ALMOST A CRAB

by JOEL W. MARTIN

I've got one." The call came from the far side of the stream—just that short sentence and no more, not even the perfunctory exclamation point to indicate that what was "got" was of any importance. And yet my skin tingled as if I had just been informed of the discovery of a living trilobite. At the time that the voice filtered down to me through a completely foreign vegetation, I was knee-deep in cold water in the Arroyo San Antonio in southern Uruguay. Wading upstream, I approached my friend with some uncertainty. After all, the animal we were seeking had not been reported from this part of the world for nearly half a century. My doubt was unjustified, and I now feel guilt when I remember my lack of faith; Dr. Bruce Means, probably the finest naturalist I shall ever know, has a reputation of sorts and (I was to find out later) makes few if any mistakes in the field. When I reached him, any questions I might have had were immediately answered. He held in his hands a living specimen of a bizarre freshwater "crab." Not a true crab (that is, a member of the infraorder Brachyura) or a crayfish (a member of the infraorder Astacidea), the animal in Bruce's hand was a member of the endemic South American crab genus *Aegla*.

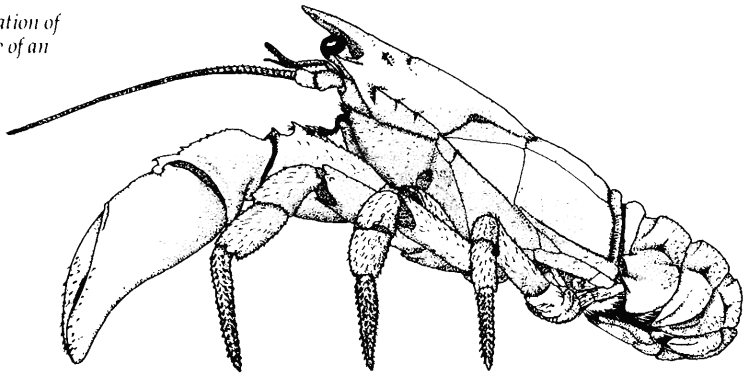
Decapod (ten-footed) crustaceans—the group of invertebrates that includes the familiar crabs, shrimps, and lobsters—are among the largest of the invertebrates. A brief perusal of the group usually leaves one staggered at the diversity of sizes and shapes. Decapods range in size from symbiotic pontiniid shrimp only a few millimeters in length to Japanese spider crabs with a leg span of several meters. In shape they may be of unbelievable delicacy and fragility, as are some of the resplendent cleaner shrimps, or they may be as massive as that culinary delight, the Maine lobster, known to exceed sixty pounds in very old individuals.

The diversity is itself somewhat misleading. All decapods, regardless of size or shape, are basically very similar. All possess eight pairs of thoracic appendages; the first three pairs are modified as feeding structures, which leaves five pairs for ambulation (hence the name Decapoda). Often the first of these five pairs are modified into large claw-bearing appendages, leaving only four pairs of walking legs. Every species possesses a large carapace, shielding the back of the fused head-thorax region, and each has an abdomen of six segments, although it may be modified from group to group. It is a simple mental exercise to envision the elongate tail of the primitive forms, such as the commercially harvested penaeid shrimps, becoming heavier and more massive with a corresponding flattening and thickening of the carapace. The result is a lobster; indeed there are few differences between "shrimps" and "lobsters" other than the number of legs that terminate in claws and the mode of reproduction (the commercial shrimps shed their unhatched eggs into the sea, whereas all other decapods carry the eggs through hatching). Continuing the exercise, one can see that a crab is built along the same plan, but with the abdomen reduced and tucked away beneath the thorax and with the carapace greatly widened.

This unity of form serves to unite the decapods into a natural, clearly defined taxon. The basic architectural design can be followed without interruption as one proceeds from group to group. But this same cohesiveness makes the job of the taxonomist devilishly hard. How does one divide the decapods into subgroups? A crab is a crab, and a shrimp a shrimp, but in reality the boundaries of "crabdom" are poorly delimited, and there are many groups that seem to fall somewhere in between.

