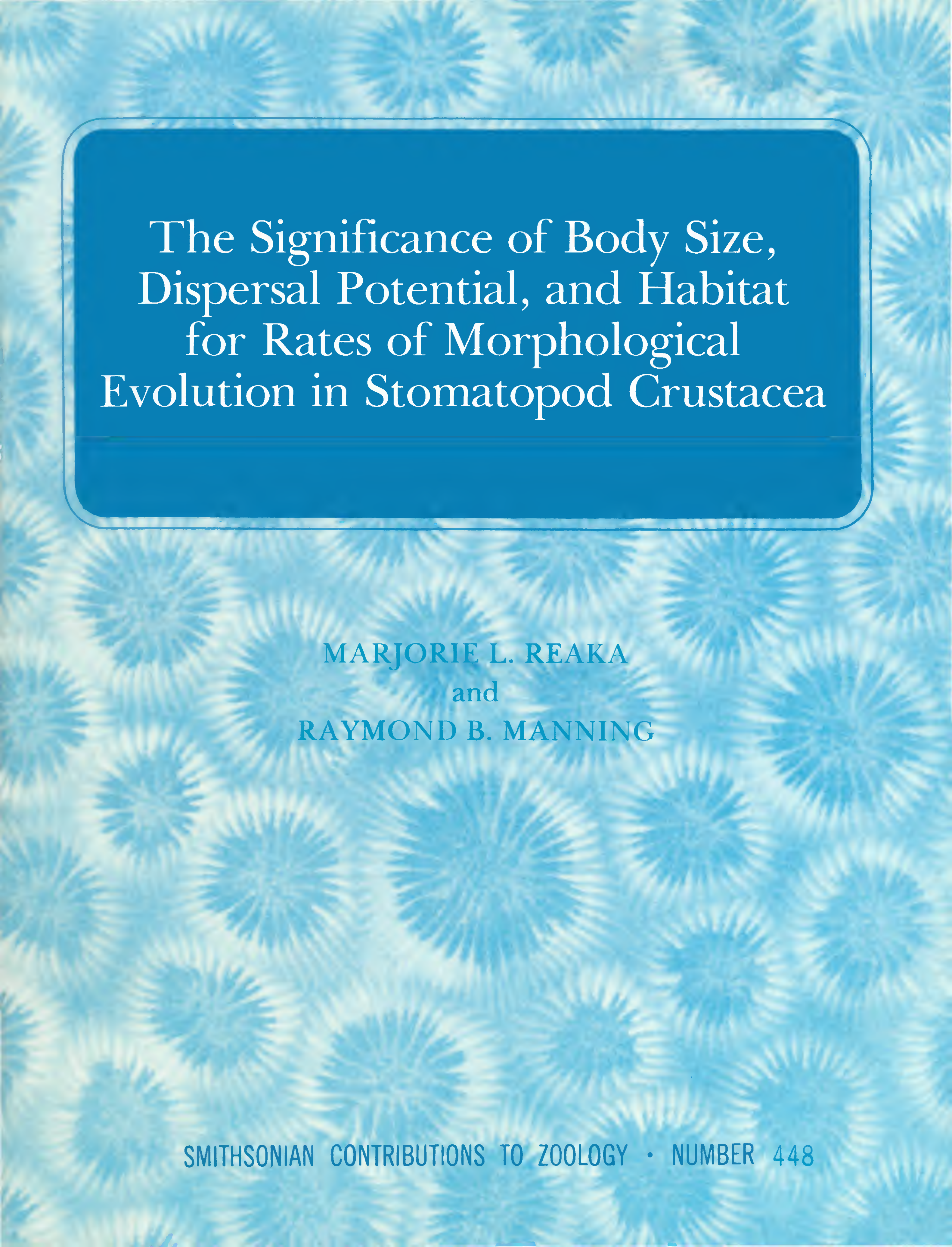

The Significance of Body Size, Dispersal Potential, and Habitat for Rates of Morphological Evolution in Stomatopod Crustacea

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and
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SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 448

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SMITHSONIAN INSTITUTION PRESS
Washington, D.C.
1987

ABSTRACT

Reaka, Marjorie L., and Raymond B. Manning. The Significance of Body Size, Dispersal Potential, and Habitat for Rates of Morphological Evolution in Stomatopod Crustacea. *Smithsonian Contributions to Zoology*, number 448, 46 pages, 11 tables, 1987.—This study reviews the world-wide distribution and status of all families and genera of stomatopod Crustacea, and tests a number of hypotheses about factors that alter rates of morphological evolution of stomatopods from the Atlanto–East Pacific region. The degree of morphological divergence of lineages among geographic subregions (East Pacific, West Atlantic, East Atlantic) and the incidence of local species radiation is both inversely and highly significantly related to species body size. Similarly, postlarval size and dispersal potential are significantly and inversely related to morphological divergence among subregions; local species multiplication is especially highly correlated with small postlarvae and restricted dispersal. Our data suggest that speciation may be higher for taxa inhabiting reef and rock substrates than level bottoms; these taxa also experience greater competition for resources and exhibit more complex behavior than those from level bottoms. However, other environmental attributes, such as depth, temperature, and latitude, were consistently unrelated to measures of divergence and speciation. Although further study is needed, extinctions appear to be more common in the gonodactyloids than in the lysiosquilloids or squilloids, in taxa with small postlarvae and restricted dispersal, in lineages inhabiting coral reefs compared to level bottoms, in tropical versus temperate latitudes, and in the East Atlantic followed by the East Pacific and then the West Atlantic geographic subregions.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Reaka, Marjorie L.
The significance of body size, dispersal potential, and habitat for rates of morphological evolution in stomatopod Crustacea.
(Smithsonian contributions to zoology ; no. 448)
Bibliography: p.
Includes index.
Supt. of Docs. no.: SI 1.27 : 448
1. Stomatopoda—Morphology. 2. Stomatopoda—Evolution. 3. Crustacea—Morphology. 4. Crustacea—Evolution. I. Manning, Raymond B., 1934- II. Title. III. Series.
QL1.S54 no. 448 591s 86-600272 [QL444.M375] [595.3'82]

Contents

The Significance of Body Size, Dispersal Potential, and Habitat for Rates of Morphological Evolution in Stomatopod Crustacea

Marjorie L. Reaka and Raymond B. Manning

Introduction

Rates of Evolution

Factors that Influence Evolutionary Rates

Evolutionary biologists long have sought to understand how some lineages flourish while others fail, how some epochs produce major radiations and others extinctions, and how some environments support diverse but others impoverished faunas. Rates of evolution, including divergence and multiplication within lineages and extinction, are thought to vary among taxa and over time (Simpson, 1983; but see Van Valen, 1973; Raup, 1975). Dispersal ability, extent of geographic range, body size, behavior, genomic traits, and various environmental characteristics have been implicated in rates of evolution. Here we examine how biotic and environmental characteristics influence rates of evolutionary divergence and apparent extinctions in the Atlanto–East Pacific Stomatopoda. We are aware of the diversity of levels at which evolutionary rates can be considered (Eldredge, 1982; Schopf, 1984a), and we restrict our discussion to rates of morphological evolution in extant stomatopods.

Scheltema (1971, 1977, 1978, 1979) and Shuto (1974) have shown that larval dispersal ability is associated with broad geographic ranges in both fossil and contemporary species of gastropods (but see Thresher and Brothers, 1985, for a counterexample in angelfishes). East and West Atlantic gastropods whose planktonic larvae frequently are collected in mid-oceanic areas resemble each other morphologically more than gastropods whose larvae do not frequently disperse into oceanic waters (Scheltema, 1972). Hansen (1978, 1980, 1982) and Jablonski and his co-workers (Jablonski and Valentine, 1981; Jablonski, 1982; Jablonski and Lutz, 1983) also have shown that species of gastropods and bivalves with dispersing larvae have broader geographic distributions, persist longer in the fossil record, and generally form fewer new species than those without planktonic larvae. Jablonski (1982) and Jablonski and Valentine (1983) suggest that shifts from planktotrophic to abbreviated development (e.g., due to extinction of particular clades) may alter the mechanisms as well as the rates of speciation, and that modes of larval development are better predictors of evolutionary rates and patterns (including the generation of evolutionary novelties) than are many aspects of adult ecology.

Characteristics of the habitat, perhaps in association with larval dispersal, may influence evolutionary rates, although there is considerable controversy over whether intrinsic (e.g., genomic) or extrinsic factors fuel evolutionary change (Stebbins, 1949; Lewin, 1984; Schopf, 1984b; Cronin, 1985). Gastropod and bivalve mollusks living in shallow, physically stressful, and potentially disturbed environments occur over broader geographic ranges, appear to have greater dispersal ability, and have persisted longer in the fossil record than species living at greater depths (Jackson, 1974, 1977; Jablonski, 1980; Jablonski and Valentine, 1981; but see Jablonski et al., 1983, for a discussion of the complexities of this issue). Species in shallow, warm, or tropical habitats are thought to have evolved more rapidly, or to have given rise to evolutionary novelties more frequently, than those in very deep, cold, or temperate environments (Kauffman, 1977; also see Vermeij, 1978; Jablonski et al., 1983). In addition, trophic position and predation, as well as competition, may accelerate rates of species turnover and divergence (Mayr, 1963; Stanley, 1973a, 1979;

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Jackson, 1977; Kauffman, 1977). Several groups of West Atlantic and East Pacific organisms (fishes, mollusks, crustaceans, polychaetes) living on hard substrates show greater taxonomic divergence (Rosenblatt, 1967; Vermeij, 1978) and possibly suffer more intense predation and competition than those on soft substrates. It also has been argued that complex social behavior associated with small demes is a major contributor to rapid evolutionary change and speciation (Bush et al., 1977; Bush, 1981; see also discussion in Reaka and Manning, 1981). Raup (1986:1530) noted that "some aspects of organismal biology appear to be related to resistance to extinction. Large population size, broad geographic distribution, and high dispersal potential should help to protect species and higher taxa from extinction . . . ."

In addition, evolutionary divergence and extinction have been related to body size and morphological complexity. It is generally accepted that adaptive breakthroughs occur at small body size, that species within lineages tend to evolve toward larger body sizes (or away from small body sizes), and that extinctions often occur in large, structurally specialized lineages (see Simpson, 1944; Newell, 1949; Stanley, 1973b). Compared to other groups (e.g., the decapod crustaceans), the Order Stomatopoda is relatively homogeneous morphologically, with small and large members of all superfamilies conforming to one basic body plan. Thus, we avoid the bias of differential morphological complexity, where greater numbers of characters can be measured in taxa that are relatively more complex morphologically, and where less change thus is artificially inferred in morphologically simple lineages (Schopf et al., 1975; Eldredge, 1982).

Predictions of Evolutionary Rates

Our purpose here is specifically to investigate the relationship of body size, larval characteristics, and habitat to evolutionary rates in stomatopod Crustacea. The stomatopods or mantis shrimps represent an ancient order of crustacean carnivores. Several lineages (Bathysquillidae, Harpiosquillidae, Squillidae, Lysiosquillidae, Erythrosquillidae, Nannosquillidae, Eurysquillidae, and Pseudosquillidae) possess a toothed raptorial maxilliped that is used to smash, grasp, or spear relatively soft-bodied prey. Other lineages (Coronididae, Hemisquillidae, Gonodactylidae, Protosquillidae, and Odontodactylidae), have a hammer-like maxilliped that is used to smash prey (bivalves, gastropods, barnacles, and other crustaceans; see Holthuis and Manning, 1969; Caldwell and Dingle, 1975; Manning, 1980; Reaka and Manning, 1981; Reaka, in press). This raptorial maxilliped also is used in potentially lethal intraspecific and interspecific combat, usually in association with defense or acquisition of a burrow. Previous work on coral-dwelling mantis shrimps has shown that, in general, the size and number of eggs, growth rates, and aggressive levels increase with species body size (Reaka, 1978, 1979a,b). In addition, the extent of the geographic range and probable dispersal ability increase with body size among species in this guild (Reaka, 1980).

Storms and disturbances frequently affect stomatopods (Reaka, 1980, 1985). Local catastrophes, however, are unlikely to affect the entire geographic range of a species, particularly for widely distributed taxa (see Shuto, 1974; Endean, 1976; Scheltema, 1977; Connell, 1978). Following a local disturbance, larger species of coral-dwelling stomatopods should be able to recolonize a locally disturbed area more rapidly than smaller species because of their life history characteristics (Reaka, 1979a, 1980).

Thus, larger species with broad geographic ranges should show greater larval exchange and lower rates of extinction, as well as lower rates of phyletic change, than small species. Because of their small geographic ranges and apparently low dispersal abilities, populations of small species are more likely to be isolated; thus, small species of stomatopods may speciate more rapidly as well as suffer higher rates of extinction than large species. More small than large coral-dwelling species are known, and small species show some tendencies for ecological innovations (Reaka, 1980; Reaka and Manning, 1980; and below).

We will examine the following hypotheses: (1) large species of stomatopods have lower rates of morphological and taxonomic divergence among geographic subregions than small species; (2) species with large, long-lived planktonic larvae have lower rates of divergence among geographic subregions than those with small, short-lived larvae; (3) species from level bottom habitats have low rates of divergence among subregions compared to those from rocky or coral rubble environments; (4) species from deep or cold habitats have lower rates of divergence than those living in warm or shallow environments; and (5) species from temperate latitudes have lower rates of divergence than those from the tropics. Although fraught with obvious difficulties, we examine the problem of differential extinction in these different groups of stomatopods in different habitats and zoogeographic subregions as well. We previously have reviewed the behavior of stomatopods as now known, and have tested the hypothesis that rates of evolution are correlated with complexity of behavior (Reaka and Manning, 1981). Since that time we have compiled considerable newly available data, and analyses of these results are presented here.

THE STUDY AREA

We have chosen to examine most intensively the Atlanto–East Pacific stomatopods. Their taxonomy is relatively well known (Manning, 1969a; 1970a,b; 1971c; 1972a,c; 1974a; 1977a). Information on the size of settling larvae in a number of species (providing an estimate of duration of planktonic life, discussed in more detail below) is available for comparisons among species. Furthermore, these species occur in a variety of habitats and depths, and their field distributions are relatively well documented compared to many other groups. Many species and generic lineages of stomatopods span the Atlanto–East Pacific region, and we examine the incidence of taxonomic and morphological divergence as well as conspicuous gaps in expected distributions in the East Pacific vs. West Atlantic vs. East Atlantic subregions to obtain a quantitative estimate of evolution in lineages with different biotic or environmental characteristics.

Affinities between West Atlantic and East Pacific faunas provide insights for rates of divergence, since these regions have been separated by the Central American isthmus since the Pliocene, about 3.1 to 3.5 million years ago (Keigwin, 1978, 1982). Consideration of evolutionary divergence, speciation, and extinction in lineages that have been isolated for this period is especially appropriate, since various workers have estimated that the mean species durations of most animal groups range from 0.5–25 (usually <5) million years (Schopf, 1984a). Lessios (1979, 1981) has compared biochemical and morphological variation in geminate species pairs of sea urchins (*Diadema, Eucidaris,* and *Echinometra*) on each side of the Central American isthmus. He found that East Pacific and West Atlantic populations of the smaller rock-boring *Echinometra* have diverged more extensively in both biochemical and morphological traits than have those of *Diadema.* Even in *D. mexicanum* and *D. antillarum,* however, the lunar spawning cycles have diverged so that these species would be reproductively isolated if they were to come into contact again (Lessios, 1984). Whereas the data from Lessios' study suggest that protein molecules do not evolve at a constant rate in different sea urchin taxa, Vawter et al. (1980) reported relatively consistent patterns of divergence in the electrophoretic attributes of 10 pairs of fish populations on each side of Central America. Based upon the "molecular clock," the latter authors estimated that these fish populations had been separated about 3.9 (range 2.5–6.8) million years ago, a figure that agrees well with the geological record.

The East Atlantic and East Pacific faunas also have been separated since the Pliocene and have been partially isolated since continental divergence between the Late Triassic and Middle Jurassic 200–150 million years ago (Phillips and Forsyth, 1972). Species that occur in the East Atlantic and East Pacific (but not in the West Atlantic), in the West Atlantic and Indo–West Pacific (but not in the East Pacific), and in the Americas and Indo–West Pacific (but not in the East Atlantic) can provide insights for patterns of extinction in these regions if these data are carefully scrutinized for alternative interpretations.

Thus, we examine the degree of taxonomic divergence and possible extinctions within lineages that span different zoogeographic subregions as indicators of rates of evolution in organisms that possess different biotic characteristics and occupy different types of environments. While fossil evidence on these issues would be exceptionally valuable, the inadequacy of the fossil record for many groups of animals and the numerous critical biases in the nature of fossil evidence (e.g., Gingerich, 1983; Schopf, 1984a) would never allow testing of the detailed hypotheses presented above with the large sample sizes and statistical rigor that we use here. Thus, while our results at this time are restricted to rates of morphological change, they provide valuable new insights, not otherwise obtainable, into the factors that mold evolutionary change at this level, and they provide justified hypotheses for further research using paleontological or other methods on this or other groups of organisms.

THE FOSSIL RECORD

The stomatopods are known but relatively sparsely represented in the fossil record. Lineages leading to the subclass Hoplocarida probably diverged from other malacostracan Crustacea as early as the Devonian (Schram, 1969a,b, 1977, 1979a, 1981, 1982; Reaka, 1975; Kunze, 1983; Dahl, 1983). Schram (1977) reports that the hoplocarids had a well-established Laurentian range by the Late Carboniferous period. Following the breakup of Pangea in the Permian, many crustacean groups became extinct or were restricted to deep sea or fresh water (Gondwana) refugia. The only Late Paleozoic group of malacostracans that persisted and radiated were the stomatopod hoplocaridans; Schram (1977) attributes their success in part to the unique specialization of their raptorial claw.

Members of the Orders Aeschronectida (*Kallidecthes, Aratidecthes, Joanellia, Crangopsis, Aenigmacaris*), Paleostomatopoda (*Perimecturus, Bairdops, Archaeocaris*), and Stomatopoda (*Tyrannophontes theridion* Schram, a primitive species linking the paleostomatopods and the stomatopods; and *Gorgonophontes peleron* Schram) were present in North America and Britain during the Carboniferous period (Schram, 1969a,b, 1979a,b,c, 1984; F. Schram and J. Schram, 1979, J. Schram and F. Schram, 1979; Factor and Feldmann, 1985). Schram (1979c) indicates that the paleostomatopods, which possessed subchelate claws, were the dominant carnivores in the Lower Carboniferous of Mazon Creek. However, they became less abundant, occurring together with the tyrannophontid stomatopods, by the Middle Carboniferous. By the Upper Carboniferous, the tyrannophontids, with their raptorial claws, were the only active carnivores in this habitat. The natant, filter feeding aeschronectids also apparently became extinct during this time.

