

A Review of the Crayfish
Genus *Astacoides*
(Decapoda: Parastacidae)

HORTON H. HOBBS, JR.

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ABSTRACT

Hobbs, Horton H., Jr. A Review of the Crayfish Genus *Astacoides* (Decapoda: Parastacidae). *Smithsonian Contributions to Zoology*, number 443, 50 pages, 23 figures, 1987.—The crayfish fauna of Madagascar consists of six species belonging to the endemic genus *Astacoides*. Four of them, originally recognized as varieties of a single species *Astacoides madagascarensis* and subsequently accorded subspecific status, are elevated to specific rank. Two, *A. crosnieri* and *A. petiti*, are described as new. Following remarks on the limited range of the genus, which appears to be confined to higher elevations in the eastern part of the island between 18° and 25° South latitude and 46° to 49° East longitude, are notes on the organization of the text and a resumé of our previous knowledge of the genus. This is followed by discussions of the taxonomic characters considered in the study, the common origin of the disjunct *Astacoides* with other parastacid stocks, and the evolution and interrelationships of the Madagascan species. A diagnosis of the genus accompanies a key provided for the recognition of its members. A synonymy, diagnosis, description, statement of range, list of localities and specimens examined, and illustrations are provided for each species.

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A Review of the Crayfish Genus *Astacoides* (Decapoda: Parastacidae)

Horton H. Hobbs, Jr.

Introduction

To students of crayfishes, the genus *Astacoides*, endemic on the Island of Madagascar, holds a number of special interests. For more than a hundred years those interested in zoogeography have been puzzled as to the origin of its members and how they reached the island. Their isolated position, emphasized by the absence of crayfishes in Africa and the Indian subcontinent, has led to interesting, if not satisfying speculations. In only a few parts of the world—Mexico (See Villalobos, 1955, 1983), Guatemala, Honduras, and Cuba (see Hobbs and Villalobos, 1964) in the Western Hemisphere, and Madagascar, New Guinea, Aru Islands, and Misol (see Holthuis, 1949, 1950, 1982), and northern Australia in the Eastern Hemisphere—have crayfishes been successful in invading the tropics. Where they have done so, many, if not most, of the species live at higher elevations as they do on Madagascar where most of the known localities occur between 800 and 2000 meters above sea level. Few crayfishes living in temperate latitudes have been found at elevations so high as the latter. Unique in appearance is the seemingly excessively spiny *Astacoides betsileoensis* Petit, 1923, which probably exhibits the most ornate appearance of any extant, and very likely extinct, species in the ancestry of the two crayfish superfamilies, Astacoidea and Parastacoidea. Although none of the crayfishes living on Madagascar attain a size approaching that of the Tasmanian *Astacopsis gouldi* Clark, 1936, all are comparatively large, sometimes attaining carapace lengths of more than 80 mm.

Intriguing also is the fact that the several recognized forms, some even having been accorded different vernacular names, have been recognized as "varieties" of a single species (Monod and Petit, 1929). That such extreme variation exhibited by the crayfish fauna of the island might occur in a single gene pool appeared unlikely to me, and their subsequently being recognized as subspecies (Pretz-

mann, 1961) does not seem a satisfactory nomenclature. Holthuis (1964) reluctantly accepted the infraspecific designation of at least one of the varieties recognized by Monod and Petit, for he remarked (page 316):

The differences from the other forms are so striking that I would be inclined to consider *A. m. betsileoensis* an independent species. As however, Monod and Petit's opinion that it is only a subspecies of *A. madagascarensis* is based on much more material than that which I have at my disposal, I abide, for the time being at least, by their decision.

Monod and Petit (1929:29–37) provided a rather detailed discussion of the surprisingly small known range of the genus that extends on the Hauts Plateaux from the region of Anjozorobe, a short distance north of Tananarive, southward for about 700 kilometers to the Isaka Valley. On the east the range is limited largely by the escarpment bounding the plateau, the crayfishes descending the rivers to about 800 meters. On the west they are not known to be present beyond the headwaters of the westward flowing streams. Thus the genus occupies a range of some 700 by 100 kilometers in the southeastern part of the island (Figure 1).

It is regrettable that so little detailed habitat data are available for these crayfishes. On the basis of what has been reported, one would conclude that they are virtually limited to streams of the high plateaus where they are most abundant in headwaters, brooks, and swifter rivers flowing through forests. Moreover, little information concerning the habitats or habits of previously unrecorded specimens accompanies them. The reason for lamenting the lack of such data is that, judging by combinations of morphological features exhibited by the several forms, adaptive radiation appears to have played a more important role in the evolution of *Astacoides* than existing information suggests.

My active interest in the Madagascan crayfishes was kindled when a decade ago my friend Alain Crosnier asked if I might be interested in examining several lots of specimens he had collected on the island. Aware that the fauna had been reported to consist of four varieties of a single species, I assumed that the specimens could be assigned quickly to one or more of them and returned. Such prompt identifi-

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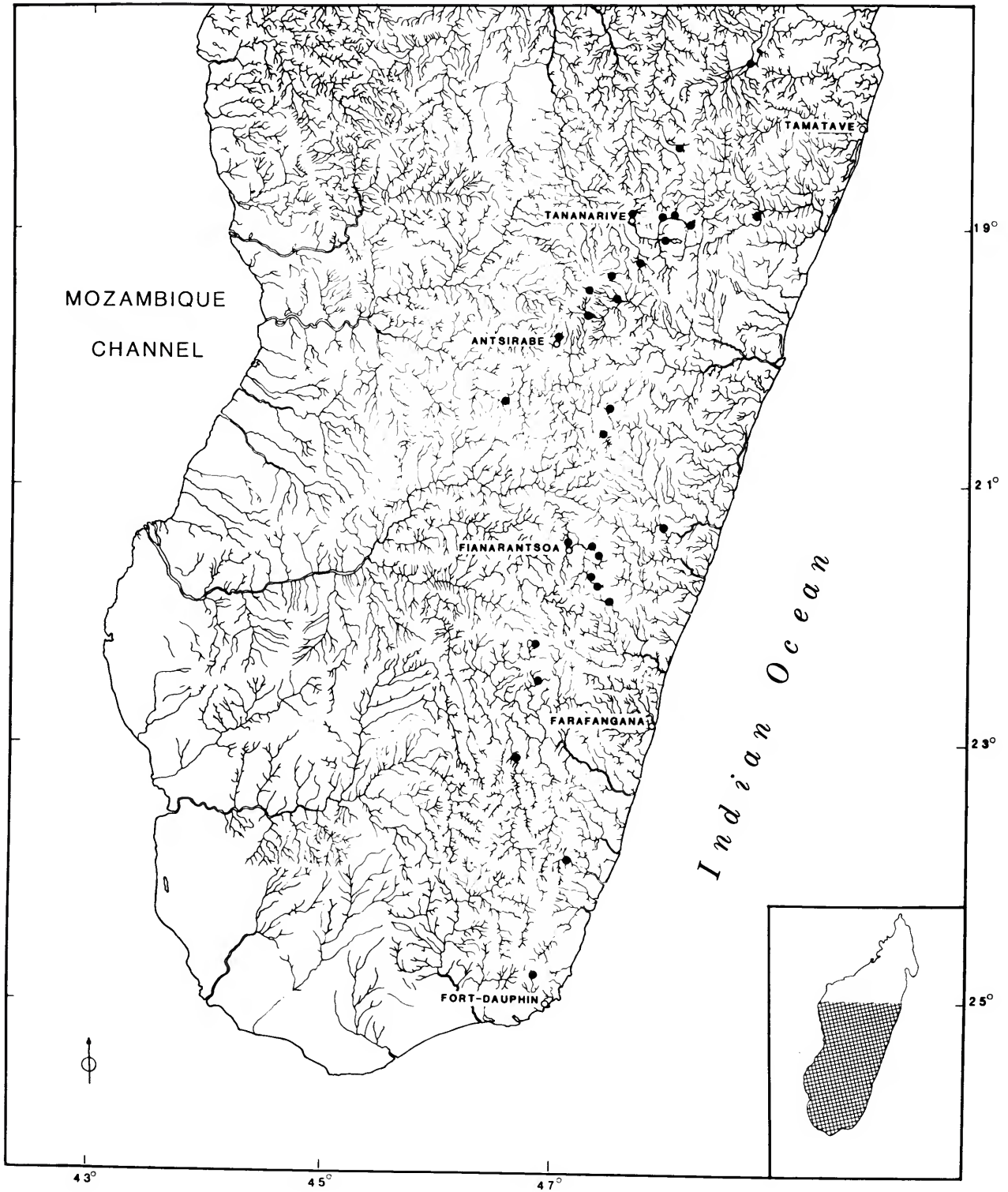


FIGURE 1.—Range of the genus *Astacoides*.

cations were not realized, and now, some ten years after accepting the specimens proffered, I reluctantly close the containers and pen this introduction to a compilation and analysis of all of the information of which I am aware concerning the genus *Astacoides*. Just as Monod and Petit (1929:4) remarked of their study made almost sixty years ago, the review herein should by no means be considered a definitive account of the crayfishes of Madagascar. It may be hoped, however, that the assumptions and hypotheses offered will incite an intensive study by others of these unique crayfishes, the natural history of which so little is known.

As a result of this study, including an examination of all of the representatives of the genus in the collections of the British Museum (Natural History), the Muséum National d'Histoire Naturelle (Paris), the Rijksmuseum van Natuurlijke Historie, Leiden, and the National Museum of Natural History, Smithsonian Institution, I am recognizing the presence of six species of *Astacoides* on Madagascar. Representatives of all of them were known to Monod and Petit, who treated four of them as varieties of *Astacoides madagascarensis* (H. Milne Edwards and Audouin, 1839a). One of the remaining two was considered to be a variant of their variety *granulimanus*. The other, represented in material available to them by a single specimen from Ikongo, was said to be too different from the latter to be considered a member of that variety but was not given a name. The varieties were subsequently treated as subspecies (see below).

To explain a viewpoint leading to some of the taxonomic changes proposed herein, I am continuing a practice of a number of years. It is my opinion that the recognition of subspecies implies a greater knowledge of a gene pool than can be anticipated when specific names are attached to what appear to be different crayfishes. In my assigning subspecific rank to populations some evidence has been at hand suggesting that they are sharing in a common gene pool. In the absence of such evidence in the Madagascan crayfishes available to me, I am admitting my limited knowledge of their affinities in according them specific rank. That at least some of them should indeed be so recognized became apparent when representatives of three were found in the same locality (Marais de Ampamaherana, east of Fianarantsoa), none of which exhibited any of the unique features of the other five. Possibly I am being hasty in according specific status to *A. betsileoensis*, for there is suggestive evidence that a gene exchange might occur between it and *A. caldwelli* (Bate, 1865), but the data are too fragmentary to be convincing. This is discussed more fully under the "Remarks" in the section devoted to *A. betsileoensis*.

As will be gleaned from the descriptions and discussions that follow, three species pairs appear to exist on the island with *Astacoides crosnieri* and *A. petiti* (the two forms described as new herein) at one end of the spectrum of diversity linked by *A. granulimanus* and *A. madagascarensis*

to the opposite, comprising *A. caldwelli* and *A. betsileoensis*.

ACKNOWLEDGMENTS.—I am deeply indebted to a number of persons for the assistance and encouragement they have given me in this study. Alain Crosnier of the Office de la Recherche Scientifique et Technique Outre Mer (ORSTOM) is responsible for my having developed an active interest in the crayfishes of Madagascar by providing me with several collections that he had made on the Island. He was my host when I visited the Muséum National d'Histoire Naturelle in Paris, extended every courtesy possible while I was there, and personally forwarded a sizable segment of the Museum collection to me for further study. For his patience and invaluable assistance, I am most grateful. Jacques Forest and Michèle de Saint Laurent of the Paris Museum were most cordial during my visit to the Museum and did much to facilitate my endeavors. A visit to examine the crayfishes in the Rijksmuseum van Natuurlijke Historie in Leiden was made enjoyable and productive through the many kindnesses of Lipke B. Holthuis. The British Museum holdings of *Astacoides* were lent to me through the courtesy of Raymond W. Ingle. My appreciation is extended to all of them, without whose cooperation and assistance this study could not have been undertaken.

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Remarks on Presentation

The initial segment of this report consists of a summary of previous work on the genus *Astacoides*. Because in the diagnoses and descriptions that comprise the major part of the study, several characters that have not been considered in other taxonomic studies of the genus have been used, a discussion and illustrations of them and comments on others are offered to clarify certain elements of the text that follows. Postulates concerning adaptations and the evolu-

tion and dispersal of the species composing the genus precede a key to the members of *Astacoides*, which is followed by accounts of the individual species. Each of these consists of a synonymy, diagnosis, description, remarks on the type-locality and types, a statement of the range and a list of the specimens examined, data on the maximum sizes, and remarks that seem pertinent.

SYNONYMIES.—Introducing each species is a complete synonymy including all of the references to it that I have encountered. Inasmuch as virtually all of the pertinent materials referred to are summarized in the historical summary of previous work on the genus, most of the comments following the list of references are limited to items that might possibly be misinterpreted.

DIAGNOSES.—The diagnoses are based on adults because few juveniles are among the collections examined. Characteristics of the chelipeds are limited to those appendages believed not to have been regenerated, and are applicable to both males and females. The ratios cited represent means followed by the standard deviation.

DESCRIPTIONS.—The descriptions, too, are based on what I presume to be adult specimens but do not take into account variations that result from regenerated appendages. Unfortunately, I am not aware of an infallible method of determining whether or not an appendage has been lost and replaced by a new one. The cheliped is the most important of those employed in distinguishing between the species, and in most, if not all, regenerated appendages the palm of the chela is decidedly short, the fingers are long, and their opposable margins bear no conspicuous basal tubercles; instead, the margins are provided with a broad, longitudinal band of minute denticles. Here, instead of repeating from the "Diagnoses" the mean and standard deviation of the several ratios cited, the minimum and maximum values encountered in the study are given.

TYPE-LOCALITIES.—In none of the forms described prior to this study except the variety "*betsileoensis*" could more than a general regional type-locality be assumed. Locality data other than "Madagascar" were unavailable for the other "varieties." Only for Monod and Petit's *A. granulimanus* does there seem a need for restricting the type-locality, and this need is discussed and a restriction proposed in the treatment of that species. The type-localities of *Astacoides madagascarensis* and *Astacoides caldwelli* are left unrestricted to "Madagascar."

TYPES.—The dispositions of the types are pointed out in the paragraphs so labeled, and, again, only for *A. granulimanus* does there seem a need for selecting a specimen from among those that must be considered to be syntypes to represent the species. To my knowledge, there are no problems surrounding the types of the other three forms recognized by Monod and Petit (1929).

RANGE AND SPECIMENS EXAMINED.—A brief statement of the range of each of the recognized species is followed by a list of the specimens that were examined in the present

study. All of the locality data available for each are included, as are the sex, carapace length, postorbital carapace length, date of collection, and collector, if available. The current disposition of the collection terminates the entry for each lot examined. The collections are identified as follows:

ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania, U.S.A.
BMNH	British Museum (Natural History), London, England
PM	Muséum National d'Histoire Naturelle, Paris, France
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
USNM	former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution

Most of the localities listed have been cited by previous authors and are summarized by Holthuis (1964). Others that have been reported but from which specimens were not available for this study are set off in a final paragraph under this heading.

Considerable difficulty was encountered in determining the coordinates of a number of localities—some of those mentioned in the literature as well as those cited on data accompanying previously unrecorded specimens. Alain Crosnier was most helpful in pinpointing a number of them, but, because of the inexact notations (for example; "between Vondrozo and Fort-Carnot") and identical names applied to more than one village, others could not be plotted in Figures 1, 15, 17, and 20. Moreover, a number of specimens were purchased in local markets, and the source of the material must be questioned; it is very unlikely that those specimens bearing labels marked "Farafangana" and "Tamatave" came from the immediate vicinity of these principalities. Thus in preparing the distribution maps, the localities indicated are those from which specimens were examined in this study and are limited to ones for which I am reasonably certain of the coordinates of their sources.

REMARKS.—The remarks that follow the listing of the specimens examined are highly varied, from noting differences in specimens from different localities to the inclusion of any life history data that are available, such as the dates upon which ovigerous females were obtained, and the diameters of their oval eggs. Certain specific characters are also sometimes emphasized.

VERNACULAR NAMES.—The local names that have been applied to the several species are included herein. Some of these have appeared in the literature, in which instances, bibliographic citations are noted, and some have been taken from field data recorded on the labels accompanying the specimens. I have been unable to associate the following common names reported by Dubois (1938:517) with any of the species: oranjatsa, orambarange, oramena, and oram-bare.

Resumé of Previous Knowledge

Uncertainty surrounded the name of the first two crayfishes described from Madagascar for 125 years following

the appearance of the descriptions of *Astacus madagascariensis* by H. Milne Edwards and Audouin on 9 May 1839 and *Astacoides Goudotii* by Guérin between 29 April and 13 May of the same year. Not until 1964, when Holthuis, who had successfully proposed to the International Commission on Zoological Nomenclature that Guérin's name be suppressed, reviewed the nomenclatural problems involved summarized the history of previous work on the crayfishes of the island, and presented a convincing defense for the nomenclature he proposed was a stability established. All of the literature reviewed herein has been perused during this study, and most of the summary that follows appears in Holthuis (1956 and/or 1964).

According to Holthuis (1964:313),

When in 1839 the traveller Goudot came back to Paris from a visit to Madagascar, he had in his collection the first Madagascar crayfish ever to reach the attention of scientific circles in Europe. Part of his material was donated by him to the Paris Museum, part came into the hands of Mr. F. E. Guérin Méneville of Paris.

That part of the material that went to the Paris Museum was described by H. Milne Edwards and Audouin (1839a, 1839b; identical descriptions) under the name *Astacus madagascariensis*, and at about the same time Guérin (1839a), considering the specimens in his possession to be worthy of generic distinction, applied to them the combination *Astacoides Goudotii*. Aware of the almost simultaneous appearance of the two names, and assuming that he and the authors of *Astacus madagascariensis* had described the same species, Guérin (1839b) published an addendum to Lucas' account of the "Thalassine, *Thalassina* (Crust.)" in the "Dictionnaire pittoresque d'Histoire naturelle" claiming priority for his name. In it he repeated the precise description that had just appeared along with the first illustrations of the crayfish and a statement to the effect that his original article had appeared in April, before that of H. Milne Edwards and Audouin, which followed on 9 May. A much more detailed description of *Astacus madagascariensis* [sic], comparing their crayfish with *Astacus fluviatilis* Fabricius, 1775 (= *A. astacus* (Linnaeus, 1758)), was presented by Audouin and Milne Edwards in 1841.

A few years later, Gray (1845:409) pointed out the close relationship of *Astacus Madagascariensis* to the Australian *A. franklinii* Gray (1845), noting that "Madagascar appears to be the tropical confines of the genus." Erichson (1846) treated *Astacoides Goudotii* as a junior synonym of *A. madagascariensis* and, in accepting *Astacoides* as a supraspecific taxon, reduced it to subgeneric rank, introducing the combination *Astacus (Astacoides) madagascariensis*. Dana (1852:521), although accepting the subgeneric designation of *Astacoides*, noted the fact that "Guérin erred in overlooking the small basal scale at the outer antennae, and based his genus on its supposed absence."

A male crayfish from Madagascar was transmitted to the Zoological Society of London by Mr. J. Caldwell and was referred to Spence Bate, who, judging from his statement

(1865:470) "Species [of *Astacus*] have been taken from . . . and now from the African island of Madagascar," was unaware of the descriptions of Guérin and those of H. Milne Edwards and Audouin. Apparently believing he had the first crayfish that would be reported from the island, he published a comparatively detailed description of the specimen from near Tananarive, naming it *Astacus Caldwelli*.

Brocchi (1875) was hesitant to accept the assignment of the Madagascar crayfishes to a genus other than *Astacus* (apparently he had overlooked Erichson's proposal of placing them in a separate subgenus of the genus *Astacus*), for he considered the characters cited by Guérin as not justifying such an arrangement. The absence of first pleopods in the males of specimens obtained in Madagascar by Granddier, however, seemed almost to persuade him that the crayfish from the island should be referred to *Astacoides*, stating that if adopted, then *Astacus madagascariensis* would become *Astacoides madagascariensis*.

Miers (1876) remarked only on characters of *Astacoides* that had been previously mentioned by others. Huxley (1879a,b) studied and illustrated the gills of a specimen of *Astacoides madagascariensis* and determined that the branchial count is 12 + epr + 5r, the least number of any known crayfish. He recognized two families of crayfishes: Potamobiidae, embracing the genera *Astacus* and *Cambarus*, and the Parastacidae, encompassing the crayfishes of the Southern Hemisphere, which was divided into six genera. In his classic, "The Crayfish . . ." (1880a, 1880b, 1881, 1883) he added little to our knowledge of *Astacoides* that had not appeared in his 1879 contributions but pointed out the "peculiar truncated rostrum" and long, flat epistome, and included an illustration of an animal in dorsal view (Figure 65).

Neither Moleyre (1885) nor Bate (1888) added anything new, but Keller (1887:291, and 1898) presented the first indication as to where on Madagascar crayfish occur: "in the central province." Vayssière (1892), whose interest was in temnocephalids that infest the Parastacidae, noted their occurrence on *Astacoides madagascariensis*.

Stebbing (1893) remarked that *Astacoides*, with its solitary species *madagascariensis*, is found only in Madagascar, presumably assuming *A. goudotii* and *A. caldwelli*, if known to him, to be synonyms. Faxon (1898:668) presented a brief diagnosis of *A. madagascariensis*, including a detailed count of the gills, and clearly treating Guérin's and Bate's names as synonyms of the species described by H. Milne Edwards and Audouin.

Not until 1900 was anything more specific pertaining to the range of the Madagascan crayfish recorded; Bertrand (1900:348) noted that it is abundant in the "torrents et ruisseaux du massif de l'Ankaratra." Moreover he remarked that although this crayfish resembles those that were becoming more and more rare in France, it was of a size unknown among its "congénères européennes," attaining 0.25 to 0.30 meter in length. Ortmann (1902) discussed the affinities of

Astacoides madagascariensis, pointing out similarities to other parastacids and remarked that there are certain similarities to *Cambaroides*; he also suggested possible past land connections with Madagascar, including an island chain and links to India and Africa. He seemed to favor the hypothesis that *Astacoides* had reached Madagascar "across India" (p. 391) before the Middle Cretaceous.

Calman (1910) made no new contribution, but, in the same year, Lenz reported two specimens from Tamatave. The isolated distribution of *Astacoides*, similar to that of "many freshwater fish, crustacea, mollusca, etc." was pointed out by Smith (1912:148). Gadow (1913) contained no original information, and Faxon (1914), in his list of described crayfishes, again treated *Astacoides goudotii* and *Astacus caldwelli* as synonyms of *Astacoides madagascariensis*.

Gravel (1922) provided a photograph of *A. madagascariensis* and noted that it occurred in great abundance in the more or less swift streams descending from the plateaus and was common in the brooks of the forest areas. He reported that it attains lengths of almost 25 centimeters and weighs 100 to 130 grams. Their consumption was said to be limited largely to Europeans.

Real progress toward an understanding of the diversity and ranges of the Madagascar crayfishes began with Petit (1923) when he recognized a new "variety," *betsileoensis*, on the basis of two females collected by him in March 1922 in the vicinity of Fianarantsoa. Its outstanding features were cited as including the substitution on the cephalothorax of strong spines for tubercles that occur on the typical form, the distinctive structure of the antennal scale, and that of the epistome.

Calman (1927) added no new information, but Petit (1927), aware of the need for clarifying the priority involved in two of the names applied to the Madagascar crayfish, concluded that documents are lacking to prove that Guérin's description had appeared in April, as he had claimed, and he accepted the name *Astacoides madagascariensis* for which the date of publication was certain. Why Petit did not adopt the original spelling is not clear. He briefly outlined the ranges of the typical variety and that of the variety *betsileoensis*, recognizing two "groups" within the genus: (1) "macrophthalmes," those possessing large eyes, a convex carapace, and flattened chelae; and (2) "microphthalmes," those exhibiting small eyes, a cylindrical carapace, and massive chelae. He also stated that the crayfish are particularly abundant at an altitude of about 1000 meters but occur as low as 800 meters above sea level. Other items do not differ from those that are offered in more detail by Monod and Petit (1929, see below). In his discussion of the fauna of Madagascar, Perrier de la Bathie (1927) mentioned a special variety that is abundant in all of the streams below 2000 meters. Harrison (1928) described *Stratiodrilus haswelli* infesting *A. madagascariensis* but no specific locality was cited; hence, uncertainty must attend the identity of the host.

Monod and Petit (1929) made one of the two most important contributions to our knowledge of the crayfishes of Madagascar. They again adopted, with reservation, H. Milne Edwards and Audouin's specific name for the Madagascar crayfish, but employed the combination *Astacoides madagascariensis*, recognizing four varieties: *madagascariensis*, *betsileoensis* Petit, *brevirostris*, new, and *granulimanus*, new. A key was provided for their recognition, and a discussion of the terminology applied to the rostrum and chela precedes the taxonomic section of the paper in which they refer to the first two varieties as "macrophthalmic forms" and to the other two as "microphthalmic forms." They also emphasized the intraspecific differences in the chelae, referring to those with long palms as "longipalmes," and those with short palms as "brevipalmes." All of the known localities for each of the varieties were cited. *Astacus caldwelli*, which was treated as a nomen nudum, was placed in the synonymy of the variety *betsileoensis*; Perrier de la Bathie's "*Astacoides madagascariensis* var." was considered a member of their variety *granulimanus*. As for interrelationships among the four varieties, the authors visualized two lines, the more primitive, embracing their *madagascariensis* (= *caldwelli*) and *betsileoensis*, and the advanced, consisting of the other two of which *granulimanus* was considered to be the more divergent. The range of the genus, according to them, is almost congruent with the "High Plateaus" below 2000 meters, forming a long oval over 600 kilometers in length and 100 kilometers at its greatest width; only in the southeast does it extend beyond this physiographic region. There the crayfishes were said to descend into the "Isaka" (= Isaha?) River valley (to about 800 meters). In the northernmost sector of the oval, the variety *brevirostris* was reported to occur in the vicinity of Tananarive; the typical variety, immediately southward on the eastern slopes of Ankaratra, and in the southern part of its range, in the province of Ambohitra; it was believed to intergrade with *betsileoensis*, which dominates streams in the region of Fianarantsoa and the Ikongo massif. The range of the latter overlaps that of the most southern variety *granulimanus* that occurs from the Andringitra massif southward to the vicinity of "Isaka." Their interpretation of the dispersal of the parastacids is most interesting, and, at least in part remarkably modern, employing "continental drift." They visualized a Middle Cretaceous parastacid stock occurring in an epicontinental sea covering segments of all (?) of the isolated areas now inhabited by the Parastacidae, and with localization occurring prior to their becoming adapted to fresh water, thus necessitating a postulate of multiple independent invasions of this new, to these crayfish, habitat. This allowed them to propose that the stock invading Madagascar had not been acquired secondarily from other land masses, rather directly from a salt water ancestor living in the epicontinental sea covering at least a part of the eastern versant of the island mass. Their treatment is concluded with a discussion of the crayfish fishery on the island, the

detriment to crayfish populations by deforestation and the introduced trout, and a plea for crayfish culture on the part of local land owners.

In addition to presenting a photograph of three living members of the variety "*madagascariensis*," Louvel (1930) noted that the vernacular name of the Madagascan crayfishes is "orana," that they are usually greenish brown in color, but in the vicinity of Ifanadiana they are completely red, and one specimen collected in Ankaratra was entirely sky blue. He also noted that the crayfishes are generally collected by hand at times of low water; they hide in excavations under the bank during the day where the natives use a spade to dislodge them. Night fishing aided by torches also seemed to be profitable. The crayfish were reported to be sold in the markets of Tananarive for five or six francs per dozen.

Grandidier and Petit (1932) added little that had not been previously reported by the latter. They stated that the natives of Manjakandriana and Ambotolaona take crayfish to the railroad between Tamatave and Tananarive, where they are sold to travelers, and also that they are sold cooked or alive at the market place in Tananarive on Fridays.

André (1937) noted that *Astacoides madagascariensis* harbors a species of *Stratiodrilus* and *Dactylocephala madagascariensis* Bayssiere. The following briefly mentioned the crayfish on Madagascar but presented no new data concerning them: Joleaud (1939), Bouvier (1940), Van Straelen (1942), Decary (1946, 1950), and Villalobos (1953, 1955, 1983).

In addition to reviewing the literature pertaining to the crayfishes of the island, Poisson (1947) presented an admirable summary of the then-current knowledge of Madagascan crayfishes, pointing out, among other information, that color does not furnish features that will permit distinguishing the varieties; at most, color is consistent for only local races. Most of the crayfishes on the island were said to be reddish or greenish brown, sometimes with yellowish, clear green, or blue marbled markings tinted with red. In Betsileo, the crayfish were blue or red. The colors of three varieties were specifically mentioned: a blackish form inhabiting swamps was described as having limited grayish flesh with a muddy taste. Although he suspected that this crayfish was the "variété *madagascariensis*" (= *A. caldwelli*), I am inclined to believe that it might have been a representative of either *A. crosnieri* or *A. petiti*. A second color type, exhibited by the "variété *brevirostris*" (= *A. madagascarensis*) was said to be blue or blue-gray, its plump flesh white or light gray and "good." The third described was the "variété" *betsileoensis*, which was vermilion red, its slender chelae with very little meat, but its abdomen quite plump, white, and very savory. Crayfish were reported to frequent waters having a pH of 4 to 8. They were described as being crepuscular and nocturnal, spending the day in cavities in the stream banks. In the mountains, they hid under rocks. The vernacular names "Ora" and "Orana," suggesting large

size, were applied to freshwater and marine crustaceans used for food. In Betsileo, the small crayfishes ("Oranakely" or "Zanak'orana") were called "Kitihy" or "Kitika." In the region of Fort-Dauphin the name "Deda" was applied to shrimps, lobsters, and crayfishes. In Betsileo, the swamp-dwelling crayfish were referred to as "Orangena" or "Oranjena," and the red crayfish there as "Oranjetsy" or "Pepeo." Poisson noted that "Oranjena" are the crayfish that burrow and plug the chimney, and that "Oranjetsy" are the red crayfish having a large abdomen. In Imerina, the crayfish were called "Orambato," and the larger ones "Orambranja." Enemies of crayfishes on Madagascar were reported to include trout, eels, and rats. Methods of fishing for crayfishes were also discussed.

