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The hermit crabs (crustacea, decapoda, anomura) collected by the International Indian Ocean Expedition, 1963-1964, with notes on their distribution and the zoogeography of the western Indian Ocean

Philip Dalton Witherington
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THE HERMIT CRABS (Crustacea, Decapoda, Anomura)
COLLECTED BY THE INTERNATIONAL INDIAN OCEAN
EXPEDITION, 1963-1964, WITH NOTES ON THEIR
DISTRIBUTION AND THE ZOOGEOGRAPHY OF THE
WESTERN INDIAN OCEAN.

The College of William and Mary in Virginia, Ph.D.,
1973
Biology

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THE HERMIT CRABS (Crustacea, Decapoda, Anomura) COLLECTED
BY THE INTERNATIONAL INDIAN OCEAN EXPEDITION, 1963-1964,
WITH NOTES ON THEIR DISTRIBUTION AND THE ZOOGEOGRAPHY OF
THE WESTERN INDIAN OCEAN

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

By
Philip D. Witherington
1973
APPROVAL SHEET

This dissertation is submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

[Signatures]

Approved, Aug. 1973

[Signatures]
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ABSTRACT

The biological collections made by the R/V *Anton Bruun* and R/V *TeVega* during the International Indian Ocean Expedition, 1963-64 contain 38 species of hermit crabs in 15 genera. New species described are *Aniculus acanthochirus*, *Paguristes plumosus*, *P. mossambicus*, *Pylcopagurus guardafuensis* and *P. mabberensis*.

Diagnostic keys to the families, genera and species are given to assist in identification of the 29 genera and 102 species of coenobitid, diogenid and pagurid hermit crabs known to occur in the Indian Ocean. Diagnoses, descriptions and distribution ranges for each species in the collection are given with diagnostic figures for newly described species.

Analysis of distribution ranges is used to propose the existence of three distinct faunal provinces lying within the Indian Ocean.
THE HERMIT CRABS (Crustacea, Decapoda, Anomura) COLLECTED
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THE WESTERN INDIAN OCEAN
INTRODUCTION

History of the collection

As part of the United States' participation in the International Indian Ocean Expedition, 1963-64, the R/V Anton Bruun conducted a series of cruises in the tropical Indian Ocean. During these cruises, hauls were made at a series of stations using the Gulf of Mexico shrimp trawl, the Menzies and Agassiz trawls, Campbell and Van Veen grabs and various other types of benthic collecting gear, resulting the collection of a large quantity of biological material. In addition, shallow-water and intertidal animals were collected from the various reefs and islands visited by shore parties from the ship. Methods used for collecting on the reefs and in the shallows included hand dipnets, beach seines, SCUBA and rotenone poisoning. Besides the material collected during the cruises of the Anton Bruun, a large number of reef and intertidal animals was collected by Mr. Jack Rudloe in the vicinity of Nossi Be, Madagascar. The R/V Te Vega, during its participation in the International Indian Ocean Expedition, made numerous collections in the southwestern Pacific Ocean and the East Indies. All of these collections were forwarded to the Smithsonian Oceanographic Sorting Center, Washington, D.C.
After being sorted, the pagurids were sent to Dr. Marvin L. Wass at the Virginia Institute of Marine Science for study. These specimens, plus a small collection of pagurids personally collected by Dr. Wass while he was a member of the scientific party on Cruise 8 of the *Anton Bruun* were made available to the author for study through the kind offices of Dr. Wass.

This collection consists of 1,091 specimens representing 15 genera and 38 species. A list of the stations and localities where pagurids were collected is given in Appendix B.

**Current Knowledge of the Indian Ocean Pagurids**

Most of the information on Indian Ocean hermit crabs is based on the collections and reports of individuals who were associated with the efforts of European countries to colonize the lands and islands of the Indian Ocean during the nineteenth century and from the results of exploratory and oceanographic expeditions of the late nineteenth and early twentieth centuries. As a consequence the literature is widely scattered and, in many instances, the scope of individual papers is limited to a restricted region or a single locality. This diverse literature has resulted in a disproportionately large number of synonyms and confusion of ranges and distribution of species. It is hoped that some of the confusion will be resolved by this paper.
Forskal (1775) described four species of hermit crabs from the Red Sea. Almost a century later Heller (1861) described three new species of pagurids from the Red Sea. The Crustacea of East Africa was reviewed by Hilgendorf (1869). Paulson (1875) proposed the genus Dardanus, described Eupagurus cavicarpus and listed four other species of hermit crabs occurring in the Red Sea. The crustaceans from the Gulf of Aqaba and from the island of Rodriguez were reported by Miers (1878, 1879). De Man (1880, 1881) reviewed the pagurids of the Red Sea and later (De Man 1892), the hermit crabs of the East Indies. In a series of publications, Lenz and Richters (1881) and Lenz (1905, 1910, 1912) described the pagurid fauna of Madagascar and the east coast of Africa. Nobili (1903, 1905, 1906) reported on the crustaceans of Singapore and the pagurids of the Persian Gulf and the Red Sea. The terrestrial hermit crabs of the Indian Ocean and the island of Aldabra were listed by Borradaile (1907, 1910). An extensive catalogue of the South African crustaceans was given by Stebbing (1908, 1910, 1916, 1917, 1920, 1924) in a series of publications by the South African Museum. Calman (1909a, 1909b) described collections of pagurids from Christmas Island and Cocos-Keeling Atoll. Balss (1911, 1916, 1926, 1931), in the reports of the Valdivia and Pola expeditions, described new species of hermit crabs from the Indian Ocean and the Red Sea. Delsman (1923) reviewed the crabs, including
pagurids, of Christmas Island. Barnard (1926, 1946, 1947, 1950, 1955, 1962) has provided an extensive catalogue of the pagurid fauna of the coast of East Africa from Mozambique to the Cape of Good Hope, with detailed notes on the distribution. Barnard included keys to the genera and species of South African pagurids. A list of pagurids collected by the *Snellius* Expedition was given by Buitendijk (1937), along with descriptions of four new species, *Clibanarius demani, C. snelliusi, C. boschmai,* and *Calcinus minutus.*

Thompson (1943) listed 26 species of pagurids collected by the John Murray Expedition in the northwestern Indian Ocean and the Red Sea, along with a description of a new parapagurid species, *Sympagurus burkenroadi.* More recently, Dechance (1963, 1964) reviewed the *Paguristes* of the western Indian Ocean and described a collection of pagurids from Madagascar, including a new species, *Diogenes crosnieri.*

Among the papers dealing with Indian Ocean pagurids, the monograph by Alcock (1905) is the only one that gives a comprehensive review of all the species from the Indian Ocean and summarizes the distribution pattern of each. In addition to descriptions and figures of new species of hermit crabs in the Indian Museum collections, Alcock included keys to the genera and species collected from the Indian Ocean and South Pacific. In the interval since the publication of Alcock's work, revision of genera and descriptions of new species, as well as the reporting of
collections from new localities, has made much of his work obsolete.

In the present study, I have sought to clarify the taxonomic status of certain Indian Ocean hermit crabs and to give descriptions of new species, in addition to cataloguing the collection of the International Indian Ocean Expedition. This paper is not a revision of pagurid systematics, therefore no attempt has been made to discuss or to test the validity of certain morphological characters that have been used to distinguish genera. However, it is my opinion that a number of genera have been erected on the basis of questionable or invalid taxonomic characters and that these genera should be critically re-examined. A full discussion and analysis of this aspect of pagurid systematics would require the examination and discussion of genera and species not included in the present collection and for that reason is considered beyond the scope of this study.
SYSTEMATIC ACCOUNT

Historical Resume

The classification of the hermit crabs, like that of most of the other crustaceans, has undergone frequent revision and modification. This instability has produced several different systems of pagurid taxonomy that, while differing in terminology and in the characters and relationships emphasized, retain a rather remarkable similarity and thereby attest to the basic soundness of the taxonomic principles involved.

In 1802, Latreille erected the order Decapoda and subdivided it into the Macroures and Brachyures, based on the relative development of the abdomen. The Macroures included, in the section Anomaux, most of the forms now referred to as hermit crabs. In 1834, H. Milne-Edwards elevated the Anomaux to the rank of suborder and changed the name to Anomoures to parallel Macroures and Brachyures. Milne-Edwards then divided the Anomoures into two families, the Pterygures and the Apterures, based on the presence or absence of uropods respectively. In his Fauna Japonica, DeHaan (1839) divided the Decapoda into five sections, one of which, the Anomala, contained those forms considered intermediate between the true crabs and the shrimps and lobsters with their well-developed abdomens. The Anomala
was subdivided into five families, one of which, the Paguroidea, contained the hermit crabs. Dana, in 1852, considered the Anomura to represent degenerate forms of Macrura and, on this basis, divided them into four grades, Anomura superior, Anomura media, Anomura submedia and Anomura inferior, on the presumed degree of degeneration. While this system was never widely accepted, certain features of its nomenclature were retained by some authors well into the twentieth century (Stebbing, 1910, 1920). Reversing the work of his father, Alphonse Milne-Edwards in 1860 abolished the suborder Anomoures and returned the forms contained therein to either the Macroures or the Brachyures. Boas (1883) re-established the Anomala of DeHaan, but included in it only three branches, the Paguridae, the Galatheidae and the Hippidae. Henderson (1888), in his report on the Anomura collected by the Challenger expedition, reasserted the name Anomura with its spelling modified from that of Milne-Edwards and pointed out that, although Latreille's Anomaux predated this name, it referred to a differently constituted group and therefore did not have priority. In the Anomura, Henderson divided the Paguridea into two sections, the Lithodea and the Paguroidea. The latter section was divided on the basis of gill structure into the Laminibranchiata, with flattened gill filaments (phyllobranchiae) and the Fibribranchiata with slender gill filaments (trichobranchiae). In the latter
branch, he placed a single family, the Parapaguridae, erected by S. I. Smith in 1883. Ortmann (1893) revised the family Paguridae and divided it into two subfamilies, the Pagurinae and the Eupagurinae, on the basis of the width of the sternal plate separating the bases of the third maxillipeds. This distinction is retained in the present system, but at a higher rank. Borradaile (1907b) proposed a system of classification in which three superfamilies, Thalassinoidea, Paguroidea and Galatheoidea, were placed in the Anomura. The Paguroidea were divided into the Paguridae and the Coenobitidae, and the Paguridae were subdivided into the subfamilies Diogeninae and Pagurinae. In 1911 Balss erected a third family of pagurids, the Pylochelidae, for those forms that retained a symmetrical abdomen and six paired pleopods.

Boas (1924) proposed an entirely new scheme of classification in which the principal character considered was the reduction of pleopods. Boas' system divided the pagurids into four families: (1) the Pylochelinen, with six pairs of pleopods; (2) the Paguristinen, with one or two pairs of pleopods in the male; (3) the Pagurinen, with no paired pleopods in the male and possessing 14 pairs of gills; and (4) the Eupagurinen, with no paired pleopods in the male and with 11 pairs of gills. This system has been largely ignored by later authors, with the exception of Wolff (1961), although the phylogenetic value of the relative reduction of
pleopods and gills cannot be denied.

Bouvier (1940) proposed that the Paguroidea be divided into two series, the Pagurienne, with the third maxillipeds approximated at the base and the Eupagurienne, with the third maxillipeds widely separated by a sternal plate.

MacDonald, Pike and Williamson (1957), on the basis of characteristics of larval development as well as the morphology of adults, proposed that the Paguridea be divided into two superfamilies, the Coenobitoidea and the Paguroidea, thereby allowing the Diogenidae and Coenobitidae to be elevated to the rank of family. The system of MacDonald et al. (1957), with the addition of the family Parapaguridae, as proposed by de Saint Laurent (personal communication), will be used in this paper. A short outline of this system is given below:

<table>
<thead>
<tr>
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<td>Family Pylochelidae Bate 1888</td>
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<td>Family Diogenidae Ortmann 1892</td>
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<td>Family Coenobitidae Dana 1852</td>
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<td>Family Lomisidae Bouvier 1894</td>
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<tr>
<th>Superfamily PAGUROIDEA MacDonald et al. 1957</th>
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<td>Family Parapaguridae Smith 1879</td>
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<tr>
<td>Family Paguridae Latreille 1802</td>
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<td>Family Lithodidae Leach 1819</td>
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Pagurid Terminology

In order to prevent confusion of terms that may have different meaning when applied to other crustacean groups, a glossary of terms used in this paper and their definitions is given below.

A Glossary of Pagurid Terminology

Abdomen - Posterior tagma of pagurid body; usually twisted or coiled; uncalcified except in the terga, uropods and telson.

Accessory tooth - Prominent tooth or spine on median surface of ischium of third maxilliped; associated with crista dentata.

Acicle - Elongate, movable scale-like process on dorsal surface of antennal peduncle; homologous with exopodite of antenna.

Antennae - Second pair of cephalic appendages; each terminating in long tapered flagellum.

Antennal angle - One of a pair of projections on anterior border of shield; usually extending into space between eyestalks and antennal peduncles.

Antennule - One of first pair of cephalic appendages; located between and in front of eyestalks; with relatively long peduncles and a pair of short flagella, the inferior of which is usually greatly reduced.
Anterior margin (of shield) - Border of shield adjacent to bases of antennules, eyestalks and antennae; bears median (rostral) process and pair of lateral (antennal angles) processes.

Branchiostegites - Portion of carapace covering gills; usually feebly calcified, if at all.

Calcareous - Composed of calcium carbonate, or having chalky appearance.

Callosity - Raised, round or oval process, usually on venter of thorax; used as friction surface to hold carcinoecium.

Carapace - Dorsal portion of anterior exoskeleton; composed of expanded epimeres and protecting cephalothorax.

Carcinoecium - Object used as "house" by hermit crab; usually gastropod shell, sponge, coral, piece of bamboo, etc.

Cardiac plate - Portion of carapace lying medial to branchiostegites; usually more or less calcified.

Cephalothorax - Combination of two anterior tagmata of body; head and thorax forming single unit.

Cervical groove - Prominent sulcus dividing cephalic shield from branchiostegites and cardiac plate.

Chela - modification of dactylus and propodus to form pinching, grasping or cutting organ by opposition of dactylus against extended distal angle of propodus.

Chelate - Possessing or bearing a chela.

Cheliped - Fourth thoracic appendage, bearing a large, well-developed chela.
Major cheliped - Larger of paired chelipeds.
Minor cheliped - Smaller of paired chelipeds.
Cornea - Distal portion of eyestalk, bearing functional optic organs (ommatidia).
Corneal peninsula - Calcareous extension of eyestalk into dorsal margin or cornea.
Corneous - Composed of chitin or having horn-like texture.
Crista dentata - Row or crest of denticles on antero-medial border of ischium and merus of third maxillipeds; masticatory structure.
Denticle - Tooth-like tubercle or spine.
Eyescale - Small calcareous dorsal projection at base of eyestalk.
Eyestalk - Movable projection bearing cornea at distal end.
Flagellum - Flexible, usually tapered, terminal portion of appendage, usually sensory in function (e.g. antennae).
Gibbous - Humped or bearing projection; used in describing produced, distal articles of flagellum.
Gonopod - Paired, usually modified, pleopods used in copulation and oviposition.
Hand - Large, prominent chela.
Interocular plate - Small, usually bilaterally symmetrical plate lying medially between bases of eyestalks.
Nude - Devoid of setae or bristles.
Orectoculiform - Used as, or shaped like operculum.
Operculum - Structure used to close or cover opening of shell or carcinoecium.

Palm - Portion of chela proximal to articulation of dactylus.

Peduncle - Basal portion of appendage.

Pereiopods - Appendages of peraeon; thoracic appendages.

Phyllobranchiae - Gills in which filaments are flattened and leaf-like.

Pleopods - Appendages of pleon; abdominal appendages on segments 1-5; may be paired or unpaired.

Preungueal process - Tubercle on dorsal margin of dactylus, proximal to corneous claw.

Rasp - A group or cluster of corneous, imbricating scales used as friction organ to retain animal in carcinoecium.

Rostriform process - A movable, spine-like process located on midline between eyestalks; characteristic of Diogenes.

Rostrum - Medial projection of anterior border of shield.

Shield - Portion of carapace anterior to cervical groove; usually heavily calcified.

Sternum - Plate forming ventral exoskeleton of body segment.

Subchelate - Modification of terminal articles of appendage in which extension of propodus does not reach tip of dactylus; tip of dactylus not opposed by propodus.

Subequal - Length of two or more structures differing by less than ten percent of length of longer.

Sulcus - Prominent or distinct groove.
Telson - Unpaired terminal appendage at posterior end of body.

Tergum - Plate forming dorsal exoskeleton of abdominal segment.

Trichobranchiae - Gills in which filaments are slender and hair-like.

Uropods - Paired appendages of sixth abdominal segment.
Keys to the Families and Genera of Paguroidea

The characters used in the following keys were selected principally for the ease with which they may be observed without great magnification or extensive dissection and in which the alternate choices are easily differentiated. Because these keys are entirely artificial, the user is cautioned against drawing any phylogenetic inferences from either the sequence or the grouping of the taxa within the keys.

Key to the Families of Paguridea
1. Bases of third maxillipeds widely separated by a sternal plate (Superfamily Paguroidea) ............... 2
   Bases of third maxillipeds not separated by sternal plate (Superfamily Coenobitoidea) .................. 3
2. Sternal plate between third maxillipeds divided by a median notch or sulcus ................ Parapaguridae
   Sternal plate between third maxillipeds not divided ................................................. Paguridae
3. Abdomen and abdominal appendages symmetrical ....................................................... Pylochelidae
   Abdomen twisted or flexed, with at least some appendages unpaired ................................. 4
4. Antennular flagellum ending bluntly .......... Coenobitidae
   Antennular flagellum ending in a tapered filament .................................................. Diogenidae
Key to the Genera of Coenobitidae

1. Abdominal terga heavily calcified; fourth pereiopods chelate, longer than fifth pereiopods ...... Birgus
   Abdominal terga not heavily calcified; fourth pereiopods subchelate and not markedly longer than the fifth ...................... Coenobita

Key to the Genera of Pylochelidae

1. Third maxillipeds chelate ...................... Pylocheles
   Third maxillipeds not chelate .................... 2
2. Eyes well-developed ................................ 3
   Eyes reduced ...................................... Parapylocheles
3. Chelae operculiform ............................. Pomatocheles
   Chelae not operculiform ........................... Mixtopagurus

Key to the Genera of Diogenidae

1. Fourth pereiopods chelate ...................... Paguroopsis
   Fourth pereiopods subchelate or simple .......... 2
2. Fourth pereiopods simple ........................ Paguristopsis
   Fourth pereiopods subchelate .................... 4
3. First gonopods of male armed with recurved hooks;
   female lacking gonopods and brood pouch .... Paguristopsis
   First gonopods of male not armed; female with one pair of gonopods and four unpaired pleopods enclosed within a fleshy brood pouch .......... Paguristes
4. Chelipeds equal or subequal ........................ 5
Chelipeds markedly unequal in size ..................... 8
5. Chelipeds and first two pereiopods sculptured with overlapping transverse ridges ...................... 6
   Chelipeds and pereiopods not sculptured as above .... 7
6. Chelipeds with stridulating rasps on inner face of hand ......................................... Trizopagurus
   Chelipeds without stridulating rasps ........ Aniculus
7. Antennal flagellum with two rows of setae ...... Isocheles
   Antennal flagellum nude ..................... Clibanarius
8. Right cheliped larger than left .............. Petrochirus
   Left cheliped larger than right ....................... 9
9. Rostrum integral with anterior border of shield .... 10
   Rostrum replaced by a movable spine lying between bases of eyestalks .......................... Diogenes
10. Antennal flagellum setose .................. Troglopagurus
    Antennal flagellum nude .......................... 11
11. Fingertips of chelae calcareous ............ Calcinus
    Fingertips of chelae corneous .................... 12
12. Cardiac plate divided by a transverse suture ................................... Alloidardanus
    Cardiac plate without a transverse suture .......... 13
13. Endopods of maxillae with prominent lateral process; female pleopods biramous .... Pseudopagurus
    Endopods of maxillae without a lateral process;
    first three pleopods of female triramous ..... Dardanus
Key to the Genera of Parapaguridae

1. Eyes normally developed and pigmented ................. 2
   Eyes reduced or absent ......................... Typhlopagurus
2. Eyescales present ..................................... 3
   Eyescales absent .................................. Tylaspis
3. Abdomen strongly calcified and only slightly twisted ........................................ Probeebei
   Abdomen soft and coiled .......................... Parapagurus

Key to the Genera of Paguridae

1. Male specimens (gonopores present on coxae of fifth pereiopods or tubular vas deferens protruding from one or both coxae) ........................................ 2
   Female specimens (gonopores on one or both coxae of third pereiopods) .......................... 27
2. Gonopores simple, vas deferens not produced ........ 3
   One or both vasa deferentia produced as tubular extensions ...................................... 17
3. Paired gonopods present ............................. 4
   Paired gonopods absent ............................. 8
4. Only one pair of gonopods present ..................... 5
   Two pairs of gonopods present ...................... Xylopagurus
5. Unpaired pleopods present ........................... 6
   No unpaired pleopods present .................... Lithopagurus
6. Right cheliped much larger than left .................. 7
   Chelipeds subequal ............................... Tomopaguropsis
7. Eyestalks dilated in corneal region .......... **Tomopagurus**
   Eyestalks narrowed distally .............. **Tomopaguroides**
8. Unpaired pleopods present ......................................... 9
   No unpaired pleopods present ......................... 2
9. Three unpaired pleopods present ....................... 10
   Four unpaired pleopods present .................. **Pagurus**
10. Both chelae fitting together to form an
    operculum ....................................... 11
    Chelae not operculiform ........................ **Orthopagurus**
11. Eleven pairs of gills present ............. **Pylorpagurus**
    Thirteen pairs of gills present ........ **Pyloropaguropsis**
12. Chelipeds greatly enlarged and elongate, longer
    than body; a prominent spine produced on the basis
    of both uropods ................................ **Munidopagurus**
    Chelipeds of normal proportions .................. 13
13. Sixth abdominal tergum divided by a median longi-
    tudinal groove ................................ **Paguritta**
    Sixth abdominal tergum not divided ............... 14
14. Eight pairs of gills present ............... **Octopagurus**
    More than eight pairs of gills present ........... 15
15. Abdomen reduced and strongly calcified on dorsal
    surface ............................................. 16
    Abdomen not reduced ............................... **Orthopaguropsis**
16. Dactylus of fourth pereiopod simple; branchi-
    ostegites strongly calcified ............... **Ostraconotus**