The fossil stomatopod family Sculdidae is known from the Upper Jurassic (three species of *Sculda* in Bavaria; Holthuis and Manning, 1969). In contrast to the two segmented exopod of all living stomatopods (except for one species of the extant Bathysquillidae, *Indosquilla manihinei* Ingle and Merrett (1971), in which the distal segment is separated from the proximal by an indistinct suture), the sculdids possessed an undivided uropodal exopod. The Sculdidae persisted at least as long as the Cretaceous (*Sculda, Pseudosculda*) and possibly into the Eocene. Members of all three major Recent superfamilies (Squilloidea, Gonodactyloidea, Lysiosquilloidea) appeared as early as the Cretaceous; because of their apparent ancient derivation, the bathysquillids were likely present also. In addition to *Sculda* and *Pseudosculda, Squilla cretacea* Schlüter, *Squilla angolia* (Berry), and a stomatopod previously misidentified as an eryonid decapod are known from the Cretaceous of West Germany, Angola, and Israel, respectively (Holthuis and Manning, 1969). Schram (1968) described a gonodactylid, *Paleosquilla brevicoxa,* from the Cretaceous of Colombia, and Förster (1982) recently described a lysiosquillid, *Lysiosquilla nkporoensis,* from the early Maestrichtian (late Cretaceous) of Nigeria. *Squilla antiqua* Münster and *S. wetherellii* Woodward have been found in Eocene rocks from northern Italy and England, respectively. Holthuis and Manning (1969) suggest that *S. cretacea* and *S. antiqua* do not represent the genus *Squilla* but may belong to the Sculdidae. Förster (1982) also described a clearly defined squillid, *Squilla hollandi,* and a pseudosquillid, *Pseudosquilla wulfi,* from the late Eocene of northern Germany. Interestingly, all of Förster's Cretaceous and Eocene specimens were recovered from sediments of shallow tropical-subtropical seas, the predominant habitat of modern stomatopods. In addition, *?Squilla miocenica* Lovisato and *Squilla sonomana* (Rathbun) are recorded from Spain (Miocene) and California (probably Pliocene), respectively (Holthuis and Manning, 1969). These data must be interpreted cautiously, however, since several authors have registered doubt about the generic and familial affinities of many of the stomatopods in the fossil record (Holthuis and Manning, 1969; Förster, 1982).

The eyes of stomatopods, which have been demonstrated to be different in members of each superfamily (Manning et al., 1984a,b), also suggest that the currently recognized lineages were differentiated very early in the history of the group. The eyes are far more diverse within the stomatopods, comprising about 400 Recent species, than they are in the Decapoda, comprising more than 10,000 species (see Fincham, 1980).

DISTRIBUTION PATTERNS OF STOMATOPODS

World-wide Distribution Patterns

The Stomatopoda generally are tropical shallow water organisms. Some genera, especially *Hemisquilla* and *Pterygosquilla* (see Manning, 1977a), and some species of other genera, such as *Heterosquilla, Heterosquilloides, Platysquilla,* and *Platysquilloides* (see Manning, 1969a, 1977a) are warm or cold temperate organisms, occurring in or frequenting latitudes above 30° N or S. Others, such as species of *Bathysquilla* (see Manning, 1969a), are found in outer shelf or upper slope habitats. The vast majority of stomatopods, however, live in relatively shallow tropical habitats.

As pointed out by Manning (1977a:161), the stomatopods "provide good examples of Tethyan distribution patterns as described by Ekman," who (1953:11) distinguished two main warm water regions of the marine shelf faunas. The larger Indo–West Pacific region was comprised of the area from the western Indian Ocean (including the Red Sea) eastward to the oceanic islands of the Pacific, Hawaii, the Marquesas, and the Tuamotus. The smaller Atlanto–East Pacific region included American and West African subregions. In contrast, Briggs (1974:13) recognized four major zoogeographic regions: the Indo–West Pacific, Eastern Pacific, Western Atlantic, and Eastern Atlantic.

The Stomatopoda support the recognition of two major marine zoogeographic regions, as proposed by Ekman, rather than the four recognized by Briggs. The distribution patterns of three taxa representing three distinct lineages within the Atlanto–East Pacific region provides the strongest evidence for recognizing the Atlanto–East Pacific as a major region distinct from the Indo–West Pacific. The squilloid *Squilla aculeata* is represented in the East Atlantic and East Pacific subregions by distinct subspecies, but it does not occur in the West Atlantic. Similarly, the gonodactyloid and lysiosquilloid genera *Pseudosquillopsis* and *Coronida* each are represented by related species in the East Atlantic and the East Pacific, but neither genus is known in the West Atlantic. The Atlanto–East Pacific region is considered to be a unit herein, comprising distinct East Atlantic, West Atlantic, and East Pacific subregions.

The distribution patterns of families and genera of Stomatopoda are summarized in Tables 1 and 2 (see also Manning, 1980). Of 76 currently recognized genera, 59 are represented in the Indo–West Pacific region, and 39 or 51% of all genera are endemic there. In particular, 88% of all gonodactylid, 75% of all protosquillid, and 59% of all squillid genera are endemic to the Indo–West Pacific. Thirty-seven genera are known in the Atlanto–East Pacific region, and 17 or 22% of all genera are endemic there. The Nannosquillidae are notable in this region because 88% of all nannosquillid genera are endemic there. Twenty genera are shared by the two regions. Three of the most species-rich genera, each containing more than 20 species, are largely or entirely restricted to one of the two regions: within the squillids, *Squilla* (27 species or subspecies) occurs only in the Atlanto–East Pacific, while *Oratosquilla* (with 33 species; Manning, 1978d) and *Clorida* (including about 27 species) are (with one exception) restricted to the Indo–West Pacific region. Within the lysiosquilloids, *Nannosquilla*

TABLE 1.—Numbers of genera within families of Stomatopoda in different zoogeographic regions (AEP = Atlanto–East Pacific; IWP = Indo–West Pacific).

Family	AEP genera	AEP endemic genera	Genera in both AEP and IWP	IWP genera	IWP endemic genera	Total no. genera
Bathysquilloidea						
Bathysquillidae	1	0	1	3	2	3
Gonodactyloidea						
Eurysquillidae	2	0	2	5	3	5
Gonodactylidae	1	0	1	8	7	8
Hemisquillidae	1	0	1	1	0	1
Odontodactylidae	1	0	1	1	0	1
Protosquillidae	1	1	0	3	3	4
Pseudosquillidae	3	1	2	3	1	4
Lysiosquilloidea						
Coronididae	3	2	1	2	1	4
Erythrosquillidae	0	0	0	1	1	1
Lysiosquillidae	5	1	4	4	0	5
Nannosquillidae	8	7	1	5	4	12
Squilloidea						
Harpiosquillidae	0	0	0	1	1	1
Squillidae	11	5	6	22	16	27
Totals	37	17	20	59	39	76

(comprising 20 species) is restricted to the Americas; species are subregionally distinct there. Within the gonodactyloids, species of *Gonodactylus* (45 species) occur in both major regions, but Indo–West Pacific and American lineages are distinct, and no species occurs in both major regions. Species of *Gonodactylus* also are subregionally distinct in the Americas, with no species occurring on both sides of the Americas.

Although all stomatopods have pelagic larvae (Provenzano and Manning, 1978), their larvae in general do not appear to disperse outside of their subregion. For example, of approximately 250 species of stomatopods found in the Indo–West Pacific, few (possibly only *Clorida mauiana*; Manning, 1976b) Indo–West Pacific stomatopods have crossed the East Pacific barrier (Briggs, 1974:102). Four otherwise circumtropical species (*Pseudosquilla ciliata, P. oculata, Alima hieroglyphica, A. hyalina*) have not successfully traversed this barrier; the only stomatopod known to occur in all four world oceans is the lysiosquillid *Heterosquilloides mccullochae*. Of approximately 400 species of stomatopods known, only seven (*Odontodactylus brevirostris, Pseudosquilla ciliata, P. oculata, Heterosquilloides mccullochae, Alima hieroglyphica, A. hyalina, Bathysquilla microps*) are shared by the tropical Indo–West Pacific and the Atlantic. Furthermore, little exchange has occurred even between the East and West Atlantic. No members of the genera *Gonodactylus* and *Nannosquilla*, each represented by numerous species in the West Atlantic and East Pacific, are known from the East Atlantic. Of the 30 species and subspecies occurring in the East Atlantic and the 78 species and subspecies known from the West Atlantic, only 5 (*Pseudosquilla ciliata, P. oculata, Heterosquilloides mccullochae, Alima hieroglyphica, A. hyalina*) are shared, and all five also occur in the Indo–West Pacific. For the stomatopods, both the East Pacific and the mid-Atlantic barriers described by Briggs (1974:102, 109) are real.

Atlanto–East Pacific Distribution Patterns

The kind of analysis presented here can be made only for groups in which the systematics are relatively well known. The systematics of few, if any, other tropical marine invertebrate groups with pelagic larvae are as well known in the Atlanto–East Pacific region as the stomatopods. The systematics of the Atlantic stomatopods have been reported in two basic monographs, one including the West Atlantic species (Manning, 1969a) and a second for the East Atlantic species (Manning, 1977a). The East Pacific species, although not monographed so far, are almost as well known. The Atlanto–East Pacific stomatopods are listed by subregion in Table 3.

LARVAL-POSTLARVAL STAGES AND DISPERSAL

Although stomatopods produce larvae whose planktonic phase varies from approximately one to many months (Provenzano and Manning, 1978; Pyne, 1972), dispersal among different geographic subregions appears to be relatively rare, as is shown by their distribution patterns (discussed above). As noted for coral reef fishes by Brothers and Thresher (1985), breadth of distribution may not correlate with the duration of pelagic developmental stages. Diurnal

TABLE 2.—Distribution patterns of all Stomatopod genera (EP = East Pacific; WA = West Atlantic; EA = East Atlantic; IWP = Indo-West Pacific; total numbers of taxa within each genus are given in parentheses).

Taxon	EP	WA	EA	IWP
BATHYSQUILLOIDEA				
BATHYSQUILLIDAE				
Altosquilla (1)	–	–	–	1
Bathysquilla (2)	–	1	–	2
Indosquilla (1)	–	–	–	1
GONODACTYLOIDEA				
EURYSQUILLIDAE				
Coronidopsis (3)	–	–	–	3
Eurysquilla (10)	2	4	2	2
Eurysquilloides (1)	–	–	–	1
Manningia (9)	–	–	1	8
Sinosquilla (2)	–	–	–	2
GONODACTYLIDAE				
Gonodactyloideus (1)	–	–	–	1
Gonodactylolus (1)	–	–	–	1
Gonodactylopsis (2)	–	–	–	2
Gonodactylus (45)	8	11	–	26
Hoplosquilla (1)	–	–	–	1
Hoplosquilloides (1)	–	–	–	1
Mesacturoides (2)	–	–	–	2
Mesacturus (5)	–	–	–	5
HEMISQUILLIDAE				
Hemisquilla (4)	2	1	–	1
ODONTODACTYLIDAE				
Odontodactylus (5)	–	1	–	5
PROTOSQUILLIDAE				
Chorisquilla (10)	–	–	–	10
Echinosquilla (1)	–	–	–	1
Haptosquilla (14)	–	–	–	14
Protosquilla (2)	–	–	2	–
PSEUDOSQUILLIDAE				
Faughnia (3)	–	–	–	3
Parasquilla (5)	1	3	1	–
Pseudosquilla (8)	1	2	2	7
Pseudosquillopsis (4)	2	–	1	1
LYSIOSQUILLOIDEA				
CORONIDIDAE				
Acoridon (1)	–	1	–	–
Coronida (3)	2	–	1	–
Neocoronida (3)	1	–	–	2
Parvisquilla (3)	–	–	–	3
ERYTHROSQUILLIDAE				
Erythrosquilla (1)	–	–	–	1
LYSIOQUILLIDAE				
Heterosquilla (3)	1	2	–	1
Heterosquilloides (9)	2	3	1	5
Lysiosquilla (12)	2	3	2	5
Lysiosquilloides (2)	–	–	1	1
Tectasquilla (1)	–	1	–	–
NANNOSQUILLIDAE				
Acanthosquilla (12)	2	2	1	9
Allosquilla (1)	–	–	1	–
Austrosquilla (2)	–	–	–	2
Coronis (1)	–	1	–	–
Hadrosquilla (2)	–	–	–	2
Keppelius (1)	–	–	–	1
Mexisquilla (1)	–	1	–	–
Nannosquilla (20)	7	13	–	–
Nannosquilloides (1)	–	–	1	–
Platysquilla (1)	–	–	1	–
Platysquilloides (2)	–	1	1	–
Pullosquilla (3)	–	–	–	3
SQUILLOIDEA				
HARPIOSQUILLIDAE				
Harpiosquilla (10)	–	–	–	10
SQUILLIDAE				
Alima (4)	–	2	2	4
Alimopsis (1)	–	–	–	1
Anchisquilla (2)	–	–	–	2
Anchisquilloides (1)	–	–	–	1
Areosquilla (3)	–	–	–	3
Busquilla (2)	–	–	–	2
Carinosquilla (2)	–	–	–	2
Clorida (27)	1	–	–	27
Cloridopsis (7)	1	1	–	6
Crenatosquilla (1)	1	–	–	–
Dictyosquilla (1)	–	–	–	1
Distosquilla (1)	–	–	–	1
Fennerosquilla (1)	–	1	–	–
Kempina (3)	–	–	–	3
Lenisquilla (4)	–	–	–	4
Leptosquilla (1)	–	–	–	1
Levisquilla (2)	–	–	–	2
Lophosquilla (4)	–	–	–	4
Meiosquilla (7)	2	5	–	–
Natosquilla (1)	–	–	–	1
Oratosquilla (33)	–	–	1	33
Pterygosquilla (4)	2	1	1	1
Rissoides (5)	–	–	4	1
Schmittius (2)	2	–	–	–
Squilla (27)	8	16	3	–
Squilloides (2)	–	–	–	2
Tuleariosquilla (1)	–	–	–	1
Total (387)	50	77	30	249

migrations from benthic or near bottom habitats during the day into the water column at night (often with peaks just after sunset and before dawn) are known in many marine plankton communities (Emery, 1968; Alldredge and King, 1977, 1980; Porter et al., 1977; Hobson and Chess, 1978, 1979; Ohlhorst, 1982; Robichaux et al., 1981; Ohlhorst and Liddell, 1985). These local vertical migrations also have been observed extensively for stomatopod larvae (Reaka, unpublished data). Such behavioral patterns, in combination with reduced activity during periods of heavy wave action (Robichaux et al., 1981; Reaka, unpublished data), may well reduce the potential for long distance dispersal in many nearshore meroplankters such as stomatopod larvae (see also Thresher and Brothers, 1985, for fish larvae). The great variation in length of the larval period among stomatopod taxa, however, still provides a relative indicator of different potentials for dispersal among species. For example, larvae that persist in the plankton even in local habitats for a number of months undoubtedly are more likely to be carried away from local areas by currents than are larvae that are planktonic for no more than a month.

In the Stomatopoda, the postlarva is the transitional stage between the pelagic larval phase and the benthic adult phase. Morphologically, the postlarva is intermediate between the late larva and the adult; the rostral plate is jointed, the claw often is provided with teeth, and some of the spination and carination of the adults make their first appearance. Postlarvae often show enough adult characters so that they can be identified to species; most larval stages as yet can not be identified to species.

We use the size of the postlarva as an indication of the length of the larval period. Squillids and lysiosquillids, species of which are known to have as many as 8 or 9 pelagic instars and/or to persist in the plankton for a number of months, have considerably larger postlarvae than *Gonodactylus,* species of which are known to pass through only 4 pelagic stages in about a month (Giesbrecht, 1910; Komai and Tung, 1929; Gurney, 1937, 1946; Gohar and Al-Kholy, 1957; Alikunhi, 1944, 1950, 1952, 1967; Manning, 1962c; Manning and Provenzano, 1963; Michel, 1968 [1969], 1970; Pyne, 1972; Provenzano and Manning, 1978; Morgan and Provenzano, 1979; Reaka and Manning, 1981). Whereas the sizes of postlarvae vary dramatically among species (from 6–33 mm), the sizes of eggs vary relatively little (0.3–1.8 mm diameter) among groups of stomatopods (Reaka, 1979a; Williams et al., 1985). We presume that, in general, growth through more instars to these considerably larger terminal sizes imposes a longer planktonic feeding period than that required for larvae that settle at small sizes. We recognize that larvae of some species of stomatopods may grow more rapidly than those of other species, that growth rates and terminal sizes in some populations occasionally may be variable, that some species of stomatopods spend extended periods in the plankton yet settle at moderate sizes (see Alikunhi, 1944; Michel and Manning, 1972; and below), and that the tremendously diverse decapods may exhibit more heterogeneous relationships between larval and postlarval size and length of larval period (A. H. Hines, personal communication); however, our studies show that, in general, species of stomatopods with larger larval and postlarval sizes spend longer periods in the plankton before settling than do those with very small postlarvae. We treat this subject in greater detail in a separate publication (Reaka and Manning, in prep.).

METHODS

The body sizes, postlarval sizes, habitat affiliations, and phyletic affinities of stomatopods occurring in the Atlanto–East Pacific region are shown in Tables 4–7. Indo–West Pacific species are too numerous for detailed presentation and their body sizes and habitat characteristics generally are much less well known; thus, only Indo–West Pacific cognates of species in the Atlanto–East Pacific region are given. "Cognates" here indicates closely related, morphologically similar species in different geographical subregions or regions that apparently are derived from a common ancestor (see Manning (1969a, 1977a) for examples and discussion of morphological characters used to differentiate and establish relationships among species and genera). Many of the species thus identified have been validated repeatedly by observations on live animals (color pattern, courtship and mating behavior, habitat, and geographic field distributions), and the classification appears to represent natural phyletic relationships.

Body lengths are comparable measures of body size among lineages, since the empirical relationship between body volume and body length does not vary significantly among different groups of stomatopods. All measurements, taken either from the literature or our own records, are rounded to the nearest millimeter here. The sample size indicates the minimum number of animals measured, since published reports sometimes presented the body sizes of only the largest and smallest individuals; these were collated here simply as two individuals. Small sample sizes can provide erroneous estimates of body sizes of some species in given regions; however, our comparisons are drawn from relatively large numbers of species, and we treat only general trends in body size. We define species as small, moderate, or large if maximum body length of individuals is <50 mm, 50–149 mm, or ≥150 mm, respectively. The category of body size for each taxon that was used in our statistical analyses is given in the tables, so that the impact of future data upon our results and conclusions can be evaluated easily.

Similarly, Tables 4–7 provide the known range of total body lengths for postlarvae in each taxon. These are categorized as small (<10 mm), moderate (10–19 mm), and large (≥20 mm). While the pelagic larva sometimes can be considerably larger than the settling postlarva (e.g., a 30 mm larva of *Alima hieroglyphica* settled as a 17 mm postlarva; Alikunhi, 1944), the size of a postlarva (double asterisk in Tables 4–7) usually is smaller than that of a juvenile (single asterisk in Tables 4–7), so that the postlarval size category could be estimated in a number of cases (e.g., as small in *Gonodactylus zacae,* where a 8 mm juvenile is known). Also, sizes of postlarvae are remarkably consistent among related species within a lineage, and usually conform to a single size category within the entire genus. For example, all known postlarvae within *Gonodactylus* and within *Protosquilla* are small, all those known for *Meiosquilla* are moderately sized, and all those known for *Parasquilla, Pseudosquillopsis,* and *Lysiosquilla* are large. Consequently, it is possible to estimate the sizes of postlarvae (category in parentheses in Tables 4–

TABLE 3.—Stomatopod Crustacea known from the Atlanto-East Pacific region (EP = East Pacific, WA = West Atlantic, FA = East Atlantic; + indicates present, dash indicates absent, parentheses indicate questionable records).

