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A Revision of the Recent Indo-west Pacific Species of the Genus *Lyreidus* De Haan (Crustacea, Decapoda, Raninidae)

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Abstract

A KEY is provided to the Recent species of *Lyreidus*. Three species are distributed throughout the northern Indo-west Pacific and one throughout the western Pacific and south-eastern Indian Ocean; one species occurs in the eastern Atlantic Ocean. The four Indo-west Pacific species are compared with each other and illustrated.

Examination of 257 specimens of the Indo-west Pacific species shows that all vary considerably with growth and that there are also sexual differences. Morphometric analysis reveals no statistically significant differences between Australian and New Zealand populations of *Lyreidus* and Japanese specimens of *L. tridentatus* De Haan. *L. australiensis* Ward from Australia and *L. fossor* Bennett from New Zealand are therefore considered to be junior synonyms of *L. tridentatus*. *L. stenops* Wood-Mason is shown to be a senior synonym of *L. integra* Terazaki and *L. politus* Parisi.

The known geographic distribution of all Indo-west Pacific species is extended to the South China Sea—Philippine area and *L. tridentatus* is recorded from the southern part of the western coast of Australia. The species are distributed along the continental shelf and down the continental slope to over 400 fathoms.

INTRODUCTION

A LARGE number of specific names have been given to different forms of *Lyreidus* without full investigation of morphological variation in previously named species. A few species of the genus are very widely distributed geographically while a larger number are rather localised. Both these features are common to many groups of animals. Most previous accounts of the genus *Lyreidus* recognise five Recent species—four Indo-west Pacific and one western Atlantic (Sakai, 1937). However, no less than 10 names are in existence for the Indo-west Pacific species. Since the beginning of the present century it has been recognised that the first described species, *L. tridentatus*, was very widely distributed—from Japan (De Haan, 1841) to East Africa on the one hand (Doflein, 1904) and to eastern Australia and New Zealand on the other (Haswell, 1882; Chilton, 1906). However, within the last 40 years both the Australian and New Zealand populations have, after examination of but a few specimens, been considered specifically distinct from the Japanese form (Ward, 1933; Bennett, 1964). There has been no claim that more than one species exists in New Zealand waters yet three different specific names have been used in the New Zealand brachyuran literature of the last 20

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years. The different supposed "species" within the *Lyreidus* group have been separated by features obviously amenable to simple statistical analysis; phrases such as "longer than", "stouter than", "more projecting than", occur throughout both Ward's and Bennett's discussions of the distinctness of their "species".

This study began as an examination of the morphological variation in the "species" of the *Lyreidus tridentatus* group. Material was obtained from Japan, eastern Australia and New Zealand; the distinctive features of *L. brevifrons,* which closely resembles *L. tridentatus* in many ways, were also investigated. Recent collections from the south China Sea made by the Fisheries Research Station, Hong Kong, from the Philippines and Hawaii by Mrs Mary E. King on the "Pele", from Western Australia by staff of the Western Australian Museum during investigations of the benthic invertebrate fauna of Western Australia, and from

TABLE I.—Summary of morphological characters of Indo-west Pacific *Lyreidus* species.

Character	*tridentatus*	*brevifrons*	*stenops*	*channeri*
Frontal width	1/3 carapace width or more	ca 2/5 carapace width	ca 1/5 carapace width	2/5 carapace width or more
Rostrum	subacute, basal width ca 1½ length	acute, basal width equal to length	subacute or rounded, basal width equal to length	acute, basal width ¾ length
External orbital spine	strong, divergent, no longer than rostrum	parallel or subparallel, longer than rostrum	strongly divergent, no longer than rostrum	subparallel, longer than rostrum
Anterolateral margin	granular, naked, straight or weakly concavo-convex from front backwards	strongly granular, naked, strongly concavo - convex from front backwards	smooth, naked, very weakly concavo - convex from front backwards or straight	granular, hirsute, concavo - convex from front backwards
Lateral carapace spines	1 short to moderately long, straight or weakly curved	1 short, curved	none	2 very long, straight
Sternum	anterolaterally rounded or blunt	anterolaterally acute or rounded	anterolaterally obliquely truncate	anterolaterally acute
Cheliped merus dorsal spines	1 small, blunt, 1/3 from base	1 small, blunt, 1/3 from base	none	1 or 2 short, sharp, 1/3 from base
Cheliped carpus dorsal spines	2 sharp, slender: 1 halfway along, 1 subdistal	2 long, sharp, slender: 1 halfway along, 1 subdistal	1 sharp or blunt, subdistal, sometimes 1 small, blunt, half-way along	1 sharp, slender, subdistal
Chela palm ventral spines	3 or 4 increasing regularly in size distally	3 or 4 increasing regularly in size distally	3 increasing regularly in size distally	1 or 2 short, proximal, 1 large distal
Abdomen segment 3 spine	1 small, blunt, 1/3-½ from base in midline	1 small, blunt, close to distal edge in midline	none	1 long, curved, 2/3 from base in midline
Abdomen segment 4 spine	1 long, curved, 1/3-½ from base in midline	1 long, curved, sharp, central	1 short, weakly curved or straight, backwardly directed, 1/3 from base	1 long, curved, 2/3 from base in midline

northern New Zealand by the N.Z. Oceanographic Institute, allowed revisionary studies well beyond those originally envisaged.

This paper reports on a morphometric analysis of available material of *Lyreidus tridentatus* from throughout its geographic range. The dimensions chosen for analysis include those used by Ward and Bennett to distinguish Australian and New Zealand forms from the Japanese one and those used by Sakai (1937) to distinguish *L. brevifrons*. The geographic ranges previously accorded the four species recognised here are modified. Full synonymies and lists of previously recorded localities are given for all species. The morphological features of the four species are summarised in Table I; adequate descriptions have been given previously by Alcock (1896), Parisi (1914), Sakai (1937) and Bennett (1964). The geographic distribution of three species is shown in Fig. 1; geographic and ecological distribution of the four Indo-west Pacific species are summarised in Table II.

