

# THE EVOLUTION OF SPINY LOBSTERS (PALINURIDAE): A STUDY OF EVOLUTION IN THE MARINE ENVIRONMENT

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Received October 18, 1966

The purpose of this paper is to evaluate relationships in the light of morphological and paleontological evidence, and to propose an evolutionary scheme which accounts for the present distribution of extant palinurid species. The spiny lobsters, because of their large size, commercial importance, benthic habits as adults and pelagic habit as larvae, and their wide geographic and vertical distribution, are well suited for a study of evolution in the marine environment. In 1946 Holthuis provided an excellent basic taxonomic revision of the Palinuridae and, sometimes with colleagues, he followed this up with more detailed studies of smaller groups within the family, particularly in the genus *Panulirus*. But some of the less well known genera inhabiting deeper waters still require revision and for this reason it has been necessary to include some taxonomic discussion in the paper; this has been kept to a minimum and will be reported on more fully in an appropriate publication at a later date. The deficiencies in our knowledge of palinurid systematics and evolution have been realized by Glaessner (1960) who stated (p. 42), "There is still some doubt about homologies and evolution in the Scyllaridea [Palinuridae and Scyllaridae] . . . for which groups more morphological information on recent and fossil forms is required." We have attempted to overcome these deficiencies and to present speciation mechanisms applicable to the marine environment.

## PHYLOGENETIC RELATIONSHIPS

We have based our phylogenetic scheme entirely on external morphology. In order

to assess "significant" characters upon which to base our phylogenetic arrangement, we first tabulated the major external morphological features which varied most between genera. For some features no meaningful arrangement could be obtained. For instance, the form of the abdominal sculpturing could be arranged as follows: no sculpture, one transverse groove interrupted medianly, one continuous transverse groove, four transverse grooves, seven transverse grooves. However, other abdominal sculpture patterns are found which are not easily fitted to this series, e.g. squamiform sculpture or longitudinal carina. Because of the inconsistency in the trend of this feature, and because similar forms of abdominal sculpture occur in many other crustacean groups which are unrelated to palinurids, and also because the partial trend given above is not supported by the trends of any of the other features, abdominal sculpture is considered to be a random development rather than a phylogenetic indicator. Two other features were also placed in this category (see p. 807).

We were searching for morphological characters which: (a) could be arrayed in order and accommodate all the genera of the family in each arrangement; (b) were consistent with one another in their trends; (c) were based on features characteristic of the family and rarely, if at all, found in other crustacean groups; (d) were judged most likely to have a selective advantage in certain environments.

Four features examined fulfilled these requirements but before presenting these data (see p. 805) it is essential to present

TABLE 1. *Morphological relationships of living palinurid genera. The parallel trend of the Silentes and Stridentes for the same morphological characters is noteworthy. For the Stridentes genera the shape and armature of the antennular plate has also been included.*

Carapace	Supra-orbital process	Eye position	Distal joints of endopod of female second pleopod		SILENTES	STRIDENTES	Antennular plate
			Penultimate	Ultimate			
Cylindrical	strong vertical	elevated	full expansion	absent		PANULIRUS	broad, 2-4 large spines
Cylindrical	strong almost vertical	elevated	full expansion	vestigial	JASUS	JUSTITIA PALINURUS	triangular, unarmed
Subcylindrical	moderate slightly elevated	horizontal	moderate expansion	reduced	PROJASUS	PALINUSTUS	triangular, unarmed
Subcylindrical	small flattened	horizontal	slight expansion	large		LINUPARUS PUERULUS	narrow, unarmed

a brief taxonomic statement on the genera of the family and to point out that the presence or absence of a stridulating apparatus is regarded by us as indicating a major divergence within the family. The stridulating apparatus is formed by a lateral and anterior expansion of the antennular segment, a dislocation of the interior margin of the first free antennal joint from this segment, and a latero-internal expansion of the first free antennal segment. This expanded stridulating pad of the antenna is ribbed ventrally and when the antenna is moved, it rubs across a polished ridge on the lateral margin of the antennular segment. Those genera which do not have the ability to stridulate have a narrow, vertical antennular plate, the antero-external margin of which serves as the fixed articulation point of the antenna.

The possession of a stridulating apparatus is well known to be an advantage to the species for warning (and probably recognition and mating, as well) purposes and we consider it most unlikely that dislocation and relocation of the antenna to the antennular plate has occurred more than once in the history of the family. Our conclusion that the development of a "stridulating line" from a nonstridulating stock is also supported by palaeontological evidence (given later in this paper) which

shows that the two lines were present at an early stage of palinurid development. These structures have been described and illustrated by George and Grindley (1964) who support the long-neglected proposal of Parker (1884) to use "Silentes" for the non-stridulating group and "Stridentes" for the stridulating group.

#### PALINURID GENERA

Holthuis (1946) listed eight genera in the family Palinuridae and since that time one additional genus, *Projasus* George and Grindley 1964, has been described. However we are of the opinion that *Palinurellus*, one of the genera mentioned by Holthuis, should be removed from the palinurid list since it has obvious affinities with the Scyllaridae and Polychelidae as well as with the Palinuridae. These affinities have been discussed at length by de Man (1881, 1882), Bate (1881), and Boas (1882). After examination of male specimens from Florida, we support their conclusions which may be summarized by the statement of Bate (1881:226) "The eyes are those of the Scyllaridae; the second pair of antennae are those of the Palinuridae. The legs are common to both forms, and the carapace belongs to neither. The frontal region resembles neither; and the posterior resembles both, as also does the pleon,

whereas the pleopoda are modelled on the type of those of the Scyllaridae, and the tail fan is that of both." We agree with Bate and de Man that *Palinurellus* should be placed in a separate family, the Synaxidae. Nevertheless, *Palinurellus* assumes special significance since several workers have acknowledged its primitiveness (e.g., Boas, 1882) and its morphological affinities with fossil genera (Winkler, 1882).

The review by Holthuis (1946) provides basic distributional data for the species of Palinuridae. This has been brought up to date by reference to unpublished data (R.W.G.) and to publications after Holthuis (1946). These include Anon (1964), Barnard (1950), Bruce (1965), Edmondson (1951), Forest and Postel (1964), George (1962), George and Grindley (1964), George and Holthuis (1965), Gordon (1960), Holthuis (1954, 1961, and 1963), Holthuis and Villalobos (1962), Holthuis and Zaneveld (1958), Holthuis and Loesch (1967) and Kubo (1955, 1963). The descriptions given by Woods (1931) have served as a basis for the fossil genera with reference also to Glaessner (1960) and Piveteau (1953). An estimate of the number of fossil species in each genus is not attempted here. In the Palinuridae, there are eight extant and six fossil genera recognized by us as follows:

#### Silentes

*Projasus* George and Grindley, 1964. One extant species off East Africa.

*Archaeocarabus* McCoy, 1849. Nummulitic = Eocene of England, USA, and Fiji.

*Jasus* Parker, 1884. Seven extant species at separate southern circumpolar localities; one Miocene species from New Zealand (Glaessner, 1960).

#### Stridentes

*Puerulus* Ortman, 1897. Four extant species near New Guinea, off Zanzibar, Arabian Sea, and East Indies.

*Linuparus* White, 1847. Two extant species named (Bruce, 1965). Possibly embraces four separate species, off East Africa, Japan, South China Sea, and off north eastern Australia; numerous fossil species mainly in the Cretaceous of Europe and North America. Four subgenera have been recognized (Piveteau, 1953).

*Palaeopalinurus* Bachmeyer, 1954. Jurassic.

*Palinustus* A. Milne-Edwards, 1880. Three (possibly four) extant species in East Indies, off East Africa, Japan, and West Indies.

*Astacodes* Bell, 1863. Lower Cretaceous of Europe.

*Justitia* Holthuis, 1946. Accepting Gordon's (1960) broad concept to include *Nupalirus* Kubo, 1955, three named (possibly five involved actually) extant species off Mauritius (two spp.), Japan, Hawaii, and West Indies.

