

# THE DEEP-SEA ISOPODS: A BIOGEOGRAPHIC AND PHYLOGENETIC OVERVIEW

ROBERT R. HESSLER, GEORGE D. WILSON & DAVID THISTLE

## SARSIA



HESSLER, ROBERT R., GEORGE D. WILSON & DAVID THISTLE 1979 05 31. The deep-sea isopods: A biogeographic and phylogenetic overview. *Sarsia* 64:67-75. Bergen. ISSN 0036-4827.

Isopod crustaceans are among the most numerous and diverse macrofaunal taxa in the deep sea. In contrast to the situation in shallow water, the Asellota encompasses the majority of the deep-sea fauna. Taxa within the Asellota exhibit marked depth zonation. Its most primitive superfamily is limited to fresh water. The rest are marine, where with increasing depth the incidence of more specialized taxa increases. Within its most advanced superfamily, Janiroidea, the most primitive families are primarily restricted to shallow water, while the more specialized families dominate in the deep sea. The most notable exception is the occurrence of these specialized families in shallow water at high latitudes.

On the basis of this pattern, it has been suggested that the deep-sea fauna is a result of invasion from shallow water, primarily at high latitudes. The present paper argues that, on the contrary, the specialized deep-sea families evolved *in situ*, and that their presence at shallow high latitudes is the result of subsequent emergence. Several lines of evidence support this conclusion. Their primary diversity is in the deep sea. In some families, the most primitive genera or their progenitors in other families live in the abyss. Finally, the deep-sea families all lack eyes, regardless of locality, whereas the more primitive families that dominate in shallow water have them, except where they are found in the deep sea. The only simple and consistent explanation for these facts is a deep-water origin for the deep-sea families.

*Robert R. Hessler and George D. Wilson, Scripps Institution of Oceanography, La Jolla, California 92093, USA. - David Thistle, Department of Oceanography, Florida State University, Tallahassee, Florida 32306, USA.*

Viewed from the human perspective, the floor of the deep sea is one of the most extreme environments on the face of the planet. It is an environment where temperature is near freezing and physically derived light is totally lacking, where nutritional input is at extremely low levels, and where all environmental factors display great temporal constancy. Not surprisingly, the deep-sea fauna is very different from what we see in shallow marine environments. Nowhere is this more true than with the isopod crustaceans.

Isopods live in most environments, from forests to the bottom of the deepest trenches. In the deep sea, they comprise one of the most important components of the community, where up to 100 species may be collected in a single sample (Table 1). Only the polychaete worms display a greater variety of species in a typical deep-sea bottom sample (HESSLER & SANDERS 1967). These species display a range of morphologies which is spectacular, and many of them are truly bizarre (see below).

Where did this remarkable array of isopods come from? Did they evolve in the deep sea, or did they migrate in from shallow water? For

Table 1. Isopod species diversity of epibenthic sled samples from various regions of the deep sea in the Atlantic Ocean. Rarefaction to 500 individuals according to the method of HURLBERT (1971) has been used in order to facilitate comparisons.

Station	General locality	Approx. depth (m)	Number of individuals	Number of species	Number of species if rarefied to 500 ind.
64	NE U.S.A.	2890	1198	51	42
128	"	3810	916	39	35
326	Ireland	3860	1282	60	46
328	"	4430	1111	69	59
293	Surinam	1490	1124	75	61
301	"	2490	899	61	55
142	W.Africa	1710	747	58	54
156	Mid-equatorial	3760	2008	90	68
245A	Argentina	2710	2521	109	74
256	"	3910	1593	87	68

many kinds of deep-sea organisms this is a difficult question. Fortunately, with the isopods there are sufficient data to yield a rather convincing answer.

Deep-sea isopod faunas are dominated by the suborder Asellota (CALMAN 1909). In contrast, other suborders (especially Flabellifera and Valvifera) have their main development in shallow marine environments, where asellotes are far less prevalent (Table 2). Within the Asellota there is a remarkably strong correlation of evolutionary advancement with depth.