MATERIALS AND METHODS

A total of 257 specimens of all four Indo-west Pacific species were examined from throughout the western Pacific and south-eastern Indian Oceans. The specimens were obtained from the following institutions (abbreviations given are those used in the lists of material examined for each species):

Australian Museum, Sydney (AM);

British Museum (Natural History), London (BM);

Bernice P. Bishop Museum, Honolulu (BPBM);

Commonwealth Scientific and Industrial Research Organisation, Division of Fisheries and Oceanography, Cronulla near Sydney (CSIRO);

Dominion Museum, Wellington (DM);

Fisheries Research Station, Hong Kong (FHK);

Rijksmuseum van Natuurlijke Historie, Leiden (LM);

New Zealand Oceanographic Institute, Wellington (NZOI);

Musée Zoologique de l'Université et de la Ville, Strasbourg (SM);

United States National Museum, Washington (USNM);

Western Australian Museum, Perth (WAM); and

Institut für Spezielle Zoologie und Zoologisches Museum, Berlin (ZMB).

The shape and ornmentation of the carapace, sternum, abdomen, chelipeds and legs were studied in all specimens.

The following measurements were taken where possible:

1. carapace length in the midline from the tip of the rostrum to the posterior edge of the carapace;
2. carapace width at its widest part (excluding spines);
3. carapace width between the tips of the lateral spines;
4. interorbital width—distance between the tips of the external orbital spines projecting forwards on each side of the eyestalks;
5. anterolateral margin length—distance along anterolateral border from tip of the external orbital spine to the widest part of the carapace;
6. external orbital spine length—distance along lateral edge of external orbital spine from its tip to a point opposite the middle of the orbital concavity on the dorsal surface;
7. cheliped merus length—distance along dorsal surface from junction with ischium to distal edge;
8. cheliped merus height at its greatest convexity, about midway along its length;
9. chela length—distance along dorsal edge from junction with carpus to tip of dactyl;

10. chela height—distance between dorsal and ventral borders measured at its widest part (at distal edge of palm from junction of palm and fixed finger);
11. second ambulatory dactyl length—measured along dorsal surface;
12. second ambulatory dactyl width—distance across widest part of segment (beyond its base);
13. third ambulatory dactyl length—measured along dorsal edge;
14. third ambulatory dactyl width—distance across widest part of segment (about midway along its length);
15. abdominal segment 5 length—measured along midline;
16. abdominal segment 5 width—distance across segment at widest part;
17. abdominal segment 6 length—measured along midline;
18. abdominal segment 6 width—distance across segment at widest part.

The shape of the first pleopod of the male was also studied in all species.

In the lists of material examined given below the measurement given is the carapace length. Measurements were made with dial calipers to the nearest 0.1mm. Drawings were completed with the aid of a camera lucida. The number following the institution's abbreviation in the lists of material examined is the registered number of the specimen.

SYSTEMATICS

Family RANINIDAE Dana, 1852.

Reptant decapods with carapace remarkably elongate but not covering abdominal terga, the first four or five of which lie exposed in dorsal view. Last pair of legs raised in dorsal plane of body. Antennae large; antennules large but not folding into fossae. Thoracic sternum broad anteriorly, very narrow or linear posteriorly; posterior thoracic epimera largely exposed by reduction of branchiostegite. Third maxillipeds narrow, completely covering buccal cavern, palp concealed in rest; exopodite little longer than ischium (after Alcock, 1896; and Rathbun, 1937; modified).

REMARKS. The above diagnosis includes only external morphological features.

The Raninidae have historically been placed within the Oxystomata (which also includes the dorippids, leucosiids and calappids) (Alcock, 1896). The family was separated as a subtribe of the Brachyura—the Gymnopleura—distinct from the Oxystomata—by Bourne (1922) in a detailed account of the morphology and anatomy of the members of this group of crabs; recent classifications have accepted Bourne's subtribe (Rathbun, 1937; Sakai, 1965).

A large number of fossil genera are known (Balss, 1957) and several genera have fossil as well as Recent species; *Lyreidus* is among these. Most of the fossil species are known from fragments only (Glaessner, 1960). Keys to most of the Recent genera represented in the Indo-west Pacific are given by Alcock (1896) and Sakai (1937) and nothing is to be gained by repeating them here. In these keys *Lyreidus* is grouped with the genus *Raninoides* H. Milne Edwards. Both have very reduced last ambulatory legs, small antennary peduncles and flagella but differ in the relative width of the fronto-orbital border (interorbital width) and the relative lengths of the merus and ischium of the third maxillipeds. In addition, most species of *Raninoides* have several sets of spines along the fronto-orbital border, and the dactyls of the first and second, as well as the third, ambulatory legs are markedly expanded near the base; in both these features there are differences from *Lyreidus* species. Finally, both genera share with other raninids a markedly flattened chela which is much wider along the distal border of the palm than at the proximal junction with the carpus.

Genus *Lyreidus* De Haan

Lyreidus De Haan, 1841: 138. Alcock, 1896: 294. Rathbun, 1937: 21. Sakai, 1937: 168; 1965: 5.

TYPE SPECIES: *Lyreidus tridentatus* De Haan, 1841; by monotypy.

DIAGNOSIS. Carapace elongate-ovate, anterolateral margins gradually convergent; strongly convex from side to side and weakly convex from front to back; smooth and polished, regions undefined. Fronto-orbital border less than half greatest carapace width. Orbits hardly oblique; eyestalks short, broad at base, cornea small. Antennules about equal in size to antennae. Antennae with stoutish peduncle, not concealing antennular peduncle; antennal flagellum short, slender. Merus of third maxillipeds a little longer than ischium. Sternum broad anteriorly as far as first pair of ambulatory legs, widening in front of chelipeds. First and second ambulatory legs with dactyls narrowly triangular, dactyls of third ambulatories expanded close to base; last pair of legs extremely short and slender, arising above and in advance of third pair. Abdomen in both sexes of seven distinct segments (modified after Alcock and Rathbun).