*Unpublished genus proposed by Wass (1959)
Fourth pereiopod subchelate; branchiostegites membranous ........................ Porcellanopagurus
17. Left vas deferens longer than right ................ 18
   Right vas deferens longer than left .............. 19
18. Left vas deferens strongly coiled into a
   spiral ............................................. Spiropagurus
   Left vas deferens only slightly curved ..... Anapagurus
19. Four unpaired pleopods present .................. 20
   Three unpaired pleopods present ............... 21
20. Ten pairs of gills present .................... Decaphyllus
   Thirteen pairs of gills present ............ Catapagurus
21. Chelipeds subequal .............................. Solenopagurus
   Right cheliped larger than left ............... 22
22. Ten pairs of gills present .................... Catapaguroides
   Eleven pairs of gills present ............... 23
23. Gills with filamentous lamellae
   (trichobranchiae) ............................. Pagurodes
   Gills with flattened lamellae (phyllobranchiae) .... 24
24. Vas deferens terminating in slender
   filament ............................................ Nematopagurus
   Vas deferens ending abruptly, not tapering ........ 25
25. Vas deferens extending under the abdomen
   toward left side of body ..................... Cestopagurus
   Vas deferens extending outward to right .......... 26
26. Terminal article of antennular peduncle bearing
   a tuft of setae near distal end ........ Acanthopagurus
No tuft of setae on terminal segment of
antennular peduncle ........................... *Trichopagurus*
27. Gonopods present ........................................ 28
    Gonopods absent .................................... 33
28. Three unpaired pleopods present ........ *Munidopagurus*
    Four unpaired pleopods present .................. 29
29. Thirteen pairs of gills present .................... 30
    Eleven pairs of gills present ..................... 31
30. Corneal region of eyestalks slightly
dilated .................................................. *Pylopaguropsis*
    Eyestalks narrowed distally; cornea
    reduced ............................................... *Tomopaguroides*
31. Chelae operculiform; bent sharply at wrist and
    incapable of being straightened .............. *Pylopagurus*
    Chelae not operculiform; wrist can be straightened.. 32
32. Gills trichobranchiate ............................. *Pagurodes*
    Gills phyllobranchiate ........................... *Nematopagurus*
33. Abdomen reduced; body flattened and crab-like ..... 34
    Abdomen not reduced; body not crab-like ............ 35
34. Dactylus of fourth pereiopod simple; branchi-
    ostegites strongly calcified .................... *Ostraconotus*
    Fourth pereiopod subchelate; branchiostegites
    membranous ......................................... *Porcellannapagurus*
35. Three unpaired pleopods present .................... 36
    Four unpaired pleopods present .................... 39
36. Thirteen pairs of gills present .................... 37
Eleven pairs of gills present .......................... 38

37. Fourth pereiopods chelate ......................... Xylopagurus

Fourth pereiopods subchelate ..................... Lithopagurus

38. Sixth abdominal tergum divided by median longitudinal groove ............................ Paguritta

Sixth abdominal tergum not divided .......... Anapagurus

39. Female gonopores paired .......................... 40

Female gonopores unpaired ....................... 47

40. Eight pairs of gills present ................. Octopagurus

More than eight pairs of gills present ........ 41

41. Thirteen pairs of gills present ............... 42

Eleven pairs of gills present ....................... 43

42. Antennal flagellum setose .................... Tomopaguropsis

Antennal flagellum nude .......................... Catapagurus

43. Chelipeds equal or subequal ...................... 44

Right cheliped markedly larger than left ........ 45

44. Preunngueal process on dactylus of fourth pereiopod ........................................... Solenopagurus

No preunngueal process on dactylus of fourth pereiopod ........................................... Spiropagurus

45. Terminal article of antennular peduncle with a tuft of setae near distal end .......... Acanthopagurus

No tuft of setae near distal end of terminal article of antennal peduncle .......................... 46

46. Gill lamellae entire ............................... Pagurus

Gill lamellae bifid at tips ........................ Cestopagurus
47. Eleven pairs of gills present .......... Trichopagurus
   Ten pairs of gills present .................. 48

48. Two longitudinal lines of tubercles on dorsal
   surface of right chela ....................... Decaphyllus
   No lines of tubercles on dorsal surface of
   right chela .................................. Catapaguroides
Methods and Materials

Each specimen in the collection was examined individually, except in those cases where large numbers of individuals of the same species were collected from a single locality. From these latter samples, a few individuals were selected at random for detailed examination and the remainder were examined only sufficiently to verify that all the specimens were of the same species. Each specimen was identified by first determining the appropriate family and then carrying it through one or more identification keys for that family. Keys found to be most useful and to have a high degree of reliability were those in Barnard (1950), Fize & Serene (1955), Forest (1954) and Wass (1959). Each identification was subsequently verified by referring to the original description or, if this was not available, to descriptions and figures by later authors. In those cases where no satisfactory identification could be made from either keys or descriptions and figures, a search of the literature on the genus or subgenus determined if the species had been previously described. Where no existing description or reference could be found, it was assumed that the specimen represented an undescribed species.

All measurements were made using small dividers in which the usual points were replaced by stainless steel insect pins, size #7 and #000. These pins extended the length of the points and provided extremely fine tips,
thereby facilitating the measurement of very small structures. Dimensions were taken from the dividers by means of metric vernier calipers. Replication of sample measurements taken in this manner have been shown to have a precision of 0.1 mm. All measurements and dimensions are given in millimeters. Unless otherwise noted, the dimensions given for the material examined refer to the carapace length.

Morphometric measurements used in the descriptions were taken as described below. The carapace length was measured on the dorsal midline from the rostrum to the most posterior point on the midline not including the rearward expansion of the branchiostegites. The shield length was also measured on the midline. The shield width was measured at the point of greatest breadth. The length of the anterior margin of the shield was taken from the point on either side at which the margin takes a definite turn toward the rear or, in those species which possess spines at these points, the measurement was taken between these spines. The lengths of the antennular and antennal peduncles were measured while the articles of these appendages were extended in a straight line. The length of the eyestalk was measured from the proximal point of the calcified stem to the distal tip of the cornea. The lengths of merus, carpus, propodus and dactylus of the appendages were taken from the most dorsal point
of the proximal articulation to the most distal point of that article. The width of these articles, including the hand of the chelae, was measured at the point of greatest breadth. Comparisons of whether flagella, chelipeds, pereiopods, etc. exceed others in extent or reach were made while these structures were in their normal attitude attached to the body.

The colors of living specimens are described for only those species that were collected by M. L. Wass, who made notes on the colors of the specimens before preservation had altered the pigments. The coloration of preserved specimens was described only for those species which retained a distinctive pigmentation pattern after years of preservation.

The range of each species was determined by combining the ranges given by previous authors with the localities represented in this collection. In cases where only a few localities are recorded and these are widely separated geographically, the range was assumed to be disjunct even though it might be suspected that further collection efforts would prove the range to be continuous.

In the process of collection, preservation and sorting, most of the specimens had been removed from the shell or carcinoecium that each had inhabited. For this reason, information on the shell preferences and on the commensal organisms associated with the pagurids cannot be given for
all species. In those cases in which the animal had been preserved in the shell, observations on the types of shells utilized by the crab and commensals, if any, are given in the remarks about that species. Most of the shells so described are identified only to the genus. These identifications were made by referring to the figures in Smith (1940) and to the descriptions of Barnard (1963).

The synonymy given for each species contains only references to the original description of the species and to its junior synonyms and to the paper in which the name in its present form was first published. This system of citing synonymy is used in preference to the traditional extensive list of all references to the species and its synonyms regardless of the significance of their contribution to the biology of the species.

Station numbers with the "JR" prefix refer to collecting stations of Jack Rudloe. In the interest of brevity, a telegraphic style is used wherever practicable.
Superfamily COENOBITOIDEA MacDonald et al. 1957

Family Coenobitidae Dana 1852

Genus Coenobita Latreille 1826

Terrestrial hermit crabs with a heavily calcified carapace. Antennular peduncle extremely long; flagellum ending bluntly. Eyestalks somewhat compressed; cornea almost obscured dorsally by corneal peninsula. Antennal peduncles strongly compressed and appressed closely to front edge of carapace. Left cheliped much larger than right; chela inflated and somewhat globose. Fourth pereiopods subchelate; propodus bearing large round rasp of corneous scales. Coxae of fifth pereiopods expanded into blade-like extensions. Three biramous pleopods on left in female; pleopods of male extremely reduced.

Key to the Indian Ocean Species of Coenobita
1. Antennal acicle movable; both chelae with a "brush" of hair-like setae; superior flagellum of antennule five times as long as inferior flagellum ........... brevimanus
   Antennal acicle fused (immovable); "brush" of hair-like setae on right chela only ........................ 2
2. Row of elongate tubercles near dorsal margin of outer face of left chela (stridulation rasp) ........ 3
   No stridulation rasp present on left chela ...... cavipes
3. Superior antennular flagellum more than twice length of inferior flagellum ......................... rugosus
Superior antennular flagellum less than twice length of inferior flagellum ....................... *scaevola*

(*) *C. scaevola* is found only in the Red Sea.

**Coenobita brevimanus** Dana 1852

**Coenobita clypeata** var. *brevimanus* Dana, 1852: 473

**Coenobita clypeata** Latreille, 1826:

**Coenobita clypeatus** Alcock, 1905: 142

**Coenobita hilgendorfi** Terao, 1913: 388

**MATERIAL EXAMINED:**

One female, 34 mm, Sta. JR-14

One male, 12 mm, *Te Vega* Sta. 32

**DIAGNOSIS:** Antennal acicle not fused to peduncle; "brush" of hair-like setae on both chelae; eyescales lanceolate, medial borders divergent; inferior antennular flagellum one-fifth length of superior flagellum.

**DESCRIPTION:** Shield quadrate, narrowing toward front, smoothly convex on dorsum, marked with evenly distributed punctae; rostrum obsolete, exceeded by antennal angles; cervical groove forming a straight line across posterior of shield; sides of shield strongly compressed. Cardiac plate strongly calcified; branchiostegites strongly calcified and divided into plates posteriorly. Eyescales lanceolate, approximated at
base, medial borders divergent, lateral borders feebly denticate. Eyestalks slightly dilated proximally, compressed distally. Antennular peduncle long, exceeding length of carapace; superior flagellum compressed, five times length of inferior flagellum; Antennal peduncle strongly compressed, closely appressed to side and front edge of carapace, exceeding eyestalk by three-fourth of terminal article; acicle small, movable.

Third maxillipeds approximated at base; thin line of denticles forming crista dentata obliquely across inner face of ischium. Right cheliped extremely massive, chela wider than long, outer face inflated and smooth, except few low tubercles near dorsal and ventral borders. Movable finger with crest of low tubercles on dorsal surface; fingertips blunt, calcareous. Inner face of all articles flattened, fitting closely to corresponding faces of right cheliped. Both chelipeds with prominent brush of setae arising from inner face and dorsal margin of propodus. Right cheliped slender, length-width ratio of chela 1.5:1, outer face relatively flat, armed with evenly scattered corneous tubercles; fingertips corneous. Second and third pereiopods massive; articles compressed, fitting closely together and to outer face of chelae. Propodus of fourth pereiopods very broad, bearing a circular rasp of corneous scales. Fifth pereiopods minutely chelate. Gill pairs 14, four anterior pairs rudimentary, remainder phyllobranchiate.
Male genitalia a pair of gonopores on coxae of fifth pereiopods, these coxae produced into thin blade-like processes in both sexes, but more so in males; female genitalia a pair of gonopores on coxae of third pereiopods.

Abdomen soft and membranous, terga widely separated; three biramous pleopods on left side in female, pleopods of male greatly reduced. Sixth abdominal tergum well calcified; uropods with friction rasps on exopods and endopods; telson bilobed, posterior margin entire, fringed with stiff setae.

RANGE: East coast of Africa throughout Indian Ocean and Indo-Pacific region to Tuamotu Islands.

REMARKS: Due to an unfortunate error, the locality of Herbst's Coenobita clveatus was given as the East Indies when, in fact, it was from the West Indies. This error has resulted in confusion of the literature of the two species.

Coenobita cavipes Stimpson 1858

Coenobita cavipes Stimpson, 1858: 245
Coenobita violascens Heller, 1862: 524
Coenobita compressus Ortmann, 1892: 318
MATERIAL EXAMINED:

One male, 6 mm, *Te Vega* Sta. 34
One female (ovig.), 34 mm, and three males, 20-23 mm,
   Sta. JR-14
Two females (1 ovig.), 22 & 25 mm, and two males, 18 & 13 mm, Sta. JR-28
Three females, 33-39 mm, and three males, 36-43 mm,
   Sta. JR-27

DIAGNOSIS: Antennal acicle fused to peduncle; "brush" of hair-like setae on right chela only; no stridulation rasp on left chela; fingertips of major chela minutely corneous; inferior antennular flagellum one-third length of superior flagellum.

DESCRIPTION: Shield quadrate, narrowing anteriorly, lateral margins sparsely setose; rostrum obsolete, exceeded by antennal angles. Eyescales narrowly triangular, medial borders approximated and parallel; eyestalks only slightly dilated proximally and compressed distally; corneal peninsula on medial border, cornea exposed laterally. Antennal peduncle equal to or barely exceeding carapace length; inferior flagellum one-third superior flagellum. Antennal peduncles strongly compressed and appressed to side and front edge of carapace; acicle fused to peduncle. Antennal peduncle exceeds eyestalks by three-fourths of terminal
article.

Third maxillipeds approximated at base; crista dentata on ischi um almost obscured by fringe of setae. Left cheli ped massive, inner face of merus, carpus and propodus flattened and fitting closely to corresponding faces of right cheliped; dorsal and lateral faces of merus with faint rugose striations; carpus with numerous flattened corneous tubercles on outer face; length of chela 1.25 times its width, proximal portion of ventral border lobed; a prominent brush of hair-like setae arising from inner face and dorsal margin of hand; movable finger with scattered corneous tubercles on dorsal surface, but not forming any semblance of a crest. Finger and thumb with rounded calcareous teeth; fingertips minutely corneous. Right cheliped much smaller than left, merus and carpus strongly compressed; chela 1.5 times as long as wide; "brush" of setae arising from dorsal margin of hand; fingertips corneous. Second and third pereiopods fitting closely together and to surface of chelipeds, inner face of each article concave and fitting closely to outer face of articles of proximal anterior appendage. Ventral surface of dactylus of third left pereipod with a narrow longitudinal rasp of corneous tubercles. Fourth pereiopods subchelate, propodus with circular rasp of corneous scales. Fifth pereiopods minutely chelate, elongate patch of corneous scales on propodus. Gill pairs 14, 10 pairs phyllobranchiate, 4 anterior pairs rudimentary.
Male and female genitalia normal. Coxae of fifth pereiopods expanded and blade-like in both sexes, those of male more so.

Abdomen soft and membranous, terga widely separated; three biramous pleopods on left side in female; pleopods of male greatly reduced. Sixth abdominal terga, uropods and telson well calcified, friction rasp on endopods and exopods of uropods well developed; posterior margin of telson with median notch, not denticulate, but fringed with stiff setae.

Pigmentation of these specimens, after eight to nine years in preservative, a prominent blotch of brown on outer face of major chela and narrow line of brown on outer face of carpus of left cheliped; merus and carpus of second and third pereiopods with blotch of brown on outer face. One specimen from Nossi Be in shell of Murex sp., two other specimens in shells of indeterminate species of land snail.

RANGE: East coast of Africa and Madagascar throughout Indo-Pacific to Solomon Islands.

REMARKS: This species appears to be the largest of the species of Coenobita in the Indian Ocean, far exceeding C. rugosus in size and averaging larger than C. brevimanus in the collection.
**Coenobita rugosus** H. Milne-Edwards 1837

**Coenobita rugosa** H. Milne-Edwards, 1837: 241

**Coenobita rugosus** Hilgendorf, 1878: 824

**Coenobita compressa** Bouvier, 1891-92, IV: 35

**MATERIAL EXAMINED:**

One male, 8 mm, Sta. HA-17

One male, 19 mm, Sta. JR-14

Three males, 7-10 mm, and five females, 7-10 mm,

*Te Vega* Sta. 27

One male, 15 mm, *Te Vega* Sta. 44

Two males, 6 and 7 mm, *Te Vega* Sta. 121

**DIAGNOSIS:** Antennal acicles fused to peduncles; "brush" of hair-like setae on both chelae; eyescales broadly triangular; large stridulation rasp on outer face of major chela.

**DESCRIPTION:** Shield quadrate, narrowing anteriorly, posterior margin straight; rostrum absent, anterior margin of shield a smooth concave curve between antennal angles; central portion of shield smooth, nude; sides and anterior portion with scattered bristles and punctae. Eyescales broadly triangular (base equals height) with medial borders approximated and parallel. Eyestalks not markedly dilated at base; compressed distally, corneal peninsula on medial margin. Antennular peduncles shorter than carapace;
inferior flagellum one-third length of superior flagellum. Antennal peduncles strongly compressed, acicle fused. Third maxillipeds approximated at base; crista dentata partially obscured by fringe of setae.

Left cheliped much more massive than right; inner faces of merus and carpus strongly flattened; inner face of hand divided by distinct longitudinal crest at level of articulation with finger, region bordering crest flat dorsally, concave ventrally. Outer face of chela strongly convex, row of obliquely elongate tubercles near dorsal border. Movable finger with small setiferous punctae arranged in parallel longitudinal rows; fingertips minutely corneous. Right cheliped slender, strongly compressed; length-width ratio of chela 1.3:1; setiferous punctae scattered uniformly over surface. Second and third pereiopods fitting closely together and to surface of chelipeds, forming almost continuous pavement of armor. Dorsal margins of meri of pereiopods and chelipeds slightly rugose. Dactylus of third left pereiopods with narrow longitudinal rasp on ventral face. Fourth pereiopod subchelate; fifth pereiopod minutely chelate. Gill pairs 14. Male and female genitали normal. Coxae of fifth pereiopods in male flattened and blade-like.

Abdomen soft, terga widely separated, coiled to right; three biramous pleopods on left side of female, pleopods of male reduced. Pigmentation of most specimens badly
faded, but Madagascar specimens with large chocolate colored spot on outer face of major chela; carpus of minor cheliped, second and third pereiopods with narrow longitudinal lines of same pigment on outer faces. Bougainville Island specimens much lighter in general appearance, with orange-red spot on outer face of major chela and transverse bands of same pigment at each joint of chelipeds and pereiopods. Morphologically, there appears to be little to distinguish these two types of specimens, but the color pattern is strikingly different. Fize and Serene (1955) described several forms distinguished principally by coloration and it appears likely that the Bougainville Island specimens represent yet another variation of pigmentation in this species.

RANGE: East coast of Africa and Madagascar throughout Indo-Pacific to the west coast of Central America.

DIOGENIDAE Ortmann 1892
(=Dardaninae Schmitt 1926)

_Dardanus_ Paulson 1875

Shield strongly calcified, branchial region feebly calcified. Rostrum obsolete, ophthalmic somite exposed; eyescales large, widely separated, a small interocular plate lying on upper surface of somite between eyescales. Antennal peduncle with well developed acicle, flagellum
nude. Chelipeds usually dissimilar and unequal, left larger than right, fingertips corneous. Second and third pereiopods, especially on left side, frequently sculptured or modified in distinctive manner. Fourth pereiopods sub-chelate; fifth pair chelate. Male genitalia a pair of gonopores on coxae of fifth pereiopods; female genitalia a pair of gonopores on coxae of third pereiopods. Abdomen soft, spirally coiled to right; four uniramous pleopods on left side in male; three biramous and one uniramous pleopod on left side in female. Gill pairs 14, lamellae phyllobranchiate.

Key to the Indian Ocean Species of Dardanus

1. Chelipeds and pereiopods with distinctive sculpture of overlapping transverse ridges .................. 2
   Chelipeds and pereiopods not sculptured as above ..... 3

2. Major chela twice as long as wide ............... arrosor
   Major chela 1.5 times as long as wide ............. imbricatus

3. Cornea not greatly dilated, occupying less than one-fourth length of eyestalk ....................... 4
   Cornea greatly dilated and flattened, occupying one-third or more of eyestalk ...................... 10

4. Shield slightly wider than long .................... 5
   Shield longer than wide .......................... 6
5. Dactylus and propodus of third left pereiopod regularly and transversely striated, with dense fringe of setae ................. *guttatus*
   Dactylus not striated, but with longitudinal sulcus on outer face .............. *scutellatus*
6. Outer face of left chela spinose ....................... 7
   Outer face of left chela not spinose except for few spines on upper margin ............. *fabimanus*
7. Left cheliped much larger, but only slightly longer than right; distal segments of antennal flagellum gibbous .............. *lagopodes*
   Left cheliped longer than right; antennal segments not gibbous ....................... 8
8. Chelipeds and pereiopods setose ....................... 9
   Chelipeds and pereiopods nude or sparsely setose .................................... *wood-masoni*
9. Propodus and dactylus of third left pereiopod flattened and regularly tesselated .......... *setifer*
   Propodus and dactylus of third left pereiopod not flattened or tesselated .............. *megistos*
10. Chelipeds subequal and similar ....................... *hessi*
    Left cheliped much larger than right ............. 11
11. Inner margin of upper face dactylus of left cheliped marked by sharp crest; outer face of dactylus of third left pereiopod without longitudinal keel .................................... *deformis*
Inner border of upper face of dactylus of left cheliped with row of low tubercles (no crest);
outer face of dactylus of third left pereiopod with longitudinal keel ...................... 12

12. Upper border of outer face of propodus of third left pereiopod defined by sharp keel .......... tinctor
Upper border of outer face of propodus of third left pereiopod not sharply defined ............. asper

**Dardanus arrosor** (Herbst 1796)

*Cancer arrosor* Herbst, 1796: 170

*Pagurus striatus* Latreille, 1804:

*Petrochirus arrosor* Rathbun, 1900: 302

*Pagurus arrosor* Pallary, 1900: 221

*Dardanus arrosor* Rathbun, 1907: 206

MATERIAL EXAMINED:

Nine males, 6-23 mm, *Anton Bruun* Sta. 394B
Six females, 9-17 mm, *Anton Bruun* Sta. 394B
One female, 29 mm, *Anton Bruun* Sta. 423
Two males, 33 and 40 mm, *Anton Bruun* Sta. 463

DIAGNOSIS: Chelipeds with transverse scute-like ridges; major cheliped twice as long as wide.

DESCRIPTION: Shield depressed, somewhat tetragonal, heavily
calcified; rostrum broad, exceeded by antennal angles (Plate I, Fig. 1.). Cardiac plate calcified only in anterior part; posterior part and entire branchiostegites membranous. Eyestalks short, approximately two-thirds anterior margin of shield; strongly dilated distally, cornea occupying one-third of eyestalk, corneal peninsula with prominent tuft of setae distally. Eyescales large, rounded posteriorly, triangular anteriorly, with 2-4 apical teeth; interocular plate separating eyescales. Antennular peduncle exceeding eyestalk by half length of distal article. Antennal peduncle barely exceeding eyestalk; acicle elongate, medial border with 4-5 teeth.

Exopods of second and third maxillipeds with recurved flagellum distally; bases of third maxillipeds approximated, opposing surfaces of coxae heavily calcified. Left cheliped much more massive than right; carpus, propodus and dactylus distinctively sculptured with overlapping setiferous ridges (Plate I, Fig. 2.), fingertips corneous. Right cheliped shorter and more slender than left, sculpture similar to that of left, except scutellations on dactylus more obscure, fingertips corneous. Outer surfaces of second and third pereiopods with scutellations similar to those of chelipeds (Plate II, Fig. 1.). Fourth pereiopod subchelate; propodal rasp elongate; single row of corneous tubercles on ventral margin of dactylus (Plate II, Fig. 2.). Fifth
pereiopods minutely chelate.

Abdomen soft, coiled to right; sixth abdominal tergum strongly calcified, divided by transverse sulcus, posterior of two plates so formed divided by longitudinal furrow; uropods with friction rasps on endopods and exopods, Telson with median posterior notch, both lobes armed with 4-6 marginal spines and fringed with stiff setae.

REMARKS: This species apparently is tolerant of a variety of commensal organisms. The large female from Sta. 423 inhabited a large shell of *Phalium sp.* bearing four large anemones. Several pedunculate barnacles were attached to the shield, chelipeds and maxillipeds. A female from Sta. 394B was heavily parasitized by a copepod. In addition to the *Phalium* shell at Sta. 423, other specimens were found in shells of *Cymatium lotorium* Linn., *Latirus lancea* Gmelin and *Voluta* sp.. The specimens from Sta. 423 represent a range extension for this species. Previously reported on the east coast of Africa as far north as Delagoa Bay, it is now recorded from Mombasa.