It is generally agreed that the most primitive members of the suborder Asellota belong to the superfamily Aselloidea. Among the asellotans, aselloideans show the strongest general resemblance to the most primitive of all isopods, the Flabellifera. This is seen in the degree of fusion of the abdominal segments, the degree of modification of the anterior abdominal limbs for reproductive purposes, and the general body shape (Figs 1, 2) (SARS 1899; BIRSTEIN 1964; AMAR 1957; MENZIES 1962). The Aselloidea are restricted to fresh water (Table 3).

The Stenetrioidea and Gnathostenetrioidea are superfamilies of intermediate advancement. Their general body plan and degree of abdominal fusion are much like that of the Aselloidea, but reproductive modification of the abdominal limbs is more advanced. These two superfamilies are found in shallow marine environments (mainly 0-500 m).

The Janiroidea (= Paraselloidea) is the most advanced superfamily. The abdomen shows greater fusion, and the first two abdominal limbs are highly modified. Janiroideans are found from fresh water down to the greatest depths of the ocean, but within the superfamily, the pattern is further refined (Table 3).

The most primitive family is the Janiridae. This determination is based on its strong general resemblance to members of the Aselloidea (Fig. 2). The Janiridae is most prevalent in shallow water, as are four other families. As we will see, these others are also primitive in some very important respects.

The remaining 15 families are all specialized (Fig. 3). Some (Haplomniscidae) are shaped like pill bugs and are capable of complete enrollment. Others (Ishnomesidae) have extremely elongate body segments and walking legs, much like walking-stick insects. In some (Mesosignidae, Dendrotionidae, and many others) extreme spinosity is the rule. The body may be slender

(Table 2). The broad environmental distribution of isopodan suborders. Primary habitat shown by capital letters; secondary habitats shown by lower case letters. Abbreviations: terr, terrestrial; f-w, fresh water; s-w, shallow marine; d-s, deep sea.

Suborder	Primary Habitat	Secondary Habitats
Oniscoidea	TERR	
Phreatoicoidea	terr	F-W
Asellota		f-w s-w D-S
Anthuridea		S-W d-s
Valvifera		S-W d-s
Flabellifera		S-W d-s
Gnathiidea		S-W d-s
Epicaridea		S-W d-s

Table 3. The broad environmental distribution of asellotan superfamilies and janiroidean families. The list of families includes some not mentioned in KUSSAKIN 1973 and therefore not present in Figure 4. Abbreviations as in Table 2.

Superfamily	Primary Habitat	Secondary Habitats
Aselloidea	F-W	
Stenetrioidea		S-W d-s
Gnathostenetrioidea		S-W
Janiroidea		
Janiridae	f-w	S-W d-s
Jaeropsidae		S-W d-s
Antiasidae		S-W
Munnidae		S-W d-s
Pleurogoniidae		S-W d-s
Haplomunnidae		D-S
Dendrotionidae		D-S
Acanthaspidae		D-S
Abyssianiridae		s-w D-S
Janirellidae		D-S
Mesosignidae		D-S
Ishnomesidae		s-w D-S
Haplomniscidae		D-S
Thambematidae		D-S
Macrostylidae		s-w D-S
Nannoniscidae		s-w D-S
Desmosomatidae		s-w D-S
Eurycopidae		s-w D-S
Ilyarachnidae		s-w D-S
Munnopsidae		s-w D-S

(Nannoniscidae, Thambematidae) or fat (Eurycopidae). The head may be enlarged to accommodate crushing jaws (Ilyarachnidae). The thoracic segments may be condensed together, and some may even be lost (Haplomunnidae).

