

COPEPOD-CHONDRICHTHYAN COEVOLUTION:
A CLADISTIC CONSIDERATION

by

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ABSTRACT

A revision of the species of *Eudactylina* (Eudactylinidae : Siphonostomatoida) and *Kroyeria* (Kroyeriidae : Siphonostomatoida) was conducted, based on type and other specimens of parasitic copepods from museums and personal collections. A description of the external morphology of each genus is included. Taxonomic, phylogenetic, and functional significance of the morphology of the general habitus, first and second antennae, oral and thoracic appendages are discussed.

The taxonomic account of the above genera recognized all nominal species in the literature. Illustrations and phylogenetic analyses, however, were necessarily restricted to only the material examined in an attempt to standardize the abstractions and interpretations associated with character observation. Detailed redescriptions are given of *E. acuta*, *E. aspera*, *E. chilensis*, *E. corrugata*, *E. indivisa*, *E. insolens*, *E. longispina*, *E. myliobatidos*, *E. oliveri*, *E. papillosa*, *E. peruensis*, *E. pollex*, *E. pusilla*, *E. similis*, *E. spinifera*, *E. squamosa*, *E. tuberifera*, *E. turgipes*, and new descriptions (all in press) are given of, *E. aphioxenus*, *E. dactylocerca*, *E. diabolophila*, *E. epaktolampter*, *E. hornbosteli*, *E. nykterimyzon*, *E. pristiophori*, *E. urolophi*, and *E. vaquetillae* followed by the detailed redescriptions of *K. carchariaeglauci*, *K. caseyi*, *K. dispar*, *K. elongata*, *K. gemursa*, *K. lineata*, *K. longicauda*, *K. papillipes*, *K. spatulata*, *K. sphyrnae*, *K. triakos* and new descriptions (all in press) of *K. branchioecetes*, *K. cresseyi*, *K. decepta*, *K. procerobscena*, and *K. rrophemophaga*.

In an attempt to unravel evolutionary relationships of their elasmobranch hosts and themselves a phylogenetic analysis of each genus is presented. In the heuristic analysis of *Eudactylina*, 75 morphological characters resulted in a single tree with a consistency index of 0.77 and a retention index of 0.88, indicating a high degree of character congruence. An exact search of nine species of *Eudactylina* with 55 characters resulted in a single tree with a consistency index of 0.88 and a retention index of

0.88. The *Eudactylina*-derived host cladograms posit monophyly of the shark-like squaloids, squatinids, pristiphorids, and batoids. This suggests that shark-like squaloids, angelsharks, and sawsharks are more closely related to rays than to other galeomorph sharks, whereas the pristiphorids represent the sister taxon to batoids. The eudactylinid clade found on the rhinopterids and mobulids appears to represent a colonization event followed by tight cospeciation. *Eudactylina*-derived carcharhinid relationships approximate conventional or currently accepted hypotheses. *Eudactylina*-derived phylogenetic relationships of a subset of species from *Squatina* and *Myliobatis* indicate speciation patterns consistent with major vicariant events associated with the breakup of Pangaea during the Jurassic period approximately 160 MY.

The phylogenetic analysis of *Kroyeria*, using 44 morphological characters resulted in a single tree with a consistency index of 0.75 and a retention index of 0.75. The *Kroyeria*-derived and *Kroyeria-Kroeyerina*-derived host cladograms posit an unconventional placement for *Galeocerdo*. *Galeocerdo* diverges at the bottom of the tree before the Triakidae. A sphyrnid clade follows, functioning as the sister taxon to remaining members of the Carcharhinidae. The genus *Carcharhinus* appears paraphyletic with *Negaprion* and *Prionace* imbedded within this clade, corroborating similarly held views by other systematists.

Congruent host and parasite cladogram topologies from both holocephalan and elasmobranch hosts suggest the existence of well-established and specific host-parasite associations as early as the late Devonian, approximately 400 MY.

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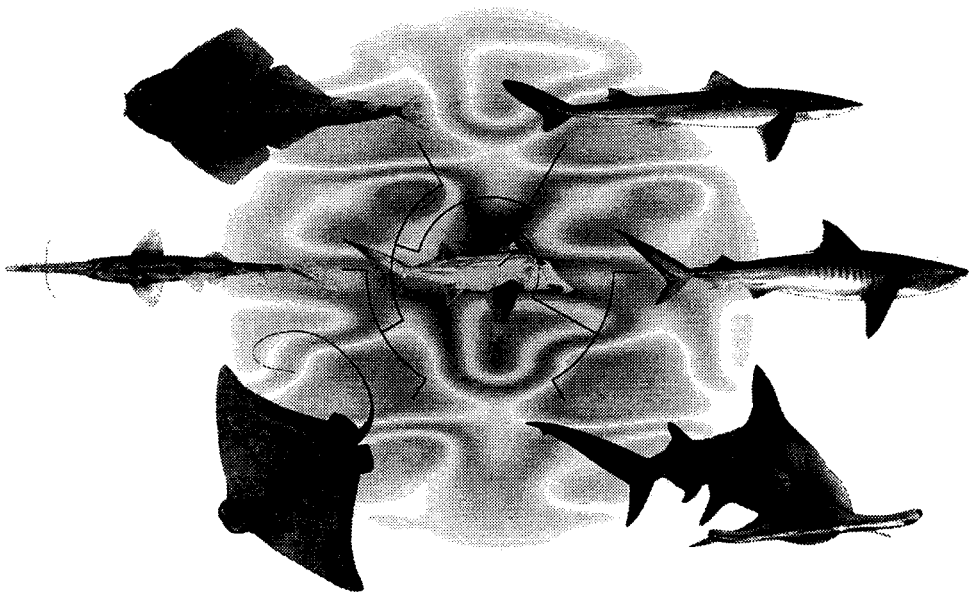
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Finally, this is dedicated to the memory of my parents, Hubert and Florence Deets, both passing away during this long process.

When I was a boy, world was better spot.
what was so was so,
what was not was not.
Now I am a man
world have changed a lot
Some things nearly so, others nearly not.



There are times I almost think
I am not sure of what I absolutely know.
Very often find confusion in conclusion
I concluded long ago.
In my head are many facts that as a student
I have studied to procure.
In my head are many facts of which
I wish I was more certain I was sure.

Oscar Hammerstein II
The King & I
A Puzzlement
1956

INTRODUCTION

Coevolution has become an increasingly popular sub-discipline within the field of evolutionary biology. Ehrlich and Raven (1964) defined coevolution as an ecological phenomenon, a matter of "stepwise reciprocal response" between any two species with "close and evident" ecological relationships. Parasitologists citing von Ihering (1891) have recognized a more restricted sense of coevolution; the historical relationships between hosts and parasites. Coevolution embodies two components, togetherness (co-) and history (evolution) (Mitter and Brooks, 1983). The study of togetherness (the functional fit of organisms to their environment) is usually restricted to the field of ecology. The study of history (phylogeny) is enveloped within the realm of systematics (Brooks, 1985a). Although this historical component is missing from most of the earlier assessments of putatively coevolved systems (Brooks, 1979a; Brooks and Mitter, 1984; Mitter and Brooks, 1983), recent efforts have attempted to incorporate it (Brooks and McLennan, 1991, 1993; Paterson, Gray & Wallis, 1993).

Whether one studies free-living or parasitic organisms, the species associations a given taxon exhibits are usually well defined, quite specific and brought about by a combination of descent and proximal or contemporaneous causes (colonization). Hence, it is of interest to determine whether most species associations are maintained as equilibrium systems fueled by constant dispersal or maintained as historically constrained associations.

Recent advances in systematics, among them the development of cladistics, allow one to approach the question from a phylogenetic standpoint. Specific questions regarding coevolution, the evolution of ecological life-history traits, historical biogeography and classification can be addressed if an explicit phylogenetic hypothesis is available.

Cladistics, or phylogenetic systematics, attempts to reconstruct genealogical

relationships among taxa by determining the sequence of the origin of their distinguishing features (Hennig, 1966; Wiley, 1981). The major interest in cladistics is centered on construction of branching sequences and defining monophyletic groupings or natural taxa. In practicing cladistics, phylogeneticists subscribe strictly to a structural, as opposed to a functional, approach to systematics. Observations of character structure are used to construct a hierarchical pattern of taxa, then from these patterns the validity of hypotheses concerning evolutionary mechanisms is scrutinized (Brooks and Wiley, 1986). Therefore, cladistic analyses attempt to dissociate inferences of organismic relationships and evolutionary pattern from assumptions concerning process (Ho and Saunders, 1984). Indeed, one of the most important contributions of cladistics has been to focus attention on the vital importance of pattern analysis, for it is only by having some aspect of pattern that science has something to explain (Cracraft, 1983).

Formal statements concerning modern cladistic methods were made by Hennig (1950, 1966). He proposed a general reference system for comparative biology based on two major points. First he distinguished between special reference systems and general reference systems in biological classifications. Special reference systems emphasize a particular kind of relationship among different species. For example, a classification that placed all parasitic copepods inhabiting shark gills in one category, and all those on batoid gills in another would be a special reference system useful for categorizing parasitic copepods in given host assemblages. This classificatory procedure would place distantly related organisms in the same taxonomic category. A general reference system should provide the most efficient summary of the maximum amount of information about the taxa being classified (Brooks, 1985b). Hennig suggested that the general reference system in biology should be based on the genealogical or phylogenetic relationships of the species involved. The choice of genealogy was based on two observations: (1) the one attribute of any organism or species that would always be constant was its history, so phylogenetic history should be the most stable criterion for classifying and (2) genealogical relationships, like classifications, are inherently hierar-

chical.

Secondly, Hennig argued for a formal method of deducing phylogenetic relationships. He objected to phylogenetic schemes that were based on hypothetical idealized archetype ancestors. Since species are composites of ancestral and derived traits, it is unlikely such things as archetypes exist. Thus, homologous traits shared by two or more species will be indicators of phylogenetic relationship. Shared primitive traits indicate general phylogenetic relationships while shared derived traits indicate more particular phylogenetic relationships. The terms plesiomorphy (plesio - near the source) and apomorphy (apo - away from the source) refer to these relatively primitive and relatively derived traits. Two taxa that share derived homologous characters (synapomorphies) are each other's closest relatives and are called *sister taxa* (Hennig, 1966).

There are two comparative methods for evaluating the degree of primitiveness of characters. These are the "ontogenetic criterion" and the "outgroup criterion". Both approaches seek to establish the direction or path of transformation from the primitive to a more derived character state. A primitive or plesiomorphic character is more general because it defines a group that is more inclusive than one defined by a less general, more derived or apomorphic condition of that character. Hence, the diagnostic features of each grouping in the genealogical hierarchy would be those traits viewed as apomorphic at that level of that particular grouping (Wiley, 1981).

The outgroup criterion states that any trait found in at least one member of the group being studied that also occurs in taxa outside the study group is plesiomorphic. Since outgroups are not archetypes and, therefore, may possess derived character states, it is often necessary to use more than one outgroup (composite outgroup) to establish enough apomorphic traits to classify a taxon (Maddison, et al., 1984).

The ontogenetic criterion states that, where two organisms possess different adult states, if one organism exhibits the other's adult trait during development, its adult trait is apomorphic and that of the other adult trait is plesiomorphic. This approach is more limited than outgroup analysis, since it works only for cases in which evolution

has proceeded by adding characteristics to the ancestral developmental program (Brooks and Wiley, 1986).

After determining which traits are apomorphic and which are plesiomorphic, one is sometimes faced with apomorphic traits that suggest conflicting groupings. The reason for this is parallel and/or convergent evolution, given the general name homoplasy, where similarity causes one to misattribute homology. Truly homologous traits of various taxa will yield congruent groupings. As long as homoplasious traits do not co-vary in larger numbers than the homologous traits, parsimony analyses will pinpoint the proper phylogenetic relationships. The possible occurrence of great amounts of parallel evolution requires only that many traits be used in the analysis, since the pattern of relationships indicated by a plurality of traits is the best estimate of phylogenetic relationships (Brooks, 1985b). Since this requires that large numbers of traits be analyzed simultaneously, phylogenetic computer packages such as PAUP (Phylogenetic Analysis Using Parsimony) and MacClade have been developed to generate and analyze phylogenetic trees.

As previously stated, concordance between phylogenetic relationships of parasites and their hosts has been recognized since the nineteenth century (von Ihering, 1891). Hennig (1966) discussed the concordance briefly and the resultant possibility of inferring host phylogenies from parasite data. The continued discovery of co-varying associations between parasites and their hosts has led to the formulation of various "rules" of coevolution. The rules form a small group of interrelated concepts:

1. Eichler's Rule (for review see, Inglis, 1971): *The more genera of parasites a host harbors, the larger the systematic group to which the host belongs.*

2. Manter's Rules (for review see Inglis, 1971): (1) *Parasites evolve more slowly than their hosts;* (2) *the longer the association with a host group, the more pronounced the specificity exhibited by the parasite group;* (3) *a host species harbors the largest number of parasite species in the area where it has resided longest, so if the same or two closely related species of host exhibit a disjunct distribution and possess similar*

parasite faunas, the areas in which the hosts occur must have been contiguous at a past time.

3. Szidat's Rule (see Szidat, 1956; 1960): *The more primitive the host, the more primitive the parasite it harbors.*

Finally, and probably the best known:

4. Farenholz's Rule (for reviews see Brooks, 1979a, 1981, 1985a; Inglis, 1971): *Parasite phylogeny mirrors host phylogeny.*

Brooks (1981) developed this latter concept of coevolution in terms of phylogenetic systematics (cladistics) and suggested that host-parasite coevolution can arise through processes comparable to those that produce homologous and homoplasious characters. This analogous relationship between character state transformation series and parasite phylogenies allows one to view cospeciatiated or historically associated parasites as homologies or autapomorphies of their hosts and colonizing parasite species as homoplastic characters of their hosts. Thus, evolutionary relationships can be taken into consideration by first doing a phylogenetic analysis of the parasites and then treating that cladogram as a multistate character tree of the hosts that are inhabited by the parasite species.

Such a tree is constructed with a source of information that is not available in standard multistate analyses, namely the cladistic analysis of the parasites themselves. The characters have characters, so to speak, that are used to infer their relationship.

Various methods exist for converting the topology of a phylogenetic into a matrix of numerical characters. This permits multiple parasite taxa to be analyzed simultaneously (a common data matrix), in order to generate host phylogenies (O'Grady and Deets, 1987).

Additionally, historical approaches to ecology rely on an *a priori* phylogenetic analyses. Replacing the names of the terminal taxa from the parasite cladogram with their respective ecological life history traits produces an ecological summary cladogram. The result is a spatiotemporal interpretation of the evolution of the parasites

infection-site associations (Brooks, 1985a; Deets, 1987). In the same vein, historical approaches to biogeography are analyzed by replacing the names of the terminal taxa with their distributions.

Phylogenetic systematics has been applied mostly to free-living taxa. Only recently has this method entered the field of parasitology. The first study to demonstrate the feasibility and applicability of cladistics with parasitic taxa was made by Brooks (1977). The phylogenetic relationships of plagiorchoid trematodes in this analysis were shown to be congruent with their anuran hosts as well as exhibiting a definite vicariant distribution consistent with the Pangaeian breakup. This was followed by a series of papers utilizing cladistic methods on parasitic taxa including crocodylians and their digenean parasites (Brooks, 1979a), vicariance biogeography, potamotrygonid stingrays and their helminth parasites (Brooks, et. al, 1981), pinworms and primates (Brooks and Glen, 1982), nematodes and primates (Glen and Brooks, 1985; 1986), and other papers formulating other applications with cladistics and evolutionary theory (Brooks, 1979b; 1980). Recently, Adamson and van Waerebeke (1985) employed cladistics to analyze parasitic nematode classification and evolution, and Boeger and Kritsky (1989) tested Compagno's (1977) various hypotheses of elasmobranch evolution with their cladistic analysis of the genera within the Hexabothriidae (Monogenea).

In the midst of this blitzkrieg of phylogenetic analyses on worms, workers on the parasitic copepods (Crustacea), staging more of a sitzkrieg, gradually entered the cladistic arena. The first authors to investigate the phylogenetic relationships and historical zoogeography of a host group of fishes (*Merluccius*) as inferred from the phylogenetic relationships of their parasitic copepods were Kabata and Ho (1981). Though their work is free of any formal cladistic analysis, and devoid of associated jargon, it is phylogenetic in its approach. Both authors were keenly aware that when drawing conclusions on host zoogeographical or phylogenetic problems, one must be conscious of the phylogenetic relationships of the parasites considered. Hence, the relatively plesiomorphic or apomorphic conditions of the characters of their "indicator" species were taken into

consideration.

Cressey, Collette and Russo (1983), specialists on parasitic copepods and scombrid teleosts, were the first authors to investigate phylogenetic relationships of parasitic copepods using formal quantitative cladistic methodology. Ho's (1984) discovery of the Spiophanicolidae, a family of highly modified copepods on polychaetes prompted him to analyze phylogenetically a certain suite of poecilostomatoid families [informally termed the Nereicoliform Group by Gooding (1963), Illg, (1970) and Gotto (1979)] that are parasitic on various invertebrate phyla. This resulted in the clarification of some classificatory problems embedded in the literature for nearly 20 years. A year later, Ho and Do (1985) analyzed the genera in the Lernanthropidae, highly derived parasites of teleost gills. That same year, Collette and Russo (1985) looked into the phylogeny of the Spanish Mackerels and their copepod parasites in order to determine which evolutionary events of the parasites could be explained by the evolutionary events of their hosts. Following this, Deets (1987) conducted a phylogenetic analysis and systematic revision of the genus *Kroeyerina* and a higher level analysis of the genera within the family Kroyeriidae. The apparent static nature of the parasites' life-history traits (specific infection sites) coupled with the congruent phylogenetic pattern with their elasmobranch hosts suggested both hosts and parasites experienced the same vicariant events and subsequent allopatric speciation. After this work a phylogenetic analysis of the Eudactylinidae (Deets and Ho, 1988), resulted in the resurrection of the previously synonymized genus *Protodactylina* Laubier, 1966. A Tethyan distribution was speculated for a single monophyletic subset (clade) of 3 monotypic genera parasitic on batoids. Next, Benz and Deets (1988), with the rediscovery of a rare parasite specific to mobulid branchial filters, carried out a phylogenetic analysis of the genera within Cecropidae. Finally, Dojiri and Deets (1988) with the finding of a new genus *Norkus* (Sphyriidae) phylogenetically analyzed the sphyriid genera. Again tight phylogenetic congruence with the hosts and parasites were the result. Additionally, parasite life history traits mirrored the cladogram's topology.

In order to apply these methods and aforementioned concepts it is imperative to possess detailed knowledge of the studied taxon's morphology. At present the morphology of parasitic copepods is only poorly known. It appears morphological details of minute animals are often ignored just because of their dimunitiveness (Kabata, 1979).

Kabata (1979) redefined the family Eudactylinidae and removed from it *Kroyeria* van Beneden, 1853 and *Kroeyerina* Wilson, 1932 to form a new family Kroyeriidae. Recently, Deets (1987) established a new genus *Prokroyeria* to accommodate *Kroeyerina meridionalis* Ramirez, 1975. The revised Eudactylinidae then consisted of seven genera, but since then three have been discovered (Deets and Benz, 1987; Deets and Ho, 1988) bringing the total to ten, namely *Bariaka* Cressey, 1966; *Carnifossorius* Deets and Ho, 1988, *Eudactylina* van Beneden, 1853, *Eudactylinella* Wilson, 1932, *Eudactylinodes* Wilson, 1932, *Eudactylinopsis* Pillai, 1966, *Heterocladius* Deets and Ho, 1988, *Jusheyus* Deets and Benz, 1987, *Nemesis* Risso, 1826, and *Protodactylina* Laubier, 1966.

This elasmobranch-copepod system is a good model to work on for many reasons. The host group has been shown to be monophyletic (Compagno, 1977; Maisey, 1984), and this coupled with their antiquity as shown by paleontological data (Maisey, 1984) and molecular data (Davies, et al., 1986) should result in a host-parasite system with a strong historical core. The phylogenetic relationships of living sharks and rays remain unsettled partly because too few of the taxa have received investigation beyond the superficial statements needed for taxonomic identification (not unlike the parasitic copepods), and partly due to the depauperate fossil record of extant and extinct elasmobranchs (Compagno, 1977). Other problems obscuring elasmobranch interrelationships are their morphological conservatism and the fact that character polarity in elasmobranchs is difficult to define due to a lack of understanding of the characters in plesiomorphic outgroup taxa (Fechhelm and McEachran, 1984). Though there are some phylogenetic analyses in the literature (Compagno, 1977, 1984a,b, 1988; Maisey, 1984; Heemstra and Smith, 1980; Nishida, 1990 and Shirai 1992a, 1992b),

there is little agreement on any one phylogeny and it appears that more morphological work and other modes of investigation (such as phylogenetic analyses of their parasites) are needed to aid in resolution and/or corroboration of these issues. Additionally, the parasite species associated with this host group have not had sufficient attention paid to those morphological details that should be used for the specific discriminants in phylogenetic analyses, and therefore are in need of this revision.

Specifically, this effort involves the previously discussed coevolutionary concepts and cladistic methods, and empirically revolves around this fascinating complex (Eudactylinidae and Kroyeriidae) of parasitic crustaceans that inhabit olfactory and branchial lamellae of an equally intriguing host group, the elasmobranchs. I intend to provide a comprehensive taxonomic revision and phylogenetic analysis for the two genera *Eudactylina* and *Kroyeria*. Specific rationale regarding the choice of these two genera follow.

Eudactylina, world-wide in distribution, is found amongst the branchial lamellae of a systematically broad range of elasmobranchs. It is the most species-rich genus of any gill-dwelling group of parasitic copepods on elasmobranchs. The principal attachment organ is the large chelate maxilliped, reminiscent of the second antenna in *Kroyeria*. *Eudactylina* exhibits a definite host preference for squaloid, squatinoid, pristiophoroid and batoid elasmobranchs (only 6 species found on carcharhiniform hosts). This host association for *Eudactylina* is very interesting as some elasmobranch systematists (Maisey, 1984; Shirai, 1992a, 1992b) have radically hypothesized that this squaloid-squatinoid-pristiophoroid "shark" lineage to be more closely related to batoids than to the other "sharks". The conventional notion of shark monophyly would therefore, degrade into paraphyly. Recently, this complex has been elevated to a monophyletic superorder the Squalea Shirai, 1992 when batoids and hexanchoids are included (Shirai, 1992a). The Hypnosqualea of Shirai (1992a) is a monophyletic subunit within the Squalea composed of the squatinoids plus pristiophoroids plus the batoids, all hosts of *Eudactylina*. Hence, a taxonomic revision and systematic analysis

of *Eudactylina* could aid in corroboration of this recently formulated, novel hypothesis that not all sharks are sharks.

Kroyeria occurs worldwide and is the second most species-rich genus of gill-dwelling copepods parasitic on elasmobranchs. All but one of the species are found attached to the gill lamellae of their hosts (Benz and Dupre, 1987; Deets, 1987). *Kroyeria caseyi* Benz and Deets, 1986 is atypical of the entire family in that the female is mesoparasitic (fossorial, anterior portion of the animal usually modified into a hold-fast and rooted into the host tissue, posterior portion exposed and freely trailing), deeply embedded within the host's interbranchial septa. The male of *K. caseyi*, like those of other members of the genus, primarily attach themselves to the secondary lamellae and secondarily to the underlying excurrent water channels of their host's gills (Benz and Dupre, 1987) by means of their modified chelate second antennae. The long vermiform body trails behind, nestled between the gill filaments of its host. The carcharhiniform families Carcharhinidae (requiem sharks), Sphyrnidae (hammerhead sharks) and the Triakidae (hound sharks or whiskery sharks) are the primary hosts reported for this genus. Although these families are closely related (Compagno, 1977, 1988) phylogenetic relationships within this carcharhiniform complex are considered to be in a state of disarray (Maisey, 1984). In fact, both morphological and molecular evidence continues to mount suggesting the possible paraphyly of the Carcharhinidae, *Carcharhinus*, and Triakidae (Compagno, 1988; Lavery, 1992; Naylor, 1992). A taxonomic revision and systematic analysis of *Kroyeria*, specific to the Carcharhiniformes may assist in answering these aforementioned questions.

This research therefore, is an effort to apply phylogenetic systematics or cladistics to this parasitic crustacean-elasmobranch host system in order to reveal and hopefully resolve the uncertain phylogenetic relationships of these hosts and parasites. This effort proceeds by initial historical and biological reviews and the subsequent taxonomic revision and redescription of two parasitic copepod genera, *Eudactylina* and *Kroyeria*. Additionally, both genera are in need of revision. Each revision is followed by a phylo-

genetic analysis of that genus, from which parasite-derived host cladograms are constructed, and in two instances, area summary-cladograms are produced. Competing independent host phylogenies are then compared with the parasite-derived host cladograms. Finally, the *Kroyeria* cladogram will be numerically recoded and combined with yet another recoded tree from a previous revision and phylogenetic analysis of the parasitic copepod genus *Kroeyerina* (cf. Deets, 1987), into a common matrix to generate a single host phylogeny based on all the parasite data from the Kroyeriidae.

MATERIAL AND METHODS

Chondrichthyan hosts were captured in three general localities. Specimens from the southern California bight (San Diego to Point Conception, California) were obtained from the San Pedro, California based commercial fishermen using set coastal gill nets and pelagic drift nets. Material from the Sea of Cortez or Gulf of California was caught with gill nets, long lines and harpoon by the fishermen at Bahia de Los Angeles and Punta Arena de la Ventana. Sampling proceeded intermittently from October 1980, through January 1994.

Additionally, type and non-type material was obtained from the U.S. National Museum of Natural History, Washington, D.C., U.S.A., The Natural History Museum, London, England, and the Museum National D'Histoire Naturelle, Paris, France. Specimens were also received from the Instituto de Biologia Marina, Mar del Plata, Argentina and Instituto de Investigaciones Oceanologicas, Universidad de Antofagasta, Antofagasta, Chile. The California Academy of Sciences in San Francisco and the National Museum of Natural History, Smithsonian Institution's support center allowed me to inspect preserved elasmobranchs for parasitic copepods during my short-term visitor appointment in June of 1988.

Additional specimens were donated to me from the personal collections of George Benz, (Tennessee Aquarium); Dr. Roger Cressey, (National Museum of Natural History, Smithsonian Institution), Dr. Ju-Shey Ho, (California State University, Long Beach), Dr. Z. Kabata, (Pacific Biological Station, Nanaimo, British Columbia), and Raul Castro Romero, (Universidad de Antofagasta, Antofagasta, Chile).

Parasites recovered from the host's branchial and olfactory lamellae were immediately preserved and subsequently stored in 70% ethanol. Later, copepods were cleared in 85% lactic acid, lightly stained with lignin pink, and transferred to wooden

slides according to procedures of Humes and Gooding (1964). The parasitic copepods were then dissected to permit a detailed morphological examination of the appendages. All drawings were made with the aid of a camera lucida. Illustrations were drawn on Canson Vidalon Tracing Vellum, no. 110 (extra heavy), and inked with Rotring Rapidograph technical pens.

Phylogenetic analyses were carried out using the following protocol: *Eudactylinodes* Wilson, 1932, recently revealed to be the sister taxon of *Eudactylina*, and at times *Eudactylinella*, *Carnifossorius*, and *Eudactylinopsis*, sister group to the *Eudactylina-Eudactylinodes* clade (Deets and Ho, 1988), functioned as outgroups for *Eudactylina*. *Kroeyerina*, the sister taxon to *Kroyeria*, and at times, *Prokroyeria meridionalis* (Ramirez), the most basally placed member of the Kroyeriidae (Deets, 1987) were chosen as outgroups for *Kroyeria*. These outgroups were selected in order to determine character polarity for their respective ingroups.

Character data were defined, produced and coded (see appendices). All character data were treated and analyzed as unordered to avoid risk of predetermining the topology of the resultant cladogram (O'Grady and Deets, 1987; Dojiri and Deets, 1988). Non-linear, multistate transformation series (the recoded cladograms) were standardized by coding techniques reviewed and outlined by O'Grady and Deets (1988). Upon completion of the character data matrix the computer program PAUP (Phylogenetic Analysis Using Parsimony; D. Swofford, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560) version 3.0S was used to analyze the data. Specifically, the exact search algorithm BRANCH AND BOUND for small data sets and the heuristic search algorithm TREE-BISECTION AND RECONNECTION (TBR) for large data sets, were utilized to generate the most parsimonious hierarchy of parasite and parasite-derived host relationships. The computer program MacClade (W. Maddison and D. Maddison, University of Arizona) version 3.0 was used interactively as a tool to increase insight on character evolution.

Parasite cladograms were perceived as character state trees of their hosts, con-

verted into numerical codes, combined and placed into a data matrix and phylogenetically analyzed in order to generate the final host phylogenies (Brooks, 1981; Brooks and McClennan 1991, 1993).

Elasmobranch figures were lifted and modified from Last and Stevens (1994), and from Stevens (1987).

HISTORICAL REVIEW

Since their inception in 1853 neither *Eudactylina* van Beneden or *Kroyeria* van Beneden have suffered any nomenclatural restructuring. However, they have experienced some shuffling at the familial level. Originally, both genera were assigned to the convenient catch-all taxon Dichelesthidae, the "tribu des Dichelestiens" of Edwards, 1840. (For a comprehensive review of the history of Dichelesthidae, see Kabata, 1979). In 1853 the family was composed of the genera *Anthosoma* Leach, 1816, *Dichelesthium* Hermann, 1804 and *Nemesis* Risso, 1826.

Streenstrup and Lütken (1861) accepted "Dichelestiner" as a valid higher taxon. They included in it more genera than any previous authors, namely: *Anthosoma*, *Congericola* van Beneden, 1854, *Dichelesthium*, *Eudactylina*, *Kroyeria*, *Lamproglena* van Nordmann, 1832, *Lernanthropus* de Blainville, 1822, *Nemesis* and *Pagodina* (= *Nemesis*). The concept of Dichelesthidae was similar in the work of Krøyer (1863, 1864), and von Nordmann (1864) used the structure of the egg sacs as the basic division between the genera. His group "Dichelestini" with filiform uniseriate egg sacs (as distinct from saccular multiseriate) consisted of: *Anthosoma*, *Congericola*, *Dichelesthium*, *Donusa* Nordmann, 1864, *Ergasilina* van Beneden, 1851 (= *Nemesis*), *Eudactylina*, *Kroyeria*, *Lamproglena* (a cyclopoid), *Lernanthropus*, *Nemesis*, *Pagodina* and *Stalagmus* Nordmann, 1864 (*Donusa*, *Ergasilina*, *Pagodina*, and *Stalagmus* are no longer valid taxa).

It wasn't until Heller (1865) provided a key to the "Familia Dichelestina" that someone offered an idea of intrafamilial groupings by way of a key to the genera. *Pagodina* was concomitantly synonymized with *Nemesis*.

A similar approach to dichelesthid systematics was followed by Gerstaeker (1866-1879). His key to the family "Dichelesthina" included the following genera: *Aethon* Krøyer, 1857, *Anthosoma*, *Bacculus* Lubbock, 1860 (larval stage of *Pennella* Oken, 1816), *Clavella* (= *Hatschekia* Poche, 1902), *Congericola*, *Dichelesthium*, *Donusa* (a polychaete parasite, probably a cyclopoid), *Epachthes* Nordmann, 1832 (syn. of *Lernanthropus*), *Ergasilina* (syn. of *Nemesis*), *Eudactylina*, *Kroyeria*, *Lamproglena*, *Lernanthropus*, *Nemesis*, *Norion* Nordmann, 1864, *Philichthys* Steenstrup, 1862 (type genus of Philichthyidae), *Pseudocycncus* Heller, 1865, *Stalagmus* (syn. of *Lernanthropus*) and *Tucca* Krøyer, 1837 (a poecilostome).

Brian (1906) along with Scott and Scott (1913) included subsets of above in their treatment of Dichelesthidae with representatives from their restricted areas of study,

Italian and British waters respectively.

Therefore, Dichelesthidae with its vague and over inclusive diagnostic boundaries functioned as a depository for many new genera and species that could not be accommodated in other existing well-defined families.

Wilson (1922), offered the first review of intrafamilial organization of the Dichelesthidae by generating a key to subfamilies. In his Copepoda of the Woods Hole Region, Wilson (1932) upgraded the status of his four subfamilies and established the following families with their respective genera:

- Anthosomidae (*Anthosoma, Lernanthropus*);
- Eudactylinidae (*Kroyeria, Kroeyerina, Nemesis, Eudactylina, Eudactylinodes, Eudactylinella*);
- Pseudocycnidae (*Pseudocycnus*);
- Dichelesthidae (*Hatschekia, Pseudohatschekia, Pseudocongericola, Lamproglena*)

Dichelesthium was excluded due to its absence from the Woods Hole Region.

Yamaguti (1939) accepted the familial rank of these four families, while Markevich (1956) kept them as subfamilies and transferred *Lamproglena* (the cyclopoid) to Eudactylinidae from Dichelesthidae. Later Yamaguti (1963) reunited Wilson's four families by establishing the superfamily Dichelesthioidea.

Kabata (1979), at wits end, realized the lack of relationship between the various genera within these families, and the lack of affinity amongst the families embedded in Yamaguti's Dichelesthioidea and systematically restructured this taxonomic complex.

Using body segmentation for the first time as the primary criterion for classification Kabata, (1979) distinguished six groups of genera within this miscellaneous assemblage previously recognized as Dichelesthidae. Additionally, the cephalothoracic appendages that each of these groups possess were shown to be unique. Witness the chelate second antennae of Kroyeriidae or the chelate maxillipeds of Eudactylinidae. Coupled to this, one find similar patterns with the swimming legs. Compare the four pairs of well developed, non-modified biramous, trimerite swimming legs of Kroyeriidae with the four pairs of Hatschekiidae, which have very reduced third and fourth legs and often only bimerite rami of legs one and two as examples. These pieces of evidence add layers of justification or corroboration to the groups distinguished by Kabata's tagmatic criterion. On the basis of these and many other arguments outlined in Kabata (1979), the following family units were proposed in accordance with this key:

1. Four distinct segments between cephalothorax and genital segment **Eudactylinae**
 Three segments (exceptionally four) between cephalothorax and genital trunk 2
 Segmentation indistinct, neck present between cephalothorax and genital trunk 3
 No free segments or neck between cephalothorax and genital trunk, dorsal plate usually present on trunk **Lernanthropidae**

2. Free segments distinct, cephalothorax with caligiform dorsal shield, four pairs of biramous legs **Kroyeriidae**
 Free segments rather indistinct, dorsal shield of cephalothorax not caligiform, three pairs of variously modified legs, elytra absent **Dichelesthiidae**

3. Second maxilla with bifid claw, maxilliped absent **Hatschekiidae**
 Second maxilla with simple, denticulated claw, maxilliped present, subchelate. . **Pseudocycnidae**

One genus, *Pseudohatchekia* Yamaguti, 1939, cannot be accommodated in any of these previous six families. If Yamaguti's illustrations accurately represent the morphological attributes of this genus, it would seem a new family (Pseudohatchekiidae) should formally be established upon inspection and revision of the species therein.

So, after 140 years of a tightly coupled and shared systematic history, in spite of their obvious morphological disparities (perhaps due to both being parasites of elasmobranchs) the paths of *Eudactylina* and *Kroyeria* diverge, finally finding their way into their own families, Eudactylinae and Kroyeriidae, respectively.

EUDACTYLINA

EXTERNAL MORPHOLOGY

GENERAL HABITUS

The body of *Eudactylina* is typically sub-cylindrical with seven distinct tagmata (Figure 2a): the cephalothorax (which consists of the somites bearing the first antenna, second antenna, mandible, first maxilla, second maxilla, maxilliped, and the first pedigerous somite), the well-developed pedigerous somites two, three, and four (bearing biramous and usually trimerous legs), a reduced pediger five (bearing a reduced fifth leg), a genital segment (bearing the genital orifices), and a multi-segmented abdomen (posteriorly bearing the caudal rami).

The cuticle is equipped with posteriorly directed cuticular expansions. These cuticular flaps or outgrowths vary in size and shape from species to species, thereby possessing some taxonomic importance. *Eudactylina* orients itself upstream relative to the flow of water over the gills (Figure 1), and these posteriorly directed flaps may function as tiny brakes keeping the parasite relatively secured at that location on the gill.

The cephalothorax houses the main "organs" (appendages) of attachment for *Eudactylina*. These are the first antenna with a few setae modified into large claws on the second and third segments, the second antenna with its unciniate apical segment, and primarily the huge robust chelate maxilliped.

The major articulation of the body is between the fifth pedigerous somite and the genital somite.

The genital somite of the female appears to be located on the sixth thoracic somite. Close examination of the ventrolateral area adjacent to the oviducal openings reveal three well developed albeit small spines (Fig. 3D detail) which most likely represent the vestigial sixth legs. Additionally, the position of this putative sixth leg roughly corresponds to the position that the reduced sixth leg occupies on the male. If this homology in structure and position is true, then it is likely that the abbreviated number of segments in the abdomen of the female (two) relative to the supposedly more plesiomorphic condition of the male (three or four segments), is due to the suppression not incorporation (into a genital complex) of these somites during ontogeny.

CAUDAL RAMUS

The caudal rami originate posteriorly from the last abdominal somite. The caudal ramus is undoubtedly an organ of slippage prevention. The parasite plunges the paired rami down into the secondary lamellae of the host's gills (Figure 1), helping to wedge the entire animal in place amongst the secondary lamellae. It seems the posteriorly-directed cuticular flaps on the ventral surface of the rami coupled with the well developed, often digitiform terminal spines (modified setae) suggest a stopping function. Within the genus caudal rami vary markedly in form, from the relatively unmodified state possessing four relatively long pinnate apical setae plus two relatively long naked setae as seen in the male *Eudactylina epaktolampter* (Figure 22B), to the extremely derived condition of possessing four stout apical spines barely larger than the adjacent cuticular flaps as in female *Eudactylina oliveri* (Figure 36B), and the bizarrely modified digitiform condition found in the female of *Eudactylina dactylocerca* (Figure 14B). The striking differences exhibited by the caudal rami between the different species of *Eudactylina* make this a useful taxonomic character.

FIRST ANTENNA

The first antenna of female *Eudactylina* (Figure 2C) is indistinctly four-, five- or six-segmented, exhibiting geniculate flexion between the second and third segments. Although no physiological work has been done on this appendage it is safe to presume similar (homologous) innervation exists here as seen in other siphonostome copepods indicating an organ capable of chemosensory and tactile functions (see Kabata, 1979). Additionally, the large dorsally-directed claw-like spine (often toothed) on the second segment would seem to be an auxiliary attachment structure especially in light of the way the parasite lodges its cephalothorax into the secondary lamellae of the gills (Figures 1A, 1B). The first antenna of the male has a greater number of more clearly delimited segments. The males of *E. epaktolampter* and *E. oliveri* (Figures 22C and 38C, respectively) have eight or nine segments, and more setae are found on the segments. In general (with regards to the female) the first or basal segment always bears one small seta on the outer margin. The apical segment appears to possess a maximum of 14 setae plus one aesthete. Although some descriptions in this revision and by other authors show fewer setae I believe some of this may be an artifact of specimen damage coupled with the fact we are pressing the limits of light microscopy with the minutiae involved.

The remaining segments between the basal segment and apical segment exhibit different degrees of fusion or segment incorporation in the different species.

SECOND ANTENNA

The second antenna (Figure 2D) is five-segmented, not sexually dimorphic. The basal segment is small, unarmed and pedunculate. The second segment is relatively elongate, sometimes armed with a styliform process (appears to have a prehensile function), and sometimes possessing cuticular flaps. The third segment usually bears a large claw-like extension and always has two slender setae at its base and cuticular flaps. The fourth segment sometimes exhibits cuticular flaps. The fifth segment forms a large uncinat terminal claw bearing a large accessory spine on the lateral surface. Two small slender setae are always found at the base of the fifth segment.

The many different combinations and states of these characters listed above make the second antenna an important taxonomic discriminant.

ORAL CONE and MANDIBLE

The mandible is typically siphonostome being a uniramous subcylindrical structure with a dentiferous distal end (Figure 2E). The mandible also appears to be divided into two parts, their boundaries demarcated by a suture. The dentiferous margin bears from five to eight teeth.

The oral cone (Figure 36D), consisting of labium and labrum houses the mandible. The possession of the mouth tube is the distinguishing characteristic of the suborder Siphonostomatoida. The structure is rather uniform throughout the genus with some differences seen in the nature of the cuticular flaps found on both the labium and labrum. The use of this structure for systematic purposes was not pursued.

FIRST MAXILLA

The first maxilla found adjacent to the mandible is the first segmental appendage found in the post-naupliar stages of copepods (Kabata, 1979). It is biramous consisting of an endopod and an exopod (Figure 2F). The exopod is armed with two setae which may bear setules or denticulations. The endopod terminates with one long seta and two short setae the former bearing setules or small denticulations in certain species. The

body of the first maxilla also bears small spinulations or cuticular flaps in some species.

SECOND MAXILLA

The second maxilla is a large brachiform appendage (Figure 2G). The orifice of the maxillary gland is present at the base as is the basal process, a small fleshy extension of cuticle. The most proximal segment is the lacertus. The lacertus is typically "fortified" by the presence of well developed sclerites, and is armed with cuticular flaps. This segment articulates with the brachium by means of the cubital joint. The brachium is also armed with the cuticular flaps and distally bears what appears to be a tuft or paired tuft of setae, and a patch of prickles or denticles termed the crista at the base of what may represent a third segment the calamus or claw. The claw usually bears a series of comb-like serrated membranes or, as in a few species, well developed teeth. Although the comb-like membranes suggest a grooming function, the closely related species *Nemesis robusta* (van Beneden, 1851) also a member of Eudactylinidae has been shown to use the second maxilla to assist in feeding on the secondary lamellae of the thresher shark (*Alopias vulpinus* (Bonnaterre, 1758)). Feeding by these gill parasites involves the mechanical rasping of host tissue and the second maxillae were shown in histological sections to be the appendage responsible for host tissue excavation (Benz and Adamson, 1990). The second maxilla has also been implicated in manipulation of the frontal filament during the developmental stages of most siphonostomes in which they are known (Kabata, 1979). Unfortunately, the specific function of the second maxilla in *Eudactylina* is unknown.

MAXILLIPED

The maxilliped is the posteriormost oral appendage borne upon the first thoracic segment incorporated into the cephalon. Sexually dimorphic, the male maxilliped occurs as a sub-chelate structure (Figure 22D), while the female form exists as a remarkable, fully chelate structure (Figure 2H). The female maxilliped appears to consist of four segments. The unarmed pedunculate basal segment supports the main body or corpus maxillipedis. The corpus maxillipedis is always armed with cuticular flaps, a small spine-like seta, at times a lateral flange, and a greatly produced posterolateral region, the myxa, forming a large scoop-like receptacle. By means of the cubital joint the corpus articulates with the subchela. The subchela is composed of the proximal shaft bearing one seta approximately midway along the outer margin and another

located distally near the base of the claw along the inner margin. A membrane is also found adjacent to the latter along the inner margin of the most distal reaches of the shaft. The shaft may bear cuticular flaps. The most terminal segment of the subchela is the claw. This is an uncinata structure accompanied along the lateral surface by a quadrangular expansion of varying sizes. When clasped, the claw and quadrangular expansion are perfectly accommodated by the receptacle-like myxa, forming a pincer. This structure is the primary attachment appendage that the copepod uses to grip the secondary lamellae of the host's gills (Figure 1).

LEG ONE

The first thoracic leg is the only leg incorporated into the cephalothorax (Figures 2A and 3A). The pair of legs is connected by an interpodal bar allowing their synchronous movement. The sympod is well delimited by a medial suture separating the proximal coxa from the adjacent basis. Both coxa and basis are armed ventrally with cuticular flaps or scales. The basis bears one lateral and one somewhat medial seta along its distal margin. The leg is always biramous, composed of a lateral exopod and a medial endopod. Both rami are usually three-segmented (trimerous) and rarely bimerous. The proximal (first) and middle (second) segments of the exopod bear a distolateral spine-like seta (pinnate setae are found in legs one through four in the male). The terminal (third) segment typically bears three or four variously modified setae. The endopod is also a trimerous or rarely bimerous ramus with only the terminal segment armed with two setae.

LEG TWO

The second thoracic legs (Figure 7B) are united by an interpodal bar. In a few species the interpodal bar of leg two has a non-articulated medial extension creating a single ventroposteriorly directed interpodal stylet (Figure 15C). The coxa and basis are distinct, with the basis armed with one seta along the distolateral edge. The second thoracic appendage is also biramous, with both rami trimerous except in a few cases in which the endopod is two-segmented. The terminal segment of the endopod carries two setae. The exopod with few exceptions (e.g., *E. acanthii*) is a bizarrely modified ramus. It has few if any cuticular flaps, in contrast to the other three leg pairs. The proximal segment is greatly enlarged, often tremendously elongate and bears a single curved

spine distolaterally. The middle segment is armed with a single spine-like seta of various sizes. The terminal segment is reduced in size bearing a small lateral seta, an odd quadrangular or thick seta is found terminally and a strongly hooked seta located on the medial margin of the segment. The sometimes strongly produced spine on the middle segment and the strongly hooked seta on the medial edge of the terminal segment when viewed in context with the *in situ* illustration of Figure 1, suggests the ramus functions in slippage prevention if not as an auxiliary attachment appendage.

LEGS THREE AND FOUR

The third and fourth pairs of legs (Figure 3C) are nearly identical in all species of *Eudactylina* with the exception of *E. dollfusi* where the endopod of the fourth leg is modified into a robust uncinat process (Figure 19D). Each leg pair is joined by an interpodal bar. In a few species the interpodal bar of leg three has a non-articulated medial extension creating a single ventroposteriorly directed interpodal stylet (Figure 33E). Both pairs of legs are adorned with cuticular flaps. The sympod is well delimited into a proximal coxa and more distal basis. The basis bears a single spiniform seta on the lateral margin. Both legs are biramous and the rami trimerous with the appearance of a few bimerous endopods on leg four being the exception. The terminal segment bearing a single seta is the only setal armature found on the endopod. The exopod bears a single spine-like seta on both segment one and two, and three spine-like setae on the terminal segment. The third and fourth pair of legs with their posteriorly directed cuticular flaps probably aid in slippage prevention. Additionally, Figure 1 shows *Eudactylina* using their endopods and exopods independently, in fact, at right angles to each other to what appears to be separating the secondary lamellae in order to more securely wedge itself amongst the lamellae. This would seem to cause the secondary lamellae to attempt to return to their normal positions possibly pressuring or pushing back down and around the parasite aiding in its attempt to remain securely affixed to the host tissue.

LEG FIVE

The fifth leg is a uniramous, one-segmented appendage found on the last and fourth free thoracic somite (Figure 2A and 3D). The sympod consists of a single segment and a small seta is found distodorsally. The ramus bears three naked or pinnate

slender setae distally. Depending on the species, both sympod and ramus may be unarmed or covered with cuticular flaps.

The sixth leg of the female is rarely seen (or looked for) as it appears to be composed of three minute stout spine-like setae adjacent to the opening of the oviducal orifice (Figure 3D detail) on the genital segment. The sixth leg of the male is found on the distolateral edge of the genital segment. It is represented by two or three setae arising from a small flap, presumably the sympod (Figure 22A and 23G).

LIFE HISTORY

GENERAL DESCRIPTION

The first mention of a larval eudactylinid was given by Wilson (1922) for *Eudactylinodes nigra*. Devoid of illustrations, the narrative description tells us little more than that the organism was a nauplius. The next time any mention of a eudactylinid larva appears is by Kabata (1976) for *Eudactylina similis*. Unfortunately, Kabata was unable to culture the parasite beyond the first naupliar stage. Hence, nothing is known about the infective stage of *Eudactylina*.

In general, most fish-parasitizing siphonostomatoid copepods with known ontogenies possess a three part post-embryonic development consisting of the nauplius, copepodid, and adult (Raibaut, 1985). The number of naupliar stages varies from one to six. Next is a single copepodid stage, followed by four modified copepodite stages, chalimus I - IV, that possesses, in many but not all species, the remarkable anchoring device, the frontal filament. According to Raibaut (1985), the frontal filament is formed during the copepodid stage and is extruded for attachment to the host immediately prior to the molt into the first chalimus stage. In contrast, Wilson (1911, Pl. 30, Fig. 10) shows a nauplius of the lernaeopodid, *Achtheres ambloplitis* with an already formed, coiled frontal filament. Although this chalimus larva had been considered to be present in all of the siphonostome copepods of fish, Cabral, Coste, and Raibaut (1984) demonstrated this was not the case. Experimental infestations of *Lernanthropus kroyeri* van Beneden, 1852 on *Dicentrarchus labrax* (Linne, 1758) revealed that this species possessed two free swimming naupliar stages but lacked the chalimus stages. It did have one free living copepodid stage followed by the infectious second fixed copepodid. Fixed copepodids III, IV and V preceded the two sub-adult stages before finally transforming into the adult. Furthermore, Kabata and Khodorevski (1977) described a copepodid, not a chalimus, from another gill inhabiting siphonostome *Dichelesthium oblongum*

(Abildgaard, 1794). The fact that I could not find any evidence of any frontal filament remnants or frontal gland scars on the many eudactylinids I have examined suggests that a similar life cycle prevails in this group of copepods. It can be presumed that they become infective as copepodids, attach themselves presumably with the second antennae and maxillipeds, suppress or skip the chalimus stage and molt finally into the pre-adult or adult stage. Indeed, Kabata (1981) suggests with regard to the absence of the frontal filament in the relatively primitive (minimal cephalization) siphonostome *Dissonus nudiventris* that the frontal filament is probably a relatively derived character.

Additionally, the majority of fish parasitizing siphonostome copepods exhibit a holoxene or direct life-cycle, requiring only a single host to live out their life. Again the evidence suggests this is probably the case with the eudactylinids, if not all of the gill dwelling families of possible dichelesthoid affinities (Eudactylinidae, Kroyeriidae, Hatchekiidae, Lernanthropidae and Dichelesthiidae).

REPRODUCTION

Copulation apparently occurs between the adult stages of the parasites. I have observed preserved specimens in the presumed copulatory embrace similar to what has been described by Benz and Adamson (1990) for *Nemesis robusta* (van Beneden, 1851), also a member of the Eudactylinidae parasitizing the common thresher shark (*Alopias vulpinus* (Bonnaterre, 1758)). The male attaches to the female using the prehensile second antennae and subchelate maxillipeds. The male then somehow transfers two spermatophores to the lateral surfaces of the female's genital segment which attach at the female's oviducal openings (Figure 3D and 16A) (see Benz and Adamson, 1990 for a detailed description of the morphology and attachment of the brown body and seminal vesicle in *N. robusta*). When the eggs exit the oviducal opening, they are fertilized by the males gametes from the seminal receptacle. Ovigerous females produce uniseriate egg sacs, presumably secreted by cement glands located in the genital segment.

HOST-PARASITE RELATIONSHIPS

DELETERIOUS EFFECTS / FEEDING

Eudactylina always attach themselves to the secondary lamellae of their elasmobranch host's gill, principally by their clasping chelate maxilliped (Figure 1). When extracting these parasites from the gills I have never observed gill tissue pathologies induced by *Eudactylina*. Certainly, some damage is being done since most of the specimens still had gill tissue gripped in their maxillipeds which had to be carefully removed before the microscopic examination and illustrations could proceed.

Additionally, over the last 14 years of collecting *Eudactylina* from elasmobranch gills I have observed a general trend for this genus to exhibit a rather low parasite load relative to other elasmobranch gill infecting siphonostome genera such as *Nemesis* and *Kroyeria*. For example, the maximum number of *Eudactylina acanthii* A. Scott, 1901 I collected from a spiny dogfish (*Squalus acanthias* Linnaeus, 1758), was 60 (average of five specimens was 35). Similarly, a single Pacific electric ray (*Torpedo californica*, Ayres) yielded a maximum of 77 *Eudactylina similis* T. Scott, 1902. These maximum numbers are reported here because it is very common to recover less than five individual *Eudactylina* from a single batoid or squaloid host.

Because individual *Eudactylina* seem to be attached to the secondary lamellae, presumably they feed directly on these respiratory surfaces. Unfortunately, no studies have been done on gut contents in *Eudactylina*. Benz and Adamson (1990) studied histological sections in the closely related eudactylinid *Nemesis robusta*, and found dark staining granules (partially digested blood?) reminiscent of those commonly found in the diverticula of haematophagus monogenetic trematodes.

SPECIFICITY

Eudactylina exhibits a high degree of both ecological and host specificity. General observations reveal *Eudactylina* to distribute itself in no apparent pattern or preferred areas across the host's hemibranchs, and *Eudactylina* will only be found on elasmobranch gills. Regarding host specificity, the majority of the species of *Eudactylina* are specific to a given host species or genus, making them good biological tags. A few species are apparently more flexible with their choice of hosts but still show specificity at a more general level in the hierarchy, restricting themselves to hosts within a

given family. Specifics are detailed in both the taxonomic account and phylogenetic analysis below.

SYSTEMATIC ACCOUNT

Genus *Eudactylina* van Beneden, 1853

Eudactylinidae: Female. Cephalothorax covered by well demarcated dorsal shield; four succeeding thoracic segments bearing cuticular flaps on terga. Genital segment small, quadrate and bearing oviducal openings and reduced uniramous leg five. Abdomen two-segmented. Caudal ramus bearing from four to six sometimes modified setae. Posteriorly directed cuticular flaps present on ventral surfaces of genital segment, abdomen, and caudal ramus.

First antenna indistinctly four to six segmented with geniculate flexion between second and third segments. Second segment bearing large curved prehensile claw. Terminal segment generally bearing one medial seta, one lateral aesthete, plus an additional 13 to 14 slender setae. Second antenna five-segmented with prehensile terminal claw. Mouth tube siphonostome. Mandible two-segmented; distal end dentiferous, bearing five to eight teeth. First maxilla biramous with endopod and exopod armed with three and two apical setae respectively. Second maxilla brachiform, two- possibly three-segmented. Maxilliped chelate, myxa produced into a large expanded receptacle. Legs one through four biramous, rami bimerous to trimerous. Exopod of leg two usually, though not always, modified (cf. *E. acanthii*). Leg five one-segmented and uniramous bearing three distal setae. Leg six represented by three minute spines at oviducal orifice.

Male: Similar to female. Abdomen three- to four-segmented. Caudal ramus less modified. Maxilliped subchelate, myxal area bearing a strong spinous process. First four pairs of less modified legs, with more plesiomorphic armature (long pinnate setae). Leg six on posterolateral edge of genital segment represented by two or three setae.

TYPE-SPECIES: *Eudactylina acuta* van Beneden, 1853.

COMMENTS: In spite of the general uniformity of habitus, the species in this genus differ from another in a multitude of structural details such as morphology of the cuticular flaps, armature of the second antenna, armature and segmentation of thoracic

legs and in specific character attributes of the caudal ramus.

Currently, *Eudactylina* consists of the 26 species illustrated and phylogenetically analyzed herein plus 12 nominal but unfortunately for this investigation unobtainable species, bringing the total to 38. The unobtainable nominal species will be reviewed at the end of the following section. An additional four species (*E. carchariaeglauci* Hesse, 1884, *E. mustellilaevis* Hesse, 1884, *E. puriensis* Tripathi, 1956, and *E. squatinaeangeli* Hesse, 1884) have been inadequately described to be recognized and are considered *species inquirendae*. The majority of the species described are parasites of squaloids (dogfish, lantern sharks), squatinids (angel sharks), pristiphorids (sawsharks), and batoids (skates, guitarfish and rays). The remaining species are found on the Carcharhinidae (requiem sharks) and Sphyrnidae (hammerheads). There are approximately 350 species of "sharks" (Compagno, 1984a), and 425-450 species of rays (Eschmeyer et al, 1983), and only 38 species of the highly host specific *Eudactylina* are known. This information suggests this genus is potentially enormous with many more species waiting to be discovered.

***Eudactylina acanthii* A. Scott, 1901**

(Figures 2-3)

Material examined. Several co-type females, BMNH 1911.11.8.48318-322, 1913.9.18.272-281, 1963.4.29.15, 1975.379-392 from British waters. Many females from the Vancouver Island region on loan from Dr. Z. Kabata, Pacific Biological Station, Nanaimo, British Columbia. Numerous females from the southern California Bight. All specimens were found attached to the branchial lamellae of the spiny dogfish, *Squalus acanthias* Linnaeus (1758).

Description

Female (Figure 2A)

Overall length in lateral view approximately 2.25 mm. Cephalothorax longer than wide, lateral margin notched accomodating the second maxillae. Ventrolateral margin of cephalothorax bearing small cuticular flaps. Tergum of first free thoracic somite with small cuticular flaps on ventrolateral margin. Second and third free thoracic somites with naked and indistinct terga. Fourth free thoracic somite bearing fifth leg smaller than previous two. Genital segment smaller than preceeding somite. Abdomen two-segmented, second segment ventrally bearing cuticular flaps. Caudal ramus (Figure 2B) longer than wide, bearing four terminal naked setae, one slender, medial seta, and one lateral naked seta; ventral surface armed with posteriorly directed cuticular flaps.

First antenna (Figure 2C) indistinctly five- or six-segmented, armature (proximal to distal) as follows: one stout seta, one small spinule, eight stout setae plus one large curving (prehensile) claw, nine stout setae, one short seta, 14 slender setae plus one aesthete. Second antenna (Figure 2D) five-segmented, uncinata, prehensile. Basal segment stout, second and third segments with sparse cuticular flaps, third segment bearing two slender setae arising from atypically reduced spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one stout auxiliary spine approximately 1/4 length of claw. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 2E) of two parts, dentiferous margin with six teeth. First maxilla (Figure 2F) biramous; endopod bearing two apical setae; exopod longer surmounted by two stout setae and one longer bilaterally denticulated seta. Second maxilla (Figure 2G) brachiform, lacertus larger than brachium armed with triangular cuticular flaps, brachium with triangular cuticular flaps and a tuft of coarse, sparse setae at base of terminal claw (calamus). Claw bearing two rows of denticles and proximal serrated membrane. Maxilliped (Figure 2H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust, bearing small stout spine on distal margin; myxal area expanded into large receptacle to accommodate claw of opposable chela. Shaft with single spine on lateral convex margin and strip of membrane along concave distal margin. Claw unciform with quadrangular cuticular expansion producing lateral shield.

First four pairs of legs biramous with three-segmented rami and two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial seta. Ventral surfaces of all four legs bearing triangular cuticular flaps. Armature of rami as follows: (non-pinnate setae in Roman numerals, pinnate setae (bearing setules) in Arabic numerals).

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 3A) terminal segment of exopod compressed bearing two small spiniform seta, lateral seta with single denticle; terminal segment of endopod with two most lateral setae denticulated, most medial seta papilliform. Leg two (Figure 3B) with atypically unmodified exopod, all setae on exopod and endopod spiniform and smooth. Legs three and four (Figure 3C) similar; all setae spine-like and denticulated, terminal segment of endopod compressed. Leg five (Figure 3D) suboval; distally bearing three

long slender setae plus one similar seta arising dorsally from the base. Leg six (Figure 3D detail) represented by three small, stout setae on a posterodorsal ridge adjacent to the oviducal opening.

Male: Unknown

Comments: Kabata (1979) mentions the possibility of misinterpreting cuticular flaps for the very tiny spine-like setae and vice-versa on the swimming legs of *E. acanthii*. In spite of this word of caution, I have found the number of apical elements on endopods one, two, three, and four to be two, two, one, and one respectively, in contrast to Kabata's three, three, three, and three, the former being generally more consistent with the endopodal formula exhibited by the genus.

Eudactylina typically exhibits a bizarrely modified exopod on leg two. This species however stands out as the anomaly within the genus in possessing a normal endopod (resembling endopods of legs one, three, and four).

All previous host records of *Eudactylina acanthii* come specifically from the branchial lamellae of the spiny dogfish *Squalus acanthias*. Like most parasitic copepods, the geographic range of this parasite is coincident with that of its host. This copepod has been reported from the Irish Sea, eastern and western North Atlantic, Sea of Japan, Vancouver Island region, coastal Angola in the southern Atlantic (see Kabata, 1979), Quehui, Chiloe', Chile (Castro and Baeza, 1991), and now from southern California waters.

***Eudactylina acuta* van Beneden, 1853**

(Figures 4-5)

Syn: *Eudactylina complexa* Brian, 1924 (see Kabata, 1979)

Material examined. Several females, MNHN, CP 156 and CP 173 from the branchial lamellae of the angelshark, *Squatina squatina* (Linnaeus, 1758) restricted to the western North Atlantic and the Mediterranean (no specific site collection data).

Description

Female (Figure 4A)

Overall length in lateral view approximately 3.3 mm. Cephalothorax longer than wide, lateral margin notched accomodating lacertus of second maxillae. Ventrolateral

and dorsal surfaces of cephalothorax bearing small cuticular flaps. Tergum of first free thoracic somite with small cuticular flaps on dorsal surface. Second and third free thoracic somites with cuticular flaps on the dorsal surface and distinct terga. Fourth free thoracic somite smaller than previous two, bearing leg five. Genital segment smaller than preceding somite, with cuticular flaps on ventral surface. Abdomen two-segmented, ventral surface bearing cuticular flaps. Caudal ramus (Figure 4B) longer than wide, bearing two terminal stout setae, one slender medial seta, and one lateral naked seta; ventral surface armed with patches of posteriorly directed cuticular flaps. Oviducal opening dorsal, egg strings uniseriate (Figure 4C).

First antenna (Figure 4D) indistinctly five-segmented, armature (proximal to distal) as follows: one stout seta, four stout setae plus one large serrated, curving (prehensile) claw, three slender setae, two short setae plus two well developed denticulated claws, two large stout setae and 12 slender setae plus one aesthete. Second antenna (Figure 4E) five-segmented, prehensile. Basal segment stout (not shown), second segment with stout spiniform process, third segment bearing rectangular cuticular flaps, two slender setae arising from large, curving spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one stout auxiliary spine nearly reaching the end of the claw. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 4F) of two parts, dentiferous margin with seven teeth. First maxilla (Figure 4G) biramous; endopod bearing two apical setae; exopod longer surmounted by two stout setae and one longer seta. Second maxilla (Figure 4H) brachiform, lacertus larger than brachium armed with cuticular flaps, brachium with crescent-shaped cuticular flaps and two tufts of setae (one coarse and one fine) at base of terminal claw (calamus). Claw bearing three distal rows of serrated membranes and one proximal serrated membranous flap. Maxilliped (Figure 4I) chelate, indistinctly segmented, proximal segment pedunculate (omitted in illustration); corpus maxillipedis robust bearing small stout spine on distal margin, rectangular cuticular flaps and a large transverse cuticular flange; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft with two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw unciform with quadrangular cuticular expansion producing lateral shield.

First four pairs of legs biramous with three-segmented rami and two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing crescent shaped cuticular flaps. Armature of rami as follows: (non-pinnate setae in Roman numerals, pinnate setae (bearing setules) in Arabic numerals).

Leg one	Exopod	I-0	I-0	IV	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 5A) all setae denticulated. Exopod two (Figure 5B) typically modified without cuticular flaps, first segment greatly enlarged bearing one smooth seta, second segment smaller with huge stout spine, third segment compressed apically armed with one stout seta, one truncate seta and one recurving slender seta. Leg two endopod (Figure 5C) with naked proximal segment, segments two and three with cuticular flaps and two finely spinulated setae on apical segment. Legs three and four (Figure 5D) similar; endopodal seta denticulated, exopodal setae curving with branching tips (Figure 5E). Leg five (Figure 5F) oval; lateral surface covered with rectangular cuticular flaps, distally bearing three long slender setae plus one similar seta arising dorsally from the base.

Male: Not obtained (see Kabata, 1979)

Comments: *E. acuta* appears to be specific to the angelshark *Squatina squatina*. Kabata (1979) mentions this parasite has been recorded (Valle, 1880; Brian, 1906; Oorde-de-Lint and Schuurmans Stekhoven, 1936) from the spiny dogfish *Squalus acanthias*, but neither he nor I have ever seen this copepod on that host (hundreds of which I have examined) suggesting a suspect association.

The geographical distribution of *Squatina squatina* ranges from southern Norway, Sweden and Shetland Island to Morocco off the western Sahara, Canary Islands, and the Mediterranean (Compagno, 1984a). Predictably, the copepod has been reported from most of this range.

Additionally, Kabata (1979) has tentatively synonymized *E. complexa* (Brian, 1924) with *E. acuta*. Besides similarities between descriptions of the two species, both are found on the same host in the same area. Hence, the records of *E. complexa* (= *E. acuta*) from the host genera *Torpedo*, *Pteromylaeus*, *Raja*, and *Myliobatis* reported by Essafi and Raibaut (1977) from the Mediterranean will be treated as uncertain host associations.

This species is easily distinguished by the nature of the caudal ramus, the huge, stout spine on the second segment of the modified exopod of leg two, and the branching, digitiform claw-like setae on the exopods of legs three and four.

***Eudactylina aphioxenos* sp. nov.**

(Figures 6-7)

Material examined. Numerous females from the branchial lamellae of the Pacific angelshark *Squatina californica* Ayres, 1859 from the southern California bight. Female holotype (USNM 266519) and 7 female paratypes (USNM 266520) deposited at the United States National Museum of Natural History.

Etymology : The specific name *aphioxenos* is derived from the greek *aphilo*, for unwanted or hateful and from the greek *xenos* for guest. Thus, the unwanted guest.

Description

Female (Figure 6A)

Overall length in lateral view approximately 2.2 mm. Cephalothorax longer than wide, lateral margin notched near base of maxilliped and lacertus of second maxillae. Ventrolateral and dorsal surfaces of cephalothorax bearing small triangular cuticular flaps. Tergum of first free thoracic somite with small triangular cuticular flaps on dorsal surface. Second and third free thoracic somites with triangular cuticular flaps on the dorsal surface and distinct terga. Fourth free thoracic somite smaller than previous two, with distinct tergum and triangular cuticular flaps, bearing leg five. Genital segment smaller than preceding somite, with cuticular flaps on ventral surface. Abdomen two-segmented, ventral surface bearing cuticular flaps. Caudal ramus (Figure 6B) slightly longer than wide, bearing two stout terminal setae, one naked dorsal seta, and one lateral naked seta; ventral surface armed with posteriorly directed triangular cuticular flaps.

First antenna (Figure 6C) indistinctly five-segmented, armature (proximal to distal) as follows: one stout seta; six smooth slender setae, two denticulated setae (one short (ghosted in near lateral margin), one long) plus one large serrated, curving (prehensile) claw; four slender setae plus one stout bilaterally denticulated seta; two short setae plus two well developed denticulated spines; 14 slender setae, one unilaterally denticulated seta plus one aesthete. Second antenna (Figure 6D) five-segmented, prehensile. Basal segment stout, second segment with stout spiniform process, third segment bearing triangular cuticular flaps, two slender setae arising near base of large styliform process. Fourth segment elongate with small cuticular flaps along convex margin; fifth segment an unciform terminal claw bearing two slender setae and one stout auxiliary spine. Mouth tube siphonostome and similar to that of other species.

Mandible (Figure 6E) of two parts, dentiferous margin with seven teeth. First maxilla (Figure 6F) biramous; endopod bearing two apical denticulated setae; exopod longer surmounted by two stout setae and one longer denticulated seta. Second maxilla (Figure 6G) brachiform, lacertus slightly larger than brachium armed with triangular cuticular flaps, brachium with triangular cuticular flaps and two tufts of setae and possibly a small reduced spine at base of terminal claw (calamus). Medial surface of claw bearing three distal rows of serrated membranes and one proximal serrated membranous flap, lateral surface only armed with two serrated membranous flaps. Maxilliped (Figure 6H) chelate, indistinctly segmented, proximal segment pedunculate (omitted in illustration); corpus maxillipedis robust bearing small stout spine on distal margin, triangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft with two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw unciform with transverse cuticular flange bearing quadrangular cuticular expansion producing lateral shield.

First four pairs of legs biramous with three-segmented rami and two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing triangular cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	IV	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 7A) all setae (except most medial seta on terminal segment of exopod) denticulated. Exopod two (Figure 7B) typically modified without cuticular flaps, first segment greatly enlarged bearing one smooth seta, second segment smaller with slender seta, third segment compressed apically armed with one short seta, one truncate seta and one recurving slender seta. Leg two endopod (Figure 7B) with two finely denticulated slender setae (one long, one short) on apical segment. Legs three and four (Figure 7C) similar; endopodal seta denticulated, exopodal setae curving with branching tips (Figure 7C detail). Leg five (Figure 7D) elongate; lateral surface covered with triangular cuticular flaps, distally bearing three long slender setae plus one seta arising dorsally from the base.

Male: Not found

Comments: *E. philoxenos* appears to be specific to the Pacific angelshark *Squatina californica*.

Squatina californica ranges from southeastern Alaska to the Gulf of California (Compagno, 1984a). Interestingly, Kato, Springer and Wagner (1967) synonymized the southern angelote *Squatina armata* (Philippi, 1887) from off the eastern South Pacific shores of South America with this host species. Compagno (1984a) mentions there is evidence against this taxonomic interpretation and adds that the Gulf of California angelshark may in fact be different from the Pacific angelshark. Evidence in support of Compagno's position is added here with parasite data. The southern angelote originally *Squatina armata* is parasitized by *Eudactylina tuberifera* Castro and Baeza (1987) from off the West coast of Chile, a species unmistakably distinct (and redescribed later herein) from the new species infecting *Squatina californica*.

E. philoxenos is similar to *E. acuta* and *E. tuberifera*, both parasites of angelsharks. All three species possess relatively large (almost digitiform) branching tips on the setae of exopods three and four. *E. philoxenos* can be distinguished from its other two allies by its relatively elongate fifth leg, the relatively small and slender seta on the second segment of the modified second exopod, its very small and numerous triangular-shaped cuticular flaps, and its lack of the transverse cuticular flange on the corpus of the maxilliped.

***Eudactylina aspera* Heller, 1865**

(Figures 8-9)

Material examined. One female, BMNH 1968.1.5.3 from the branchial lamellae of the brownbanded bamboo shark, *Chiloscyllium punctatum* Müller and Henle, 1838 collected from Moreton Bay, Queensland. Several females USNM 153636 from the branchial lamellae of the milk shark, *Rhizoprionodon acutus* (Rüppel, 1837), several females USNM 153634 from the spinner shark, *Carcharhinus brevipinna* (Müller and Henle, 1839), (= *Carcharhinus maculipinnis* (Poey, 1865)), and numerous females USNM 153639 from the scalloped hammerhead, *Sphyrna lewini* (Griffith and Smith, 1834), all collected from the Indian Ocean near Nosy Be, Madagascar.

Description

Female (Figure 8A)

Overall length in lateral view approximately 1.5 mm. Cephalothorax longer than

wide, lateral margin notched accomodating lacertus of second maxillae. Ventrolateral and dorsal surfaces of cephalothorax covered with cuticular flaps. Tergum of first, second, third, and fourth free thoracic somites covered with cuticular flaps. Fourth free thoracic somite smaller than previous three, bearing leg five. Genital segment smaller than preceeding somite, with cuticular flaps on ventral surface. Abdomen two-segmented, ventral surface bearing cuticular flaps. Caudal ramus (Figure 8B) longer than wide, bearing two stout setae, one dorsal naked seta, and one lateral naked seta; ventral surface armed with posteriorly directed cuticular flaps.

First antenna (Figure 8C) five-segmented, armature (proximal to distal) as follows: one slender seta; seven smooth slender setae, one small denticulated seta plus one large denticulated, curving (prehensile) claw; seven smooth setae, one large spine plus one well developed denticulated spine; one large denticulated spine; terminal segment with 12 smooth slender setae, two denticulated setae plus one aesthete. Second antenna (Figure 8D) five-segmented, prehensile. Basal segment short and unarmed, second segment with well developed spiniform process and triangular cuticular flaps, third segment bearing wavy quadrangular cuticular flaps, two slender setae arising from large, curving spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one stout auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 8E) of two parts, dentiferous margin with six teeth. First maxilla (Figure 8F) biramous; endopod bearing triangular cuticular flaps and two apical denticulated setae; exopod longer surmounted by two small setae and one longer denticulated seta. Second maxilla (Figure 8G) brachiform, lacertus larger than brachium armed with cuticular flaps (omitted in illustration), brachium with crescent-shaped cuticular flaps and two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or hair-like) at base of terminal claw (calamus). Claw bearing one serrated membrane parallelling the distal half of the claw and two pendulous strips of membrane, one hanging from each side. Maxilliped (Figure 8H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, narrow rectangular cuticular flaps and a large transverse cuticular flange; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing many fine triangular cuticular flaps with two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw unciform with quadrangular cuticular expansion producing lateral shield.

First four pairs of legs biramous with three-segmented rami and two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial seta. Ventral surfaces of all four legs bearing crescent to sub-triangular shaped

cuticular flaps. Armature of rami as follows:

Leg one	Exopod	0-0	0-0	IV	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	1-0	1-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	1-0	1-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	1-0	1-0	III	Endopod	0-0	0-0	I

Leg one (Figure 9A) all setae slender and denticulated. Exopod two (Figure 9C) typically modified, first segment greatly enlarged with proximal crescentic cuticular flap patch, one distal stout seta, second segment smaller with stout seta, third segment armed with one small sub-apical seta, one apical slightly curving seta plus one large serrated curving claw-like seta. Leg two endopod (Figure 9B) completely covered with crescentic and sub-triangular cuticular flaps with two finely denticulated slender setae on terminal segment. Legs three and four (Figures 9D and 9E) similar; endopodal seta (Figure 9D) claw-like and unilaterally denticulated with a single setule or flagelliform process arising midpoint on the seta, exopodal setae (Figure 9E) stout with largest most apical seta curving with bifid tip. Leg five (Figure 9F) longer than wide; lateral surface covered with crescent shaped cuticular flaps, distally bearing three long bifurcate slender setae plus one seta arising dorsally from the base.

Male: Unknown

Comments: *E. aspera* was originally reported from *Carcharias pleurotaenia*, Bleeker, 1852 (= *Carcharhinus limbatus* (Valenciennes, 1839)), the blacktip shark from Java (Heller, 1865). Since then this parasite has been reported from the branchial lamellae of the sharpnose shark, *Rhizoprionodon terraenovae*, (Richardson, 1836), the smooth tooth or fine tooth shark *Aprionodon isodon* (= *Carcharhinus isodon* (Valenciennes, 1839)), collected from Lemon Bay, Florida (Gulf of Mexico) (Bere, 1936). Cressey (1967) reported *E. aspera* from the spinner shark, *Carcharhinus brevipinna* (Müller and Henle, 1839), the scalloped hammerhead, *Sphyrna lewini* (Griffith and Smith, 1834), and from *Rhizoprionodon acutus* (Rüppel, 1837) all collected from the Indian Ocean near Nosy Be, Madagascar. Kabata (1970) added to the host list an unidentified requiem shark, *Carcharhinus* sp., and a member of the Hemiscylliidae, the brownbanded bamboo shark, *Chiloscyllium punctatum* Müller and Henle, 1838 both from Moreton Bay, Queensland. Finally, Essafi and Raibaut (1977) collected the parasite from the spinner shark from Tunisian waters. The parasite seems to have an affinity for hosts of the family Carcharhinidae, with only the one record from the Sphyrnidae

and one record from the Hemiscylliidae, an orectolobid (carpet sharks) as the host group exceptions.

Heller (1865) shows pointed processes arising from the lateral margins of the cephalothorax. This appears to be an erroneous interpretation of the notches in the lateral margins of the dorsal shield.

This species is easily distinguished by the large spatulate process on the second segment of the second antenna, the pendulous membranous flaps on the claw of the second maxilla, the elongate proximal segment and large denticulated claw-like seta on the distal segment of the second exopod, and the branching setae of leg five.

Eudactylina chilensis Ho and McKinney, 1981
(Figures 10-11)

Material examined. Several females, from the personal collections of Dr. Ju-Shey Ho, California State University, Long Beach and Raul Castro Romero, Universidad de Antofagasta, Antofagasta, Chile, all specimens collected from the branchial lamellae of the black shark or hooktooth dogfish, *Aculeola nigra* De Buen, 1959 collected from Coquimbo, Chile (eastern South Pacific).

Description

Female (Figure 10A)

Overall length in lateral view approximately 2.3 mm. Cephalothorax longer than wide, lateral margin notched accommodating area of lacertus of second maxillae. Ventrolateral and dorsal surfaces of cephalothorax bearing small crescentic cuticular flaps. Tergum of first, second, and third free thoracic somites covered with small cuticular flaps on dorsal surface. Fourth free thoracic somite not as densely covered with flaps and smaller than previous somites and bearing leg five. Genital segment smaller than preceding somite, with cuticular flaps on ventral surface. Abdomen two-segmented, ventral surface bearing cuticular flaps. Caudal ramus (Figure 10B) longer than wide, distal margin bearing three large denticulated setae and one small smooth stout seta, dorsal surface with one smooth slender seta, ventral surface armed with triangular shaped posteriorly directed cuticular flaps and one tiny seta.

First antenna (Figure 10C) five-segmented, armature (proximal to distal) as follows: first segment with one unilaterally denticulated seta, second segment with six smooth slender setae, one thick spine, one unilaterally denticulated seta plus one large denticulated curving (prehensile) claw, third segment with nine smooth setae plus one

well developed unilaterally denticulated seta, fourth segment bearing one unilaterally denticulated seta, fifth segment with one unilaterally denticulated seta, 13 slender setae plus one aesthete. Second antenna (Figure 10D) five-segmented, prehensile. Basal segment short, second segment with sub-triangular cuticular flaps, third segment bearing rectangular cuticular flaps, two slender setae arising near base of spinous process. Fourth segment elongate with small triangular cuticular flaps; fifth segment an unciform terminal claw bearing two slender setae and one stout auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 10E) of two parts, dentiferous margin with eight teeth. First maxilla (Figure 10F) biramous; endopod with triangular cuticular flaps and bearing two apical spinulated setae; exopod longer surmounted by two stout setae and one longer slender seta. Second maxilla (Figure 10G) brachiform, lacertus larger than brachium armed with crescent shaped cuticular flaps, basal process located at base of lacertus, brachium with crescent-shaped cuticular flaps and two tufts of setae, one tuft composed of fine hair-like setules the other consisting of coarse rope-like, possibly fused setules at base of terminal claw (calamus). Claw bilaterally bearing two strips of serrated membranes. Maxilliped (Figure 10H) chelate, indistinctly segmented, proximal segment pedunculate (omitted in illustration); corpus maxillipedis robust bearing small stout spine on distal margin, rectangular and semicircular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing triangular cuticular flaps with two setae: one near midpoint on lateral convex margin and the other along concave distal margin. Claw unciform with quadrangular cuticular expansion producing lateral shield.

First four pairs of legs biramous with three-segmented rami and two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing sub-triangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 11A) all setae on rami slender and denticulated. Exopod two (Figure 11B) typically modified generally devoid of cuticular flaps, first segment greatly enlarged proximally bearing small patch of cuticular flaps and distally bearing one smooth, slender seta, second segment smaller with slender seta, third segment armed with two small curving seta and one large bilaterally denticulated curving seta. Leg two

endopod (Figure 11B) with two finely denticulated slender setae on apical segment. Legs three and four similar; exopod three and four (Figure 11C) with stout setae and one large bilaterally denticulated seta on terminal segment, endopod three and four (Figure 11D) bearing a single bilaterally denticulated seta on terminal segment. Leg five (Figure 11E) oval; lateral surface covered with fine triangular cuticular flaps, distally bearing three slender setae plus one seta arising dorsally from the base.

Male: Not obtained (see Ho and McKinney, 1981)

Comments: This parasite has not been reported since its initial discovery on *Aculeola nigra* (Dalatiiformes: Etmopteridae) from Chilean waters by Ho and McKinney (1981).

This species can be distinguished by the presence of cuticular flaps on the second, third, and fourth segments of the second antenna with the reduced spiniform process on the third segment, the three apical slender, bilaterally, denticulated setae plus the unique, tiny lateral seta on the caudal ramus.

***Eudactylina corrugata* Bere, 1930**

(Figures 12-13)

Material examined. One female, USNM 60469 from the branchial lamellae of the little skate, *Raja erinacea* Mitchell collected from St. Andrews, New Brunswick, one female, USNM 79619 from the branchial lamellae of *Raja erinacea* collected from Woods Hole, Massachusetts July 17, 1914.

Description

Female (Figure 12A)

Overall length in lateral view approximately 1.7 mm. Specimen unnaturally bloated due to lactic acid absorption during microscopic examination. Cephalothorax longer than wide, lateral margin notched accommodating lacertus of second maxillae. Ventrolateral and dorsal surfaces of cephalothorax covered with cuticular flaps. Terga of first, second, third, and fourth free thoracic somites sparsely covered with cuticular flaps; terga of third and fourth free thoracic somites indistinct. Second and third free thoracic somites bearing posteriorly directed cuticular flaps on ventral surface. Fourth free thoracic somite smaller than previous three, bearing leg five. Genital segment smaller than preceding somite, with cuticular flaps on ventral surface. Abdomen two-

segmented, ventral surface bearing cuticular flaps. Egg string (Figure 12B) uniseriate. Caudal ramus (Figure 12C) suboval, bearing two terminal slightly curved stout setae, one medial naked seta, and one lateral naked seta; ventral surface armed with posteriorly directed cuticular flaps.

First antenna (Figure 12D) indistinctly five-segmented, armature (proximal to distal) as follows: first segment bearing one slender seta; second segment with seven smooth setae, one denticulated seta plus one large denticulated, curving (prehensile) claw; third segment with nine smooth setae plus one large uncinata spine; fourth segment with one slender seta; terminal segment with 14 smooth setae plus one aesthete. Second antenna (Figure 12E) five-segmented, prehensile. Basal segment short, second segment with stout spiniform process, third segment bearing quadrangular cuticular flaps, two slender setae arising from near base of large curving spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one stout auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (not illustrated) of two parts, dentiferous margin with eight teeth. First maxilla (Figure 12F) biramous; endopod bearing two apical spinulated setae; exopod longer surmounted by two small slender setae and one longer spinulated seta. Second maxilla (Figure 12G) brachiform, lacertus larger than brachium, brachium with sub-triangular and crescent-shaped cuticular flaps and two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or hair-like) at base of terminal claw (calamus). Claw bearing two pairs of serrated membranes parallelling the claw plus one distal strip of membrane along the convex margin. Maxilliped (Figure 12H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, narrow rectangular cuticular flaps and region of small triangular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw unciform with quadrangular cuticular expansion producing lateral shield.

First four pairs of legs biramous with two-segmented endopods, three-segmented exopods and two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing rectangular to sub-triangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	IV	Endopod	0-0	-	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	-	II

Leg three	Exopod	I-0	I-0	III	Endopod	0-0	-	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	-	I

Leg one (Figure 13A) exopod indistinctly three-segmented; exopodal setae slender unilaterally denticulated with or without spinules, endopodal setae bilaterally spinulated. Exopod two (Figure 13B) typically modified, first segment greatly enlarged with proximal triangular cuticular flaps along the medial margin, one distal stout seta, second segment smaller with stout spine, third segment armed with one small sub-apical seta, another sub-apical recurving slender seta plus one large, blunt apical truncate seta. Leg two endopod (Figure 13C) with two finely spinulated slender setae on terminal segment. Legs three and four (Figure 13D) similar; setae slender and denticulated. Leg five (Figure 13E) longer than wide; lateral surface covered with rectangular cuticular flaps, distally bearing three slender setae plus one seta arising dorsally from the base.

Male: Unknown

Comments: *E. corrugata* has only been reported by Bere (1930) occurring on the skates *Raja erinacea* Mitchell, 1825 collected from St. Andrews, New Brunswick and Woods Hole, Massachusetts and from *Raja scabrata* Garman, 1913 (= *Raja radiata* Donovan, 1807) collected from Woods Hole, Massachusetts.

This species is easily distinguished by the large truncate seta on the terminal segment of the second exopod and by the two-segmented endopods of legs one through four.

***Eudactylina dactylocerca* sp. nov.**

(Figures 14-15)

Material examined. Several females from the branchial lamellae of the shovel-nose guitarfish *Rhinobatus productus* (Ayres) collected from inshore waters from the southern California Bight. Female holotype (USNM 266521) and 4 female paratypes (USNM 266522) deposited at the United States National Museum of Natural History.

Etymology: The specific name *dactylocerca* is derived from the Greek *dactylos* meaning finger or digit and *cerco* from *kerkos* meaning tail, referring to the digitiform processes on the caudal rami.

Description

Female (Figure 14A)

Overall length in lateral view approximately 1.9 mm. Cephalothorax longer than wide, lateral margin notched accomodating lacertus of second maxillae. Anterolateral and dorsal surfaces of cephalothorax covered with cuticular flaps. Dorsal and ventrolateral surfaces of tergum of first, second, and third free thoracic somites covered with cuticular flaps; terga of first and second free thoracic somites aliform. Fourth free thoracic somite smaller than previous three, bearing leg five. Genital segment smaller than preceeding somite. Abdomen (Figure 14C) two-segmented, ventral surface bearing a pair of blunt tubercles on each segment, and a pair of semicircular cuticular flaps on the posterior segment. Egg string (Figure 14D) uniseriate. Caudal ramus (Figure 14B) beautifully modified into a tridentate digitiform structure composed of three strongly sclerotized tuberculous processes (fused modified setae?), one tiny proximal seta (sensilla?), one dorsomedial slender seta, one small stout ventral seta plus two ventrodistal slender setae; ventral surface armed with a single posteriorly directed semicircular cuticular flap.

First antenna (Figure 14E) five-segmented, armature (proximal to distal) as follows: first segment bearing one slender seta; second segment with four smooth slender setae, one large smooth seta, three denticulated slender setae plus one large denticulated, curving (prehensile) claw; third segment with eight smooth setae, one denticulated slender seta plus one large uncinat denticulated spine; fourth segment with one slender seta and an atypical conical process; terminal segment with 13 smooth spiniform plus one aesthete. Second antenna (Figure 14F) five-segmented, prehensile. Basal segment short, second segment with unciform process and truncated quadrangular cuticular flaps, third segment bearing quadrangular cuticular flaps and two slender setae arising from near base of well produced spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one stout uncinat auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 14G) of two parts, dentiferous margin with five teeth. First maxilla (Figure 14G) biramous; endopod bearing tiny triangular cuticular flaps and two apical denticulated setae; exopod longer surmounted by two small setae and one longer slender seta. Second maxilla (Figure 14H) brachiform, lacertus larger than brachium, brachium with crescent-shaped cuticular flaps and two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or hair-like) at base of terminal claw (calamus). Claw bearing two rows of serrated membranes parallelling the claw plus one distal pendulous strip of membrane along the convex margin of other side. Maxilliped (Figure 14I) chelate, indistinctly segmented, proximal segment pedun-

culate; corpus maxillipedis robust bearing small seta on distal margin and narrow rectangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one with enlarged proximal region near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw (Figure 14J) complex, unciform with tiny proximal seta, cuticular expansions producing a fused complex of claw and cuticle.

First four pairs of legs biramous, except leg four with two-segmented endopod, three-segmented exopods and endopods on remaining rami, sympods two-segmented. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing rectangular to sub-triangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	-	I

Leg one (Figure 15A) rami three-segmented; exopodal setae unilaterally bearing serrated flange with medial denticulations on largest apical seta on terminal segment, largest endopodal seta unilaterally bearing serrated flange, smaller bilaterally denticulated. Exopod two (Figure 15B) typically modified, first segment greatly enlarged with quadrangular cuticular flaps along the lateral margin, one distal seta, second segment smaller with seta, third segment armed with two smooth curving setae plus one large curving bilaterally denticulated seta. Leg two endopod (Figure 15B) with one slender seta and one large bilaterally serrated seta on terminal segment. Sclerite bar between leg two and leg three (Figure 15C) with single, large medial stylet. Legs three and four (Figure 15D) similar; except leg four has a two-segmented endopod; exopodal setae claw-like and unilaterally denticulated, endopodal seta unilaterally bearing denticles and serrated membranous flange. Leg five (Figure 15E) slightly longer than wide; lateral surface smooth, distally bearing three pinnate setae plus one seta arising dorsally from the base.

Male: Unknown

Comments: *E. dactylocerca* is specific to the shovelnose guitarfish *Rhinobatus productus*. It is the third eudactylinid to be reported from this genus of host. *Eudactylina rhinobati* Raibaut and Essafi, 1979 has been found from *Rhinobatus rhino-*

batus (Linne', 1758), and from *Rhinobatus cemiculus* (Geoffrey Saint-Hilaire, 1817) collected from Tunisia, and recently Luque and Farfan (1991) acquired *Eudactylina peruensis* from *Rhinobatus planiceps* Garman, 1880 from eastern South Pacific waters off the west coast of Peru.

Some of the illustrations of *E. rhinobati* (Raibaut and Essafi, 1979) lack detail but imply something atypical, yet vaguely similar (digitiform elements) among the caudal rami of these three rhinobatid-infesting species. All three species share the dorsolateral aliform expansions of free thoracic somites one and two, suggesting a very close relationship between these species despite the great geographical distances that separate them.

This species is easily distinguished from all other species in the genus by the modified caudal rami. The interesting fine denticulations along the lateral margin of the setae on exopods three and four are shared by *E. peruensis*.

***Eudactylina diabolophila* sp. nov.**

(Figures 16-17)

Material examined. Two females from the branchial lamellae of the Manta or Devil Ray *Manta birostris* (Donndorff, 1798), (California Academy of Sciences Fish Collection) collected August 20, 1951 during the George Vanderbilt Equatorial Pacific Expedition from station 49 located at 5° 51.9' N X 162° 7.6' N, near Sand and Line Islands. Female holotype (USNM 266523) deposited at the United States National Museum of Natural History.

Etymology: The specific name *diabolophila* is derived from the Greek *diabolos* meaning devil and *philia* meaning loving, referring to this species predilection for feeding upon the devil ray.

Description

Female (Figure 16A)

Overall length in lateral view approximately 3.8 mm. Cephalothorax longer than wide, lateral margin notched. Anterolateral and dorsal surfaces of cephalothorax covered with cuticular flaps. Dorsolateral surfaces of first, and second free thoracic somites covered with cuticular flaps. Fourth free thoracic somite smaller than previous three, bearing leg five. Genital segment smaller than preceding somite. Abdomen two-segmented; lateral surface of posterior segment with cuticular flaps. Caudal ramus (Figure

16B) atypically elongate with six distal, relatively unmodified naked setae, a distal area of anteriorly directed rectangular flaps and the lateral margin armed with subtriangular cuticular flaps.

First antenna (Figure 16C) six-segmented, armature (proximal to distal) as follows: first segment atypically bearing a lateral patch of semicircular cuticular flaps and bearing one reduced stout seta; second segment with five naked and one large denticulated, curving (prehensile) claw; third segment with three naked setae; fourth segment with three small naked seta plus one large styliform seta, fifth segment with a single naked seta; terminal segment with 13 setae plus one aesthete. Second antenna (Figure 16D) five-segmented, prehensile. Basal segment short, second segment elongate and unarmed, third segment bearing thin rectangular cuticular flaps and two slender setae arising from near base of greatly reduced spinous process (this may only be the distomedial corner of this segment). Fourth segment elongate with fine triangular cuticular flaps along convex margin; fifth segment an elongate, unciform terminal claw bearing two slender setae and one small auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 16E) of two parts, dentiferous margin with five teeth. First maxilla (Figure 16F) biramous; sympod with three rows of fine triangular cuticular flaps, endopod bearing tiny triangular cuticular flaps and two stout apical setae; exopod longer with tiny triangular cuticular flaps and surmounted by two small stout setae and one longer seta. Second maxilla (Figure 14G) brachiform, lacertus larger than brachium bearing small triangular cuticular flaps and basal process, brachium with triangular cuticular flaps and two tufts of setae (one coarse or rope-like (possibly fused setae)) and one fine or hair-like at base of terminal claw (calamus). Claw bearing two rows of denticles proximally plus a row of denticles along both the concave and convex margins. Maxilliped (Figure 16H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small naked seta on distal margin and tiny triangular cuticular flaps; myxal area proximally bearing triangular cuticular flaps and expanded into a receptacle to accommodate claw of opposable segment. Shaft with proximal patch of small triangular flaps and bearing two setae: one very small near midpoint (not illustrated) on lateral convex margin and the other along concave distal margin. Claw (Figure 16H) complex, unciform with a very small lateral shield.

First four pairs of legs biramous and trimerite, sympods two-segmented. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing triangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 17A) rami three-segmented; exopodal setae unilaterally to bilaterally denticulated, largest endopodal seta bilaterally denticulated, smaller smooth. Leg two (Figure 17C) atypically unmodified, setae stout with and without denticulations. Legs three and four (Figure 17B) similar; distolateral areas on first and second segments of exopods greatly extending past segmental boundaries, with ventral face devoid of cuticular flaps, largest of three stout setae on terminal segment bilaterally denticulated. Leg five (Figure 17D) subquadrate, slightly wider than long, distally bearing three slender setae plus one similar seta arising dorsally from the base; lateral surface with small triangular cuticular flaps

Male: Unknown

Comments: *E. diabolophila* is the first record of *Eudactylina* from the genus *Manta*. Although Pacific and Atlantic mantas are presently considered conspecific, it would be of interest to examine this host from the Atlantic for additional corroborative evidence.

This species is easily distinguished from all other species in the genus by the greatly extended distolateral regions of the first and second segments on the third and fourth exopods, the unusually elongate caudal rami, the very large strongly curved claw of the second antenna, and the greatly reduced "lateral shield" of the claw of the maxilliped. The unmodified condition of the exopod of leg two found in this species is similarly found in *E. acanthii* and *E. squamosa*.

***Eudactylina dollfusi* Brian, 1924**

(Figures 18-19)

- Syn: *Eudactylina spinifera* Wilson, 1932, *syn nov.*
Eudactylina spinifera Wilson, 1932; of Bere (1936)
Eudactylina spinifera Wilson, 1932; of Yamaguti (1963)
Eudactylina spinifera Wilson, 1932; of Cressey (1970)

Material examined. Several females (types?) MNHN CP 174 from the branchial lamellae of the host squale (Marao); Several female specimens USNM 63915 from the branchial lamellae of *Carcharias commersoni* (= ?) collected from Wood's Hole, July 25, 1927; female "holotype" USNM 56621 from gills of *Carcharhinus milberti*; from Wood's Hole; numerous females USNM 153650, 153651, 153652, 63915, 79087 from the gills of *Carcharhinus milberti* (Valenciennes, in Müller and Henle, 1839), (= *Carcharhinus plumbeus* (Nardo, 1827)).

Description

Female (Figure 18A)

Overall length in lateral view approximately 1.8 mm. Cephalothorax longer than wide, lateral margin notched accomodating lacertus of second maxillae. Anterolateral and dorsal surfaces of cephalothorax sparsely covered with spiniform cuticular flaps. Dorsal and ventrolateral surfaces of terga of first, second, third, and fourth free thoracic somites sparsely covered with spiniform cuticular flaps. Fourth free thoracic somite smaller than previous three, bearing leg five. Genital segment smaller than preceding somite and sparsely covered with spiniform cuticular flaps. Abdomen (Figures 18A, B) two-segmented, ventral surface bearing a pair of slender setae on anterior segment, and posteriorly directed triangular cuticular flaps on both segments. Caudal ramus (Figure 18B) longer than wide with posteriorly directed triangular cuticular flaps on ventral surface, rami bearing one lateral and one medial seta, distally one stout unilaterally denticulated seta, two terminal finely denticulated or spinulated seta and possibly one tiny unilaterally denticulated or spinulated seta.

First antenna (Figure 18C) indistinctly five-segmented, armature (proximal to distal) as follows: first segment bearing one short seta; second segment with eight smooth stout setae of various sizes, plus one large denticulated, curving (prehensile) claw; third segment with nine smooth stout setae; fourth segment with one stout seta; terminal segment with 14 smooth slender setae plus one aesthete. Second antenna (Figure 18D) five-segmented, prehensile. Basal segment short, second segment naked, third segment bearing six small semicircular cuticular flaps and two slender setae arising from near base of well produced spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae, one very small stout seta, and one stout uncinat auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 18E) of two parts, dentiferous margin with five teeth. First maxilla (Figure 18F) biramous; endopod bearing tiny triangular cuticular flaps, one apical denticulated seta, and one smooth with papilliform tip; exopod longer surmounted by two small setae and one longer slender seta all

tipped with tiny setule. Second maxilla (Figure 18G) brachiform, lacertus larger than brachium with triangular cuticular flaps; brachium with triangular-shaped cuticular flaps and two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or hair-like) at base of terminal claw (calamus). Claw bearing two rows of serrated membranes paralleling the claw plus six claw-like denticles along the concave distal surface. Maxilliped (Figure 18H) chelate, indistinctly segmented, proximal segment pedunculate (not illustrated); corpus maxillipedis robust apparently devoid of typical small spiniform seta on distal margin, two patches of triangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one small slender seta near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw complex, unciform with tiny membrane or membranous flange along concave margin.

First four pairs of legs biramous and trimerite except for two-segmented endopod of leg one and the endopod of leg four fused into a large claw, sympods two-segmented. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing small triangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	-	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	-	-

Leg one (Figure 19A) rami three-segmented; exopodal setae bearing bilaterally or unilaterally serrated membranous flange, denticulations on medial edge of largest apical seta on terminal segment, largest endopodal seta bilaterally denticulated, smaller seta smooth. Leg two (Figure 19B) with exopod typically modified, first segment greatly enlarged with proximal patch of triangular cuticular flaps, distally bearing one naked seta, second segment smaller with naked seta, third segment armed with two stout setae each bearing a single denticle, plus one smaller naked seta. Leg two endopod (Figure 19B) with one slender seta and one large bilaterally spinulated seta on terminal segment. Leg three (Figure 19C) exopodal setae stout and unilaterally denticulated, largest seta on terminal segment bilaterally denticulated; endopodal seta stout and bilaterally denticulated. Leg four (Figure 19D) exopod similar to leg three but with smooth setae except for large bilaterally denticulated on terminal segment, endopod modified into a heavily sclerotized, fused unciform claw with a proximal patch of cuticular flaps. Leg five (Figure 19E) slightly longer than wide; lateral surface with few cuticu-

lar flaps, distally bearing three spiniform setae plus one seta arising dorsally from the base.

Male: Unknown

Comments: *E. dollfusi* Brian, 1924 was originally reported from the gills of a shark (squale (Marao)) collected from Mauritius. It was later discovered on the branchial lamellae of the brown or sandbar shark, *Carcharhinus milberti* (Valenciennes, in Müller and Henle, 1839), (= *Carcharhinus plumbeus* (Nardo, 1827)) from the Wood's Hole region but was described as a new species, *E. spinifera* by Wilson (1932). Bere (1936) reported *E. spinifera* from the dusky shark *C. obscurus* (LeSueur, 1818). Yamaguti (1963) transferred the errors into his compilation, and finally Cressey (1970) reported Wilson's *E. spinifera* from the sandbar shark, *C. plumbeus* and the blacknose shark *C. acronotus* (LeSueur, 1818).

Examination of several specimens confirms *E. spinifera* Wilson, 1932 is a junior synonym of *E. dollfusi* Brian, 1924.

Eudactylina dollfusi seems to be specific to the few aforementioned species of sharks of the Carcharhinidae, with a preference for the sandbar shark *Carcharhinus plumbeus*.

This species is readily identified by the huge, modified claw-like fused endopod of leg four.

***Eudactylina epaktolampter* sp. nov.**

(Figures 20-23)

Material examined. Two females and one male from the branchial lamellae of the smooth lanternshark *Etmopterus pusillus* (Lowe, 1839), (California Academy of Sciences, CAS 1967 VII:6) collected from off the Mississippi Delta, August 24, 1962 on the R/V *Oregon*, station 3724, located 29°04'N X 88°31'; and two females from the gills of *E. pusillus* (USNM 220344) collected from Atlantic Liberia at a depth of 400 m, station location 06°08'N X 10°57'W. Female holotype (USNM 266524) deposited at the United States National Museum of Natural History.

Etymology: The specific name *epaktolampter* is derived from the Greek *epakter* meaning hunter and *lampter* meaning lantern, referring to the predilection of this parasite for

lantern sharks.

Description

Female (Figure 20A)

Overall length in lateral view approximately 3.1 mm. Cephalothorax longer than wide, lateral margin notched. Surface of cephalothorax, first, second, and third free thoracic somites covered with cuticular flaps. Fourth free thoracic somite smaller than previous three, bearing leg five. Genital segment slightly smaller than preceding somite. Abdomen two-segmented; ventrodistal surface of posterior segment with cuticular flaps. Caudal ramus (Figure 20B) with three stout setae, one very tiny setule, plus two elongate slender setae (one medial, one lateral).