RANGE: West Indies to Brazil, Mediterranean Sea and west coast of Africa to Cape of Good Hope, east coast of Africa to Mombasa; Philippine Islands to Australia.
Dardanus guttatus (Olivier 1811)

Pagurus guttatus Olivier, 1811: 640
Pagurus setifer Hess, 1865: 161
Dardanus guttatus Holthuis, 1953: 48

MATERIAL EXAMINED:
One male, 10 mm, Sta. JR-22
Two females, 12 and 11 mm, Sta. JR-35
One male, 5 mm, Andromache Reef, Mombasa

DIAGNOSIS: Body greatly flattened, carapace depressed; shield as wide as long; chelipeds and pereiopods setose, except for prominent bald spot on face of carpi; second and third pereiopods exceeding chelipeds.

DESCRIPTION: Body extremely flat and widened; width of shield equalling or slightly exceeding length; branchiostegites greatly expanded, membranous; cardiac plate uncalcified except in anterior region. Rostrum obsolete, antennal angles prominent; lateral sides of shield with dense fringe of setae. Eyescales separated by interocular plate; anterior lobe rounded, fringed with stiff setae. Eyestalks slightly more than half anterior margin of shield; slightly distally; exceeding antennular peduncles by length of cornea (Plate IV, Fig. 1). Antennal peduncles extend to base of cornea; acicle short, barely reaching base of distal
article; flagellum nude, exceeding tips of periopods.

Second and third maxillipeds with recurved flagellum on exopod; coxae slightly separated. Chelipeds similar and subequal, left slightly larger than right; chelae twice as long as wide, outer face with uniformly scattered cornaceous-tipped spiniform tubercles and tufts of long, stiff setae, except lower margin of left chela densely setose (Plate III, Fig. 2); fingertips corneous. Carpus of chelipeds, second and third pereiopods with large bald white spot on upper face; outer face of carpus, propodus and dactylus of third left pereiopod with regular transverse striations and fringed with dense row of setae (Plate III, Fig. 3). Sternal plates of thorax greatly flattened and widened.

Fourth pereiopod subchelate; dorsal border of three distal articles with dense fringe of setae; propodal rasp ovate; single row of corneous tubercles on ventral margin of dactylus (Plate III, Fig. 4). Fifth pereiopod chelate; propodal rasp extended onto immovable finger; dactylar rasp narrow.

Abdomen soft, coiled to right; appendages typical of genus; a feebly calcified "spur" on left side posterior to third pleopod. Sixth abdominal tergum well calcified; uropods with typical rasps on endopods and exopods; telson asymmetrical to left, posterior margin with median notch, each lobe with 4-7 marginal teeth and fringe of stiff setae.

REMARKS: The combination of a flattened body with a prominent
fringe of setae on the appendages makes this an easily recognized species. The extreme flattening of the body is correlated with the habit of choosing shells with narrow, slit-like apertures. The two specimens from Sta. JR-35 were in shells of *Pterocera chiragra* Linn. and a species of cowrie.

**RANGE:** East coast of Africa and Madagascar throughout Indo-Pacific to Hawaiian Islands.

*Dardanus scutellatus* (Milne-Edwards 1848)

*Pagurus scutellatus* Milne-Edwards, 1848: 62

*Pagurus fabimanus* Dana, 1852: 270

*Dardanus scutellatus* Buitendijk, 1937: 273

**MATERIAL EXAMINED:**

Six males, 4-15 mm, and four females, 8-10 mm, Aldabra Shore Coll.

**DIAGNOSIS:** Left chela with spiniform tubercles near upper margin only, hand of chela with ventral region twisted, thumb deflexed slightly. Propodus of third left pereiopod with outer face moderately flat and set off from upper face by sharp crest; dactylus of third left pereiopod with outer face depressed and longitudinal groove extending full length.
DESCRIPTION: Shield only moderately depressed, length equalling width; rostrum obsolete, exceeded by antennal angles. Cardiac plate calcified only in anterior region; branchiostegites membranous, not greatly expanded. Eye-stalks equal anterior margin of shield; slightly dilated proximally, moderately dilated distally; cornea equal one-sixth of eyestalk; eyescales large, triangular with rounded bases, separated by interocular plate; 3-4 apical teeth. Antennular peduncles short, barely reaching to base of cornea. Antennal peduncles extend to distal third of eyestalks; acicle barely reaching base of distal article, armed with a single subdistal tooth on lateral margin; antennal flagellum nude, exceeding tips of chelipeds and pereiopods.

Left cheliped much larger and longer than right, large chela twice as long as wide, contributing over half length of appendage, outer face strongly convex, with low granular tubercles becoming spiniform near dorsal border. Ventral margin sinuous, immovable finger slightly deflexed; movable finger short, less than half length of hand; finger-tips corneous. Carpus of left cheliped trigonal in outline; three spiniform teeth on dorsal margin. Right cheliped extending to midway between base of major chela and articulation of finger. Length-width ratio of chela 2:1, movable finger long, more than half length of chela, two rows of corneous-tipped spines on dorsal face; outer face of chela
and fingers with scattered tufts of long setae; fingertips corneous. Propodus of third left pereiopod with outer face slightly flattened and set off from upper face by distinct keel; dactylus with outer face concave and a longitudinal sulcus extending entire length. Propodal rasp of fourth pereiopod a narrow oval; row of corneous tubercles on ventral margin of dactylus. Fifth pereiopods chelate; propodal rasp extended onto fixed finger; dactylar rasp narrow. Gills and genitalia typical of genus.

Abdomen soft, terga hardly distinguishable except fifth and sixth; pleopods typical of genus; telson with posterior median notch, left lobe markedly longer than right, margins not denticulate. Pigmentation of preserved specimens consisting of blotches of orange on anterior of shield, dorsal faces of articles of chelipeds and second and third pereiopods; these blotches marked with white punctae. Distal article of antennal peduncle with longitudinal line of pigment on dorsal surface; eyestalks without evidence of pigmentation.

REMARKS: The short synonymy of this species indicates that it is an easily recognized species. The two forms, with the names *Pagurus scutellatus* and *P. fabimanus* were shown by Buitendijk (1937) to be distinguishable only by relatively minor differences in the shape and armature of the chelipeds and pereiopods. Fize and Serene (1955) pointed out
that these differences might be correlated with the type of shells chosen by the animals, making the two species synonymous.

RANGE: East coast of Africa, Zanzibar, Aldabra, Mauritius, Philippine Islands, Fiji Islands and Tahiti.

**Dardanus lagopodes** (Forskal 1775)

- *Cancer lagopodes* Forskal, 1775: 93
- *Pagurus sanguinolentus* Quoy and Gaimard, 1824: 532
- *Pagurus affinis* H. Milne-Edwards, 1836: 274
- *Pagurus euopsis* Dana, 1852: 542
- *Pagurus depressus* Heller, 1861: 248
- *Dardanus helleri* Paulson, 1875: 90
- *Dardanus euopsis* Buitendijk, 1937: 275
- *Dardanus sanguinolentus* Gordon, 1955: 315 (literature)
- *Dardanus affinis* Gordon, 1955: 312 (literature)
- *Dardanus lagopodes* Lewinsohn, 1969: 32

**MATERIAL EXAMINED:**

One male, 11 mm, Anton Bruun Sta. 19
One male, 6 mm, Anton Bruun Sta. 412-D
Four males, 6-14 mm, and five females, 9-19 mm, Aldabra (shore collection)
Two males, 10 and 6 mm, Nossi Be, Madagascar (coll. M. L. Wass)
One male, 15 mm, Andromache Reef, Mombasa
One male, 11 mm, Sta. JR-16
One male, 19 mm, Sta. JR-20
Two males, 14 and 19 mm, Sta. JR-22
One male, 14 mm, Sta. JR-25B
Two females, 19 and 20 mm, Sta. JR-35
One male, 18 mm, Te Vega Sta. 34

DIAGNOSIS: Carapace moderately to strongly depressed; eyestalks equalling length of anterior margin of shield; propodus and dactylus of third left pereiopod unmodified; distal articles of antennal flagellum gibbous.

DESCRIPTION: Carapace moderately to strongly (var. depressus) depressed, shield barely longer than wide; cardiac plate uncalcified except in extreme anterior region; rostrum broad, exceeded by antennal angles. Eyestalks slightly exceed length of anterior margin of shield, slightly dilated distally. Eyescales triangular, 3-4 apical teeth interspersed with stiff setae; eyescales separated by interocular plate. Antennular peduncles short, not reaching base of cornea. Antennal peduncles barely reaching midway on eyestalks; acicle short, extending only to base of distal article, 3-4 teeth on lateral margin; antennal flagellum long, exceeding tips of chelipeds and pereiopods, medio-distal angle of distal articles produced, giving the flagellum a
"notched" appearance. Base of third maxillipeds slightly separated; exopods of second and third maxillipeds with recurved flagellum at tip; crista dentata on ischium of third maxillipeds.

Chelipeds of approximately equal length, but left cheliped more massive; length-width ratio of chela 2:1, outer face of hand and fingers with scattered spiniform tubercles, each associated with tuft of long stiff setae; fingertips corneous; carpus with prominent spine near middle of disto-dorsal margin. Right cheliped similar to left but less massive. Second and third pereiopods long, exceeding chelipeds by half length of dactylus; distal margin of carpi with corneous-tipped spines; propodus and dactylus with numerous corneous-tipped spines, each almost obscured by tuft of setae arising from its base. Fourth pereiopods subchelate; propodal rasp a narrow oval; dactylus with 3-4 corneous tubercles on ventral margin. Fifth pereiopods chelate, propodal rasp continued onto finger as narrow line of scales; dactylus with narrow rasp. Sternal plates of posterior thorax greatly expanded. Fourteen pairs phyllobranchiate gills. Male with pair of gonopores on coxae of fifth pereiopods; female with pair of gonopores on coxae of third pereiopods.

Abdomen soft, coiled to right; terga of males hardly distinguishable, four uniramous pleopods on left side; terga of females more heavily calcified, widely separated;
four pleopods on left side, three triramous, one uniramous. Sixth tergum and telson well calcified; uropods with well-developed rasps on both rami; telson with posterior margin divided by median notch, left lobe more elongate, with 5-7 marginal teeth; both lobes fringed with stiff setae.

REMARKS: The variation observed in the degree of flattening of the body evidently results from environmental factors, most logically the type of shell chosen as the carcinoecium. All of the specimens in the present collection were removed from their shells prior to preservation, so a definite test of this presumed correlation cannot be made. Lewinsohn (1969) stated that the "depressus" form is usually found in shells with small apertures.

RANGE: East coast of Africa, Madagascar, Aldabra, Mauritius, the Red Sea and Gulf of Aden, Andaman Islands, Malaysia to Fiji Is.

**Dardanus wood-masoni** (Alcock 1905)

**Pagurus wood-masoni** Alcock, 1905: 85

**Dardanus wood-masoni** Gordan, 1956: 316

MATERIAL EXAMINED:

One male, 11 mm, Sta. JR-19
DIAGNOSIS: Eyestalks slightly exceeding antennular peduncles, slightly dilated distally; left cheliped massive, outer face spinose, ventral border dentate; outer face of dactylus of third left pereiopod with longitudinal groove.

DESCRIPTION: Carapace moderately depressed; shield slightly longer than wide; cardiac plate calcified only in anterior region; branchiostegites soft, membranous. Rostrum obsolete, antennal angles obtuse. Eyescales triangular, bases rounded, separated by interocular plate, medial borders convergent, apices with 4-5 teeth on lateral margin. Eyestalks slightly exceed antennular peduncles, cornea only slightly dilated. Antennal peduncles reaching only to base of cornea, acicle narrowly triangular, 2-3 teeth on medial border; flagellum long, nude, distal articles somewhat gibbous. Left cheliped of specimen missing; Right cheliped slender, length-width ratio of hand slightly greater than 2:1, outer face and fingers with numerous procurred spines and tufts of setae, fingertips corneous and extending back along fingers to form cutting edges; outer face of carpus spinose. Second and third pereiopods slender, faces of distal articles setose; outer face of dactylus of third left pereiopod with longitudinal groove and spinose upper margin. Fourth pereiopod subchelate; propodal rasp extending beneath edge of dactylus; tip of dactylus corneous. Fifth pereiopod chelate; propodal rasp continued onto finger
as narrow line; dactylar rasp broad, narrowing distally.

Abdomen soft and coiled to right; terga widely separated; pleopods of both sexes typical of genus.

REMARKS: This species is closely related to *D. scutellatus* Milne-Edwards from which it is distinguished principally by the spinose condition of the chelipeds. Alcock (1905) described the left cheliped as follows: "Left cheliped vastly the larger, its length measured in a straight line (chord) is about twice that of the sagittal line of the carapace; its hand, which is long and comparatively narrow, is inclined inwards somewhat as in *Diogenes miles*; the merus has its borders spinose, especially the cristiform inner border; the wrist has its inner border and the lower part of its outer surface spinose; the hand and dactylus are abundantly spinose on the outer and upper surface, the spines on the inner border being enlarged and those of the lower border forming a serrate crest." Fize and Serene (1955) suggested that this species may be merely a "spinose form" of *D. scutellatus*. This record of *D. wood-masoni* from Madagascar represents a major range extension of this species, it having previously been reported from the Philippines and Vietnam westward to the Andaman Islands and the Maldives.
Dardanus setifer (H. Milne-Edwards 1836)

**Pagurus setifer** H. Milne-Edwards, 1836: 274

**Pagurus sculptipes** Stimpson, 1859: 246

**Pagurus pavimentatus** Hilgendorf, 1878: 816

**Dardanus setifer**, Gordan, 1956: 316 (literature)

**MATERIAL EXAMINED:**

One male, 10 mm *Anton Bruun* Sta. 372C

One female, 10 mm *Anton Bruun* Sta. 393A

Two males, 8 and 9 mm, *Anton Bruun* Sta. 400C

One male, 9 mm, *Anton Bruun* Sta. 403A

One female, 7 mm, Sta. JR-19

**DIAGNOSIS:** Shield only slightly longer than wide; eyestalks three-fourths length of anterior margin of shield; antennal flagellum with distal articles gibbous; left cheliped larger, ventral portion of chela less setose than remainder; propodus and dactylus of third left pereiopod remarkably flattened and regularly tesselated.

**DESCRIPTION:** Carapace somewhat depressed; shield barely longer than wide. Cardiac plate uncalcified except in extreme anterior part. Rostrum obsolete, exceeded by antennal angles. Eyestalks three-fourths length of anterior margin of shield, slightly dilated at base, moderately dilated distally; eyescales large, triangular with
bases rounded, 2-3 apical teeth; separated medially by interocular plate. Antennular peduncles equalling eye-stalks. Antennal peduncles short, barely reaching base of cornea; acicle short and setose, barely exceeding base of distal article; antennal flagellum long, exceeding tips of chelipeds and pereiopods; distal articles with disto-medial angles produced, giving flagellum a "notched" appearance. Bases of third maxillipeds slightly separated; low crista dentata on medial surface of ischium.

Left cheliped considerably larger and longer than right; length-width ratio of chela 1.8:1, outer face without spines but long setae uniformly scattered over face; upper margin of propodus with row of 4-5 teeth; lower margin a row of rounded tubercles with narrow spaces between. Both fingers of chela with 2-3 calcareous teeth; fingertips corneous. Right cheliped more slender than left; hand slightly more than twice as long as wide; ventral border smooth; corneous tips of fingers extended as cutting edges for one-third length of fingers. Second and third pereiopods reaching tip of major cheliped, surfaces of articles with scattered stiff setae. Outer face of propodus of third left pereiopod with longitudinal keel separating an upper and lower concave portion; this keel and these surfaces regularly crossed by transverse striations; dactylus with similar sculpture, but keel less prominent. Fourth pereiopod subchelate; propodal rasp a
narrow oval extending beneath ventral edge of dactylus; dactylus with 3-4 corneous-tipped teeth on ventral edge. Fifth pereiopod minutely chelate; propodal rasp hardly extended onto finger; dactylar rasp very narrow. Male and female genitalia typical of genus.

Abdomen soft, coiled to right; terga uncalcified, hardly distinguishable; female with four pleopods on left, three biramous and one uniramous; male with four uniramous pleopods on left. Sixth abdominal tergum well calcified; uropods with well developed rasps; telson lightly calcified, posterior margin with median notch, left lobe slightly longer.

REMARKS: This species is closely allied to *D. guttatus*, sharing with it the remarkably sculptured third left pereiopod and the flattened body form. *Dardanus setiferus* may easily be distinguished from *D. guttatus* by the lack of spiniform tubercles on the outer face of the major chela and the absence of a dense fringe of setae on the third left pereiopod. In all other respects, the two species are very similar. The specimens from Sta. 400C were in shells of *Murex* sp., one of which was host to a commensal pedunculate barnacle attached deep within the shell. The specimen from Sta. 403A was living in a *Fusinus* sp. shell.

RANGE: East coast of Africa, Madagascar, Ceylon, India
and throughout the Indo-Pacific region to Australia and Hong Kong.

**Dardanus megistos** (Herbst 1804)

- *Cancer megistos* Herbst, 1804: 23
- *Pagurus punctulatus* Olivier, 1811: 641
- *Pagurus megistos* Stebbing, 1908: 21
- *Dardanus megistos* Rathbun, 1907: 205

**MATERIAL EXAMINED:**

- One female, 31 mm, Anton Bruun Sta. HA-16
- One female (ovig.), 44 mm, Sta. JR-3
- One female, 29 mm, Sta. JR-17
- One male, 22 mm, Sta. JR-20
- One female, 17 mm, Sta. JR-22
- One female, 34 mm, Sta. JR-34A
- One female, 14 mm, Sta. JR-36
- Two males, 22 and 24 mm, Aldabra (shore coll.)
- One female, 25 mm, Small island SW of Fedu Addu Atoll

**DIAGNOSIS:** Left chela much larger than right; chelipeds and pereiopods covered with long stiff bristles; eyestalks equalling antennular peduncles; cardiac plate calcified except at posterior extremity; branchiostegites feebly calcified, with tufts of setae in longitudinal rows.
DESCRIPTION: Shield strongly calcified, elongate tufts of bristles on sides and front, rostrum obsolete, antennal angles prominent, (Plate IV, Fig. 1). Cardiac plate strongly calcified, except for posterior one-fourth, tufts of setae in two longitudinal rows. Branchiostegites feebly calcified, with tufts of stiff setae arranged in longitudinal rows. Eyescales large, triangular, with rounded bases and 2-3 apical teeth interspersed with stiff setae; interocular plate separating eyescales. Eyestalk equals three-fourths anterior margin of shield, cylindrical; corneal region slightly dilated. Antennular peduncles barely reaching base of cornea; acicle short, barely reaching base of distal article, a single tooth and several tufts of setae on mesial margin. Antennal flagellum long, nude, extending to tips of chelipeds and pereiopods. Exopods of second and third maxillipeds with recurved flagella; base of third maxillipeds approximated; crista dentata of corneous tubercles.

Left cheliped extremely massive, chela comprising half length of appendage. Length-width ratio of hand 1.5:1, outer face strongly convex, armed with scattered corneous spines, each spine with a tuft of setae arising from base; dorsal margin of hand armed with 4-5 procurred spines; ventral border with stiff setae (Plate IV, Fig. 2). Finger and thumb armed with low calcareous teeth, forming a relatively straight edge; corneous fingertips extended back...
along fingers to form short cutting edges; inner face of thumb and finger flat. Outer face of carpus with spination similar to the chela, dorsal margin with 3-4 spines; medio ventral margin of merus and ischium armed with series of corneous spines. Right cheliped much smaller than left, chela twice as long as wide, armed with spines and bristles in same manner as left; corneous fingertips forming cutting edge as in left, inner surfaces of fingers curved, not meeting when chela is closed, (Plate V, Fig. 1). Second and third pereiopods slender and somewhat compressed; dactylus and propodus covered by long stiff setae, carpus and merus setose only on dorsal margins (Plate V, Fig. 2). Fourth pereiopod subchelate; propodal rasp twice as long as wide, continuing beneath ventral edge of dactylus; dactylus with 4-5 corneous tubercles on ventral edge, (Plate V, Fig. 3). Propodal rasp of fifth pereiopod continued onto thumb as a single row of scales; dactylar rasp short, partially obscured by setae. Gills and genitalia typical of genus.

Abdomen soft, coiled to right; terga 1-5 feebly calcified and widely separated; three unpaired biramous pleopods and one uniramous pleopod on left side in female; four uniramous pleopods on left side of male. Sixth tergum well calcified, uropods well-developed, left longer; telson strongly calcified, posterior margin with median notch, left lobe twice as long as right, posterior margin not denticulate.
In alcohol, chelipeds and pereiopods deep orange, more pale on proximal articles; shield pale orange; all orange areas marked by distinct white punctae with dark borders. Eyestalks uniformly dark maroon, eyescales orange.

REMARKS: The large size, distinctive coloration and setose appendages make this an easily recognized species. Only one specimen in the collection exhibited any variation; a specimen from Sta. JR 34A in which the orange ground color and white punctae were not distinguishable. It seems unlikely that the preservative would have affected this specimen differently, therefore it is assumed that this specimen represents a form in which the normal pigmentation does not develop.

RANGE: East coast of Africa, Red Sea, throughout Indo-Pacific to Australia and Hawaii.

**Dardanus hessi** (Miers 1884)

*Pagurus hessii* Miers, 1884: 185

*Pagurus similimanus* Henderson, 1888: 59

*Pagurus hessi* Fize and Serene, 1955: 214

*Dardanus hessi* Gordan, 1956: 314
MATERIAL EXAMINED:

One male, 23 mm, Anton Bruun Sta. 260A
One male, 21 mm, Anton Bruun Sta. 262A
One female, 22 mm, Anton Bruun Sta. 266A

DIAGNOSIS: Eyestalks equalling antennular peduncles; cornea strongly dilated and flattened; chelipeds subequal and similar.

DESCRIPTION: Shield and carapace moderately flattened; branchiostegites not markedly expended. Rostrum broad, partially obscured by tuft of setae, exceeded by antennal angles. Eyescales large, postero median angles appressed to interocular plate; posterior margins a smooth curve extending laterally and anteriorly from their contact with interocular plate; triangular lobe arising from antero-medial margin with 3-4 apical teeth. Eyestalks equal antennular peduncles; greatly dilated distally and flattened on dorsal surface; cornea large with broad corneal peninsula. Antennal peduncle equals eyestalks; acicle narrow, armed with 2-4 teeth on medial border; extending to base of distal article. Third maxillipeds with corneous crista dentata on medial face of ischium. Chelipeds subequal, similar shape and sculpture. Chelae twice as long as wide, finger half length of hand; outer face of hands with rows of cornaceous-tipped spines and tufts of long bristles, dorsal margin
with procurred spines, ventral margin with low, rounded tubercles. Dactylus with scattered tufts of setae and row of spines on dorsal margin; tips of both fingers corneous, extending back along opposing margins to form cutting edges. Carpi of chelipeds with row of corneous spines on dorso-medial border and two rows of spines parallel to dorso-medial border on upper face; meri with 3-4 spines on disto-dorsal margin and one spine subdistal on dorsal face. Second and third pereiopods long, exceeding chelipeds by length of dactylus; dactyli very slender, 2-4 spines on dorsal proximal margin, entire dorsal surface with long setae; ventral surface of carpi of left pereiopods with 5-8 low rounded tubercles. Fourth pereiopods subchelate; propodal rasp a narrow oval; dactylus with 3-5 small corneous tubercles on ventral margin. Fifth pereiopods chelate, propodal rasp extended onto thumb, dactylar rasp reduced.