Holthuis (1956, 1958), endeavoring to stabilize the name of the Madagascan crayfishes, petitioned the International Commission on Zoological Nomenclature to suppress the name "Goudotii" in the combination *Astacoides Goudotii* and to add *madagascariensis* to the "Official Index of Rejected and Invalid Specific Names in Zoology." This petition was adopted in Opinion 519 (Hemming, 1958:162), suppressing *Goudotii* in synonymy but not in homonymy, and adding *madagascariensis* to the list of rejected names. Thus it appeared that the long uncertainty about the name of the Madagascan crayfishes had been clarified.

In 1961, Paulian added nothing new, but Pretzmann accorded the varieties recognized by Monod and Petit subspecific rank and cited a few new locality records.

Holthuis' (1964) invaluable study brought together virtually all of the important information pertaining to the Madagascan crayfishes. Most of the bibliographic references cited herein were included in his synonymies, and in a convincing nomenclatural analysis he recognized four subspecies of *Astacoides madagascarensis*: (1) the nominate subspecies, of which the variety *brevirostris* Monod and Petit was considered a synonym; (2) *caldwelli* Bate, which was the form described by Guérin as *Astacoides Goudotii* and designated the variety *madagascariensis* by Monod and Petit; (3) *granulimanus* Monod and Petit; and (5) *betsileoensis* Petit. All of the localities known at that time for each subspecies were also cited. Not until Holthuis undertook this study does it seem that anyone investigating the crayfishes of Madagascar thought to compare the types of *Astacus madagascarensis* and *Astacoides Goudotii*. An inquiry made by Holthuis to M. Jacques Forest of the Muséum National d'Histoire Naturelle in Paris brought to light a syntype of the former in the Paris Museum, and another was found in the Rijksmuseum van Natuurlijke Historie, Leiden. The former specimen was designated the lectotype by Holthuis (1964:311). These specimens were compared with the only extant type of *Astacoides Goudotii*, which he borrowed from the Academy of Natural Sciences of Philadelphia. (This crayfish, listed by Faxon (1898, 1914), had been obtained from Guérin by a patron of the Academy, T.B. Wilson). To Holthuis' surprise, the specimen from the Academy was

distinctly different from the types of *Astacus madagascarensis* that had been described by H. Milne Edwards and Audouin. Thus Guérin's *Astacoides Goudotii* was not a synonym of the latter after all, but the name had been suppressed by the International Commission of Zoological Nomenclature! As a result, it appeared that Guérin's specimens were lacking a name, but upon comparing the type from the Academy with the description and illustration of *Astacus caldwelli* Bate, the type of which could not be located, Holthuis (1964:315) was convinced that "there cannot be the least doubt that his [Bate's] specimen belongs to the same subspecies as *Astacoides goudotii*." Thus Guérin's long rejected name was replaced by *Astacoides madagascarensis caldwelli* (Bate). Holthuis pointed out that Monod and Petit (1929:18) had found a specimen in the Paris Museum labeled "*Astacoides Caldewelli* Sp. Bate," but being unaware of Bate's description, treated it as a nomen nudum and relegated the name to the synonymy of *Astacoides madagascariensis* var. *betsileoensis*. According to Holthuis (1964:315), "That the Paris Museum specimen was incorrectly identified and that Bate's type is different from *A. m. betsileoensis* is clearly shown by Bate's original description and his figures of *Astacus caldwelli*, especially by the shape of the scaphocerite and by that of the exorbital spine." As for Bate's type, "no trace of it could be found at the British Museum; it may even have gotten lost before the collection of the Zoological Society was transferred to the British Museum" (1964:315). Particularly valuable among Holthuis' contributions in this study are the photographs of the types of *Astacus madagascarensis* and *Astacoides goudotii*, together with reprints of the two illustrations of the latter published by Guérin (1839b).

Bishop (1967:112) observed that the distribution of the Parastacidae "has never been satisfactorily explained. There is little or no evidence to suggest that contemporary crayfish can cross oceanic barriers." In his study of the phylogeny of the Parastacidae, Riek (1972) concluded that *Astacoides* shares more in common with members of the Tasmanian genus *Astacopsis* than with the Australian *Euastacus* and *Euastacoides*. "*Astacoides* has a few apomorphic attributes, including a reduced number of gills, very flattened body, and a spined margin of the antennal scale, as compared with *Astacopsis*" (p. 382). He also included an illustration of *A. madagascarensis*.

Neither Bott (1972) nor Miyake (1973) added to our knowledge of *Astacoides*, and the only pertinent contributions of Hobbs (1974) are a diagnosis of the genus *Astacoides* and illustrations of *A. betsileoensis*. Similarly, Yassini (1977), Brodsky (1981), Villalobos (1983), and Griveaud (1984) offered no new information.

Adegboye (1983), in discussing possible explanations for the presence of a crayfish on Madagascar and their absence from the African continent, listed four hypotheses but seemed to favor none. Only the theory that perhaps they

were introduced on Madagascar by man has not, to my knowledge, been previously offered. The most recent reference encountered to a crayfish from Madagascar is that of Vila and Bahamonde (1985) who referred to the study of Harrison (1928) in which he described a new histriobdellid infesting *Astacoides madagascariensis*.

COMMENTS ON PREVIOUS STUDIES.—Because of the importance of the contributions to our knowledge of *Astacoides* by Monod and Petit (1929), the number of references to their study herein, and the confusion that might arise to those references, a list of the names assigned to the crayfishes of Madagascar by them and the equivalents employed herein might prove helpful.

Monod and Petit (1929)	herein
<i>A. madagascariensis</i> var. <i>madagascariensis</i>	<i>A. caldwelli</i>
<i>A. madagascariensis</i> var. <i>brevirostris</i>	<i>A. madagascarensis</i>
<i>A. madagascariensis</i> var. <i>betsileoensis</i>	<i>A. betsileoensis</i>
<i>A. madagascariensis</i> var. <i>granulimanus</i>	<i>A. crosnieri</i>
	<i>A. granulimanus</i>
	<i>A. petiti</i>

In their analysis of variations in the chela of members of the genus *Astacoides*, Monod and Petit (1929) recognized "individus brevipalmes" and "individus longipalmes," pointing out that both chela of an individual may have short or long palms, or that of one may be short and the other long. They suggested further that the latter condition might be a manifestation of a tendency similar to that occurring in lobsters in which there is a slender (cutting) chela and a large (crushing) one. Indeed, in the lectotype of *A. madagascarensis* both chelae are short-palmed, and in the paralectotype the left is long-palmed and the right, short-palmed (see Holthuis, 1964, pl. 9) and the reverse condition obtains in the extant type of *A. goudotii* (1964, pl. 10). After examining as many specimens of *Astacoides* as are available, I am convinced that the long-palmed chelae are ones that have not been subject to loss and regeneration, and the short-palmed ones are those that have been regenerated. Similar differences occur in the chelae of many, if not all, cambarid crayfishes. Such dimorphic forms of the chelae are as evident in the cambarid genus *Fallicambarus* as they are in *Astacoides* (see Figure 2).

Perhaps significant is the observation that in addition to other similarities between the existing syntype of *A. goudotii* and Guérin's illustrations (1839b), the left chelae are short-palmed (regenerated) ones, and the right ones are long-palmed, indicating that in all probability the illustrations were executed using the specimen in the Academy of Natural Sciences of Philadelphia as the model.

Taxonomic Characters of the Genus *Astacoides*

SEXUAL DIMORPHISM.—An effort has been made to determine in which, if any, of the taxonomic features a measure of sexual dimorphism could be recognized in members

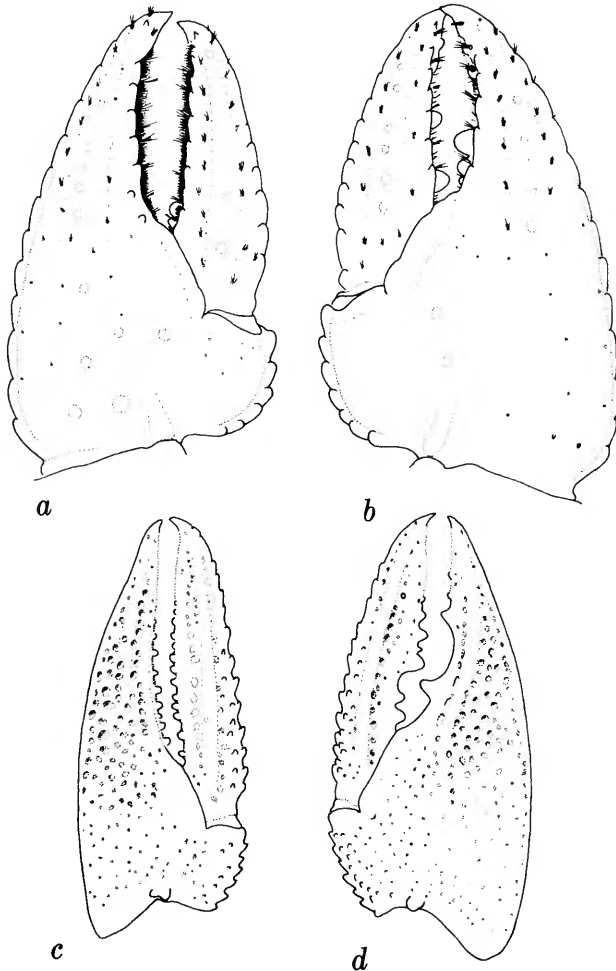


FIGURE 2.—Dorsal view of left and right chelae from two male crayfishes; a, b, *Astacoides crosnieri*; c, d, *Fallicambarus hedgpethi* (Hobbs, 1948) (a, c, regenerated (short-palmed); b, d, "normal" (long-palmed)).

of the genus *Astacoides*. The only readily evident differences between the sexes that could be found were (1) the position and features associated with the external apertures of the gonoducts on the coxae of the fifth (in males) and third (in females) pereopods, and (2) in the abdominal segments, which in most adult females are less arched transversely, resulting in a broader spread of the terga and pleura. No other secondary sexual features, such as larger chelae in males, accessory copulatory apparatus, modifications of the thoracic or abdominal sterna, could be found. Thus all of the following taxonomic features, except those concerning the width of the abdomen and references to the phallic papillae, employed in the key, diagnoses, and/or descriptions, apply equally to males and females.

ROSTRUM.—Detailed features of the rostrum in members of the genus *Astacoides* are highly variable, but basically it

is shovel- or spoon-like, subtruncate anteriorly, with slightly bowed or subparallel margins. The lateral carinae bear at least rudiments of a series of dorsal tubercles ranging from as few as two very low ones on each side and none on the anterior margin in *A. crosnieri* to as many as six prominent lateral ones in *A. caldwelli*, and three anterior ones in *A. betsileoensis*. But the numbers in both the lateral and anterior series are not consistent for any of the five species, and apparently some of the tubercles coalesce to form short ridges, particularly in larger, presumably older, individuals. Sometimes, especially in *A. betsileoensis*, the carinae of the rostrum are rather markedly concave laterally, causing the rostrum to appear somewhat broader anteriorly than basally, but in the other species the lateral carinae are almost always either subparallel or weakly convergent anteriorly. The degree of deflection anteriorly is somewhat variable but is less so in *A. crosnieri* and *A. granulimanus* than in the others. The length of the rostrum, as determined from the difference between the total length and the postorbital length of the carapace, ranges from 6.6 to 10.3 percent of the total carapace length in *A. crosnieri*, 7.9 to 11.2 in *A. petiti*, 7.9 to 12.7 in *A. granulimanus*, 5.8 to 10.0 in *A. madagascarensis*, 7.5 to 12.4 in *A. caldwelli*, and 9.9 to 16.1 in *A. betsileoensis*. Thus the only feature of the rostrum that can be relied upon to distinguish members of one species of *Astacoides* from another is the relative length, which, if constituting more than 12.7 percent of the length of the carapace, can be assumed to be that of *A. betsileoensis*.

AREOLA.—The areola in members of the genus *Astacoides* ranges from 1.8 to 5.9 times as long as broad: 3.7–5.9 in *A. crosnieri*, 2.5–3.2 in *A. petiti*, 2.3–4.2 in *A. granulimanus*, 3.2–4.9 in *A. madagascarensis*, 2.6–4.3 in *A. caldwelli*, and 1.8–3.5 in *A. betsileoensis*. The intrusion of the postcervical groove into the areola is not always readily evident, but, in general, it is somewhat V-shaped in *A. crosnieri*, *A. petiti*, *A. granulimanus*, and *A. caldwelli* but more U-shaped and situated more anteriorly in the other two.

POSTORBITAL RIDGE.—These ridges are comparatively poorly developed in all members of the genus, often represented by virtually nothing other than a small tubercle, which also is occasionally absent, situated lateral to the base of the rostrum. Occasionally a short, weak ridge extends posteriorly from the tubercle, but in none of the five is a well-developed carina present, and rarely is there even a weak posterior tubercle or spine that occurs in some *Eus-tacus*.

SPINATION OF CARAPACE AND ABDOMEN.—A considerable range of intra- and interspecific variation in the spination of the carapace and abdomen occurs in the genus *Astacoides*. The most spectacular exhibit of spines occurs in *A. betsileoensis* in which virtually all of those studding the lateral surface of the carapace are bowed with their apices directed anteriorly, and at least one of those on the pleura of the second and third segments of the abdomen is strong

with a needle-sharp tip. The spines of the carapace and abdominal pleura of the other members of the genus are not nearly so strongly developed as they are in *A. betsileoensis*, many represented by tubercles, particularly in *A. crosnieri*, *A. petiti*, and in *A. madagascarensis*. In these, even many of the tubercles are small. A marked contrast in the number of tubercles present in the mandibular region of the carapace occurs in *A. granulimanus*, in which they are crowded, and *A. crosnieri* and *A. petiti*, in which there are virtually none in this region or in the anteroventral branchiostegal region. The mandibular arc, a curved ridge, often bearing tubercles or spines, located ventrally in the mandibular region of the carapace and disposed subparallel to the anteroventral part of the cervical groove, is a feature shared by all members of the genus. It may be inconspicuous, almost concealed by the series of two to four prominent spines borne on it in *A. betsileoensis*, prominent and bearing as many as five or six tubercles, or may be comparatively weak and devoid of tubercles as it sometimes is in *A. crosnieri* and *A. petiti*.

EYES.—Monod and Petit (1929) recognized two groups among their "varieties" of *A. madagascarensis* based in part on the size of the eyes: the "forme macrophthalmale" encompassing the varieties *betsileoensis* and *madagascarensis* [= *caldwelli*], and the "forme microphthalmale" composed of the varieties *brevirostris* [= *madagascarensis*] and *granulimanus*. Indeed the eyes of *A. betsileoensis* are proportionately much larger than those of their other "varieties"; those of *caldwelli* are a little less conspicuously so.

ANTENNAL SCALE.—The presence of spines or tubercles on the lateral margin of the scaphocerite, a feature shared by all members of the genus *Astacoides*, occurs sparingly or not at all in other crayfish genera. The scale of *A. betsileoensis* (Figure 23*f*) is the most distinctive of that of the crayfishes of Madagascar in possessing at least one (and as many as three) strong, procurved spines on the lateral margin. Whereas a strong spine on the lateral surface of the antennal scale of other *Astacoides* is of rare occurrence, all exhibit one or two lateral rows of tubercles and sometimes a stray one. The ventral keel of this structure may be smooth or bear one or two tubercles or spines; such spines are strongest in *A. betsileoensis*, but an occasional specimen of this species may lack even a tubercle on the keel.

MANDIBLE.—A comparison of the mandibles of the Madagascan crayfishes and of them with mandibles of representatives of *Astacopsis* and *Euastacus* reveals striking similarities, but a few distinct differences were found. The terminology employed in Bouchard's (1977) study of the mandibles of the Astacidea, to the extent possible, is employed herein (Figure 3). The incisor lobe consists typically of a dentate-crenate row of eight or nine corneous denticles, but in *Astacoides madagascarensis* there may be as many as 11. Of these the penultimate tooth is always the largest. The shape of the elongate oval cephalic molar process is rather

uniform in all three genera, but it is situated distinctly closer to the caudal molar process in *Astacopsis* and *Euastacus* (Figure 3*b,a*) than it is in *Astacoides*. Depending apparently on the amount of wear, this process may be almost smooth, marked with subtransverse, anastomosing ridges, or with elongate, median concavities. Also, it is a little closer to the caudal molar process in *A. madagascarensis* and *A. caldwelli* than it is in the other members of the genus.

In none of the members of the parastacid genera examined does the caudal molar process exist in a distinct triangular ridge, rather (apparently basically, and perhaps primitively) there are prominences marking what one might consider to be apices of a triangle that is probably homologous to that illustrated for the Cambaridae by Bouchard (1977, fig. 4). These apices were designated by him as follows: "c-d," that between the cephalic and distal sides of the triangle; "p-c," that between the proximal and cephalic sides, and "d-p," that between the distal and proximal sides. Since it seems more appropriate to emphasize the angles rather than the sides of the triangle in the parastacids, I am designating the "cusps" at the angles as the "cephalodistal," "proximocephalic," and "distoproximal" cusps, thus essentially maintaining Bouchard's terminology. The most conspicuous (perhaps because of the sclerotization) of the three cusps in all of the mandibles examined is the proximocephalic; it is always at least partly sclerotized, and even when abraded it is somewhat dome-shaped and lies in the same transverse plane as, and almost in line with, the long axis of the cephalic molar process. The smallest of the three cusps is consistently the tuberculiform or slightly compressed distoproximal cusp, which is situated closer to the basal denticle of the incisor ridge than are the other two cusps; too, it is always sclerotized. Most variation occurs in the proximocephalic cusp, which in the *Astacopsis* and *Euastacus* examined forms a short corneous ridge not far removed from the smaller distoproximal cusp. It, the proximocephalic cusp, is more prominent in *Astacoides madagascarensis* and *A. petiti*, and almost abuts the distoproximal cusp in *A. betsileoensis*, *A. caldwelli*, and *A. granulimanus*. In *A. crosnieri*, it is more massive, mammiform, and cornified only apically. One of the most distinctive of the apical features of the mandible in *Astacoides* is the nodular cluster (best illustrated herein in Figure 3*h*) situated between the proximocephalic cusp and the cephalodistal cusp and mesial part of the distoproximal one. Not even a remnant of the nodular cluster was found in the mandibles of the *Euastacus* I examined. The cluster is represented by only one nodule in *Astacopsis franklinii* Huxley, 1879a, and the nodules are very sparse in *Astacoides crosnieri* and *A. caldwelli*; more are present in the mandible of *A. madagascarensis* and *A. petiti*, and they are most abundant in *A. betsileoensis*, in which there are as many as 13, and *A. granulimanus*. In individuals at a late intermolt stage, the abraded nodules in *A. betsileoensis* resemble an irregular tile paving.

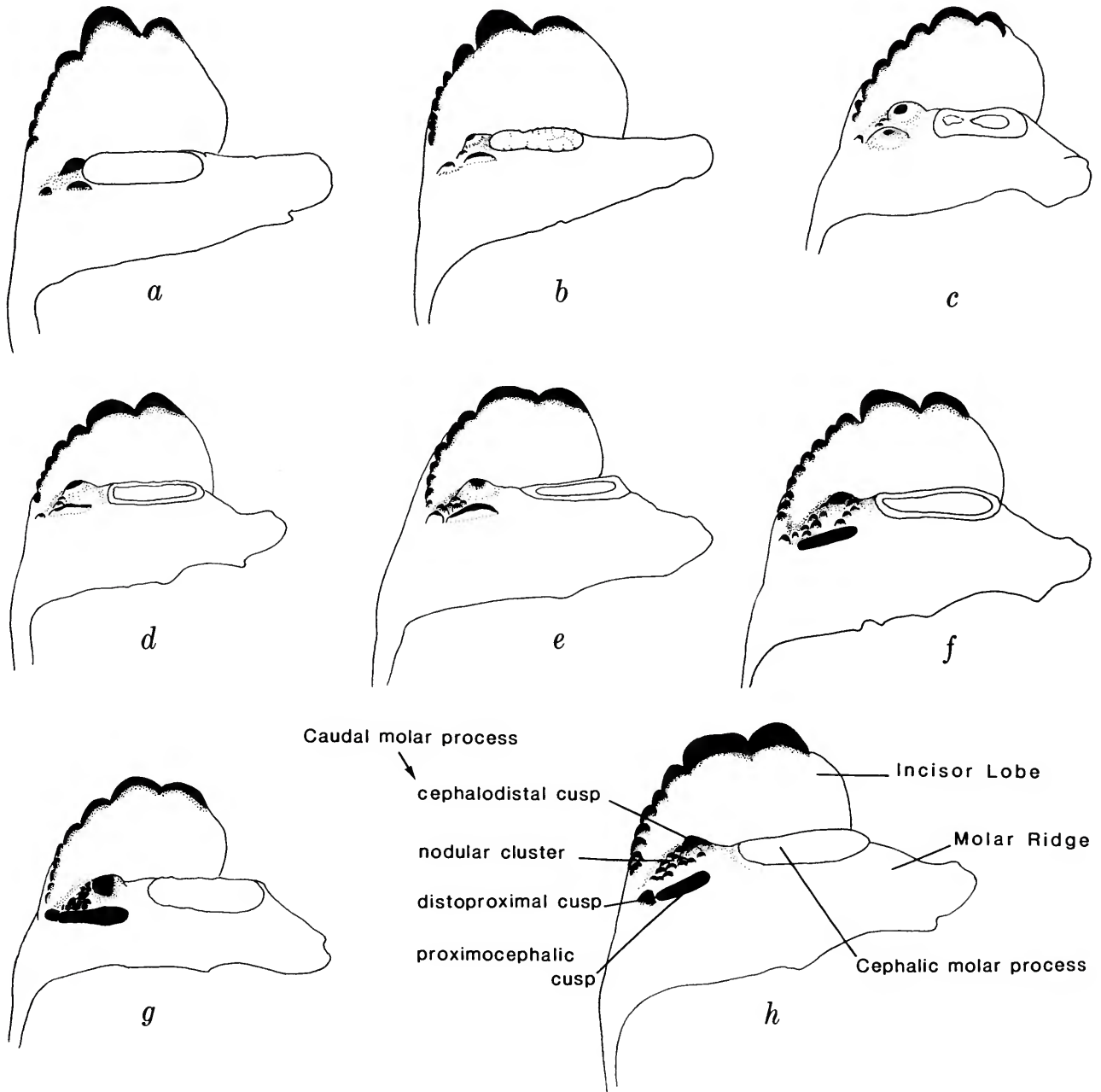


FIGURE 3.—Postaxial view of distal part of mandible, palp omitted: a, *Eustacus yarraensis*; b, *Astacopsis franklinii*; c, *Astacoides crosnieri*; d, *Astacoides caldwelli*; e, *Astacoides petiti*; f, *Astacoides madagascarensis*; g, *Astacoides betsileoensis*; h, *Astacoides granulimanus*.

THIRD MAXILLIPED (Figure 4).—The merus of the third maxilliped displays an array of spines and tubercles that, while somewhat variable in number and position in each species, aid in the recognition of at least two of the five crayfishes occurring in Madagascar. Both the mesial and

lateral margins of this flattened podomere lack or bear from one to a linear series of several tubercles or spines. The most prominent spines occur, as might be anticipated, in *A. betsileoensis* in which one to three comparatively prominent spines are situated mesially and one or none laterally (ad-

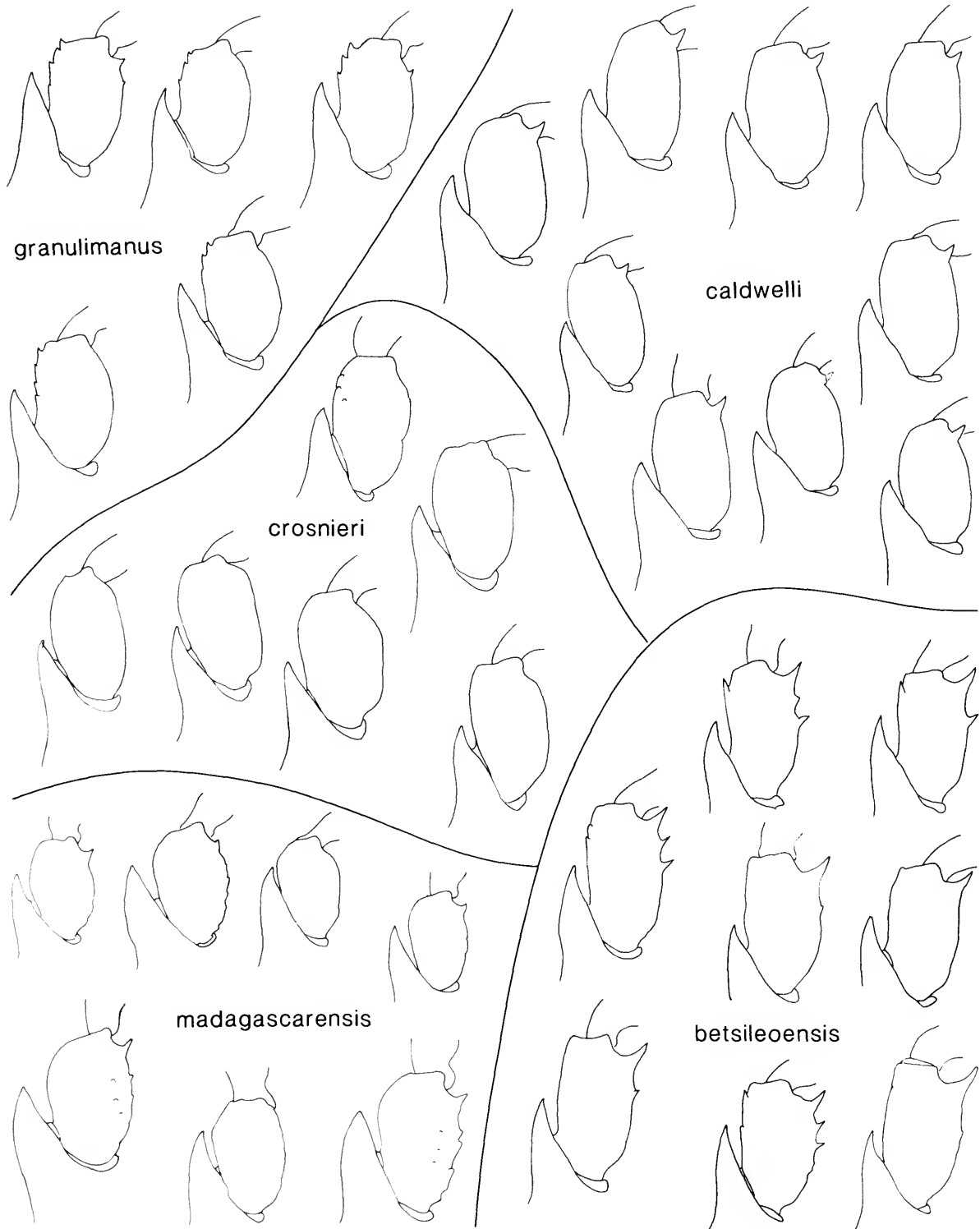


FIGURE 4.—Postaxial view of merus of third maxilliped in members of the genus *Astacoides*.

ditional tubercles may be present on either margin). In *A. caldwelli*, a single mesiodistal spine is present but none occurs on the lateral margin. In *A. madagascarensis*, there may be none, one, or several spines or tubercles on the mesial margin but none occurs on the lateral border. In *A. crosnieri*, both the mesial and lateral margins are devoid of spines although occasionally a row of rounded tubercles may be present laterally. In *A. granulimanus*, one or two distomesial spines are infrequently present, but more often the mesial margin lacks them; the lateral margin, however, always supports a linear series of at least three. Tubercles and spines are lacking on the mesial border in *A. petiti*, but a distolateral row seems always to be present.

STERNAL KEEL (Figure 5).—The basic structure of the sternal keel is perhaps best understood by considering that element of it comprising the sternite of segment XIV (that supporting the fifth pereopods), which is the only "free" sternite of the thoracic sternum. This skeletal element consists of a pair of alate projections, "lateral processes," and a small anteromedian prominence, the rudiment of what is termed here the "median keel." The more anterior sternites, although fused, are composed of the same elements, and the generalized condition is clearly represented by sternite XII. In this sternite, shaped somewhat like an inverted "T," the slender median keel extends lengthwise along the thorax, between the coxae of the third pereopods. Posteriorly the keel supports the alate lateral processes with which the coxae of the third pereopods articulate, and anteriorly it merges imperceptibly with the posterior end of the adjacent median keel of sternite XI. Sternites XI and XIII differ little from XII, chiefly in the size of the lateral

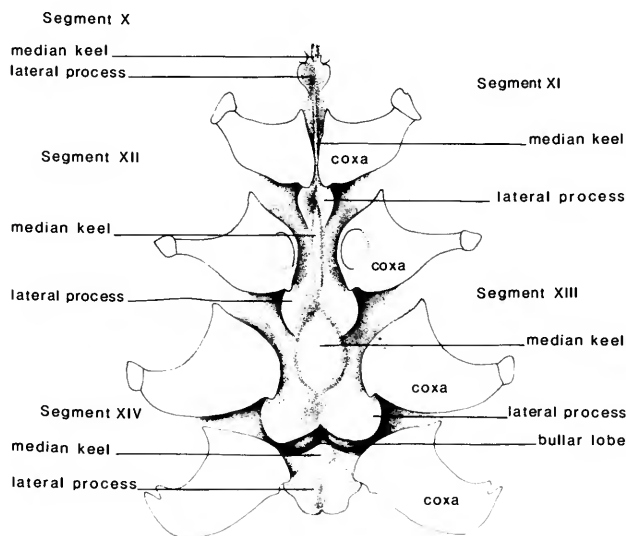


FIGURE 5.—Sternal area and coxae of associated pereopods of body segments X through XIV in female of *Astacoides madagascarensis*.

processes which are smaller and less splayed in XI, and larger and more spread in sternite XIII. A progressive reduction occurs in both the median keel and in the lateral processes in the more anterior sternites: the keels become shorter, narrower, and more recessed between the appendages, and the lateral processes smaller and directed more ventrally. In some members of *Astacoides*, sternite XIII bears a pair of bulbous prominences, the "bullar lobes," situated dorsal or posterodorsal to the lateral processes. They are prominent on the sternum of *A. crosnieri*, *A. granulimanus*, *A. petiti*, and *A. madagascarensis*, but they appear to be lacking in *A. caldwelli* and *A. betsileoensis* as they are in *Euastacus yarraensis* (McCoy, 1888), *Astacopsis franklinii*, and *Samastacus spinifrons* (Phillippi, 1882) (cf. Figures 6–8). The corresponding elements of sternite XIV are flanked laterally by the paired vertical arm of the sternopleural bridge (Figure 9b). In all members of the genus except *A. crosnieri* and *A. petiti*, the vertical arms are widely separated so that the bullar lobes are prominent and clearly evident in caudal aspect (Figure 10). In the two species just mentioned (Figure 10e,h,i), the vertical processes course nearer the median line, at least occasionally (in some members of *A. petiti*) becoming contiguous and almost completely obscuring the bullar lobes. These lobes lie dorsal to and abut the posteroventral side of the lateral lobes of the sternal keel, and, in all *Astacoides*, except some members of *A. caldwelli*, these elements are distinct. In the latter and in the more distantly related *Astacopsis franklini* (Figure 10c) and *Euastacus yarraensis* (Figure 10f), the lines of contact become less and less obvious, and in *Samastacus spinifrons* (Figure 10j), the bullar lobes, if present, are insensibly fused with the lateral processes of the sternite.