*Palinurus* Fabricius, 1798. Four extant species, three in the east Atlantic, and one off East Africa. This genus has had many fossil species included in it but a critical examination of them has not been attempted.

*Panulirus* White, 1847. Nineteen species in the tropic and subtropic waters of the Indian, Pacific, and Atlantic Oceans.

#### Incertae Sedis

*Cancrinus* Munster, 1839. This Liassic genus is regarded as intermediate between the palinurids and the scyllarids because of the club-shaped antenna.

*Palinurina* Munster, 1839. Liassic of Europe.

*Eurycarpus* Schluter, 1868. Upper Cretaceous of Germany.

#### *Characters indicating phylogenetic trend.*

—After separation into Silentes and Stridentes, the extant genera have been arranged (Table 1) according to the degree of development of the following four morphological features: (a) the relative size and disposition of the supraorbital processes; (b) the elevation of the eyestalks; (c) the structure of the pleopod on the second abdominal segment of the female; (d) the general shape of the carapace.

Except for the last, these generic features conform to the four criteria given earlier for good phylogenetic indicators. In the Table, the size and degree of spination of the antennular plate in the Stridentes is also included and a trend from a narrow to a broad structure is seen. There is a similar trend in each group towards the formation, lateral separation and elevation of the supraorbital processes; the elongation and elevation of the eyestalks; the enlargement of the endopod of the pleopod of the female second abdominal somite (see illustrations at the top of Figure 1) and the rounding of the carapace.

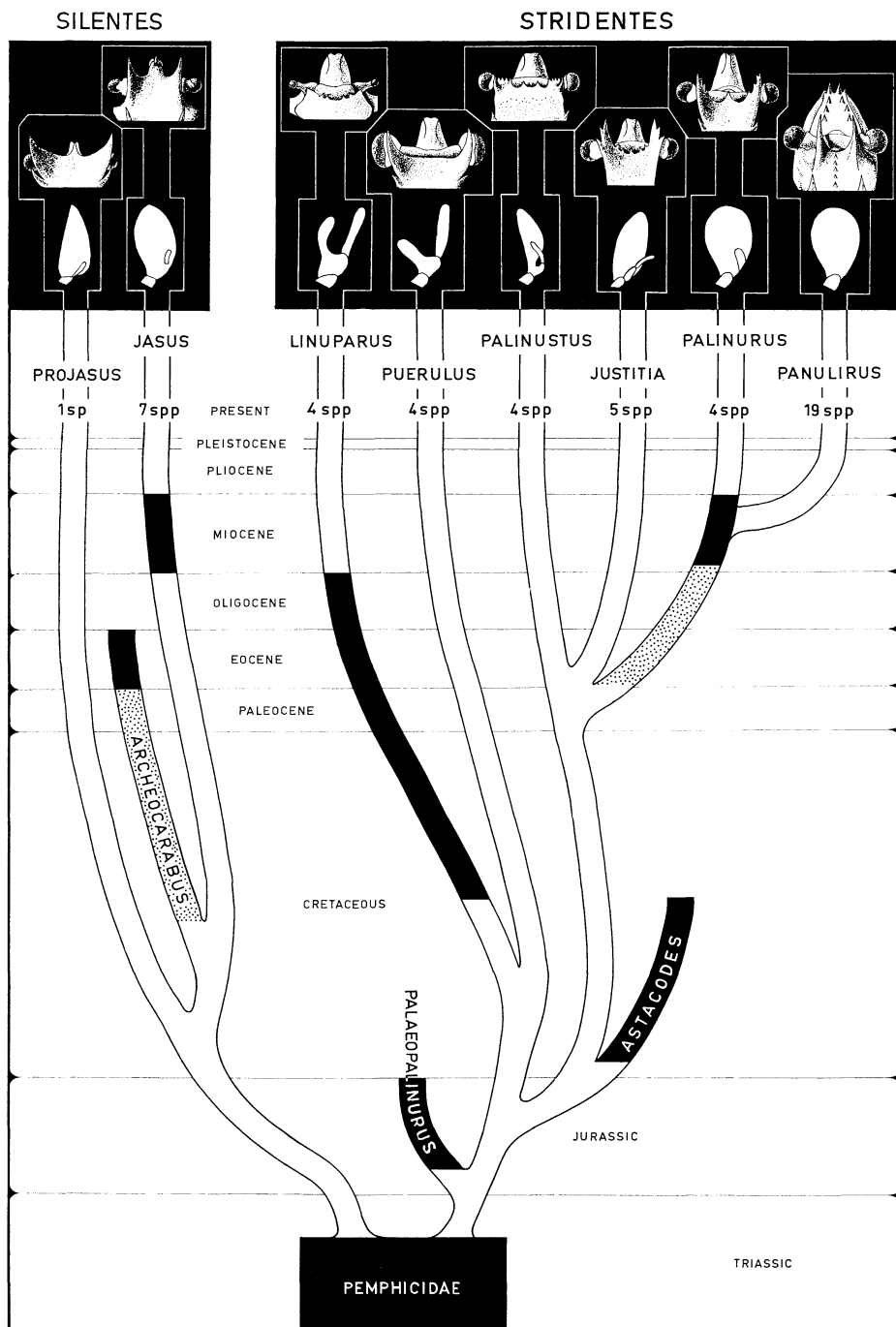


FIG. 1. Postulated palinurid evolution. Positive fossil records are indicated black, probable records are dotted. The form of the front of the carapace and of the endopod of the female pleopod on the second abdominal segment is illustrated for the extant genera.

The effect of the morphological trend of the first two structures is to provide the animal with better vision by raising the eyes and still protect them by the development of the forward-directed, curved supraorbital horns. The full expansion of the endopod of the most anterior pleopod of the female considerably increases the effective area of the whole pleopod. It appears that this correlates with a trend from deep to shallow water. It will be shown later that the genera with raised eyes and well expanded endopods (e.g. *Panulirus*, *Palinurus*, and *Jasus*) live at much shallower depths than those with lowered eyes and small endopods (e.g., *Linuparus*, *Puerulus*, and *Projasus*). It may be interpreted that improved vision is an advantage in shallow well-lit waters and that an increased surface area of the pleopod provides better mechanical aeration for the eggs in the shallow warm waters of lowered oxygen levels. It might also be argued that the less calcified carapaces of the deeper inhabitants rely on longitudinal ridging for strength and that in the shallows, the shell is strengthened by calcification.

*Characters considered to be of little phylogenetic importance.*—In addition to the abdominal sculpturing mentioned previously, there are three features which probably are readily reversed in their evolutionary development. These are: (a) the relative proportions of the legs; (b) the distal expansion of the propodus of the first walking leg to form a subchela with the dactyl; (c) the dentition of the abdominal pleura.

It is noteworthy that these same features and their variations are often observed in species of many other crustacean groups in both the living and the fossil forms. The value of these characteristics for subgeneric identification is undoubted.

#### PALEONTOLOGICAL EVIDENCE

The family Palinuridae has evolved from the Pemphidea in the early Mesozoic, according to Glaessner (1960) following his

analysis of the carapace furrows of the living and fossil decapod crustacea. Our interpretation of the phylogenetic relationships within the Palinuridae is given in Figure 1.

The emergence of the Stridentes from the pemphicid stock occurred early in the fossil record of the family since the Stridentes *Palaeopalinurus* was already developed in the Jurassic; the presence of its poorly developed supraorbital processes places it close to the *Puerulus*—*Linuparus* group in Table 1. Of these two genera, *Linuparus* is well represented from the Cretaceous to the present, suggesting that *Linuparus* (and probably *Puerulus* too) was established by the beginning of the Cretaceous. Another fossil Stridentes which can be placed with confidence in Table 1 is the Lower Cretaceous *Astacodes*; its features of subcylindrical carapace, moderate-sized slightly elevated supraorbital horns and a triangular antennular plate place it close to *Palinustus*. As mentioned earlier, revision of the fossil forms referred to *Palinurus* is required; Piveteau (1953) records it with certainty in Lower Tertiary but not with certainty before that time.