Abdomen soft, coiled to right; terga 1-5 of female calcified and only slightly separated; those of male hardly calcified and rather widely separated; pleopods of both sexes typical of genus. Sixth tergum strongly calcified in both sexes, uropods with well-developed rasps on endopods and exopods. Telson with left lobe slightly larger, margin of both lobes feebly denticulate and setose.

After eight to nine years in alcohol, entire body a light cream except deep orange on distal region of chelae
and ventral surfaces of carpi and dactyli of second and third pereiopods. Tubercles on ventral surfaces of left carpi light cream in contrast to deep orange surrounding them. Eyestalks show evidence of darker pigmentation, but original color indeterminable.

RANGE: Gulf of Oman, coasts of India, Thailand, Indonesia, throughout the Celebes Sea and Arafura Sea. The three stations at which this species was collected are all in the Gulf of Oman, where this species was previously reported by Thompson (1943).

*Dardanus deformis* (H. Milne-Edwards 1836)

*Pagurus deformis* H. Milne-Edwards, 1836: 272

*Dardanus deformis* McNeill, 1927: 303

MATERIAL EXAMINED:

- One female, 10 mm, Sta. HA-2
- One male, 21 mm, Sta. HA-8
- One male, 13 mm, Sta. HA-19
- One female, 17 mm, Sta. HA-20
- One male, 20 mm, and two females, 18 and 32 mm, Sta. JR-22
- One male, 19 mm, Sta. JR-29
- One female, 13 mm, Sta. JR-36
One male, 22 mm, and one female, 12 mm,
Aldabra (Shore Coll.)
One male, 15 mm, Tulear, Madagascar (offshore reef)
One female, 30 mm, Te Vega Sta. 98

DIAGNOSIS: Eyestalks short, one-half length of anterior margin of shield; dorsal margin of dactylus of major chela with keel-like crest; outer face of propodus of third left pereiopod sharply separated from dorsal face by a keel; outer face lacking longitudinal keel; males with openings on coxae of third pereiopods corresponding to female gonopores.

DESCRIPTION: Shield longer than wide; rostrum very broad, antennal angles prominent and exceeding rostrum; cardiac plate and branchiostegites calcified only in anterior region. Eyescales triangular with bases rounded, separated by interocular plate, apices convergent, 4-5 teeth distally on lateral margin. Eyestalks extremely short, strongly dilated and flattened distally, cornea reniform with pronounced corneal peninsula. Antennular peduncles exceeding the eyestalks by two-thirds of terminal article. Antennal peduncles barely exceeding eyestalks; acicle narrow, curved and armed with 4-5 teeth on medial margin; flagellum nude, not extending to tips of chelipeds or pereiopods. Exopods of second and third maxillipeds with recurved terminal flagellum; ischium of third maxillipeds with corneous crista
dentata on medio-dorsal margin and three prominent teeth on medio-ventral margin. Left cheliped much larger and longer than right; carpus trigonal, dorsal surface with scattered spiniform tubercles, medio-dorsal margin with three procurved spines; length-width ratio of chela 2:1, outer face smooth, except for one row of tubercles parallel to axis of hand; dorsal margin of hand flattened and armed with spiniform tubercles; ventral margin with row of low, rounded tubercles. Dorsal margin of dactylus with sharp crest, fingertips corneous. Right cheliped setose, two rows of corneous-tipped spines on dorsal margin of carpus and propodus; length-width ratio of chela 2:1; fingers with corneous tips extended back to form cutting edges. Second and third pereiopods long, exceeding chelipeds; dactyli longer than propodi and covered with scattered tufts of setae; propodus of third left pereiopod with outer face flattened, dorsal and ventral margins sharply cristate; a longitudinal groove on outer face of dactylus, upper margin of face with denticulate crest. Fourth pereiopods subche­late; propodal rasp elongate and continuing beneath ventral edge of dactylus; dactylus with row of corneous tubercles on ventral margin. Fifth pereiopods chelate; propodal rasp not continued onto finger; dactylar rasp reduced. Genitalia of male a pair of gonopores on coxae of fifth pereiopods, plus a pair of openings resembling female gonopores on coxae of third pereiopods. Female genitalia typical of genus.
Abdomen coiled to right; terga of female feebly calcified and widely separated, those of males uncalcified and hardly distinguishable. Pleopods typical of genus, except that those of male are considerably reduced. Sixth tergum well calcified in both sexes, uropods well developed, with prominent rasps; telson with median posterior notch, left lobe only slightly longer, 2-3 marginal denticles and fringe of setae; right lobe not denticulate, marginal setae only.

REMARKS: Males of this species are unique in possessing a pair of accessory openings on the coxae of the third pereopods apparently corresponding to the female gonopores. Because of this, the sexes are most easily distinguished by observing the pleopods rather than the gonopores. This species apparently selects shells with large apertures for their carcinoecia; the specimen from Sta. HA-8 was found in a shell of Casmarea achatina which also carried four commensal anemones. The specimens from Sta. HA-20 were in shells of Phalium sp. and Cymatium sp., each of which also bore several commensal anemones. The large female from Te Vega Sta. 98 was in a shell of Tonna olearium.

RANGE: East coast of Africa, Red Sea, Indian seas and the Indo-Pacific region eastward to Tahiti.
**Dardanus asper** (DeHann 1849)

**Pagurus asper** DeHaan, 1849: 208

**Dardanus haani** Rathbun, 1903: 34

**Pagurus haani** Laurie, 1926: 158

**MATERIAL EXAMINED:**

One female (ovig.), 15 mm, *Anton Bruun* Sta. 409C

(removed from stomach of *Carcharinus leucas*)

One male, 21 mm, *Anton Bruun* Sta. 445

One female, 26 mm, Tulear, Madagascar

One male 32 mm, Mauritius (rotenone station)

One male, 38 mm, Patong Phuket, Thailand

**DIAGNOSIS:** Eyestalks short, cornea strongly dilated; no crest on dorsal face of dactylus of major cheliped; border between upper face and outer face of propodus of third left pereiopod not sharply defined.

**DESCRIPTION:** Carapace moderately depressed; shield strongly calcified; anterior portion of cardiac plate strongly calcified; posterior less so; branchiostegites show calcification in parallel lines on either side of cardiac plate, membranous laterally and posteriorly. Rostrum obsolete, antennal angles prominent. Eyescales triangular, bases widely separated by interocular plate; medial borders convergent; antero-lateral borders with six teeth. Eyestalks
short, half length of anterior border of shield; strongly
dilated distally and flattened; cornea occupying almost
half the length. Antennular peduncles exceed the eyestalks
by two-thirds distal article. Antennal peduncles barely
exceed eyestalks; acicles broad posteriorly, sharply nar-
rowed distally, extending beyond base of distal article,
three teeth on medial border. Antennal flagellum nude,
barely reaching tip of major cheliped. Second and third
maxillipeds with setose flagellum on exopods; ischium of
third maxilliped with well-developed crista dentata. Left
cheliped extremely massive; chela half length of cheliped;
length-width ratio of hand 1.5:1, outer face inflated,
uniformly covered with low calcareous tubercles; dorsal
margin with longitudinal row of calcareous tubercles; inner
face of hand with 3-4 longitudinal rows of setae. Dactylus
with row of low tubercles on dorsal face, but not forming
crest; outer face randomly tuberculate, inner face sparsely
setose; fingertips corneous. Carpus trigonal, dorso-medial
border with three prominent procurred spines, outer face
sparsely spinose; medio-ventral border produced and blade-
like, armed with 6-8 denticles. Minor cheliped short,
reaching only to middle of dorsal border of major chela;
length-width ratio of minor chela 2.5:1, outer face smooth,
with 2-3 rows of setae; dactylus half length of chela;
fingertips corneous, forming short cutting edges. Second
pereiopod extending only to base of dactylus of major
cheliped. Third pereiopod extending to tip of major chela; propodus and dactylus sparsely setose on dorsal and medial faces. Outer face of dactylus of third left pereiopod with longitudinal keel extending full length and a serrulate crest on dorsal border; upper margin of outer face of propodus not sharply defined. Fourth pereiopods subchelate; propodal rasp extending beneath edge of dactylus; row of dark corneous tubercles on ventral margin of dactylus. Fifth pereiopods chelate; propodal rasp extended onto immovable finger; dactylar rasp well-developed. Gills and genitalia typical of genus.

Abdomen soft; terga feebly calcified, well separated, pleopods in both sexes typical of the genus. Sixth abdominal tergum strongly calcified; uropods more developed on left; telson with posterior margin bilobed, left larger, margins of both lobes setose, not denticulate.

In life, shield purple on sides and anterior, gastric region shading to yellow posteriorly; antennal angles yellow, eyescales reddish-purple, eyestalks banded with brick red; chelipeds and pereiopods purple with irregular spots of cream or white.

RANGE: East coast of Africa from Delagoa Bay to Cape Guardafui, Madagascar, India and Indonesia to Australia and Hawaii.
REMARKS: The ovigerous female from Sta. 409C, collected from the stomach of a bull shark (*Carcharinus leucas*) was found in the shell of *Fusinus* sp.; the male from Sta. 445 was in a *Cymatium* sp. shell; the Patong Phuket specimen was in a *Tonna olearium* shell. While these shells vary greatly in overall shape, all possess a large, round aperture. The massive left cheliped of *D. asper* probably limits it to shells of this type.

*Aniculus* Dana 1852

Chelipeds similar and subequal; chelipeds and second and third pereiopods with regular transverse, scute-like ridges. Fingertips corneous and deeply spooned. Fourth pereiopod subchelate, fifth pereiopod chelate. Abdomen soft, coiled to right; terga widely separated. Female pleopods biramous, the fourth reduced in overall size and one ramus rudimentary; first three pleopods with leaf-like bract on peduncles and enclosed within brood flap. Fourteen pairs of phyllobranchiate gills as in *Dardanus*.

Key to the Indo-Pacific Species of *Aniculus*

1. Eyestalks shorter than anterior border of shield; chelipeds scutellate, but not spinose .......... *aniculus*
   Eyestalks exceed anterior border of shield; chelipeds with corneous spines on dorsal and distal regions ......................... *acanthochirus*
Aniculus acanthochirus, new species

MATERIAL EXAMINED:

One female, 10 mm, Té Vega Sta. 34 (Holotype)

DIAGNOSIS: Carapace not depressed, shield longer than wide; eyestalks long, equalling length of shield and exceeding antennular peduncles. Chelipeds with rows of corneous spines on transverse ridges, most numerous distally (Plate VI, Fig. 2). First three pleopods of female with foliaceous bract arising from peduncle; membranous flap arising from left side of abdomen and enclosing first three pleopods.

DESCRIPTION: Carapace not markedly flattened, shield moderately convex dorsally; cardiac plate and branchioste-gites calcified only on anterior border. Rostrum broadly triangular, equalling antennal angles. Sides of shield sparsely setose; a prominent tuft of setae directly posterior to each antennal angle (Plate VI, Fig. 1). Ey-scales broadly triangular, bases rounded, apices convergent, not denticulate. Eyestalks extremely long, equalling length of shield, twice length of antennal peduncles and exceeding length of antennular peduncles; strongly dilated at base, narrowest medially, cornea dilated. Few scattered setae near base of eyestalks. Antennal peduncle setose, acicle extending beyond base of distal article; flagellum
nude, reaching to tips of chelipeds. Exopods of second and third maxillipeds with terminal recurved flagella; crista dentata present. Chelipeds similar and subequal, right very slightly the larger; articles sculptured with regular, transverse scutellations fringed with short cilia on their distal margins. These ridges on the dorsal and disto-lateral regions of chelae armed with regularly spaced, corneous spines. Long, white-tipped setae scattered among these spines. Opposing faces of the fingers curved, not touching, except at the deeply spooned and corneous tips (Plate VI, Fig. 2). Carpus, propus and dactyli of second and third pereiopods with scutellations similar to chelipeds, but more obscure and lacking corneous tips; dactyli shorter than propi, tips corneous. Fourth pereiopod subchelate; propodal rasp broadly oval, ventral margin serrulate; dactyli with row of corneous tubercles on ventral margin, terminating in corneous claw (Plate VI, Fig. 3). Fifth pereiopod chelate; propodal rasp occupying distal half of propodus and extending onto thumb; dactyli narrow and restricted to edge of finger. Fourteen pairs phyllobanchiante gills, arranged as in Dardanus. Female gonopores paired, on coxae of third pereiopods.

Abdomen soft, membranous and coiled to right; terga hardly calcified. Segments 2-4 in female with a single pleopod on left side, biramous with a foliaceous membrane hooping
and partially enclosing the two rami (Plate VI, Fig. 4). A thin membranous brood flap originating on fourth somite and extending forward to envelop the bases of the pleopods and dorsally to completely enfold the pleopods. Fifth somite bears a small biramous pleopod in which one ramus is so reduced as to appear uniramous. Sixth abdominal tergum well calcified; uropods well developed, longer on left side; rasps on exopods and endopods well developed. Telson with median notch in posterior margin, left lobe more produced; margins setose.

Color of preserved specimen uniformly pale reddish-yellow over carapace and appendages, except dull purple on distal half of eyestalks. Setae on carapace and appendages deep rust-red with white tips.

REMARKS: This species is closely allied to A. aniculus with which it shares the foliaceous bracts on the female pleopods and the membranous brood flap. The principal differences are the longer eyestalks and the spinose chelipeds. The male of this species is unknown. The specific name is derived from the Greek, acanthus: spine and chiros: hand, alluding to the spinose condition of the chelae. The holotype is deposited in the U. S. National Museum.

RANGE: Known only from the type locality, Vanikoro Island (11° 42' S, 167° 07' E.).
**Trizopagurus** Forest 1952

Chelipeds similar and subequal; chelipeds and second and third pereiopods with regular transverse scutellated ridges. Dorsal and inner face of chelipeds with stridulation organs consisting of longitudinally elongate tubercles arranged in transverse rows corresponding to the ridges characterizing the remainder of chelipeds. Finger-tips corneous and deeply spooned. Antennal flagella sparsely setose. Thirteen pairs of phyllobranchiate gills. Four unpaired biramous pleopods on left side in both sexes, those of male with one ramus greatly reduced.

Key to the Indian Ocean Species of **Trizopagurus**
1. Carapace not markedly depressed; eyestalks much longer than anterior border of shield ....... *tenebrarum*
   Carapace greatly depressed and flattened ............ 2
2. Eyestalks barely equalling anterior border of shield ........................................... *strigatus*
   Eyestalks slightly exceeding length of anterior border of shield .......................... *kremphi*

**Trizopagurus tenebrarum** (Alcock 1905)

*Aniculus tenebrarum* Alcock, 1905: 96

**Trizopagurus tenebrarum** Forest, 1952b: 17
MATERIAL EXAMINED:
One female, 3 mm, Anton Bruun Sta. 444
One female, 2.5 mm, Anton Bruun Sta. 442
One male, 4 mm, Anton Bruun Sta. 18-A

DIAGNOSIS: Shield not markedly flattened; longer than broad; eyestalks slender, equalling length of shield and extending beyond antennular peduncles. Antennal peduncles short, barely reaching midpoint of eyestalks; acicle extending nearly midway on terminal article; flagellum short, reaching only to base of fingers of chelipeds.

DESCRIPTION: Shield strongly calcified, slightly longer than wide. Cardiac plate and branchiostegites membranous and translucent, calcified only in proximity of cervical groove. Rostrum broadly triangular, extending only to the level of the equally broad antennal angles. Eyescales small, triangular and approximated; eyestalks slender, equalling length of shield, dilated proximally and distally, narrowed medially; corneal peninsula short, triangular. Antennular peduncles short, barely reaching halfway on eyestalks; acicle narrowly triangular, with three teeth on medial border, reaching middle of distal article of peduncle; antennal flagellum short, reaching only to base of dactylus of chelipeds (Plate VII, Fig. 1). Chelipeds similar and subequal; merus, carpus, propodus and dactylus regularly
scutellated, each scute-like ridge with a distal fringe of setae (Plate VII, Fig. 2,3). Length-width ratio of chelae 2:1, fingers less than half length of hand, tips corneous and deeply spooned. Second and third pereiopods with sculpture similar to chelipeds, ridges becoming obscure on dactylus. Propodus and dactylus with tufts of long setae scattered sparsely on dorsal and ventral surfaces (Plate VII, Fig. 4). Fourth pereiopods subchelate; scales on ventral edge of propodal rasp produced and forming serrate margin; dactylus with black corneous tip; dorsal margin of propodus and dactylus with tufts of long setae. Fifth pereiopods chelate; propodal rasp barely extended onto base of thumb; dactylus with narrow rasp. Gills and male and female gonopores typical of genus.

Abdomen soft, coiled to right, terga feebly calcified and widely separated; four biramous pleopods on left side in female, male with one ramus of pleopods reduced. Sixth abdominal tergum well calcified, uropods longer on left, rasps on exopods and endopods well developed. Telson feebly calcified; lateral margins almost parallel, each with a small notch; posterior margin with median notch, left lobe slightly longer; margins with fringe of stiff setae, not denticulate.

Color of preserved specimens unremarkable, except for bands of orange pigment associated with ridges on chelipeds and pereiopods; dactyli of pereiopods more or less
mottled with the same deep orange pigment. Dorsal surface of eyestalks pigmented, ventral surface white.

REMARKS: These specimens, although much smaller, agree very closely with Alcock’s (1905) original description, differing principally in the degree of pigmentation remaining after preservation.

RANGE: Cape Comorin, Gulf of Aden and Cape Guardafui.

**Trizopagurus strigatus** (Herbst 1804)

*Cancer strigatus* Herbst, 1804: 25
*Pagurus strigatus* Olivier, 1911: 647
*Aniculus strigatus* Henderson, 1893: 422
*Trizopagurus strigatus* Forest, 1952b: 19

MATERIAL EXAMINED:

One male, 3 mm, *Anton Bruun* Sta. 408-D
One female, 7 mm, Andromache Reef, Mombasa
One male, 4 mm, Aldabra (shore collection)

DIAGNOSIS: Carapace and body greatly flattened and depressed; shield broader than long; anterior border almost straight, rostrum obsolete, antennal angles absent. Eyescales separated, eyestalks shorter than anterior margin of shield.
DESCRIPTION: Carapace and body extremely flattened, shield slightly wider than long, rostrum extremely reduced, antennal angles completely absent (Plate VIII, Fig. 1). Cardiac plate calcified only in anterior region; branchiostegites greatly expanded, calcified only in vicinity of cervical groove. Eyescales widely separated, triangular, apex armed with 3-4 teeth; eyestalks cylindrical, shorter than anterior margin of shield, slightly dilated proximally, hardly at all distally, cornea small, less than one-eighth length of eyestalk, corneal peninsula short, hardly distinguishable. Antennular peduncles very short, reaching only two-thirds length of eyestalks. Antennal peduncles slightly exceeding midpoint of eyestalks; acicle triangular, 1-3 denticles on lateral border, extending slightly less than halfway distal article; antennal flagellum short, slightly exceeding base of chelae, each article with two setae. Coxae of third maxillipeds somewhat separated due to flattening of body; crista dentata of low corneous denticles. Flagellum on exopod of second maxilliped reduced, that of third maxilliped normally developed. Chelipeds subequal; regularly marked with low, imbricating transverse ridges, each with a distal fringe of short setae; length-width ratio of chelae 1.5:1, dorsal margin of palm strongly convex (Plate VIII, Fig. 2); dorsal part of inner face with stridulation rasp composed of transverse rows of parallel elongate tubercles; dactylus half length of hand, fingertips
corneous and deeply spooned (Plate VIII, Fig. 3). Second and third pereiopods with sculpture similar to chelipeds, lacking stridulation rasps; tips of dactyli corneous (Plate VIII, Fig. 4). Fourth pereiopods subchelate; merus, carpus and propodus with faint traces of sculpture similar to that of chelipeds, the ridges short and relatively obscure (Plate VIII, Fig. 5); propodal rasp broadly ovate; dactylus with dorsal margin inflated and bearing a prominent fringe of setae, ventral margin with row of corneous tubercles terminating with fingertip. Fifth pereiopods chelate; propodal rasp covering two-thirds of hand, extending onto thumb as single row of scales; dactylar rasp obscure. Sternal plates of last four thoracic somites greatly expanded.

Abdomen soft, membranous; terga widely separated; four biramous pleopods on left side in both sexes, those of female with longer rami. Sixth abdominal tergum strongly calcified; left uropods more developed; telson feebly calcified, posterior margin setose, not denticulate; bilobed, left lobe no larger than right.

In living animal, shield white, eyescales and eyestalks yellowish-orange; antennae and peduncles yellow. Chelipeds and pereiopods white with regular transverse yellow bands fringed with red setae; dactyli uniformly yellow.

REMARKS: The striking coloration and extreme flattening of the body easily distinguish this species from its congeners.
It is most likely to be confused with *T. krempfi*, from which it is distinguished by the eyestalks being shorter than the anterior margin of the shield and the presence of 3-4 apical teeth on the eyescales.

**RANGE:** East coast of Africa, Red Sea and Gulf of Aden throughout the Indo-Pacific westward to Tahiti and Hawaii.

*Calcinus Dana* 1852

Shield, chelifeds and pereiopods strongly calcified, surfaces nude and glossy; rostrum distinct, obtuse or acute; eyescales simple or denticulate, eyestalks long and slender. Antennal flagellum nude. Chelipeds unequal, left much larger than right, fingertips calcareous. Tips of dactyli of pereiopods corneous. Gill pairs 13, phyllobranchiate. Male with pair of gonopores on coxae of fifth pereiopods; female gonopores on coxae of third pereiopods. Abdomen soft, coiled to right; four biramous pleopods on left side in both sexes.

**Key to the Indian Ocean Species of Calcinus**

1. Eyestalks equalling anterior margin of shield; upper margin of palm of right chela entire .. *laevimanus*
   Eyestalks exceeding anterior margin of shield; upper margin of palm of right chela serrate or tuberculate .................. 2
2. Ventral surface of propodus and dactylus of third left pereiopod with large tufts of setae forming a prominent "brush"; upper border of right chela serrate .................................................. 3
Ventral surfaces of propodus and dactylus of third left pereiopod sparsely setose; upper border of right chela with low, rounded tubercles ........ rosaceus

3. Eyestalks one and one-third length of anterior margin of shield; second and third pereiopods with cross-bands of pigment ...................... elegans
Eyestalks one and one-half length of anterior margin of shield; second and third pereiopods not cross-banded ........................................ 4

4. Lower margin of left chela with serrate keel .... latens
Lower margin of right chela without serrate keel ........................................... gaimardi

**Calcinus laevimanus** (Randall 1839)

*Pagurus laevimanus* Randall, 1839: 135
*Pagurus tibicen* H. Milne-Edwards, 1836: 278
(not *P. tibicen* Herbst, 1791)
*Calcinus herbstii* de Man, 1887: 437
*Calcinus laevimanus* Rathbun, 1907: 208

**MATERIAL EXAMINED:**

One male, 3 mm, Anton Bruun Sta. KA-9
One male, 10 mm, Anton Bruun Sta. HA-8
One male, 5 mm, and one female, 6 mm, Anton Bruun Sta. HA-13
One male, 12 mm, Anton Bruun Sta. HA-16
One male, 11 mm, Sta. JR-4
One male, 9 mm, Sta. JR-14
Six males, 9-14 mm, and three females (two ovig.),(9-10 mm, Sta. JR-22
Fourteen males, 8-13 mm, and eighteen females (six ovig.), 5-10 mm, Sta. JR-23
One male, 8 mm, Sta. JR-25
Two males, 11-13 mm, and six females, 6-12 mm, Sta. JR-25B
Two males, 12-13 mm, and six females, 11-13 mm, Sta. JR-33
One male, 10 mm, and one female, 11 mm, Sta. JR-38
Two males, 13-17 mm, and seven females (four ovig.), 7-14 mm, Aldabra Is. (shore coll.)
Five males, 7-12 mm, and five females (ovig.), 10-11 mm, Nossi Be, Madagascar (M. L. Wass, coll.)
One male, 6 mm, and one female (ovig.), 10 mm, Te Vega Sta. 15
One male, 6 mm, Te Vega Sta. 16
Six males, 6-15 mm, and two females (ovig.), 8 mm, Te Vega Sta. 21
One male, 12 mm, and one female, 8 mm, Te Vega Sta. 27
Three males, 4-8 mm, and one female, 9 mm, *Te Vaga*
Sta. 39

**DIAGNOSIS:** Eyestalks equal anterior margin of shield; left cheliped extremely massive, chela inflated and globose; right chela with upper margin of palm entire. Dactyli of pereiopods with band of pigment and pigmented spot near proximal end. Chelipeds uniformly dark, except white fingers.