BRANCHIAE (Figure 11).—As pointed out by Huxley (1879a:775), *Astacoides madagascarensis* has fewer gills than any other crayfish. Whereas it has been assumed that all members of the genus exhibit a gill count of $I_2 + epr + 5r$, variation does exist. Except for the rudiments, all of the gills are trichobranchs, and even some of the rudimentary ones bear one to several short filaments. As in all crayfishes, the gills occur in three series: (1) The podobranchiae extend dorsally from plate-like epipodites, the individual filaments arising from the basal plate and from the tapering axial stem. The stem is not produced in wing-like expansions. (2) The arthrobranchiae are basically similar to the podobranchiae with the filaments borne on a tapering axial stem; the rudimentary arthrobranchiae, however, may appear to be no more complex in appearance than a single filament or a filament bearing one to several knobs or short finger-like processes. (3) The single pleurobranchia, on segment XIV, although often appearing to be more robust, strongly resembles the anterior arthrobranchiae.

The most conspicuous variation in the branchiae of *Astacoides* occurs in the degree of development of the anterior arthrobranch on segment VIII (that bearing the second

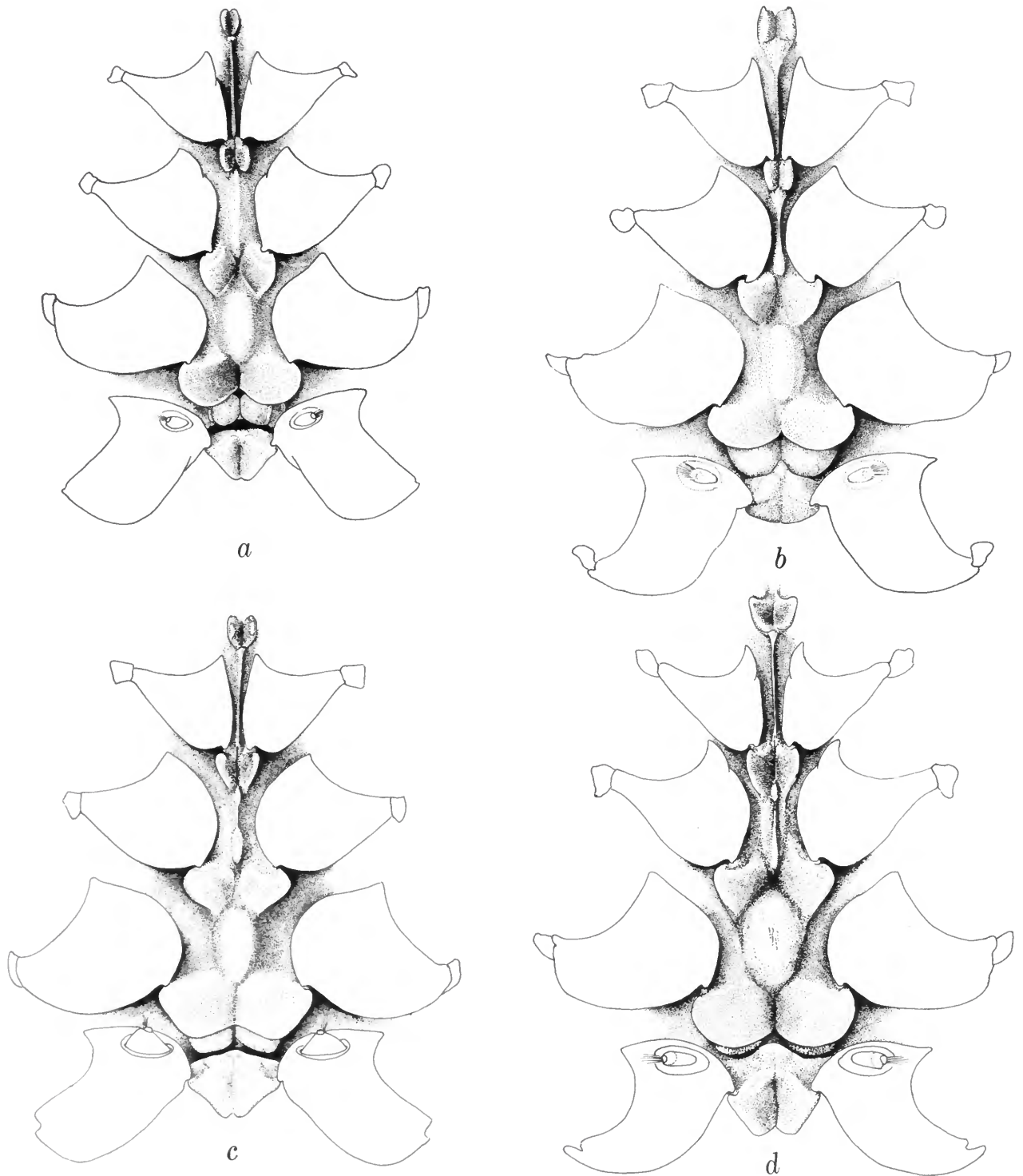


FIGURE 6.—Sternal area of segments X through XIV and coxae of associated pereiopods of males of the genus *Astacoides*: a, *A. crosnieri*; b, *A. petiti*; c, *A. granulimanus*; d, *A. madagascarensis*.

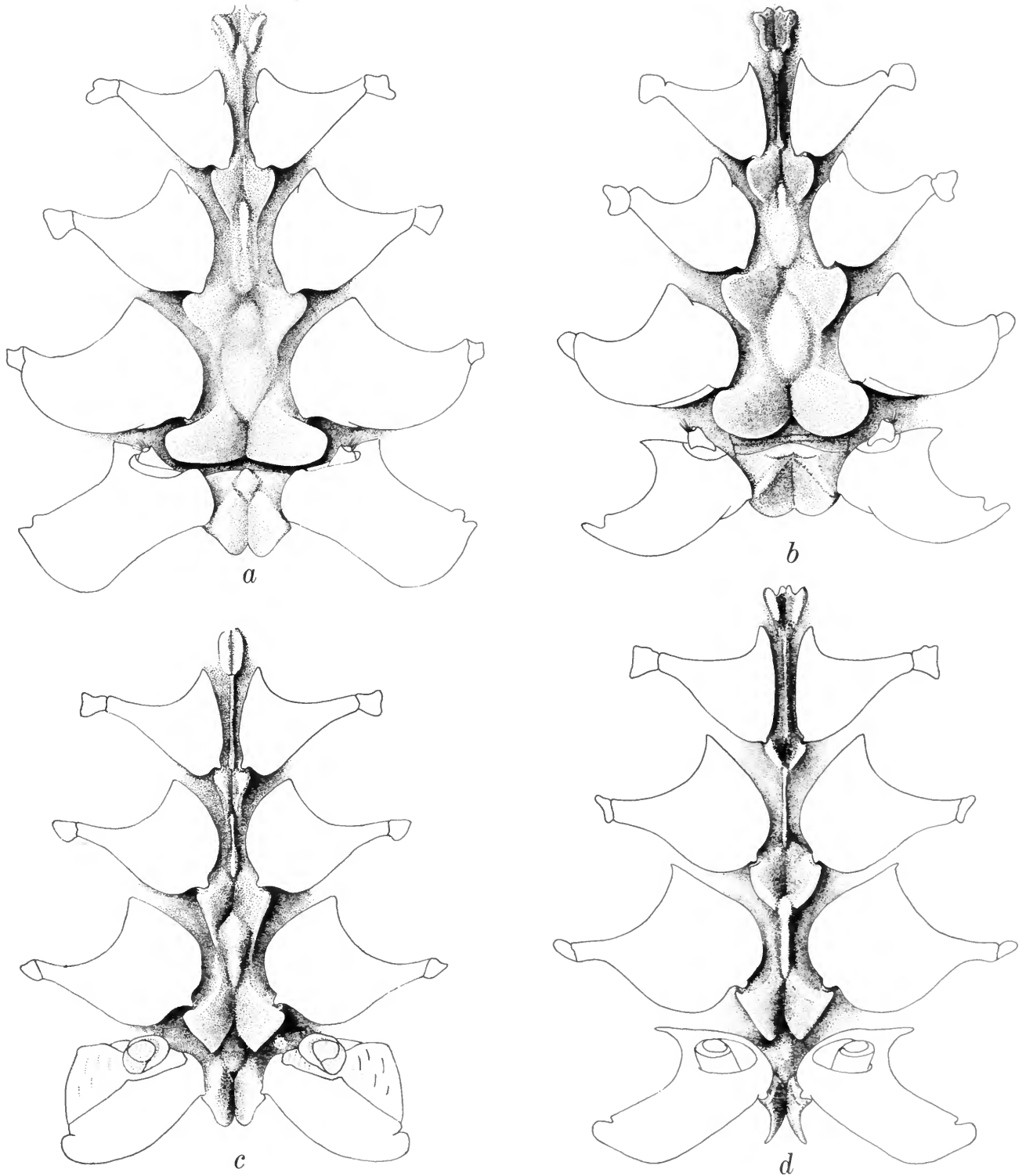


FIGURE 7.—Sternal area of segments X through XIV and coxae of associated pereiopods in males: *a*, *Astacoides caldwelli*; *b*, *Astacoides betsileoensis*; *c*, *Euastacus yarraensis*; *d*, *Astacopsis franklini*.

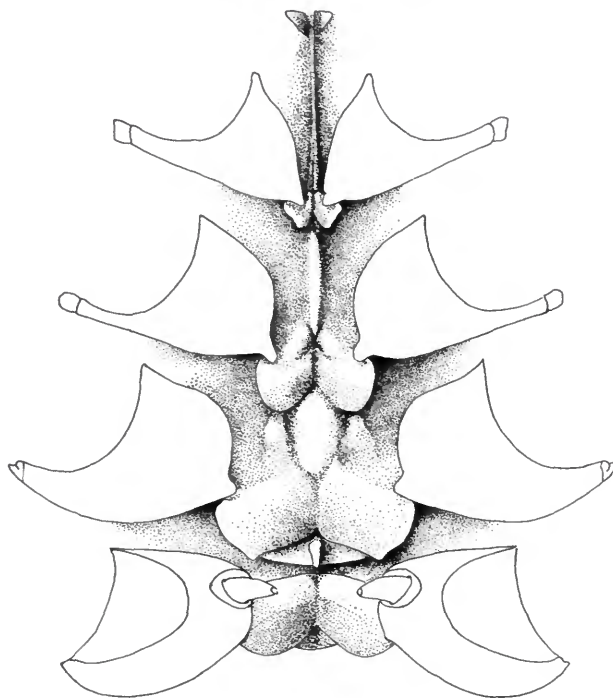


FIGURE 8.—Sternal area of segments X through XIV and coxae of associated pereopod in *Samastacus spinifrons*.

maxilliped). It is comparatively well developed in *A. betsileoensis*, *A. caldwelli*, and in at least some individuals of *A. madagascarensis*; it is rudimentary in *A. crosnieri*, and absent in *A. petiti* and *A. granulimanus*. Rudimentary posterior arthrobranchs are present on segments IX through XIII in *A. petiti*, *A. caldwelli* (Figure 11a,b), and *A. madagascarensis*; on IX through XII in *A. betsileoensis*; X through XII in *A. crosnieri* (Figure 11c,d); and XI through XIII in *A. granulimanus*.

Inasmuch as all other crayfishes have a greater number of gills than does any member of *Astacoides*, an assumption that the fewer gills in these crayfishes is the derived condition seems warranted. Thus, in this respect, *A. caldwelli* and *A. madagascarensis* are the most primitive of the Madagascan crayfishes, with a count of 13 + epr + 5r (Figure 12); *A. betsileoensis* has only one fewer rudiment, 13 + epr + 4r; *A. petiti*, one fewer gill but with five rudiments, 12 + epr + 5r; *A. crosnieri*, one fewer gill and rudiment, 12 + epr + 4r; and *A. granulimanus*, one or two yet fewer rudiments, 12 + epr + 3 (or 2) r. The data presented on the variation in the numbers of branchiae in each of the species belonging to the genus *Astacoides* were obtained from only one or two of each of the six species, thus their gill counts may be more variable than those reported herein. The counts are summarized for each species in Figure 12.

One of the most striking differences noted in the gills of

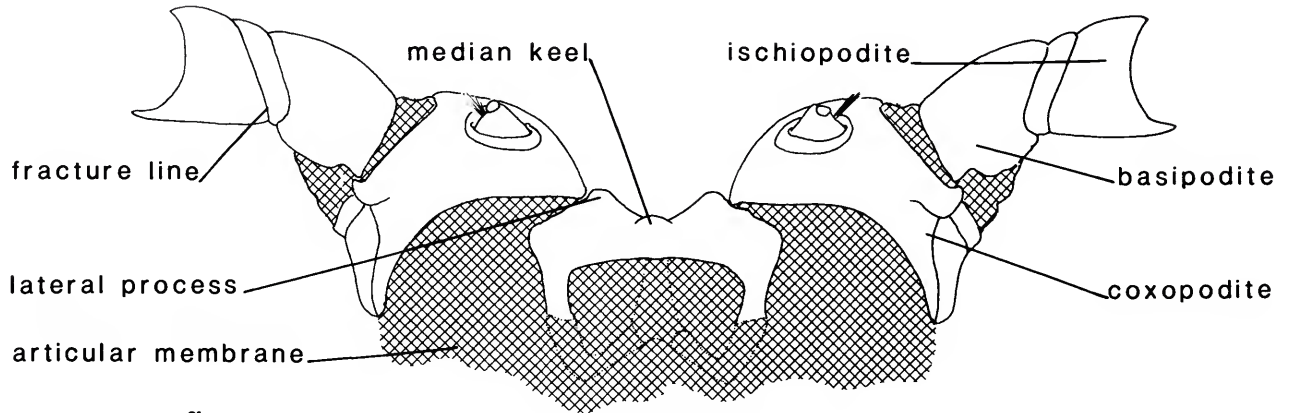
Astacoides can be seen by comparing Figure 11a and c. The podobranchs in *A. caldwelli* do not extend nearly so far anterodorsally as do those of *A. crosnieri*, a species in which the carapace is decidedly more highly vaulted, the areola comparatively narrow, and other features are similar to those that I have come to associate with cambarids that spend much of their lives in burrows (compare Figures 15a,b and 22a,b).

PLEUROCOXAL LAPPETS.—Many years ago, I observed a small setiferous lappet borne on the lateral membranous exoskeleton between the coxae of segments XIII and XIV in members of the family Cambaridae. Since all of the crayfishes that I had examined exhibited this paired feature I did not mention it in my taxonomic studies. When the late R.E. Snodgrass was preparing his textbook on arthropod anatomy (1952), he noted this structure and asked if I knew what it was. I did not know then, and even now have no evidence as to its function. At the time I suggested to him that judging from its position alone, lying in one of the principal water intake channels to the gill chamber, one might suspect it to have a chemosensory function. He clearly illustrated the lappet in figs. 43G, and 45E,F, and described it as a pendant setiferous lobe arising from the pleurocoxal membrane posterior to the fourth pereopods (page 170), and as a brush-like appendage (page 191). I have encountered no other references to it.

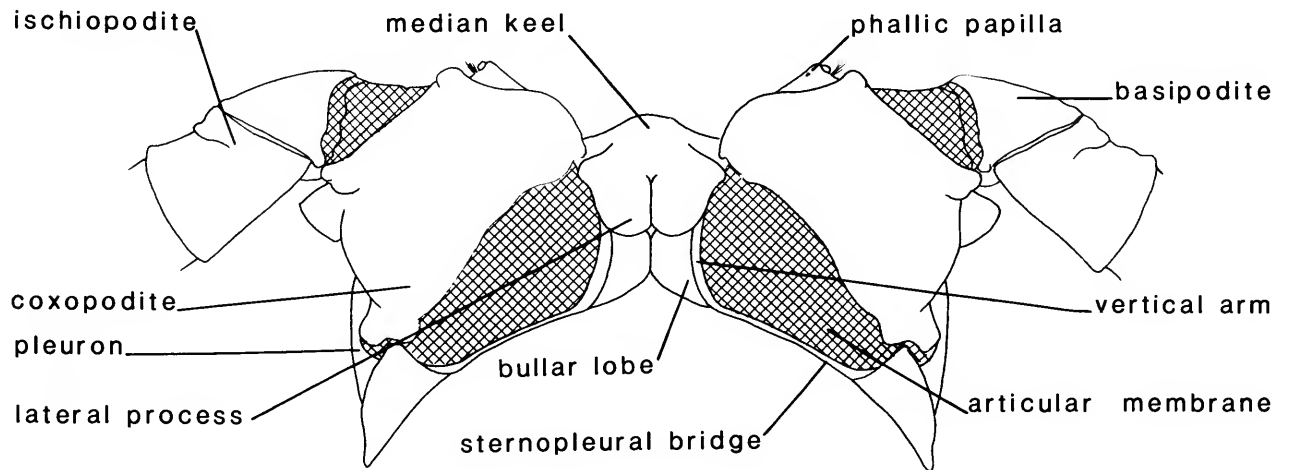
Being familiar with this lappet in the cambarids, I was surprised when I removed one of the branchiostegites of a member of *Astacoides crosnieri* to find four pairs of such lappets situated between the coxae of segments X through XIV (Figure 11c,d, pla). A similar arrangement of lappets occurs in all *Astacoides* and appears to be present in representatives of most, if not all, parastacid genera.

Whereas in members of the genus *Astacoides* the pleurocoxal lappets are not conspicuously different in the six species recognized herein, the degree to which they are readily seen does differ. For example, in *A. caldwelli* (Figure 11a) the plate-like epipodites bearing the podobranchs are disposed in such a manner that when viewed laterally they completely conceal the lappets. In contrast, the epipodites in *A. crosnieri* (Figure 11c), particularly those of segments XI through XIII, are positioned at more of an angle to the horizontal, and the posteroventral extremities are situated far more dorsally than the anteroventral angles; this tilt exposes at least the ventral part of all four of the lappets.

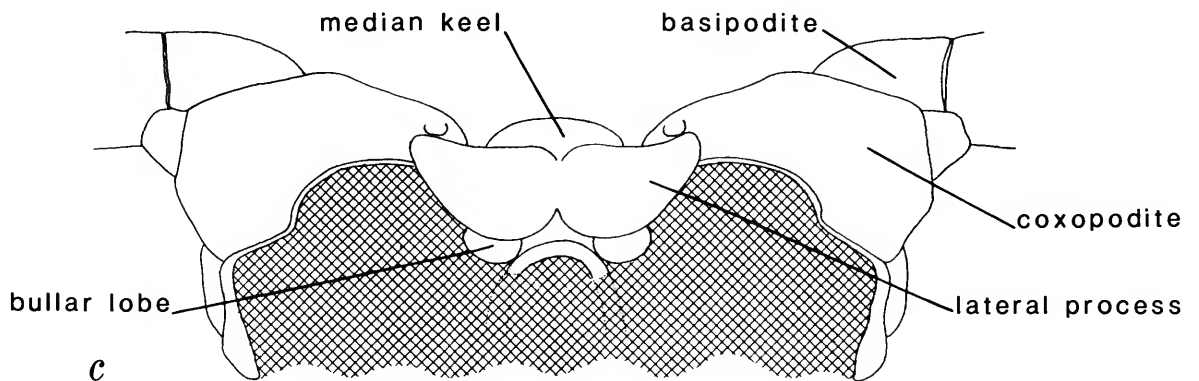
ABDOMEN.—Differences between the abdomen of the male and that of the female are noted elsewhere, but attention should be called to the presence or absence of spines and tubercles on the pleura of the second and third abdominal segments (Figure 13). Strong, sharp spines on the second segment are typical of *A. betsileoensis* (Figure 13d) and are represented by tubercles, which are especially weak in *A. petiti*, in the other members of the genus. The pleura of the third through fifth segments taper ventrally



a



b



c

FIGURE 9.—Semi-diagrammatic representation of sternal area and basal podomeres of appendages of body segments XIII and XIV in male *Astacooides granulimanus*: *a*, cephalic view of XIV; *b*, caudal view of XIV; *c*, caudal view of XIII.

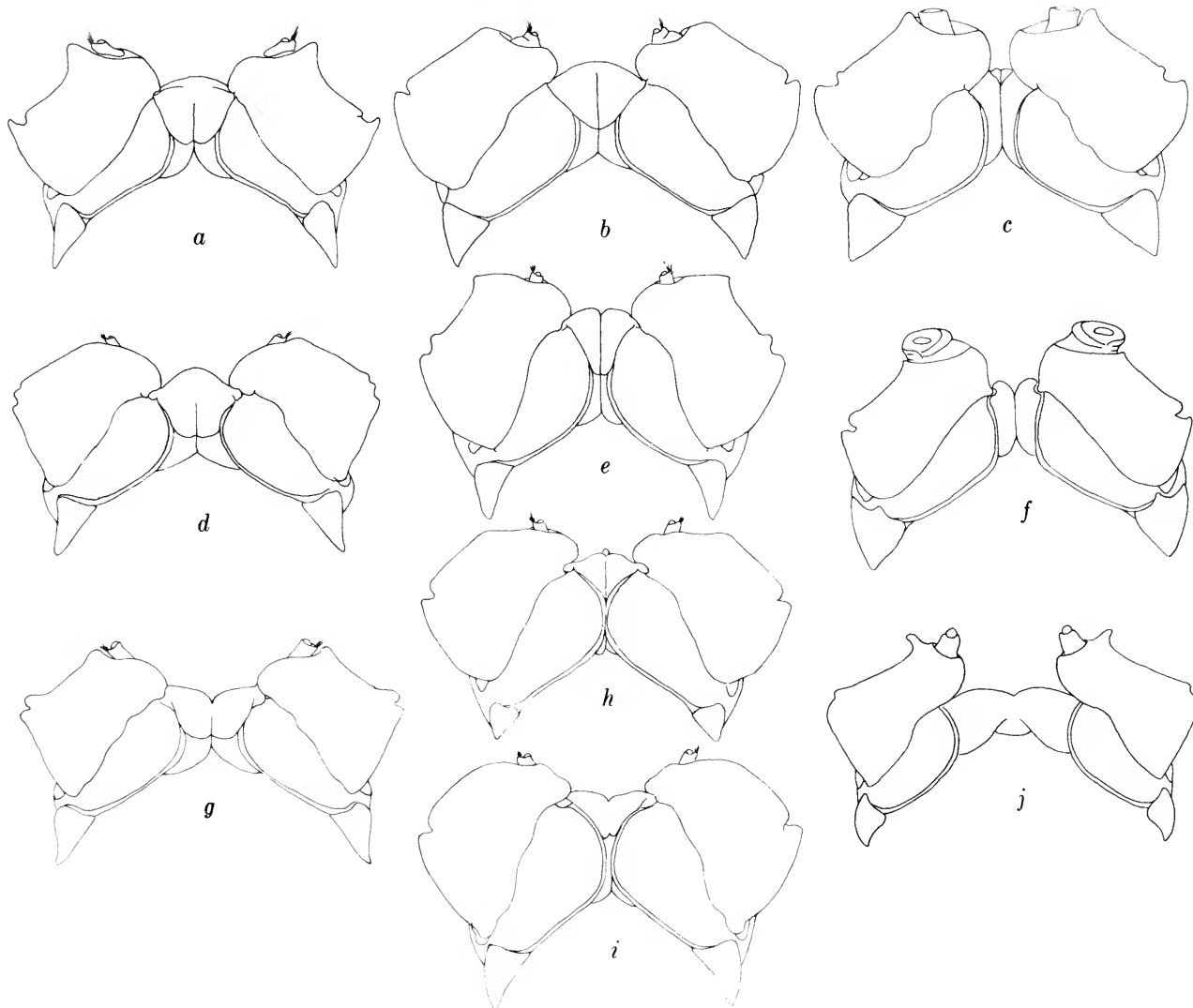


FIGURE 10.—Caudal view of ventral part of body segment XIV, associated coxae, and phallic papillae: a, *Astacoides madagascarensis*; b, *Astacoides granulimanus*; c, *Astacopsis franklinii*; d, *Astacoides caldwelli*; e, *Astacoides crosnieri*; f, *Euastacus yarraensis*; g, *Astacoides betsileoensis*; h, *Astacoides petiti* (holotype); i, same (paratype); j, *Samastacus spinifrons*.

and are subangular to rounded in all except *A. crosnieri*, in which they are subtruncate (Figure 13e).

Origin and Interspecific Relationships

As pointed out by Riek (1972:382), almost certainly the members of the genus *Astacoides* have more features in common with the Tasmanian *Astacopsis* than they have with any other species group, and despite the size of the gap between their current ranges, it seems likely that they shared a more recent common ancestry than either did with the several other early parastacid stocks. Among the many features common to modern members of these two genera

are a rostrum in which the lateral carinae are studded with a series of tubercles, branchiae the stems of which lack wing-like lobes, and a telson that is rather uniformly calcified. If the closest allies of the Madagascan crayfishes are indeed members of the genus *Astacopsis*, the question arises immediately as to how did an ancestral common stock arrive on such disparate islands as Madagascar and Tasmania and leave no traces of having been elsewhere. That no fossils of these stocks are known to exist is hardly surprising, for few preserved crayfish remains have been discovered anywhere, but for more than a century occasional speculations have been offered to explain the presence of the disjunct assemblage of crayfishes on Madagascar. The proximity of Tas-

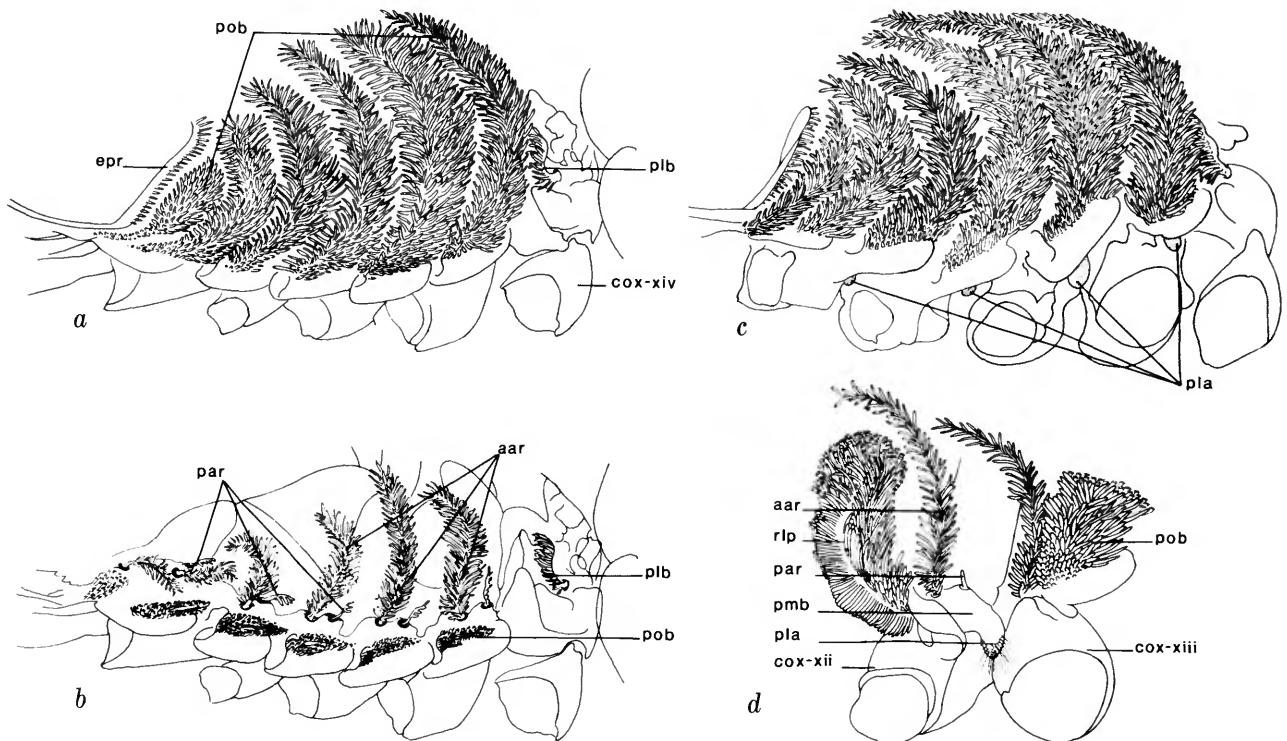


FIGURE 11.—Branchiae and associated structures in *Astacoides* (*a, b*, *A. caldwelli*; *c, d*, *A. crosonieri*): *a, c*, lateral view of podobranchiae and pleurobranchiae; *b*, lateral view of same region with podobranchiae cropped, revealing series of arthrobranchiae; *d*, lateral view of coxae of third and fourth pereopods, associated branchiae, and pleurocoxal lappet. (aar, anterior arthrobranchia; cox, coxae of twelfth, thirteenth, and fourteenth body segments; epr, epipodite of first maxilliped with rudimentary branchiae; par, rudimentary posterior arthrobranchiae; pla, pleurocoxal lappet; plb, pleurobranchia; pmb, pleurocoxal membrane; pob, podobranchia; rlp, reflexed podobranchia.

mania to the Australian Continent, the center of diversity of the Parastacidae, and the general similarities of their crayfish faunas has perhaps been responsible for less spectacular hypotheses concerning the crayfish invasion of that island.