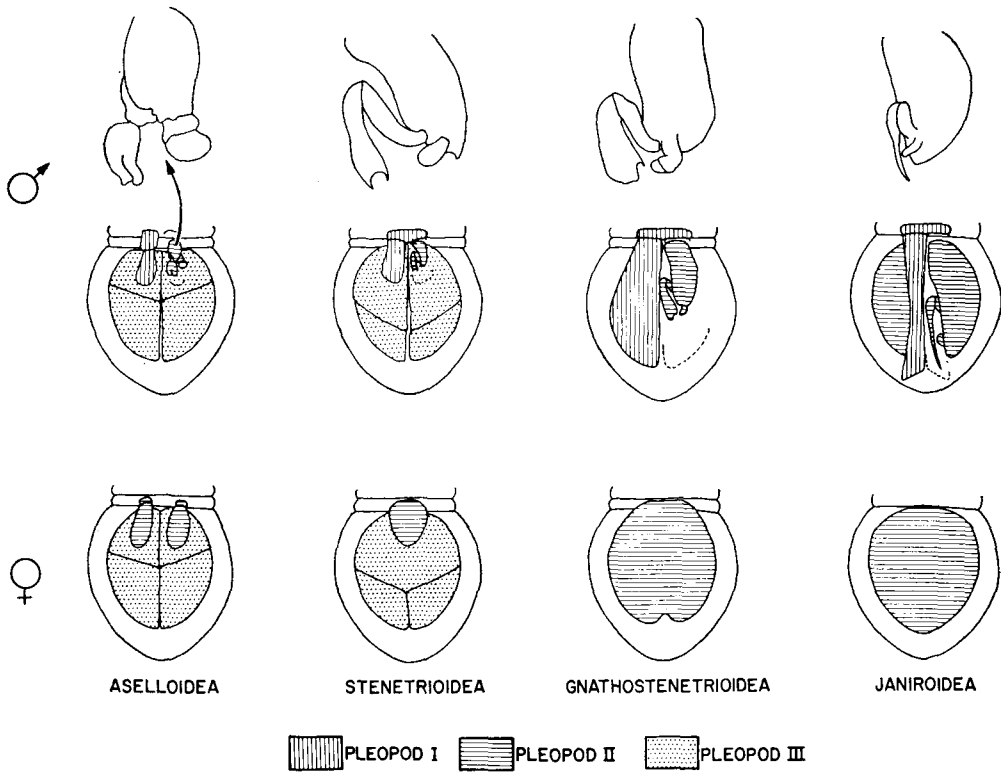


Fig. 1. The abdomen and abdominal appendages of the four superfamilies of the suborder Asellota, showing the evolutionary gradation from the primitive aselloidean condition to that of the advanced janiroidean. Note that pleopod I is always absent in females.

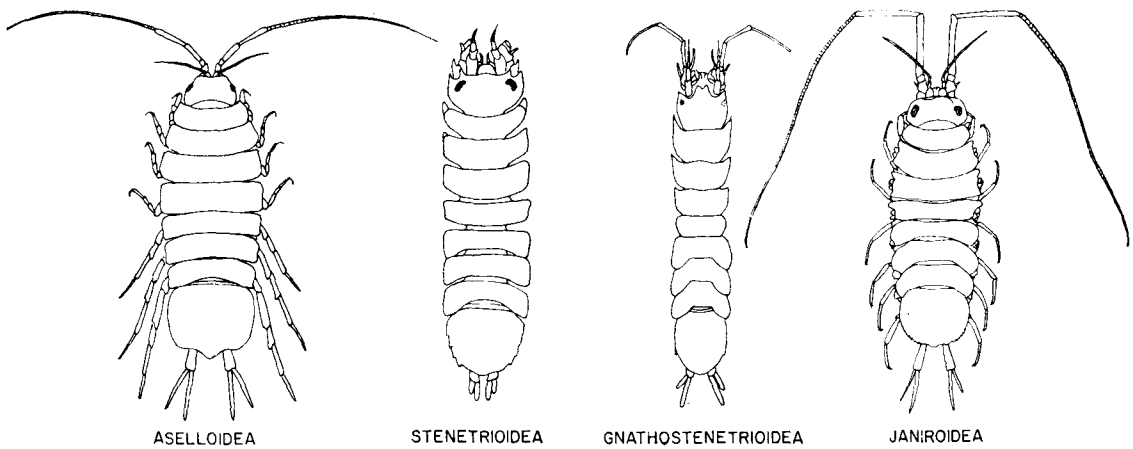


Fig. 2. General body morphology of the four superfamilies of the suborder Asellota. Note their similarity, particularly between the aselloidean and janiroidean.