**DESCRIPTION:** Shield strongly calcified, cardiac plate and branchiostegites calcified only in proximity of cervical groove, remainder soft and membranous; shield moderately arched, surface glossy; rostrum acute, antennal angles obsolete. Eyescales narrow, separated only by width of rostrum; eyestalks cylindrical, dilated slightly at base, narrowest just beyond basal dilation, expanding smoothly to the slightly dilated cornea; corneal peninsula obsolete. Antennular peduncle short, not reaching base of cornea. Antennal peduncle extending three-fourths length of eyestalks; acicle triangular, 3-4 teeth on dorsal face; antennal flagellum nude, barely reaching to base of dactylus of major cheliped. Exopods of second and third maxillipeds flattened, with recurved flagellum at tip; crista dentata absent. Left cheliped much more massive than right; length of chela subequal to length of carapace; surfaces of all
articles glossy, almost vitreous in texture, nude except on inner edge of opposing surfaces of fingers; carpus with prominent oblique groove near proximal margin of dorsal surface. Length-width ratio of left chela 1.25:1, outer face inflated and strongly convex; dorsal and ventral margins smooth; dactylus short, one-third length of hand; fingertips calcareous. Right cheliped much smaller and shorter, reaching only to base of finger of left cheliped; length-width ratio 1.5:1, less inflated than left, dorsal margin produced, somewhat keel-like, but not dentate; setae present only on finger and thumb. Fingertips calcareous, spooned. Second and third pereiopods compressed, dactylus shorter than propodus; setae present only as scattered tufts on ventral surface of dactyli. Tips of dactyli corneous and sharply curved. Fourth pereiopods subchelate; propodal rasp semi-circular in outline, dorsal margin straight; dactylus with single row of corneous tubercles on ventral margin, terminating with corneous claw. Fifth pereiopods minutely chelate; propodal rasp extended onto dorsal surface; dactylar rasp reduced. Telson short, wider than long; calcified only at margins; posterior margin with shallow median notch, both lobes of equal length, with setose margins.

Shield olive in living animal, shading to blue-green posteriorly; eyestalks bright blue proximally, distal two-thirds bright orange; antennular peduncles bright blue, flagellum orange. Antennal peduncles dark green, acicle
white; flagellum orange. Both chelipeds dark maroon, except dactylus and ventro-distal region of propodus clear white. Pereiopods orange dorsally, shading to brown ventrally; a longitudinal brown stripe on outer face of merus and carpus. Dactyli with brown spot near proximal border and brown band on distal half.

REMARKS: A widespread and very common species, *C. laevimanus* is easily recognized by the massive left chela with its striking contrast of colors and the nonserrate right chela. This species apparently prefers shells with large, round apertures, probably due to the massive size of the left chela. Most of the specimens in the collection were found in shells of *Nerita* spp. and *Murex* sp..

RANGE: East coast of Africa and Madagascar, throughout the Indian Ocean and Indo-Pacific region to Tahiti and Hawaii.

*Calcinus rosaceus* Heller 1861

*Calcinus rosaceus* Heller, 1861: 23

*Calcinus nitidus* var. *australis* Bouvier, 1915: 207

MATERIAL EXAMINED:

One female, 3 mm, *Anton Bruun* Sta. 412-D

One female, 4 mm, *Anton Bruun* Sta. 412-K
DIAGNOSIS: Left cheliped larger, but not longer than right; right chela with row of low tubercles on dorsal margin; eye­stalks exceed length of anterior margin of shield.

DESCRIPTION: Shield longer than wide, moderately arched; rostrum prominent, exceeding the antennal angles which are tipped with a small spine. Cardiac plate and branchioste­gites uncalcified except in proximity of cervical groove. Eyescales triangular, base exceeding height; apex bidentate. Eyestalks long, exceeding anterior margin of shield, left slightly longer than right; dilated proximally, slightly dilated distally, the stalks slightly curved outward; cor­neal peninsula obsolete. Antennular peduncles short, only three-fourths length of eyestalks. Antennal peduncles short, reaching only midpoint of eyestalks, acicle slender, triangular, armed with 3-4 teeth on dorsal surface; anten­nal flagellum barely reaching to tip of chelipeds. Left cheliped larger, but not noticeably longer than right; length-width ratio of chela 2:1, finger less than half length of hand, dorsal margin of palm with row of five low tubercles, but not keeled or cristiform; ventral margin smooth; outer face of hand convex, with only scattered low tubercles; fingertips calcareous and deeply spooned. Carpus with prominent tubercle near center of outer face. Right cheliped more slender than left, length-width ratio of chela 2.25:1, dorsal margin of palm with row of procurved
spines, but not cristiform. Carpus with prominent tubercle in center of outer face. Second and third pereiopods without noticeable armament, nude except for sparsely scattered tufts of setae on ventral face of dactylus. Fourth pereiopods subchelate. Fifth pereiopods chelate; propodal rasp extremely short, occupying only the distal one-fifth of propodus and hardly extended onto thumb.

Shield of living animal bright crimson with yellow spots, large white spots directly behind each antennal angle; eyestalks purple proximally shading through yellow to clear white distally; cornea black. Chelipeds ochre with white denticles and scattered white spots. Second and third pereiopods light purple with yellow spots.

REMARKS: Forest (1956) described this species as being closely related to and very similar to C. nitidus Heller and gave an excellent comparison of the two species. Examination of the two females in the present collection fails to demonstrate as great a degree of sexual dimorphism as that described by Forest.

RANGE: East coast of Africa, the Red Sea and Gulf of Aden, and Mauritius.

*Calcinus elegans* (Milne-Edwards 1836)

*Pagurus elegans* Milne-Edwards, 1836: 278
Pagurus pictus Owen, 1839: 83
Pagurus decorus Randall, 1839: 134
Calcinus elegans Dana, 1852: 458

MATERIAL EXAMINED:

One male, 7 mm, Sta. HA-18
One female, 4 mm, Sta. KA-9
One male, 10 mm, and one female, 9 mm, Sta. JR-19
One male, 8 mm, and one female, 5 mm, Sta. JR-16
One male, 9 mm, Sta. JR-20
One female, 7 mm, Sta. JR-22
One male, 8 mm, Sta. JR-31
One female (ovig.), 8 mm, Sta. JR-36
Two males, 7-10 mm, Andromache Reef, Mombasa
Seven males 4-10 mm, and two females, 4-7 mm, Aldabra
  (shore coll.)
One male, 9 mm, Te Vega Sta. 34
Three males 8-12 mm, Te Vega Sta. 44
Two males, 4-8 mm, and one ovig. female, 5 mm, Te Vega
  Sta. 45-5

DIAGNOSIS: Right chela with upper margin cristiform and serrate; dactylus and propodus of third left pereiopod with "brush" of setae on ventral surface; eyestalks exceed length of anterior margin of shield by one-fourth their length; carpus of left cheliped with elongate tubercle in center of
outer face and oblique depression posteriorly; antennular peduncles reaching base of cornea.

DESCRIPTION: Carapace moderately arched; shield well calcified, nude, posterior margin rounded; anterior margin with prominent rostrum, antennal angles broad, less prominent than rostrum. Eyescales narrowly triangular, medial borders convergent, single apical spinule; eyestalks longer than anterior margin of shield, dilated proximally and distally, corneal peninsula extremely short. Antennular peduncles extend to base of cornea. Antennal peduncles short, extending only slightly beyond midpoint of eyestalks; acicle reaching beyond base of terminal article, armed with 5-7 teeth; flagellum nude, reaching to tip of minor cheliped. Crista dentata on dorsal margin of ischium of third maxillipeds. Left cheliped of male vastly larger and longer than right; length-width ratio of hand 1.8:1, hand inflated, margins smooth, fingers curved, in contact only at tips which are calcareous and deeply spooned. Carpus trigonal, inflated, armed with a single elongate tubercle near center of outer face, an oblique groove or depression lying posterior to this tubercle. Left cheliped of female subequal to right, hand with row of low, rounded tubercles on dorsal margin; carpus as in male. Right cheliped of male more setose than left; dorsal margin of palm produced and forming a high, serrate crest, lower margin smooth; fingers curved,
meeting only at the calcareous and spooned tips. Carpus with upper margin produced slightly and armed with three teeth, outer face smooth. Left cheliped of female similar to male, except dorsal margin not so produced and teeth on dorsal margin more rounded; carpus unarmed. Second and third pereiopods sparsely setose, except ventral side of propodus and dactylus which bears series of tufts of long setae forming a distinct "brush"; dactyli with prominent corneous tips. Fourth pereiopods subchelate; propodal rasp with dorsal margin straight; dactylus with row of corneous tubercles on ventral margin. Fifth pereiopods chelate; propodal rasp occupying distal one-third of article, extended onto thumb; dactylus with rasp of 4-5 rows of scales. Telson feebly calcified except along margins; small median notch on posterior margin, left lobe more produced; both lobes fringed with stiff setae. Preserved specimens uniform light tan, except dactyli of chelipeds shade to light ivory; dactyli of pereiopods with band of dark pigment on proximal half.

REMARKS: The distinctively crested right chelipeds and the bands of pigment on the dactyli of the walking legs distinguish this species. The sexual dimorphism of the chelipeds is more marked than in other species of Calcinus. A few of the specimens have the "brush" of setae on the third left pereiopod less well developed than in the majority. This
condition is more likely the result of normal attrition of the setae between ecdyses than to genetic variation.

RANGE: Throughout the Indian Ocean from the east coast of Africa and the Gulf of Aden to the Indo-Pacific and Hawaii.

_Clibanarius_ Dana 1852

Shield longer than wide; rostrum short; eyestalks long and slender; eyescales usually approximated; antennal flagellum nude. Chelipeds subequal and similar, tips corneous and deeply spooned; fourth pereiopods subchelate, fifth pereiopods chelate. Thirteen pairs phyllobranchiate gills. Male gonopores paired, on coxae of fifth pereiopods; female gonopores paired, on coxae of third pereiopods. Abdomen soft, terga widely separated; four unpaired pleopods on left side in both sexes.

Key to the Indian Ocean Species of _Clibanarius_

(after Fize and Serene, 1955)

1. Dactylus of third left pereiopod longer than propodus ......................................................... 2
2. Dactylus of third left pereiopod does not exceed propodus ..................................................... 11

2. Longitudinal lines of pigment on dorsal surfaces of eyestalks ................................................. 3
Dorsal surfaces of eyestalks without longitudinal lines of pigment ........................................ 7

3. Second and third pereiopods with longitudinal lines of pigment ........................................ 4
   Second and third pereiopods lacking longitudinal lines of pigment .................................. olivaceus

4. Eyestalks exceed antennular peduncles; two rows of spines on dorsal margins of chelipeds ...... taeniatus
   Eyestalks not exceeding antennular peduncles .......... 5

5. Eyestalks equal antennular peduncles ........ padavensis
   Eyestalks distinctly shorter than antennular peduncles ................................................. 6

6. Large prominent tooth on medio-ventral margin of merus of chelipeds ....................... infraspinatus
   Merus of chelipeds without tooth as above .. clibanarius

7. Eyestalks longer than antennular peduncles ........ padavensis
   Eyestalks equal length of antennular peduncles .......... 9

8. Dorsal margin of left chela with ridge of 4-5 sharp, spiniform tubercles ....................... striolatus
   Dorsal margin of left chela with row of low, rounded tubercles ............................... laevimanus

9. Eyestalks short, flattened, cornea occupying one-fourth of eyestalk ......................... lineatus
   Eyestalks long and slender; cornea occupying one-fifth or less of eyestalk ...................... 10

10. Hands of chelipeds covered with long setae .. longitarsus
Hands of chelipeds covered with short setae .... demani

11. Dactylus of third left pereiopod approximately equal to propodus .......................................... 12
   Dactylus of third left pereiopod clearly shorter than propodus ........................................... 18

12. Color uniformly dark, without lighter spots or lines ........................................ arethusa
   Dark ground color interrupted by lighter bands or spots .................................................. 13

13. Outer face of third left pereiopod strongly flattened; upper margin with dense fringe of long setae ........................................ carnifex
   Third left pereiopod not flattened or setose ........ 14

14. Chelae armed with sharp-tipped spines .............. 15
   Chelae not spinose .................................. bimaculatus

15. Carapace, chelipeds and pereiopods marked with longitudinal white bands ................ eurysternus
   Longitudinal bands and spots on chelipeds and pereiopods, but not on carapace ................. 16

16. Outer face of third left pereiopod with longitudinal bands .................................................. 17
   Outer face of third pereiopod with white spots only, no longitudinal bands ...................... cruentatus

17. Dactyli of second and third pereiopods with two white transverse bands ....................... nathi
Dactyli of second and third pereiopods with longitudinal lines ................................ snelliusi

18. Propodus of third left pereiopod flattened and densely setose ................................. corallinus

Propodus of third left pereiopod not densely setose ..................................................... 19

19. Longitudinal line of pigment on medio-dorsal surface of eyestalks ......................... 20

Eyestalks without medio-dorsal line of pigment .... 22

20. Carapace marked with longitudinal lines of pigment .............................................. zebra

Carapace without longitudinal lines of pigment .... 21

21. Propodi of second and third pereiopods with transverse white bands at each end .......... boschmai

Propodi of pereiopods without transverse bands ......................................................... signatus

22. Third pereiopod with longitudinal bands of pigment .............................................. 23

Third pereiopods without longitudinal bands of pigment ........................................... 24

23. Merus, carpus, propodus and dactylus of second pereiopod with longitudinal lines of pigment ...... ransonii

Second pereiopod with longitudinal lines of pigment on dactylus only ......................... merguiensis

24. Dactylus of third left pereiopod with transverse bands of clear yellow ................... virescens
Dactylus of third left pereiopod without transverse bands ......................... humilis

Clibanarius padavensis de Man 1888

Clibanarius padavensis de Man, 1888: 242

MATERIAL EXAMINED:

Two males, 5-7 mm, Sta. JR-4
One male 11 mm, Sta. JR-11
One female, 17 mm, Sta. JR-24A
Two males, 8-10 mm, Sta. JR-33
One female (ovig.), 20 mm, Sta. JR-34A
Six males, 8-15 mm, and seven females (3 ovig.),
  10-15 mm, Te Vega Sta. 24

DIAGNOSIS: Dactylus of third left pereiopod longer than propodus; eyestalks equal antennular peduncles and exceed anterior margin of shield; length of chelae twice the width; longitudinal line of pigment on dorsal side of eyestalks.

DESCRIPTION: Carapace not depressed; shield convex, longer than wide, gastric region nude, lateral margins with scattered tufts of setae; rostrum prominent, acute, exceeding antennal angles; transverse sulcus lying posterior to rostrum and antennal angles. Eyescales triangular, a single corneous spinule at apex; eyescales cylindrical, slightly dilated
proximally, moderately dilated distally with broad corneal peninsula. Antennular peduncles equal eyestalks. Antennal peduncles barely reaching base of cornea, acicle triangular, short, little longer than wide, medial border with a single tooth; flagellum nude, exceeding pereiopods. Third maxillipeds approximated at base, exopods flattened and paddle-like, terminating in recurved flagellum.

Chelipeds subequal and similar; length-width ratio of hands 2:1, dactylus half length of chela, outer face of hand and dactylus with corneous-tipped spines, sparsely setose; opposing surfaces of fingers with 1-2 calcareous teeth; fingertips corneous, hoof-shaped. Carpus and merus of chelipeds slender, unarmed except for single spine on distal margin of carpus; sparsely setose. Articles of second and third pereiopods moderately compressed, unarmed, sparsely setose; dactyli longer than propodi, tips corneous. Fourth pereiopod subchelate, a single corneous spine on disto-dorsal margin of carpus; dorsal edge of propodal rasp straight single row of corneous tubercles on ventral margin of dactylus. Fifth pereiopod minutely chelate; propodal rasp short, roughly triangular; dactylar rasp truncate.

Abdomen soft, coiled to right; terga widely separated; pleopods of female equally biramous, those of male with rami unequal; telson with left lobe slightly larger, both lobes with 3-4 marginal teeth and fringe of stiff setae.
RANGE: East coast of Africa from Delagoa Bay northward and Madagascar, Bay of Bengal to Singapore and the East Indies to Australia.

*Clibanarius taeniatus* (H. Milne-Edwards 1848)

*Pagurus taeniatus* H. Milne-Edwards, 1848: 63

*Clibanarius taeniatus* de Man, 1890: 113

MATERIAL EXAMINED:

One male, 12 mm, and two females, 9-11 mm, Sta. JR-38

One male, 15 mm, and one female (ovig.), 11 mm,

Nossi Be, Madagascar (M. L. Wass, coll.)

DIAGNOSIS: Dactylus of third left pereiopod longer than propodus; eyestalks exceed antennular peduncles by length of cornea; longitudinal lines of pigment on dorsal surface of eyestalks; chelipeds, pereiopods and carapace with longitudinal lines of pigment. Body greatly depressed, shield barely longer than wide.

DESCRIPTION: Body depressed; shield width subequal to length; rostrum acute, prominent, antennal angles obsolete. Shield nude except a few setae on lateral margins. Cardiac plate calcified in anterior half, membranous posteriorly; branchiostegites calcified only in proximity of cervical groove, calcified portion divided into calcareous ossicles.
Eyescales triangular, base exceeding height, medial margins convergent, antero-lateral margin with 2-4 teeth near apex; eyestalks slender, slightly dilated proximally, not at all distally, corneal peninsula triangular. Antennular peduncles short, hardly reaching base of cornea; antennal peduncles reaching slightly beyond midpoint of eyestalks, acicle with single tooth on lateral margin, 5-6 teeth on medial margin; flagellum nude, exceeding chelipeds and reaching halfway on dactyli of second pereiopods. Exopods of second and third maxillipeds flattened and paddle-shaped, terminating in recurved flagella. Chelipeds subequal and similar, almost reaching to base of dactylus of second pereiopods; length-width ratio of chelae 2:1, two rows of setiferous tubercles parallel to dorsal margin of palm, continued on dactylus; outer face of hand with scattered tufts of setae arising from low tubercles. Fingers armed with 1-2 calcareous teeth; tips corneous and hoof-shaped. Carpus of chelipeds with corneous-tipped spine at disto-dorsal extremity and scattered setiferous tubercles on outer face; merus unarmed. Second and third pereiopods unarmed, sparsely setose, becoming more dense on dorsal and ventral margins; dactylus of third left pereiopod slightly flattened on outer face, dorsal margin with regularly spaced tufts of setae. Fourth pereiopods with prominent fringe of setae on dorsal margin; propodal rasp well-developed; dactylus with single row of corneous
tubercles on ventral margin. Fifth pereiopod with propo­
dal rasp occupying half of outer face of propodus; dacty­
lar rasp uniseriate; a prominent tuft of stiffly hooked
setae arising from base of dactylus. Abdominal terga un­
calcified and hardly distinguishable, except sixth tergum
well calcified. Uropods with well-developed rasps on endo­
pods and exopods; posterior median notch of telson obsolete,
left lobe slightly longer and armed with 2-3 marginal teeth,
both lobes with setose fringe.

REMARKS: These specimens constitute a major range extension
for this species. At present the range appears to be dis­
 junct, but it is likely that more extensive collections will
show it to be continuous.


Clibanarius striolatus Dana 1852

Clibanarius striolatus Dana, 1852: 463

MATERIAL EXAMINED:

One male, 9 mm, Sta. FT-9

Four males, 4-6 mm, and five females, 4-7 mm, Sta. JR-36

DIAGNOSIS: Eyestalks equal anterior margin of shield and
exceed antennular peduncles; length-width ratio of chelae
1.6:1, outer face of propodus of third left pereiopod with low keel on dorsal margin.

DESCRIPTION: Similar to C. padavensis, except in the characters given in the diagnosis.

RANGE: East coast of Africa (Delagoa Bay), Madagascar, Seychelles Is., Gulf of Aden and Red Sea eastward to Tahiti.

Clibanarius longitarsus (de Haan 1849)
   Pagurus longitarsus de Haan, 1849: 211
   Clibanarius longitarsus Dana, 1852: 464

MATERIAL EXAMINED:
   One female, 17 mm, Nossi Be, Madagascar (M. L. Wass, coll.)

DIAGNOSIS: Differs from C. striolatus only in having blue lines on the pereiopods rather than red.

DESCRIPTION: Body structures and proportions similar to C. striolatus and C. padavensis, differing only in the coloration. Shield brown with grey spots; eyestalks greenish buff, cornea black; chelipeds olive with blue spots; second and third pereiopods with blue stripes.
REMARKS: Direct comparison of this specimen with specimens of *C. striolatus* revealed no differences by which the species may be distinguished morphologically, even the pattern of pigmentation after fading in the preservative was not distinctive. Barnard (1950) p.434, stated that the two species may be distinguished by the coloration, citing Henderson, 1915. The color notes of the living specimen, made by M. L. Wass are the basis for identifying this specimen as *C. longitarsus*.

RANGE: East coast of Africa and Madagascar throughout the Indo-Pacific to the Philippine Islands and Japan.

*Clibanarius eurysternus* Hilgendorf 1878

*Clibanarius eurysternus* Hilgendorf, 1878: 822

MATERIAL EXAMINED:

Eight males, 8-13 mm, and five females (4 ovig.),
8-12 mm, Nossi Be, Madagascar (M. L. Wass, coll.)

DIAGNOSIS: Dactylus of third left pereiopod equals propodus; body strongly depressed, shield wider than long; chelae spinose; width of sternal plate between fourth pereiopods equal to width of shield; carapace and appendages with longitudinal white lines.
DESCRIPTION: Similar to *C. taeniatus*, but differing in the length of dactylus and in having the eyescales narrower.

REMARKS: The remarkable flattening and broadening of the body of this species is probably correlated with the type of shells selected. Because most of the features distinguishing *C. eurysternus* from *C. taeniatus* are due to the flattening of the body, it is possible that *C. eurysternus* is a synonym of *C. taeniatus*.

RANGE: East coast of Africa and Madagascar to East Indies.