First antenna (Figure 20C) five-segmented, armature (proximal to distal) as follows: first segment bearing one stout seta; second segment with seven slender setae, one large stout seta, and one large smooth, curving (prehensile) claw; third segment with ten slender setae; fourth segment with one long slender seta; terminal segment with 14 slender setae plus one aesthete. Second antenna (Figure 20D) five-segmented, prehensile. Basal segment short, second segment elongate and unarmed, third segment bearing proximally directed triangular cuticular flaps and two slender setae, segment apparently devoid of typical spinous process. Fourth segment elongate and unarmed; fifth segment an elongate, unciform terminal claw bearing two slender setae and one small auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 20E) of two parts, dentiferous margin with seven teeth. First maxilla (Figure 20F) biramous; endopod bearing tiny triangular cuticular flaps and two stout apical setae, one unilaterally denticulated and one with proximal patch of spinules; exopod longer with tiny triangular cuticular flaps and surmounted by two small stout setae (one omitted in illustration) and one longer seta. Second maxilla (Figure 20G) brachiform, lacertus larger than brachium bearing semicircular cuticular flaps, brachium with semicircular cuticular flaps and two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or hair-like) at base of terminal claw (calamus). Claw atypically bearing a patch or bilobed patch of fine spinulations along concave surface. Maxilliped (Figure 20H) chelate, indistinctly segmented, proximal segment pedunculate (not shown); corpus maxillipedis robust bearing small spiniform seta on distal margin and small rectangular cuticular flaps; myxal area expanded into a receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint and the other along concave distal margin near membranous strip (see detail). Claw (Figure 20H detail) complex, unciform with a large orbicular lateral shield.

First leg biramous and bimerite, legs two, three and four biramous and trimerite, sympods two-segmented. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing semicircular cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	-	IV	Endopod	0-0	-	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 21A) rami two-segmented (possibly indistinctly three); exopodal and endopodal setae bilaterally denticulated. Leg two exopod (Figure 21B) typically modified, first segment greatly elongated with proximal patch of flaps, all setae smooth and stout, endopod (Figure 21C) tipped with two slender setae. Legs three and four (Figure 21D) similar; all setae smooth and stout except bilaterally denticulated middle seta on terminal segment of exopod. Leg five (Figure 21E) subquadrate, longer than wide distally bearing three slender setae plus one similar seta arising dorsally from the base; lateral surface with small triangular cuticular flaps.

Male: (Figure 22A)

Overall length in lateral view approximately 1.8 mm. Similar to female, except abdomen four-segmented, leg five and leg six arising from genital complex. Caudal ramus (Figure 22B) bearing four pinnate setae and two smooth slender setae.

First antenna (Figure 22C) indistinctly of nine segments; armature (proximal to distal) as follows: first segment bearing one stout seta, second segment with nine slender setae plus one large curving (prehensile) claw, third segment armed with four slender setae, fourth segment with two setae, fifth segment with one seta, sixth segment with four slender setae, seventh segment armed with two setae, eighth segment bearing a single small stout seta and long aesthete, ninth segment bearing 12 slender setae. Maxilliped (Figure 22D) subchelate; corpus bearing many small rectangular cuticular flaps, myxal area bearing a well produced styliform process, subchela bearing two stout setae, claw produced into a large curving process proximally producing a bifid spine which in concert with the claw creates a concavity for the myxal process to act upon.

First pair of legs (Figures 23A and 23B) biramous and bimerite, legs two, three and four biramous and trimerite. Sympods two-segmented. Semicircular cuticular flaps on ventral surfaces of legs I - IV. Armature of rami as follows:

Leg one	Exopod	I-0	-	V	Endopod	0-0	-	II
Leg two	Exopod	I-I	I-I	VII	Endopod	0-0	0-I	III
Leg three	Exopod	I-I	I-I	VII	Endopod	0-I	0-I	IV
Leg four	Exopod	I-I	I-I	VII	Endopod	0-0	0-0	III

Exopod one (Figure 23A) two-segmented; first segment with single smooth seta, second segment bearing two long pinnate setae plus three smaller naked setae. Endopod one (Figure 23B) tipped with two naked setae. Leg two (Figure 23C) exopodal setae predominately pinnate medially and smooth and along lateral margin, proximal segment of endopod with large sclerotized lateral process, remaining setae pinnate. Leg three (Figure 23D) exopodal and endopodal setae smooth along lateral margin, pinnate along medial margin. Leg four similar to leg three except for terminal segment of endopod (Figure 23E) bearing only three instead of four setae. Leg five (Figure 23F) armed with three slender setae on distal edge and one pinnate seta at base. Leg six (Figure 23G) consists of three slender naked setae on distal edge of finely spinulated lobe.

Comments: *E. epaktolampter* is the first record of *Eudactylina* from the genus *Etmopterus*. Both of my finds come from the smooth lanternshark, *Etmopterus pusillus* (Lowe, 1839), collected in the Gulf of Mexico off the Mississippi Delta and off the Liberian Atlantic.

The male of this species exhibits a very unusual blunt spinous process on the lateral margin of the basal segment of the second endopod. This character has only been reported once before from the entire order Siphonostomatoida, predictably from another male eudactylinid, *Eudactylina chilensis* Ho and McKinney, 1981 from the black shark *Aculeola nigra* De Buen, 1959. This shared derived character indicates a close phylogenetic relationship between these species of parasites. Interestingly, both hosts have been removed from the family Squalidae and recently placed in a common family Etmopteridae. The parasites support this systematic restructuring.

This species is easily distinguished from all other congeners by the spinulations covering the concave surface of the second maxilla, the minute apicomedial seta on the caudal rami, the large orbicular lateral shield on the claw of the maxilliped. The absence of the spiniform process on the third segment of the second antenna is shared by *E. acanthii*, *E. diabolophila*, *E. insolens*, *E. longispina*, *E. oliveri*, *E. pollex*, and *E. vaquetillae*, all strikingly different from this species in a multitude of characteristics.

Eudactylina hornbosteli sp. nov.

(Figures 24-25)

Material examined. Several females from the branchial lamellae of the bat ray *Myliobatis* sp., captured from waters off Nosy Be', Madagascar. Donated from the personal collection of Dr. Roger Cressey, National Museum of Natural History, Smithsonian Institution, Washington, D.C. Female holotype (USNM 266525) and 5 female paratypes (USNM 266526) deposited at the United States National Museum of Natural History.

Etymology: The specific name *hornbosteli* is in honor of Mr. Bernard Horn-Bostel for computer hardware support for this effort.

Description

Female (Figure 24A)

Overall length in lateral view approximately 1.6 mm. Cephalothorax longer than wide, lateral margin slightly concave. Surface of cephalothorax, first, second, third and, fourth free thoracic somites covered with wavy cuticular flaps. Fourth free thoracic somite, genital segment and, two-segmented abdomen all bearing wavy cuticular flaps on ventral surface. Caudal ramus (Figure 24B) with two stout curving setae, plus two elongate slender setae (one dorsal, one lateral).

First antenna (Figure 24C) apparently four-segmented, armature (proximal to distal) as follows: first segment bearing one tiny seta; second segment with four small setae, three elongate blunt setae and one large denticulated, curving (prehensile) claw; third segment with seven slender setae plus two large denticulated spines; fourth segment an elongate process with 14 setae of various shapes and sizes plus one aesthete. Second antenna (Figure 24D) five-segmented, prehensile. Basal segment short, second segment elongate with a very long, proximally directed spiniform process, third segment elongate bearing proximally directed wavy rectangular cuticular flaps and two slender setae arising from near base of long curving spiniform process. Fourth segment elongate and unarmed; fifth segment an elongate, unciform terminal claw bearing two slender setae and one extremely elongate auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 24E) of two parts, dentiferous margin with five teeth. First maxilla (Figure 24F) biramous; endopod more robust bearing two slender apical setae, one unilaterally denticulated and one smooth; exopod longer and surmounted by two small stout setae and one longer slender seta. Second maxilla (Figure 24G) brachiform, lacertus larger than brachium bearing wavy cuticular flaps, brachium with wavy cuticular flaps (some triangular), distal patch of triangular

prickles two tufts of setae (one coarse or rope-like (possibly fused setae), one fine or hair-like (omitted in illustration)) at base of terminal claw (calamus). Claw bearing four strips of serrated membrane plus one serrated strip on other side. Maxilliped (Figure 24H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small seta on distal margin and large wavy cuticular flaps; myxal area expanded into a receptacle to accommodate claw of opposable segment. Shaft with long membranous flange, bearing two setae: one elongate near midpoint and the other along concave distal margin near membranous strip (see detail). Claw (Figure 20H detail) complex, unciform with a large orbicular lateral shield.

First four pairs of legs biramous and trimerite, sympods two-segmented. All basipods with lateral pinnate slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of legs two, three, and four bearing wavy cuticular flaps. Armature of rami as follows:

Leg one	Exopod	1-0	1-0	IV	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	1-0	1-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	1-0	1-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	1-0	1-0	III	Endopod	0-0	0-0	I

Leg one (Figure 25A) with single row of fine triangular cuticular flaps fringing distal margins of all segments except terminal segment of exopod; lateral exopodal setae unilaterally bearing serrated membranous flange, apical setae smooth and slender, endopodal setae naked and slender. Leg two exopod (Figure 25B) typically modified, first segment greatly enlarged with stout seta, second segment swollen with stout seta, terminal segment with two small slender setae plus one truncate seta, endopod (Figure 25B) tipped with two slender setae. Legs three and four (Figure 25C) similar; lateral margins of endopodal segments one and two with fringes of fine setae, all exopodal setae stout bearing large subapical tines, endopod tipped by single finely spinulated seta. Leg five (Figure 25D) longer than wide; lateral surface with wavy cuticular flaps and distally bearing three semipinnate slender setae plus one pinnate seta arising dorsally from the base.

Male: Unknown

Comments: *E. hornbosteli* is easily distinguished from its congeners by the extremely elongate setae on the second, third and fourth segments of the first antenna, the extremely elongate and spiniform apical segment of the first antenna, the elongated

segments of the second antenna, the very long, curving claw and auxiliary spine on the second antenna, the elongate spiniform process found on the second segment of the second antenna, the large digitiform subapical tines found on the setae of exopods three and four, and the fringe of spinules or cuticular flaps along the distomedial margins of the exopodal and endopodal segments of leg one.

Eudactylina indivisa Castro and Baeza, 1991
(Figures 26-27)

Material examined. Several females from the branchial lamellae of the eastern South Pacific bat ray, *Myliobatis peruvianus* (Garman, 1913) collected from Antofagasta, Chile. Donated from the personal collection of Mr. Raul Castro Romero, Universidad de Antofagasta, Chile.

Description

Female (Figure 26A)

Overall length in lateral view approximately 1.8 mm. Cephalothorax longer than wide, lateral margin notched accomodating lacertus of second maxillae. Surface of cephalothorax covered with cuticular flaps. Terga of first, second, third, and fourth free thoracic somites covered with cuticular flaps. Fourth free thoracic somite, genital segment and abdomen bearing posteriorly directed cuticular flaps on ventral surface. Fourth free thoracic somite smaller than previous three, bearing leg five. Genital segment smaller than preceeding somite. Abdomen two-segmented. Caudal ramus (Figure 26B) longer than wide, bearing two distal apically curved stout setae, one dorsal slender seta, one lateral slender seta, and one proximal setule; ventral surface armed with posteriorly directed cuticular flaps.

First antenna (Figure 26C) apparently four-segmented, armature (proximal to distal) as follows: first segment bearing one slender seta; second segment with four small setae, one stout seta, one slender denticulated seta, one long slender seta, plus one large denticulated, curving (prehensile) claw; third segment bearing eight slender naked setae plus one large spine armed with rectangular flaps; terminal segment with 14 smooth spiniform setae plus one aesthete. Second antenna (Figure 26D) five-segmented, prehensile. Basal segment short, second segment with spiniform process, third segment bearing six rectangular cuticular flaps, two slender setae arising from near base of elongate styliform process. Fourth segment elongate and unarmed; fifth

segment an unciform terminal claw bearing two slender setae and one elongate auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 26E) of two parts, dentiferous margin with seven teeth. First maxilla (Figure 26F) biramous; endopod with tiny triangular cuticular flaps and bearing two apical bilaterally denticulated setae; exopod longer surmounted by two small setae and one longer seta. Second maxilla (Figure 26G) brachiform, lacertus larger than brachium bearing large round rectangular cuticular flaps, brachium with wavy, rectangular, and semicircular cuticular flaps, a distal patch of triangular prickles and two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or hair-like)) at base of terminal claw (calamus). Claw bearing four strips of serrated membranes parallelling the distal portion of the claw plus one proximal strip of membrane along the convex margin, two strips present on other side. Maxilliped (Figure 26H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, narrow wavy, rectangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw unciform with quadrangular cuticular expansion with thinner cuticular expansion on distal edge producing lateral shield.

First four pairs of legs biramous and trimerite, two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing various shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	IV	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 27A) lateral exopodal setae unilaterally bearing serrated membranous flange, apical setae slender with small setules (spinules), endopodal setae bilaterally spinulated. Exopod two (Figures 27B and 27C) modified, first segment greatly enlarged with a few tiny triangular cuticular flaps along the medial margin, one distal denticulated seta, second segment smaller with large, stout spine, third segment armed with one small subapical seta, another subapical recurving seta plus one blunt apical truncate seta. Leg two endopod (Figure 27B) with subtriangular expansion in distolateral corner of first segment, one small spinulated seta and one large bilaterally denticulated seta on terminal segment. Legs three and four (Figures 27D and 27E)

similar; exopods three and four (Figure 27E) with denticulated setae, endopods three and four (Figure 27D) tipped with a single bilaterally denticulated seta. Leg five (Figure 27F) subtriangular, longer than wide, distally bearing three slender setae plus one pinnate seta arising dorsally from the base; lateral surface covered with triangular cuticular flaps. Leg six (Figure 27G) represented by three very tiny spines located on the rim of the aperture of the oviducal opening.

Male: Unknown

Comments: *E. indivisa* seems to be a parasite of temperate eastern South Pacific bat rays. So far, it has been reported from the gills of *Myliobatis peruvianus* (Garman, 1913) and *Myliobatis chilensis* Phillipi, 1892, from near Antofagasta, Chile.

The unusual presence of cuticular flaps on the large spine on the third segment of the first antenna, the difficult to characterize claw of the maxilliped, and the long straight, denticulated spine-like seta on the second segment of exopod two are ready discriminants for this species.

***Eudactylina insolens* Scott and Scott, 1913**
(Figures 28-29)

Material examined. Several females (BMNH 1913.9.18.292-293) from the branchial lamellae of the tope shark, *Galeorhinus galeus* (Linnaeus, 1758) collected from the Irish Sea.

Description

Female (Figure 28A)

Overall length in lateral view approximately 1.8 mm. Cephalothorax longer than wide, lateral margin notched accommodating lacertus of second maxillae. Anterolateral surface of cephalothorax covered with cuticular flaps. Terga of first, second, third, and fourth free thoracic somites atypically devoid of cuticular flaps. Genital segment and abdomen bearing posteriorly directed cuticular flaps on ventral surface. Fourth free thoracic somite bearing leg five. Genital segment smaller than preceding somite. Abdomen two-segmented. Caudal ramus (Figure 28B) longer than wide, bearing three terminal denticulated setae, one dorsomedial seta, and one lateral naked seta; ventral surface armed with posteriorly directed triangular cuticular flaps.

First antenna (Figure 28C) five-segmented, armature (proximal to distal) as fol-

lows: first segment bearing one spiniform seta; second segment with six smooth setae, two unilaterally denticulated spiniform setae plus one large denticulated, curving (prehensile) claw; third segment bearing nine smooth setae; fourth segment bearing a single seta. Terminal segment atypically exhibiting the presence of cuticular flaps, and armed with 13 smooth slender setae plus one aesthete. Second antenna (Figure 28D) five-segmented, prehensile. Basal segment short, second segment with triangular cuticular flaps, third segment bearing three rectangular cuticular flaps, two slender setae arising from near base of reduced spiniform process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one tiny seta near auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 28E) of two parts, dentiferous margin with six teeth. First maxilla (Figure 28F) biramous; endopod with tiny triangular cuticular flaps, bearing one apical bilaterally denticulated seta, and one smooth seta; exopod longer surmounted by two small setae and one longer seta. Second maxilla (Figure 28G) brachiform, lacertus subequal to brachium bearing large triangular cuticular flaps, brachium with triangular cuticular flaps, and one tuft of setae at base of terminal claw (calamus). Claw bearing two rows of denticles parallelling the concave margin. Maxilliped (Figure 28H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, and tiny triangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw unciform with ovoid cuticular expansion producing lateral shield.

First four pairs of legs biramous and trimerite except two-segmented exopod and the fused to partially fused endopod of leg one, two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing triangular shaped cuticular flaps except for thin rectangular flaps found on the basal segment of modified exopod two. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	-	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 29A) exopodal setae spiniform, bilaterally bearing serrated membranous flange, smaller endopodal seta bilaterally spinulated, larger unilaterally

bearing denticles. Exopod two (Figure 29B) modified, first segment greatly enlarged with many thin rectangular cuticular flaps and one distal curving seta, second segment smaller with distally extending lateral lobe bearing single curved seta, third segment armed with three curved setae. Leg two endopod (Figure 29C) with one small spinulated seta and one large bilaterally spinulated seta on terminal segment. Legs three and four (Figures 29D) similar; exopods three and four with smooth styliform setae, endopods three and four tipped with a single unilaterally denticulated seta. Leg five (Figure 29E) ovoid, barely longer than wide; lateral surface covered with triangular cuticular flaps, distally bearing three slender setae plus one similar seta arising dorsally from the base.

Male: Unknown

Comments: *E. insolens* seems to be a rarely reported parasite of temperate eastern North Atlantic and Mediterranean sharks. So far, it has been reported from the gills of the tope shark, *Galeorhinus galeus* (Linnaeus, 1758) collected from the Irish Sea (Scott and Scott, 1913), and off Norfolk in the North Sea (Hamond, 1969). Essafi and Raibaut (1977) have found this parasitic copepod on the gills of the smooth-hound *Mustelus mustelus* (Linnaeus, 1758), the blackspotted smooth-hound *Mustelus mediterraneus* Quignard and Capape, 1972 (= *Mustelus punctulatus* Risso, 1826), and the starry smooth-hound *Mustelus asterias* Cloquet, 1821 all collected in the Mediterranean Sea near Tunis.

It should be noted that the genera this copepod parasitizes, *Galeorhinus* and *Mustelus* are members of the carcharhiniform family Triakidae.

The unusual absence of cuticular flaps on the dorsal surfaces of the cephalothorax and free thoracic somites one through four coupled with the distally extended lobe of the second segment of the modified second endopod and denticulated claw of the second maxilla help to identify this copepod.

***Eudactylina longispina* Bere, 1936**

(Figures 30-31)

Material examined. One holotype female (USNM 69839) from the branchial lamellae of the bonnethead shark, *Sphyrna tiburo* (Linnaeus, 1758) collected from Lemon Bay, Florida in the Gulf of Mexico, and one female (USNM 153653) from the

same species of host from Tampa Bay, Florida.

Description

Female (Figure 30A)

Overall length in lateral view approximately 1.1 mm. Cephalothorax longer than wide, lateral margin notched accommodating lacertus of second maxillae. Lateral surface of cephalothorax covered with cuticular flaps. Cuticular flaps restricted to lateral surfaces of first and second free thoracic somites. Third and fourth free thoracic somites atypically devoid of cuticular flaps. Fourth free thoracic somite bearing leg five. Genital segment and abdomen bearing posteriorly directed cuticular flaps on ventral surface. Genital segment smaller than preceding somite. Abdomen two-segmented. Caudal ramus (Figure 30B) longer than wide, bearing three terminal slender setae, one dorso-medial slender seta, and one lateral slender seta; ventral surface armed with posteriorly directed triangular cuticular flaps.

First antenna (Figure 30C) five-segmented, armature (proximal to distal) as follows: first segment bearing one small stout seta; second segment with eight smooth stout setae, plus one curving (prehensile) claw; third segment bearing seven smooth setae; fourth segment bearing a single seta. Terminal segment armed with 14 smooth slender setae plus one aesthete. Second antenna (Figure 30D) five-segmented, prehensile. Basal segment short, second segment naked, third segment devoid of cuticular flaps, two slender setae arising from distal margin. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one elongate auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 30E) of two parts, dentiferous margin with six teeth. First maxilla (Figure 30E) biramous; endopod bearing two slender setae, exopod longer surmounted by two small setae and one longer seta. Second maxilla (Figure 30F) brachiform, lacertus subequal to brachium bearing elongate, triangular cuticular flaps, brachium with long, triangular cuticular flaps, and one tuft of setae at base of terminal claw (calamus). Claw bearing two rows of denticles paralleling the concave margin. Maxilliped (Figure 30G) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, and large triangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw unciform with ovoid cuticular expansion producing lateral shield.

First four pairs of legs biramous and trimerite except two-segmented endopod of leg two, two-segmented sympods. All basipods with lateral slender seta; first basipod

bears additional distomedial stout seta. Ventral surfaces of all four legs bearing triangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	-	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	0-0
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	0-0

Leg one (Figure 31A) exopodal setae smooth and blunt, endopodal setae slender, largest seta denticulated, smallest seta smooth. Exopod two (Figure 31B) typically modified, first segment greatly enlarged with proximal patch of large triangular cuticular flaps and one distal curved seta, second segment smaller bearing single curved seta, third segment armed with three curved setae, one armed with a single setule. Leg two endopod (Figure 31C) with two smooth slender setae. Legs three and four similar; sympods and exopods three and four (Figure 31D) with denticulated styliiform setae, terminal segment of endopods three and four (Figure 31E) modified into a long blunt sclerotized process, patch of large triangular cuticular flaps on basal segment. Leg five (Figure 31F) longer than wide, distally bearing three slender setae plus one similar seta (not illustrated) arising dorsally from the base; lateral surface sparsely covered with triangular cuticular flaps.

Male: Unknown

Comments: *E. longispina* was reported originally by Bere (1936), and later by Pearse (1952) and Cressey (1970) from the gills of the bonnethead shark *Sphyrna tiburo* (Linnaeus, 1758). All collections were from the West coast of Florida in the Gulf of Mexico.

The bizarrely modified terminal segment on the endopod of legs three and four forming a long, blunt process is unique to this species.

Eudactylina myliobatidos Luque and Farfan, 1991
(Figures 32-33)

Material examined. One female (USNM 251291) from the branchial lamellae of the bat ray *Myliobatis chilensis* Phillippi, 1892 collected from inshore waters near

Chorrillos, Peru.

Description

Female (Figures 32A)

Overall length in lateral view approximately 1.8 mm. Cephalothorax longer than wide, lateral margin slightly notched accomodating lacertus of second maxillae. Dorsolateral surface of cephalothorax covered with wavy cuticular flaps. Wavy cuticular flaps present on dorsolateral surfaces of first, second, third and fourth free thoracic somites. Fourth free thoracic somite bearing leg five. Fourth free thoracic somite, genital segment, and abdomen bearing posteriorly directed cuticular flaps on ventral surface. Genital segment smaller than preceeding somite. Abdomen two-segmented. Caudal ramus (Figure 32B) longer than wide, bearing two relatively elongate, apically curved terminal setae, one dorsal slender seta, and one lateral slender seta; ventral surface armed with posteriorly directed triangular cuticular flaps.

First antenna (Figure 32D) indistinctly four-segmented, armature (proximal to distal) as follows: first segment bearing one small seta; second segment with five smooth setae (one elongate, two minute, two stout), one small, unilaterally denticulated seta, plus one curving, denticulated (prehensile) claw; third segment bearing six smooth setae, plus two large distal auxiliary spines (one unilaterally bearing teeth and the other with four semicircular cuticular flaps), Terminal segment armed with 11 slender setae, one large stout seta, plus one aesthete. Second antenna (Figure 32D) five-segmented, prehensile. Basal segment short, second segment armed with spinous process, third segment bearing six rectangular cuticular flaps and two slender setae arising from base of well produced spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing a single slender seta and one elongate auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 32E) of two (possibly three) parts, dentiferous margin with six teeth. First maxilla (Figure 32F) biramous; endopod bearing two setae, both unilaterally denticulated, exopod longer surmounted by two small naked setae and one longer, unilaterally denticulated seta. Second maxilla (Figure 32G) brachiform, lacertus larger than brachium bearing large, semicircular cuticular flaps, brachium with large slender, rectangular cuticular flaps, a distal patch of prickles, plus two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or hair-like) at base of terminal claw (calamus). Claw bearing four rows of serrated membranes distally, plus one longer serrated strip proximally, two similar strips parallelling the concave margin present on other side. Maxilliped (Figure 32H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust, typical small stout spine on distal margin not observed,

corpus with rectangular cuticular flaps; myxal area bearing large transverse cuticular flange and expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw unciform bearing membranous flange with quadrate cuticular expansion producing lateral shield (see detail).

First four pairs of legs biramous and trimerite except for the two-segmented endopod of the first leg, two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing variously shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	IV	Endopod	0-0	-	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 33A) exopodal setae bearing lateral serrated membranous flange except for the two most distomedial setae (largest seta appears to bilaterally bear spinules or tiny denticles, smallest seta naked), endopodal setae bilaterally denticulated / spinulated. Exopod two (Figure 33B) modified, first segment greatly enlarged with two thin, rectangular cuticular flaps and one distal denticulated seta, second segment smaller bearing single stout seta, third segment armed with one small slender seta, one slender recurving seta, and one truncate seta. Leg two endopod (Figure 33C) with two slender setae, longest bilaterally bearing stout setules or minute denticles and the other smooth. Legs three and four similar; exopods three and four (Figure 33D) with denticulated styliform setae, terminal segment of endopods three and four (Figure 33D) bearing single spinulated seta. Medial stylet (Figure 33E) stout and blunt, located between pedigers three and four and not directly arising from either somites interpodal bars. Leg five (Figure 33F) longer than wide; lateral surface sparsely covered with small triangular cuticular flaps, distally bearing three slender setae plus one pinnate seta arising dorsally from the base.

Male: Unknown

Comments: This redescription of *E. myliobatidos* brings attention to detail missing in the original description of this species (Luque and Farfan, 1991). This species shares the characters of a four-segmented first antenna, elongated segments of the

second antenna, and wavy cuticular flaps with *E. hornbosteli*, *E. indivisa*, and *E. nykterimyzon* all parasites of *Myliobatis* sp. from their respective waters.

The large semicircular flaps and denticulations on the two large distal auxiliary spines on the third segment of the first antenna, the denticulated seta on the proximal segment of exopod two and the relatively elongate terminal setae on the caudal rami are found in *E. indivisa*, also a parasite of *Myliobatis chilensis*. Both *E. indivisa* and *E. myliobatidos* are so similar to one another that synonymization may be warranted. Although, the two large rectangular cuticular flaps on the proximal segment of the modified second exopod separate this species from *E. indivisa*, additional collecting of these parasites may show this trait not to be as taxonomically unique as this present effort suggests.

***Eudactylina nykterimyzon* sp. nov.**

(Figures 34-35)

Material examined. Several females from the branchial lamellae of the bat ray *Myliobatis californica* Gill, collected from inshore waters near El Segundo, California; and several females from the same host species from Punta Arena de la Ventana, in the southern Sea of Cortez (Gulf of California). Female holotype (USNM 266527) and 7 female paratypes (USNM 266528) deposited at the United States National Museum of Natural History.

Etymology: The specific name *nykterimyzon* is derived from the Greek *nykteris* meaning bat, and *myzo* meaning suck, referring to this species' predilection for feeding upon bat rays.

Description

Female (Figures 34A and 34B)

Overall length in lateral view approximately 2.0 mm. Cephalothorax longer than wide, lateral margin notched accomodating lacertus of second maxillae. Dorsolateral surface of cephalothorax covered with cuticular flaps. Cuticular flaps present on dorso-lateral surfaces of first, second, third and fourth free thoracic somites. Fourth free thoracic somite bearing leg five. Fourth free thoracic somite, genital segment, and abdomen bearing posteriorly directed cuticular flaps on ventral surface. Genital segment smaller than preceeding somite. Abdomen two-segmented. Caudal ramus

(Figure 34C) longer than wide, bearing two terminal, apically curved setae, one dorso-medial slender seta, and one lateral slender seta; ventral surface armed with posteriorly directed triangular cuticular flaps.

First antenna (Figure 34D) indistinctly four-segmented, armature (proximal to distal) as follows: first segment bearing one naked seta; second segment with seven setae (four small, three large), plus one curved, denticulated (prehensile) claw; third segment bearing nine (six small, one elongate, and two large distally placed auxiliary spines (setae)) setae, terminal segment armed with 14 setae plus one aesthete. Second antenna (Figure 34E) five-segmented, prehensile. Basal segment short, second segment armed with spiniform process, third segment bearing three cuticular flaps and two slender setae arising from base of well produced spiniform process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one elongate auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 34F) of two parts, dentiferous margin with six teeth. First maxilla (Figure 34G) biramous; endopod bearing two slender setae, longer seta unilaterally denticulated, exopod longer surmounted by two small setae and one longer slender seta. Second maxilla (Figure 34H) brachiform, lacertus larger than brachium bearing large, wavy cuticular flaps, brachium with large wavy, and triangular cuticular flaps, a distal patch of prickles, possibly a small spine plus two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or hair-like) at base of terminal claw (calamus). Claw bearing three rows of serrated membranes distally, plus one longer serrated strip proximally, two similar strips paralleling the concave margin present on other side. Maxilliped (Figure 34I) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, and large wavy cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw unciform bearing membranous flange with subquadrate cuticular expansion producing lateral shield.

First four pairs of legs biramous and trimerite, two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial seta. Ventral surfaces of all four legs bearing variously shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	IV	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg four Exopod I-0 I-0 III Endopod 0-0 0-0 I

Leg one (Figure 35A) exopodal setae bearing lateral serrated membranous flange, endopodal setae bilaterally denticulated. Exopod two (Figure 35B) modified and devoid of cuticular flaps, first segment greatly enlarged with one distal seta, second segment smaller bearing single stout seta and conical protuberance, third segment armed with two small setae, and one truncate seta. Leg two endopod (Figure 35B) with two smooth setae. Legs three and four similar; exopods three and four (Figure 35C) with denticulated styliform setae, terminal segment of endopods three and four (Figure 35C) bearing single denticulated seta. Leg five (Figure 35D) longer than wide, distally bearing three slender setae plus one seta arising dorsally from the base; lateral surface sparsely covered with cuticular flaps.

Male: Unknown

Comments: *Eudactylina nykterimyzon* seems to be specific to the California bat ray *Myliobatis californica* Gill, 1865.

Other species possessing a distinctly 4-segmented first antenna are: *E. hornbosteli*, *E. indivisa*, *E. myliobatidos*, *E. pristiophori*, *E. squamosa*, *E. turgipes*, and *E. urolophi*. *E. acuta*, *E. aphioxenous*, and *E. tuberifera* all possess an indistinctly 4- or 5-segmented first antenna, as segments three and four show incomplete fusion. Six of the aforementioned species possess serrated membranes on the setae of the first exopod, these are: *E. hornbosteli*, *E. indivisa*, *E. myliobatidos*, *E. pristiophori*, *E. turgipes*, and *E. urolophi*. Five of these species possess only four setae on their caudal rami, they are: *E. hornbosteli*, *E. indivisa*, *E. myliobatidos*, *E. pristiophori*, and *E. urolophi*. Only three of these species, *E. hornbosteli*, *E. indivisa*, and *E. myliobatidos* possess elongate spiniform processes on segments two and three of the second antennae, as does *E. nykterimyzon*. *E. nykterimyzon* can be distinguished from this small group of allies by being the only member with three cuticular flaps on segment three of the second antenna; the others all have six. The extremely elongate components of the second antenna of *E. hornbosteli* set that species apart from the rest of this group. The possession of a denticulated seta on the second segment of the second exopod and cuticular flaps on the auxiliary spine of *E. indivisa* and *E. myliobatidos* additionally guarantee the uniqueness of this new species.

Eudactylina oliveri Laubier, 1968
(Figures 36-39)

Syn: *Eudactylina oliveri*, of Pillai (1985)

Material examined. Several females and males from the branchial lamellae of the spinetail mobula, *Mobula japonica* (Müller and Henle, 1841) collected from Punta Arena de la Ventana (Gulf of California), Mexico and from the same host species from near Anacapa Island (southern California Channel Islands); several females from the smoothtail mobula *Mobula thurstoni* (Lloyd, 1908) (= *Mobula lucasana* Beebe and Tee-Van, 1938) collected from Punta Arena de la Ventana, Mexico; several females from *Mobula* sp. collected from Nosy Be, Madagascar from the personal collection of Dr. Roger Cressey, Smithsonian Institution, Washington, D.C.

Description

Female (Figure 36A)

Overall length in lateral view approximately 1.9 mm. Cephalothorax longer than wide, lateral margin notched accomodating lacertus of second maxillae. Lateral surfaces of cephalothorax covered with cuticular flaps. Cuticle of first, second, and third free thoracic somites laterally covered with cuticular flaps. Fourth free thoracic somite smaller than previous three with cuticular flaps on ventral surface and bearing leg five. Genital segment smaller than preceeding somite, with cuticular flaps on ventral surface. Abdomen two-segmented, ventral surface bearing cuticular flaps. Caudal ramus (Figure 36B) longer than wide, bearing four terminal small stout setae, one subterminal small stout seta, plus one dorsal slender seta; ventral surface covered with posteriorly directed triangular cuticular flaps. Egg string (Figure 36C) uniseriate.

First antenna (Figure 36E) six-segmented, armature (proximal to distal) as follows: first segment with triangular and rectangular cuticular flaps along lateral margin bearing one stout seta; second segment with eight naked setae of various sizes plus one large smooth, curving (prehensile) claw; third segment with four slender setae plus one small papilliform seta; fourth segment with two large seta, one small stout seta, and one large distal spine; fifth segment bearing one tiny seta, terminal segment with 14 setae plus one aesthete. Second antenna (Figure 36F) five-segmented, prehensile. Basal segment short, second segment elongate bearing long rectangular cuticular flaps, third segment bearing rectangular cuticular flaps, two slender setae arising from near base of very reduced spinous process. Fourth segment elongate with many rectangular cuticular flaps (only two visible in illustrated view), fifth segment an elongate

unciform terminal claw bearing two slender setae and one long slender spine. Mouth tube (Figure 36D) siphonostome and similar to that of other species; labrum with sub-rectangular flaps, distal edge of frons labri bearing membrane; lateral surface of labium with elongate triangular cuticular flaps, ventrodistal surface with small prickles. Mandible (Figure 36G) of two parts, dentiferous margin with six teeth. First maxilla (Figure 36H) biramous; sympod with small patches of spinules, endopod bearing two stout spinulated setae; exopod longer surmounted by two small naked setae and one longer denticulated seta. Second maxilla (Figure 36I) brachiform, lacertus larger than brachium, with small triangular cuticular flaps, brachium with rectangular and triangular cuticular flaps, a distal patch of prickles a tiny seta and a single tuft of fine setae at base of terminal claw (calamus). Distal region of claw bearing two rows of denticles, proximal region with three pairs of serrated membranes. Maxilliped (Figure 37A) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, small semicircular cuticular flaps and small triangular flaps; myxal area expanded into large receptacle to accommodate claw of opposite segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw (Figure 37B) unciform with reduced quadrangular cuticular expansion producing a very small lateral shield.

First four pairs of legs biramous with three-segmented endopods, three-segmented exopods and two-segmented sympods. All basipods with lateral seta, (basipods two, three and four with spatulate setae); first basipod bears additional disto-medial seta. Ventral surfaces of all four legs bearing triangular and semicircular cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Exopodal setae of leg one (Figure 37C) small and denticulated on the most proximal two segments, endopodal setae unilaterally denticulated. Exopod two (Figure 37D) somewhat modified, first segment elongate with a proximal patch of triangular cuticular flaps along lateral margin, one distal naked seta, second segment smaller with small, naked seta, third segment armed with two small sub-apical naked setae, plus one longer unilaterally denticulated (two teeth) seta. Leg two endopod (Figure 37D) with

two finely spinulated/denticulated setae on terminal segment. Setae of legs three and four (Figure 37E) stout with largest endopodal and exopodal seta bearing well developed spinules. Leg five (Figure 37F) elongate distally bearing three spatulate setae plus one seta arising dorsally from the base; lateral surface with rectangular and triangular cuticular flaps along ventral surface.

Male: (Figure 38A)

Overall length in lateral view approximately 1.6 mm. More slender than female, abdomen four-segmented, leg five arising from fourth free thoracic somite and leg six arising from genital segment. Caudal ramus (Figure 38B) bearing four robust setae (three semipinnate), one dorsal pinnate seta and one small lateral naked seta.

First antenna (Figure 38C) indistinctly eight- or nine-segmented; armature (proximal to distal) as follows: first segment bearing one small seta and triangular cuticular flaps along lateral margin, second segment with eleven slender setae plus one large curving (prehensile) claw, third segment armed with nine slender setae, fourth segment with four distal setae and one proximal slender seta, fifth segment with two slender setae, sixth segment with two slender setae, seventh segment armed with two setae, terminal segment bearing a single aesthete plus 13 slender setae of various heights. Second antenna (Figure 38D) five-segmented, prehensile; proximal segment short, second segment elongate with proximally directed rectangular cuticular flaps, third segment with proximally directed cuticular flaps and two slender setae arising from near base of small spiniform process, fourth segment elongate and naked, terminal segment an elongate claw with one small auxiliary spine and two proximal slender setae. Mandible (Figure 38E) similar to that of female. First maxilla (Figure 38F) biramous; endopod bearing small triangular cuticular flaps and two apical setae, one smooth and one unilaterally denticulated; exopod with triangular cuticular flaps, two small setae and one long seta. Second maxilla (Figure 38G) similar to that of female. Maxilliped (Figure 38H) subchelate; corpus bearing many small rectangular cuticular flaps, myxal area bearing a well produced denticulated, styliform process, shaft bearing two small slender setae, claw produced into a large curved process proximally producing a robust spine along the concave margin.

First four pair of legs (Figures 39A-39E) biramous and trimerite. Sympods two-segmented. Various shaped cuticular flaps on ventral surfaces of legs. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	IV	Endopod	0-0	0-0	II
Leg two	Exopod	I-I	I-I	VI	Endopod	0-I	0-I	V

Leg three	Exopod	I-I	I-I	VII	Endopod	0-I	0-I	IV
Leg four	Exopod	I-I	I-I	VII	Endopod	0-I	0-I	III

Exopod one (Figure 39A) three-segmented; first segment with single smooth seta, second segment bearing single short seta, terminal segment with four apical naked setae. Endopod one (Figure 39A) tipped with two short setae. Leg two (Figure 39B) lateral exopodal setae with membranes along lateral margins, medial setae pinnate, lateralmost long seta semipinnate with membrane along lateral margin; endopodal setae pinnate. Exopod three and four (Figure 39C) with stout setae along lateral margin and pinnate setae along medial margin. endopodal setae pinnate along medial margin, apical setae naked. Terminal segment of endopod three (Figure 39D) with one naked plus three pinnate setae. Terminal segment of endopod four (Figure 39E) with one naked and two pinnate setae. Leg five (Figure 39F) composed of three pinnate setae on distal edge of leg with one similar seta at base. Leg six (Figure 39G) consists of two pinnate setae on distal edge of small lobe.

Comments: *E. oliveri* was originally described by Laubier, 1968 from gills of *Mobula mobular* (Bonnaterre, 1788) captured near Narbonne Beach, along the French Mediterranean. The next record of this parasite was from gills of *Mobula diabolus* Smith, 1943 (= *Mobula kuhlii* (Valenciennes in Müller and Henle, 1841)) from Cape Comorin, India (Pillai, 1985). This redescription adds to the list *Mobula japonica* (Müller and Henle, 1841) from the southern Sea of Cortez (Gulf of California) and from off the Channel Islands, southern California, *Mobula thurstoni* (Lloyd, 1908) (previously known as *M. lucasana* Beebe and Tee-Van, 1938) from the southern Sea of Cortez and, *Mobula sp.* from Nosy Be, Madagascar.

This host list is interesting in light of the recent revision of the genus *Mobula* by Notarbartolo-di-Sciara (1987) in which he mentions the possible synonymy of *Mobula mobular* and *Mobula japonica* and, the possibility of some records of *M. kuhlii* being in error and probably representing *M. thurstoni*. In absence of more reliable host identification one can speculate that *E. oliveri* may be specific only to the spine-tail mobula, *Mobula japonica* and the smooth-tail mobula, *Mobula thurstoni*.

Recently, another new species, *Eudactylina mobuli* was described by Hameed et al, (1990) from *Mobula diabolus* from off the coast of Kerala in the Indian Ocean. The hideous cartoon-like abstractions used for illustrations add nothing but pain and confusion to the researcher from that literature. Key attributes such as the unique spatulate setae found in *E. oliveri* are not shown or compared with features found on *E. mobuli*. Hameed et al, (1990) claim their new species is morphologically similar to *E. oliveri*,

but differ by an unarmed claw of the second antenna (this does not occur anywhere in the genus that I am aware of), and a two-segmented exopod on the first leg. The highly abstracted illustrations of these characters coupled with the lack of so much detail make these claims difficult to agree with. The general appearance of the illustrations (the elongate exopods of legs three and four resulting in an ant-like appearance) and the possibility of the host being *M. thurstoni*, suggest to me that *E. mobuli* may be synonymous with *E. oliveri*.

Eudactylina oliveri is easily distinguished from all other congeners by the spatulate spine-like setae located on the basipods of legs two, three, and four and on reduced leg five.

***Eudactylina papillosa* Kabata, 1970**

(Figures 40-41)

Material examined. One paratype female (BMNH 1968.1.5.2) from the branchial lamellae of the stingray, *Dasyatis kuhli* (Müller and Henle, 1838) collected from Moreton Bay, Queensland, Australia.

Description

Female (Figure 40A)

Overall length in lateral view approximately 1.3 mm. Cephalothorax longer than wide, lateral margin slightly notched accommodating lacertus of second maxillae. Dorsolateral surfaces of cephalothorax covered with wavy cuticular flaps. Cuticle of first, second, third and fourth free thoracic somites covered with cuticular flaps. Fourth free thoracic somite smaller than previous three with cuticular flaps on ventral surface and bearing leg five. Genital segment smaller than preceding somite, with cuticular flaps on ventral surface. Abdomen two-segmented, ventral surface bearing cuticular flaps. Caudal ramus (Figure 40B) longer than wide, bearing three stout terminal setae (one very small, two well produced) plus one dorsomedial slender seta and, one lateral slender seta; ventral surface covered with posteriorly directed cuticular flaps.

First antenna (Figure 40C) five-segmented; armature (proximal to distal) as follows: first segment bearing one slender seta; second segment with six naked setae, three short setae with proximal denticulations / serrations plus one large curving, denticulated (prehensile) claw; third segment with nine slender setae plus one large distal spine; fourth segment with one slender seta; fifth (terminal) segment bearing 14 slen-

der setae plus one aesthete. Second antenna (Figure 40D) five-segmented, prehensile. Basal segment short, second segment with short spiniform process and proximally directed subtriangular cuticular flaps, third segment bearing rectangular cuticular flaps and two slender setae arising from base of well developed spiniform process. Fourth segment elongate with many small triangular cuticular flaps along convex margin, fifth segment an elongate unciform terminal claw bearing two slender setae and a very long, slender auxiliary spine. Mandible (not shown) of two parts, dentiferous margin with eight teeth. First maxilla (Figure 40E) biramous; sympod naked, endopod bearing two apical setae (one smooth and one unilaterally denticulated); exopod longer surmounted by two small setae and one longer slender seta. Second maxilla (Figure 40F) brachiform, lacertus larger than brachium, with semicircular cuticular flaps, brachium with semicircular cuticular flaps, a distal patch of prickles and two tufts of setae at base of terminal claw (calamus). Claw bearing two pairs of serrated membranes. Maxilliped (Figure 40G) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small spiniform seta on distal margin, and rectangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposite segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw (Figure 40G detail) unciform with reduced subquadrangular cuticular expansion producing a small lateral shield.

First four pairs of legs biramous with three-segmented endopods, three-segmented exopods and two-segmented sympods. All basipods with lateral slender seta, first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing various shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-I	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 41A) exopod three-segmented; exopodal setae with serrated membrane along lateral margins, largest seta on terminal segment additionally bears denticulations along the distal portion of the medial edge, endopodal setae bilaterally denticulated. Exopod two (Figure 41C) modified, first segment elongate with four rectangular cuticular flaps near proximal region and one distal papilliform seta, second segment smaller, naked and bearing one papilliform seta, third segment armed with one small sub-apical seta plus two papilliform setae. Leg two endopod (Figure 41B) with

two naked setae on terminal segment. Legs three and four (Figure 41D) setae stout with largest exopodal seta bearing denticles. Leg five (Figure 41E) subcircular, distally bearing three small pinnate setae plus one similar seta arising dorsally from the base; lateral surface with subquadrangular and subtriangular cuticular flaps along lateral surface.

Comments: *Eudactylina papillosa* has not been reported since its discovery and description by Kabata (1970) from gills of the stingray, *Dasyatis kuhli*.

E. papillosa is easily distinguished from all other congeners by the papilliform (nipple-like) setae located on the modified exopod of leg two.

Eudactylina peruensis Luque and Farfan, 1991.

(Figures 42-43)

Material examined. Six females (USNM 251289) from the branchial lamellae of the shovelnose guitarfish *Rhinobatos planiceps* Garman, 1880 collected from inshore waters near Chorrillos, Peru.

Description

Female (Figure 42A)

Overall length in lateral view approximately 1.4 mm. Cephalothorax longer than wide, lateral margin slightly notched accommodating lacertus of second maxillae. Anterolateral and dorsal surfaces of cephalothorax covered with cuticular flaps. Dorsal and ventrolateral surfaces of first, second, and third free thoracic somites covered with cuticular flaps; first and second free thoracic somites aliform. Fourth free thoracic somite smaller than previous three, bearing leg five. Genital segment smaller than preceding somite. Abdomen two-segmented, ventral surface bearing a pair of semicircular cuticular flaps on the posterior segment. Caudal ramus (Figure 42B) modified into a digitiform structure bearing two strongly sclerotized processes (fused modified setae?), one tiny proximal seta (sensilla?), one dorsomedial slender seta, one lateral slender seta plus two ventrodiscal short naked setae.

First antenna (Figure 42C) five-segmented, armature (proximal to distal) as follows: first segment bearing one seta; second segment with five small slender setae, two large naked setae, one large bilaterally denticulated seta plus one large denticulated, curving (prehensile) claw; third segment with seven slender setae, two large stout

naked spines, plus one large uncinat denticulated spine; fourth segment with one slender seta; terminal segment with one tiny seta, 11 long slender setae plus one aesthete. Second antenna (Figure 42D) five-segmented, prehensile. Basal segment short (not shown), second segment with long unciform process and triangular cuticular flaps, third segment bearing large hook-like process, three cuticular flaps and two slender setae arising from near base of well produced spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one stout uncinat auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 42E) of two parts, dentiferous margin with five teeth. First maxilla (Figure 42F) biramous; endopod bearing tiny triangular cuticular flaps and two apical setae, the longer with spinules or minute denticles; exopod longer surmounted by two small setae and one longer seta. Second maxilla (Figure 42G) brachiform, lacertus with large semicircular cuticular flaps, brachium with crescentic and subquadarangular cuticular flaps and one patch of prickles and one tuft of rope-like setae at base of terminal claw (calamus). Claw bearing two rows of serrated membranes parallelling the claw plus two strips of membrane along the convex margin of other side, small basal process at base of lacertus. Maxilliped (Figure 42H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing slender seta on distal margin and narrow cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one with pedunculate proximal region near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw complex, cuticular expansions producing a fused complex of claw and cuticle.

First four pairs of legs biramous, leg four with two-segmented endopod, three-segmented exopods and endopods on remaining rami, sympods two-segmented. All basipods with lateral slender seta; first basipod bears additional distomedial naked seta. Ventral surfaces of all four legs bearing semicircular to subtriangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	-	I

Leg one (Figure 43A) exopodal setae unilaterally bearing serrated membranes, largest endopodal seta unilaterally bearing serrated flange, smaller naked. Exopod two

(Figure 43B) modified, first segment greatly elongated with tiny triangular cuticular flaps along the lateral margin and one distal naked seta, second segment smaller with naked seta, third segment armed with one short naked seta, one longer curved naked seta, plus one large curved unilaterally denticulated seta. Leg two endopod (Figure 43B) with one small naked seta and one large bilaterally spinulated seta on terminal segment. Sclerite bar between leg two and leg three (Figure 43C) giving rise to a single, large medial stylet. Exopodal setae of legs three and four (Figures 43D and 43E) large and unilaterally denticulated, endopodal seta unilaterally bearing serrated membranous flange. Leg five (Figure 43F) longer than wide; lateral surface smooth, probably bearing three pinnate setae (only one intact in my specimens) plus one similar seta arising dorsally from the base.

Male: Unknown

Comments: *E. peruensis* can be readily identified by the uniquely modified caudal ramus. The similarities of this structure with the caudal ramus of the new species *Eudactylina dactylocerca*, described herein, plus the two-segmented endopod of leg four, suggest a close phylogenetic relationship. Interestingly, these two species and *Eudactylina rhinobati* Essafi and Raibaut, 1979 share the posteriorly extended terga of free thoracic somites one and two, overlapping free thoracic somites two and three, respectively. All three infect *Rhinobatos*, from their respective waters.

***Eudactylina pollex* Cressey, 1967**

(Figures 44-45)

Material examined. Several females (USNM 271635) from the branchial lamellae of the great hammerhead, *Sphyrna mokarran* (Rüppell, 1837) collected from Sarasota, Florida, and several females (USNM 262099) from the same host species collected from the Caribbean Sea during a shark tagging expedition.

Description

Female (Figure 44A)

Overall length in lateral view approximately 3.5 mm. Cephalothorax longer than wide, lateral margin slightly notched accommodating lacertus of second maxillae.

Dorsolateral surfaces of cephalothorax covered with tiny triangular cuticular flaps. Cuticle of all body somites covered with patches of tiny triangular cuticular flaps. Fourth free thoracic somite smaller than previous three with cuticular flaps on ventral surface and bearing leg five. Genital segment smaller than preceding somite, with cuticular flaps on ventral surface. Abdomen (Figure 44B) two-segmented, ventral surface covered with tiny triangular cuticular flaps. Caudal ramus (Figure 44B) longer than wide, bearing two very large bilaterally denticulate setae plus one or two (too small for certainty) very tiny setae tipped with a tiny setule, one lateral slender seta plus one dorso-medial slender seta; ventral surface covered with posteriorly directed tiny triangular cuticular flaps.

First antenna (Figure 44C) five-segmented, armature (proximal to distal) as follows: first segment bearing one stout seta; second segment with nine stout setae; third segment with ten stout setae, plus one very robust seta (only eight total in figure); fourth segment with one short stout seta; fifth (terminal) segment bearing 13 slender setae plus one aesthete. Second antenna (Figure 44D) five-segmented, prehensile. Basal segment short, second segment without spiniform process, bearing triangular cuticular flaps, third segment bearing a patch of rectangular cuticular flaps and a patch of tiny triangular flaps along convex margin, two slender setae arising from distal end of concave edge. Fourth segment elongate with many small triangular cuticular flaps along convex margin, fifth segment forming a stout unciform terminal claw bearing two short naked setae and a slender auxiliary spine. Mandible (Figure 44E) of two parts, dentiferous margin with five teeth. First maxilla (Figure 44F) biramous; sympod naked or with spinules, endopod bearing two apical setae (one smooth and one sparsely semipinnate or denticulated); exopod longer with or without spinules surmounted by two small stout setae and one longer seta with or without tiny spinules. Second maxilla (Figure 44G) brachiform, lacertus larger than brachium, with triangular cuticular flaps, brachium also with triangular cuticular flaps, a distal patch of densely packed triangular flaps and four large elongate triangular flaps (modified setal tuft?) at base of terminal claw (calamus). Claw bearing two rows of teeth. Maxilliped (Figure 44H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small seta on distal margin, and two patches of tiny triangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two short stout setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw (Figure 44H detail) unciform with amorphous cuticular expansion bearing some very fine spinules along outer edge producing lateral shield.

First four pairs of legs biramous with two-segmented endopod one, modified

endopod four and indistinctly three-segmented endopods two and three, three-segmented exopods and two-segmented sympods. All basipods with lateral slender seta, first basipod bears additional distomedial denticulated seta. Ventral surfaces of all four legs bearing triangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	-	II
Leg two	Exopod	I-0	I-0	III	Endopod	0-0	0-0	III
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	-	I

Leg one (Figure 45A) exopodal setae powerful claws with largest seta on terminal segment additionally bilaterally denticulate, endopodal setae bilaterally denticulated. Exopod two (Figure 45B) not modified, all exopodal setae manifest as powerful claws with largest seta on terminal segment bilaterally denticulated, leg two endopod (Figure 45B) with two denticulated stout setae and one seta on terminal segment. Legs three and four (Figure 45C) with powerful claw-like setae, largest exopodal seta bilaterally denticulate, endopod indistinctly segmented of leg three and partially fused in leg four (Figure 45D) into a two-segmented, bilaterally denticulated claw. Leg five (Figure 45E) ovoid; lateral surface with a few triangular cuticular flaps along lateral surface, distally bearing three small slender setae plus one similar seta arising dorsally from the base.

Comments: *Eudactylina pollex* was reported by Cressey (1967 and 1970) from the great hammerhead, *Sphyrna mokarran* (Rüppell, 1837), collected from Madagascar and the West coast of Florida (Sarasota), and from the scalloped hammerhead, *Sphyrna lewini* (Griffith and Smith, 1834) from off the west coast of Florida. This redescription extends the known geographic range of *E. pollex* to the Caribbean.

E. pollex is easily distinguished from all other congeners by the fused uncinete claw-like nature of the third and especially the fourth endopod, and the lateral expansion of the proximal segment of endopods two, three, and four. Although the unusual absence of an uncinete claw on the second segment of the first antenna appears to be unique to this species, it is probable that the large stout spine on the proximal portion on the third segment represents this structure. It is also possible this apparent displacement is more apparent than real. The highly sclerotized condition of the first antenna makes it very difficult to accurately follow segmental boundaries.

Eudactylina pristiophori sp. nov.

(Figures 46-47)

Material examined. Three females from the branchial lamellae of the longnose sawshark, *Pristiophorus cirratus* (Latham, 1794) captured from near Green's Beach at the Tamar River mouth, northern Tasmania. Specimen (USNM 205516) examined at the Smithsonian's Support Center, National Museum of Natural History, Smithsonian Institution, Washington, D.C. Female holotype (USNM 266529) and 1 female paratype (USNM 266530) deposited at the United States National Museum of Natural History.

Etymology: The specific name *pristiophori* refers to the generic name of the host.

Description

Female (Figure 46A)

Overall length in lateral view approximately 1.8 mm. Cephalothorax longer than wide, lateral margin slightly concave. Surface of cephalothorax, first, second, third and, fourth free thoracic somites covered with cuticular flaps. Fourth free thoracic somite, genital segment and, two-segmented abdomen all bearing cuticular flaps on ventral surface. Caudal ramus (Figure 46B) bearing terminally two very squat curved setae, plus two elongate slender setae (one dorsomedial, one lateral).

First antenna (Figure 46C) apparently four-segmented, armature (proximal to distal) as follows: first segment bearing one slender seta; second segment with four denticulated setae (3 small, one large), four naked setae (two small, one large, one papilliform), and one large denticulated, curving (prehensile) claw; third segment with eight naked setae, one stout naked spine, plus one large denticulated spine; fourth segment with 14 slender setae plus one aesthete. Second antenna (Figure 46D) five-segmented, prehensile. Basal segment short, second segment devoid of cuticular flaps with short spinous process, third segment bearing proximally directed irregular rectangular cuticular flaps and two slender setae arising from near base of curving spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one curving auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 46E) of two parts, dentiferous margin with eight teeth. First maxilla (Figure 46F) biramous; endopod more robust bearing two unilaterally denticulated apical setae; exopod longer and surmounted by two small setae and one longer, unilaterally denticulated seta. Second maxilla (Figure 46G) brachiform, lacertus larger than brachium bearing semicircular cuticular flaps and small basal process, brachium with semicircular and rectangular cuticular flaps, a distal

patch of triangular prickles and two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or hair-like at base of terminal claw (calamus)). Claw bearing four pairs of serrated membranes. Maxilliped (Figure 46H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small seta on distal margin and small rectangular cuticular flaps; myxal area expanded into a receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint and the other along concave distal margin near membranous strip (see detail). Claw (Figure 46H detail) unciform bearing cuticular flange and a quadrate lateral shield.

First four pairs of legs biramous and trimerite, sympods two-segmented. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of legs two, three, and four bearing cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	IV	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 47A) lateral margins of proximal segments with single row of fine triangular cuticular flaps; lateral exopodal setae unilaterally bearing serrated membranous membrane, largest apical exopodal seta bilaterally denticulated, smallest slender and naked, endopodal setae bilaterally denticulated. Leg two exopod (Figure 47C) modified, first segment greatly enlarged with thick seta, second segment with stout seta, terminal segment with one small naked setae, one small recurving seta plus one truncate seta, endopod (Figure 47B) tipped with two bilaterally denticulated setae. Legs three and four (Figure 47D) similar; all exopodal setae denticulated, endopods tipped by single finely denticulated seta. Leg five (Figure 47E) slightly longer than wide, distally bearing three spiniform setae plus one seta arising dorsally from the base; lateral surface with small subquadrangular cuticular flaps.

Male: Unknown

Comments: *Eudactylina pristiophori* is the first record of a parasitic copepod inhabiting the Pristiophoriformes (sawsharks).

This species is readily identified by the very short, stout, and apically curving terminal setae on the caudal rami. Additionally, it is the only species in the genus with a

stout papilliform seta on segment two of the first antenna. Also, no other species bears the unique combination of two slender setae with lateral serrated membranes, an elongate bilaterally denticulated (not semipinnate) seta, and a medial small slender seta on the terminal segment of the first exopod.

Eudactylina pusilla Cressey, 1967
(Figures 48-49)

Material examined. Several females (USNM 153628) from the branchial lamellae of the tiger shark, *Galeocerdo cuvier* (Peron and LeSueur, 1822) collected from Sarasota, Florida.

Description

Female (Figure 48A)

Overall length in lateral view approximately 4.4 mm. Cephalothorax longer than wide, lateral margin deeply notched accommodating lacertus of second maxillae. Dorsolateral surfaces of cephalothorax covered with cuticular flaps. Cuticle of free thoracic somites one-four covered with cuticular flaps. Fourth free thoracic somite smaller than previous three with cuticular flaps on ventral surface and bearing leg five. Genital segment smaller than preceding somite, with cuticular flaps on ventral surface. Abdomen two-segmented, ventral surface bearing cuticular flaps. Caudal ramus (Figure 48B) longer than wide, bearing three terminal large blunt (nearly amorphous) setae (the two lateralmost with a row of fine denticles), one lateral slender seta plus one dorsomedial slender seta; ventral surface with a few posteriorly directed tiny triangular cuticular flaps.

First antenna (Figure 48C) five-segmented, armature (proximal to distal) as follows: first segment bearing one stout seta; second segment with six thick naked setae, two slender naked setae, plus one finely denticulated curving (prehensile) claw; third segment with nine thick naked setae and one large spine; fourth segment with one slender seta; fifth (terminal) segment bearing 13 slender setae plus one aesthete. Second antenna (Figure 48D) five-segmented, prehensile. Basal segment short, second segment without spinous process, bearing subrectangular cuticular flaps, third segment bearing a patch of subrectangular cuticular flaps and two slender setae arising from base of small spinous extension. Fourth segment elongate with many small triangular cuticular flaps along convex margin, fifth segment forming a stout unciform termi-

nal claw bearing two slender setae and a single thick auxiliary spine. Mandible (Figure 48E) of two parts, dentiferous margin with five teeth. First maxilla (Figure 48F) biramous; endopod with triangular cuticular flaps bearing two denticulated setae; exopod longer with subtriangular flaps surmounted by two small denticulated setae and one longer denticulated seta. Second maxilla (Figure 48G) brachiform, lacertus larger than brachium with semicircular cuticular flaps and basal process, brachium also with semicircular cuticular flaps, and distal patch of coarse setae at base of terminal claw (calamus). Claw bearing two rows of teeth distally and two strips of serrated membranes proximally. Maxilliped (Figure 49A) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small seta on distal margin, and patches of tiny triangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two stout setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw (Figure 49A detail) unciform with small cuticular expansion producing lateral shield.

First four pairs of legs biramous and trimerite. All basipods with lateral pinnate to semipinnate setae, first basipod bears additional distomedial denticulated seta. Ventral surfaces of all four legs bearing triangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one exopodal setae (Figure 49B) denticulated, endopodal setae (Figure 49C) bilaterally denticulated. Exopod two (Figure 49D) modified, all exopodal setae naked except largest seta on terminal segment unilaterally denticulated, terminal segment atypically hemispherical in shape with setae displaced to medial margin, leg two endopod (Figure 49E) with two small naked setae on terminal segment. Setae of legs three and four (Figure 49F) claw-like with largest exopodal seta unilaterally denticulated, endopod tipped with a single bilaterally denticulated seta. Leg five (Figure 49G) wider than long, distally bearing three sparsely pinnate setae plus one seta arising dorsally from the base; lateral surface covered with subtriangular cuticular flaps along lateral surface.

Comments: *Eudactylina pusilla* was reported by Cressey (1967, 1970) from gills of the tiger shark, *Galeocerdo cuvier* (Peron and LeSueur, 1822), collected from Madagascar and the West coast of Florida near Sarasota.

E. pusilla is easily distinguished from all other congeners by the large blunt (nearly amorphous) denticulated setae on the caudal rami and by the unusual shape of the terminal segment on the second (modified) exopod and the lateral displacement of the three setae which are usually found terminally.

***Eudactylina similis* T.Scott, 1902**
(Figures 50-51)

Syn: *Eudactylina rachelae* Green, 1958, (see Kabata, 1979)

Material examined. Numerous females from the branchial lamellae of the Pacific electric ray, *Torpedo californica* (Ayres), and the big skate *Raja binoculata* Girard, captured near Palos Verdes, southern California.

Description

Female (Figure 50A)

Overall length in lateral view approximately 4.5 mm. Cephalothorax longer than wide, lateral margin slightly concave. Dorsolateral surface of cephalothorax, first, second, third and, fourth free thoracic somites covered with cuticular flaps. Fourth free thoracic somite, genital segment and, two-segmented abdomen all bearing cuticular flaps on ventral surface. Caudal ramus (Figure 50B) with two terminal stout setae, one lateral slender seta, and one dorsomedial slender seta.

First antenna (Figure 50C) apparently four-segmented, but could be interpreted as seven-segmented; armature (proximal to distal) as follows: first segment bearing one short seta; second segment with three denticulated slender setae (two small, one large), five naked setae and one large denticulated, curving (prehensile) claw; third segment with a proximal group of five slender setae (one denticulated) and a distal group of three setae (two slender, one stout) plus one large denticulated spine; fourth segment elongate with one proximal slender seta, and either 13 or 14 setae with either one or two aesthetes respectively. Second antenna (Figure 50D) five-segmented, prehensile. Basal segment short, second segment devoid of cuticular flaps with small spinous process, third segment bearing proximally directed subrectangular cuticular

flaps, distally directed subtriangular flaps along convex margin, and two slender setae arising from near base of large spinous process. Fourth segment elongate with cuticular flaps along convex margin; fifth segment an unciform terminal claw bearing two slender setae and one curving auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 50E) of two parts, dentiferous margin with seven teeth. First maxilla (Figure 50F) biramous; endopod with triangular cuticular flaps bearing two denticulated apical setae; exopod longer and surmounted by two small naked setae and one longer, bilaterally denticulated thick seta. Second maxilla (Figure 50G) brachiform, lacertus slightly larger than brachium bearing semicircular cuticular flaps, brachium with semicircular cuticular flaps, a distal patch of triangular prickles and two tufts of setae and possibly a small spine at base of claw (calamus). Claw bearing multiple strips of serrated membranes. Maxilliped (Figure 50H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing minute seta on distal margin and small rectangular cuticular flaps; myxal area expanded into a receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint and the other along concave distal margin near membranous strip (see detail). Claw (Figure 50H detail) unciform bearing cuticular flange and a subquadrate lateral shield.

First four pairs of legs biramous and trimerite, sympods two-segmented. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of legs two, three, and four bearing cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	IV	Endopod	0-0	0-0	II
Leg two (modified)	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 51A) lateral margins of proximal segments with single row of fine triangular cuticular flaps; lateral exopodal setae unilaterally bearing serrated membranous flange, largest apical exopodal seta bilaterally denticulated, smallest with distal setules, endopodal setae slender and bilaterally denticulated. Leg two exopod (Figure 51C) modified, first segment greatly enlarged with stout seta, second segment with squat papilliform seta, terminal segment with one small naked seta, one small recurving seta plus one truncate seta, endopod (Figure 51B) tipped with two slender bilaterally spinulated setae. Legs three and four (Figure 51D) similar; all exopodal setae denticulated, endopod tipped by single finely denticulated slender seta. Leg five (Figure 51E)

longer than wide, distally bearing three slender setae plus one seta arising dorsally from the base; lateral surface with small cuticular flaps.

Male: Not obtained

Comments: *Eudactylina similis* was first described by Scott (1902) in British waters from gills of the thorny skate, *Raja radiata* Donovan, and the skate *Raja fullonica*. Green (1958) discovered it on the Atlantic torpedo, *Torpedo nobiliana* Bonaparte, and erroneously established a new species *E. rachelae*, for that record. Also, Delamare Deboutteville and Nunes-Ruivo (1958) discovered *E. similis* on *Raja asterias* in the Mediterranean. Boxshall (1974) found it on *Raja montagui* and *Raja naevus* in the North Sea, and Kabata (1979) found this copepod on the longnose skate, *Raja rhina* Jordan and Gilbert, and on the starry skate, *Raja stellulata* Jordan and Gilbert, in the eastern North Pacific near Vancouver Island. This report adds the big skate, *Raja binoculata* Girard and the Pacific electric ray, *Torpedo californica* Ayres both from near Palos Verdes in southern California to the list. The finding of *E. similis* on *Torpedo californica* supports the synonymy of *E. rachelae* and *E. similis*. This copepod is apparently a common parasite of both *Raja* and *Torpedo* worldwide.

This species can be readily identified by the many small denticles scattered over the convex surface of the large prehensile claw on the second segment of the first antenna, and the apparently unique possession (in the genus) of two aesthetes on the distal segment (s) of the first antenna.

***Eudactylina squamosa* Bere, 1936**

(Figures 52-53)

Material examined. Several females from the branchial lamellae of the cow nose ray *Rhinoptera bonasus* (Mitchill, 1815) collected from the West Coast of Florida (Gulf of Mexico), donated to me by Dr. Roger Cressey (personal collection), Smithsonian Institution; and two females from the gills of the cow nose ray, *Rhinoptera steindacheri* Evermann and Jenkins, 1891 collected from Punta Arena de la Ventana, in the southern Sea of Cortez (Gulf of California).

Description

Female (Figures 52A, B)

Overall length in lateral view approximately 1.2 mm. Cepalothorax longer than

wide, lateral margin notched accomodating lacertus of second maxillae. Entire surface of cephalothorax covered with cuticular flaps. Cuticular flaps present on surfaces of first, second, third and fourth free thoracic somites. Fourth free thoracic somite bearing leg five. Fourth free thoracic somite, genital segment, and abdomen bearing posteriorly directed cuticular flaps on ventral surface. Genital segment smaller than preceeding somite. Abdomen two-segmented. Caudal ramus (Figure 52C) longer than wide, bearing two terminal stout setae, one very small medial seta, one dorsomedial slender seta, one lateral slender seta, and one proximal seta near the lateral edge (possibly homologous to the typical setule seen in this area in other species); ventral surface armed with posteriorly directed subtriangular cuticular flaps.

First antenna (Figure 52D) apparently four-segmented, armature (proximal to distal) as follows: first segment bearing one seta; second segment with five small naked setae, two large setae plus one curving, denticulated (prehensile) claw; third segment bearing nine naked setae, terminal segment armed with 15 smooth slender setae plus one aesthete. Second antenna (Figure 52E) five-segmented, prehensile. Basal segment short, second segment armed with blunt spinous process, third segment bearing three cuticular flaps and two setae (one of them nearly the size of spinous process) arising from base of well produced spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one stout auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 52F) of two parts, dentiferous margin with seven teeth. First maxilla (Figure 52G) biramous; endopod larger bearing two elongate setae, longer seta unilaterally denticulated, exopod shorter surmounted by two small naked setae and one longer slender seta. Second maxilla (Figure 52H) brachiform, lacertus larger than brachium with basal process and bearing cuticular flaps, brachium with irregular triangular cuticular flaps, a distal patch of coarse setae and apparently a small spine at base of terminal claw (calamus). Claw bearing three rows of serrated membranes distally, plus one longer serrated strip proximally. Maxilliped (Figure 52I) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, and devoid of cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other near concave distal margin. Claw unciform with small lateral shield.

First four pairs of legs biramous and trimerite, two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial seta tipped with two setules. Ventral surfaces of all four legs bearing subtriangular cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 53A) exopodal setae thick bearing lateral denticulations, endopod with one slender seta and one larger seta bilaterally denticulated. Leg two (Figure 53B) exopod not modified and bearing subtriangular cuticular flaps, first segment largest with one distal stout seta, second segment smaller bearing single stout seta, third segment armed with three small stout setae. Leg two endopod (Figure 53B) with two bilaterally denticulated setae (one small, one large). Exopods of legs three and four (Figure 53C) with claw-like setae, largest seta on terminal segment with denticles, terminal segment of endopods three and four (Figure 53C) bearing single thick bilaterally denticulated seta. Leg five (Figure 53D) longer than wide, distally bearing three slender setae plus one similar seta arising dorsally from the base; lateral surface sparsely covered with triangular cuticular flaps.

Male: Unknown

Comments: *E. squamosa* has not been reported since its discovery by Bere (1936) on *Rhinoptera bonasus* from Lemon Bay, Florida. This report from *Rhinoptera steindacheri* extends the host spectrum and geographic range of the parasite. The specimen dissected and studied from the Gulf of California from *R. steindacheri* differed from its counterpart from the Gulf of Mexico by possessing cuticular flaps on the maxilliped, cuticular flaps on the fourth segment of the second antenna, cuticular flaps on the penultimate segment of the first antennae, and terminal elements on the caudal rami appearing a bit more amorphous and claw-like. Until more specimens are looked at I feel it is best to treat these differences as intraspecific. In either case, this (or these) species seem to be specific to the rhinopterids.

The squat habitus, the relatively short expansion of the corpus maxillipedis coupled with the transverse palm of the corpus (resulting in a reduced aperture) readily distinguish this species. Additionally, the thick setae approximating the dimensions of the spiniform process of the third segment of the second antenna are unique to the species. The relative lengths of the terminal setae on the third segment of the unmodified second exopod decrease from the lateral to the medial margins, in sharp contrast to what occurs in the other species.

Eudactylina tuberifera Castro and Baeza, 1987

(Figures 54-55)

Material examined. Several females (USNM 213114) from the branchial lamellae of the southern angelote, *Squatina armata* (Philippi, 1887), collected from the eastern South Pacific near Antofagasta, Chile.

Description

Female (Figure 54A)

Overall length in lateral view approximately 1.8 mm. Cephalothorax longer than wide, lateral margin notched accommodating lacertus of second maxillae. Entire surface of cephalothorax covered with cuticular flaps. Cuticular flaps present on surfaces of first, second, third and fourth free thoracic somites. Fourth free thoracic somite bearing leg five. Fourth free thoracic somite, genital segment, and abdomen bearing posteriorly directed cuticular flaps on ventral surface. Genital segment smaller than preceding somite. Abdomen two-segmented. Caudal ramus (Figure 54B) longer than wide, bearing two terminal apically curved stout setae, one dorsomedial slender seta, and one lateral slender seta; ventral surface armed with posteriorly directed cuticular flaps.

First antenna (Figure 54C) indistinctly four-segmented, armature (proximal to distal) as follows: first segment bearing one naked seta; second segment with five small naked setae, two large naked setae (one elongate, one stout), one elongate bilaterally denticulated seta plus one curving, denticulated (prehensile) claw; third segment bearing six slender setae, one short stout seta, one large naked spine, and one large denticulated spine, terminal segment armed with 14 naked slender setae, one long unilaterally denticulated seta plus one aesthete. Second antenna (Figure 54D) five-segmented, prehensile. Basal segment short second segment armed with spiniform process, third segment bearing proximally directed cuticular flaps and two slender setae arising from base of well produced spinous process. Fourth segment elongate and unarmed; fifth segment an unciform terminal claw bearing two slender setae and one well developed auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 54E) of two parts, dentiferous margin with eight teeth. First maxilla (Figure 54E) biramous; endopod with triangular cuticular flaps and bearing two slender setae, longer seta denticulated, exopod longer surmounted by two small setae and one longer bilaterally denticulated seta. Second maxilla (Figure 54F) brachiform, lacertus larger than brachium and bearing cuticular flaps, brachium with irregular cuticular flaps, and two tufts of setae (one coarse or rope-like (possibly fused setae) and one fine or setule-like at base of terminal claw (calamus)). Claw bearing four rows

of serrated membranes distally, plus one longer serrated strip proximally, two strips of serrated membranes flanking concave surface on opposite side. Maxilliped (Figure 55A) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, and large patch of cuticular flaps; myxal area bearing large transverse cuticular flap along anteroventral margin and expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to membranous strip along concave distal margin. Claw (Figure 55A, detail) unciform with subrectangular lateral shield.

First four pairs of legs biramous and trimerite, two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing variously shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	1-0	1-0	III	Endopod	0-0	0-0	II
Leg two	Exopod	1-0	1-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	1-0	1-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	1-0	1-0	III	Endopod	0-0	0-0	I

Leg one (Figure 55B) exopodal setae bearing lateral serrated cuticular expansions, endopodal setae and bilaterally denticulated. Leg two exopod (Figure 55C) modified and bearing subtriangular cuticular flaps along lateral margin, first segment greatly enlarged with one distal, toothed stout seta, second segment smaller, bearing single stout, naked seta, third segment armed with one small slender seta, one truncate seta, and one recurving seta. Leg two endopod (Figure 55D) with two bilaterally denticulated slender setae. Exopods of legs three and four (Figure 55E) with stout toothed setae, terminal segment of endopods three and four (Figure 55F) bearing single thick bilaterally denticulated seta. Leg five (Figure 55G) longer than wide, distally bearing three slender naked setae plus one pinnate seta arising dorsally from the base; lateral surface with cuticular flaps.

Male: Not obtained

Comments: *E. tuberifera*, the parasite of the southern angelote *Squatina armata*, is very similar to *E. acuta*, a parasite of the Mediterranean angelshark, *Squatina squatina* and to the new species *E. aphioxenos*, parasitizing the Pacific angelshark, *Squatina californica* off the southern California coast. Castro and Baeza (1987) claim

the swollen third segment of the second antenna of the female is a diagnostic character of this species. However, this is not so; the second antenna is quite typical of the entire genus and the specimens examined did not display this accentuated trait.

This species, and its two aforementioned allies, *E. acuta* and *E. aphioxenous*, share the large tines found on the setae of exopods three and four, and the difficult to distinguish four- or five-segmented first antenna. The serrated membranes on the lateral edge of the setae on exopod one, possessing three setae on the terminal segment of exopod one (not four), and the row of cuticular flaps along the lateral edge of the modified exopod of leg two, separate this species from the two remaining squatinid parasitizing copepods.

***Eudactylina turgipes* Bere, 1936**

(Figures 56-57)

Material examined. Several females (USNM 155196) from the branchial lamellae of the butterfly ray *Gymnura* sp. collected from Lemon Bay, Florida (Gulf of Mexico), additional specimens from same host species and locality donated to me by Dr. Roger Cressey (personal collection), Smithsonian Institution.

Description

Female (Figure 56A)

Overall length in lateral view approximately 1.7 mm. Cephalothorax longer than wide, lateral margin notched accommodating lacertus of second maxillae. Entire surface of cephalothorax covered with cuticular flaps. Cuticular flaps present on surfaces of first, second, third and fourth free thoracic somites. Fourth free thoracic somite bearing leg five. Fourth free thoracic somite, genital segment, and abdomen bearing posteriorly directed cuticular flaps on ventral surface. Single median intersomitic stylet present between leg three and four (Figure 57A). Genital segment smaller than preceding somite. Abdomen two-segmented. Caudal ramus (Figure 56B) longer than wide, bearing four terminal setae (two small unilaterally denticulated setae, one small naked seta, and one elongate bilaterally denticulated seta), one dorsomedial slender seta, and one lateral slender seta; ventral surface armed with posteriorly directed subtriangular cuticular flaps.

First antenna (Figure 56C) indistinctly four-segmented, armature (proximal to distal) as follows: first segment bearing one small slender seta; second segment with

four small naked setae, one small unilaterally denticulated seta, two elongate naked setae, one large stout seta plus one curving, denticulated (prehensile) claw; third segment bearing eight slender naked setae, one stout naked spine, and one large denticulated spine, terminal segment armed with 15 slender setae plus one aesthete. Second antenna (Figure 56D) five-segmented, prehensile. Basal segment short, second segment armed with spinous process, third segment bearing two rows of proximally directed subrectangular cuticular flaps and two slender setae arising from base of long spinous process. Fourth segment elongate and unarmed; fifth segment an elongate, unci-form terminal claw bearing two slender setae and one elongate auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 56E) of two parts, dentiferous margin with eight teeth. First maxilla (Figure 56F) biramous; endopod bearing one unilaterally denticulated seta and one longer bilaterally denticulated seta, exopod longer surmounted by two small naked setae and one longer bilaterally spinulated (sparsely pinnate) slender seta. Second maxilla (Figure 56G) brachiform, lacertus larger than brachium and bearing a proximal patch of triangular cuticular flaps adjacent to basal process and wavy cuticular flaps on other side, brachium with wavy (sinusoidal) cuticular flaps, a distal patch of triangular flaps (prickles) and one tuft of coarse setae at base of terminal claw (calamus). Claw bearing one pair of serrated membranes distally and another pair proximally, two strips of serrated membranes flanking concave surface on opposite side. Maxilliped (Figure 56H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin, and large patch of sinusoidal cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one large stout seta near midpoint on lateral convex margin and the other adjacent to elongate membranous strip along concave distal margin. Claw (Figure 56H, detail) complex with ovoid lateral shield.

First leg biramous and bimerite, legs two three and four biramous and trimerite, two-segmented sympods. All basipods with lateral pinnate seta; first basipod bears additional distomedial slender seta. Ventral surfaces of all four legs bearing semicircular, triangular, and rectangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	-	IIII	Endopod	0-0	-	II
Leg two	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 57A) exopodal setae distally bearing serrated cuticular expan-

sions, longest seta on terminal segment bilaterally bearing tiny spinules, endopod with unusual array of semicircular cuticular flaps wrapping around lateral margin of elongated terminal segment, setae bilaterally spinulated. Leg two exopod (Figure 57B) modified, bearing minute triangular cuticular flaps along lateral margin, first segment greatly enlarged, second and third segments compressed with a few tiny triangular flaps, all setae robust and papilliform. Leg two endopod (Figure 57C) with relatively large proximal segment and rectangular cuticular flaps, terminal segment apically bears two pinnate slender setae. Exopods of legs three and four (Figure 57D) with apically toothed setae, largest seta on terminal segment pinnate, terminal segment of endopods three and four bearing single pinnate seta. Leg five (Figure 57E) longer than wide, distally bearing three pinnate setae plus one similar seta arising dorsally from the base; lateral surface with triangular cuticular flaps. Intersomitic stylet (Figure 57F) plunging down between pediger three and pediger four.

Male: Unknown

Comments: *E. turgipes* was first recorded by Bere (1936) from gills of the butterfly ray *Pteroplatea maclura* (= *Gymnura maclura*); it was subsequently found by Pearse (1952a) from the smooth butterfly ray, *Aetoplatea micrura* (= *Gymnura micrura*, (Bloch and Schneider)), and most recently it turned up again (Raibaut et al., 1971) in Tunisian waters (Mediterranean Sea) from the gills of the spiny butterfly ray, *Gymnura altevela* (Linnaeus). This additional record from *Gymnura* sp. from Lemon Bay, Florida strongly suggests *E. turgipes* is specific to butterfly rays of the genus *Gymnura*.

This species is easily distinguished by the peculiarly swollen modified exopod of leg two, the papilliform setae of exopod two, the unique combination of setal characteristics on the caudal ramus, the bimerite condition of the exopod and endopod of leg one, the apparently bifid ventral stylet, and the four semicircular flaps wrapping around the lateral margin of the elongated terminal segment of the endopod of leg one.

***Eudactylina urolophi* sp. nov.**

(Figures 58-59)

Material examined. Several females from the branchial lamellae of the round stingray *Urolophus halleri* Cooper collected from Los Angeles Harbor and Seal Beach, California. Female holotype (USNM 266566) and 1 female paratype (USNM 266567)

deposited at the United States National Museum of Natural History.

Etymology: The specific name *urolophi* refers to the generic name of the host.

Description

Female (Figure 58A)

Overall length in lateral view approximately 2.3 mm. Cephalothorax longer than wide, lateral margin notched accommodating lacertus of second maxillae. Dorsolateral surface of cephalothorax covered with cuticular flaps. Cuticular flaps present on surfaces of first, second, third and fourth free thoracic somites. Fourth free thoracic somite bearing leg five. Fourth free thoracic somite, genital segment, and abdomen bearing posteriorly directed cuticular flaps on ventral surface. Genital segment smaller than preceding somite. Abdomen two-segmented. Caudal ramus (Figure 58B) longer than wide, bearing two stout setae, one dorsomedial slender seta (not illustrated), and one lateral slender seta; ventral surface armed with posteriorly directed triangular cuticular flaps.

First antenna (Figure 58C) apparently four-segmented, armature (proximal to distal) as follows: first segment bearing one small slender seta; second segment with only four slender setae observed (certainly more exist but were missed) plus one curving, denticulated (prehensile) claw; third segment bearing three small setae and one elongate slender seta (again, more are certain to exist but were missed) plus one stout seta and one large denticulated spine, terminal segment with only 10 slender setae observed plus one aesthete. Second antenna (Figure 58D) five-segmented, prehensile. Basal segment short, second segment armed with spinous process and single subrectangular cuticular flap, third segment bearing proximally directed subrectangular cuticular flaps with two slender setae arising from base of spinous process. Fourth segment elongate and unarmed; fifth segment an elongate, unciform terminal claw bearing two slender setae and one elongate auxiliary spine. Mouth tube siphonostome and similar to that of other species. Mandible (Figure 58E) of two parts, dentiferous margin with six teeth. First maxilla (Figure 58F) biramous; endopod bearing two naked setae, exopod longer surmounted by two small naked setae and one longer naked seta. Second maxilla (Figure 58G) brachiform, lacertus larger than brachium, brachium with rectangular cuticular flaps, a distal patch of triangular flaps (prickles) and two tufts of setae (one coarse and one fine) at base of terminal claw (calamus). Claw bearing serrated membrane distally and another strip along concave margin. Maxilliped (Figure 58H) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout seta on distal margin, and five large rectangular cuticu-

lar flaps; myxal area expanded into large receptacle to accommodate claw of opposite segment. Shaft bearing two setae: one large naked seta near midpoint on lateral convex margin and the other adjacent to elongate membranous strip along concave distal margin. Claw with subquadrangular lateral shield.

First leg biramous and bimerite, legs two three and four biramous and trimerite, two-segmented sympods. All basipods with lateral slender seta; first basipod bears additional distomedial seta (not shown). Ventral surfaces of all four legs bearing triangular and rectangular shaped cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	-	IIII	Endopod	0-0	-	II
Leg two	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 59A) exopodal setae laterally bearing serrated cuticular expansions (membranes), longest seta on terminal segment slender and naked, endopod with elongated terminal segment, setae slender and naked. Leg two exopod (Figure 59B) modified, bearing minute cuticular flaps along lateral margin and small triangular flaps along medial edge, first segment greatly enlarged, second and third segments smaller, terminal segment with truncate seta, one short slender seta, and one recurving seta. Leg two endopod (Figure 59B) with relatively large lateral protuberance on proximal segment, terminal segment apically bears two naked slender setae. Exopods of legs three and four (Figure 59C) with unilaterally denticulated setae, seta on proximal segment of endopods with serrated membrane. Leg five (Figure 59D) longer than wide, distally bearing three slender setae plus one seta arising dorsally from the base; lateral surface with rectangular and triangular cuticular flaps.

Male: Unknown

Comments: *E. urolophi* is the first eudactylinid to be reported from the genus *Urolophus*. Only three species possess both a two-segmented endopod and two-segmented exopod on the first leg. These species are *E. epaktolampter*, *E. corrugata*, and *E. turgipes*. Of these three species, both *E. epaktolampter* and *E. turgipes* possess caudal rami bearing six setae, *E. urolophi* bears only four setae on the caudal ramus. This simple combination sets *E. urolophi* apart from the remaining species in the genus.

Eudactylina vaquetillae sp. nov

(Figures 60-61)

Material examined. Several females branchial lamellae of the vaquetilla, *Mobula tarapacana* (Philippi, 1892) collected from Punta Arena de la Ventana in the southern Sea of Cortez (Gulf of California). Female holotype (USNM 266531) and 5 female paratypes (USNM 266532) deposited at the United States National Museum of Natural History.

Etymology: The specific name *vaquetillae* refers to the local vernacular name ascribed to this very large mobulid.

Description

Female (Figure 60A)

Overall length in lateral view approximately 3.3 mm. Cephalothorax longer than wide, lateral margin notched accomodating lacertus of second maxillae. Lateral and dorsal surfaces of cephalothorax covered with cuticular flaps. Cuticle of first, second, and third free thoracic somites covered with cuticular flaps. Fourth free thoracic somite smaller than previous three with cuticular flaps on ventral surface and bearing leg five. Genital segment smaller than preceeding somite, with cuticular flaps on dorsal and ventral surfaces. Abdomen two-segmented, ventral surface bearing cuticular flaps. Caudal ramus (Figure 60B) ellipsoid, bearing four terminal short stout setae (only three illustrated), one dorsomedial slender seta and one ventrolateral slender seta; ventral surface covered with variously directed semicircular cuticular flaps.

First antenna (Figure 60C) indistinctly five-segmented, armature (proximal to distal) as follows: first segment with cuticular flaps along lateral margin bearing one tiny stout seta; second segment with eight naked setae plus one large, curving (prehensile) claw; third segment with a proximal cluster of six naked setae (only four illustrated) plus a distal cluster of three naked setae and a stout spine; fourth segment bearing one slender seta, terminal segment with 14 slender setae plus one aesthete. Second antenna (Figure 61A) five-segmented, prehensile. Basal segment short, second segment elongate bearing many small semicircular cuticular flaps, third segment bearing proximally directed rectangular cuticular flaps, two slender setae arising from near base of very reduced spinous (possibly absent) process. Fourth segment elongate with many semicircular cuticular flaps, fifth segment an elongate unciform terminal claw bearing two slender setae and one similar in size, slender auxiliary spine. Mouth tube

siphonostome and similar to that of other species. Mandible (Figure 60D) of one part, dentiferous margin with six teeth. First maxilla (Figure 60D) biramous; sympod with small patches of spinules, endopod bearing two stout setae, one unilaterally denticulated; exopod longer surmounted by two small naked setae and one longer bilaterally denticulated seta. Second maxilla (Figure 60E) brachiform, lacertus larger than brachium, with small triangular and larger semicircular cuticular flaps, brachium with semicircular cuticular flaps, a distal patch of prickles a tiny naked seta and a single tuft of fine setae at base of terminal claw (calamus). Distal region of claw bearing two rows of denticles, proximal region with three pairs of serrated membranes. Maxilliped (Figure 60F) chelate, indistinctly segmented, proximal segment pedunculate; corpus maxillipedis robust bearing small stout spine on distal margin and small triangular cuticular flaps; myxal area expanded into large receptacle to accommodate claw of opposable segment. Shaft bearing two setae: one near midpoint on lateral convex margin and the other adjacent to a strip of membrane along concave distal margin. Claw (Figure 60F detail) unciform with reduced subquadrangular cuticular expansion producing a very small lateral shield.

First four pairs of legs biramous with three-segmented endopods, three-segmented exopods and two-segmented sympods. All basipods with short lateral slender seta; first basipod bears additional distomedial short slender seta. Ventral surfaces of all four legs bearing triangular and semicircular cuticular flaps. Armature of rami as follows:

Leg one	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg two	Exopod	I-0	I-0	III	Endopod	0-0	0-0	II
Leg three	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I
Leg four	Exopod	I-0	I-0	III	Endopod	0-0	0-0	I

Leg one (Figure 61B) exopod reduced; exopodal setae small, stout and denticulated, endopodal setae unilaterally denticulated with elongate triangular cuticular flaps near bases. Exopod two (Figure 61C) elongate; first segment long with triangular cuticular flaps along lateral margin and one enlarged, distal papilliform seta, second segment smaller with papilliform seta, third segment armed with three slightly more elongated papilliform setae. Leg two endopod (Figure 61C) with two unilaterally denticulated setae on terminal segment and three elongate, triangular cuticular flaps near bases. Legs three and four (Figure 61D); setae short and denticulated on terminal segments. Terminal segments of exopod of leg four (Figure 61E) and endopod of leg four (Figure 61F) not as elongate as leg three with smoother setae on exopod of leg four. Leg five

(Figure 61G) elongate, distally bearing three slender setae plus one seta arising dorsally from the base; lateral surface with semicircular and triangular cuticular flaps. Leg six (Figure 61H) represented by three short stout spines near oviducal opening.

Male: Unknown

Comments: Predictably, *Eudactylina vaquetillae* shares many characteristics with other mobulid-infecting species, *Eudactylina diabolophila* and *Eudactylina oliveri*. The long legs, giving these species an ant-like appearance, the reduced lateral shield on the claw of the maxilliped, the relatively reduced exopods and elongated endopods of legs one and two, the relatively straight five- or six-segmented first antenna with relatively reduced auxiliary spines on the third or fourth segment, the relatively elongated caudal rami bearing six setae, the two rows of thick denticles found on the distal half of the second maxilla, the transverse palm of the maxilliped coupled to the short extension of the myxa resulting in a reduced aperture, separate these species from their remaining congeners. Undoubtedly, close phylogenetic relationships exist among species of this complex.

Eudactylina vaquetillae is distinguished from other species of this complex and all other congeners by the globose, mammiform setae located on the exopod of leg two, the unusual and irregular orientation of the very large semicircular cuticular flaps on the caudal rami and the very elongate leg five.

REMAINING UNOBTAINABLE NOMINAL SPECIES

As previously stated, *Eudactylina* now consists of 38 nominal species. Five of them, (*E. carchariaeglauci* Hesse, 1884, *E. mustelillaevis* Hesse, 1884, *E. sqautinaeangeli* Hesse, 1884, *E. puriensis* Tripathi, 1956, and *E. mobuli* Hameed et al, 1990) have not been sufficiently described to be recognized and are considered *species inquirendae*. Yamaguti (1963) includes *E. versicolor* Wilson, 1913 in the genus. Strangely enough, the only eudactylinid featured in Wilson (1913) is *Nemesis versicolor*. Thus, *E. versicolor* is presumably a *lapsus calami* due to Yamaguti's transcriptional error. *E. rachelae* and *E. complexa* have been relegated to synonymy (see Kabata, 1979), as has *E. dollfusi* and *E. spinifera* herein, bringing the number of accepted taxa within the genus to 30.

For the sake of completeness and cohesiveness for future reference, this section

is a brief (alphabetical) account of the females of the uncertain species above and the remaining species that were not available for this revision of *Eudactylina*.

Eudactylina alata Pillai, 1968 was described from *Rhynchobatus* sp. from near Kerala, India. This species is relatively well described and exhibits many unique if not bizarre characteristics. The first free thoracic somite immediately posterior to the cephalothorax is greatly enlarged with lateral aliform expansions overlapping the majority of the following somite. The second segment of the second antenna bears three stout spines or processes, and the prehensile claw of the first antenna appears to be bifid.

Eudactylina bicornis Hameed et al, 1990 was described from the smooth hammerhead, *Sphyrna zygaena* (Linnaeus, 1758) near Trivandrum, India. The illustrations are recognizable as *Eudactylina*, but the fine detail needed for specific identification is lacking.

Eudactylina breviabdomina Pearse, 1952 was originally reported from the black-tip shark, *Carcharhinus limbatus* (Valenciennes, 1839) from the Gulf of Mexico near Texas. I examined the old, colorless, flattened specimen preserved on a slide and could not use it for the current purposes. The original description also lacks sufficient detail.

Eudactylina brevicauda Hameed et al, 1990 described from gills of *Rhynchobatus djiddensis* (Forsskal, 1775) from near Cape Comorin, India. Despite the specific name bestowed upon it, this species stands out amongst its congeners due to the presence of very long posteriorly directed extensions of the cephalothorax. Illustrations are insufficient for comparison of systematically important fine detail.

Eudactylina chelata Hameed et al, 1990 was collected from gills of the whitecheek shark, *Carcharhinus dussumieri* (Valenciennes, 1839). The authors claim this species is unique within the genus due to the modification of the terminal segment of the endopod into a chela on legs three and four. Again, the illustrations make it difficult to distinguish the exact nature of their claim, however it appears there is a large curving spine on that segment.

Eudactylina carchariaeaglauci Hesse, 1883 was reported from the blue shark, *Prionace glauca* (Linnaeus, 1758) from the French Atlantic. Inadequate description relegates this to a *species inquirendum* (see Kabata, 1979).

Eudactylina lancifera Pillai, 1968 was reported from gills of the sawfish, *Pristis* sp. and *Rhynchobatus* sp. from Kerala, India. This species possesses a long median interpodal stylet extending from the basipod of leg three, hence the specific name. It also exhibits what appears to be two instead of the typical single seta near the midpoint of the shaft on the maxilliped and along the distal medial margin of the myxal area

of the maxilliped. These latter two traits are unique within the genus if they truly do exist.

Eudactylina minuta T. Scott, 1904 was recently redescribed by Kabata (1979) from the gills of the stingray *Dasyatis pastinaca* (Linnaeus). The fine illustrations allow the researcher to easily identify this species and as always keen attention is paid to the fine detail. Because I was not able to obtain specimens of this parasite, this species was not included in this analysis. This species has also been reported from the rough-tail stingray *Dasyatis centroura* (Mitchill), and from *Dasyatis pastinaca* (Linnaeus, 1758), both from Tunisian waters (Mediterranean) (Essafi and Raibaut, 1977).

Eudactylina mobuli Hameed et al, 1990 was described from *Mobula diabolus* Smith, 1943 (= *Mobula kuhlii* (Valenciennes in Müller and Henle, 1841)). Although the illustrations appear unrealistic, the elongated legs unmistakably alert one to the similarity of this species to the other mobulid-infecting eudactylinids. The two-segmented modified exopod of leg two is very atypical for this genus. Unfortunately, the fine detail is lacking and since correct identification of mobulids is not an easy task, this species was not included in the analyses.

Eudactylina mustelillaevis Hesse, 1884 was considered a *species inquirendum* by Kabata (1979) due to insufficient description. This parasite was originally described from gills of the smooth-hound shark, *Mustelus laevis* Linck, 1790 (= *Mustelus mustelus* (Linnaeus, 1758)). One wonders if subsequent records of *E. insolens* (redescribed herein) from this host and from the blackspotted smooth-hound, *Mustelus mediterraneus* (Quignard and Capape, 1972) (= *Mustelus punctulatus* Risso, 1826) from the same geographic locality represent the same parasite species.

Eudactylina parva Castro and Baeza, 1991 was recently described from the gills of the skate *Sympterygia brevicaudata* Cope, 1877 from Antofagasta, Chile. This appears to be a rather non-descript species. It does possess what appears to be a four-segmented first antenna, two large claw-like setae at the distal margin of the third segment of the first antenna, a medium length spiniform process on both second and third segment of the second antenna, four rows of serrated membranes along the distal portion of the claw of the second maxilla, a subquadrangular lateral shield on the claw of the maxilliped, denticulated setae of exopods three and four, setae on the first exopod bearing lateral serrated membranes, and a truncate medial seta on the terminal segment of the modified second exopod. All these characteristics should place this species in with the other species of *Eudactylina* infecting batoids (see following cladistic analyses).

Eudactylina puriensis Tripathi, 1962 was described from gills of *Rhynchobatus djiddensis* from Puri, India. This description allows one to recognize the

organism as *Eudactylina* but little else. The general habitus does resemble *E. lancifera* that Pillai (1968) described from the same host genus. Interestingly, male *E. puriensis* possess two posteriorly-directed cephalothoracic extensions. These same attributes are also shown to be shared by the male of *E. alata* described by Pillai (1968), again from the same genus of host. It would appear this confused and insufficient description should relegate this taxon to a *species inquirendum*.

Eudactylina rhinobati was described by Raibaut and Essafi (1979) from gills of the shovenose guitarfish, *Rhinobatos rhinobatos* (L., 1758) and *Rhinobatos cemiculus* Geoffrey, 1817 both from southern Tunisia. The description suggests this species is closely related to the other rhinobatid-infecting eudactylinids described herein; all species show similarities in structures of the caudal rami and in the two-segmented endopods on some if not all thoracic legs.

Eudactylina spinula Pearse, 1950 parasitizes the sand devil, *Squatina dumeril* Lesueur, 1818. This species could not be used in this analysis due to it being curled up and mounted on a slide. Kabata (1979) mentions *E. spinula* is unmistakably different than *E. acuta* which parasitizes squatinids on the European side of the Atlantic.

Eudactylina squatinaeangeli Hesse, 1883 exists as a *species inquirenda* due to the insufficient description originally provided by Hesse (1883) (see Kabata, 1979). This parasite was originally reported from the angelshark, *Squatina angelus* Blainville, 1816 (= *Squatina squatina* (Linnaeus, 1758)). One wonders if this does not represent *Eudactylina acuta*, a common parasite of this host, found along European and northern African continental shelves.

Eudactylina valei Nunes-Ruivo, 1956 was reported from the dusky smoothhound, *Mustelus canis* (Mitchill, 1815) from Angola, and from the spiny dogfish, *Squalus acanthias* Linnaeus, 1758, from southwest Africa.

Eudactylina vilelai Nunes-Ruivo, 1956 was originally found on the little gulper shark, *Centrophorus uyato* (Rafinesque, 1810), and on the longnose spurdog, *Squalus fernandinus* Molina, 1782 (= *Squalus blainvillei* (Risso, 1826)) both members of the Squalea (see Shirai, 1992b), from off the coast of Angola. Essafi and Raibaut (1977) collected this species from the blackmouth catshark, *Pristiurus melanostomus* (= *Galeus melastomus* Rafinesque, 1810) from the western Mediterranean, and off the coast of France. The latter two species of *Eudactylina*, though both adequately described were left out of the analysis to maintain the standardized interpretations generated by a single illustrator/author.

PHYLOGENETIC ANALYSIS

CLADOGRAM CONSTRUCTION

A phylogenetic analysis was conducted for the 28 species of *Eudactylina* revised herein. Deets and Ho (1988) generated a cladogram (Figure 62) and host-summary cladogram (63) of the Eudactylinidae. The outgroup used herein was composed of the supposed sister taxon *Eudactylinodes* and at times members of their sister clade namely, *Eudactylinella*, *Carnifossorius*, and *Eudactylinopsis* (Figure 62; see Deets and Ho, 1988 for details). 75 characters (see Appendix A for data matrix and definition of characters) were analyzed using the heuristic Tree-Bisection and Reconnection (TBR) algorithm from the phylogenetic computer program PAUP (Phylogenetic Analysis Using Parsimony), version 3.0S (developed by Dr. David Swofford, Museum of Natural History, Smithsonian Institution, Washington, D.C.). The most parsimonious tree for *Eudactylina* (Figure 64) had a tree length of 239, a consistency index of 0.77 (maximum value = 1.00), a retention index of 0.88 (maximum value = 1.00), and an *F* - ratio of 0.0589 (maximum value=0). Due to the large number of characters, it became problematical mapping them back on the tree, therefore change and/or synapomorphy lists may be obtained from the author.

The tree posits that one species *E. aspera* is the sister taxon to the remaining species in the genus. The next node separates the tree into two major lineages, one clade is composed of the *E. diabolophila* - *E. insolens* group, while the other clade is composed of the remaining 18 species.