Taxon	EP	WA	EA
BATHYSQUILLOIDEA Manning, 1967			
BATHYSQUILLIDAE Manning, 1967			
Bathysquilla microps (Manning, 1961)	–	+	–
GONODACTYLOIDEA Giesbrecht, 1910			
EURYSQUILLIDAE Manning, 1977			
Eurysquilla chacei Manning, 1969	–	+	–
Eurysquilla galatheae Manning, 1977	–	–	+
Eurysquilla holthuisi Manning, 1969	–	+	–
Eurysquilla leloeuffi Manning, 1977	–	–	+
Eurysquilla maiaguesensis (Bigelow, 1901)	–	+	–
Eurysquilla plumata (Bigelow, 1901)	–	+	–
Eurysquilla solari Manning, 1970	+	–	+
Eurysquilla veleronis (Schmitt, 1940)	+	–	–
Manningia posteli Manning, 1977	–	–	+
GONODACTYLIDAE Giesbrecht, 1910			
Gonodactylus albicinctus Manning and Reaka, 1979	+	–	–
Gonodactylus austrinus Manning, 1969	–	+	–
Gonodactylus bahiahondensis Schmitt, 1940	+	–	–
Gonodactylus bredini Dingle, 1969	–	+	–
Gonodactylus costaricensis Manning and Reaka, 1979	+	–	–
Gonodactylus curacaoensis Schmitt, 1924	–	+	–
Gonodactylus festae Nobili, 1901	+	–	–
Gonodactylus lacunatus Manning, 1966	–	+	–
Gonodactylus lalibertadensis Schmitt, 1940	+	–	–
Gonodactylus lightbourni Manning and Hart, 1981	–	+	–
Gonodactylus minutus Manning, 1969	–	+	–
Gonodactylus moraisi Fausto Filho and Lemos de Castro, 1973	–	+	–
Gonodactylus oerstedii Hansen, 1895	–	+	–
Gonodactylus petilus Manning, 1970	–	+	–
Gonodactylus pumilus Manning, 1970	+	–	–
Gonodactylus spinulosus Schmitt, 1924	–	+	–
Gonodactylus stanschi Schmitt, 1940	+	–	–
Gonodactylus torus Manning, 1969	–	+	–
Gonodactylus zacae Manning, 1972	+	–	–
HEMISQUILLIDAE Manning, 1980			
Hemisquilla braziliensis (Moreira, 1903)	–	+	–
Hemisquilla ensigera californiensis Stephenson, 1977	+	–	–
Hemisquilla ensigera ensigera (Owen, 1832)	+	–	–
ODONTODACTYLIDAE Manning, 1980			
Odontodactylus brevirostris (Miers, 1884)	–	+	–
PROTOSQUILLIDAE Manning, 1980			
Protosquilla calypso Manning, 1974	–	–	+
Protosquilla folini (A. Milne Edwards, 1867)	–	–	+
PSEUDOSQUILLIDAE Manning, 1977			
Parasquilla boschii Manning, 1970	–	+	–
Parasquilla coccinea Manning, 1962	–	+	–
Parasquilla ferussaci (Roux, 1830)	–	–	+
Parasquilla meridionalis Manning, 1961	–	+	–
Parasquilla similis Manning, 1970	+	–	–
Pseudosquilla adiastalta Manning, 1964	+	–	–
Pseudosquilla ciliata (Fabricius, 1787)	–	+	+
Pseudosquilla oculata (Brullé, 1837)	–	+	+
Pseudosquillopsis cerisii (Roux, 1828)	–	–	+
Pseudosquillopsis lessonii (Guérin, 1830)	+	–	–
Pseudosquillopsis marmorata (Lockington, 1877)	+	–	–
LYSIOSQUILLOIDEA Giesbrecht, 1910			
CORONIDIDAE Manning, 1980			
Acoridon manningi Adkison, Heard, and Hopkins, 1983	–	+	–
Coronida bradyi (A. Milne Edwards, 1869)	–	–	+
Coronida glasselli Manning, 1976	+	–	–
Coronida schmitti Manning, 1976	+	–	–
Neocoronida cocosiana (Manning, 1972)	+	–	–
LYSIOSQUILLIDAE Giesbrecht, 1910			
Heterosquilla platensis (Berg, 1900)	–	+	–
Heterosquilla polydactyla (von Martens, 1881)	+	+	–
Heterosquilloides armata (Smith, 1881)	–	+	–
Heterosquilloides insolita (Manning, 1963)	(+)	+	–
Heterosquilloides mccullochae (Schmitt, 1940)	+	+	+
Lysiosquilla campechiensis Manning, 1962	–	+	–
Lysiosquilla desaussurei (Stimpson, 1857)	+	–	–
Lysiosquilla glabriuscula (Lamarck, 1818)	–	+	–
Lysiosquilla hoevenii (Herklots, 1851)	–	–	+
Lysiosquilla monodi Manning, 1977	–	–	+
Lysiosquilla panamica Manning, 1971	+	–	–
Lysiosquilla scabricauda (Lamarck, 1818)	–	+	–
Lysiosquilloides aulacorhynchus (Cadenat, 1957)	–	–	+
Tectasquilla lutzae Adkison and Hopkins, 1984	–	+	–
NANNOSQUILLIDAE Manning, 1980			
Acanthosquilla biminiensis (Bigelow, 1893)	+	+	–
Acanthosquilla digueti (Coutière, 1905)	+	+	–

7) in a number of taxa for which the pattern of postlarval sizes within the lineage (e.g., those connected by horizontal or vertical lines in Tables 4–7) was clear. The sizes of postlarvae are known in 39 Atlanto–East Pacific taxa, and we either know or can reliably estimate the sizes for 121 taxa. We document both known and estimated size categories for each taxon in the tables so that the reader can evaluate our conclusions as new information becomes available.

Types of substrate are categorized as "coarse bottom" (coral, rock, coralline algal mat) and "level bottom" (mud, sand, sometimes mixed with shell). Depths are defined as "shallow" (where the species is recorded only from depths <100 m), "moderate" (100–300 m), or "deep" (>300 m). These depth categories differ from those used in Reaka (1980), where finer subdivisions of depth distribution were analyzed for coral-dwelling stomatopods. Latitudinal distributions are classified as "tropical" and "temperate". Tropi-

TABLE 3.—Continued.

Taxon	EP	WA	EA
Acanthosquilla septemspinosa (Miers, 1881)	–	–	+
Allosquilla africana (Manning, 1970)	–	–	+
Coronis scolopendra Latreille, 1828	–	+	–
Mexisquilla horologii (Camp, 1971)	–	+	–
Nannosquilla adkisoni Camp and Manning, 1982	–	+	–
Nannosquilla anomala Manning, 1967	+	–	–
Nannosquilla antillensis (Manning, 1961)	–	+	–
Nannosquilla baliops Camp and Manning, 1982	–	+	–
Nannosquilla californiensis (Manning, 1961)	+	–	–
Nannosquilla canica Manning and Reaka, 1979	+	–	–
Nannosquilla carolinensis Manning, 1970	–	+	–
Nannosquilla chilensis (Dahl, 1954)	+	–	–
Nannosquilla dacostai Manning, 1970	–	+	–
Nannosquilla decemspinosa (Rathbun, 1910)	+	–	–
Nannosquilla galapagensis Manning, 1972	+	–	–
Nannosquilla grayi (Chace, 1958)	–	+	–
Nannosquilla hancocki (Manning, 1961)	–	+	–
Nannosquilla heardi Camp and Manning, 1982	–	+	–
Nannosquilla schmitti (Manning, 1962)	–	+	–
Nannosquilla similis Manning, 1972	+	–	–
Nannosquilla taguensis Camp and Manning, 1982	–	+	–
Nannosquilla taylori Manning, 1969	–	+	–
Nannosquilla vasquezi Manning, 1979	–	+	–
Nannosquilla whitingi Camp and Manning, 1982	–	+	–
Nannosquilloides occultus (Giesbrecht, 1910)	–	–	+
Platysquilla eusebia (Risso, 1816)	–	–	+
Platysquilloides enodis (Manning, 1962)	–	+	–
Platysquilloides lillyae (Manning, 1977)	–	–	+
SQUILLOIDEA Latreille, 1803			
SQUILLIDAE Latreille, 1803			
Alima hieroglyphica (Kemp, 1911)	–	+	+
Alima hyalina (Leach, 1817)	–	+	+
Clorida mauiana (Bigelow, 1931)	+	–	–
Cloridopsis dubia (H. Milne Edwards, 1837)	+	+	–
Crenatosquilla oculinova (Glassell, 1942)	+	–	–
Fennerosquilla heptacantha (Chace, 1939)	–	+	–
Meiosquilla dawsoni Manning, 1970	+	–	–
Meiosquilla lebouri (Gurney, 1946)	–	+	–
Meiosquilla quadridens (Bigelow, 1893)	–	+	–
Meiosquilla randalli (Manning, 1962)	–	+	–
Meiosquilla schmitti (Lemos de Castro, 1955)	–	+	–
Meiosquilla swetti (Schmitt, 1940)	+	–	–
Meiosquilla tricarinata (Holthuis, 1941)	–	+	–
Oratosquilla massavensis (Kossmann, 1880)	–	–	+
Pterygosquilla armata armata (H. Milne Edwards, 1837)	+	+	–
Pterygosquilla armata capensis Manning, 1969	–	–	+
Pterygosquilla gracilipes (Miers, 1881)	+	–	–
Rissoides africanus (Manning, 1974)	–	–	+
Rissoides calypso (Manning, 1974)	–	–	+
Rissoides desmaresti (Risso, 1816)	–	–	+
Rissoides pallidus (Giesbrecht, 1910)	–	–	+
Schmittius peruvianus Manning, 1972	+	–	–
Schmittius politus (Bigelow, 1891)	+	–	–
Squilla aculeata aculeata Bigelow, 1893	+	–	–
Squilla aculeata calmani Holthuis, 1959	–	–	+
Squilla biformis Bigelow, 1891	+	–	–
Squilla bigelowi Schmitt, 1940	+	–	–
Squilla brasiliensis Calman, 1917	–	+	–
Squilla cadenati Manning, 1970	–	–	+
Squilla caribaea Manning, 1969	–	+	–
Squilla chydaea Manning, 1962	–	+	–
Squilla deceptrix Manning, 1969	–	+	–
Squilla decimdentata Manning, 1970	–	+	–
Squilla discors Manning, 1962	–	+	–
Squilla edentata australis Manning, 1969	–	+	–
Squilla edentata edentata (Lunz, 1937)	–	+	–
Squilla empusa Say, 1818	–	+	–
Squilla grenadensis Manning, 1969	–	+	–
Squilla hancocki Schmitt, 1940	+	–	–
Squilla intermedia Bigelow, 1893	–	+	–
Squilla lijdingi Holthuis, 1959	–	+	–
Squilla mantis (Linnaeus, 1758)	–	–	+
Squilla mantoidea Bigelow, 1893	+	–	–
Squilla neglecta Gibbes, 1850	–	+	–
Squilla obtusa Holthuis, 1959	–	+	–
Squilla panamensis Bigelow, 1891	+	–	–
Squilla parva Bigelow, 1891	+	–	–
Squilla prasinolineata Dana, 1852	–	+	–
Squilla rugosa Bigelow, 1893	–	+	–
Squilla surinamica Holthuis, 1959	–	+	–
Squilla tiburonensis Schmitt, 1940	+	–	–
Total	50	78	30

cal species are defined as those which occur at any depth within the latitudes where reef coral is known to grow ($\geq 20°$ C surface temperature, although note that this definition is delimited by latitude rather than temperature, since all depths, i.e., even cold deep waters, are included). Temperate species are those that occur at any depth outside of tropical latitudes or whose ranges extend into temperate latitudes. (Thus, species which also are recorded in tropical localities but extend into high latitudes will be classified as temperate, whereas species categorized as tropical do not extend into high latitudes.) Warm environments are categorized here as those in tropical latitudes at shallow or moderate depths; species that live in temperate regions or in deep tropical water are classified as inhabiting cold environments.

We analyzed our data in $r \times k$ contingency tables as explained in Tables 8 and 10 or the text; $p \leq 0.05$ is used as the criterion of statistical significance, although instances of $p < 0.10$ are brought to the reader's attention in the text. We tested the relationship of biotic and environmental characteristics to four different measures of affinity to relatives elsewhere and endemicity or local species radiation. Taxa were scored as either having (+1) or not having (+0) relatives (conspecifics, cognates) in another subregion, even though a given taxon may be related to several different cognates in different subregions. To avoid possible bias, we repeated the analysis presented in Table 8 when the total number of relatives in other subregions were summed for each of the categories in Table 8, but the statistical results were essentially unchanged from those presented here. In addition, the relationship of biotic and environmental characteristics to the number of endemic species without cognates elsewhere was tested. We also tested the number of endemic species alone, regardless of whether or not cognates were present in other subregions; however, the results were not essentially different from those presented in Table 8. These several tests, available upon request from the authors, showed that different analytical approaches yielded essentially the same results as presented here.

ACKNOWLEDGMENTS

We thank Roy L. Caldwell of the University of California at Berkeley; Roger F. Cressey, Jr., and Anson H. Hines, Jr., of the Smithsonian Institution; Geerat J. Vermeij and Roy K. Kropp of the University of Maryland; and David K. Camp of the Florida Department of Natural Resources, all of whom either contributed valuable discussions or provided constructive criticism on earlier drafts of the manuscript. This research was supported by the Smithsonian Institution under a grant from its Scholarly Studies Program (to RBM) and by grants from the NSF (Biological Oceanography) and NOAA (Undersea Research Program) (to MLR). Space and facilities at the Museum of Comparative Zoology, Harvard University, were kindly made available by Professor E.O. Wilson while one of us (MLR) was on sabbatical leave there. This paper represents contribution number 161 from the Smithsonian Marine Station at Fort Pierce, Florida, and contribution number 158 from the West Indies Laboratory, St. Croix, U. S. Virgin Islands, where some of the work was completed. We gratefully acknowledge all of these sources of support.

GONODACTYLOIDEA

ODONTODACTYLIDAE, GONODACTYLIDAE, AND PROTOSQUILLIDAE

Within the study area, the superfamily Gonodactyloidea is represented by six families. Members of three relatively closely related families, the Odontodactylidae, Gonodactylidae, and Protosquillidae inhabit holes in or under coral rubble, rocks, coralline algae, or shells (Table 4). The first family includes one species of *Odontodactylus*, the second 19 species of *Gonodactylus*, and the third 2 species of *Protosquilla*. All representatives of these families possess smashing claws. Most of these coarse bottom species occupy shallow (less than 50 m) warm water habitats. Thus habitat is held relatively constant within the group, while genera and species vary in body size, and, in some cases, postlarval size. Three other families, treated below, include species that usually live in burrows on level bottoms of sand or mud.

ADULT BODY SIZE.—Species of *Odontodactylus* attain the largest sizes of stomatopods in this group of families, and one species of the genus, *O. brevirostris*, occurs in both the West Atlantic and the Indo-West Pacific (Table 4). Four other species of *Odontodactylus* (maximum lengths from 102–171 mm) are known from the Indo-West Pacific.

Gonodactylus and related genera, all of small or moderate body size (lengths up to 105 mm), include many more species and show considerably more regional divergence than *Odontodactylus*. All West Atlantic species of *Gonodactylus* have diverged at the species level from sibling lineages in the East Pacific (Table 4). Two main lineages, those with Bredini-type telsons (e.g., *G. bredini*, *G. zacae*) and those with Oerstedii-type telsons (e.g., *G. oerstedii*, *G. pumilus*), are found on both coasts of the Americas (Manning, 1969a, 1971c). Extensive radiation has occurred in the Oerstedii lineage in both the West Atlantic and the East Pacific, and species within each subregion are more closely related to each other than to species in the other subregion (e.g., *G. oerstedii–G. curacaoensis–G. torus–G. moraisi*; *G. festae–G. bahiahondensis–G. lalibertadensis–G. costaricensis–G. albicinctus*). All of the American *Gonodactylus* show major morphological differences from Indo-West Pacific lineages of this genus (Manning, 1969a, 1971c, 1977a). At least 26 species of *Gonodactylus* are present in the Indo-West Pacific.

In the East Atlantic, the endemic protosquillid genus *Protosquilla* (Table 4) is closely related to a small Indo-West Pacific relative, *Chorisquilla* (maximum lengths usually less than 50 mm). Comparisons among gonodactyloid genera from coarse substrates therefore are consistent with the hypothesis that lower rates of divergence are found in taxa of large rather than small body size.

POSTLARVAL SIZE.—Postlarvae are considerably larger and probably require longer planktonic periods in species of *Odontodactylus* (13–27 mm) than in species of *Gonodactylus* and *Protosquilla* (6–10 mm) (Manning, 1969a, 1977a; Provenzano and Manning, 1978; Table 4). Although we have classified the postlarvae of *O. brevirostris* from the Indo-West Pacific as large based on the median of the recorded range, the recorded postlarvae appear to fall into two size groups, and it is likely that these records include the young of two different species (Manning, 1969a); since we do not include Indo-West Pacific taxa in our statisitical analyses, however, this does not bias our results. Larvae of

TABLE 4.—Sizes, habitats, and taxonomic relationships for morphologically related families of Gonodactyloidea that occupy coarse habitats. In this and following tables, the size category (S = small, M = moderate, L = large; see text for further definition of these categories) of postlarvae (pl) is given beneath each species; parentheses around the size category indicate that postlarval size was estimated from juvenile size or a consistent pattern of postlarval size in closely related taxa (see text). The known size ranges (mm total length) of postlarvae (**) and juveniles (*) that were used to establish the postlarval size category follow. Where a range of postlarval sizes spans two categories, the median was used to assign the category (also see text for further discussion of postlarval size in *O. brevirostris*). On the second line beneath each species, the adult size (as) category is given (S = small, M = moderate, L = large; see text for further explanation), followed by the range of body sizes (mm total length) recorded for juveniles through adults in the species. Environmental characteristics known for the species are presented together on the third line beneath the species (CB, LB = coarse or level bottoms; SH, MD, DP = shallow, moderate, or deep water; TR, TE = tropical-subtropical or temperate-warm temperate latitudes; W, C = warm or cold water; see text for further discussion of these environments). Dashes for a size or habitat category indicate that data were not available or were inadequate to assign a category. The number of measured individuals (see text) is given on the last line beneath each species. Horizontal solid lines (e.g., *O. brevirostris*) indicate conspecific lineages in different geographic subregions; horizontal dashed lines (e.g., *G. bredini*—*G. zacae*; *G. spinulosus*—*G. festae*) designate closely related species in different subregions. Vertical solid lines indicate that species within a subregion are more closely related to each other than to those in another subregion; an x or + to the left of the genus name indicates species that form species clusters within the endemic group. Vertical dashed lines show that a group of species or even genera are very closely related.

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
	ODONTODACTYLIDAE		
	Odontodactylus brevirostris —— pl M (**13, *20) as M (20–78) CB, DP, TR, C N = 21		—— *O. brevirostris* pl L (**13–27, *13–30) as M (13–79) CB, DP, TR, C N = 33
GONODACTYLIDAE			
Gondactylus zacae – – – pl (S) (*8) as M (8–59) CB, SH, TR, W N = 394	*G. bredini* pl S (**8, *9) as M (9–75) CB, SH, TR, W N = 725		
	G. lacunatus pl S (**8–9, *9) as M (9–59) CB, SH, TR, W N = 77		
	× *G. oerstedii* pl S (**6–10, *8–10) as M (8–76) CB, SH, TR, W N = 1404		
	× *G. curacaoensis* pl (S) (*9–12) as M (9–72) CB, SH, TR, W N = 139		
+ *G. festae* – – – pl (S) as S (15–49) CB, SH, TR, W N = 25	*G. spinulosus* pl (S) (*8–12) as M (8–54) CB, SH, TR, W N = 131		
+ *G. bahiahondensis* pl (S) (*7) as S (7–49) CB, SH, TR, W N = 63	*G. austrinus* pl (S) as M (10–53) CB, SH, TR, W N = 72		
+ *G. stanschi* pl (S) as S (10–41) CB, SH, TR, W N = 20	× *G. torus* pl S (**9) as S (12–34) CB, DP, TR, C N = 56		
+ *G. costaricensis* pl (S) as S (25–37) CB, SH, TR, W N = 10	*G. minutus* pl (S) (*9–10) as S (9–31) CB, SH, TR, W N = 47		
+ *G. lalibertadensis* pl (S) (*9) as S (9–32) CB, SH, TR, W N = 14	*G. lightbourni* pl (S) (*10) as S (10–25) CB, SH, TR, W N = 4		
+ *G. albicinctus* pl (S) as S (13–25) CB, SH, TR, W N = 3	*G. petilus* pl (S) as S (18–22) CB, SH, TR, W N = 5		
G. pumilus pl (S) as S (8–20) CB, SH, TR, W N = 22	× *G. moraisi* pl (S) as S (20) CB, SH, TR, W N = 2		
		PROTOSQUILLIDAE	
		Protosquilla calypso pl S (**8, *10–13) as S (10–36) CB, SH, TR, W N = 635	
		P. folini pl (S) (*7–8) as S (7–28) CB, SH, TR, W N = 408	

Sources of data are as follows: ODONTODACTYLIDAE: Manning, 1965, 1966, 1967a, 1968a, 1969a. GONODACTYLIDAE: Fausto-Filho and Lemos de Castro, 1973; Gurney, 1946; Manning, 1969a, 1970b, 1971c, 1974a, 1976a; Manning and Hart, 1981; Manning and Reaka, 1979; Provenzano and Manning, 1978; Reaka and Manning, 1980; Schmitt, 1940; authors' unpublished observations. PROTOSQUILLIDAE: Manning, 1970a, 1974c, 1977a.