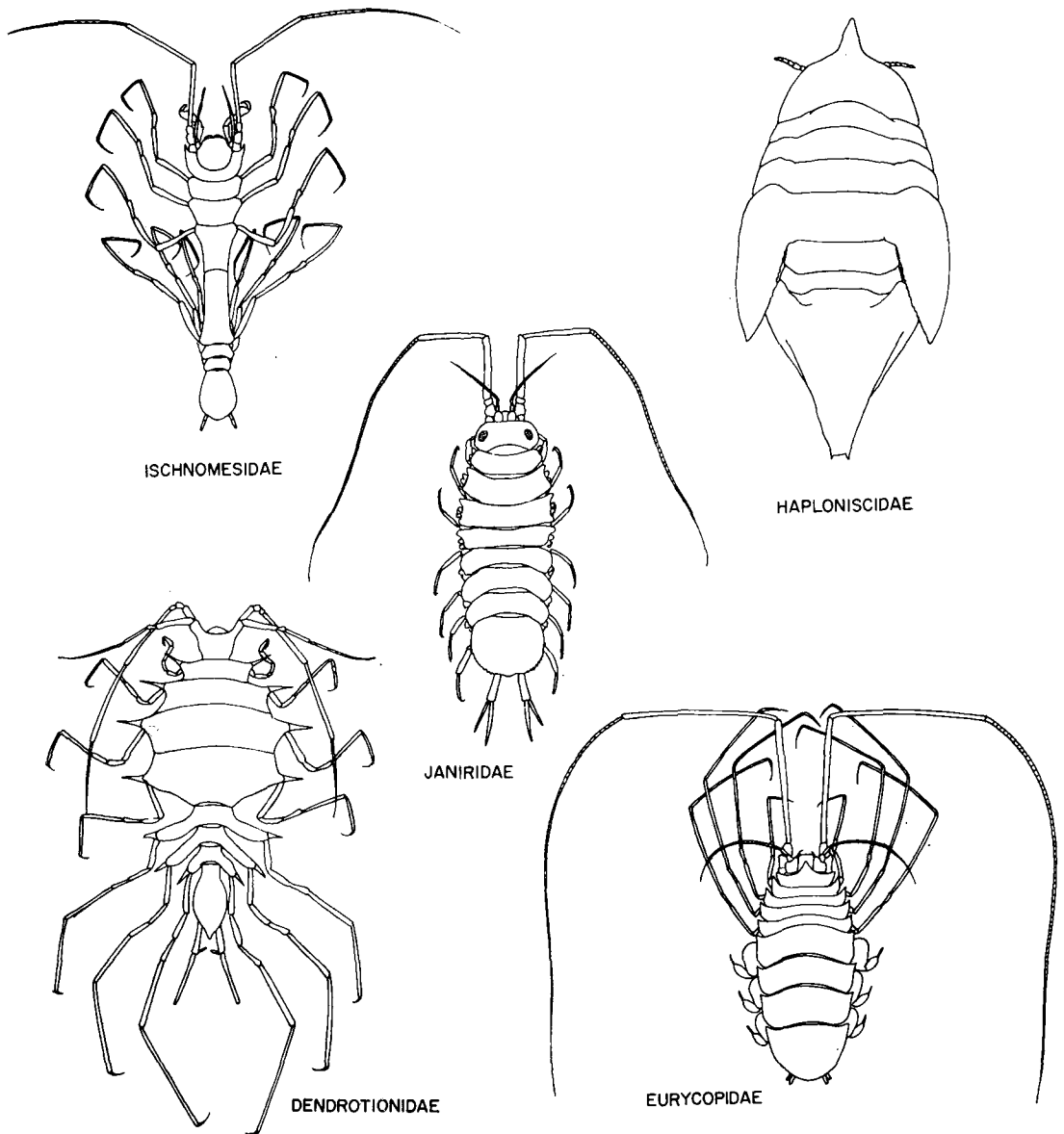


Fig. 3. Four specialized, deep-sea families of Janiroidea (Dendrotionidae, Ischnomesidae, Haploneiscidae, Eurycopidae) contrasted with the most primitive shallow-water family (Janiridae), which was also illustrated in Fig. 2.

Whereas the primitive janirid body plan is adapted for walking, some deep-sea families are modified for burrowing (Macrostylidae) or swimming (Munnopsidae, Eurycopidae, Ilyarachnidae). In the latter case, the posterior thoracic limbs are converted into paddles, and

the corresponding segments are fused and enlarged to accommodate a massive musculature. No other group of isopods can begin to equal this degree of fundamental morphological variation. All these families have their center of abundance in the deep sea (Table 3).