Huxley (1880a) summarized what was known about the distribution of crayfishes throughout the world and called particular attention to the isolated position of *Astacoides* in respect to the range of the remaining members of the family. Postulating the existence of "... marine primitive crayfishes south of the equator . . ." (page 332), he made the following statement:

that they should have ascended the rivers of New Zealand, Australia, Madagascar, and South America, and become fresh water *Parastacidae*, is an assumption which is justified by the analogy of the fresh-water prawns. It remains to be seen whether marine *Parastacidae* still remain in the South Pacific and Atlantic Oceans, or whether they have become extinct.

Huxley continued,

At present, I confess that I do not see my way to a perfectly satisfactory explanation of the absence of crayfishes in so many parts of the world in which they might, *a priori*, be expected to exist; and I can only suggest the directions in which an explanation may be sought.

The first of these is the existence of physical obstacles to the spread of crayfishes, at the time at which the Potamobine [= Astacidae and Cambariidae] and the Parastacine stocks respectively began to take possession of the rivers, some of which have now ceased to exist; and the second is the probability that, in many rivers which have been accessible to crayfishes, the ground was already held by more powerful competitors . . .

With respect to the Southern hemisphere, the absence of crayfishes in Mauritius and in the islands of the Indian Ocean, though they occur in Madagascar, may be due to the fact that the former islands are of comparatively late volcanic origin; while Madagascar is the remnant of a very ancient continental area, the oldest indigenous population of which, in all probability, is directly descended from that which occupied it at the beginning of the tertiary epoch. If Parastacine *Crustacea* inhabited the southern hemisphere at this period, and subsequently became extinct as marine animals, their preservation in the freshwaters of Australia, New Zealand, and the older portions of South America may be understood. The difficulty of the absence of crayfishes in South Africa remains; and all that can be said is, that it is a difficulty of the same nature as that which confronts us when we compare the fauna of South Africa in general with that of Madagascar. The population of the latter region has a more ancient aspect than that of the former; and it may be that South Africa, in its present shape, is of very much later date than Madagascar.

With respect to the second point for consideration, it is to be remarked that, in the temperate regions of the world, the crayfishes are by far the largest and strongest of any of the inhabitants of freshwater, except the *Vertebrata*; and that while frogs and the like fall an easy prey to them, they

A. caldwelli					A. madagascarensis					A. betsileoensis				
Body Segment	Podobranchiae	Arthrobranchiae		Pleurobranchiae	Body Segment	Podobranchiae	Arthrobranchiae		Pleurobranchiae	Body Segment	Podobranchiae	Arthrobranchiae		Pleurobranchiae
		anterior	posterior				anterior	posterior				anterior	posterior	
VII	epr	0	0	0	VII	epr	0	0	0	VII	epr	0	0	0
VIII	1	1	0	0	VIII	1	1	0	0	VIII	1	1	0	0
IX	1	1	r	0	IX	1	1	r	0	IX	1	1	r	0
X	1	1	r	0	X	1	1	r	0	X	1	1	r	0
XI	1	1	r	0	XI	1	1	r	0	XI	1	1	r	0
XII	1	1	r	0	XII	1	1	r	0	XII	1	1	r	0
XIII	1	1	r	0	XIII	1	1	r	0	XIII	1	1	0	0
XIV	0	0	0	1	XIV	0	0	0	1	XIV	0	0	0	1

A. granulimanus					A. crosnieri					A. petiti				
Body Segment	Podobranchiae	Arthrobranchiae		Pleurobranchiae	Body Segment	Podobranchiae	Arthrobranchiae		Pleurobranchiae	Body Segment	Podobranchiae	Arthrobranchiae		Pleurobranchiae
		anterior	posterior				anterior	posterior				anterior	posterior	
VII	epr	0	0	0	VII	epr	0	0	0	VII	epr	0	0	0
VIII	1	0	0	0	VIII	1	r	0	0	VIII	1	0	0	0
IX	1	1	0	0	IX	1	1	0	0	IX	1	1	r	0
X	1	1	0	0	X	1	1	r	0	X	1	1	r	0
XI	1	1	r	0	XI	1	1	r	0	XI	1	1	r	0
XII	1	1	r	0	XII	1	1	r	0	XII	1	1	r	0
XIII	1	1	r (0)	0	XIII	1	1	0	0	XIII	1	1	r	0
XIV	0	0	0	1	XIV	0	0	0	1	XIV	0	0	0	1

FIGURE 12.—Branchial counts in *Astacoides*.

must be formidable enemies and competitors even to fishes, aquatic reptiles, and the smaller aquatic mammals. In warm climates, however, not only the large prawns which have been mentioned, but *Atya* and fluviatile crabs (*Thelphusa* [= several potamonids]) compete for the possession of the freshwaters; and it is not improbable that under some circumstances, they

may be more than a match for crayfishes . . .

In connection with this speculation, it is worthy of remark that the area occupied by the fluviatile crabs is very nearly the same as that zone of the earth's surface from which crayfish are excluded, or in which they are scanty. That is to say, they are found in the hotter parts of the eastern side

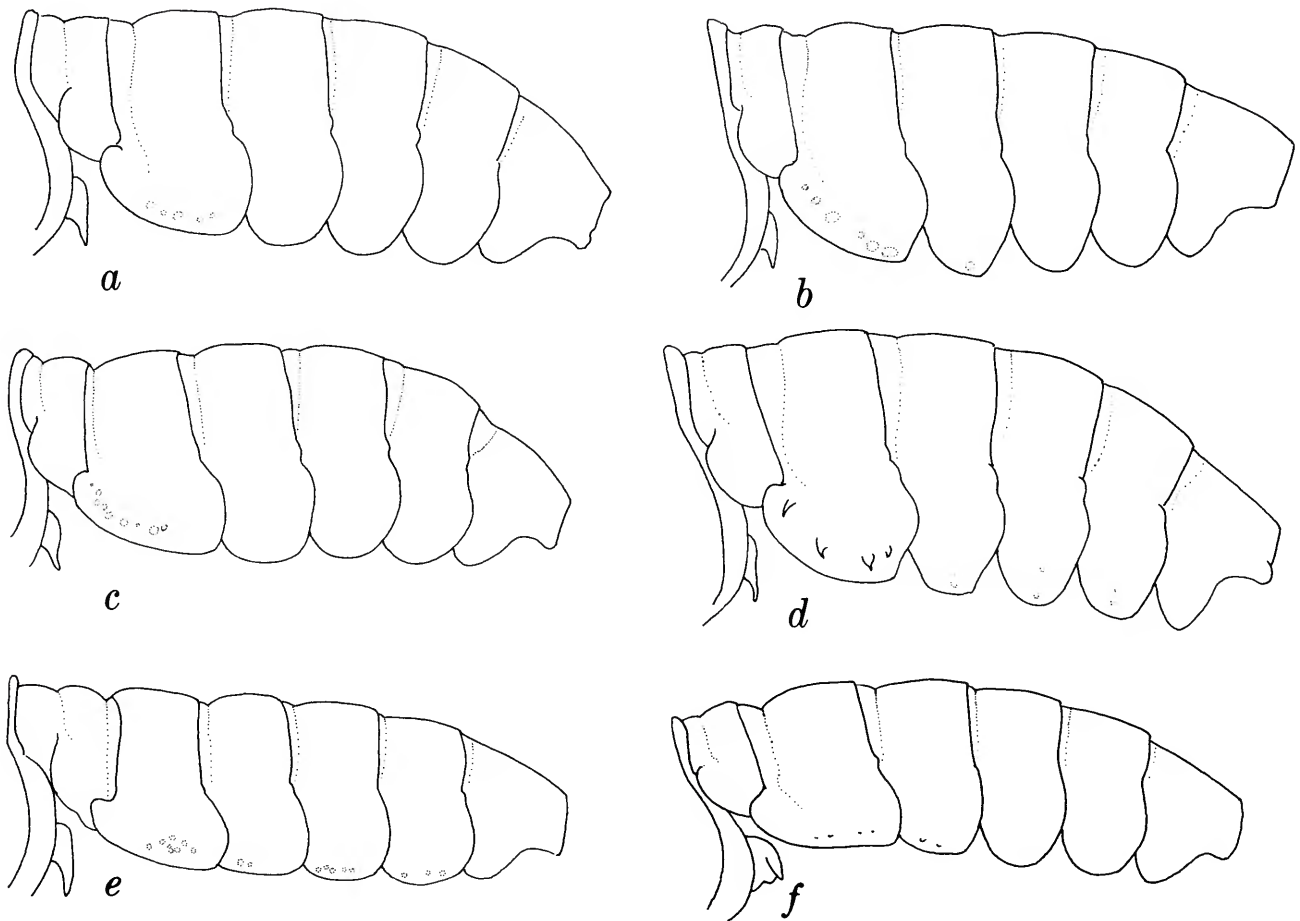


FIGURE 13.—Lateral view of abdomen in *Astacoides*: a, *A. madagascarensis*; b, *A. caldwelli*; c, *A. granulimanus*; d, *A. betsileoensis*; e, *A. crosnieri*; f, *A. petiti*.

of the two Americas, the West Indies, Africa, Madagascar, Southern Italy, Turkey and Greece, Hindostan [sic], Burmah [sic], China, Japan, and the Sandwich Islands

The hypothesis respecting the origin of crayfishes which has been tentatively put forward in the preceding pages, involves the assumption that marine Crustacea of the astacine type were in existence during the deposition of the middle tertiary formations, when the great continents began to assume their present shape. That such was the case there can be no doubt, inasmuch as abundant remains of Crustacea of that type occur still earlier in the mesozoic rocks. They prove the existence of ancient crustaceans, from which the crayfishes may have been derived, at that period of the earth's history when the conformation of the land and sea were such as to admit of their entering the regions in which we now find them (pages 335-338).

Ortmann (1902:295), in attempting to explain how the disjunct parastacid stock became so broadly dispersed, suggested several "connections" between areas now inhabited by them, beginning with the assumption that "crayfishes formerly existed in southeastern Asia": (1) "Southeastern Asia with Madagascar and Australia," (2) "New Zealand

with Australia, possibly over the Fiji Islands and New Guinea," and (3) "New Zealand or Australia with South America."

He proposed (page 387) that in the Lower Cretaceous the Potamobiidae and Parastacidae lived in Sino-Australia, possibly having reached Antarctica, and that during the Middle Cretaceous, *Astacoides* arrived on Madagascar by way of the Lemurian landbridge, coming from the Sinic continent. In the Upper Cretaceous, Eastern Asia became separated from Australia "resulting in the differentiation of the families Potamobiidae (in the Sinic continent) and Parastacidae (in Archinotis)." He further pointed out that "the distribution of crayfishes and crabs in Mesozonia is almost mutually exclusive" (page 388). Noting again the advent of *Astacoides* on Madagascar from India in the Middle Cretaceous (page 391), he proposed that the arrival of freshwater crabs in the Upper Cretaceous resulted in the extermination of crayfishes throughout the southern part

of Asia (from India to China), acting not only as "a check to the distribution of the crayfishes, but directly annihilated them. Only on Madagascar *Astacoides* survived, probably because in this island it inhabits parts that have not been occupied by the crabs. Possibly the large size of *Astacoides* has something to do with its survival." He believed that the presence of crabs in Africa either prevented crayfishes from colonizing the Continent or were responsible for their extinction if they preceded the crabs.

Others have remarked on the isolated position of *Astacoides* on Madagascar, but only Monod and Petit (1929) have offered an alternative to Ortmann's hypothesis that appears to me to warrant a summary herein. It was proposed that the ancestral parastacid lived in an epicontinental sea bordering or flooding parts of the land masses constituting Gondwana. With the fragmentation and progressive separation of the resulting pieces, segments of the ancestral stock accompanying them became differentiated, so that the stock that invaded the freshwaters of South America was different from that moving into the streams on Madagascar or those adapting to the fresh waters of Australia. They concluded (translating freely, with some omissions) that (pages 38, 39)

The same stock, or related species, from which the Australian genera and Madagascan genus were descended, was obliged to have lived in some portion of the Indian Ocean before emigrating to the fresh waters of the large southern islands. Without doubt, it found itself in the sea which had left a series of deposits on the east coast of Madagascar, and which, in the upper Cretaceous, definitely isolated Madagascar from Australia.

Thus the disjunct distribution of the Parastacidae probably had its origin in an ancient localization, progressively acquired by marine ancestors before their specialization to life in fresh water.

They suggested that the almost exclusive localization of *Astacoides* on the eastern slope of Madagascar is consistent with such an hypothesis and obviates the necessity for postulating a secondary acquisition of a freshwater stock from elsewhere.

Thus far, neither extant nor fossil representatives of a stock believed to be the immediate marine ancestor of any freshwater crayfish group have been found. In the more than one hundred years since Huxley (1880a) demonstrated an interest in the evolution of *Astacoides*, the advancement of our knowledge concerning it is virtually limited to the hypotheses proposed by Ortmann and by Monod and Petit (1929), the latter embracing the concept of Continental Drift, and the subsequent embellishments by geologists and geomorphologists involving the historical relationships of the continents and major islands.

There seems to be no reason to doubt that the immediate ancestors of freshwater crayfishes were marine astacideans, and it is unlikely that members of this littoral stock suddenly moved from the sea into fresh water. Rather, is it not more probable that the transition was a more gradual one? Even after problems associated with osmoregulation had been at

least partly solved, some degree of ambivalence for tolerating fresh and salt water must have existed in them. It is tempting to assume that at that stage they wandered, perhaps even seasonally, back and forth from near-salt to brackish and fresh water as some astacids have been found to do in recent times (Miller, 1965; Lamanova, 1970). As they moved about in the littoral or sublittoral zones of the sea, currents might have taken them for at least short distances across waters of considerable depth to other shallows. Thus, if these pro-parastacids in the transition stage were also immigrating actively or passively, refinement of multiple invasions of a varying, wide-ranging stock on a number of land masses could well have occurred. Since no well-fixed time frame for the existence of such a stock has been established, if it existed as Australia and Tasmania began to move away from Madagascar, then in essence a single physiological transition from salt to fresh water in the middle to late Mesozoic could have become perfected within a plastic stock (perhaps almost simultaneously) in a number of river systems on the drifting, fragmented Gondwana land masses.

Although I favor the account just offered for the invasion of Madagascar by the primitive *Astacoides*, I could be almost equally satisfied by an assumption that the invasion did not occur directly through a riverine environment but through a lentic one resulting from a land-locked segment of an epicontinental sea in which the marine ancestor was trapped, and from there moved to streams and swamps.

If Monod and Petit (1929) were right in believing that the immediate ancestors of the parastacids were marine forms occurring in an epicontinental sea in which sediments were being deposited, one would expect that under such conditions somewhere in the Southern Hemisphere remains of them might be found. Their absence from the fossil record does not, however, inhibit one's pondering the question as to their appearance and their habits.

Following the lead offered by Monod and Petit, that all parastacids probably did not have an origin in a single stock that invaded fresh water, I offer herein my concept of the appearance of that segment of the marine pro-parastacid stock that I believe might have been immediately ancestral to the Madagascan genus *Astacoides*.

The body was likely subcylindrical, bearing a subtruncate, perhaps spoon-shaped rostrum, the lateral carinae of which bore a series of erect corneous tubercles; the postorbital ridges were distinct but rather weak, and carried only an anterior tubercle. The areola was broad and deeply invaded by the postcervical groove. The tubercles borne on the branchiostegites were numerous and comparatively large ventrally but diminished in number and size dorsally to the sparsely studded area approaching the weakly punctate areola. Tubercles in the cephalolateral area of the carapace were most dense in the ventral hepatic and mandibular adductor regions; a row of them capped the well-defined

mandibular arc, but they were sparse and weak or lacking in the orbital and dorsalmost hepatic areas. The abdomen was strong, joined to the thorax by a broad first abdominal segment; the pleura of the second and third abdominal segments bore a submarginal ventral row and an anterior patch of tubercles; the pleura of the third through sixth segments were tapered ventrally to rounded apices. The telson was rather uniformly calcified, and a pair of lateral spines marked the position of the primitive transverse suture that was reduced to shallow sinuses from which short sutures extended anteromesially. Spines were borne on the dorsal submedian keels and on the dorsolateral parts of the rami of the uropods. The eyes were comparatively large, resembling those of *Astacoides betsilensis*. The antennal scale exhibited a row of tubercles laterally, and the epistome was provided with lateral patches of tubercles and was produced anteriorly in a median, subserrate, sagittiform prominence. The incisor element of the mandible consisted of a sclerotized dentate ridge on which the penultimate tooth was the largest; the cephalic molar process formed a non-sclerotized, elongate ridge; and the caudal molar process comprised a triangular arrangement of three tubercles, the rounded apices of which were sclerotized. The merus of the third maxilliped was studded with one or two tubercles on the distal dorsolateral margin and several on the ventromesial margin. The chelae were moderately robust, bearing a serrate row of tubercles on the mesial and lateral margins of the propodus and a row on the mesial margin of the dactyl; both fingers carried a dorsal row of tubercles flanking the opposable surfaces, each of which was studded with a row of five to seven tubercles. Tubercles were lacking on the dorsal surface of the palm as they were on the corresponding surface of the carpus, but the latter was provided with a longitudinal row of five or six tubercles mesially and a cluster of several laterally. The second through fifth pereopods lacked conspicuous spines on the merus. Noteworthy features of the sternal keel include a deeply situated, narrow, uninflated median keel and small vertically disposed lateral processes on segment XI; an inflated but rather small median keel and slightly splayed lateral processes on segment XII; a conspicuously inflated, broad median keel and lateral processes splayed at about 100 degrees on segment XIII; and a greatly reduced, but distinctly produced, median keel and narrow, splayed lateral processes on segment XIV. Segment XIII had at least rudiments of bullar lobes; and on segment XIV, the bullar lobes were well developed, clearly visible posteriorly, and a well-defined suture marked their junctions with the corresponding lateral processes. The phallic papillae were small, somewhat cone-shaped, and bore an eccentric patch of apical setae. The primitive ancestral gill complement had been reduced to 13 + epr + 5r.

In any postulated history of the invasion of Madagascar by a proastacoides stock and its radiation on the island, an

assumption must be made that it occurred when this land mass enjoyed a more temperate climate than that in which its descendants exist at the present time. As was pointed out by Huxley (1880a) and subsequent students of crayfishes, these animals are essentially elements of temperate faunas, and few of them have successfully invaded the tropics. This observation is bolstered by their distribution on Madagascar where *Astacoides* is largely restricted to the higher, cooler altitudes.

When the island gained its first crayfish stock, it is possible, if not probable, that the animals spread to virtually all of the existing streams and became the dominant invertebrate group on Madagascar. Perhaps it was the combination of warming climates and the rapid spread of potamonid crabs (nine species and subspecies were reported to occur there by Bott, 1965) that were responsible for their later restriction to the higher altitudes existing on the island. It is perhaps significant, however, that crabs have been reported from the same areas in which crayfishes have been collected.

Radiation from this stock appears to be more to have followed much the same pattern that it seems to have taken in parastacids in Australia and South America, and in cambarids in North America. But due to my very limited knowledge of the habitat distribution of *Astacoides*, much of the following must be considered to be little more than speculation with an unquestioned need to be substantiated or refuted.

Probably the earliest crayfishes on the island were stream dwellers having a body similar to that of *A. caldwelli*, but more tuberculate, as were the chelipeds and other pereopods which were more similar to those of *A. crosnieri* and *A. petiti*. Thus, whereas it could tolerate riverine conditions, it was not nearly so well adapted to flowing water as are *A. caldwelli* and *A. madagascarensis*. But the ecological vacuum into which they had entered had more to offer than the comparatively slow-flowing subestuarine areas. Few modifications were required of the invading stock in conquering the rapidly flowing, rock-littered segments of the rivers and larger tributaries. This was accomplished mostly through the reduction or loss of ornamentation which, while perhaps having protective qualities in the marine habitat of their ancestors, could well have been to some degree disadvantageous in rapidly flowing water. Their forbears also probably lived in a rocky environment where a strong thigmotactic tendency had already been established. Also, finding themselves in a medium in which the oxygen content was close to saturation, there was no necessity for making special adaptations that would do more than assure their conquest of flowing water. A well-developed abdomen was still important for swimming and it remained large and broadly joined to the thorax. *Astacoides caldwelli* most reflects such modifications and retentions.

As adaptations were better fitting this stock to live in the

lower sectors of the creeks and rivers, some individuals began to make excursions into the mountains where the streams were flowing more swiftly, and, at least seasonally, becoming torrential. For these wanderers importance became attached to the acquisition of some recess in which they might find safety from the shifting substrate, a wet, or at least damp, environment when the rills and creeks were reduced to trickles or ceased to flow during dry seasons, and a place in which they might defend themselves from terrestrial predators. Somehow they discovered that all of these needs could be satisfied by constructing retreats in the form of tunnels in the banks of the streams. In such habitats where they were either bathed in strong currents or secluded in minicaverns, indeed a reduction in the ornamentation of the exoskeleton and in the size of the eyes was hardly disadvantageous. At this stage the body pattern of *A. madagascarensis* had been attained. Such modifications did not necessarily restrict their possessors to the smaller tributary streams; rather, they allowed those crayfish exhibiting such features to live successfully in a habitat that could not have been exploited by their ancestors.

When, or soon after, the early crayfish stock obtained a foothold on Madagascar there must have existed a comparatively quiet body of water of some size with an outlet to the sea. It is inconceivable to me that the mien exhibited by *A. betsileoensis* could have come into existence in any environment other than one lacking a current or possessing a very sluggish one. The refinement of its features must have occurred in a lentic or sublentic environment. The spiny thorax, broad abdomen, and comparatively weak but spiny chelipeds surely did not come into existence in the cascading streams of the highlands. Neither is it likely that this stock could have found a congenial habitat in fast-flowing water, and the modern descendant appears ill-suited to a life centered in burrows.

Of the remaining three crayfishes occurring on Madagascar, *A. granulimanus* was probably derived from the same stock that gave rise to *A. madagascarensis* but was descended from an early offshoot that discovered agreeable surroundings in the turbulent waters associated with rocky riffles where it sought refuge in crevices between the rocks and dug shallow excavations beneath them. In moving into such habitats, it retained, among others, several primitive features of the cheliped (for example, a serrate lateral margin of the propodus, a row of tubercles on the mesial surface of the carpus, and stronger tubercles on the merus) that were lost or became modified in its close relative.

Early after the proastacoides stock had become established in the lowland rivers, and perhaps during a period of high water, some crayfish moved out of, or were dislodged from, the low-lying stream bed and became stranded in floodplain pools. With a background in their lineage for burrowing under objects for protection from predators and during the molting period, as the pools began to dry, instead

of wandering overland in search for water, they simply dug into the mud, tunneling deeper as the water table receded. Finding in the floodplain swamps and temporary pools a tolerable, uncrowded habitat, adaptations primarily associated with obtaining adequate oxygen and becoming acclimated to a more sedentary existence resulted in the mien presented by *A. crosnieri* and *A. petiti*. The differences between these two crayfishes are ones that could well have developed after their immediate ancestors had become adapted to living in swamps and seepages. It should be pointed out, however, that *A. crosnieri* has progressed farther, as evinced particularly by the abdomen and narrow areola, toward limiting itself to a style of living centered around burrows than has *A. petiti*.

I should like to emphasize that in suggesting a possible adaptive evolutionary pattern in the racial history of *Astacoides*, I have no first-hand knowledge of the habits of any of the six taxa recognized herein and have based this account on an assumed correlation with morphological features and habitats that seem to exist in crayfishes belonging to the family Cambaridae. Tentatively assuming that such parallel correlations exist in the Parastacidae and that subsequent ecological studies support at least the broad aspects of the ecological distribution as suggested herein, one should anticipate that, in all probability, none of the six is so perfectly adapted to any one environmental condition that it is limited to that niche. I suspect that any one of these crayfishes might at least occasionally invade the habitats generally occupied by the others.

Seeking further evidence that the conclusions drawn concerning the interrelationships in the Genus *Astacoides* are not entirely amiss, 34 features (see "Characters Compared") were selected for an objective comparison. The Wagner Program of computer analysis (Farris, 1970; Farris, Kluge, and Eckardt, 1970) was used to prepare a series of cladograms, the most parsimonious of which is depicted in Figure 14. It is in such close agreement with the views already expressed that further discussion, for the most part, seems unnecessary.

In the preceding account of adaptive radiation of *Astacoides* on Madagascar, the invasions of the habitats by the ancestral stocks of the six species are recounted in almost the reverse order as the appearance of the species names on the cladogram. Whereas the primitive *A. crosnieri* and *A. petiti* have preserved the greatest number of primitive features considered, thus presumably more nearly resembling the marine ancestor than do the remaining species, at the same time, these two crayfishes have become the most specialized ecologically. Their ability to tolerate the conditions in swamps (and presumably burrows) is reflected in modifications of their thoracic region permitting a proportional increase in the lengths of their gills. These changes in the exoskeleton are ones that are unlikely ever to have occurred in the ancestral lineage of the stream dwellers or

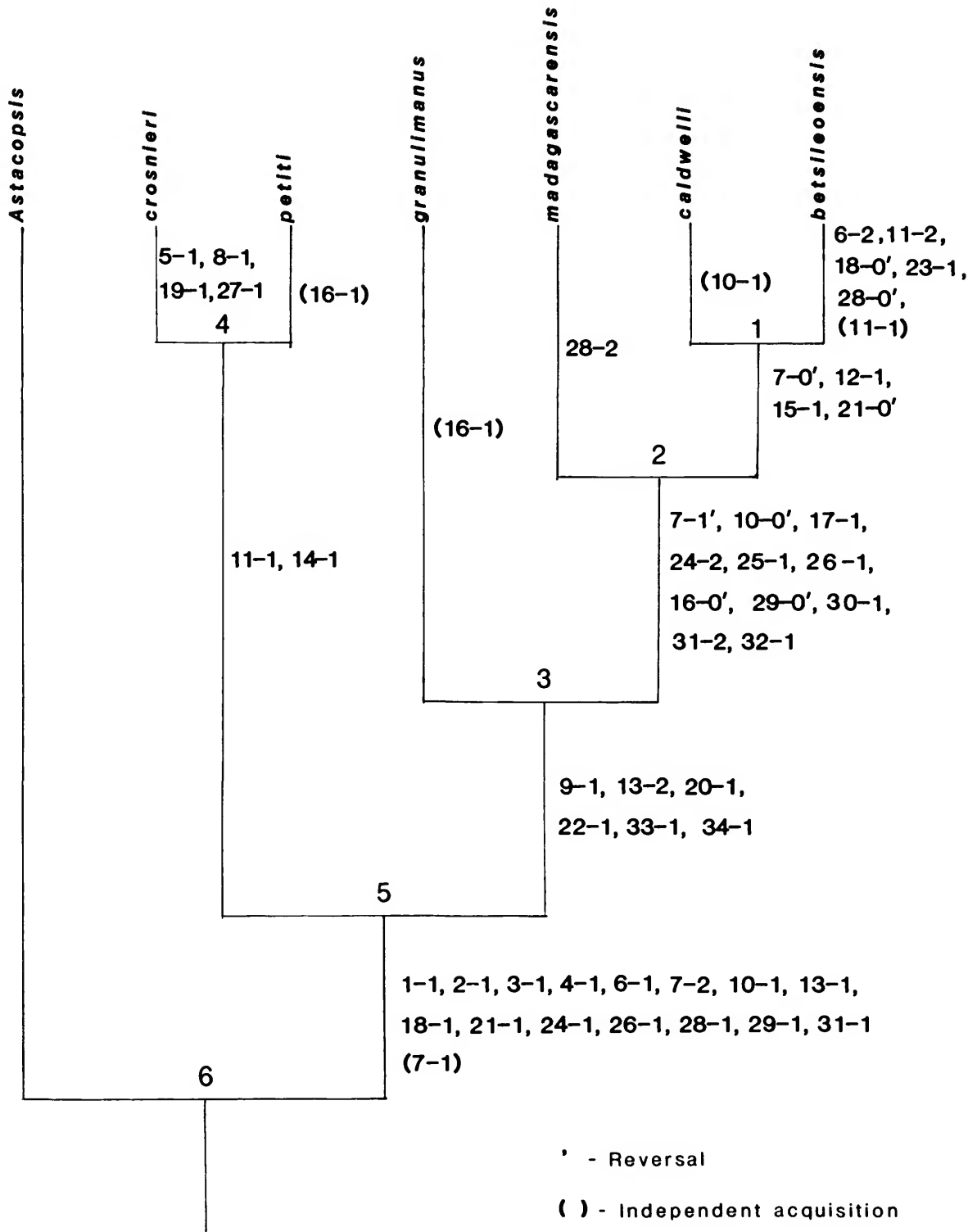


FIGURE 14.—Cladogram expressing relationships of members of the genus *Astacoides*. (*Astacopsis*, the out-group, based largely on *A. franklinii*.)

occupants of well-oxygenated lacustrine habitats. Thus one might suggest that they, along with *A. granulimanus*, es-

caped the channeling effect of becoming adapted to lotic and lacustrine environments.

Characters Compared

The first condition listed for each character is considered to be plesiomorphic.