Gonodactylus pass through four pelagic stages in about a month (Provenzano and Manning, 1978).

HABITAT.—All members of these families occupy coarse substrates (coral rubble, rocks, shell) in tropical waters. Deep distributions are not correlated consistently with low morphological divergence among regions. The broadly distributed *Odontodactylus brevirostris* occurs in deep environments (55–439 m), but *O. hawaiiensis* Manning, 1967, known only from Hawaii, also occurs at considerable depths (109–276 m). In *Gonodactylus*, both small and moderately sized species occupy exclusively shallow (<10 m; *G. bredini, G. spinulosus, G. festae*) or moderately broad (0–73 m; *G. zacae, G. austrinus*) depth ranges, but only smaller species live exclusively in deeper water (*G. minutus* 13–66 m; *G. petilus* 51–59 m; *G. lightbourni* 64–91 m; *G. moraisi* 76m; *G. torus* 50–364 m; see also Reaka, 1980). No evidence suggests that these small, moderately deep-dwelling species with small geographic ranges have lower rates of morphological divergence than those in exclusively shallow habitats.

GAPS IN DISTRIBUTION.—Since *O. brevirostris* occurs in the West Atlantic and the Indo–West Pacific but not the East Pacific or the East Atlantic, extinction of this lineage may have occurred in the latter subregions. We have discussed above (p. 5) the evidence that stomatopod larvae in general disperse outside of their subregions infrequently. Furthermore, it seems unlikely that larvae of *O. brevirostris* could disperse from the Indo–West Pacific into the West Atlantic without colonizing the East Atlantic or central Atlantic islands (as do *Alima hyalina* and *Pseudosquilla oculata*, see Manning, 1969a). If *Odontodactylus brevirostris* has reached the East Pacific from the Indo–West Pacific, it has not survived there.

If one assumes prior Tethyan faunal distributions (Manning, 1977a; Scheltema, 1977; Schram, 1977), the absence of *Gonodactylus* from the East Atlantic also suggests that this lineage may have become extinct in the latter area.

The East Atlantic genus *Protosquilla*, on the other hand, has Indo–West Pacific affinities but is absent in the Americas. Possibly a *Chorisquilla*-like ancestor immigrated into or was already present in the East Atlantic, where it evolved into the present *Protosquilla* without dispersing to the New World. It is also likely, however, that either *Protosquilla* or a pre-existing relative with a Tethyan distribution may have disappeared in the Americas.

HEMISQUILLIDAE, PSEUDOSQUILLIDAE, AND EURYSQUILLIDAE

Within the Atlanto–East Pacific region, these families, only recently separated from the gonodactylids (Manning, 1977a, 1980) are represented by one, three, and two genera, respectively (Table 5). These stomatopods often inhabit level bottom (sometimes deep or cold) habitats, possess toothed spearing claws (except *Hemisquilla*), include fewer species, produce larger postlarvae, have wider distributions, and show closer taxonomic affinities to taxa in other geographic subregions than do the gonodactyloid genera treated above and in Table 4.

ADULT BODY SIZE.—The largest (lengths to 174 mm) members of these families belong to the Hemisquillidae. *Hemisquilla* is represented by *H. ensigera*, with subspecies off California, Chile, and Australia, and a related congener, *H. braziliensis*, which occurs off Brazil.

In the Pseudosquillidae, species of *Parasquilla* reach moderately large body sizes (lengths to 160 mm), and related species are found in each of the subregions of the study area; in the Indo–West Pacific *Parasquilla* is replaced by the cognate genus *Faughnia* (length to at least 157 mm; Manning and Makarov, 1978). Species of *Pseudosquillopsis* also reach moderate to large body sizes (lengths to 150 mm), and are widely distributed. Although cognates occur in the East Atlantic and East Pacific, the *Pseudosquillopsis* lineage is absent in the West Atlantic. In a genus of moderate (lengths to 125 mm) body size, the distributions of two species, *Pseudosquilla ciliata* and *P. oculata*, span remarkably wide areas (East and West Atlantic, Indo–West Pacific), but do not include the East Pacific. Instead, *P. adiastalta* (a relative of *P. oculata* and *P. guttata* Manning, 1972 in the Indo–West Pacific) is endemic in the East Pacific. Five additional species of *Pseudosquilla*, with maximum lengths from 35 to 83 mm, are known from the Indo–West Pacific. Thus, the largest species in this genus show the broadest distributions.

In the Eurysquillidae, *Eurysquilla galatheae* and *E. leloeuffi* (East Atlantic), *E. plumata* (West Atlantic), *E. veleronis* and *E. solari* (East Pacific), and *E. sewelli* (Chopra, 1939) (Indo–West Pacific), form a closely related, widespread group of moderately small (length to about 50 mm) species. An additional small species of *Eurysquilla* and eight species of *Manningia*, all of relatively small body size, are known from the Indo–West Pacific.

POSTLARVAL SIZE.—Postlarvae of these taxa settle at unusually large, sometimes variable sizes (30 mm in *Hemisquilla ensigera*; 20–21 mm in *Parasquilla coccinea*, 40 mm in *P. ferussaci*, and 21 mm in the related species *Faughnia haani* (Holthuis, 1959); 30–32 mm in *P. lessonii*, 30–33 mm in *Pseudosquillopsis cerisii*, <20–22 mm in *P. dofleini* (Balss, 1910), and 25–33 mm in *P. marmorata*; 16–24 mm in *Pseudosquilla ciliata*, 24–33 mm in *P. oculata*, and 25 mm in *P. guttata* (see Komai, 1927; Manning, 1968a, 1969a,b, 1971c, 1972a,b, 1974c, 1977a). In contrast, the postlarvae of eurysquillids are only moderately sized (15 mm in an unidentified species of *Eurysquilla* from West Africa (not listed in Table 5): <14 mm, <10 mm, <15 mm, and <13 mm in *E. veleronis, E. plumata, E. galatheae*, and *E. leloeuffi*; <17 mm in an Indo–West Pacific species, *E. pacifica* Manning, 1975; and 11–12 mm in *Manningia posteli* (Camp, 1973; Manning, 1975a, 1977a; authors' unpublished data). Therefore, these lineages generally show much closer taxonomic relationships and possess considerably larger, prob-

TABLE 5.—Sizes, habitats, and taxonomic relationships for morphologically related families of Gonodactyloidea that generally occupy level bottoms (symbols and format are as in Table 4).

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
HEMISQUILLIDAE			
Hemisquilla ensigera ensigera pl L (**30) as L (141–163) LB, MD, TE, C N = 3 *H. e. californiensis* pl (L) as L (90–166) LB, MD, TE, C N = 9	*H. braziliensis* pl (L) as L (78–163) LB, SH, TE, C N = 17		*H. e. australiensis* pl (L) as L (127–174) LB, MD, TE, C N = 26
PSEUDOSQUILLIDAE			
Parasquilla similis pl (L) as L (117–160) LB, MD, TR, W N = 7	*P. boschii* pl (L) as M (108–128) LB, MD, TE, C N = 3 *P. meridionalis* pl (L) as M (55–99) LB, SH, TR, W N = 4	*P. ferussaci* pl L (**40) as M (79–120) LB, DP, TE, C N = 13	
	Parasquilla coccinea pl L (**20–21, *27) as M (27–117) LB, DP, TR, C N = 24		
Pseudosquillopsis lessonii pl L (**30–32, *35) as L (35–150) LB, —, TE, C N = 6		*P. cerisii* pl L (**30–33) as M (84) LB, —, TE, C N = 3	*P. dofleini* pl L (**22, *20) as M (20–85) —, —, —, — N = 6
Pseudosquillopsis marmorata pl L (**25–33, *40–50) as M (40–120) LB, SH, TR, W N = 15			
	Pseudosquilla ciliata pl L (**16–24, *16–18) as M (16–89) CB, SH, TR, W N = 339	*P. ciliata* pl (L) (**18–19, *18) as M (18–61) CB, SH, TR, W N = 18	*P. ciliata* pl L (**18–24) as M (18–95) CB, SH, TR, W N = 180
Pseudosquilla adiastalta pl (L) as M (23–89) CB, SH, TR, W N = 52	*P. oculata* pl L (**29–33, *30) as M (30–125) CB, SH, TR, W N = 6	*P. oculata* pl L (**25–33, *24–25) as M (24–65) CB, SH, TR, W N = 78	*P. oculata* pl L (**24–31) as M (34–54) CB, SH, TR, W N = 27 *P. guttata* pl L (**25) as S (33–35) CB, SH, TR, W N = 3

TABLE 5.—Continued

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
EURYSQUILLIDAE			
Eurysquilla veleronis pl (M) (*14–18) as S (14–43) LB, SH, TR, W N = 13 *E. solari* pl (M) as S (47) LB, MD, TR, W N = 1	*E. plumata* pl (M) (*10) as S (10–32) LB, SH, TR, W N = 10	*E. galatheae* pl (M) (*15) as S (15–31) LB, SH, TR, W N = 2 *E. leloeuffi* pl (M) (*13) as S (13–33) LB, SH, TR, W N = 3	*E. sewelli* pl (M) as S (32–42) LB, DP, TR, C N = 2
	Eurysquilla chacei pl — as M (50) LB, DP, TR, C N = 1 *E. holthuisi* pl — as S (35) LB, MD, TR, W N = 1 *E. maiaguesensis* pl — as S (19–23) LB, MD, TR, W N = 5		*E. pacifica* pl — as S (17) —, —, TR, — N = 1
		Manningia posteli pl M (**11–12, *12) as S (12–39) LB, SH, TR, W N = 39	

Sources of data are as follows. HEMISQUILLIDAE: Dahl, 1954; Holthuis, 1941; Manning, 1963a, 1966, 1969a,b, 1974a; Schmitt, 1940; Stephenson, 1953, 1967; Stephenson and McNeill, 1955. PSEUDOSQUILLIDAE: Balss, 1910; Bigelow, 1901, 1931; Camp, 1973; Giesbrecht, 1910; Hansen, 1895; Holthuis, 1941; Komai, 1927; Manning, 1964, 1968a, 1969a,c, 1970a,b,c, 1971c, 1972b, 1973, 1974a,c, 1976a, 1977a,b, 1978a; Reaka and Manning, 1980; Schmitt, 1940; Stephenson and McNeill, 1955; authors' unpublished observations. EURYSQUILLIDAE: Camp, 1973; Chopra, 1939; Gore and Becker, 1976; Manning, 1969a, 1970b, 1971c, 1974a, 1975a, 1977a; authors' unpublished observations.

ably longer-lived larvae than the reef-dwelling gonodactylids treated above.

HABITAT.—Members of these families have been collected in diverse, usually soft muddy or sandy level bottom environments. Individuals of some species, e.g., those of *Hemisquilla*, are known to dig burrows in mud or muddy sand, whereas others, e.g., those of *Pseudosquilla*, inhabit burrows in grass flats, coralline algae, sponges, or beneath coral rubble (Hatziolos, 1980). Juveniles of large species and even adults of small species of *Pseudosquilla* are found in holes within coral rubble.

Although some of these gonodactyloids live in shallow water, others frequent deep or cold environments. *Hemisquilla ensigera* and *H. braziliensis* occupy moderately deep (33–200 m and 37–100 m) temperate environments and show low geographic divergence. West Atlantic species of *Parasquilla* live in relatively deep water (21–194, 46–92, and 73–382 m for *P. boschii, P. meridionalis, P. coccinea*), and have close affinities to East Pacific and East Atlantic species that also occur in deep environments (73–125 m and 100–550 m, respectively). On the other hand, most species of *Pseudosquilla* inhabit shallow, warm, coralline sand and rubble environments and also show unusually low geographic divergence. Several species of *Eurysquilla* are found in relatively shallow water (less than 100 m except for *E. solari*, which is known from 160 m) and have close relatives in other subregions. However, *E. holthuisi, E. chacei*, and *E. maiaguesensis* live in relatively deep waters (to 291, 419, and 315 m), as does one of the Indo–West Pacific species, *E. sewelli* (220–695 m). Thus, habitat type, temperature, and depth do not influence rates of divergence in a predictable manner in this group of families.

Gaps in Distribution.—Extinction appears to have occurred in at least one of these families, since a lineage of *Pseudosquillopsis* occurs in the East Pacific and East Atlantic, but, assuming a Tethyan distribution, has disappeared in the West Atlantic.

Two species of *Pseudosquilla* occur in all subregions except for the East Pacific. One of these lineages apparently has disappeared and the other has diverged into the East Pacific endemic, *P. adiastalta*. One lineage of *Eurysquilla* (*E. maiaguesensis–E. pacifica*) is present in the West Atlantic and Indo–West Pacific, but is conspicuously absent from both the East Pacific and East Atlantic.

Hemisquilla is not present in the East Atlantic, but members of this genus may not have reached there due to their generally southerly distribution; *H. ensigera californiensis*, however, reaches Californian waters.

The genus *Manningia*, represented by one species in the East Atlantic and several in the Indo–West Pacific, is absent from the Americas.

LYSIOSQUILLOIDEA

LYSIOSQUILLIDAE, NANNOSQUILLIDAE, AND CORONIDIDAE

These families are represented by five, eight, and three genera, respectively, within the study area (Table 6). All have toothed claws, but these are inflated into smashing appendages in the coronidids. Many lysiosquilloids excavate U-shaped or vertical burrows in sandy or muddy bottoms, but the coronidids and some nannosquillids live in coarse substrates. The lysiosquilloids include the largest and some of the smallest stomatopods known.

Adult Body Size.—Almost all lysiosquillids reach moderate or large body sizes and are broadly distributed, with close taxonomic relationships among distant geographic regions and subregions. The genus *Lysiosquilla* includes the largest known species of stomatopod, the Indo–West Pacific *L. maculata* (Fabricius, 1793), which can attain a total length of up to 385 mm. Several lineages of closely related species of *Lysiosquilla*, all of large body size (maximum lengths from 132–385 mm), occur over broad geographic regions (Table 6). *Lysiosquilla desaussurei* (East Pacific) is more closely related to *L. hoevenii* (East Atlantic) than to the West Atlantic *L. scabricauda*. Also, *L. panamica* (East Pacific) is more closely related to the Indo–West Pacific *L. tredecimdentata* Holthuis, 1941 than to any of the West Atlantic species. In contrast, the distribution of the *L. glabriuscula–L. maculata* lineage includes the West Atlantic and Indo–West Pacific but not the East Pacific or East Atlantic. A related genus of large body size (lengths to 266 mm), *Lysiosquilloides*, is known from both the East Atlantic and from Thailand in the Indo–West Pacific.

The lysiosquillids *Heterosquilla* and *Heterosquilloides* are moderately sized (maximum lengths from 76–109 mm), but show remarkably low rates of divergence in different geographic regions and subregions (Table 6); these and several other stomatopod genera appear to exhibit relict distribution patterns (Manning, 1977a). Although relatively uncommon, *Heterosquilloides mccullochae* has the widest distribution of any stomatopod, having been collected from Ascension Island (authors' unpublished data; included as East Atlantic in Table 6), the West Atlantic, the East Pacific, and the Indian Ocean. *Heterosquilloides insolita* has been taken off Florida and possibly the Galapagos (where only a fragmented specimen has been taken), and *Heterosquilla polydactyla* is an austral species known from both Chile and Argentina. However, *Heterosquilloides armata* occurs only between Massachusetts and Texas, *Heterosquilla platensis* is recorded only from Uruguay and Argentina, and a newly discovered species, *Tectasquilla lutzae* Adkison and Hopkins, 1984, is known only from the Gulf of Mexico. In addition to *Heterosquilloides mccullochae, H. insignis*, and *Heterosquilla tricarinata*, at least three species of *Heterosquilloides* and an additional undescribed species of *Heterosquilla* are endemic in Indo–West Pacific waters.

Species within the Nannosquillidae reach only small or moderate body sizes. One of the lineages of largest body size, *Acanthosquilla*, is characterized by broadly distributed, closely related taxa. The widespread *Acanthosquilla biminiensis–A. septemspinosa* lineage is related to *A. acanthocarpus* (Claus, 1871) and *A. multifasciata* (Wood-Mason, 1875) in the Indo–West Pacific; at least seven other Indo–West Pacific species of *Acanthosquilla* are known. Conspecific populations of *A. biminiensis* and *A. digueti* inhabit both coasts of the Americas. Closely related species of *Platysquilloides* occur in both the North West and North East Atlantic, members of *Allosquilla, Mexisquilla*, and *Platysquilla* each are found only in one subregion (Manning, 1977; Manning and Camp, 1981; Froglia and Manning, 1986). However, *Coronis* also reaches moderate sizes (to 75 mm), but is found only in the West Atlantic.

All of the 20 species in the genus *Nannosquilla* are small (≤42 mm) and all are endemic to either the West Atlantic or East Pacific. Most species resemble others in their own subregion (e.g., species clusters in Table 6), indicating local radiation. *Nannosquilloides*, a related genus of similar small size (<48 mm), is endemic to the East Atlantic.

In contrast, the coronidids are characterized by small body size but widespread distributions at the generic level, often with close taxonomic relationships among taxa in distant regions or subregions. East Pacific species of *Coronida* and *Neocoronida* resemble relatives in the East Atlantic and Indo–West Pacific, respectively (Table 6). Only the species shown in table 6 are known. The recently discovered *Acoridon manningi* (related to both *Coronida* and *Neocoronida*) may reflect either a remnant of an ancestral Tethyan lineage that has become extinct in the East Atlantic and East Pacific or a branch of *Coronida* or *Neocoronida* that has diverged in the West Atlantic.

Therefore, large and particularly some moderately sized

TABLE 6.—Sizes, habitats, and taxonomic relationships for species of Lysiosquilloidea in different geographic subregions (symbols and format are as in Table 4; within *Nannosquilla*, +, ×, O, and ● signify local species clusters that are more closely related to each other than to other species).

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
	LYSIOSQUILLIDAE		
		Lysiosquilla monodi pl (L) as M (79–135) LB, SH, TR, W N = 4	*L. sulcirostris* pl L (**20–22, *26) as L (26–325) LB, SH, TR, W N = 12
Lysiosquilla desaussurei pl (L) as L (68–210) LB, SH, TR, W N = 8	*L. scabricauda* pl (L) as L (52–275) LB, SH, TR, W N = 82	*L. hoevenii* pl (L) as L (75–265) LB, SH, TR, W N = 40	
Lysiosquilla panamica pl (L) as L (90–205) LB, SH, TR, W N = 7			*L. tredecimdentata* pl (L) as L (72–259) LB, SH, TR, W N = 17
	L. glabriuscula pl L (**22–25) as L (61–214) LB, SH, TR, W N = 43 *L. campechiensis* pl (L) as M (64–132) LB, SH, TR, W N = 6		*L. maculata* pl L (**22–23, *26–29) as L (26–385) LB, SH, TR, W N = 76
		Lysiosquilloides aulacorhynchus pl — as L (161–266) LB, SH, TR, W N = 3	*L. siamensis* pl — as L (102–155) —, —, TR, — N = 5
Heterosquilla polydactyla pl L (**19–22) as M (42–95) LB, SH, TE, C N = 17	*H. platensis* pl (L) as M (68–109) LB, —, TE, C N = 15 *H. polydactyla* pl L (**19–22) as M (36–65) LB, SH, TE, C N = 12		*H. tricarinata* pl M (**12–13) as M (51–80) LB, SH, TE, C N = 14
Heterosquilloides insolita pl — as M (ca. 76) LB, MD, TR, W N = 1	*H. insolita* pl — as (M) (48) LB, MD, TR, W N = 1		*H. insignis* pl — as M (42–52) LB, —, TR, — N = 4

TABLE 6.—Continued.