Since heuristic methods do not guarantee finding the most parsimonious tree (see Swofford, 1991, for a discussion on global versus local optima), nine species of *Eudactylina* were then selected in order to employ the Branch and Bound algorithm which is capable of identifying all most parsimonious trees in PAUP. This analysis was pursued as a check or test of the general phylogenetic framework revealed from the initial heuristic TBR method. Hence, the selection of these nine species required this subset to span across the cladogram, and to preferably represent parasites of major supraspecific host taxa (i.e., Triakidae, Carcharhinidae, squalids, squatinids, pristiphorids, and batoids in order to generate a general parasite-derived phylogeny for these systematically more inclusive host taxa. The 9 species chosen to fulfill these systematic needs were: *E. acanthii*, *E. chilensis*, *E. epaktolampter*, *E. acuta*, *E. pristiphori*, *E. myliobatis*, *E. insolens*, *E. pusilla* and, *E. pollex*.

A phylogenetic analysis was conducted for the 9 aforementioned species of *Eudactylina*. 55 characters (see Appendix B for data matrix and definition of characters) were analyzed using the Branch and Bound algorithm. The most parsimonious tree for the subset of *Eudactylina* on supraspecific host taxa (Figure 65) had a tree length of 102, a consistency index of 0.88 (maximum value = 1.00), a retention index of 0.88 (maximum value = 1.00), and an *F* - ratio of 0.0642 (maximum value=0). Again, change and/or synapomorphy lists may be obtained from the author if the reader wishes to map character state changes back on to the tree.

The resultant cladogram is composed of two major lineages. The smaller clade composed of three species reveals *E. insolens* to be the sister taxon to the clade composed of *E. pusilla* and *E. pollex*. The other clade composed of the remaining six species places *E. acanthii* as the sister taxon to the remaining species which sort themselves out into two distinct clades. The first group is composed of *E. chilensis* and *E. epaktolampter*. The remaining clade appears quite closely related and derived relative to the other species in this analysis. This group is composed of *E. acuta*, which is the sister taxon to the remaining two species, *E. pristiophori* and *E. myliobatidos*.

PARASITE-DERIVED HOST CLADOGRAMS

In an attempt to reconstruct the history of this association between species of *Eudactylina* and their elasmobranch hosts and to infer possible phylogenetic relationships of the host taxa, the parasite cladogram was recoded by the additive binary coding technique (O'Grady and Deets, 1987), and a host by parasite data matrix was created (Table I). Treating the parasites as characters and the phylogeny of the species as a character state tree was formally introduced by Brooks (1981). Accordingly, the most-parsimonious reconstruction from the data describes the evolution of the host-parasite association.

The phylogenetic analysis conducted from the recoded species of *Eudactylina* by host matrix (Table I) resulted in a single most-parsimonious tree (Figure 66). The TBR generated tree had a tree length of 55, and a consistency index with a maximum value of 1.00 .

The parasite-derived host cladogram postulates an unresolved group composed of *Chiloscyllium*, *Sphyrna*, *Rhizoprionodon*, and two *Carcharhinus* species (all sharing *E. aspera*) to be the sister group to the rest of the tree. The next node separates the tree into two major clades. The smaller complex enveloped by *Manta birostris* and

Mustelus asterias, is composed of carcharhiniforms and a closely related group of highly derived batoids. Specifically, an unresolved clade composed of the genera *Galeorhinus* and *Mustelus* both members of the Triakidae exist as the sister group to a clade containing one lineage housing the genera *Carcharhinus* and *Sphyrna*, and another clade with the tiger shark, *Galeocerdo cuvier* which in turn is the sister taxon to a group of highly derived epipelagic tropical rays, the rhinopterids and mobulids.

Although at first this appears a very unlikely phylogeny for the hosts in question, a partial dismantling of the tree suggests otherwise. First, if one can apply a naive hypothesis to this chronicled pattern (see O'Hara, 1992 for an interesting discussion on the use and misuse of evolutionary chronicle and narrative), two distinct (and believable) patterns emerge. If a horizontal transmission or colonization event occurred with the emergence of the rhinopterids in the lower Eocene (Eocene=35-55 MY) (Maisey, 1984) from some carcharhinid parasitizing eudactylinid, as the cladogram suggests, then we are left with two separate or independent phylogenetic hypotheses (a carcharhinid clade and a batoid clade) to inspect. The carcharhinid clade now shows the triakid clade composed of *Galeorhinus* and *Mustelus spp.*, as the sister group to the clade which now posits *Galeocerdo cuvier* as the sister taxon to the clade housing an unresolved polytomy of *Carcharhinus plumbeus*, *C. acronotus*, and *C. obscurus* which in turn is the sister group to the *Sphyrna* (hammerheads) clade with these nested relationships (*Sphyrna tiburo* (*Sphyrna lewini*, *Sphyrna mokarran*)). These relationships between the Triakidae, *Galeocerdo*, Sphyrnidae, and Carcharhinidae are congruent with those hypotheses presented by Maisey (1984b) and most recently by Compagno (1988). The relationships of the three sphyrnids revealed by their parasitic copepods shows the same pattern as the cladogram of Sphyrnidae offered by Compagno (1988) in his monumental treatise on the Carcharhiniformes. The colonized batoid clade posits that the two species of *Rhinoptera* (cownose rays) is the sister group to the clade composed of *Manta* which itself is the sister group to the (*Mobula tarapacana* (*Mobula japanica*, *Mobula thurstoni*)) clade. Again, these relationships are congruent with the phylogenetic relationships of this closely related subset of rays set forward by Nishida (1990), except the parasites show more resolution between the three species of *Mobula* and the single species of *Manta*. Nishida (1990) is left with an unresolved polytomy between the taxa used in his analysis: *Manta birostris*, *Mobula japanica*, *Mobula lucasana* (= *Mobula thurstoni*), and *Mobula diabolus* (= *M. kuhlii*), which is often a misidentified *M. thurstoni* (cf. Notarbartolo-di-Sciara, 1987).

The remaining clade contains taxa spanning from *Squalus acanthias* to *Urolophus halleri*. Fascinatingly, this portion of the parasite-generated host phylogeny proposes the monophyly of the squaloids, squatinids, pristiophorids and batoids. This

corroborates the revolutionary findings of Shirai (1992a, b) in which he proposed a radically new systematic framework for squaloids and related taxa, the Squalea and Hypnosqualea.

The basal clade of this portion of the parasite generated host phylogeny is represented by the spiny dogfish, *Squalus acanthias* (Squalidae), the next branch contains the lantern sharks (Etmopteridae). The next node up the tree mirrors the relationships of the supraspecific taxa comprising Shirai's Hypnosqualea, which contains three species of angel sharks, *Squatina*, a single species of sawshark, *Pristiophorus*, and 22 species of batoids or Rajiformes, hierarchically arranged as follows: (*Squatina* (*Pristiophorus*, Rajiformes)).

The batoid clade is characterized by a major dichotomy. The first clade is composed primarily of members from the Rajoidei plus two species of electric rays, *Torpedo*. This rajoid clade contains one completely unresolved polytomy of eight species of *Raja* and two species of *Torpedo*. Since, these ten species of rays all possess the same parasite *Eudactylina similis*, any additional *Eudactylina*-derived host resolution is impossible. This complex is the sister group to a small group composed of two species of *Rhinobatos* which is the sister group to two species of *Raja*. It is surprising to see some species of *Raja* more related to *Rhinobatos* than to the other species of *Raja*. This incongruence may be due to the author's inability to find and/or discriminate more characters or character states in order to resolve these inconsistencies. It is also possible, as has been realized by others that some minor incongruencies (such as the aforementioned paraphyletic parasite derived host relationships of *Raja* versus the monophyletic relationships which supposedly distinguish a taxon) in host and associate cladograms might be more apparent than real. Recent advances (software not available to the author at this point in time) comparing "host and associate" trees (i.e. gene trees and species trees, host trees and parasite trees and, organism trees and areas) generate a single hypothesis called a reconciled tree. This hypothesis which maximizes the amount of codivergence (shared history) between the associated, represents the combined host and associate tree and makes explicit the cost of a strict cospeciation hypothesis (Page, 1994). Future studies involving these rival methods with these data should provide added insight regarding the historical association of this host - parasite system.

The remaining and most apical clade of the cladogram is strictly composed of myliobatoids. The first subclade contains 4 species of *Myliobatis*. The other subclade contains 3 myliobatoid genera that are hierarchically arranged as follows: (*Urolophus* (*Dasyatis* (*Gymnura*))).

The phylogenetic analysis conducted from the recoded subset of nine species of

Eudactylina by host matrix (Table II) resulted in a single most-parsimonious tree (Figure 67). The Branch and Bound generated tree had a tree length of 17 and a consistency index with a maximum value of 1.00. This cladogram supports the relationships of the supraspecific host taxa revealed in the initial analysis containing all 28 recoded species revised herein. Additionally, with the serendipitous removal of the supposed colonization (horizontal transfer) event of the rhinopterid - mobulid clade, the putative relationships of the four carcharhiniform taxa used in this analysis break down into two distinct clades. One clade contains *Galeorhinus galeus* and various species of *Mustelus* as sister groups, both members of the Triakidae. The other clade contains *Galeocerdo cuvier* and *Sphyrna mokarran*, two of the largest carcharhinoids. The remainder of the tree once again shows the very interesting monophyly (the Squalea of Shirai, 1992a, b) of the squaloids, squatinids, pristiophorids and, batoids. Again, *Squalus acanthias* branches off first becoming the sister taxon to the remainder of the squalean clade. The next clade composed of shark-like squalids contains *Etmopterus pusillus* and *Aculeola nigra* both members of the bioluminescent Etmopteridae. The relationships of the remaining three taxa confirm the relationships uncovered by the heuristic search using the TBR algorithm. This clade is composed of *Squatina squatina*, the sister taxon to the final clade containing *Pristiophorus* and *Myliobatis*, further corroborating the validity of Shirai's (1992a, b) Hyposqualea.

HISTORICAL BIOGEOGRAPHY

Historical biogeography is completely reliant on phylogenetically accurate systematics. Describing the distributional relationships of a taxon is useless, unless its members constitute a monophyletic group (Futuyma, 1986). Cladistics can provide original hypotheses on the history of the continents by means of vicariance biogeography. This rests on the postulate that allopatric speciation is due to the origin of natural barriers (e.g. the breakup of Pangaea), so that the phylogeny of the monophyletic groups under study is a reflection of the geological history of the areas they occupy. Vicariance biogeography offers the advantage of hypotheses about the history of areas that can be independently tested with geological data, without noise from intervening, narrative, *ad hoc* hypotheses. Thus, it can suggest to geologists inconsistencies between the reported biogeographical patterns and plate tectonic models (Janvier, 1984).

Fortunately, two monophyletic groups of hosts the angelsharks, *Squatina* and the bat rays, *Myliobatis* appear to be parasitized by monophyletic subsets of *Eudactylina* (Figure 66).

The 3 species of *Squatina*, are held together as a monophyletic unit by the parasites *Eudactylina tuberifera*, *Eudactylina aphioxenous*, and *Eudactylina acuta*. What does the parasite-derived host and area summary-cladogram (Figure 68) tell us about the possible evolutionary history of this subset of angelsharks, and land masses? First, the summary-cladogram posits that *Squatina armata* (refer to discussion section of *Eudactylina aphioxenous* for competing ideas regarding the synonymy of *S. armata* and *S. californica*) is the sister taxon to the clade housing *S. californica* and *S. squatina*. Nothing in the literature is available for comparison regarding those specific relationships. However, the cladogram suggests two possible vicariant events, represented by the nodes in the cladogram, were responsible for the differentiation of ancestral stock into these three descendants. Fossils recognizable as *Squatina* have been found in Jurassic period deposits (Maisey, 1984), pushing their divergence time as far back as 140-180 MY during the Mesozoic era. Assuming an intimate association was already established between *Eudactylina* and *Squatina* is interesting and I believe quite likely. Phylogenetically congruent host - parasite patterns found between holocephalans and elasmobranchs with the Kroyeriidae (Deets, 1987) may reflect a very ancient copepod-chondrichthyan association and co-divergence event. This possibly occurred in the late to post Devonian with the emergence of the Chondrichthyes approximately 400 MY. In any case, the first node separates the eastern South Pacific (*S. armata*) from the eastern North Pacific (*S. californica*) plus eastern North Atlantic and Mediterranean (*S. squatina*). This apparent Gondwanaland - Laurasia distribution is likely the result of the Tethys Seaway separating North and South America in the late Jurassic approximately 160 MY (Haq, 1984). Another concurrent mid-Jurassic event, the opening of the North Atlantic began approximately 160-165 MY (Windley, 1984). Perhaps it is this latter event that is represented by the node uniting the eastern North Pacific and eastern North Atlantic plus the Mediterranean. Thus, a possible explanation for the speciation patterns of this subset of *Squatina* interpreted from the summary cladogram would posit an initial separation of eastern Pacific ancestral stock into southern and northern components with the opening of Central America. The Tethys Seaway must have allowed some of the northern population to migrate far enough East to eventually find themselves rifted away with western Europe during the evolution of the North Atlantic. Future collections of *Eudactylina* from the remaining nine or ten species of *Squatina* found worldwide, would be a fascinating study and test of the aforementioned scenario.

The 4 species of *Myliobatis*, are held together as a monophyletic unit by the par-

asites *Eudactylina hornbosteli*, *Eudactylina indivisa*, *Eudactylina myliobatidos*, and *Eudactylina nykterimyzon*. What does the parasite-derived host and area summary-cladogram (Figure 69) tell us about the possible evolutionary history of this subset of bat rays, and their associated coastal land masses? The summary-cladogram posits that *Myliobatis* sp. is the sister taxon to the clade housing *M. californicus* which is in turn the sister taxon to *M. chilensis* and *M. peruvianus*. The literature is devoid of data regarding those specific myliobatid relationships. However, the cladogram posits three possible speciation events represented by the nodes in the cladogram, responsible for the differentiation of ancestral stock into these four descendants. The earliest fossils recognizable as *Myliobatis* are from Tertiary deposits (Maisey, 1984b), postulating their latest time of emergence occurred during the Eocene epoch 35-55 MY. This very recent emergence would place all the continents nearly in their present position (see Windley, 1984; Figure 11.3 a-h), and would make a vicariant interpretation of the relationships of the myliobatid hosts and their respective associated land masses impossible. Is there any way to infer a much earlier emergence time, independent of the relationships revealed by the parasite-derived summary-cladogram? I believe so. If Nishida's (1990) Dasyatidoidea (Urolophidae plus Dasyatididae) is the sister taxon to his Myliobatidoidea (Gymnuridae plus Myliobatididae), then these groups share a common node or a common point of divergence in space and time. Although, paleontological data is lacking for the Gymnuridae (butterfly rays), there is a record of a few late Cretaceous teeth which have been referred to dasyatids (Case, 1978). Additionally, there appears to have been a rapid diversification of stingrays towards the end of the Cretaceous; the group may primitively be represented by the extinct *Cyclobatis* (upper Cretaceous, Lebanon; Capetta, 1980) which approaches recent dasyatid myliobatoids but still maintains uncertain systematic status (Maisey, 1984b). Hence, it seems likely the Dasyatidoidea and Myliobatidoidea diverged in the Cretaceous, and *Myliobatis* is possibly much more ancient than what the current paleontological data base has uncovered. Working with these assumptions, telling the tree with an accommodating tectonic history is now possible. The first branch leads to an unidentified sp of *Myliobatis* living in the Indian Ocean (Mozambique Channel) off Madagascar. This node may represent the incipience of the South Atlantic with the separation of South America and Africa during the mid-Jurassic approximately 160 MY. Some reconstructions suggest Madagascar might have been located more southerly than its current position, thereby being in relatively close proximity to the tip of South America. Additionally, the southern tip of South America may have been slightly tucked around the southern tip of southern Africa (see Windley, 1984). Perhaps continued separation of these two continents and concurrent expansion of the South Atlantic carried away and separated those parts of a

formerly contiguous population of *Myliobatis* in that southern region. The next major event represented by the following node on the cladogram appears to once again represent the separation of the northern and southern hemispheres (eastern North Pacific and eastern South Pacific) due to the opening of Central America by the Tethyan Seaway approximately 160 MY. The final node separates two eastern South Pacific countries, Chile and Peru from one another, sharing *Myliobatis chilensis* but with *Myliobatis peruvianus* exclusive to Chile. This final node is difficult to assess without any obvious potential past vicariant events or any strong geological landmarks to refer to. Note that *E. indivisa* and *E. myliobatidos* may be synonymous. Although small differences were found between the two parasite species it is possible a larger sample may find synonymy a better choice in the future. The author prudently leaves them with their own taxonomic integrity in this revision, but wonders how unique their two myliobatid hosts actually are.

KROYERIA

EXTERNAL MORPHOLOGY

GENERAL HABITUS

The body of *Kroyeria* is typically elongate and cylindrical with six distinct tagmata (Figure 70 and 71A): the cephalothorax (consisting of the segments bearing the first antenna, second antenna, mandible, first maxilla, second maxilla, maxilliped, and the first pedigerous somite bearing leg one), the well developed pedigerous somites two, three, and four (bearing biramous, trimerite legs), a greatly elongated tube-like genital complex housing the gonads, and bearing the reduced fifth leg, and a multi-segmented abdomen (posteriorly giving rise to the caudal rami).

The cephalothorax comprises the somites bearing the principal appendages of attachment for *Kroyeria*. The main appendages of attachment are the remarkable chelate second antenna, the slender subchelate maxilliped, and the dagger-like dorsal stylets arising dorsolaterally along the posterior margin of the cephalothorax, from within the posterior sinuses. Additionally, large paired interpodal stylets arising from swimming legs two, three, and four (stylets usually reduced on leg one) (Figures 72A-72D) undoubtedly function as brakes with regards to the upstream orientation of this parasite on carcharhiniform gills (see Benz and Dupre, 1987).

The major articulation of the body exists between the third free thoracic somite and the genital complex.

The genital complex of the female bears the reduced fifth leg (leg six is never found), and the genital complex of the male bears reduced legs five and six. The abdomen of the male is composed of three segments, while the abdomen of the female exists in various states of indistinctness ranging from one to three segments. Again, this seems to indicate that the "missing" abdominal segments are not being incorporated into the genital complex but are being suppressed or becoming less distinct due to vague segmental boundary areas (sutures less sclerotized?).

Many of the previous functional and anatomical comments mentioned in the section regarding the appendages of *Eudactylina* apply to *Kroyeria* and need not be repeated in the following discourse.

CAUDAL RAMUS

The caudal rami (Figure 71C) originate terminally from the posteriormost abdominal somite. They are rather generalized in their appearance. The six setae arising from the distal region are similarly rather generalized in their structure, though all homologous elements have the ability to exhibit the slender pinnate state to a naked stout state with intermediate character states exhibited by different species. The flat lamelliform shape of the ramus might allow it to function as a rudder as suggested by Kabata and Hewitt (1971), for the Caligidae. Additionally, the more derived claw-like setae when present on certain species of the upstream oriented *Kroyeria*, may function to brake the parasite from slipping back and off the gill filament.

DORSAL AND INTERPODAL STYLETS

The dorsal stylet (Figures 70, 71A and 71B) is a novel structure in parasitic copepods. Other parasitic copepods possess posteriorly-directed cephalothoracic expansions such as in female *Eudactylina brevicauda* Hameed et al, 1990, and male *Eudactylina alata* Pillai, 1968. In the monotypic *Jusheyus* Deets and Benz, 1987 dorsal spines arise from a thick, dorsal sclerotized bar along the posterior margin of the cephalothorax. However, *Kroyeria* is the only genus in which these styliform processes (arising from within the posterior sinuses of the cephalothorax) are articulated. The articulation of this structure appears to be due to a complex ball and socket joint. Observations on living specimens reveal that the stylets have the ability to rotate freely in all directions. Undoubtedly, these structures are wedged into the secondary lamellae of the host's gills securing the parasite in its upstream orientation (Figure 70). It has been found that for *Kroyeria carchariae* Hesse, 1879, on the blue shark, *Prionace glauca* (Linnaeus, 1758), 80 percent of individuals were attached to the secondary lamellae and the remaining 20 percent were found in the excurrent water channels clinging to the interbranchial septa (Benz and Dupre, 1987).

Dorsal stylets differ between the species. They may occur as sweeping, elongate, lissome stylets as in *Kroyeria sphyrnae* Rangnekar, 1957, as stout, blunt processes as in *Kroyeria dispar* Wilson, 1932, as slightly curved spines with a flanged terminus as in *Kroyeria branchioetes* sp. nov., or possessing a deeply incised bifid tip as seen in *Kroyeria longicauda* Cressey, 1970. Hence, they are helpful characters for identification.

With the exception of Lewis' (1966b) discussion on the possibility of the interpo-

dal stylets giving rise to the sternal furca of Dissonidae, Trebiidae and Caligidae, the origins and homologies of dorsal and interpodal stylets have never been critically discussed. During this revision, an interesting event recurred with each dissection of the available species in this genus, which may shed some insight on the homology of these unique structures. Whenever the maxillipeds were carefully dissected from the cephalothorax, the dorsal stylets became disjoined from the cephalothorax and were removed in conjunction with the maxillipeds. This structural complex of maxillipeds, sclerites, and dorsal stylets is illustrated in Figure 83A. The maxillipeds are united by a heavily sclerotized interpodal bar. Dorsally, the base of the maxillipeds appear to articulate with a complex sclerotized ring dorsolaterally giving rise to the articulated dorsal stylets.

Maxillipeds are appendages of the first or anteriormost thoracic somite that have been incorporated into the cephalosome thus becoming a cephalothorax during the process of cephalization (see Huys and Boxshall 1991, Kabata, 1979, and Schram 1986). Crustaceans are metameric organisms (see Barnes, 1984), therefore different structures having the same segmental origin are said to be serially homologous. Thus, the maxilliped is serially homologous not only to the remaining thoracic appendages but also to the cephalic appendages, for all evolved from originally similar segmental appendages. Interestingly, all non-reduced thoracic appendages (maxillipeds and legs) possess paired sclerotized styliform processes.

Not unlike the external cuticular structures such as setae, appendages, processes, and the like, other cuticular structures such as sclerites or sclerotized bars or rods have serial homologues. Hence, we should be able to use this type of information in tracing morphological homologies.

The thoracic legs are connected by an interpodal bar which gives rise to the paired interpodal stylets (Figures 82B, 83A, and 83B). Although the interpodal stylets are not articulated, there are some soft, joint-like areas at the junction of the leg and the interpodal bar. The interpodal bar anteriorly butts up against a large sclerite ring not associated with an appendage. Anterior to this is a small gap before the pattern repeats itself with legs united by an interpodal bar giving rise to paired interpodal stylets. This bar anteriorly butting up against a large non-appendage associated sclerite ring and so forth. Upon inspecting the complex of sclerites associated with the maxilliped (Figure 83B), one can see the interpodal bar of the first leg with its typically reduced interpodal stylets anteriorly butting up against a non-appendage associated ring (as with the legs mentioned above), albeit not complete. This is followed anteriorly by a large gap, and then another interpodal bar uniting the maxillipeds. This serially repeating pattern of sclerites and appendages suggests that the interpodal stylets and the dorsal stylets

found in *Kroyeria* are one and the same. This is an economical explanation for the origination of these novel structures. One must only hypothesize a single evolutionary event giving rise to paired, styliform, interpodal thoracic processes for their presence to be explained on all thoracic appendages on non-reduced thoracomeres (thoracic legs five and six are often absent). Perhaps a homeotic mutation, known in arthropods, which causes all or part of a segment to develop in a manner inappropriate to itself but in approximate conformity to the normal development of some other segment (see Arthur, 1984), could explain the manifestation of an interpodal stylet associated with a maxilliped (the dorsal stylet).

FIRST ANTENNA

The first antenna of *Kroyeria* (Figure 71D) is indistinctly seven- or eight-segmented. Assuming similar (homologous) innervation exists here as seen in other siphonostomes (see Kabata, 1979), this appendage has chemosensory and tactile functions. The apical segment bears 13 setae (12 terminal, 1 sub-terminal) and one aesthete. Due to differential fusion of segments amongst species within the genus, the details regarding specific armature on each segment will be covered in taxonomic descriptions.

SECOND ANTENNA

The principle attachment organ for *Kroyeria* is the extraordinary four-segmented, chelate second antenna (Figure 71E). The heavily sclerotized, indistinctly divided first and second segments form a base allowing great freedom of movement (Kabata, 1979, Deets, unpublished observations of living specimens). The third segment forms the corpus of the chela, its distal end greatly produced and terminally expanded forms a receptacle to receive tip of the terminal segment or claw. The receptacle can be quite expansive when possessing membranous extensions of the cuticle as in *Kroyeria longicauda* Cressey, 1970 (Figure 93E), or simply a small indentation barely large enough to accommodate the tip of the opposable claw as in *Kroyeria dispar* Wilson, 1935 (Figure 85F). Likewise, the tip of the claw as in *Kroyeria longicauda* Cressey, 1970 (Figure 93E) may possess membranous cuticular expansions giving it a cup-like appearance similar to the receptacle which typically houses it, alternatively, the tip may exist smooth and unornamented as in *Kroyeria dispar* Wilson, 1935 (Figure 85F). Additionally, the proximal area of the claw is typically armed with a pair of spines as in *Kroyeria cresseyi* Deets, sp.nov. (Figure 79F), or a set of three spines as in *Kroyeria longicauda* Cressey, 1970 (Figure 93E). Different combinations and states of these characters make the

second antenna a valuable taxonomic and phylogenetic discriminant.

MANDIBLE AND ORAL CONE

The mandible, with a dentiferous distal end (Figure 74G), uniramous, subcylindrical, is typically siphonostome. It appears to be of two parts. Their boundaries demarcated by a proximal suture. The dentiferous margin bears from seven to ten teeth, with some species exhibiting teeth uniform in size (Figure 74G) and other species with different-sized teeth (Figure 93F), reminiscent of the primary and secondary teeth in the Lernaepodidae/Sphyriidae/Tanypleuridae complex.

The oral cone (Figures 81H and 89I) consisting of anterior labrum and posterior labium house the mandibles. The labrum typically bears distolateral patches of prickles and terminal membranes, the labium is equipped with two rows of prickles along the lateral surface and a terminal membrane. This structure being quite uniform throughout the genus was not utilized for taxonomic purposes.

FIRST MAXILLA

The first maxilla (Figure 71G) located adjacent to the oral cone and mandible is a biramous appendage composed of a relatively elongate endopod and smaller exopod. Both the exopod and endopod are tipped with two setae. Setae may occur as naked or pinnate depending on the species.

SECOND MAXILLA

The second maxilla of *Kroyeria* is a large brachiform appendage (Figure 71H), consisting proximally of a heavily sclerotized lacertus and distally of a robust brachium. The orifice of the maxillary gland is present near the base of the lacertus as is the previously undescribed (probably unnoticed) basal process. The basal process in some species may approach half the length of the second maxilla. The brachium is typically armed with two contiguous patches of densely packed prickles. Distal to these patches at the base of the claw is a tuft of long fine setae. The most terminal component is the claw which may or may not represent a third segment. It is a robust, curving structure, typically armed along the lateral surfaces with lamelliform membranes and a prickly membrane along the convex surface. No specific function for the second maxilla of *Kroyeria* has yet been observed.

MAXILLIPED

The maxilliped (Figure 71I) is a subchelate structure. The corpus appears to be two-segmented. The subchela is not divided into a proximal shaft and distal claw as in many siphonostomes. A minute slender seta is present near the distal end of the subchela. A membranous flange is present along the distal margin of the corpus in some species. Additionally, a series of three transverse cuticular flanges occur on the corpus of *Kroyeria dispar* Wilson, 1935 (Figure 86A) and *Kroyeria longicauda* Cressey, 1970 (Figure 93I).

LEG ONE

The first thoracic leg (Figure 72A) pair is connected by an interpodal bar. As previously mentioned, interpodal stylets arise from the interpodal bar. Interpodal stylets of the first thoracic leg are always reduced in relation to those of thoracic legs two, three, and four. The sympod is composed of the proximal coxa and distal basis. The coxa usually bears two strips of membrane, although in a few species only one or none were observed. The basis similarly bears two strips of membrane, one lateral seta, and one distomedial seta. The first leg is always biramous, composed of a lateral exopod and medial endopod. Both the exopod and endopod are trimerite throughout the genus.

The first (proximal) segment of the exopod bears a row of setules along the medial margin, a distomedial pinnate seta, a distolateral seta, and a smooth and / or pectinate membrane along the lateral edge. The second segment possesses the same characteristics except the distolateral seta is absent in some species. The third segment shares similar characteristics to the first two segments and bears one small lateralmost seta, one elongate slender seta occurring in various states (see detailed species descriptions), and four long pinnate setae.

The first endopodal segment bears a single distomedial pinnate seta, a distolateral membrane, and a row of setules along the lateral margin.

The second endopodal segment in most species has a row of setules along the lateral edge and in some species a series of triangular denticulations connected by a webbing of membrane. Under both light microscopy and scanning electron microscopy (unpublished data and Oldewage unpublished data), these denticulations or teeth found on some endopodal segments appear to be thickened, fused, or fortified regions of the membrane that typically run along that lateral margin. Under close examination, the membranous webbing running along these teeth appear to fuse with the teeth or endopodal denticulations. Hence, both the membrane and the teeth or endopodal den-

ticulations appear to be one in the same. Additionally, in cases where these endopodal denticulations or teeth are absent, the typical membrane is present. Typically this segment is devoid of pinnate distomedial setae but in *Kroyeria dispar* Wilson, 1935 from the tiger shark, *Galeocerdo cuvier* (Peron and LeSeuer, 1822), two pinnate setae are present.

The third or terminal endopodal segment from the first leg similarly exhibits membranous denticulations or a smooth membrane and the fringing row of setules was not always observed. Six long, pinnate setae are found on this segment throughout the genus. Very minute pectinate membranes reminiscent of those present in the Caligidae (see Kabata, 1979), are present at the setal bases (of some leg pairs) of some species (possibly most) but are clearly seen only with scanning electron microscopy.

LEG TWO

The second thoracic legs (Figure 72B) are united by an interpodal bar which gives rise in the majority of species to well developed interpodal stylets. The exceptions are *Kroyeria caseyi* Benz and Deets, 1987 on the night shark, *Carcharhinus signatus* (Poey, 1868), *Kroyeria dispar* Wilson, 1935, and *Kroyeria papillipes* Wilson, 1932 both parasitic on the tiger shark, *Galeocerdo cuvier* (Peron and LeSeuer, 1822). The coxa and basis are well delimited with the basis distally bearing two well developed membranes, and a single lateral seta.

The first segment of the second exopod typically bears a medial row of setules, pinnate seta, a distolateral slender seta, and a lateral smooth or pectinate membrane. The second segment is similar to the first with the lateral slender seta absent in some species. The third segment similarly bears a smooth or pectinate membrane along the lateral margin and seven pinnate and variously modified slender setae.

The first segment of the endopod bears a distomedial pinnate seta, a lateral membrane, and a lateral fringe of setules. The second segment generally bears a lateral fringe of setules, membranous denticulations in some species, and the atypical presence of pinnate setae on the distomedial edge in *Kroyeria dispar* Wilson, 1935. The terminal segment harbors six pinnate setae.

LEG THREE

The third thoracic legs (Figure 72C) are connected by an interpodal bar possessing large interpodal stylets with the exception of *K. caseyi*, *K. dispar*, and *K. papillipes*. The coxa is unarmed, but a lateral seta and two distal membranes are found on the

basis.

The proximal segment of the exopod typically bears a medial fringe of setules, a distomedial pinnate seta, a lateral slender seta, and a smooth and / or pectinate membrane. The second segment is similar to the first, with the lateral slender seta absent in certain species. The terminal segment similar to the previous two segments bears four elongate pinnate setae and three variously modified slender setae.

The first segment of the endopod is equipped with a lateral fringe of setules, a distolateral membrane, and a single distomedial pinnate seta. The second segment may possess membranous denticulations, a medial pinnate seta, or a medial fringe of setules depending on the species. The third, or terminal, segment shares similar attributes with the preceding segments and generally bears four pinnate setae. However, in *K. caseyi* and *K. dispar*, there are three pinnate setae, one slender seta, and another pinnate seta for a total of five setae.

LEG FOUR

The fourth thoracic legs (Figure 72D) as in the previous three are connected by an interpodal bar which gives rise to interpodal stylets which are well-developed except in *K. caseyi*, *K. dispar*, and *K. papillipes*. The sympod is composed of an unarmed coxa and a basis with a single lateral seta and two membranes along the distal edge.

The first exopodal segment bears a medial fringe of setules, a single distomedial pinnate seta, a single distolateral slender seta, and a smooth and / or pectinate membrane flanking the lateral margin. The second segment is similar to the first with exception of the absence of both the fringing setules on the medial edge and the distolateral slender seta in some species. The terminal segment differs from these two segments by possessing four pinnate setae plus three variously modified setae.

The first segment of the endopod bears a lateral membrane, a lateral fringe of setules, and a single distomedial pinnate seta. The second segment bears a single distomedial pinnate seta and may or may not possess lateral membranous denticulations and fringing setules. The terminal segment generally bears two pinnate setae plus one variously modified seta. *K. dispar* is an exception bearing two pinnate setae, one slender seta, and one more pinnate seta, as is *K. papillipes* bearing three pinnate setae.

LEGS FIVE AND SIX

The fifth leg (Figure 81J) is located approximately 1/2 to 2/3 the length of the genital complex down the lateral side of the genital complex and is rarely found.

However, in species where it is known it is a uniramous appendage consisting of four setae. A sixth leg does not appear to exist.

In the males, the fifth and sixth legs (Figure 73A) are found on the genital complex. The fifth and sixth leg both setiform are represented by four and two setae respectively.

LIFE HISTORY

GENERAL DESCRIPTION

There have been few published attempts of culturing *Kroyeria*, or descriptive accounts of life history stages other than the adult and first nauplius.

The first report of the nauplius accompanied the first description of this genus by van Beneden (1853) for *Kroyeria lineata*, the type species. Carli and Bruzzone (1973) were able to hatch first-stage of the nauplius 60 minutes after the egg was shed from the egg strand of *Kroyeria carchariaeglauci* Hesse, 1878. The most recent description of the first nauplius was offered by Benz and Deets (1986), and illustrated the three naupliar appendages, the uniramous first antenna, the biramous second antenna, and the biramous mandible. Also shown were the two dorsal ocelli of the tripartite naupliar eye (the ventral ocellus was not shown), and the two well developed filiform balancers on the posterior end.

It would not be surprising if *Kroyeria* exhibited a holoxenous life-cycle similar to that demonstrated by Cabral, et al (1984) in *Lernanthropus kroyeri*, from the percichthyid (temperate bass) *Dicentrarchus labrax* (see Raibaut, 1985 for a general life history review of different parasitic copepod taxa).

REPRODUCTION

Copulation and reproduction probably occurs in a manner similar to that in *Eudactylina*, but no reports or observations have been published. I have not seen members of this genus in the presumed copulatory embrace.

HOST-PARASITE RELATIONSHIPS

DELETERIOUS EFFECTS / FEEDING

As previously stated, *Kroyeria* attach themselves to the secondary lamellae of the gill primarily with their clasping chelate second antenna, and secondarily with their articulate posterolaterally oriented dorsal stylets and the ventroposteriorly directed interpodal stylets (Figure 70). Benz and Dupre (1987), have shown that 80 percent of all *K. carchariaeaglauri* Hesse, 1879, attach themselves in an upstream-oriented fashion to the secondary lamellae on the gills of its favored host, the blue shark, *Prionace glauca* (Linnaeus, 1758). The remaining 20 percent were found clipped on to the soft tissue in the underlying excurrent water channels. The dorsal stylets and interpodal stylets with their supposed braking function probably allow *Kroyeria* increased mobility in its environment by not having to rely entirely on the second antennae for its security. It is speculated that the second antennae may be used to reach out and align itself upstream and possibly crawl with them, assuming the stylets have the ability to hold the parasite in place, as suggested by Figure 70.

I have not witnessed gill tissue pathologies induced by *Kroyeria* in the carcharhiniform hosts I have inspected over the years. During microscopic examination, many specimens of *Kroyeria* still had tissue from the secondary lamellae grasped in their chelate second antennae. Hence, some damage is occurring to the respiratory surfaces of the host. *In situ*, the copepods are reddish, suggesting these parasites feed at least in part on blood. Blood would be easily accessible from the secondary lamellae since respiratory blood sinuses are only one epithelial cell thick in this region (Benz, 1984). With up to 1,250 individuals per host as reported for *K. carchariaeaglauri* on *Prionace glauca* (Benz and Dupre, 1987) some physiological effects on the host shark would be expected.

The specific feeding mechanics have yet to be observed for any gill dwelling copepod, but morphological evidence (from scanning electron microscopy, Oldewage, unpublished) suggests that it is similar to that of caligids as described by Kabata (1974, 1979).

A dentiferous ridge, the strigil, appears to be present along the inner edge of the labium (Oldewage, unpublished SEM micrographs,). The strigil possibly saws away at the epithelial cells, while the mandibles equipped with their dentiferous margins, may continue the maceration process and then convey the host tissue into the buccal cavity. Patches of prickles along the distolateral region of the labrum and the two rows of spin-

ules flanking the lateral surfaces of the labium may anchor the oral cone to the feeding site.

SPECIFICITY

Although the literature suggests a few species such as *K. lineata* and *K. carchariaeglauci* have the ability to infect a broad range of hosts, my personal collections over the last 13 years, suggest that host specificity is the general rule for the species in this genus. One problem that undoubtedly beleaguers this host-parasite system is the morphological conservatism that both *Kroyeria* and its hosts, the Carcharhiniformes exhibit. Hence, host and/or parasite may have been misidentified and the apparent broad host range of these species may be artifactual.

With the exception of the mesoparasitic *Kroyeria caseyi* Benz and Deets, 1986, which embeds approximately 80% of its body into the interbranchial septa of its host *Carcharhinus signatus* (Poey, 1868), *Kroyeria* typically attach by the chelate second antenna to the gills (secondary lamellae).

Microniche specificity and the functional morphological requirements associated with it has only recently been examined in parasitic copepods of elasmobranchs (see Benz 1980, 1992; Benz and Adamson, 1990; Benz and Dupre, 1987). Reports of microniche have typically not been given in sufficient detail (e.g., skin, gill, or branchial lamellae) to assess the ecological or morphological significance of the association.

When collecting eudactylinids or kroyeriids from branchial lamellae, I have noticed that genera that possess fully chelate attachment organs, such as the second antenna of *Kroyeria* or the maxilliped of *Eudactylina* or *Eudactylinodes*, secure themselves primarily to the secondary lamellae of their host. On the other hand, *Nemesis*, attaches itself by surrounding the efferent branchial arterioles near the gill filaments' free distal tips with its large subchelate maxillipeds (Benz and Adamson, 1990), a microniche quite unlike that occupied by its fully chelate allies.

SYSTEMATIC ACCOUNT

Genus *Kroyeria* van Beneden, 1853

Kroyeriidae: Female. Cephalothorax covered by well demarcated dorsal shield. Dorsal stylets arising from posterior sinuses of cephalothorax. Three pedigerous segments between cephalothorax and genital complex. Genital complex composed of pedi-

gerous somites five and six, together constituting more than 50% of length of body. Abdomen one- to three-segmented. Caudal ramus lamelliform bearing six setae distally.

First antenna indistinctly seven- or eight-segmented, terminal segment bearing one aesthete and thirteen slender setae. Second antenna four-segmented and chelate; third segment distally produced into a receptacle to accommodate claw of terminal segment. Mouth tube siphonostome. Mandible of two parts, distal end dentiferous bearing from seven to ten teeth. First maxilla biramous with both endopod and exopod bearing two apical setae. Second maxilla brachiform, two- possibly three-segmented (including claw). Maxilliped subchelate, subchela not divided into shaft and claw. Legs one through four biramous and trimerite. Leg five when found represented by four setae.

Male: Similar to female; abdomen three-segmented. Legs five and six setiform and represented by four and two setae respectively.

TYPE-SPECIES: *Kroyeria lineata* van Beneden, 1853

COMMENTS: Previous to this account, the literature contained references to 19 nominal species (see Kabata, 1979 for review). An additional description of an unnamed male by Capart (1953) is devoid of illustrations making correct identification difficult. The description suggests affinity with *K. papillipes*, and this possibility is further suggested by the fact that Capart's material came from the tiger shark, *Galeocerdo cuvier* (Peron and LeSueur, 1822), the principal host to *K. papillipes*. Three species (*K. acanthiasvulgaris* Hesse, 1879, *K. galeivulgaris* Hesse, 1884, and *K. scyllicaniculae* Hesse, 1879) have been insufficiently described to be recognized and are treated as *species inquirendae*. *K. trecai* Delamare Deboutteville and Nunes-Ruivo, 1953 was never fully described and remains a *nomen nudum*. *K. aculeata* (Gerstaecker, 1854) and *K. sublineata* Yamaguti and Yamasu, 1959 have been relegated to junior synonyms of *K. lineata* van Beneden, 1853. This revision resurrects *K. elongata* Pillai, 1967 from synonymy, and treats it as a valid species. Five species new to science, *K. branchiocetes*, *K. cresseyi*, *K. decepta*, *K. procerobscena*, and *K. rhophemophaga* are described herein.

Kroyeria consists of the 16 species illustrated and phylogenetically analyzed herein, plus two unobtainable species for this current effort bringing the total number of accepted species to 18. As in the previous section, the unobtained species will be reviewed at the end of the following taxonomic account.

The systematics of *Kroyeria* has suffered in the past from insufficient attention to morphological detail that can be used as specific discriminants (Kabata, 1979). Additionally, this genus is superficially morphologically conservative, and also difficult to

distinguish.

The major host taxon for *Kroyeria*, is the Carcharhiniformes (see Raibaut, 1982). The latest revision of this host group was by Compagno (1988). He estimates that this largest group of living sharks comprises nearly 60 percent or 200 species of the approximately 350 known shark species. This information coupled to the apparently high degree of host fidelity exhibited by *Kroyeria*, suggests (as is true of *Eudactylina*) there are many species yet to be discovered in the genus.

***Kroyeria branchiocetes* sp.nov**

(Figures 71-73)

Material examined. Several females (on loan from Dr. Z. Kabata, Pacific Biological Station, Nanaimo, Canada) collected by Dr. Paperna, University of Israel, from the gills of the grey reef shark, *Carcharhinus amblyrhynchos* (Bleeker, 1856) from the Red Sea. Female holotype (USNM 266533) and 3 female paratypes (USNM 266534) deposited at the United States National Museum of Natural History.

Etymology: The specific name *branchiocetes* is derived from the greek *Branchia*, meaning gill and *oecetes* an inhabitant, referring to the typical gill-dwelling nature of this rather attractive, albeit nondescript species.

Description

Female (Figure 71A)

Overall length in dorsal view approximately 3.8 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 71A and 71B) extending posteriorly to nearly 30 % down the length of the third free thoracic somite, stylets curving slightly inward and distolaterally bearing a flange-like cuticular expansion. Three free thoracic somites with overlapping terga. Genital complex cylindrical, constituting 60 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 71C) lamelliform, longer than wide with medial fringe of setules, distally bearing four pinnate and two semipinnate setae.

First antenna (Figure 71D) indistinctly eight-segmented, armature (base to apex) as follows: 10, 1, 5, 2, 3, 1, 1, 12 +1 aesthete. Second antenna (Figure 71E) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized

in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a membranous receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing two prominent setae proximally and similarly expanded into a membranous receptacle distally. Mandible (Figure 71F) of two parts (only distal portion illustrated), dentiferous margin with nine teeth, tiny apical tooth followed by one large, two small, two large, and three small. First maxilla (Figure 71G) biramous; endopod longer bearing two apical elongate, naked setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 71H) brachiform; lacertus heavily sclerotized with elongate basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; claw bearing lateral membranous lamellae with small prickles scattered upon convex surface. Maxilliped (Figure 71I) subchelate; corpus two-segmented; subchela not divided into shaft and claw, distally uncinata and bearing a single small, slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and one or two distomedial membranes; first basipod bears additional distomedial pinnate seta; first coxopod bears additional distolateral membrane. All four interpodal bars bearing interpodal stylets; interpodal stylets of leg one very small. Lateral fringe of setules on each endopodal segment, medial fringe of setules on each of first exopodal segment. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 72A) bearing distolateral membrane on first (proximal) segment; pectinate lateral membrane on segments two and three. Segment three with four pinnate setae, one elongate slender seta bearing a lateral membrane, and one small naked seta. Endopod of leg one (Figure 72A) with distolateral membrane on first segment; segment two with four to five (only four shown) endopodal denticulations; segment three with four to six (only four shown) endopodal denticulations. Exopod of leg two (Figure 72B) similar to leg one, except second segment bears additional seta (bilaterally bearing membranes), and third segment with four pinnate setae, one semi-pinnate seta with setules along the medial edge and a membrane along the lateral, one slender seta bearing a membrane along the lateral edge, and one seta bearing mem-

branes on both lateral and medial edges. Endopod of leg two similar to leg one, except five to six endopodal denticulations (five shown) are present on the second segment; five endopodal denticulations on the third segment. Exopod of leg three (Figure 72C) as in leg two, except seta adjacent to lateralmost seta bilaterally bears membranes (unilaterally in leg two). Endopod of leg three (Figure 71C) with six and five endopodal denticulations on segments two and three respectively; segment three with four pinnate setae. Exopod of leg four (Figure 72D) as in leg three. Endopod of leg four (Figure 72D) with seven and five endopodal denticulations on segments two and three respectively; segment three with two pinnate setae and one bilaterally bearing serrated membranes. Fifth leg (not shown) represented by four setae.

Male: (Figure 73A)

Overall length in lateral view approximately 2.8 mm. Cephalothoracic appendages and swimming legs similar to those of female. Genital complex bearing fifth and sixth legs represented by four and two setae respectively. Dorsal stylet (Figure 73B) shorter and more stout than that of female with a hyaline flange along the proximal medial margin. Caudal ramus (Figure 73C) more elongate than that of female, setules fringing medial margin; six distal setae (two semipinnate, four pinnate).

Comments: *Kroyeria branchiocetes* is the first kroyerid reported from the grey reef shark, *Carcharhinus amblyrhynchos* (Bleeker, 1856). This non-descript parasite resembles *K. cresseyi*, *K. lineata*, *K. rrophemophagus*, and *K. triakisae*, in possessing only two slender setae on the claw of the second antenna. It can be distinguished from these species by the presence of endopodal denticulations on segments two and three of all four swimming legs. Interestingly, all four of the aforementioned parasites lacking the complete set of endopodal denticulations and possessing only two (not the more common condition of three) slender setae on the claw of the second antennae are found on various hosts of the family Triakidae. *Kroyeria branchiocetes* is found on *Carcharhinus amblyrhynchos*, a member of Carcharhinidae as opposed to Triakidae.

***Kroyeria carchariaeglauci* Hesse, 1879**

(Figures 74-76)

Syn: *Kroyeria gracilis* Wilson, 1932, (see Delamare-Deboutteville and Nunes Ruivo)

Material examined. Several males and females collected by George Benz, Tennessee Aquarium, Chatanooga, Tennessee, U.S.A., from the gills of the blue shark, *Prionace glauca* (Linnaeus, 1758) from the western North Atlantic; numerous males and females collected from the same host species from the southern California bight near the Channel Islands and from the southern Sea of Cortez (Gulf of California) near Isla Cerralvo; a few specimens were collected from the silky shark, *Carcharhinus falciformis* (Bibron, 1839) near Punta Arena de la Ventana and Isla Cerralvo in the southern Sea of Cortez; a few specimens collected from the pelagic white tip shark, *Carcharhinus longimanus* (Poey, 1861) near the Revillagigedos Islands in the tropical eastern North Pacific, Mexico.

Description

Illustrated specimen from blue shark, *Prionace glauca* (Linnaeus, 1758).

Female (Figure 74A, B)

Overall length in dorsal view approximately 5.5 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 74A-C) extending posteriorly to approximately 60 % down the length of the second free thoracic somite, stylets curving slightly inward and distally bifurcating. Three free thoracic somites with overlapping terga. Genital complex cylindrical, constituting approximately 65 % of total body length. Posterolateral corners of latter bearing oviducal openings; egg strand bearing 44 eggs. Abdomen indistinctly three-segmented. Caudal ramus (Figure 74D) lamelliform, longer than wide with medial fringe of setules, distally bearing six pinnate setae (one short, one short and pyriform, and four elongate).

First antenna (Figure 74E) indistinctly seven- or eight-segmented, armature (base to apex) as follows: 11 (only nine shown), 5, 2, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 74F) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing three prominent slender setae proximally. Mandible (Figure 74G) of two parts, dentiferous margin with nine teeth. First maxilla (Figure 74H) biramous; endopod longer bearing two apical elongate, naked setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 74I) brachiform; lacertus heavily sclerotized with elongate basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; claw bearing paired lateral membranous lamellae with small prickles scattered upon convex surface. Maxilliped (Figure 75A) subchelate; corpus two-segmented,

proximal segment bearing two conical processes, and proximal end of adjacent segment bearing single small, conical process; subchela not divided into shaft and claw, distally uncinata and bearing a single small, slender seta.

All four legs biramous and trimerite. Symopods two-segmented. All basipods with lateral pinnate seta and one or two distomedial membranes; first basipod bears additional distomedial pinnate seta; first coxopod bear additional distolateral membranes. All four interpodal bars bearing interpodal stylets; interpodal stylets of leg one relatively small. Lateral fringe of setules on each endopodal segment, medial fringe of setules on each of first exopodal segment. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 75B) bearing distolateral membranes on segments one, two and three. Segment three with four pinnate setae, one elongate, slender seta bearing a finely serrated, lateral membrane, and one small naked seta. Endopod of leg one (Figure 75B) with distolateral membrane on first segment; segment two with six to eight (only six shown) endopodal denticulations; segment three with six to seven (only six shown) endopodal denticulations (specimens collected from the pelagic white tip, *Carcharhinus longimanus* (Poey, 1861), bear nine). Exopod of leg two (Figure 75C) similar to leg one, except second segment bears additional lateral, slender seta, and third segment with four pinnate setae, one semipinnate seta with setules along the medial edge and a membrane (smooth or finely serrated, too small for certainty) along the lateral edge, one slender seta bearing a membrane along the lateral edge, and one naked, slender seta. Endopod of leg two similar to leg one, except seven endopodal denticulations (eight in the specimens collected from the pelagic white tip) are present on the second segment and eight to ten (ten shown) endopodal denticulations on the third segment. Exopod of leg three (Figure 75D) as in leg two, except seta adjacent to lateralmost seta appears to be devoid of lateral membrane (unilaterally in leg two). Endopod of leg three (Figure 75D) with seven and ten endopodal denticulations on segments two and three respectively (eight are present on both segments from specimens collected from the pelagic white tip); segment three with four pinnate setae. Exopod of leg four (Figure 75E) as in leg three. Endopod of leg four (Figure 75E) with seven and nine endopodal denticulations on segments two and three respectively (specimens col-

lected from the pelagic white tip bear seven to eight on segment three); segment three with two pinnate setae and one bilaterally bearing serrated membranes; bases of setae bearing small pectinate membranes (reminiscent of those in Caligidae). Fifth leg (see Figures 74A and 74B) represented by four setae.

Male: (Figure 76A)

Overall length in lateral view approximately 4.4 mm. Cephalothoracic appendages and swimming legs similar to those of female. Genital complex bearing fifth and sixth legs represented by four and two setae respectively. Dorsal stylet shorter and more stout than that of female. Caudal ramus (Figure 76B) more elongate than that of female, setules fringing medial margin; six distal setae (two semipinnate, four pinnate).

Comments: *Kroyeria carchariaeoglauca* Hesse, 1879 was originally described from gills of the blue shark, *Carcharhinus glaucus* (= *Prionace glauca* (Linnaeus, 1758)) near Brest, France in the eastern North Atlantic. It was subsequently redescribed from from the same host in the Mediterranean (Delamare Deboutteville & Nunes Ruivo, 1953), from Japanese waters (Shiino, 1957), from off Valaparaíso, Chile (Stuardo and Fagetti, 1961), from the West coast of South Africa (Kensley and Grindley, 1973), from the western North Atlantic and Mediterranean (Carli and Bruzzone, 1972; 1973), from Tunisian waters (Essafi and Raibaut, 1977), from the western North Atlantic (Benz, 1986; Benz and Dupre, 1987), and herein from the eastern North Pacific from the southern Sea of Cortez, Mexico, Revillagigedos Islands, Mexico, and Channel Islands, southern California Bight.

K. carchariaeoglauca has also been reported from carcharhiniform hosts other than the blue shark. The first report of this occurred with the description of *K. gracilis* by Wilson (1932). He reported *K. gracilis* from the blue shark and brown shark, *Carcharhinus milberti* (Valenciennes, in Müller and Henle, 1839) (= the sandbar shark, *Carcharhinus plumbeus*, Nardo, 1827). Additionally, *K. gracilis* is considered a junior synonym of *K. carchariaeoglauca* by Delamare-Deboutteville and Nunes-Ruivo (1953) and Shiino (1957). Kabata and Gusev (1966) report *K. carchariaeoglauca* from *Eulamia* sp. from near Cocos Island, Indian Ocean but provided no illustrations. Finally, Essafi and Raibaut (1977) add questionable records of *K. carchariaeoglauca* inhabiting the starry smooth-hound, *Mustelus asterias* Cloquet, 1821, and the smooth-hound *Mustelus mustelus* (Linnaeus, 1758) from France. Equally suspect, is their report of *K. carchariaeoglauca* from gills of the longnose spurdog, *Squalus blainvillei* (Risso, 1826).

I have examined specimens from Dr. Roger Cressey's personal collection from

elasmobranchs from both the Indian Ocean and Florida coast, (see Cressey, 1967 and 1970) and conclude that the many unillustrated records of *K. gracilis* (= *K. carchariaeglauci*) on hosts other than blue shark, *Prionace glauca* (Linnaeus, 1758), pelagic white tip, *Carcharhinus longimanus*, (Poey, 1861), and silky shark, *Carcharhinus falciformis* (Bibron, 1839) should be viewed with caution (see following new species descriptions of *K. decepta* and *K. procerobscena*).

The combined characteristics of the bifid dorsal stylet, the relative length to width ratio of the males' caudal rami (see *K. decepta*), and the stout, pyriform, pinnate seta adjacent to the two elongate pinnate setae of the caudal rami, readily distinguish this species from its congeners.

***Kroyeria caseyi* Benz and Deets, 1986**

(Figures 77-78)

Material examined. Two females and one male collected from the interbranchial septa of the night shark, *Carcharhinus signatus* (Poey, 1868) from the western North Atlantic.

Description

Female (Figure 77A-C)

Overall length in dorsal view approximately 60 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 77A-D) very short and robust, extending posteriorly to approximately 50 % down the length of the first free thoracic somite, stylets curving inward slightly and terminating somewhat bluntly. Three free thoracic somites with overlapping terga. Genital complex cylindrical, inflating distally and constituting approximately 95 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen swollen, one-segmented bearing tiny posteroventrally directed spinules. Caudal ramus (Figure 77E) lamelliform, longer than wide devoid of typical medial fringe of setules, distally bearing six stout, naked, setae.

First antenna (Figure 77F) indistinctly seven- or eight-segmented, armature (base to apex) as follows: 7, 2, 5, 2, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 77G) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest the capability of relatively unrestricted movement. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a receptacle to accommodate tip of fourth segment. Latter forming heavi-

ly sclerotized robust claw, bearing one elongate, somewhat blunt seta near midpoint, one tiny seta along concave margin in aperture of chela, and one proximal seta. Mandible (Figure 77H) of two parts, dentiferous margin with nine teeth. First maxilla (Figure 77I) biramous; endopod longer bearing two apical elongate, naked setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 77J) brachiform; lacertus heavily sclerotized with stout basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; claw very elongate, bearing paired lateral membranous lamellae. Maxilliped (Figure 77K) subchelate; corpus two-segmented, proximal segment bearing two conical processes, and proximal end of adjacent segment bearing single small, conical process; subchela not divided into shaft and claw, distally uncinat and bearing a single small, slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta; first coxopod bears additional membranes. All four interpodal bars bearing small interpodal stylets; interpodal stylets of leg one smaller than others. Lateral fringe of setules on each endopodal segment; medial fringe of setules on the proximal segment of each exopod. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	I-1	II,4	Endopod	0-1	0-1	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	1,1,3
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	1,2

Exopod of leg one (Figure 78A) bearing distolateral membranes on segments one, two and three. Segment three with four pinnate setae, plus two naked setae. Endopod of leg one (Figure 78A) with distolateral membrane on first segment; segment two with three to eight (only three shown) endopodal denticulations; segment three with three to six (four shown) endopodal denticulations. Exopod of leg two (Figure 78B) similar to leg one, except third lateral most seta is semipinnate with setules along the medial edge and a finely serrated membrane along the lateral edge, and two lateralmost seta bilaterally bearing smooth or finely serrated membranes (too small for certainty). Endopod of leg two similar to leg one, with three to six endopodal denticulations (three shown) present on the second segment and four to six (four shown) endopodal denticulations on the third segment. Exopod of leg three (Figure 77C) as in leg two. Endopod

of leg three (Figure 78C) with three to five and four to five endopodal denticulations on segments two and three respectively (three and four are shown, respectively); segment three bears one medial pinnate seta followed laterally by one stout seta, and three elongate pinnate setae. Exopod of leg four (Figure 78D) as in leg three. Endopod of leg four (Figure 78D) with three to five (three shown) endopodal denticulations on segment two, and two to seven (three shown) endopodal denticulations on segment three. Fifth leg not found.

Male: (Figure 78E)

Overall length in dorsal view approximately 3.0 mm. Cephalothoracic appendages and swimming legs similar to those of female. Genital complex bearing fifth and sixth legs represented by four and two setae, respectively. Dorsal stylet slightly more stout than that of female. Caudal ramus (Figure 78F) more elongate than that of female, with setules fringing medial margin; six elongate distal setae (two pinnate).

Comments: *Kroyeria caseyi* has been reported only once from the night shark, *Carcharhinus signatus* (Poey, 1868) by Benz and Deets (1986) from the western North Atlantic. *Kroyeria caseyi* is perhaps the most remarkable member of the entire Kroyeriidae. It not only is the largest member of the family at approximately 60 mm, but it is also the only known member to date of this family to be mesoparasitic, embedded up to 80% of its body (anteriorly) into the interbranchial septa. The extremely elongate genital complex (comprising approximately 95% of the total body length) coupled to the very elongate claw of the second maxilla, the reduced seta in the aperture of the second antenna, the 1,1 3 formula of the terminal segment of endopod three, the inflated one-segmented abdomen, and the very derived caudal rami devoid of the typical medial fringe of setules, and bearing stout naked setae, distinguish this species from all other kroyeriids.

***Kroyeria cresseyi* sp. nov.**

(Figures 79-80)

Material examined. Several females collected from the secondary lamellae of the leopard shark, *Triakis semifasciata* Girard, 1854 from inshore waters off El Segundo, Seal Beach, and Palos Verdes, California, U.S.A. Female holotype (USNM 266535) and 5 female paratypes (USNM 266536) deposited at the United States National Museum of

Natural History.

Etymology: The specific name honors my good friend and pioneer in the studies of the parasitic copepods infecting elasmobranchs. Dr. Roger Cressey, Curator of Crustacea, USNM, Smithsonian Institution, Washington D.C.

Description

Female (Figure 79A)

Overall length in dorsal view approximately 5.0 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 79A and 79B) extending posteriorly to approximately 50 % down the length of the second free thoracic somite, stylets curving inward slightly with a bifid terminus. Three free thoracic somites with overlapping terga. Genital complex cylindrical, constituting approximately 66 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 79C) lamelliform, longer than wide bearing the typical medial fringe of setules, distally bearing four elongate pinnate setae and two shorter semipinnate setae. Egg strands (Figure 79D) containing six eggs.

First antenna (Figure 79E) indistinctly seven- or eight-segmented, armature (base to apex) as follows: 11, 1, 5, 2, 3, 1, 1, 13 (only 12 shown) +1 aesthete. Second antenna (Figure 79F) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest the capability of relatively unrestricted movement. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing one elongate seta along concave margin in aperture of chela, and one proximal elongate seta. Mandible (Figure 79G) of two parts, dentiferous margin with nine (1 apical, 2 large, 2 small, 2 large, and 2 small) teeth. First maxilla (Figure 79H) biramous; endopod longer bearing two apical elongate, naked setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 80A) brachiform; lacertus heavily sclerotized with large basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae (not shown) near base of claw. Claw bearing paired lateral membranous lamellae, with a unilaterally serrated membrane enveloping the latter. Maxilliped (Figure 80B) subchelate; corpus two-segmented, proximal segment bearing two conical processes, and proximal end of adjacent segment bearing single small, conical process; subchela not divided into shaft and claw, distally uncinat and bearing a single small slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta; first coxopod bears two additional membranes. All four interpodal bars bearing elongate interpodal stylets; interpodal stylets of leg one smaller than others. Lateral fringe of setules on each endopodal segment, medial fringe of setules on the proximal segment of each exopod. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	0-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	II,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 80C) bearing lateral membranes on segments one, two and three. Segment three with four pinnate setae, plus two slender setae; longer of the two with membrane along lateral edge. Endopod of leg one (Figure 80C) with distolateral membrane on first segment; segment two with six endopodal denticulations; segment three with distolateral membrane, and six pinnate setae. Exopod of leg two (Figure 80D) similar to leg one, except third lateral most seta is semipinnate with setules along the medial edge and a finely serrated membrane along the lateral edge, the two lateralmost setae slender and apparently naked. Endopod of leg two similar to leg one, with three to six endopodal denticulations (six shown) present on the second segment, and a distolateral membrane and six pinnate setae on the third segment. Exopod of leg three (Figure 80E) similar to leg two except second segment bears a small lateral seta, and the terminal segment bears only 2 lateral setae laterally bearing serrated membranes; longer of the two semipinnate. Endopod of leg three (Figure 80E) with three to seven endopodal denticulations on segment two (four shown); segment three bears four pinnate setae and one distolateral membrane. Exopod of leg four (Figure 80F) as in leg two. Endopod of leg four (Figure 80F) with six to thirteen (thirteen shown) endopodal denticulations on segment two; one lateral stout seta bilaterally bearing serrated membranes, and two pinnate setae tip segment three. Fifth leg not found.

Comments: *Kroyeria cresseyi* along with *K. branchiocetes*, *K. lineata*, *K. rhophemophagus*, and *K. triakos* all possess second antennae with the claw armed with only two slender setae, as opposed to three found amongst the remaining congeners.

K. cresseyi differs most notably from *K. branchiocetes* and *K. lineata* by not possessing the large membranous expansions found distally on the claw and the corpus of the second antennae of these two species. *K. cresseyi* is easily distinguished from *K. triakos* by possessing only four pinnate setae (plus two slender setae (one with serrated membrane and one semipinnate)) on the terminal segment of exopod three, while *K. triakos* bears five pinnate setae (plus one naked seta). Finally, the orbicular cephalothorax of *K. cresseyi* is quite dissimilar from the distinctly subquadrangular cephalothorax of *K. rrophemophagus*. Additionally, *K. cresseyi* stands apart from this species complex in being the only member with a bifid dorsal stylet.

As noted above, *K. branchiocetes* differs from these species in that it occurs in the Carcharhinidae not the Triakidae.

***Kroyeria decepta* sp. nov**

(Figures 81-84)

Material examined. Several males and females collected by Dr. Roger Cressey, from the gills of the dusky shark, *Carcharhinus obscurus* (LeSueur, 1818) from the West coast of Florida; numerous males and females collected from the same host species from near the Revillagigedos Islands in the tropical northeastern Pacific, Mexico. Female holotype (USNM 266537) and 7 female paratypes (USNM 266538) deposited at the United States National Museum of Natural History.

Etymology: The specific name *decepta* is derived from the Latin *decipio*, to deceive, in reference to the subtle morphological differences possessed by this species, relative to *K. carchariae glauci*, making specific identification difficult.

Description

Female (Figure 81A, B)

Overall length in dorsal view approximately 7.6 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 81A, B, and 81D) extending posteriorly to approximately 60 % down the length of the second free thoracic somite, stylets curving slightly inward and distally bifurcating. Three free thoracic somites with non-overlapping terga. Genital complex cylindrical, constituting approximately 66 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus

(Figure 81C) lamelliform, longer than wide with medial fringe of setules, distally bearing six pinnate setae (two stout and four elongate).

First antenna (Figure 81E) indistinctly seven- or eight-segmented, armature (base to apex) as follows: 10, 5, 2, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 81F) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing three prominent slender setae proximally. Mandible (Figure 81G) of two parts, dentiferous margin with nine teeth (2 large, 2 small, 2 large, 3 slightly smaller). Labrum of oral cone (Figure 81H) typical of the genus. First maxilla (Figure 81I) biramous; endopod longer bearing two apical elongate pinnate setae; exopod shorter bearing two short, naked setae. Second maxilla (only claw detailed) (Figure 82A) brachiform; lacertus heavily sclerotized with elongate basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; claw bearing paired lateral membranous lamellae with small prickles scattered upon convex surface. Maxilliped (Figures 82B, 83A, 83B) subchelate; corpus two-segmented, proximal segment bearing two conical processes; subchela not divided into shaft and claw, distally uncinat and bearing a single small slender seta. [The possible homologous relationships between the interpodal and dorsal stylets' sclerites illustrated in Figures 82B, 83A, B have been discussed in the previous dorsal and interpodal stylet section dealing with this hypothesis].

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and one or two distomedial membranes; first basipod bears additional distomedial pinnate seta; first coxopod bears two additional distolateral membranes, and a small patch of spinules. All four interpodal bars bearing interpodal stylets; interpodal stylets of leg one relatively small. Lateral fringe of setules on each endopodal segment, medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 82C) bearing distolateral membranes on segments

one, two and three (membranes pectinate on segments two and three). Segment three with four pinnate setae, plus two lateral setae bearing finely serrated, lateral membranes. Endopod of leg one (Figure 82C) with distolateral membrane on first segment; segment two with eight endopodal denticulations; segment three with eight to nine (nine shown) endopodal denticulations (specimens of *K. carchariaeglauci* collected from the pelagic white tip, *Carcharhinus longimanus* (Poey, 1861), similarly bear nine). Exopod of leg two (Figure 82D) similar to leg one, except second segment bears additional lateral seta, and third segment with four pinnate setae, plus one semipinnate seta with setules along the medial edge and a membrane along the lateral edge, and two slender setae bearing membranes along their lateral edge. Pectinate membranes are present along the lateral margin of segments two and three. A strip of pectin is also present paralleling the typical membrane along the lateral margin if the first segment of both exopod one and two. Endopod of leg two (Figure 82D) similar to leg one, except eight to nine (nine shown) endopodal denticulations (eight in the specimens of *K. carchariaeglauci* collected from the pelagic white tip) are present on the second segment and nine to ten (ten shown) endopodal denticulations on the third segment. Exopod of leg three (Figure 82E) as in leg two, except the two lateralmost setae appear to be devoid of lateral membrane (unilaterally in leg two). Endopod of leg three (Figure 82E) with eight to nine endopodal denticulations on segments two and nine to ten endopodal denticulations on segment three (eight are present on both segments from specimens of *K. carchariaeglauci* collected from the pelagic white tip); segment three with four pinnate setae. Exopod of leg four (Figure 82F) as in leg three. Endopod of leg four (Figure 82F) with seven to eight and eight to ten endopodal denticulations on segments two and three respectively (specimens of *K. carchariaeglauci* collected from the pelagic white tip bear seven to eight on segment three); segment three with two pinnate setae and one bilaterally bearing serrated membranes. Fifth leg (Figure 81J) represented by four setae (three pinnate and one naked).

Male: (Figure 84A and 84B)

Overall length in lateral view approximately 4.6 mm. Cephalothoracic appendages and swimming legs similar to those of female. Genital complex bearing fifth and sixth legs represented by four and two pinnate setae respectively. Dorsal stylet shorter and more stout than that of female. Caudal ramus (Figure 84C) more elongate than that of female, setules fringing medial margin; six distal setae (one stout and semipinnate, one stout and naked, two large and two small pinnate). Leg one endopod (two most distal segments illustrated) (Figure 84D) similar to female, bearing four and five endopodal denticulations on segments two and three respectively. Endopods of

legs two, three and four similar to leg one, all bearing four to five endopodal denticulations on segments two and three.

Comments: *Kroyeria decepta* is very similar to *K. carchariaeaglauci*, and this undoubtedly has led to confusion in my mind and in the literature. Having examined specimens of *Kroyeria* from *Carcharhinus obscurus* from both the West coast of Florida and off the Revillagegedos Islands in the tropical eastern North Pacific, I believe this represents a distinct form and have treated it herein as such. Many specific differences, albeit subtle, contribute to this decision. First, the caudal rami of male *K. decepta* are greatly elongated relative to that of male *K. carchariaeaglauci*, being approximately 9.5 times the width, compared with about 6.5 times the width in male *K. carchariaeaglauci*. The length of the genital complex of female *K. decepta* is approximately 10.25 times its width, compared with that of *C. carchariaeaglauci* which is only about 7.6 times its width. The endopod of the first maxilla of *K. decepta* bears pinnate setae, these setae are naked in *K. carchariaeaglauci*. The lateral membranes on the second and third segments of the exopod from leg one are pectinate in *K. decepta*, while those of *C. carchariaeaglauci* are thin and smooth. The two species are different in size; *K. decepta* is approximately 7.6 mm in total length, while *K. carchariaeaglauci* is about 5.5 mm long, or about 72% the length of the former. The length of the dorsal stylet of *K. decepta* is approximately 6.5 times its width, compared to that of *K. carecharchiaeaglauci*, which is nearly 8.8 times its width. And finally, the teeth on the mandible from *K. decepta* exhibit alternating sizes; teeth are more uniform in size in *K. carchariaeaglauci*.

K. decepta appears to be confined to the dusky shark, *Carcharhinus obscurus*. Interestingly, Kabata and Gusev (1966) report *K. carchariaeaglauci* from *Eulamia* sp. in the Indian Ocean. The copepod was reported to be 6.72 mm, large for that species, and a genital complex length approximately 9 times that of its width. These measurements suggest that copepod may be *K. decepta*, but without examining the specimen or being more certain what *Eulamia* sp. represents, no conclusion should be drawn.

***Kroyeria dispar* Wilson, 1932**

(Figures 85-86)

Material examined. Several females and males (USNM 153870) collected by Dr. Roger Cressey, from the gills of the tiger shark, *Galeocerdo cuvier* (Peron & LeSueur, 1822) from the West coast of Florida; numerous males and females (USNM 153864)

collected from the same host species from the Indian Ocean near Madagascar.

Description

Female (Figure 85B)

Overall length in dorsal view approximately 13.1 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Cephalothorax laterally extended relative to congeners. Dorsal stylets (Figures 85B and 85C) extending to just below posterior margin of first free thoracic somite, stylets curving slightly inward with blunt tips. Three free thoracic somites with non-overlapping terga. Genital complex cylindrical, constituting approximately 65 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly one- or two-segmented. Caudal ramus (Figure 85D) lamelliform, longer than wide with medial fringe of setules, distally bearing two stout semipinnate setae, two long thick pinnate setae, and two small slender pinnate setae; two duct-like openings (see detail) are present ventrodistally.

First antenna (Figure 85E) indistinctly nine-segmented, armature (base to apex) as follows: 9, 1, 1, 5, 2, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 85F) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a small receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, proximally bearing three prominent setae (one seta nearly half the length of claw and very blunt). Aperture of chela nearly circular due to strongly curving claw. Mandible (Figure 85G) of two or three parts as suggested by divisions of the sclerites, dentiferous margin with nine teeth. First maxilla (Figure 85H) biramous; endopod longer bearing two apical elongate setae with rows of denticles; exopod shorter bearing two short, naked setae. Second maxilla (Figure 85I) brachiform; lacertus heavily sclerotized with elongate basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; the latter bearing paired lateral membranous lamellae with small prickles scattered upon convex surface. Maxilliped (Figure 86A) subchelate; corpus two-segmented, proximal segment bearing two conical processes; myxal region of corpus with large protuberance bearing three cuticular expansions reminiscent of the cuticular flaps in *Eudactylina*; subchela not divided into shaft and claw, distally uncinat and bearing a single minute seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta; first coxopod bears two additional membranes. All four interpo-

dal bars with poorly developed (absent?) interpodal stylets. Lateral fringe of setules on each endopodal segment, medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	I-1	II,4	Endopod	0-1	0-2	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-2	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	1,1,3
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	1,1,2

Exopod of leg one (Figure 86B) bearing distolateral membranes on segments one, two and three (additional pectinate strips on segments two and three). Segment three with four pinnate setae, plus two lateral setae bilaterally bearing membranes. Lateral short setae on all exopods with flagellate tips. Endopod of leg one (Figure 86B) with distolateral membranes on each segment. Exopod of leg two (Figure 86C) similar to leg one, except third segment with four pinnate setae, plus one semipinnate seta with setules along the medial edge and a membrane along the lateral edge, and the two lateralmost setae bilaterally bearing membranes. Pectinate membranes paralleling the typical membranes are present along the lateral margin of segments one, two, and three. Endopod of leg two (Figure 86C) similar to leg one. Exopod of leg three (Figure 86D) as in leg two, except pectinate membranes not observed. Endopod of leg three (Figure 86D) with only one pinnate seta on segment two and segment three bears (laterally to medially) one pinnate seta, one short seta bearing membranes followed by three pinnate setae. Exopod of leg four (Figure 86E) as in leg three. Endopod of leg four (Figure 86E) similar to leg three except terminal segment bears one pinnate seta followed by one short seta bearing membranes, followed by only two pinnate setae. Fifth leg (not illustrated) represented by four setae (three pinnate and one naked).

Male: (Figure 85A)

Overall length in lateral view approximately 7.2 mm. Cephalothoracic appendages and swimming legs similar to those of female. Genital complex bearing fifth and sixth legs represented by four and two pinnate setae respectively. Dorsal stylet shorter and more stout than that of female. Caudal ramus more elongate than that of female.

Comments: *Kroyeria dispar* was originally described by Wilson (1935) from an unnamed shark. Since then, (see Cressey, 1967, 1970) all subsequent records have

been from gills of the tiger shark, *Galeocerdo cuvier* (Peron & LeSueur, 1822).

The unusually wide cephalothorax, the absence of endopodal denticulations, plus the presence of two elongate, pinnate setae arising from the medial margin of legs one and two, the spinulated / denticulated endopod of the first maxilla, and the peculiar cuticular flaps found on the myxal area of the maxilliped distinguish this species from all others in the genus. This species shares several attributes with *K. papillipes* also from *Galeocerdo cuvier*: short dorsal stylets, very reduced interpodal stylets, circular aperture of the second antenna, and an indistinctly nine-segmented first antenna.

Kroyeria elongata Pillai, 1967

Syn: Kroyeria spatulata Pearse, 1948 of Pillai, 1985

nec Kroyeria spatulata Pearse, 1948

nec Kroyeria elongatus Fukui, 1965

(Figures 87-88)

Material examined. Several females (USNM 154002) collected by Dr. Roger Cressey, from the gills of the spot-tail shark, *Carcharhinus sorrah* (Valenciennes, 1839) from the Indian Ocean near Madagascar.

Description

Female (Figure 87A)

Overall length in dorsal view approximately 3.0 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 87A, C) extending into anterior quarter of free thoracic somite three, stylets curving inward with expanded distolateral portion forming a cuticular flange. Three free thoracic somites with non-overlapping terga. Genital complex cylindrical, constituting approximately 63 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 87B) lamelliform, longer than wide with medial fringe of setules, distally bearing two stout setae (the longer distally pinnate, the shorter semipinnate), two thick longer pinnate setae, and two slender pinnate setae.

First antenna (Figure 87D) indistinctly seven- to eight--segmented, armature (base to apex) as follows: 10, 1, 5, 2, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 87E) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way to suggest relatively unrestricted movement capabilities.

Third segment forming corpus of chela, extending into a rigid arm distally expanded into a large receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, distally bearing membranous expansions forming a large cuticular receptacle fitting into the large receptacle of the corpus. Claw additionally bearing three prominent slender setae proximally (middle seta shorter and blunt). Aperture of chela elliptical due to elongated corpus and claw, reminiscent of the maxilliped in *Eudactylina*. Mandible (Figure 87F) of two or three parts as suggested by divisions of the sclerites, dentiferous margin with nine teeth (1 apical, 1 large, 2 small, 2 large, and 3 small decreasing in size). First maxilla (Figure 87G) biramous; endopod longer bearing two apical elongate naked setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 87H) brachiform; lacertus heavily sclerotized with elongate basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; the latter bearing paired lateral membranous lamellae with small prickles scattered upon convex surface. Maxilliped (Figure 87I) subchelate; corpus two-segmented, proximal segment bearing three conical processes; subchela not divided into shaft and claw, distally uncinata and bearing a single small slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta; first coxopod bears two additional membranes. Interpodal bars with interpodal stylets (leg one interpodal stylet very small or absent). Lateral fringe of setules probably present on each endopodal segment, though not seen on all segments from specimens inspected, medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 88A) bearing distolateral membranes on segments one, two and three (membranes pectinate on segments two and three). Segment three with four pinnate setae, plus two lateral slender setae (the lateralmost seta naked, the adjacent seta bearing a membrane along lateral edge). Endopod of leg one (Figure 88A) with distolateral membrane on first segment, five to six endopodal denticulations on the second segment, and three to five endopodal denticulations on the terminal seg-

ment. Exopod of leg two (Figure 88B) similar to leg one, except second segment bears lateral spiniform seta, and third segment bears four pinnate setae, plus one semipinnate seta with setules along the medial edge and a membrane along the lateral edge, and the two lateralmost setae laterally bearing membranes. Endopod of leg two (Figure 88B) similar to leg one. Exopod of leg three (Figure 88C) as in leg two. Endopod of leg three (Figure 88C) similar to leg two but segment three bears only four pinnate setae. Exopod of leg four (Figure 88D) as in leg three. Endopod of leg four (Figure 88D) similar to leg three except second segment medially bears pinnate seta, and terminal segment bears one stout seta bilaterally bearing short setules plus two pinnate setae.

Male: not acquired

Comments: *Kroyeria elongata* was originally described by Pillai (1967) from milk shark, *Scoliodon sorrokowah* (Bleeker, 1853) (= *Rhizoprionodon acutus* (Rüppel, 1837)). Pillai (1985) synonymized this species with *K. spatulata* Pearse, 1948. No reasons were given for the action, but the two species are quite distinct from another.

K. elongata can be distinguished from its congeners easily by the structure of the second antenna alone. No other *Kroyeria* has such an elongated claw and corpus of the second antenna. These attributes give the second antenna a very elongate elliptical aperture resulting in a general morphology that is reminiscent of that seen in the chelate maxilliped of *Eudactylina*. *K. elongata* is further distinguished from *K. spatulata* in that the terminus of the dorsal stylet of *K. elongata* is an inward curving flange, while that of *K. spatulata* is bifid (see following species description of *K. spatulata*). The cephalothorax of *K. elongata* is subtriangular not subquadrangular as in *K. spatulata*. This report adds the spot-tail shark, *Carcharhinus sorrah*, as the second known host for this species. Both records come from the Indian Ocean.

***Kroyeria gemursa* Cressey, 1967**
(Figures 89-90)

Material examined. Two paratype females (USNM 113296) collected from the gills of the great hammerhead, *Sphyrna mokarran* (Rüppel, 1837) from the Indian Ocean near Madagascar; numerous females (USNM 153855) from the same host species from near Sarasota, Florida.

Description

Female (Figure 89A)

Overall length in dorsal view approximately 14.4 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Ventral surface of rostrum (Figure 89C) with two small spinous processes. Dorsal stylets (Figures 89A-C, E) extending near anterior quarter of free thoracic somite three, stylets relatively straight, with a tiny bifid terminus. Three free thoracic somites with non-overlapping terga. Genital complex cylindrical, constituting approximately 73 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 89D) lamelliform, longer than wide with medial fringe of setules along proximal half, bearing four pinnate setae distally (2 large, two small), and distolaterally bearing two stout semipinnate setae each with a ventromedial row of tiny denticles.

First antenna (Figure 89F) indistinctly seven-segmented, armature (base to apex) as follows: 11, 3, 1, 3, 1, 1, 12 +1 aesthete. Second antenna (Figure 89G) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a small receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, proximally bearing three setae. Aperture of chela small due to stout claw and stout pollex of corpus. Mandible (Figure 89H) of two parts, dentiferous margin with nine teeth (1 apical, 1 large, 2 small, 2 large, and 3 small decreasing in size). Oral cone (Figure 89I) typical kroyeriid type but with lateral patches of spinules on the labrum much larger than those of congeners. First maxilla (Figure 89J) biramous; endopod longer bearing two apical elongate, pinnate setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 90A) brachiform; lacertus heavily sclerotized with elongate basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; the latter bearing paired lateral membranous lamellae with small prickles scattered upon convex surface. Maxilliped (Figure 90B) subchelate; corpus two-segmented, proximal segment bearing two conical processes, one conical process on proximal part of main corpus; subchela indistinctly divided into shaft and claw, distally uncinat and bearing a single small slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta. Interpodal bars with interpodal stylets (leg one interpodal stylet very small and blunt). Lateral fringe of setules present on segment one of the first

endopod and on the first and second segments of endopods two, three, and four, medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 90C) bearing distolateral membranes on segments one, two and three. Segment three with four pinnate setae, plus two shorter lateral setae (lateralmost seta with membrane along medial edge, the adjacent seta bearing a finely serrated membrane along lateral edge). Endopod of leg one (Figure 90C) with distolateral membrane on first segment, 28 to 30 endopodal denticulations on the second segment, and 29 to 31 endopodal denticulations on the terminal segment. Exopod of leg two (Figure 90D) similar to leg one, except second segment bears lateral seta, and third segment bears four pinnate setae, plus one semipinnate seta with setules along the medial edge and a finely serrated membrane along the lateral edge, one spiniform seta bilaterally bearing finely serrated membranes and a small naked seta. Endopod of leg two (Figure 90D) similar to endopod of leg one, except second segment bears 25-32 endopodal denticulations, and segment three bears 28-33 endopodal denticulations. Exopod of leg three (Figure 90E) as in leg two, except lateral seta on second segment bears a finely serrated lateral membrane. Endopod of leg three (Figure 90E) similar to leg two but segment three bears only four pinnate setae, segment two bears 10-12 endopodal denticulations, and segment three bears 15 endopodal denticulations. Exopod of leg four (Figure 90F) as in leg three. Endopod of leg four (Figure 90F) similar to leg three except second segment medially bears pinnate seta, and terminal segment bears one stout seta bilaterally bearing serrated membrane plus two pinnate setae. Second and third segments bear 10-12 and 11-13 endopodal denticulations respectively.

Male: not acquired

Comments: *Kroyeria gemursa* was originally described by Cressey (1967) from the great hammerhead, *Sphyrna mokarran* from off Madagascar. Since then it has been reported from the same host from the West coast of Florida (Cressey, 1970) and from

the Indian Ocean near Trivandrum, India (Pillai, 1985).

The laterally bulging, heavily sclerotized distal region of the last segment of the abdomen, the thickened claw and thickened extension of the corpus with the resultant reduced aperture of the second antenna, the large patches of spinules on the distolateral surfaces of the labrum, and the numerous (25-33) endopodal denticulations found on the second and third segments of leg one and leg two, readily distinguish this species.

Kroyeria lineata van Beneden, 1853

Syn: Lonchidium aculeatum Gerstaecker, 1854

Lonchidium lineatum; of Bassett-Smith (1899)

Krøyeria lineata Beneden; of Brian (1906)

Krøyeria aculeata Gerstaecker; of Brian (1906)

Krøyeria lineata Beneden; of Wilson (1932)

Krøyeria sublineata Yamaguti and Yamasu, 1959

(Figures 91-92)

Material examined. One female (BMNH 1928.6.11.6-15); one female (BMNH 1913.9.18.250-259) both collected by Andrew Scott from the gills of the tope shark, *Galeus canis* Bonaparte, 1834 (= *Galeorhinus galeus* (Linnaeus, 1758) from the Irish Sea; one female (BMNH 23.5.1975) collected by G.A. Boxshall from the gills of the smooth-hound, *Mustelus mustelus* (Linnaeus, 1758).

Description

Female (Figure 91A)

Overall length in dorsal view approximately 4.9 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 91A and 91B) extending near hind margin of first free thoracic somite, stylets curve sharply inward, forming an uncinatè terminus. Three free thoracic somites with non-overlapping terga. Genital complex cylindrical, constituting approximately 68 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 91C) lamelliform, longer than wide with medial fringe of setules, bearing two pinnate setae distally, one distomedial pinnate seta, one distal thick semipinnate seta, and distolaterally bearing one stout semipinnate setae, and one slender pinnate seta.

First antenna (Figure 91D) indistinctly seven- to eight-segmented, armature (base to apex) as follows: 10, 1, 5, 2, 3, 1, 1, 12 +1 aesthete. Second antenna (Figure

91E) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a large membranous receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing two prominent setae proximally, and distally expanded into a large membranous receptacle. Mandible (Figure 91F) of two parts, dentiferous margin with nine teeth (1 apical, 1 large, 2 small, 2 large, and 3 small decreasing in size). First maxilla (Figure 91G) biramous; endopod longer bearing two apical elongate, pinnate setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 91H) brachiform; lacertus heavily sclerotized with short basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; the latter bearing paired lateral membranous lamellae with small prickles scattered upon convex surface, and atypically, a large distal, subquadrangular membranous flap. Maxilliped (Figure 90I) subchelate; corpus two-segmented; subchela not divided into shaft and claw, distally uncinatè and bearing a single small, slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta. Interpodal bars with interpodal stylets (leg one interpodal stylet very small). Lateral fringe of setules present on all endopodal segments, medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1 0-1 II,4	Endopod	0-1 0-0 6
Leg two	Exopod	I-1 0-1 III,4	Endopod	0-1 0-0 6
Leg three	Exopod	I-1 I-1 III,4	Endopod	0-1 0-0 4
Leg four	Exopod	I-1 I-1 III,4	Endopod	0-1 0-1 I,2

Exopod of leg one (Figure 92A) bearing lateral membranes on segments one, two and three. Segment three with four pinnate setae, plus two lateral slender setae (lateralmost seta smaller and naked, adjacent seta bearing membrane along lateral edge). Endopod of leg one (Figure 92A) with distolateral membranes on all three segments, and devoid of endopodal denticulations. Exopod of leg two (Figure 92B) similar to leg one, except third segment bears four pinnate setae, plus one semipinnate seta with setules along the medial edge and a membrane along the lateral edge, one seta laterally bearing a membrane, and a small naked seta. Endopod of leg two (Figure

92B) similar to endopod of leg one. Exopod of leg three (Figure 92C) as in leg two, except second segment bears a lateral slender seta. Endopod of leg three (Figure 92C) similar to leg two but segment three bears only four pinnate setae. Exopod of leg four (Figure 92D) as in leg three. Endopod of leg four (Figure 92D) similar to leg three except second segment medially bears pinnate seta, and terminal segment bears one stout seta bilaterally bearing serrated membrane plus two pinnate setae.

Male: not acquired

Comments: *Kroyeria lineata* van Beneden, 1853, type species of the genus, was originally reported from tope shark, *Galeus canis* Bonaparte, 1834 (= *Galeorhinus galeus* (Linnaeus, 1758)). Since then, a few questionable records come from hosts in the family Carcharhinidae, such as the smooth hammerhead, *Sphyrna zygaena* (Linnaeus, 1758) (cf. Wilson, 1932), the blacktip shark, *Carcharhinus limbatus* (Valenciennes, 1839), and the lemon shark, *Hypoprion brevirostris* (= *Negaprion brevirostris* (Poey, 1868)), (cf. Wilson, 1936), and the blue shark, *Prionace glauca* (Linnaeus, 1758) (cf. Rokicki and Bychawska, 1991; Kabata, 1979), the species has been reported principally from tope sharks, smooth-hounds or whiskery sharks of the genera *Galeorhinus* and *Mustelus*, of the family Triakidae. *K. lineata* has been reported from the tope shark, *Galeorhinus galeus* (Linnaeus, 1758) from Belgian waters (van Beneden, 1853 and 1861), from the Mediterranean (Claus, 1858), (Brian, 1906); from the Irish Sea (Scott and Scott, 1913, A.Scott, 1929), and from off England (Leigh-Sharpe, 1933). *K. lineata* has also been reported from the smooth-hound *Mustelus mustelus* (Linnaeus, 1758), (= *Mustelus equestrius*, see Compagno, 1984b), from the Adriatic Sea (Valle, 1880), the North Sea (Boxshall, 1974), and the Mediterranean off Tunisia (Essafi and Raibaut, 1977). The species has also been found on the starry smooth-hound, *Mustelus asterias* Cloquet, 1821 and *Mustelus punctulatus* Risso, 1826 (= *M. mediterraneus* according to Compagno (1984b)), and off Tunisia in the Mediterranean (Essafi and Raibaut, 1979). Finally, the relegation of *K. sublineata* Yamaguti and Yamasu, 1959 to synonymy with *K. lineata* by Kabata (1979) extends the host and geographic range to include the starspotted smooth-hound, *Mustelus Manazo* Bleeker, 1854 from Japanese waters (Inland Sea).

Kabata (1979) suggested that *K. lineata* may be a synonym of the incompletely described *Lonchidium aculeatum* Gerstaecker, 1854, collected from *Galeorhinus galeus*, in the eastern North Atlantic. Brian (1906) and Delamare Debutteville and Nunes-Ruivo (1953) agreed with this synonymy. Evidence accumulated over the years indicates that *G. galeus* is one of the preferred hosts for *K. lineata*, and supports this synonymy.

K. lineata is the only species in the genus that has endopods without endopodal denticulations and a second antenna bearing only two prominent setae on the proximal region of the claw. Additionally, no other *Kroyeria* has the distal membranous extensions near the tip of the claw of the second maxilla. The relatively short, sharply incurving dorsal stylets coupled with the angular cephalothorax, aid in specific identification of this parasite.

***Kroyeria longicauda* Cressey, 1970**
(Figures 93-95)

Material examined. One paratype female (USNM 128497) collected from the gills of the blacktip shark, *Carcharhinus limbatus* (Valenciennes, 1839) from Sarasota, Florida; numerous females and a male (USNM 128496) collected by Dr. Roger Cressey, from the same host species from near Sarasota, Florida; and a few females (USNM 154003) collected from the gills of the spinner shark, *Carcharhinus brevipinna* (Müller and Henle, 1839) collected by Dr. Roger Cressey from Nosy Bé Island, near Madagascar in the Mozambique Channel.

Description

Female (Figure 93A)

Overall length in dorsal view approximately 3.5 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 93A and 93B) extending near anterior quarter of third free thoracic somite, stylets slightly curving inward with a deeply bifid terminus, lateral tine approximately 20% the length of the other. Three free thoracic somites with non-overlapping terga. Genital complex cylindrical, constituting approximately 65 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 93C) lamelliform, longer than wide without medial fringe of setules along proximal half, but with a lateral cuticular flange not a membrane as represented by Cressey (1970) or Pillai (1985), bearing five pinnate setae and one stout, plumose seta.

First antenna (Figure 93D) indistinctly seven- to eight-segmented, armature (base to apex) as follows: 10, 1, 5, 2, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 93E) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities.

Third segment forming corpus of chela, extending into a rigid arm, distally expanded into a large receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, distally expanded into a large membranous receptacle similar to corpus, and bearing three prominent setae proximally. Aperture of chela small due to the large membranous expansions of both claw and corpus. Mandible (Figure 93F) of two parts, dentiferous margin with nine teeth (1 apical, 1 large, 2 small, 2 large, and 3 small decreasing in size). First maxilla (Figure 93G) biramous; endopod longer bearing two apical elongate, naked setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 93H) brachiform; lacertus heavily sclerotized with basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; the latter bearing paired lateral membranous lamellae with small prickles scattered upon an inflated convex surface. Maxilliped (Figure 93I) subchelate; corpus two-segmented, myxal area bearing three crescent-shaped, membranous, cuticular flaps reminiscent of those in *Eudactylina*; subchela not divided into shaft and claw, distally uncinata and bearing a single small, slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta. Interpodal bars with interpodal stylets (leg one interpodal stylet very small and blunt). Lateral fringe of setules present on segments one and two of all endopods, medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 94A) bearing pectinate lateral membranes on segments one, two and three. Segment three with four pinnate setae, plus two lateral slender setae (lateralmost seta naked, the adjacent seta semipinnate and bearing a membrane along lateral edge). Endopod of leg one (Figure 94A) with distolateral membrane on first segment, five to six endopodal denticulations on the second segment, and four endopodal denticulations on the terminal segment. Exopod of leg two (Figure 94B) similar to leg one, except second segment bears lateral seta, and third segment bears four pinnate setae, plus one semipinnate seta with setules along the medial edge and a finely serrated membrane along the lateral edge, and two slender seta bearing a mem-

brane along their lateral edge. Endopod of leg two (Figure 94B) similar to endopod of leg one, except second segment bears six to seven endopodal denticulations, segment three bears four endopodal denticulations. Exopod of leg three (Figure 94C) as in leg two, except lateral seta on second segment bears a lateral membrane. Endopod of leg three (Figure 94C) similar to leg two but segment three bears only four pinnate setae, segment two bears five endopodal denticulations, and segment three bears three endopodal denticulations. Exopod of leg four (Figure 94E) as in leg three. Endopod of leg four (Figure 94D) similar to leg three except second segment medially bears pinnate seta, and terminal segment bears one stout seta bilaterally bearing smooth membranes plus two pinnate setae. Second and third segments bear three to four and three endopodal denticulations respectively. Leg five composed of four setae.

Male: (Figure 95A)

Overall length in lateral view approximately 2.1 mm. Cephalothoracic appendages and swimming legs similar to those of female. Genital complex bearing fifth and sixth legs represented by four and two pinnate setae respectively. Dorsal stylet (Figure 95B) more stout than that of female, and similarly bearing a small lateral tine. Caudal ramus (Figure 95C) more elongate than that of female, lacking setules fringing medial margin; six distal setae (one stout and semipinnate, one stout and naked, and four slender and pinnate).

Comments: *Kroyeria longicauda* was originally described by Cressey (1970) from the blacktip shark, *Carcharhinus limbatus* from off Sarasota, Florida. It has been reported from this host from the Indian Ocean near Kerala, India (Pillai, 1985). This report adds the spinner shark, *Carcharhinus brevipinna* (Müller and Henle, 1839) from the Mozambique Channel to the host and geographic range of this parasite. Interestingly, both the spinner shark, *Carcharhinus brevipinna* and the blacktip shark, *Carcharhinus limbatus* are members of Garrick's (1967) "*C. limbatus* group" and Garrick's (1982) "*C. limbatus-amblyrhynchoides* group" (see Compagno, 1988). The presence of *K. longicauda* is consistent with the hypothesized close relationship between these species.

The lateral tine on the deeply incised, bifid dorsal stylet, the lateral cuticular flange (the hyaline fringe of Cressey (1970)) on the caudal rami, and the small number of unusually large endopodal denticulations are unique to this species. The three atypical cuticular flaps on the myxal area of the maxilliped are also found on *K. dispar*, a species obviously unrelated.

The dorsal stylet of male *K. elongata* (Pillai, 1967), is very similar to that of *K. longicauda*.

***Kroyeria papillipes* Wilson, 1932**
(Figures 96-97)

Material examined. One holotype female (USNM 56672) collected from the tiger shark, *Galeocerdo cuvier* (Peron & LeSueur, 1822); several females and a male (USNM 153884-153899) collected by Dr. Roger Cressey, from the same host species from the West coast of Florida.

Description

Female (Figure 96A)

Overall length in dorsal view approximately 12.0 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Cephalothorax laterally extended relative to congeners. Dorsal stylets (Figures 96A, B) extending to midpoint of first free thoracic somite, stout, and curving slightly outward with blunt tips. Three free thoracic somites with non-overlapping terga. Genital complex cylindrical, constituting approximately 68 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly one- or two-segmented. Caudal ramus (Figure 96C) lamelliform, longer than wide, devoid of typical medial fringe of setules, distally bearing six pinnate setae.

First antenna (Figure 96D) indistinctly nine-segmented, armature (base to apex) as follows: 9, 1, 1, 5, 2, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 96E) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a small receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing three small setae proximally. Aperture of chela nearly circular due to strongly curving claw. Mandible (Figure 96F) of two parts, dentiferous margin with ten teeth somewhat uniform in size. First maxilla (Figure 96G) biramous; endopod longer bearing two elongate pinnate (short pinnules) setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 96H) brachiform; lacertus (not illustrated) heavily sclerotized with elongate basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; the latter

bearing paired lateral membranous lamellae with small prickles scattered upon convex surface. Maxilliped (Figure 96I) subchelate; corpus two-segmented, proximal segment bearing two conical processes; myxal region of corpus with a tiny conical process; subchela not divided into shaft and claw, distally uncinata and bearing a single small, slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta. Interpodal bars with poorly developed (absent?) interpodal stylets. Lateral fringe of setules on each endopodal segment, medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	3

Exopod of leg one (Figure 97A) bearing lateral membranes on segments one, two and three (additional pectinate strips on segments one, two and three). Segment three with four pinnate setae, plus two lateral naked setae. Endopod of leg one (Figure 97A) with distolateral membranes on segments one and three; second segment bears five endopodal denticulations. Exopod of leg two (Figure 97B) similar to leg one, except second segment bears a lateral seta, third segment with four pinnate setae, plus one semipinnate seta with setules along the medial edge and a membrane along the lateral edge, and two naked lateralmost setae. Pectinate membranes paralleling the typical membranes are present along the lateral margin of segments one, two, and three. Endopod of leg two (Figure 97B) similar to leg one, except second segment bears seven endopodal denticulations. Exopod of leg three (Figure 97C) as in leg two. Endopod of leg three (Figure 96C) similar to endopod of leg two except second segment bears five to eight endopodal denticulations, and terminal segment bears four pinnate setae. Exopod of leg four (Figure 96D) as in leg three. Endopod of leg four (Figure 96D) similar to leg three except terminal segment bears three pinnate seta, second segment similarly bears five to eight endopodal denticulations. Fifth leg not observed.

Male: (Figure 97E)

Total length approximately 5.4 mm. Appendages similar to female. Caudal rami

more elongate than that of female, and leg five and six represented by four and two setae respectively.

Comments: *Kroyeria papillipes* was originally described by Wilson (1932) from the tiger shark, *Galeocerdo cuvier* (Peron & LeSueur, 1822). The record of this species parasitizing the smooth hammerhead, *Sphyrna zygaena* (Linnaeus, 1758) has been found to be in error (see Cressey, 1970). All subsequent records have been from gills of *Galeocerdo cuvier*.

This species is the only member of the genus with all six setae on the caudal rami elongate and pinnate, making it readily identifiable. Additionally, the endopodal denticulations are restricted to the second segment of each endopod, similar to that in *K. cresseyi*.

The short dorsal stylets, reduced or absent interpodal stylets, circular aperture of the chelate second antenna, and the indistinctly nine-segmented first antennae are attributes shared with *K. dispar* Wilson, 1935, which occurs on the same host and geographic locality.

***Kroyeria procerobscena* sp. nov.**

(Figures 98-99)

Material examined. A few females (USNM 153860, 153858, 153857) collected by Dr. Roger Cressey, from the gills of the bull shark, *Carcharhinus leucas* (Valenciennes, 1839) from near Nosy Bé Island, near Madagascar in the Mozambique Channel. Female holotype (USNM 266541) and 2 female paratypes (USNM 266542) deposited at the United States National Museum of Natural History.

Etymology: The specific name *procerobscena* derived from the Latin *procerus*, meaning slender, long, stretched out, and from the Latin *obscenus*, meaning indecent, or private part, in reference to the extremely elongated genital complex of this species.

Description

Female (Figure 98A)

Overall length in dorsal view approximately 17.7 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 98A-C) extending posteriorly to anterior margin of the second free thoracic

somite, stylets curving slightly inward. Dorsal stylets distally bifurcated with a sharp tine (Figure 98B) or protuberance (Figure 98C) on the proximolateral edge approximately 30% down the length of the stylet. Three free thoracic somites with overlapping terga. Genital complex cylindrical, constituting approximately 80 % of total body length. Posterolateral corners of latter bearing oviducal openings. Egg strands (Figure 98A) containing 89 and 97 eggs. Abdomen (Figures 98A, D) indistinctly two- or three-segmented. Caudal ramus (Figure 98E) lamelliform, longer than wide without medial fringe of setules, distally bearing two large pinnate setae (setules along inflated proximal halves), two slender pinnate setae, one robust semipinnate seta, and one stout plumose seta (a small setule arises from a raised crypt near the lateral border).