Fossils of two Silentes, *Archaeocarabus* and *Jasus*, are known. *Archaeocarabus* from the Eocene has a well marked rostrum with small pedate clasp processes; the carapace is cylindrical, the supraorbital horns are moderate sized and slightly raised, and the eyes are probably elevated rather than horizontal. Placed in Table 1 it would be between *Projasus* and *Jasus*, probably closer to *Jasus*. A distinguishing feature of *Archaeocarabus* is the well developed, subchela first leg, a feature not obvious in the other Silentes genera. *Jasus flemingi* (the only fossil *Jasus* known) has been recorded by Glaessner (1960) from the Miocene of New Zealand and it has close affinities to one of the present species, *J. verreauxii*. Thus the chronological order of appearance of fossil genera in the geological column (Figure 1) is in general agreement with the order of arrangement of extant genera presented in Table 1.

TABLE 2. *Classification of living palinurid genera based on environmental temperature.*

Subpolar	Temperate	Subtropic	Tropic
<i>Puerulus</i> 2 spp. <i>Projasus</i> 1 sp.	<i>Puerulus</i> 2 spp. <i>Linuparus</i> 2 spp. <i>Palinustus</i> 2 spp.  <i>Justitia</i> 2 spp. <i>Palinurus</i> 3 spp. <i>Jasus</i> 6 spp.	<i>Palinustus</i> 1 sp. and 1 sp. (part) <i>Justitia</i> 1 sp. <i>Palinurus</i> 1 sp. <i>Jasus</i> 1 sp. <i>Panulirus</i> 5 spp. and 2 spp. (part)	<i>Panulirus</i> 14 spp.

#### GEOGRAPHICAL AND VERTICAL DISTRIBUTION

Members of the Palinuridae live in all the major oceans of the world. Some are of commercial importance and inhabit the coastal waters in tropic, subtropic, or temperate temperature zones (see Vaughan, 1940 for description of zones) while others are less frequently taken since they live at much greater depths (down to 1400 m) where subpolar temperatures exist (Table 2).

In Figure 2, the distributions of extant genera have been plotted against depth and latitude and it is apparent that, with few exceptions, the spatial distributions of genera do not overlap. Isotherms of selected temperatures are also given in this figure, indicating the approximate temperature preferences of each genus. Although several genera (e.g., *Palinustus*, *Linuparus*, *Palinurus*, and *Jasus*) all have approximately the same temperature preferences of 10–20°C (Table 2), they in fact rarely inhabit geographic regions which correspond in latitude and depth. This is well illustrated by the palinurids living off the east, south, and lower west coasts of South Africa where every genus in the family is represented by one species; on present evidence it appears that each species occupies a region to the exclusion of other species of the family, thus:

*Jasus lalandii*—west coast of South Africa lat. 20–35°S, 0–50 m depth; *Palinurus gilchristi*—south-east coast of South Africa lat. 25–35°S, 60–520 m depth; *Projasus*

*parkeri*—south-east coast of South Africa lat. 33°S, 620 m depth; *Palinustus mossambicus*—Mossambique lat. 25°S, 406 m depth. *Linuparus trigonus*—Portuguese East Africa lat. 24°S, 360 m depth; *Justitia mauritiana*—off Mauritius lat. 20°S, 80 m depth. *Panulirus* spp. (5)—upper east coast of South Africa lat. 20–0°S, 0–30 m depth; and *Puerulus carinatus*—Saya de Mahla lat. 11°S, 250 m depth.

#### CORRELATION OF PHYLOGENY AND DISTRIBUTION

Comparing Table 1 and Figure 2, the sequences of genera show a marked correlation which we interpret as showing that the primitive genera live in deeper, higher latitude areas whereas the advanced genera live in shallower warmer regions in lower latitudes.

The opinion expressed here of an evolutionary trend in the Palinuridae from the relatively stable conditions of the deeper waters to the more varied and fluctuating conditions of the shallow waters is in accord with the generally held zoogeographical principles of Darlington (1957:547) who describes the main pattern of dispersal (for the terrestrial and freshwater animals he examined) as directional, “. . . from the largest and most favorable areas, . . . . . , into smaller and less favorable areas.” In the sense of Darlington, the deeper parts of the zones inhabited by palinurids are the largest and most favorable areas, while the shallow littoral areas are less favorable.

For the extant palinurids, the most re-

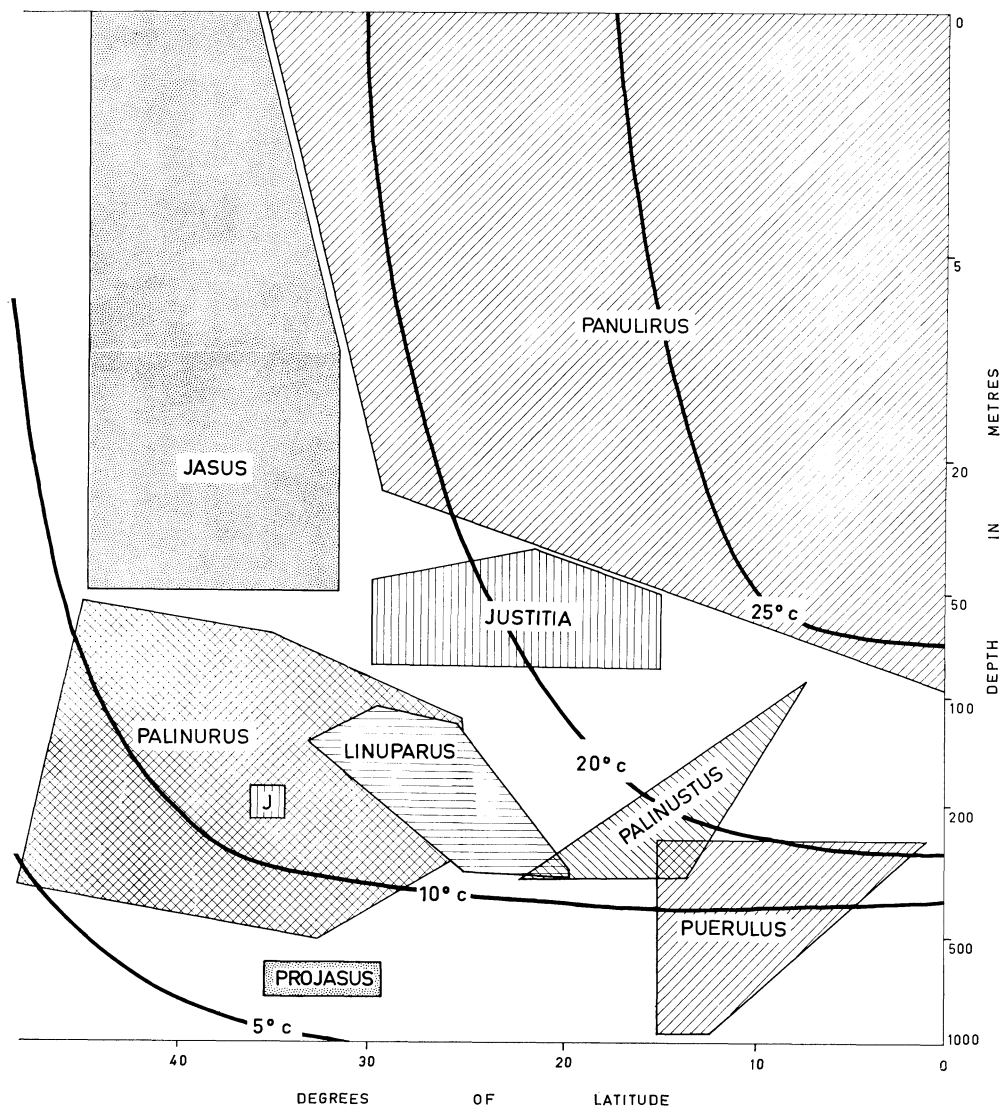


FIG. 2. Distribution by depth and latitude of extant palinurid genera. Approximate isotherms are included.

cent radiations into the many varied habitats of the shallower areas are found in the genus *Panulirus* (19 species). That similar radiations into relatively shallow regions have occurred in the past (as indicated by fossil deposits in shallow waters) is strongly suggested by the presence of many species of *Linuparus* in the Cretaceous and early Tertiary of Europe and North America as well as the more isolated occurrences of

*Archaeocarabus* (England, North America, and Fiji), *Palaeopalinurus* (Europe) and *Astacodes* (Europe). Most of the marine fossil deposits have been described from shallow water faunas. Little is known of the ancient faunas which lived in the deeper waters since these are rare in fossil deposits. Perhaps the fossils known today represent specialized shallow water species which died out at that time and the actual ancestors of

the modern fauna survived in deeper, cooler waters and were not directly represented in the fossil deposits.