*Clibanarius signatus* Heller 1861

*Clibanarius signatus* Heller, 1861: 252

MATERIAL EXAMINED:
One male, 10 mm, and one female, 11 mm, Sta. LW-1
Two males, 7-11 mm, Sta. HA-27
One male, 14 mm, Gulf of Kutch

DIAGNOSIS: Chelipeds subequal and similar; eyestalks equal anterior margin of shield, exceeding antennular and antennal peduncles; dactylus of third left pereiopod shorter than propodus.

DESCRIPTION: Shield longer than wide; moderately convex;
nude, except for 2-3 tufts of bristles on lateral margins; rostrum short, but distinct; antennal angles broad and rounded, equalling rostrum. Cardiac plate and branchio-stegites feebly calcified, lateral margins of branchio-stegites densely setose. Eyescales broadly triangular, medial borders parallel; 2-4 apical teeth on antero-lateral margin. Eyestalks slender, subequal to anterior margin of shield and slightly exceeding antennular and antennal peduncles; corneal peninsula obsolete. Proximal article of antennal peduncle with spine on anterolateral angle; acicle narrowly triangular, barely reaching base of distal article, 4-5 teeth on medial border; antennal flagellum nude, short, barely reaching tips of chelipeds. Chelipeds subequal and similar, reaching only to base of dactylus of second pereiopods; length-width ratio of chelae 2:1, finger half length of hand; outer face of chelae with scattered spiniform tubercles, sparsely setose. Carpus trigonal with scattered tubercles; dorsal margin with 3-4 spines. Merus with subdistal ridge, paralleling distal margin. Second and third pereiopods exceed chelipeds by length of dactyli; unarmed except single longitudinal row of 4-6 corneous spines on ventral faces of dactyli. Outer face of propodus of third left pereiopod flattened, dorsal margin carinate or subcarinate. Fourth pereiopod subchelate; propodal rasp well-developed; dacty-lus with single row of corneous spinules on ventral margin. Fifth pereiopod minutely chelate; propodal rasp short,
extended onto dorsal surface of fixed finger; dactylar rasp narrow, restricted to edge of finger.

After eight to nine years in alcohol, gastric region of shield cream with two orange spots posteriorly and a transverse bar of orange just posterior to anterior margin; lateral sides of shield orange. Eyestalks with longitudinal orange line on dorsal side. Chelipeds with broad longitudinal bands of orange, tubercles white. Pereiopods with distinct longitudinal stripes.


Genus *Diogenes* Dana 1852

Shield longer than wide, lateral margins rectilinear, posterior margin sinuous; rostrum absent, replaced by a rostriform process (interocular plate) which may be denticulate or entire. Eyescales broadly triangular, anterolateral margins denticulate. Antennal flagellum sparsely setose; crista dentata on third maxillipeds. Left cheliped much larger and longer than right; fingertips of both chelipeds calcareous. Female gonopores paired, on coxae of third pereiopods; male gonopores paired, on coxae of fifth pereiopods. Thirteen pairs phyllobranchiate gills. Abdomen coiled to right, no paired gonopods; four unpaired biramous pleopods on left side in female, four uniramous pleopods in male.
Identification of species of Diogenes is difficult due to the variability of many of the species. The armament and shape of the chelipeds exhibit considerable variation with the development of the individual. Small or immature specimens usually will not fit in the following key.

Key to the Indian Ocean Species of Diogenes
1. Rostriform process denticulate ................................ 2
   Rostriform process entire ..................................... 8
2. Carapace broader than long ................................... miles
   Carapace longer than broad ..................................... 3
3. Acicle bifurcate ................................................ 4
   Acicle not bifurcate ............................................ 6
4. Medial (shorter) ramus of acicle barely reaching base of terminal article of peduncle .... merguiensis
   Medial ramus of acicle reaching only halfway on penultimate article of peduncle ......................... 5
5. Outer face of major chela spinose; lateral ramus of acicle barely reaching base of terminal article of peduncle ......................... diogenes
   Outer face of major chela granulous; lateral ramus of acicle exceeding base of terminal article of peduncle ..................... custos
6. Palm of major chela wider than long ............... affinis
Length of palm of major chela equalling or exceeding width ........................................... 7

7. Length of palm of major chela equalling width ........................................ planimanus
Palm of major chela longer than wide ........... violaceus

8. Eyestalks exceeding both antennal peduncles and anterior margin of shield ...................... 9
Eyestalks not exceeding both antennal peduncles and anterior margin of shield .................. 11

9. Eyestalks exceeding antennular peduncles ........... serenei
Antennular peduncles exceeding eyestalks ............. 10

10. Antennal acicle finely serrate ............... gardineri
Antennal acicle with 2-3 prominent teeth ........ senex

11. Ventral margin of major chela sinuous; fixed finger more or less deflexed ....................... 12
Ventral margin of major chela not sinuous; fixed finger not deflexed .............................. 16

12. Eyestalks barely reaching base of terminal article of antennular peduncle ....................... 13
Eyestalks extending beyond base of terminal article of antennular peduncle ...................... avarus

13. Outer face of major chela with two obliquely longitudinal crests ............................ bicristimanus
Outer face of major chela with single obliquely longitudinal crest .................................. 14
14. Dorsal margin of side-wall of carapace finely serrate throughout whole length .......... costatus
Dorsal margin of side-wall of carapace with only 2-3 teeth posteriorly, anterior margin smooth ................................. 15

15. Upper face of carpus of left cheliped convex, with irregularly scattered tubercles .......... brevirostris
Upper face of carpus of left cheliped with a flat surface between two rows of tubercles.. extricatus

16. Antennular peduncle clearly longer than antennal peduncle .............................. rectimanus
Antennular peduncle equals antennal peduncle ...................................... investigatoris

Diogenes diogenes (Herbst 1791)
   Cancer diogenes Herbst, 1791: 17
   Pagurus miles Fabricius, 1798: 412
   Diogenes diogenes Henderson, 1893: 412

MATERIAL EXAMINED:
Three males, 11-18 mm, and one female, 11 mm,
   Anton Bruun Sta. 201A
One male, 12 mm, Anton Bruun Sta. 204A
One male, 21 mm, Anton Bruun Sta. 209A
One male, 22 mm, Anton Bruun Sta. 224A
Six males, 9-14 mm, and three females (ovig.),
10-13 mm, Sta. JR-19
Two males, 5-7 mm, Beira, Mozambique (M. L. Wass, coll.)

DIAGNOSIS: Rostriform process denticulate; antennal acicle bifurcate, lateral point reaching base of terminal article, medial point reaching middle penultimate article; major cheliped remarkably spinose.

DESCRIPTION: Shield wider than long; sparsely setose except nude gastric region; with scattered vesiculous tubercles; anterior margin and antennal angles obscurely denticulate, prominent spine on antero-lateral angles (Plate IX, Fig. 1). Cardiac plate and adjacent regions of branchiostegites calcified, with scattered vesiculous tubercles; remainder of branchiostegites feebly calcified or not at all. Rostriform process long, one-third to one-half length of eyestalks; denticulate, denticles more prominent distally. Eyescales broad, trapezoidal, anterior margins finely denticulate; eyestalks two-thirds length of anterior margin of shield, obliquely compressed distally, corneal peninsula narrowly triangular and lying on medio-dorsal surface of cornea. Antennular and antennal peduncles exceed eyestalks by length of terminal article. Antennal acicle bifurcate, internal margins of both rami denticulate; lateral ramus
reaching base of terminal article, mesial ramus reaching midway on penultimate article; antennal flagellum setose, reaching to base of major chela.

Left cheliped much larger than right; length-width ratio of hand 1.5:1, outer face covered with numerous long spines; dorsal margin of palm with a prominent row of spines, ventral margin not spinose; inner face with scattered low, rounded tubercles. Dorsal face of dactylus with two prominent rows of spines; opposing edges of fingers straight, feebly dentate and meeting over the whole length; fingertips calcareous. Outer face of carpus with spines similar to chela; outer face of merus trigonal, feebly spinose (Plate IX, Fig. 2). Right cheliped slender; length-width ratio of hand 2:1, outer face with four longitudinal rows of setiferous spines; dorsal margin spinose; dactylus two-thirds length of hand, setose, fingertips calcareous (Plate IX, Fig. 3). Armament of carpus and merus similar to chela. Second and third pereiopods exceeding major cheliped by half length of dactylus; propodus armed with parallel rows of procurred spines, sparsely setose; dactylus slender, longer than propodus, unarmed except single row of spines on dorso-lateral margin flanked by longitudinal rows of dense setae (Plate IX, Fig. 4). Fourth pereiopods subchelate, dactylus very small, propodal rasp well-developed. Fifth pereiopod chelate; propodal rasp ovate, not extended onto fixed finger; dactylar rasp uniseriate.
Gills and genitalia typical of genus.

RANGE: West coast of India and Arabian Sea, East Coast of Africa southward to Mozambique and Madagascar.

Genus **Paguristes** Dana 1852

Carapace longer than wide; rostrum broad or slender, acute; eyescales separated. Chelipeds equal and similar or unequal, the left larger; fingertips corneous. Fourth pereiopods simple, not subchelate; fifth pereiopods chelate. Thirteen pairs gills. Male gonopores paired; females with exception of *P. marocanus* and *P. oculatus* var. *rubropictus,* with unpaired gonopore on left side. Male with two pairs gonopods and three unpaired pleopods on left; female with single pair gonopods and four unpaired pleopods, the first three of which are enclosed within a brood pouch.

Key to the Indian Ocean Species of **Paguristes**

1. Antennal flagellum longer than carapace ............... 2
   Antennal flagellum shorter than carapace ............... 5
2. Eyestalks shorter than antennular peduncle ...... *calvus*
   Eyestalks exceed antennular peduncle .................... 3
3. Chelipeds densely tomentose ..................... *ciliatus*
   Chelipeds nude or nearly so ............................. 4
4. Eyestalks slender; rostrum slender ........ *balanophilus*
   Eyestalks stout; rostrum broad ...................... *mundus*
5. Fingers of chelipeds with cutting edges in contact through whole length; chelipeds nude or sparsely setose ........................................... 6

Fingers of chelipeds with gap between cutting edges near base of fingers; chelipeds setose or tomentose ........................................... 10

6. Outer surface of cheliped with imbricating, ciliated, squamiform tubercles .......... longirostris
Tubercles on surface of cheliped not imbricated ...... 7

7. Outer face of chelipeds finely granulous ...... puniceus
Outer face of cheliped with conical tubercles and spinules ........................................... 8

8. Eyestalks strongly dilated at base .......... jousseaumei
Base of eyestalks not dilated or only slightly so .... 9

9. Outer face of carpus of cheliped with randomly scattered tubercles ....................... perspicax
Single row of tubercles on inner and outer margins of carpus of cheliped, face unarmed medially ........................................... abbreviatus

10. Eyestalks exceeding antennular peduncles ........ hians
Eyestalks not exceeding antennular peduncles ........ 11

11. Cephalic shield tomentose .................... incomitatus
Cephalic shield nude ........................................... 12

12. Eyestalks tapering distally, dorsal surface slightly carinate .............................. mossambicus
Eyestalks cylindrical, not tapering ................. 13
13. Eyescales approximated ................. \textit{plumosus}
Eyescales separated ....................... \textit{gamianus}

\textbf{Paguristes balanophilus} Alcock, 1905

\textbf{Paguristes balanophilus} Alcock, 1905:

\textbf{MATERIAL EXAMINED}:
One male, 20 mm, \textit{Anton Bruun} Sta. 202A

\textbf{DIAGNOSIS}: Antennal flagellum longer than carapace; antennular peduncle shorter than eyestalks; shield longer than wide, rostrum narrowly triangular; left cheliped much larger than right, cutting edges of fingers in contact throughout length, tips minutely corneous.

\textbf{DESCRIPTION}: Cephalic shield moderately arched; rostrum slender, exceeding antennal angles. Cardiac plate feebly calcified, branchiostegites membranous. Eyescales large, separated, triangular anteromedially; eyestalks slender, slightly exceeding antennular peduncles; cornea dark, corneal peninsula short, broad. Antennal peduncle reaching only to base of cornea; acicle elongate, extending to distal third of terminal article, spinose on both margins; flagellum sparsely setose. Ischium of third maxilliped with crista dentata obliquely on medial surface; Ventral margin of merus with 5-6 spines. Left cheliped larger,
but not longer than right; outer face of hand somewhat depressed, with dorsal and ventral margins sharply carinate. Length-width ratio of hand 2:1; movable finger two-thirds length of hand; opposing edges of fingers straight, regularly denticulate, in contact throughout length, tips minutely corneous. Right cheliped more slender than left; length-width ratio of hand 3:1, armature similar to left. Second and third pereiopods slender, upper margin of propodus and carpus of second pair spinose, third pair unarmed; dactylus of both pairs with two longitudinal rows of stiff setae, tips of dactylus with small corneous spur in addition to corneous tip. Fourth pereiopod simple; propodus with small rasp of corneous scales on disto-ventral angle; dactylus with single row of corneous spinules on ventral margin. Fifth pereiopod chelate; rasp covering distal third of propodus, extending onto fixed finger; dactylus with narrow row ventrally. Abdomen soft, coiled to right; appendages typical of genus; telson long and narrow, posterior margin with deep median notch, left lobe greatly elongate.

RANGE: Gulf of Oman, E. coast of India and Andaman Islands.

*Paguristes mossambicus* new species

MATERIAL EXAMINED:

Three males, 5, 3 and 2 mm, one female (ovig.) 3 mm,
Anton Bruun Sta. 409-I
Three males, 3, 3 and 2 mm, Anton Bruun Sta. 409-K
Holotype: Male, 5 mm, Anton Bruun Sta. 409-I

DIAGNOSIS: Carapace longer than antennal flagellum; shield nude; fingers of cheliped with prominent gap; eyestalks separated.

DESCRIPTION: Shield longer than wide, roughly triangular in outline; rostrum rounded, not exceeding antennal angles (Plate X, Fig. 1). Eyescales simple, triangular, moderately separated; eyestalks slender, 1 ½ times width of shield, widest at base, tapering smoothly to small rounded cornea. Antennular peduncles exceeding eyestalks by half terminal article. Antennal peduncle short, not reaching base of cornea, two prominent spines on mesial margin of second article; acicle narrowly triangular, lateral and mesial borders minutely serrate, antennal flagellum short, barely exceeding antennular flagellum, sparsely setose. Third maxilliped with crista dentata on merus, accessory tooth absent, two spiniform tubercles on mesial margin of carpus. Chelipeds subequal and similar, left very slightly larger, reaching to midpoint of second pereiopod dactylus; merus trigonal, mesial margin with 2–4 teeth; carpus length 1 ½ times width, three longitudinal rows of spines on outer face, middle row most prominent; length of chela 2 ½ times
width, finger half length of hand, outer face of palm with three longitudinal rows spiniform tubercles, those on mesial margin most prominent; cutting edges of fingers not meeting except at tip, thumb with single large tooth, finger with 5-6 smaller teeth, tips corneous (Plate X, Fig. 2); both fingers densely tomentose, density of tomentum diminished on palm and carpus. Second and third pereiopods slender, unarmed except dense fringe of stiff setae on dorsal margin of dactylus. Fourth pereiopod simple; dactylus \( \frac{1}{2} \) length propodus, sharply flexed; propodal rasp uniseriate. Fifth pereiopod chelate, propodal rasp reduced, dactylar rasp absent. Eleven pairs extremely reduced gills, none on last two thoracic somites. Gonopores of male with vasa deferentia produced as L-shaped tubes, distal ends opening into grooved portion of first gonopods (Plate X, Fig. 3); female with paired gonopores. Male with two pairs gonopods, first pair deeply grooved and receiving distal ends of vasa deferentia, three unpaired pleopods on left; female with single pair of gonopods, four unpaired pleopods on left.

Specimens in alcohol cream to light brown. In life, shield mottled with red, branchiostegites buff, eyestalks crimson fading to pink dorsally, eyescales rose, chelipeds and pereiopods with indistinct transverse bands of brown on pale ground.

RANGE: Known only from single locality (Sta. 409-I and
Paguristes olumosus new species

Holotype (male, 5 mm, Sta. 409-I) deposited in USNM

Paguristes plumosus new species

MATERIAL EXAMINED:

Three males, 5, 4 and 4 mm, Anton Eruun Sta. 412-D

DIAGNOSIS: Antennal flagellum shorter than carapace; eye-stalks subequal to antennular peduncle; shield longer than wide, rostrum broad, not exceeding antennal angles; eye-scales approximated.

DESCRIPTION: Carapace elongate, shield nude, except lateral margins sparsely setose; cardiac plate feebly calcified;
branchiostegites membranous, numerous plumose setae on anterior and lateral regions. Rostrum broad, exceeded by antennal angles. Eyescales approximated, longer than wide, 3-4 teeth on tip. Eyestalks slender, slightly dilated proximally, corneal region not dilated; equalling antennal peduncles and exceeding antennal peduncles (Plate XI, Fig. 1). Antennal acicle long, almost reaching distal end of peduncle, weak spines on both margins obscured by fringe of plumose setae. Antennal flagellum hardly long as shield, setose to tip. Chelipeds similar, equal, slightly exceeding carpus of second pereiopod; length of hand twice width, dactylus slightly exceeding half length of hand, dorsal margin of hand with 2-3 corneous tipped spines, outer face with scattered spinules, fingers curved, prominent gap at distal end of cutting edges, tips corneous, hoof-shaped; outer face of carpus flattened, dorsal and ventral margins sharply delineated, armed with 4-5 corneous-tipped spines (Plate XI, Fig. 2); merus trigonal, mesio-ventral margin dentate, outer face of all articles partially obscured by long plumose setae. Second and third pereiopods slender, exceeding chelipeds by length of propodus and dactylus; unarmed except single row of 4-5 corneous spinules on ventral margin of dactylus; dorsal and ventral margins of all articles more or less obscured by tufts of plumose setae. Fourth pereiopod simple; narrow rasp on distal 2/3 propodus; 4-5 corneous spines ventrally
on dactylus; dorsal and ventral margins of all articles with plumose setae. Fifth pereiopod minutely chelate, dactylus 1/5 propus, rasp on distal third of propus, extending onto fixed finger; dactylar rasp narrow. Gill paris 13. Vasa deferentia of male paired; two pairs gonopods, three unpaired pleopods on left side of abdomen. Female unknown.

Color after 10 years in alcohol light yellow. In life, carapace red posteriorly, shading to white with red maculae anteriorly; eyestalks white at ends, median region red, cornea wine; antennular and antennal peduncles red, flagella light purple; chelipeds dull purple; pereiopods purple with white area adjacent to mero-carpal and carpo-propodal joints.

REMARKS: This species is closely related to P. gamianus and P. mossambicus, but is easily distinguished by the shape of the eyestalks and the separated eyescales, the unarmed dorsal margins of the pereiopods and the dense plumose setae. The holotype is deposited in the collection of the USNM.

RANGE: Known only from the type locality (Castor Bank) of the northwest coast of Madagascar.

Superfamily PAGUROIDEA MacDonald et al., 1957
Family Parapaguridae Smith 1879
Genus Parapagurus Smith 1879
Shield broad, moderately calcified, posterior median region sometimes weakly calcified; branchiostegites membranous. Antennal flagellum exceeding length of carapace. Right cheliped larger and longer than left. Epistome with two median unpaired spines, one lying between bases of antennules, the other lying just anterior to the labrum. Third maxillipeds widely separated at base, sternal plate armed with pair of spines flanking median sulcus; crista dentata well developed, accessory tooth lacking. Vasa deferentia paired; female genital opening on coxa of left third pereiopod only; one or two pairs gonopods in male, female lacking gonopods, both sexes with three unpaired pleopods. Gill pairs eleven, either phyllobranchiate or trichobranchiate.

This genus has recently been reviewed by Saint Laurent (1973). Due to the extensive subspeciation in this genus and the brevity and lack of detail of many of the descriptions thereof, no attempt is made here to devise a key to the species. Because of the rather subtle distinctions described between many species and subspecies, it would necessitate detailed examination of the type materials in order to recognize valid key characters.

Parapagurus pilosimanus bouvieri Stebbing, 1910
Parapagurus bouvieri Stebbing, 1910: 357
Parapagurus pilosimanus bouvieri Saint Laurent, 1973 (in press)
MATERIAL EXAMINED:

One female (ovig.) 16 mm, Anton Bruun Sta. 390C
Two males, 10 and 12 mm, one female (ovig.), 10 mm, Anton Bruun Sta. 398B
Three males, 10, 10 and 12 mm, Anton Bruun Sta. 399C

DIAGNOSIS: Shield well calcified; eyestalks exceeding base of terminal article of antennal peduncles; cornea well developed, moderately dilated; chelae elongate, outer faces densely tomentose.

DESCRIPTION: Shield well calcified, width slightly exceeding length; cardiac plate and branchiostegites membranous; rostrum broadly triangular, antennal angles obsolete. Ophthalmic somite exposed; eyescales simple, acuminate, moderately separated, eyestalks equalling half width shield, reaching midpoint penultimate article of antennular peduncle (Plate XII, Fig. 1), slightly flattened dorsally, dilated proximally and distally, cornea reniform, corneal peninsula wider than long. Antennal peduncle reaching base of terminal article of antennular peduncle, anterolateral angle of second article with 4-5 teeth; acicle slender, reaching tip of peduncle, both margins finely denticulate, setose; flagellum long, nude, exceeding tips of pereiopods. Base of third maxillipeds widely separated, sternal plate divided by median cleft flanked by two prominent spines;
cristata well developed, lacking accessory tooth. Right cheliped massive, exceeding left by length of hand; merus trigonal, unarmed; carpus elongate, length twice width; length of chela $1\frac{1}{2}$ times width, finger less than half length of chela, axis of finger and thumb inclined to axis of hand; outer face of all articles finely granulous, becoming spinose on lateral margin of chela (Plate XII, Fig. 2), surface sculpture obscured by dense, matted tomentum. Left cheliped slender; carpus narrowly triangular, length twice width; length chela twice width, finger half length hand, cutting edges minutely corneous, contacting throughout length (Plate XII, Fig. 3). Second and third pereiopods extremely slender, exceeding major cheliped, unarmed except single on distodorsal margin of carpus and row of stiff setae on distal half dactylus; dactylus twice length propodus. Fourth pereiopod subchelate, narrow rasp on ventral margin of propodus, dactylar rasp uniseriate. Fifth pereiopod minutely chelate; propodal rasp triangular in outline. Single pair of gonopods and three unpaired pleopods in male; female with four unpaired pleopods on left side, single vestigial pleopod on right side of second abdominal somite, obscured by tuft of setae. Gill pairs eleven, filaments slender phyllobranchiae, cleft at tips.

REMARKS: The length of the eyestalks and the well developed cornea distinguish this subspecies from other subspecies
of *P. pilosimanus*.

RANGE: East coast of Africa south of Kenya to Cape of Good Hope.

**Family Paguridae Latreille 1802**

**Genus *Pagurus* Fabricius, 1775**

Shield strongly calcified; rostrum obtuse; ophthalmic somite exposed, eyescales separated; eyestalks never exceeding shield length, cornea usually dilated. Antennular peduncles equalling or exceeding eyestalks. Antennal acicle simple, flagellum nude. Right cheliped larger and longer than left. Second and third pereiopods usually slender, dactylus being longest article. Fourth pereiopod weakly subchelate. Fifth pereiopod chelate. Paired pleopods never present in either sex, male with three (rarely four) and female with four unpaired pleopods. Uropods and telson asymmetrical to the left, telson with deep median cleft in posterior margin. Vasa deferentia paired, not protruding; female gonopores paired. Eleven pairs phyllobranchiate gills.