First antenna (Figure 98F) indistinctly seven-segmented, armature (base to apex) as follows: 11, 5, 2, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 98G) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing three prominent setae (two slender and one truncate) proximally. Mandible (Figure 98H) of two parts, dentiferous margin with nine teeth (2 large, 2 small, 2 large, 3 slightly smaller). First maxilla (Figure 98H) biramous; endopod longer bearing two apical elongate, pinnate setae; exopod shorter bearing two short, naked setae. Second maxilla (only distal portion illustrated) (Figure 98I) brachiform; lacertus heavily sclerotized with basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; claw bearing paired lateral membranous lamellae with small prickles scattered upon convex surface. Maxilliped (Figure 99A) subchelate; corpus two-segmented, proximal segment bearing two spinous processes; distal portion of corpus bearing sharp cuticular flange; subchela not divided into shaft and claw, distally uncinat and bearing a single small, slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and one or two distomedial membranes; first basipod bears additional distomedial pinnate seta; first coxopod bears two additional distolateral membranes. All four interpodal bars bearing interpodal stylets; interpodal stylets of leg one acute but relatively small. Lateral fringe of setules on each endopodal segment, medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
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Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	1,2

Exopod of leg one (Figure 99B) bearing distolateral membranes on segments one, two and three (membranes finely pectinate on segments two and three). Segment three with four pinnate setae, plus two lateral slender setae, the largest bears a membrane along its lateral edge and the smaller and lateralmost seta is naked. Endopod of leg one (Figure 99B) with distolateral membrane on first segment; segment two with six to seven (six shown) endopodal denticulations; segment three with eight to ten (nine shown) endopodal denticulations. Exopod of leg two (Figure 99C) similar to leg one, except second segment bears additional lateral seta, and third segment with four pinnate setae, plus one semipinnate seta with setules along the medial edge and a membrane along the lateral edge, and two slender setae bearing membranes along their lateral edge. Pectinate membranes are present along the lateral margin of segments two and three. Endopod of leg two (Figure 99C) similar to leg one, except seven endopodal denticulations are present on the second segment and nine to twelve (nine shown) endopodal denticulations on the third segment. Exopod of leg three (Figure 99D) as in leg two, except the lateral membranes of the second and third segments are not pectinate. Endopod of leg three (Figure 99D) with seven to eight endopodal denticulations on segment two and eleven endopodal denticulations on segment three; segment three with four pinnate setae. Exopod of leg four (Figure 99F) as in leg three, but pectinate membranes on segments two and three and an additional pectinate strip parallels the typical membrane on segment one. Endopod of leg four (Figure 99E) with six and nine endopodal denticulations on segments two and three respectively; segment three with two pinnate setae and one slender seta bilaterally bearing serrated membranes. Fifth leg not observed.

Male: not acquired

Comments: *Kroyeria procerobscena* is one of the giants in the genus. At nearly 18 mm long its size is only rivalled by *K. papillipes*, *K. dispar*, and *K. gemursa*, at approximately 12.0, 13.1, and 14.4 mm respectively. Of course the mesoparasitic *K. caseyi* at nearly 60 mm in length remains in a class of its own.

K. procerobscena also has an unusually long genital complex (hence its name), comprising 80% of the body length. The unusually long genital complex, the large size, the unique lateral tine on the proximal region of the bifid dorsal stylet, and the two elon-

gate, proximally inflated, medially-pinched pinnate setae on the caudal rami distinguish this from any other species in this genus.

***Kroyeria rhophemophaga* sp. nov.**

(Figures 100-102)

Material examined. Several females collected from the secondary lamellae of the California soupfin shark, *Galeorhinus galeus* (Linnaeus, 1758) from inshore waters off El Segundo and Newport Beach, California, U.S.A. Female holotype (USNM 266539) and 5 female paratypes (USNM 266540) deposited at the United States National Museum of Natural History.

Etymology: The specific name is derived from the greek *rhomphema*, meaning soup, and the greek *phagein*, to eat, referring to this species' predilection for feeding upon soupfin sharks.

Description

Female (Figure 100A)

Overall length in dorsal view approximately 8.1 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 100A-C) extending posteriorly to approximately 50 % down the length of the second free thoracic somite, stylets curving inward slightly with an acute terminus. Three free thoracic somites with non-overlapping terga. Genital complex cylindrical, constituting approximately 67 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 100D) lamelliform, longer than wide bearing the typical medial fringe of setules, distally bearing four elongate pinnate setae and two stout, semipinnate setae. Egg strands (Figure 100E) containing six eggs.

First antenna (Figure 100E) indistinctly seven- or eight-segmented, 'armature (base to apex) as follows: 11, 5, 1, 3, 1, 1 (missing in this specimen), 13+1 aesthete. Second antenna (Figure 100G) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest the capability of relatively unrestricted movement. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing one elongate, slender seta

arising from concave margin in aperture of chela, and one proximal slender seta. Mandible (Figure 100H) of two parts, dentiferous margin with nine (2 large, 2 small, 2 large, and 3 small descending in size) teeth. First maxilla (Figure 100I) biramous; endopod longer bearing two apical elongate, pinnate setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 100J) brachiform; lacertus heavily sclerotized with large basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw. Claw bearing paired lateral membranous lamellae, with membrane bearing prickles along the convex surface. Maxilliped (Figure 101A) subchelate; corpus two-segmented; subchela not divided into shaft and claw, distally uncinat and bearing a single small slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta. All four interpodal bars bearing elongate interpodal stylets; interpodal stylets of leg one smaller than others. Lateral fringe of setules on endopodal segments one and two, and on segment three on leg four. Medial fringe of setules on the proximal segment of each exopod. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	0-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	1,2

Exopod of leg one (Figure 101B) bearing pectinate lateral membranes on segments one, two and three. Segment three with four pinnate setae, plus two slender setae; longer of the two with membrane along lateral edge. Endopod of leg one (Figure 101B) with distolateral membrane on first segment; segment two with five to six endopodal denticulations; segment three with lateral membrane, and six pinnate setae. Exopod of leg two (Figure 101C) similar to leg one, except three distolateral slender setae (two bearing lateral membranes and lateralmost seta smallest and naked) are present. Endopod of leg two (Figure 101C) similar to leg one, with five to seven endopodal denticulations present on the second segment, a distolateral membrane and six pinnate setae are present on the third segment. Exopod of leg three (Figure 101D) similar to leg two except second segment bears a small lateral slender seta, and the largest slender on the terminal segment seta is semipinnate with a membrane along the lateral edge. Endopod of leg three (Figure 101D) with three to eight endopodal den-

tenticulations on segment two (eight shown); segment three bears four pinnate setae and one lateral membrane. Exopod of leg four (Figure 101E) similar to exopod of leg three. Endopod of leg four (Figure 101E) with nine endopodal denticulations on segment two; one lateral stout seta bilaterally bearing finely serrated membranes, and two pinnate setae tip segment three. Fifth leg not found.

Male: (Figures 102A, B)

Overall length in dorsal view approximately 2.1 mm. Cephalothoracic appendages and swimming legs similar to those of female. Genital complex bearing fifth and sixth legs represented by four and two pinnate setae respectively. Dorsal stylet (Figure 102A) shorter and more stout than that of female. Caudal ramus (Figure 102C) more elongate than that of female, bearing six distal setae (two short and apically plumose; two long and pinnate, and two small slender pinnate). Second segment of endopods (Figure 102D) bears three large endopodal denticulations and a row of long setules fringing the lateral margin.

Comments: *Kroyeria rrophemophaga* resembles *K. branchiocetes*, *K. lineata*, *K. cresseyi*, and *K. triakos* in that the claw of the second antennae bears two rather than three elongate slender setae. *K. rrophemophaga* differs most notably from *K. branchiocetes* and *K. lineata* by lacking the large membranous expansions found distally on the claw and corpus of the second antennae. *K. rrophemophaga* is easily distinguished from *K. triakos* by possessing only four pinnate setae plus two lateral slender setae on the terminal segment of exopod three; *K. triakos* bears five pinnate setae plus one naked slender seta. Finally, the cephalothorax of *K. cresseyi* is orbicular rather than subquadrangular as in *K. rrophemophaga*.

I was also able to examine four specimens of *Kroyeria* from *Galeorhinus galeus* from Kaikoura, New Zealand, collected by Dr. Pilgrim. These specimens resembled *K. rrophemophaga* from southern California specimens that were only about 4.4 mm in length. This is approximately 54% the length of the specimens described herein. Until more data are acquired, populations of *Kroyeria* from the California and New Zealand soupfin sharks, *Galeorhinus galeus*, will be considered conspecific.

Interestingly, *K. lineata* from the soupfin or tope shark, *Galeorhinus galeus* from the eastern Atlantic, is markedly different from the *K. rrophemophaga* from the eastern North Pacific (California) and New Zealand. Many of species-specific elasmobranch-infecting copepods have a geographic range concomitant with that of their hosts. Perhaps the synonymy of the six species of *Galeorhinus* into *G. galeus* by Compagno (1984b) is mistaken. The different parasite species and striking difference in the size

between the aforementioned Pacific samples suggest distinct stocks of these soupfins.

***Kroyeria spatulata* Pearse, 1948**

(Figures 103-104)

Material examined. Several females (USNM 154009) collected by Dr. Cressey from the gills of the bull shark, *Carcharhinus leucas* (Valenciennes, 1839) from Sarasota, Florida; and a few females (USNM 271635) collected by Dr. Roger Cressey, from the gills of the lemon shark, *Negaprion brevirostris* (Poey, 1868) from Sarasota, Florida.

Description

Female (Figure 103A)

Overall length in dorsal view approximately 5.4 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 103A and 103B) extending near posterior margin of second free thoracic somite, stylets slightly curving inward with a bifid terminus. Three free thoracic somites with slightly overlapping terga. Genital complex cylindrical, constituting approximately 57 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 103C) lamelliform, longer than wide with fringe of setules along medial margin, bearing five pinnate setae (four elongate and one stout) and one large, stout, semipinnate seta.

First antenna (Figure 103D) indistinctly seven- to eight-segmented, armature (base to apex) as follows: 11, 5, 2, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 103E) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm, distally expanded into a receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing three prominent slender setae. Mandible (Figure 103F) of two parts, dentiferous margin with nine teeth (1 apical, 2 large, 2 small, 2 large, and 3 small decreasing in size). First maxilla (Figure 103G) biramous; endopod longer bearing two apical elongate, unilaterally denticulated setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 103H) brachiform; lacertus heavily sclerotized with large basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; the latter bearing paired lateral membranous lamellae with small prickles scattered upon convex sur-

face. Maxilliped (Figure 104A) subchelate; corpus two-segmented, proximal segment with three small spinous processes, distal region of distal segment of corpus bearing a transverse cuticular flange; subchela not divided into shaft and claw, distally uncinat and bearing a single small slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta, coxopod of leg one bears additional distolateral membrane. Interpodal bars with interpodal stylets (leg one interpodal stylet very small and blunt). Lateral fringe of setules present on segments one and two of all endopods, and on segment three of the endopod of leg four; medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 104B) bearing pectinate lateral membranes on segments one, two and three, typical membrane paralleling pectinate membrane on first segment. Segment three with four pinnate setae, plus two lateral slender setae (lateral-most seta naked, the adjacent seta bears a membrane along lateral edge). Endopod of leg one (Figure 104B) with distolateral membrane on first segment, seven to nine endopodal denticulations on the second segment, and ten to eleven endopodal denticulations on the terminal segment. Exopod of leg two (Figure 104C) similar to leg one, except second segment bears lateral seta, and third segment bears four pinnate setae, plus one semipinnate seta with setules along the medial edge and a membrane along the lateral edge, and laterally, two slender seta, the larger bearing a membrane along the lateral edge. Endopod of leg two (Figure 104C) similar to endopod of leg one, except second segment bears nine to eleven endopodal denticulations, segment three bears thirteen endopodal denticulations. Exopod of leg three (Figure 104D) as in leg two, except pectinate membrane paralleling typical membrane is present. Endopod of leg three (Figure 104D) similar to leg two but segment three bears only four pinnate setae, segment two bears nine to ten endopodal denticulations, and segment three bears thirteen to fifteen endopodal denticulations. Exopod of leg four (Figure 104F) with pectinate membranes arising medial to the distolateral setae of segments one and two, and arising medial to the second most lateral seta, and all sinuously wrapping

down along lateral margins of segments one, two, and three (obviously the diagnostic saddlelike sclerotizations noted by Cressey (1970)). Membranes present on all three segments. Endopod of leg four (Figure 104E) similar to leg three except second segment medially bears pinnate seta, and terminal segment bears one stout seta bilaterally bearing finely serrated membranes plus two pinnate setae. Second and third segments bear ten and eleven endopodal denticulations respectively. Leg five not observed.

Male: not acquired

Comments: *Kroyeria spatulata* was originally described by Pearse (1948) from the sharpnosed shark, *Scoliodon terraenovae* (Richardson, 1836) (= *Rhizoprionodon terraenovae* (Richardson, 1836)) from off Beaufort, North Carolina, U.S.A. Since then it has been reported from the sandtiger shark, *Carcharias littoralis* (= *Eugomphodes taurus* (Rafinesque, 1810)), and from the Bahamas (Pearse, 1951), from the blacktip shark, *Carcharhinus limbatus* (Valenciennes, 1839) from the Gulf of Mexico (Pearse, 1952b). Cressey (1967) reported it from the spinner shark, *Carcharhinus maculipinnis* (Poey, 1865) (= *Carcharhinus brevipinna* (Müller and Henle, 1839)), the spot-tail shark, *Carcharhinus sorrah* (Valenciennes, 1839), and from the milk shark, *Rhizoprionodon acutus* (Rüppel, 1837) all from the Indian Ocean. Following these reports, *K. spatulata* was reported by Cressey (1970) from the lemon shark, *Negaprion brevirostris* (Poey, 1868), and the bull shark, *Carcharhinus leucas* (Valenciennes, 1839) from off the West coast of Florida.

Having been fortunate enough to examine many of these specimens collected by the International Indian Ocean Expedition I found the record of *K. spatulata* on *C. brevipinna* to be in error. The correct identification of the parasite is *K. longicauda*. Furthermore, the record of *K. spatulata* on *C. sorrah* should be changed to *K. elongata* (assuming host identification is accurate).

This species is problematic in that the original description by Pearse (1948) was incomplete, and inconsistent with the illustrations. First, the corpus of the second antenna is not uniquely spatulate as described in the text. Second, Pearse states that there are no papillae (the endopodal denticulations herein) on the middle endopod segment of all legs, yet the illustrations of the apparently broken first leg and the fourth leg (legs two and three were not illustrated) distinctly show these to be present. Adding misery, the hideously distorted type specimen is distorted and compressed, and was of no value in sorting these inconsistencies out. The only illustration of this species since the original one by Pearse was a single illustration of the fourth leg by Cressey (1970) detailing the diagnostic "saddlelike sclerotizations on the distolateral corners on seg-

ments two and three of the fourth leg exopod", which corresponds to the sinuous pectinate membranes described herein. Pillai (1985) synonymized *K. spatulata* with *K. elongata*, but this is clearly in error as outlined above in the comments section under *K. elongata*.

This species is easily distinguished from all other congeners by the unique sinuous, pectinate membranes arising medial to the spiniform setae and wrapping down the lateral margins of segments two and three on the exopod of leg four.

Kroyeria sphyrnae Rangnekar, 1957

(Figures 105-106)

Syn: Kroyeria praelongacicula Lewis, 1966, *syn. nov.*

Material examined. Several paratype females of *K. praelongacicula* (USNM 110800) collected By Dr. Alan Lewis, University of British Columbia, from the gills of the scalloped hammerhead, *Sphyrna lewini* (Griffith and Smith, 1834) from the Hawaiian Islands near Kaneohe Bay; numerous females from the same host species from Punta Arena de la Ventana, in the southern Sea of Cortez (Gulf of California), Mexico; and numerous females from the smooth hammerhead, *Sphyrna zygaena* (Linnaeus, 1758) from Punta Arena de la Ventana, Mexico, and from near the Channel Islands, in the southern California bight.

Description

Female (Figure 105-106)

Overall length in dorsal view approximately 8.7 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 105A-C) extending beyond fourth free thoracic somite, stylets extremely elongate, lissome, with an acute terminus. Three free thoracic somites with non-overlapping terga. Genital complex cylindrical, constituting approximately 60 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 105D) lamelliform, longer than wide with medial fringe of setules, bearing four pinnate setae distally, and distolaterally bearing two stout semipinnate setae.

First antenna (Figure 105E and (terminal segment detail) 104F) indistinctly seven- to eight-segmented, armature (base to apex) as follows: 11, 3, 1, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 105G) chelate and prehensile, apparently four-seg-

mented. Proximal two segments heavily sclerotized in such a way as to suggest relatively unrestricted movement capabilities. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a small receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing three prominent setae proximally. Aperture of chela small due to stout claw and extension of corpus. Mandible (Figure 105H) of two parts, dentiferous margin with seven teeth (1 large, 2 small, 2 large, and 2 small decreasing in size). First maxilla (Figure 105I) biramous; endopod longer bearing two apical elongate, setae (one naked and one pinnate); exopod shorter bearing two short, naked setae. Second maxilla (Figure 106A) brachiform; lacertus heavily sclerotized with elongate basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw; the latter (see detail) bearing paired lateral membranous lamellae with small prickles scattered upon convex surface. Maxilliped (Figure 106B) subchelate; corpus two-segmented, proximal segment bearing a single conical process; subchela not divided into shaft and claw, distally uncinata and bearing a single small slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta. Interpodal bars with interpodal stylets (leg one interpodal stylet very small and blunt), remaining three legs all possess interpodal stylets relatively smaller than the majority of the genus. Lateral fringe of setules present on the first and second segments of endopods one through four, and on the third segment of leg four; medial fringe of setules on the first exopodal segment of each leg. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	III,4	Endopod	0-1	0-0	4
Leg four	Exopod	I-1	I-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 106C) bearing lateral membranes on segments one, two and three. Segment three with four pinnate setae, plus two lateral slender setae (lateralmost seta small and naked, the adjacent seta bears a membrane along lateral edge). Endopod of leg one (Figure 106C) with distolateral membrane on first segment, six to nine endopodal denticulations on the second segment, and eight to nine endopodal denticulations on the terminal segment. Exopod of leg two (Figure 106D) similar to

leg one, except second segment bears lateral seta, and third segment bears four pinnate setae, plus one semipinnate seta with setules along the medial edge and a finely serrated membrane along the lateral edge, one slender seta bearing a lateral membrane and a small naked lateralmost seta. Endopod of leg two (Figure 106D) similar to endopod of leg one, except second segment bears seven to eleven endopodal denticulations, and segment three bears eight to ten endopodal denticulations. Exopod of leg three (Figure 106E) as in leg two. Endopod of leg three (Figure 106E) similar to leg two but segment three bears only four pinnate setae, segment two bears nine to ten endopodal denticulations, and segment three bears nine to eleven endopodal denticulations. Exopod of leg four (Figure 106F) as in leg three. Endopod of leg four (Figure 106F) similar to leg three except second segment medially bears pinnate seta, and terminal segment bears one stout seta bilaterally bearing serrated membrane plus two pinnate setae. Second and third segments bear eight to nine and eight to eleven endopodal denticulations respectively.

Male: not acquired.

Comments: *Kroyeria sphyrnae* was originally described by Rangnekar (1957) from an unknown species of hammerhead, *Sphyrna* sp. in India, presumably in the Bombay region. The next record of *K. sphyrnae* came from the gills of the smooth hammerhead, *Sphyrna zygaena* (Linnaeus, 1758) from Trivandrum, India (Pillai, 1967). Kabata (1970) presented a tentative find of *K. sphyrnae* from a single non-ovigerous specimen collected from the brownbanded bamboo shark, *Chiloscyllium punctatum* Müller and Henle, 1838 (Orectolobiformes: Hemiscylliidae), from Moreton Bay, Queensland, Australia. Unfortunately, no illustrations or dimensions accompanied that report, and specific identification of the specimen remains open to question. Cressey (1970) claimed to have discovered it from the blacknose shark, *Carcharhinus acronotus* (Poey, 1860) from the West coast of Florida. Again, no illustrations accompanied that report, but Cressey did include total length of the specimens, which were reported to be very small (2.2 mm). Pillai (1985) superficially describes the species and summarizes reported host associations of this parasite.

Lewis (1966a) described a new species, *Kroyeria praelongacicula*, from the scalloped hammerhead, *Sphyrna lewini* (Griffith and Smith, 1834) from Kaneohe Bay, Oahu, Hawaii. These specimens appear to be conspecific with *K. sphyrnae*. The strange irregular bifid tip of the dorsal stylet illustrated in Lewis' description of *K. praelongacicula*, was not observed in the paratypes I examined. Based on the paratype specimens examined and specimens collected from the same host species in the

southern Sea of Cortez, and southern California Bight in the eastern North Pacific, and the descriptions offered by Rangnekar (1957) and Pillai (1967, 1985), *K. praelongacicula* is considered a synonym of *K. sphyrnae*.

Cressey's (1970) record of *K. sphyrnae* is suspect. Cressey reports the length of *K. sphyrnae* as only 2.2 mm, which is quite small considering the original description by Rangnekar measures this species at 4.7 mm. Lewis (1966a) reports a range of 6.58-8.12 mm, and a total length of approximately 8.7 mm was found herein. It is unlikely Cressey's (1970) record represents the same species. Cressey notes that the small size combined with the last two segments of the endopod of the fourth leg bearing only two or three lateral spinules (the endopodal denticulations herein) make specific identification easy. Neither of these characteristics apply to *K. sphyrnae*. What species Cressey's (1970) record represents is uncertain.

K. sphyrnae is a parasite of smooth and scalloped hammerheads, *Sphyrna zygaena* and *Sphyrna lewini*, respectively. My unpublished field observations from both southern California and the southern Sea of Cortez suggest *S. zygaena* is the preferred host as the parasite load is higher on this host.

The long, acute, lissome dorsal stylets, the formula of the seven-toothed mandible, and the relatively short interpodal stylets which barely reach the distal margin of the basipods of legs two, three, and four readily distinguish this species.

Kroyeria triakos* Fukui, 1965 *nom. emend.

(Figures 107-108)

Syn: Kroyeria elongatus Fukui, 1965

Kroyeria triakisae Fukui, 1965

nec Kroyeria elongata Pillai, 1967

Material examined. Two females collected from the secondary lamellae of the banded houndshark, *Triakis scyllium* Müller and Henle, 1839 (USNM 22607) from inshore waters off Awa, Japan.

Description

Female (Figure 107A)

Overall length in dorsal view approximately 4.6 mm. Cephalothoracic sutures arising anterolaterally and uniting posteromedially. Eyes not evident. Dorsal stylets (Figures 107A, B) extending to the posterior margin of the second free thoracic somite,

stylets curving inward slightly with a narrow distolateral flange. Three free thoracic somites with slightly overlapping terga. Genital complex cylindrical, constituting approximately 66 % of total body length. Posterolateral corners of latter bearing oviducal openings. Abdomen indistinctly three-segmented. Caudal ramus (Figure 107C) lamelliform, longer than wide bearing the typical medial fringe of setules, distally bearing two elongate pinnate setae, two shorter pinnate setae and two stout semipinnate setae.

First antenna (Figure 107D) indistinctly seven- or eight-segmented, armature (base to apex) as follows: 9, 1, 5, 1, 3, 1, 1, 13 +1 aesthete. Second antenna (Figure 107E) chelate and prehensile, apparently four-segmented. Proximal two segments heavily sclerotized in such a way as to suggest the capability of relatively unrestricted movement. Third segment forming corpus of chela, extending into a rigid arm distally expanded into a receptacle to accommodate tip of fourth segment. Latter forming heavily sclerotized robust claw, bearing one elongate slender seta along concave margin in aperture of chela, and proximally, one elongate seta. Mandible (Figure 107F) of two parts, dentiferous margin with nine (1 apical, 2 large, 2 small, 2 large, and 2 small) teeth. First maxilla (Figure 107G) biramous; endopod longer bearing two apical elongate, pinnate setae; exopod shorter bearing two short, naked setae. Second maxilla (Figure 107H) brachiform; lacertus heavily sclerotized with long basal process arising from near base. Brachium with two large patches of prickles and a tuft of fine, long setae near base of claw. Claw bearing membranous lamellae, specifics difficult to ascertain due to small size. Maxilliped (Figure 107I) subchelate; corpus two-segmented, proximal segment bearing one conical process, distolateral region of main corpus bears transverse cuticular flange; subchela not divided into shaft and claw, distally uncinata and bearing a single small, slender seta.

All four legs biramous and trimerite. Sympods two-segmented. All basipods with lateral pinnate seta and two distomedial membranes; first basipod bears additional distomedial pinnate seta; first coxopod bears two additional membranes. All four interpodal bars bearing elongate interpodal stylets; those of leg one smaller than others. Lateral fringe of setules on endopodal segments two and three, medial fringe of setules on the first segment of each exopod. Armature of rami as follows (Arabic numerals denote fully pinnate setae, Roman numerals denote conditions diverging from that state):

Leg one	Exopod	I-1	0-1	II,4	Endopod	0-1	0-0	6
Leg two	Exopod	I-1	0-1	III,4	Endopod	0-1	0-0	6
Leg three	Exopod	I-1	I-1	I,5	Endopod	0-1	0-0	4
Leg four	Exopod	0-1	0-1	III,4	Endopod	0-1	0-1	I,2

Exopod of leg one (Figure 108A) bearing lateral membranes on segments one, two and three. Segment three with four pinnate setae, plus two slender naked setae. Endopod of leg one (Figure 108A) with distolateral membrane on first segment; segment two with seven endopodal denticulations; segment three bearing six pinnate setae, and apparently devoid of typical distolateral membrane. Exopod of leg two (Figure 108B) similar to leg one, except third lateralmost seta is semipinnate with setules along the medial edge, the two lateralmost setae slender and apparently naked. Endopod of leg two (Figure 108C) similar to leg one, with six to eight endopodal denticulations (eight shown) present on the second segment, and a lateral membrane and six pinnate setae on the third segment. Exopod of leg three (Figure 108D) similar to leg two except second segment bears a small lateral seta, and the terminal segment bears only one naked, lateral setae and five pinnate setae. Endopod of leg three (Figure 108E) with seven to ten endopodal denticulations on segment two (seven shown); segment three bears four pinnate setae and one distolateral membrane. Exopod of leg four (Figure 108F) without typical lateral setae on segments one and two, terminal segment with four pinnate setae, one semipinnate seta, one slender seta bearing a serrated membrane, and the lateralmost slender seta naked. Endopod of leg four (Figure 108F) with indistinct membranous, endopodal denticulations forming the membrane, or transparent supports for the membrane (illustrated as a typical membrane) on segment two (this could be interpreted as devoid of endopodal denticulations or antithetically, possessing very many fused, membranous endopodal denticulations); one lateral stout seta bilaterally bearing serrated membranes, and two pinnate setae tip segment three. Fifth leg not found.

Comments: As noted above, *Kroyeria triakos*, *K. branchiocetes*, *K. lineata*, *K. rhopemophaga*, and *K. cresseyi* differ from their congeners in that the claw of the second antenna is armed with only two slender setae. Differences between species in this complex have already been outlined in the comments section for *K. cresseyi*.

K. triakos was originally described by Fukui (1965) from gills of a young, banded houndshark, *Triakis scyllium* Müller and Henle, 1839, from Kurihama, in the Kanagawa prefecture collected in 1955. Although his description is incomplete, the unique shape of the cephalothorax (almost arrowhead shaped; "the cobra with protrusions in the posterior corners" of Fukui (1965)), the similar dimensions, and the fact that both collections come from the same host species in Japanese waters leave no doubt that specimens examined here are conspecific with Fukui's material. Fukui (1965) assigned the new Japanese name *Dochi-zame-hoso-yadori Ken-mizinko*, (meaning, the elongated *Kroyeria* from *Triakis*) to this parasite. Strangely, he also assigns two binomens to this

copepod, keeping the Japanese name the same in both instances. *Kroyeria elongatus* is the first name to show up in the publication in the figure caption preceding the actual description. The name *Kroyeria triakisae* occurs in the narrative, describing the species. Fukui's *K. elongatus* should be *K. elongata* (*Kroyeria* is feminine), making it a homonym of Pillai's (1967) *K. elongata*. This would force one to correct the gender of Fukui's species and rename Pillai's. However, for the sake of nomenclatural stability and to minimize further taxonomic confusion in the genus, this species will retain the name *K. triakisae*. Since the name is a Greek noun, its genitive singular is *triakos*. I propose, therefore to amend Fukui's *K. triakisae* to *K. triakos*. This leaves Pillai's (1967) *K. elongata*, unchanged.

K. triakos is easily recognized by being the only species in the genus that has five elongate, pinnate setae on the third segment of the third leg. It is also the only species lacking the typical lateral setae on segments one and two of the fourth exopod. The latter feature is suggested here only tentatively, for two reasons. Firstly, it is otherwise unknown in Kroyeriidae; secondly, material available for examination was not adequate to determine it beyond a reasonable doubt.

REMAINING UNOBTAINABLE NOMINAL SPECIES

Kroyeria consists of 18 nominal species. Three of them, (*K. acanthiasvulgaris* Hesse, 1879, *K. galeivulgaris* Hesse, 1884, and *K. scyllicaniculae* Hesse, 1879) have not been sufficiently well described to be recognized and must be considered *species inquirenda*. *K. trecai* Delamare Deboutteville and Nunes-Ruivo, 1953 was never described and remains a *nomen nudum*. *K. aculeata* (Gerstaecker, 1854) and *K. sublineata* Yamaguti and Yamasu, 1959 are considered junior synonyms of *K. lineata* van Beneden, 1853. *K. gracilis* Wilson, 1932 similarly is considered a junior synonym of *K. carchariaeglauci* Hesse, 1879, and *K. praelongacicula* Lewis 1966 is a synonym of *K. sphyrnae* Rangnekar, 1957. This revision resurrects *K. elongata* Pillai, 1967.

This section is a brief (alphabetical) account of the females of the uncertain species above and the remaining species that were not available for this revision of *Kroyeria*.

Kroyeria acanthiasvulgaris Hesse, 1879 was described from the spiny dogfish, *Acanthias vulgaris* Risso, 1826 (= *Squalus acanthias* Smith and Radcliffe, 1912), from off Brest, France. I have examined literally hundreds of this host species, and they only harbored *Eudactylina acanthii* A. Scott, 1901. Since many triakids or smooth-hounds are morphologically similar to this reported squaloid host, host misidentification

is a likely explanation for this unlikely host-parasite association.

Kroyeria echinata Rangnekar, 1956 was reported from the body surface of the smooth hammerhead, *Sphyrna zygaena* (Linnaeus, 1758) from the Indian Ocean near Bombay, India. The description is too superficial for detailed comparisons. Although Pillai's (1985) redescription is helpful, some interpretations (setation on distal elements of the caudal rami and legs, and the number of slender setae on the claw of the second antennae) are suspect. Pillai (1985) reports this parasite from the smooth hammerhead from Kerala, India. The short stout dorsal stylets are reminiscent of those found in *K. dispar* and *K. papillipes*, but can be distinguished from these two by their small size (approximately 3.2-4.1 mm, compared to the 13.1 and 12.0 mm of *K. dispar* and *K. papillipes* respectively). The endopods of *K. dispar* are devoid of endopodal denticulations, and they are restricted to the second segment only of all four legs in *K. papillipes* and *K. echinata*. The orbicular cephalothorax of *K. papillipes* is quite distinct from that of *K. echinatus* as is the armature of the setae on the caudal rami and the legs.

Kroyeria galeivulgaris Hesse, 1884 was reported from the Tope shark, *Galeus vulgaris* Fleming, 1828 (= *Galeorhinus galeus* (Linnaeus, 1758)). This may represent *K. lineata*, considering the host and geographic locality (Brest, France).

Kroyeria minuta Pillai, 1968 was described from gill filaments of the milk shark, *Scoliodon sorrokowah* (Bleeker, 1853), (= *Rhizoprionodon acutus* (Rüppel, 1837)), from Kerala, India. This is a small species, only about 3.0 mm in length. The long bifid dorsal stylets reaching the posterior margin of the fourth free thoracic somite, coupled with the supposed and questionable serrated medial margins (I suspect these serrations are the typical endopodal denticulations characteristically found throughout the genus), and the atypical patch of spinules on the lateral margin of the coxopod of leg two, plus the existence of six fully pinnate setae on the terminal segment of the exopod of leg two, readily distinguish this species.

Kroyeria scyllicaniculae Hesse, 1879 was originally reported from the small-spotted catshark, *Scyllium canicula* (= *Scylliorhinus canicula* (Linnaeus, 1758)), from Brest, France. Unfortunately, *K. scyllicaniculae* a *species inquirenda* comes from the Scylliorhinidae, a host family with very little parasitic copepod information.

Kroyeria trecai Delamare Debutteville and Nunes-Ruivo, 1953 was reported from the smooth hammerhead, *Sphyrna zygaena* (Linnaeus, 1758) and from the scalloped hammerhead, *Sphyrna diplana* Springer, 1941 (= *Sphyrna lewini* (Griffith and Smith, 1834)) from off the coast of Senegal. Although no description was ever published, they mention the species is characterized by its styliform processes projecting past the level of the genital segment, by having a one-segmented abdomen and by its caudal rami ending in 4 subequal setae, the 2 longer being ciliated. The long dorsal

stylets coupled to the fact that this species is found on the same sphyrid hosts as *Kroyeria sphyrnae* suggests that these two species may be synonyms.

PHYLOGENETIC ANALYSIS

CLADOGRAM CONSTRUCTION

A phylogenetic analysis was conducted of the 16 species of *Kroyeria* revised herein. The outgroup was composed of the presumed sister taxon, *Kroeyerina*, and *Prokroyeria* (presumed sister to *Kroyeria* and *Kroeyerina*) (Figure 109; see Deets, 1987 for details). A total of 44 characters (see Appendix C for data matrix and definition of characters) were analyzed using an exact search Branch and Bound algorithm of PAUP. The most parsimonious tree for *Kroyeria* (Figure 110) had a tree length of 165, a consistency index of 0.75 (maximum value = 1.00), a retention index of 0.75 (maximum value = 1.00), and an *F*-ratio of 0.0589 (maximum value=0). Change and/or synapomorphy lists may be obtained from the author.

The first two branches arising from the base of the cladogram are represented by *K. dispar* and *K. papillipes* respectively, both parasites of the tiger shark, *Galeocerdo cuvier*. The next clade is composed of parasites specific to the Triakidae: the major dichotomy in this clade separates *K. lineata* (parasites of *Galeorhinus galeus* and *Mustelus spp.*) and *K. rrophemophaga* (parasite of Californian *Galeorhinus galeus*) from *K. triakos* and *K. cresseyi*, parasites of the Japanese and Californian leopard sharks, *Triakis scyllium* and *Triakis semifasciata*, respectively. The next clade up the cladogram holds two species, *K. sphyrnae* and *K. gemursa*, parasites of the hammerhead genus *Sphyrna*. A paraphyletic triad follows consisting of the bizarre, mesoparasitic *K. caseyi*, parasitic on the night shark, *Carcharhinus signatus*, *K. spatulata*, found on various species of *Carcharhinus*, *Negaprion*, and *Rhizoprionodon*, and *K. procerobscenum* a parasite of the bull shark, *C. leucas*. The final major bifurcation leads to one clade composed of *K. branchiocetes*, *K. longicauda*, and *K. elongata*, parasites of various species of *Carcharhinus*, and a clade composed of *K. decepta*, specific to the dusky shark, *C. obscurus*, and *K. carchariaeglauci* parasitic on the epipelagic silky shark, *C. falciformis*, the pelagic whitetip, *C. longimanus*, and the blue shark *Prionace glauca*.

PARASITE-DERIVED HOST CLADOGRAMS

The *Kroyeria* cladogram was recoded by additive binary coding and a host by parasite data matrix was created (Table III).

The phylogenetic analysis conducted from the recoded species of *Kroyeria* by host matrix (Table 3) resulted in a single most-parsimonious tree (Figure 111). The Branch and Bound generated tree had a tree length of 30, and a consistency index with a maximum value of 1.00.

The parasite-derived host cladogram shows some unexpected patterns. The first two branches at the base of the tree posit a paraphyletic relationship for the presumably monophyletic tiger shark, *Galeocerdo cuvier*. This artifact is due to this host possessing two different species of *Kroyeria*. Using parasite species as characters in this case would be analogous to coding an organism for phylogenetic analysis that possessed two different character states of a given character simultaneously. Inclusive OR'ing, a technique previously used to code for the occurrence of more than one parasite taxon per host could have been used to force *Galeocerdo* into monophyly, however this technique, if not restricted to treatment of parasite sister taxa, creates a chimera out of unmodified data, resulting in the distortion of phylogenetic information (see O'Grady and Deets, 1987 for details).

The next clade contains members of the Triakidae. This clade consists of one group housing the leopard sharks *Triakis semifasciata* from the California coast, and *T. scyllium* from Japanese waters. The remaining clade contains the soupfin shark *Galeorhinus galeus* functioning as the sister taxon to a clade composed of the *G. galeus* and various species of *Mustelus* from the western North Atlantic and Mediterranean. The monophyly of *G. galeus* with the many *Mustelus* species is due to this host complex sharing the common parasite, *K. lineata*. The other branch leading to *G. galeus* stands alone as this soupfin shark from California waters possesses its own copepod *K. rhophemophaga*.

The next clade contains all hammerheads of the genus *Sphyrna*. The great hammerhead, *Sphyrna mokarran* is sister taxon to the clade consisting of scalloped and smooth hammerheads, *Sphyrna lewini* and *S. zygaena*, respectively. The night shark, *Carcharhinus signatus* is the first *Carcharhinus* to appear on the cladogram followed by a clade consisting of the bull shark, *C. leucas* and the lemon shark, *Negaprion brevirostris* both possessing *K. spatulata*. *C. leucas* is unresolved with two clades, one with five the other with four taxa. The five taxon clade consists of the Grey reef shark, *C. amblyrhynchos* which is the sister taxon to a clade composed of two

smaller groups. The first group contains the spinner shark, *C. brevipinna* and the black-tip, *C. limbatus*. The remaining group is composed of the spot-tail shark, *C. sorrah* and the milk shark *Rhizoprionodon acutus*. The four taxon clade on consists of the dusky shark, *C. obscurus*, the sister taxon to an unresolved trichotomy of pelagic tropical to temperate carcharhinids, the silky shark, *C. falciformis*, the pelagic whitetip, *C. longimanus*, and the blue shark, *Prionace glauca*.

COMBINING PARASITE CLADOGRAMS

If parasites can be used as characters, and if they possess symplesiomorphic, synapomorphic, or autapomorphic relationships with their hosts as do typical characters in phylogenetic analyses, then we should gain resolution regarding host relationships with addition of parasite phylogenies (assuming an hypothesis of strict co-speciation). Additionally, Brooks and McLennan (1991, 1993) claim the methods applied in single clade analysis can be used for multiple clades simultaneously.

Kroeyerina Wilson, 1932 (Figure 112) is a genus of copepods dwelling in olfactory lamellae of elasmobranchs. Deets (1987) generated a parasite cladogram and a parasite-derived host cladogram of the genus. During the course of this study *Kroeyerina cortezensis* Deets, 1987, originally reported from the silky shark, *Carcharhinus falciformis*, was discovered from olfactory lamellae of the pelagic whitetip, *Carcharhinus longimanus*, captured in a tuna seine off the Revillagegedos Islands, Mexico in September of 1988. Hence the parasite-derived host cladogram for *Kroeyerina* is slightly different from the original with the incorporation of the pelagic whitetip (Figure 113).

The *Kroeyerina* cladogram from Deets (1987) was converted into a binary code (Table III), and then added to the binary code for *Kroyeria* (Table II) resulting in the combined matrix for both genera (Table IV). A phylogenetic analysis was conducted for this hybridized data set using the exact search Branch and Bound algorithm in PAUP. Three equally parsimonious trees with a tree length of 49, a CI of 0.90 (maximum value = 1.00), and an RI of 0.96 (maximum value = 1.00) resulted. One tree preserved the paraphyly of *Galeocerdo cuvier*, as in the previously generated *Kroyeria* cladogram (Figure 110). One tree had the thresher shark, *Alopias vulpinus* and the mako, *Isurus oxyrinchus* both lamnids, tucked between the triakids and *Galeocerdo cuvier* resulting in the paraphyly of the carcharhinids and lamnids. The remaining tree that maintained monophyly of the aforementioned specific and supraspecific taxa was chosen (Figure 114).

The resultant tree accommodates both sets of parasite data (the additive binary

recoded cladograms from *Kroyeria* and *Kroeyerina*) with little conflict. The holocephalan clade represented by *Callorhynchus callorhynchus* (Linnaeus, 1758) is the sister taxon to the remaining elasmobranchs. The batoid clade composed of the genera *Mobula*, *Dasyatis*, and *Rhinobatus* is the sister clade to the remaining components of the tree composed of the two lamnids, *Alopias* and *Isurus* plus the remaining carcharhinids. *Galeocerdo*, previously showing a paraphyletic relationship with itself due to the sharing of *Kroyeria dispar* and *K. papillipes* becomes a monophyletic entity held together by the presence of *Kroeyerina elongata* Wilson, 1932.

Also of interest is the placement of the blue shark, *Prionace glauca*. In the *Kroeyerina* cladogram (Figure 113) *Prionace* is basally placed in the carcharhinid-lamnoid lineage, in the *Kroyeria*-derived cladogram (Figure 111) *Prionace* was at the top of the cladogram, and the combined tree (Figure 114) (in fact all three of the combined *Kroeyerina*-*Kroyeria* trees) maintained this placement of *Prionace*. This placement of *Prionace* is consistent with that of Compagno (1988) and Lavery (1992) in their morphologically- and molecular-based cladograms, respectively. The taxonomic or phylogenetic congruence (see Lanyon, 1993) amongst three independent data sets suggests that the presence of *Kroeyerina elongata*, on *Prionace* is a result of colonization from *Galeocerdo*.

Not mentioned in other studies however, the method used equally combines parasite species from one genus with those from another genus to generate the host cladogram. The more species a cladogram contains, the more nodes and branches or information the binary code must contain, resulting in a significantly longer binary string in order to represent that topology. Having more character states in a parsimony analysis will functionally weight that set of data as graphically illustrated in this example.

Serendipitously, this combination of data sets has almost no overlap. With all the *Kroyeria* species restricted to the Carcharhiniformes, and *Kroeyerina* extending over a broad range of host taxa, minimal character conflict or competition occurs,

Although the specific results are not included in this effort, combining this hybrid data matrix composed of *Kroeyerina* and *Kroyeria* with the recoded *Eudactylina* cladogram resulted in thousands of rival trees with heavily conflicting topologies (data set may be obtained from the author). Surveying hundreds of these trees revealed that each tree possessed subsets of clades from each of the three data sets. Due to the differential possession (via sampling bias or extinction) of a given parasite group or groups, members of putative host clades apparently well resolved in the independent analyses would be ripped away from one another. The general problem here has been touched upon superficially by Page (1994) and specifically herein by me. The problem is in the treating of parasites strictly as characters and not as lineages with their own

independent histories. Generating a host phylogeny with multiple parasite lineages that are differentially possessed by the host complex under analysis is somewhat analogous to generating a copepod parasite tree based on the maxilliped from a couple of species of one genus, the antennae of another, and on the legs from yet another with only some of these characteristics overlapping across the taxa under study. The result will be uninterpretable noise and artifact at best. If cladists recognize that clades or lineages, have independent histories, then single parasite lineages are what cospeciation analyses should focus on. Despite this, informative analyses are possible if the parasite taxa are restricted to: 1) a single lineage, 2) multiple parasite taxa equally distributed and weighted across the host axis, or 3) parasite lineages that occur in different host lineages minimizing character conflict. This is nothing more than following the same protocol one follows in using typical character data. Point one is analogous to character state analysis of a single character, point two is the same as undifferentially using all character data available from organisms, and point three is equivalent to synapomorphic or autapomorphic character data distributions. Therefore, though combined analyses may consolidate information into a single tree under the above conditions, cladograms may offer more information separately than when combined in other situations. Subsequent tree comparison or tree reconciliation methodologies can proceed from that point. Of course tree comparison/reconciliation can be conducted with the parasite or associate phylogeny directly, a parasite-derived host phylogeny need not be generated *a priori*.

COMPETING HOST CLADOGRAMS

The several parasite-derived host cladograms generated herein function as independent tests or hypotheses of other elasmobranch phylogenies previously reported in the literature.

Two of the most comprehensive phylogenetic analyses of relationships of the squaloids, squatinids, pristiophorids (Shirai, 1992a, b), and batoids (Nishida, 1990) are hybridized herein for comparative purposes (Figure 115), with the irrelevant or non-parasitized host taxa excluded. The topology is not as different as it appears compared to that of *Eudactylina*-derived host trees (Figures 66 and 67). As previously mentioned, the *Eudactylina*-derived cladogram contains two distinct estimates of the host cladogram. One (read from left to right) bracketted by *Manta* and *Mustelus*, is essentially a carcharhinid clade with a host capture to derived epipelagic myliobatids. The other bracketted by *Squalus* and *Urolophus* is a clade infecting the Squalea. The parasite-derived host tree corroborates Shirai's (1992b) postulate of a paraphyletic assemblage

of shark-like squaloids, and the monophyly or existence of the hypnosqualea, consisting of *Squatina* as the sister taxon to the pristiophorid plus batoid clade. The parasite data posits a more basal placement for *Squalus* relative to the etmopterids *Aculeola* and *Etmopterus* than does Shirai (1992b).

The batoid relationships from Nishida (1990) show genera (in ascending order) *Torpedo*, *Rhinobatus*, and *Raja* existing as a paraphyletic grade. The parasite-derived host tree suggests the possibility of monophyly for these respective taxa. In a somewhat complementary approach, Heemstra and Smith (1980) hypothesize a monophyletic *Raja* plus *Rhinobatus* with *Torpedo* as the sister taxon to that clade. Nishida (1990) places both *Dasyatis* (Dasyatidae) and *Urolophus* (Urolophidae) as the sister group to *Gymnura* (Gymnuridae) plus *Myliobatis*, *Rhinoptera*, *Manta*, and *Mobula*, his Myliobatidae. The parasite-derived host tree is very similar except the group composed of ((*Urolophus*) (*Gymnura*, *Dasyatis*)) is the sister group to *Myliobatis*. The supposed horizontal transfer or colonization of the eudactylinid-infecting rhinopterid-mobulid clade from the carcharhinid lineage is congruent with the relationships proposed by Nishida (1990) with the exception that the parasite-derived host tree yields greater specific resolution between the sampled species of *Mobula* and *Manta*.

With regard to carcharhiform relationships, a cladogram deduced and hybridized from Compagno's (1988) many cladograms and text is presented in Figure 116A. An additional cladogram derived from molecular data (Naylor, 1992) is presented in Figure 116B. Again, non-parasitized host taxa have been excluded from the host trees. Keep in mind different host taxa are involved because many more squaloids and batoids host *Eudactylina* than do carcharhinids, many more carcharhinids host *Kroyeria* than do the squaloids and batoids, and different sets of hosts were used from that herein, with Compagno's (1988) and Naylor's (1992) analyses. Host relationships derived from *Eudactylina* postulate an unresolved group composed of *Chiloscyllium punctatum* (an orectolobid), *Rhizoprionodon acutus*, *Carcharhinus brevipinna*, *Carcharhinus limbatus*, and *Sphyrna lewini* to be the sister group to the rest of the tree; these four all harbor *E. aspera*. The next carcharhiform group is composed of triakids *Mustelus* and *Galeorhinus*. This is sister group to a clade composed of *Galeocerdo* which, with the clade of rhinopterid-mobulid colonizers removed, is sister taxon to a clade composed of *Sphyrna* which is the sister group to a small *Carcharhinus* clade. Additionally, if the host association of *E. aspera* on the orectolobid, *Chiloscyllium* represents host-parasite co-divergence, and if the other records of *E. aspera* indicate colonization of this species to those four carcharhinid hosts, then the parasite-derived host phylogeny closely parallels the hybrid host tree of Compagno (1988) (Figure 116A). The orectolobid is placed outside the carcharhiform group with the remaining galeomorphs. The triakid genera

Triakis, *Mustelus*, and *Galeorhinus* though shown to be monophyletic with the parasite tree, are hypothesized to be paraphyletic by Compagno (1988), even though he assigns them to Triakidae. *Galeocerdo* is the sister taxon to the sphyrnids and carcharhinids as in the *Eudactylina*-derived host tree. Interestingly, the host and parasite-derived cladograms show *Sphyrna tiburo* as sister taxon to *S. lewini* and *S. mokarran*. Additionally, both host morphological and molecular cladograms show *Carcharhinus acronotus*, well separated from the more closely related *C. plumbeus* and *C. obscurus*, while the *Eudactylina*-derived host cladogram (Figure 66) leaves the three as an unresolved polytomy. All three trees suggest *C. obscurus* and *C. plumbeus* are closely related.

The combined *Kroyeria* plus *Kroeyerina*-derived host cladogram (Figure 114) shows the holocephalan to be the sister group to the remaining members of the tree, or to all extant elasmobranchs as Maisey (1984a) has shown. The parasite-derived host cladogram shows batoids to be removed from the next node and postulates sister group relationships of Carcharhiniformes and Lamniformes (*Alopias* and *Isurus*), as Compagno (1988) has suggested. The *Kroyeria*-*Kroeyerina*-derived host tree implies that the tiger shark, *Galeocerdo cuvier* is the most basally placed carcharhinid of this data set. Hence the Triakidae is situated between sphyrnids and *Galeocerdo*. This relationship is not supported by the host morphology-based cladogram (Figure 116A) of Compagno (1988), nor by the host molecular-based cladogram (Figure 116B) of Naylor (1992). This arises because of the many plesiomorphic character states found in *Kroyeria dispar* and *Kroyeria papillipes* which are specific to *Galeocerdo*. Because cladistic analyses form groups on shared derived characters (synapomorphies) there is a possibility of species or groups of species being split off near the base of a cladogram because plesiomorphic characters invoke no particular groupings (Lamshead and Paterson, 1986). Although there is much evidence placing *Galeocerdo* outside of the main body of *Carcharhinus* (see Compagno, 1988 and Naylor, 1992) it is currently recognized as a member of the Carcharhinidae.

Lavery (1992) in his phylogenetic analysis of carcharhinids from Australia using allozyme electrophoresis concluded *Galeocerdo* may be more closely related to sharks of the Hemigaleidae (weasle sharks), traditionally placed between the Triakidae and *Galeocerdo* (Compagno, 1988 and Maisey, 1984b). Compagno (1988) mentions that little has been done to elucidate the relationships of *Galeocerdo* because of its distinctiveness and ubiquity which invites neglect. Applegate (1978) compared dental and external morphology of *Galeocerdo* with a few triakids. It also shares similarities with the Hemeigaleidae with regards to the nasal fontanelles. Additionally, many *Galeocerdo* characters (see Compagno, 1988 for a comprehensive list) are primitive

characters by virtue of comparison with hemigaleids, triakids, proscylliids, scyliorhinids, and noncarcharhinoid sharks. Many of these characters make *Galeocerdo* a transitional form between hemigaleids and the subfamily Carcharhininae, and through hemigaleids the Triakidae (Compagno, 1988). Compagno (1988) adds several characters such as the very short snout, serrated and anaulacorhizous teeth, caudal keels, basin-like rostrum, pits and keels in front of the anterior fontanelle, great size, massive jaws, *Carcharhinus*-like arrangement of dorsal and anal fins, and high vertebral number are probably derived characters, suggesting that it is specialized away from its common origin with the rest of the carcharhinids but has evolved in parallel with the large macro-predatory species of *Carcharhinus*, *Glyphis*, *Negaprion*, and *Prionace*. *Galeocerdo* is probably the most primitive living carcharhinid, and may be closer to the common ancestry of all carcharhinids than any other living member of its family. It is probably the primitive sister group of all other carcharhinids plus the Sphyrnidae. If these *Carcharhinus*-like characteristics are in fact parallelisms or homoplasies, and the aforementioned primitive characteristics are found in even more basally placed families (Proscylliidae and Scyliorhinidae) than the Triakidae, then perhaps the *Kroyeria-Kroeyerina*-derived host cladogram placing *Galeocerdo* below the Triakidae describes an accurate relationship not readily embraced by current ichthyologists. The most parsimonious explanation for the basal placement of *Kroyeria dispar*, *Kroyeria papillipes*, and *Kroeyerina elongata*, in their respective genera is one of host-parasite co-divergence, not three independent host captures by three plesiomorphic parasites, further corroborating the unorthodox placement of *Galeocerdo* in the *Kroyeria-Kroeyerina*-derived host cladogram. In any case, *Galeocerdo* appears to remain somewhat of an enigma, basally placed within the Carcharhinidae or possibly even outside that family.

The next clade of the *Kroyeria-Kroeyerina*-derived host cladogram (Figure 114) posits a monophyletic Triakidae with a monophyletic *Triakis* clade as the sister group to a clade composed of a paraphyletic *Galeorhinus* plus *Mustelus*. Host morphology (Figure 116A) depicts a paraphyletic grade consisting of, in ascending order *Triakis*, *Mustelus*, and *Galeorhinus*. A clade composed of ((*Sphyrna mokarran*)(*Sphyrna lewini*, *Sphyrna zygaena*)) is found next in the parasite-derived tree (Figure 114). Relationships among these sphyrnids are unresolved in the morphological and molecular cladograms.

The parasite-based tree suggests that *Carcharhinus* is paraphyletic, including with it *Prionace*, *Negaprion*, and *Rhizoprionodon*. This placement of *Prionace* is in general consistent with its placement in morphologically-based and molecular-based host trees. Furthermore, *Negaprion* is nested within *Carcharhinus* in the morphologically-based tree, and Lavery (1992) reached a similar conclusion in an allozyme study of car-

charhinids. Morphologically-based and molecular-based trees treat *Rhizoprionodon* as external to *Carcharhinus*. This discrepancy in the parasite-derived host tree may be the result of parasite colonization or host misidentification.

SUMMARY AND CONCLUSIONS

A systematic revision and phylogenetic analysis was conducted for 26 of the 38 nominal species of *Eudactylina*, and for 16 of the 18 nominal species of *Kroyeria*. Nine new species of *Eudactylina* and five new species of *Kroyeria* are described herein. A new host record for *Kroeyerina cortezensis* from *Carcharhinus longimanus* is included. Parasite-derived host phylogenies were generated from the recoded (additive-binary) *Eudactylina* and *Kroyeria* cladogram topologies and combined in part with the previously revised and phylogenetically analyzed *Kroeyerina*. Congruent host and parasite topologies from both holocephalan and elasmobranch hosts suggest the existence of well established host-parasite associations as early as the late Devonian approximately 400 MY.

The parasite-derived host phylogenies generated from *Eudactylina* hypothesized the monophyly of the squaloids, squatinids, pristiophorids and batoids. This corroborates the revolutionary findings of Shirai (1992a, b) in which he proposed a radically new systematic framework for squaloids and related taxa, the Squalea and Hypnosqualea. *Eudactylina*-derived batoid relationships were similar to previous hypotheses of these host groups. Parasite cladograms resolved batoid species relationships previously not addressed in the literature. The parasite-derived host phylogenies generated from *Kroyeria* and from *Kroyeria* combined with *Kroeyerina* posits the paraphyly of the genera contained within the Carcharhinidae. Again with the exception of the basal placement of *Galeocerdo* below the Triakidae, the parasite-derived cladograms are generally congruent with the molecular and morphological host cladograms previously generated by other authors and presented herein.

Parasite-derived phylogenetic relationships of a subset of species from *Squatina* and *Myliobatis* indicate a speciation pattern consistent with major vicariant events associated with the Pangaeian breakup during the Jurassic period approximately 160 MY.

If taxonomic congruence (analysis of the congruence between topologies produced from independent data sets) is preferable to character congruence (analysis of the congruence between individual characters) for estimating the accuracy of phylogenetic hypotheses (Lanyon, 1993), then it appears that parasite-derived host phylogenies offer much information in conjunction with the conventionally-derived (morphologi-

cal and molecular data) phylogenetic hypotheses. Continued host and parasite collections and future research utilizing existing (e.g., combinable components, tree reconciliation) and developing (such as Page's TREEMAP) methods for examining taxonomic congruence will improve upon the effort offered herein. Future efforts with these methods should yield more information regarding the tectonic history of our planet by generating an even more robust phylogenetic framework for both classes of these amazing biological entities, the elasmobranchs and their parasitic copepod fauna.

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FIGURES

FIGURE 1. *Eudactylina oliveri* Laubier, 1968 attached to gill filaments of *Mobula thurstoni* (Lloyd 1908). Scale: 3.0 mm.

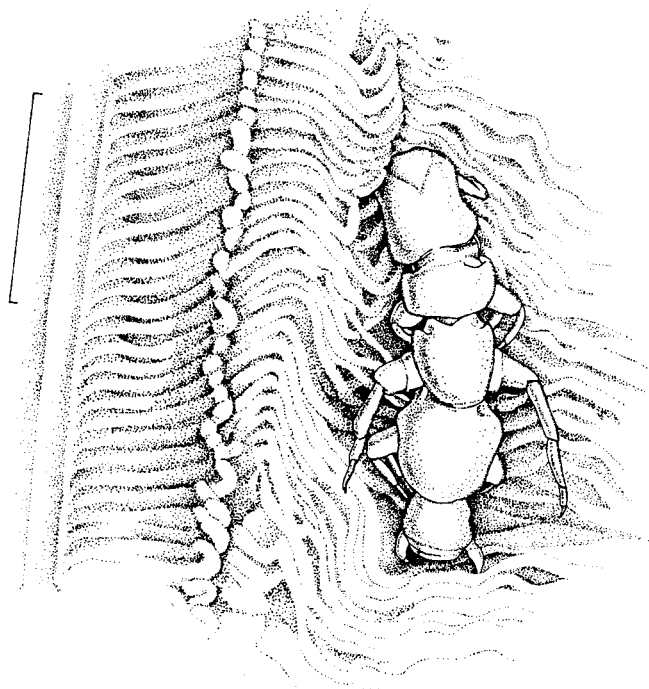
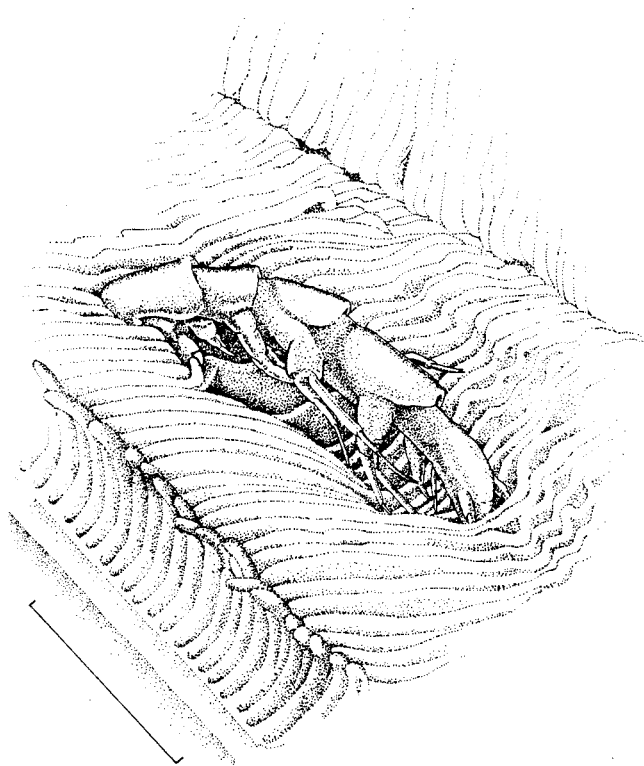


FIGURE 2. *Eudactylina acanthii* A. Scott, 1901 female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 1.0 mm in A; 0.1mm in B-F; 0.2 mm in G, H.

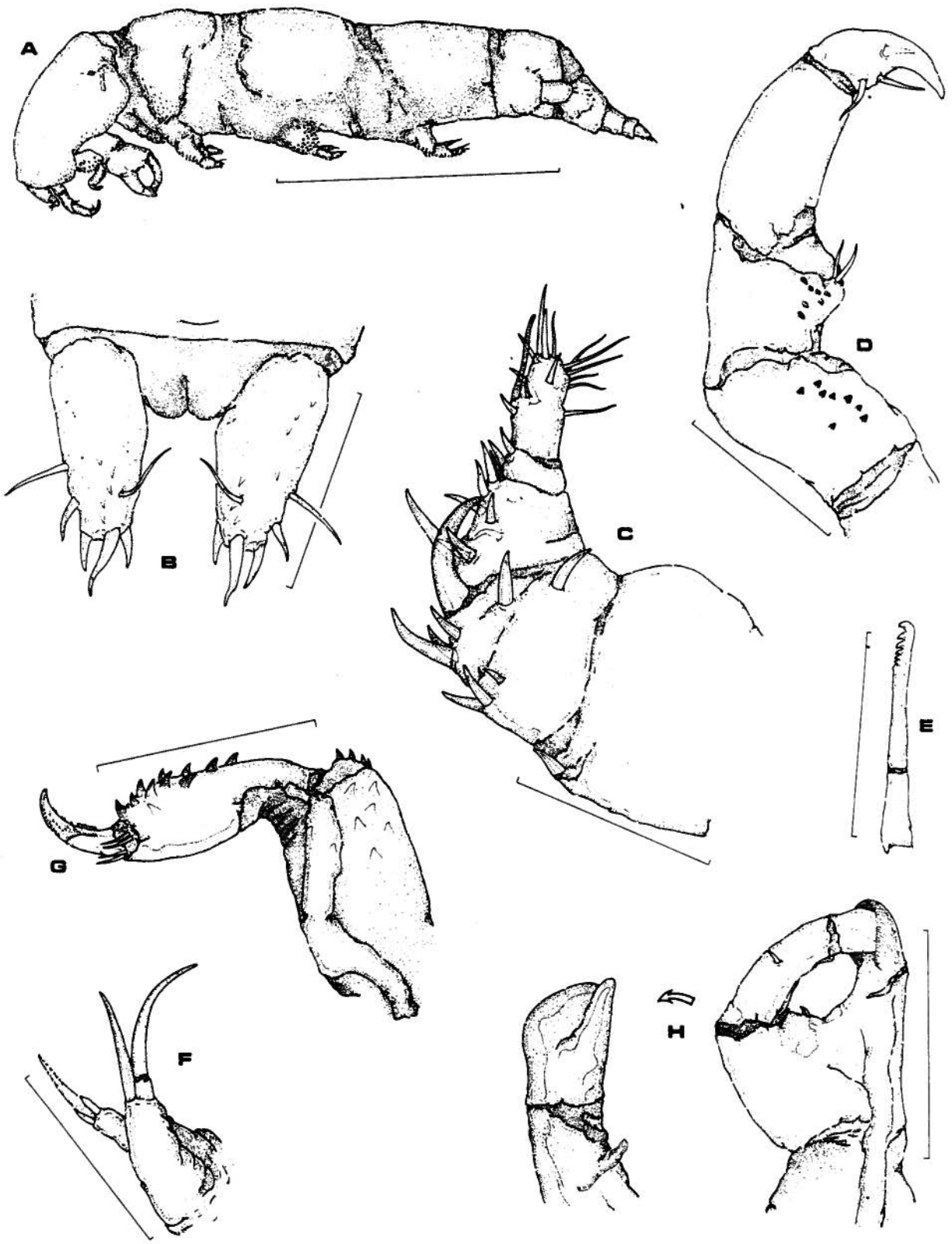


FIGURE 3. *Eudactylina acanthii* A. Scott, 1901 female: A, leg 1; B, leg 2; C, leg 3 and 4; D, leg 5 and 6. Scales: 0.1 mm in A; 0.2 mm in B-D.

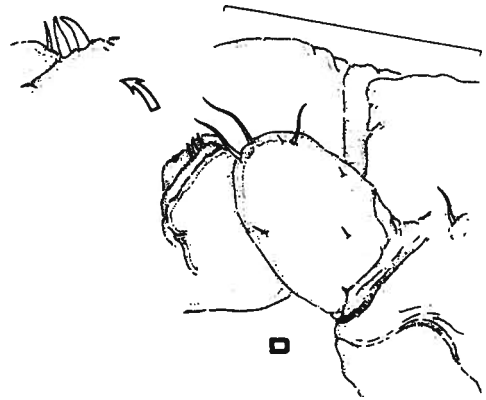
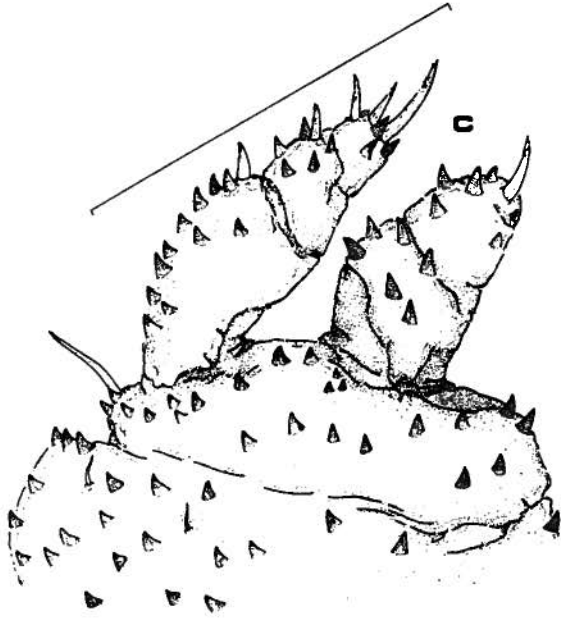
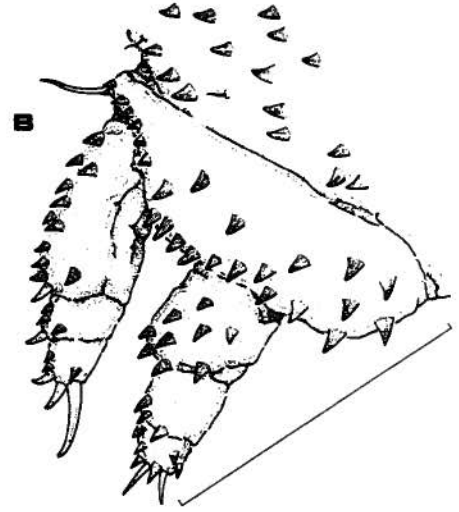


FIGURE 4. *Eudactylina acuta* van Beneden, 1853, female: A, habitus, lateral; B, caudal ramus; C, abdomen and egg strings; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H, second maxilla; I, maxilliped. Scales: 0.3 mm in A; 0.05 mm in B-I.

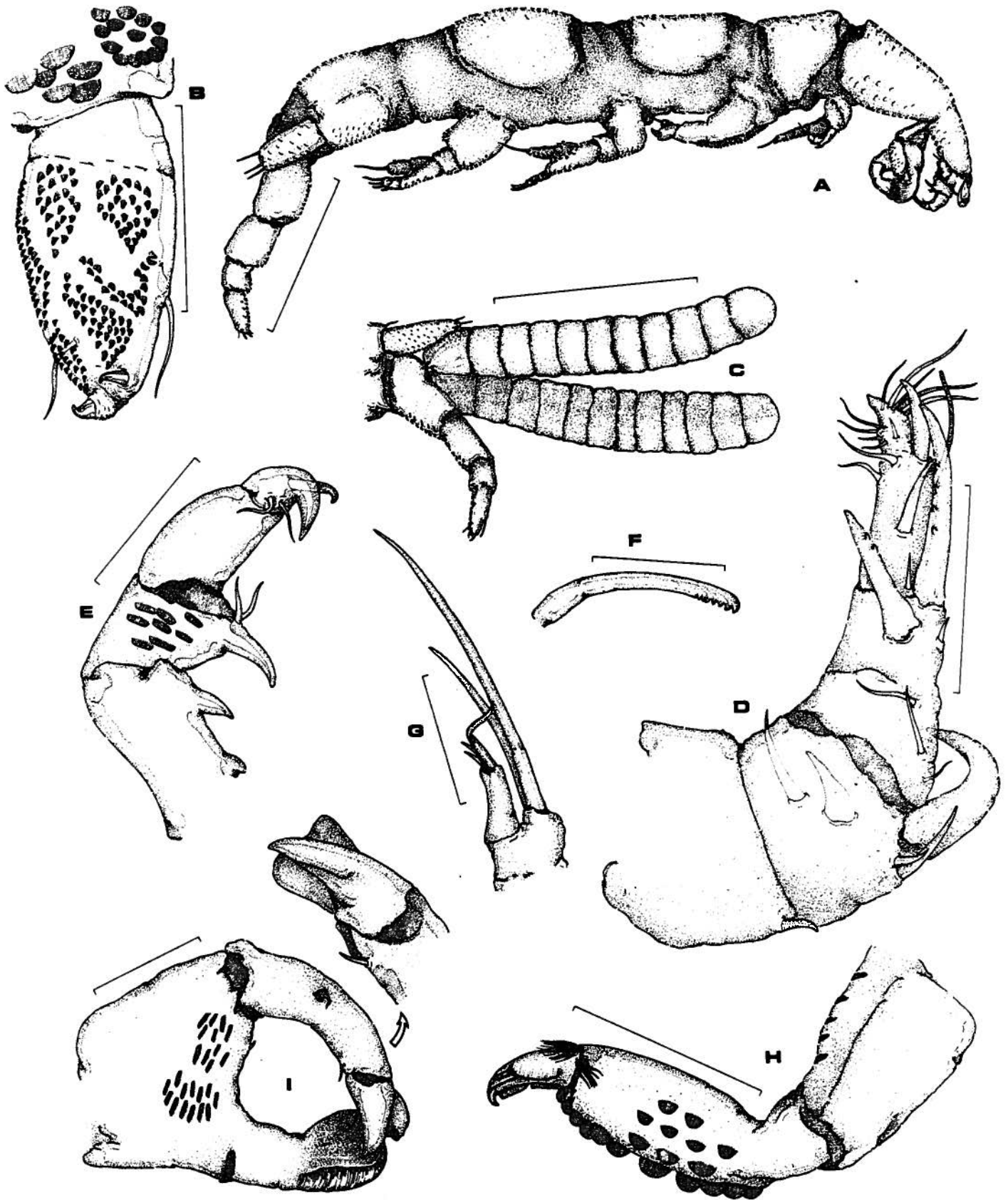


FIGURE 5. *Eudactylina acuta* van Beneden, 1853, female: A, leg 1, ; B, leg 2 exopod; C, leg 2 endopod; D, legs 3 and 4; E, tines on seta from terminal segment of exopod from legs 3 and 4. Scales: 0.05 mm in A-E.

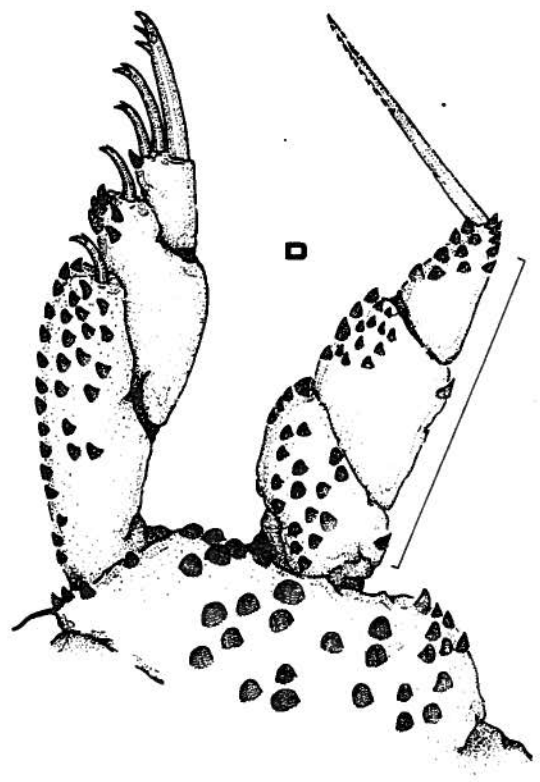
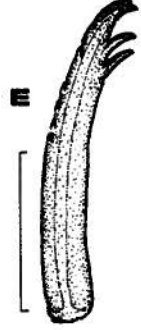
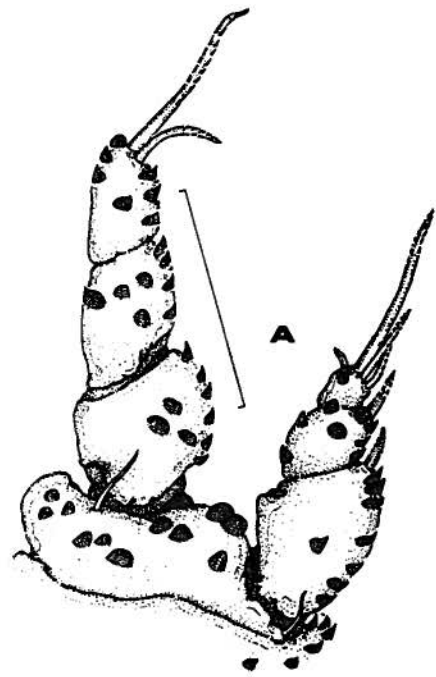
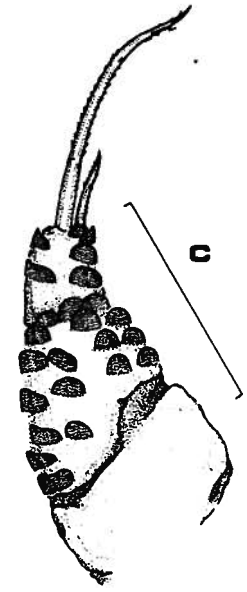
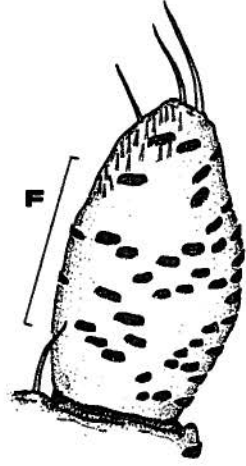
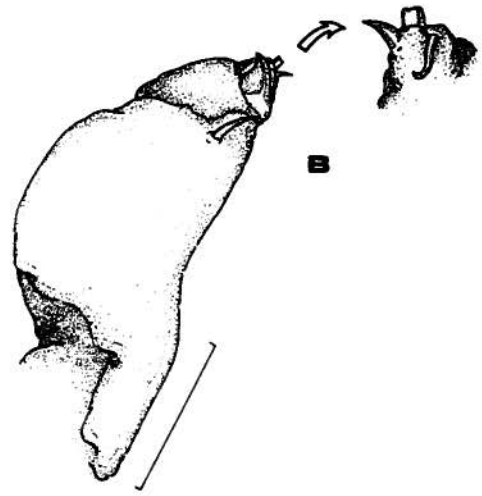


FIGURE 6. *Eudactylina aphioxenos* sp. nov., female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 1.0 mm in A; 0.2 mm in B-D; 0.1 mm in E-F; 0.2 mm in G, H.

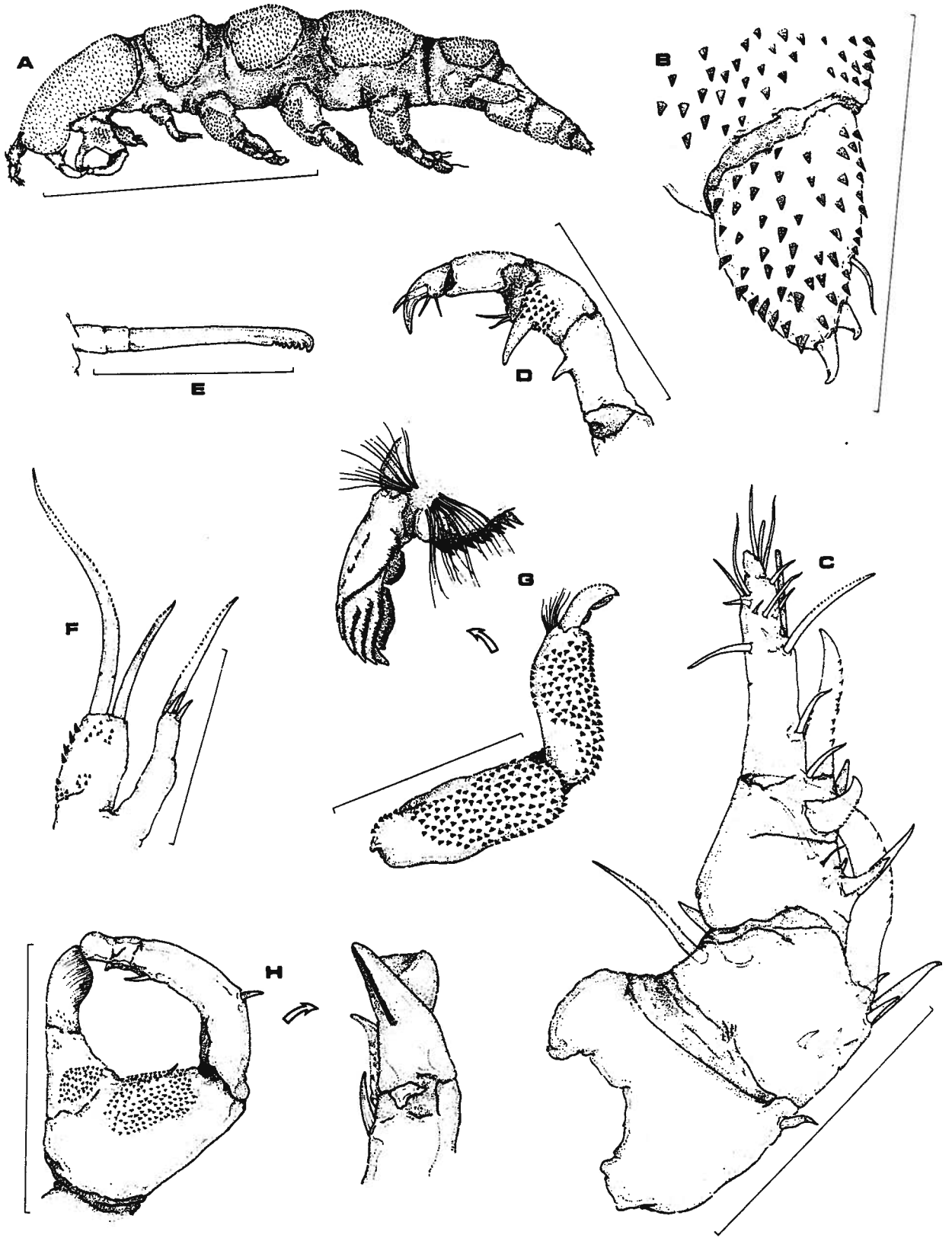


FIGURE 7. *Eudactylina aphioxenos* sp. nov., female: A, leg 1; B, leg 2; C, legs 3 and 4; D, leg 5. Scales: 0.2 mm in A-D.

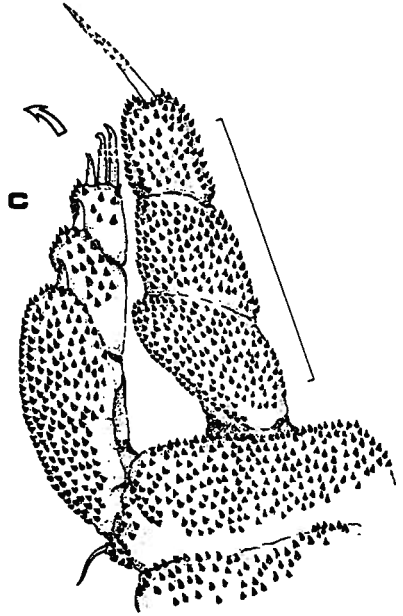
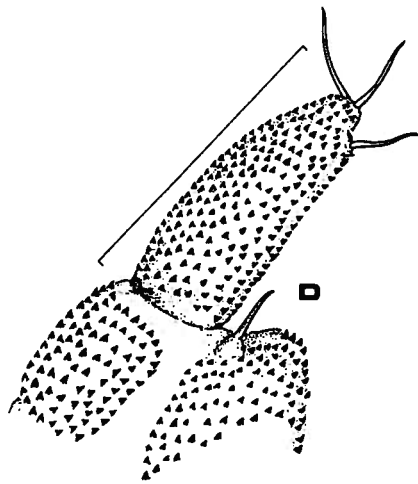
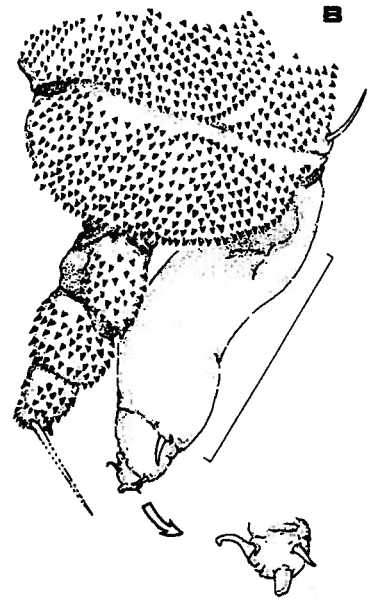
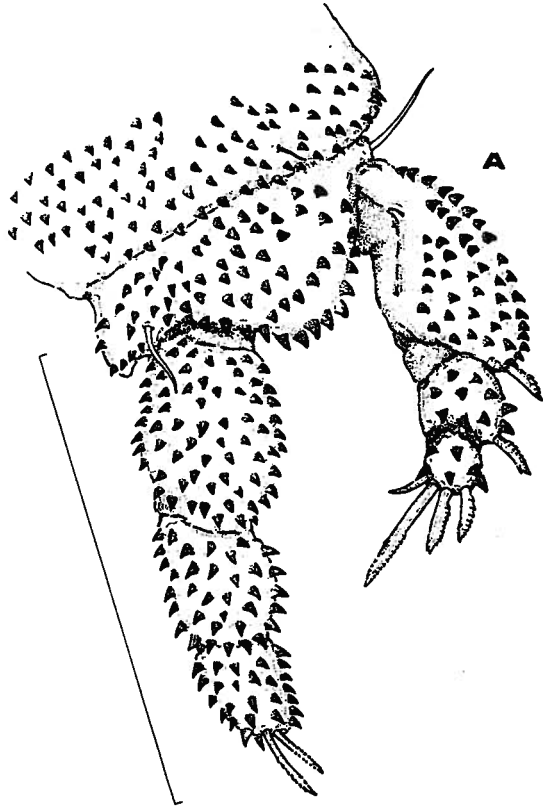


FIGURE 8. *Eudactylina aspera* Heller, 1865 female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.4 mm in A; 0.2 mm in B; 0.1 mm in C; 0.5 mm in D; 0.1 mm in E-H.

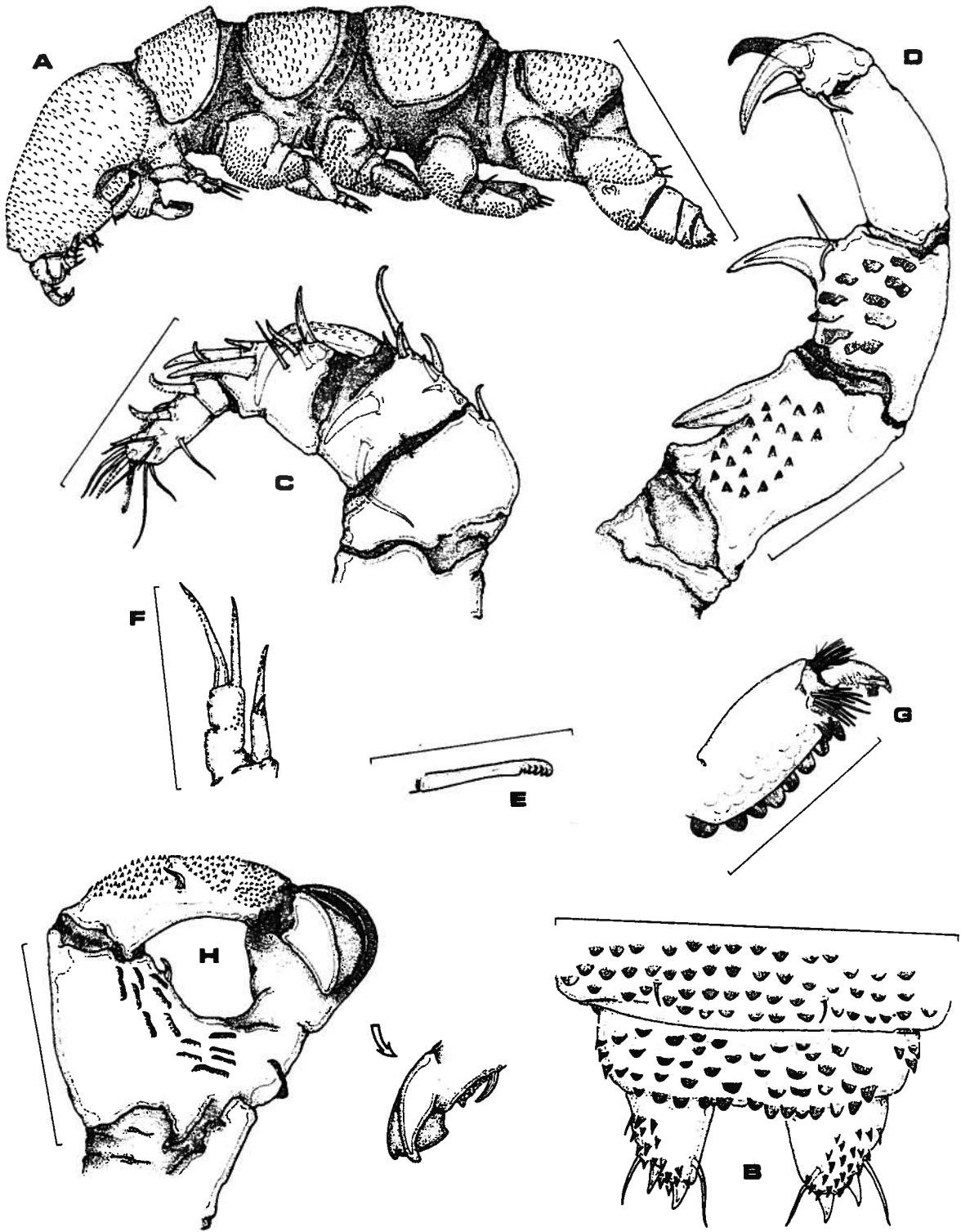


FIGURE 9. *Eudactylina aspera* Heller, 1865 female: A, leg 1; B, leg 2 endopod; C, leg 2 exopod; D, leg 3 and 4 endopod; E, leg 3 and 4 exopod; F, leg 5; maxilla. Scales: 0.1 mm in A-F.

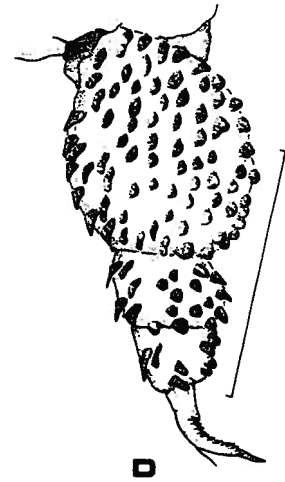
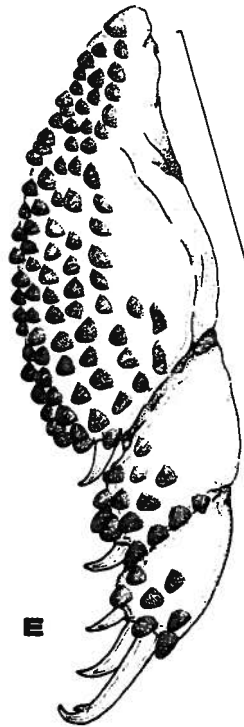
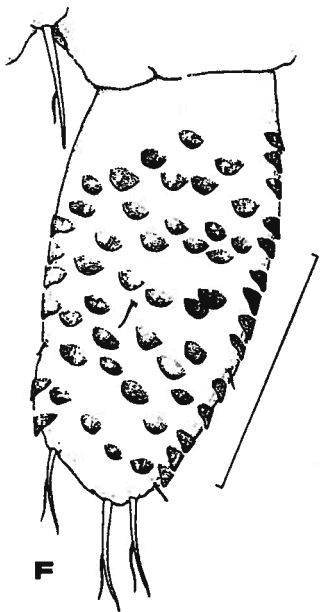
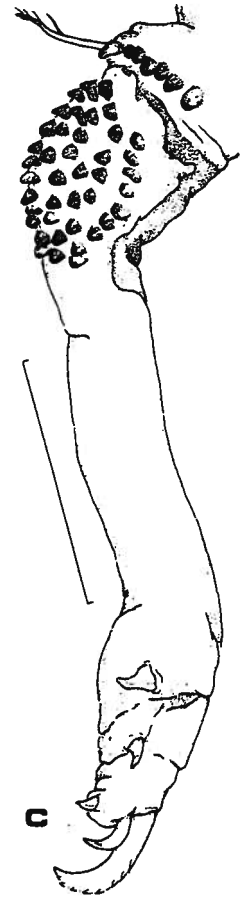
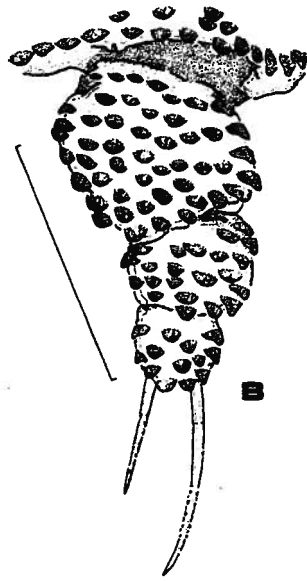
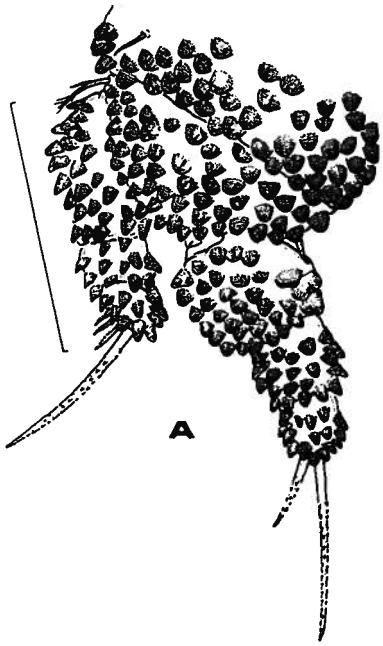


FIGURE 10. *Eudactylina chilensis* Ho and McKinney, 1981, female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.6 mm in A; 0.1 mm in B; 0.2 mm in C; 0.2 mm in D; 0.1 mm in E-G; 0.2 mm in H.

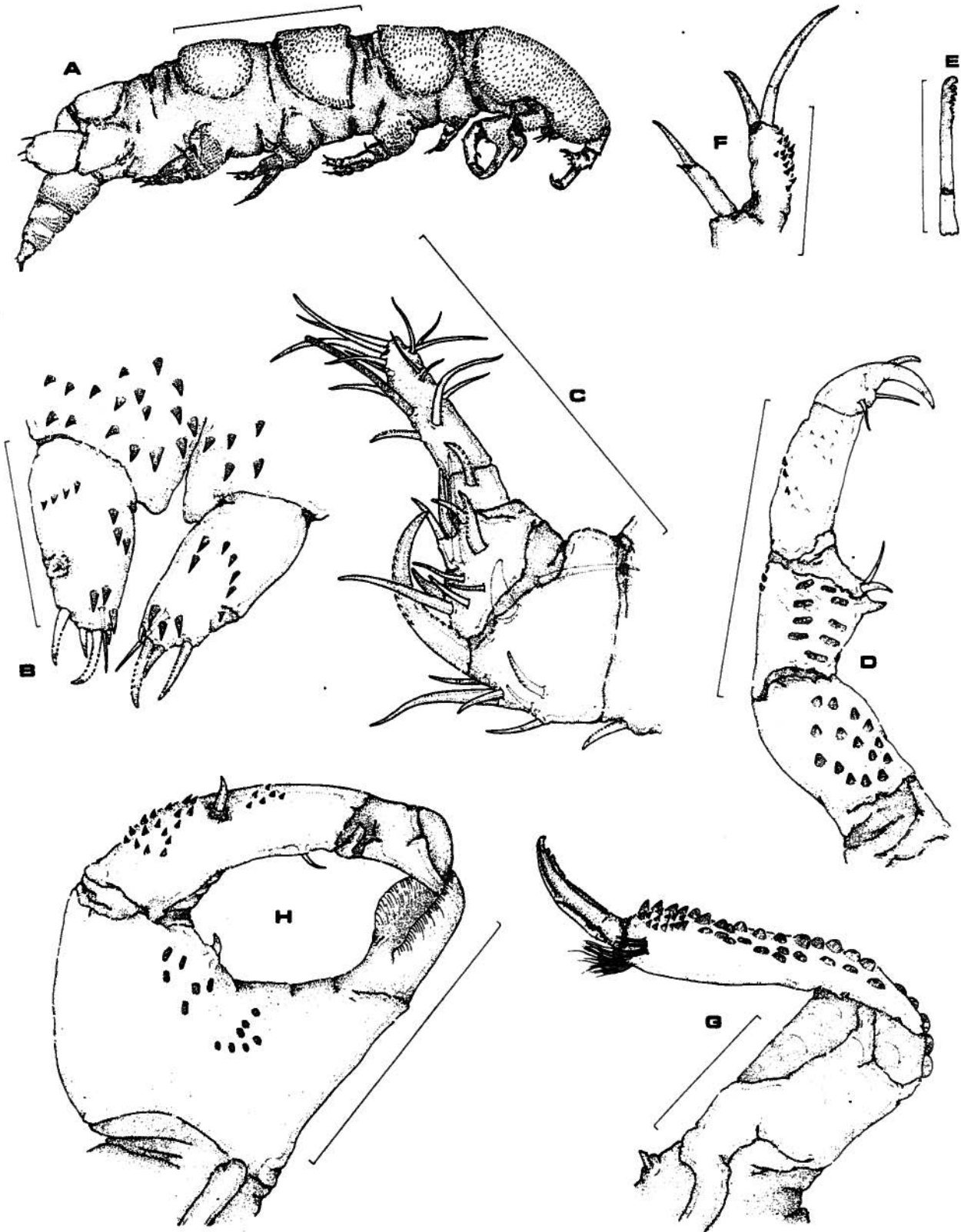


FIGURE 11. *Eudactylina chilensis* Ho and McKinney, 1981, female: A, leg 1; B, leg 2; C, leg 3 and 4 exopod; D, leg 3 and 4 endopod; E, leg 5. Scales: 0.2 mm in A-E.

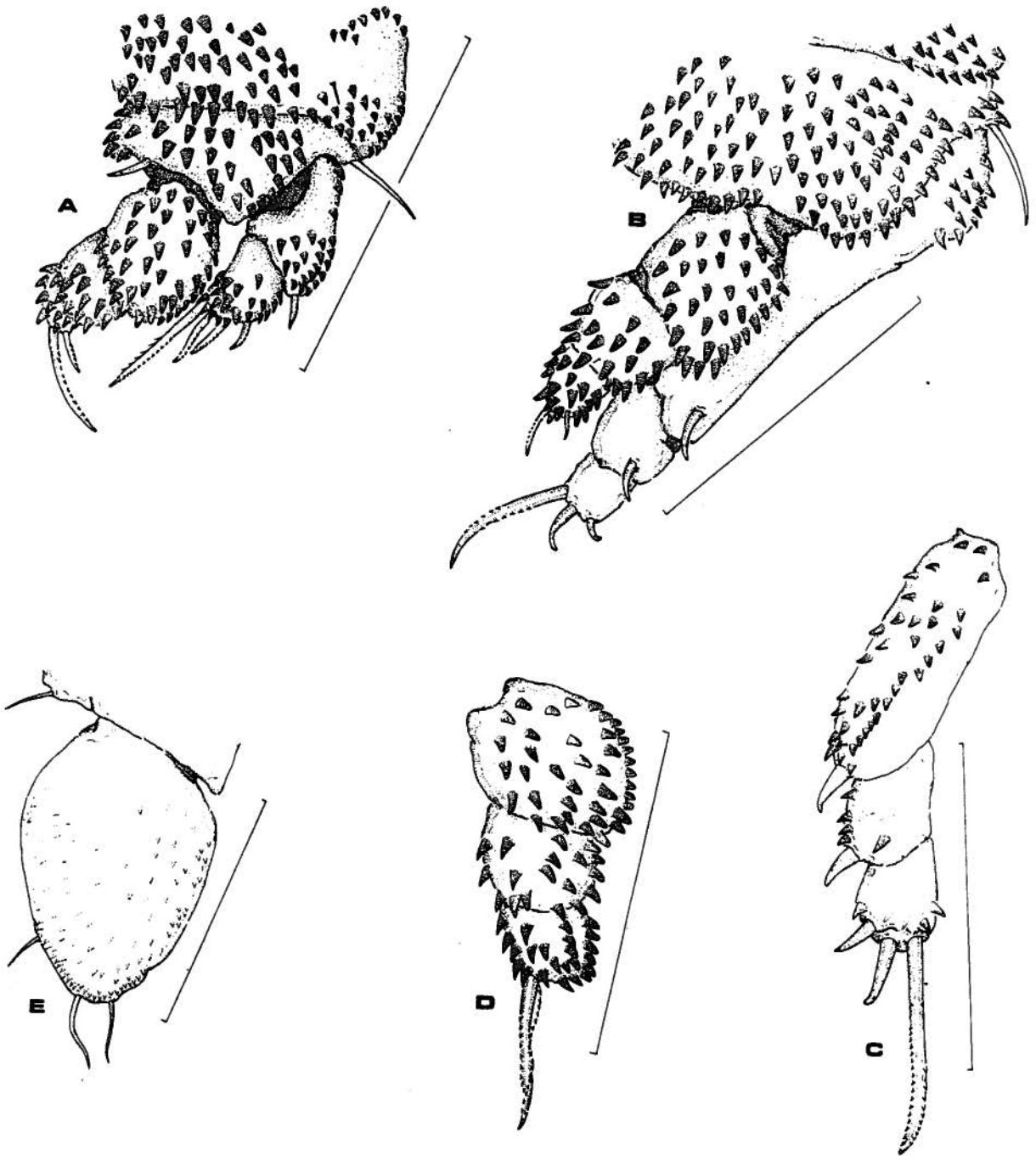


FIGURE 12. *Eudactylina corrugata* Bere, 1930, female: A, habitus, lateral; B, egg string; C, caudal ramus; D, first antenna; E, second antenna; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.6 mm in A; 0.4 mm in B; 0.1 mm in C,D; 0.2 mm in E; 0.1 mm in F-H.

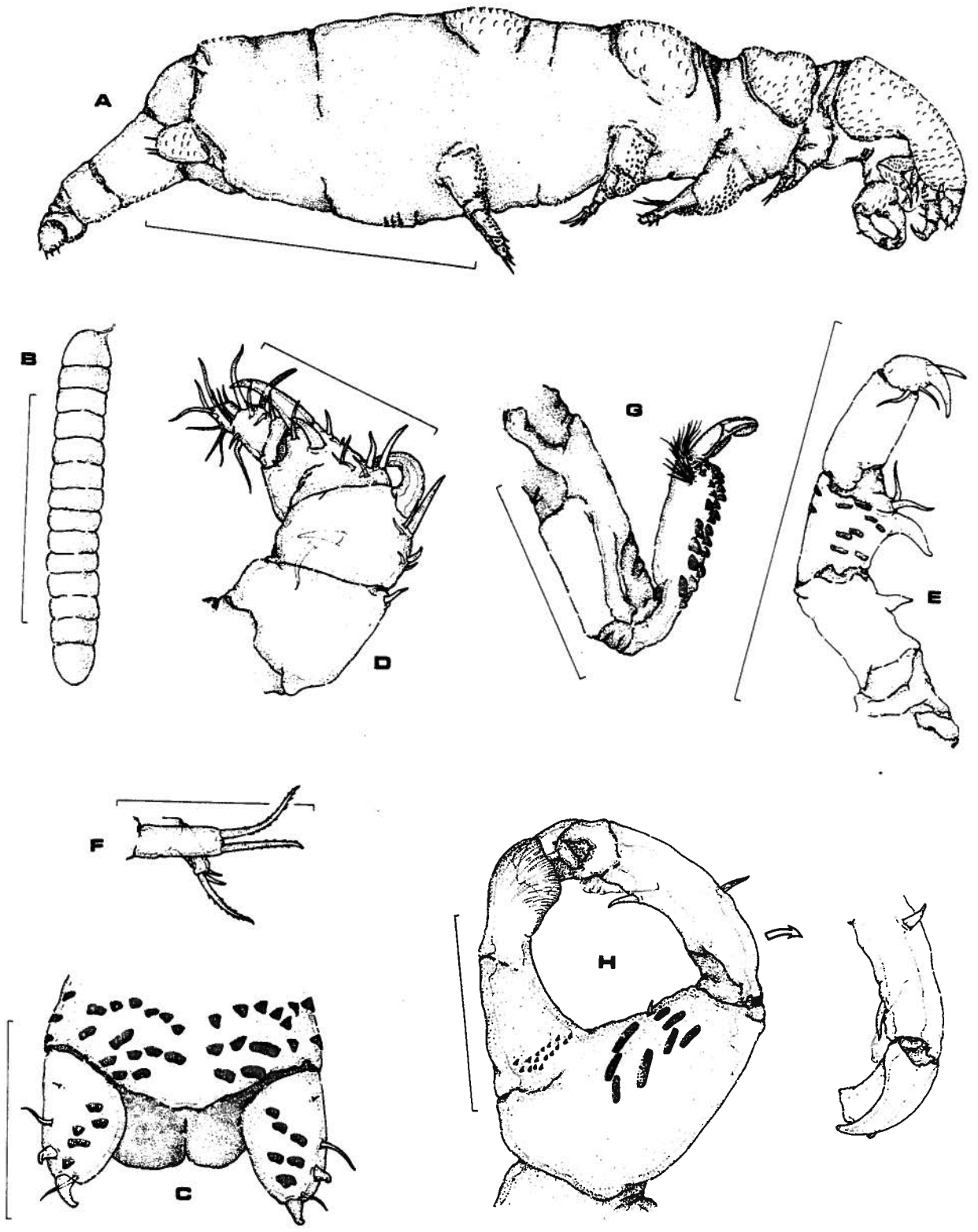


FIGURE 13. *Eudactylina corrugata* Bere, 1930, female: A, leg 1; B, leg 2 endopod; C, leg 2 exopod; D, legs 3 and 4; E, leg 5. Scales: 0.2 mm in A-E.