#### DISTRIBUTION PATTERNS

We recognize two fairly well marked distribution patterns for the Palinuridae; a high latitude, partial or complete circumpolar distribution and a low latitude, circumequatorial distribution.

*High latitude distribution.*—The genera which fall into this group are *Projasus*, *Palinurus*, and *Jasus* (Fig. 2); these may best be regarded as actual or relict representatives of circumpolar distributions. *Jasus* today has six very closely related species fragmented around the Southern Ocean; each species is endemic to one of the following areas: Tristan da Cunha, S.W. Africa, St. Paul and Amsterdam Is., southern Australia, New Zealand, and Juan Fernandez I. The remaining species of *Jasus*, *J. verreauxii*, is quite distinct from the above *J. lalandii* group of species and occurs off the North Island, New Zealand, and off New South Wales, Australia.

Only one species of *Projasus* (from one locality off East Africa) is known at present and this species may represent a survivor of a genus which once had a circumpolar distribution similar to that of *Jasus*. *Palinurus*, with all except one of its species occurring in the north-east Atlantic, might have once had a circumpolar distribution in the northern hemisphere but today survives only in the Atlantic and south-west Indian Oceans.

Both *Palinurus* and *Projasus* are generally from greater depths than *Jasus*. In view of the apparent importance of depth (and temperature) in the phylogeny of the palinurid genera it is convenient to treat the palinurids under two sub-headings: shallow water and deeper water. The shallow water region extends from 1 to 50 meters and the deeper waters from about 50 to 1400 meters. This division does not strictly correlate with faunal zones such as those proposed by Hedgpeth (1957); our

“deeper water” includes the upper part of the bathyal zone and the lower part of the sublittoral zone and our “shallow water” covers only the upper sublittoral. *Jasus* is regarded as a derivative of *Projasus* emerging at or before the Miocene (*J. flemingi* Glaessner, 1960, is from the Miocene of New Zealand) and was probably well established before the most recent genus (*Panulirus*) emerged about the close of the Pliocene. An analysis of fragmentation and isolation of the circumpolar *Jasus* species can not be attempted at this stage of our knowledge.

*Equatorial distribution.*—The remaining palinurid genera occur in a broad belt extending for about 30° on each side of the equator and at depths from littoral to over 700 fathoms. Eckman (1953) recognized four major barriers to species distribution in this region, two terrestrial (Panama and Suez Isthmuses) and two oceanic (Central Pacific and Atlantic); these barriers separate four major faunal assemblages—the Indo-West Pacific, East Pacific, West Atlantic, and East Atlantic faunal regions. Recent revisions have greatly improved our knowledge of distributions and interrelationships for the shallow water genera but the more primitive genera, living in deeper water, are not so well studied because of their rarity in collections. It is evident in the following discussions that endemic or suspected endemic species occur in the following areas: south-west Indian Ocean, East Indies, Japan, and West Indies; these are apparently areas with a wide range of suitable habitats.

a) *Deeper water equatorial distribution.*—The genera which fall into this category are *Puerulus*, *Palinustus*, *Justitia* and *Linuparus*.

*Puerulus* has four closely related species in the Indian and western part of the Pacific Ocean; the species appear to be geographically isolated from one another and inhabit the upper regions of ocean basins. *P. carinatus* has been recorded at Saya de Malha on the eastern side of the



Mascarene Basin, *P. sewelli* on the eastern and western sides of the Arabian Basin, *P. velutinus* on the western side of the Banda Basin, and *P. angulatus* on the southern side of the Caroline Basin. Since these species occur at fairly considerable depths of 250 to 1438 meters, they are rare in collections and further collecting would be essential to confirm their correlation with particular ocean basins.

There are three named species of *Palinustus*; these were originally described from Japan (*P. waguensis*), Portuguese East Africa (*P. mossambicus*), and West Indies (*P. truncatus*). Further specimens from the Sulu Sea (Holthuis, 1946) probably represent a new species according to the list of differences given by Kubo (1963). All *Palinustus* species live at shallower depths (80–400 meters) than *Puerulus* spp.

Gordon's (1960) broad generic concept of *Justitia* is represented here for discussion. She united *Justitia* and *Nupalirus* (Kubo, 1955) following her examination of the holotype of *J. mauritiana* (Miers) 1882 from Mauritius and another Mauritian specimen which she identified as *J. japonicus* (Kubo) 1955 (type locality Japan). The type of the genus is *J. longimana* (H. Milne-Edwards) 1837 from the West Indies; Edmondson (1951) and Tinker (1965) gave this name to specimens from Hawaii. Our evaluation of the species concerned in Gordon's broad generic concept suggests that two species groupings are perhaps valid. The first group has very long subchelate (in the male), dorsally spinose first pereopods; about four transverse grooves on the abdominal terga; and submedian spines on the anterior margin of the carapace—the species with these characteristics are *longimana* (West Indies), *mauritiana* (Mauritius) and the specimens from Hawaii. The second group of species, *japonicus* (Japan) and Gordon's specimen from Mauritius, have in common short non-chelate (in the male), ventrally spinose first pereopods, about six transverse grooves on the abdominal terga; and

no submedian spines on the anterior margin of the carapace. In our view, this second species group warrants subgeneric recognition and the name *Nupalirus* is available for it. The species of *Justitia* occur in intermediate depths (40–200 meters), the "*Nupalirus*" group occupying the deeper part of the range.

*Linuparus* inhabits a similar depth range (100–400 meters) to that of the "*Nupalirus*" group but four geographically isolated species are probably represented within the recorded distribution of *Linuparus*; one in Japan (*trigonus*), one in South China Sea (*sordidus*), one off Portuguese East Africa (see Barnard, 1950) and one off east Australia (see McNeill, 1953; Anon, 1964). Dr. D. J. G. Griffin (pers. comm.) has pointed out to us some differences between a male from 130 meters off Queensland and the male described by Barnard.

b) *Shallow water equatorial distribution*.—*Panulirus* is the only genus in this category. The view that *Panulirus* is the most recently evolved genus of the Stridentes has been discussed earlier. This genus is the largest in species numbers (19) and is represented in all of Eckman's (1953) equatorial regions. Some species of *Panulirus* have lost some or all of the exopods of the second and third maxillipeds. According to the degree of maxilliped modification, the species can be placed in groups (I, II, III, IV see Table 3) and since all the other palinurid genera have fully formed exopods of these appendages those species of *Panulirus* with the most reduced exopods are regarded as the most advanced. In Table 3, the distribution and temperature zonation of the recognized species of *Panulirus* is also indicated. The following detailed description of the distribution of the species in each of the faunal zones is given to facilitate the subsequent discussion of speciation mechanisms in *Panulirus*.