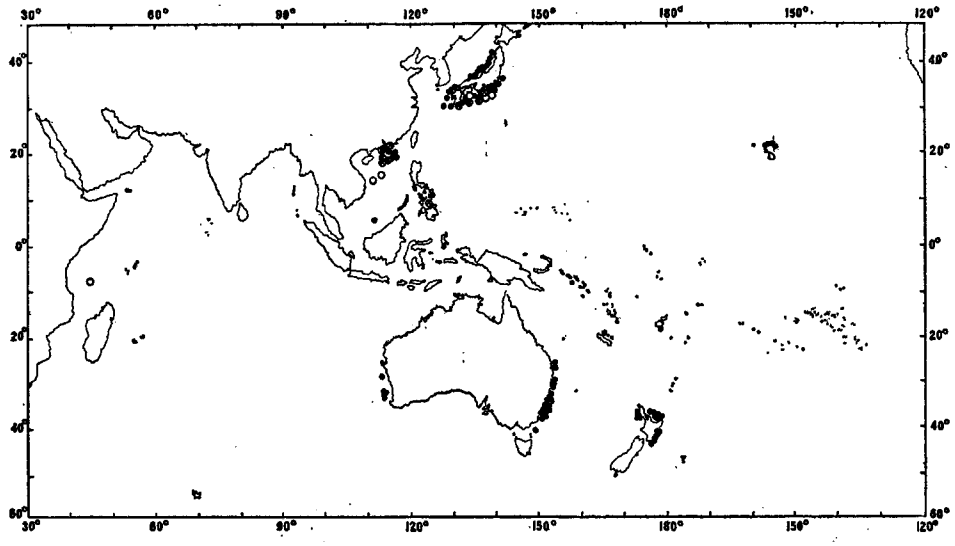


FIG. 1.—Map of the Indo-west Pacific region showing the known distribution of three species of *Lyreidus*. ●—*L. tridentatus*, ○—*L. brevifrons*, ⊗—*L. stenops*.

REMARKS. A total of eleven Recent "species" of *Lyreidus* have been described up to the present time. They are, in chronological order, as follows (the locality from which they were first described is given with each name):

1841. *L. tridentatus* De Haan—Japan.
1879. *L. elongatus* Miers—Japan (Kada Bay).
1881. *L. bardii* Smith—N.E. America (Massachusetts).
1885. *L. channeri* Wood-Mason—India (Bay of Bengal).
1887. *L. stenops* Wood-Mason—Hong Kong.
1888. *L. gracilis* Wood-Mason—India (Andaman Sea).
1902. *L. integra* Terazaki—Japan.
1914. *L. politus* Parisi—Japan (Sagami Bay).
1933. *L. australiensis* Ward—Australia (off Newcastle, N.S.W.).
1937. *L. brevifrons* Sakai—Japan (Tosa Bay).
1964. *L. fossor* Bennett—New Zealand (Bay of Plenty).

A key to the five Recent species recognised here is given below:

KEY TO THE RECENT SPECIES OF *Lyreidus*

1. Carapace laterally with two long spines, one at junction of anterolateral and posterolateral borders and one midway along anterolateral border. Both third and fourth segments of abdomen bearing a long, recurved spine .... *L. channeri* Wood-Mason

–	Carapace laterally with a single short spine at, or just forward of, junction of anterolateral and posterolateral borders or lacking lateral spines altogether. Only fourth segment of abdomen with a long, recurved spine; third segment smooth or with a small tubercle or low curved or straight spine	2
2.	(1) Carapace extremely narrow anteriorly, width between tips of external orbital spines 1/5 greatest carapace width. Lateral borders of carapace lacking spines	*L. stenops* Wood-Mason
–	Carapace rather broad anteriorly, width between tips of external spines ¼ greatest carapace width or more. Lateral borders of carapace with a single short spine	3
3.	(2) Anterolateral borders of carapace sinuous, a convex protuberance immediately in front of lateral spine. Carpus of cheliped with a single spine dorsally	*L. bairdii* Smith, 1881 (N.E. America from Greater Antilles and Gulf of Mexico to Massachusetts (see Rathbun, 1937: 23, pl. 5, figs. 5, 6).
–	Anterolateral borders of carapace straight or uniformly curved. Carpus of cheliped with two spines dorsally	4
4.	(3) Thoracic sternum anterior to bases of chelipeds laterally acute. Outer borders of external orbital spines parallel or subparallel	*L. brevifrons* Sakai
–	Thoracic sternum anterior to bases of chelipeds laterally rounded or subtruncate. Outer borders of external orbital spines divergent posteriorly	*L. tridentatus* De Haan

TABLE II.—Comparison of geographic and ecological distribution of Indo-west Pacific *Lyreidus* species.

Geographic Distribution	*tridentatus*	*brevifrons*	*stenops*	*channeri*
W. Indian O.		+		
N. Indian O.				+
E. Indian O.	+			
S. China Sea—Philippines	+	+	+	+
Japan	+	+	+	
Central Pacific	+			
W. Pacific Islands	+			
E. Australia	+			
New Zealand	+			
Depth				
Upper shelf (-50 fms)	+		+	
Lower shelf	+	+	+	
Slope	+	+		+
Sediment				
Sand		+	+	
Sand-mud	+		+	
Mud	+	+	+	+

Lyreidus tridentatus De Haan, Figs. 1–5; 6a, e, f, j-n, o; 7a, b; 8a, b, f, g. Pl. 1A.

Lyreidus tridentatus De Haan, 1841: 140, pl. 35 fig. 6 (type locality: Japan, types in Rijksmuseum van Natuurlijke Historie, Leiden—see below). Haswell, 1882: 144. Wood-Mason, 1887: 209. Henderson, 1888: 33. Ortmann, 1892: 574. Whitelegge, 1900: 165. Doflein, 1902: 654. Chilton, 1906: 266. Parisi, 1914: 306. Balss, 1922: 121. Yokoya, 1933: 110. Sakai, 1934: 283; 1936: 68, pl. 13 fig. 2; 1937: 169, text-figs. 38a, 39a, b, 40a, b, 41a, pl. 16 fig. 5; 1965: 5, pl. 2 fig. 3. Miyake, 1936: 417. Powell, 1949: 371. McNeill, 1953: 91. Dell, 1956: 148; 1963a: 243; 1963b: 20, fig.; 1968: 23. Utinomi, 1958: 73, pl. 37 fig. 4. Tinker, 1965: 82, pl. 29.