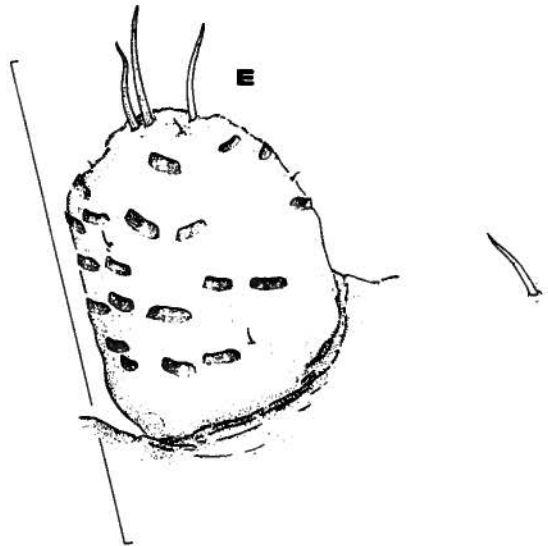
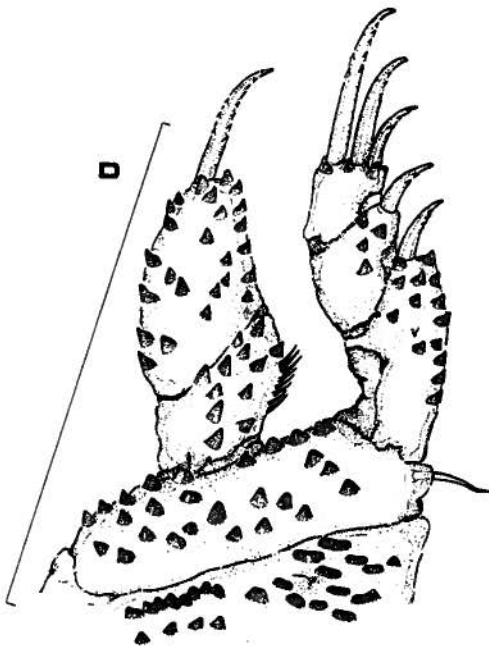
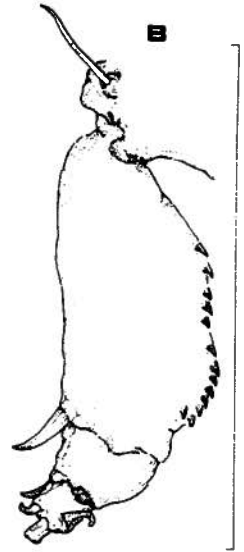
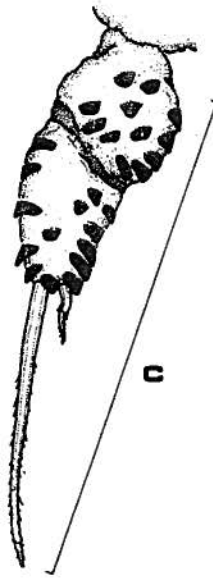
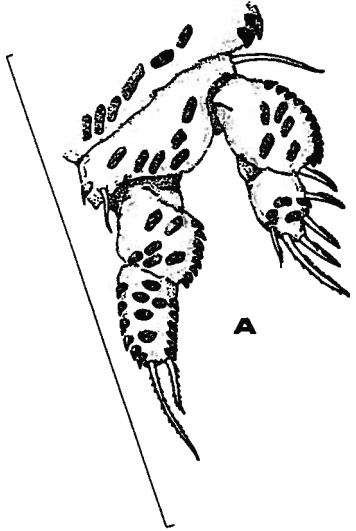


FIGURE 14. *Eudactylina dactylocerca* sp. nov., female: A, habitus, lateral; B, caudal ramus; C, caudal ramus and abdomen; D, egg string; E, first antenna; F, second antenna; G, mandible and first maxilla; H, second maxilla; I, maxilliped; J, claw of maxilliped. Scales: 0.1 mm in A, B; 0.2 mm in C; 0.4 mm in D; 0.1 mm in E-G; 0.2 mm in G, H; 0.1 mm in J.

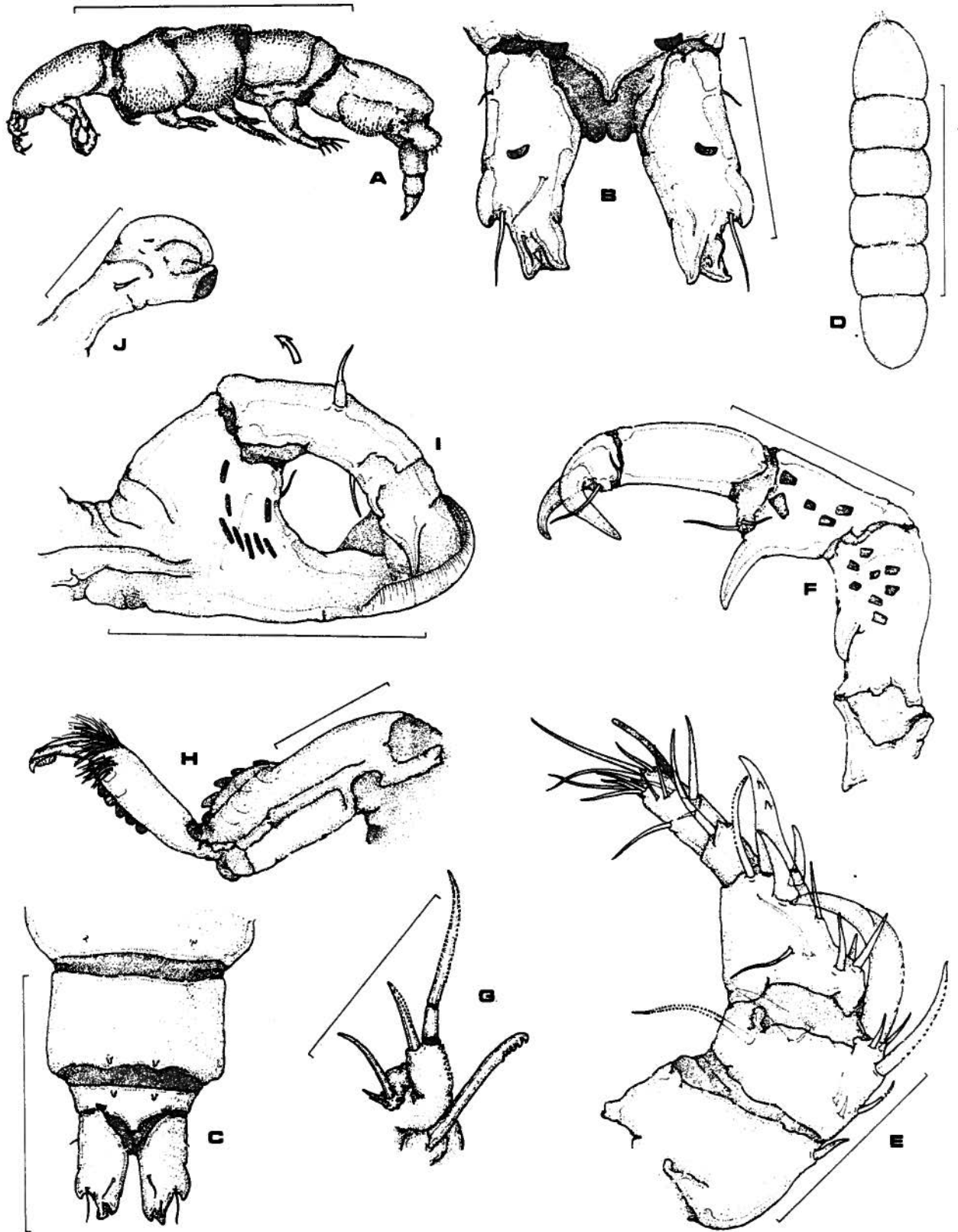


FIGURE 15. *Eudactylina dactylocerca* sp. nov., female: A, leg 1; B, leg 2; C, leg 2 with medial stylet; D, legs 3 and 4; E, leg 5. Scales: 0.1 mm in A, B; 0.2 mm in C-E.

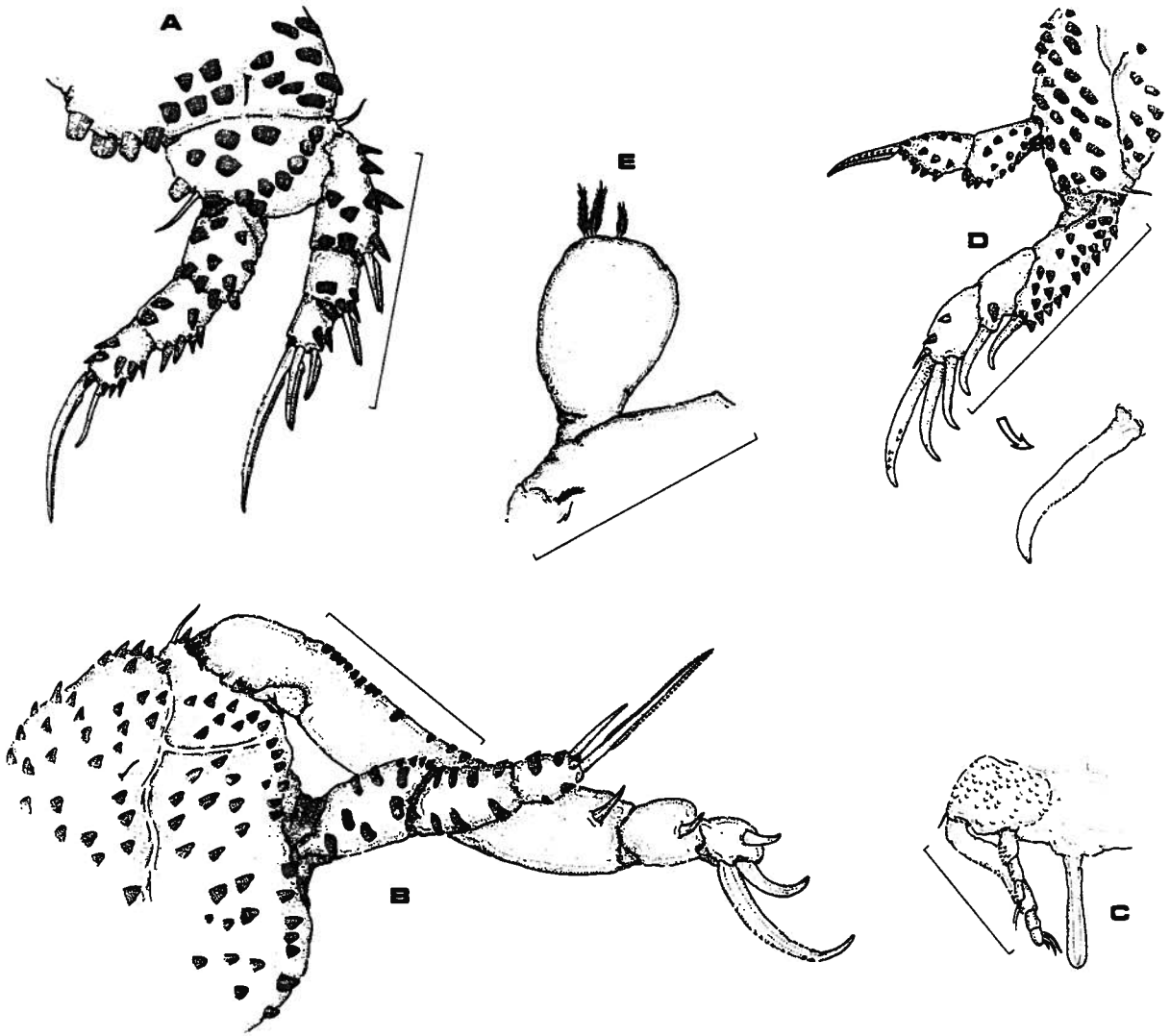


FIGURE 16. *Eudactylina diabolophila* sp. nov., female: A, habitus, dorsal; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 1.0 mm in A; 0.1 mm in B-H.

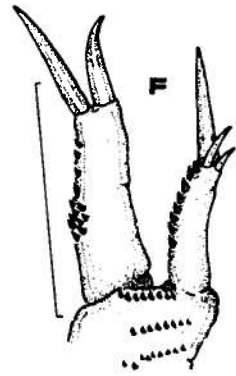
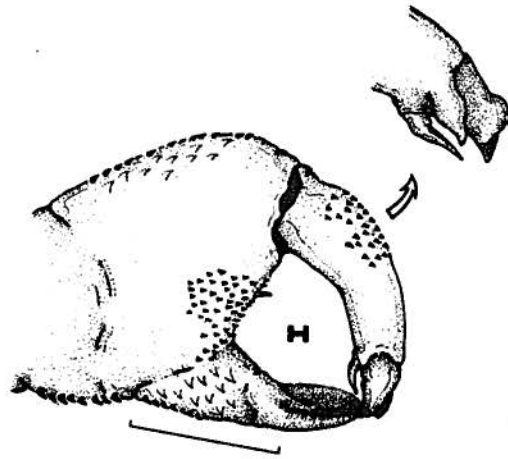
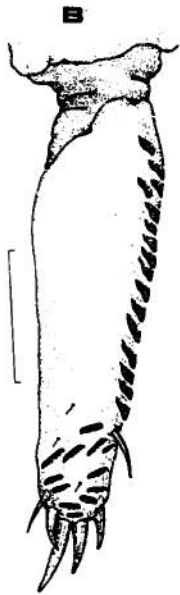
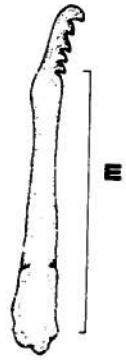
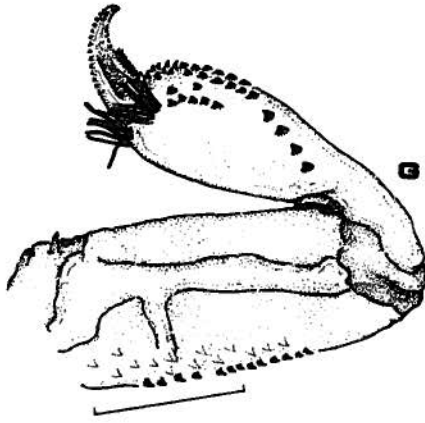
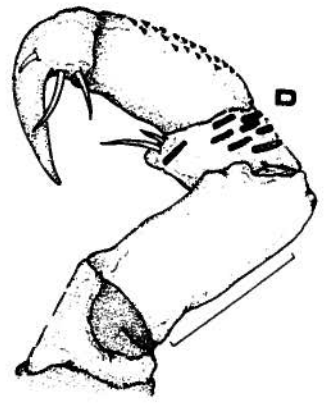
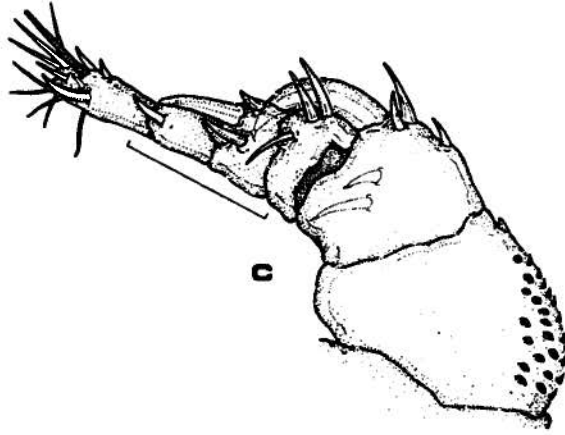
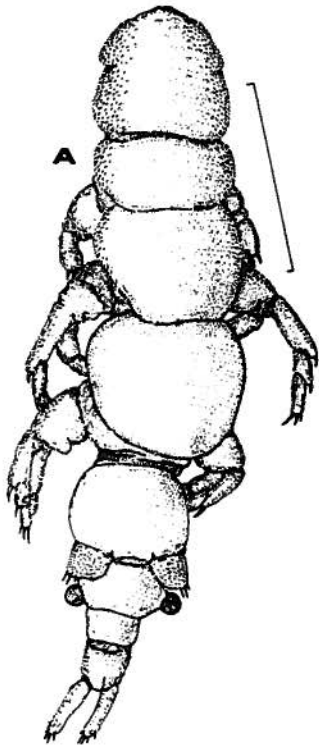


FIGURE 17. *Eudactylina diabolophila* sp. nov., female: A, leg 1; B, leg 2; C, legs 3 and 4; D, leg 5. Scales: 0.1 mm in A; 0.3 mm in B, C; 0.1 mm in D.

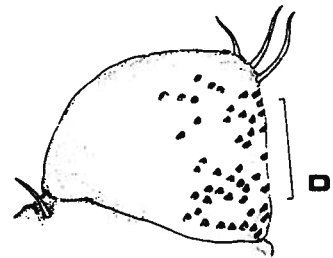
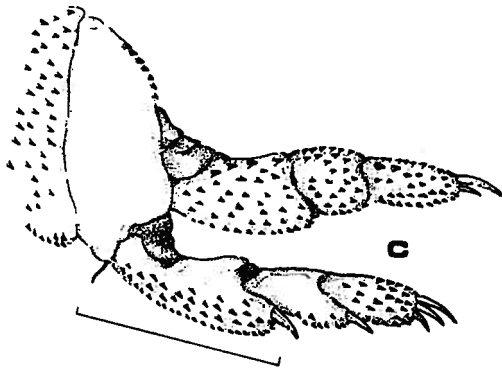
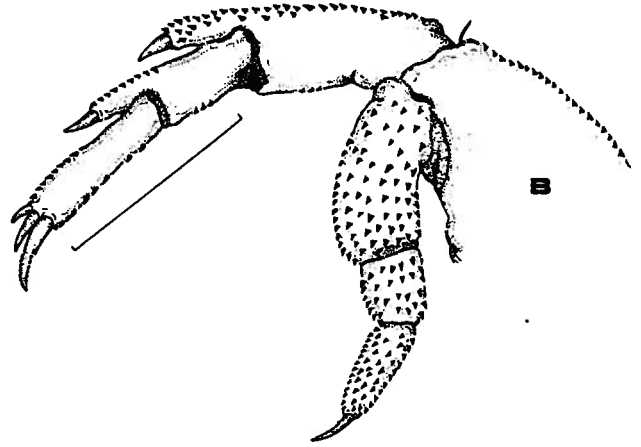
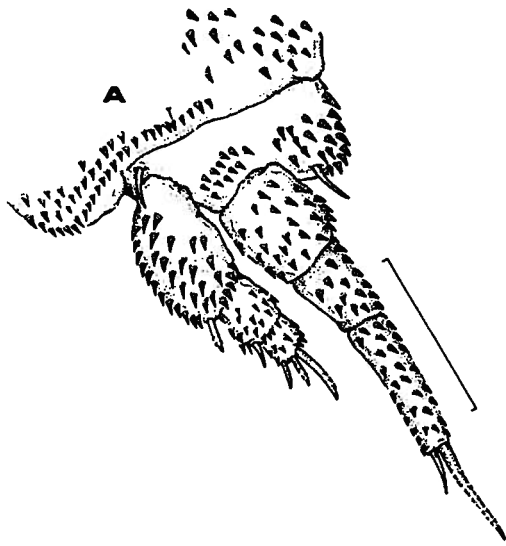


FIGURE 18. *Eudactylina dollfusi* Brian, 1924, female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.4 mm in A; 0.2 mm in B; 0.1 mm in C; 0.2 mm in D; 0.1 mm in E-G; 0.2 mm in H.

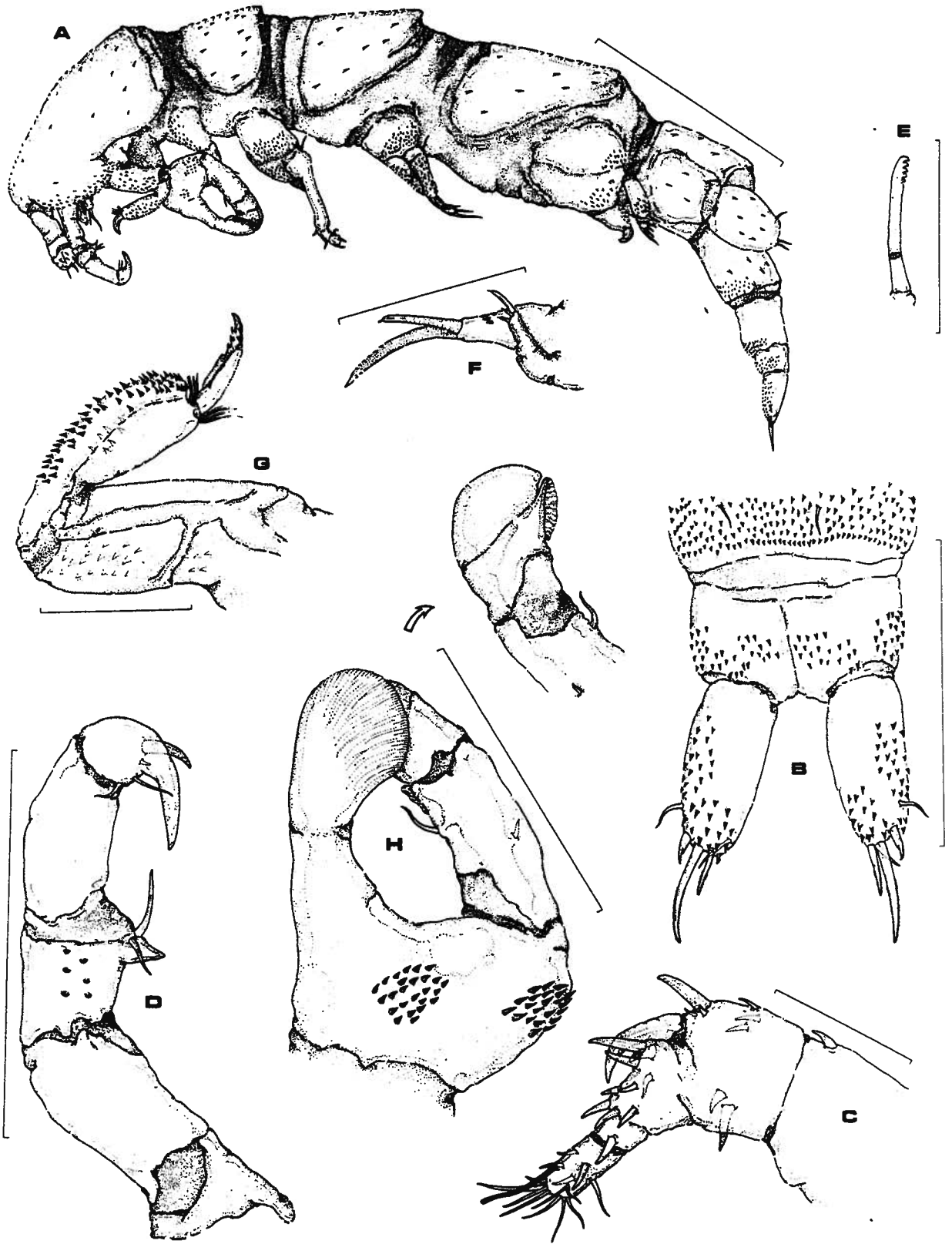


FIGURE 19. *Eudactylina dollfusi* Brian, 1924, female: A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scales: 0.2 mm in A-E.

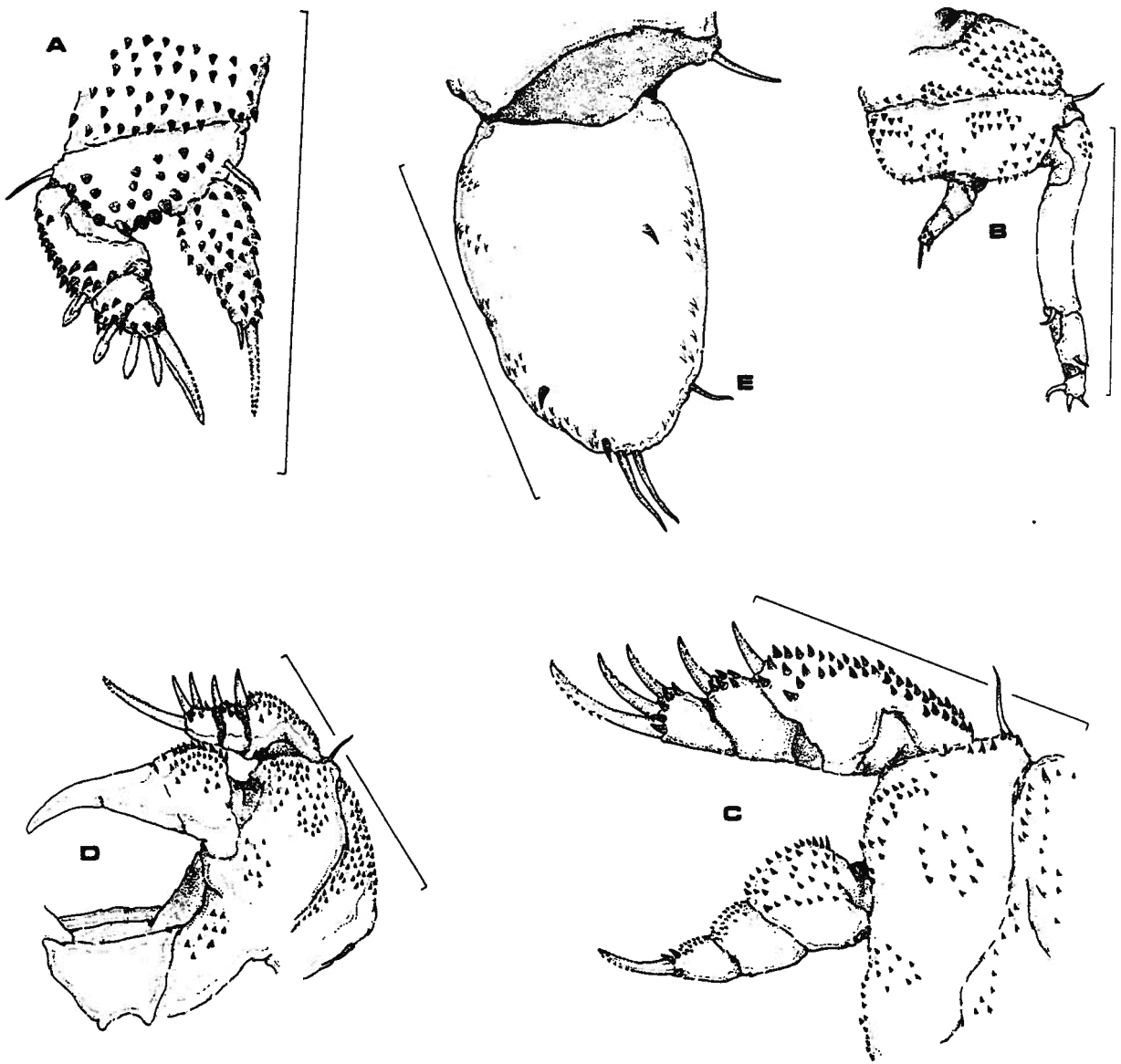


FIGURE 20. *Eudactylina epaktolampter* sp. nov., female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.4 mm in A; 0.2 mm in B-D; 0.1 mm in E-G; 0.2 mm in H.

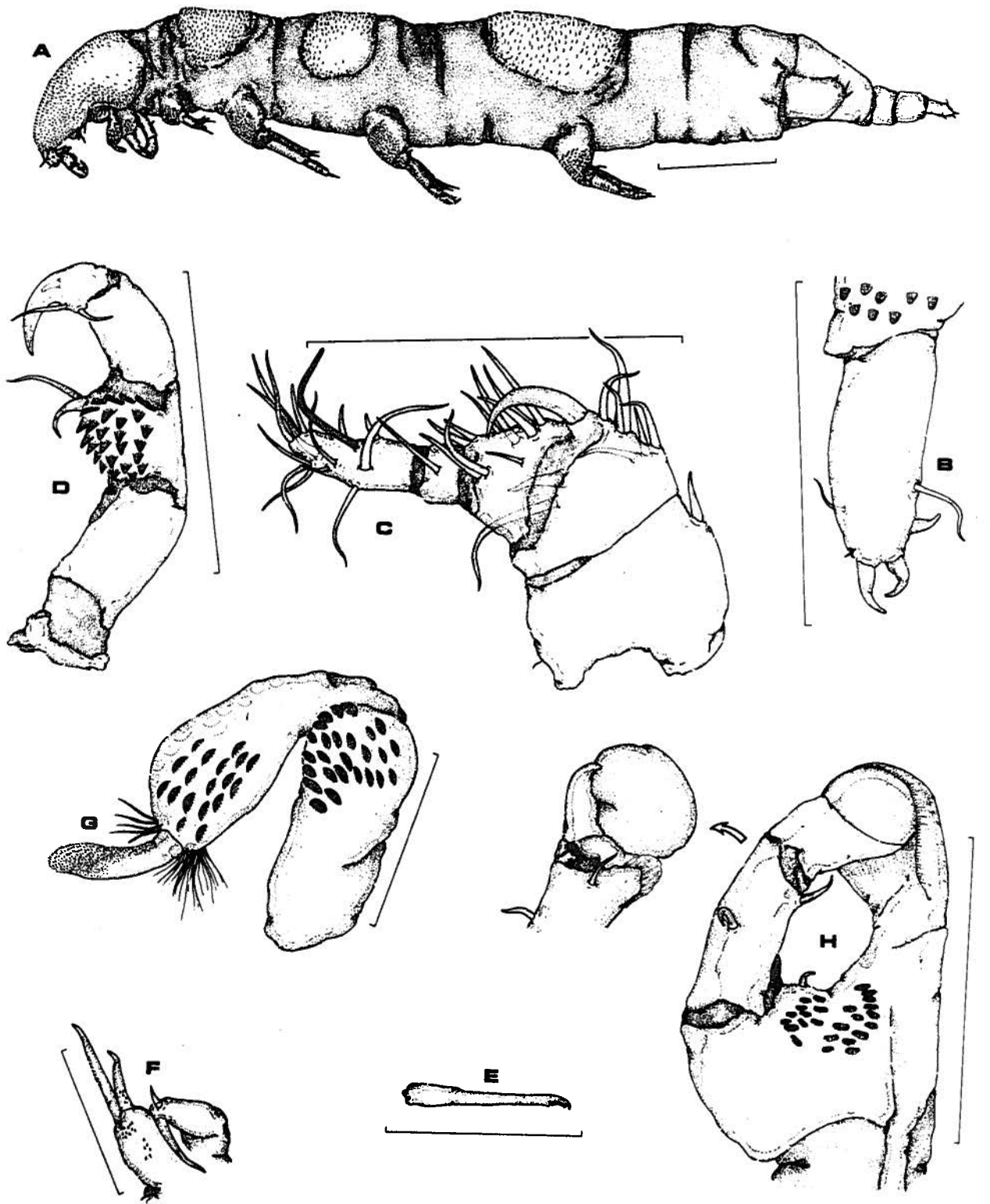


FIGURE 21. *Eudactylina epaktolampter* sp. nov., female: A, leg 1; leg 2 exopod; C, leg 2 endopod; D, legs 3 and 4; E, leg 5. Scales: 0.3 mm in A; 0.2 mm in B-E.

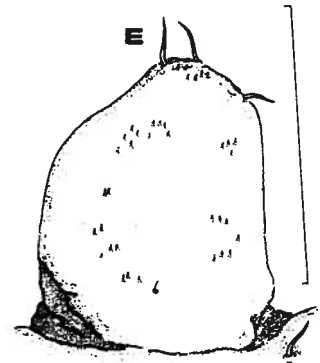
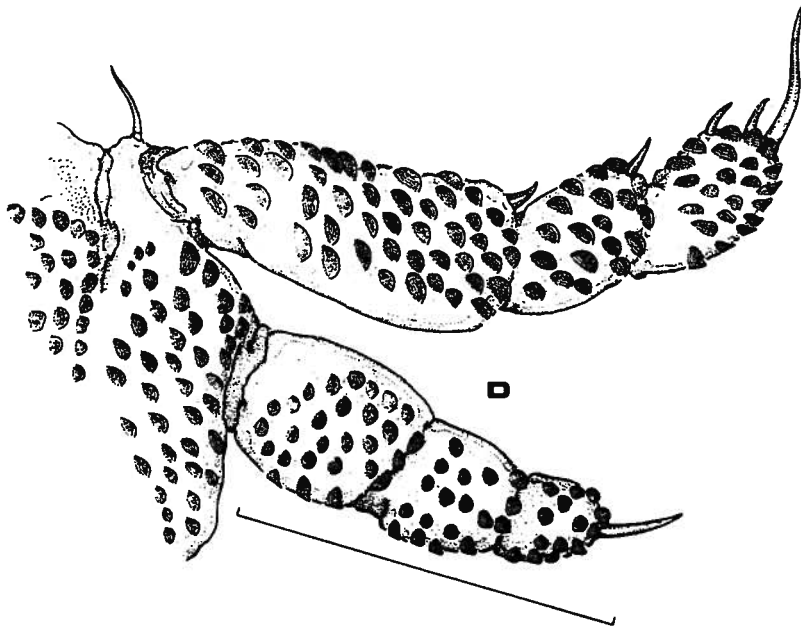
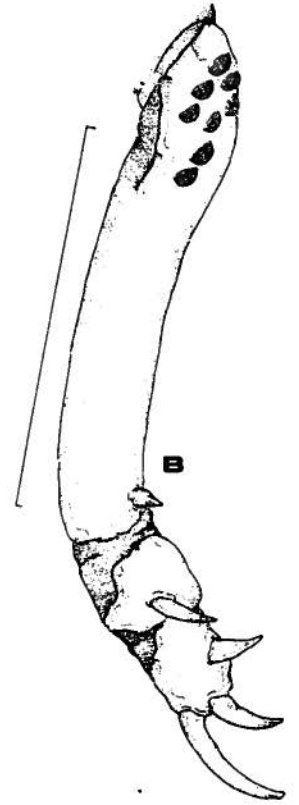
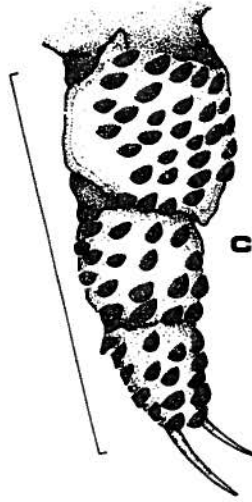
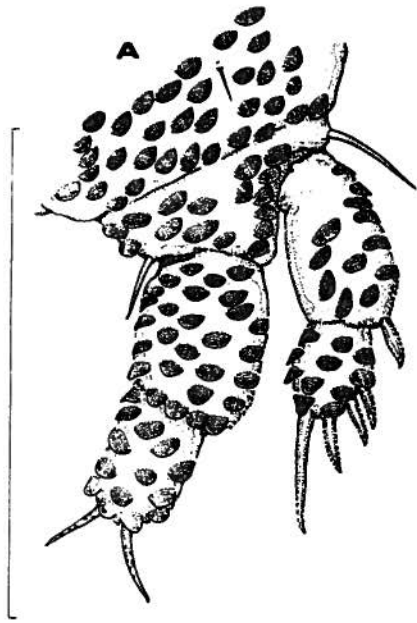


FIGURE 22. *Eudactylina epaktolampter* sp. nov., male: A, habitus, lateral; B, caudal ramus; C, first antenna; D, maxilliped. Scales: 0.5 mm in A; 0.1 mm in B-D.

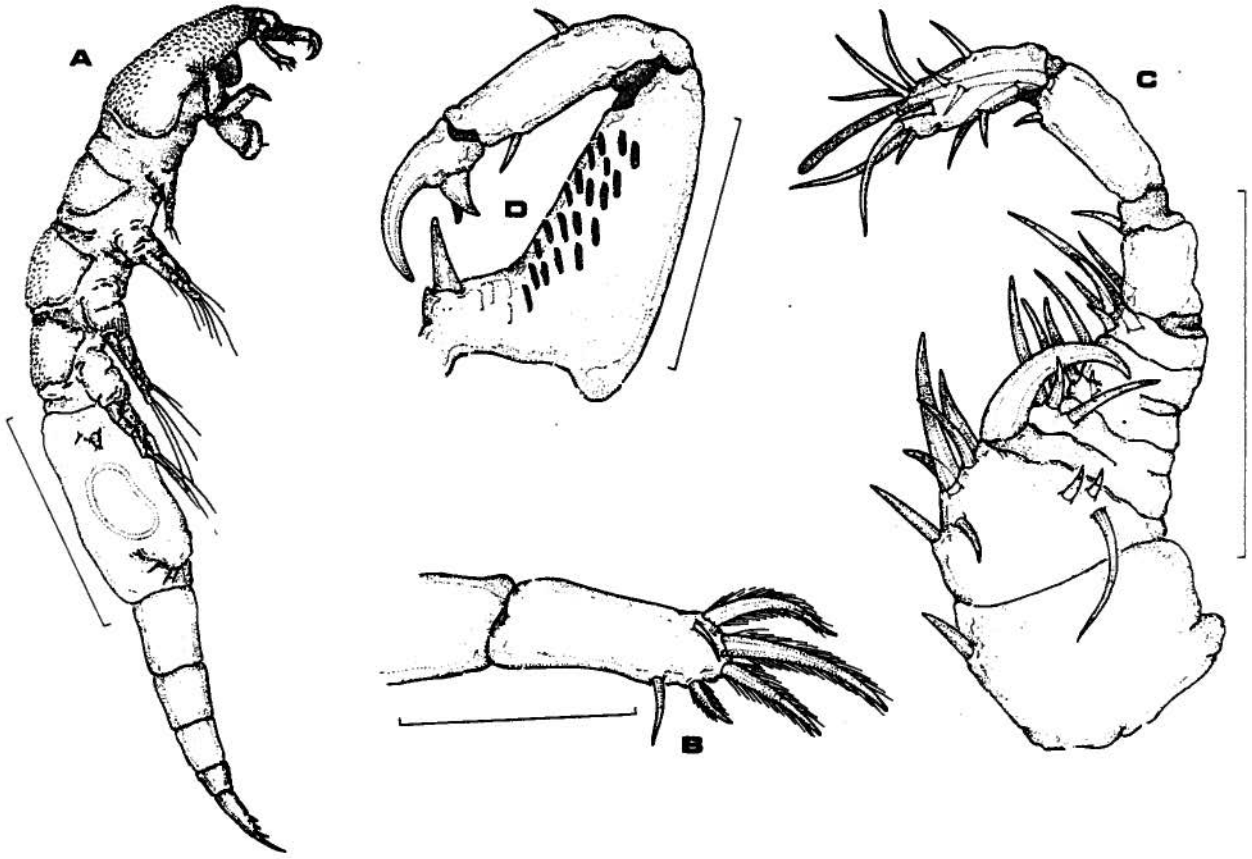


FIGURE 23. *Eudactylina epaktolampter* sp. nov., male: A, leg 1 exopod; B, leg 1 endopod; C, leg 2; D, leg 3; E, leg 4 endopod; F, leg 5; G, leg 6. Scales: 0.1 mm in A-G.

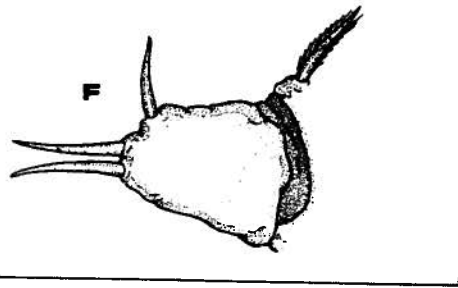
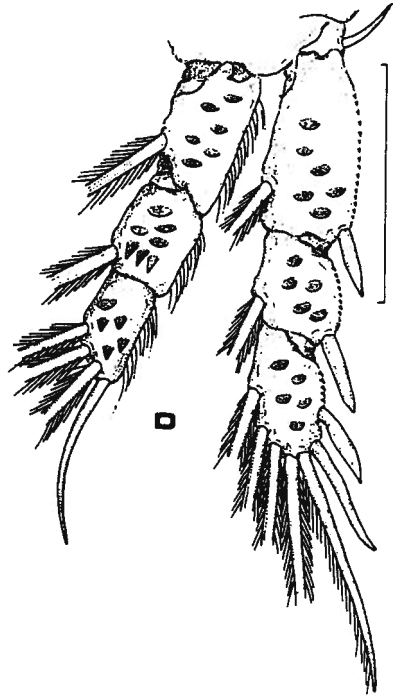
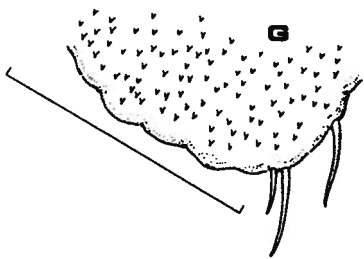
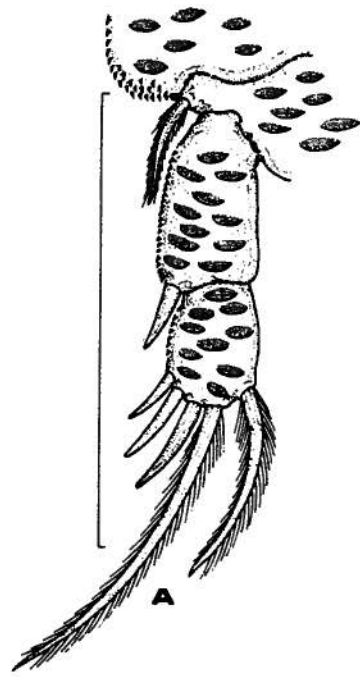
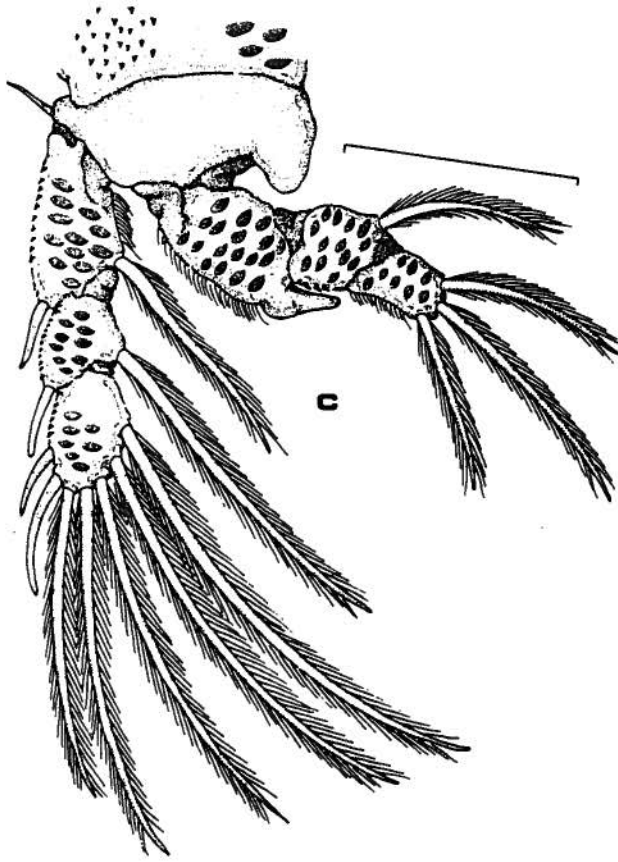


FIGURE 24. *Eudactylina hornbosteli* sp. nov., female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.4 mm in A; 0.1 mm in B-G; 0.2 mm in H.



FIGURE 25. *Eudactylina hornbosteli* sp. nov., female: A, leg 1; B, leg 2; C, legs 3 and 4; D, leg 5. Scales: 0.2 mm in A-D.

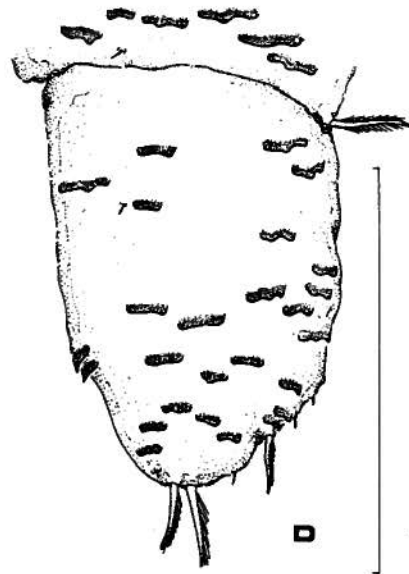
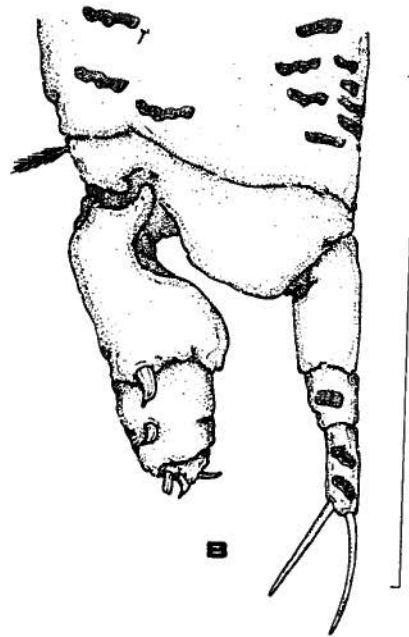
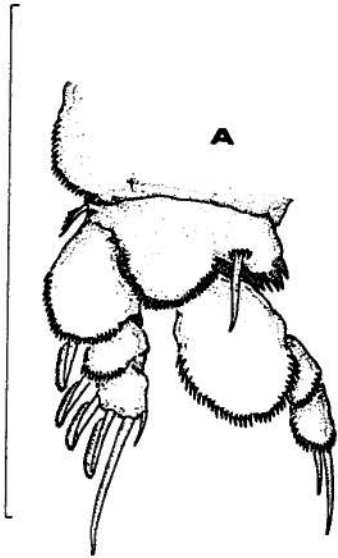


FIGURE 26. *Eudactylina indivisa* Castro and Baeza, 1991, female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped; Scales: 0.6 mm in A; 0.1 mm in B-G; 0.2 mm in H.

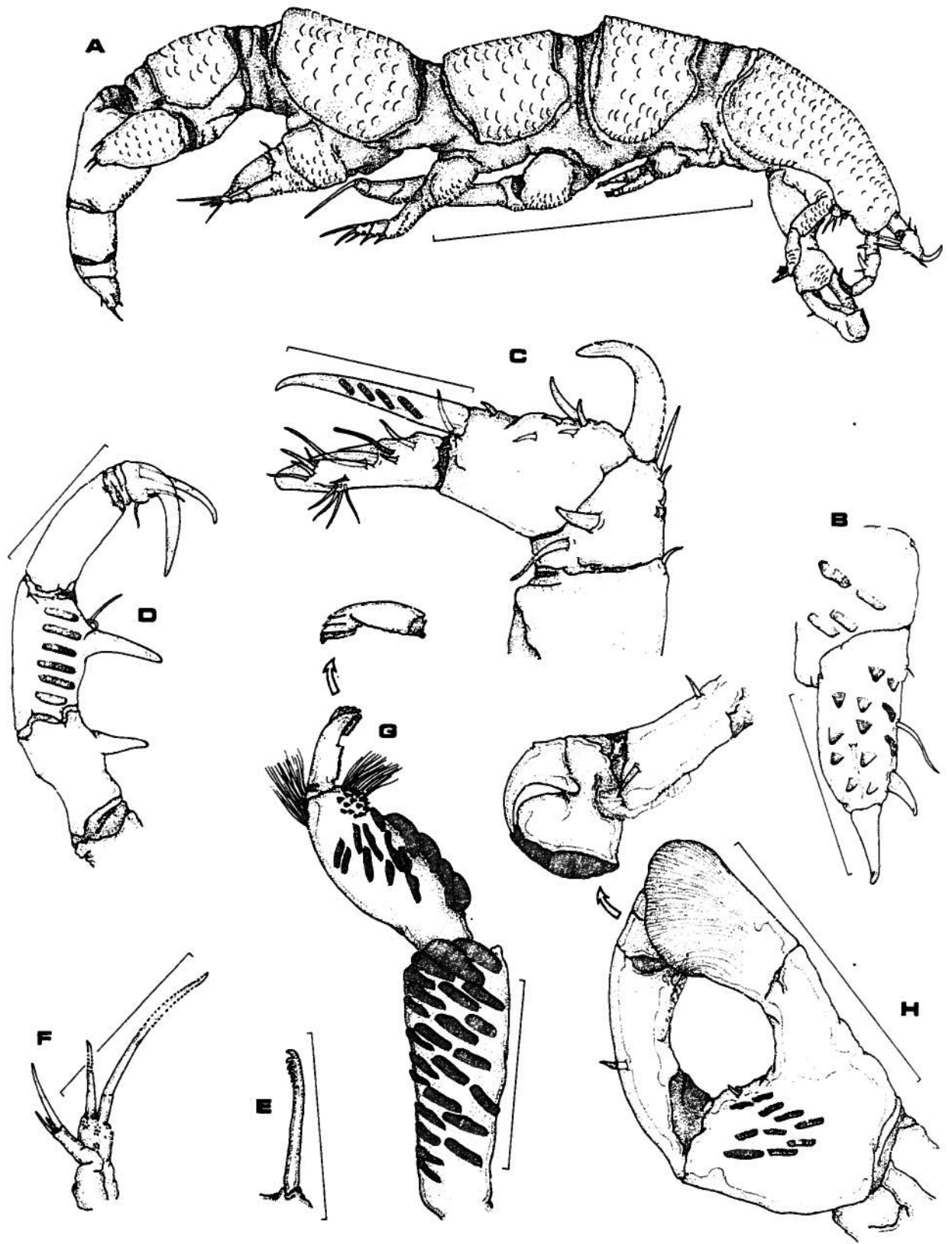


FIGURE 27. *Eudactylina indivisa* Castro and Baeza, 1991, female: A, leg 1; B, leg 2; C, leg 2 exopod; D, legs 3 and 4 endopod; E, legs 3 and 4 exopod; F, leg 5; G, gonad, leg 5. Scales: 0.2 mm in A-F; 0.1 mm in G.

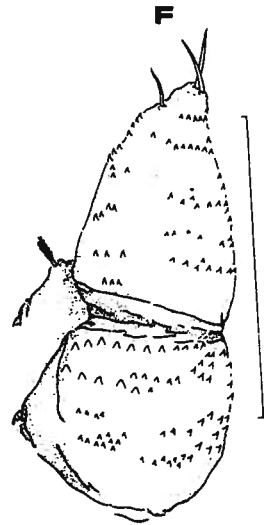
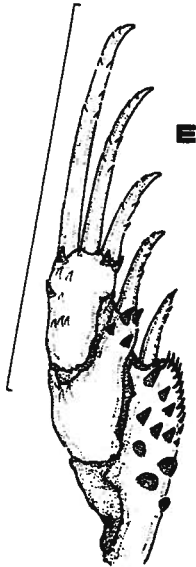
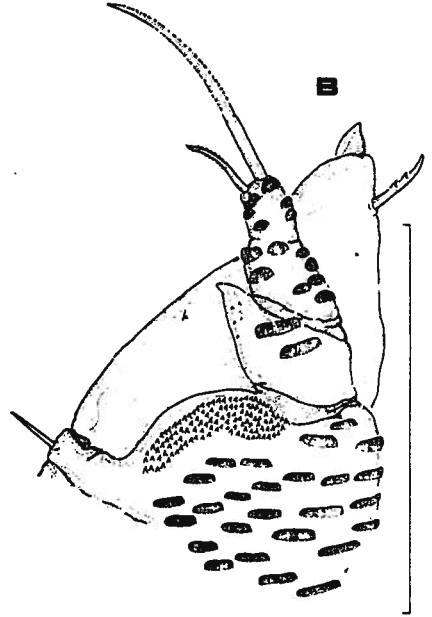
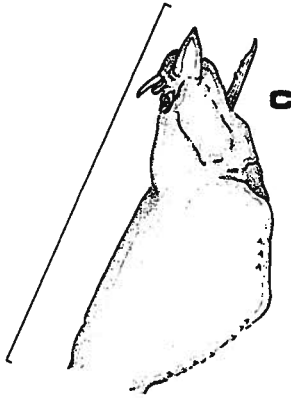
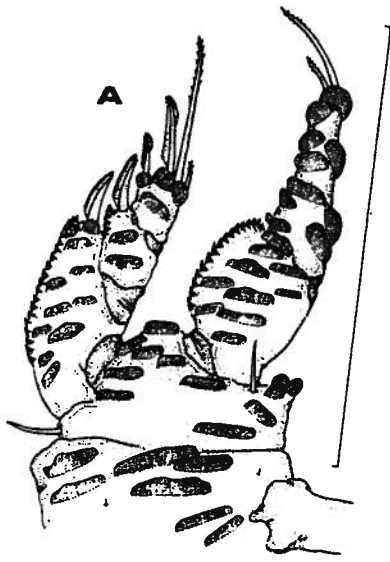


FIGURE 28. *Eudactylina insolens* Scott and Scott, 1913, female: A, habitus, lateral; B, caudal rami; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.4 mm in A; 0.1 mm in B-H.

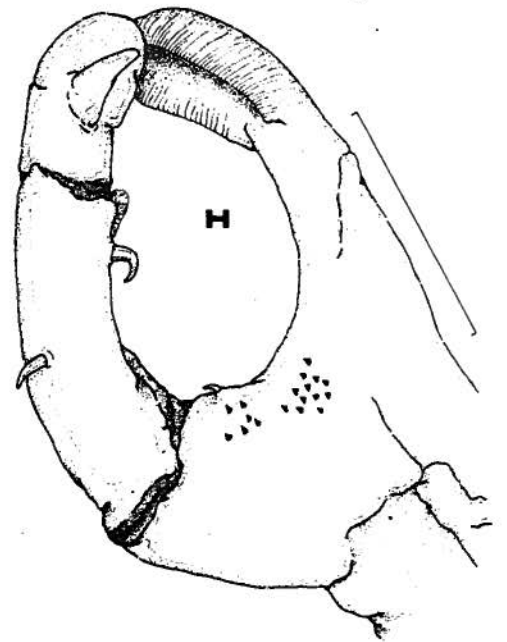
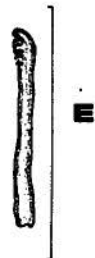
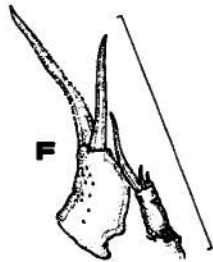
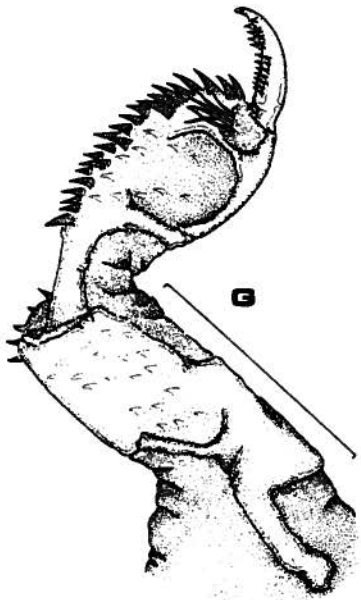
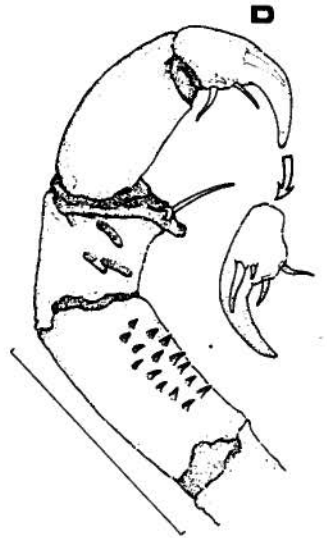
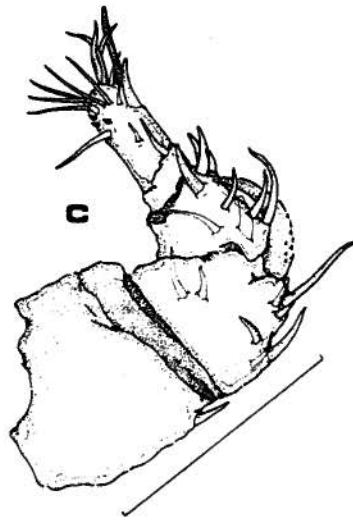
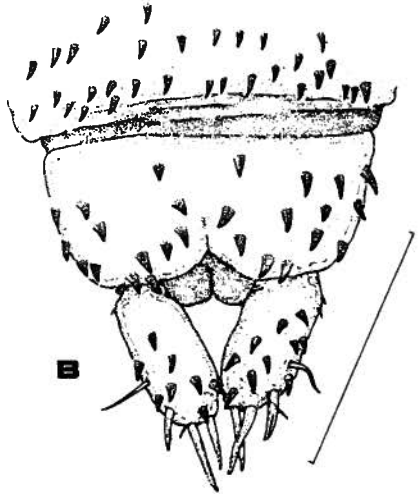
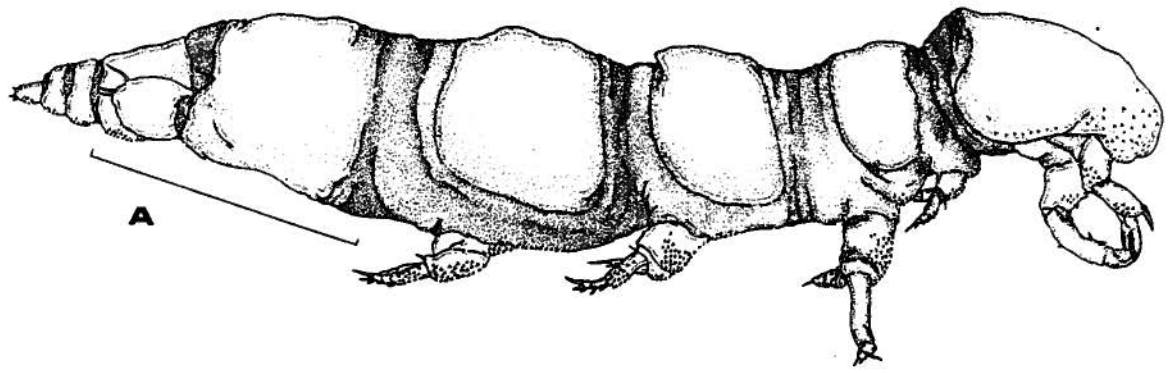


FIGURE 29. *Eudactylina insolens* Scott and Scott, 1913, female: A, leg 1; B, leg 2 exopod; C, leg 2 endopod; D, legs 3, 4; E, leg 5. Scales: 0.2 mm in A; 0.1 mm in B, C; 0.2 mm in D, E.

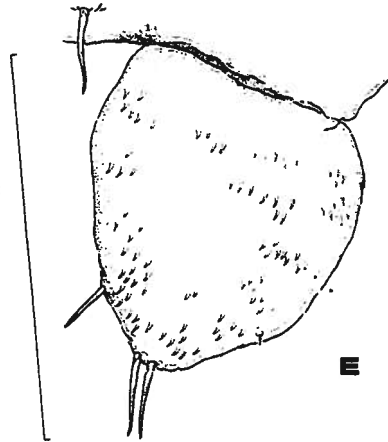
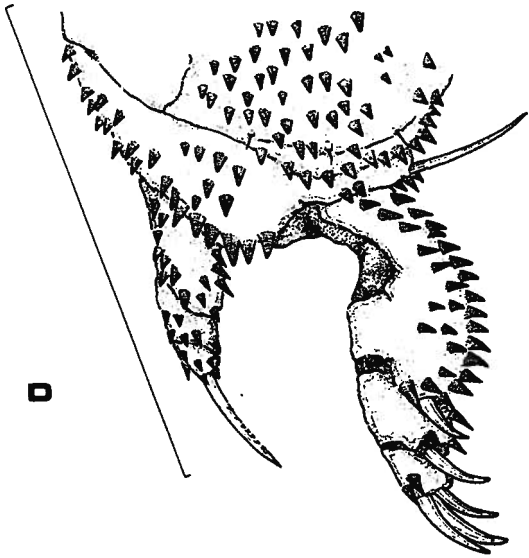
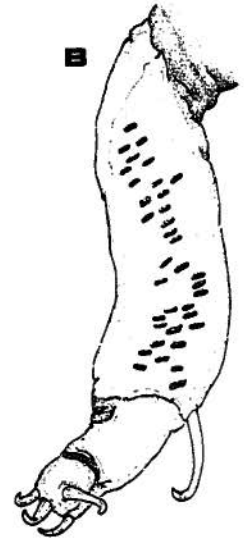
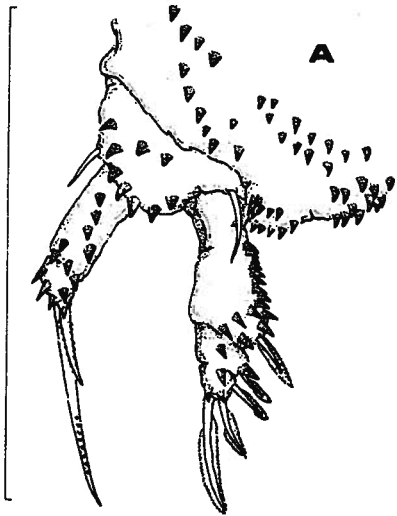


FIGURE 30. *Eudactylina longispina* Bere, 1936, female: A, habitus, lateral; B, caudal rami; C, first antenna; D, second antenna; E, mandible and first maxilla; F, second maxilla; G, maxilliped. Scales: 0.2 mm in A; 0.1 mm in B-G.

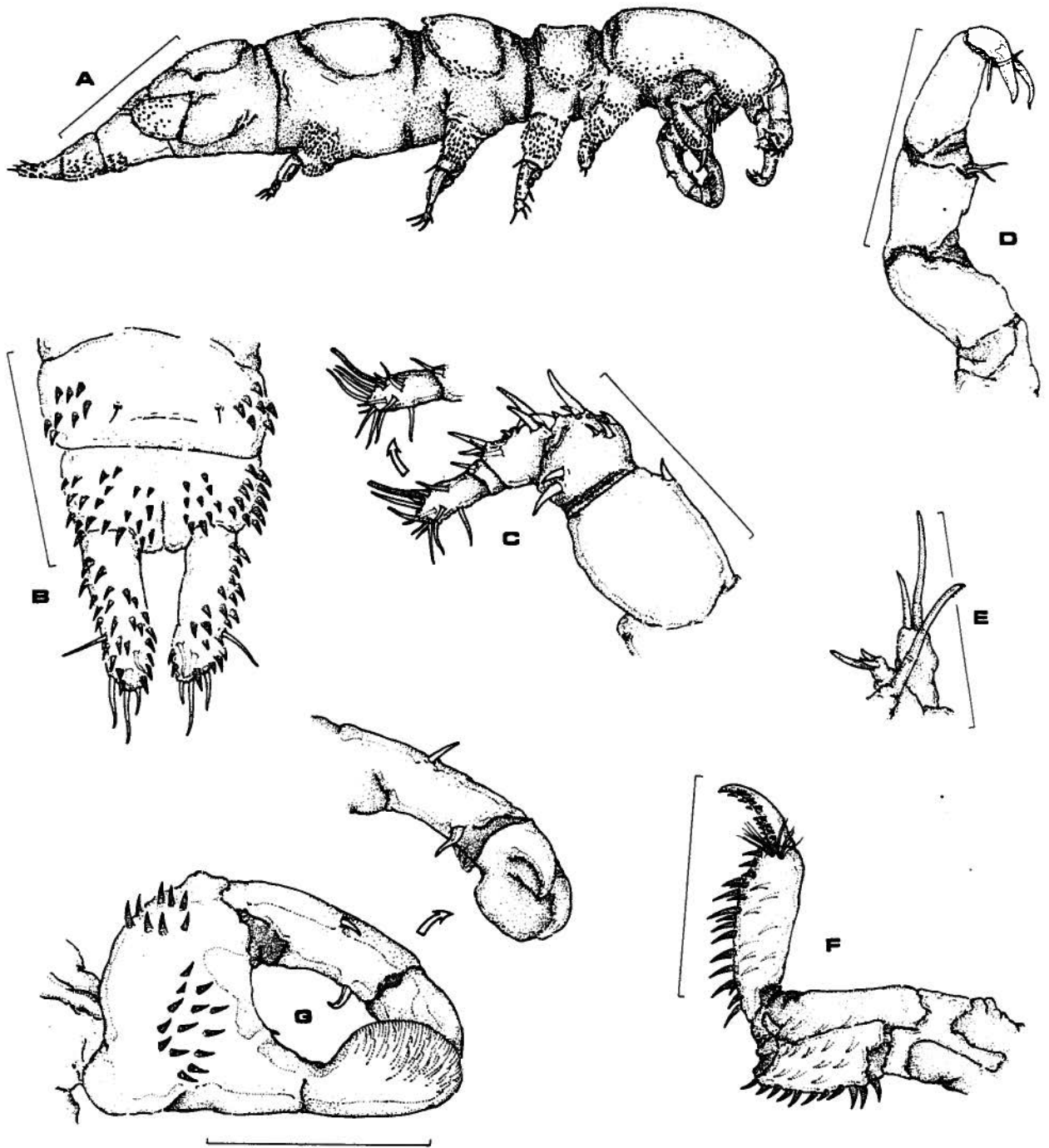


FIGURE 31. *Eudactylina longispina* Bere, 1936, female: A, leg 1; B, leg 2 endopod; C, leg 2 exopod; D, legs 3 and 4 endopods; E, legs 3 and 4 exopods; F, leg 5. Scales: 0.2 mm in A; 0.1 mm in B-G.

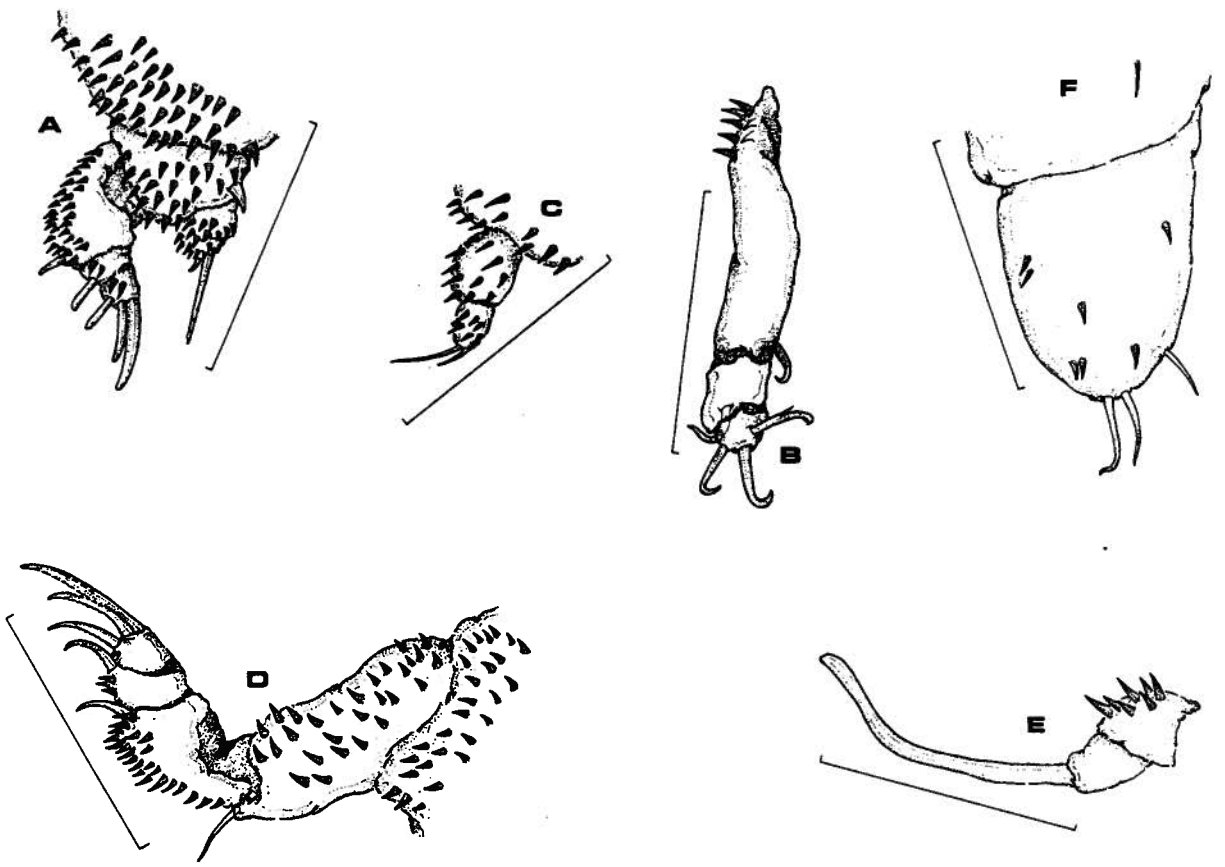


FIGURE 32. *Eudactylina myliobatidos* Luque and Farfan, 1991. female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.3 mm in A; 0.05 mm in B-H.

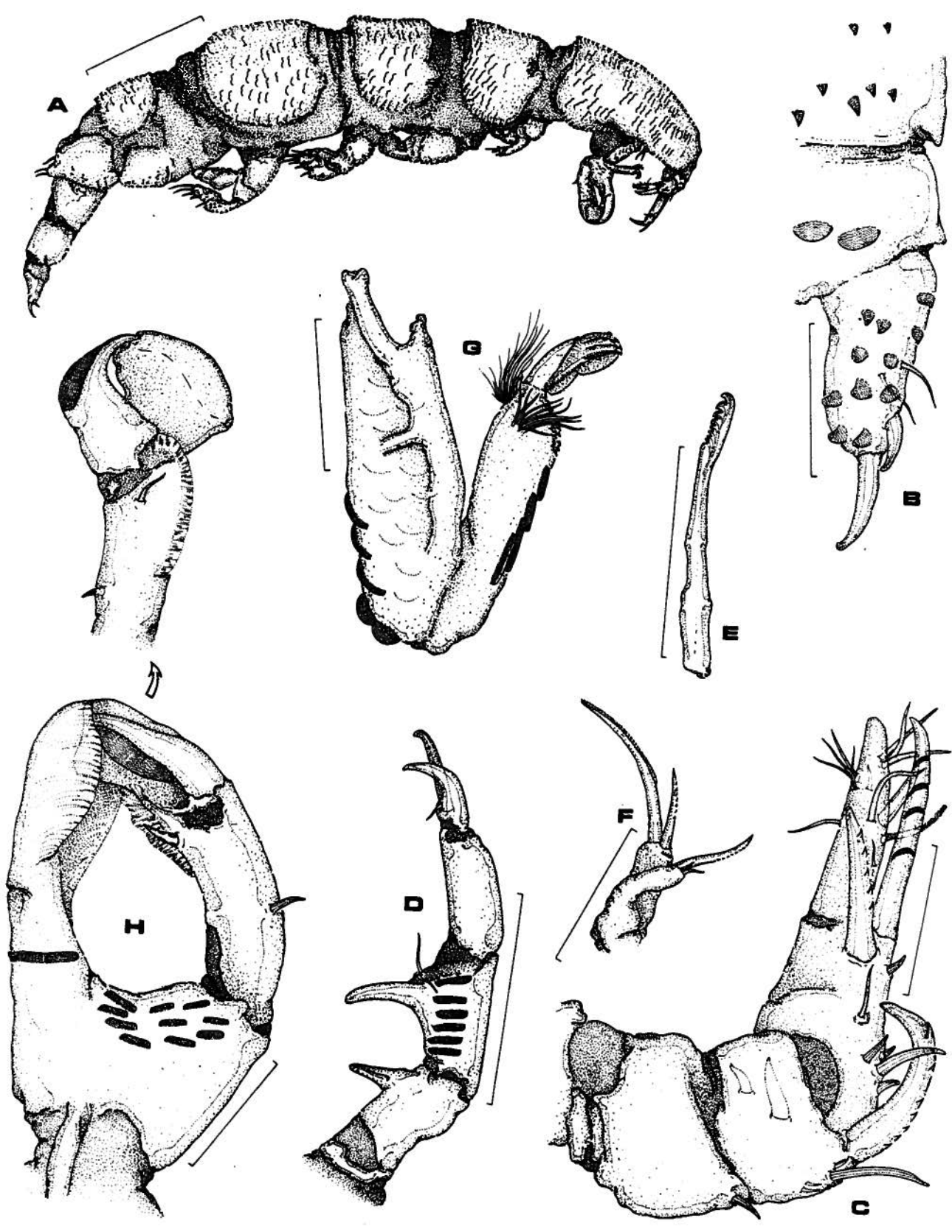


FIGURE 33. *Eudactylina myliobatidos* Luque and Farfan, 1991, female: A, leg 1; B, leg 2 exopod; C, leg 2 endopod; D, legs 3 and 4; E, medial stylet; F, leg 5; Scales: 0.4 mm in A; 0.1 mm in B-G; 0.2 mm in H.



FIGURE 34. *Eudactylina nykterimyzon* sp. nov., female: A, habitus, dorsal; B, habitus, lateral; C, caudal ramus; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H, second maxilla; I, maxilliped. Scales: 1.0 mm in A; 0.5 mm in B; 0.1 mm in C-H; 0.2 mm in I.

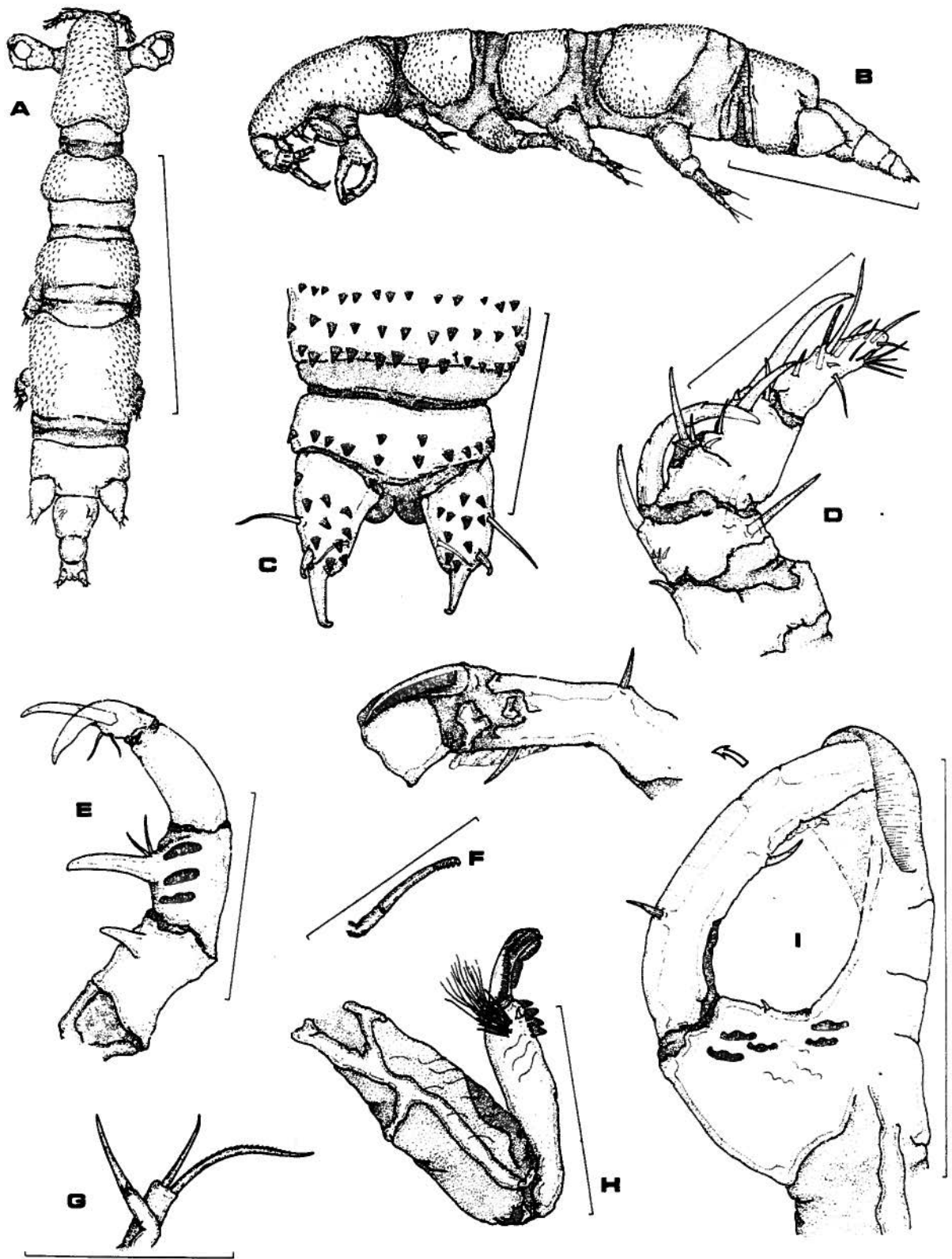


FIGURE 35. *Eudactylina nykterimyzon* sp. nov., female: A, leg 1; B, leg 2; C, legs 3 and 4; D, leg 5; Scales: 0.2 mm in A-D.

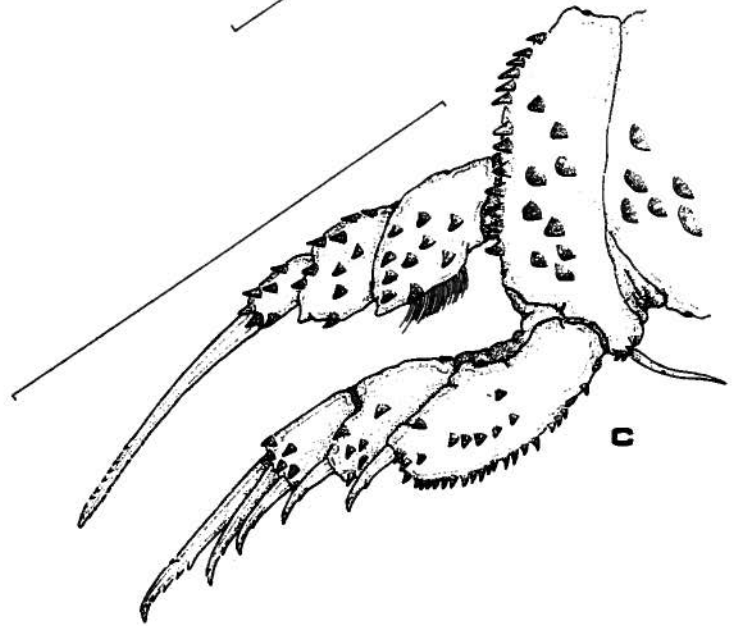
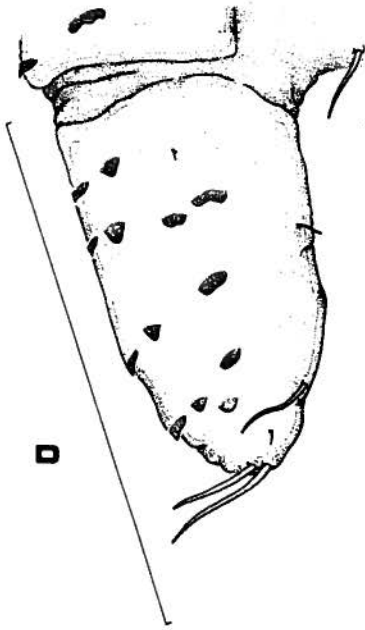
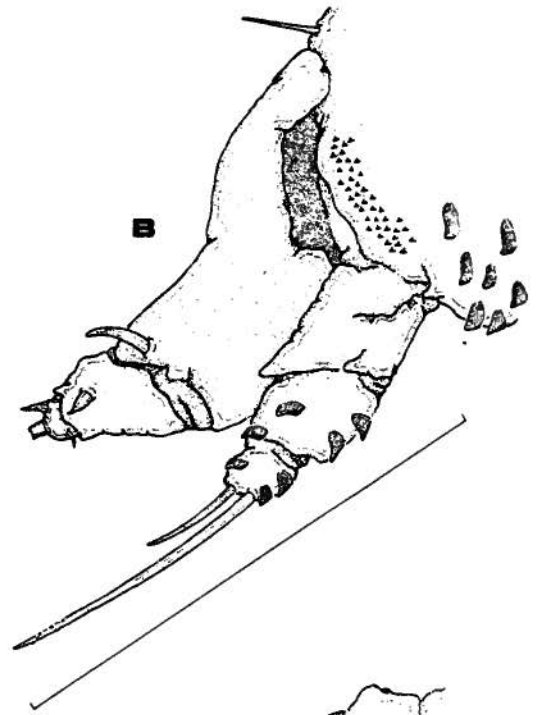
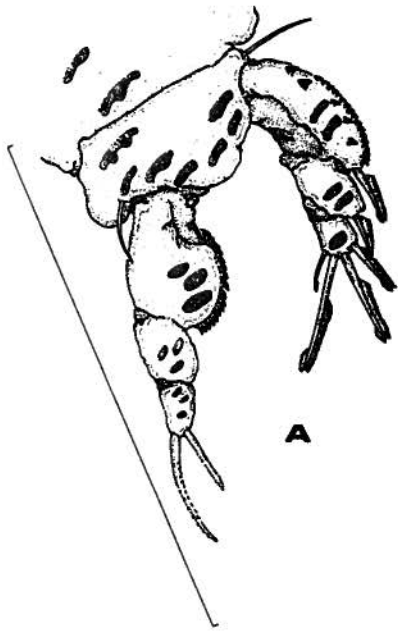


FIGURE 36. *Eudactylina oliveri* Laubier, 1968, female: A, habitus, dorsal; B, abdomen and egg string; C, caudal ramus; D, first antenna; E, second antenna; F, oral cone; G, mandible; H, first maxilla; I, second maxilla; J, maxilliped. Scales: 1.0 mm in A, B; 0.1 mm in C; 0.2 mm in D; 0.1 mm in E-H; 0.2 mm in I, J.

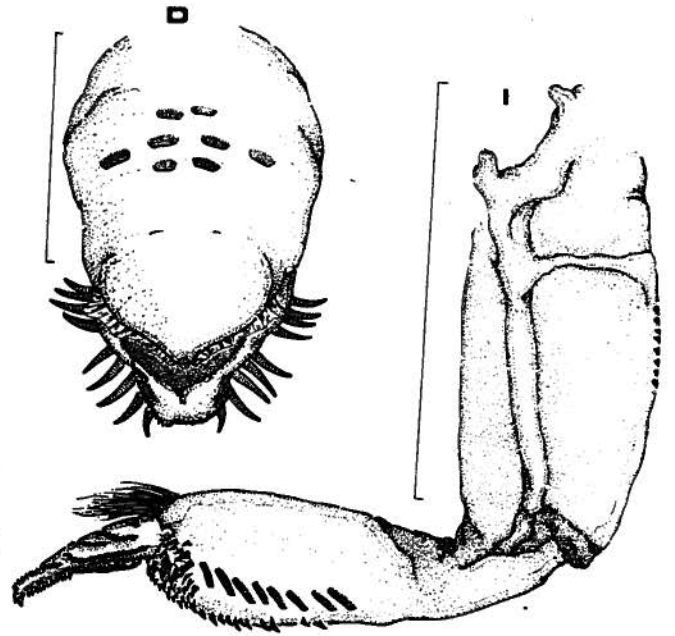
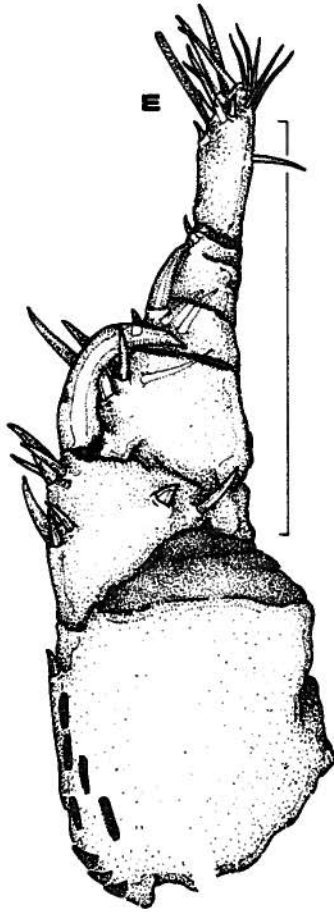
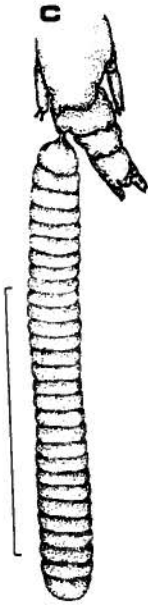
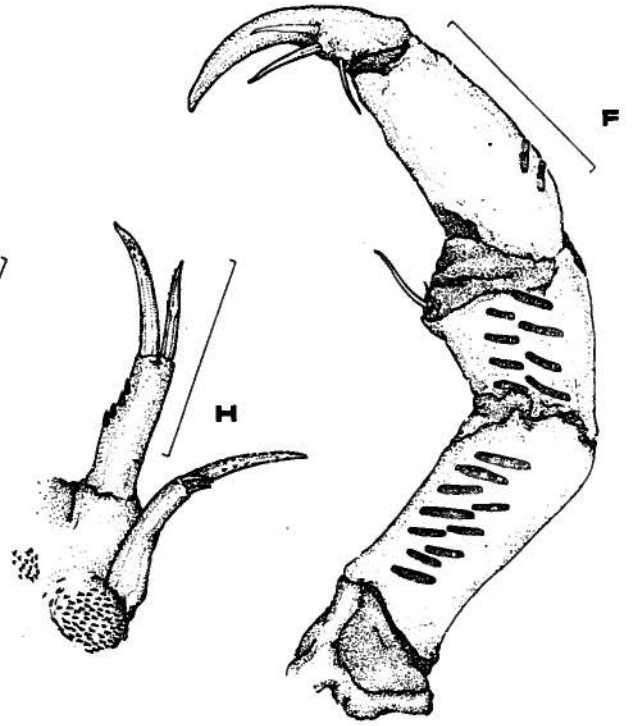
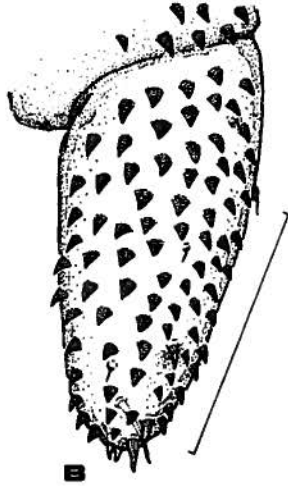
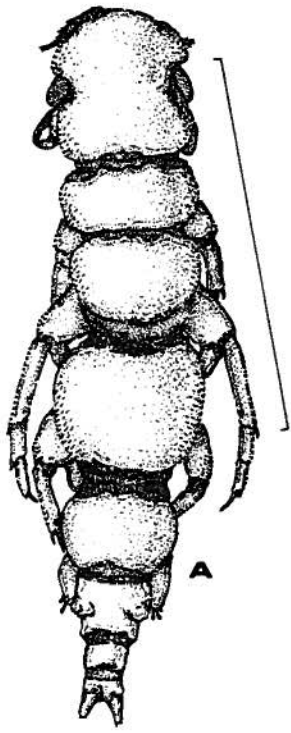


FIGURE 37. *Eudactylina oliveri* Laubier, 1968, female: A, maxilliped; B, maxilliped claw; C, leg 1; D, leg 2; E, legs 3 and 4; F, leg 5; Scales: 0.2 mm in A-F.

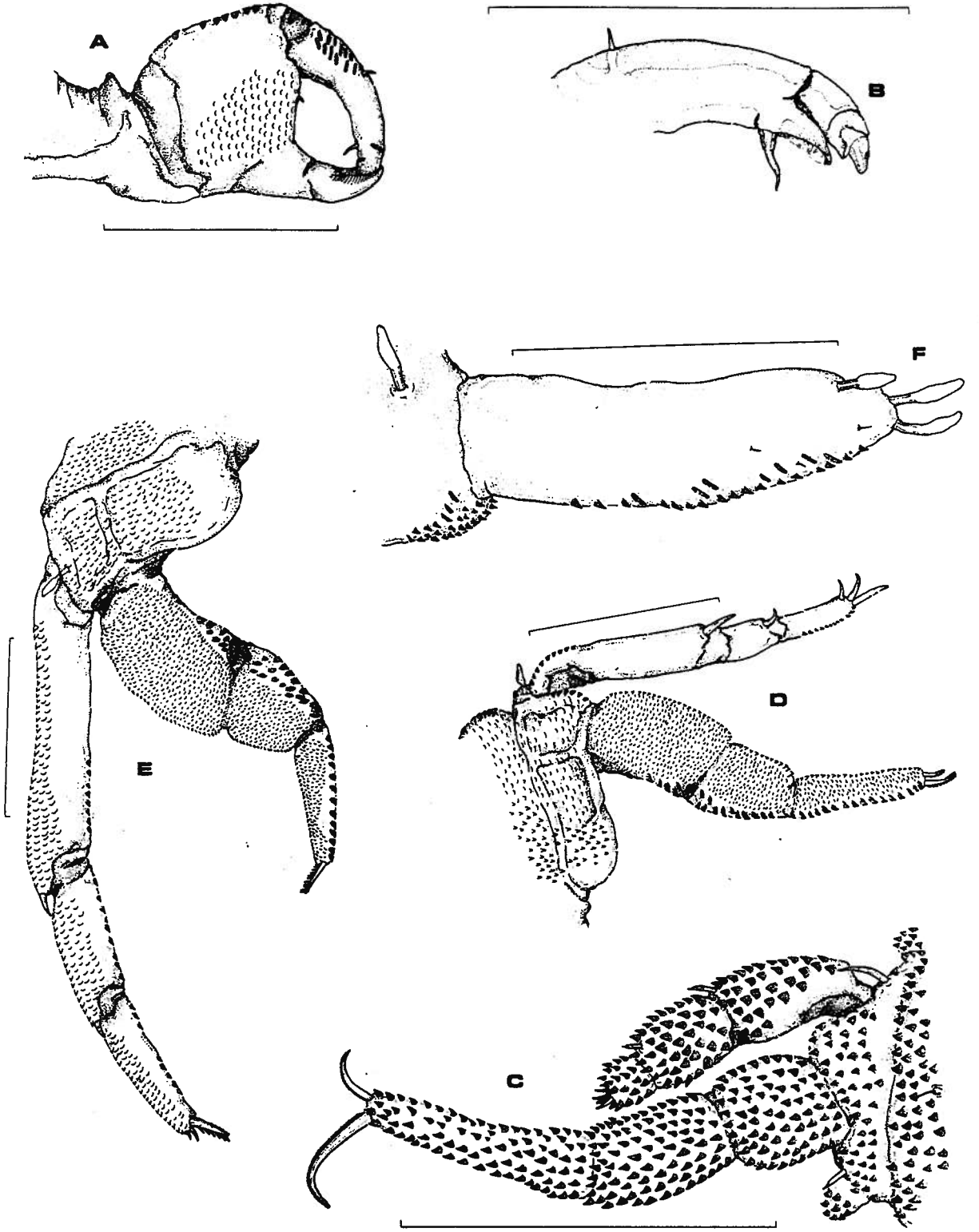


FIGURE 38. *Eudactylina oliveri* Laubier, 1968, male: A, habitus, dorsal; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.4 mm in A; 0.2 mm in B; 0.2 mm in C; 0.2 mm in D; 0.1 mm in E, F; 0.2 mm in G, H.

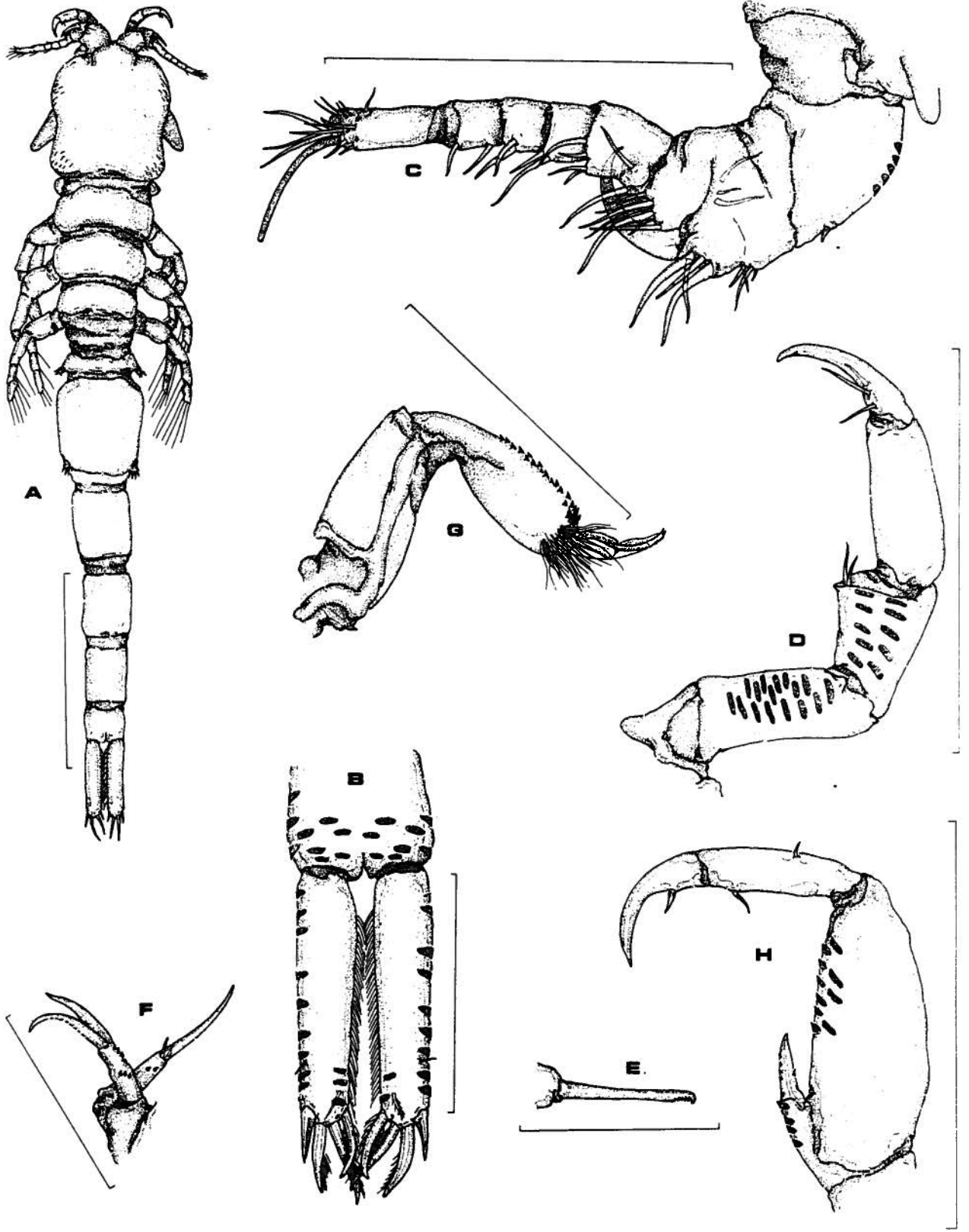


FIGURE 39. *Eudactylina oliveri* Laubier, 1968, male: A, leg 1; B, leg 2; C, legs 3 and 4 exopod; D, leg 3 terminal segment of endopod; E, leg 4 terminal segment of endopod; F, leg 5; G, leg 6. Scales: 0.1 mm in A; 0.2 mm in B, C; 0.1 mm in D-G.

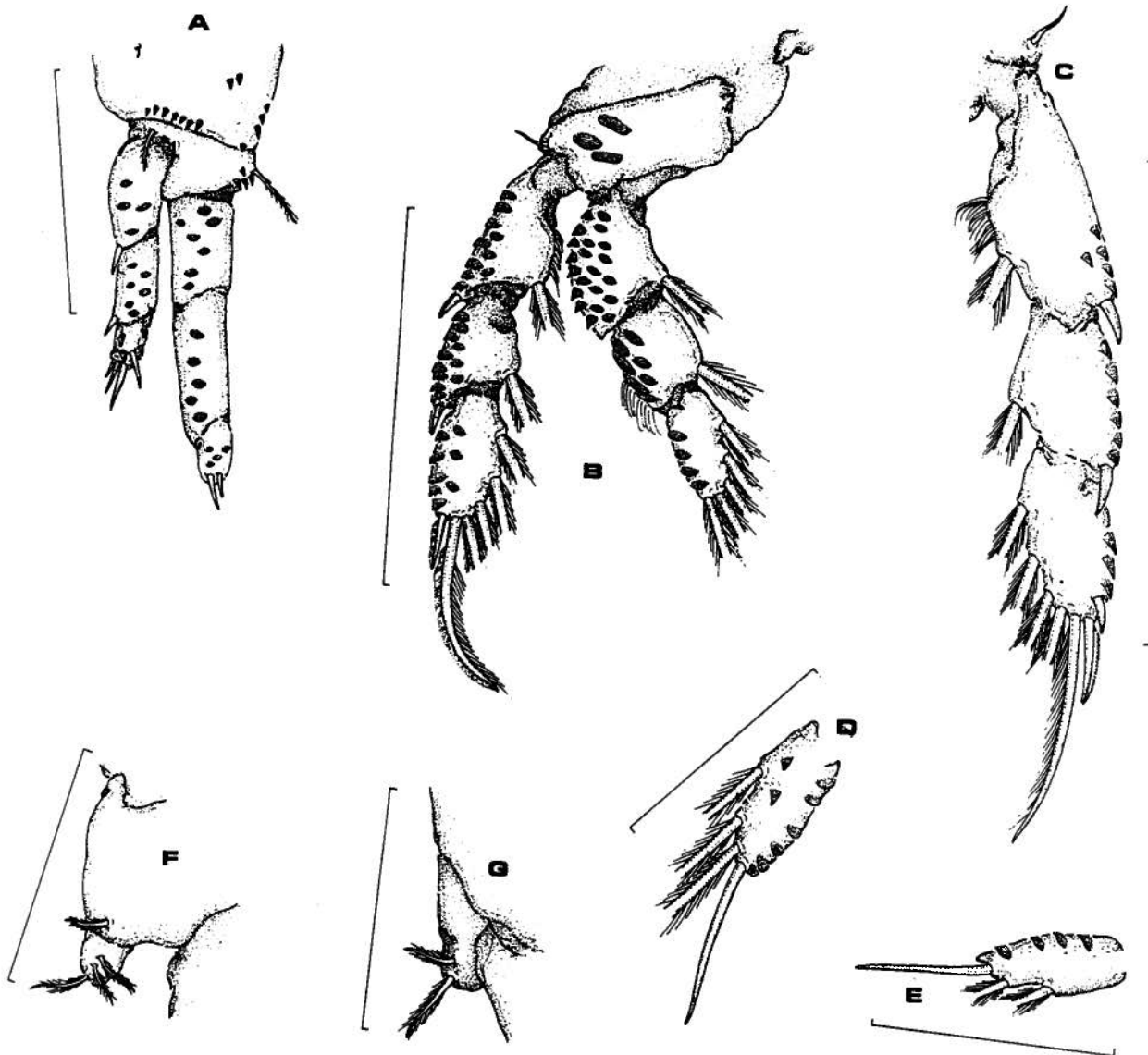


FIGURE 40. *Eudactylina papillosa* Kabata, 1979, female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, first maxilla; F, second maxilla; G, maxilliped. Scales: 0.6 mm in A; 0.1 mm in B, C; 0.2 mm in D; 0.1 mm in E; 0.2 mm in F, G.