Key to the Indian Ocean Species of *Pagurus*

1. Eyestalks equalling or exceeding anterior width of shield .......................... 2
   Eyestalks shorter than anterior width of shield ...... 4
2. Rostrum obsolete ........................ pergranulatus
   Rostrum prominent, extending between base of
   eyescales .................................................. 3

3. Second and third pereiopods longitudinally
   striped on all articles ............................ zebra
   Second and third pereiopods striped on merus
   only .................................................. investigatoris

4. Rostrum absent, margin between antennal angles
   a straight line .................................... spinulentus
   Rostrum present (may be prominent or obsolete) ...... 5

5. Rostrum exceeding antennal angles, protruding into
   space between eyescales ........................... hirtimanus
   Rostrum not exceeding antennal angles ............... 6

6. Dactylus of left cheliped strongly curved, cutting
   edges of fingers not meeting except at tips ........ placens
   Cutting edges of fingers of left cheliped in
   contact, fingers straight ................................ 7

7. Carpus of right cheliped with deep pit (foramen)
   on ventral surface ................................. cavicarpus
   No pit in ventral surface of carpus of right
   cheliped .................................................. 8

8. Right cheliped nude or nearly so, lower margins
   of merus and carpus carinate ...................... kulikarnii
   Right cheliped densely tomentose, margins of
   merus and carpus not carinate ..................... macardlei
**Pagurus spinulentus** (Henderson, 1888)

*Eupagurus spinulentus* Henderson, 1888: 68

*Pagurus spinulentus* Gordan, 1956: 335

**MATERIAL EXAMINED:**

Four males, 8-14 mm, and four females (ovig.), 8-12 mm,

Anton Bruun Sta. 391J

One male, 11 mm, and two females (ovig.), 10 mm,

Anton Bruun Sta. 394B

Two males, 3 & 7 mm, and one female (ovig.), 4 mm,

Anton Bruun Sta. 401B

**DIAGNOSIS:** Rostrum absent, median anterior margin of shield relatively straight; eyestalks less than width of shield, cornea strongly dilated; chelipeds nude or sparsely setose.

**DESCRIPTION:** Shield broader than long, margin between antennal angles smooth, antennal angles broadly rounded; cardiac plate and branchiostegites membranous. Ophthalmic somite exposed, eyescales separated, lanceolate with apical spineule, posterior region widened; eyestalks barely equalling 2/3 width of shield, cylindrical, cornea greatly dilated. Antennular peduncles exceeding eyestalks by length of distal article. Antennal peduncle equalling antennular peduncle, antero-lateral angle of second article extended as prominent spine; acicle narrow, unarmed, setose distally,
reaching to distal third of terminal article. Right cheliped long, but not massive; merus trigonal, scattered low tubercles on upper face; carpus only slightly longer than wide, inner margin of upper face with row of procurred spines, longitudinal row of low tubercles in center of face, a few tubercles scattered over remainder; length of chela twice width, outer face of palm inflated, inner margin subcristiform with row of low tubercles, outer margin with row of close-set tubercles; finger 1/3 length of hand, cutting edges straight, tips calcareous. Left cheliped similar to right, but more slender; carpus length 1½ width; length of chela 2 1/3 width, cutting edges of fingers in contact throughout length, tips reaching to base of finger of right chela. Second and third pereiopods slender, unarmed except row of low tubercles on dorsal margin of carpus; dactylus slender, exceeding right cheliped by 1/4 length of article. Fourth pereiopod subchelate, propodal rasp multiseriate, dactylar rasp uniseriate, dactylus with 4-5 corneous spines on dorsal margin. Fifth pereiopod minutely chelate, dactylus sharply flexed, axis at right angles to propodus; propodal rasp covering only distal quarter of article. Male and female genitalia typical of genus. Pleopods entirely absent in male; four unpaired pleopods in female.

REMARKS: This species is unique in the complete absence of the male pleopods. Known from the Philippine Islands
(Henderson, 1888) and from the east coast of Africa, this species appears to have a disjunct distribution, not having been reported from any islands of the Indian Ocean nor from any portion of the Asian coast.

RANGE: Philippine Islands and east coast of Africa.

*Pagurus placens* (Stebbing, 1924)

Eupagurus *placens* Stebbing, 1924: 7

*Pagurus placens* Gordan, 1956: 333

MATERIAL EXAMINED:

One male, 9 mm Anton Bruun Sta. 394B

DIAGNOSIS: Eyestalks less than anterior width of shield, cornea slightly dilated; chelipeds and pereiopods densely setose; finger of left cheliped sharply curved.

DESCRIPTION: Shield longer than wide, rostrum obtuse, barely equalling antennal angles; cardiac plate and branchio-stegites membranous. Ophthalmic somite exposed, eyescales separated, broadly triangular; eyestalks cylindrical, reaching to proximal third of terminal article of antennular peduncle, cornea slightly dilated. Antennal peduncle exceeding antennular peduncle by half terminal article, prominent spine on antero-lateral angle of second article;
acicle slender, curved, unarmed, barely exceeding base of terminal article. Right cheliped tomentose; carpus barely longer than wide, row of procurved spines on mesio-dorsal margin; outer face of hand beset with scattered conical tubercles, but obscured by dense tomentum; cutting edges of finger and thumb armed with 3-4 rounded teeth, tips minutely corneous. Left cheliped more slender than right, densely setose, finger strongly curved, cutting edges in contact only at tips. Second and third pereiopods covered with plumose setae, unarmed; dactylus short, barely longer than propodus. Fourth pereiopod subchelate, propodal rasp multiseriate, dactylus with single row of fine corneous tubercles on ventral margin. Fifth pereiopod minutely chelate, propodal rasp extending over distal half of article. Genitalia typical of genus.

RANGE: Coast of South Africa northward to Mozambique.

_Pagurus macardlei_ (Alcock, 1905)

_Eupagurus macardlei_ Alcock, 1905: 129

_Pagurus macardlei_ Gordan, 1956: 331

MATERIAL EXAMINED:

11 males, 4-18 mm, and 3 females (1 ovig.), 6-13 mm, 

_Anton Bruun_ Sta. 218A
3 males, 8-12 mm, and 1 female (ovig.), 7 mm, 
Anton Bruun Sta. 248A 
1 male, 13 mm, Anton Bruun Sta. 255A 
5 males, 6-13 mm, and 4 females, 6-9 mm, Anton Bruun 
Sta. 269A 

DIAGNOSIS: Eyestalks less than anterior width of shield; rostrum not exceeding antennal angles; antennular peduncles exceeding antennal peduncles; chelipeds densely tomentose.

DESCRIPTION: Shield wider than long, rostrum broadly triangular, not exceeding antennal angles; cardiac plate feebly calcified, branchiostegites membranous. Ophthalmic somite exposed; eyescales separated, posterior margin rounded, anterior lanceolate with apical spinule. Eyestalks cylindrical, middle slightly constricted, cornea dilated. Antennular peduncle long, exceeding cornea by length of terminal article. Antennal peduncle barely reaching midpoint of terminal article of antennular peduncle; anterolateral angle of second article spiniform; acicle slender, curved, setose, reaching distal third of terminal article. Third maxillipeds with well developed crista dentata and a single prominent accessory tooth. Right cheliped twice length of carapace; length of carpus twice width, outer face with double longitudinal row of spines in center and single row on mesial margin; length
of chela twice width, finger half length of hand, outer face of palm with distinct median row of spines and lateral and mesial margins with close-set procurved tubercles; sculpture of both articles obscured by dense tomentum. Cutting edges of fingers straight, in contact throughout length, tips calcareous. Left cheliped shorter than right, barely reaching midway right palm; carpus length 2½ times width, outer face with single median row of spines; length of chela twice width, finger half length of hand, tips calcareous; densely tomentose as in right. Second and third pereiopods slender, unarmed except 2-3 spines distally on dorsal margin of carpus; dactylus nearly equalling combined length of carpus and propodus, unarmed except double row long stiff setae on dorsal margin, tip minutely corneous.

Fourth pereiopod subchelate; propodal rasp multiseriate, dactylar rasp uniseriate. Fifth pereiopod minutely chelate, propodal rasp occupying distal half of article, dactylar rasp uniseriate. Gills phyllobranchiate, eleven pairs.

Male and female genitalia typical of genus. Abdomen soft, coiled to left, terga indistinguishable except on fifth and sixth somites; four unpaired pleopods in male, three unpaired pleopods in female.

REMARKS: This species appears to select shells that lack the capacity to contain its body and the posterior portion of the abdomen is frequently reflected back upon itself.
ventrally. All of the specimens from Sta. 218A were in examples of a Murex-like snail and one specimen from Sta. 269A was in a Melongena-like shell.

RANGE: Persian Gulf and Gulf of Oman.

Genus Pylonagurus Milne-Edwards & Bouvier 1891

Shield strongly calcified, branchiostegites membranous; rostrum prominent; eyescales separated, cornea moderately dilated; antennal flagellum nude. Right cheliped massive, chela markedly flattened, fitting with left cheliped to form operculum; outer face variously sculptured, margins usually cristiform or tuberculate. Third maxillipeds with well developed crista dentata and prominent accessory tooth. Vasa deferentia paired, not protruded; gonopores of female paired. Gill pairs eleven. Male lacking paired gonopods, possessing 3 (sometimes 4) unpaired pleopods on left; female with one pair feebly developed gonopods and single unpaired pleopod on fifth somite.

Key to the Indian Ocean Species of Pylonagurus

1. Outer face of major chela with "pavement" of mushroom-shaped tubercles .................. guardafuimensis

Outer face of major chela with low rounded tubercles, not forming continuous "pavement" ........... 2
2. Margins of major chela subcristiform and regularly serrate ...................... *ungulatus*

Margins of major chela smooth and unarmed .. *mabberensis*

_Pyllogurus guardafuiensis* new species

**MATERIAL EXAMINED:**

1 male (holotype), 12 mm, *Anton Bruun* Sta. 465

**DIAGNOSIS:** Right cheliped armed with mushroom-shaped tubercles forming a continuous pavement over the surface, cutting edges of fingers paralleling axis of chela, fingertips calcareous; four unpaired pleopods in male.

**DESCRIPTION:** Shield wide as long, rostrum broadly triangular, barely equalling antennal angles; cardiac plate and branchiostegites membranous, expanded posterolaterally. Eyescales moderately separated, broad posterior margin tapering to acute tip anteriorly; eyestalks cylindrical, 2/3 anterior width of shield, cornea dilated. Antennular peduncles exceeding eyestalks by half terminal article (Plate XIII, Fig. 1). Antennal peduncle equalling antennular peduncle, anterolateral angle of second article extended, forming triangular spine; acicle slender, mesial margin finely denticulate, partially hidden by setae, extending beyond middle of terminal article; flagellum with paired
setae at widely spaced intervals. Third maxillipeds widely separated, sternal plate unarmed; crista dentata well developed, accessory teeth corneous. Right cheliped massive, much longer than left, permanently flexed at wrist; upper face of carpus triangular with scattered spiniform tubercles and stiff setae; length of hand twice width, outer face slightly inflated, armed with mushroom shaped tubercles forming a continuous "pavement", each tubercle polygonal in outline; lateral and mesial margins subcristiform, serrate; finger 1/3 length hand, cutting edges straight, tips calcareous (Plate XIII, Fig. 2). Left cheliped short, reaching only to hinge of right finger; carpus elongate, length twice width, sculpture similar to right; width of chela 1/3 length, sculpture similar to right but reduced, margins rounded, unarmed. Second and third pereiopods slender, exceeding major cheliped by half length of dactylus, unarmed except single spine on distodorsal angle of carpus of second pereiopod, dactylus with spiniform setae. Fourth pereiopod subchelate; propodal rasp multiserial; dactylus short, hardly flexed in opposition to propodus, ventral margin and tip corneous. Fifth pereiopod chelate, propodal rasp covering distal half of articles; dactylus spatulate, entire outer surface covered by rasp. Gills phyllobranchiate, eleven pairs. Male genitalia paired, vasa deferentia not protruded. Abdomen of male with four unpaired pleopods; female unknown.
REMARKS: This species generally agrees with the description of *Pylopagurus*, except in the unarmed sternal plate separating the third maxillipeds and the presence of a fourth pleopod on the abdomen of the male. Affinities of this species are difficult to assess, there being no marked similarity to any species of the Indian Ocean. Similarities to Western Atlantic forms appear superficial. The uniqueness of this specimen might be considered sufficient grounds for establishment of a new genus or subgenus. The holotype is deposited in the collection of the USNM. The specific name refers to the type locality off Cape Guardafui.

RANGE: Known only from the type locality.

*Pylopagurus mabberensis* new species

MATERIAL EXAMINED:

1 male (holotype), 6 mm, Anton Bruun Sta. 437

DIAGNOSIS: Outer face of major chela with low, rounded tubercles on periphery, granulations in central region obsolete; left cheliped and chela extremely slender, unarmed, thumb slightly deflexed; three unpaired pleopods in male.

DESCRIPTION: Shield strongly calcified, glabrous, cardiac plate and branchiostegites uncalcified. Rostrum broadly
triangular, hardly exceeding antennal angles (Plate XIV, Fig. 1). Eyescales widely separated, rounded posteriorly, acutely triangular anteriorly; eyestalks cylindrical, slightly enlarged proximally, cornea hardly dilated. Antennular peduncles exceeding eyestalks by \( \frac{1}{4} \) terminal article; antennal peduncles barely exceeding eyestalks, anterolateral angle of second article produced, spiniform; acicle slender, curved, unarmed, moderately setose on mesial margin, reaching midpoint terminal article; flagellum sparsely setose. Third maxillipeds separated by sternal plate bearing median cleft but no spines; crista dentata moderately developed, accessory tooth present. Right cheliped extremely massive, twice length of carapace; merus trigonal, dorsal margin faintly rugose; prominent tuft setae on distal mesial margin; carpus widest distally, dorsal face convex with scattered low tubercles, mesial and distal margins with prominent row of low calcareous tubercles; length of chela \( \frac{1}{2} \) times width, outer face flattened, margins not clearly delineated, regions adjacent to mesial and lateral margins with low rounded tubercles, becoming more prominent distally and reaching maximum density and development on finger and thumb. Finger less than half length of hand, cutting edges unarmed, tips calcareous, axis of finger oblique to axis of hand (Plate XIV, Fig. 2). Left cheliped extremely slender, hardly more massive than pereiopods; merus with three procurred spines distally on outer ventral margin; carpus with
five procurve spiniform tubercles distally on upper face; length of chela three times width, finger half length of hand, tips minutely corneous. Second and third pereiopods slender, unarmed except two rows spiniform setae on dactylus; dactylus exceeding length of propodus, tips corneous. Fourth pereiopod subchelate, propodal rasp extremely narrow (2-3 irregular rows of scales); ventral margin of dactylus with single row pectinate corneous scales, tip corneous. Fifth pereiopod minutely chelate; propodal rasp extending onto thumb; dactylar rasp uniseriate. Gills phyllobranchiate, 11 pairs. Male gonopores paired, vasa deferentia not protruded. Three unequally biramous pleopods on left side in male; female unknown.

REMARKS: This species appears closely related to *P. liochele*, from which it is distinguished by the smooth margins of the major chela, the extremely slender left cheliped and the narrow rasp on the fourth pereiopod. The major chela of this species is capable of complete extension, but appears to be normally held in a sharply flexed position. The specific name refers to Ras Mabber on the coast of Somalia, the type locality. Holotype deposited in the USNM.

RANGE: Known only from the type locality.
Genus *Tomopagurus* Milne-Edwards & Bouvier 1893

Similar to Pagurus except male possessing one pair gonopods in addition to three unpaired pleopods. Gills phyllobranchiate, 11 pairs.

(?) *Tomopagurus enigmaticus* new species

**MATERIAL EXAMINED:**

Eight males, 7-9 mm, (holotype, 9 mm), Anton Bruun Sta. 22B

**DIAGNOSIS:** Male with single pair gonopods, three unpaired pleopods; sternum of third maxillipeds unarmed; outer face of major chela with low scattered tubercles; finger sharply oblique to axis of chela.

**DESCRIPTION:** Shield strongly calcified, cardiac plate and branchiostegites soft, transparent; rostrum broadly rounded, barely exceeding antennal angles. Ophthalmic somite exposed, eyescales widely separated, bases rounded, tapering to slender acute anterior point; eyestalks short, cylindrical, cornea strongly dilated. Antennular peduncles exceeding eyestalks by $\frac{4}{5}$ length of terminal article. Antennal peduncles barely equalling tip of cornea; antero-lateral angle of second article spiniform; acicle slender, curved laterally, mesial margin obscurely serrate, setose,
reaching nearly to tip of distal article (Plate XV, Fig. 1); flagellum very sparsely setose, clearly exceeding pereiopods. Third maxilliped widely separated, sternal plate unarmed; crista dentata minutely serrate, two prominent teeth at posterior end, accessory tooth absent. Right chelifed massive, exceeding twice length of carapace; merus trigonal, lateral and ventral margins dentate; carpus broadest distally, distal width equalling length, upper face with longitudinal median eminence, sloping toward lateral and mesial margins, lateral and distal margins with rows of procurred spines; chela flattened, operculiform, length barely exceeding width, outer face of palm with median eminence extending to base of finger, lateral margin regularly serrate, mesial margin carinate, mesial margin of finger serrate, cutting edge with 2-3 rounded calcareous teeth, tips calcareous, axis of finger oblique to axis of hand (Plate XV, Fig. 2). Inner face of chela deeply excavated near lateral margin, inner face of thumb strongly carinate (Plate XV, Fig. 3). Left chelifed slender, barely exceeding base of right chela; carpus subcylindrical, length 2½ times width, unarmed; chela extremely slender, length three times width, finger half length of hand, cutting edges straight, minutely serrate, tips minutely corneous. Both chelips setose, right more densely than left. Second and third pereiopods extremely long, exceeding major chelifed, unarmed except a single spine on distal margin of carpus;
dactylus 1\frac{1}{2} times length of propodus, dorsal margin with fringe of stiff setae, tip corneous. Fourth pereiopod subchelate; propodal rasp uniseriate; dactylus unarmed except corneous tip. Fifth pereiopod barely chelate; dactylus much reduced, hardly opposing propodus; propodal rasp on distal half of article. Gills phyllobranchiate, 11 pairs. Vas deferentia not protruding; female genitalia unknown. Abdomen soft, coiled to left, terga 1-5 not distinguishable. Male with one pair gonopods and three unpaired, uniramous pleopods on abdomen. Uropods and telson markedly asymmetrical to left, numerous corneous tubercles on left posterior margin of telson.

REMARKS: These specimens agree with the diagnosis of the genus Tomopagurus as presently constituted and are hereby, with reservation, assigned to that genus. A critical re-examination of the Tomopagurus-Tomopaguropsis-Tomopaguroides group is needed. The similar widely disjunct distribution of these genera (western Atlantic and northeastern Indian Oceans) seems to indicate a possible parallel development in two geographically separated groups. Considering the general evolutionary trend of reduction of gills and pleopods in the Paguridae, it is not inconceivable that two unrelated groups might simultaneously duplicate one condition of reduction of these structures, thereby achieving a superficial resemblance.
RANGE: Known only from the type locality (Bay of Bengal).

Genus Spiropagurus Stimpson 1858

Carapace flattened, shield moderately to strongly calcified. Eyestalks short, cornea strongly dilated, greatly exceeded by both antennular and antennal peduncles; antennal flagellum nude, exceeding chelipeds and pereiopods. Chelipeds short, similar and subequal. Left vas deferens of male greatly produced and sprially coiled; female gonopores paired. A single species is known from the Indian Ocean.

Spiropagurus spiriger (de Haan, 1849)

Pagurus spiriger de Haan, 1849: 206
Spiropagurus spiriger Stimpson, 1858: 248

MATERIAL EXAMINED:

2 females (ovig.), 7 & 12 mm, Anton Bruun Sta. 21
9 males, 10-12 mm, & 4 females (ovig.), 11-14 mm,

Anton Bruun Sta. 38
1 male, 11 mm, Anton Bruun Sta. 41
2 males, 9 & 11 mm, Anton Bruun Sta. 41A
1 male, 10 mm, & 1 female, 10 mm, Anton Bruun Sta. 46
5 males, 10-18 mm, & 1 female (ovig.), 12 mm,

Anton Bruun Sta. 256
1 female, 14 mm, Anton Bruun Sta. 260A
1 female, 10 mm, *Anton Bruun* Sta. 261A

**DIAGNOSIS:** Shield broader than wide, rostrum obsolete, antennal angles with minute apical spinule; chelipeds and pereiopods squamose.

**DESCRIPTION:** Carapace flattened, branchial width equalling or exceeding length, shield moderately calcified, width 1½ times length; rostrum obsolete, exceeded by antennal angles, each with minute apical spinule. Eyescales broadly lanceolate, separated, ophthalmic somite exposed; eyestalks short, half anterior width of shield, cornea strongly dilated, corneal peninsula falciform. Antennular peduncles exceeding antennal peduncles by half length of terminal article. Anterolateral angle of second article of antennal peduncle extended to form acute spine; acicle slender, barely reaching base of terminal article, prominent fringe of setae on lateral and mesial margins; flagellum nude, exceeding tips of pereiopods. Third maxillipeds widely separated; crista dentata corneous, accessory tooth present. Chelipeds similar and subequal or right very slightly the larger, barely exceeding base of dactylus of second pereiopod; single prominent spine on ventral margins of ischium and merus; length of carpus twice width, two longitudinal rows of spines on dorsal face, distal margin spinose. Outer faces of chelae with regular transverse setiferous ridges,
giving impression of imbricated squamae; length $3\frac{1}{2}$ times width, finger half length of hand, straight cutting edge with uniformly close-set corneous scales interspersed at regular intervals with 8-10 calcareous tubercles, tips minutely corneous. Second and third pereiopods exceeding chelifeds by length of dactylus; outer face of merus, carpus and propodus with imbricating ridges similar to chelae; merus with 3-4 spines distally on ventral margin; upper face and distal margin of carpus spinose; upper margin of propodus regularly spinose, partially obscured by fringe of stiff setae; dactylus slender, $1\frac{1}{2}$ times length of propodus, prominent fringe of setae on upper margin, tip corneous. Fourth pereiopod weakly subchelate, ventral angle of propodus only slightly produced, dactylus exceeding propodal "digit" by $4/5$ length; propodal rasp of 2-3 irregular rows scales; dactylus unarmed. Fifth pereiopod minutely chelate, propodal rasp covering distal half article, dactylus spatulate. Gill pairs eleven. Left vas deferens protruded as slender tapered tube forming flat spiral of $1\frac{1}{2}$ turns; right vas deferens not protruded; female gonopores paired. Abdomen soft, coiled to right; three uniramous pleopods on male; four pleopods (three biramous, one uniramous) on female.

RANGE: Gulf of Aden and Arabian Sea to Philippine Islands and South China Sea.
Genus *Nematopagurus* Milne-Edwards & Bouvier 1892

Shield strongly calcified; rostrum obsolete; eyescales small, widely separated. Third maxillipeds widely separated, crista dentata well developed, accessory tooth absent. Chelipeds similar in shape and sculpture, but markedly unequal in size, right larger and longer than left. Fourth pereiopod subchelate; fifth chelate. Right vas deferens of male protruded, directed to left, terminating in a slender filament; left vas deferens a low conical papilla. Three unpaired pleopods on abdomen of male; one pair gonopods and four unpaired pleopods on abdomen of female. Gills phyllo-branchiate, eleven pairs.