Lyreidus elongatus Miers, 1879: 46 (type locality: Kada Bay, Japan, holotype (male, ca 14mm c.l.) in British Museum (Natural History), London—reg. no. 78: 11).

Lyreidus australiensis Ward, 1933: 377, pl. 23 fig. 10 (type locality: off Newcastle, N.S.W., holotype in Australian Museum, Sydney—see below). Richardson and Krefft, 1949: 69, figs. 1–4.

Lyreidus fossor Bennett, 1964: 24–6, figs. 5–9, 106 (type locality: North of Whale Island, Bay of Plenty, New Zealand, 67fms; holotype (male) in Canterbury Museum, Christchurch).

TYPES: Dr L. B. Holthuis has kindly informed me that the material on which De Haan based his original description of *L. tridentatus* comprises 6 syntypes. On his advice I select the most complete of these as LECTOTYPE: A female, c.l. 40mm, Japan, 1823-1835, P. F. von Siebold and H. Burger, Crust. reg. no. D.23017, a dry specimen with the mouthparts dissected out and pasted on cardboard.

PARALECTOTYPES: Two dry specimens with same data as lectotype; 3 dry specimens, Japan, 1830-1835, H. Burger.

LOCALITIES PREVIOUSLY REPORTED

Japan: "Japan" (De Haan). Kada Bay (Miers). S. of Inuboe-zaki, 196 m. ("Misago" Sta. 113); E. of Bosyu, 117–269 m. ("Misago" Sta's 5, 103, 104, 105) (Yokoya). Tokyo Bay (Doflein, 1902; Parisi; Balss). Sagami Bay (Ortmann; Parisi). Misaki, Sagami Bay, 100 m., 200–300 m. (Parisi; Balss; Sakai, 1937). Dzushi, 130 m., and Ito, Sagami Bay (Balss). Manazuru and Hayama, Sagami Bay (Sakai 1937). Enoshima, Sagami Bay (Parisi). Off Enoshima, 30–80 m., off Kameki reef and off Mitohama, 30–50 m., Sagami Bay (Sakai, 1965). Suruga Bay, 123 m. ("Misago" Sta. 286); S. of Lake Hamana, 172 m. ("Misago" Sta. 195); S. of Sima, Mie-ken, 207 m. ("Misago" Sta. 199); S. of Hamazima, Mie-ken, 93 m. ("Misago" Sta. 365); N.E. of Owrase, Mie-ken, 183 m. ("Misago" Sta. 201); W. of Siwo-misaki, 165 m. ("Misago" Sta. 210) (Yokoya). Tosa Bay (Sakai, 1937). N.E. of Asizurizaki, 223 m. ("Misago" Sta. 226); S. of Kôti, 97 m. and 126 m. ("Misago" Sta's 341 and 406); Bungo Strait, 241 m. ("Misago" Sta. 304) (Yokoya). Nagasaki (Sakai, 1934, 1937). S. of Goto Is, 238 m. ("Misago" Sta. 238); Toyama Bay, 135 m. ("Misago" Sta. 580) (Yokoya). Fukuura (Balss). Off Tori-shima (Ryukyu Islands), 100 fms (Miyake).

South China Sea: Hong Kong (Wood-Mason, 1887).

South Pacific Ocean: Off Kandavu, Fiji Is, 210 fms ("Challenger" Sta. 174) (Henderson). New Caledonia (Ortmann).

Central Pacific Ocean: Hawaii (Tinker).

Australia: Pt Stephens (Haswell). Off Newcastle, 45–50 fms (Ward). Newcastle Bight, 5–7 miles off shore, 26–40 fms ("Thetis" Sta. 22); 6½–8 miles off Newcastle, 42–48 fms ("Thetis" Sta. 25) (Whitelegge). Outside the heads of Pt Jackson (Haswell). Off Pt Jackson, 30–35 fms (Henderson). Off Wata Mooli, 3½–4 miles offshore, 54–59 fms ("Thetis" Sta. 57) (Whitelegge).

New Zealand: Outside Great Barrier I., 120 fms (Chilton). Near the entrance to Hauraki Gulf, probably in about 20–25 fms (Powell, 1947). W. of Aldermen Is., Bay of Plenty, 50 fms; between Mayor I. and Motiti I., Bay of Plenty, 70–100 fms; N.E. of Motiti I., Bay of Plenty, 49 fms; 7 miles S.E. of Whale I., Bay of Plenty (Powell, 1949). Off White I., Bay of Plenty, 113–120 fms; 14 miles E. of Whale I., Bay of Plenty, 105 fms (Dell, 1963). N. of Whale I., Bay of Plenty, 67 fms (Bennett). Three miles N.E. of Hicks Bay, 100–120 fms (Dell, 1963a). Waikawa Point, near C. Runaway, 60 fms (Powell, 1949). "Ex Napier trawlers" (Dell, 1956). "Wellington area, from dogfish stomach" (Richardson and Krefft).

MATERIAL EXAMINED: A total of 243 specimens, as follows—Japan: "Japan", Reiter, 1894, 1 ♂, ca 31mm (SM unreg.—photo only). Japanese Seas, pres. T. Sakai before April 1934, 1 ♂, 39.9mm (AM P.10499), 1 ♀, 41.7mm (AM P.10500). Off Honshu, 65 fms, 7/5/1900, "Albatross" Sta. 3740, 1 ♂, 17.0mm (USNM 57686). Misaki, don. A. S. Pearse, 1 ♂, 28.3mm (USNM 63689). Sagami Bay, Doderlein, 1882, 2 ♀♀, ca 29, 44mm (SM unreg.—photos only).

South China Sea: S. of Hong Kong, 21°04.5′ to 21°05′N., 114°30.5′E., 46 fms, mud and coarse sand, Agassiz trawl, 25/7/1965, FHK Sta. 18, 1 juv., 10.9mm (AM P.15784). S.E. of Hong Kong, 21°14′N., 115°18′E., 62 fms, Agassiz trawl, 13/8/1965, FHK Sta. 21, 1 ♀, 28.9mm (AM P.15785). S.E. of Hong Kong, 21°15.2′N., 115°16.4′E., 63 fms, Agassiz trawl, 13/8/1965, FHK Sta. 19, 1 ♀, 24.6mm (AM P.15786). N.E. of Bunguran, 5°41′N., 110°07′ to 110°10′E., 103–131 fms, muddy sand, Granton trawl, 6/11/1964, FHK Sta. 41, 1 empty carapace with sternum and mandibles, 22.2mm (AM P.15783).