#### INDO-WEST PACIFIC REGION

Eleven of the 19 species of *Panulirus* inhabit this region, and for Groups I–III

TABLE 3. *Species groups in Panulirus based on condition of second and third maxilliped. Group I is considered to be the most primitive species group. Those species marked by asterisk live in subtropic water temperatures, the remainder are inhabitants of the tropic water temperature zone. Two species, P. longipes and P. argus, live in both tropic and subtropic zones.*

Exopod condition		Panulirus spp.			
	3rd maxilliped	2nd maxilliped	Indo-West Pacific	East Pacific	West Atlantic East Atlantic
I	Present, with flagellum	Present, with flagellum	* japonicus * marginatus * pascuensis * cygnus	interruptus	argus
II	Present, no flagellum	Present, with flagellum	longipes penicillatus		guttatus echinatus
III	Absent	Present, with full flagellum	polyphagus		laevicauda rissonii
IV	Absent	Present, no flagellum (except where it is reduced <i>P. homarus</i> )	homarus ornatus versicolor stimpsoni	gracilis inflatus	

there are equivalent morphological species represented in other faunal regions.

In the Indo-West Pacific species in Group I, *P. longipes* is the only species with a wide distribution; there is some evidence that subspecific recognition should be given to two forms, one inhabiting the Indian Ocean region and the other the west Pacific region (George and Holthuis, 1965). The four remaining species each have restricted distributions in peripheral areas of the Indo-West Pacific region—*P. japonicus* (Japan), *P. marginatus* (Hawaii), *P. pascuensis* (Easter and Pitcairn Is.) and *P. cygnus* (west Australia). These last four species are sufficiently abundant in their respective areas for commercial exploitation.

The species in Groups II–IV (with the exception of *P. stimpsoni* which is restricted to Hong Kong) are widely distributed over most of the region, particularly the Indian Ocean. Only *P. penicillatus* extends eastward to Hawaii; this species also crosses the east Pacific oceanic barrier where it occurs on offshore islands adjacent to the American coast from Galapagos to Revillagigedo Islands. *P. penicillatus* has the widest distribution of any palinurid and would be termed by Briggs (1961:545) “transpacific.”

In the Indo-West Pacific region it appears that each species has a different general center of abundance. *P. versicolor* is probably most abundant along the north coast of Australia, *P. ornatus* is apparently more abundant at Zanzibar, *P. homarus* is the basis of a small fishery in the Arabian Gulf area (FAO/UN, 1963), *P. polyphagus* is only recorded in any quantity on the west coast of India and *P. penicillatus* has been reported as commercially abundant from the Revillagigedo and Galapagos Islands (Holthuis and Loesch, 1967).

#### EAST PACIFIC REGION

The three species along the American west coast have adjacent distributions with little overlap; *P. interruptus* inhabits the subtropic water temperature zone of the California-Baja Californian region and is less frequently found in the Gulf of California, the region which is dominated by *P. inflatus*. *P. gracilis* dominates the Central American coast from the Gulf of California to Peru. It also occurs at the Galapagos Is. where it is displaced from the very shallow water part of its range by *P. penicillatus* (Holthuis and Loesch, 1967).

## WEST ATLANTIC REGION

Of the four species in this region, *P. argus* has the widest distribution, from North Carolina and Bermuda to Rio de Janeiro, and throughout this range is generally the most abundant species. Two other species, *P. guttatus* and *P. laevicauda*, occur in the central part of the *P. argus* range; (they are rare in the Florida-Cuba region and do not appear to extend to Brazil). *P. echinatus* extends eastwards from its only mainland occurrence in Brazil to the islands of Cape Verde, St. Helena and St. Peter, and St. Paul Rocks (Chace, 1966). In this respect, *P. echinatus* has the ability to achieve an extensive oceanic distribution similar to that of *P. penicillatus*.

## EAST ATLANTIC REGION

Only one species, *P. rissonii*, is at present recognized and it is of commercial importance to French fisherman visiting the Mauritian coast and Cape Verde Archipelago.

## DISCUSSION

Darlington (1964) expresses the view that the continents of Africa and South America were probably joined during the Palaeozoic but that separation occurred in the early Mesozoic or late Palaeozoic. In our consideration of palinurid evolution, we are primarily concerned with the post-Mesozoic when the positions of the oceans and land masses were probably much as they are today. In these oceans we can envisage distribution patterns of marine animals which differ little from those of the present day. Naturally the species may be different. Habitat zones of the oceans were probably filled by species which reacted in much the same way as do their present occupants. There is little reason to imagine habitats remaining vacant for any length of time; following extinction of a specialized group within a habitat as a result of some environmental deterioration, the habitat would be filled from a new source fairly rapidly. The reactions and interactions of *all* marine species in

the past have had to contend with the changing environment and one would expect that this would result in similar species distribution patterns regardless of the group chosen for examination. For the few examples we have considered, this appears to be so (see p. 817).

*Speciation in the most primitive deep water genera.*—Regarding the evolution of the Palinuridae, speculation on the particular events leading to the present day distribution of the older, more primitive genera of the bathyal waters can only be tentative. The extant species of these genera are few in number and, within each genus, all species are very similar morphologically. We suggest that the geological and oceanic barriers which divided the once continuous equatorial seas of the world (including the Tethys Sea) into its present day faunal regions fragmented the early stocks, and that the subsequent morphological changes in these groups were very slow.

For the genus *Puerulus*, we have already suggested that each species is associated with a separate ocean basin; perhaps each species has been evolved in response to a set of environmental conditions peculiar to each of these basin regions. One could imagine such a situation operating after the initial, larger scale, barriers were erected. The peculiarity of the fauna in other ocean regions which have very obvious topographical barriers (such as the Red Sea, Mediterranean, Philippine Basin, and the Japan Sea) is well known (Sverdrup et al., 1961). Just which environmental factors are likely to limit the distribution of the species of *Puerulus* are, at our present state of knowledge, obscure; perhaps the answer lies in a better understanding of the subsurface circulation of these and adjacent ocean basins.

*Speciation in Panulirus.*—*Panulirus* inhabits sublittoral waters and during the Pleistocene ice ages this genus would be subject to great environmental stresses, e.g., falling and rising sea levels, changes in

area of continental shelves, changes in water temperatures, and strengthening and weakening of oceanic circulation.

A consideration of the pelagic larval stages (phyllosoma) in the speciation of *Panulirus* is important since the larvae have great potential for wide dispersal. However, dispersal does not appear to be haphazard. Information on larval development, larval behavior, and the dispersal and recruitment paths of the larvae in response to current circulation are known only for a few species of *Panulirus*. Nothing is known about the phyllosoma of all the more primitive genera. Of other genera for which phyllosoma are recognized, only very few species have all stages described. Fewer species still have adequate field data of sufficient phyllosoma stages (associated with information on local current systems) to allow the presentation of possible recruitment paths. Nevertheless, the results of some field studies on the biology of commercial species of *Panulirus* suggest to us that larvae are not entirely randomly dispersed but remain reasonably confined to the general area of adult distribution; this is based on the findings of Johnson (1960a, b) for *Panulirus interruptus* off the coast of California and of George and Cawthorn (1962) and Chittleborough (1964) for *Panulirus cygnus* off the west coast of Australia. In these studies, the larval stages are shown to gradually move offshore but mechanisms which confine and return the later stages to the onshore fishing ground are as yet unknown. Whether the offshore late stages represent the "wasted" portion of the larvae or the "true" recruits remains to be shown. But the larvae are rarely found beyond the latitudinal geographical limits of the coastal adult population; this must surely be the result of behavioral responses (e.g., by vertical migrations) of the larvae within prevailing current systems.