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
Heterosquilloides mccullochae pl (M) (*19) as M (19–50) LB, SH, TR, W N = 8	*H. mccullochae* pl (M) as (M) (21–32) LB, SH, TR, W N = 2	*H. mccullochae* pl (M) as M (42–69) LB, SH, TR, W N = 3	*H. mccullochae* pl (M) as M (55) LB, SH, TR, W N = 1
	Heterosquilloides armata pl — as M (20–76) LB, MD, TE, C N = 15		
	Tectasquilla lutzae pl — as M (73) —, SH, TR, W N = 2		
	NANNOSQUILLIDAE		
Acanthosquilla biminiensis pl (S) as M (15–56) LB, SH, TR, W N = 19	*A. biminiensis* pl S (**9–10) as M (39–62) LB, SH, TR, W N = 15	*A. septemspinosa* pl M (**11, *11–12) as M (11–55) LB, SH, TR, W N = 13	*A. acanthocarpus* pl S (**9–10, *11) as M (11–79) LB, SH, TR, W N = 12
Acanthosquilla digueti pl — as S (18–27) LB, SH, TR, W N = 7	*A. digueti* pl — as S (45–48) LB, SH, TR, W N = 2		
	Coronis scolopendra pl L (**20) as M (23–75) LB, SH, TR, W N = 70		
		Allosquilla africana pl — as S (39–70) LB, MD, TR, W N = 3	
	Platysquilloides enodis pl — as M (32–67) LB, SH, TE, C N = 11	*P. lillyae* pl — as M (42–55) LB, DP, TR, C N = 4	
	Mexisquilla horologii pl (S) (*11) as S (11–16) LB, SH, TR, W N = 5	*Platysquilla eusebia* pl — as M (45–55) LB, SH, TE, C N = 3	
		Nannosquilloides occultus pl — as S (15–48) LB, MD, TE, C N = 11	

TABLE 6.—Continued.

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
● *Nannosquilla decemspinosa* pl (S) as S (15–25) LB, SH, TR, W N = 22	+ *N. grayi* pl (S) as S (21–42) LB, SH, TE, C N = 34		
N. anomala pl (S) as S (34–41) LB, SH, TE, C N = 8	+ *N. whitingi* pl (S) as S (24–30) LB, SH, TR, W N = 4		
N. californiensis pl (S) as S (17–30) CB, SH, TE, C N = 8	+ *N. taylori* pl (S) as S (28) LB, SH, TR, W N = 1		
○ *N. chilensis* pl (S) (*10) as S (10–28) LB, SH, TE, C N = 13	+ *N. baliops* pl (S) as S (23) LB, SH, TR, W N = 1		
○ *N. similis* pl (S) as S (25) —, SH, TR, W N = 1	× *N. antillensis* pl S (**6) as S (14–25) CB, SH, TR, W N = 9		
	N. schmitti pl (S) (*9) as S (9–25) LB, SH, TR, W N = 14		
○ *N. galapagensis* pl (S) as S (21–23) —, SH, TR, W N = 3	*N. vasquezi* pl (S) as S (18–24) LB, SH, TR, W N = 7		
	+ *N. hancocki* pl (S) as S (15–21) —, SH, TR, W N = 5		
● *N. canica* pl (S) as S (15–18) LB, SH, TR, W N = 3	× *N. dacostai* pl (S) as S (19) —, SH, TR, W N = 1		
	× *N. carolinensis* pl (S) as S (18) —, SH, TE, C N = 2		
	× *N. heardi* pl (S) as S (18) LB, SH, TR, W N = 1		
	× *N. adkisoni* pl (S) as S (17) —, SH, TR, W N = 1		
	N. taguensis pl (S) as S (16–17) LB, SH, TR, W N = 3		

TABLE 6.—Continued.

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
	CORONIDIDAE		
Coronida schmitti pl (S) as S (13–48) CB, SH, TR, W N = 33		*C. bradyi* pl (S) (*10) as S (10–44) CB, SH, TR, W N = 24	
C. glasselli pl (S) as S (19–36) CB, SH, TR, W N = 2			
	Acoridon manningi pl — as S (13–41) —, SH, TR, W N = 2		
Neocoronida cocosiana pl — as S (20) CB, SH, TR, W N = 1			*N. martensi* pl — as S (45) —, —, TR, — N = 1
			N. trachurus pl — as S (32–47) CB, SH, TR, W N = 10

Sources of data are as follows. LYSIOSQUILLIDAE: Adkison and Hopkins, 1984; Alikunhi, 1967; Barnard, 1950; Bigelow, 1931; Camp, 1973, 1985; Fenwick, 1975; Gore and Becker, 1975, 1976; Greenwood and Williams, 1984; Holthuis, 1941; Manning, 1962b, 1963b, 1966, 1968a, 1969a,c, 1970c,d, 1971a,b,c, 1972c, 1974a,b,c, 1977a, 1978b,c; Michel, 1970; Naiyanetr, 1980; Reaka and Manning, 1980; Schmitt, 1940; Shanbhogue, 1970 [1971]; Stephenson and McNeill, 1955; Tirmizi and Manning, 1968; Williams et al., 1985; authors' unpublished data. NANNOSQUILLIDAE: Bahamonde, 1968; Camp, 1973; Camp and Manning, 1982; Dahl, 1954; Froglia and Manning, 1986; Holthuis, 1984; Howells et al., 1980; Kocatas, 1981; Lewinsohn and Manning, 1980; Manning, 1961, 1962a,b, 1967b, 1968a, 1969a, 1970a,b,c, 1972c, 1974a,b,c, 1977a, 1979; Manning and Camp, 1981; Manning and Froglia, 1979; Manning and Reaka, 1979; Reaka and Manning, 1980; Schmitt, 1940; Stephenson and McNeill, 1955; Tirmizi and Manning, 1968; authors' unpublished observations. CORONIDIDAE: Adkison et al., 1983; Manning, 1970a, 1972c, 1974c, 1976a, 1977a,b, 1978c.

lysiosquilloids show a high incidence of close relatives or conspecifics in different regions and subregions. Of 15 American lysiosquilloids of large or moderate size, four species (27%) have conspecific populations in other subregions, and seven species (47%) are closely related to congeners in other areas. Affinities are generally as strong among as within subregions, and relatively small numbers of closely related species within subregions suggest either relatively low rates of radiation or high rates of extinction. As discussed below, the small numbers of closely related species within subregions does not appear to be explainable by postulating high rates of extinction. The largest species in this heterogeneous superfamily, however, also show some tendencies for subregional differentiation, since all species of *Lysiosquilla* and *Lysiosquilloides* are endemic to their subregion. Of 25 American lysiosquilloids of small body size, only one species (4%) is conspecific, and only five species (20%) show cognate relationships to species in other subregions. Two genera of very small body size, *Nannosquilla* and *Nannosquilloides*, inhabit only Atlanto–East Pacific waters, and show strong divergence in different geographic subregions. *Nannosquilla* has undergone considerable radiation within each American subregion.

POSTLARVAL SIZE.—Species of *Lysiosquilla* produce larvae that progress through numerous molts during long pelagic phases and settle at large sizes (22–25 mm in *L. glabriuscula*, 20–22 mm in *L. sulcirostris* Kemp, 1913, 22–23 mm in *L. maculata*; see Alikunhi, 1967; Michel, 1970; Manning, 1969a, 1978b; Table 6). Postlarvae of some species of *Heterosquilla* and *Heterosquilloides* settle at similar relatively large to moderate sizes (19–22 mm in *H. polydactyla*, <19 mm in *H. mccullochae*; 12–13 mm in *H. tricarinata*; see Greenwood, and Williams, 1984; Manning, 1971b; Reaka and Manning, 1980). Within the Nannosquillidae, species of *Acanthosquilla* produce small to moderately sized postlarvae (9–12 mm in *A. biminiensis*, *A. acanthocarpus*, *A.*

multifasciata, A. tigrina (Nobili, 1903), and *A. septemspinosa* (Alikunhi, 1967; Camp, 1973; Manning, 1977a; Table 6). In general, *Heterosquilla, Heterosquilloides,* and *Acanthosquilla* show less morphological divergence among subregions and produce larger postlarvae than comparably sized gonodactyloids.

Coronida bradyi has relatively small postlarvae (<10 mm), as does *Mexisquilla horologii* (<11 mm) (Camp, 1973; Manning, 1977a; authors' unpublished data), but both show taxonomic affinities among different subregions. However, the small size of postlarvae (6 mm in *Nannosquilla antillensis,* <9 mm in *N. schmitti,* <10 mm in *N. chilensis*; Dahl, 1954; authors' unpublished data; Table 6) and the high endemism in *Nannosquilla* are comparable to that in *Gonodactylus.*

Consequently, there is a general inverse correlation between size of postlarvae and degree of divergence within lineages among zoogeographic subregions (especially exemplified by *Lysiosquilla, Heterosquilla, Heterosquilloides,* and *Nannosquilla*), but several exceptions are apparent. Although species of *Lysiosquilla* produce large postlarvae and show affinities among taxa in different subregions, all species are endemic to their own subregion. Similarly, species of *Acanthosquilla* and *Coronida* show strong relationships among taxa in distant regions or subregions but lack large postlarvae.

HABITAT.—Where their habits are known, lysiosquilloids (except coronidids) burrow in level bottoms of sand or muddy sand. Although the wide distributions of many lineages in this family generally correlate with occupation of a sandy environment (e.g., in *Lysiosquilla, Acanthosquilla*), several exceptions exist. Some widespread species live in sand associated with coarse substrates, whereas some endemic species occupy exclusively sandy environments. One of the most widespread species, *Heterosquilloides mccullochae,* often lives in sand associated with coral rubble or rocks. Another species found in more than one subregion, *Acanthosquilla biminiensis,* sometimes is found in sand in rocky habitats. *Nannosquilla* is characterized by the greatest regional differentiation in the family. Some species of that genus occur in sand on coral reefs, but most live exclusively on beaches or in subtidal sandy environments (Reaka and Manning, 1980; personal observations). Coronidids, like gonodactylids, inhabit cavities in rocks, rubble, or coralline algae.

Furthermore, no predictable relationship occurs between depth and rate of geographic divergence in lysiosquilloids. *Heterosquilloides mccullochae* and species of *Acanthosquilla* and *Lysiosquilla* occupy shallow, warm environments and show low rates of divergence. A number of lysiosquilloids occur in cold or deep water (*Heterosquilla platensis,* Uruguay, Argentina; *H. polydactyla,* Chile, Argentina; *Heterosquilloides insolita,* Florida and perhaps the Galapagos, 91–247 m; *Heterosquilloides armata,* Massachusetts, Florida, and Texas, 96–218 m; *Platysquilla eusebia,* Ireland to the Mediterranean; *Platysquilloides enodis,* Massachusetts to North Carolina; *Platysquilloides lillyae* (Azores, 225–345 m); and *Allosquilla africana* (Adriatic and West Africa, 148–222 m).

GAPS IN DISTRIBUTION.—Extinction appears to have occurred in the *Coronida* lineage in the West Atlantic, since closely related species inhabit only East Atlantic and East Pacific waters. However, this or a preceding lineage may have diverged into the related genus, *Acoridon,* now known from the West Atlantic. *Neocoronida,* known from the Indo-West Pacific and Cocos Island in the East Pacific, either never reached or became extinct in the Atlantic. Similarly, the *Lysiosquilla panamica–L. tredecimdentata* lineage is present in the East Pacific and Indo-West Pacific but not the Atlantic. The East Atlantic endemic genera *Platysquilla* and *Allosquilla* are missing in the West Atlantic, but are closely related to the West Atlantic *Platysquilloides* and *Mexisquilla*; however, another East Atlantic endemic, *Nannosquilloides,* either never reached or became extinct in American waters. Similarly, the *Lysiosquilla monodi–L. sulcirostris* and the *Lysiosquilloides aulacorhynchus–L. siamensis* lineages extend to East Atlantic from Indo-Pacific waters but fail to inhabit the New World.

The *Lysiosquilla glabriuscula–L. maculata* lineage is conspicuously absent from East Pacific waters and may have become extinct there. The related species of *Platysquilloides* are found in the West and East Atlantic but not in the East Pacific. It is not possible to determine whether these lineages, as well as the endemic species of *Tectasquilla, Coronis, Allosquilla, Mexisquilla,* and *Platysquilla,* became extinct in the East Pacific or if they evolved in the Atlantic after elevation of the Central American isthmus.

The distributions of two lineages of *Lysiosquilla* span Indo-West Pacific and American regions without occurring in the East Atlantic (*L. panamica–L. tredecimdentata, L. glabriuscula–L. maculata*). In addition, two otherwise transregional lineages, *Heterosquilla polydactyla–H. tricarinata* and *Heterosquilloides insolita–H. insignis,* display conspicuous gaps in distribution in the East Atlantic; *H. polydactyla* may not have reached the East Atlantic, however, because of its very southerly distribution. Although related to the pantropical *Acanthosquilla biminiensis–A. septemspinosa–A. acanthocarpus* lineage, *A. digueti* includes conspecific populations on both sides of the Central American isthmus but is not present in the East Atlantic. If the broad distributions of its relatives and its own trans-American distribution are characteristic, this lineage may have previously inhabited the East Atlantic and become extinct there. The genus *Nannosquilla* is present in the Americas but lacks representation in the East Atlantic, where a pre-existing lineage may have diverged as *Nannosquilloides.* Similarly, the endemic West Atlantic genera *Tectasquilla* and *Coronis* are missing from the East Atlantic; either these genera arose in the West Atlantic or all relatives have disappeared in the East Atlantic.

SQUILLOIDEA

SQUILLIDAE

This diverse family is represented by 11 genera in the Atlanto–East Pacific region, and 6 of these (*Squilla, Fennerosquilla, Schmittius, Rissoides, Meiosquilla,* and *Crenatosquilla*) are almost entirely restricted to that region (Table 7); one species of *Rissoides* occurs in the Indo–West Pacific (Manning, 1975b). This superfamily contains one Indo–West Pacific family, Harpiosquillidae, which, like the Lysiosquillidae, includes some of the largest (to 335 mm) known stomatopods (Manning, 1969d, 1980). Most squillids excavate vertical, branched, or U-shaped burrows in level bottom habitats, and all possess toothed spearing appendages (Caldwell and Dingle, 1976; Myers, 1979; Reaka and Manning, 1981).

ADULT BODY SIZE.—Major predators in shrimp beds, species of *Squilla* reach large sizes (more than 150 mm) in each of the subregions of the study area. One of the largest species in the East Pacific, *S. aculeata,* occurs also in the East Atlantic (with morphological differences at the subspecific level), but is replaced in the West Atlantic by a large and very common relative, *S. empusa* (Table 7). Additionally, *S. biformis* reaches relatively large sizes in the East Pacific and has cognates in both the East and West Atlantic. Of six West Atlantic species larger than 130 mm, four are closely related to species in the East Pacific and two also have cognates in the East Atlantic. Species of smaller body size do not show comparable linkages (11 West Atlantic species, only one of which has an East Pacific cognate). Species in both the West Atlantic and the East Pacific form a series of related groups (*S. edentata* (two subspecies)–*S. caribaea–S. intermedia–S. brasiliensis, S. lijdingi–S. chydaea, S. rugosa–S. grenadensis, S. neglecta–S. prasinolineata, S. obtusa–S. surinamica, S. discors–S. deceptrix* (all West Atlantic); *S. panamensis–S. tiburonensis–S. bigelowi* (East Pacific)), indicating substantial radiation within each subregion, particularly the West Atlantic. Thirty-three species of *Oratosquilla,* some reaching lengths of more than 200 mm, form the Indo–West Pacific counterpart of *Squilla* (see Manning, 1978d). *Oratosquilla* is represented in the Atlanto–East Pacific by *O. massavensis* (Kossmann, 1880), a large species that recently has entered the Mediterranean Sea via the Suez Canal (Lewinsohn and Manning, 1980).

Pterygosquilla armata also reaches large sizes (to 168 mm), and subspecies occur off southern South America, New Zealand, and southern Africa. Although little is known of its ecology, a large (to 157 mm) related species, *P. gracilipes,* inhabits Chilean waters. Conspecific populations of *Cloridopsis dubia* reach relatively large body sizes (to 156 mm), and are known from both sides of the Americas; this genus is otherwise represented by six species (lengths to at least 93 mm) in the Indo–West Pacific region.

Species of *Alima* and *Schmittius* reach moderate (to about 75 mm) body sizes. Two species of *Alima* are pantropical except for the East Pacific, and two additional species occur in the Indo–West Pacific. Species of *Schmittius,* known only from the East Pacific, appear to be closely related to *Squilloides* in the Indo–West Pacific.

A smaller relative of *Cloridopsis, Clorida* includes one species, *C. mauiana,* which occurs in the East Pacific as well as in Hawaii and the Santa Cruz islands in the Indo–West Pacific (Manning, 1976b). This represents the only instance of a single species of stomatopod that lives in both the Indo–West Pacific and the East Pacific. A relatively large number of individuals have been collected, suggesting that its occurrence in the East Pacific probably is not accidental. The lineage is characterized by small to moderate body sizes; 26 other Indo–West Pacific species of *Clorida* range from 23 to 67 mm in maximum lengths. Among the smallest members of the Squillidae, the *Rissoides–Meiosquilla–Crenatosquilla* lineage is distributed in the East Atlantic and the Americas (except for *R. barnardi,* which inhabits South African waters; Manning, 1969c, 1975b). A major morphological feature, the shape and dentition of the claw, distinguishes species of *Rissoides* in the East Atlantic from the American species of *Meiosquilla* and *Crenatosquilla* (see Manning and Lewinsohn, 1982). All species of *Meiosquilla,* as well as the genus *Crenatosquilla,* are endemic to their subregions. Thus, this group illustrates the greatest degree of subregional differentiation within the squillids, even though the trend for endemism and local species radiation appears to be less extensive than that found in the comparably small species of *Gonodactylus* and *Nannosquilla.*

Therefore, as in the lysiosquilloids, large species of squillids show strong affinities to taxa in other regions or subregions (*Squilla, Pterygosquilla, Cloridopsis*), as well as some tendencies for regional divergence (generic differentiation in Atlanto–East Pacific vs. Indo–West Pacific regions, as well as large numbers of subregionally distinct species in *Squilla*). Within *Squilla,* the large species show the closest affinities to taxa in other geographic subregions. As in the pseudosquillids and the lysiosquilloids, some medium sized species (e.g., those of *Alima*) are unusually widespread. Also, as in the gonodactylids and nannosquillids, most small species (e.g., those of *Rissoides, Meiosquilla,* and *Crenatosquilla*) show strong subregional differentiation. The main exception to this general pattern is the transregional distribution of *Clorida mauiana,* a small lineage.

POSTLARVAL SIZE.—In general, sizes of squillid postlarvae exceed the sizes of postlarval protosquillids and gonodactylids, are smaller than those of the pseudosquillids, but are comparable to those of many lysiosquilloids. Some squillid larvae (e.g., those of *Pterygosquilla armata* and *Squilla empusa*) pass through eight or nine pelagic stages that can last many months (Pyne, 1972; Morgan and Provenzano, 1979). In some cases, postlarval sizes appear to vary consid-

TABLE 7.—Sizes, habitats, and taxonomic relationships for species of Squillidae and Bathysquillidae in different geographic subregions (symbols and format are as in Table 4; within *Squilla*, O, ●, +, ++, ×, and ×× indicate species clusters within the West Atlantic subregion that are more closely related to each other than to other species).