A large male aegluid, a freshwater relative of the hermit crab, from the Arroyo San Antonio, southern Uruguay. This specimen is the largest Aegla *known to science. Photograph by Joel W. Martin.*

Early naturalists divided the decapods into three somewhat artificial groups, based upon the relative development of the abdomen. The macrurans (longtails) encompassed all of the shrimps and lobsters. The brachyurans (shorttails) contained the true crabs; this assemblage is believed to be a natural (monophyletic) group, and we have retained Brachyura as a widely recognized taxon. But there remained a large number of decapods that fit into neither of these two groups. The tail was either asymmetrically twisted (the hermit crabs and their relatives) or flexed forward beneath the abdomen like that of a crab, but not as reduced. Examples of this latter group are the familiar mole crabs or sand fleas (*Emerita* and *Hippa*) of Atlantic and Pacific coasts of North America and a marine benthic (deep water) taxon, the Galatheoidea. The appropriate name Anomura was assigned, on the basis of the

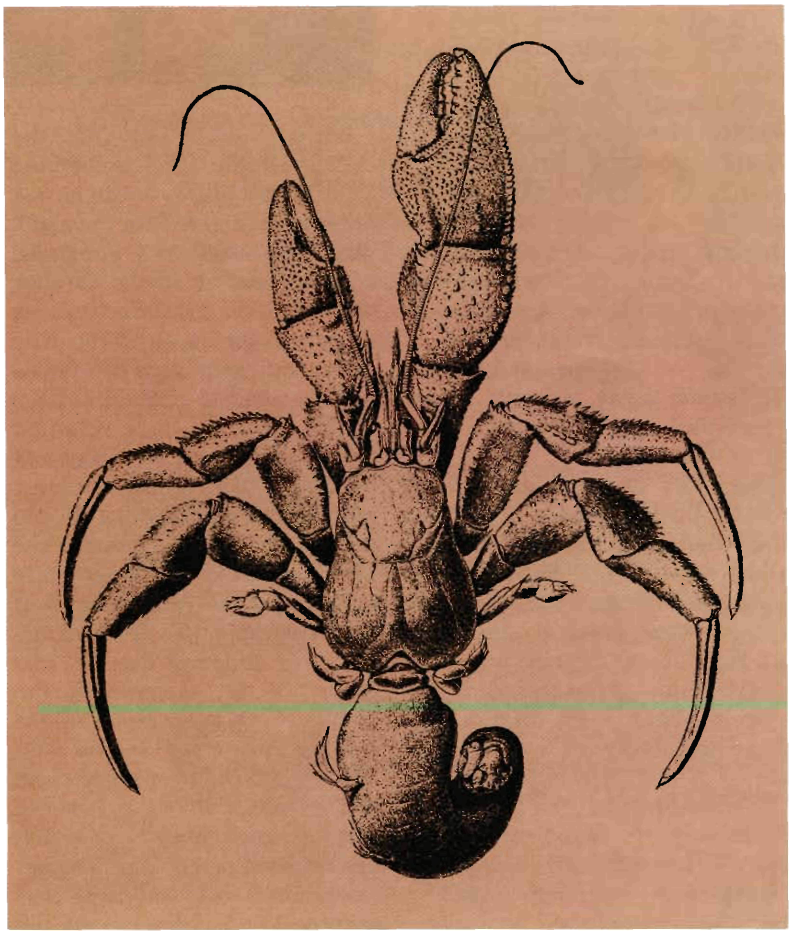


An illustration of a side view of an aeglid.

anomalous nature of the abdomen, to members of this nonconformant assemblage. It is to this group, the Anomura, that the South American aeglids belong.