If the species of *Panulirus* have evolved in response to water circulation patterns, a consideration of what might have happened to these systems in the geologic

past is of paramount importance and the following sets out our interpretation of the nature of these changes and their probable effects on *Panulirus* speciation. Oceanic circulation is driven by the wind systems of the globe and during the advances and retreats of ice in the Pleistocene the circulation is believed to have strengthened and weakened. When the wind circulation is weak, oceanic currents are probably weak and diffuse; pelagic larvae contained in these currents would be widely dispersed and settling of larvae would not be contained within limited geographical areas. When wind circulation is strong, oceanic currents are probably well defined and persistent; in these conditions strong circulation is likely to result in the fragmentation of an earlier widely-distributed adult stock into discrete populations which are unconnected by larval dispersal.

Perhaps the four species groups of *Panulirus* indicate the effects of four major Pleistocene glaciations, each glaciation producing conditions for optimum isolation and subsequent speciation. In each of three species groups in *Panulirus* (Group I, II, and III in Table 3), analogous species today occur in two or more separate faunal regions; if these groups reflect close genetic affinity, and if four species groupings are the result of previous Pleistocene glaciations, then it is reasonable to assume that there have been equatorial connections between the Pacific and Atlantic Oceans in recent times to allow such genetic interchange. Following Simpson's (1952) postulation that dispersal and interchange of terrestrial faunas does not necessarily indicate entire and persistent migration pathways during the particular geological period under discussion, the evidence of post Tertiary dispersal of terrestrial faunas between North and South America does not, by any means, rule out the possibility of intermittent marine communications between the Pacific and Atlantic oceans during the Pleistocene.

Recent marine workers such as Briggs (1961), Brinton (1962), and Davies

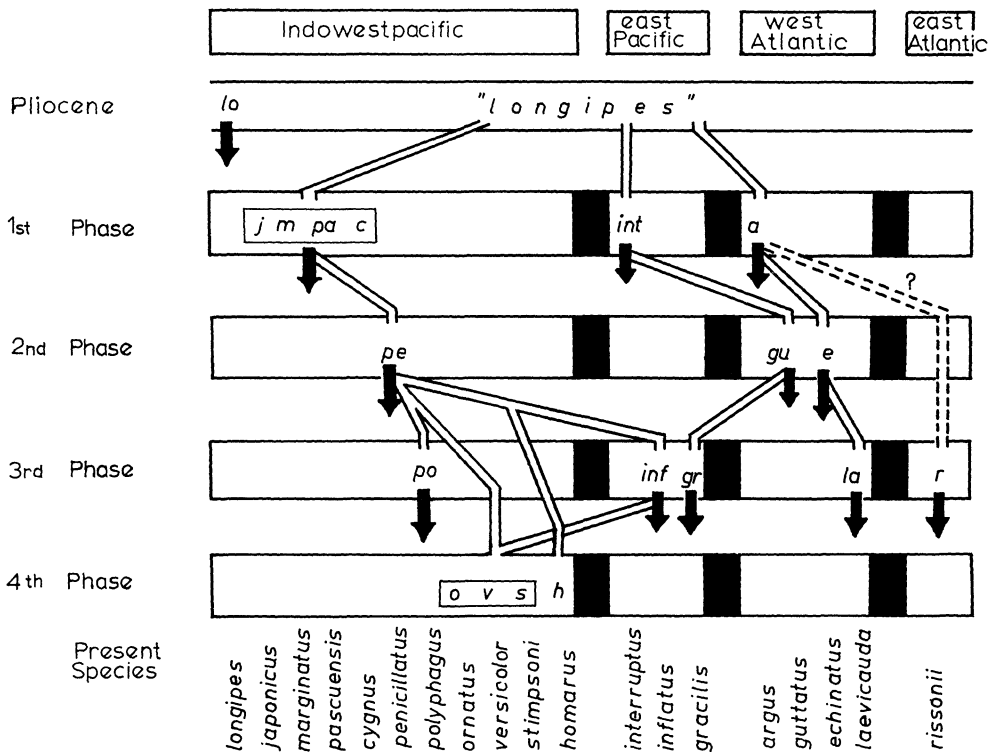


FIG. 3. Postulated speciation of *Panulirus*.

(1963), have apparently assumed an unbroken Panamanian Isthmus during the Pleistocene and have interpreted the recent evolution of marine species as resulting from changing sea temperatures. There is no doubt that temperature and other environmental changes have played a very important role in marine evolution but we believe that considerations of the changes in total current systems and the possibility of marine interchange in the Panamanian region during the Pleistocene are more significant than considerations of temperature alone. If there were no marine connections after the late Pliocene, one must envisage parallel speciation in *Panulirus* on each side of an unbroken Panamanian Isthmus with a similar parallel sequence evolving in the Indo-West Pacific with this procedure occurring three times. As an alternative, all the present species of

*Panulirus* may have evolved before the Pliocene and altered little since that time. In these latter two alternatives, the *Panulirus* groupings would have no genetic significance and their similarities would be simply convergent.

The following hypothesis for speciation in *Panulirus* assumes that there were four opportunities for marine interchange in the Panamanian region. The postulated evolution in *Panulirus* is represented in Figure 3. The ancestral species was able to inhabit the sublittoral of an extensive geographic area in the equatorial region during the late Pliocene with free access to all ocean areas and was "protected" from potential extinction by its wide environmental tolerance in both the larval and adult condition. This tolerance would permit wide dispersal of larvae over a range of temperatures (probably subtropic and

tropic) and habitats. The modern species which fit closest to this description are *P. longipes* and *P. argus*; we have chosen to represent "the" ancestral species by *P. longipes* because it is better known to us. By the end of the first glaciation, one could imagine the Indo-West Pacific species—*P. japonicus*, *P. marginatus*, *P. pascuensis*, and *P. cygnus*—as peripheral, isolated representatives of "*P. longipes*" each species perhaps responding to separate "endemic" current systems. In the east Pacific and in the west Atlantic, *P. interruptus* and *P. argus* respectively were isolated from one another by a temporary Panamanian barrier, and from the Indo-West Pacific forms by the Pacific Ocean barrier (Fig. 3).

During the succeeding interglacial, full oceanic interchange of species is again available due to diffuse current circulation and the breaking down of equatorial land bridges. Following the re-establishment of the oceanic and land barriers of the next glaciation, populations which earlier passed through the broken "barrier regions" would have been isolated, and one could imagine *P. penicillatus*, *P. guttatus*, and *P. echinatus* as further derivatives of any one of the earlier species—*P. longipes*, *P. interruptus* or *P. argus*. Following similar reasoning, at the end of the next glaciation *P. polyphagus*, *P. inflatus*, *P. gracilis*, and *P. laevicauda* probably originated from any one of the species *P. penicillatus*, *P. guttatus*, and *P. echinatus*. *Panulirus rissonii* originated from either one of the west Atlantic species of the previous glaciation or from an earlier stock which came from *P. argus* at the first glaciation.

The most recent separation of the remaining *Panulirus* species, all of which occur in the Indo-West Pacific, probably developed in response to temporary isolation within restricted parts of this vast region—suggestions of which may be indicated by the various areas of relative abundance of each species witnessed today. *P. ornatus*, *P. versicolor*, and *P. stimpsoni* might have originated from any one of the species *P. penicillatus*, *P. gracilis*, and *P.*

*inflatus*. *P. homarus* might best be explained as a development from *P. penicillatus* in particular, because of the presence of the small flagellum on its second maxilliped exopod.

An examination of the habitat preferences of each of the Indo-West Pacific species indicates that (a) where closely related species occupy a similar habitat, they are found to be geographically isolated (*japonicus*, Japan; *marginatus*, Hawaii; *pascuensis*, Easter I., and *cygnus*, Western Australia, all live in rock and coral at subtropical temperatures); and (b) where the tropic species are sympatric over a very wide area, each appears to be separated by habitat preference. For instance at Ceylon where all six tropical species occur, De Bruin (1962) showed that each species has preferential habitat, depth and behavior. The different combinations of these characteristics for each species presumably determine which one predominates in a particular area; De Bruin's work in Ceylon clearly illustrates such regional domination.