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
	SQUILLIDAE		
Squilla aculeata aculeata ——— — — — pl (M) as L (26–197) LB, SH, TR, W N = 25	—*S. empusa* — — — — ——— pl M (**12–14) as L (29–185) LB, SH, TE, C N = 1295	—*S. aculeata calmani* pl M (**13) as L (21–150) LB, SH, TR, W N = 123	
S. mantoidea pl — as L (93–200) LB, SH, TR, W N = 9	O *S. edentata* pl — as L (30–175) LB, DP, TR, C N = 70		
	O *S. caribaea* pl — as L (61–174) LB, DP, TR, C N = 63		
S. biformis — — — — — — pl (L) (*51–57) as L (51–170) LB, DP, TR, C N = 134	-O *S. intermedia* - - - - - - - - - - pl (L) as L (48–153) LB, DP, TR, C N = 37	-*S. cadenati* pl (L) as L (33–166) LB, DP, TR, C N = 120	
S. panamensis - - - - - pl (M) as M (32–140) LB, SH, TR, W N = 45	-O *S. brasiliensis* pl — as L (38–150) LB, MD, TE, C N = 75	*S. mantis* pl L (**17–23) as L (25–165) LB, DP, TE, C N = 142	
S. tiburonensis - - - - - - pl (M) (*16–21) as M (16–97) LB, MD, TR, W N = 27	-● *S. lijdingi* pl (M) as M (22–133) LB, MD, TR, W N = 136		
S. bigelowi pl (M) as M (37–132) LB, MD, TR, W N = 34	● *S. chydaea* pl (M) as M (29–125) LB, DP, TR, C N = 153		
	+ *S. rugosa* pl — as M (24–125) LB, SH, TR, W N = 112		
	++ *S. neglecta* pl — as M (43–119) LB, SH, TR, W N = 34		
	++ *S. prasinolineata* pl — as M (21–119) LB, SH, TR, W N = 48		

TABLE 7.—Continued

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
	S. decimdentata pl — as M (22–86) LB, MD, TR, W N = 41		
	× *S. obtusa* pl — as M (30–83) LB, MD, TR, W N = 55		
S. hancocki pl — as M (20–68) LB, MD, TR, W N = 27	×× *S. deceptrix* pl — as M (24–75) LB, DP, TR, C N = 55		
S. parva pl — as M (19–53) LB, SH, TR, W N = 15	×× *S. discors* pl — as M (37–67) LB, MD, TR, W N = 31		
	× *S. surinamica* pl — as S (26–44) LB, SH, TR, W N = 43		
	+ *S. grenadensis* pl — as S (24–42) LB, DP, TR, C N = 9		
	Fennerosquilla heptacantha pl M (**18) as M (37–100) LB, DP, TR, C N = 29		
		Oratosquilla massavensis pl M (**15–18, *17) as L (17–216) LB, SH, TR, W N = 303	*O. massavensis* pl (M) as M (35–126) LB, SH, TR, W N = 42
Pterygosquilla armata armata pl L (**20–32, *33) as M (33–145) LB, DP, TE, C N = 27	*P. a. armata* pl (L) as M (31–146) LB, DP, TE, C N = 14	*P. a. capensis* pl M (**12–22) as L (22–168) LB, DP, TE, C N = 36	*P. a. schizodontia* pl — as M (114–122) LB, DP, TE, C N = 4
P. gracilipes pl (L) as L (82–157) —, —, TE, C N = 9			

TABLE 7.—Continued

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
Cloridopsis dubia pl — as M (35–147) LB, SH, TR, W N = 9	*C. dubia* pl — as L (50–156) LB, SH, TR, W N = 55		
	Alima hieroglyphica pl (M) as M (49–75) LB, SH, TR, W N = 3	*A. hieroglyphica* pl M (**15) as M (16–58) LG, SH, TR, W N = 10	*A. hieroglyphica* pl M (**17) as M (48–62) LB, SH, TR, W N = 6
	Alima hyalina pl M (**16–18, *18–20) as S (18–46) LB, SH, TR, W N = 26	*A. hyalina* pl L (**22) as S (32) LB, SH, TR, W N = 4	*A. hyalina* pl (M) as S (17–46) LB, SH, TR, W N = 8
Schmittius peruvianus pl (L) (*33) as M (33–60) LB, DP, TE, C N = 2			
S. politus pl (L) (*22) as M (22–72) LB, MD, TE, C N = 17			
Clorida mauiana pl — as S (17) LB, SH, TR, W N = 1			*C. mauiana* pl — as S (21–27) LB, SH, TR, W N = 2
	Meiosquilla randalli pl (M) as S (24–39) —, SH, TR, W N = 5	*Rissoides desmaresti* pl M (**16) as M (26–89) LB, SH, TE, C N = 30	
	M. tricarinata pl M (**12) as S (14–35) LB, SH, TR, W N = 10	*R. pallidus* pl (M) as M (21–73) LB, DP, TE, C N = 31	
M. dawsoni pl (M) as S (19–47) LB, SH, TR, W N = 8	*M. quadridens* pl M (**13–16, *11–13) as S (11–35) LB, SH, TR, W N = 25	*R. africanus* pl (M) (*13–15) as S (13–36) LB, SH, TR, W N = 96	
M. swetti pl (M) as S (19–42) CB, SH, TR, W N = 7	*M. schmitti* pl M (**12–13) as S (13–33) CB, SH, TR, W N = 19	*R. calypso* pl (M) as S (35) —, SH, TR, W N = 1	*R. barnardi* pl (M) (*15) as S (15–30) —, SH, TE, C N = 4
	M. lebouri pl M (**12–14) as S (13–22) CB, SH, TR, W N = 8		

TABLE 7.—Continued

East Pacific	West Atlantic	East Atlantic	Indo-West Pacific
Crenatosquilla oculinova pl (S) (*9–14) as S (9–36) CB, SH, TR, W N = 70			
BATHYSQUILLIDAE			
	Bathysquilla microps pl — as L (45–255) LB, DP, TR, C N = 12		*B. microps* pl — as L (201) LB, DP, TR, C N = 1

Sources of data are as follows. SQUILLIDAE: Alikunhi, 1944; Bigelow, 1894; Camp, 1973; Dahl, 1954; Giesbrecht, 1910; Gurney, 1946; Holthuis, 1961, 1967; Ingle, 1963; Kemp, 1913, 1915; Kurian, 1947, 1954; Lewinsohn and Manning, 1980; Manning, 1966, 1968a,b, 1969a,c, 1970b,c, 1971c, 1972a, 1974a,c, 1975b, 1976a,b, 1977a,b, 1978a,c, 1984; Manning and Camp, 1983; Manning and Froglia, 1979; Manning and Lewinsohn, 1982; Miers, 1881; Morgan and Provenzano, 1979; Parisi, 1922; Reaka and Manning, 1980; Schmitt, 1940; Tirmizi and Manning, 1968; authors' unpublished data. BATHYSQUILLIDAE: Manning, 1969a; Manning and Struhsaker, 1976.

erably even within a species (12–22 mm in *Pterygosquilla armata capensis* and 20–32 mm in *P. a. armata*; 16–22 mm in different populations of *Alima hyalina*; Manning, 1969a, 1969c; Table 7), suggesting that number of stages or duration of larval development sometimes may be variable.

The relationships between postlarval size and morphological divergence among populations are not clear for a number of squillids with large and moderately sized postlarvae, perhaps reflecting the need for further study of the biology and systematics of members of this family. In the widely distributed *Squilla aculeata–S. empusa* lineage (Table 7), postlarvae are only 12–14 mm in length, but juveniles of the subregional endemic *S. tiburonensis* are 16–21 mm long. On the other hand, the subregional endemics *S. mantis* and *Fennerosquilla heptacantha* produce moderately large postlarvae (17–23 mm and 18 mm, respectively) (Giesbrecht, 1910; Manning 1969a, 1977a; authors' unpublished observations). Also, the transregional *Clorida mauiana* apparently has either moderate or small postlarvae (juveniles <17 mm; Manning, 1976b, Table 7). Despite their unusually broad distributions, *Alima hyalina* and *A. hieroglyphica* have only moderately large postlarvae (16–22 mm and 15–17 mm, respectively); however, pelagic larvae 54 mm and 30 mm long have been reported for these two species (Gurney, 1946; Manning, 1962c; Alikunhi, 1944). Species of *Schmittius* appear to possess relatively large postlarvae (juveniles 22–33 mm; Bigelow, 1894; Manning, 1972a). Although this genus is endemic to the East Pacific, it is related to a similar lineage (*Squilloides*) in the Indo–West Pacific. A species introduced into the Mediterranean from the Indo–West Pacific, *Oratosquilla massavensis*, produces postlarvae 15–18 mm in length; it is not known whether or not long-lived larvae were instrumental in this colonization process (Lewinsohn and Manning, 1980; Table 7).

Even though the *Rissoides–Meiosquilla–Crenatosquilla* lineage shows generic affinities among Atlantic–East Pacific subregions, this lineage is characterized by extensive endemicity and some of the smallest postlarvae among the squillids. Postlarvae are moderately small in the American *Meiosquilla* (12 mm in *M. tricarinata*, <11–16 mm in *M. quadridens*, 12–13 mm in *M. schmitti*, and 12–14 mm in *M. lebouri*; Camp, 1973; Gurney, 1946; Manning, 1969a; authors' unpublished data). Known only in the East Pacific, the related genus *Crenatosquilla* possesses even smaller postlarvae (<9 mm; Reaka and Manning, 1980), perhaps comparable in size to those of *Gonodactylus* and *Nannosquilla*. In *Rissoides*, postlarvae are 16 mm in length in *R. desmaresti* (Giesbrecht, 1910). Juveniles are <13–15 mm and 15 mm, respectively, in the East Atlantic *Rissoides africanus* and in *R. barnardi* off South Africa (Manning, 1969c, 1975b, 1977a; Table 7).

Therefore, although there are several conspicuous exceptions (e.g., *Squilla aculeata*, *Clorida mauiana*, possibly *Alima hyalina* and *A. hieroglyphica*), a general correlation exists between postlarval size and intimate taxonomic relationships among geographic subregions when groups of moderately large versus relatively small postlarvae are compared.

HABITAT.—Squillids generally dig U-shaped burrows in level bottom habitats of mud or muddy sand, frequently in association with shells or debris. However, whereas some species of *Meiosquilla* are found in mud or sand, members of the related *Crenatosquilla* occur under and among rocks in coral rubble (Reaka and Manning, 1980, 1981).

Many squillids are found in shallow water, but some species have considerable depth ranges. A number of species of *Squilla* occur in unusually deep habitats, but deep distributions do not correlate with low divergence from species in other subregions. For example, the *S. cadenati–S. intermedia–S. biformis* lineage occurs in deep water (to 300, 615, and 466 m, respectively), but the *S. aculeata–S. empusa* lineage usually is found in less than 40 m. Nevertheless, both lineages are known from all three parts of the Atlanto–East Pacific region. The *S. hancocki–S. deceptrix* lineage inhabits moderate to deep water, but *S. tiburonensis–S. lijdingi* and *S. panamensis–S. brasiliensis* occupy moderate to shallow habitats. *Pterygosquilla armata* occurs in cold, deep (to 380 m) water, and subspecies are known from all geographic subregions in the southern hemisphere. Species of *Schmittius*, an endemic East Pacific genus with Indo–West Pacific affinities, have been recorded from depths between 125 and 350 m. On the other hand, the transregional species *Clorida mauiana* is found at moderately shallow depths (26–79 m), and *Cloridopsis dubia* (0–73 m) and both species of *Alima* (0–37 m) also live in shallow water. Thus, both widespread and geographically limited lineages are found in both deep and shallow habitats.

GAPS IN DISTRIBUTION.—Several instances of apparent extinction are found in the squillids. Otherwise pantropical, both species of *Alima* are conspicuously absent from the East Pacific. It is possible that members of this genus have colonized the Atlantic rather recently, but have been unable to cross the East Pacific barrier. However, *Alima hyalina*, along with *Pseudosquilla ciliata* and *P. oculata*, has been recorded from the mid-South Atlantic island of St. Helena. All three of these species also have been recorded from Hawaii (Townsley, 1953), and *A. hyalina* and *P. ciliata* are both known from South Africa and the Red Sea (Ingle, 1958; Manning, 1969a,c; Manning and Lewinsohn, 1986). These distributional patterns suggest that these species are specialized for colonization, making it likely that these species have reached but not survived in the East Pacific.

Squilla aculeata is represented in the East Atlantic and East Pacific by distinct subspecies but is absent in the West Atlantic, where it is replaced by a cognate, *S. empusa*.

Although *Oratosquilla massavensis* is absent from the Americas, this species has invaded the eastern Mediterranean from the Red Sea in recent times (Lewinsohn and Manning, 1980). This gap in distribution clearly does not represent an American extinction but a very recent colonization of the Mediterranean.

Although absent from the East Atlantic, *Cloridopsis* includes both American and Indo–West Pacific representatives. There is no evidence to determine whether it became extinct in or never reached the East Atlantic, but the occurrence of several species of this genus in the Indo–West Pacific suggests that it may be an old lineage with a Tethyan distribution that has undergone extinction in parts of its original range.

Both *Schmittius* and *Clorida* live in the East Pacific and show Indo–West Pacific affinities. These lineages either never reached or became extinct in the Atlantic Ocean.

BATHYSQUILLOIDEA

BATHYSQUILLIDAE

The bathysquillids are believed to represent an ancient stock of stomatopods now restricted to deep, continental slope habitats (Manning and Struhsaker, 1976). They possess reduced eyes and a toothed spearing claw. One genus and species is known from the study area.

ADULT BODY SIZE.—*Bathysquilla microps* is a large species, attaining a total length of 255 mm; it has been recorded from Hawaii as well as the West Atlantic (Manning and Struhsaker, 1976). Three other Indo–West Pacific representatives of the family are known. *Bathysquilla crassispinosa* (Fukuda, 1910), length to almost 300 mm, is reported from several localities from Japan to South Africa (Manning and Struhsaker, 1976; Bruce, 1985). *Indosquilla manihinei* Ingle and Merrett, 1971, length to 176 mm, is recorded from the western Indian Ocean (Ingle and Merrett, 1971). Also, *Altosquilla soelae* Bruce, 1985, length to 120 mm, was found recently on the Australian northwest shelf.

HABITAT.—Other than depth, little is known of the habitat of bathysquillids; they presumably construct burrows in soft, level bottoms. *Bathysquilla microps* has been taken from depths of 604–1281 m (Manning and Struhsaker, 1976). *Bathysquilla crassispinosa* is recorded from 208–310 m (Fukuda, 1910; Manning and Struhsaker, 1976; Bruce, 1985); the latter author reports a specimen of this species taken from clay-mud substrate. *Indosquilla manihinei* is known from 420 m (Ingle and Merrett, 1971), and *Altosquilla soelae* was taken from cold (8.4°–9.6° C) silty substrates at 396–458 m (Bruce, 1985).

GAPS IN DISTRIBUTION.—*Bathysquilla microps* occurs in both the West Atlantic and in the Indo–West Pacific, but not in the East Atlantic or in the East Pacific. Whether this is a reflection of its extinction in one or both of those regions or reflects incomplete sampling of these relatively rare animals is not known.

Discussion

Summarizing information for all families of stomatopods, we first discuss general relationships of body size, postlarval size, and habitat to the degree of morphological change and speciation that has occurred since different lineages became isolated in the East Atlantic, West Atlantic, and East Atlantic subregions. Then we review the evidence for apparent extinctions, and relate these patterns to body size, larval settling size, habitat, and evolutionary equilibria in different geographic subregions.

ADULT BODY SIZE

Most groups of stomatopods with small body sizes are characterized by relatively large numbers of species and substantial differentiation of both lower and higher taxa among regions and/or subregions. For example, the American species of *Gonodactylus* are distinct from Indo–West Pacific lineages of this genus, and all 19 American species are endemic to either the East Pacific or West Atlantic. With 45 species, the genus *Gonodactylus* contains more species world-wide than any other genus of stomatopods (Table 2). The small gonodactylid *Protosquilla* has diverged from Indo–West Pacific relatives at the generic level in the East Atlantic. The small lysiosquilloids include nine genera endemic to the Atlanto–East Pacific area, and, in one genus restricted to the Americas (*Nannosquilla*), all 20 species are endemic to their own subregions. A related genus, *Nannosquilloides*, is unique to the East Atlantic. Of the small squillids, the *Rissoides–Meiosquilla–Crenatosquilla* lineage is largely restricted to the Atlanto–East Pacific (there is one South African species), but differentiation at the generic level has occurred between East Atlantic (*Rissoides*) and American (*Meiosquilla, Crenatosquilla*) lineages. All 13 species are subregionally endemic. On the other hand, several instances of small species with close affinities to taxa in different regions are known (members of *Eurysquilla, Coronida, Neocoronida,* and *Clorida*).

Moderately sized species sometimes show the lowest rates of divergence among all of the stomatopods. Such species include the largest gonodactyloids (*Odontodactylus*), the smallest pseudosquillids (*Pseudosquilla*), some medium-sized lysiosquilloids (*Acanthosquilla, Heterosquilla, Heterosquilloides*), and some medium-sized squillids (*Alima*). Exceptions to this trend include some lysiosquillids, nannosquillids, and squillids with subregionally endemic taxa (*Tectasquilla, Coronis,* and *Schmittius*). Even considering these exceptions, however, the level of phylogenetic affinity to taxa in other regions or subregions is considerably higher and the number of species per genus is lower in taxa of moderate than of small body size.

In taxa of relatively large body size, we find several trends in geographic divergence. One species of *Hemisquilla* occurs in different East and West Pacific subregions as distinct subspecies, and a cognate species is known from the Southwest Atlantic. Species of *Parasquilla* and *Pseudosquillopsis* show close relationships among regions and subregions, although all species are distinct. Including some of the largest known stomatopods, *Lysiosquilla* is found in all geographic regions. Although they are subregionally distinct, species of *Lysiosquilla* clearly show close affinities among distant regions. A related genus, *Lysiosquilloides*, until recently considered to be endemic to the East Atlantic, is now known to be represented by a species in the Indo–West Pacific as well (Naiyanetr, 1980). Some squillids also reach very large body sizes. Members of two genera of relatively large body size, *Cloridopsis* and *Pterygosquilla*, show particularly low divergence among regions and contain few species. *Squilla* also reaches large sizes, but, like *Lysiosquilla, Parasquilla,* and *Pseudosquillopsis*, shows both strong affinities among populations in distant regions and tendencies for regional differentiation. Atlanto–East Pacific species of *Squilla* have diverged at the generic level from all Indo–West Pacific relatives. *Squilla* includes more Atlanto–East Pacific species than any other genus in this study, and all species except one are subregional endemics. On the other hand, particularly the larger species show strong cognate relationships among subregions, and one of the largest American species, *S. aculeata*, has diverged only at the subspecific level in the East Pacific and East Atlantic subregions. The bathysquillids include an old stock of large stomatopods (Manning and Struhsaker, 1976), one species of which spans West Atlantic and Indo–West Pacific areas. Therefore, while most large stomatopods do not achieve the pantropical distributions found in some of the moderately sized stomatopods, they show conservative patterns of morphological differentiation among regions and subregions.

When the degree of taxonomic divergence in species of different body size is quantified for all stomatopods within the study area, body size shows a highly significant inverse relationship to regional divergence within lineages; similarly, species of small body size are significantly more likely to be included in local species clusters than are large species, suggesting a high incidence of local species multiplication in the former (Table 8). We conclude that evolutionary change in stomatopods proceeds at the most rapid rates in lineages of small body size, but that considerable divergence is occurring among some lineages of larger body size as well. Most large lineages and particularly a few moderately sized lineages appear to be evolutionarily conservative.