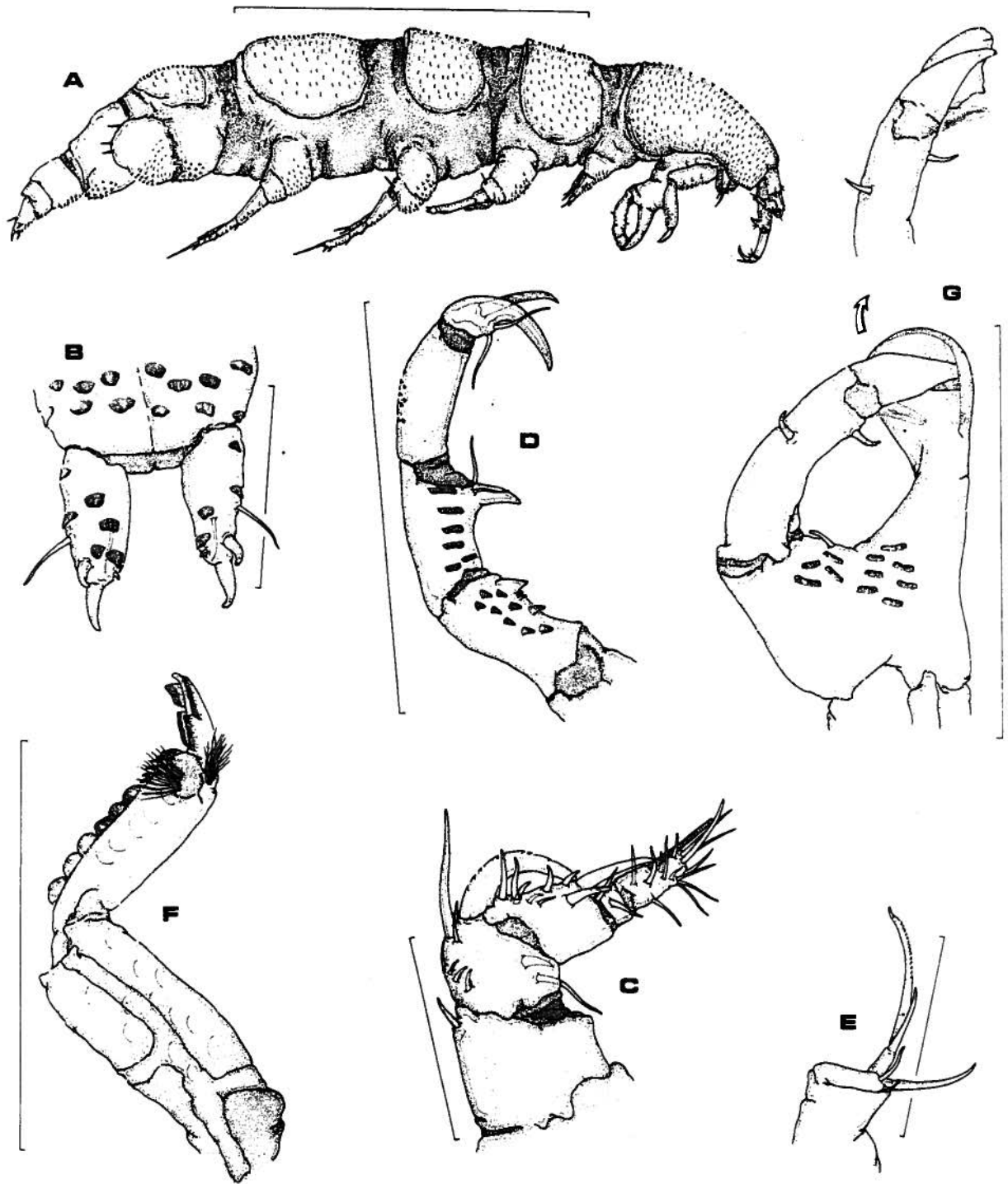


FIGURE 41. *Eudactylina papillosa* Kabata, 1970, female: A, leg 1; B, leg 2 endopod; C, leg 2 exopod; D, legs 3 and 4; E, leg 5. Scales: 0.1 mm in A, B; 0.2 mm in C, D; 0.1 mm in E.

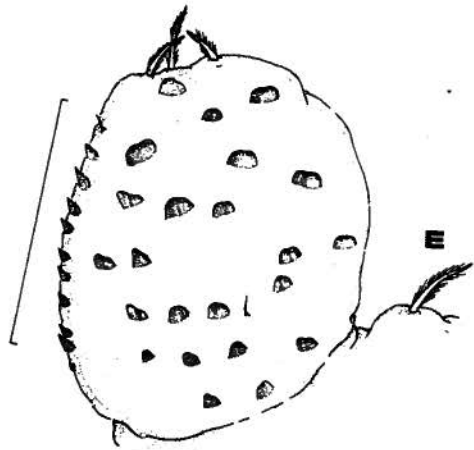
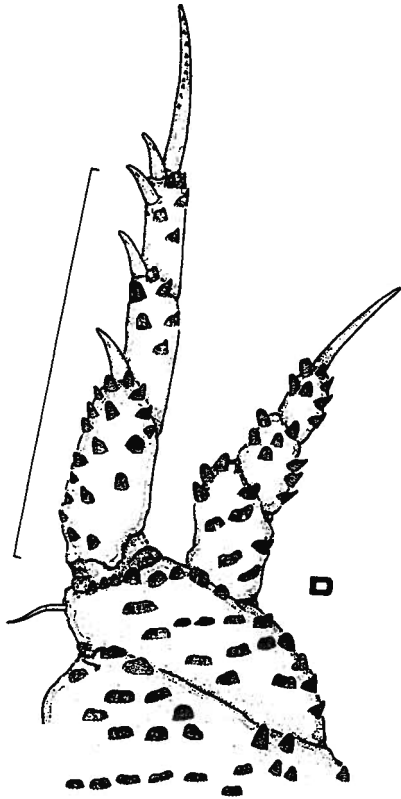
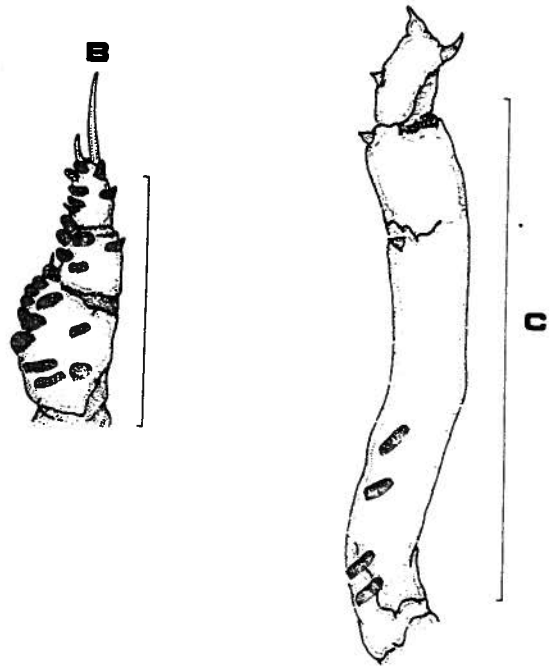
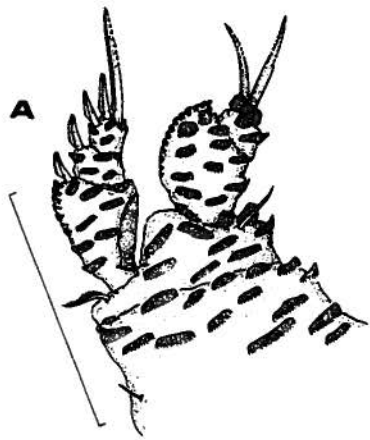


FIGURE 42. *Eudactylina peruensis* Luque and Farfan, 1991, female: A, habitus, lateral; B, caudal rami; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped; Scales: 0.3 mm in A; 0.05 mm in B-H.

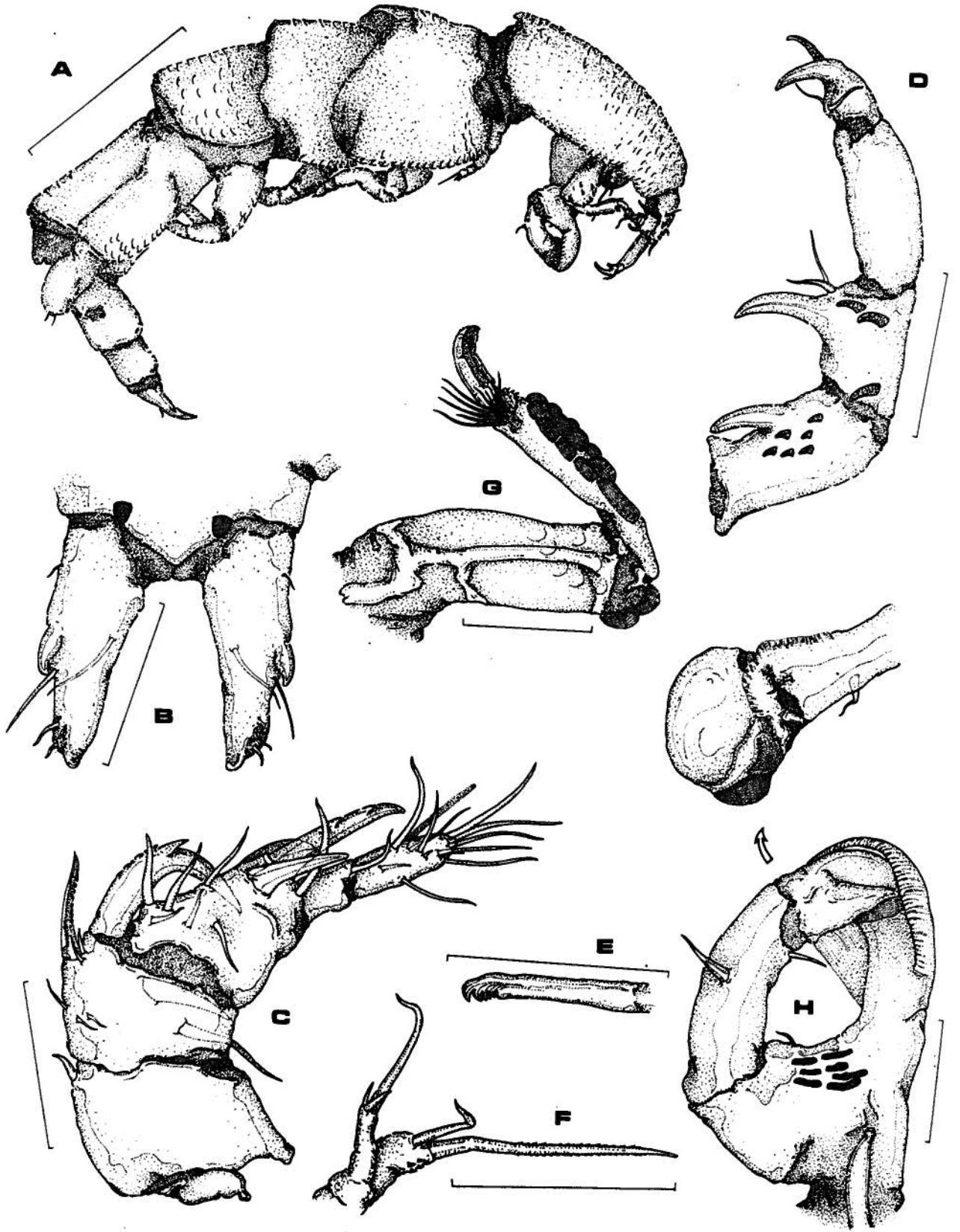


FIGURE 43. *Eudactylina peruensis* Luque and Farfan, 1991, female: A, leg 1; B, leg 2; C, leg 2 and ventromedial stylet; D, leg 3; E, leg 4 endopod; F, leg 5; Scales: 0.1 mm in A, B, D-F; 0.4 mm in C.

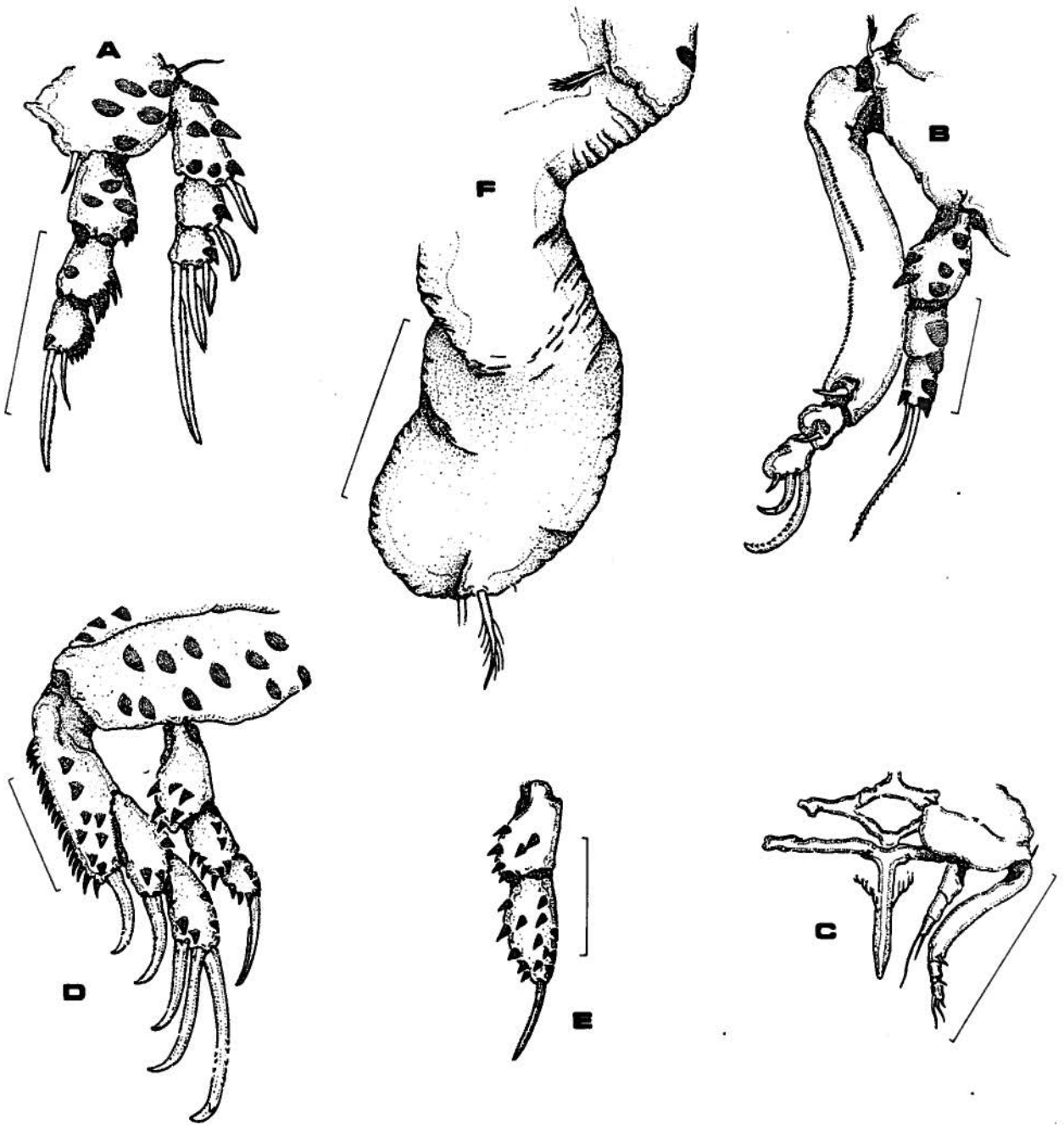


FIGURE 44. *Eudactylina pollex* Cressey, 1967, female: A, habitus, lateral; B, caudal rami and abdomen; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped; Scales: 1.0 mm in A; 0.2 mm in B; 0.1 mm in C; 0.2 mm in D; 0.1 mm in E-G; 0.2 mm in H.

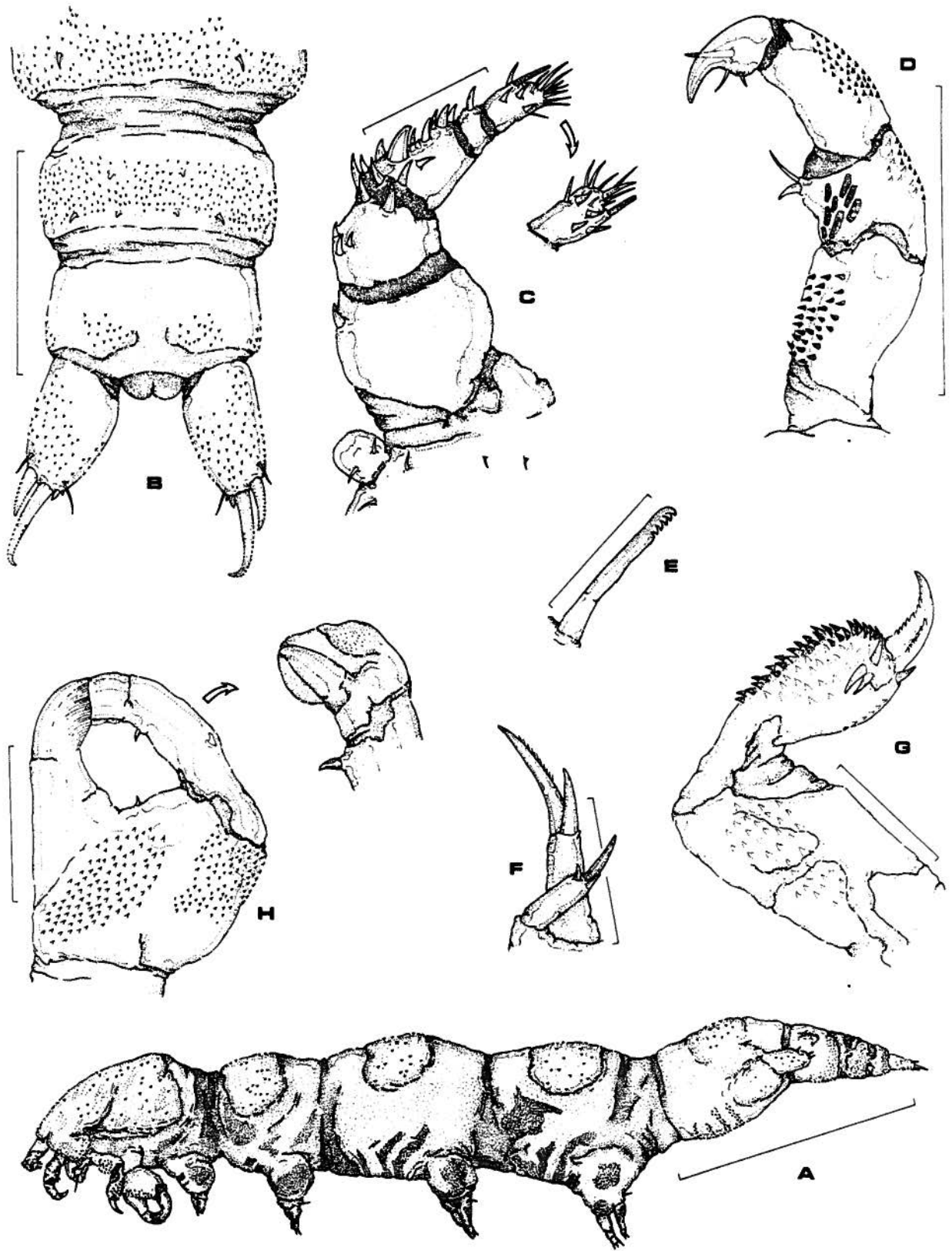


FIGURE 45. *Eudactylina pollex* Cressey, 1967, female: A, leg 1; B, leg 2; C, leg 3; D, leg 4 endopod; E, leg 5. Scales: 0.2 mm in A-E.

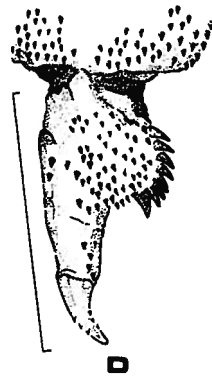
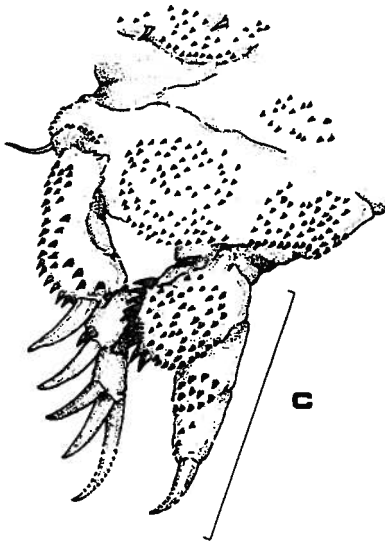
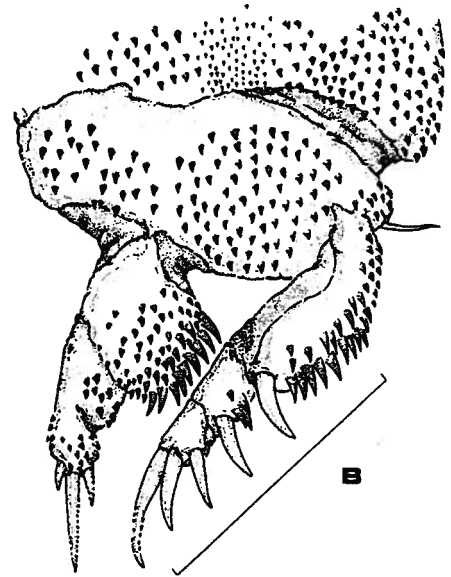
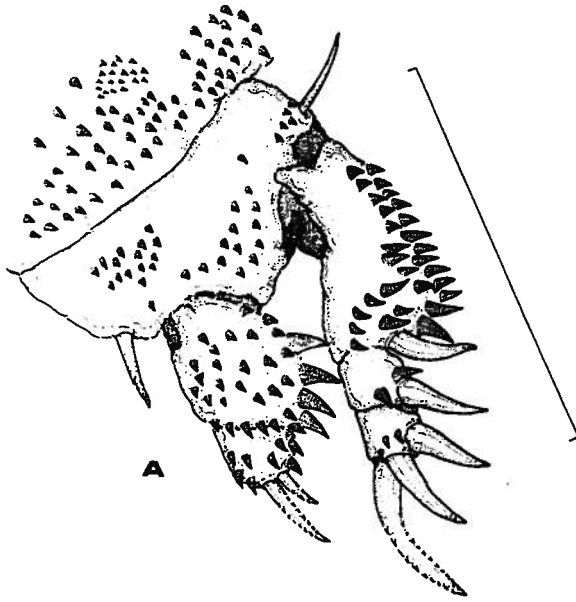


FIGURE 46. *Eudactylina pristiophori* sp. nov., female: A, habitus, dorsal; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.6 mm in A; 0.1 mm in B; 0.2 mm in C, D; 0.1 mm in E-H.

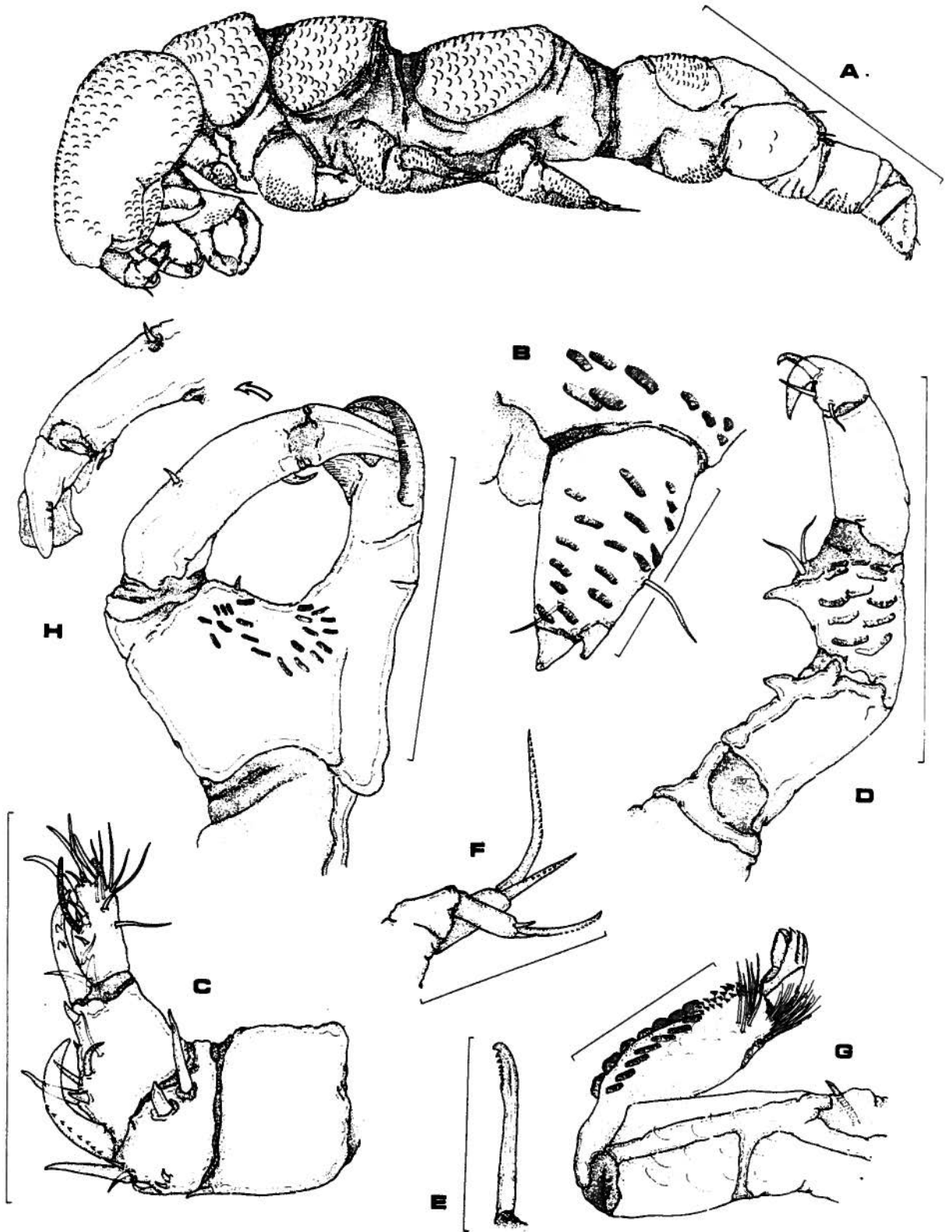
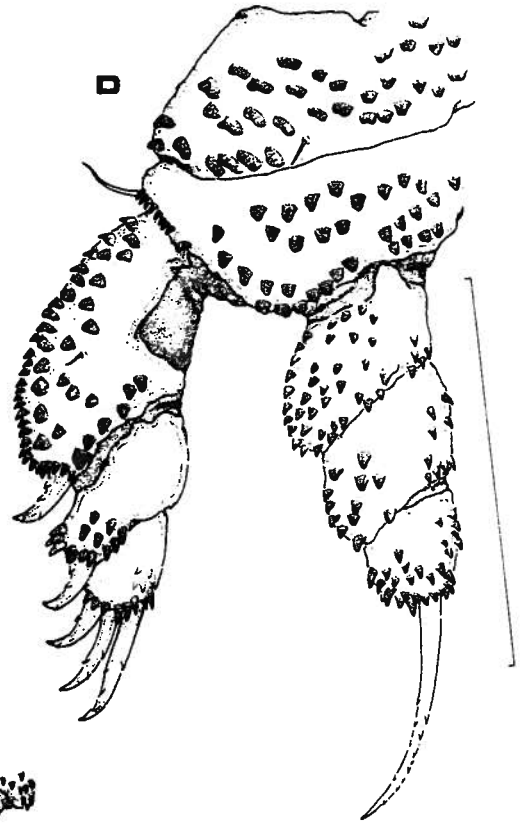


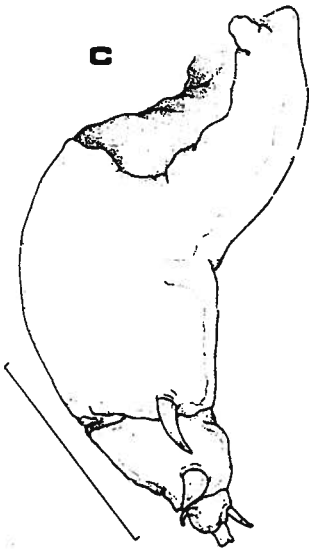
FIGURE 47. *Eudactylina pristiophori* sp. nov., female: A, leg 1; B, leg 2 endopod; C, leg 2 exopod; D, leg 3 and 4; E, leg 5. Scales: 0.2 mm in A, B; 0.1 mm in C; 0.2 mm in D; 0.1 mm in E.



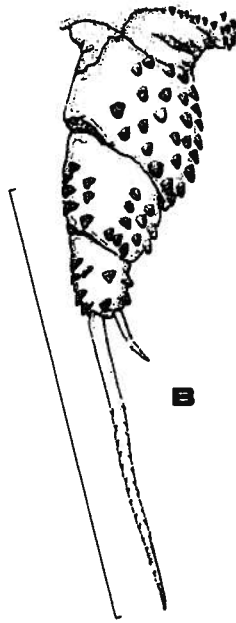
A



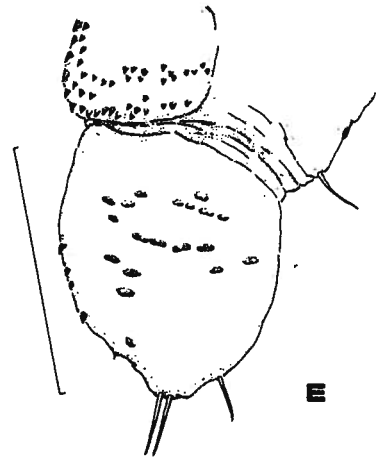
D



C



B



E

FIGURE 48. *Eudactylina pusilla* Cressey, 1967, female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla. Scales: 1.0 mm in A; 0.2 mm in B-G.

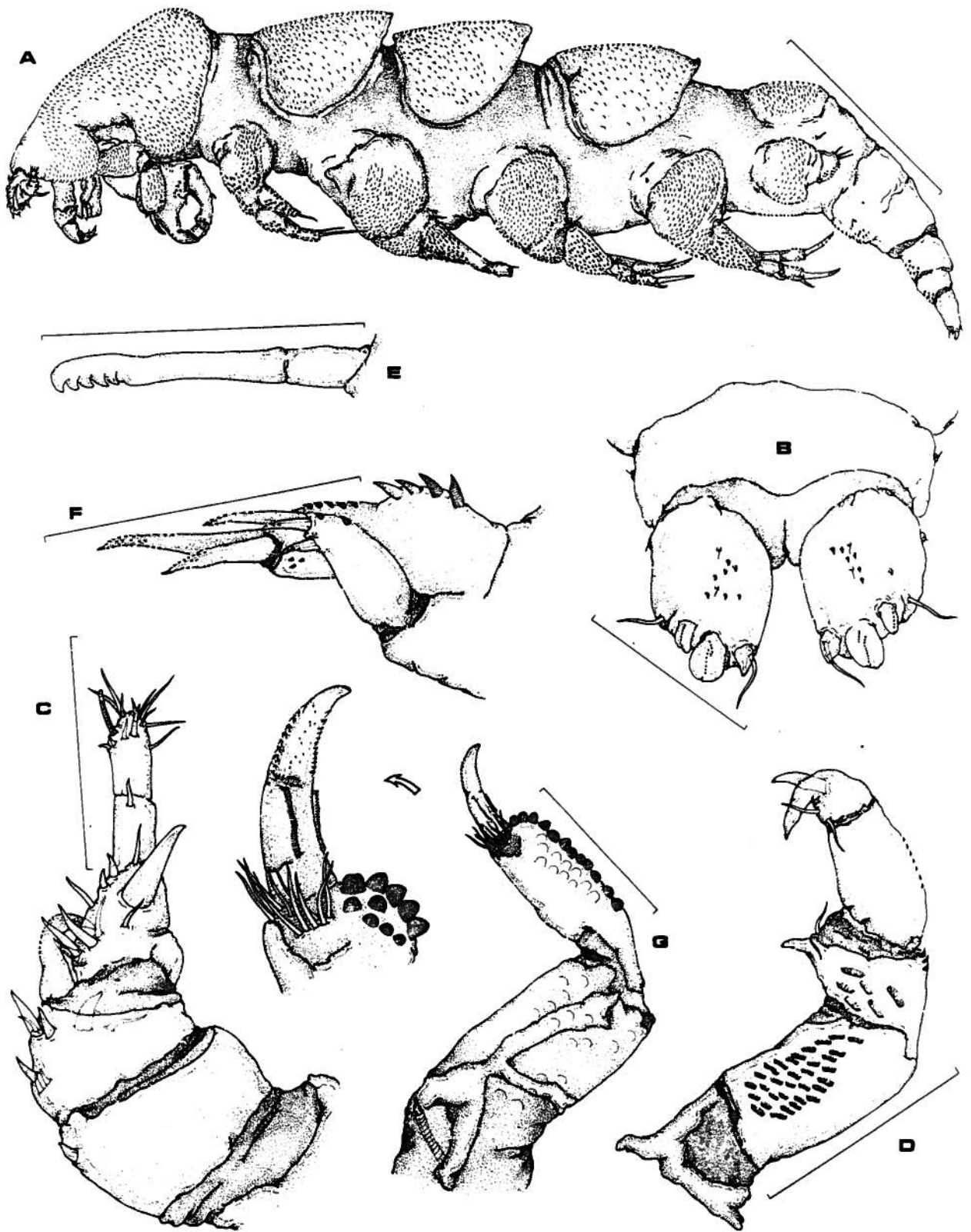


FIGURE 49. *Eudactylina pusilla* Cressey, 1967, female: A, maxilliped; B, leg 1 exopod; C, leg 1 endopod; D, leg 2 exopod; E, leg 2 endopod; F, legs 3 and 4; G, leg 5; Scales: 0.2 mm in A-E; 0.4 mm in F; 0.1 mm in G.

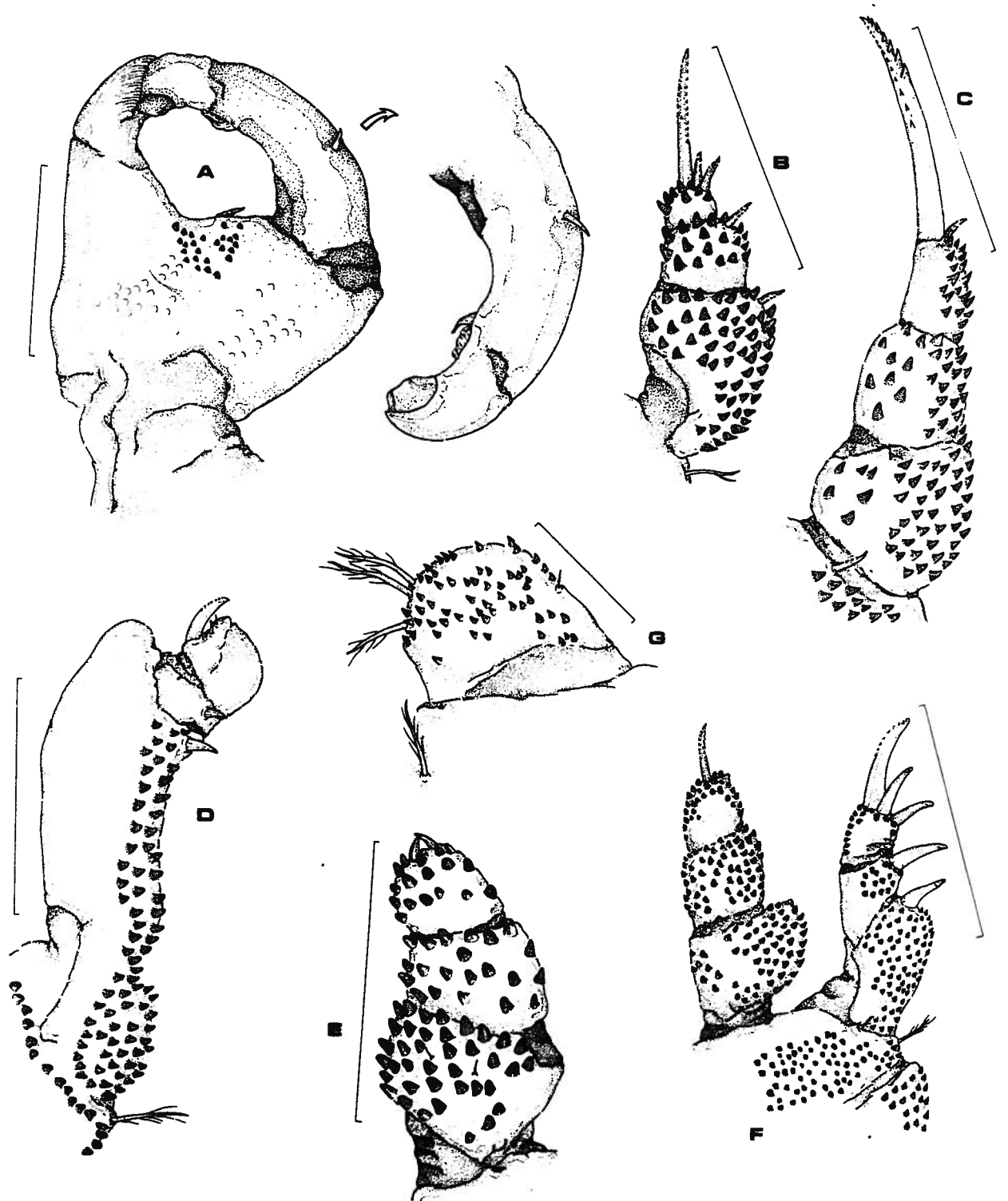


FIGURE 50. *Eudactylina similis* Scott, 1902, female: A, habitus, dorsal; B, caudal ramus; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 1.0 mm in A; 0.2 mm in B-D; 0.1 mm in E, F; 0.2 mm in G, H.

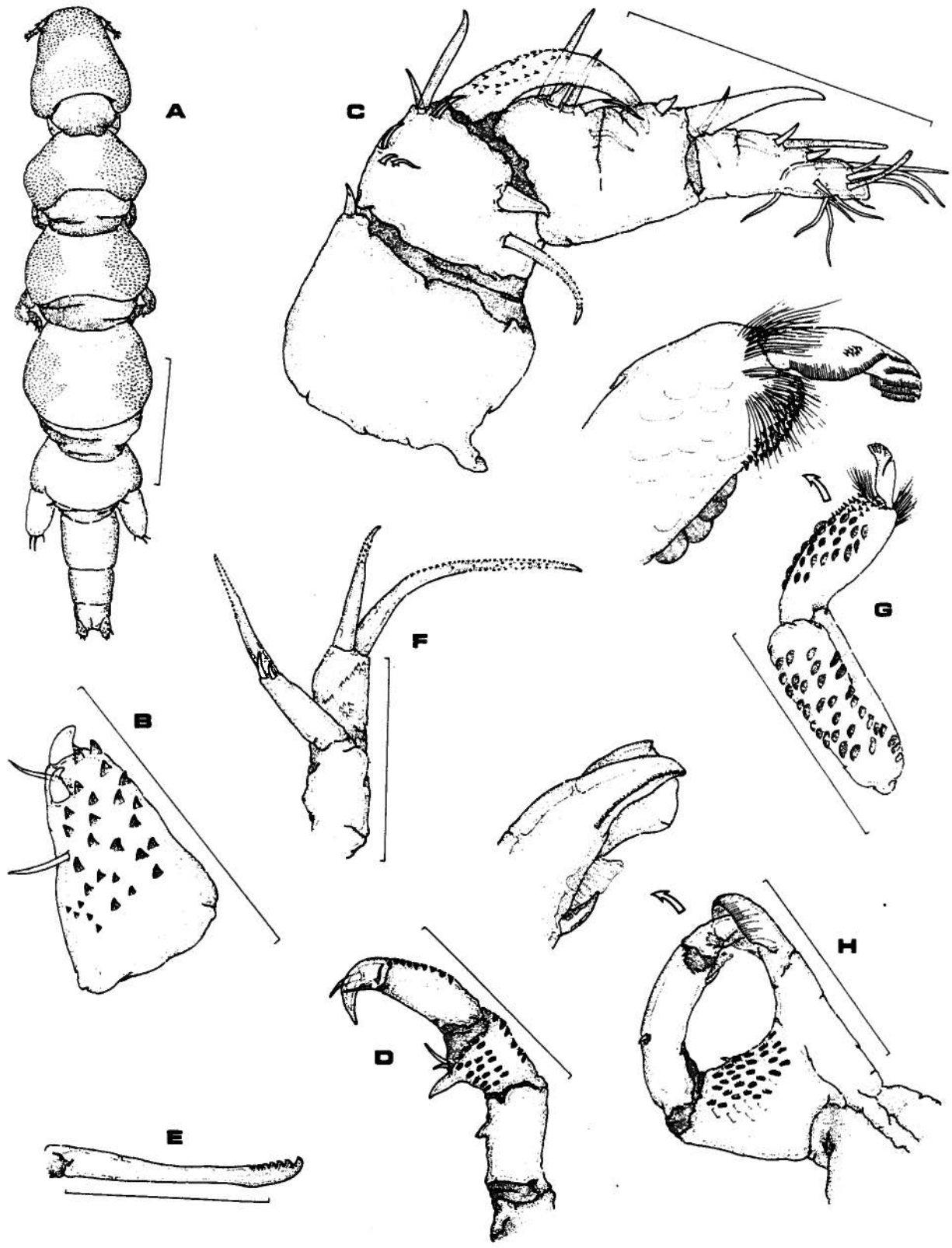


FIGURE 51. *Eudactylina similis* Scott, 1902, female: A, leg 1; B, leg 2 endopod; C, leg 3 exopod; D, legs 3 and 4; E, leg 5. Scales: 0.2 mm in A-E.

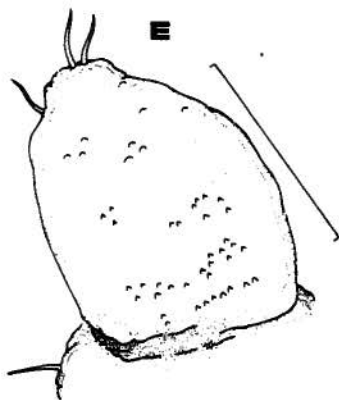
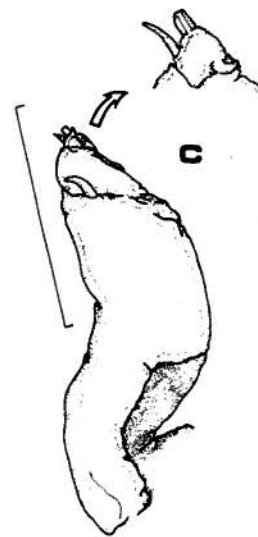
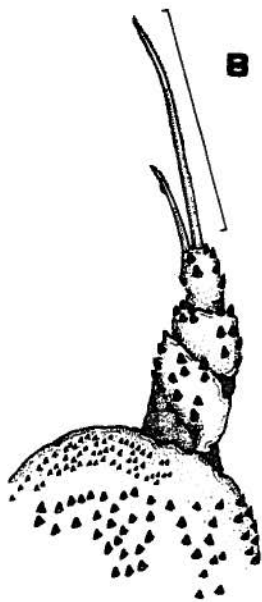
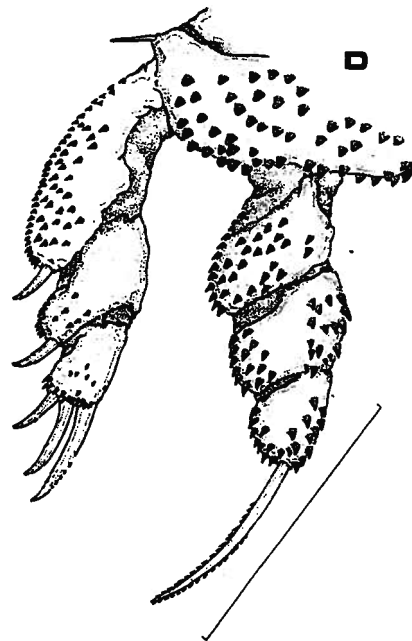
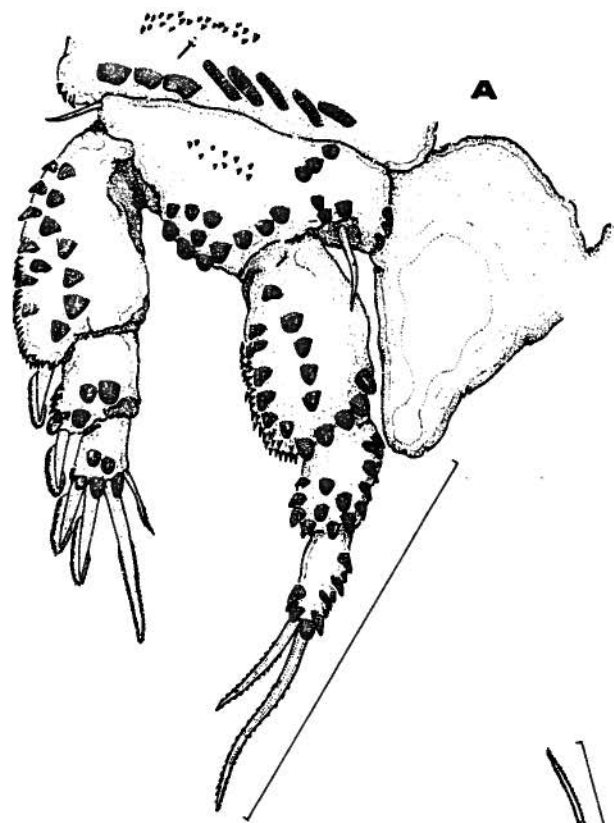


FIGURE 52. *Eudactylina squamosa* Bere, 1936, female: A, habitus, dorsal; B, lateral
C, caudal rami; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H,
second maxilla; I, maxilliped. Scales: 0.3 mm in A, B; 0.1 mm in C-F; 0.05 mm in G; 0.1
mm in H; 0.2 mm in I.

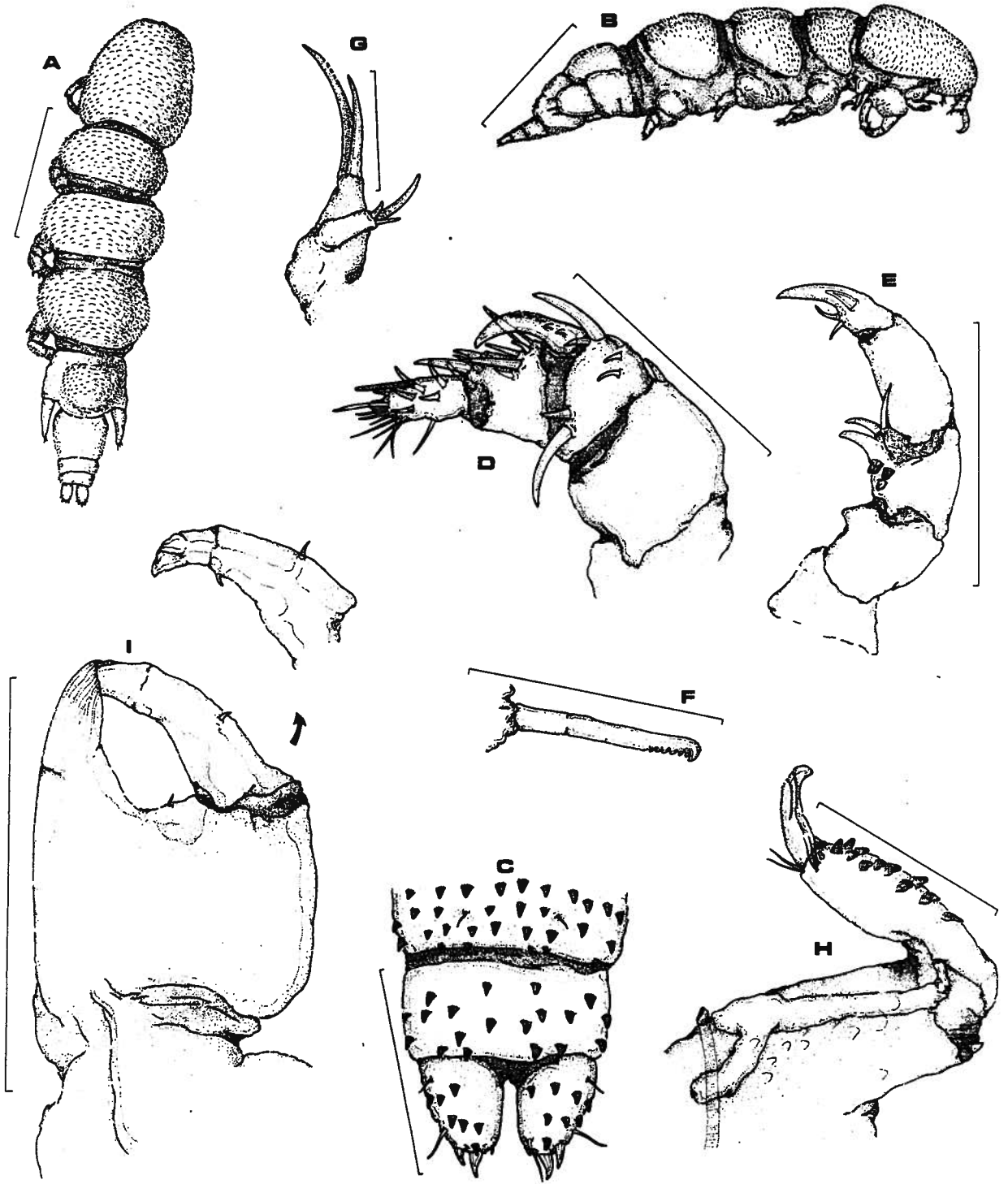


FIGURE 53. *Eudactylina squamosa* Bere, 1936, female: A, leg 1; B, leg 2; C, legs 3 and 4; D, leg 5. Scales: 0.1 mm in A-D.

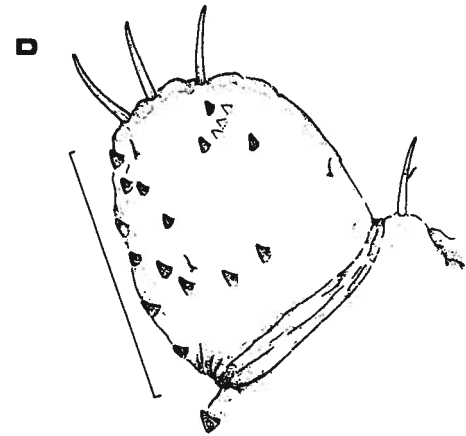
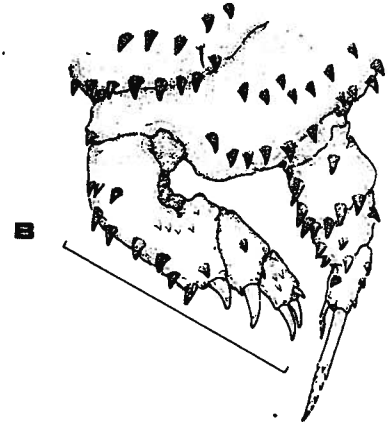
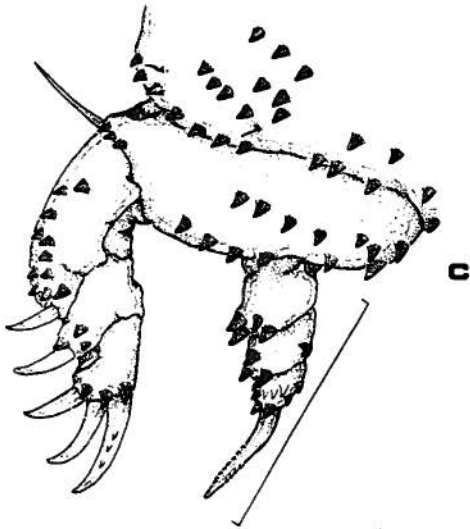


FIGURE 54. *Eudactylina tuberifera* Castro and Baeza, 1987, female: A, habitus, lateral; B, caudal rami; C, first antenna; D, second antenna; E, first maxilla and mandible; F, second maxilla. Scales: 0.4 mm in A; 0.1 mm in B-F.

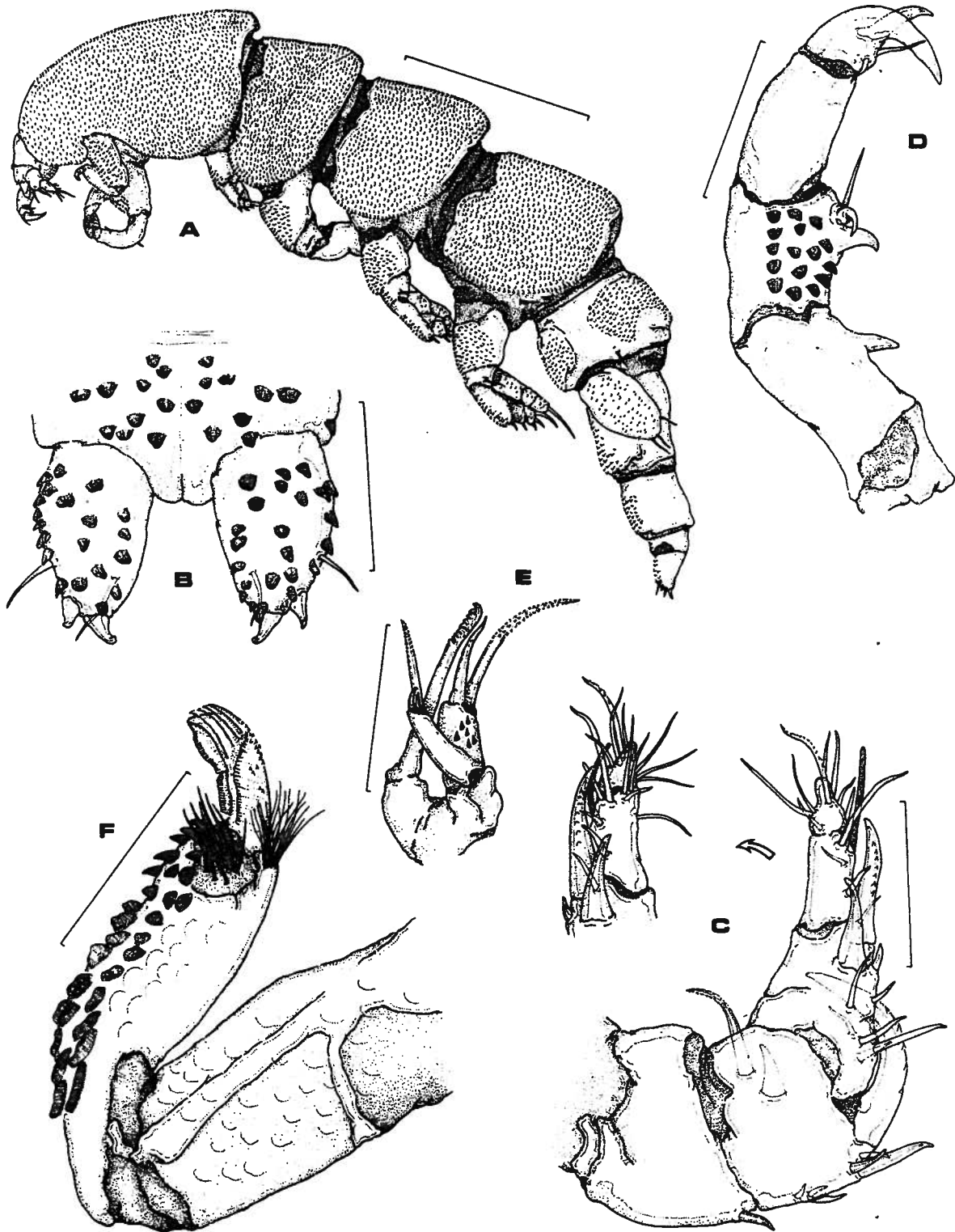


FIGURE 55. *Eudactylina tuberifera* Castro and Baeza, 1987, female: A, maxilliped; B, leg 1; C, leg 2 exopod; D, leg 2 endopod; E, legs 3 and 4 exopod; F, legs 3 and 4 endopod; G, leg 5. Scales: 0.2 mm in A; 0.1 mm in B; 0.2 mm in C-G.

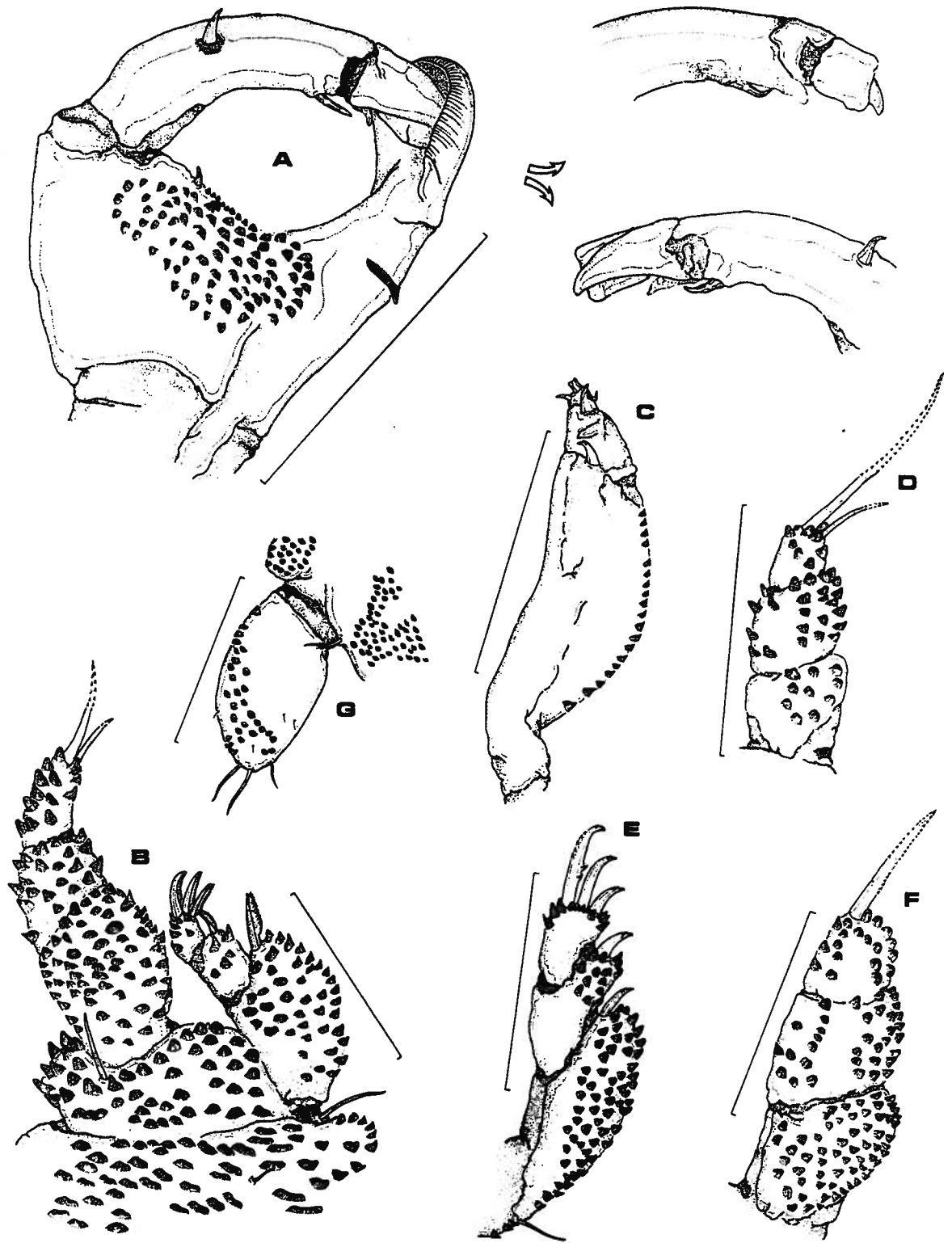


FIGURE 56. *Eudactylina turgipes* Bere, 1936, female: A, habitus, lateral; B, caudal rami and abdomen; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.4 mm in A; 0.1 mm in B-H.

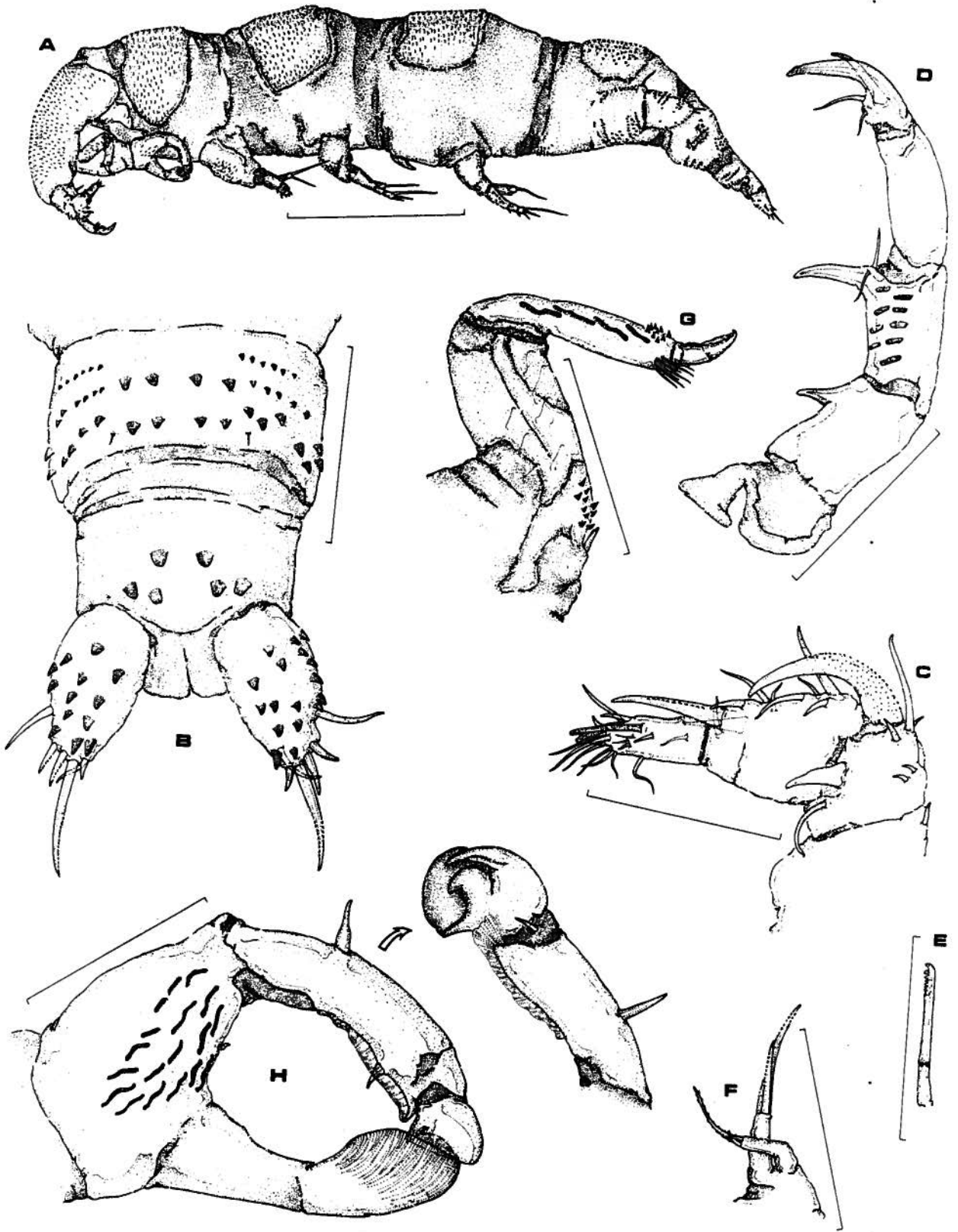


FIGURE 57. *Eudactylina turgipes* Bere, 1936, female: A, leg 1; B, leg 2; C, leg 2; D, legs 3 and 4; E, leg 5; F, ventral stylet. Scales: 0.2 mm in A; 0.1 mm in B, C. 0.2 mm in D-F.

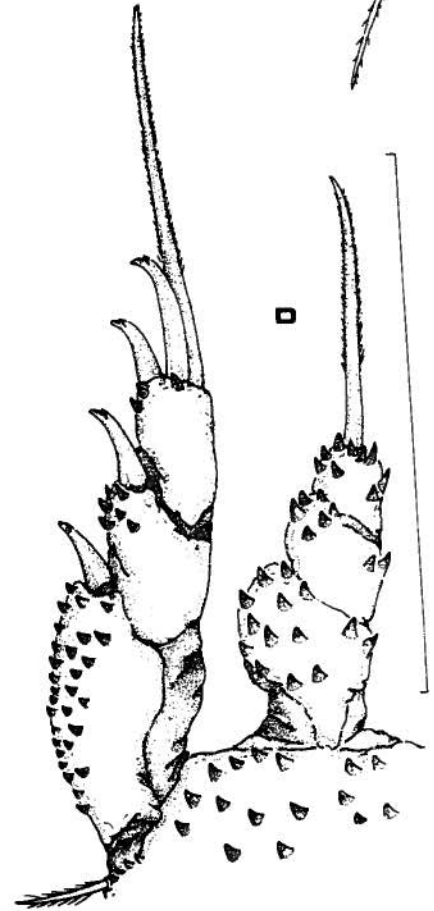
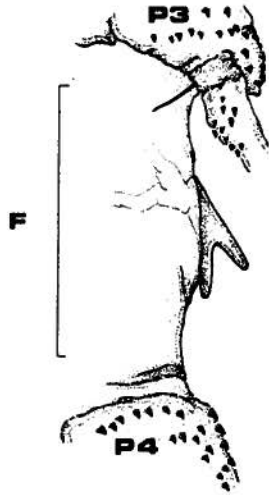
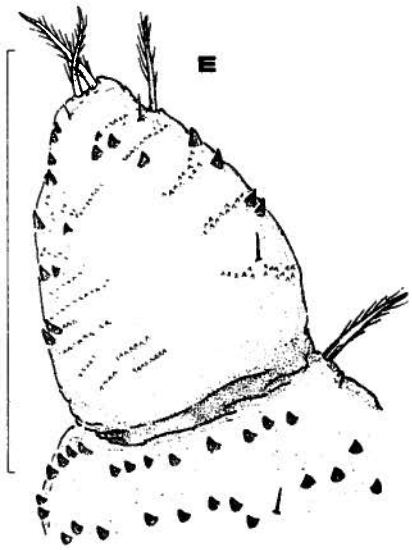
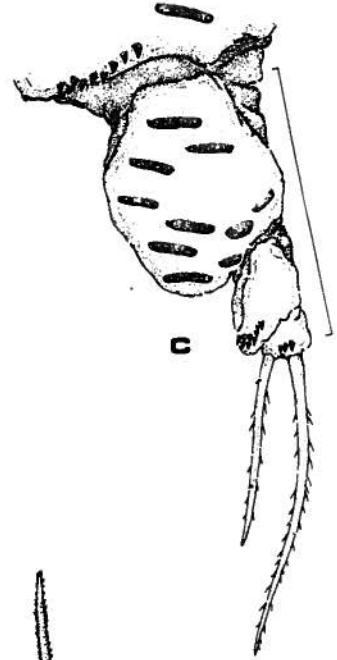
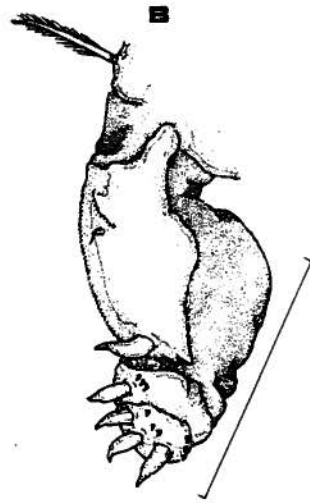


FIGURE 58. *Eudactylina urolophi* sp. nov., female: A, habitus, lateral; B, caudal rami; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped. Scales: 0.1 mm in A-H.

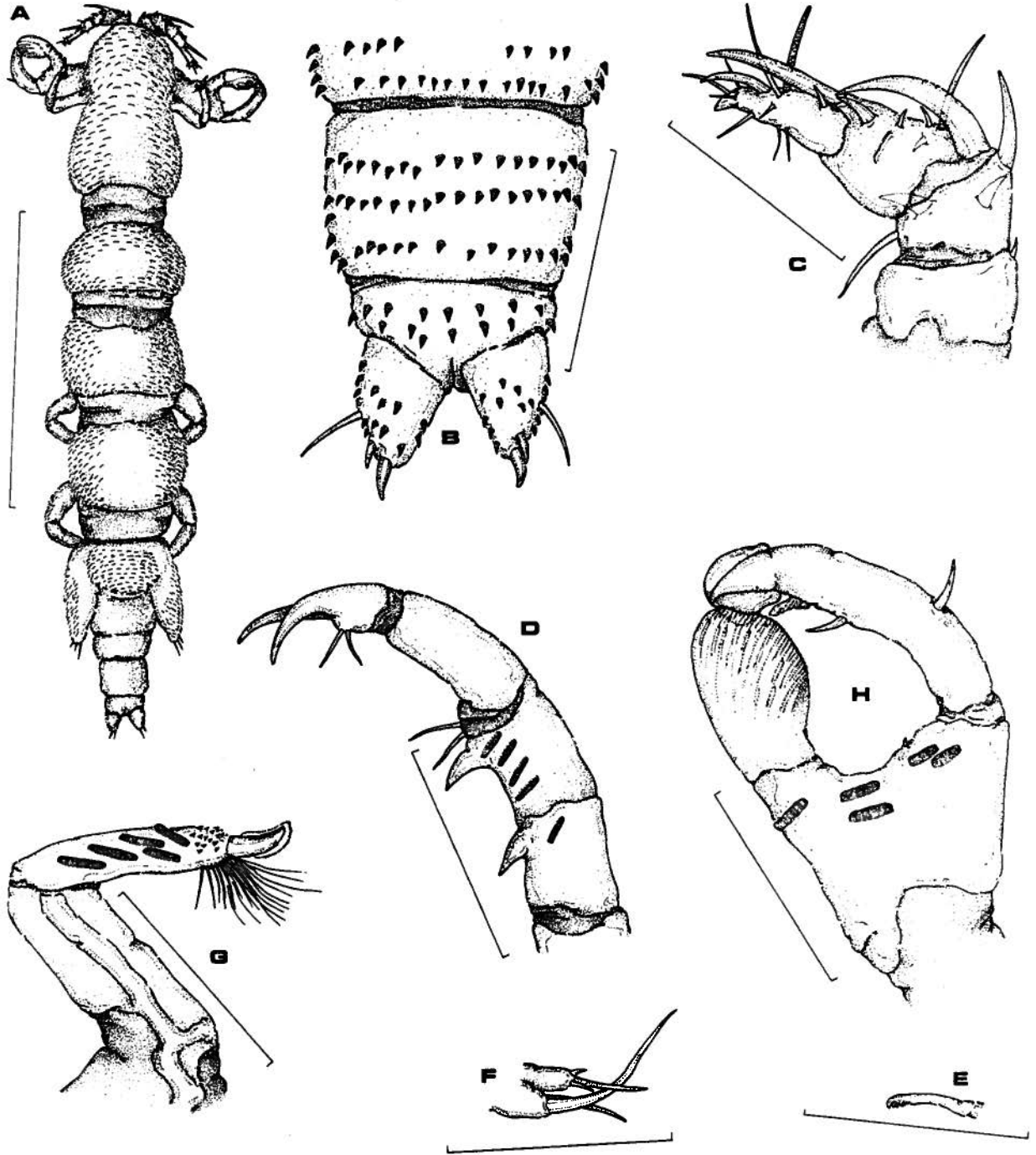


FIGURE 59. *Eudactylina urolphi* sp. nov., female: A, leg 1, lateral; B, leg 2; C, legs 3 and 4; D, leg 5. Scales: 0.1 mm in A-D.



FIGURE 60. *Eudactylina vaquetillae* sp. nov., female: A, habitus, lateral; B, caudal ramus; C, first antenna; D, mandible and first maxilla; E, second maxilla; F, maxilliped. Scales: 1.0 mm in A; 0.2 mm in B-G.

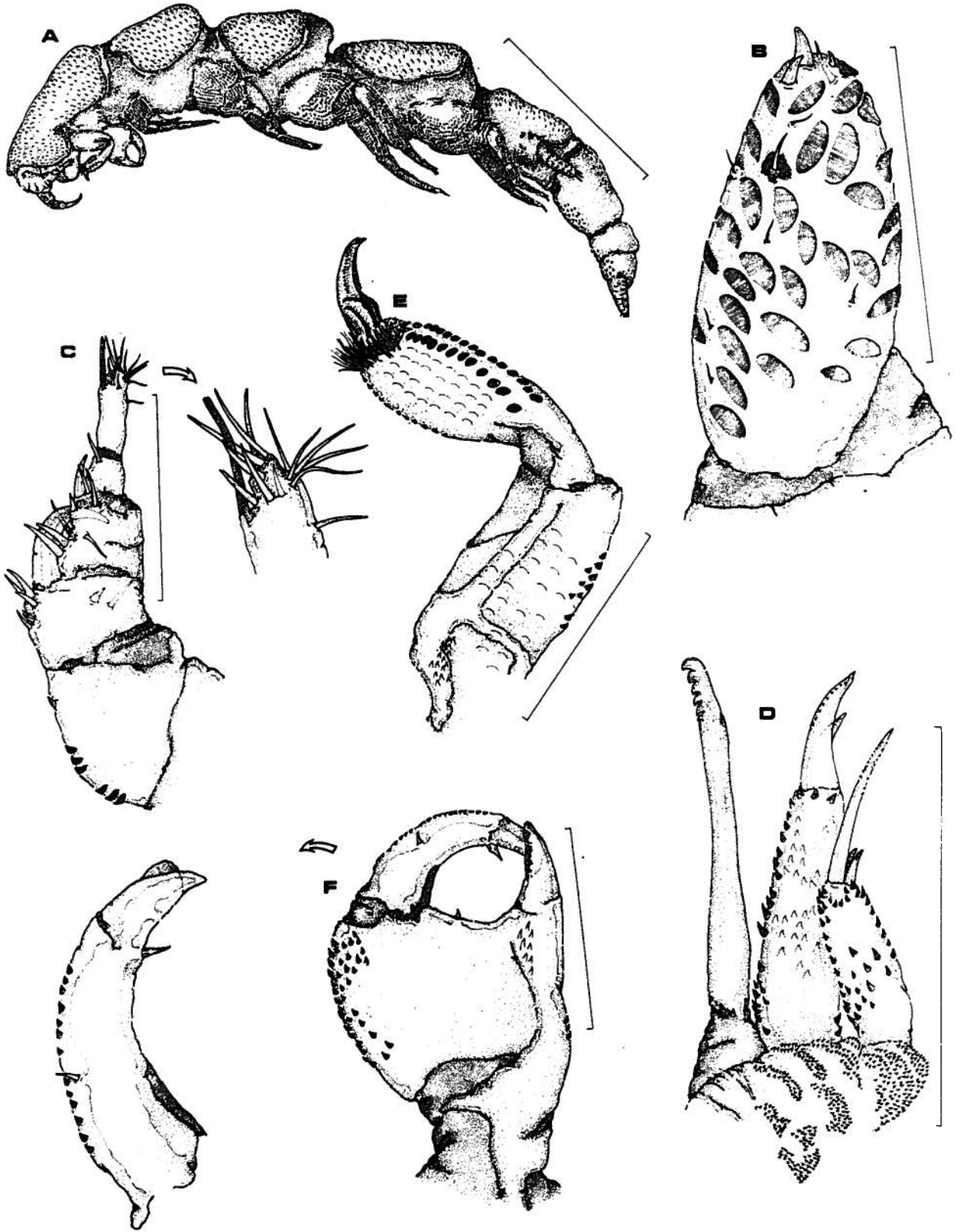


FIGURE 61. *Eudactylina vaquetillae* sp. nov., female: A, second antenna; B, leg 1; C, leg 2; D, leg 3; E, leg 4 exopod; F, leg 4 endopod; G, leg 5; H, leg 6. Scales: 0.2 mm in A; 0.38 mm in B; 0.2 mm in C-G; 0.1 mm in H.

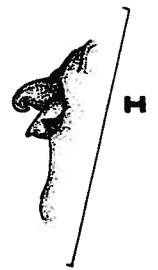
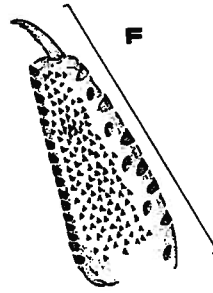
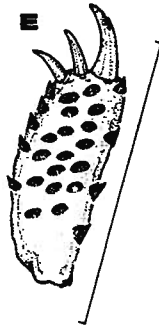
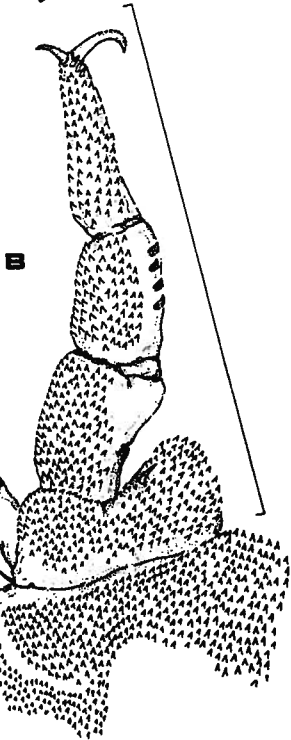
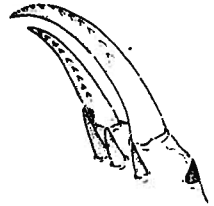
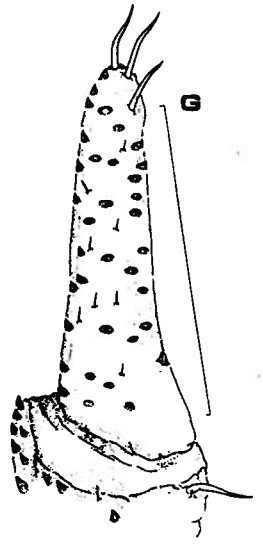
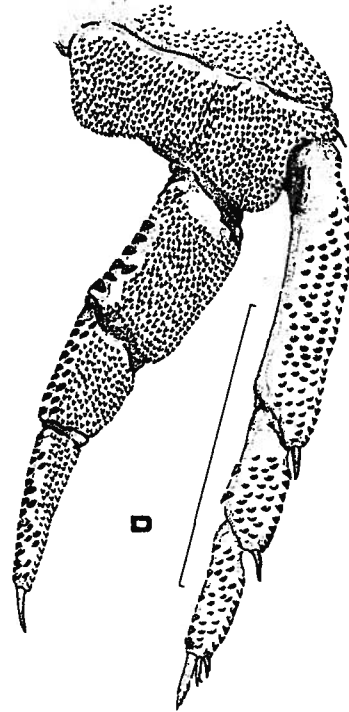
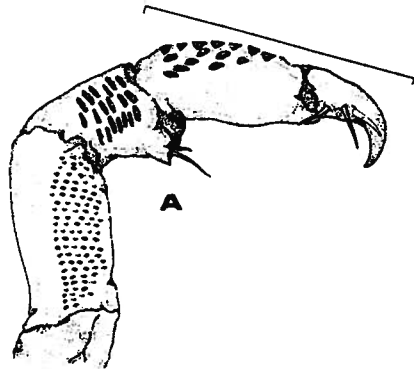


FIGURE 62. Eudactylinidae Cladogram.

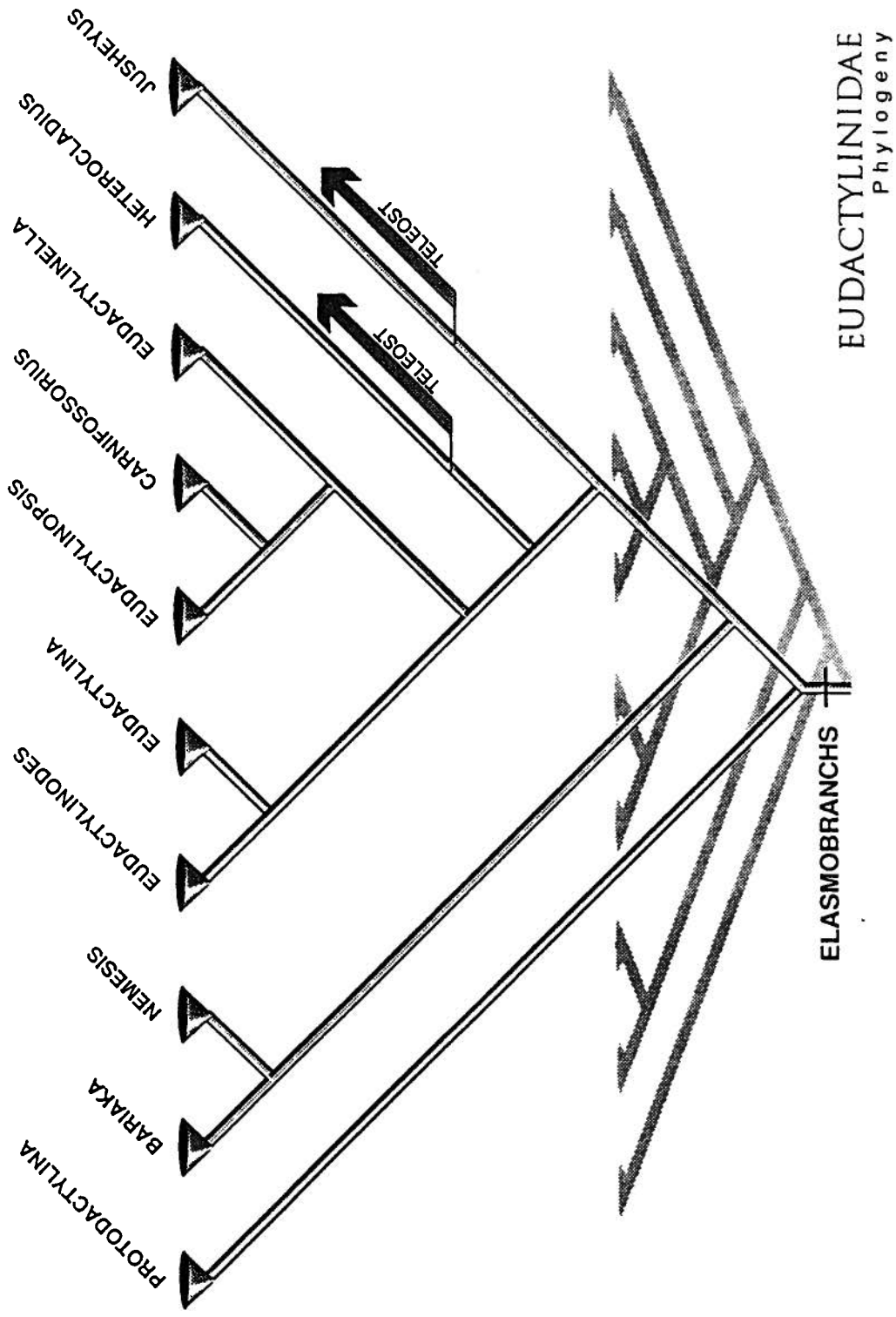
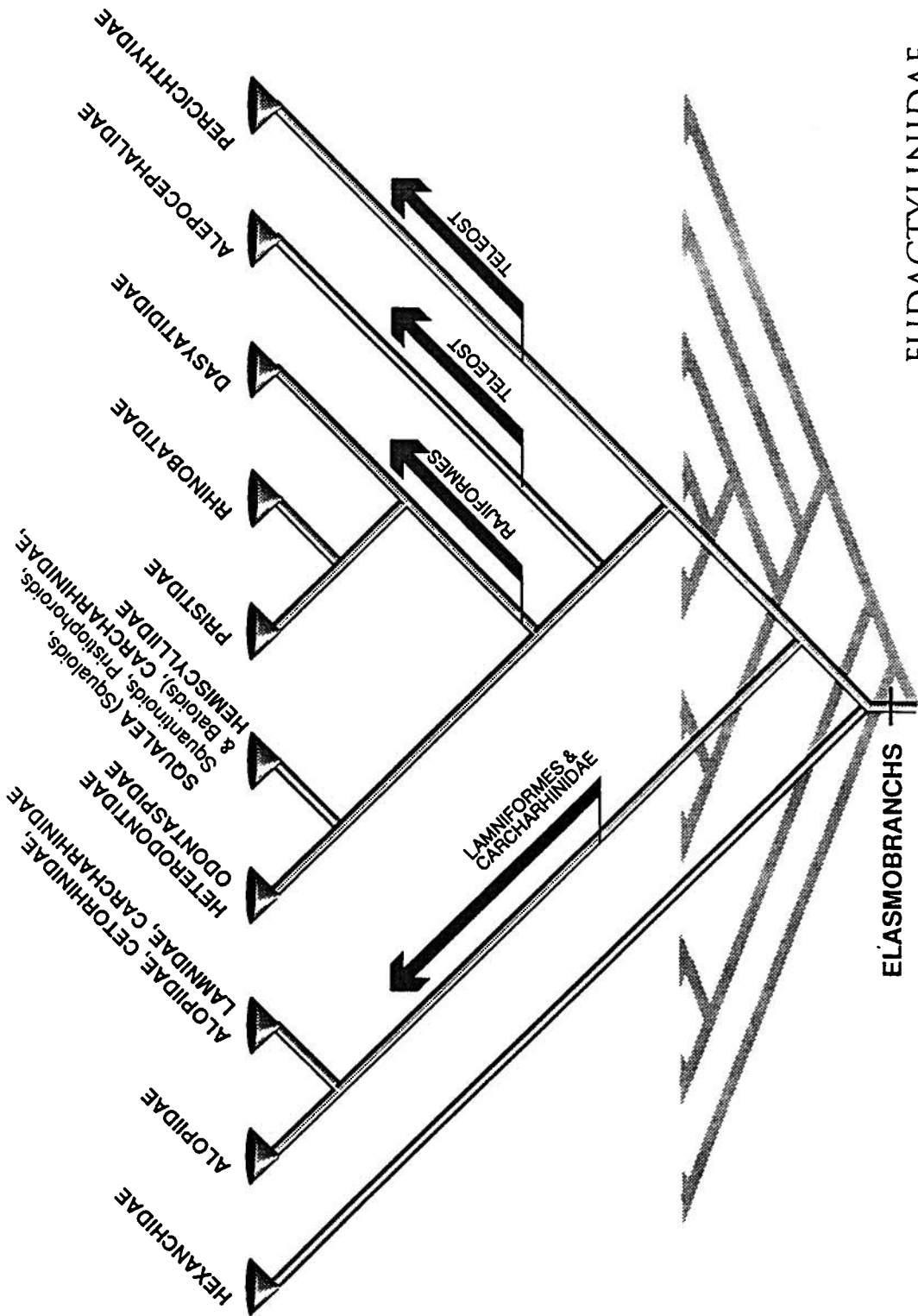
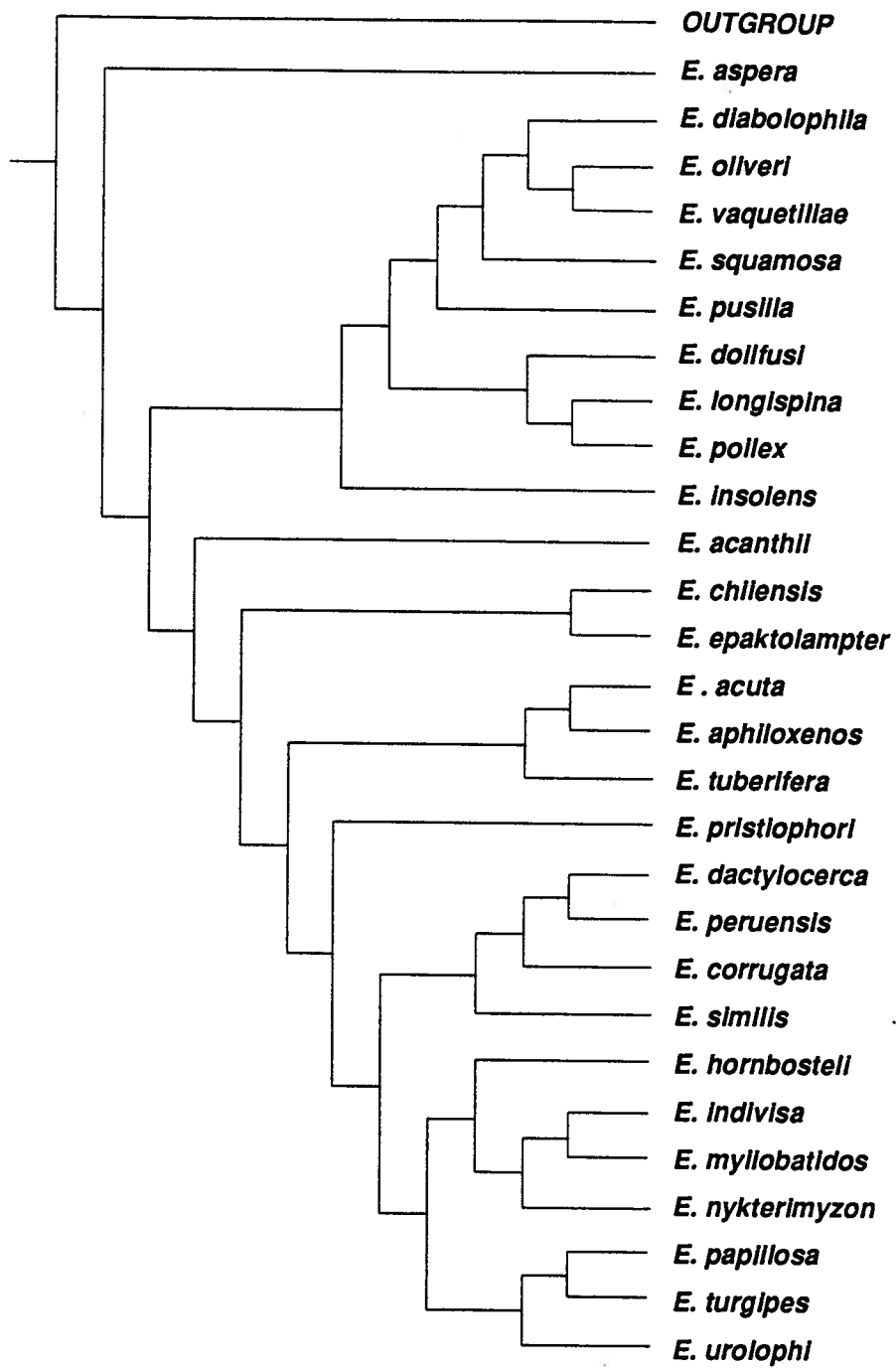


FIGURE 63. Eudactylinidae Host-Summary Cladogram.



EUDACTYLINIDAE
Host-Summary Cladogram

FIGURE 64. *Eudactylina* Cladogram (Heuristic search).



EUDACTYLINA CLADOGRAM

FIGURE 65. *Eudactylina* Cladogram (Exact search)

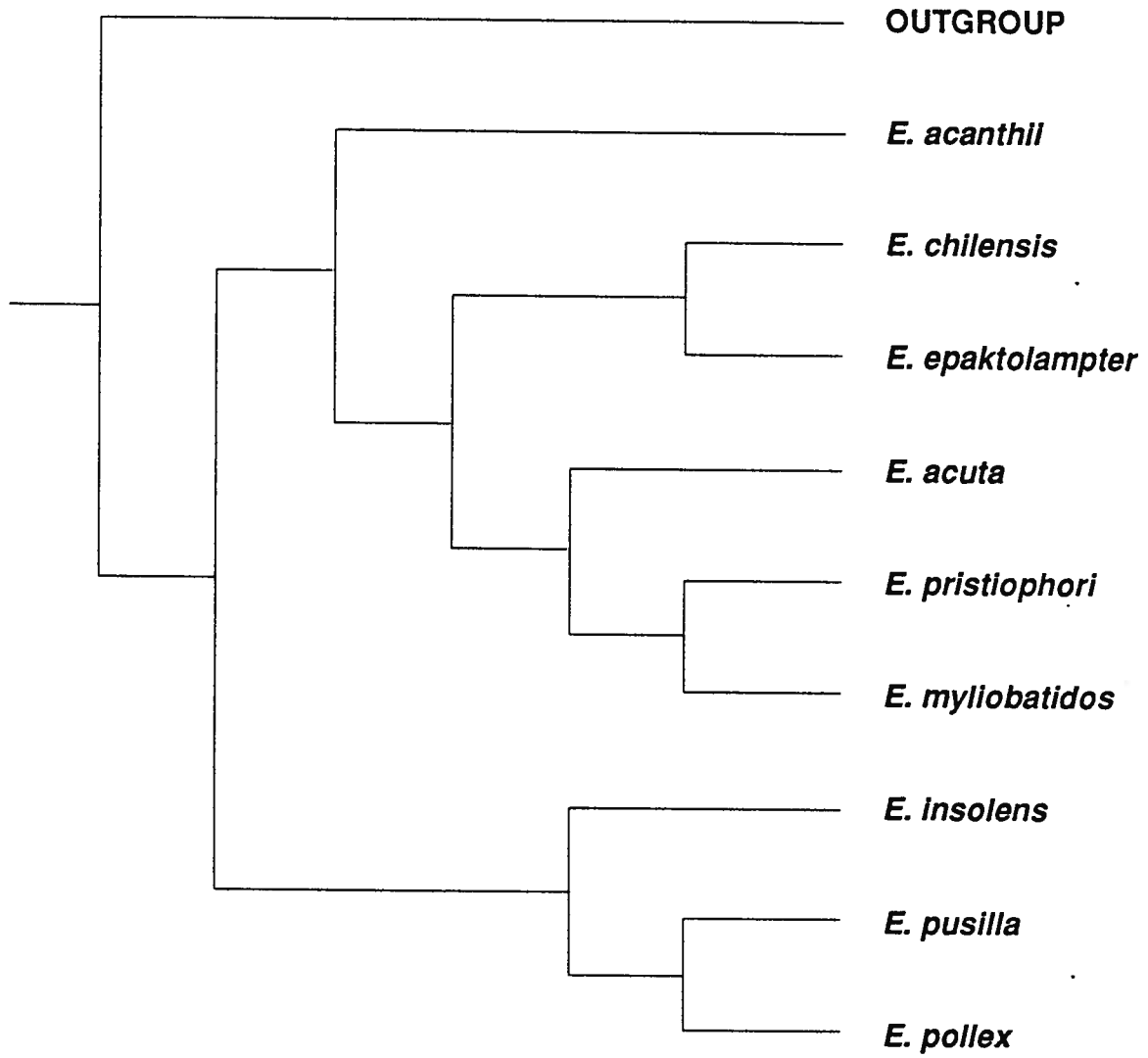
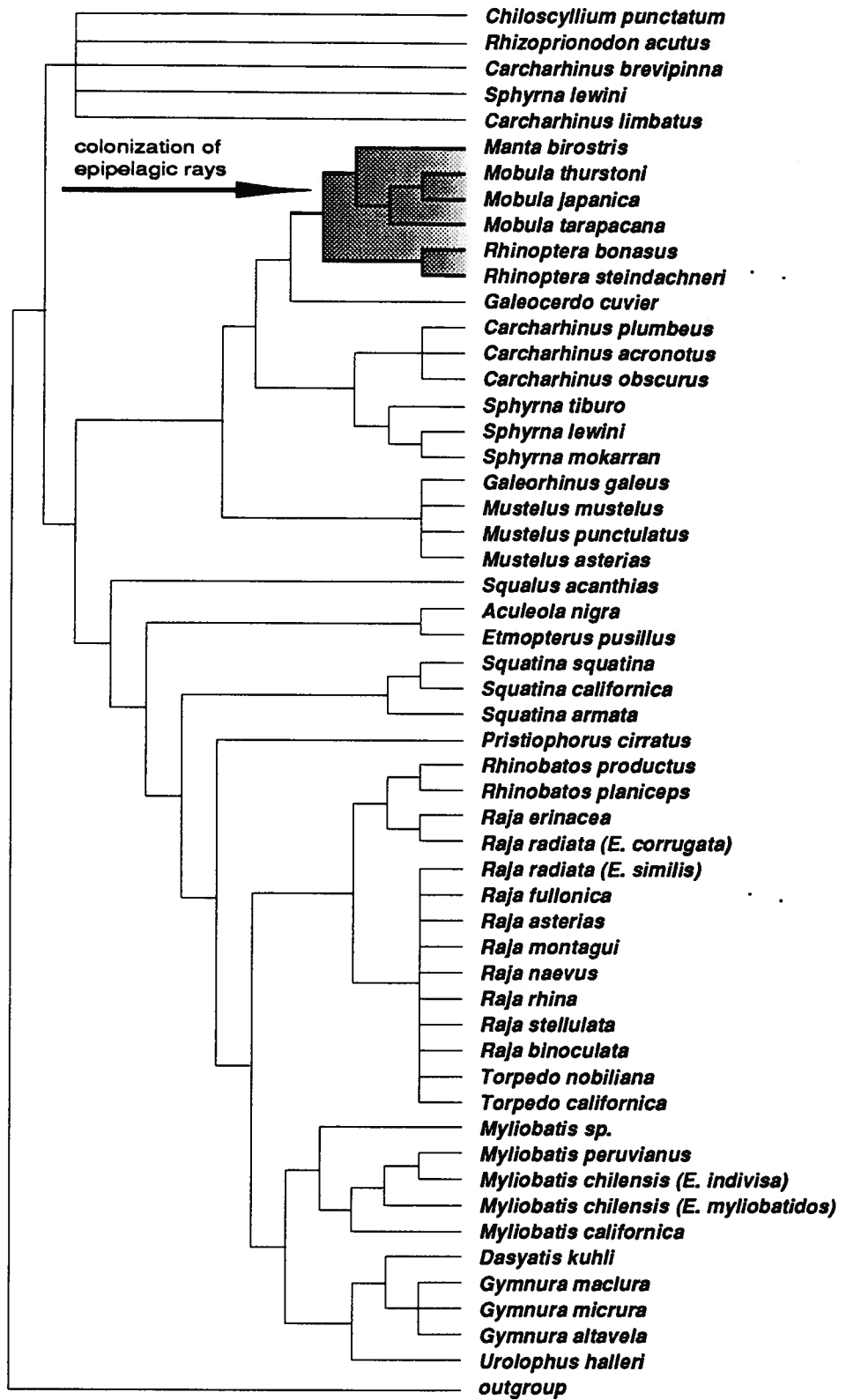
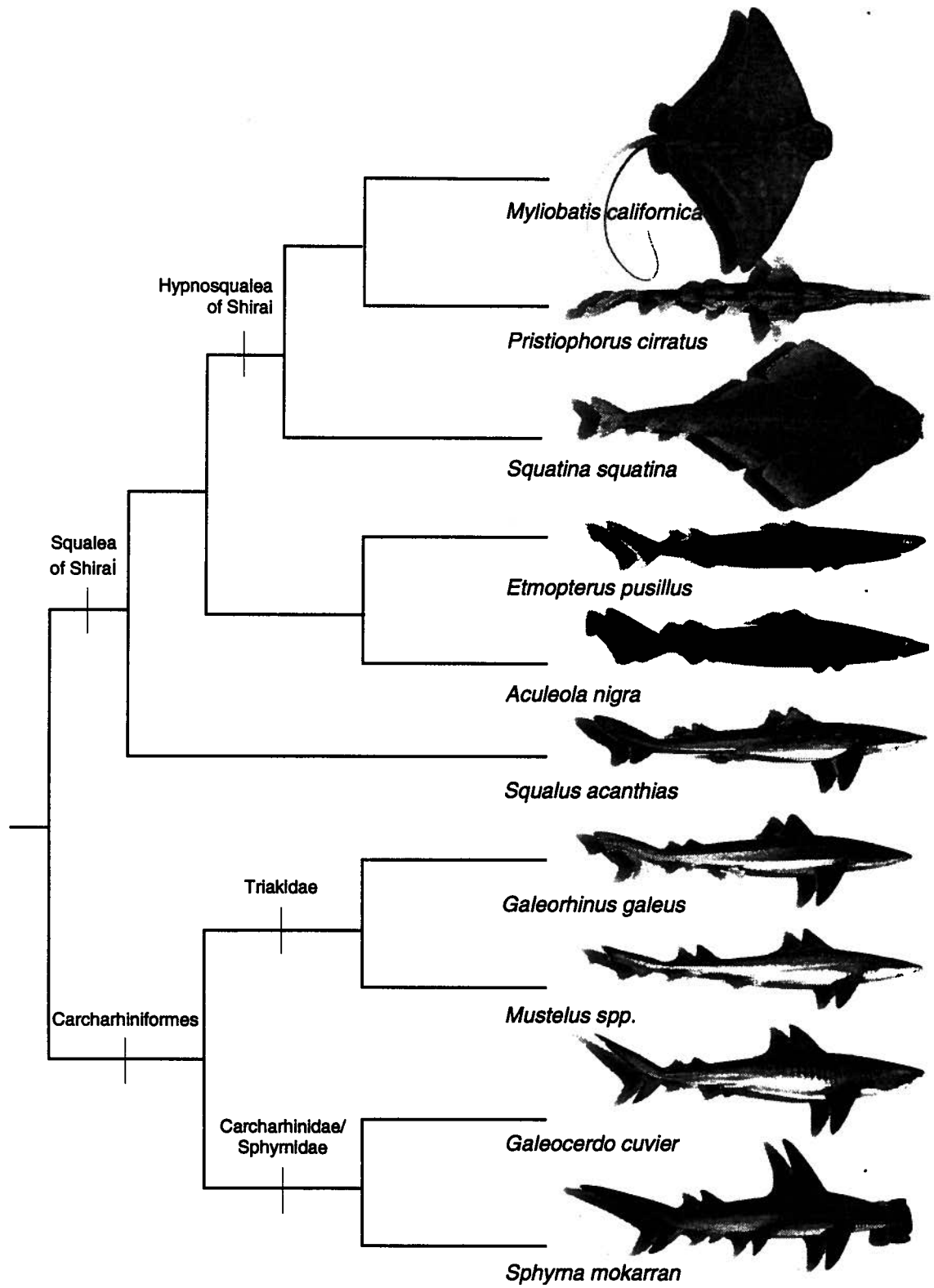


FIGURE 66. *Eudactylina*-derived host cladogram (Heuristic).