*Comparisons outside the Palinuridae.*—Comparisons can be made between the patterns of distribution of the Palinuridae and of other groups of marine animals as long as one bears in mind that groups being compared must have been classified according to similar sets of taxonomic values. Where the evolutionary relationships of a group have been worked out, such an appraisal can be used to compare such taxonomic levels. It would be surprising if distribution patterns of other groups were absolutely identical with those outlined here for the Palinuridae, but since the various marine groups of animals have been subjected to the same overall environmental stresses in the past, similarities are to be expected. Factors such as the age of the group, their habits, dispersal potential (as larvae and adults) modify the patterns of distribution. Although there are numerous examples of similar distribution patterns for a wide variety of marine animals, our remarks here are restricted to some of the decapod crustacea—the group

with which we are most familiar in this respect. In the decapod crustacean groups examined, Eckman's (1953) concept of four major shallow water, circumtropical faunal regions was closely supported as was the generally accepted thesis that the warm parts of the oceans usually contain a larger number of species than the cool waters.

Where sufficient reliable taxonomic information for the group was available to make a valid comparison with the palinurids, the distribution patterns and affinities were found to be consistent with the palinurid patterns, e.g., the evolution of the Portunidae and the distribution patterns of *Ovalipes* (Portunidae) and *Ibacus* (Scyllaridae). The general pattern of evolution from deeper to shallower water is clearly illustrated in the Portunidae. Stephenson (1962) assessed the affinities of the portunid subfamilies and he regarded the Portuninae as evolving from the more primitive Carcininae and Macropopinae. Our analysis of the depth and geographic distribution of these crabs shows that the few species that inhabit depths greater than about 100 fathoms or those living in high latitudes belong to the two primitive subfamilies. All the species of the derivative Portuninae are inhabitants of warm shallow waters. The southern circumpolar distribution pattern of closely related species, typified in the Palinuridae by *Jasus*, is shown by several decapod genera such as *Ibacus* and *Ovalipes* (this genus is currently being revised by Prof. W. Stephenson, pers. comm.). In both these examples, however, at least one species of the genus also occurs in subtropic Japanese waters (but no species occupy the intermediate tropic region). A combination of two distribution patterns (southern circumpolar and peripheral Indo-West Pacific) is thus evident for these two genera.

Where the taxonomy of a group is not well known, we have sometimes found it useful to make comparisons with our broad palinurid conclusions to assist in the unravelling of "difficult" species in these

taxonomic groups. For instance in the Indo-West Pacific *Ocypode* (beach crabs) the species distribution pattern is very similar to that shown by *Panulirus*; some are widespread (*O. ceratophthalma* and *O. cordimana*) whereas others form a group of peripheral endemics in Japan, Hawaii, western Australia, and Madagascar (comparable with the peripheral distribution pattern of the *Panulirus japonicus* species group). There are, however, more *Ocypode* species, compared with *Panulirus*, living as endemics within relatively small geographical areas in the tropical region of the Indo-West Pacific region; tropical endemics of *Ocypode* are known from South Arabia, west coast of India, east coast of India, Borneo, north coast of Australia, and Coral Sea.

Background information such as this has assisted us in our approach to a "difficult" species, *O. kuhlii*. It was originally described from Java and many subsequent workers have stated that it occurs at many widely separated localities in the Indo-West Pacific region. Recent carcinological studies in Western Australia (George and Knott, 1964) show that previous records of *O. kuhlii* from west and north Australia are misidentifications; Crosnier (1965) also showed that previous records of *O. kuhlii* from Madagascar are very doubtful. These results suggest that *O. kuhlii* is another of the tropical endemics inhabiting only a limited region (around Java) and is not a widely distributed species. We might also venture to suggest that the proliferation of species of *Ocypode* has been in response to a proliferation of different habitats along the shore during the Pleistocene and that the species probably evolved from a permanently aquatic sublittoral ancestor which in turn evolved from a deeper water ancestor.

*Origin of marine faunas.*—It is well to note that we do not suggest by extrapolation that the abyssal or hadal fauna is ancestral to the bathyal fauna which in turn is ancestral to the sublittoral and supralittoral faunas. On the contrary, we

support the suggestions by other authors (e.g., Brunn, 1956) that the abyssal and hadal fauna evolved from the *shallower* bathyal fauna. However, one must be cautious of the interpretation that the bathyal fauna might have come from the warmest, *shallowest* water. For consideration, we suggest that the intermediate (bathyal) depths may have been the original area and that radiations have proceeded up into shallower waters (the crustacean situation discussed in this paper) as well as down into deeper waters (the suggestion by Brunn, 1956 and others).

#### SUMMARY

1) Spiny lobsters occur in all major oceans of the world from sublittoral to bathyal depths. A phylogeny of the Palinuridae is proposed based on external morphology. The family is divisible into two groups—*Silentes* and *Stridentes* and within each group a parallel trend in several morphological features is apparent.

2) Coincident with these morphological trends is a habitat trend from deep (bathyal) to shallow (littoral) waters; adaptive advantages under these conditions are considered.

3) The shallow waters are the specialized habitats of spiny lobsters and the fossils indicate past radiations into shallow water but not the surviving stock; it is suggested that the "successful" ancestral line is represented by the deeper water inhabitants.

4) An analysis of depth and latitude distributions of the palinurid genera shows that the spatial distributions of the genera rarely overlap; in other words, each genus appears to have a separate set of depth and latitude parameters. In the southwest Indian Ocean one species of every palinurid genus is represented presumably because the total region provides all the separate habitats for these genera.

5) There are two basic distribution patterns in the Palinuridae, a circumpolar high latitude pattern, as exemplified by *Jasus*

(and also *Projasus* and *Palinurus* in relict form) and a circumequatorial low latitude pattern; we have made a further subdivision into the shallow water species (*Panulirus* spp.) and deep water inhabitants (the remaining genera). The species of one of these deep water genera—*Puerulus*—appear to be associated with oceanic basins.

6) The warmest shallowest regions contain the most number of species because of the greater diversity of habitat but these species are the most vulnerable in a changing total environment.

7) Speciation within the most recently evolved palinurid genus—*Panulirus*—has occurred during the Pleistocene and the four species groups probably reflect four major glaciation periods. Interglacials allowed equatorial inter-ocean dispersal of the pelagic larvae, while during glacials stocks were isolated by physical barriers and more defined current systems.

8) It is suggested that the bathyal region for many marine organisms is the original region and that radiations have proceeded both up into shallow water and down into the deeper abyssal regions.

#### ACKNOWLEDGMENTS

We wish to formally acknowledge the willing assistance given by our many colleagues from Universities, Museums and other Institutions in the compilation of material and literature for this work. We are also particularly grateful to Professor H. Waring and Dr. D. Bradshaw of the Zoology Department, University of Western Australia, Drs. W. D. L. Ride, G. M. Storr, and B. R. Wilson of the Western Australian Museum and Dr. W. G. Inglis of the British Museum for their very useful criticisms in the final stages of the preparation of the manuscript.