POSTLARVAL SIZE

Several previous workers have reported for other groups of marine invertebrates that species with dispersing larvae have low rates of morphological divergence and speciation compared to those with abbreviated larval phases (Scheltema, 1971, 1972, 1977, 1978, 1979; Shuto, 1974; Hansen, 1978, 1980, 1982; Jablonski, 1980, 1982; Jablonski and Valentine, 1981; Jablonski and Lutz, 1983). One can see how distant populations with potential larval exchange, such as those in the East and West Atlantic, could remain genetically similar. However, even if a species occurs in geographically isolated subregions, species with pelagic larvae may evolve slowly within each of the subregions. Species with dispersing larvae are likely to occupy broad geographic ranges within each subregion, encounter diverse local habitats, and exchange genetic material among populations in these different local environments. These factors can reduce the effectiveness of directional selection within each

TABLE 8.—Degree of phyletic divergence (conspecific, cognate, and endemic relationships) among taxa in different geographic subregions, and local species radiation within geographic subregions, where taxa are characterized by different adult and postlarval sizes or different habitats. The percentage figures indicate the proportion of taxa with a given phyletic affinity relative to the total number of taxa in that adult or postlarval size class or in that habitat type. The sum of these proportions sometimes does not equal 100%, since some taxa have both cognate and conspecific relationships to taxa in different subregions. The number of species within locally radiating lineages is derived from the number of taxa included in vertical brackets within subregions in Tables 4–7. Since Indo–West Pacific taxa in Tables 4–7 are biased toward cognates and conspecifics, these taxa are excluded from the present statistical analysis. Statistical tests are based on r × k contingency tables, for example the number of taxa with vs. the number of taxa without conspecifics in each size or habitat category. (* = statistically significant results; AEP = Atlanto-East Pacific)

Character	No. AEP taxa	No. (%) taxa with conspecifics elsewhere	No. (%) taxa with cognates elsewhere	No. (%) endemic species without cognates elsewhere	No. (%) species within locally radiating clusters
Adult body size					
Small (<50 mm)	67	5 (7.5)	19 (28.4)	43 (64.2)	55 (82.1)
Moderate (50–149 mm)	63	19 (30.2)	28 (44.4)	24 (38.1)	31 (49.2)
Large (≥150 mm)	27	8 (29.6)	20 (74.1)	4 (14.8)	8 (29.6)
Statistical test (df = 2)					
χ^2		12.02	16.58	21.09	27.03
P		0.0025*	0.0003*	0.0000*	<0.0000*
Known postlarval size					
Small (<10 mm)	7	1 (14.3)	2 (28.6)	5 (71.4)	6 (85.7)
Moderate (10–19 mm)	15	6 (40.0)	6 (40.0)	5 (33.3)	5 (33.3)
Large (≥20 mm)	17	9 (52.9)	9 (52.9)	4 (23.5)	4 (23.5)
Statistical test (df = 2)					
χ^2		3.07	1.33	5.01	8.37
P		0.215	0.515	0.082	0.015*
Postlarval size (known and estimated)					
Small (<10 mm)	48	2 (4.2)	11 (22.9)	38 (79.2)	43 (89.6)
Moderate (10–19 mm)	36	11 (30.6)	18 (50.0)	10 (27.8)	20 (55.6)
Large (≥20 mm)	37	11 (29.7)	26 (70.3)	6 (16.2)	13 (35.1)
Statistical test (df = 2)					
χ^2		12.29	19.32	39.39	27.67
P		0.0021*	0.0000*	0.0000*	0.0000*
Substrate type					
Coarse bottom	37	5 (13.5)	13 (35.1)	21 (56.8)	27 (73.0)
Level bottom	109	27 (24.8)	52 (47.7)	41 (37.6)	58 (53.2)
Statistical test (df = 1)					
χ^2		2.05	1.77	4.14	4.43
P		0.153	0.184	0.042*	0.035*
Latitude					
Tropical	127	27 (21.3)	51 (40.2)	60 (47.2)	75 (59.1)
Temperate	30	7 (23.3)	16 (53.3)	11 (36.7)	19 (63.3)
Statistical test (df = 1)					
χ^2		0.20	1.72	1.10	0.18
P		0.66	0.19	0.30	0.67
Depth					
Shallow (<100 m)	110	23 (20.9)	42 (38.2)	54 (49.1)	65 (59.1)
Moderate (100–300 m)	21	4 (19.0)	13 (61.9)	7 (33.3)	15 (71.4)
Deep (≥300 m)	22	5 (22.7)	9 (40.9)	10 (45.5)	12 (54.5)
Statistical test (df = 2)					
χ^2		0.09	4.09	1.77	1.45
P		0.96	0.13	0.41	0.48
Temperature					
Warm	112	23 (20.5)	45 (40.2)	53 (47.3)	66 (58.9)
Cold	45	9 (20.0)	22 (48.9)	18 (40.0)	28 (62.2)
Statistical test (df = 1)					
χ^2		0.06	1.00	0.69	0.15
P		0.94	0.32	0.40	0.70

subregion. Thus, everything else being equal, one might expect change to be conservative, even within subregionally isolated populations, in species with dispersing larvae compared to species with reduced larval phases.

As discussed in the introduction, we have assumed that length of the pelagic larval period and dispersal potential is roughly proportional to size of the settling postlarva. In the case of the Atlanto–East Pacific stomatopods, we find that size of postlarvae usually increases with increased adult body size among genera (e.g., *Gonodactylus* vs. *Odontodactylus*; *Pseudosquilla* vs. *Pseudosquillopsis* and *Hemisquilla*; *Nannosquilla* and *Acanthosquilla* vs. *Heterosquilla* and *Lysiosquilla*; *Meiosquilla* vs. *Alima*; see also Reaka, in press). Exceptions to this trend include some species of *Squilla* and possibly some populations of *Pterygosquilla*. In many cases, increased postlarval size also correlates with lower divergence among subregions (*Gonodactylus* vs. *Odontodactylus*; gonodactylids and protosquillids vs. pseudosquillids, especially *Pseudosquilla*); however, there are many exceptions. For example, *Coronida*, *Alima*, and probably *Clorida* produce relatively small or moderately sized postlarvae but show very low rates of divergence among subregions (although very large pelagic larvae have been reported for *Alima*). *Nannosquilla* and *Acanthosquilla* both have relatively small postlarvae, but the former includes numerous subregionally endemic species and the latter transregional species. Smaller postlarvae are found in *Pseudosquilla* than in *Pseudosquillopsis*, but the former is less regionally differentiated than the latter. The most widely distributed stomatopod, *Heterosquilloides mccullochae*, apparently does not have unusually large postlarvae compared to either the large lysiosquillids or the pseudosquillids and hemisquillids. In general, the correlation between postlarval and adult body size (Reaka, in press) appears to be stronger than the relationship between postlarval size and evolutionary divergence.

Nevertheless, when the degree of taxonomic divergence is quantified for all taxa with postlarvae of different sizes, postlarval size is inversely related to degree of evolutionary change (Table 8). This correlation is higher for comparisons including estimated postlarval size than for comparisons in which postlarval size is known, however. Where postlarval size is definitely known, species with small postlarvae are significantly more likely to be included within locally radiating species clusters, and probably are more likely to be endemic without relatives in other subregions, than are species that possess larger postlarvae (Table 8).

HABITAT

Rates of divergence do not correlate consistently with distributions in deep or cold waters or with latitude (Table 8). Among species that occur in relatively deep habitats, several show very low rates of geographic divergence (*Bathysquilla microps*, *Odontodactylus brevirostris*, *Hemisquilla ensigera*, *Pterygosquilla armata*; Tables 4–7), which is consistent with the hypothesis that evolution proceeds more slowly in deep than in shallow habitats. However, many shallow-dwelling species also exhibit low rates of divergence (*Pseudosquilla ciliata*, *P. oculata*, *Heterosquilloides mccullochae*, *Squilla aculeata*, *Cloridopsis dubia*, *Alima hyalina*, *A. hieroglyphica*, *Clorida mauiana*; Tables 5–7). Furthermore, many deep-dwelling taxa show restricted ranges, occupying only one or part of one geographic subregion (*Gonodactylus torus*; some species of *Parasquilla*, *Eurysquilla*, *Allosquilla*, *Squilla*, *Rissoides*, and *Schmittius*; Tables 4–7). Coral-dwelling species that occupy exclusively deep habitats have significantly smaller geographic ranges than those with shallow or broad depth distributions (Reaka, 1980). Thus, there is no significant overall correlation between depth and rate of morphological divergence among subregions or speciation within subregions (Table 8).

Although it has been postulated that rapid evolution in the tropics fosters high species diversity compared to temperate or polar environments, transregional distributions are not more frequent among lineages that inhabit temperate compared to tropical waters (Table 8); instead geographic divergence correlates with body size. For example, of the smaller species living in cold habitats (all of which are lysiosquilloids or squilloids), *Heterosquilloides armata* and *Heterosquilla platensis* each occur in only one part of one subregion (the North West and South West Atlantic, respectively), and *Heterosquilla polydactyla* is found only on the coasts of south temperate South America. *Platysquilla eusebia* is known from the North East Atlantic, while the related *Platysquilloides enodis* has been taken only from the North West Atlantic. Endemic to the East Pacific, the two species of *Schmittius* are known from as far south as Peru and as far north as Central California, while several species of another genus of moderately small body size, *Rissoides*, occur in temperate waters in the Mediterranean and South Africa (Table 7). Thus, many small or moderately sized species from temperate waters have restricted distributions. On the other hand, of the larger species that occur in temperate habitats, subspecies of *Hemisquilla ensigera* occupy ranges over a broad area (California, Chile, New Zealand, Australia), as do those of *Pterygosquilla armata* (Argentina, Chile, New Zealand, South Africa). The widely distributed *Pseudosquillopsis cerisii–P. lessonii* lineage, as well as several cognate species of *Parasquilla*, extend into temperate waters in the Mediterranean and off the Americas (Table 5). Thus, large species inhabiting temperate latitudes tend to be broadly distributed while small species do not.

Among families in the Atlanto–East Pacific region, rates of divergence for *Gonodactylus* and *Squilla*, appear to be related very generally to substrate type, as suggested by Vermeij (1978). The highest degree of subregional differentiation is found among the gonodactylids and protosquillids, which occupy holes in coral rubble and rocks. Most lysiosquillids and nannosquillids occupy sandy substrates in level bottom habitats, and most hemisquillids, pseudosquillids, eurysquillids, squillids, and bathysquillids use muddy or sand and mud substrates, also on level bottoms; in most cases these groups show greater taxonomic affinities among subregions than do the gonodactylids and protosquillids.

However, when examined closely, these trends are subject to many exceptions and in some cases are not statistically significant when all stomatopod taxa from the subregions are considered (Table 8). For example, despite the transregional distribution of *Odontodactylus brevirostris*, some species of this genus occur on reefs and have been collected from holes inside coral rubble (Manning, 1967a; Reaka, personal observations). Also, some species of *Pseudosquilla* are exceptionally widespread but live in coarse substrates and among the roots of grass beds (Hatziolos, 1980; Reaka and Manning, 1981). Both *Odontodactylus* and *Pseudosquilla* reach moderately large body sizes. The coronidids (e.g., *Coronida*, *Neocoronida*) inhabit coarse substrates, have smashing claws, and show close affinities among geographically distant populations. Some species of *Nannosquilla* occur exclusively in sandy habitats, whereas others burrow among rocks and coral rubble (Reaka and Manning, 1980); nevertheless, all species of the genus show high subregional endemism. Similarly, although all species of *Meiosquilla* and *Crenatosquilla* are endemic to a single subregion, some species live on mud flats, some in sandy environments, and others in rocks and rubble (Reaka and Manning, 1980). Therefore, except in the coronidids, the trend for high regional differentiation in species that are associated with hard substrates appears to be more closely related to body size than to type of habitat occupied.

There is no statistically significant relationship between the type of substrate inhabited and the incidence of conspecific and cognate relationships between taxa in separate subregions; however, the degree of endemism (without cognates elsewhere) and the numbers of species included within locally radiating species clusters are statistically associated with substrate type (Table 8). These results suggest that speciation events (though not necessarily subsequent morphological divergence) may be more common in species inhabiting coarse than level bottom habitats. Rapid speciation could result either from biotic pressures (predation, competition for space) that have been demonstrated to limit stomatopod populations in these environments (Reaka, 1985), or may result from the more complex social behavior known for stomatopods that occupy coarse compared to level bottom habitats (Reaka and Manning, 1981).

Divergence appears to occur most slowly in two separate conditions. First, taxa may retain close affinities to those in other subregions when several factors (body size, larval characteristics, substrate type, temperature or depth) operate together. For example, *Bathysquilla microps* reaches a large size; inhabits soft substrates; lives in cold, deep environments; and occupies a broad, probably relict, distribution (Table 7). *Hemisquilla ensigera* and *Pterygosquilla armata* reach large sizes as adults; have large, long-lived larvae; and inhabit soft substrates in cold, deep water (Tables 5, 7).

Second, broad geographic ranges and slow rates of divergence can occur in shallow-dwelling species with adaptations for colonization. For example, *Pseudosquilla ciliata* is of moderate body size; lives in shallow, sandy environments with rubble; and produces tremendous numbers of larvae that progress from tiny to relatively large settling stages (Reaka, 1979a). Also of moderate size, *Alima hyalina* produces larvae that grow to unusually large sizes; their size, the known biology of squillid larvae, and the distribution of the species (including the South Atlantic island of St. Helena, which has emerged as recently as the Miocene; Briggs, 1974:93), suggest that these larvae spend long periods in the plankton. *Pseudosquilla oculata*, *Alima hieroglyphica*, and *Heterosquilloides mccullochae* show similar biological attributes and distributions. In addition, most gonodactylids occupy shallow habitats in warm water. Especially the larger species (moderately sized in our overall classification) within the coral-dwelling lineages occupy relatively broad geographic ranges and are adapted for colonization and dispersal in disturbed reef habitats (Reaka, 1979a, 1980, 1985).

Therefore, broad geographic distributions and slow rates of evolutionary change may occur either in deep relict populations or in species adapted for dispersal and colonization in shallow environments. Species of moderate body size are more likely to show dispersal and colonization abilities, whereas those of large body size often show relict distributions. Divergence among distant populations is low in both cases. Consequently, generalizations about rates of divergence and environmental factors, particularly depth, can be obscured because these factors do not operate in isolation.

GAPS IN DISTRIBUTION

The number of species observed at any one time is a result of both rates of species multiplication and rates of extinction. In the present study, we examine conspicuous absences of taxa where, on the basis of subregional geographic distributions, a lineage can be expected to occur. This method can best evaluate possible extinctions in broadly distributed species and lineages, and probably underestimates apparent extinctions in taxa of small body size and restricted distributions. However, many transregional species lineages and genera of stomatopods are known, so that absences can be identified. The geographic method also is subject to the objection that the absence of a species from a region may indicate that the species, evolved elsewhere, merely has not yet arrived in a given area. Each example must be examined carefully, but in many cases extinction is the most parsimonious explanation of a gap in distribution. While not entirely satisfactory, this analysis provides some information on possible extinction in lineages with different body sizes, larval characteristics, and habitat requirements, and it yields new information on regional patterns of extinction and diversity.

Three species lineages are present in the East Pacific and East Atlantic, but not the West Atlantic (*Pseudosquillopsis cerisii–P. lessonii/P. marmorata*; *Coronida bradyi–C. glasselli/C. schmitti*; and *Squilla aculeata calmani–S. aculeata aculeata*; Tables 5–7). However, *Squilla aculeata* is replaced by a relative, *S. empusa*, in the West Atlantic, and a West Atlantic gap in the *Coronida* lineage is not certain since the affinities and derivation of *Acoridon*, a recently discovered West Atlantic coronidid, are not known.

This leaves one highly likely (*Pseudosquillopsis*) and a possible (*Coronida*) case of extinction in the West Atlantic (Table 9). One of these two lineages is large in body size and one small. Postlarvae are large and probably small. One of the lineages inhabits soft and the other coarse substrates; and both live in shallow or moderate depths. The distribution of one lineage extends into cold temperate waters, and the other is from tropical warm climates.

Apparent extinctions are more numerous in the East Pacific than in the West Atlantic. Eight species lineages occur in the West Atlantic and Indo–West Pacific, but not the East Pacific (the Indo–West Pacific affinities of a ninth species, *Heterosquilloides armata*, are not known). Six of these lineages are conspecific (*Odontodactylus brevirostris, Pseudosquilla ciliata, P. oculata, Alima hyalina, A. hieroglyphica,* and *Bathysquilla microps*). Cognate representatives of the other two lineages (*Eurysquilla pacifica–E. maiaguesensis/E. chacei/E. holthuisi*; *Lysioquilla glabriuscula–L. maculata*) also are absent from the East Pacific (Tables 4, 5, 7). In addition, 8 species (members of *Tectasquilla, Coronis,* the *Platysquilloides–Mexisquilla–Platysquilla–Allosquilla* complex, and *Fennerosquilla*) are known from the Atlantic but not the East Pacific. However, *Pseudosquilla oculata* is replaced by a relative, *P. adiastalta,* in the East Pacific, suggesting divergence rather than extinction. It is not known whether the seven endemic Atlantic genera arose in the Atlantic after elevation of the Central American isthmus or whether they became extinct in the East Pacific. Although extinction of the ancient *Bathysquilla microps* lineage seems likely in the East Pacific, this deep-dwelling species simply may not have been collected there.

Therefore, seven (*Odontodactylus brevirostris, Pseudosquilla ciliata, Eurysquilla maiaguesensis–E. pacifica, Lysiosquilla glabriuscula–L. maculata, Alima hieroglyphica, A. hyalina,* and *Bathysquilla microps*) conspicuous omissions of taxa in the East Pacific stomatopod fauna remain (Table 9). Five of these seven species lineages (all but *E. maiaguesensis–E. pacifica* and *A. hyalina*) are moderate-sized or large as adults. Where known, all have moderate-sized or large postlarvae. Two inhabit coral rubble, often with associated coralline sand, and the others live in muddy or muddy sand environments. Four lineages show shallow and three moderate to deep distributions. All seven apparent extinctions are from tropical latitudes, although two derive from very deep cold waters. Apparent extinctions, then, are more numerous in the East Pacific than in the West Atlantic.

Overall, however, the evidence suggests many more omissions of taxa, and probably much more extensive extinction, in the East Atlantic than in the Americas. Twelve species lineages and seven generic lineages are absent from the East Atlantic (Table 9). Eight of the species lineages (*Odontodactylus brevirostris, Eurysquilla maiaguesensis–E. pacifica, Lysiosquilla panamica–L. tredecimdentata, L. glabriuscula–L. maculata, Heterosquilla polydactyla–H. tricarinata, Heterosquilloides insolita–H. insignis, Acanthosquilla digueti, Bathysquilla microps*) are present in the Americas and have relatives in the Indo–West Pacific but are conspicuously absent in the East Atlantic. Of these, extinction is the simplest explanation for all except for the *Heterosquilla polydactyla* lineage, which because of its distribution around the southern tip of South America may never have been in the East Atlantic. We do not know if *Heterosquilloides armata* arose in the West Atlantic or became extinct in the East Atlantic and East Pacific. In addition, several species lineages of *Squilla* are known in the Americas but not the East Altantic; they may either have become extinct there or may have arisen at a later time in the new world. The seven genera that are absent from the East Atlantic include 45 American species. Extinction seems highly likely for *Gonodactylus* and *Cloridopsis* (including 20 American species), since these genera are well represented in both subregions of the Americas and in the Indo–West Pacific; either these genera or their precursors must have been present in the East Atlantic during continental divergence. *Nannosquilla* possibly became extinct in the East Atlantic. However, this genus is known only from the Americas, and may have arisen there. Alternatively, if a pre-existing *Nannosquilla*-like lineage was present throughout the Atlanto–East Pacific, this lineage may have diverged into the endemic genus *Nannosquilloides* in the East Atlantic. *Tectasquilla, Coronis,* and *Fennerosquilla* also are endemic to the West Atlantic, but there is no way to determine whether they arose there or became extinct in the East Atlantic. *Hemisquilla* either became extinct or may have never been in the East Atlantic because of its southerly distribution around South America.