EUDACTYLINA-DERIVED HOST CLADOGRAM

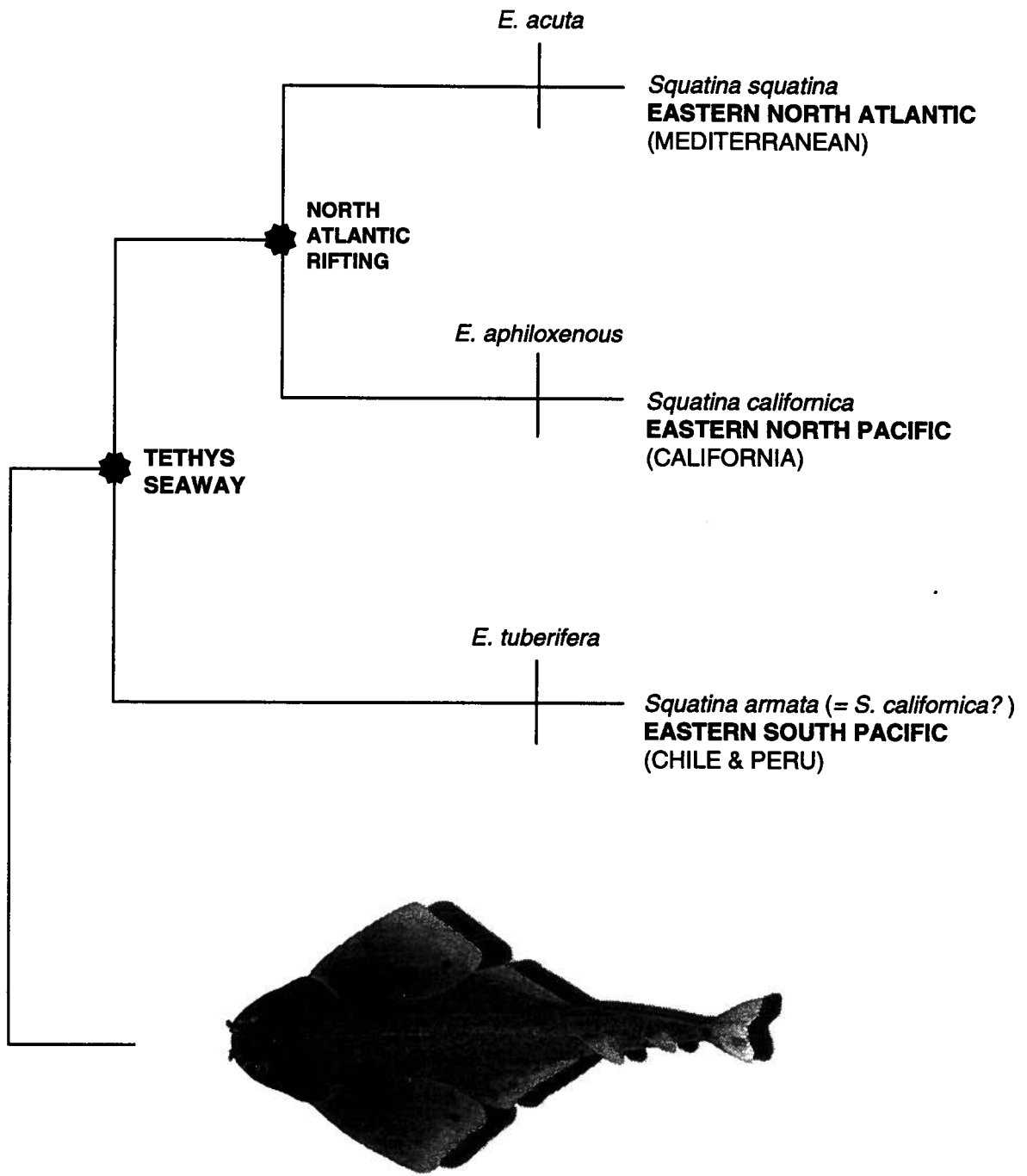
FIGURE 67. *Eudactylina*-derived host cladogram (Exact).



EUDACTYLINA - derived

Host Cladogram

FIGURE 68. Area- and host-summary cladogram for species of *Eudactylina* found on *Squatina*.



SQUATINA

FIGURE 69. Area- and host-summary cladogram for the species of *Eudactylina* found on *Myliobatis*.

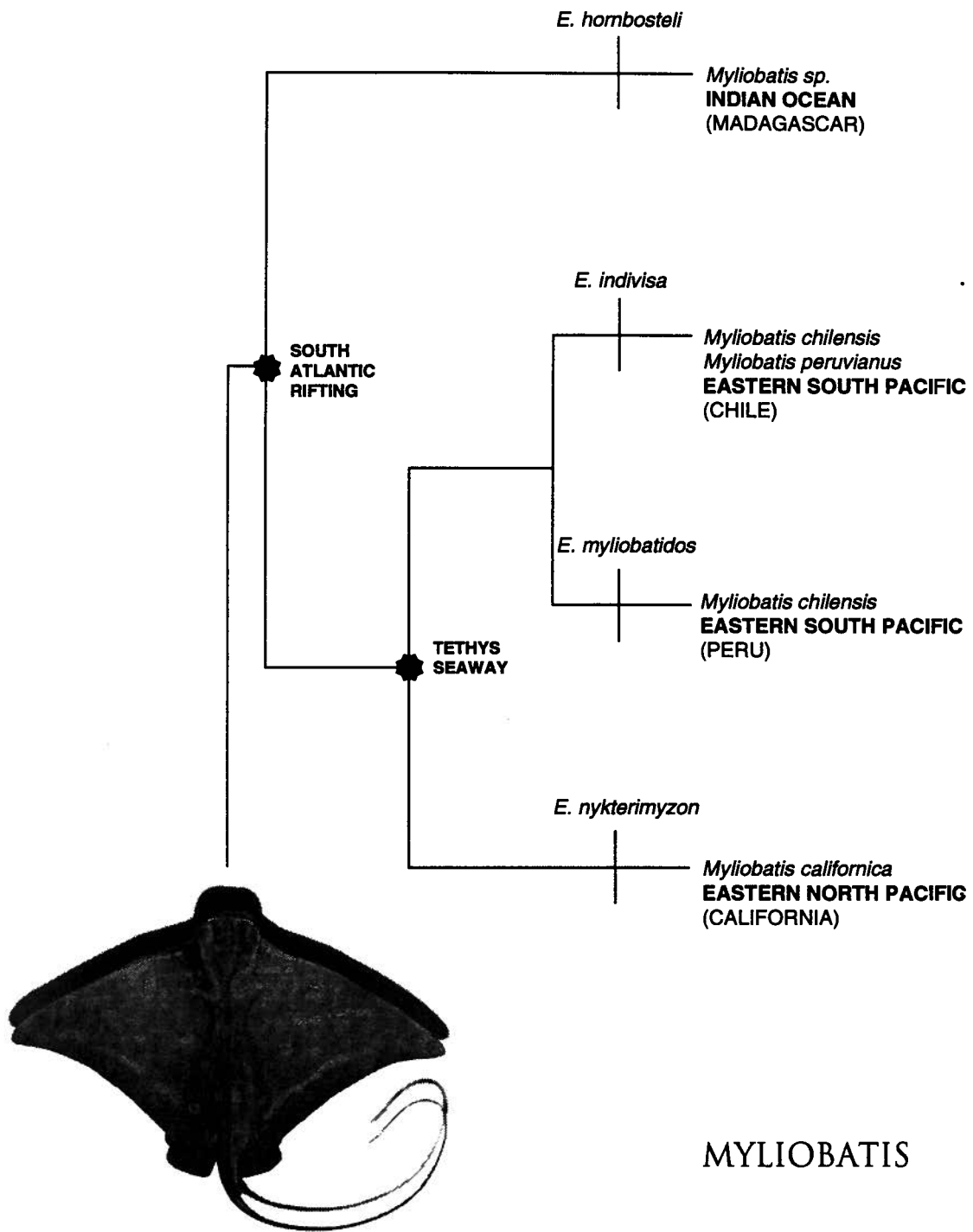


FIGURE 70. *Kroyeria carchariaeglauci* attached to gill filament (*in situ*) of the blue shark, *Prionace glauca*.

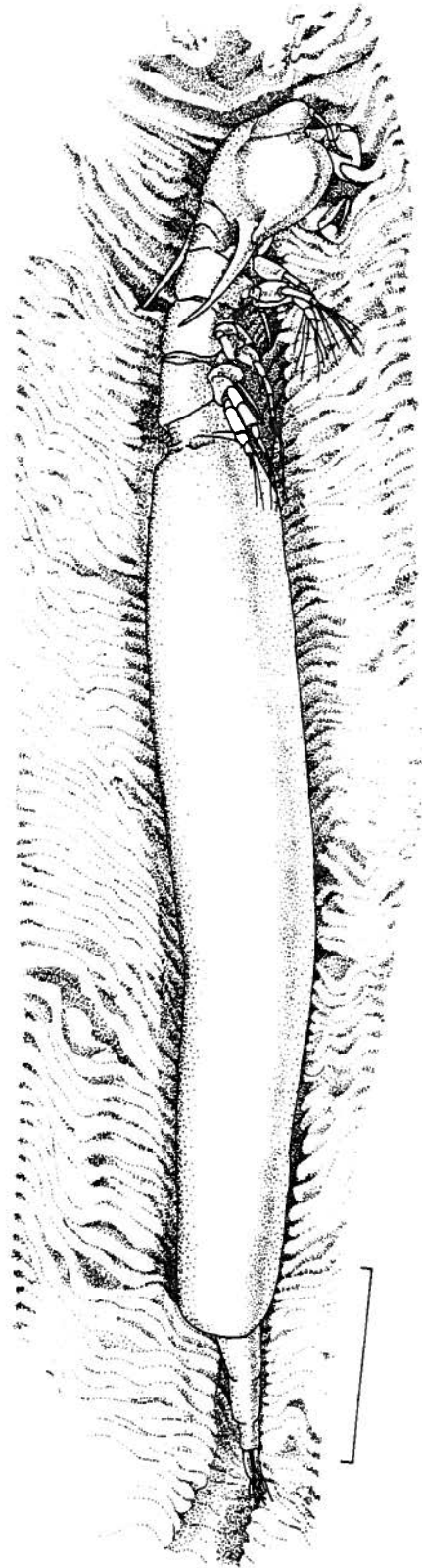


FIGURE 71. *Kroyeria branchiocetes* sp. nov., female: A, habitus, lateral; B, dorsal stylet; C, caudal ramus; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H, second maxilla; I, maxilliped. Scales: 1.0 mm in A; 0.360 mm in B; 0.070 mm in C, D; 0.180 mm in E; 0.035 mm in F; 0.070 mm in G, H; 0.180 mm in I.

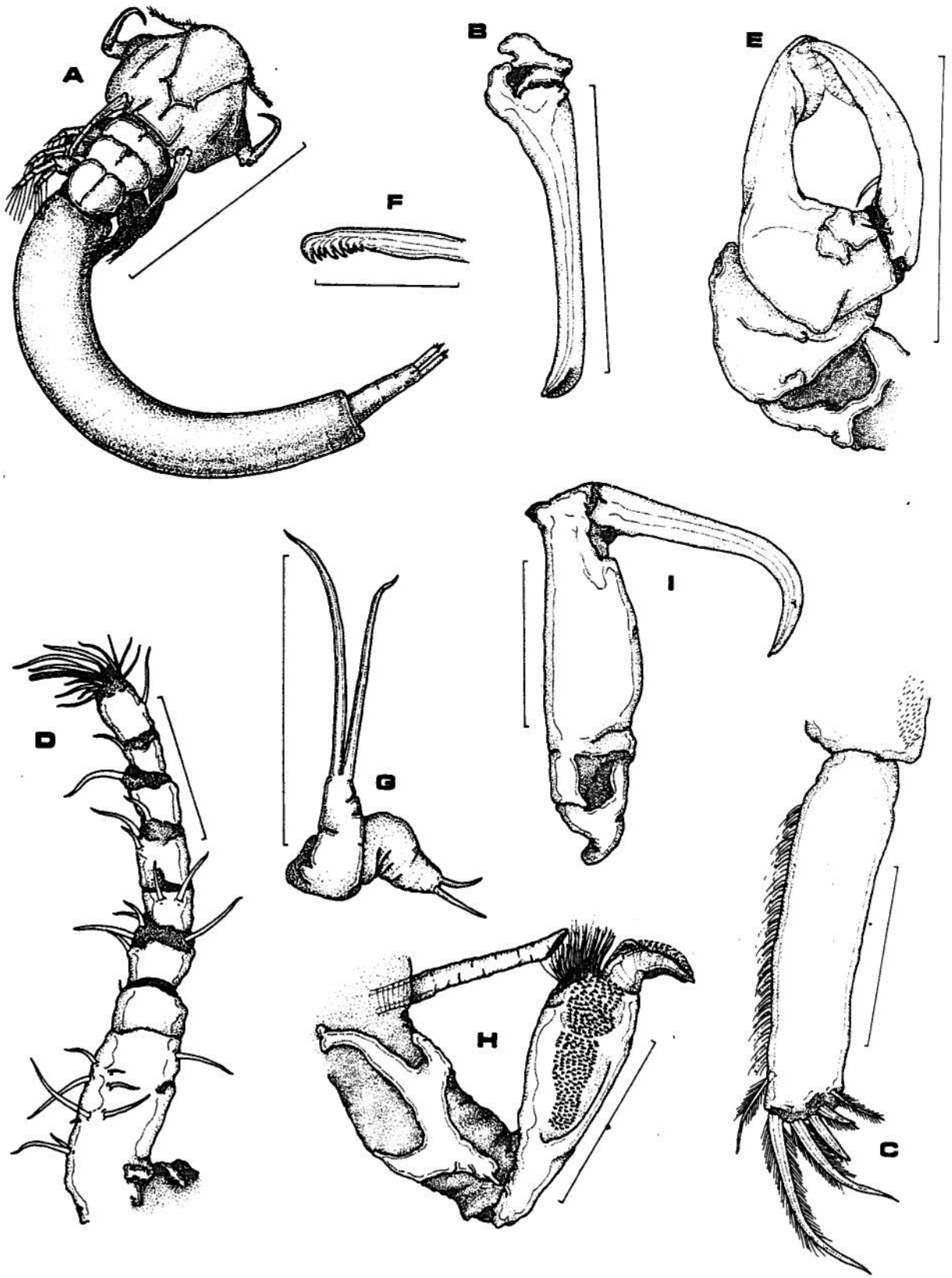


FIGURE 72. *Kroyeria branchiocetes* sp. nov., female: A, leg 1; B, leg 2; C, leg 3; D, leg 4. Scales: 0.180 mm in A-D.

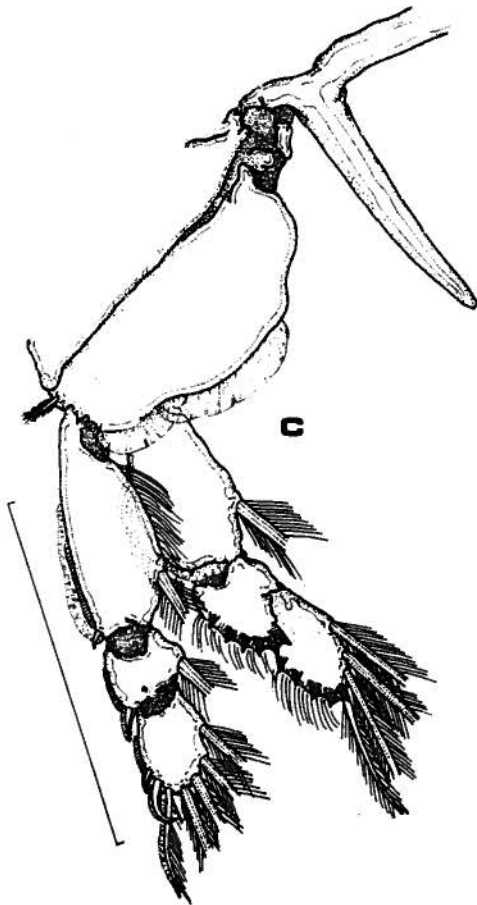
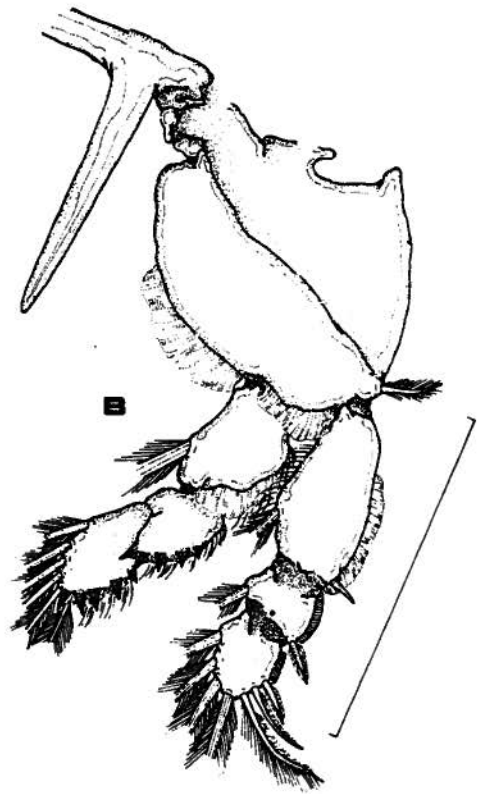
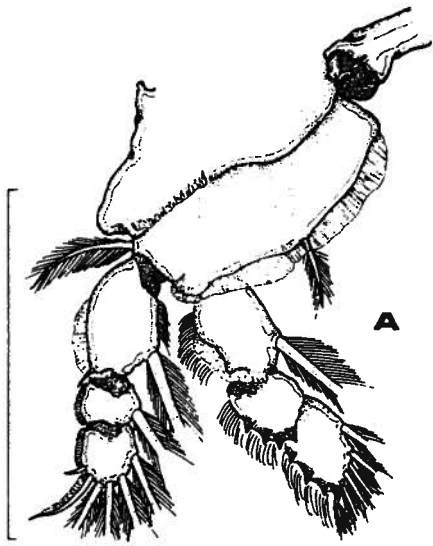


FIGURE 73. *Kroyeria branchiocetes* sp. nov., male: A, habitus, lateral; B, dorsal stylet; C, caudal ramus. Scales: 1.0 mm in A; 0.180 mm in B; 0.180 mm in C.

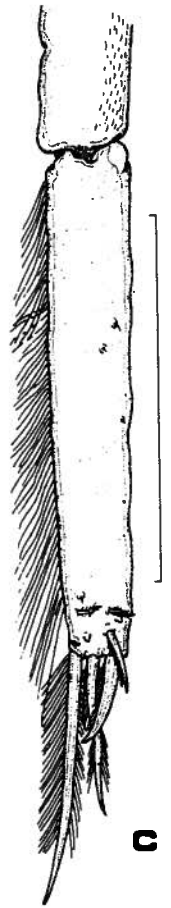
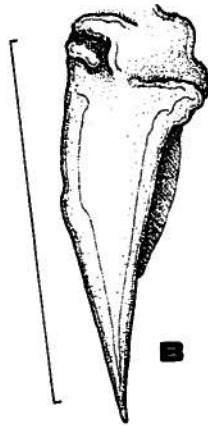
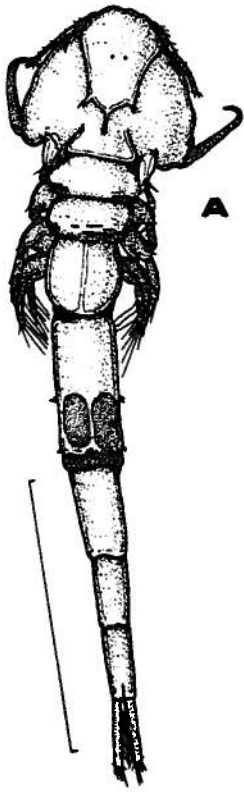


FIGURE 74. *Kroyeria carchariaeglauci* Hesse, 1879, female: A, habitus, dorsal; B, body lateral; C, dorsal stylet; D, caudal ramus; E, first antenna; F, second antenna; G, mandible; H, first maxilla; I, second maxilla. Scales: 1.0 mm in A, B; 0.360 mm in C; 0.180 mm in D; 0.02 mm in E, F; 0.01 mm in G, H; 0.090 mm in I.

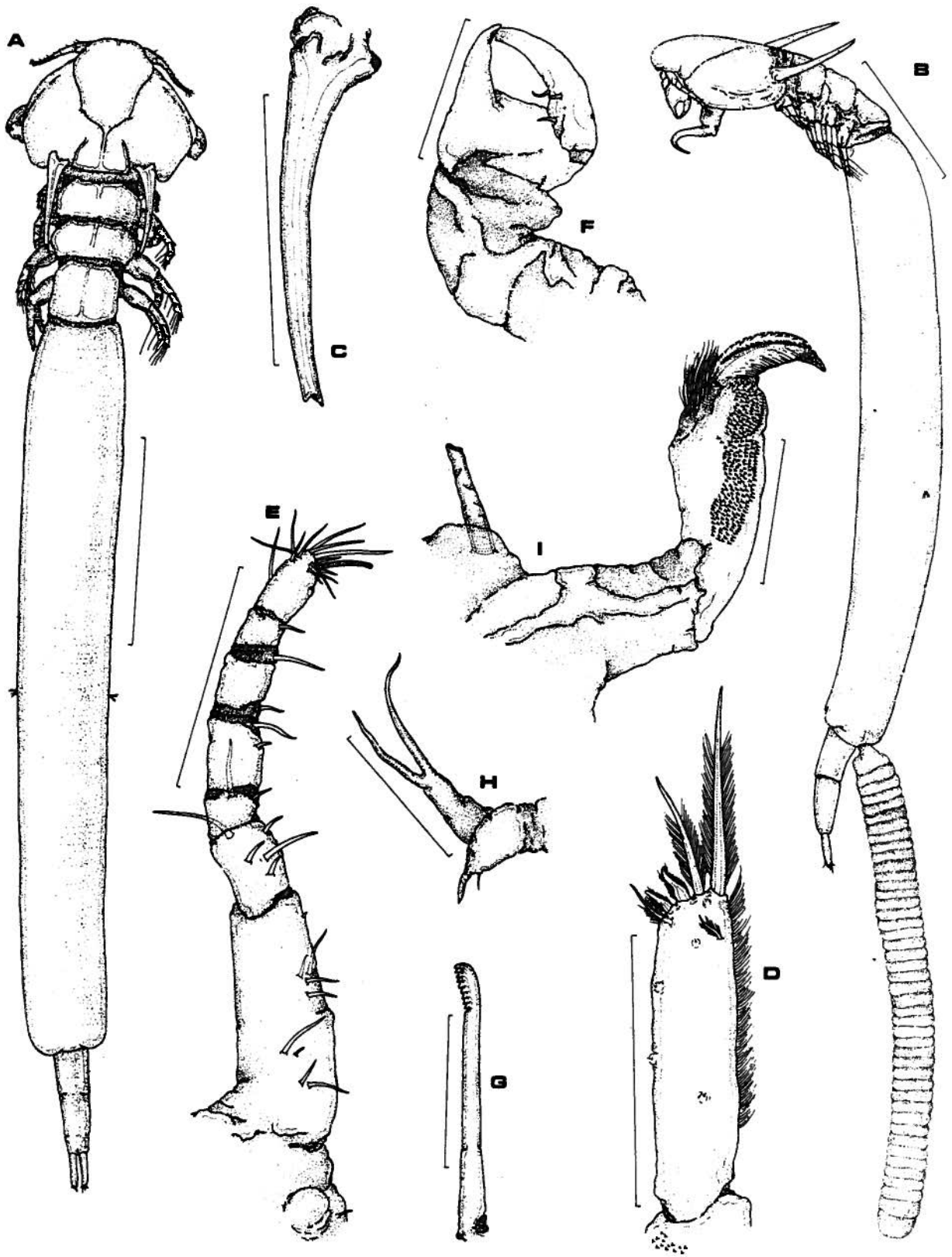


FIGURE 75. *Kroyeria carchariaeglauci* Hesse, 1879, female: A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 4. Scales: 0.2 mm in A-E.

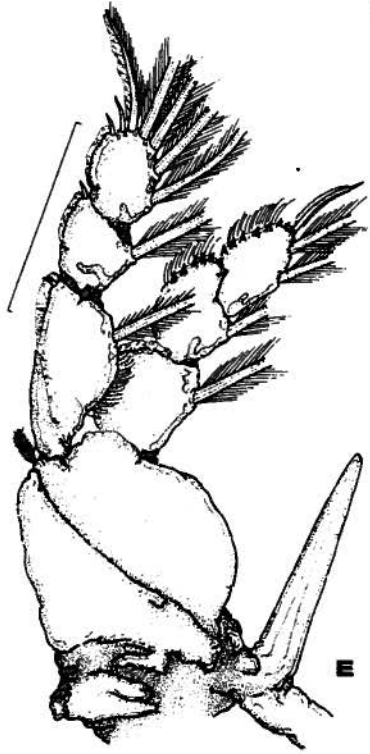
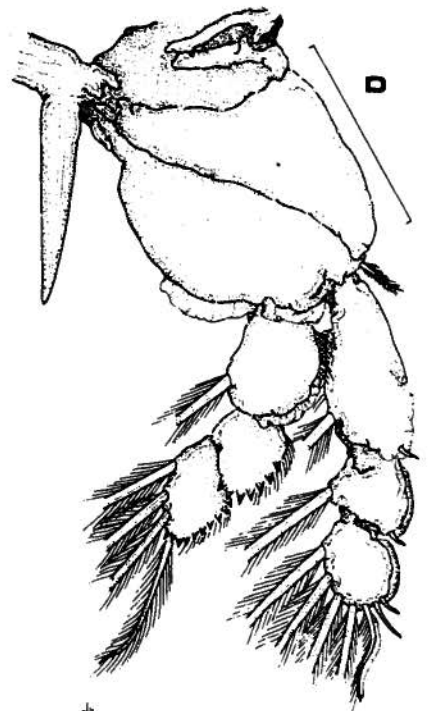
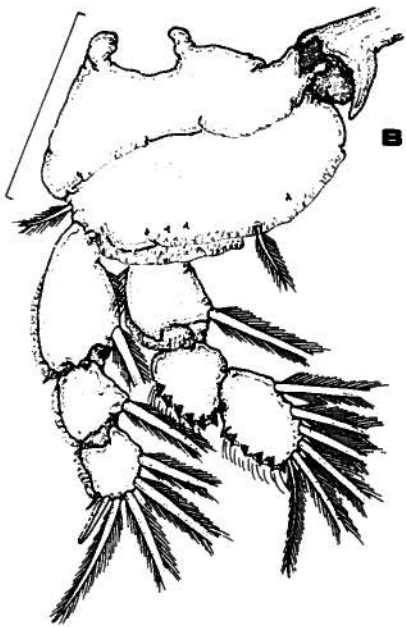


FIGURE 76. *Kroyeria carchariae* Hesse, 1879, male: A, habitus; B, caudal ramus. Scales: 1.0 mm in A; 0.090 mm in B.

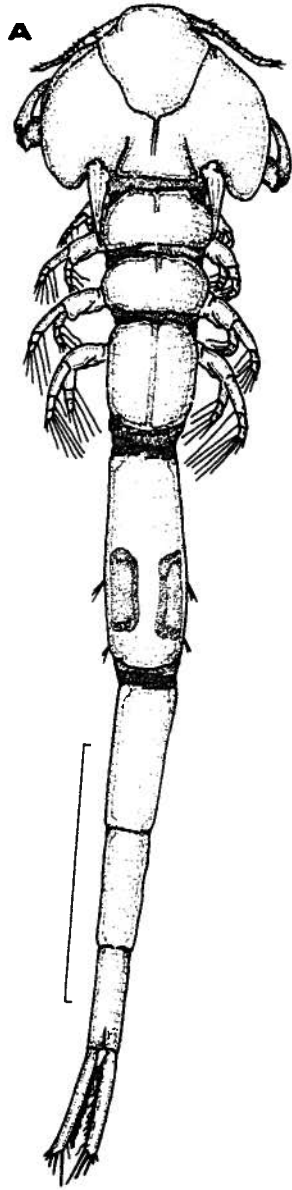


FIGURE 77. *Kroyeria caseyi* Benz and Deets, 1986, female: A, habitus, dorsal; B, habitus, dorsal; C, lateral cephalothorax; D, dorsal stylet; E, caudal ramus; F, first antenna; G, second antenna; H, mandible; I, first maxilla; J, second maxilla; K, maxilliped. Scales: 1.0 mm in A, B; 0.2 mm in C, D; 0.1 mm in E-K.

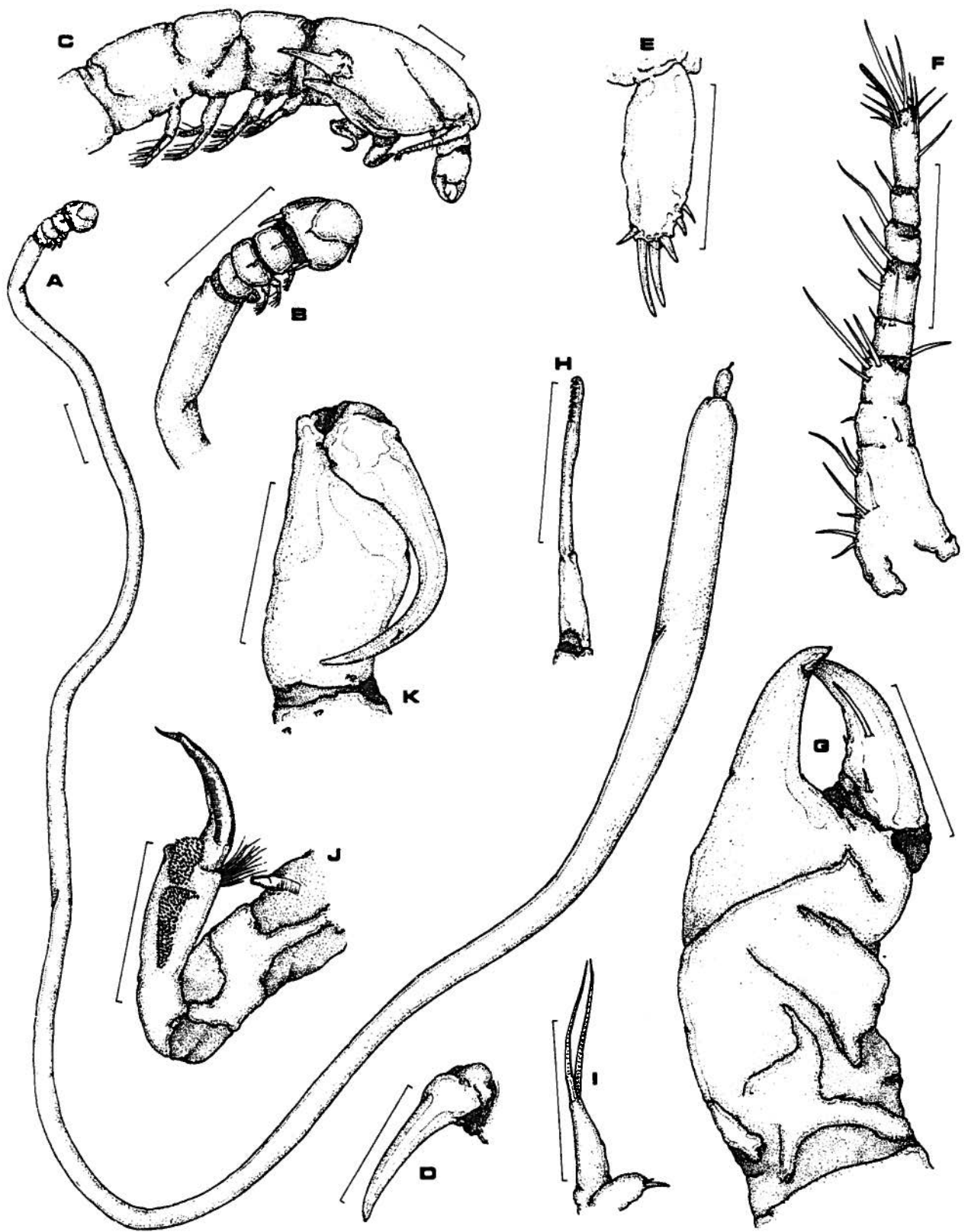


FIGURE 78. *Kroyeria caseyi* Benz and Deets, 1986, female: A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, male, dorsal; F, male, caudal ramus. Scales: 0.2 mm in A-D; 1.0 mm in E; 0.1 mm in F.

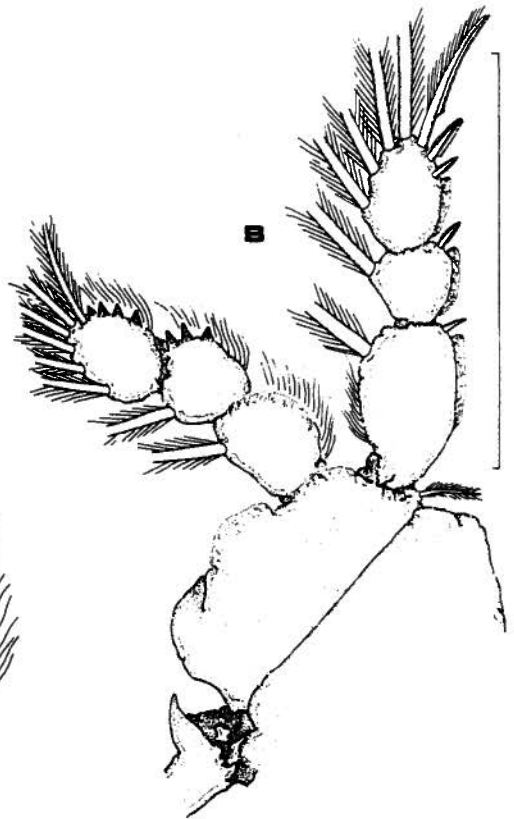
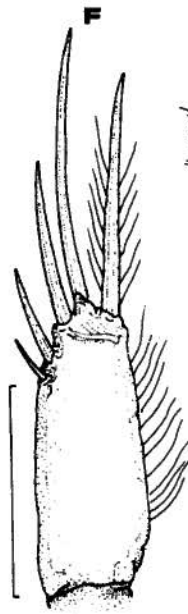
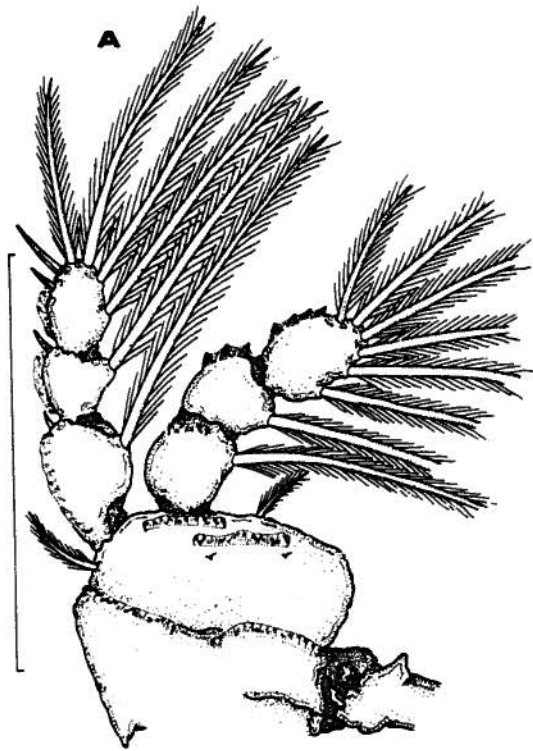
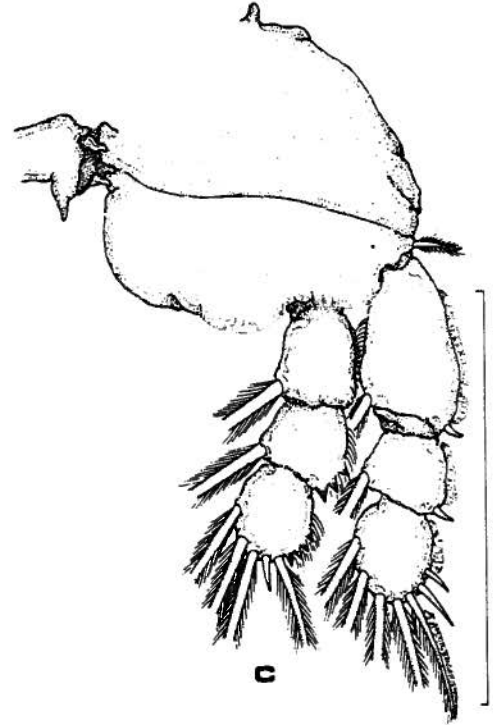
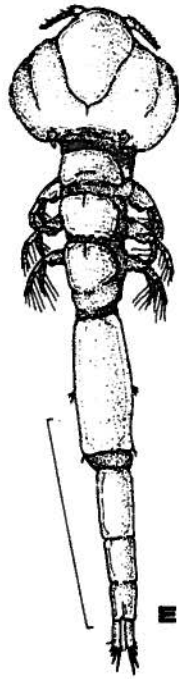
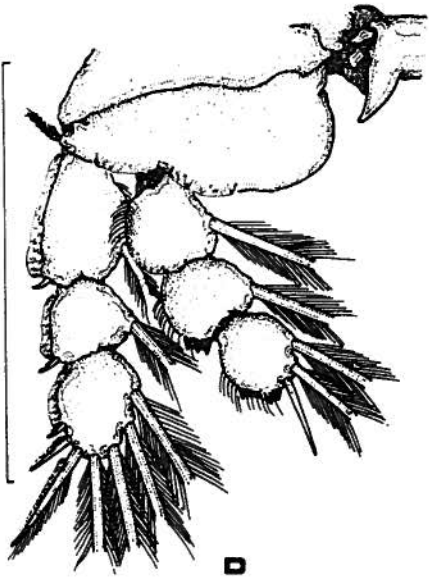


FIGURE 79. *Kroyeria cresseyi* sp. nov., female: A, habitus, dorsal; B, dorsal stylet; C, caudal ramus; D, egg sac; E, first antenna; F, second antenna; G, mandible; H, first maxilla. Scales: 1.0 mm in A; 0.2 mm in B, C; 1.0 mm in D; 0.2 mm in E, F; 0.1 mm in G, H.

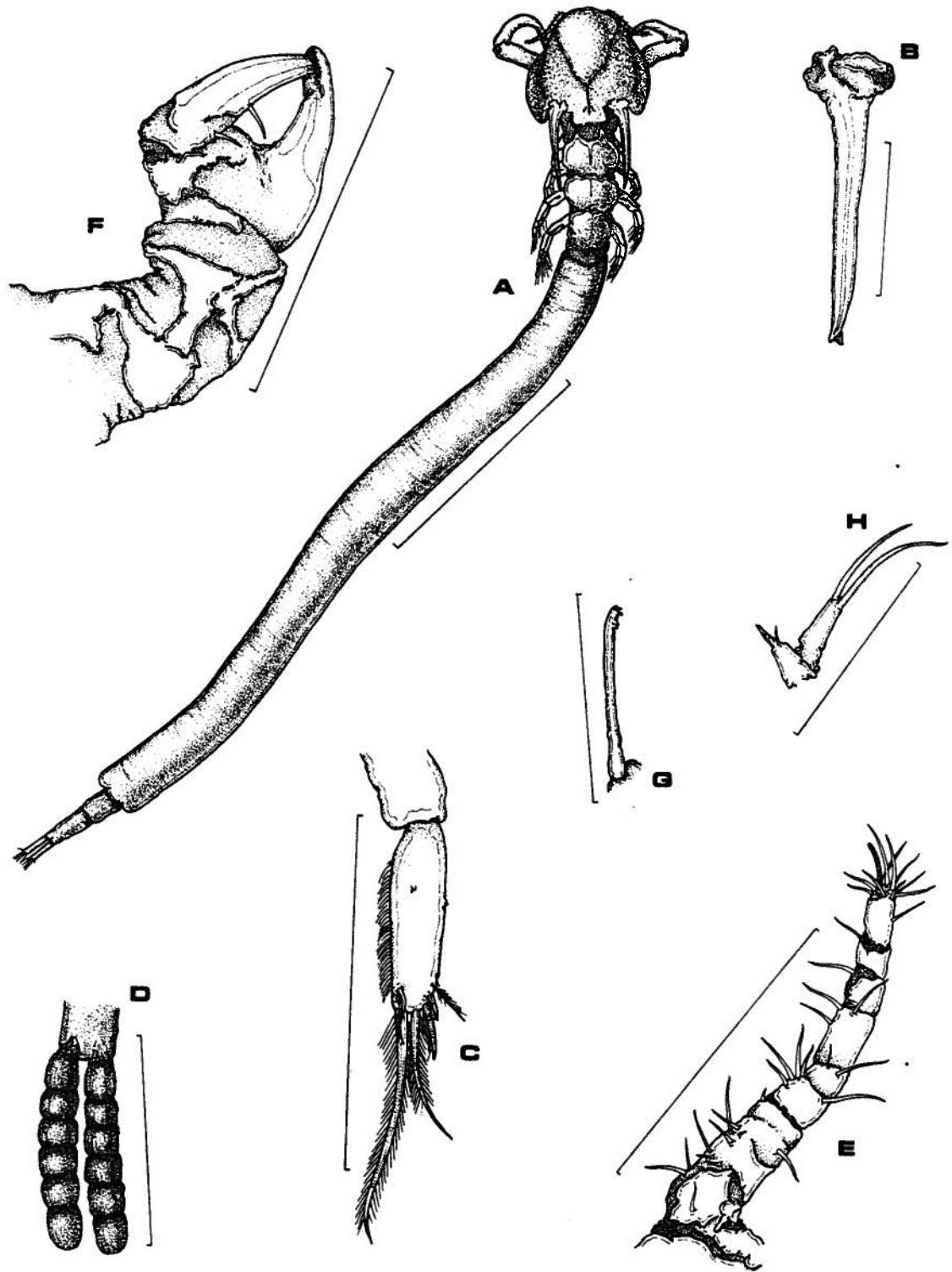


FIGURE 80. *Kroyeria cresseyi* sp. nov., female: A, second maxilla; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 4. Scales: 0.1 mm in A; 0.2 mm in B; 0.1 mm in C, D; 0.2 mm in E, F.

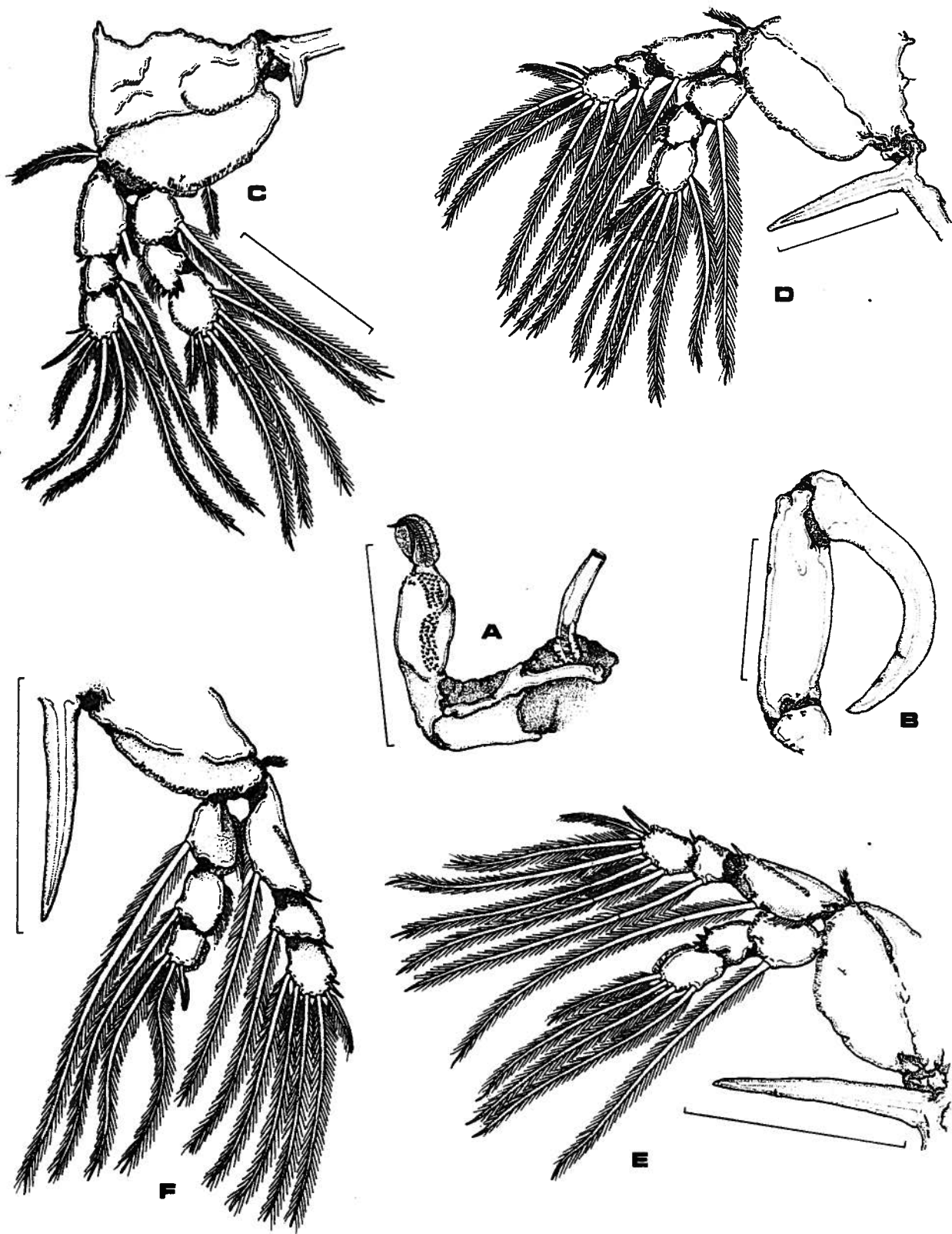


FIGURE 81. *Kroyeria decepta* sp. nov., female: A, habitus, lateral; B, habitus, dorsal; C, caudal ramus; D, dorsal stylet; E, first antenna; F, second antenna; G, mandible; H lambrum; I, first maxilla; J, leg 5. Scales: 1.0 mm in A, B; 0.090 mm in C; 0.360 mm in D; 0.180 mm in E, F; 0.070 mm in G; 0.090 mm in H; 0.070 mm in I; 0.035 mm in J.

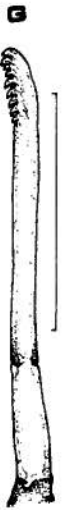
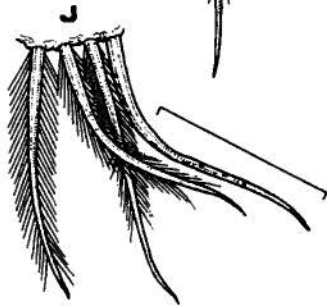
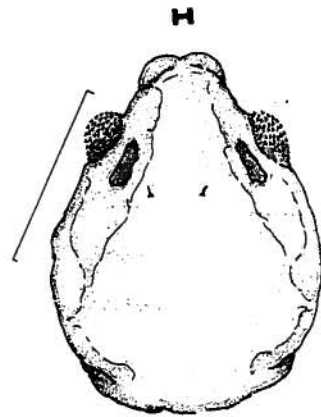
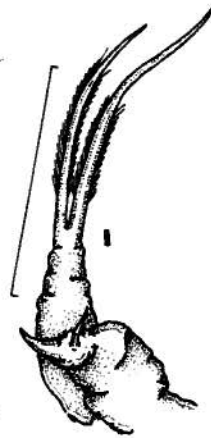
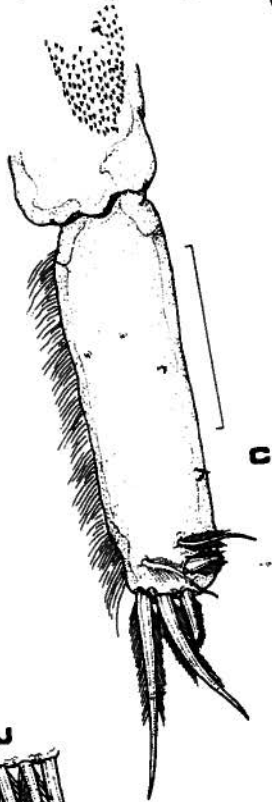
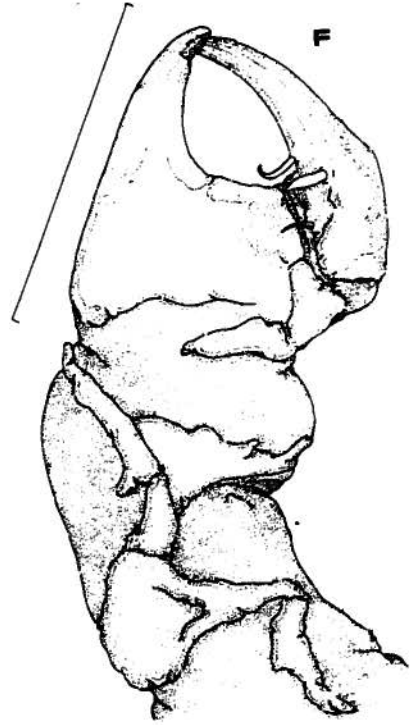
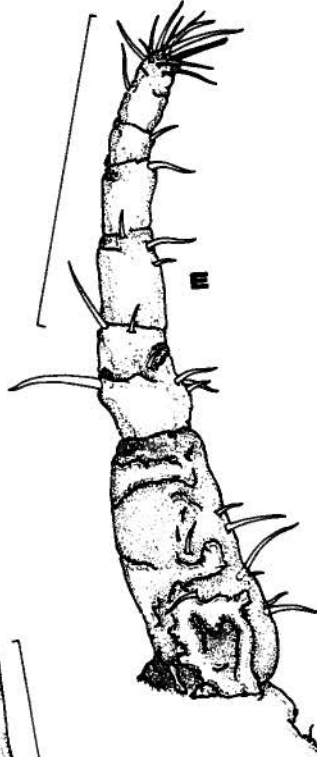
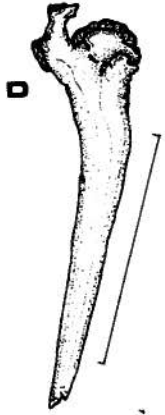
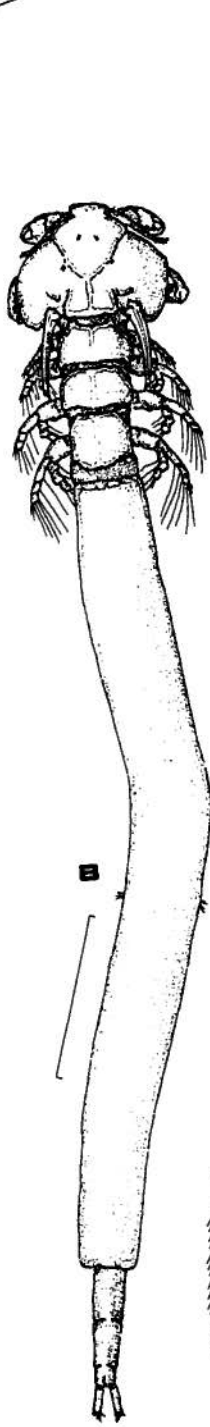
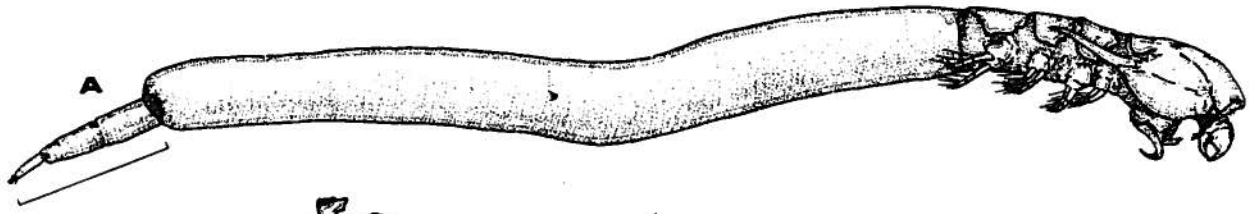
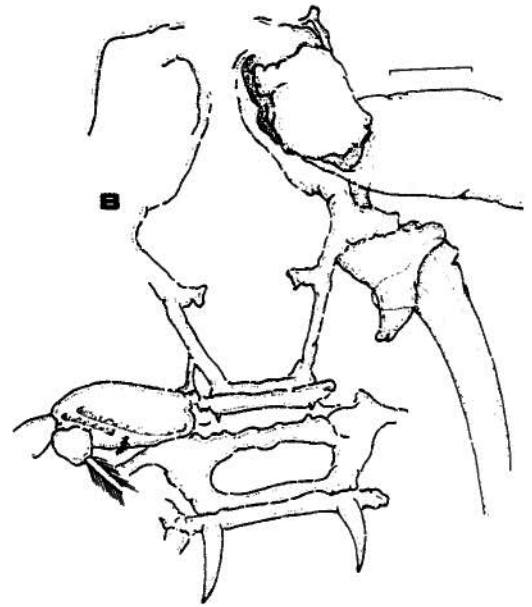
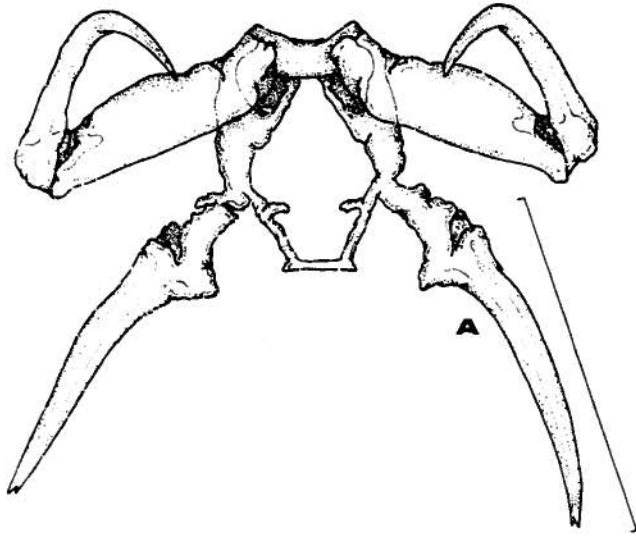


FIGURE 82. *Kroyeria decepta* sp. nov., female: A, second maxilla; B, maxilliped; C, leg 1; D leg 2; E, leg 3; F, leg 4; Scales: 0.05 mm in A; 0.360 mm in B; 0.180 mm in C, D; 0.360 mm in E, F.



FIGURE 83. *Kroyeria decepta* sp. nov., female: A, maxilliped, dorsal stylet; B, maxilliped, dorsal stylet. Scales: 0.710 mm in A; 0.1 mm in B.



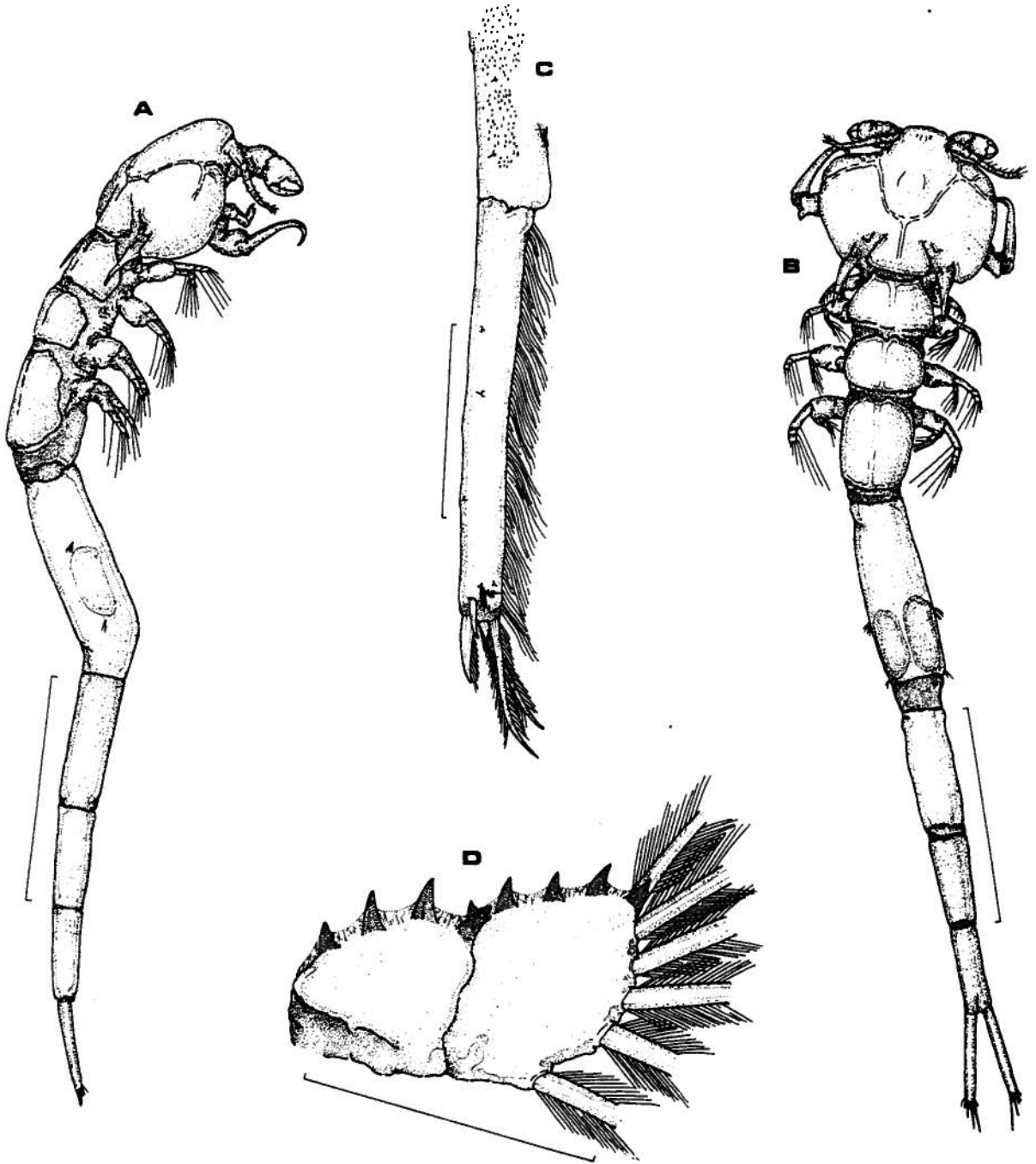


FIGURE 85. *Kroyeria dispar* Wilson, 1932, male: A, habitus, lateral; B, female, dorsal; C, dorsal stylet; D, caudal ramus; E, first antenna; F, second antenna; G, mandible; H first maxilla; I, second maxilla. Scales: 1.0 mm in A; 3.0 mm in B; 0.360 mm in C-F; 0.180 mm in G; 0.070 mm in H; 0.360 mm in I.

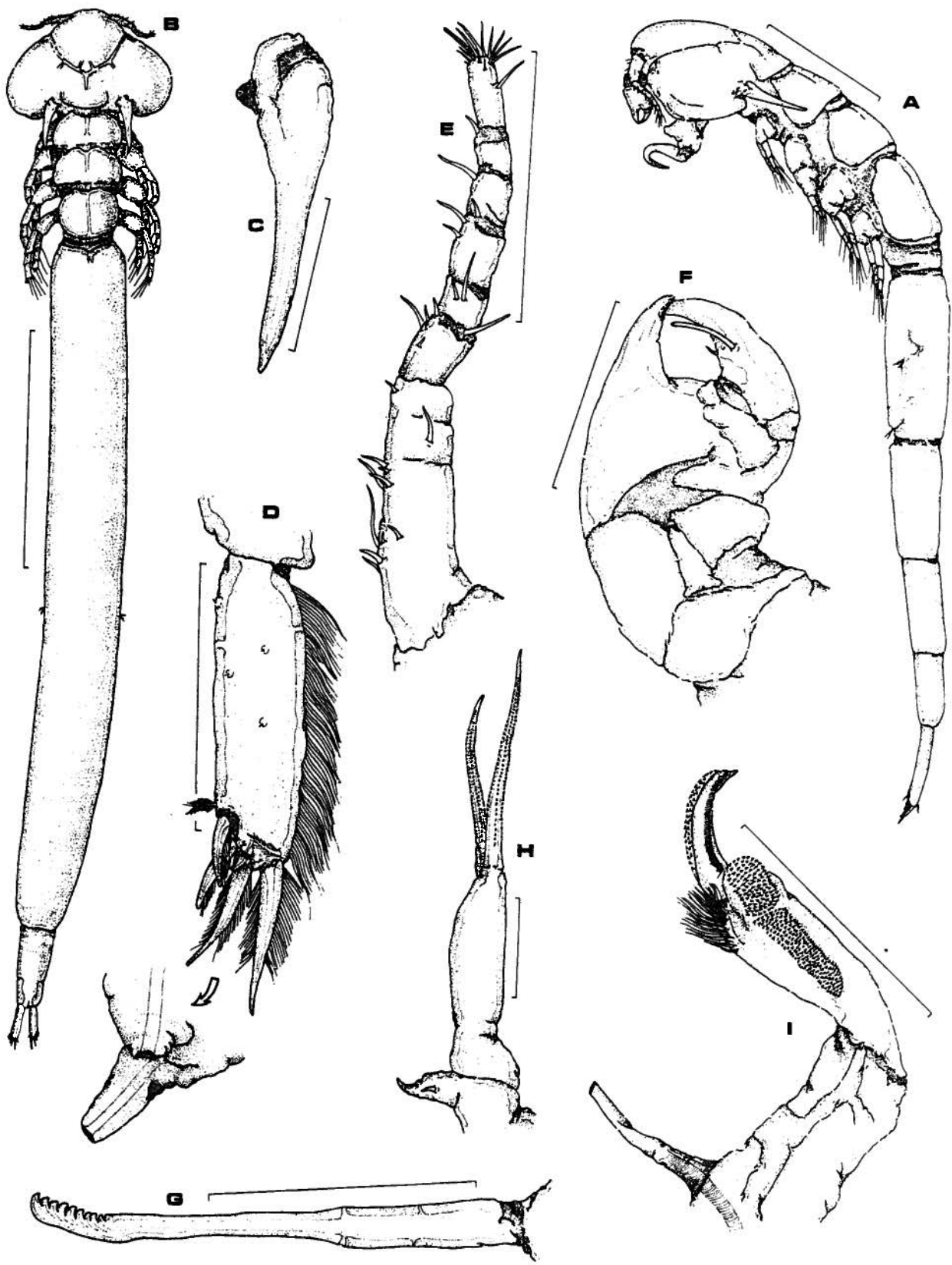


FIGURE 86. *Kroyeria dispar* Wilson, 1932, female: A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 4. Scales: 0.090 mm in A; 0.360 mm in B; 0.710 mm in C-E.

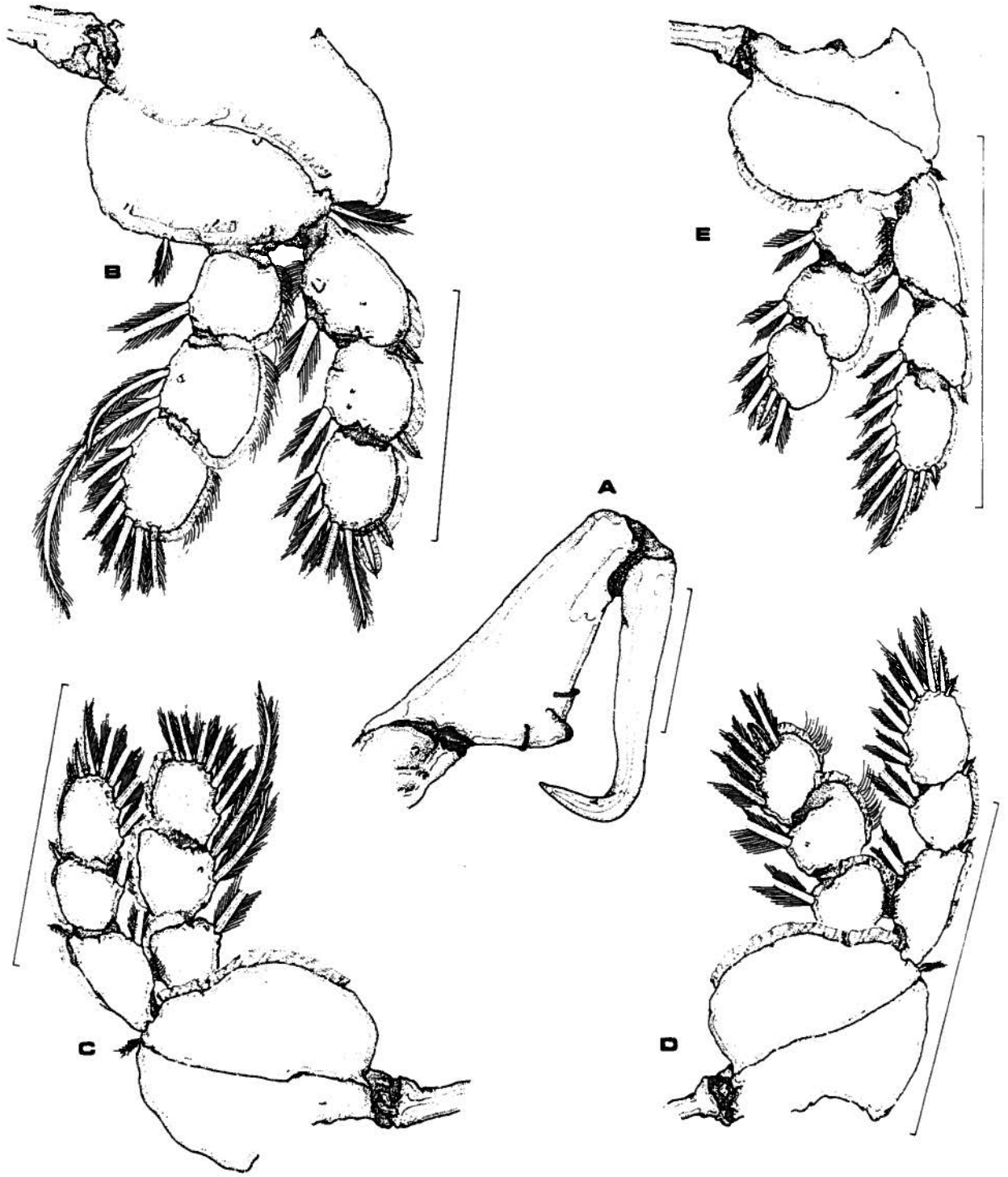


FIGURE 87. *Kroyeria elongata* Pillai, 1967, female: A, habitus, dorsal; B, caudal ramus; C, dorsal stylet; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H, second maxilla; I, maxilliped; Scales: 0.4 mm in A; 0.2 mm in B, C; 0.1 mm in D-H; 0.2 mm in I.

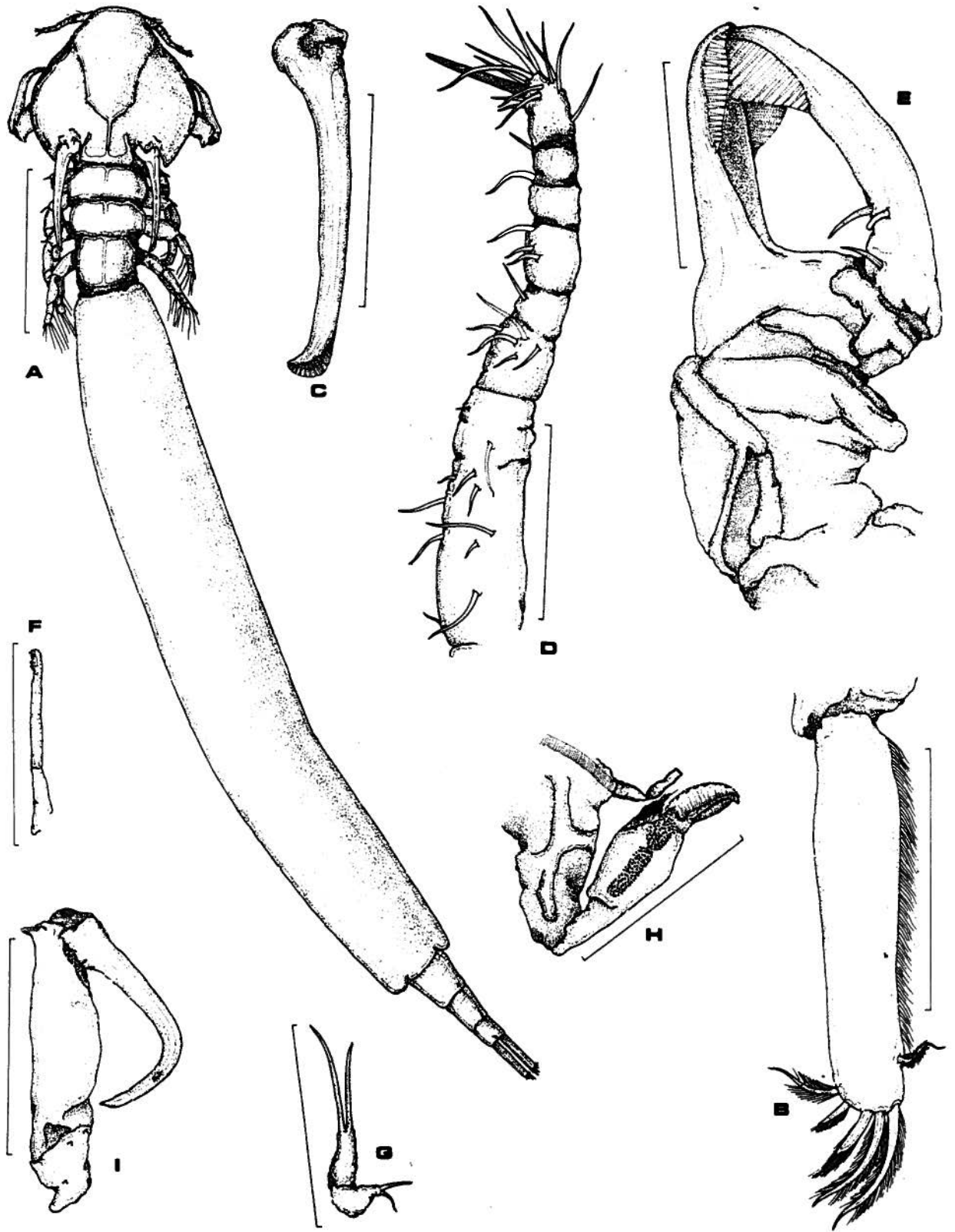


FIGURE 88. *Kroyeria elongata* Pillai, 1967, female: A, leg 1; B, leg 2; C, leg 3; D, leg 4.
Scales: 0.2 mm in A-D.

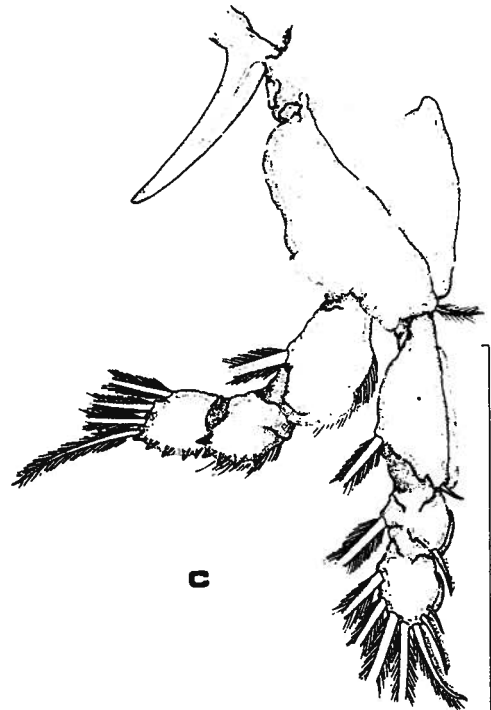
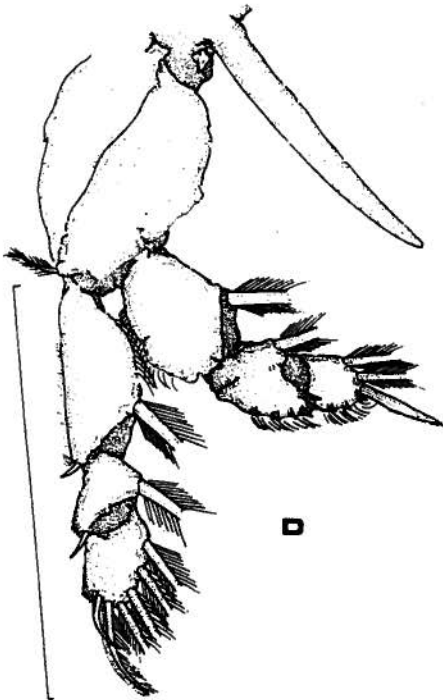
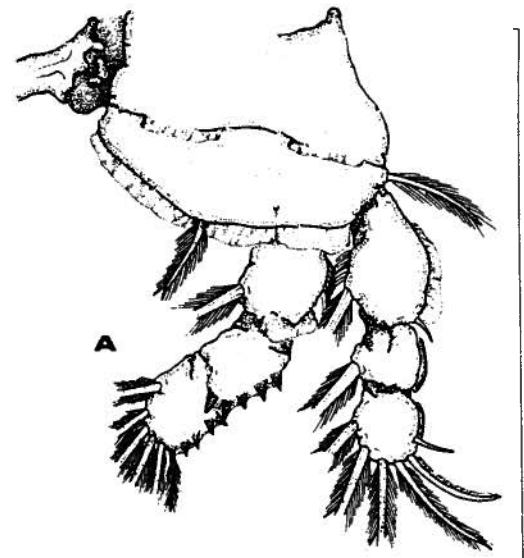
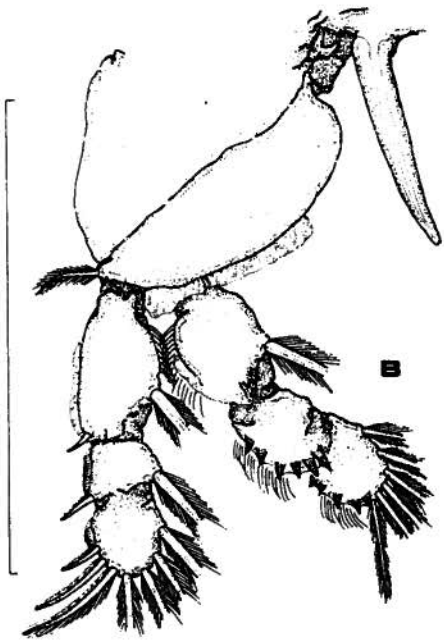


FIGURE 89. *Kroyeria gemursa* Cressey, 1967, female: A, habitus, dorsal; B, habitus, lateral; C, ventral cephalothorax; D, caudal ramus; E, dorsal stylet; F, first antenna; G, second antenna; H, mandible; I, mouth; J, first maxilla; Scales: 1.0 mm in A-C; 0.090 mm in D; 0.360 mm in E; 0.180 mm in F; 0.090 mm in G; 0.070 mm in H; 0.090 mm in I; 0.035 mm in J.

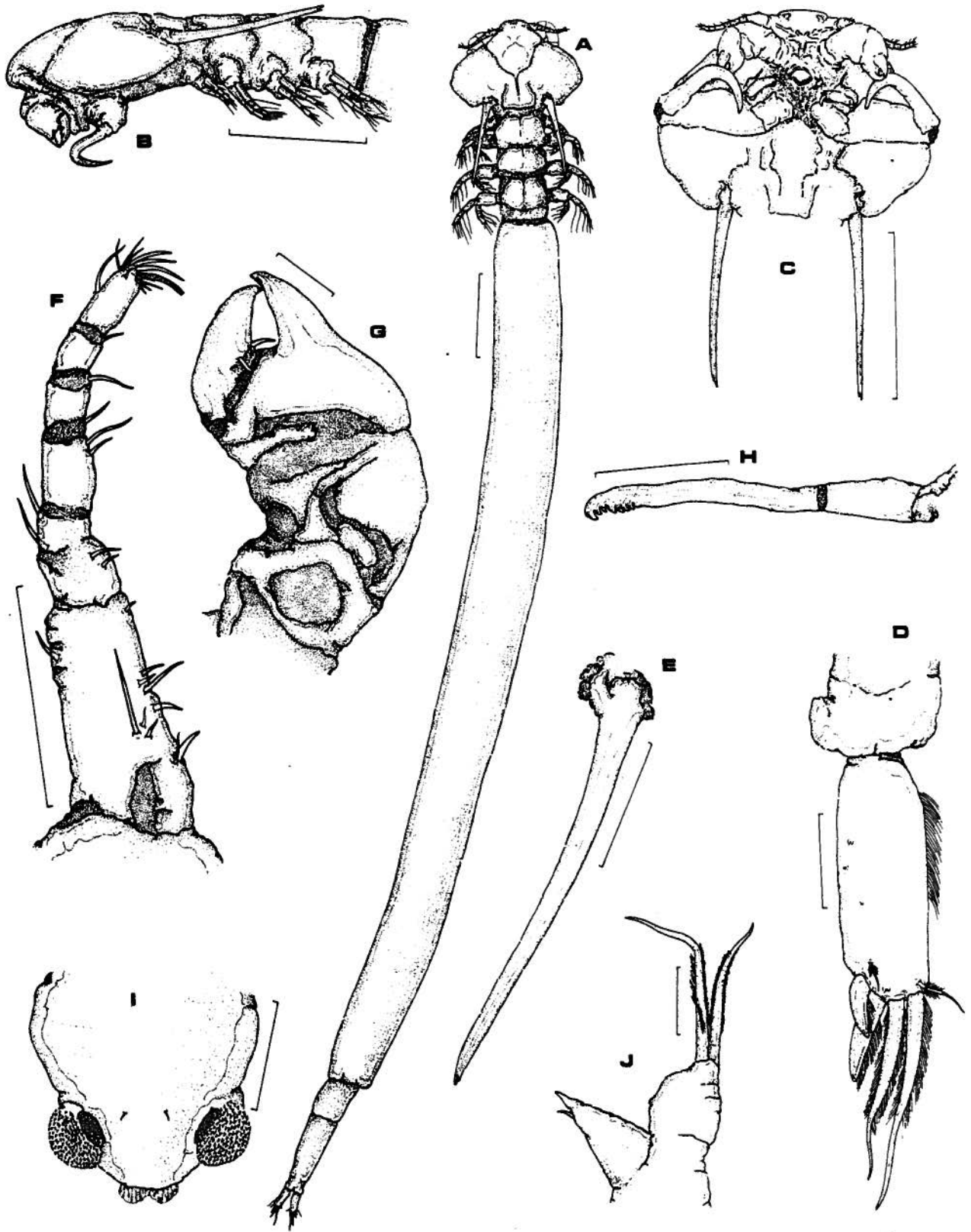


FIGURE 90. *Kroyeria gemursa* Cressey, 1967, female: A, second maxilla; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 4. Scales: 0.090 mm in A; 0.2 mm in B; 0.090 mm in C; 0.180 mm in D-F.

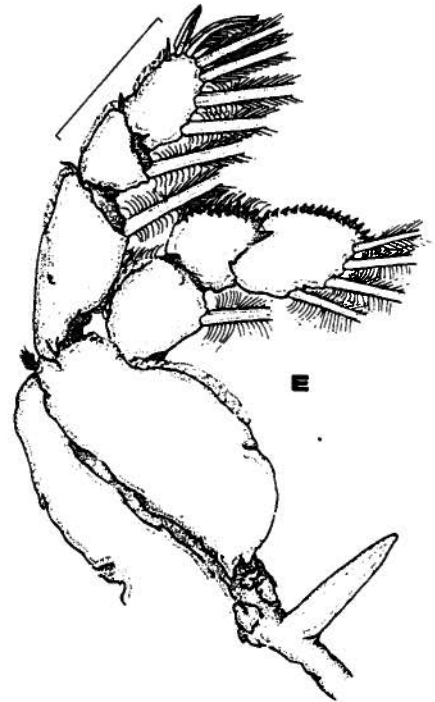
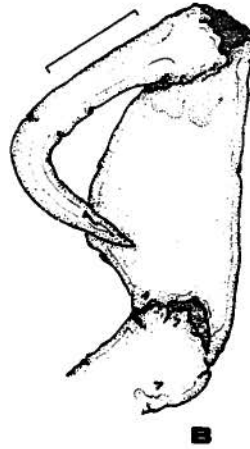
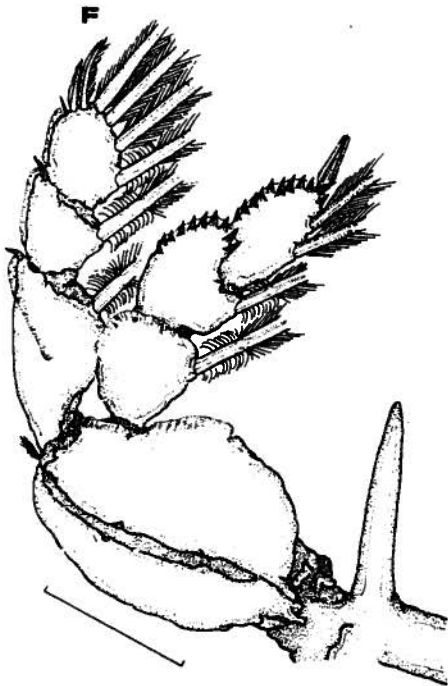
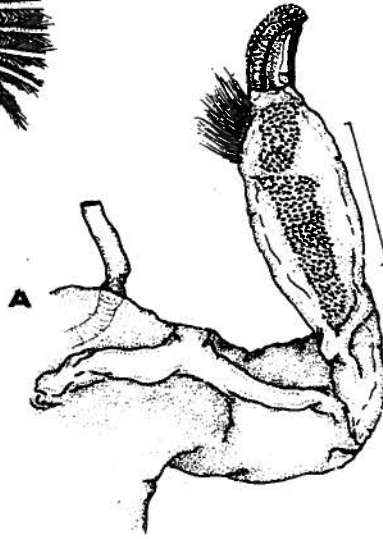
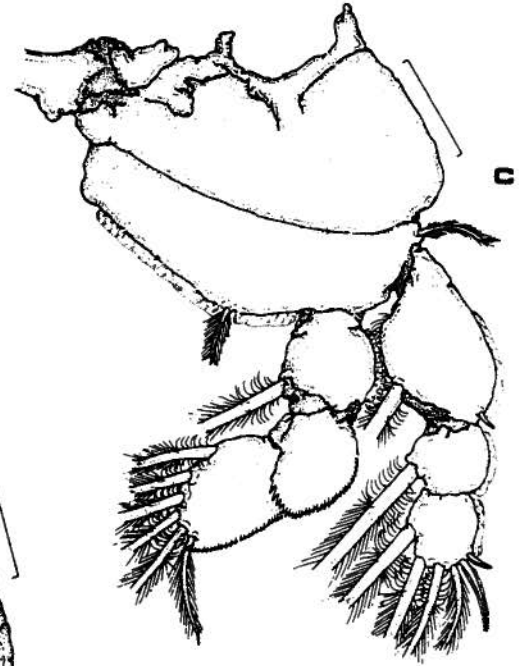
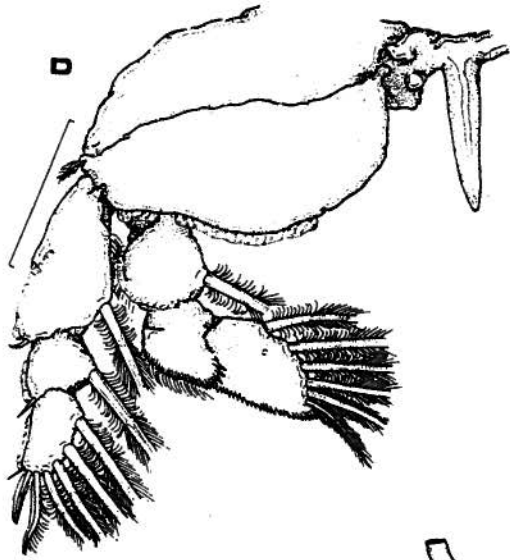


FIGURE 91. *Kroyeria lineata* van Beneden, 1853, female: A, habitus, dorsal; B, dorsal stylet; C, caudal ramus; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H, second maxilla; I, maxilliped. Scales: 1.0 mm in A; 0.2 mm in B; 0.2 mm in C, D; 0.1 mm in E-H; 0.2 mm in I.

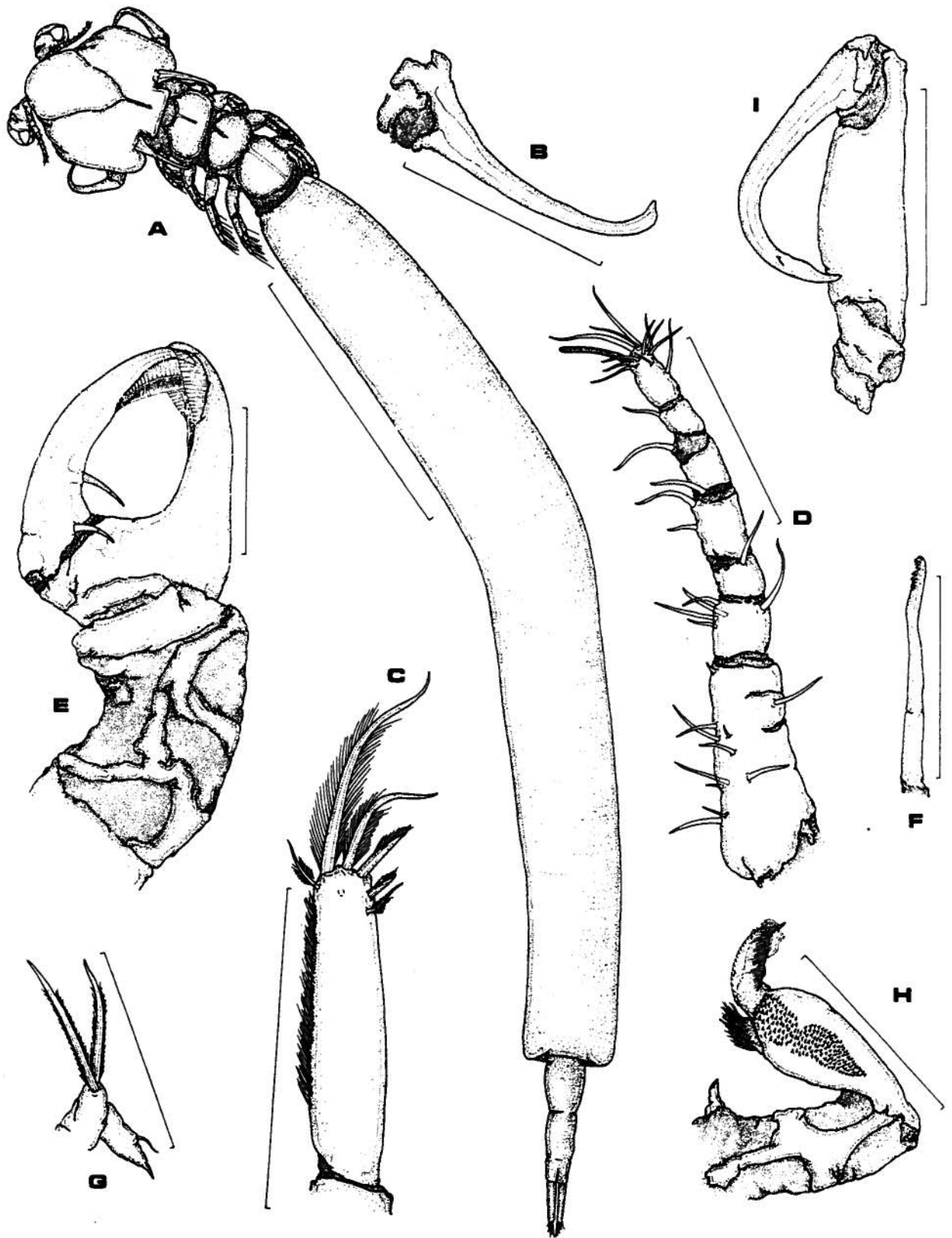


FIGURE 92. *Kroyeria lineata* van Beneden, 1853, female: A, leg 1; B, leg 2; C, leg 3; D, leg 4. Scales: 0.1 mm in A; 0.2 mm in B-D.

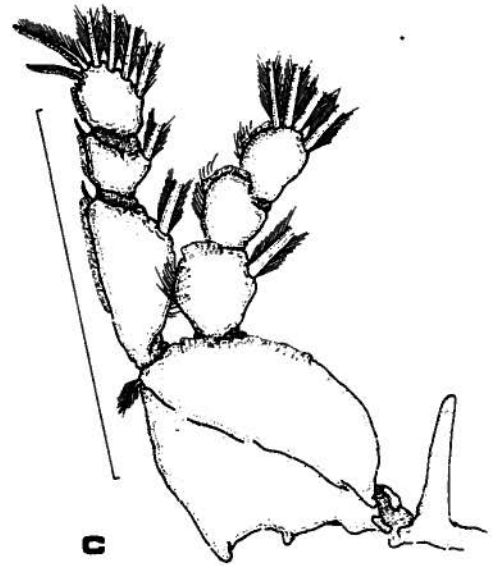
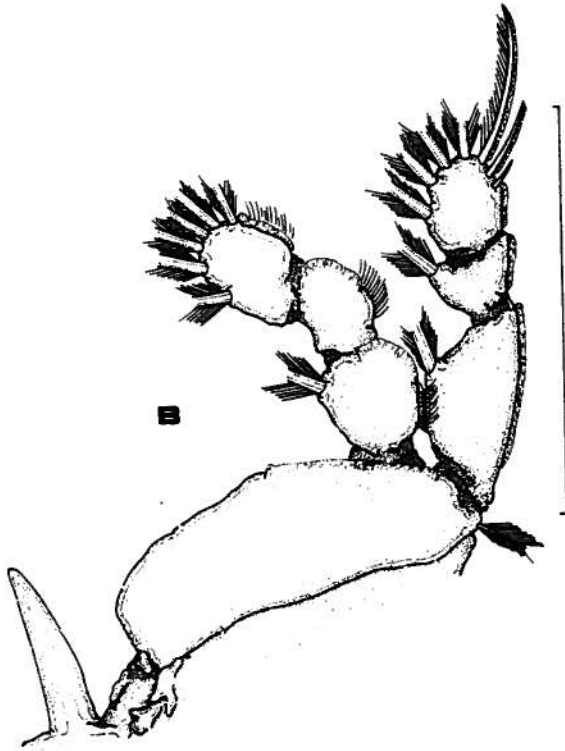
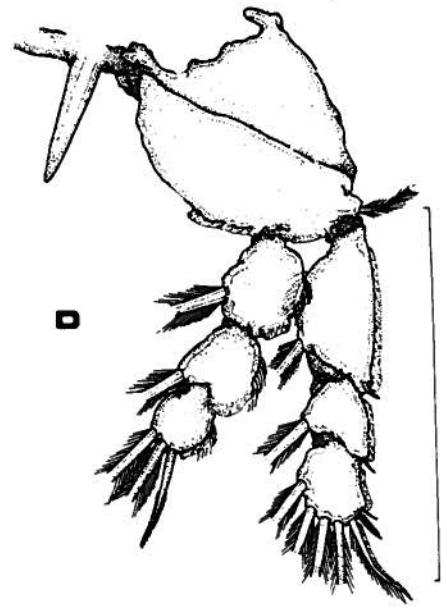
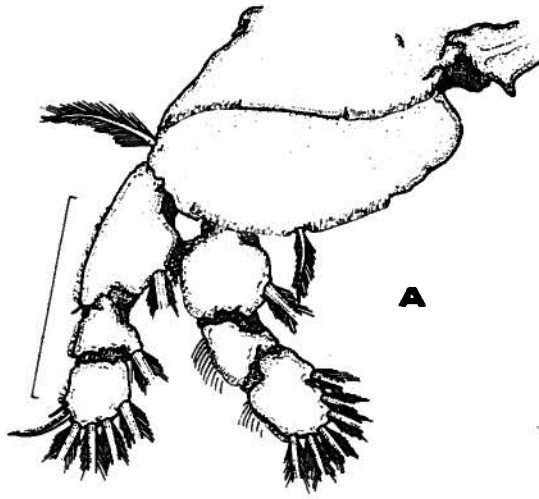


FIGURE 93. *Kroyeria longicauda* Cressey, 1970, female: A, habitus, dorsal; B, dorsal stylet; C, caudal ramus; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H, second maxilla; I, maxilliped. Scales: 0.360 mm in A; 0.180 mm in B; 0.070 mm in C-E; 0.035 mm in G; 0.070 mm in H; 0.180 mm in I.

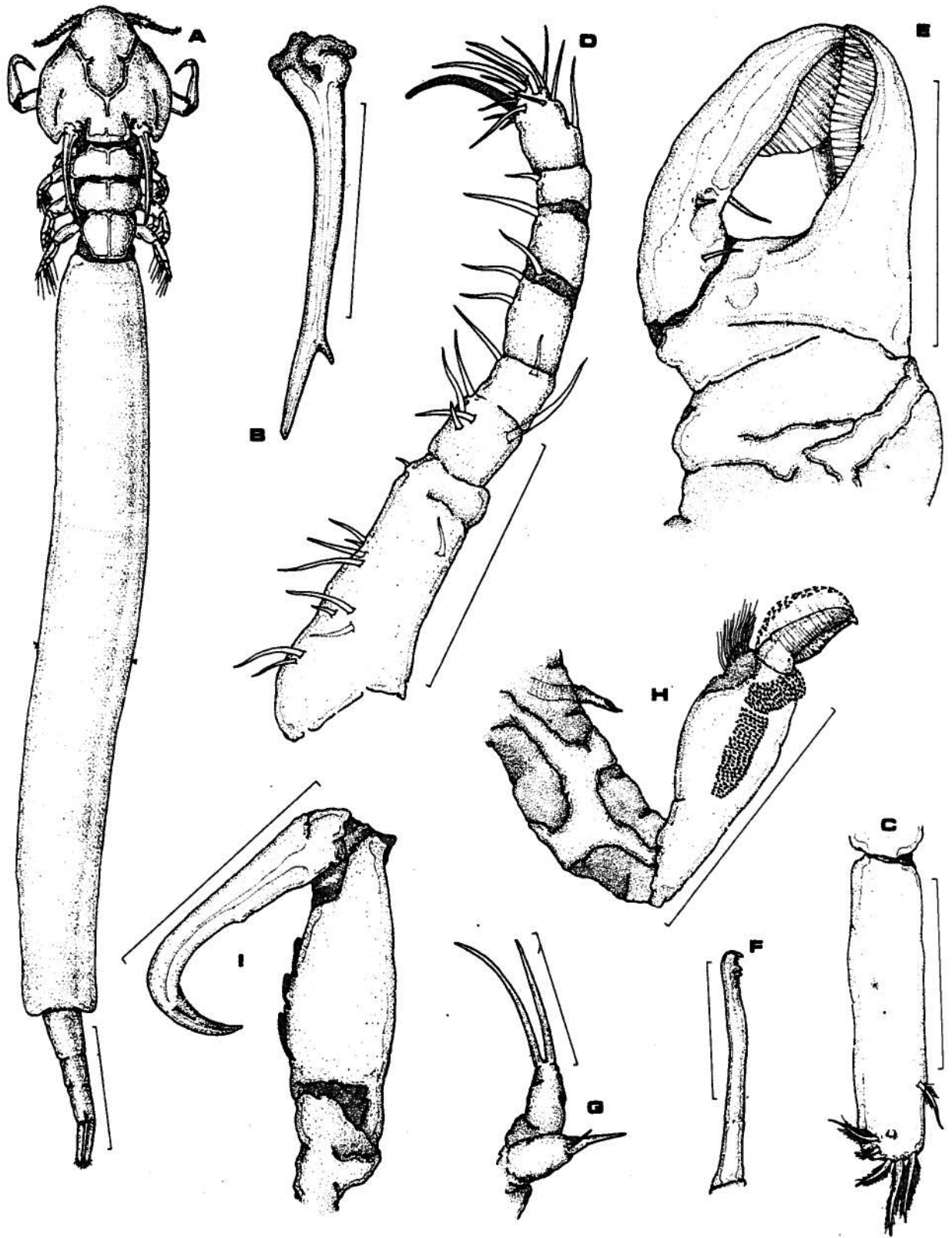


FIGURE 94. *Kroyeria longicauda* Cressey, 1970, female: A, leg 1; B, leg 2; C, leg 3; D, leg 4 endopod; E, leg 4 exopod. Scales: 0.070 mm in A; 0.180 mm in B; 0.070 mm in C-E.

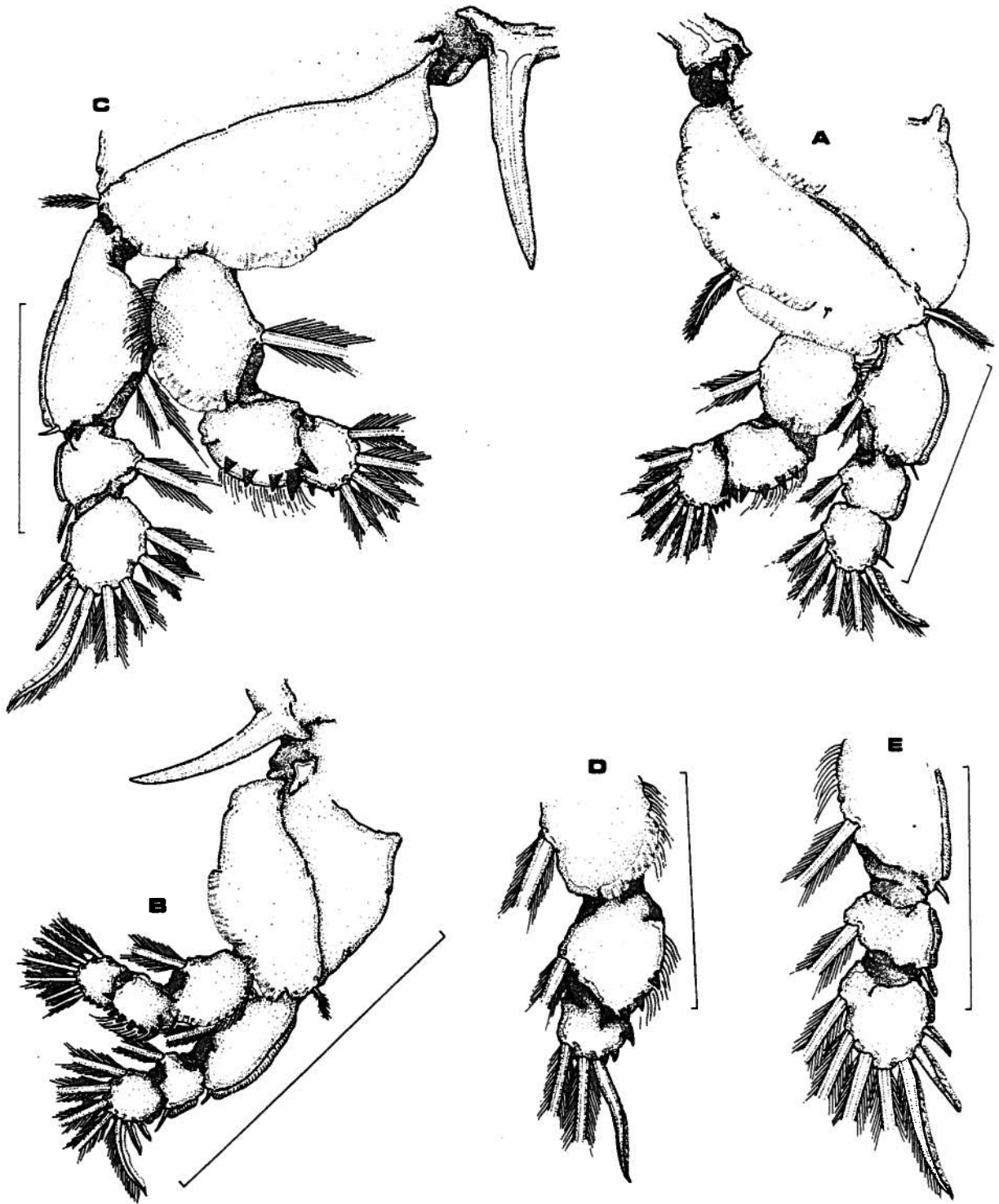


FIGURE 95. *Kroyeria longicauda* Cressey, 1970, male: A, habitus, dorsal; B, dorsal stylet; C, caudal ramus. Scales: 0.360 mm in A; 0.180 mm in B, C.