Central Pacific Ocean: Hawaii, T. Richert, 1 ♀, 20.3mm (WAM 351–67). Hawaii, 200 fms, T. Richert, 2 ♂♂, 2 ♀♀, 16.7–41.7mm (WAM 352–67). Off Sand I., Oahu, Hawaii, 60 fms, 18/7/1959, "Pele" Expedition Sta. 168, 1 juv., 1 ♀, 13.2, 27.8mm (BPBM 6796). Off Waikiki, Oahu, Hawaii, 90–102 fms, "Pele" Expedition, 8/4/1959, 2 juvs., 3.5, 13.5mm (BPBM 6797).

South Pacific Ocean: New Caledonia, Krieger collection, 1864, 2 ♂♂, 37.7, 39.6mm (SM unreg.).

Eastern Australia: Twelve to 15 miles N.N.E. of C. Moreton, Qld, 80–100 fms, 1964, D. Harris, pres. T. Garrard, 1 (sex indet.), 1 ♂, 28.0, 49.5mm (AM P.15288). Outside Moreton Bay, N. of C. Moreton, Qld, 20 fms, University of Queensland Department of Zoology, September 1966, pres. J. M. Thomson, 1 ♂, 1 ♀, 34.6, 47.9mm (AM P.15289). Off Broughton I., N.S.W., ca 70 fms, trawler "Bar-ea-mul", October 1925, pres. M. Ward 1 ♂, 37.5mm (AM P.8409). Off Pt. Stephens, N.S.W. 40–45 fms, mud, trawled, D. F. McMichael and J. C. Yaldwyn, 22/6/1963, 10 ♂♂, 10 ♀♀, (9 ovig.), 25.0–33.8mm (AM P.14787). Between Point Perpendicular and Wreck Bay, N.S.W., 30–40 fms, trawler "Barracouda", W. Barnes, November 1941, 1 ♂, 40.2mm (AM P.11394). Off mouth of Manning River, N.S.W., 45–50 fms, trawler "Ben Bow", pres. K. Moller, 1 ♀, 12.2mm (AM P.11404). Newcastle Bight, N.S.W., 26–40 fms, grey sand to mud and shell, E. R. Waite, 2/3/1898, "Thetis" Expedition Sta. 22, 1 ♂, 41.8mm (AM G.2183). Off Newcastle, N.S.W., 42–48 fms, soft mud, E. R. Waite, 4/3/1898, 1 ♂, 35.5mm (AM G.2176). Ten to 15 miles off Newcastle, N.S.W., 45–50 fms, November 1931, pres. M. Ward, 1 ♂, 43.8mm (AM P.10623—HOLOTYPE of *Lyreidus australiensis* Ward). Nine and three-quarter miles off Norah Head, N.S.W., 42–45 fms, mud, trawled, "Endeavour" Expedition, 1 ♂, 6 ♀♀, 31.0–37.0mm (AM E.4525). E. of Sydney, N.S.W., 150 fms, May 1920, pres. D. G. Stead, 1 ♂, 23.9mm (AM P.4909). Off Pt Jackson, N.S.W., 30–35 fms, "Challenger" Expedition, 1 ♂, 1 ♀, 20.2, 22.5mm (AM G.1645). Eleven to 12 miles E. of Pt Jackson, N.S.W., ca 75 fms, trawler "Durimbee", pres. M. Ward, 1 ♂, 37.0mm (AM P.8428). Six miles E. of Maroubra, near Sydney, N.S.W., 55–60 fms, trawled, 31/5/1955, pres. A. A. Racek, 2 ♀♀, 27.8mm, 33.3mm (AM P.12954). Off Botany, N.S.W., 55–60 fms, State trawler "Goonambee", pres. Capt. A. G. Flett, 1 ♂, 50.0mm (AM P.5309). Off Botany, N.S.W., 33–56 fms, State trawler "Goonambee", F. A. McNeill and A. A. Livingston, August 1921, 1 ♂, 16.1mm (AM P.5545). Off Botany, N.S.W., 50 fms, pres. General Manager, State Trawling Dept., 1 ♀, 41.5mm (AM P.4435). E. of Cronulla, N.S.W., 60 fms, Danish Seine Net, 6/6/1947, pres. C.S.I.R. Fisheries, 1 ♀ (ovig.), 32.1mm (AM P.11808). Off Cronulla, N.S.W., 80 m., dredged, R. J. MacIntyre, 26/5/1965, 16 ♂♂, 14 ♀♀, 14.9–42.0mm (C.S.I.R.O.). Off Jibbon, N.S.W., 66–50 fms, mud and abattoir refuse, 16/3/1898, "Thetis" Expedition Sta. 46, 1 ♀, 33.3mm (AM P.1118). Five miles E. of Point Jibbon, N.S.W., 100 m., mud, trawled, 24/7/1943, pres. K. Sheard, 1 ♀, 16.0mm (AM P.11494). N. of Montagu I., N.S.W., 62 fms, "Endeavour" Expedition, 4 small carapaces and assorted legs (AM E.6148). Off Wata Mooli, N.S.W., 59–54 fms, E. R. Waite, 1898, "Thetis" Expedition Sta. 57, 1 ♂, 12.1mm (AM G.2378). Shoalhaven Bight, N.S.W., 15–45 fms, "Endeavour" Expedition, 1 ♂, 26.2mm (AM E.284). Off southern coast of N.S.W., 40 fms, trawled, pres. Capt. K. Moller, 1 ♀, 24.3mm (AM P.11437). Southern coast of N.S.W., 90–100 fms, dredged, May 1923, 1 ♀, 39.0mm (MP unreg.). New South Wales, D. G. Stead, "Thetis" Expedition, 1 ♂, 41.8mm (AM P.4786). Off Flinders I., Bass Strait, pres. Commonwealth Fisheries Bureau, 1909, 1 ♂, 33.7mm (AM P.2324).