1. Branchiae	(0) 21 + epr, (1) no more than 13 + epr + 5r
2. Merus of pereopods	(0) spines present, (1) spines absent
3. Phallic papilla	(0) no apical setal tuft, (1) apical setal tuft
4. Phallic papilla	(0) large tubular, (1) small cone-shaped
5. Rostral tubercles	(0) erect, (1) flattened
6. Antennal scale: lateral spines or tubercles	(0) absent, (1) tubercles, (2) spines
7. Postorbital ridges	(0) strong, (1) weak, (2) tubercles only
8. Areola length/carapace length	(0) less than 0.39, (1) more than 0.39
9. Width 1st abdominal segment/carapace length	(0) less than 0.35, (1) more than 0.35
10. Postcervical groove invasion in areola	(0) shallow, (1) deep
11. Thoracic tubercles	(0) moderate, (1) weak or absent (2) procurved spines
12. Cervical spine	(0) weak or absent, (1) moderate
13. Mandibular arc	(0) absent, (1) with weak tubercles, (2) with strong tubercles or spines
14. Anteroventral branchiostegal region	(0) tuberculate, (1) few if any tubercles
15. Epistome, lateral tubercles	(0) in patch, (1) only 1 or 2 spines or tubercles
16. Third maxilliped, lateral tubercles or spines	(0) 0 to 2, (1) usually 3 or 4
17. Third maxilliped, mesial tubercles or spines	(0) 0 or 1, (1) 2 or more
18. Abdominal pleuron II	(0) spines strong, (1) weak spines or tubercles
19. Abdominal pleura III-VI	(0) tapering, (1) truncate
20. Dorsal surface of telson	(0) without spines, (1) with spines
21. Bullar lobe, Segment XIII	(0) absent, (1) present
22. Sternite XI, lateral process	(0) vertical, (1) splayed
23. Sternite XII, median keel	(0) slender, (1) inflated
24. Sternite XIII, median keel	(0) narrow (1) moderately inflated, (2) broadly inflated
25. Cheliped, dorsodistal part of merus	(0) row of spines or tubercles, (1) no spines, if tubercles, very weak
26. Cheliped, dorsodistal extremity of merus	(0) smooth, (1) crenulate
27. Carpus of cheliped	(0) no dorsal tubercles, (1) dorsal tubercles present
28. Carpus, mesial surface	(0) row of spines, (1) row of tubercles, (2) tubercles fused in massive prominence
29. Chela, width of palm/length of propodus	(0) average less than 0.49, (1) average more than 0.49
30. Cheliped, lateral tubercles on carpus	(0) moderate to strong, (1) weak or absent
31. Chela, lateral tubercles on propodus	(0) double row, (1) single row, (3) absent
32. Chela, tubercles on mesial margin of propodus	(0) forming cristiform row, (1) if present, not forming cristiform row
33. Chela, mesial margin of dactyl	(0) tubercles present, (1) tubercles absent
34. Chela, dorsal margin of dactyl	(0) tubercles present, (1) tubercles absent

The Genus *Astacoides*

Astacoides Guérin, 1839a. [Type-species, by monotypy, *Astacoides Goudotii* Guérin, 1839a: 109, a subjective senior synonym of *Astacus caldwelli* Bate, 1865: 470. For explanation of the nomenclature involved, see paragraph beginning "Holthuis (1964) . . ." on page 7. Gender: masculine.]

DIAGNOSIS.—Carapace with truncate to subtruncate rostrum bearing multituberculate lateral carinae; mandibular arc usually well developed and studded with tubercles or spines, sometimes rudimentary; branchiostegal spine absent; anterolateral part of postcervical groove extremely nar-

rowly separated from, and subparallel to, cervical groove; cervical groove broadly U-shaped and deeply impressed; postorbital ridges weak to almost obsolete, usually with anterior extremity marked by small corneous tubercles; abdomen with spines or tubercles on pleura of one or more segments; pleuron of first abdominal segment distinct and partly overlapped by that of second; telson never with posterior membranous section; pleurocoxal lappets on segments X through XIII; branchial count 12 or 13 + epr + 3 to 5r; pleurobranchiae on segment XIV only; anterior arthrobranchiae on segment VIII moderately well developed,

rudimentary, or absent, and posterior arthrobranchiae on three or more segments of IX through XIII rudimentary; stems of podobranchiae without wing-like expansion. Phallic papilla with eccentric, distal tuft of setae. (Modified from Hobbs, 1974:18, 19.)

RANGE.—Endemic on Madagascar (Figure 1) where it occupies an area of about 60,000 square kilometers in the southeastern part of the island (latitude 18° to 25°S and longitude 46° to 49°E) at altitudes of about 500 to 2000 meters.

Key to the Species of the Genus *Astacoides*

1. Sternite XIII with bullar lobe [Figures 5, 6] 2
 Sternite XIII without bullar lobe 5
2. Mesial surface of carpus of cheliped with coalescing tubercles (sometimes forming single massive prominence); mesial margin of palm of chela with row of low tubercles *A. madagascariensis*
 Carpus of cheliped with row of distinctly separated tubercles mesially; mesial margin of palm of chela with cristiform row of tubercles 3
3. Dorsal surface of carpus and palm of cheliped with few to many low flattened tubercles
 *A. crosnieri*, new species
 Except for 1 or 2 small tubercles on dorsal mesiodistal angle of carpus, dorsal surface without tubercles 4
4. Dactyl of chela with tubercles mesially and dorsally *A. petiti*, new species
 Dactyl of chela without tubercles mesially or dorsally *A. granulimanus*
5. Antennal scale with lateral spines; branchiostegites armed with conspicuous procurved spines
 *A. betsileoensis*
 Antennal scale without lateral spines; branchiostegites lacking procurved spines *A. caldwelli*

***Astacoides crosnieri*, new species**

FIGURES 2a,b, 3c, 4, 6a, 10e, 11c,d, 12, 13e, 14, 15, 16

Astacoides madagascariensis var. *granulimanus*.—Monod and Petit, 1929:22, 23 [in part], 24, fig. 7e.

Astacoides madagascariensis granulimanus.—Holthuis, 1964:315, 316 [in part].

DIAGNOSIS.—Rostrum short (8.4±1.0 percent of carapace length). Areola 4.7±0.7 times as long as wide, constituting 40.5±1.2 percent of carapace length and 44.6±1.3 percent of postorbital carapace length. Branchiostegites comparatively weakly tuberculate, never bearing strong tubercles or spines. Width of first abdominal segment in males equivalent to 31.8±1.5 percent of carapace length, that of second in males, 45.3±1.2 percent. All abdominal pleura lacking spines, that of third through sixth subtruncate ventrally. Dorsal surface of telson and uropods lacking spines except laterally and forming row along proximal margin of diarsis on lateral ramus of uropods. Antennal scale with tuberculate lateral margin. Merus of third maxilliped lacking spines and tubercles mesially and laterally. Carpus of cheliped with 2 rows of low, polished, sclerotized tubercles dorsally and row of distinct tubercles mesially, but lacking 1 or 2 tubercles on dorsal distomesial margin. Width of palm of chela 55.2±1.9 percent of length of propodus; lateral and mesial margins of propodus each with cristiform row of tubercles; mesial and dorsal surfaces of dactyl with rows of tubercles. Keel of sternite XIII provided with bullar lobes. Median keel of sternite XII slender, not inflated, that of sternite XIII inflated but comparatively slender. Space between verticle arms of paired sternopleural bridge of sternite XIV narrow, but bullar lobes well exposed.

DESCRIPTION.—Rostrum (Figure 15a,b), constituting 6.6

to 10.3 percent of carapace length, with lateral carinae slightly convergent to weakly divergent, bearing low, elongate, subsymmetrically arranged tubercles; dorsal surface moderately to deeply excavate. Postorbital ridge obsolete, sometimes lacking even anterior tubercle. Suborbital angle subtruncate, bearing single, procurved, postmarginal spine that rarely reduced to weak tubercle. Branchiostegal spine absent and no spines or tubercles present on margin of anteroventral branchiostegal region, lateral surface of which weakly, if at all, tuberculate. Antennal and hepatic regions with low tubercles, and row of tubercles flanking anterior margin of mandibular and ventral part of antennal regions. Mandibular arc comparatively inconspicuous, and row of tubercles on it sometimes scarcely noticeable; ridge and tubercles almost obsolete in specimens from Ikongo. Lateral surface of branchiostegal region rather densely studded with small tubercles. Cervical spine unrecognizable or represented by low tubercle only slightly larger than others nearby. Areola 3.7 to 5.9 times as long as broad and constituting 38.7 to 43.6 percent of carapace length (42.5 to 47.5 percent of postorbital carapace length).

Basal podomere of antennular peduncle sublamelliform, its anteroventral margin with 2 subacute tubercles. Antennal peduncle (Figure 15e) usually with acute distomesial tubercle on coxa, distolateral one rudimentary or absent; weak ventral, distoventral, and distolateral tubercles on basis, and lacking tubercle on merus. Antennal scale (Figure 15f) with 3 tubercles in lateral marginal row, 0 to 2 on proximal part of dorsolateral ridge, and 0 to several forming subserrate row on ventral keel (right scale on specimen from Ikongo lacking lateral tubercles). Antennal flagellum reaching third or fourth abdominal tergum.

Epistome (Figure 15e) with cluster of 10 or 12 tubercles

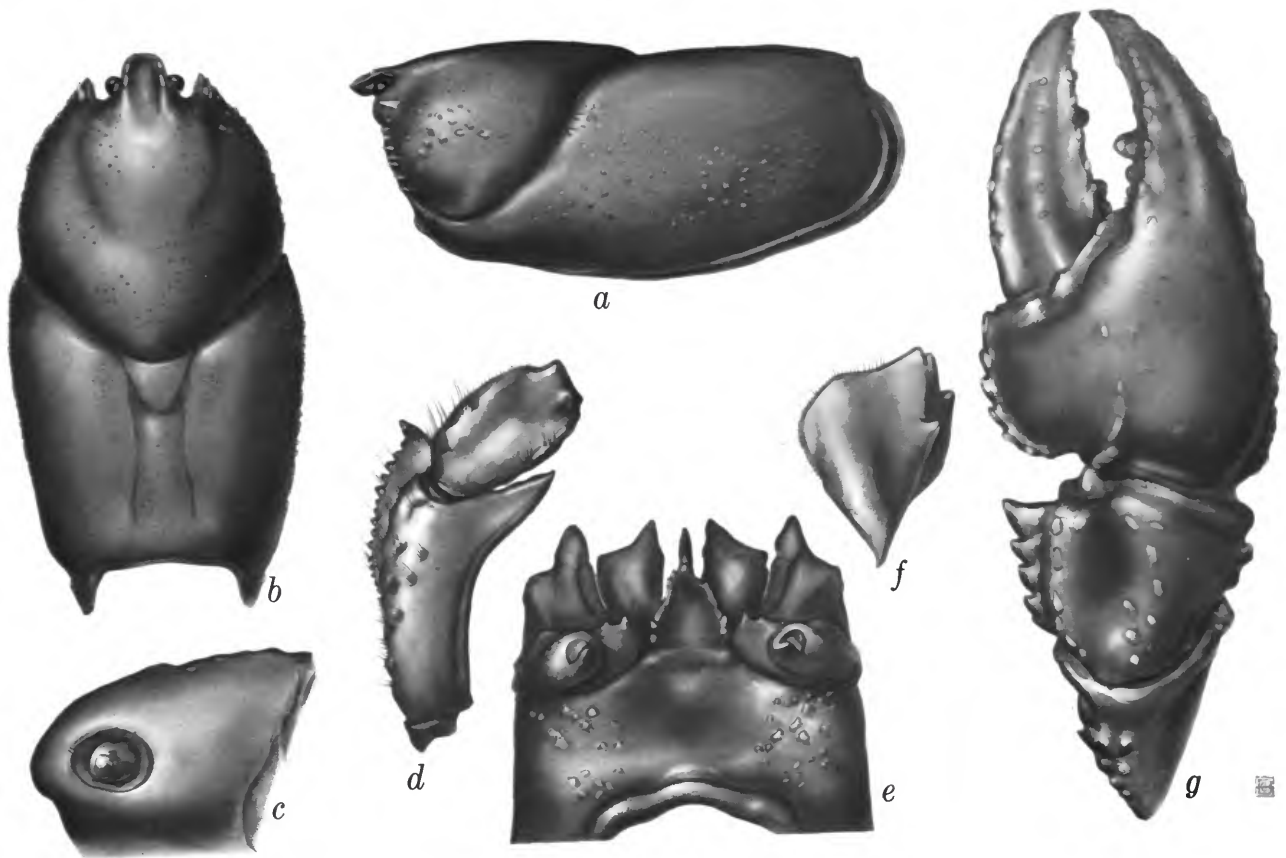


FIGURE 15.—*Astacoides crosnieri*, new species (all from holotype): *a*, lateral view of carapace; *b*, dorsal view of carapace; *c*, phallic papilla on coxa of fifth pereopod; *d*, distal part of basis, ischium, and merus of left third maxilliped; *e*, epistome and basal podomeres of antennae; *f*, dorsal view of right antennal scale; *g*, dorsal view of distal podomeres of right cheliped.

in each posterolateral section; deep median depression at base of sagittiform anteromedian lobe, latter with serrate or subserrate lateral margins, usually reaching level of distal end of merus of antennal peduncle.

Keel of sternite XIII (Figure 6*a*) provided with bullar lobe. Median keel of sternite XII not inflated, distinctly keel-like; that of XIII inflated but comparatively slender. Lateral processes of sternite XI small and directed almost ventrally, never so much as at 45 degree angle, those of sternites XII at about 110, and those of XIII at about 125 degree angle. Verticle arms of paired sternopleural bars of sternite XIV (Figure 10*e*) narrowly separate but intervening bullar lobes clearly visible.

Mandible (Figure 3*c*) with mammiform proximocephalic cusp of caudal molar process contiguous with similar but larger cephalodistal cusp and lying close to very small distoproximal cusp; nodular cluster consisting of only 1 or 2 tiny nodules lying at mesial bases of cephalodistal and proximocephalic cusps.

Ischium of third maxilliped (Figures 4, 15*d*) strongly produced distolaterally in acute projection. Merus without spines or tubercles mesially and laterally (one specimen with 1 lateral tubercle).

Cheliped (Figures 2*a,b*, 15*g*) with ischium bearing none or row of as many as 3 tubercles anteromesially. Ventral surface of merus with mesial row of 4 to 6 tubercles and lateral row of 2 or 3; dorsal surface with row of low tubercles on ridge becoming progressively larger distally, several additional tubercles present near distal end, only 1 or 2 of more distally situated ones spiniform; dorsodistal margin irregular but not crenulate. Carpus with mesial cristiform row of 5 or 6 tubercles increasing in size toward distal end of podomere, lateral surface with 2 or 3 low tubercles, dorsal surface with median depression flanked by prominent sublinear series of large sclerotized tubercles, and ventral surface with as many as 8, sometimes arranged in arched transverse row; lateral surface with row of 2 to 5 tubercles. Propodus, with width 52.7 to 58.5 percent of length, bear-

ing lateral serrate row of sclerotized tubercles extending for almost entire length of podomere, more distally situated ones more widely spaced; mesial margin of palm with cristiform row of 5 to 7 similar tubercles; dorsal surface of palm with few tubercles (including 1 immediately lateral to more distal one in mesial row) distal to strongly elevated proximo-medial socket, and few conspicuous setiferous punctations. Opposable margin of fixed finger bearing row of 5 to 7 corneous tubercles below which another row of 6 or 7 present, fourth or fifth from base largest; row of minute denticles borne between rows of tubercles; low, rounded, mid-dorsal ridge weak and delimited by rows of setiferous punctations, that on ventral surface similarly flanked, but by row of 2 or 3 tubercles proximomesially. Opposable margin of dactyl with 5 to 7 tubercles and oblique ventral excavation present proximally; mesial surface with longitudinal row of as many as 10 corneous tubercles, median longitudinal ridge on both fingers bearing row of low, rounded sclerotized tubercles.

Width of first abdominal segment in males 27.6 to 34.2 percent of carapace length, that of second 43.7 to 47.3. Pleuron of second abdominal segment (Figure 13e) with cluster of very low tubercles flanking ventral region, those on pleuron of third segment few in number, some of which hardly visible. Third through sixth pleura little, if at all, tapering, and subtruncate ventrally.

Telson scabrous, junction of cephalic and caudal sections recognizable only in those specimens bearing single pair of small to minute caudolateral spines at base of caudal sixth or seventh of length. Proximal podomere of uropod lacking spines and tubercles; mesial ramus with low median carina bearing very small tubercles, few spiniform, and 1 to 3 spines on distal part of median keel and 1 strong, curved, marginal spine at end of keel; crowded small tubercles, accompanied by very short setae, on lateral half of mesial and lateral rami, some of those on lateral half of lateral ramus spiniform. Diarsis on lateral ramus flanked proximally by 14 to 17 spines.

TYPE-LOCALITY.—Marais d'Ampamaherana, situé à 25 km de Fianarantsoa sur la ligne de Chemin de fer, Fianarantsoa-Manakara, Madagascar. Specimens were collected there by Alain Crosnier on 30 July 1973.

TYPES.—The specimens listed under "Range and Specimens Examined" constitute the type series and are deposited as indicated there.

RANGE AND SPECIMENS EXAMINED.—*Astacoides crosnieri* is known from only five localities, all situated in headwaters of westward-flowing streams between latitudes of 20° and 22°S, longitude 47° and 48°E. Three of the localities are so close together, perhaps all virtually one, that only three are identified in Figure 16.

The specimens examined are as follows (carapace length and postorbital carapace length, respectively, in mm, follow sex symbols): (1) Type-locality, holotypic ♂ 48.7, 44.4; PM

As328. ♂ 45.8, 42.1; ♂ 49.2, 45.4; ♂ 53.6, 49.2; ♂ 38.5, 35.3; ♀ 43.7, 39.7; PM As329. ♂ 51.2, 46.5; ♂ 45.8, 32.8; USNM 218797. (2) Madagascar, purchase of E. Bartlet, ♀ 36.4; 33.0; ♂ 32.3, 29.3; ♂ 31.3, 28.5; BMNH 1881.9. ♂ 46.3, 42.3; ♂ 43.9, 40.2; USNM 147263. (3) Forêt d'I-kongo, Vinanitelo, Sep 1898, ♀ 40.6, 37.3; PM As212. (This is probably the specimen recorded by Monod and Petit (1929:26) as "(e) 1♀ exemplaire aberrant" and partly described by them on page 24.) (4) Station Ampamaherana, Fianarantsoa District, 22 Jul 1970, M. Vincke, coll., ♂ 31.5, 29.1; ovig. ♀ 35.1, 32.3; RNHL 27275. (5) On the margin of the swamp on the highway to Ranomena, Fianarantsoa District, 24 Nov 1961, Y. Thérézien, coll., ♂ 21.7, 19.5; ♀ 23.1, 21.1; RNHL 18368. (6) Ampamaherana on way (near) Ranomena, 1962, M. Vincke, coll., ♀ 28.0, 25.5; RNHL 26485.

SIZE.—The largest specimen examined is a male from the type-locality having a carapace length of 53.6 mm, postorbital carapace length of 49.2 mm. The largest female, also from the type-locality, has corresponding lengths of 43.7 and 39.7 mm. Those of the only ovigerous female are 35.1 and 32.3 mm.

REMARKS.—This swamp-dwelling crayfish is easily recognized by the narrow areola, the highly vaulted carapace, and the flattened, sclerotized tubercles on the dorsal surface of the carpus and palmar part of the propodus of the cheliped.

The 21 oval eggs carried by the single ovigerous female, obtained on 22 July 1970, have diameters of approximately 3.8 and 2.6 mm.

As has been pointed out in the introductory pages of this review, Monod and Petit (1929) recognized the distinctive characteristics of this crayfish but considered it to belong to their variety *granulimanus* because of the intermediates, which appeared to them to exist between the typical form and this "extreme" one. The features they pointed out were the abundance of striking, knob-like tuberculiform granules on the chelae, which stand out by their yellow, glossy appearance, and their distribution on the propodus, which is described in detail; moreover, they noted that the external orbital angle, instead of being rounded, is truncate. They did not mention the apparently unique presence of the same kind of tubercles they noted on the propodus on the dorsal surface of the carpus of the cheliped, the narrower areola, and several other features (compare the "Diagnosis" with that of *A. granulimanus* herein) that suggest the distinctness of this crayfish from that they considered to be the typical form of *A. granulimanus*. In none of the specimens that I have examined do there appear to be "intermediates" between them and specimens that are herein considered to be typical of the latter species or of *A. petiti*.

VERNACULAR NAME.—*Astacoides crosnieri* is known in the region of the type-locality as "Oramboro" (fide Alain Crosnier).

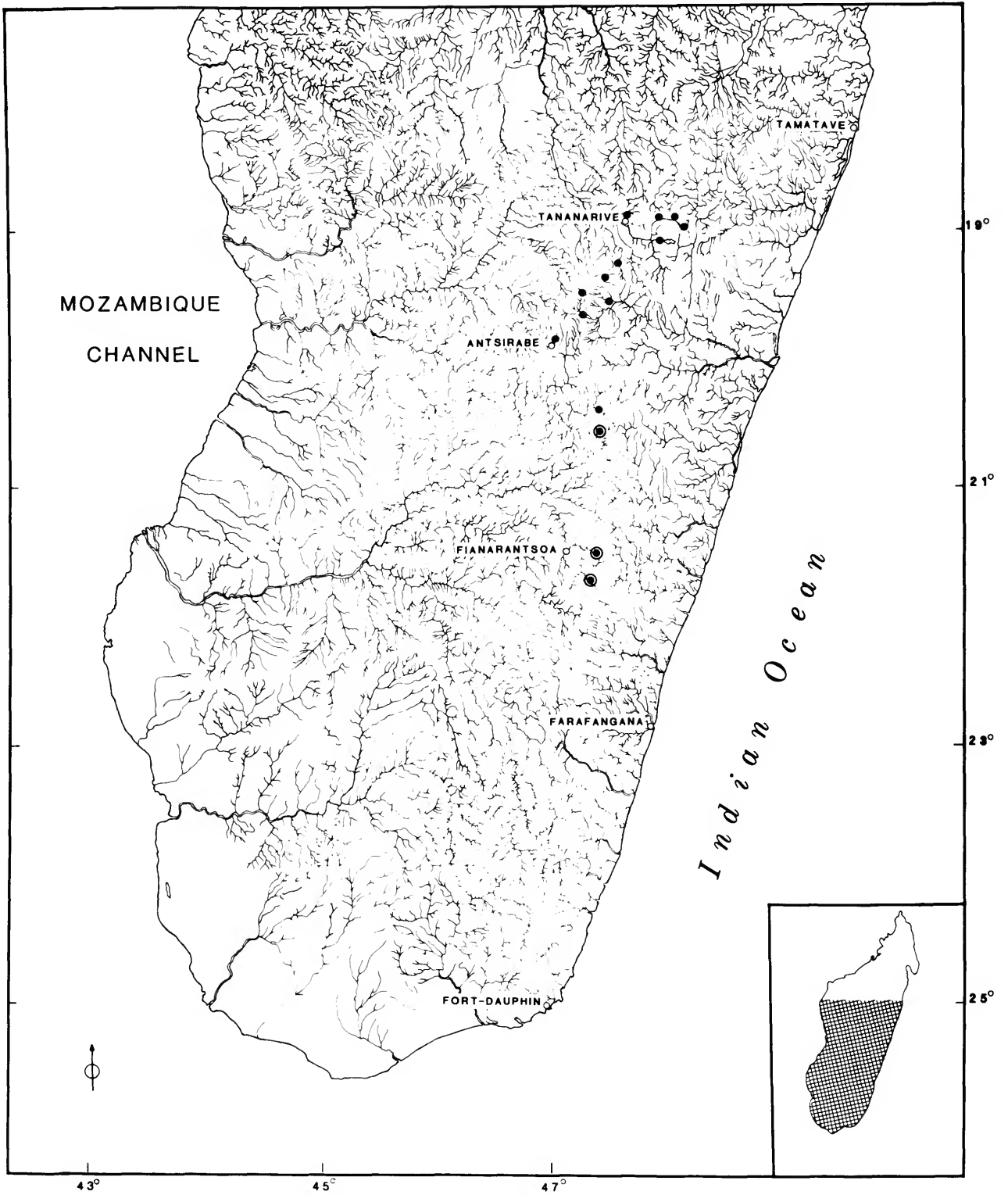


FIGURE 16.—Distribution of *Astacoides crosnieri*, new species (open circle with dot) and *A. caldwelli* (solid circle).

ETYMOLOGY.—This crayfish is named in honor of my friend Alain Crosnier who is responsible for arousing my interest in the crayfish fauna of Madagascar when he asked if I might be interested in examining specimens that he had collected on the island in the early 1970s.

Astacoides petiti, new species

FIGURES 3e, 6b, 10h, 12, 13f, 14, 17, 18

Astacoides madagascariensis var. *granulimanus*.—Monod and Petit, 1929:22, 23 [in part], fig. 7i.

Astacoides Madagascariensis var. *granulimanus*.—Poisson, 1947:63, pl. III: fig. 1.

Astacoides madagascariensis granulimanus.—Holthuis, 1964:22, 23 [in part].

DIAGNOSIS.—Rostrum of moderate length (9.6 ± 1.4 percent of carapace length). Areola 2.9 ± 0.3 times as long as wide, comprising 37.4 ± 0.9 percent of carapace length and 41.4 ± 0.7 percent of postorbital carapace length. Branchiostegites comparatively weakly tuberculate, never with spines. Width of first abdominal segment in males equivalent to 34.5 ± 0.7 percent of carapace length; that of second 48.0 ± 1.9 percent. All abdominal pleura lacking spines, that of third through sixth gently tapering and rounded ventrally. Dorsal surface of telson lacking spines; uropods with row of spines on median keel of mesial ramus, along diarsis of lateral ramus, and on distal margin of both rami. Antennal scale with tuberculate lateral margin. Merus of third maxilliped lacking spines mesially but with row of 3 to 5 tubercles laterally. Carpus of cheliped usually with 1 or 2 submarginal, dorsomesial, distal tubercles, lacking tubercles dorsally, but with distinct row of tubercles mesially; width of palm of chela 50.1 ± 1.7 percent of length of propodus; lateral and mesial margins of propodus each with cristiform row of tubercles; mesial and dorsal surfaces of dactyl with rows of acute or subacute tubercles. Keel of sternite XIII with bullar lobes. Median keel of sternite XII slightly inflated anteriorly and posteriorly but slender, that of XIII inflated but comparatively slender. Vertical arms of paired sternopleural bridges of sternite XIV almost or quite contiguous, sometimes completely obscuring all but extreme ventral part of bullar lobes.

DESCRIPTION.—Rostrum (Figure 17a,b), constituting 7.9 to 11.2 percent of carapace length, with lateral carinae weakly convergent to slightly divergent anteriorly, bearing 3 pairs of well-defined, elevated, corneous tubercles, anteromedian one also present; rostral margins in specimens from Isaka (Fort-Dauphin) area also ending in corneous tubercles (lacking in specimens from Farafangana). Surface of rostrum deeply excavate; short median carina extending into concavity from anteromedian tubercle. Postorbital ridge obsolete but represented by paired corneous tubercles situated immediately lateral to pair of smaller ones belonging to series on lateral rostral carinae. Suborbital angle truncate and bearing anteriorly directed postmarginal tubercle or

spine. Branchiostegal spine absent, and only 1 or 2 minute tubercles present in anteroventral branchiostegal region, lateral surface bearing very weak tubercles, strongest along ventral flank of cervical groove. Orbital region rather strikingly delimited from hepatic region by conspicuous sinuous groove; antennal, anterior part of hepatic, and mandibular regions with many small tubercles (more prominent in small specimens); mandibular arc clearly defined, abutting cervical groove but very weakly tuberculate. Lateral surface of branchiostegites granulate. Cervical "spine" not distinguishable from other small tubercles in region. Areola 2.5 to 3.2 times as long as broad and constituting 36.1 to 38.9 percent of carapace length (40.6 to 42.4 percent of postorbital carapace length).

Basal podomere of antennular peduncle sublamelliform, bearing 2 or 3 subacute tubercles on distoventral margin. Antennal peduncle (Figure 17e) bearing small mesial and lateral tubercles distally (latter usually larger) on coxa, weak distomesial and distolateral tubercles on basis, and lacking spines on merus. Antennal scale (Figure 17f) with row of 3 to 5 tubercles in lateral row, 1 or 2 dorsal to row, and 3 or 4 on ventral keel. Antennal flagellum reaching third or fourth abdominal tergum.

Epistome (Figure 17e) with cluster of tubercles laterally, some buttressed and some sometimes spiniform; deep median depression at base of sagittiform anteromedian lobe; latter with serrate or toothed lateral margins almost or quite reaching distal end of merus of antennal peduncle.

Keel of sternite XIII (Figure 6b) provided with bullar lobe. Median keel of sternite XII slightly inflated; that of XIII also inflated but comparatively slender. Lateral process of sternite XI rather small and directed almost ventrally, never so much as at 45 degree angle, those of XII at about 100 degrees, and those of XIII at about 140 degree angle. Vertical arms of paired sternopleural bridges (Figure 10h) of sternite XIV contiguous or almost so, obscuring almost all of bullar lobes.

Mandible (Figure 3e) with proximocephalic cusp of caudal molar process rather long, almost contiguous with distoproximal cusp. Nodular cluster consisting of 4 or 5 nodules crowded between distoproximal and cephalodistal cusps.

Ischium of third maxilliped strongly produced distolaterally in acute projection. Merus (Figure 17d) like that of *A. granulimanus* (Figure 4) with 4 to 6 subacute tubercles forming serrate row on dorsolateral margin of podomere, none on mesial margin.