There is one major exception to this pattern. Many of the deep-sea families are also found in shallow water at high latitudes, such as the fjords of Norway and western Sweden, and the Antarctic and Arctic oceans. This fact has given rise to the hypothesis that the kinds of animals found in the deep sea today evolved in high-latitude, shallow waters, and subsequently migrated into the deep sea (KUSSAKIN 1973).

This hypothesis has considerable appeal because it makes good sense. The ultimate source of life for the deep sea must have been shallow water. One of the most important environmental factors restricting downward migration is temperature. The constantly cold temperatures of the deep sea would be difficult to adapt to by tropical or summer-breeding temperate organisms. That temperature differences create important barriers to distribution is well known to biogeographers of terrestrial and shallow marine communities. Because shallow waters at high latitudes are also cold, this important barrier would be absent.

However, this distribution pattern could also be explained as resulting from deep water evolution with subsequent migration into shallow water. The lack of a thermal barrier would apply in this case as well.

Three criteria are available to us as tests of these alternate hypotheses. The center of origin may be the center of diversity. It may also be the habitat of the most primitive species. Finally, the animals from both habitats may bear a morphological imprint that could only have been evolved in one of the areas. If use of these criteria yielded different answers, the dilemma would remain, but fortunately, they all suggest the same thing: the janiroidean families which dominate in the deep sea evolved there rather than having been introduced from elsewhere.

The known depth distribution of the Janiroidea (= Paraselloidea) has been summarized by WOLFF (1962, table 18, fig. 176) and KUSSAKIN (1973, fig. 11). These summaries differ from each other and with the list in Table 3 regarding usage of some minor families and details of family composition, but for the most part they agree. Most species in the families Janiridae, Jaeropsidae, Munnidae, and Antiasidae are found in shallow water (Fig. 4). Their diversity decreases markedly with depth, yielding what KUSSAKIN aptly calls a funnel-like distribution. Only 22 % of their species listed by WOLFF (1962) are restricted to depths greater than 200 m, and these comprise only 15 % of the janiroidean species which are

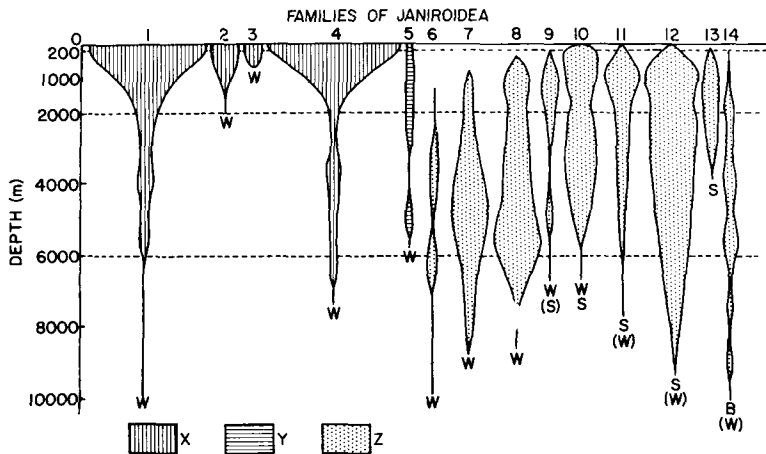


Fig. 4. Relative abundance of species in janiroidean families according to depth (modified from, and using the classification of KUSSAKIN 1973). 1: Janiridae; 2: Jaeropsidae; 3: Antiasidae; 4: Munnidae; 5: Dendrotionidae; 6: Janirellidae; 7: Haploniscidae; 8: Ischnomesidae; 9: Nannoniscidae; 10: Desmosomatidae; 11: Ilyarachnidae; 12: Eurycopidae; 13: Munnopsidae; 14: Macrostyliidae. Abbreviations are as follows: X, families primarily found in shallow water and typically having eyes; Y, family primarily found in the deep sea, but having bathyal representatives with eyes; Z, families primarily found in the deep sea and never possessing eyes; W, having the ability to walk; S, having the ability to swim; B, having the ability to burrow.