Western Australia: N.W. of Bluff Point, Geraldton, 27°40'S., 113°03'E., 70 fms, sponge and bryozoans, 22/8/1963, C.S.I.R.O. Sta. 131, 1 ♂, 1 ♀, 15.9, 16.3mm (WAM 59–64). W. of West End, Rottnest I., 30–100 fms, dredged, "Bluefin", R. W. George and B. R. Wilson, 12/3/1962-16/9/1965, 6 ♂♂, 4 ♀♀, 15.7–28.0mm (WAM 52–64, 54–64, 57–64, 1–67 to 3–67).

New Zealand: West of Tauroa Point, 35°20.1'S., 172°52'E., 97–91 fms, grey muddy sand, Agassiz trawl, 17/2/1962, NZOI Sta. C753, 10 ♂♂, 5 ♀♀, 16.9–31.0mm (NZOI). Off Kaipara Heads, 36°40'S., 174°17'E., 12 fms, Agassiz trawl, 26/10/1962, NZOI Sta. B672, 1 ♂, 1 ♀, 29.2mm (NZOI). W. of Kaipara Heads, 36°40'S., 173°53'E., 107 fms, Agassiz trawl, 26/10/1962, NZOI Sta. B674, 1 ♂, 31.8mm (NZOI). W. of Kaipara Heads, 36°40'S., 173°56.5'E., 68 fms, fine grey black muddy sand, Agassiz trawl, 26/10/1962, NZOI Sta. B673, 1 ♂, 34.0mm (NZOI). W. of Manakau Heads, 36°41'S., 173°58'E., 104 fms, Devonport dredge, 24/10/1959, NZOI Sta. C306, 1 ♂, 15.7mm (NZOI). W. of Manakau Heads, 37°18.7'S., 174°06.2'E., 71 fms, mud, Agassiz trawl, 26/10/1962, NZOI Sta. B669, 3 ♂♂, 1 ♀, 22.7–32.1mm (NZOI). W. of Manakau Heads, 37°18.7'S., 174°03.8'E., 93 fms, Agassiz trawl, 26/10/1962, NZOI Sta. B670, 1 ♀, 31.9mm (NZOI). W. of Raglan, 37°41.8'S., 174°13.9'E., 85 fms, sandy mud, Devonport dredge, 26/10/1959, NZOI Sta. C342, 1 ♀, 24.3mm (NZOI). Twelve miles off Flat Head, Doubtless Bay, 82–87 fms, N.Z. Marine Dept, 16/6/1963, 1 ♂, 1 ♀, 11.7, 19.9mm (DM Cr. 1369). Twelve miles S.E. of Poor Knights Is, 90 fms, N.Z. Marine Dept, 1962, 1 ♂, 2 ♀♀, 18.5–26.5mm (DM Cr. 1346). N. of Cuvier I., 60 fms, N.Z. Marine Dept, 7/11/1962, 1 ♀, 25.8mm (DM Cr. 1206). Waipiro Bay, 40 fms, pres. Auckland Inspector of Fisheries, 1 ♂, 32.1mm (DM Cr. 1055). Auckland District, pres. Auckland Inspector of Fisheries, 1 ♀, 37.2mm (DM Cr. 1056). Hauraki Gulf, 5 fms, stomachs of shark (*Mustelus*), J. Moreton, June 1949, 1 ♂, 1 ♀, 3 ovig. ♀ (fragments), 24.1–27.6mm (DM Cr. 1057). Six miles N.E. of Aldermen Is, 82–89 fms, N.Z. Marine Dept, 1962, 2 ♀♀, 8.6, 8.9mm (DM Cr. 1345). Five miles N.W. of Oreti Point, 65 fms, N.Z. Marine Dept, 3/4/1963, 2 ♀♀, 11.0, 11.8mm (DM Cr. 1343), 3 ♂♂, 5 ♀♀, 9.3–22.6mm (DM Cr. 1337). S. of Mayor I., Bay of Plenty, 37°20.1'S., 176°19'E., 103–95 fms, grey sandy mud, Agassiz trawl, 23/2/1962, NZOI Sta. C798, 1 ♂, 2 ♀♀, 29.9–32.2mm (NZOI).