Cheliped with ischium bearing anteromesial row of 4 or 5 tubercles. Ventral surface of merus with mesial row of 5 to 7 tubercles and lateral one of 4 to 6; dorsal surface with row of low tubercles on ridge, more distal ones larger and sometimes spiniform, additional few tubercles lateral to row, dorsodistal margin crenulate (Figure 17g). Carpus with mesial cristiform row of 5 to 6 subacute tubercles and with 1 (occasionally 2) rounded tubercles dorsolateral to distal-

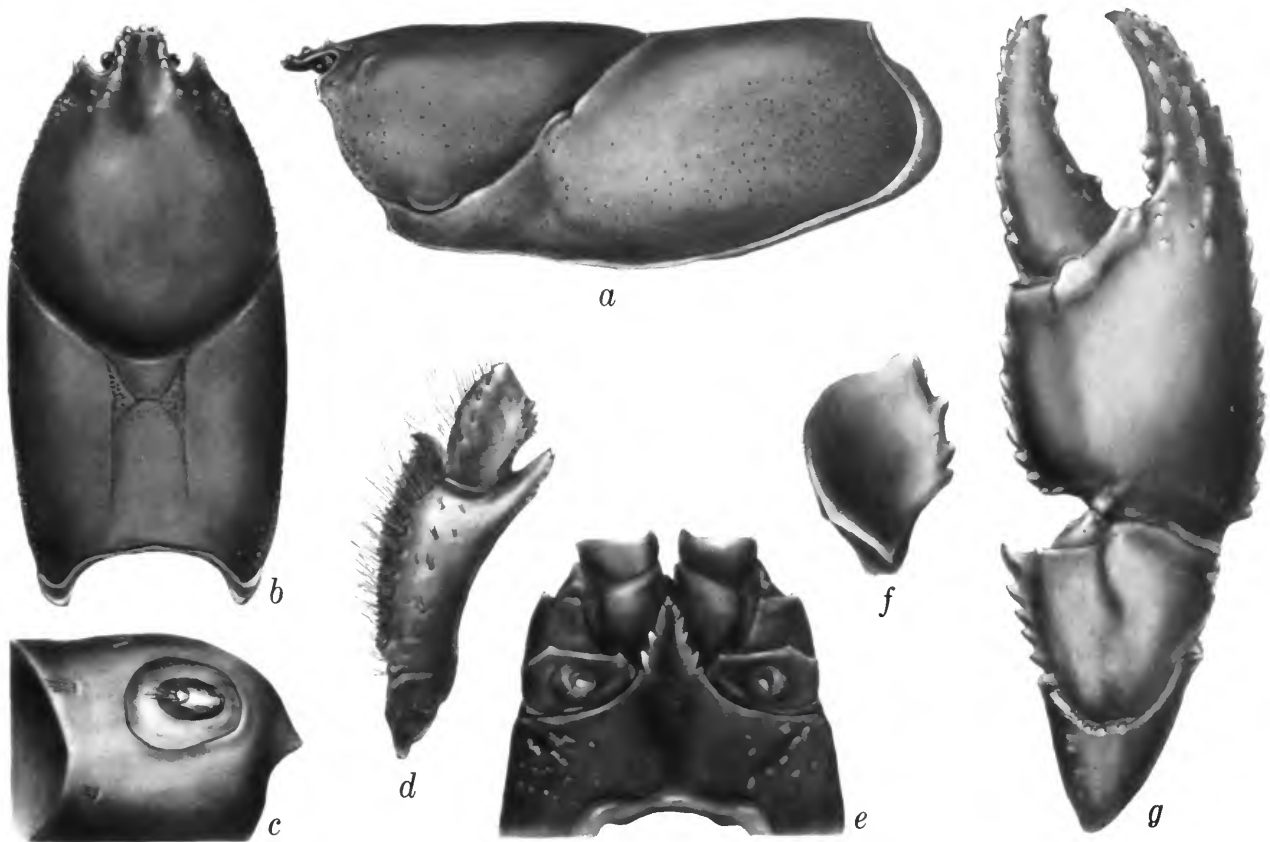


FIGURE 17.—*Astacoides petiti*, new species (all from holotype): *a*, lateral view of carapace; *b*, dorsal view of carapace; *c*, phallic papilla on coxa of fifth pereopod; *d*, distal part of basis, ischium, and merus of left third maxilliped; *e*, epistome and basal podomeres of antennae; *f*, dorsal view of right antennal scale; *g*, dorsal view of distal podomeres of right cheliped.

most in row; remainder of dorsal surface devoid of tubercles; ventral surface with 4 or 5 tubercles variously arranged, and lateral surface with 3 to 7, one of which usually on distal margin. Propodus, with width 47.9 to 52.6 percent of length, bearing lateral serrate row of sclerotized tubercles extending almost entire length of podomere, more distal ones not markedly farther apart than those on proximal half of podomere; mesial margin of palm with cristiform row of 7 or 8 sclerotized tubercles (sometimes fewer on regenerated chelae). Opposable margin of fixed finger with 4 well-defined tubercles in proximal half, dorsomesial row of 6 distally directed corneous tubercles extending along almost entire length of finger, and dorsomedian row of 9 similarly oriented ones. Opposable margin of dactyl with row of 5 large rounded tubercles (second from base not visible in Figure 17*g*), proximalmost slightly larger than others; row of 6 or 7 distally directed, corneous-tipped tubercles immediately above opposable margin spanning most of length of finger; dorsal surface with 2 similar tubercles near corneous tip, and mesial margin with 1 row

of about 10 tubercles (Isaka) or 2 rows of approximately 6 (lower) and 11 (Farafangana) extending almost from base to distal corneous tip; 1 or 2 preapical tubercles situated ventromesially. Single inconspicuous row of minute denticles present on opposable margin of both fingers, that on dactyl becoming multiple between penultimate tubercle and corneous tip; median longitudinal ridge on both fingers poorly defined, scarcely recognizable as such except for presence of flanking setiferous punctations.

Width of first abdominal segment in males 33.7 to 35.5 percent of carapace length, that of second, 46.0 to 51.0. Pleuron of second and third abdominal segments (Figure 13*f*) with marginal row of small tubercles and few scattered ones dorsal to it. Third through sixth pleura tapering, and, except for truncate margin of third, rounded ventrally.

Telson rugose to scabrous, with or without paired marginal spines, which if present (in specimens from Isaka) constituting only indication of division into anterior and posterior sections; in specimens from Farafangana, two sections more clearly delineated by shallow sinuses and weak

furrows; one pair of small, submarginal, corneous tubercles usually present posteriorly. Proximal podomere of uropod lacking spines and tubercles; mesial ramus with median carina bearing row of spines extending along almost entire length, few spines also often present lateral to distal part of carina and along distomedian and lateral margins; lateral ramus with low median carina bearing 1 or 2 tubercles, and 1 marginal spine present at end of carina; lateral half distinctly rugose with few to several spiniform tubercles. Diarsis on lateral ramus flanked proximally by 8 to 11 spines.

TYPE-LOCALITY.—Fond de la vallée d'Isaka (= Isaha?), Madagascar; torrents de la montagne. Two male specimens were collected there by Ch. Alluaud in 1901 (See Monod and Petit, 1929:26).

TYPES.—The specimens (three males and one female) constituting the type series are listed in the first three localities cited immediately below. All are in the Muséum National d'Histoire Naturelle, Paris, except the paratypic male from the type-locality, which is deposited in the National Museum of Natural History, Smithsonian Institution. The specimens from Farafangana (Locality 4) are excluded from the series because of the unique features pointed out in the "Remarks" that follow.

RANGE AND SPECIMENS EXAMINED.—*Astacoides petiti* has been found in only five localities (possibly only four, for the source of the specimens purchased in Farafangana is not known), all of which are situated on the eastern versant of the island between latitudes of 22° and 25°S, longitude 46° and 48°E (Figure 18).

The specimens examined are as follows (carapace length and postorbital carapace lengths, respectively, in mm, follow sex symbols): (1) Type-locality, holotypic ♂ 54.0, 49.7; PM As211. ♂ 49.1, 45.0; USNM 218799. (2) Isaka, near Fort-Dauphin, at altitude of 700 m, 1934, received from M. Catala, ♂ 41.9, 38.5; PM As208. (3) Andringitra, ♀ 46.2, 42.0, PM As189. (4) Farafangana (purchased, not collected), Marseille Expédition, 1907, ♂ 40.0, 35.6; ♂ 27.4, 24.4; ♀ 34.2, 30.6; ♀ 29.4, 26.1; PM As209. (5) Rivière Isandra, à Aukaiobe à l'est de Befotaka, Province de Farafangana; altitude 500 m, 13 Aug 1926, Mission R. Decary, ♂ 21.4, 18.9; ♀ 29.3, 26.3; PM As226.

SIZE.—The largest specimen available is the holotypic male that has a carapace length of 54.0 mm, postorbital carapace length, 49.7 mm. The largest female has corresponding lengths of 46.2 and 42.0 mm.

REMARKS.—This crayfish can be readily distinguished from the other members of the genus by the combination of having serrate or subserrate rows of tubercles on the lateral surface of the propodus of the cheliped and on the mesial surface of the dactyl but lacking flattened tubercles on the dorsal surface of the carpus and propodus of the cheliped. These characters are also evident in the regenerated chelipeds of all of the specimens that I have examined.

If I am correct in interpreting the short-palmed chelae in *Astacoides* as resulting from a loss and regeneration of this appendage, then only half of the available specimens of *A. petiti* have unregenerated chelae, and in two of these one of the members of the pair is a regenerated one, and a third has only a bud of one member. The assumed regenerated chela in *A. petiti* is easily recognized by the usually shorter palm and the paucity of large tubercles and the consistent dense longitudinal band of minute denticles on the opposable margins of the fingers.

In addition to the features already mentioned, the specimens from Isaka and Andringitra can be distinguished from those collected in Farafangana by possessing a single row of tubercles on the lateral margin of the propodus of the chela, but the specimens from Isaka exhibit traces (remnants?) of a second row: a stray tubercle adjacent to the row, or by one of the tubercles of the row having two partly fused corneous tips. Double rows of tubercles on the lateral surface of the propodus are characteristic of at least some representatives of several genera of parastacids, common in, if not typical of, both *Astacopsis* and *Euastacus*, the probable closest allies of *Astacoides*.

Ovigerous females are not among the material available.

ETYMOLOGY.—This species is named for G. Petit who exerted considerable effort in surveying the Madagascan fauna, contributing to our knowledge of the crayfishes, and pointing out the need for steps to be taken toward their conservation.

Astacoides granulimanus Monod and Petit, new status

FIGURES 3h, 4, 6c, 9, 10b, 12, 13c, 14, 19, 20

Astacoides madagascariensis-var.—Perrier de la Bathie, 1927:24.

Astacoides madagascariensis var. *granulimanus* Monod and Petit, 1929:11, 22–26, 28, 34 [in part], figs. 1E, 4C,F,H,J; 6E, 7D,F-H, 8C,D, 9A,B, 10; pl. 1: figs. 1, 2.—Louvel, 1930:18.

Astacoides madagascariensis.—Decary, 1946:201 [in part].

Astacoides madagascariensis granulimanus.—Poisson, 1947:13.

Astacoides madagascariensis (granulimanus type).—Decary, 1950:167.

Astacoides madagascariensis granulimanus.—Pretzmann, 1961:161.

Astacoides madagascariensis granulimanus.—Holthuis, 1964:309, 315, 316 [in part].

DIAGNOSIS.—Rostrum of moderate length (10.3 ± 1.1 percent of carapace length). Areola 3.0 ± 0.4 times as long as wide, constituting 38.0 ± 1.3 percent of carapace length and 42.5 ± 1.4 percent of postorbital carapace length. Branchiostegites tuberculate, never bearing strong spines. Width of first abdominal segment in males equivalent to 36.8 ± 2.0 percent of carapace length, that of second in males 51.1 ± 2.6 percent. All abdominal pleura lacking spines, that of third through sixth tapering ventrally and with distinctly rounded ventral margins. Dorsal surface of telson and uropods usually with spiniform tubercles. Antennal scale with tuberculate lateral margin. Merus of third maxilliped with row of 4 or more tubercles, mesial margin with or without

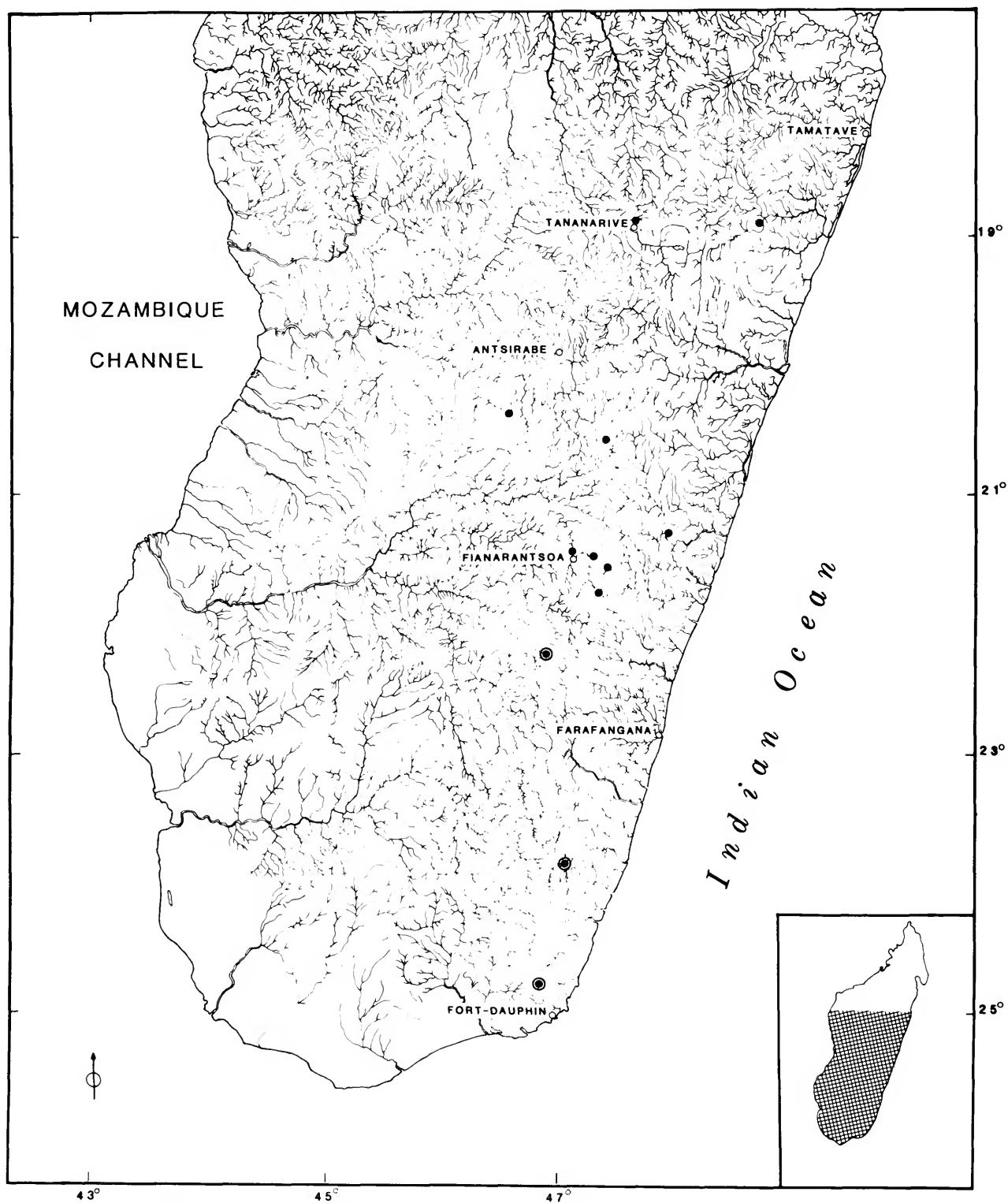


FIGURE 18.—Distribution of *Astacoides petiti*, new species (open circle with dot) and *A. betsiloensis* (solid circle).

few tubercles. Carpus of cheliped lacking low polished tubercles dorsally; width of palm of chela 48.7 ± 2.3 percent of length of propodus; lateral and mesial margins of latter each with cristiform row of tubercles; mesial and dorsal surface of dactyl lacking tubercles. Keel of sternite XIII provided with bullar lobes. Median keel of sternites XII and XIII inflated but comparatively slender. Vertical arms of paired sternopleural bars of sternite XIV broadly separated, clearly exposing bullar lobes.

DESCRIPTION.—Rostrum (Figure 19*a,b*) 7.1 to 12.7 percent of carapace length, with weakly convergent to slightly divergent lateral carinae, each bearing row of 3 or 4 corneous tubercles and usually 1 anteromedian one; dorsal surface comparatively deeply excavate. Postorbital ridges virtually obsolete, but small, usually paired, corneous tubercles resembling those on rostral carinae marking anterior extremities. Suborbital angle subtruncate but bearing 1 or 2 strong, acute, procurved tubercles. Branchiostegal spine absent. Antennal, mandibular, and hepatic regions with conspicuous to small, procurved, acute to subacute tubercles; mandibular arc well defined and bearing row of rather strong tubercles, both ridge and tubercles weak in small

individuals. Anteroventral branchiostegal region with few, if any, tubercles other than those sometimes flanking cervical groove; branchiostegal region with many tubercles laterally, most below level of cervical spine which scarcely larger than others nearby. Areola 2.3 to 4.2 times as long as broad and constituting 33.6 to 40.0 percent of carapace length (37.5 to 44.4 percent of postorbital carapace length).

Basal podomere of antennular peduncle with distal ventromesial margin bearing 2 spiniform tubercles. Antennal peduncle (Figure 19*e*) with obtuse to subacute distomesial and distolateral tubercles on coxa, distoventral, distolateral, and usually smaller ventral tubercle on basis, and small tubercle on ventrodistal margin of merus. Antennal scale (Figure 19*d*) with lateral marginal row of 3 or 4 (not counting apical tubercle) tubercles, mesial margin slightly undulant, and ventral keel with 2 or 3 small, often spiniform tubercles. Antennal flagellum reaching as far as sixth abdominal tergum.

Epistome (Figure 19*e*) with oblique row of 3 or 4 spiniform tubercles in each posterolateral angle, and with few additional smaller ones flanking row; deep anteromedian depression situated at base of subserrate, sagittiform, an-

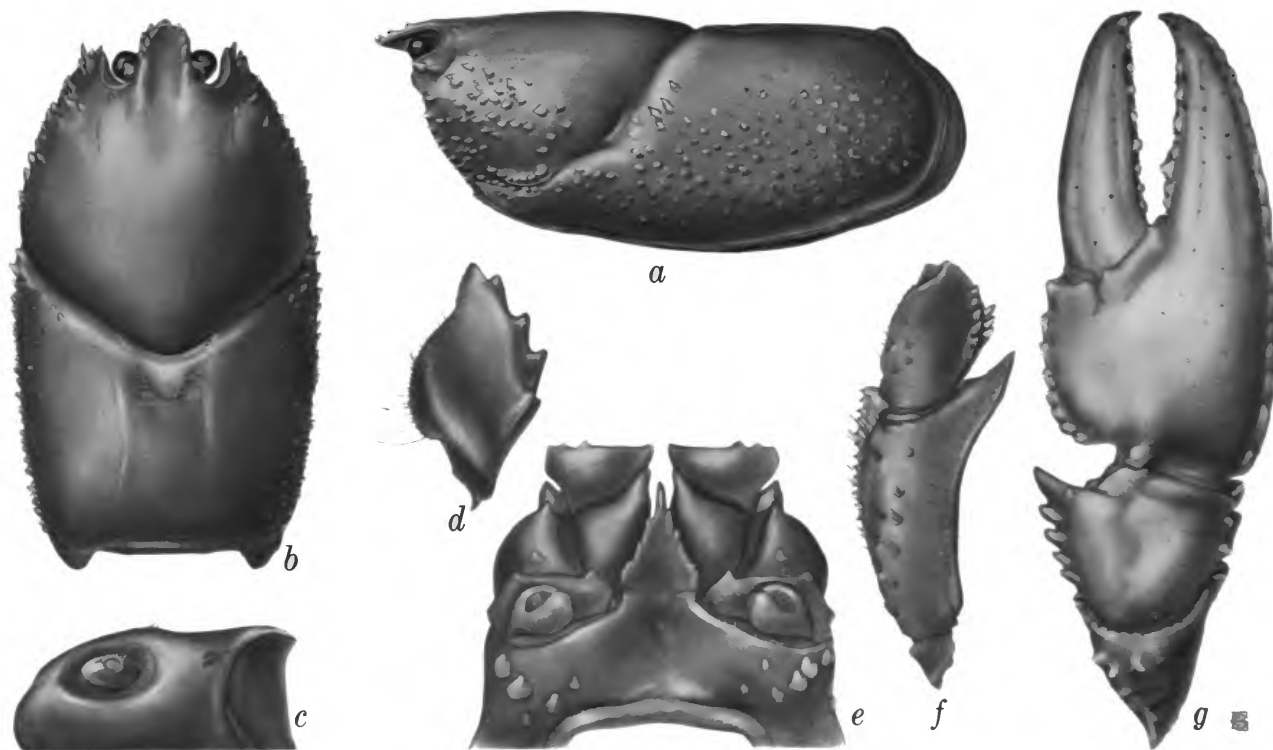


FIGURE 19.—*Astacoides granulimanus* (all from Marais d'Ampanaherana, 25 km from Fianarantsoa on rail line to Manakara): *a*, lateral view of carapace; *b*, dorsal view of carapace; *c*, phallic papilla on coxa of fifth pereopod; *d*, dorsal view of right antennal scale; *e*, epistome and basal podomeres of antennae; *f*, distal part of basis, ischium, and merus of left third maxilliped; *g*, dorsal view of distal podomeres of right cheliped.

teromedian lobe, apex almost or quite reaching ventrodistal extremity of merus of antennal peduncle.

Keel of sternite XIII (Figure 6c) provided with bullar lobes. Median keel of sternite XII slightly inflated, that of XIII more inflated but comparatively slender. Lateral processes of sternites XI through XIII splayed but forming broad V-shaped angle. Vertical arms of paired sternopleural bars (Figures 9c, 10b) of sternite XIV widely separated, not obscuring most of intervening bullar lobes which distinctly delimited from lateral processes.

Mandible (Figure 3h) with long proximocephalic cusps of caudal molar process very close to distoproximal cusp; nodular cluster consisting of as many as 12 nodules, none almost abutting proximocephalic or distoproximal cusps.

Ischium of third maxilliped (Figures 4, 19f) strongly produced distolaterally in acute projection. Merus with 0 to 2 small, often spiniform, tubercles on mesial margin, 1 to 3 spines present on distolateral margin and 1 to several serially arranged tubercles on ventrolateral surface just mesial to marginal row.

Cheliped (Figure 19g) with ischium bearing no prominent tubercles, but usually with row of 3 or 4 small ones on mesial margin. Ventral surface of merus with mesial row of 4 to 9 spike-like tubercles and lateral one of 4 to 6; dorsal surface bearing sublinear arrangement of small tubercles along ridge and scattered ones (mesiodistal member of which larger than others) more distally; dorsodistal extremity distinctly crenulate. Carpus with mesial row of 4 or 5 spiniform tubercles increasing in size toward distal end of podomere, row of 3 or 4 more rounded ones laterally, none dorsally, and 4 to 6 subspiniform tubercles ventrally. Propodus, with width 41.0 to 52.9 percent of length, subserrate laterally almost from base to tip of finger and bearing cristiform row of 7 or 8 tubercles mesially; dorsal and ventral surfaces sparsely and shallowly punctate. Opposable margin of fixed finger with 7 or 8 tubercles, one of third, fourth, or fifth from base large, others low and rounded, especially those distal to large tubercle; dorsomedian longitudinal ridge low, its lateral limits sometimes hardly recognizable except for presence of rows of shallow setiferous punctations. Opposable margin of dactyl with row of 6 to 8 tubercles of approximately same size; mesial margin with row of punctations. Distolateral part of propodus and distomesial part of dactyl sometimes with few very small tubercles, and occasionally with row of 3 or 4 dorsally, flanking opposable margins.

Width of first abdominal segment in males 31.0 to 40.4 percent of carapace length, that of second in males 44.8 to 54.3. Pleuron of second abdominal segment (Figure 13c) with row of small spiniform tubercles subparallel to anteroventral margin, that of third slightly rugose but lacking tubercles. Pleura of third through sixth segments tapering and rounded ventrally.

Telson approximately subequal in length and width, studded with short tubercles, many spiniform; caudal section

short and set off by pair of lateral tubercles or occasionally only by paired, short, weak sutures or shallow emarginations, otherwise continuous with basal section. Proximal podomere of uropod lacking spines and tubercles; mesial ramus with 1 or 2, usually row of, spiniform tubercles on median carina, and others, mostly smaller, in lateral half; lateral ramus lacking tubercles on keel but scattered ones over dorsal surface of lateral half; sometimes 1 or few small marginal spines present on either or both rami. Row of 6 (in small individuals) to 13 tubercles flanking proximal side of diarsis.

TYPE-LOCALITY.—Forêt d'Ikongo, Vinanitelo, Madagascar (here restricted). Unfortunately, Monod and Petit (1929) did not designate specimens they considered to typify the varieties of *Astacoides madagascarensis* they recognized, nor did they select a single locality from which they had specimens they believed best to represent them. None of the specimens listed that were in the "Collection du Laboratoire des Pêches et Productions Coloniales," (pages 24, 25), could be located. Four lots were reported: "a," the exact locality for which was unknown; "b," Massif de l'Andringitra; "c," Entre Vondrozo et Ifanadiana; and "d," Environs de Fort-Carnot. Of the specimens in the "Collection du Muséum National d'Histoire Naturelle" cited on page 26, those from "a," Massif de l'Ikongo, are dry and fragmentary. Those from "b," Farafangana (?), Expédition de Marseille, "c," Fond de la vallée d'Isaka, and "d, e," Forêt d'Ikongo, Vinanitelo, are in good condition. Of these five lots, however, only two, those from "a" and "d," contain the form that I believe Monod and Petit considered to be typical of their variety *granulimanus*. Those from localities "b" and "c" are members of one of the "extreme" forms with the lateral margin of both fingers of the chela serrate and which are being included in the type series of *Astacoides petiti*. That from "e" is the "unique" specimen (page 24), which they recognized as distinct but did not name. Herein it is assigned to the type series of *A. crosnieri*. Thus only two lots of the syntypic series known to be extant contain the typical form of *A. granulimanus*. To associate the latter name with members of one of the three species represented in what must be considered the syntypic series of *Astacoides granulimanus* Monod and Petit, I designate the large male (carapace length 68.5 mm) from Forêt d'Ikongo, Vinanitelo, as the lectotype of *A. granulimanus*, thereby restricting the type-locality to that cited above. (See "Types" below).

TYPES.—(See "Type-Localities.") Lectotype, ♂ cl. 68.5 mm, MP As214. Paralectotypes: MP As213, 2♂, 5♀; MP As215, 4♂, 4♀ (dry and fragmentary).

RANGE AND SPECIMENS EXAMINED.—On the basis of the material at hand, *Astacoides granulimanus* appears to have the largest range of any of the crayfishes of Madagascar, occurring in watersheds draining to the east and west between latitudes of 18° to 24°S, longitudes 46° to 48°E (Figure 20).

The specimens examined are as follows (Carapace length

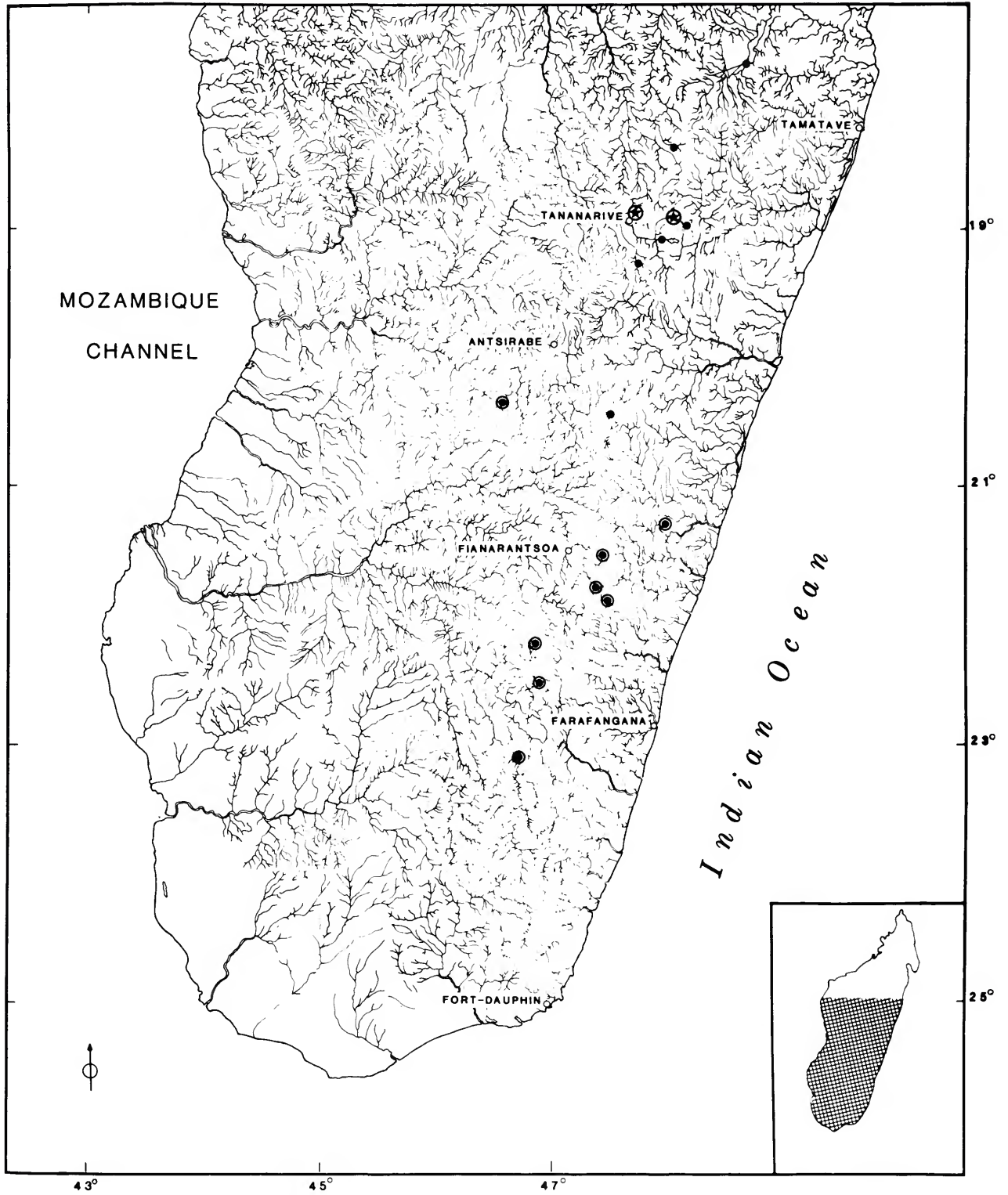


FIGURE 20.—Distribution of *Astacoidea granulimanus* (open circle with dot) and *A. madagascarensis* (solid circle); both in localities marked by encircled star.

and postorbital carapace length, respectively, in mm, follow sex symbols): (1) Marais d'Ampamaherana, situé à 25 km de Fianarantsoa sur la ligne de chemin de fer Fianarantsoa-Manakara, Alain Crosnier, coll. 30 Jul 1973, ♂ 49.0, 43.5; ♂ 36.8, 32.7; ♂ 23.0, 20.4; ♀ with young 50.7, 45.0; ovigerous ♀ 55.7, 49.4; ♀ 38.2, 33.8; PM As330. (2) Tananarive market place, E. Gould, 25 Jan 1963, ovigerous ♀ 48.9, 43.4; USNM 145294. (3) Betsileo, no other data, ♂ 41.2, 37.2; ♂ 35.4, 31.6; ♂ 58.2, 52.1, ♂ 46.1, 41.3; BMNH 1880.27. (4) Ivohibe, Forêt Marovitsoika, FDHMA, 4 Nov 1970, ♂ 30.7, 27.7; PM As217. (5) Between Vondrozo and Fort-Carnot, ♂ 49.1, 43.6; ♂ 60.2, 53.8; ♀ 53.2, 48.0; PM As140. (6) Andringitra, Andrianony, Blanc, rec., ♂ 34.2, 30.9; ♂ 23.9, 21.4; PM As210. (7) Fort-Carnot, ♂ 34.3, 30.9; ♂ 37.5, 33.8; ♀ 32.5, 29.5; ♀ 19.3, 17.3; ♀ 17.0, 15.6; PM As190. (8) Massif de l'Ikongo, Province of Farafangana, 800 to 1000 m, Jan 1927, Mission R. Decary, ♂ 55.3, 49.8; ♂ 51.1; ♂ 63.5, 57.6; ♂ 61.5, 56.5; ♀ 64.9, 58.8; ♀ 60.0, 54.0; ♀ 58.0, 52.5; ♀ 54.1, 48.6; PM As215. (9) Région Vondrozo, Fort-Carnot, ♂ 53.5, 48.2; ♂ 41.9, 37.6; ♀ 50.0, 45.0; ♀ 6♂, 11♀, and 2 carapaces; PM As186. (10) Lakera (= Iakora?), ♂ 48.4, 43.0; ♂ 36.2, 31.8; ♂ 33.9, 30.0; ♂ 20.2, 17.8; PM As225. (11) Andringitra, ♂ 46.7, 42.1; PM As188. (12) Sakalava River, Fianarantsoa District, 1 Dec 1961, Y. Thérezien, coll., ♂ 44.9, 39.2; RNHL 17725. (13) Station Ampamaherana, Fianarantsoa District, 22 Jul 1970, M. Vincke, coll., ♂ 46.7, 42.2; ♂ 43.9, 39.1; ovig. ♀ 45.6, 40.6; RNHL 27275. (14) Forêt d'Ikongo, Vinanitelo, Sep 1898, G. Grandidier, coll., ♂ 68.5, 60.9; ♂ 34.8, 30.7; ♂ 34.4, 30.5; ♀ 25.9, 22.9; ♀ 21.9, 19.2; ♀ 20.3, 17.8; ♀ 20.1, 17.5; ♀ 17.5, 15.3; PM As214. In addition, I have examined three lots that are without data: (15) ♀ 30.9, 27.2; PM As216. (16) ♂ 64.5, 58.0; PM As137. (17) ♂ 66.7, 60.5; PM As230.