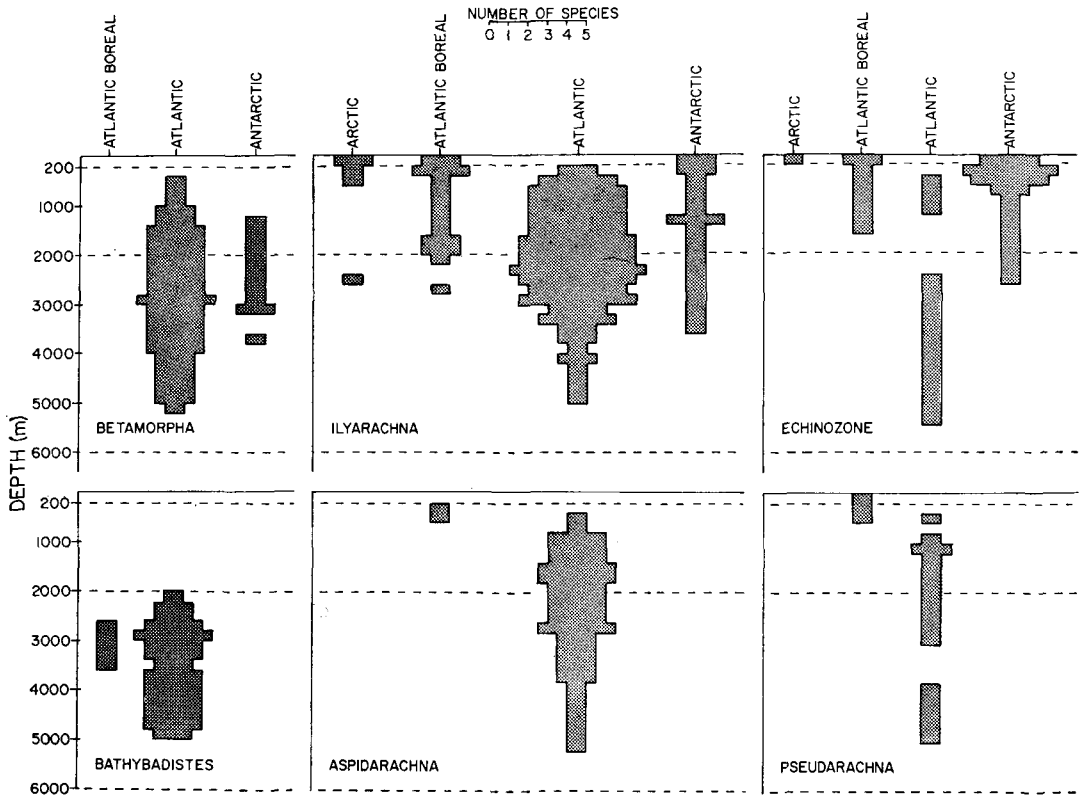


Fig. 5. Known depth range of genera of Ilyarachnidae and the precursor genus, *Betamorpha*, according to geographic region (modified from HESSLER & THISTLE (1975)).

limited to those depths. Shallow-water species are found in both warm and cold waters.

The other janiroidean families have quite a different depth distribution. Here, most species are found in deep water, resulting in a 'spindle-like' distribution (KUSSAKIN 1973). Only 17 % live shallower than 200 m and comprise only 16 % of the janiroidean species living there (WOLF 1962). The vast majority of the shallow-water species are limited to high latitudes.

These data clearly indicate that the center of diversity of all the janiroidean families except for the Janiridae, Jaeropsidae, Munnidae, Antiasidae, and Pleurogoniidae, is in the deep sea.

To date, very little effort has been made on the study of the origin and evolution of individual janiroidean families. As a result, for the most part it is not possible to discuss the distribution of primitive members. An outstanding exception to this is the case of the Ilyarachnidae,

where it has been possible to identify the precursor genus, *Betamorpha*, in an entirely different family, the Eurycopidae (HESSLER & THISTLE 1975). Knowing the origin of primitive and advanced genera within it. The pattern of distribution of these genera is clearest in the Atlantic, where sampling has been most intense (Fig. 5). Here, all the genera except one extend from the upper deep-sea boundary (200–500 m) to the greatest depth for which samples are available (approximately 5000 m). The single exception is *Bathybadistes*, which is limited to the abyssal zone (greater than approximately 2000 m). Only at high latitudes do ilyarachnids extend routinely into the littoral zone (< 200 m).