Off Mayor I., Bay of Plenty, 37°22.5'S., 176°22'E., 113–120 fms, M.V. "Alert", 27/2/1957, DM Bottom Sta. 208, 6 ♂♂, 13 ♀♀, 19.6–37.1mm (DM Z. Cr. 663). Off Motiti Is, Bay of Plenty, 37°27'S., 176°26'E., 70–90 fms, 28/8/1956, 1 ♂, 33.7mm (DM Cr. 1052). Off Plate I., Astrolove Reef, Bay of Plenty, 70–100 fms, 16/8/1956, 2 ♂♂, 25.0, 36.7mm (DM Cr. 1051). Fourteen miles E. of White I., Bay of Plenty, 105 fms, N.Z. Marine Dept, 3/4/1963, 2 ♂♂, 3 ♀♀, 9.0–35.7mm (DM Cr. 1340). Bay of Plenty, trawled, pres. Marine Dept, 1955, 1 ♂, 46.8mm (DM Cr. 593). Bay of Plenty, 30–70 fms, pres. Auckland Inspector of Fisheries, 1953, 1 ♂, 45.3mm (DM Cr. 1050). N. of Hicks Bay, 37°33'S., 178°35'E., 138 fms, soft grey mud, Agassiz trawl, 24/3/1967, NZOI Sta. E720, 1 ♂, 38.1mm (NZOI). Three miles N.E. Hicks Bay, 100–120 fms, N.Z. Marine Dept, 4/4/1963, 1 ♂, 2 ♀♀, 17.9–43.4mm (DM Cr. 1338), 1 ♀, 11.5mm (DM unreg.). Three miles N.E. of Hicks Bay, 60–70 fms, N.Z. Marine Dept, 4/4/1963, 1 ♂, 27.6mm (DM Cr. 1341). Sixteen miles S.E. of East Cape, 70 fms, N.Z. Marine Dept, 5/4/1963, 2 ♀♀, 28.0, 30.3mm (DM Cr. 1339). Twelve miles E. of Tetara Head, 80 fms, N.Z. Marine Dept, 5/4/1963, 4 ♀♀, 8.9–31.6mm (DM Cr. 1342). Twelve miles E.N.E. of Marau Point, 70 fms, N.Z. Marine Dept, 5/4/1963, 1 ♀, 27.5mm (DM Cr. 1344). Off Napier, A. G. Clark, October 1953, 1 ♂, 38.4mm (DM unreg.). S.E. of C. Kidnappers, 39°20'S., 178°35'E., 140 fms, soft grey mud, Agassiz trawl, 22/3/1967, NZOI Sta. E710, 3 ♀♀, 25.8–32.5mm (NZOI). Between C. Kidnappers and C. Turnagain, 39°33.8'S., 177°13.6'E., 40 fms, grey green sandy mud, cone dredge, 4/9/1957, NZOI Sta. B55, 1 ♀, 20.6mm (NZOI). Between C. Kidnappers and C. Turnagain, 39°31.4'S., 177°39.4'E., 70 fms, soft grey mud, Agassiz trawl, 27/2/1962, NZOI Sta. C827, 2 ♂♂, 9 ♀♀, 20.2–39.7mm (NZOI). Between C. Kidnappers and C. Turnagain, 39°30.8'S., 177°18.4'E., 46 fms, grey green sandy mud, cone dredge, 4/9/1957, NZOI Sta. B56, 1 ♀, 21.4mm (NZOI). E. of C. Turnagain, 40°36.7'S., 177°01.6'E., 110 fms, shelly sand, orange-peel grab, 20/6/1960, NZOI Sta. C511, 1 ♀ (ovig.), 31.0mm (NZOI). Off Castlepoint Light, 40 fms, F. Abbernethy, 24/8/1955, 1 ♂, 43.0mm (DM Z. Cr. 615). Off Castlepoint, 30–60 fms, trawled, F. Abernethy, 7/7/1956, 3 ♂♂, 1 ♀, 39.8–42.1mm (DM Cr. 1058). Off Castlepoint, 60 fms, F. Abernethy, 17/9/1956, 1 ♂, 46.0mm (DM Z. Cr. 644). C. Campbell, 40 fms, trawled, F. Abernethy, October 1952, 1 ♀, 32.3mm (DM Cr. 1054).

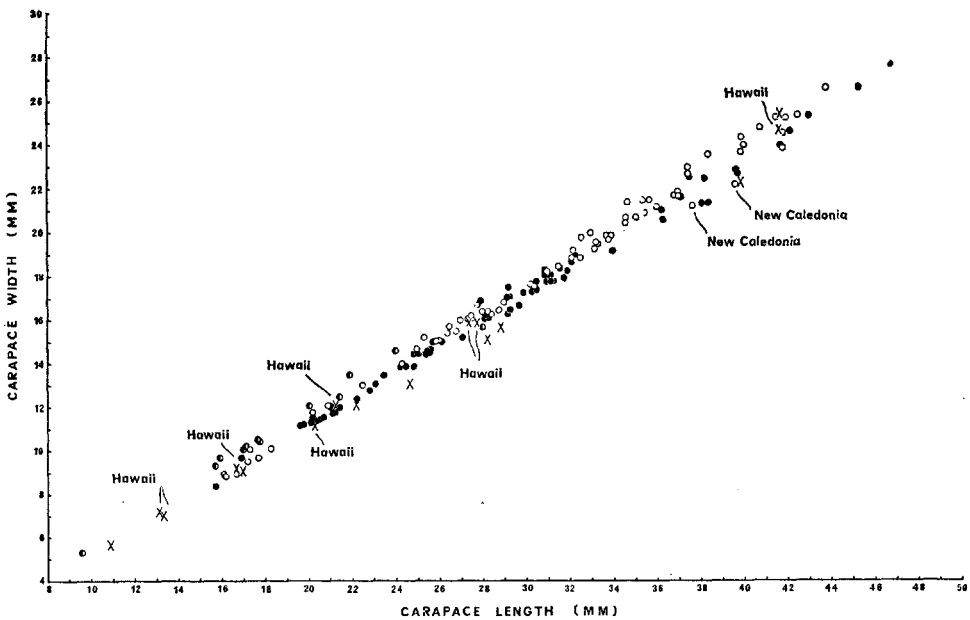


FIG. 2.—Relative growth in *Lyreidus tridentatus.* ○—Eastern Australia and New Caledonia, ◐—Western Australia, ●—New Zealand, ×—Japan, South China Sea and central Pacific (Hawaii). (See Table III.)

REMARKS: Workers on Japanese Brachyura from the time of De Haan (1841) have, with one exception, accepted the name *Lyreidus tridentatus* for this species of raninid (Doflein, 1902; Parisi, 1914; Balss, 1922; Yokoya, 1933; Sakai, 1934, 1936; Miyake, 1936; Sakai, 1937, 1965). The name has also been used for speci-

mens from Hong Kong (Wood-Mason, 1887), Fiji (Henderson, 1888), New Caledonia (Ortmann, 1892), eastern Australia (Haswell, 1882; Whitelegge, 1900; McNeill, 1953), New Zealand (Chilton, 1906; Powell, 1949; Dell, 1956, 1963a, 1963b, 1965, 1968) and Hawaii (Tinker, 1965). The name *Lyreidus elongatus* was given to Japanese specimens by Miers (1879), Ward (1933) described Australian specimens as *Lyreidus australiensis* and this name was used for New Zealand specimens by Richardson and Krefft (1949), while recently Bennett has described the New Zealand form as *Lyreidus fossor*. In general, none of these names has been accepted by later workers. Doflein's (1904) record of *L. tridentatus* from off Dar-es-Salaam is shown here to rest on a misidentification of *L. brevifrons*.

Ward considered that Australian specimens differed from Japanese ones in that the orbits extended further back, the carapace was broader, the sternum broader, the chelae longer and more slender, the fixed finger (of the chela) more constricted basally, the dactyl stouter, the ambulatory dactyls more slender and the fifth abdominal segment of the male longer and narrower.

Bennett stated that the New Zealand form differed from others in having more projecting lateral carapace spines, shorter chelipeds, stouter cheliped meri, more slender cheliped dactyls and differently shaped third ambulatory dactyls.