Inasmuch as three species are recognized herein among the collections reported previously for *A. granulimanus*, the following localities from which no specimens were available to me are perhaps in need of confirmation. (This is especially apropos for localities 20 and 21 where *A. petiti* was found.) (18) Massif d'Andringitra (Perrier de la Bathie, 1927:14). (19) Region of Fort-Carnot (Petit, 1927:103). (20) Region of Isaka (Petit, 1927:103). (21) Midongy to Fort-Carnot (Monod and Petit, 1929:34). (22) Farafangana (Monod and Petit, 1929:26). (23) Southeast Madagascar (Monod and Petit, 1929:34). (24) Between Vondrozo and Ifanadiana (Monod and Petit, 1929:25). (25) Andrambovato and Beromazava creeks near Ampamaherana, Fianarantsoa District (Pretzmann, 1961:161).

SIZE.—The largest specimen that I have examined is a female from the Massif d'Ikongo (Locality 8, above) having a carapace length of 64.9 mm, postorbital carapace length 58.8 mm. The largest male, which is from the same locality, has corresponding lengths of 63.5 and 57.6 mm. The smallest female carrying eggs or young has corresponding lengths of 45.6 and 40.6 mm.

REMARKS.—This crayfish is readily recognizable by the combination of a serrate lateral margin of the propodus (at least the fixed finger) of the chela and a smooth or punctate mesial surface on the dactyl.

It is regrettable that virtually nothing is known of the habitat/s it occupies, and all that is known of its life history is that females carrying oval eggs, with diameters of 2.9 × 3.6 mm occur in late January and late July, and with young in late July.

That this crayfish appeared to Perrier de la Bathie (1927:24) to be different from that which he considered the typical crayfish of Madagascar is made clear by his statement that "un variété spéciale de l'écrevisse malagache d'altitude." In the same year, a more concrete assessment concerning it was made by Petit's (1927:103) pointing out the existence of two groups of crayfishes on the island: one having large eyes, an inflated cephalothorax, and flattened chelae (his variety *betsileoensis* and the crayfish occurring in the rivers around Ankaratra and Vakinankaratra); the other, consisting of those with small eyes, a cylindrical cephalothorax, and massive chelae (the "ordinary variety"), which occurs east of Tananarive and Manjakandriana, and another that lives in the "massifs de l'Andringitra, de l'Ikongo, la région de Fort-Carnot et aussi la région d'Isaka." (The crayfish occurring in the latter region is described herein as *Astacoides petiti*.) This small-eyed crayfish was designated a distinct variety by Monod and Petit (1929), who listed several localities where it had been found. The only subsequent additions to our knowledge of it are two new localities cited by Pretzmann (1961) and two others by Holthuis (1964).

VERNACULAR NAME.—According to Alain Crosnier, natives in the vicinity of the Marais d'Ampamaherana know this crayfish as "orambato." He pointed out that "Cela devrait indiquer que cette espèce vit au milieu des pierres se trouvant dans les petits rapides, à fort courant, des rivières."

Astacoides madagascarensis (H. Milne Edwards and Audouin), new status

FIGURES 3f, 4, 5, 6d, 10a, 12, 13a, 14, 20, 21

Astacus madagascarensis H. Milne Edwards and Audouin, 9 May 1839a:152; 1839b:32.—Monod and Petit, 1929:5.—Holthuis, 1956:107, 108, 112, 116, 118; 1958:147, 156, 158; 1964:309, 310, 311, 317.—Hemming, 1958:141, 147, 151, 156.—Hobbs, 1974:18.

Astacus madagascariensis.—Guérin-Méneville, 1839b:390.—Brocchi, 1875:25.—Huxley, 1879a:752.—Keller, 1887:291; 1898:44.—Monod and Petit, 1929:5, 6.—Poisson, 1947:12.—Holthuis, 1956:108, 118; 1958:147, 158.—Hemming, 1958:143.—Adegboye, 1983:564, 565, 567.

Astacus Madagascariensis.—Audouin and H. Milne Edwards, 1841:35, 36, 39, pl. 3: figs. 1-5.—Gray, 1845:409-411.

Astacoides Madagascariensis.—Erichson, 1846:89, 90.

Astacoides madagascariensis.—Dana, 1852:521.—Brocchi, 1875:25.—Miers, 1876:412.—Huxley, 1879a:752, 759, 772, 773-775, figs. 2b, 7;

- 1879b:79, 92, 93, figs. 2b, 7; 1880a:308; 1880b:225, fig. 65; 1881:258; 1883:278, 327.—Stebbing, 1893:209.—Ortmann, 1902:293.—Calman, 1910:56; 1927:52.—Lenz, 1910:567, 575.—Gadow, 1913:92.—Gravel, 1922:3, 1 fig.—Petit, 1923:219; 1927:102, 103.—Harrison, 1928:116, 120.—Monod and Petit, 1929:5.—Louvel, 1930:18, 19.—Grandidier and Petit, 1932:236.—André, 1937:32, 33, 35.—Bouvier, 1940:60.—Decary, 1950:167.—Villalobos, 1953:348, 349; 1955:8, 9, pl. 1; 1983:10, 12, pl. 1.—Bott, 1972:178.—Brodsky, 1981:120.—Vila and Bahamonde, 1985:349.
- Astacoides madagascariensis*.—Huxley, 1880a, fig. 65; 1881, fig. 65; 1883, fig. 65.—Bate, 1888:201, 207, 208.—Petit, 1927:102.—Riek, 1972, figs. 14, 33A,B.
- Astacoides madagascariensis*.—Huxley, 1879b:92, 93.—Decary, 1946:201 [in part].
- Astacoides madagascariensis*.—Huxley, 1880b, fig. 65.
- Astacoides Madagascariensis*.—Moleyre, 1885:680.
- Astacopsis Madagascariensis*.—André, 1937:32 [lapsus calami].
- Astacoides madagascariensis* var. *madagascariensis*.—Petit, 1927:103 [by implication].—Monod and Petit, 1929:10, 12–14, 18, 26, 28, 29, figs. 1C,I,J, 4G,O,P, 5F, 6A–C, 8E,F, 10; pl. 11: fig. 1.—Louvel, 1930, photograph on unnumbered page.
- Astacoides madagascariensis madagascariensis*.—Monod and Petit, 1929:33.—Pretzmann, 1961:161.
- Astacoides madagascariensis* var. *brevirostris* Monod and Petit, 1929:10, 12, 18, 19, 22, 26, 28, 33, figs. 1A,F,H, 3D, 4D,M,N, 5A,C–E,H, 6D, 8A,B, 10, pl. 3.
- Astacoides madagascariensis brevirostris*.—Monod and Petit, 1929:33.—Pretzmann, 1961:162.—Holthuis, 1964:309, 311, 312, 317.
- Astacoides madagascariensis*.—Poisson, 1947:12.
- Astacoides madagascariensis brevirostris*.—Poisson, 1947:13.
- Astacoides madagascariensis* var. *brevirostris*.—Poisson, 1947:63, pl. 3: fig. 4.
- Astacoides madagascariensis (brevirostris type)*.—Decary, 1950:167.
- Astacoides madagascariensis madagascariensis*.—Holthuis, 1964:309–313, 316, 317, pl. 1X: figs. a, b.

DIAGNOSIS.—Rostrum short, comprising 8.5 ± 0.8 percent of carapace length. Areola 3.8 ± 0.4 times as long as wide, constituting 37.7 ± 1.3 percent of carapace length and 41.3 ± 1.5 percent of postorbital length. Branchiostegites comparatively weakly tuberculate, never bearing strong tubercles or spines. Width of first abdominal segment in males equivalent to 39.7 ± 1.3 percent of carapace length, that of second 54.6 ± 1.3 percent. All abdominal pleura lacking spines, that of third through sixth tapering and rounded ventrally. Dorsal surface of telson and uropods usually with spiniform tubercles. Antennal scale with tubercles laterally. Merus of third maxilliped with or without 1 or 2 spines or tubercles mesially and laterally. Carpus of cheliped without low, polished tubercles dorsally, with single massive prominence (usually bearing rudiments of fused tubercles) mesially; width of palm of chela 47.6 ± 2.0 percent of length of propodus; lateral and mesial margins of propodus lacking cristiform row of tubercles; mesial and dorsal surfaces of dactyl without tubercles. Keel of sternite XIII with bullar lobes. Median keel of sternite XII inflated but narrow, that of sternite XIII very broad and usually elevated. Vertical processes of paired sternopleural bridges of sternite XIV widely separated, clearly exposing bullar lobes.

DESCRIPTION.—Rostrum (Figure 21a,b), 5.8 to 11.0 percent of carapace length, strongly deflected, chamfered,

quadrangular, with lateral carinae weakly divergent anteriorly and bearing 2 or 3 very weak (scarcely recognizable) tubercles on each side; anterior margin weakly scalloped but often lacking well-defined tubercles. Postorbital ridge weak or obsolete except for inconspicuous knob representing anterior extremity. Suborbital angle rounded and bearing 1 prominent postmarginal tubercle and 1 or 2 very small marginal ones, latter frequently absent. Branchiostegal spine absent. Antennal region of carapace with few, small, postmarginal tubercles, none spiniform, and submarginal row of small tubercles continuing onto mandibular region; ventral mandibular area with row of 5 to 8 tubercles along crest of mandibular arc; hepatic region with hemispherical arrangement of small tubercles, none spiniform. Anteroventral branchiostegal region with number of very small tubercles, some flanking cervical groove; branchiostegal region with comparatively small tubercles laterally, those in area occupied by cervical spines slightly larger than others but none spiniform. Areola 3.1 to 4.9 times longer than broad and constituting 34.4 to 40.8 percent of carapace length (38.2 to 46.8 percent of postorbital carapace length).

Basal podomere of antennular peduncle with or without small spine on mesial ventrodial angle. Antennal peduncle (Figure 21e) with ventrodial margin of coxa subtruncate, distomesial and distolateral angles sometimes weakly produced but otherwise without spines or tubercles, basis bearing small subacute tubercle on ventro- and laterodistal surfaces. Antennal scale (Figure 21f) with 2 or 3 lateral tubercles proximal to apical one, and 1 or 2 tubercles on ventral keel. Antennal flagellum reaching as far as sixth abdominal tergum.

Epistome (Figure 21e) with posterolateral areas rugose and bearing cluster of mostly small tubercles, 2 or 3 spiniform; anteromedian depression with distinct fovea; anteromedian lobe sagittiform, its lateral margins weakly tuberculate, apex reaching well beyond tip of ventral spine on basis of antennal peduncle.

Keel of sternite XIII (Figure 6d) with bullar lobes. Median keel of sternite XII inflated but comparatively slender, that of XIII conspicuously inflated and broad. Lateral processes of sternite XI through XIII strongly splayed. Vertical arms of paired sternopleural bridges of sternite XIV (Figure 10a) widely separated, not obscuring most of intervening bullar lobes, which distinctly delimited from lateral processes.

Mandible (Figure 3f) with proximodistal cusp of posterior molar process long, distinct gap separating it from cephalodistal cusp; nodular cluster with as many as 13 nodules lying between proximocephalic and other two cusps.

Ischium of third maxilliped (Figures 4, 21d) produced in strong, subacute distolateral process; merus with or without spine on distoventral margin, few tubercles sometimes present proximal to spine; both absent on dorsolateral distal margin.

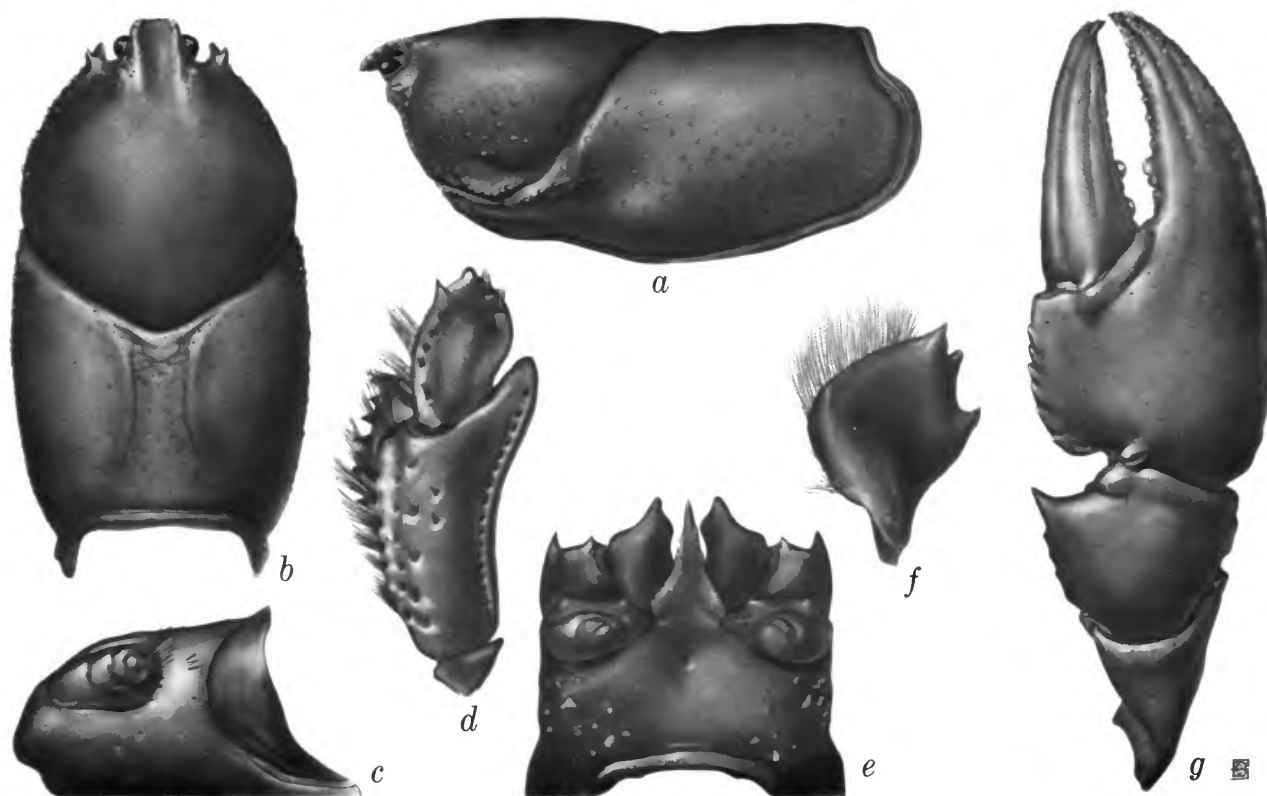


FIGURE 21.—*Astacoides madagascarensis* (all from Manjakandriana, Mantasoa): *a*, lateral view of carapace; *b*, dorsal view of carapace; *c*, phallic papilla on coxa of fifth pereiopod; *d*, distal part of basis, ischium, and merus of left third maxilliped; *e*, epistome and basal podomeres of antennae; *f*, dorsal view of right antennal scale; *g*, dorsal view of distal podomeres of right cheliped.

Cheliped (Figure 21g) with ischium bearing 3 or 4 short spines on mesial surface. Ventral surface of merus with mesial row of 4 to 7 mostly spiniform tubercles and lateral one of 4 to 8, dorsal surface of podomere irregular but not bearing distinct tubercles or spines; dorsodistal extremity punctate but not crenulate. Carpus with mesial row of 5 tubercles: distalmost conspicuous but others markedly smaller, and decreasing in size proximally, and in larger individuals becoming more adnate and hardly discernible; ventral surface with no large tubercle or spines but 2 or 3 small ones situated near middle of podomere and 1 on distomedian margin. Propodus with width of palm 43.0 to 51.1 percent of length of podomere, very weakly scalloped, costate lateral margin marked by row of some 18 to 28 punctations; scallops very short and subserrate distally; mesial margin of palm with row of 7 or 8 low tubercles, dorsal and ventral surfaces sparsely punctate. Opposable margin of fixed finger with row of 15 or 16 sclerotized tubercles (fourth from base largest) extending along almost entire length of finger, and single row of minute denticles (interrupted by tubercles) present between fifth tubercle from base and corneous tip of finger; in addition, row of 10 or

11 small corneous tubercles situated dorsal to primary row and extending distally from about sixth tubercle from base; dorsal surface of finger with low, submedian, longitudinal ridge flanked by setiferous punctations, ridge on ventral surface of finger not so well defined. Opposable margin of dactyl with row of 10 sclerotized tubercles (second and fourth from base larger than others) extending along proximal three-fourths; clusters of minute denticles present between most tubercles and forming band along distal fourth of finger, and row of 4 small tubercles flanking dorsal side of band of denticles; dorsal and ventral surfaces of dactyl with low median longitudinal ridges and mesial surface with row of punctations. Fewer tubercles on opposable margins of both fingers in smaller males.

Width of first abdominal segment in males 37.7 to 44.1 percent of carapace length, that of second 52.5 to 58.0 percent. Pleuron of second abdominal segment (Figure 13a) with or without submarginal row of 3 or 4 low tubercles, none spiniform. That of third with 0 to 3 small submarginal tubercles. Pleura of third through sixth segments tapering and rounded ventrally.

Telson subequal in length and width, divisible into ce-

phalic and caudal sections by shallow lateral incisions and attendant sutures, but lacking marginal spines; dorsal surface with few tubercles in caudal half, 4 to 6 spiniform. Proximal podomere of uropod lacking spines and tubercles; dorsal surface of mesial ramus with row of 4 to 8 acute tubercles on median carina, few scattered ones in lateral half, and 1 small tubercle on lateral margin; lateral ramus lacking spines on median carina but lateral half of dorsal surface with many small ones, series of 4 or 5 small spines on lateral margin proximal to diarsis, latter flanked proximodorsally by row of 9 to 13 small spines.

TYPE-LOCALITY.—"Madagascar." In view of the range of this crayfish, the types probably were collected in the vicinity of Tananarive.

TYPES.—Two of the specimens on which H. Milne Edwards and Audouin based their description of *Astacus madagascarensis* are extant. The male in the Muséum National d'Histoire Naturelle, Paris, (As193) was designated the lectotype by Holthuis (1964:311); the paralectotype in the Rijksmuseum van Natuurlijke Historie, Leiden, (5592), is also a male.

RANGE AND SPECIMENS EXAMINED.—The range of *Astacoides madagascarensis* extends a little farther north than that of any of the other Madagascan crayfishes, and lies at latitudes of 18° to 21°S, longitudes 47° to 49°E (Figure 20).

The specimens examined are as follows (carapace length and postorbital carapace length in mm, respectively, follow sex symbols): (1) "Madagascar," Lectotype ♂ 87.1, 79.3; PM As193. Paralectotype ♂ 80.0, 74.3; RNHL 5592. (2) Marché de Tananarive ♂ (hermaphrodite?) 58.3, 54.1; PM As221. ♀ 38.2, 34.6; ♀ 36.5, 33.5; USNM 145293, 25 Jan 1963, purchased by E. Gould. (3) Région de Tananarive, ♂ 60.0, 55.3; PM As198. (4) Imerina, Exp. Marseille 1907, ♂ 49.7, 46.8; PM As200. (5) Marché de Tananarive: Fenoarivo près de Tananarive, ovig. ♀ 45.2, 41.4; PM As202. ♂ 60.0, 55.5; PM As203. (6) Madagascar Centre, Manjakandriana, Mantasoa, Cammas, rec., ♂ 49.8, 46.0; ♂ 42.6, 39.3; ♀ 57.8, 53.2; ♂ 54.1, 49.5; PM As334. ♂ 42.6, 39.3; ♀ 42.1, 38.6; USNM 218801. (7) "Near" or "from" Lake Alaotra (Ambatolaona), C.S. Webb, coll., ♂ 45.1, 40.1; ♂ 36.4, 33.4; ♂ 41.6, 38.0; BMNH 1936.2.5.2-3. (8) Mantasoa, lake complex about 60 km east of Tananarive, 1974, Cammas, rec., ♂ 62.5, 59.6; ♂ 54.0, 49.6; ♂ 40.2, 36.7; ♂ 40.0, 36.4; ♂ 39.2, 36.0; ♂ 34.6, 31.6; ♀ 58.9, 54.2; ♀ 47.6, 44.0; ♀ 42.9, 39.7; ♀ 36.0, 32.9; PM As335. ♂ 60.1, 54.9; ♂ 37.6, 34.3; ♀ 44.4, 40.6; ♀ 37.7, 34.3; USNM 218802. (9) Forester's house at Ambatolaona, Manjakandriana District, Tananarive Province, 16 Oct 1961, Y. Thérézien, coll., ♂ 36.4, 32.9; RNHL 17726. (10) Andasibe near Mandraka, east of Tananarive, 3 Jun 1970, M. Vincke, ♂ 50.0, 45.1; RNHL 27270.

The following lots bore no locality data: (11) ♂ 76.3, 70.0; ♂ 75.4, 68.9; PM As196. (12) ♂ 77.4, 70.3; ♂ 77.3, 69.6; PM As197. (13) M. d'Anthouard, coll., ♂ 65.0, 59.4; ♂ 58.6,

♂ 58.3, 53.0; PM As199. (13) 1900, M. Grandidier, coll., ♂ 72.3, 66.2; ♂ 65.5, 59.6; ♀ 82.9, 76.4; PM As206. (14) ♂ 47.5, 43.7; ♂ 43.7, 40.0; BMNH 1888:5.

The following localities from which I have examined no specimens were reported as indicated. (15) Est de Tananarive (Petit, 1927:103). (16) Mandraka (Monod and Petit, 1929:33). (17) Maroangoatra, Antsihambavy, Andranomahera, and Antanjona brooks in the Manjakandriana District (Monod and Petit, 1929:33). (18) Ankazondrano, Ampatoka, and Andomba creeks in the Andramasina District (Monod and Petit, 1929:33). (19) Tamatave (Lenz, 1910:567); almost certainly purchased at market. (20) Région d'Anjozorobe (Grandidier and Petit, 1932:236).

SIZE.—The largest specimen examined was a male, lacking data, in the Muséum National d'histoire Naturelle, Paris, having a carapace length of 87.1 mm (postorbital carapace length 79.3 mm). The largest female, also lacking data, has corresponding lengths of 82.9 and 76.4 mm. Those of the single ovigerous female, which was purchased in a Tananarive market, are 45.3 and 41.4 mm.

REMARKS.—Whereas the presence of apertures to gonopods on the coxae of the third and fifth pereopods is typical of all members of certain species (e.g., members of the South American genus *Parastacus*) of the family Parastacidae, such apparent hermaphrodites (to my knowledge, whether these crayfishes are functional hermaphrodites, protandrous, or protogonous ones is not known) seem to be of rare occurrence in members of the genus *Astacoides*. One such specimen of *A. madagascarensis* was purchased in a market in Tananarive.

The diameters of the oval eggs borne by the single ovigerous female are 3.0 and 4.0–4.6 mm.

Astacoides caldwelli (Bate), new status

FIGURES 3d, 4, 7a, 10d, 11a, b, 12, 13b, 14, 15, 22

Astacoides Goudotii Guérin-Méneville, 29 April–13 May, 1839a:109 [Type: 1♂, Academy of Natural Sciences of Philadelphia. Type-locality: Madagascar.]; 1839b:390, pl. 686: figs. 4, 4a.—Dana, 1852:521.—Brocchi, 1875:24.—Miers, 1876:412.—Petit, 1927:102.—Monod and Petit, 1929:5, 6.—Holthuis, 1964:313.—Hobbs, 1974:18.

Astacus caldwelli Bate, 1865:469, 470, pl. 27.—Holthuis, 1964:315.

Astacoides madagascariensis.—Faxon, 1898:668; 1914:404.

Écrevisse malgache Bertrand, 1900:348.

Astacoides madagascariensis var. Petit, 1927:103.

Astacoides madagascariensis var. *madagascariensis*.—Monod and Petit, 1929:10, 12, 33, figs. 1c, 1j, 4g, o, p, 5f, 6a–c, 8e, f, 10; pl. 2: fig. 1.—Decary, 1950:167.—Pretzmann, 1961:161.

Astacoides Caldwelli.—Monod and Petit, 1929:7, 14.

Astacoides madagascariensis.—Decary, 1946:201 [in part].

Astacoides Goudotii.—Poisson, 1947:12.

Astacoides Caldwelli.—Poisson, 1947:13.

Astacoides madagascariensis madagascariensis.—Poisson, 1947:13, 62, pl. 1. *Astacoides madagascariensis* var. *madagascariensis*.—Poisson, 1947:63, pl. 3: fig. 2.

Astacoides madagascariensis (*madagascariensis* type).—Decary, 1950:167.

Astacoides goudotii.—Holthuis, 1956:107, 108, 112, 115, 116, 118; 1958:147, 151, 156, 158.—Hemming, 1958:135, 143, 146, 147, 151,

156, 158, 167.—Holthuis, 1964:313–315, 317, fig. 1c,d, pl. 10: figs. a–c.
Astacoides madagascariensis caldwelli.—Holthuis, 1964:310, 312, 313–317, fig. 1c, d, pl. 10.

DIAGNOSIS.—Rostrum moderately long, constituting 10.5 ± 1.5 percent of carapace length. Areola 3.6 ± 0.4 times as long as wide, constituting 38.5 ± 1.2 percent of carapace length and 43.0 ± 1.5 percent of postorbital carapace length. Branchiostegites weakly to moderately strongly tuberculate, never spiniform. Width of first abdominal segment in males equivalent to 42.9 ± 2.0 percent of carapace length, that of second 55.1 ± 3.5 . All abdominal pleura lacking spines, that of third through sixth tapering and rounded ventrally. Dorsal surface of telson and uropods almost always with spiniform tubercles. Antennal scale with low tubercles laterally. Merus of third maxilliped usually with single spine mesially, sometimes with 2 or 3 both distomesially and distolaterally. Carpus of cheliped without low, polished tubercles dorsally, with row of 3 or 4 tubercles mesially; width of palm 44.2 ± 3.3 percent of length of propodus; lateral and mesial margins of propodus lacking cristiform row of tubercles but sometimes with subserrate row of small ones on distal half or fourth of former; mesial

and dorsal surfaces of dactyl without tubercles except apically. Keel of sternite XIII lacking bullar lobes. Median keel of sternites XII inflated but narrow, that of sternite XIII very broad and depressed. Vertical arms of paired sternopleural bridges of sternite XIV broadly separated, clearly exposing bullar lobes.