*Betamorpha*, the ilyarachnid precursor, is limited to deep water, even at high latitudes. The most primitive species within the Ilyarachnidae, *Ilyarachna abyssorum*, is found only in the abyss. All the ilyarachnid genera except *Echino-*

zone have their greatest diversity in deep water. *Echinozone* shows its highest diversity in shallow water at high latitudes, but this is an advanced genus in the family.

Thus, on the basis of the distribution of primitive members, as well as general diversity pattern, the Ilyarachnidae evolved *de nova* in the deep sea. The only other family for which there is some information on intrafamilial evolution is the Desmosomatidae (HESSLER 1970). Here, the most primitive genus, *Balbidocolon*, is also limited to the deep sea.

The final criterion for discernment of place of origin is a morphological one. The five families with primary diversity in shallow water all have

well-developed eyes. The primarily deep-sea families lack all traces of eyes, except in the Dendrotonidae, whose most primitive genus, *Acanthomunna*, has them. Even the shallow-water, high-latitude members of these deep-sea families lack eyes.

It is not difficult to understand why eyes are lacking in the deep-sea environment. There is no light from the sun, and isopods lack bioluminescence. Therefore, as seen with cave faunas, there would not be sufficient selective advantage to prevent eyes from regressing completely. This process is even evident in the five shallow-water families. In their deep-water representatives, eyes are either strongly reduced or absent.