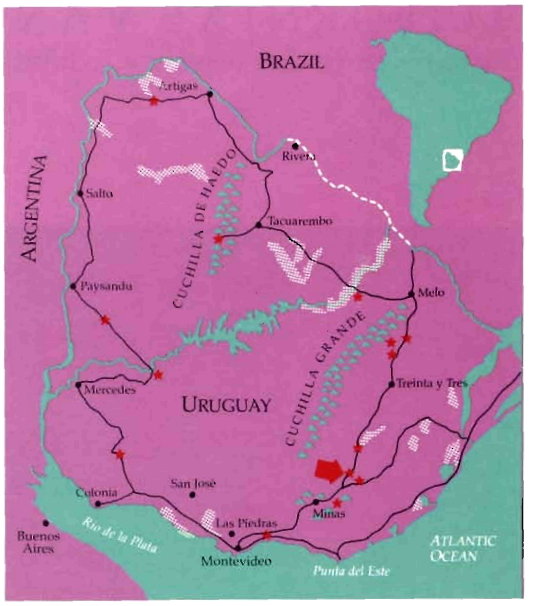
I began studying aeglids long before I had the opportunity to see my first specimen. That specimen, a small crab on loan from the Smithsonian Institution, had been preserved for over fifty years. Yet they are not rare. During the few weeks we were to spend in Uruguay, Bruce Means and I would collect several hundred specimens, returning many living specimens to our Florida State University laboratories. In fact the family is fairly well represented in most of temperate South America; the absence of reported sightings in Uruguay stems probably from inadequate sampling. So why are aeglids of interest? There are two reasons. First, like so many zoological enigmas, they may not be what they appear to be. Second, their habitat is undergoing drastic reduction and perturbation; natural freshwater habitat in Uruguay is increasingly difficult to find.

Aeglid crabs traditionally are grouped with a marine superorder of decapods, the Galatheoidea, an assemblage that contains galatheid crabs (often called "squat lobsters"), porcelain crabs, and rare deep-sea chirostylids, which tend to associate with gorgonian sea fans. Superficially, aeglids resemble the squat lobsters of the family Galatheidae, but this entire assemblage, except the aeglids, consists of species restricted to a marine environment. Aeglids are strictly freshwater animals. They need never return to the sea, not even to deposit eggs as do many freshwater or terrestrial crabs and shrimps, but instead undergo direct development (there is no larval stage) in fresh water. In addition to this ecological difference, there exist in *Aegla* a host of morphological peculiarities found in no galatheid. The connection between aeglids and their supposed marine relatives appears tenuous at best. Are there any more likely candidates for aeglid relatives?



Aegla *is an anomuran crab like the hermit crab* Pagurus alaskensis. *If* Aegla *is closely related to hermit crabs, then the evolutionary divergence must have occurred before hermits became asymmetrically coiled for life in snail shells.*

As I stared in amazement at the crustacean in my friend's hand, I began comparing the crab to all other decapods with which I was familiar. The flat, cockroachlike appearance and the slow forward crawl of the crab were not reminiscent of any of their supposed relatives in the Galatheoidea. Over the next few weeks we were to make many observations on aeglids in their natural environment (cold rocky streams); each encounter further convinced me that aeglids were very different from any of the squat lobster group. The most striking feature of the aeglids is the carapace. It is oval and flat, with serrated margins. This combination of features is not unique—indeed it is not too different from that seen in several squat lobsters—but the carapace is crossed by a series of thin lines, effectively dividing the carapace into distinct regions. Preserved specimens can be teased apart along these sutures. It is a condition shared by no member of the galatheoidea. However, one other group of decapods does have a similarly divided carapace.



A map of Uruguay showing localities where the author found aeglids.

Along the shores of almost all continents swarm legions of hermit crabs. These ubiquitous decapods walk in a more or less forward direction, as do the aeglids. Their right and left claws are almost always asymmetrical, like those of the aeglids. The carapace is subdivided by a series of suture lines nearly identical to that seen in *Aegla*. In fact, it seems possible that aeglids represent a freshwater offshoot of the hermit crabs that branched off long before asymmetry (as an adaptation to living in snail shells) proved to be the predominant hermit theme.