DESCRIPTION.—Rostrum (Figure 22*a,b*), 7.5 to 12.0 percent of carapace length, with slightly divergent lateral carinae, each bearing row of 4 or 5 submarginal corneous-tipped tubercles; anteromedian prominence short, with or without 1 or 2 weak corneous tubercles; dorsal surface deeply excavate. Postorbital ridge weak, and terminating anteriorly in small tubercle. Suborbital angle truncate and bearing strong, subacute, postmarginal tubercle. Branchiostegal spine absent. Antennal, mandibular, and hepatic regions with conspicuous, anteriorly directed, acute to subacute tubercles, those on lower mandibular region flanking cervical groove forming distinct mandibular arc with row of tubercles on crest; submarginal row of well-developed tubercles extending from ventral base of suborbital angle to anterior extremity of cervical groove. Anteroventral branchiostegal region with crowded small tubercles; lateral surface of branchiostegites with many small to moderately

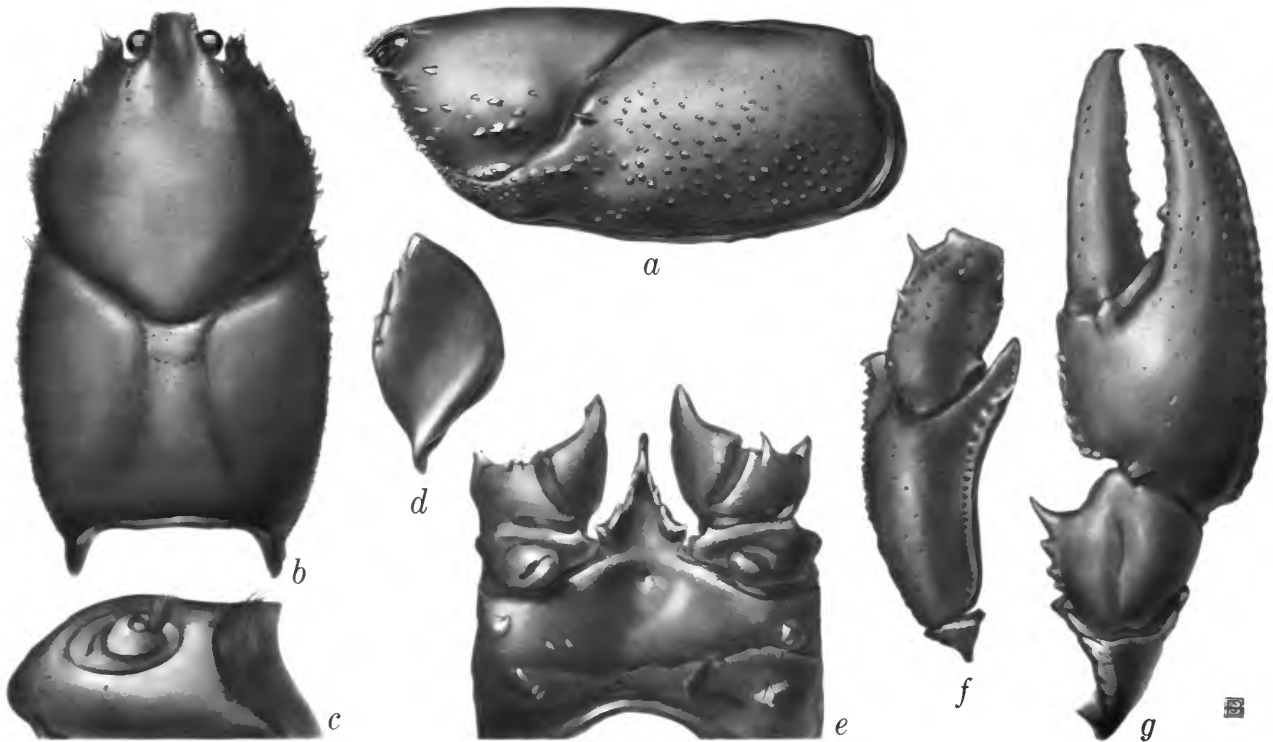


FIGURE 22.—*Astacoides caldwelli* (all from lectotype): *a*, lateral view of carapace; *b*, dorsal view of carapace; *c*, phallic papilla on coxa of fifth pereiopod; *d*, dorsal view of left antennal scale; *e*, epistome and basal podomeres of antennae; *f*, distal part of basis, ischium, and merus of left third maxilliped; *g*, dorsal view of distal podomeres of right cheliped.

large tubercles laterally, most below level of well-developed, single, cervical spine. Areola 2.6 to 4.4 times as long as broad and constituting 35.8 to 41.2 percent of carapace length (39.1 to 46.1 percent of postorbital carapace length).

Basal podomere of antennular peduncle with or without spine on distal mesioventral margin. Antennal peduncle (Figure 22e) with obtuse to subacute distomesial (and sometimes distolateral) tubercles on coxa, and strong distoventral and dorsolateral spines on basis. Antennal scale (Figure 22d) with mesial margin gently rounded, lateral surface with 1 or 2 rows of 2 to 4 rounded tubercles (sometimes only 1 row and additional tubercle out of line), and distolateral tip with single one; ventral keel with 0 to 2 weak tubercles. Antennal flagellum reaching sixth abdominal tergum.

Epistome (Figure 22e) with 1 to 3, usually 2, spiniform tubercles in each posterolateral area; deep anteromedian depression present, and conspicuous, laterally subserrate, sagittiform anteromedian lobe extending as far anteriorly as ventrodorsal spine on basis of antennal peduncle.

Sternal keel of segment XIII (Figure 7a) lacking bullar lobes. Median keel of sternite XII slightly inflated; that of sternite XIII distinctly inflated, frequently with slight constriction between anterior and middle segment. Lateral processes of sternites XI through XIII strongly splayed. Vertical arms of paired sternopleural bridges of sternite XIV (Figure 10d) widely separated, not obscuring most of bullar lobes which distinctly delimited from lateral processes.

Mandible (Figure 3d) with proximocephalic cusp decidedly largest of three elements of caudal molar process; proximodistal cusp long and ridge-like with distal edge corneous; only 2 or 3 small nodular elements present.

Ischium of third maxilliped (Figures 4, 22f) produced distolaterally in subacute prominence. Merus usually with single spine on mesiodistal margin but type with 2 spines on that margin and 2 small tubercles proximolateral to them; in addition, submarginal lateral row of small tubercles and row of 3 weak ones on distodorsal margin also present; most of lateral surface with prominent punctations.

Cheliped (Figure 22g) with ischium bearing no more than 1 prominent spine distomesially and 2 small tubercles proximal to it; merus with ventromesial row of 5 to 7 spines (becoming increasingly spike-like distally) and ventrolateral row of 3 or 4, dorsal surface devoid of spines and bearing only 2 small, subsquamous tubercles; dorsodistal margin rather smooth, never crenulate. Carpus with mesial row of 4 tubercles, distalmost forming large spine, others frequently almost rudimentary; 2 prominent, often spiniform tubercles and sometimes 1 or 2 small ones present ventrally, and lateral surface sparsely punctate and bearing 0 to 2 very small tubercles. Propodus with width 40.7 to 59.3 percent of length, bearing well-defined lateral costa flanked by prominent row of punctations, and studded with row of

small corneous tubercles, row becoming subserrate along distal half to fourth of finger; mesial surface of palm with row of 6 to 8 (usually 7) tubercles. Opposable margin of fixed finger with row of 8 to 10 tubercles, third from base largest, linear series of minute denticles interspersed between tubercles, distal segments of series broadening to 2 or 3 denticles; dorsal surface of finger with low submedian ridge flanked by rows of punctations. Dactyl with row of punctations mesially; opposable margin with row of 9 or 10 tubercles and 2 or 3 small ones situated dorsal to row along distal fourth of finger; linear band of denticles interspersed between members of longer row of tubercles, and distal segments of band conspicuously broader than those on fixed finger.

Width of first abdominal segment 37.5 to 46.4 percent of carapace length, that of second 46.8 to 65.1 percent. Pleuron of second abdominal segment (Figure 13b) with row of tubercles subparallel to anteroventral and ventral margins; that of third sometimes with 1 or 2 near ventral margin.

Telson subequal in length and width and studded with small acute tubercles. Anterolateral margin of shallow sutures marking cephalic and caudal sections provided with fixed spine, sections not otherwise recognizable. Proximal podomere of uropod lacking spines and tubercles; dorsal surface of mesial ramus with 0 to 6 spines on median carina, and 0 to 4 others on lateral half; lateral spine usually well developed but occasionally rudimentary; lateral ramus lacking spines on carina, but as many as 5 or 6, often well-developed ones, present dorsolaterally, distolateral margin of proximal section of lateral ramus of uropod with row of 3 spiniform tubercles; 10 to 13 spines on proximal margin of diarsis.

TYPE-LOCALITY.—“Madagascar.” In view of our far from perfect knowledge of the range of this crayfish and the nature of its relation to *A. betsileoensis*, it seems inadvisable to consider suggesting a limitation to the now vague type-locality.

TYPE.—Lectotype of *Astacoides Goudotii* Guérin, senior synonym of *Astacus caldwelli* Bate, ♂ (dry and dismembered), Academy of Natural Sciences of Philadelphia, No. 290. (See “Resumé of Previous Knowledge,” herein.)

RANGE AND SPECIMENS EXAMINED.—The range of *Astacoides caldwelli* is apparently largely confined to tributaries of western watersheds on the island lying at latitudes of 18° to 21°S, longitudes 46° to 48°E (Figure 15).

The specimens examined are as follows (carapace length and postorbital carapace length, respectively, in mm, follow sex symbols): (1) “Madagascar,” lectotype ♂ 58.4, 52.8; ANSP 290. (2) Antsampandrano (Ambatolampy), alt. 1900 m, 3 Feb 1942, R. Decary, ♂ 40.9, 36.3; PM As204. (3) Imerina, Exp. Marseille, 1907, ♀ 57.1, 52.2; ♀ 46.9, 43.2; ♀ 21.5, 19.3; PM As194. ♀ 61.4, 56.4; PM As136. (4) Ankaratra, ♂ 55.9, 50.2; ♀ 45.9, 41.4; PM As141. ♂ 61.4, 54.9; ♂

46.7, 41.4; ♂ 40.0, 35.8; ♂ 39.5, 35.1; ♂ 35.2, 31.0; ♂ 32.3, 28.5; ♀ 61.4, 55.1; ♀ 54.3, 48.6; ♀ 40.6, 35.8; ♀ 36.6, 32.6; PM As185. ♂ 48.2, 42.5; PM As207. (5) Marche de Tananarive, ♂ 55.8, 49.5, PM As220. (6) Behenjy (?), 2 Mar 1897, Dorr 64–97, ♂ 40.6, 35.8; PM As205. (7) Vakinankaratra, Exp. Marseille, 1907, ♀ 46.5, 40.9; ♀ 46.1, 40.5; PM As219. (8) Antsirabe, Petit, coll.?, ♂ 79.1, 70.5; PM As222. (9) Mantasoa, lake complex situated about 60 km E of Tananarive, 1974, Cammas and Alain Crosnier, rec., ♂ 58.2, 53.1; ♂ 44.1, 40.6; ♀ 41.6, 38.2; ♀ 46.8, 43.1; PM As167. (10) Rivière Antezina, Face est du Massif de l'Ankaratra, alt. 1800 m, 12 Dec 1973, Alain Crosnier, coll., ♂ 61.5, 54.9; ♂ 54.5, 48.4; ♂ 50.4, 45.2; ♂ 44.5, 40.0; ♂ 36.2, 31.9; ♀ 55.1, 48.8; ♀ 51.5, 46.2; ♀ 42.7, 37.6; PM As331. ♂ 58.4, 52.3; ♂ 50.8, 45.3; ♀ 44.6, 39.7; USNM 218800. (11) Anbatolampy about 70 km south of Tananarive, 8 May 1970, 6 Jun 1970, M. Vincke, ♂ 60.8, 58.1; ♂ 50.6, 45.4; ♂ 45.4, 40.3; ♀ 54.8, 49.1; ♀ 43.3, 38.2; RNHL 27272 and 27273. (12) Andasibe near Mandraka, east of Tananarive, 3 Jun 1970, ♂ 47.8, 41.9; RNHL 27274. (13) Antsampandrano, Antsirabe District, 17 Apr 1966, M. Vincke, ♀ 36.4, 31.9; RNHL 26486.

The following localities from which I have examined no specimens were reported as indicated: (14) "torrents et ruisseaux du massif de l'Ankaratra" (Bertrand, 1900:349). (15) Manjakatomo (Monod and Petit, 1929:14). (16) Sambaina, Vakinankaratra Province (Monod and Petit, 1929:14). (17) Vakinankaratra (Monod and Petit, 1929:14). (18) Ambositra Province (Monod and Petit 1929:33). (19) Soahindrahiny (Antsirabe) (Monod and Petit, 1929:33).

SIZE.—The largest specimen available is a male from Antsirabe having a carapace length of 79.1 mm, postorbital carapace length, 70.5 mm. The corresponding lengths of the largest female, from Ankaratra, are 61.4 and 55.1 mm.

REMARKS.—Few remains of a color pattern exist in any crayfishes examined during the course of this study, but that of *A. caldwelli* from Rivière Antezina on the eastern slope of the Massif de l'Ankaratra is rather striking and, to some degree, persistent. The basic color of specimens preserved in alcohol is greenish tan. The surface of the rostrum is dark; the carapace over the origins of the mandibular adductor muscles is marked by an almost black reticulate pattern as are the branchiocardiac grooves. Each of the second through fifth abdominal terga exhibits a narrow, median longitudinal, almost black stripe that falls short of the caudal margins of the terga and a pair of oblique sublinear stripes laterally above the pleura. These diverging dark lines broaden and bleed posteriorly in reddish gray splotches. The sixth tergum bears a more ornate pattern resembling the outline of a stretched pelt of a small mammal, in which the "arms" are extended anterolaterally to the anterior base of the pleura; the "tail" does not quite reach the caudal margin of the tergum. The anterior part of each tergum is suffused with red, rendering it an orange

tan. The dorsal and lateral surfaces of the merus and carpus of the cheliped also bear reticulate blotches of black as does the dorsal surface of the palm of the chela. The fingers are increasingly suffused with red distally, and the tips are scarlet to crimson.

Astacoides betsileoensis Petit, new status

FIGURES 3g, 4, 7b, 10g, 12, 13d, 14, 17, 23

Astacoides madagascariensis var. *betsileoensis* Petit, 1923:219, 220 [Types: not known to be extant. Type-locality: vicinity of Fianarantsoa, Madagascar.]; 1927:103.—Monod and Petit, 1929:7, 10, 12, 14, 16, 18, 26, 28, 33, 34, figs. 1B,D,G, 3C, 4A,B,E,I,K,L, 5B,C, 6F, 7A–C, 10; pl. 2: fig. 2.—Louvel, 1930:18.

Astacoides madagascariensis.—Decary, 1946:201 [in part].

Astacoides madagascariensis betsileoensis.—Poisson, 1947:12, 13.

Astacoides madagascariensis var. *Betsileoensis*.—Poisson, 1947:63, pl. 3: fig. 3.

Astacoides madagascariensis, betsileoensis type.—Decary, 1950:167.

Astacoides madagascariensis betsileoensis.—Pretzmann, 1961:161, 162.

Astacoides madagascariensis betsileoensis.—Holthuis, 1964:309, 315–317.—Hobbs, 1974:19, fig. 14a–e.

DIAGNOSIS.—Rostrum long, comprising 13.8 ± 2.0 percent of carapace length. Areola 3.0 ± 0.4 times as long as wide and constituting 35.7 ± 1.1 percent of carapace length, 41.5 ± 1.4 percent of postorbital carapace length. Branchiostegites bearing conspicuous array of procurved spines. Width of first abdominal segment in males equivalent to 44.2 ± 1.4 percent of carapace length, that of second 56.9 ± 3.0 . Pleuron of second abdominal segment with row of as many as 6 spiniform tubercles, that of third often with few; pleura of third through sixth segments tapering and rounded ventrally. Dorsal surface of telson and lateral sectors of both rami of uropods with spines or spiniform tubercles. Antennal scale with prominent spine laterally. Merus of third maxilliped with 1 to 3 spines on distal mesioventral margin, occasionally 1 or 2 on dorsolateral border. Carpus of cheliped without low, polished tubercles dorsally, with row of spiniform tubercles and spines mesially; width of palm 40.6 ± 3.4 percent of length of propodus; lateral and mesial margins of propodus lacking cristiform row of tubercles although distal part of latter sometimes suberrate; mesial and dorsal surfaces of dactyl lacking tubercles except apically. Keel of sternite XIII lacking bullar lobes. Median keel of sternite XII and XIII inflated and broad. Vertical arm of paired sternopleural bridges of sternite XIV broadly separated, clearly exposing bullar lobes.

DESCRIPTION.—Rostrum (Figure 23a,b) 9 to 16.8 percent of carapace length, spoon-shaped with distinctly divergent lateral carinae bearing 3 or 4 corneous tubercles on each side and 1 to 3 smaller ones on convex anterior margin; dorsal surface deeply excavate. Postorbital ridge hardly recognizable except for anterior extremity which produced in small tubercle. Suborbital angle rounded but bearing 1 or 2 short marginal spines and 1 often compound or 2 very prominent, procurved, postmarginal spines, if compound

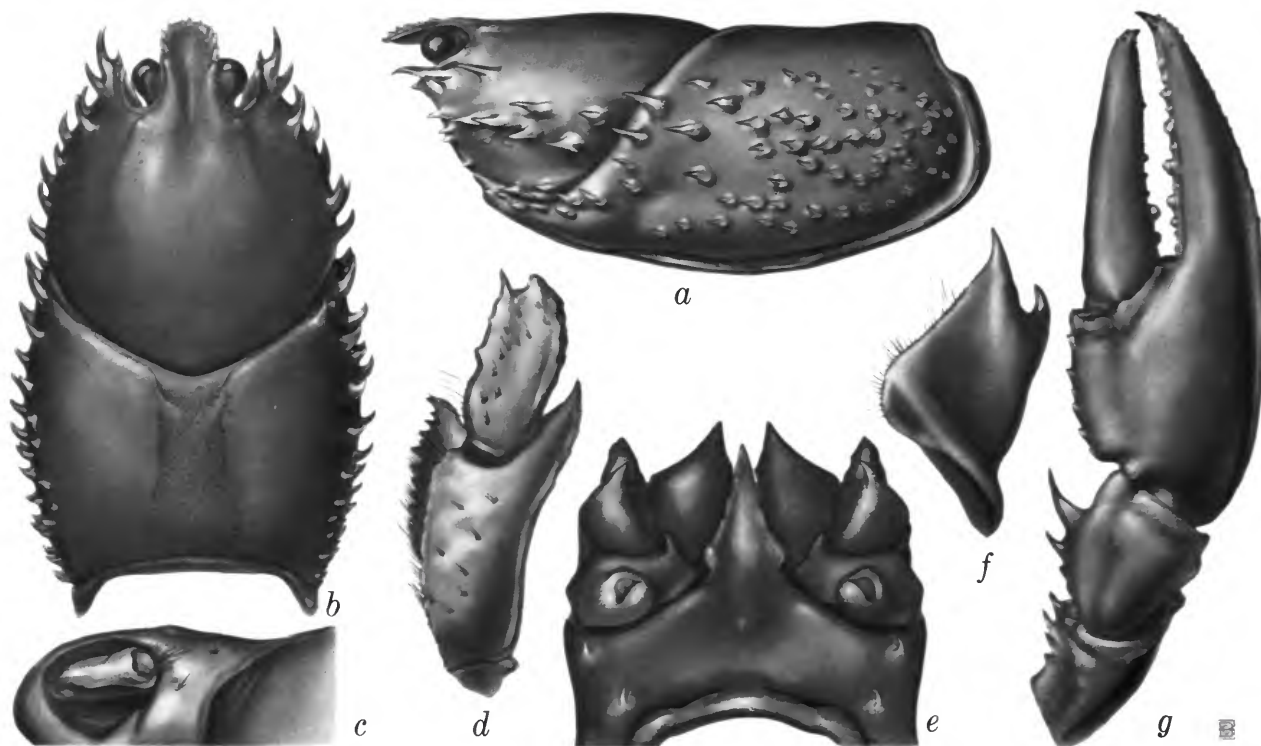


FIGURE 23.—*Astacoides betsileoensis* (all from Marais d'Ampamaherana, 25 km from Fianarantsoa on rail line to Manakara): *a*, lateral view of carapace; *b*, dorsal view of carapace; *c*, phallic papilla on coxa of fifth pereiopod; *d*, distal part of basis, ischium, and merus of left third maxilliped; *e*, epistome and basal podomeres of antennae; *f*, dorsal view of right antennal scale; *g*, dorsal view of distal podomeres of right cheliped.

or 2, more anterior one conspicuously large. Branchiostegal spine absent. Antennal region of carapace with 3 to 5 spines; mandibular region with 2 or 3 small, acute submarginal tubercles and row of 3 or 4 spines on weak mandibular arc on dorsal flank of cervical groove; hepatic region with longitudinal band of 6 to 12 prominent spines. Anteroventral branchiostegal region bearing 4 to 7 spines or acute tubercles; branchiostegites with number of procurved spines laterally, 1 to 5 corresponding to cervical spines in other crayfishes bearing 1 or more spines along caudolateral margin of cervical groove. Areola 1.8 to 3.8 times as long as broad and constituting 33.1 to 38.6 percent of carapace length (38.6 to 44.1 percent of postorbital carapace length).

Basal podomere of antennular peduncle with small spine on mesiodistal margin. Antennular peduncle (Figure 23*e*) with strong distomesial spine and low distolateral tubercle (both sometimes reduced) on coxa; basis bearing strong spine on ventro- and laterodistal surfaces. Antennal scale (Figure 23*f*) with sharp distolateral spine (sometimes small additional spine between it and apical spine), and usually 1 or 2 on ventral keel. Antennal flagellum overreaching telson when bent caudally.

Epistome (Figure 23*e*) with 2 to 8 (2 usually prominent) spines in each posterolateral angle; moderately deep antero-medial depression situated at base of sagittiform antero-medial lobe bearing weakly scalloped anterolateral margins; apex of lobe reaching slightly beyond tip of ventral spine on basis of antennal peduncle.

Sternal keel of segment XIII (Figure 7*b*) lacking bullar lobes. Median keel of sternite XII distinctly inflated, that of XIII even more so, both broad. Lateral processes of sternites XI through XIII strongly splayed. Vertical arms of paired sternopleural bridges of sternite XIV (Figure 10*g*) widely separated, not obscuring most of intervening bullar lobes, which distinctly delimited from lateral processes.

Mandible (Figure 3*g*) with proximocephalic cusp of posterior molar process long and often contiguous with disto-proximal cusp; nodular cluster consisting of as many as 10 nodules of variable sizes filling most of gap between cusps of process.

Ischium of third maxilliped (Figures 4, 23*d*) produced in strong distolateral spine. Merus with prominent distoventral spine and 1 or 2 proximal to it on ventromesial border; dorsolateral margin usually lacking spines, sometimes with

1 or 2 small tubercles, distalmost rarely spiniform; distal part of lateral surface with few very small tubercles.

Cheliped (Figure 23g) with ischium bearing 1 to 4 prominent procurves spines on ventromesial surface, more proximal ones often tuberculiform. Ventral surface of merus with mesial and lateral rows of 3 or 4 and 4 to 6 curved spines, respectively; dorsal surface rugose but lacking prominent tubercles; dorsodistal margin smooth or punctate but never crenulate. Carpus with mesial row of usually 3 tubercles, distal 2 always procurved and spiniform, distalmost very large, spanning proximal third of mesial margin of palm when chela adducted; lateral and dorsal surfaces lacking tubercles, and ventral surface bearing single procurved spine almost as large as distomesial spine just mentioned, no spine or tubercle present on ventral articular condyle. Propodus, with width 34.7 to 52.5 percent of length, and with costate lateral margin almost smooth proximally, becoming subserrate distally; mesial margin of palm bearing row of 7 or 8 rather low tubercles, dorsal and ventral surfaces sparsely punctate; tubercle present on ventrodistal margin of palm at base of dactyl. Opposable margin of fixed finger with row of 12 (to as few as 9 in smaller individuals) sclerotized tubercles, sixth from base largest, and single row of minute denticles (interrupted by tubercles) extending from third tubercle from base to corneous tip of finger, dorso- and ventromedian longitudinal ridges poorly delimited. Opposable margin of dactyl with row of 6 to 12 (as few as 4 in small specimens) tubercles, second from base largest, and band of minute denticles extending distally from second tubercle from base, band beginning as single row; dorsal, ventral, and mesial surfaces of dactyl with comparatively few punctations. Apical parts of both fingers with few, very small, corneous-tipped tubercles.

Width of first abdominal segment of males 41.1 to 46.6 percent of carapace length, that of second 52.5 to 62.6 percent. Pleuron of second abdominal segment (Figure 13d) with J-shaped row of 5 or 6 tubercles, 2 or 3 distinctly spiniform; that of third with 2 to 4 inconspicuous ones, in large specimens one sometimes spiniform.

Telson subequal in length and width (slightly longer than wide in females), clearly divisible into cephalic and caudal sections by pair of marginal spines and remnants of transverse suture; dorsal surface studded with about 12 caudally directed spines. Proximal podomere of uropod lacking spines and tubercles; dorsal surface of mesial ramus with row of 3 or 4 strong spines on median carina, 2 or 3 others in lateral half, and 1 spine on lateral margin; lateral ramus lacking spines on median carina but well-developed ones on lateral half of dorsal surface and series of 2 to 5 on lateral margin proximal to diarsis, latter flanked proximodorsally by row of 9 to 11 small spines.

TYPE-LOCALITY.—No more specific locality than the vicinity of Fianarantsoa was stipulated by Petit (1923) as the place where he obtained the two syntypes, and Monod and

Petit (1929:32) referred to this crayfish as "the usual variety of Fianarantsoa."

TYPES.—There are no specimens in the Muséum National d'Histoire Naturelle, Paris, that can be assumed unquestionably to be those on which Petit based his differential characters of his new variety. Perhaps the fragmentary specimens (As139), cited in locality 3 below, are what remains of them.

RANGE AND SPECIMENS EXAMINED.—*Astacoides betsileoensis*, which appears to be more widespread in streams flowing westward on the island than in those flowing to the east, ranges at latitudes of 18° to 20°S, longitudes of 46° to 49°E (Figure 17).

The specimens examined are as follows (carapace length and postorbital carapace lengths in mm, respectively, follow sex symbols): (1) Forêt d'Ikongo, Vinanitelo, Sep 1898 [G. Grandidier, 1900], ♂ 35.7, 30.1; PM As213. (2) Moramanga, G. Grandidier, coll., ♂ 45.5, 40.8; ♀ 58.5, 52.6; ♀ 34.2, 30.6; PM As218. (3) Fianarantsoa, fragmentary specimens, PM As191. ♀ 59.2, 49.8; PM As139. (4) Andranoroa, au nord d'Ambohimalaza, canton de Vatomitana, district de Fianarantsoa au sud de Vohiparara, ♂ 77.5, 66.6; ♂ 76.5, 65.5; PM As171. (5) Écrevisse bleue de la rivière Tantamala (est de Fianarantsoa, alt 540 m), 1934, don de M. René Catala, ♂ 81.5, 70.0; PM As172. (6) Fianarantsoa, ♀ 84.2, 72.5; PM As223. Ovig ♀ 85.3, 74.2; PM As224. (7) Fianarantsoa, ♂ 59.4, 51.1; ♀ 46.3, 39.0; PM As228. (8) Région d'Ifanadiana, N.E. de Fianarantsoa, 2 fragmentary specimens, PM As229. (9) Sahambavy River, Fianarantsoa, 12 Jan 1962, Y. Thérézien, coll., ♂ 48.2, 40.9; ♀ 25.0, 20.8; RNHL 17724. (10) Station Ampamaherana, Fianarantsoa District, ♀ 58.4, 49.4; ♀ 55.2, 46.6; RNHL 27271. (11) Ambodiriana, near Moramanga, between Tananarive and Andevoranto, 1969, M. Vincke, ♀ 34.2, 30.1; RNHL 26487. (12) Marais d'Ampamaherana, 25 km de Fianarantsoa sur la ligne de Chemin de fer Fianarantsoa-Manakara, 10 Jul 1973, ♂ 41.8, 34.9; ♂ 40.4, 33.6; ♀ 67.1, 57.4; ♀ 54.8, 46.8; PM As332. 30 Jul 1973, ♂ 38.1, 31.8; ♀ 64.0, 54.6; ♀ 47.8, 40.5; ovig ♀ 64.9, 55.5; PM As333. (13) 22 km SE of Ambohimahasoa, Namorona River, Fianarantsoa Province, 1 Nov 1962, H.E. Uible, ♂ 56.7, 49.5; ♂ 40.8, 35.0; ♀ 43.8, 38.0; USNM 144976. (14) Tananarive Market, 25 Jan 1963, E. Gould, ♂ 57.7, 50.0; ♂ 47.7, 41.0; ♂ 40.0, 35.4; ♂ 42.3, 36.9; ♂ 35.4, 31.4; ♂ 33.9, 29.7; ♀ 59.5, 49.0; ♂ 43.1, 37.1; ♀ 31.8, 28.0; ♀ 35.3, 31.2; ♀ 35.3, 31.8; ♀ 30.1, 26.5; USNM 129944. (15) "Madagascar," purchased by E. Bartlett, ♂ 59.5, 52.7; ♂ 56.1, 47.2; ♀ 59.3, 52.8; ♀ 49.8, 43.3; BMNH 1881:9.

The following localities from which I have examined no specimens were reported as indicated: (16) "le massif de l'Ikongo" (Petit, 1927:103). (17) Betsileo (Decary, 1950:167).

SIZE.—The largest specimen examined is an ovigerous female from Fianarantsoa (locality 6 above) having a cara-

pace length of 85.3 (postorbital carapace length 74.2) mm. The smallest ovigerous female has corresponding lengths of 64.9 and 55.5 mm, and the largest male, 81.5 and 70.0 mm.

REMARKS.—In remarking on the range of *A. betsileoensis*, Monod and Petit (1929:32) expressed the opinion that the specimens they had from Moramanga had probably been collected elsewhere in the province, suspecting that they had come from much farther south. The subsequent collection made by M. Vincke (see locality 11 above) seems to make possible, if not probable, the correctness of at least the vicinity of the locality from which the specimens were said to have come.

The four specimens in the British Museum (locality 15 above), for which locality data are wanting, appear to combine the characters of *A. betsileoensis* and *A. caldwelli*. The large female appears to be typical of the former in every respect, but, in contrast, the three other specimens are not clearly assignable to either. In them, the spines on the carapace are much weaker than they are in the large female but are more strongly developed than they are in typical *A. caldwelli*. The antennal scales exhibit a weaker spiny pattern but are similar to that of *betsileoensis*. The chelae are rather robust, resembling those of the latter, and the tubercles on

the mesial surface of the carpus are likewise more similar to those of *caldwelli*. Likewise, the sternal keels are more like that of *caldwelli*, the lateral processes being more flattened than they are in typical *betsileoensis*. The spines on the second abdominal pleura are not nearly so well developed as they are in the large female. Possibly these specimens are indeed members of *A. caldwelli* that were even collected in a locality other than that from which the large female was taken. The fact that locality data are not available for these specimens is even more regrettable when one realizes that the life history of not a single species occurring on Madagascar has been investigated. Such knowledge might aid in recognizing morphological changes with increasing age in the several species.

Two of the three ovigerous females available were collected on 30 July 1973, and their oval eggs were approximately 2.9 by 3.8 mm in diameter. The date of collection of the third is not known.

VERNACULAR NAMES.—Holthuis (1964:316) noted that "According to field notes by Mr. Therezien the present form is named 'orambanonga' or 'orambato' by the natives." See also the remarks on vernacular names in the contributions of Poisson (1947) recorded in the "Resumé of Previous Knowledge" herein.

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