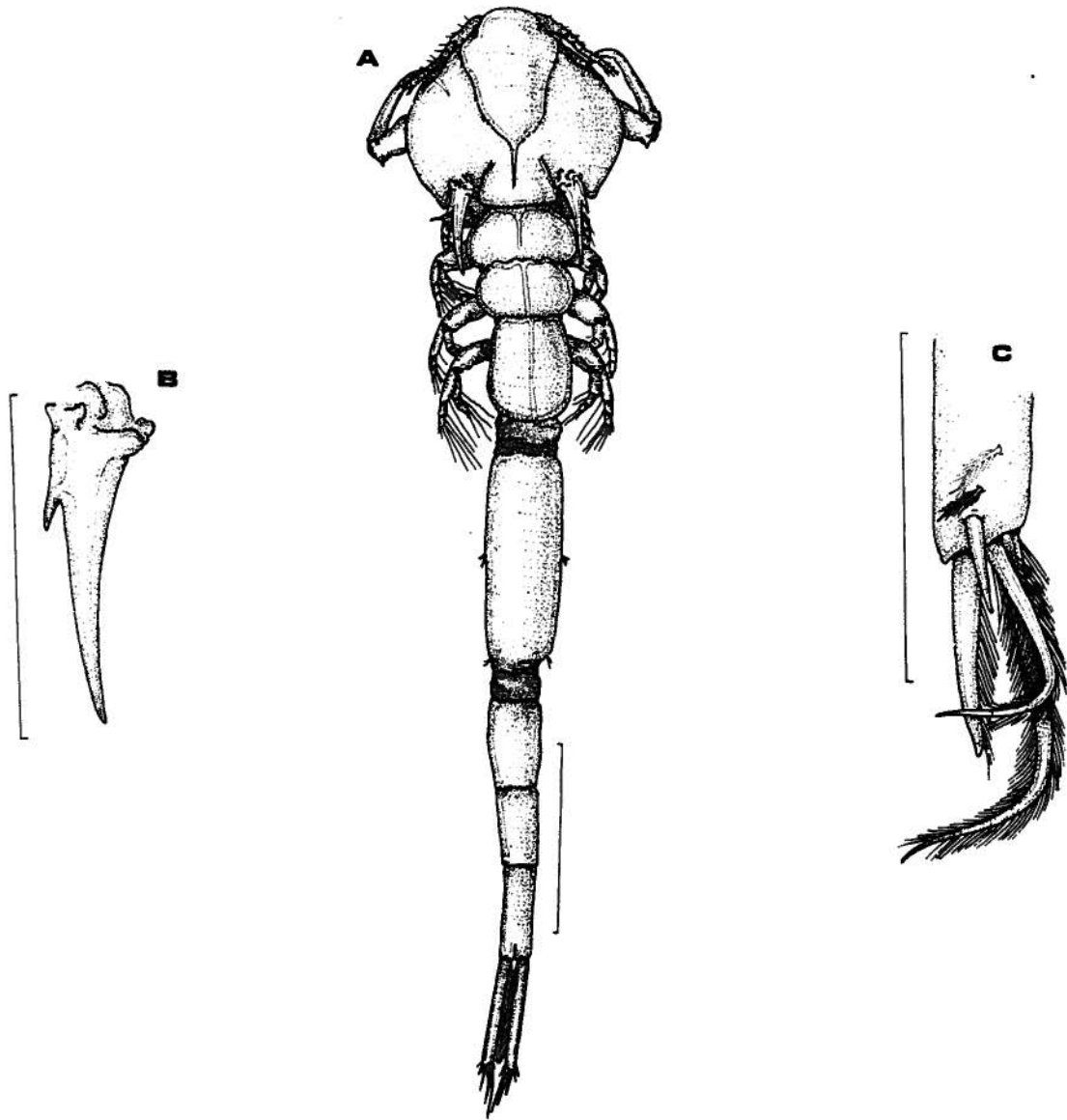


FIGURE 96. *Kroyeria papillipes* Wilson, 1932, female: A, habitus, lateral; B, dorsal stylet; C, caudal ramus; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H, second maxilla; I, maxilliped. Scales: 2.0 mm in A; 0.180 mm in B; 0.070 mm in C; 0.180 mm in D, E; 0.070 mm in F-H; 0.360 mm in I.

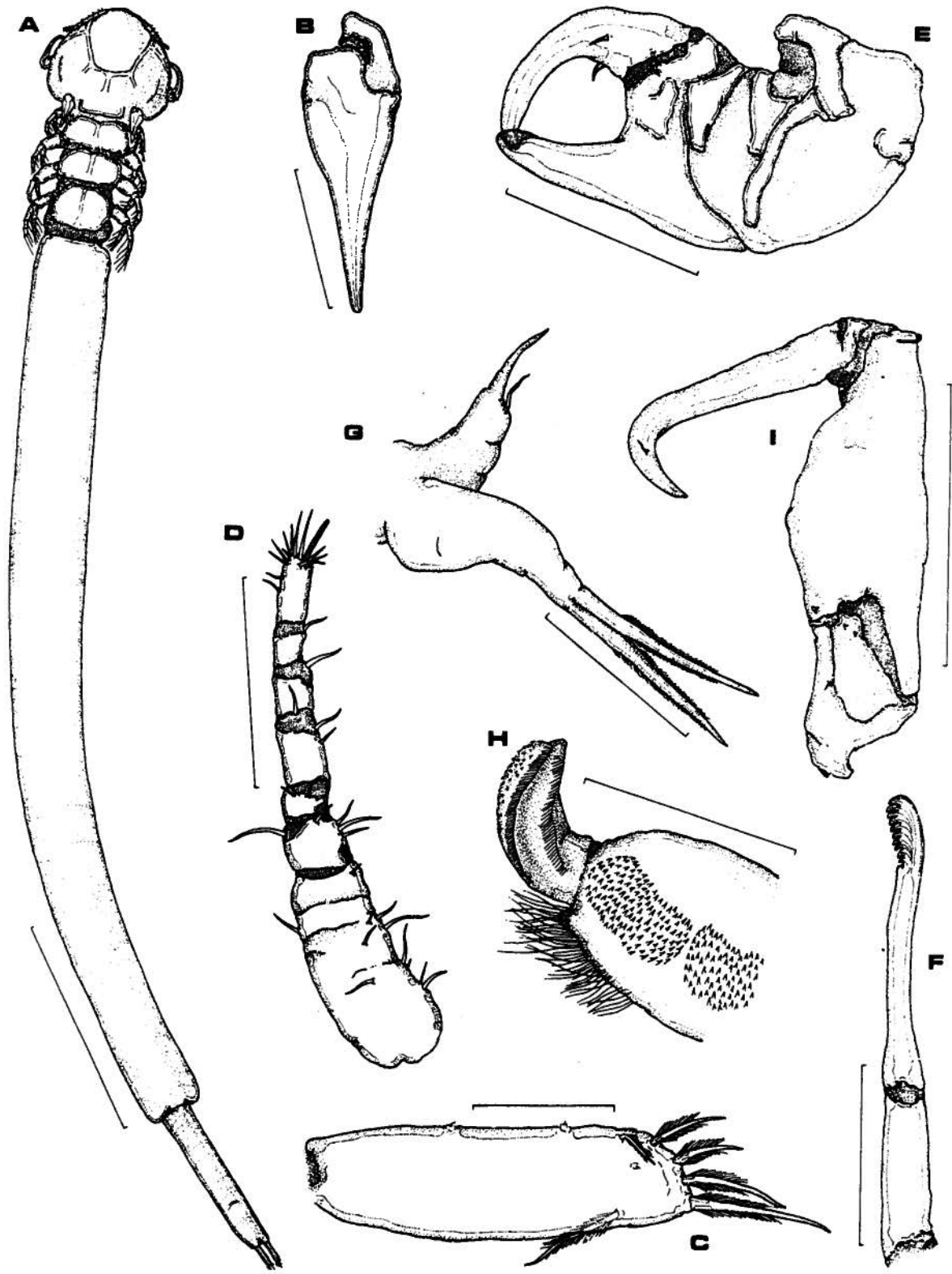


FIGURE 97. *Kroyeria papillipes* Wilson, 1932, female: A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, male. Scales: 0.180 mm in A-C; 0.360 mm in D; 1.0 mm in E.

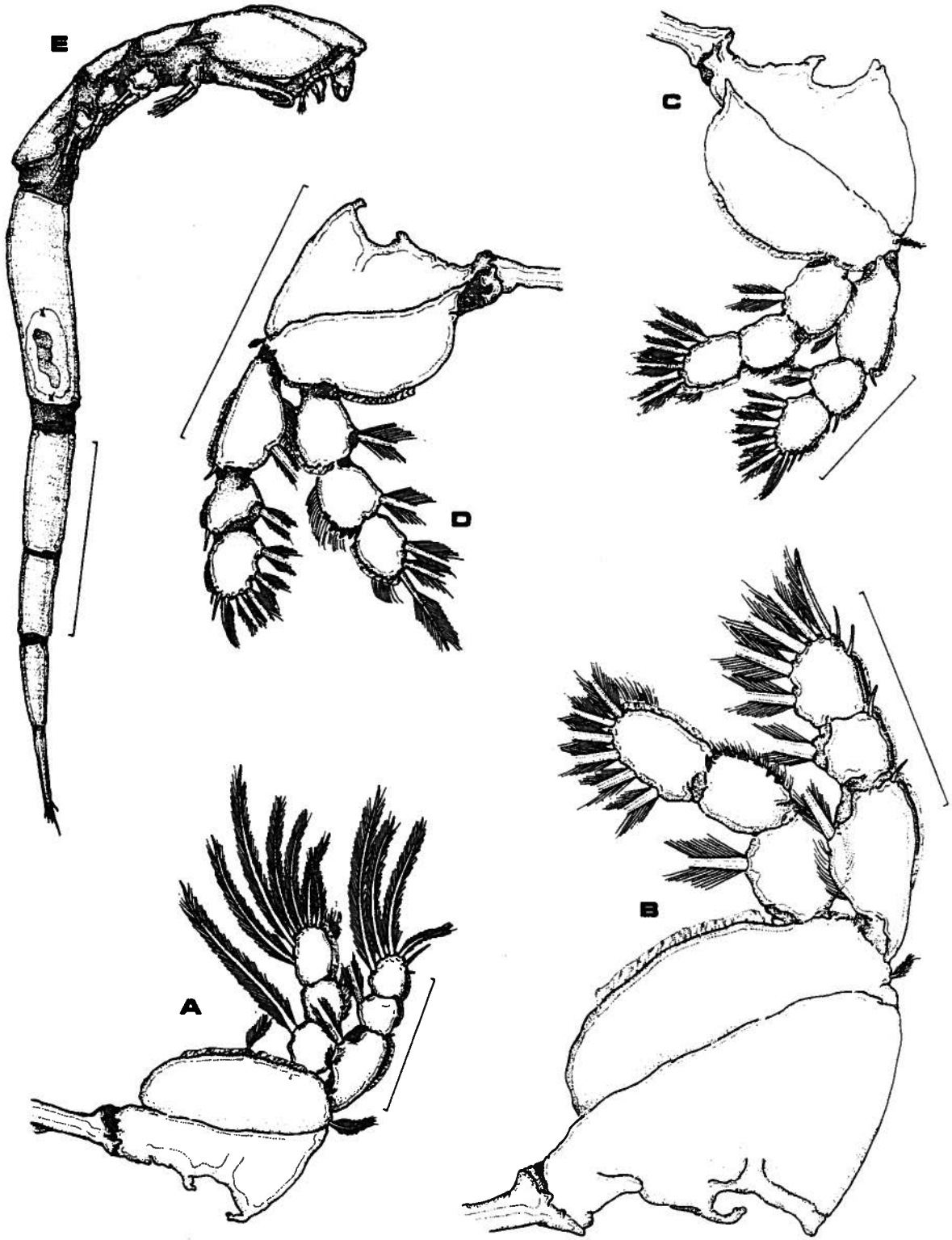


FIGURE 98. *Kroyeria procerobscena* sp. nov., female: A, habitus, dorsal; B, cephalothorax; C, dorsal stylet; D, abdomen and caudal ramus; E, tip of caudal ramus; F, first antenna; G, second antenna; H, mandible and first maxilla; I, second maxilla. Scales: 1.0 mm in A, B; 0.2 mm in C; 1.0 mm in D; 0.1 mm in E; 0.02 mm in F-G; 0.1 mm in H, I.

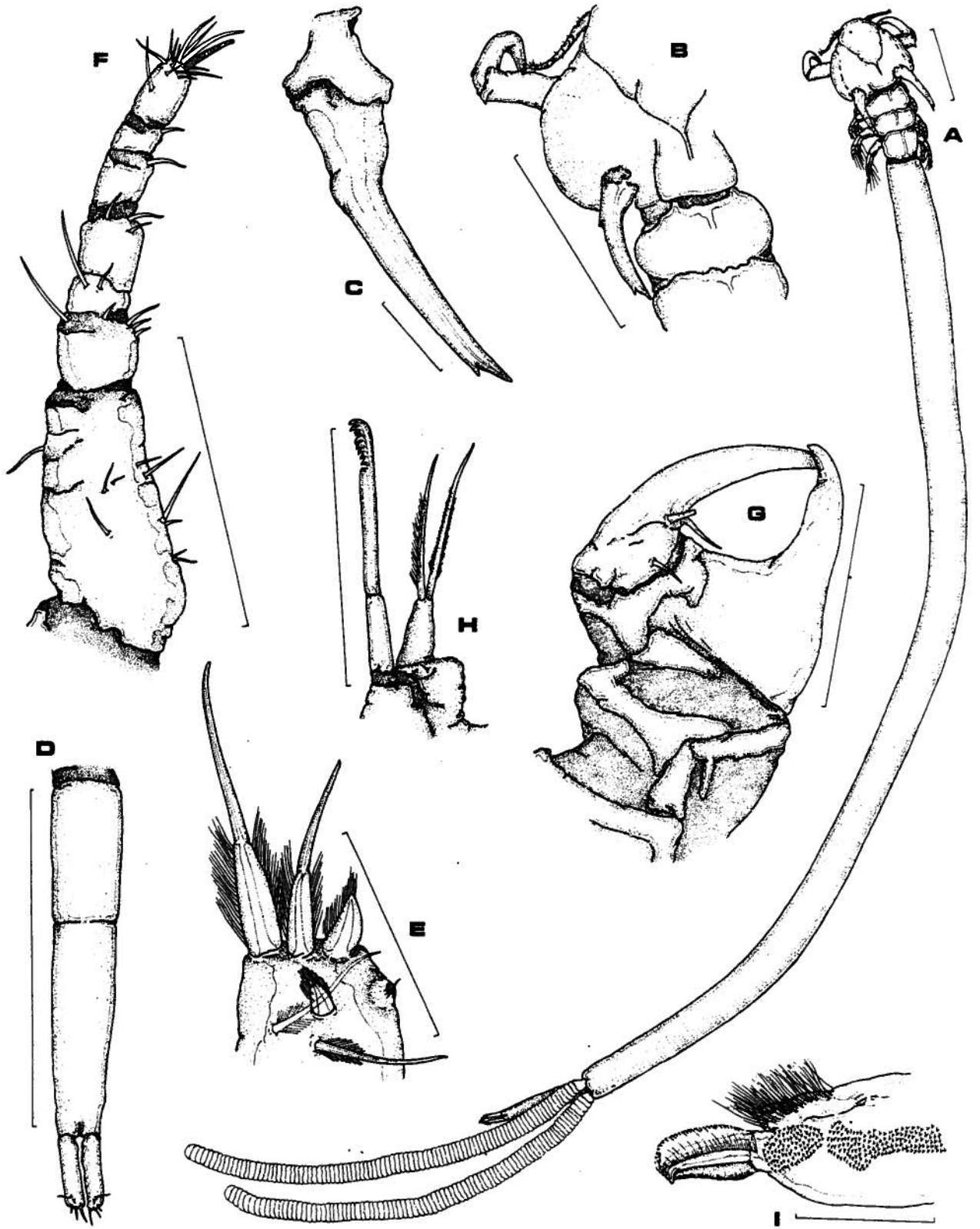


FIGURE 99. *Kroyeria procerobscena* sp. nov., female: A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 4 endopod; F, leg 4 exopod. Scales: 0.4 mm in A; 0.2 mm in B-F.

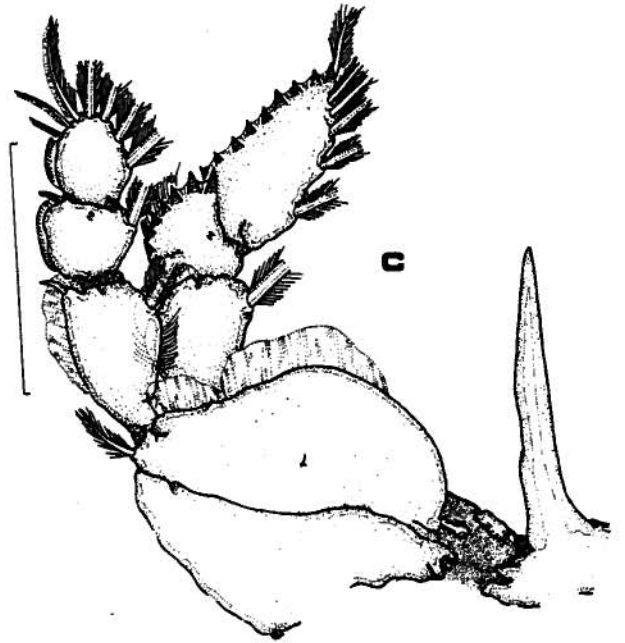
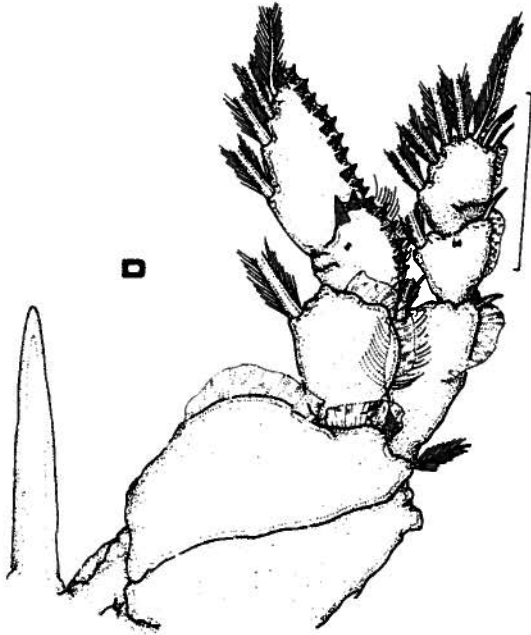
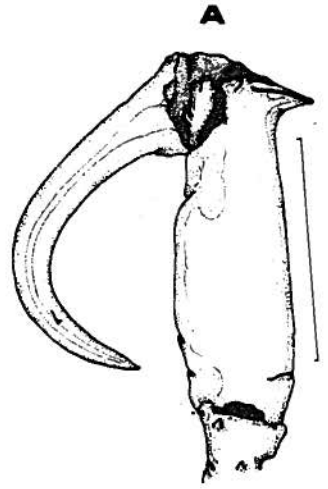
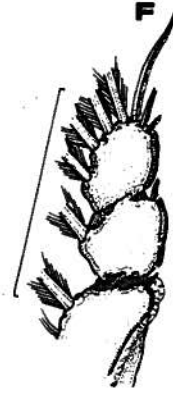


FIGURE 100 . *Kroyeria rrophemophaga* sp. nov., female: A, habitus, dorsal, B, cephalothorax, oblique; C, dorsal stylet; D, caudal ramus; E, egg strings; F, first antenna; G, second antenna; H, mandible; I, first maxilla; J, second maxilla. Scales: 1.0 mm in A, B; 0.4 mm in C; 0.2 mm in D; 1.0 mm in E; 0.180 mm in F; 0.09 mm in G; 0.07 mm in H, I; 0.09 mm in J.



FIGURE 101 . *Kroyeria rrophemophaga* sp. nov., female: A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 4; Scales: 0.180 mm in A-E.



FIGURE 102 . *Kroyeria rrophemophaga* sp. nov., male: A, habitus, dorsal; B, habitus, lateral; C, caudal ramus; D, middle segment of endopods. Scales: 1.0 mm in A, B; 0.180 mm in C, D.

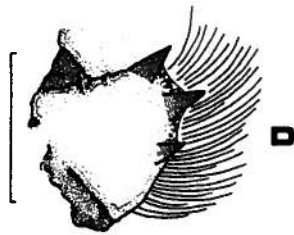
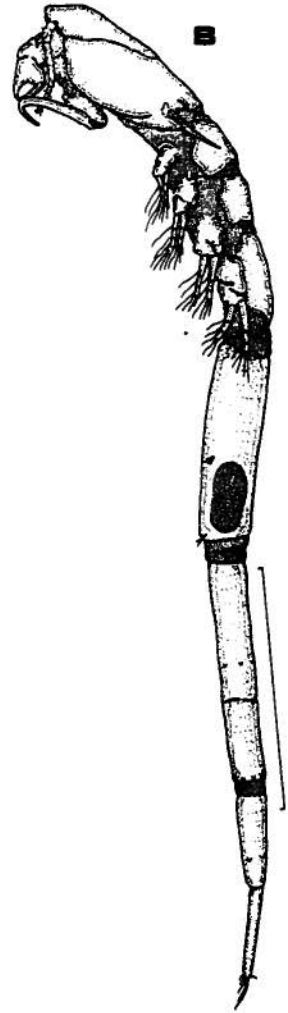
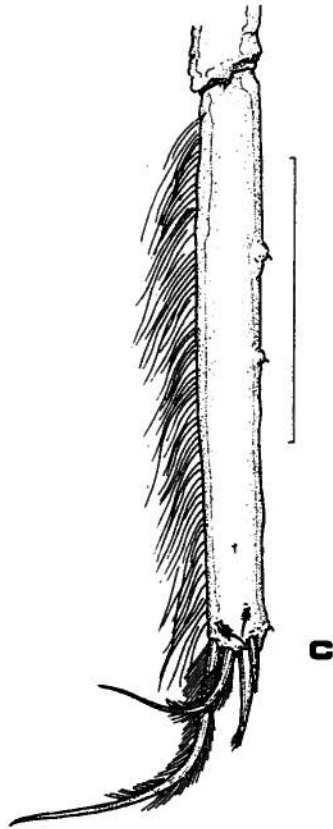
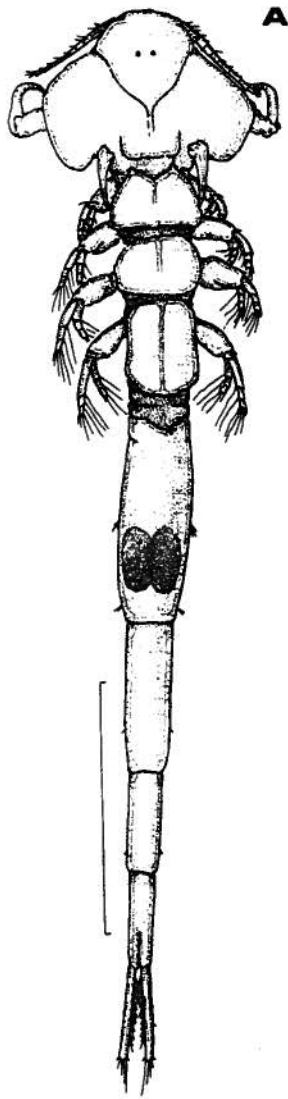


FIGURE 103 . *Kroyeria spatulata* Pearse, 1948, female: A, habitus, dorsal; B, dorsal stylet; C, caudal ramus; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H, second maxilla. Scales: 1.0 mm in A; 0.360 mm in B; 0.070 mm in C; 0.180 mm in D, E; 0.07 mm in F-H.

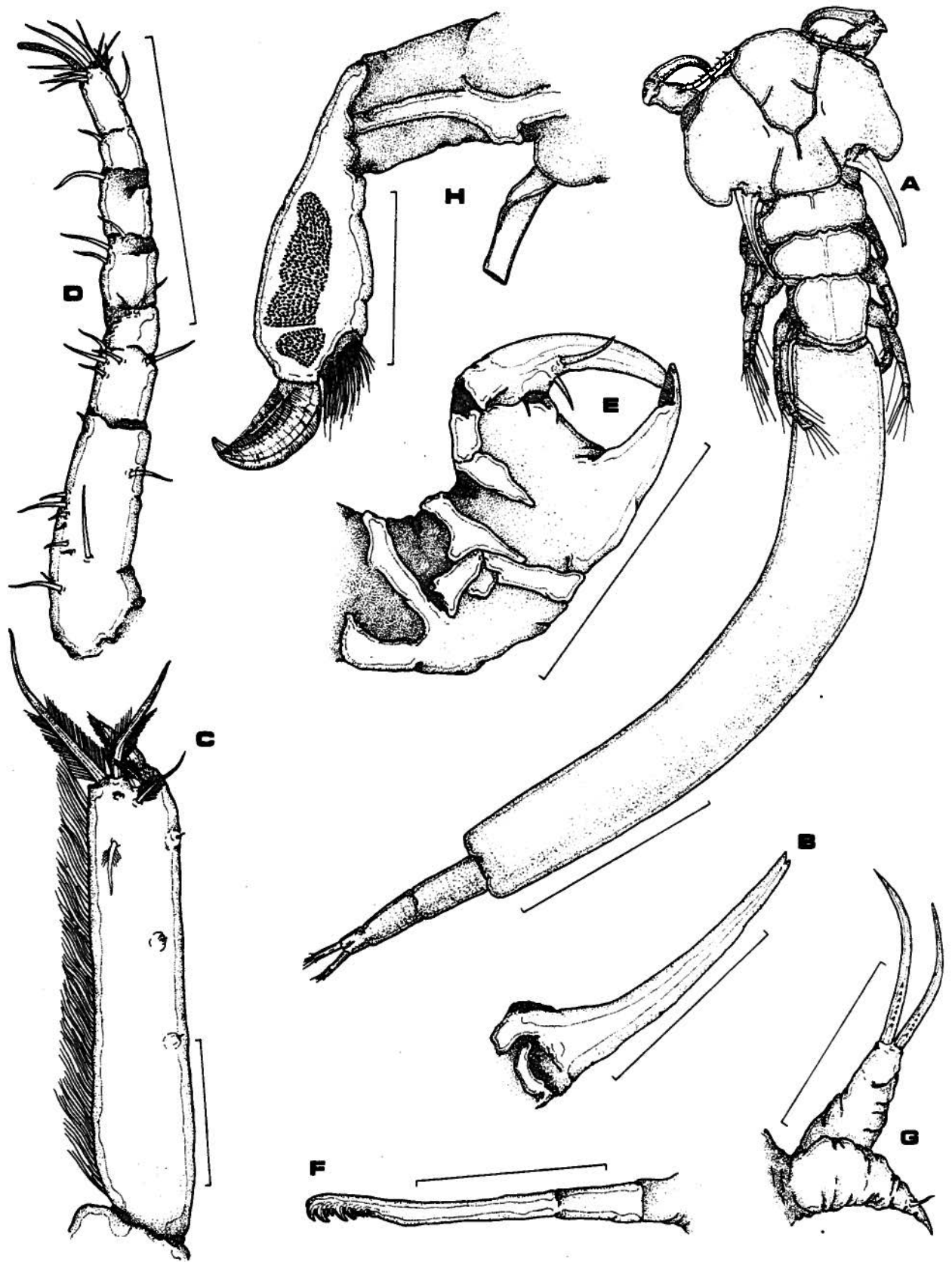


FIGURE 104 . *Kroyeria spatulata* Pearse, 1948, female: A, maxilliped; A, leg 1; B, leg 2; C, leg 3; D, leg 3; E, leg 4 endopod; F, leg 4 exopod Scales: 0.360 mm in A; 0.180 mm in B, C; 0.360 mm in D; 0.180 mm in E, F.

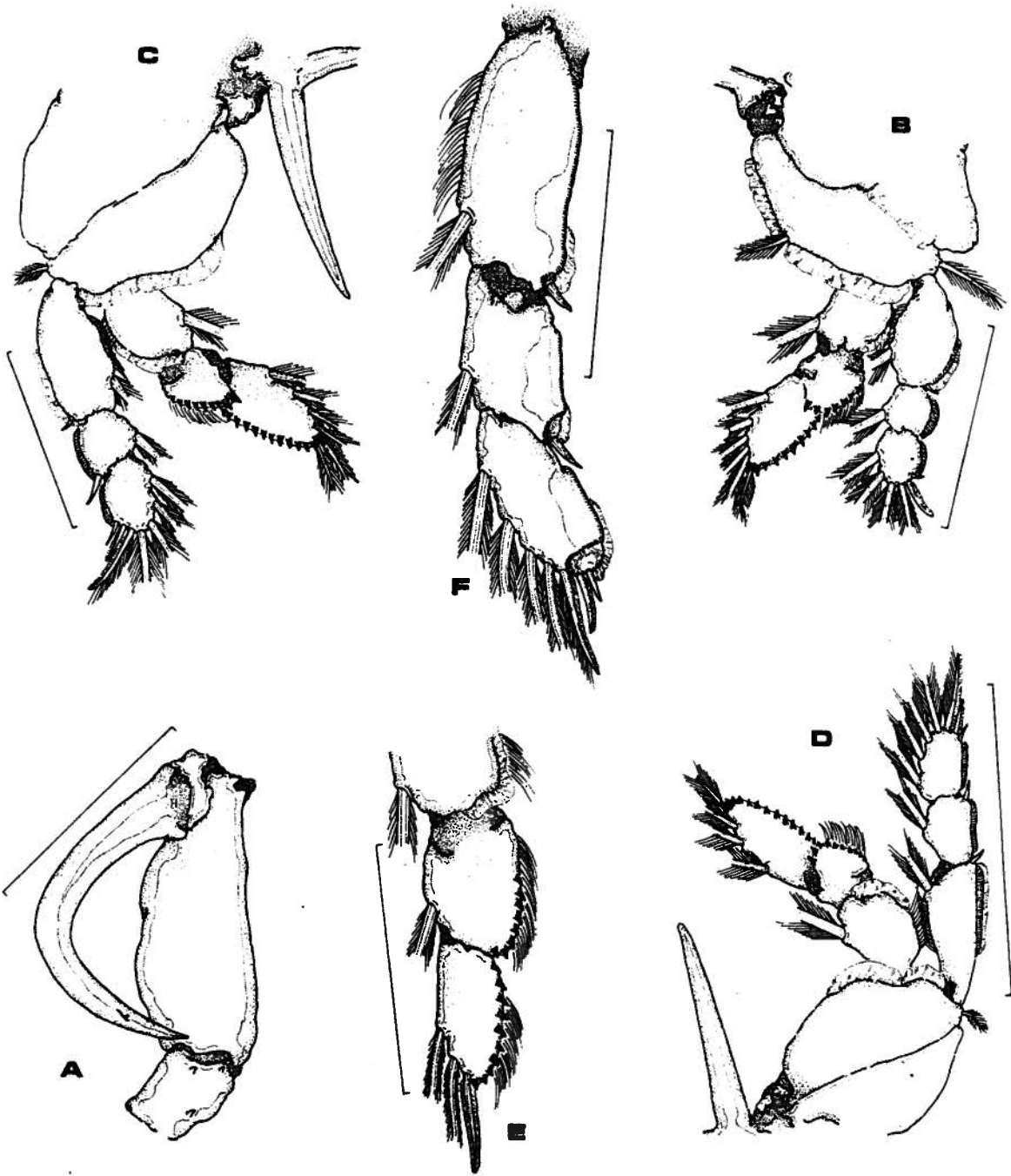


FIGURE 105 . *Kroyeria sphyrmae* Rangnekar, 1957, female: A, habitus, dorsal; B, cephalothorax, lateral; C, dorsal stylet; D, caudal ramus; E, first antenna; F, tip of first antenna; G, second antenna; H, mandible; I, first maxilla. Scales: 1.0 mm in A, B; 0.2 mm in C; 0.090 mm in D; 0.180 mm in E; 0.035 mm in F; 0.090 mm in G; 0.070 mm in H; 0.090 mm in I.

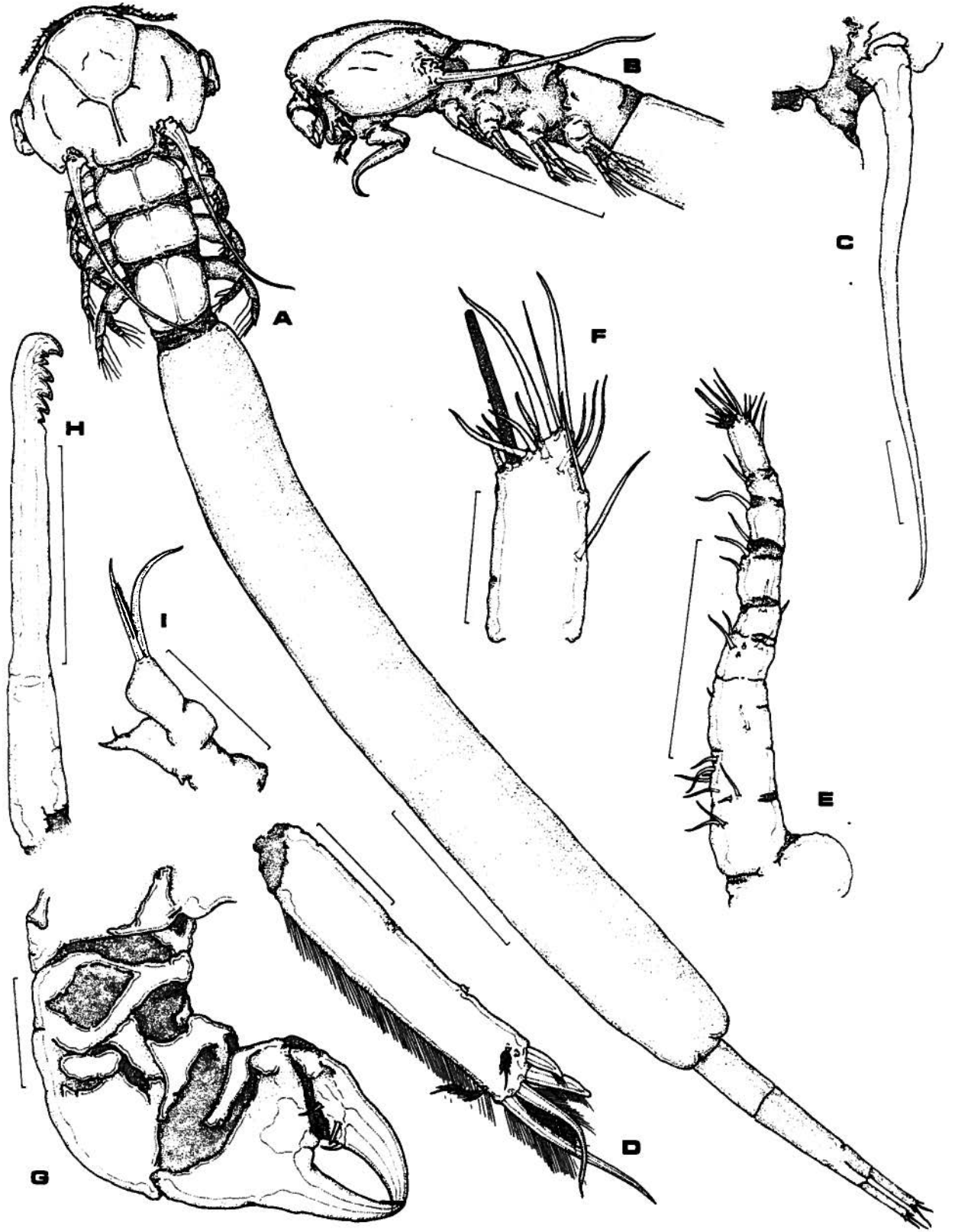


FIGURE 106 . *Kroyeria sphyrnae* Rangnekar, 1957, female: A, second maxillae; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 4. Scales: 0.090 mm in A; 0.180 mm in B; 0.090 mm in C, D; 0.180 mm in E, F.

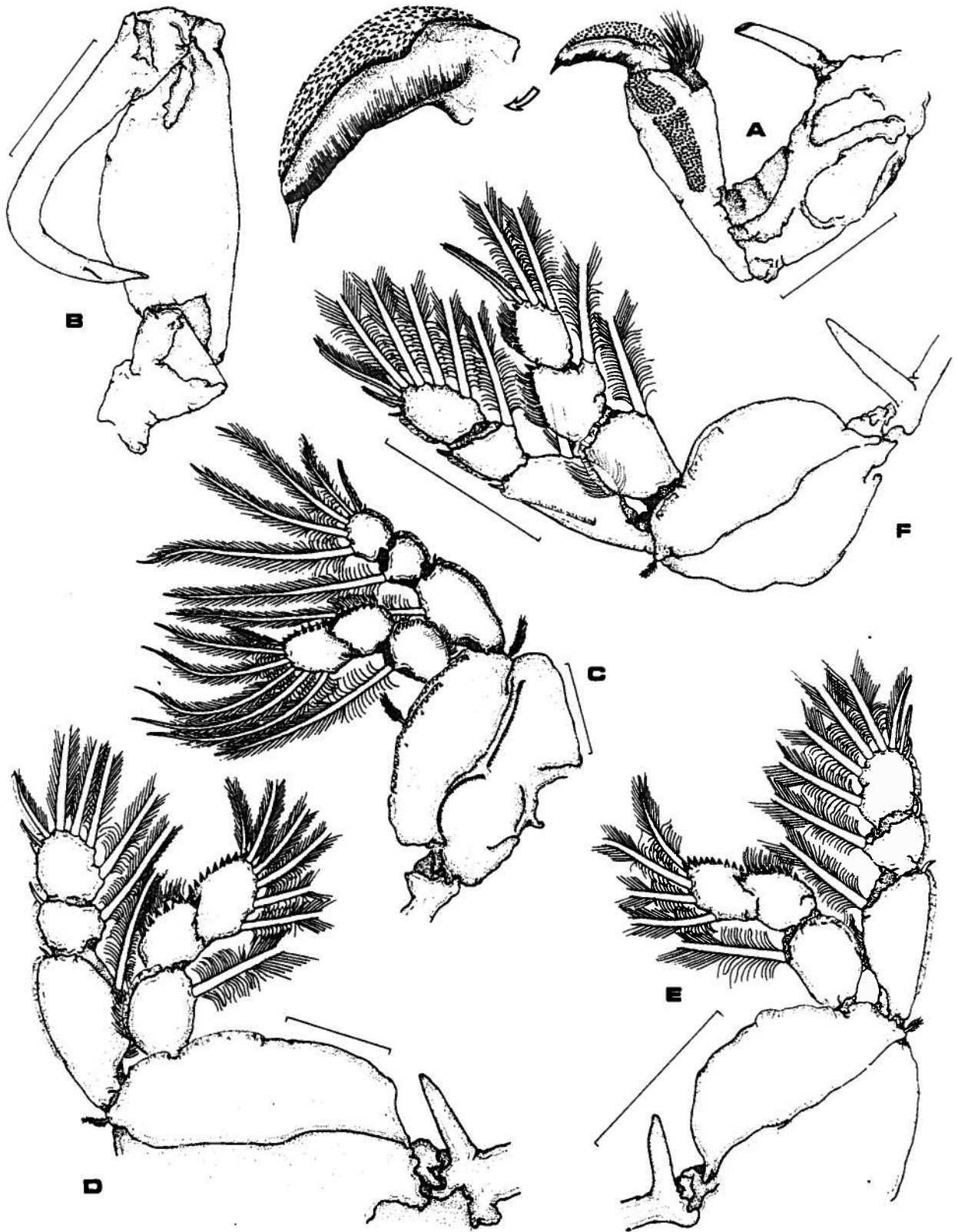


FIGURE 107 . *Kroyeria triakos* Fukui, 1965, female: A, habitus, dorsal; B, dorsal stylet; C, caudal ramus; D, first antenna; E, second antenna; F, mandible; G, first maxilla; H, second maxilla; I ,maxilliped. Scales: 0.6 mm in A; 0.2 mm in B; 0.01 mm in C-E; 0.05 mm in F; 0.1 mm in G, H; 0.2 mm in I.

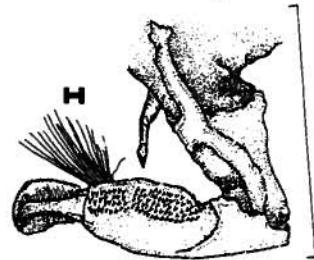
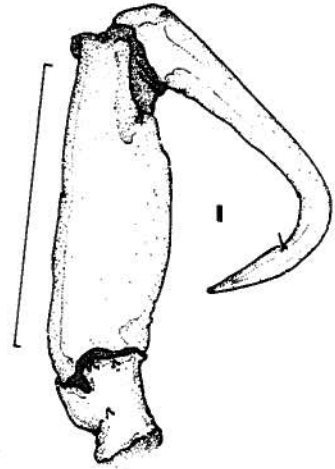
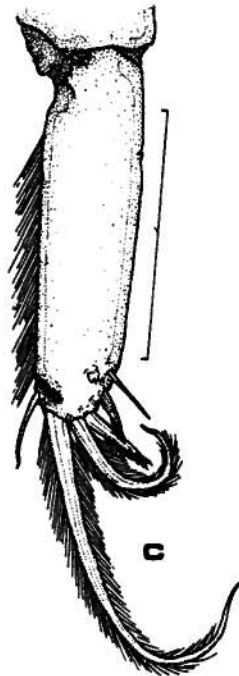
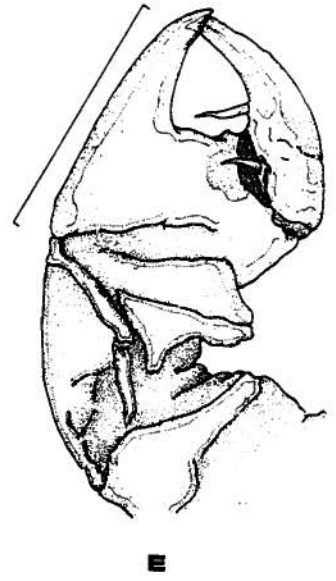
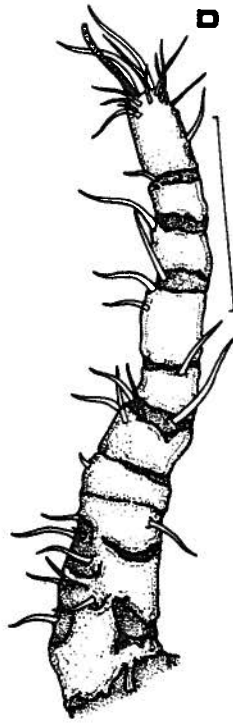
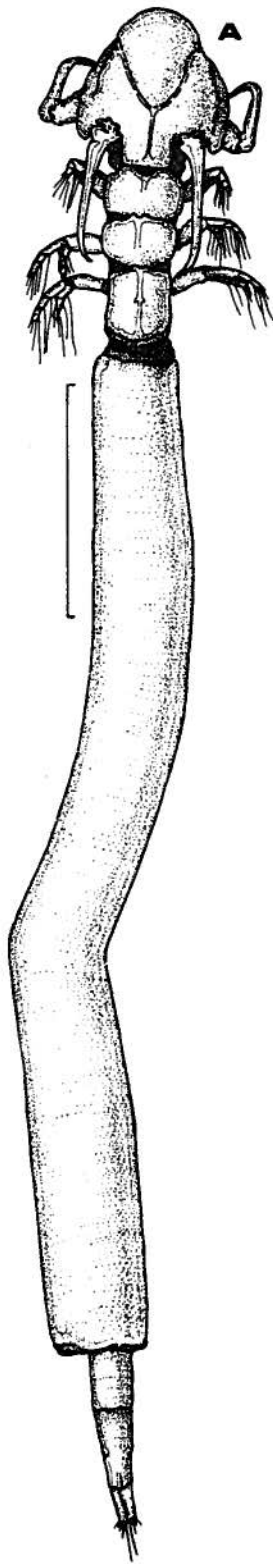


FIGURE 108. *Kroyeria triakos* Fukui, 1965, female: A, leg 1; B, leg 2, exopod; C, leg 2 endopod; D, leg 3, exopod; E, leg 3 endopod; F, leg 4. Scales: 0.1 mm in A-F.

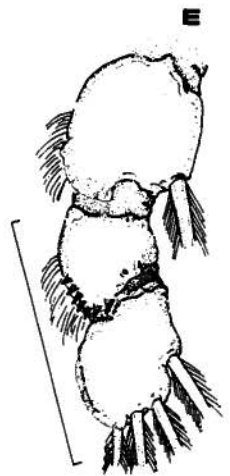
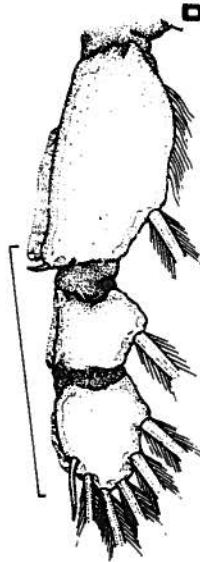
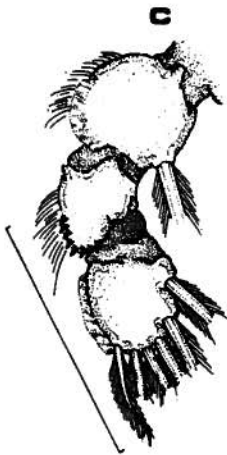
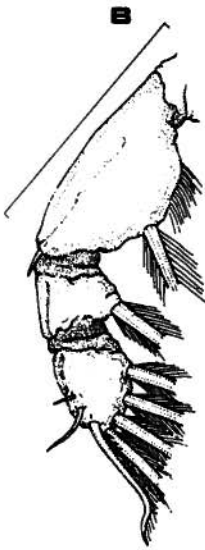
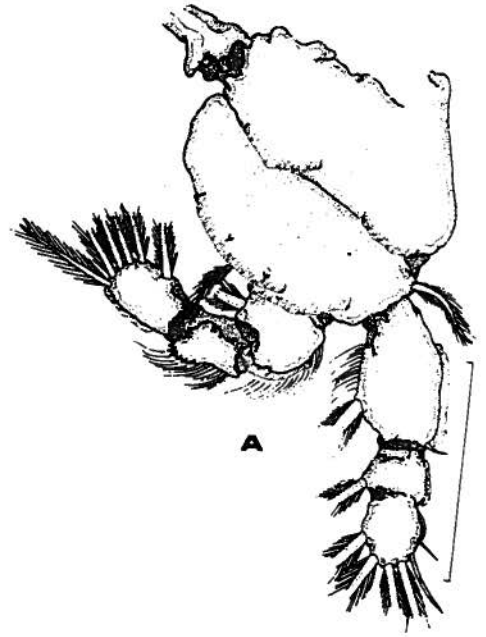
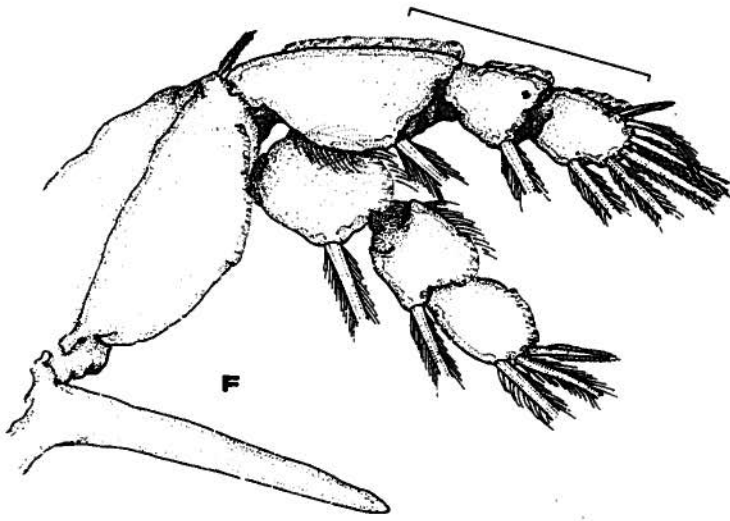


FIGURE 109 . Kroyeriidae Cladogram.

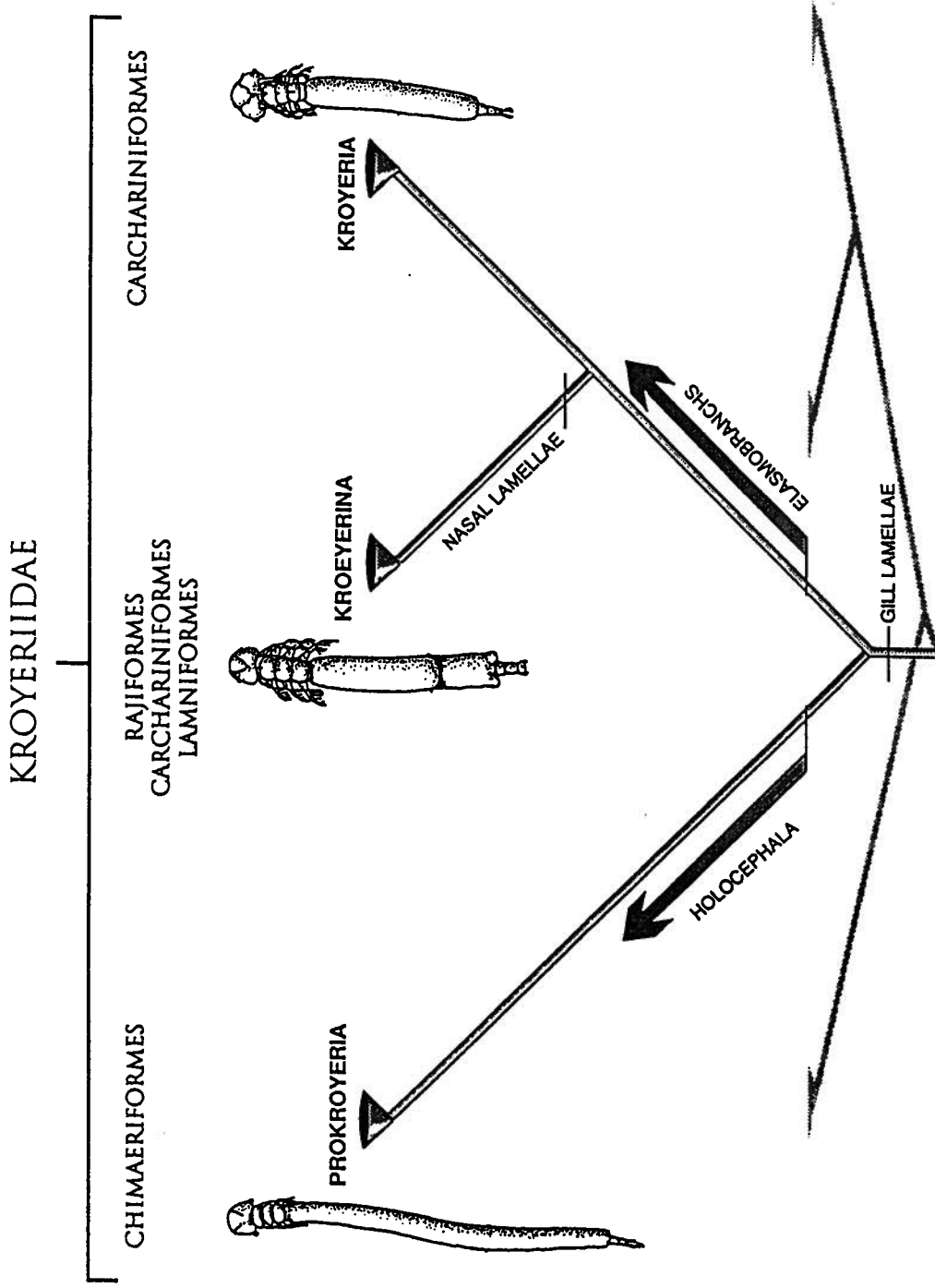


FIGURE 110 . *Kroyeria* Cladogram.

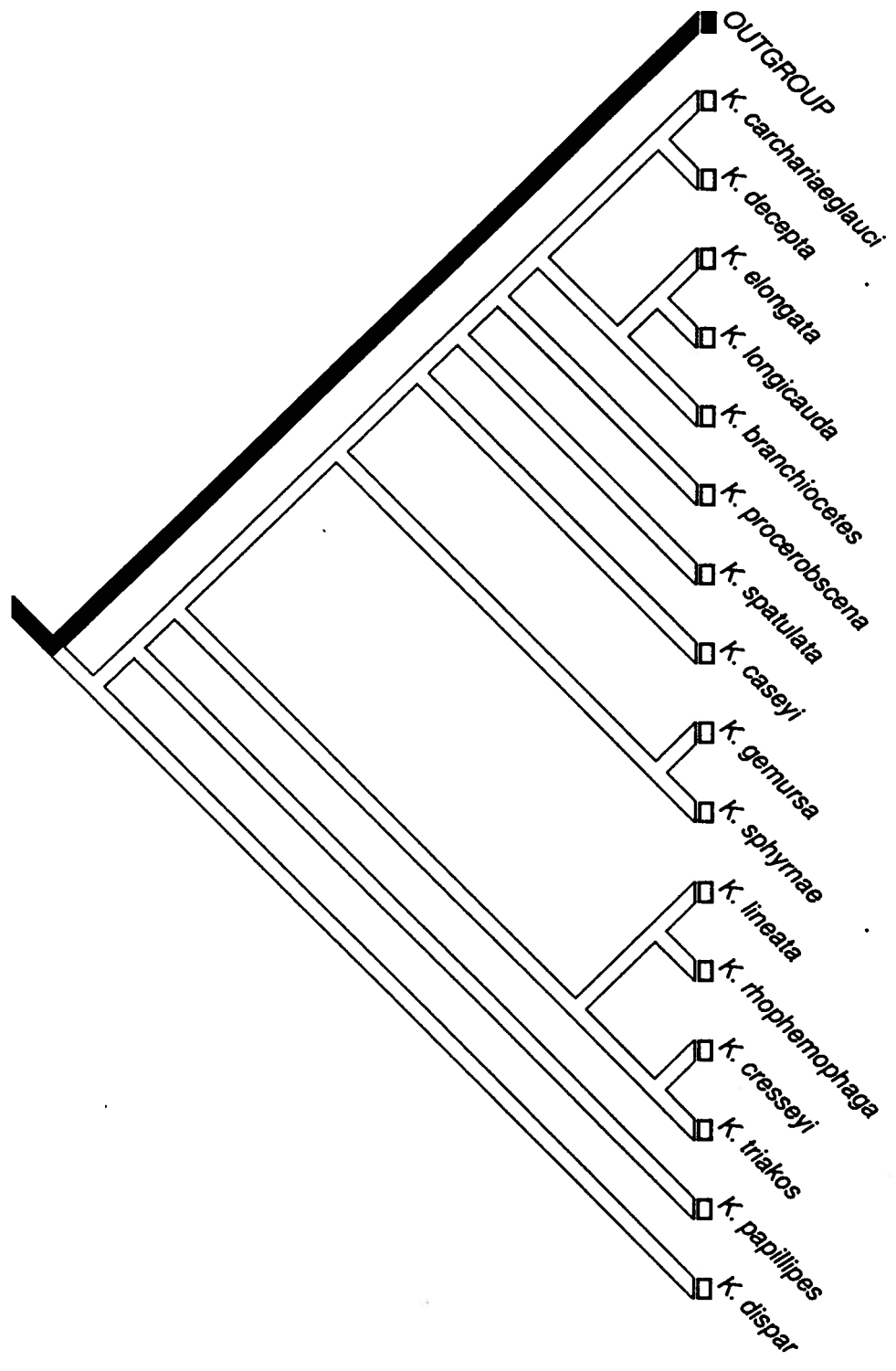


FIGURE 111 . *Kroyeria*- derived host cladogram.

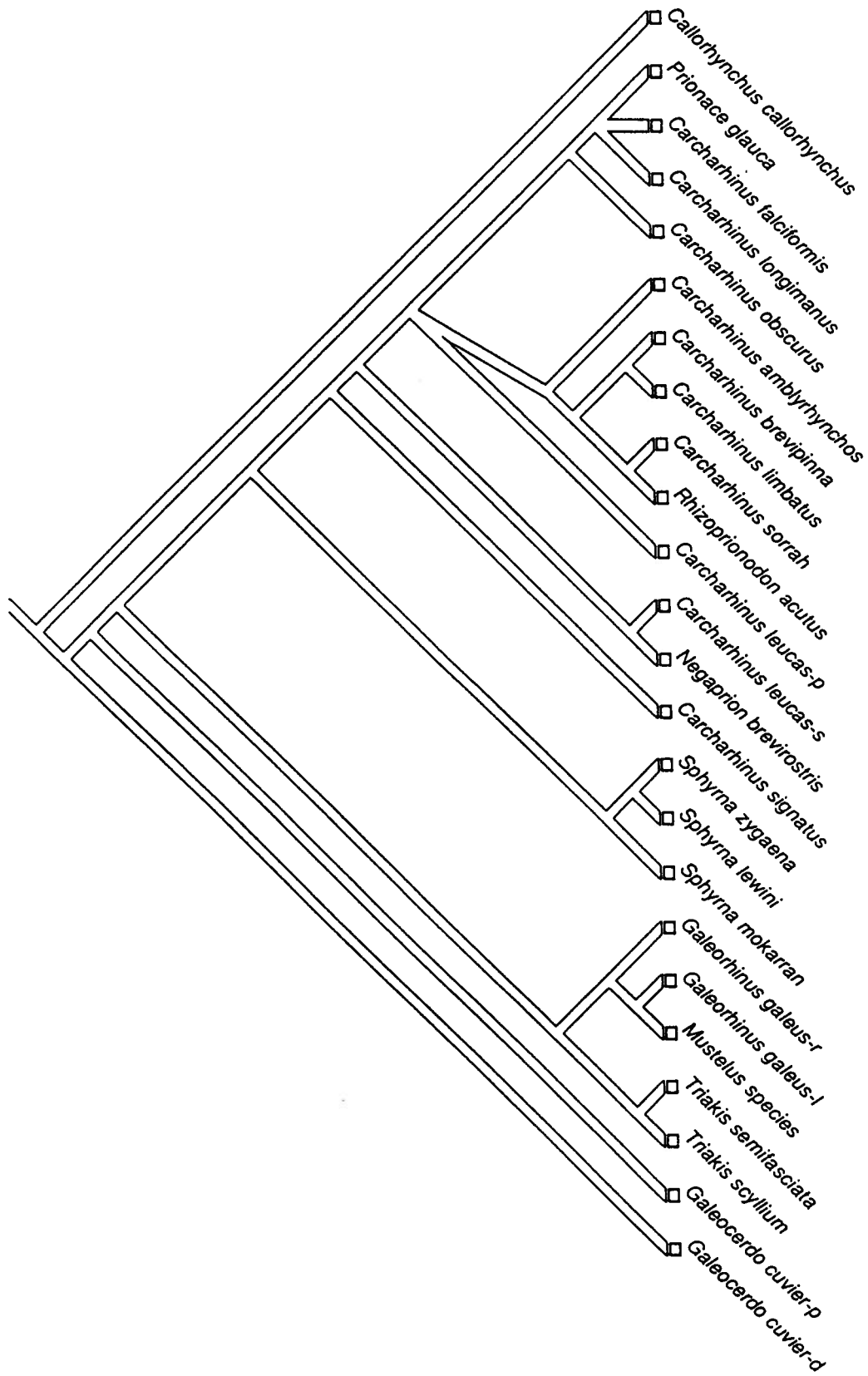


FIGURE 112 . *In situ* illustration of *Kroeyerina elongata* Wilson, 1932, attached to the olfactory lamellae of the blue shark, *Prionace glauca* Linnaeus, 1758.

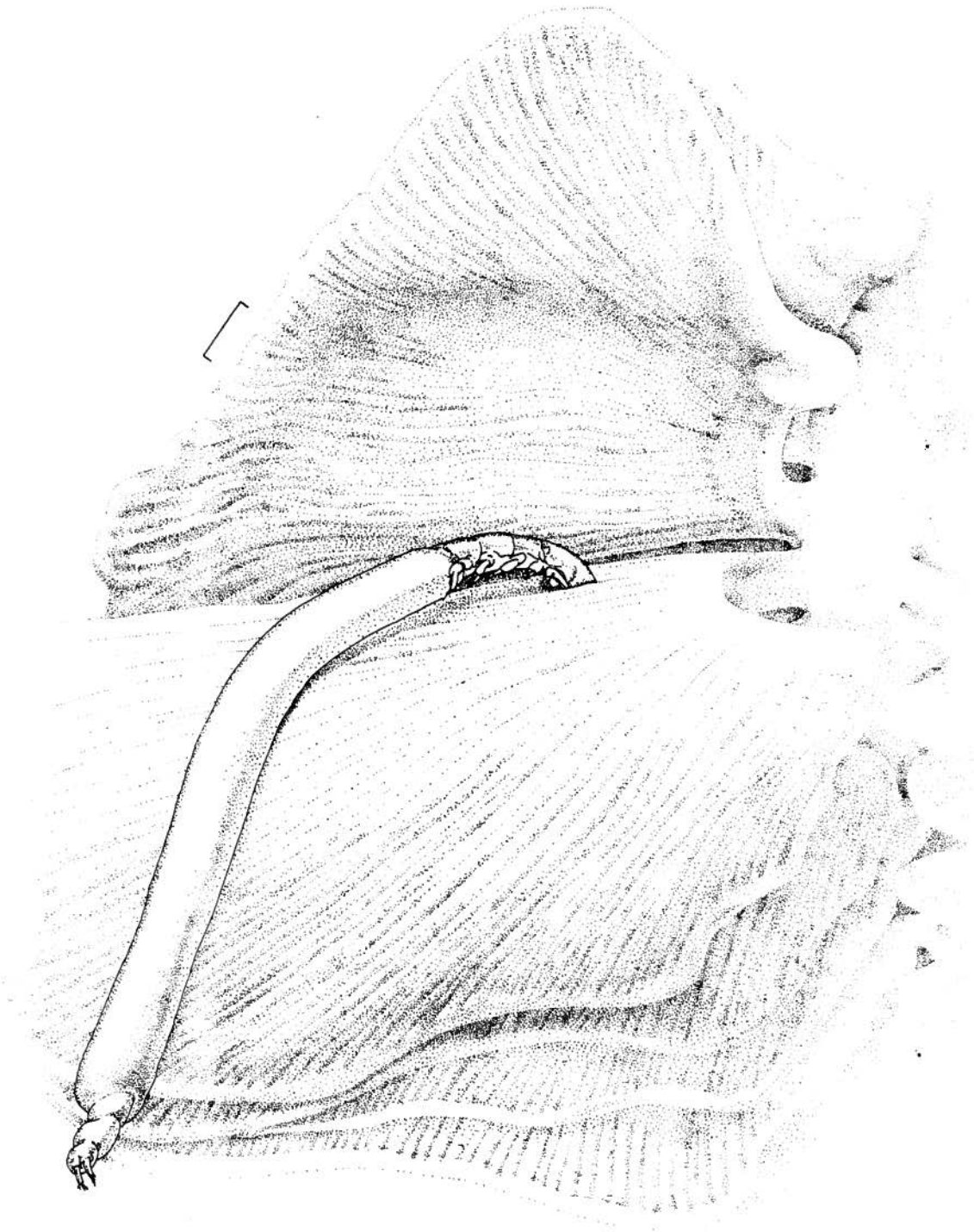
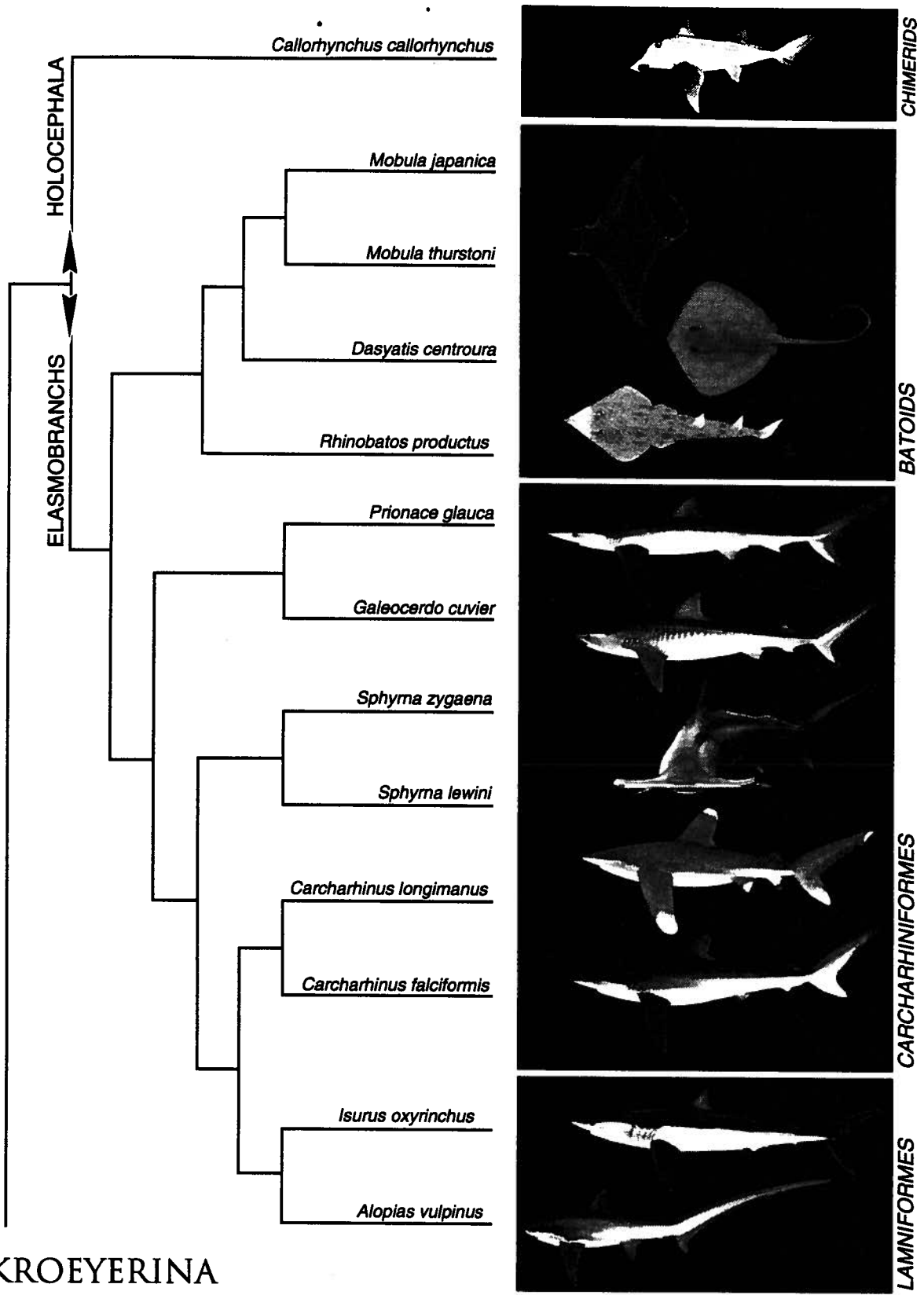


FIGURE 113 . *Kroeyerina*-derived host cladogram.



KROEYERINA

Host-Summary Cladogram

FIGURE 114 . Combined *Kroyeria-Kroeyerina*-derived host cladogram.

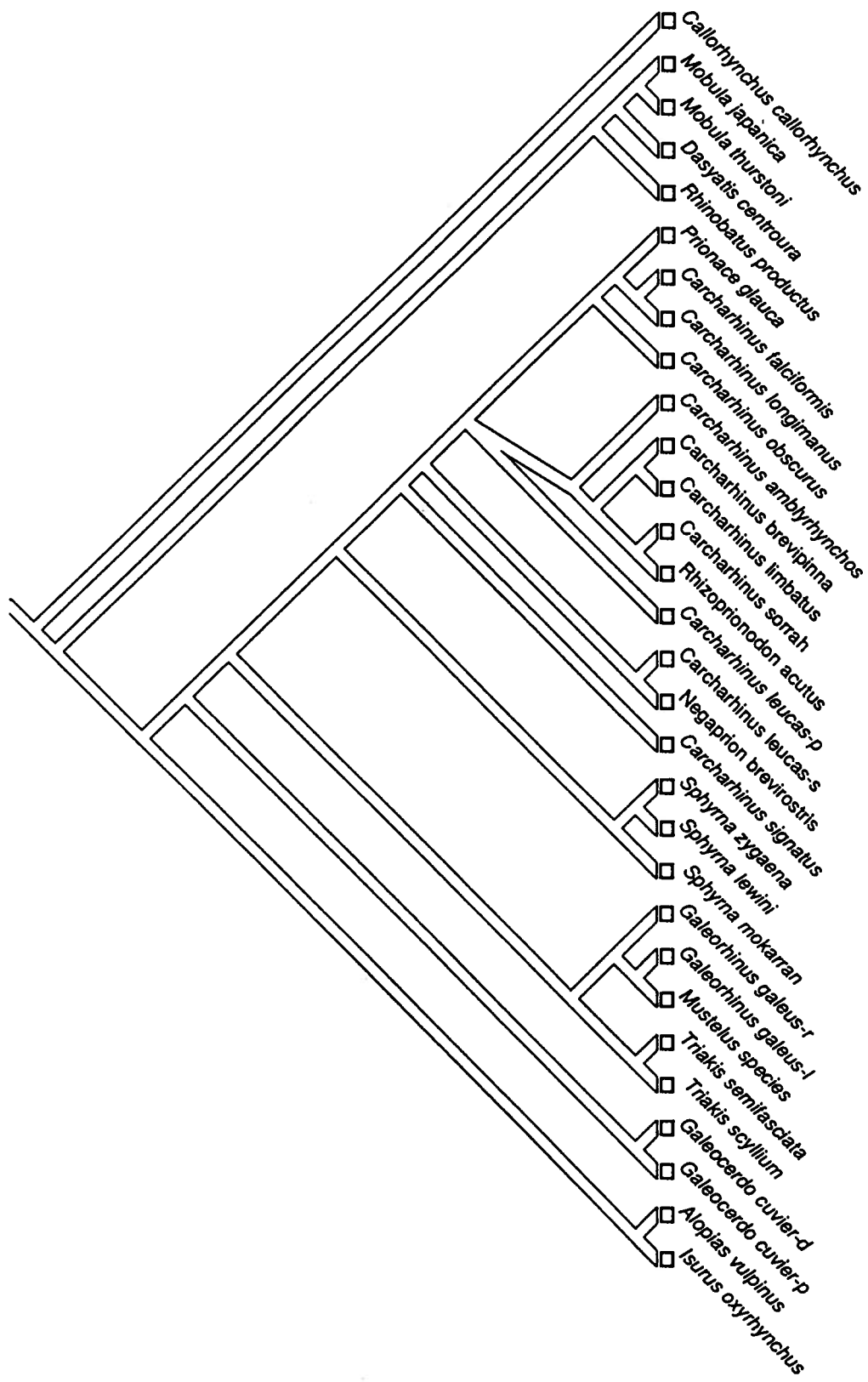


FIGURE 115 . *Squalia* and *Hypnosqualia* relationships from Shirai 1992. Rajiform relationships from Nishida 1990. Irrelevant and non-parasitized host taxa excluded.

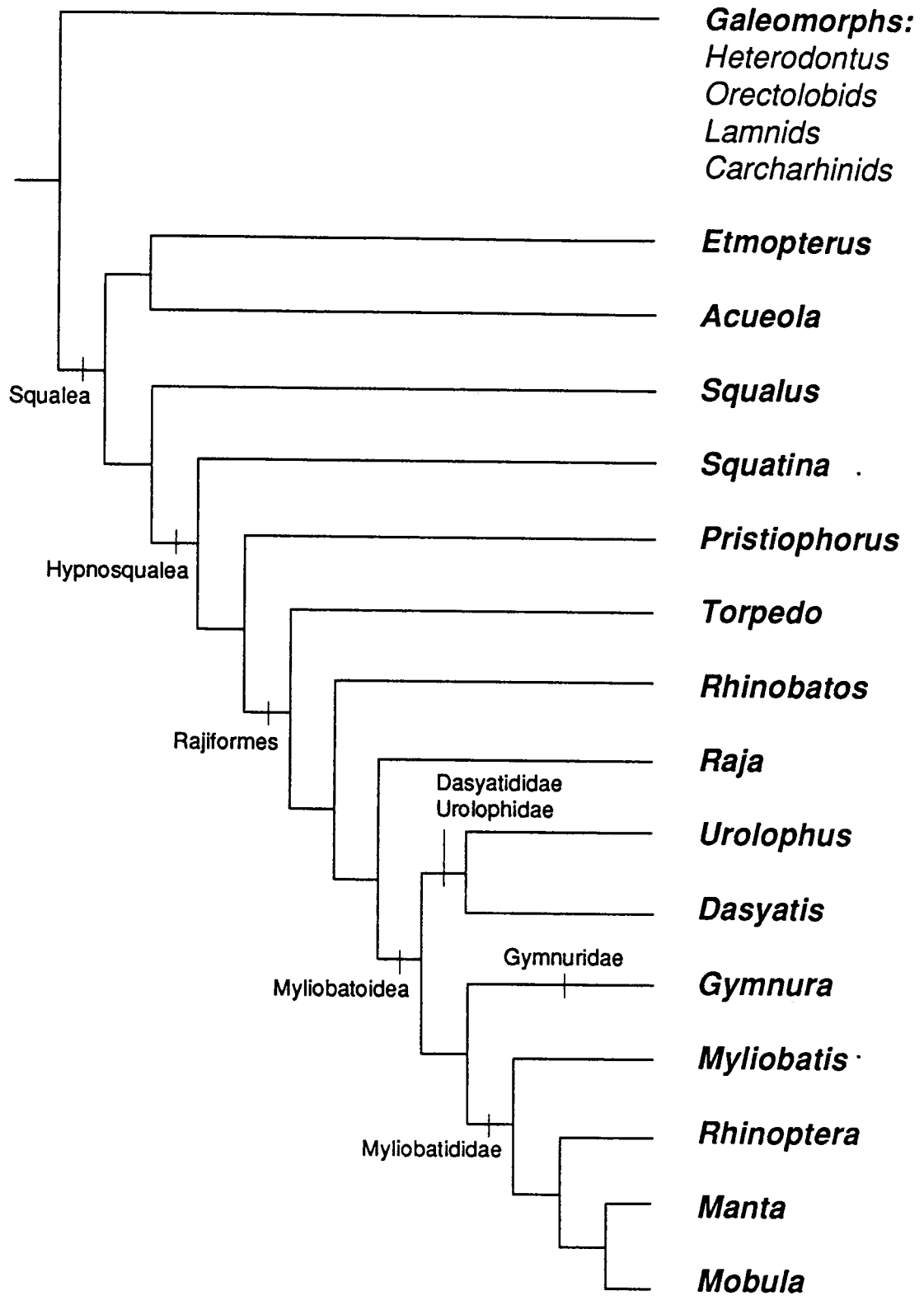
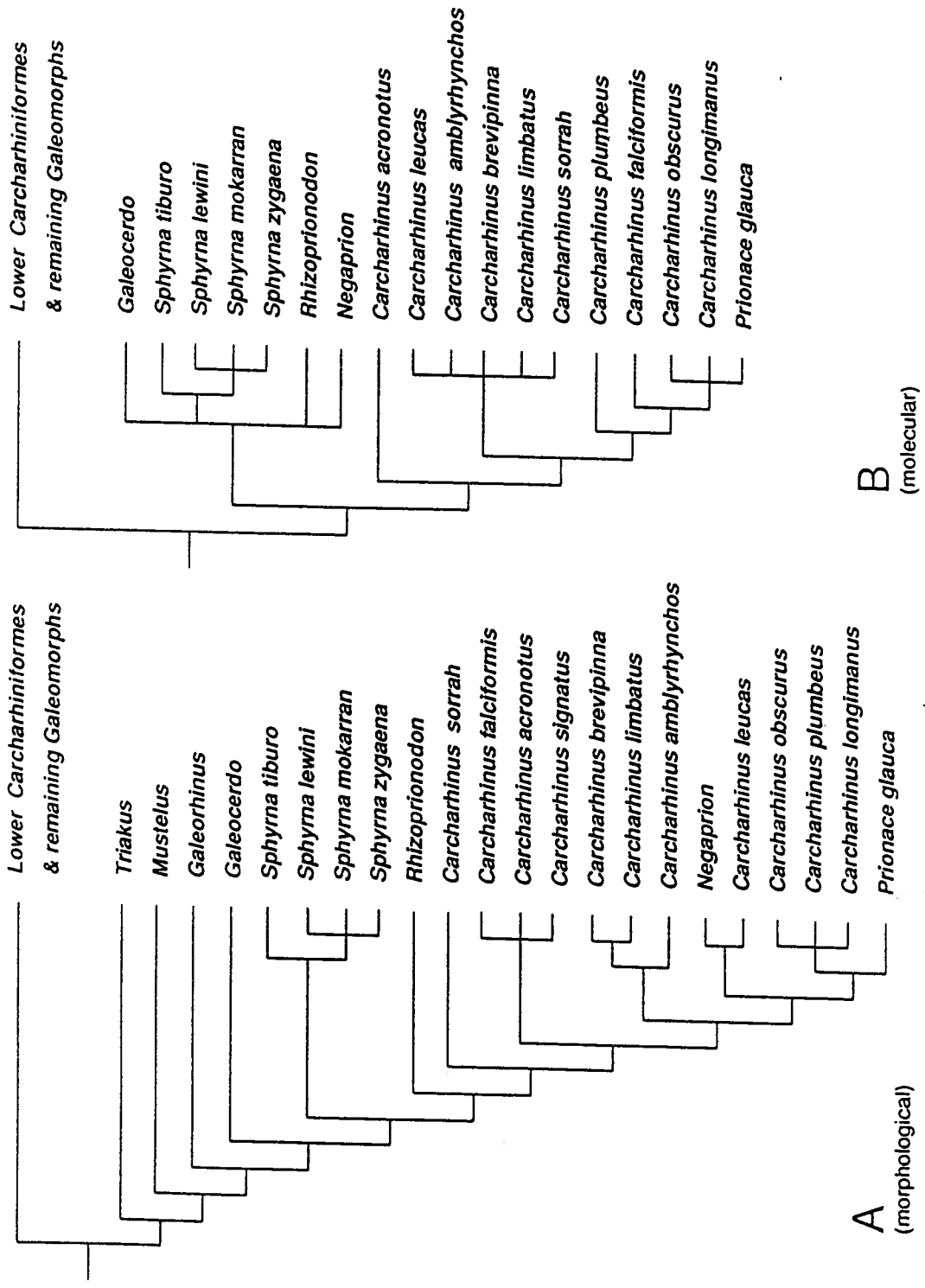


FIGURE 116 . Competing morphological and molecular cladograms of carcharhinids.



TABLES

TABLE II - Binary codes of select species of *Eudactylina* from major host taxa.

OUTGROUP	000000000000000000
<i>Myliobatis californica</i>	100000000000111011
<i>Pristiophorus cirratus</i>	010000000000111011
<i>Squatina squatina</i>	001000000000111010
<i>Etmopterus pusillus</i>	000100000000111100
<i>Aculeola nigra</i>	000010000000111100
<i>Squalus acanthias</i>	000001000000110000
<i>Galeorhinus galeus</i>	000000100001100000
<i>Mustelus sp.</i>	000000100001100000
<i>Galeocerdo cuvier</i>	00000001011110000

TABLE IV - Recoded *Kroeyerina* phylogeny by host matrix.

<i>Callorhynchus callorhynchus</i>	1 0 0 0 0 0 0 0 1 0 0 0 0 0 0
<i>Mobula japonica</i>	0 1 0 0 0 0 0 0 1 1 1 1 0 0 0
<i>Mobula thurstoni</i>	0 1 0 0 0 0 0 0 1 1 1 1 0 0 0
<i>Rhinobatos productus</i>	0 0 0 1 0 0 0 0 1 0 1 1 0 0 0
<i>Dasyatis centroura</i>	0 0 1 0 0 0 0 0 1 1 1 1 0 0 0
<i>Prionace glauca</i>	0 0 0 0 1 0 0 0 1 0 0 1 1 0 0
<i>Galeocerdo cuvier</i>	0 0 0 0 1 0 0 0 1 0 0 1 1 0 0
<i>Sphyrna zygaena</i>	0 0 0 0 0 1 0 0 1 0 0 1 1 1 0
<i>Sphyrna lewini</i>	0 0 0 0 0 1 0 0 1 0 0 1 1 1 0
<i>Carcharhinus falciformis</i>	0 0 0 0 0 0 1 0 1 0 0 1 1 1 1
<i>Carcharhinus longimanus</i>	0 0 0 0 0 0 1 0 1 0 0 1 1 1 1
<i>Alopias vulpinus</i>	0 0 0 0 0 0 0 1 1 0 0 1 1 1 1
<i>Isurus oxyrinchus</i>	0 0 0 0 0 0 0 1 1 0 0 1 1 1 1

APPENDICES

APPENDIX A (Continued) -

Description of characters, code 0 followed by 1-9, respectively.

1. Number of setae on caudal rami: 6; 5; 4.
2. Terga of first free thoracic somite: typical; aliform, overlapping posterior somite.
3. Terga of second free thoracic somite : typical; aliform, overlapping posterior somite.
4. Number of segments of first antenna: many; 6; 5; indistinct 4-5; 4.
5. Auxiliary spine on first antenna: absent; present in penultimate segment; present on antipenultimate segment; as in the latter but shorter.
6. Secondary auxiliary spine on penultimate segment of first antenna: present; absent.
7. Second segment of second antenna: unarmed; bearing spiniform process.
8. Third segment of second antenna: unarmed; bearing spiniform process.
9. If third segment bears a process: unarmed; bearing slender elongate process; with a short process; with a stout curving process.
10. Third segment of second antenna: shorter than segment two; longer than or, subequal to segment two.
11. If third segment of second antenna is longer than or subequal to segment two: shorter; subequal; longer.
12. Formula of terminal segment of exopod 1: 4; III; 3; 2,1; 3,1.
13. Proximal segment of exopod two: typical; swollen and enlarged; elongate.
14. Leg one: rami similar in length; exopod greatly reduced.
15. Rami of leg three: typical proportions; elongate.
16. Rami of leg four: typical proportions; elongate.
17. Endopod leg four: 3 segments; 2 segments.
18. Terminal segment of endopod 4; not modified; modified into spinous process.
19. Caudal rami: not modified; modified into a digitiform structure.
20. Lateral shield of claw of maxilliped: large ovoid: small and quadrate; large, quadrate; reduced.
21. Proximal portion of claw of second maxillae: denticulated; with row(s) of finely serrated membranes; row of pendulous membrane; spinulated patch.
22. Distal portion of claw of second maxilla: denticulated; bearing finely serrated membranes; spinulated patch.

23. If distal portion of claw of second maxilla bears membranes: denticulated; multiple rows; two rows; single row.
24. Setae on endopod of first maxilla: stout; elongate.
25. Setae on exopod of first maxilla: stout; elongate.
26. Endopod of leg two: with 3 terminal setae; with 2 terminal setae.
27. Middle seta on terminal segment of exopod two: spiniform; truncate quadrangle or nipple.
28. If truncate: spiniform; quadrangular; papilliform.
29. First segment of endopod one of male: unarmed; with thumb-like process.
30. Medial most seta on terminal segment of exopod two: claw-like; recurved; papilliform.
31. Seta on first segment of exopod one: pinnate; slender with finely serrated membrane; medium small, denticulated; claw-like, small, naked; with coarsely serrated membrane; absent.
32. If claw-like: pinnate; small; large.
33. If large: pinnate; stout, naked; stout with serrated membrane; slender with serrated membrane; denticulated.
34. Setae on second segment of exopod one: pinnate; slender with lateral serrated membrane; medium length, semi-stout denticulated; short, stout, acute; absent; coarsely serrated membrane; large claw; tiny denticulated; tiny naked; tiny, naked; stout, tiny.
35. If a large claw: pinnate; naked; with apical membrane; bilateral bearing membrane; slender; denticulated.
36. Lateral most seta on terminal segment of exopod one: elongate, pinnate; slender with lateral serrated membrane; medium-short, denticulated; short, skinny, bilaterally denticulated: minute, with coarsely serrated membrane; short, stout and bilaterally denticulated; claw-like.
37. Seta adjacent to lateralmost seta on terminal segment of exopod one: pinnate; with finely serrated membrane; with coarsely serrated membrane; medium length, semi-stout, denticulated; stout claw; short.
38. If short: pinnate; stout; slender; minute.
39. If a stout claw: pinnate; naked; denticulated; membraned.
40. Large setae on terminal segment of exopod one: pinnate; with finely serrated membrane; with coarsely serrated membrane: medium length, semi-stout, denticulated; stout claw; short.
41. If claw-like: pinnate; large; minute.
42. If large: pinnate; stout; relatively slender.

43. If elongated and slender: pinnate; with a serrated membrane; naked; with scattered denticles; bilaterally denticulated; unilaterally denticulated.
44. Seta on proximal segment of exopod three; stout, claw-like; medium length; more slender, slightly curved.
45. If seta is medium length: stout, claw-like; slender with large teeth; stout, denticulated; slender, denticulated; shorter and naked.
46. If slender and denticulated: stout, claw-like; typical denticulations; row of fine denticulations; naked or single denticle.
47. Corpus of maxilliped: typical with oblique inner margin; massive with transverse inner margin.
48. Receptacle of corpus: large; small.
49. Subchela of maxilliped: without cuticular flaps; with cuticular flaps.
50. Seta on proximal segment of exopod four: as in #44 above.
51. Seta on second segment of exopod three: claw-like; more slender; slightly curving.
52. Seta on second segment of exopod four as in #51 above.
53. If seta on second segment of exopod three and four is slender and slightly curved: claw-like; short, slender: bearing large teeth (tines); medium length with or without denticulations; stout with typical denticulations.
54. If short and slender: claw-like; bearing 2 tiny denticles: naked.
55. If medium in length: claw-like; slender with row of fine denticulations along lateral margin; with single large tine; naked or one apical denticle; with typical denticulations; slightly longer and more slender than the latter.
56. Lateralmost segment on terminal segment of exopod three: claw-like; relatively more slender, slightly curved.
57. Lateralmost setae on terminal segment of exopod four: claw-like; relatively more slender, slightly curved.
58. If lateralmost seta on terminal segment of exopod three and four is relatively more slender and curved; claw-like; short, slender; stout, denticulated; elongate with large distal tines; with row of fine denticulations along lateral margin; medium length with typical denticulations or naked.
59. If medium length: claw-like; with small apical tooth; naked; with large lateral tine; with typical denticulations.
60. Seta adjacent to lateralmost seta on terminal segment of exopod three: claw-like; relatively more slender; slightly curved.
61. Seta adjacent to lateralmost seta on terminal segment of exopod four: claw-like; relatively more slender; slightly curved.

62. If seta adjacent to lateralmost seta terminal segment of exopod three and four is slender and slightly curved: claw-like; short, slender; with large teeth or tines; relatively stout with typical denticulations; medium length with typical denticulations.
63. If seta is medium length: claw-like; with small apical tooth; with typical denticulations; slender with row of fine denticulations along lateral margin; naked; with single large tine.
64. Medialmost seta on terminal segment of exopod three; claw-like; relatively more slender; slightly curved.
65. Medialmost seta on terminal segment of exopod four; claw-like; relatively more slender; slightly curved.
66. If medialmost seta on terminal segment three and four is relatively more slender: claw-like; medium length, naked or with few tiny teeth; elongate, bilaterally bearing many teeth; stout with typical denticulations; bearing large tines; erect, bearing upwardly directed teeth; pinnate; elongate bearing typical denticulations; long, strongly curved with few denticles.
67. If medialmost seta on terminal segment of exopod three and four is claw-like: large, long; short, stout.
68. If large and long: naked; with large apical tine; stout, bilaterally denticulated; stout, unilaterally denticulated.
69. If claw-like: large; small.
70. If large: naked; strongly curved, unilaterally denticulated with a subapical setule; stout and bilaterally denticulated; slender and denticulated; modified.
71. If second segment of second antennae has spiniform process: absent; medium in length; medium in length, stout, curved downward; elongate; short; slight nub-like extension.
72. Auxiliary spine on penultimate segment of antenna one: not bearing cuticular flaps; bearing cuticular flaps.
73. Components of second antenna: typical proportions; elongate.
74. If first antenna is four segmented with elongate terminal segment: with elongate setae; with generally shorter setae.
75. Terminal segment of first antenna: with typical length aesthete; with elongate aesthete, extending beyond the tip of atypically elongate terminal segment.

APPENDIX B (continued) -

Description of characters. Code 0 given first, followed by character states 1-4, respectively.

1. Number of setae on caudal ramus: 6; 5; 4.
2. Number of segments on first antenna: many; 4; 5; 6.
3. Second segment of second antennae: unarmed; with spinous process.
4. Third segment of second antennae: unarmed; with spinous process.
5. Huge auxiliary spine on penultimate segment of first antenna: absent; present.
6. Secondary auxiliary spine on penultimate segment of first antennae: absent; present.
7. Setae of first antennae: elongate; slender; short, stout.
8. Proximal portion of claw of second maxilla: denticulated; with serrated membrane; spinulated patch.
9. Distal portion of claw of second maxilla: denticulated; with serrated membranes; spinulated patch.
10. Setal formula for terminal segment of exopod one: 4; III; I,3.
11. If with a formula of III: 4; 3 of medium length and in ascending height: 3 stout and claw-like; 3 elongate and slender.
12. Seta on proximal segment of exopod one: pinnate; slender, denticulated and medium in length; slender, elongate, bearing serrated membrane; claw-like.
13. Leg two exopod: unmodified; swollen and enlarged; elongate and enlarged.
14. Middle seta on terminal segment of exopod two: claw-like; quadrate.
15. Medialmost seta on terminal segment of exopod two: spiniform; claw-like; thin and recurved; stout and papilliform.
16. Setae on exopod of first maxilla: stout; elongate.
17. Setae on endopod of first maxilla: stout; elongate.
18. Seta on second segment of exopod one: claw-like; small, spiniform and denticulated; with lateral serrated membrane; bilaterally bearing serrated membrane.
19. Lateralmost seta on terminal segment of exopod one: claw-like; laterally bearing serrated membrane; tiny.
20. Seta adjacent to lateralmost seta on terminal segment of exopod one: claw-like; medium length, slender; with lateral serrated membrane; bilaterally bearing membrane; reduced.

21. Largest segment on terminal segment of exopod one: claw-like; pinnate; slender, bilaterally denticulated; bilaterally membraned; elongate, naked; unilateral membrane; tiny; claw-like.
22. Seta on proximal segment of exopod three: large; claw-like; shorter; spiniform.
23. Seta on proximal segment of exopod four: large: claw-like; shorter; spiniform.
24. If seta on proximal segment of exopod three is not claw-like: large claw; short and stout; curving, semi-slender; reduced.
25. If seta on proximal segment of exopod four is not claw-like: large, claw-like; short and stout; curving, semi-slender; reduced.
26. Seta on second segment of exopod three: Large, claw-like; slender, medium length, more slender.
27. Seta on second segment of exopod four: large, claw-like; slender, medium length.
28. If seta on second segment of exopod three is medium, slender: claw-like; shorter, stout; curving, denticulated, as latter but shorter; very stout.
29. If seta on second segment of exopod four is medium, slender: claw-like: shorter, stout; curved, denticulated; as latter but stout; very slender.
30. Lateralmost seta on terminal segment of exopod three: large, claw-like; medium length; spiniform.
31. Lateralmost setae on terminal segment at exopod four: large, claw-like; medium length, spiniform.
32. If lateralmost seta on terminal segment of exopod three is medium in length: large, claw-like; short; slender and curved.
33. If lateralmost seta on terminal segment of exopod four is medium in length: large, claw-like; short; slender and curved.
34. If lateralmost seta on terminal segment of exopod three is short: large, claw-like; slender and denticulated; stouter, naked.
35. If lateralmost seta on terminal segment on exopod four is short: large, claw-like; slender and denticulated; stout, naked.
36. If lateralmost seta on terminal segment of exopod three is slender and curved: claw-like; with large apical teeth; bilaterally denticulated; as latter but stouter.
37. If lateralmost seta on terminal segment of exopod four is slender and curved: claw-like, with large apical teeth; bilaterally denticulated; as latter but slender.
38. Seta adjacent to lateralmost seta on terminal segment of exopod three: large, claw-like; short, spiniform; slender.
39. Seta adjacent to lateralmost seta on terminal segment of exopod four: large, claw-like; short, spiniform; slender.

40. Medialmost seta on terminal segment of exopod three: large, claw-like; slender, spiniform.
41. Medialmost seta on terminal segment of exopod four: large, claw-like; slender, spiniform.
42. If medialmost seta on terminal segment of exopod three is claw-like: naked; denticulated.
43. If medialmost seta on terminal segment of exopod four is claw-like: naked; denticulated.
44. If medialmost seta on terminal segment of exopod three is slender: claw-like; semi-stout; very long, curving; medium length and slender; long and erect.
45. If medialmost seta of terminal segment of exopod four is slender: claw-like; semi-stout; very long, curving; medium length, slender; long and erect.
46. Proximal segment of second endopod of male: unarmed; with lateral thumb-like process.
47. Large seta on endopod of first maxilla: naked; short, laterally denticulated; short, semipinnate; short, covered with denticles; elongate and denticulated; long, pinnate.
48. Cuticular flaps on brachium of second maxilla: absent; crescent shaped; triangular, irregular.

Appendix C (continued)

Description of characters

Code 0 state is given first, followed by character states 1-7, respectively.

1. Armature of claw of second antennae: 1 setae; 2 setae; 3 setae.
2. Segmentation and armature of first antennae: nine-segmented, 4, 5, 4, 1, 1, 1, 1, 1, 13+1; nine-segmented, (4,5), 1, 1, 5, 2, 3, 1, 1, 13+1; eight -segmented, 9 or 10, 1, 5, 1 or 2, 3, 1, 1, 13+1; seven-segmented, 11, 2 or 3, 1 or 2, 3, 1, 1, 13+1; seven-segmented, 9 or 11, 5, 1 or 2, 3, 1, 1, 13+1
3. Condition of claw of second antenna: robust bearing single setae; naked bearing 3 setae; bearing distal membranous receptacle and 3 setae; stout , naked with compressed aperature and 3 setae; strongly curved, naked forming circular aperature and 3 setae.
4. Dorsal stylet: absent; medium length, strongly incurved; medium length, apically bifid; medium length with large distolateral tine; medium length with flanged terminus; short and stout; greatly elongate.
5. Pollex of second antennae: small pocket; large membranous receptacle.
6. Mandible: 9-10 teeth; 7-8 teeth.
7. Endopodal denticulations on second segment of leg one: absent; present.
8. Endopodal denticulations on third segment of leg one: absent; present.
9. Endopodal denticulations on second segment of leg two: absent; present.
10. Endopodal denticulations on third segment of leg two: absent; present.
11. Endopodal denticulations on second segment of leg three: absent; present.
12. Endopodal denticulations on third segment of leg three: absent; present.
13. Endopodal denticulations on second segment of leg four: absent; present.
14. Endopodal denticulations on third segment of leg four: absent; present.
15. Formula of second segment of endopod one: 0,2; 0,1; 0,0.
16. Formula of second segment of endopod two: 0,2; 0,1; 0,0.
17. Formula of second segment of endopod three: 0,1; 0,0.
18. Lateral margins of cephalothorax: non-parallel, parallel.
19. Posterior sinus: shallow; deeply recessed.
20. Interpodal stylets of leg two: absent; short; medium; elongate.
21. Interpodal stylets of leg three: absent, short, medium, elongate.
22. Interpodal stylets of leg four: absent, short, medium, elongate.
23. Formula of second segment of exopod one: 1, 1; 0,1.
24. Number of setae on segment three of exopod three: 7; 6.
25. Formulae of segment three of endopod three: 1, 1, 3, 4.

26. Setae in aperture on claw of second antenna: minute; elongate (approaching width of aperture); medium length and slender; recurved; stout.
27. Middle setae on claw of second antennae: absent; pinched; long and blunt ; medium length and slender; short and stout; truncate; tiny; elongate and acute
28. Medial most distal setae of caudal ramus: elongate and entirely pinnate; medium length and entirely pinnate: slender with proximal half pinnate; naked; thick with proximal half pinnate; proximally inflated, proximally pinnate and medially pinched.
29. Distal seta adjacent to medial-most seta of caudal ramus: elongate and entirely pinnate; medium length and entirely pinnate; slender with proximal half pinnate; naked; thick with proximal half pinnate; proximally inflated, proximally pinnate
30. Lateralmost distal seta of caudal ramus: elongate and fully pinnate; short blunt, pinnate; slender and semi-pinnate; stout and semi-pinnate; naked; long, thick and semi-pinnate; semi-pinnate curved claw.
31. Distal seta adjacent to lateralmost seta on caudal ramus: elongate, fully pinnate; semipinnate; slightly more robust semi-pinnate seta; stout irregular shaped pinnate seta; naked; semi-pinnate curved claw; large thick semi-pinnate seta; stout and semi-pinnate.
32. Lateralmost seta of segment three of exopod two: naked; bearing smooth lateral membrane; bilaterally bearing serrated membranes; pin-tipped with large smooth membranes bilaterally.
33. Abdomen: 3-segmented; 2-segmented; 1-segmented.
34. Proximal seta on claw of second antenna: small; medium and stout; elongate and slender.
35. Seta adjacent to lateralmost seta on segment three of exopod four: naked; with lateral smooth membrane; lateral serrated membrane; bilaterally bearing smooth membranes and pin-tipped; bilaterally bearing membranes.
36. Exopod of first maxilla: both setae pinnate; one pinnate, one naked; both setae with proximal denticles; both setae entirely denticulated.
37. Corpus of maxilliped: naked; with transeverse lateral flange.
38. Intermediate or transitional seta of exopod four: semi-pinnate; semipinnate with smooth lateral membrane; semipinnate with serrated lateral membrane.
39. Lateralmost seta of segment three of exopod three: robust and naked; slender and naked; extremely small; absent; bilateral smooth membranes; lateral membrane.
40. Lateralmost seta of segment two on exopod two: robust and naked; slender and naked; absent; lateral smooth membrane; bilaterally bearing membranes and

- pin-tipped; bilaterally bearing serrated membranes; bilaterally bearing smooth membranes.
41. Lateralmost seta of segment two of exopod three: robust and naked; slender and naked; lateral smooth membrane; serrated lateral membrane; pin-tipped bilaterally bearing smooth membranes; bilaterally bearing smooth membranes.
 42. Lateralmost seta on segment two of exopod four: robust and naked; slender and naked; lateral smooth membrane; lateral serrated membrane; pin-tipped and bilaterally bearing smooth membranes; bilaterally bearing smooth membranes; absent.
 43. Formula of second segment of exopod two: 11; 0,1.
 44. Middle seta on claw of second antenna: absent; distal to seta in aperture; between proximal and aperture seta.