The surrounding countryside should have been my first clue to this surprising possibility. Uruguay is a flattened speck of delta; the highest elevation in the country is less than fifteen hundred feet. Over the past millennia the adjacent Rio de la Plata has leveled the lowlands of Uruguay and eastern Argentina into a gently rolling, incredibly rich landscape. Indeed, over evolutionary time and considering the large number of marine inundations, the vast expanse of the Argentine and Uruguayan flatlands could be considered one large estuarine mud flat—a not surprising habitat in which to find hermit crabs. Marine waters have spread across Uruguay and eastern Argentina numerous times in the past. Epicontinental seas persisted over the Amazon and Rio de la Plata basins well into the late Cretaceous (some 65 million years ago), the time period that contains the only known fossil aeglid. That fossil, from marine deposits in New Zealand, allows us to postulate the approximate time at which aeglids may have been stranded in freshwater in South America. As the seas receded, numerous organisms were undoubtedly left behind in pools of brackish water. Although the majority probably did not survive, those hardy enough to adapt to brackish and eventually fresh waters have persisted until today. Thus the aeglids, long thought to be relatives of the marine squat lobsters, may instead have descended from shell-less hermit crabs left behind when the seas receded from the Argentine pampas.

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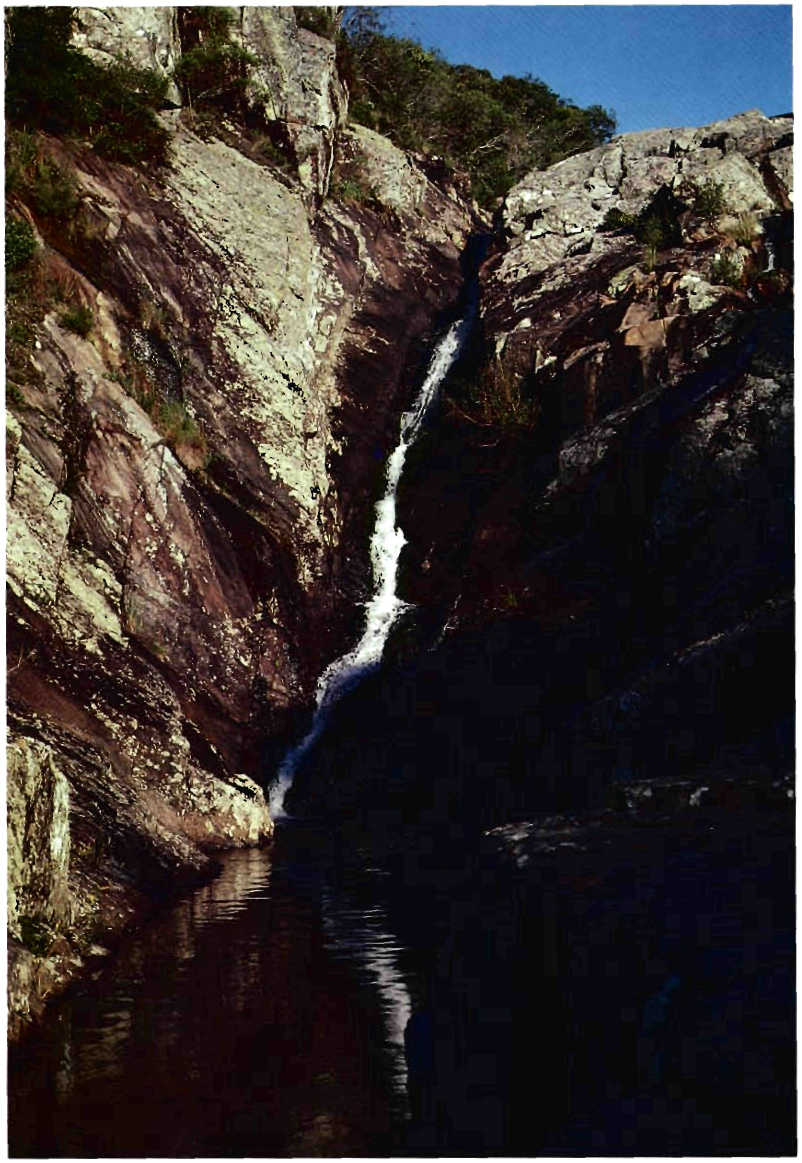

Aeglid habitat. Salto de Penitente (the falls of the Penitente River), southern Uruguay. This area is one of the highest points in the country. Photograph by Joel W. Martin.