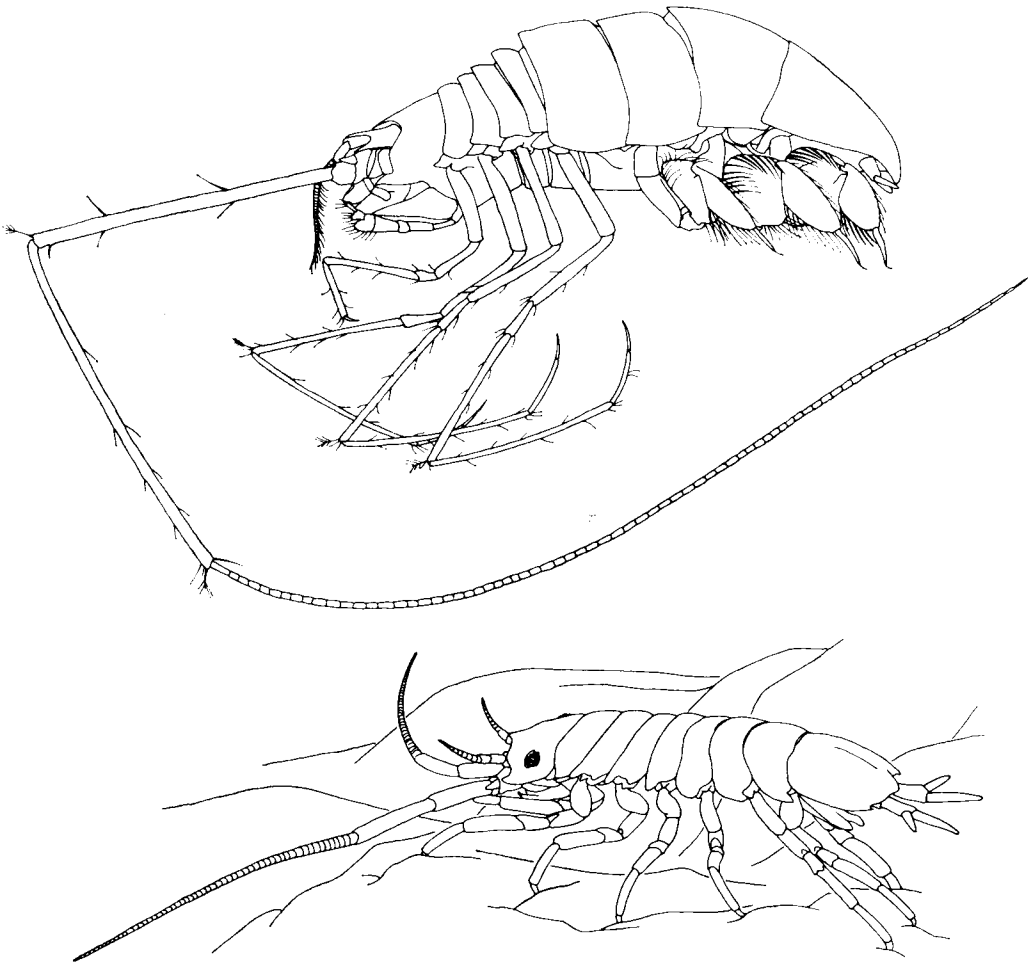


Fig. 6. Habitus views of *Janira lata* (bottom), showing the presence of eyes in a primitive, walking, shallow-water family (Janiridae), and *Eurycope* (top), showing the lack of eyes in an advanced, swimming family (Eurycopidae), even when found in shallow water.

Once lost, eyes are not regained. This explains why shallow-water representatives of the deep-water families lack them. It might be argued that even exclusively shallow-water animals sometimes lack eyes, and therefore it is possible that these deep water families lost their eyes in shallow water prior to deep migration. The life style of the isopods involved makes this unlikely. All of the shallow-water families are ambulatory, that is, move about by walking (Fig. 6). Their possession of eyes in shallow water clearly demonstrates the adaptive advantage of vision there. Some of the deep-sea families are also ambulatory, but in four of them, the ability to swim is well developed. It is precisely these swimming families that most frequently have shallow-water representatives. Thus, the argument for a shallow-water origin for the deep-sea families must explain why vision has greater adaptive advantage for ambulatory animals than swimming ones. This would be difficult to do.

In short, the distribution of eyes reinforces the conclusion based on evidence from distribution of diversity centers and primitive forms by showing unambiguously that the deep-sea families must have evolved in the deep sea. The presence of these families in shallow water at high latitudes is a result of upward migration into areas of similar temperature regime. Since deep-sea genera tend to be cosmopolitan, they are potentially available for emergence into any suitable shallow-water environment. This could explain how many genera could have bipolar distributions in shallow water.

The presence of the most primitive asellotes in shallow water tells us that even the janiroidean families that evolved in the deep sea had progenitors with a shallow-water ancestry. Unfortunately the ability to discern the ancestor of the Ilyarachnidae is an unusual circumstance. For the most part the other families are distinct, allowing few insights into the details of their origin. All one can be reasonably confident of is that the ancestor was similar to the Janiridae. However, the lack of identifiable intermediates suggests that evolution of the deep-sea families occurred so long ago that there is no reason to think the ultimate ancestor was closely related to any extant genus.

Furthermore, since the Janiridae is nearly cosmopolitan, there is no *a priori* way to detect what portion of the globe was the site of downward migration. Today's shallow-water center of diversity tells nothing about distributions

before global cooling, when some or all of the invasion might have taken place. It is not even necessary to assume that the invasion must have emanated from a diversity center, as opposed to some more restricted but nonetheless healthy fauna. Finally, until we know more about the evolution of the deep-water families, one cannot even be sure of how many invasion events took place. Deep-water species with vestigial eyes are a likely indication that such invasions are taking place today. For such recent invasions – the Serolidae is an example (MENZIES & al 1973:296–300) – cold, high-latitude waters are apparently the center of origin.

While similarity in climate apparently eases the passage between shallow and deep water, physical factors may not be the primary forces which determine whether a species is a potential invader. The low rate of food supply may be an even more stringent problem (HESSLER & JUMARS 1974). Temperature adaptation requires metabolic adaptations, but adjustment to a different food supply requires far more extensive modifications, involving size, ambit (the amount of space covered during the activity of an individual), feeding morphology, reproductive strategy, digestive physiology, growth rate, life span, behavior, and so on.

The present discussion argues strongly for *in situ* evolution of a major component of the deep-sea fauna. It is perfectly possible that other deep-sea groups have a similar history. However, it is also possible that others display very different patterns. Each group requires individual scrutiny before we can determine the extent to which generalizations can be made about the origin of life in the deep sea.

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Received 16 November 1978.