#### LITERATURE CITED

- ANON. 1964. Prawn trawler nets rare "Barking crayfish." *Fish. News Lett. Aust.* **23**(11): 26.  
 BARNARD, K. H. 1950. Descriptive catalogue of



- South African decapod Crustacea. *Ann. S. Afr. Mus.* **38**: 1-864.
- BATE, C. S. 1881. On *Synaxes*, a new genus of Crustacea. *Ann. Mag. Nat. Hist.* (ser. 5) **7**: 220-228.
- BOAS, J. E. V. 1882. Die Gattung *Synaxes* Sp. *Bate. Zool. Anz.* 1882: 111-114.
- BRIGGS, J. C. 1961. The east Pacific barrier and the distribution of marine shore fishes. *Evolution* **15**: 545-554.
- BRINTON, E. 1962. The distribution of Pacific euphausiids. *Bull. Scripps Inst. Oceanogr.* **8**: 51-270.
- BRUCE, A. J. 1965. A new species of the genus *Linuparus* White, from the South China Sea (Crustacea Decapoda) *Zool. Meded., Leiden* **41**: 1-13.
- BRUNN, A. FR. 1956. The abyssal fauna: its ecology, distribution and origin. *Nature, Lond.* **177**: 1105-1108.
- CHACE, F. A. 1966. Decapod crustaceans from St. Helena Island, South Atlantic. *Proc. U.S. Nat. Mus.* **118**: 622-662.
- CHITTLEBOROUGH, R. G. 1964. Western Australian crayfish-recruitment phase; in Western Fisheries Research Group, Half-yearly Report January-June 1964, Fisheries Department, Western Australia (Mimeo.).
- CROSNIER, A. 1965. Crustacés décapodes. Grapridae et Ocypodidae. *Faune Madagascar* **18**: 1-143.
- DARLINGTON, P. J. 1957. Zoogeography: the geographical distribution of animals. Wiley, New York, 675 p.
- . 1964. Drifting continents and late Paleozoic geography. *Proc. Acad. Nat. Sci. Philad.* **52**: 1084-1091.
- DAVIES, J. L. 1963. The antitropical factor in cetacean speciation. *Evolution* **17**: 107-116.
- DE BRUIN, G. H. P. 1962. Spiny Lobsters of Ceylon. *Fish. Res. Stat. Dept. of Fish. Ceylon. Bull. No.* **14**: 1-28.
- ECKMAN, S. 1953. Zoogeography of the sea. William Clowes, London.
- EDMONDSON, C. H. 1951. Some central Pacific crustaceans. *Occ. Pap. Bishop Mus.* **20**: 183-243.
- FAO/UN. 1963. Report to the Government of Aden on the Crawfish Resources of Eastern Aden Protectorate. Based on the work of R. W. George. *Rep. FAO/EPTA*, (1966) 1-23.
- FOREST, J., AND E. POSTEL. 1964. Sur une espèce nouvelle de langouste des îles du Cap Vert, *Palinurus charlestoni* sp. nov. *Bull. Mus. Hist. Nat. Paris* (ser. 2) **36**: 100-121.
- GEORGE, R. W. 1962. Description of *Panulirus cygnus* sp. nov., the commercial crayfish (or spiny lobster) of Western Australia. *J. Roy. Soc. W. Aust.* **45**: 100-110.
- GEORGE, R. W., AND P. CAWTHORN. 1962. Investigations on phyllosoma larvae of the Western Australian crayfish; in Western Fisheries Research Committee, Fisheries Department, Western Australia (Mimeo.).
- GEORGE, R. W., AND J. R. GRINDLEY. 1964. *Projasus*—a new generic name for Parker's crayfish, *Jasus parkeri* Stebbing (Palinuridae: "Silentes"). *J. Roy. Soc. W. Aust.* **47**: 87-90.
- GEORGE, R. W., AND L. B. HOLTHUIS. 1965. A revision of the Indo-west Pacific spiny lobster of the *Panulirus japonicus* group. *Zool. Verh., Leiden* **72**: 1-36.
- GEORGE, R. W., AND MARY E. KNOTT. 1964. The Ocypode ghost crabs of Western Australia (Crustacea: Brachyura) *J. Roy. Soc. W. Aust.* **48**: 15-21.
- GLAESSNER, M. F. 1960. The fossil decapod Crustacea of New Zealand and the evolution of the order Decapoda. *Palaeont. Bull. N.Z.*, no. **31**: 1-63.
- GORDON, I. 1960. On the genus *Justitia* Holthuis Decapoda, Palinuridae). *Crustaceana* **1**: 295-306.
- HEDGPETH, J. W. 1957. Classification of marine environments. In: *Treatise on marine ecology and paleoecology*. *Mem. Geol. Soc. Amer.* **67**: 18-28.
- HOLTHUIS, L. B. 1946. The Decapoda Macrura of the Snellius Expedition. *Temminckia* **7**: 1-178.
- . 1954. On a collection of decapod Crustacea from the Republic of El Salvador (Central America). *Zool. Ver.* **23**.
- . 1961. The taxonomic status of *Panulirus echinatus* Smith 1869 (Decapod Macrura, Palinuridae). *Crustaceana* **2**: 223-227.
- . 1963. Preliminary descriptions of some new species of Palinuridea (Crustacea, Decapoda, Macrura, Reptantia). *Proc. Acad. Sci. Amst.*, (ser. c) **66**: 54-60.
- HOLTHUIS, L. B., AND A. VILLALOBOS. 1962. *Panulirus gracilis* Streets y *Panulirus inflatus* (Bouvier), dos especies de langosta (Crustacea, Decapoda) de la costa del Pacifico de America. *An. Inst. Biol. Univ. Mex.* **32**: 251-276.
- HOLTHUIS, L. B., AND J. S. ZANEVELD. 1958. De kreeften van de Nederlandse Antillen. *Zool. Bijdr. no.* **3**: 1-26.
- HOLTHUIS, L. B., AND H. LOESCH. 1967. The lobsters of the Galapagos Islands (Decapoda, Palinuridea). *Crustaceana* **12**: 214-222.
- JOHNSON, M. W. 1960a. The offshore drift of larvae of the Californian spiny lobster *Panulirus interruptus*. *Symposium. California Cooperative Oceanic Fisheries Investigations Report no.* **17**: 147-161.
- . 1960b. Production and distribution of larvae of the spiny lobster, *Panulirus interruptus* (Randall) with records on *P. gracilis* Streets. *Bull. Scripps Inst. Oceanogr.* **7**: 413-462.
- KUBO, I. 1955. Systematic studies on the Japa-

- nese macrurous decapod Crustacea. 5. A new palinurid, *Nupalirus japonicus*, gen. et sp. nov. J. Tokyo Coll. Fish. **41**: 185-188.
- . 1963. Systematic studies on the Japanese macrurous decapod Crustacea. 6. A new and imperfectly known species of palinurid lobster. J. Tokyo Coll. Fish. **49**: 63-71.
- MCNEILL, F. 1953. Carcinological notes, no. 2. Rec. Aust. Mus. **23**: 89-96.
- MAN, J. G. DE. 1881. Carcinological studies in the Leyden Museum, No. 1. Notes Leyden Mus. **3**: 121-144.
- . 1882. On the genus *Araeosternus* de M. Notes Leyden Mus. **4**: 161, 162.
- PARKER, J. J. 1884. On the structure of the head in *Palinurus* with especial reference to the classification of the genus. Trans. N.Z. Inst. **16**: 297-307.
- PIVETEAU, J. (ed.). 1953. *Traité de Paléontologie*. Masson, Paris. **3**.
- SIMPSON, G. G. 1952. Probabilities of dispersal in geologic time, p. 163. In E. Mayr [ed.]. *The problem of land connections across the South Atlantic with special reference to the Mesozoic*. Bull. Amer. Mus. Nat. Hist. **99**: 81-258.
- STEPHENSON, W. 1962. Evolution and ecology of portunid crabs, with special reference to Australian species, p. 311-327. In: G. W. Leeper [ed.]. *The evolution of living organisms*. Melb. University Pr., Melbourne.
- SVERDRUP, H. W., M. W. JOHNSON, AND R. H. FLEMING. 1961. *The Oceans*. Prentice Hall, New York.
- TINKER, S. W. 1965. *Pacific crustacea*. Tuttle Company, Tokyo.
- VAUGHAN, W. T. 1940. Ecology of modern marine organisms with reference to paleogeography. Bull. Geol. Soc. Amer. **51**: 433.
- WINKLER, T. C. 1882. Carcinological investigations on the genera *Pemphix*, *Glyphea* and *Araeosternus*. Ann. Mag. Nat. Hist. (ser. 5) **10**: 133-149, 306-317.
- WOODS, H. 1931. *A monograph of the fossil macrurous crustacea of England*. Palaentol. Soc., London.