Of the seven species lineages and two generic lineages where we judge extinction to be likely in the East Atlantic (Table 9), six are characterized by moderate to large body size; however, the three remaining small or moderately sized lineages (*Gonodactylus, Eurysquilla maiaguesensis* and relatives, *Acanthosquilla digueti*) include 23 American species. The postlarvae of only four of these taxa are known; they are small in *Gonodactylus* (19 species), moderately sized in *Odontodactylus* (1 species lineage), and large in *Lysiosquilla*

TABLE 9.—Instances of possible and very likely (*) extinctions of stomatopod Crustacea (cases of gaps in distribution but where extinction was not judged probable are omitted from this list; [ ] = lineage replaced by a relative, probably due to endemic divergence; where entire genera are missing from an area, the genus name and the number of AEP species are given; for the Gonodactyloidea, group A includes the Odontodactylidae, Gonodactylidae, and Protosquillidae (Table 4); group B includes the Hemisquillidae, Pseudosquillidae, and Eurysquillidae (Table 5).

Absent EP	Absent WA	Absent EA	Absent Americas	Absent Atlantic
GONODACTYLOIDEA, Group A: 2 (*2) absences of species lineages 2 (*1) absences of generic lineages, 21 (*19) species				
* *Odontodactylus brevirostris* pl M, as M CB, DP, TR, C		* *O. brevirostris* pl M, as M CB, DP, TR, C		
		* *Gonodactylus* (19 sp) pl S, as S-M CB, SH, TR, W		
			Protosquilla (2 sp) pl S, as S CB, SH, TR, W	
GONODACTYLOIDEA, Group B: 5 (*4) absences of species lineages 2 (*0) absences of generic lineages, 3 (*0) species				
		Hemisquilla (2 sp) pl L, as L LB, MD, TE, C		
	* *Pseudosquillospsis lessonii–P. cerisii* pl L, as M-L LB, SH-MD, TE, C			
* *Pseudosquilla ciliata* pl L, as M CB, SH, TR, W				
[*P. oculata*] pl L, as M CB, SH, TR, W				
* *Eurysquilla maiaguesensis–E. pacifica* pl —, as S LB, MD, TR, W		* *E. maiaguesensis–E. pacifica* pl —, as S LB, MD, TR, W		
			Manningia (1 sp) pl M, as S LB, SH, TR, W	
LYSIOSQUILLOIDEA: 13 (*6) absences of species lineages 7 (*0) absences of generic-suprageneric lineages, 30 (*0) species				
		* *Lysiosquilla panamica–L. tredecimdentata* pl (L), as L LB, SH, TR, W		* *L. panamica–L. tredecimdentata* pl (L), as L LB, SH, TR, W
* *Lysiosquilla glabriuscula–L. maculata* pl L, as L LB, SH, TR, W		* *L. glabriuscula–L. maculata* pl L, as L LB, SH, TR, W		
			Lysiosquilla monodi–L. sulcirostris pl (L), as M-L LB, SH, TR, W	
			Lysiosquilloides aulacorhynchus–L. siamensis pl —, as L LB, SH, TR, W	
		Heterosquilla polydactyla–H. tricarinata pl L, as M LB, SH, TE, C		
		* *Heterosquilloides insolita–H. insignis* pl —, as M LB, MD, TR, W		
Heterosquilloides armata pl —, as M LB, MD, TE, C		*H. armata* pl —, as M LB, MD, TE, C		
Tectasquilla (1 sp) pl —, as M —, SH, TR, W		*Tectasquilla* (1 sp) pl —, as M —, SH, TR, W		
		* *Acanthosquilla digueti* pl —, as S LB, SH, TR, W		

TABLE 9.—Continued.

Absent EP	Absent WA	Absent EA	Absent Americas	Absent Atlantic
Coronis (1 sp) pl L, as M LB, SH, TR, W		*Coronis* (1 sp) pl L, as M LB, SH, TR, W		
Platysquilloides–Mexisquilla–Platysquilla–Allosquilla (5 sp) pl —, as S-M LB, SH-DP, TE-TR, C-W				
			Nannosquilloides (1 sp) pl —, as S LB, MD, TE, C	
		Nannosquilla (20 sp) pl S, as S LB-CB, SH, TE-TR, C-W		
	Coronida schmitti–C. bradyi pl (S), as S CB, SH, TR, W			
				Neocoronida cocosiana–N. martensi pl —, as S CB, SH, TR, W
SQUILLOIDEA: 6 (*2) absences of species lineages 5 (*1) absences of generic lineages, 6 (*1) species				
	[*Squilla aculeata*] pl M, as L LB, SH, TR, W			
		Squilla panamensis–S. brasiliensis pl (M), as M-L LB, SH-MD, TE-TR, C-W		
		S. tiburonensis–S. lijdingi pl (M), as M LB, MD, TR, W		
		S. hancocki–S. deceptrix pl —, as M LB, MD-DP, TR, C-W		
Fennerosquilla (1 sp) pl M, as M LB, DP, TR, C		*Fennerosquilla* (1 sp) pl M, as M LB, DP, TR, C		
		* *Cloridopsis* (1 sp) pl —, as M-L LB, SH, TR, W		
* *Alima hieroglyphica* pl M, as M LB, SH, TR, W				
* *A. hyalina* pl M, as S LB, SH, TR, W				
				Schmittius (2 sp) pl (L), as M LB, MD-DP, TE, C
				Clorida (1 sp) pl —, as S LB, SH, TR, W
BATHYSQUILLOIDEA: 2 (*2) absences of species lineages				
* *Bathysquilla microps* pl —, as L LB, DP, TR, C		* *B. microps* pl —, as L LB, DP, TR, C		
TOTAL GAPS IN DISTRIBUTION:				
9 (*7) species lineages 4 (*0) generic-suprageneric lineages, 8 species	3 (*1) species lineages 0 generic lineages	12 (*7) species lineages 7 (*2) generic lineages, 45 (*20) species	2 (*0) species lineages 3 (*0) generic lineages, 4 species	2 (*1) species lineages 2 (*0) generic lineages, 3 species

(2 species lineages). Likely extinction occurs in lineages containing 20 American species that inhabit coarse bottoms (*Gonodactylus* and *Odontodactylus*) and in seven species lineages from level bottoms. Gaps in distribution are found in taxa including 23 American species (*Gonodactylus, Lysiosquilla, Acanthosquilla, Cloridopsis*) from shallow and 4 species lineages from moderate or deep water. All likely extinctions occurred in tropical latitudes, and temperatures were warm except for two species lineages inhabiting very deep waters (*Odontodactylus, Bathysquilla*).

Relatively few taxa are found in the Indo–West Pacific and East Pacific but not in the Atlantic (Table 9). *Neocoronida* and *Clorida* may have dispersed from the Indo–West Pacific into either the offshore islands or the continental East Pacific, and we do not regard extinction throughout the Atlantic to be highly likely in these lineages. It is difficult to determine whether a pre-existing *Schmittius–Squilloides* lineage was pantropical but became extinct in the Atlantic, or whether *Schmittius* arose in the East Pacific after the Miocene elevation of Central America. Because all of the lineages within the genus *Lysiosquilla* tend to be very widely distributed, however, the failure of the *Lysiosquilla panamica–L. tredecimdentata* lineage to inhabit the Atlantic indicates a possible instance of extinction in this area. This lineage is moderate to large in adult body size, probably has large postlarvae, and inhabits level bottoms in shallow, warm tropical waters.

Two species lineages in the genera *Lysiosquilla* and *Lysiosquilloides* are present in the Indo–West Pacific and the East Atlantic but are absent from and possibly became extinct in the Americas (Table 9). In addition to one species in the East Atlantic, a number of species of *Manningia* are known in the Indo–West Pacific. It is difficult to determine, however, whether extinction occurred in the New World, or whether *Lysiosquilla monodi, Lysiosquilloides aulacorhyncus,* and *Manningia posteli* arrived and diverged in the East Atlantic after separation of the continents. *Oratosquilla massavensis* has invaded the Eastern Mediterranean via the Suez Canal in recent times (Lewinsohn and Manning, 1980); otherwise, *Oratosquilla* is restricted to the Indo-Pacific, being replaced in the Atlanto–East Pacific by *Squilla*. Two additional generic lineages (*Protosquilla, Nannosquilloides*) are present in the East Atlantic but absent in the New World. Although the genus *Protosquilla* is endemic to the East Atlantic, it may have been derived from Indo–West Pacific relatives (*Chorisquilla*). *Protosquilla* may have become extinct in the Americas or it may have evolved after the opening of the Atlantic. *Nannosquilloides* and *Nannosquilla* are uniquely Atlanto–East Pacific genera and may have diverged from an ancient common stock in the East Atlantic and Americas, respectively; thus it is not clear that the absence of *Nannosquilloides* in American waters represents extinction. The biotic and environmental characteristics of taxa that are absent from the Americas are given in Table 9.

The number of gaps in distribution is higher for the Gonodactyloidea than for the other superfamilies. The number of species lineages plus the number of Atlanto–East Pacific species within generic lineages that are absent from given geographical areas due to possible extinction is 29, 43, and 12 in the Gonodactyloidea, Lysiosquilloidea, and Squilloidea, respectively. Of these, we judge that the absence of 25, 6, and 3 species are very probably due to extinction in these three groups, respectively. Likely instances of extinction thus represent 53% (25/47), 11% (6/55), and 6% (3/54) of the numbers of Atlanto–East Pacific taxa in these three superfamilies, respectively.

Table 10 shows the biotic and environmental characteristics associated with instances of possible and likely extinctions. We emphasize that these data on gaps in distribution must be interpreted with extreme caution awaiting fossil or other comparative evidence. In addition, using our methods, gaps in distribution are less likely to be detected in lineages with narrow rather than with broad geographical distributions. Thus, the geographic method probably underestimates extinctions in species of small body size because species lineages in these groups are likely to occur in fewer regions than those of larger body size (e.g., *Gonodactylus, Nannosquilla, Meiosquilla*). However, extinctions appear to occur in species with large as well as small adult and postlarval body sizes, in species that inhabit soft as well as hard substrates, and in species from shallow, warm environments as well as in deep or cold habitats. Despite their limitations, these preliminary data do suggest working hypotheses for further testing, either in Crustacea or in other animal groups, and we present the statistically significant trends in our data so that they can be further tested and modified as more information becomes available. For example, our data on likely extinctions suggest that extinctions may be more frequent in lineages with dispersing than nondispersing larvae, in taxa that occupy reefs and rock compared to mud and sand habitats, and in animals from warm or tropical compared to cold or temperate environments (Table 10). These predictions need to be tested further on other groups where fossil evidence is available.

Furthermore, apparent extinction rates vary substantially among geographic subregions, as do rates of divergence. The equilibrium between these processes determines the species diversity in a region. Approximately 77 species and subspecies of stomatopods occur in the West Atlantic, 50 in the East Pacific, and 30 in the East Atlantic (Table 3). Of these three subregions, apparent extinctions are most frequent in the East Atlantic, where extinction is likely in seven species lineages and two generic lineages including 20 American species (Table 9). However, very extensive divergence also has occurred in that subregion. An endemic representative of one family (Protosquillidae) and 5 endemic genera with 9 species (*Protosquilla, Platysquilla, Allosquilla, Nannosquilloides,* and *Rissoides*) apparently have diverged in the East Atlantic. All East Atlantic species (except for the

TABLE 10.—Summaries of biological and environmental characteristics associated with instances of possible or likely extinction (see text for discussion). Data are drawn from the number of species lineages plus the number of Atlanto–East Pacific species within generic lineages that are absent from the geographic areas given in Table 9. The total number of species known in each biotic or environmental category (see Table 8) is given to show the number of species with apparent extinctions that one might expect to find in each category; statistical tests based on the two sets of numbers are given below each data set (* = statistically significant results).

Character	No. AEP taxa	Number of species lineages with	
		possible extinctions	likely extinctions
Adult body size			
Small	67	43	16
Moderate	63	34	14
Large	27	14	8
Statistical test			
χ^2		0.50	0.34
p		0.78	0.84
Postlarval size			
Small	48	42	19
Medium	36	10	4
Large	37	15	6
Statistical test			
χ^2		9.69	6.53
p		0.008*	0.038*
Substrate			
Coarse bottom	37	29	22
Level bottom	109	50	14
Statistical test			
χ^2		3.19	16.86
p		0.074	0.000*
Depth			
Shallow	110	66	28
Moderate	21	13	3
Deep	22	9	4
Statistical test			
χ^2		0.87	1.03
p		0.65	0.60
Latitude			
Tropical	127	71	35
Temperate	30	17	1
Statistical test			
χ^2		0.00	5.79
p		0.97	0.02*
Temperature			
Warm	112	49	31
Cold	45	20	5
Statistical test			
χ^2		0.00	3.33
p		0.96	0.07

pantropical lineages of *Pseudosquilla, Heterosquilloides, Alima,* and the south temperate *Pterygosquilla*) are morphologically distinct from American relatives. Three species lineages (*Eurysquilla galatheae, E. leloeuffi, Acanthosquilla septemspinosa*) have diverged into cognate species from relatives in both surrounding (West Atlantic, Indo–West Pacific) areas. Eleven of the 30 East Atlantic species (36.7%) are included within locally radiating species clusters (vertical brackets in Tables 4–7). When the number of species within versus those not included in local species clusters are compared, species multiplication varies significantly among the three subregions (χ^2 = 10.17, df = 2, p = 0.006). In particular, the incidence of species radiations as here measured is lower in the East Atlantic than in the West Atlantic (χ^2 = 10.14, df = 1, p = 0.001) and probably is less than in the East Pacific (χ^2 = 3.41, df = 1, p = 0.065). Therefore, the East Atlantic stomatopod fauna has undergone major phyletic divergence but has suffered high extinction and relatively limited species multiplication, thus it includes relatively few extant species.

Our evidence suggests that the rate of extinction may be lower and phyletic divergence and speciation considerably greater in the West Atlantic than the East Pacific. Seven species lineages are absent and very likely extinct in the East Pacific in contrast to only one from the West Atlantic. Five endemic monospecific genera are known in the West Atlantic (*Tectasquilla, Coronis, Mexisquilla, Acoridon,* and *Fennerosquilla*). Only two endemic genera with three species have developed in the East Pacific (*Schmittius, Crenatosquilla*). At the species level, lineages have diverged from conspecific relatives in both surrounding subregions in *Squilla empusa* (West Atlantic) and *Pseudosquilla adiastalta* (East Pacific). Five West Atlantic species (*Parasquilla boschii, P. meridionalis, Eurysquilla plumata, Lysiosquilla scabricauda,* and *Squilla intermedia*) have diverged from cognate relatives in both surrounding subregions, and two East Pacific species (*Eurysquilla veleronis* and *E. solari*) have diverged from cognate relatives in both surrounding regions. Speciation tends to be somewhat more extensive in the West Atlantic than in the East Pacific, since 54 of 77 (70.1%) of the species in the West Atlantic in contrast to 29 of 50 (58.0%) of those in the East Pacific are included within radiating endemic species groups (Tables 4–7); however, this difference is not statistically significant when the numbers of species within versus those not included in species clusters are tested for the two subregions (χ^2 = 1.97, df = 1, p = 0.16).

Therefore, the considerably fewer species known from the East Pacific than in the West Atlantic probably is due both to higher rates of extinction and lower rates of phyletic divergence in the former. Rates of evolutionary divergence of West Atlantic taxa appear to approach those of East Atlantic stomatopods (Table 11), but high extinction and low rates of local speciation appear to have played a prominent role in reducing the numbers of East Atlantic compared to West Atlantic species.

Area of stomatopod habitat is smaller in the East Atlantic and East Pacific subregions than in the West Atlantic (Ekman, 1953, fig. 19; Reaka, 1980, fig. 1). Rates of extinction as here measured are inversely proportional and the num-

TABLE 11.—Summary of phyletic divergence, species multiplication (% taxa within locally radiating species clusters), and probable extinction (Table 9) in the Atlanto-East Pacific subregions.

	East Pacific	West Atlantic	East Atlantic
Divergence			1 endemic family
	2 endemic genera, 3 species	5 endemic genera, 5 species	5 endemic genera, 9 species
	3 cognate species diverged	6 cognate species diverged	3 cognate species diverged
Species multiplication (%)	58.0	70.1	36.7
Extinction	7 taxa	1 taxon	27 taxa

ber of extant species is directly proportional to total area of habitat in each subregion.

Conclusions

This study reviews the distribution and status of all families and genera of stomatopod Crustacea from both major zoogeographic regions (Atlanto–East Pacific and Indo–West Pacific), and tests a number of hypotheses about intrinsic or environmental factors that enhance or retard rates of morphological evolution in the well-studied Atlanto–East Pacific stomatopods.

The degree of morphological and taxonomic divergence among geographic subregions (East Pacific, West Atlantic, East Atlantic) is consistently correlated with body size. In small taxa, most species are subregionally endemic, considerable radiation of species has occurred within subregions, and groups of species or genera frequently have diverged among subregions. Some moderate-sized species show unusually low divergence, and a number of transregional species are known. Most large species show low rates of divergence, although several taxa or lineages of large body size also show tendencies for regional divergence at the generic and specific level. Lineages of large body size generally have fewer closely related species within subregions than taxa of small body size, suggesting lower species radiation in the former. When all taxa are considered, rates of evolutionary divergence since geographic isolation in different subregions and species multiplication within subregions show a highly significant decline with increased body size.

We suggest that size of settling postlarvae is related to duration of dispersal phases. Size of postlarvae generally increases with adult body size, and species with postlarvae of large known and estimated sizes show lower regional and subregional divergence than those with moderately sized or small postlarvae. Taxa with known small postlarvae are significantly more prone to local speciation than those with known large postlarvae.

Different types of habitat (coral and rock vs. sand and mud substrate; deep or cold vs. shallow and warm water, tropical vs. temperate latitudes) generally were not related to rates of morphological change among geographic subregions. However, the number of endemic species and the number of species within locally radiating lineages were significantly higher for species inhabiting coarse than level bottoms, suggesting that the former habitat (or competition and complex behavior associated with this habitat) may enhance speciation. Low regional divergence occurs in lineages with large body sizes and deep, relict distributions as well as in shallow-dwelling species with dispersing and colonizing tactics. Environmental temperature and latitude were consistently unrelated to rates of evolutionary change. Trends in regional divergence are more coherently related to adult and postlarval size than to habitat characteristics.

Extinction, estimated from conspicuous gaps in distribution, appears to occur in taxa of all body sizes, postlarval sizes, and habitat types. Our data suggest that extinction is more frequent in the gonodactyloid than in the squilloid or lysiosquilloid stomatopods, in lineages with dispersing than nondispersing larvae, in taxa that occupy reefs and rock compared to mud and sand substrates, and in animals from warm or tropical compared to cold or temperate environments. These hypotheses need to be further tested with paleontological evidence and data from other groups of organisms.

Apparent extinctions are most prominent in the East Atlantic, followed by the East Pacific, then the West Atlantic. Although phyletic divergence also is dramatic in the East Atlantic, this subregion supports the fewest extant species of the three subregions. The West Atlantic stomatopods have undergone extensive phyletic divergence from relatives in other regions; however, this fauna has been subject to relatively low extinction rates and high local species multiplication. The West Atlantic supports the largest extant stomatopod fauna of the three subregions. Stomatopods in the East Pacific have undergone somewhat less speciation and considerably lower rates of phyletic divergence from relatives in surrounding regions than those in the West Atlantic; in addition, higher rates of extinctions probably have contributed to the reduced numbers of species observed in this geographic subregion compared to the West Atlantic.

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