Key to the Indian Ocean Species of *Nematopagurus*

1. Outer face of chelae with flat, imbricating squamae ................................................................. 2

Outer face of chelae with spines or tubercles (not squamiform plates) ........................................ 3

2. Squamiform plates on chelae in two longitudinal rows ................................................................. *scutellichelis*

Squamiform plates on chelae in several longitudinal rows ......................................................... *squamicichelis*

3. Armature of right chela spiniform ............................... 4

Right chela armed with rounded tubercles, several forming a cluster in center of outer face ...... *diadema*
4. Armature of right chela consisting only of single
   median longitudinal row of spines ....................... 5
Armature of right chela consisting of scattered
spiniform tubercles in addition to median
row .............................................. muricatus
5. Eyestalks equal or exceed anterior width of
   shield ........................................ gardineri
Eyestalks less than anterior width of shield ... indicus

Nematopagurus diadema Lewinsohn, 1969

Nematopagurus diadema Lewinsohn, 1969: 74-79

MATERIAL EXAMINED:

1 male, 2 mm, Anton Bruun Sta. 403E (M. L. Wass, coll.)

DIAGNOSIS: Eyestalks exceeding width of shield, equalling
antennular peduncles; outer face of both chelae with pecu­
liar sculpture of mushroom-shaped tubercles, 14-18 of which
form prominent boss in center of face.

DESCRIPTION: Shield longer than wide, generally triangular;
rostrum obsolete, antennal angles prominent. Ophthalmic
somite exposed, eyescales small, separated; eyestalks cy­
lindrical, equalling antennular peduncles, cornea moderate­
ly dilated, corneal peninsula short, two stiff bristles
near base. Antennal peduncle barely reaching cornea; acicle
slender, sparsely setose, reaching distal third of terminal article; (flagellum missing on specimen). Third maxillipeds widely separated, crista dentata well developed, accessory tooth absent. Right cheliped short, barely exceeding propodus of second pereiopod; merus triangular, unarmed; carpus length 1½ times width, outer face with indistinct median row of spines, lateral margin spinose; chela length twice width, finger less than half length of chela, outer face of palm with 3-4 low mushroom-shaped tubercles on lateral and mesial margins, a single median row of tubercles with a prominent boss of 14-18 clustered tubercles in center of outer face, row continued onto fixed finger. Left cheliped similar to right, but shorter and smaller. Second and third pereiopods slender, unarmed except for 4-6 corneous spines on ventral margin of dactylus, dactylus 1½ times length of propodus. Fourth pereiopod missing from specimen. Fifth pereiopod minutely chelate, dactylus partially obscured by prominent tuft of setae. Right vas deferens protruded, forming slender, tapered tube, coiled once and terminating as slender filament directed toward left side; left vas deferens with low conical papilla, tip directed toward right side. Gills phyllobranchiate, eleven pairs. Male with three unpaired pleopods.

REMARKS: This species, previously described and reported only from the Red Sea (Gulf of Aqaba), is here recorded from
the coast of Mozambique at a depth of 85 m.

RANGE: Reported only from the Gulf of Aqaba and the Mozambique Channel.
Zoogeography and Distribution of Indian Ocean Shelf Pagurids

A study of the distribution of the pagurid fauna of the Indian Ocean (Appendix C) indicates that the distribution patterns of the hermit crabs of the continental shelf reflect the existence of three distinct faunal regions. The easternmost of these regions extends from the northwest coast of Australia through the Indonesian archipelago and coasts of Indochina and the Bay of Bengal, with the western limit at Ceylon and the Gulf of Manaar. The western Indian Ocean comprises two regions; one extends along the east coast of Africa from the vicinity of Durban northward to Mombasa and includes the islands of Madagascar, Aldabra, Mauritius, Rodriguez, the Comoro Islands and the Seychelles Islands; the second region includes the coasts of Somalia and Arabia, including the Gulf of Aden, the Red Sea, Gulf of Oman and the Persian Gulf with the eastern limit occurring on the Malabar Coast of India. For convenience, these regions are designated Indo-Malayan, Africa-Mascarene and Arabian-Red Sea, respectively.

Comparison of the species diversity and distribution of genera (Table 1) indicates that the fauna of the Arabian-Red Sea region is markedly distinct from that of either of the other regions. The genus Cestopagurus occurs in the Indian Ocean only within this region, while three other genera Nematopagurus, Spiropagurus and Paguristes, exhibit
Table 1. REGIONAL DISTRIBUTION OF SEVERAL PAGURID GENERA IN THE INDIAN OCEAN

The numbers of species in each genus that occur in each region compared to the number of species that occur in both regions.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Indo-Malayan</th>
<th>Common</th>
<th>Africa-Madagascar</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coenobita</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Dardanus</td>
<td>11</td>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td>Clibanarius</td>
<td>15</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>Calcinus</td>
<td>5</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Paguristes</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Spiropagurus</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nematopagurus</td>
<td>2</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Cestopagurus</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

B. Genus     | Indo-Malayan | Common | Arabian-Red Sea |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
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<tr>
<td>Coenobita</td>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Dardanus</td>
<td>11</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Clibanarius</td>
<td>15</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Calcinus</td>
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<td>2</td>
<td>2</td>
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<tr>
<td>Paguristes</td>
<td>2</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Spiropagurus</td>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Nematopagurus</td>
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<td>4</td>
</tr>
<tr>
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<td>3</td>
</tr>
<tr>
<td>C. Genus</td>
<td>Arabian-Red Sea</td>
<td>Common</td>
<td>Africa-Madagascar</td>
</tr>
<tr>
<td>----------</td>
<td>----------------</td>
<td>--------</td>
<td>-------------------</td>
</tr>
<tr>
<td>Coenobita</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Dardanus</td>
<td>7</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>Clibanarius</td>
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<td>4</td>
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</tr>
<tr>
<td>Clcinus</td>
<td>2</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Paguristes</td>
<td>11</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Spiropagurus</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nematopagurus</td>
<td>4</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Cestopagurus</td>
<td>3</td>
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</tr>
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</table>
greater diversity within this region, and have limited
distribution outside its boundaries. It is interesting
to note that other species of these genera are found only
in the Mediterranean Sea and the Atlantic Ocean.

Even in genera with more widespread occurrence, e.g.
Dardanus, Clibanarius, and Calcinus, certain anomalies of
distribution are observed. The Arabian-Red Sea region has
higher degree of endemism than either the Indo-Malayan or
Africa-Mascarene regions (Table 1, B and C). A similar
comparison (Table 1, A) of the Africa-Mascarene region with
the Indo-Malayan region reveals a greater number of shared
species, indicative of the faunal affinities of these re­
gions.

The affinities recognized in the Indo-Malayan and
Africa-Mascarene regions appear difficult to reconcile with
the vast oceanic basin separating them and the intervening
Arabian-Red Sea region preventing direct connection along
the coastline. On the basis of the larger overall number
of species, the Indo-Malayan region may be assumed to be
the original center of dispersion of the Indian Ocean
pagurids. From this center, two possible dispersion routes
to the Africa-Mascarene region may be postulated. The
first route, involving migration by "island hopping" pro­
ceeds from the coast of Indochina to the Nicobar Island,
thence across the Bay of Bengal to Ceylon and southward
to the Chagos Archipelago. From Chagos, a series of banks
and shoals (Saya de Malha, Nazareth Bank, Cargados Carajos) and islands (Amirante Islands and Seychelles Islands) forms a bridge to the coasts of Africa and Madagascar. The simplicity and forthrightness of this route is attractive, but a serious weakness of this "stepping-stone" hypothesis lies in the adverse currents encountered in the Chagos-Saya de Malha region. The Equatorial Countercurrent sweeps eastward across these shoals, carrying both planktonic larvae and flotsam on which adults might be rafting away from the necessary landfall and into the central basin of the Indian Ocean. The second possible route to the Africa-Mascarene region involves oceanic dispersal directly from the Indo-Malayan region to the continental shelf of Africa and Madagascar. This dispersion might occur as planktonic larvae or as adults being "rafted" by drifting flotsam. The principal appeal of the direct oceanic dispersal route lies in the fact that the South Equatorial Current flows westward directly from the Indo-Malayan region toward the coast of Africa and in the strong prevailing winds blowing from Australia toward Africa. The strongest adverse factor of this route is the extremely long drift from Cocos-Keeling atoll to the islands lying north and east of Madagascar, a minimum distance of 5000 to 5500 kilometers. Whether the planktonic stage of pagurids is sufficiently long to allow the larvae to traverse this distance is questionable. Laboratory rearing of pagurid larvae (Bookhout, 1964, 1972)
indicates that the larval life spans 29 to 47 days before reaching the glaucothoe stage with an additional 11 to 17 days before molting of the glaucothoe. Application of data derived from laboratory studies to conditions in the field may not be valid, but if we assume an average larval life-span of 30 days, we find that the larva must travel an average of 166 km per day in order to complete the voyage. If we assume that the average larval life is 60 days, then the average speed required is 84 km per day. Speeds of this magnitude are highly unlikely to be achieved, therefore, in order to complete the voyage the larval lifetime must be assumed to be longer than those determined in the laboratory or the final metamorphosis of the larva must be delayed. Instances of delayed metamorphosis and setting of larvae are known in the Crustacea, but no reports of this phenomenon in pagurids have been made. Observations of the activity of glaucothoe in the laboratory indicate a longer active swimming period in cases where suitable shells are not available (Bookhout, 1964).

The probability of transport of adults associated with flotsam is quite easily accepted for members of some intertidal and subtidal pagurids, e.g. Coenobita, Clibanarius, Dardanus, but it is difficult to visualize circumstances in which adults of certain shelf pagurids would become associated with floating debris. Recognizing the lack of corroborative evidence relating to the length or extension of the
planktonic stage and assessing the significance of the negative aspects of the alternative routes, oceanic dispersal of planktonic larvae appears to offer the most likely explanation of the affinities observed between the Indo-Malayan and the Africa-Mascarene regions.

Both the Africa-Mascarene region and the Arabian-Red Sea region have their principal affinities with the Indo-Malayan region, but each also exhibits affinities with the pagurid fauna of the Atlantic Ocean and the Mediterranean Sea. The Atlantic components of the Africa-Mascarene fauna are recognized as immigrants from the South Atlantic and Gulf of Guinea via the Cape of Good Hope. The only explanation for the Atlantic-Mediterranean component of the Arabian-Red Sea fauna is that its species are relicts of the Tethyan fauna.
APPENDIX A

List of Unidentifiable Specimens

The following specimens were not identified due to missing appendages, mutilation of body, immature or juvenile stage, etc.

(?) *Catapaguroides* sp.  
1 female  Sta. 407I
1 male  Sta. 408A
1 female  Sta. 409L

*Catapagurus* sp.  
1 male  Sta. 425

(?) *Cestopagurus* sp.  
1 male  3 mi. S. of Moroni
1 male  Sta. 453
1 female  Sta. 400C

*Clibanarius* sp.  
1 female  Aldabra

*Diogenes* sp.  
2 ?  Cocos-Keeling
3 ?  Sta. 246A
1 male  Sta. 201A
1 ?  Sta. JR22
1 ?  Sta. 371G

(?) *Nematopagurus* sp.  
1 male  Sta. 403E

*Pagurus* sp.  
1 male  Cocos-Keeling
1 ?  Sta. 370G
1 ?  Sta. 372C
1 male  Sta. 390S
<table>
<thead>
<tr>
<th>Species</th>
<th>Quantity</th>
<th>Gender</th>
<th>Station</th>
</tr>
</thead>
<tbody>
<tr>
<td>(?)Pagurus sp.</td>
<td>1 ?</td>
<td></td>
<td>Sta. 124F</td>
</tr>
<tr>
<td></td>
<td>1 male</td>
<td></td>
<td>Sta. 202B</td>
</tr>
<tr>
<td></td>
<td>1 ?</td>
<td></td>
<td>Sta. 221A</td>
</tr>
<tr>
<td>Parapagurus sp.</td>
<td>2 ?</td>
<td></td>
<td>Sta. 373H</td>
</tr>
<tr>
<td></td>
<td>3 males</td>
<td></td>
<td>Sta. 399B</td>
</tr>
<tr>
<td>(?)Pylopagurus sp.</td>
<td>1 male</td>
<td></td>
<td>Sta. 393A</td>
</tr>
</tbody>
</table>
APPENDIX B

LIST OF COLLECTING STATIONS AND LOCALITIES

Station numbers preceded by "AB" refer to stations occupied by R/V Anton Bruun, those preceded by "TV" refer to stations of R/V Te Vega and the letters "JR" identify those stations in the vicinity of Nossi Be, Madagascar that were collected by Mr. Jack Rudloe.

<table>
<thead>
<tr>
<th>Sta. #</th>
<th>Date</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Depth (m.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AB 22B</td>
<td>24 Mar. 1963</td>
<td>10°39' N.</td>
<td>97°06' E.</td>
<td>290</td>
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<tr>
<td>AB 201A</td>
<td>13 Nov. 1963</td>
<td>17°54' N.</td>
<td>72°27' E.</td>
<td>50</td>
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<tr>
<td>AB 202A</td>
<td>13 Nov. 1963</td>
<td>17°25' N.</td>
<td>71°39' E.</td>
<td>100</td>
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<tr>
<td>AB 203A</td>
<td>14 Nov. 1963</td>
<td>19°07' N.</td>
<td>71°41' E.</td>
<td>74</td>
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<tr>
<td>AB 204A</td>
<td>15 Nov. 1963</td>
<td>20°30' N.</td>
<td>70°41' E.</td>
<td>35</td>
</tr>
<tr>
<td>AB 209A</td>
<td>16 Nov. 1963</td>
<td>20°49' N.</td>
<td>68°41' E.</td>
<td>66</td>
</tr>
<tr>
<td>AB 213A</td>
<td>17 Nov. 1963</td>
<td>21°11' N.</td>
<td>69°16' E.</td>
<td>74</td>
</tr>
<tr>
<td>AB 218A</td>
<td>18 Nov. 1963</td>
<td>22°03' N.</td>
<td>68°19' E.</td>
<td>81</td>
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<tr>
<td>AB 221A</td>
<td>18 Nov. 1963</td>
<td>22°31' N.</td>
<td>68°07' E.</td>
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<td>AB 224A</td>
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<td>23°00' N.</td>
<td>68°10' E.</td>
<td>25</td>
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<td>AB 233A</td>
<td>21 Nov. 1963</td>
<td>24°01' N.</td>
<td>66°33' E.</td>
<td>86</td>
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<tr>
<td>AB 241A</td>
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<td>63°52' E.</td>
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<td>60°45' E.</td>
<td>122</td>
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<td>29 Nov. 1963</td>
<td>25°10' N.</td>
<td>60°27' E.</td>
<td>84</td>
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<tr>
<td>AB 253A</td>
<td>29 Nov. 1963</td>
<td>25°25' N.</td>
<td>58°20' E.</td>
<td>87</td>
</tr>
<tr>
<td>AB 255A</td>
<td>30 Nov. 1963</td>
<td>25°30' N.</td>
<td>57°07' E.</td>
<td>97</td>
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<tr>
<td>AB 256A</td>
<td>30 Nov. 1963</td>
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<td>57°02' E.</td>
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</tr>
<tr>
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<td>Date</td>
<td>Latitude</td>
<td>Longitude</td>
<td>Depth (m.)</td>
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<td>------------</td>
<td>---------------</td>
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<td>------------</td>
</tr>
<tr>
<td>AB 260A</td>
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<td>56°53' E.</td>
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<td>56°34' E.</td>
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<td>AB 266A</td>
<td>2 Dec. 1963</td>
<td>24°27' N.</td>
<td>56°50' E.</td>
<td>51</td>
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<td>3 Dec. 1963</td>
<td>23°35' N.</td>
<td>58°49' E.</td>
<td>130</td>
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<tr>
<td>AB 356J</td>
<td>29 Jul. 1964</td>
<td>29°10' S.</td>
<td>31°51' E.</td>
<td>42</td>
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<td>AB 372C</td>
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<td>34°50' E.</td>
<td>22</td>
</tr>
<tr>
<td>AB 373F</td>
<td>22 Aug. 1964</td>
<td>26°02' S.</td>
<td>33°08' E.</td>
<td>366</td>
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<tr>
<td>AB 373H</td>
<td>23 Aug. 1964</td>
<td>26°58' S.</td>
<td>33°54' E.</td>
<td>896</td>
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<tr>
<td>AB 380C</td>
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<td>32°58' S.</td>
<td>43°41' E.</td>
<td>950</td>
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<tr>
<td>AB 390C</td>
<td>8 Sep. 1964</td>
<td>29°45' S.</td>
<td>31°40' E.</td>
<td>440</td>
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<tr>
<td>AB 390S</td>
<td>9 Sep. 1964</td>
<td>29°35' S.</td>
<td>31°42' E.</td>
<td>138</td>
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<tr>
<td>AB 391F</td>
<td>9 Sep. 1964</td>
<td>29°26' S.</td>
<td>31°46' E.</td>
<td>77</td>
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<tr>
<td>AB 391J</td>
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<td>29°21' S.</td>
<td>31°35' E.</td>
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<tr>
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<td>29°18' S.</td>
<td>31°33' E.</td>
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<td>AB 393A</td>
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<td>17°19' S.</td>
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<td>are in vicinity of</td>
<td>less than</td>
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<tr>
<td></td>
<td></td>
<td>Nossi Be</td>
<td>5 meters</td>
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<td>JR-38</td>
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<td>155°37' E.</td>
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### APPENDIX C

**Distribution of Indian Ocean Pagurids**

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<tr>
<th>Genus</th>
<th>Species</th>
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<tr>
<td>Anapagurus</td>
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<td>acanthochirus</td>
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<td>E. coast Africa to Indonesia</td>
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<tr>
<td>Birgus</td>
<td>latro</td>
<td>Indian Ocean and South Pacific</td>
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<td>Calcinus</td>
<td>elegans</td>
<td>E. coast Africa and Gulf of Aden throughout Indo-Pacific to Hawaii</td>
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<tr>
<td></td>
<td>gaimardii</td>
<td>Maldive Is. and Indo-Pacific to Tahiti</td>
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<tr>
<td></td>
<td>laevimanus</td>
<td>E. coast Africa and Indo-Pacific to Hawaii and Tahiti</td>
</tr>
<tr>
<td></td>
<td>latens</td>
<td>Red Sea and Indo-Pacific to Hawaii</td>
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<td>minutus</td>
<td>Indonesia</td>
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<td>rosaceus</td>
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<td>investigatoris</td>
<td>Gulf of Manaar</td>
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<td>Red Sea, Madagascar and Burma</td>
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<td>Cestopagurus</td>
<td>coutieri</td>
<td>Red Sea and Gulf of Aden</td>
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<tr>
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<td>helleri</td>
<td>Red Sea</td>
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<td>boschmai</td>
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<td>carnitex</td>
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<td>clibanarius</td>
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<td>Indonesia and South Pacific</td>
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<td><em>signatus</em></td>
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<td>E. coast Africa throughout Indo-Pacific</td>
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<td><em>asper</em></td>
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**Dardanus**

- **deformis**
  - E. coast Africa and Indo-Pacific to Tahiti
- **fabimanus**
  - E. coast Africa and Indonesia
- **guttatus**
  - E. coast Africa and Indo-Pacific to Hawaii
- **hessi**
  - Gulf of Oman and Indo-Pacific to New Guinea
- **imbricatus**
  - Bay of Bengal and Indonesia
- **lagopodes**
  - E. coast Africa, Red Sea, Persian Gulf and Indo-Pacific
- **megistos**
  - E. coast Africa and Indo-Pacific to Hawaii
- **scutellatus**
  - E. coast Africa and Indo-Pacific
- **setifer**
  - E. coast Africa and Indo-Pacific
- **tinctor**
  - Red Sea, Gulf of Aden and Persian Gulf
- **wood-masoni**
  - Red Sea, Arabian Sea and Indo-Pacific

**Diogenes**

- **affinis**
  - Bay of Bengal and Indonesia
- **avarus**
  - E. coast Africa, Red Sea and Indo-Pacific
- **bicristimanus**
  - E. Indian Ocean
- **costatus**
  - Red Sea, E. coast Africa and Seychelles Is. to Gulf of Manaar
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### Pagurodes

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### Pagurus

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LITERATURE CITED


Forskal, P. 1775. Descriptiones animalium, avium, piscium, amphibiorum, insectorum, vermium; quae in itinere orientili observavit. 164 pp.


PLATES
Plate I. *Dardanus arrosor*

Fig. 1. Shield and cephalic appendages

Fig. 2. Left chela (outer face)

Scale = 5.0 mm
Plate II. Dardanus arrosor

Fig. 1. Second pereiopod (left)
Fig. 2. Fourth pereiopod (left)
Scale = 5.0 mm
Plate III. *Dardanus guttatus*

Fig. 1. Shield and cephalic appendages
Fig. 2. Left cheliped (outer face)
Fig. 3. Second pereiopod (left)
Fig. 4. Fourth pereiopod (left)

Scale = 5.0 mm
Plate IV. *Dardanus megistos*

Fig. 1. Shield and cephalic appendages

Fig. 2. Left cheliped

Scale = 5.0 mm
Plate V. *Dardanus megistos*

Fig. 1. Right cheliped

Fig. 2. Second pereiopod (left)

Fig. 3. Fourth pereiopod (left)

Scale = 5.0 mm
Plate VI. *Anicus acanthochirius*

Fig. 1. Shield and cephalic appendages
Fig. 2. Left cheliped
Fig. 3. Fourth pereiopod (left)
Fig. 4. Pleopod 2 (female)

Scale = 5.0 mm
Plate VII. *Trizopagurus tenebrarum*

Fig. 1. Shield and cephalic appendages
Fig. 2. Left cheliped (outer face)
Fig. 3. Left cheliped (inner face)
Fig. 4. Second pereiopod (left)

Scale = 1.0 mm
PLATE VIII. *Trizopagurus strigatus*

Fig. 1. Shield and cephalic appendages

Fig. 2. Left cheliped (outer face)

Fig. 3. Left cheliped (inner face)

Fig. 4. Second pereiopod (left)

Fig. 5. Fourth pereiopod (left)

Scale = 5.0 mm
Plate IX. *Diogenes diogenes*

Fig. 1. Shield and cephalic appendages

Fig. 2. Left cheliped

Fig. 3. Right cheliped

Fig. 4. Second pereiopod (left)

Scale = 5.0 mm
Plate X. *Paguristes mossambicus*

Fig. 1. Shield and cephalic appendages

Fig. 2. Left cheliped

Fig. 3. Fourth pereiopod (left)

Fig. 4. Male genitalia and gonopods (not to scale)

Scale = 5.0 mm
Plate XI. _Paguristes plamosus_

Fig. 1. Shield and cephalic appendages

Fig. 2. Left cheliped

Fig. 3. First pleopod (left)

Scale = 5.0 mm
Plate XII. *Parapagurus pilosimanus bouvieri*

Fig. 1. Shield and cephalic appendages
Fig. 2. Right cheliped (tomentum removed)
Fig. 3. Left cheliped (tomentum removed)

Scale = 5.0 mm
Plate XIII. *Pylcopagurus guardafuiensis*

Fig. 1. Shield and cephalic appendages

Fig. 2. Right cheliped

Fig. 3. Left cheliped

Scale = 5.0 mm
Plate XIV. *Pylopagurus mabberensis*

Fig. 1. Shield and cephalic appendages

Fig. 2. Right cheliped

Fig. 3. Left cheliped

Scale = 5.0 mm
Plate XV. *Tomopagurus enigmaticus*

Fig. 1. Shield and cephalic appendages
Fig. 2. Right cheliped (outer face)
Fig. 3. Right cheliped (inner face)

Scale = 5.0 mm
VITA

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