The results of the morphometric analyses and study of features not amenable to measurement are now given.

TABLE III.—Values for constants associated with regression analysis of relative growth in *Lyreidus tridentatus*. The x and y columns give the name of the dimensions concerned (the independent and dependent variables respectively). The a and b columns give the mean values for these two constants (in equation of type $y = a + bx$) and their standard errors are given in brackets below. The category column specifies the locality and/or size of the specimens considered (n is the number of specimens).

x	y	category (n)	a (S.E.)	b (S.E.)
carapace length	carapace width	Eastern Australia (70)	0.90 (0.074)	0.62 (0.010)
		New Zealand (71)	−0.43 (0.073)	0.59 (0.011)
carapace width	carapace width between spines	Eastern Australia (70)	0.46 (0.050)	0.97 (0.011)
		New Zealand (70)	0.68 (0.050)	0.99 (0.012)
carapace length	anterolateral margin length	Eastern Australia (39)	3.27 (0.201)	0.38 (0.041)
		New Zealand (27)	0.23 (0.122)	0.49 (0.014)
cheliped merus length	cheliped merus height	Eastern Australia (70)	0.29 (0.047)	0.44 (0.013)
		New Zealand (72)	0.40 (0.081)	0.40 (0.023)
ambulatory dactyl 2 length	ambulatory dactyl 2 width	Eastern Australia (36)	0.36 (0.031)	0.16 (0.014)
		New Zealand (23)	−0.10 (0.049)	0.22 (0.017)
ambulatory dactyl 3 length	ambulatory dactyl 3 width	Eastern Australia (35)	0.19 (0.032)	0.34 (0.020)
		New Zealand (25)	−0.13 **(0.038)**	0.39 **(0.018)**

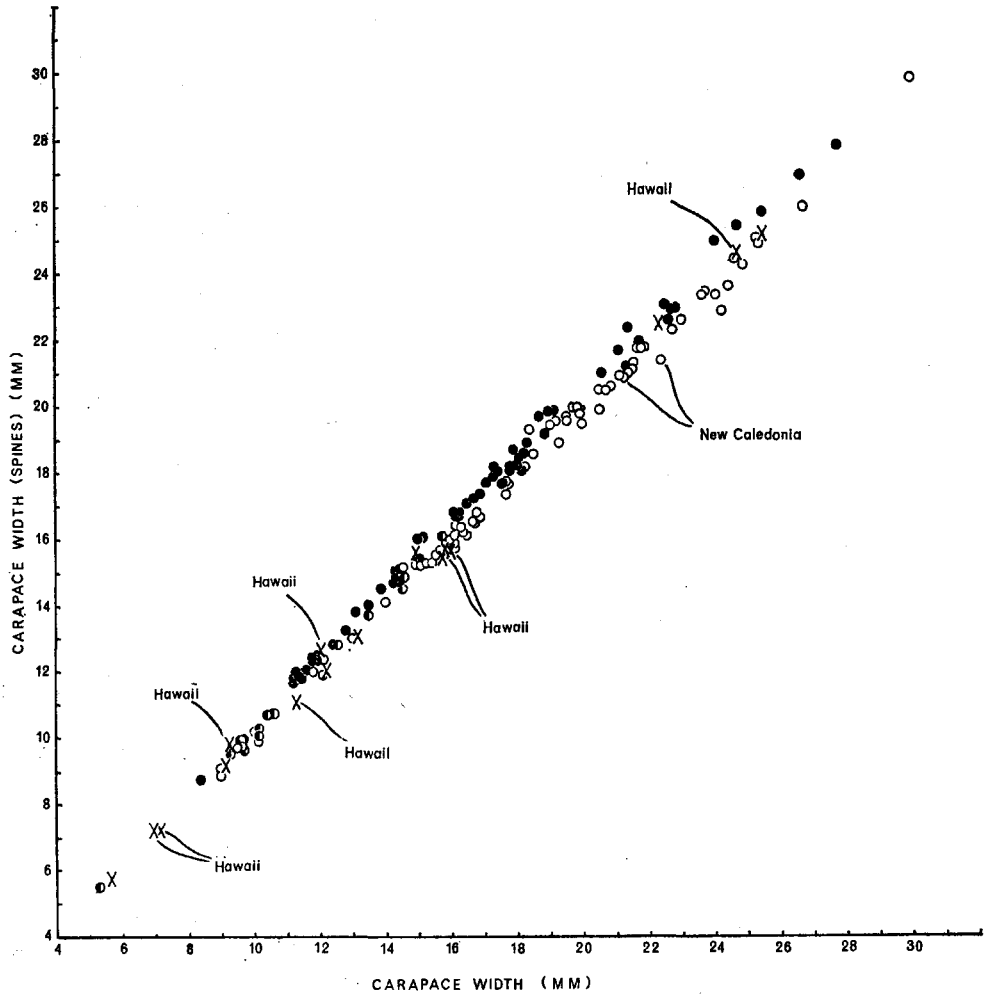


FIG. 3.—Relative growth in *Lyreidus tridentatus* (see Table III). Symbols as in Fig. 2.

MORPHOMETRICS

1. Carapace length, carapace width and width between lateral spines. In the specimens from all areas examined the carapace length ranges from 1.6 to 1.9 times carapace width. Relative growth of these two dimensions is isometric (see Table III and Fig. 2).

New Zealand specimens examined have the lateral spines projecting outwards slightly further than do specimens from other areas in which the carapace width is equal to, or slightly exceeds, the distance between the lateral spines (see Table III and Fig. 3). This difference, is, however, not significant at the 5 percent level ($0.25 > P > 0.10$). The relationship between carapace width and distance between the lateral spines does not appear to change markedly with increasing overall size.

2. Anterolateral margin length. Relative growth of the length of the anterolateral margin is isometric (anterolateral margin length about 0.5 carapace length) (see Table III). There is no difference at the 5 percent level between the eastern Australian and New Zealand samples in this feature ($P > 0.25$).

3. Interorbital width and external orbital spine length. Relative growth of the interorbital width is negatively allometric (see Table IV and Fig. 4). New Zealand

specimens are very slightly wider across the orbits than Australian ones. The external orbital spines decrease very slightly in length relative to carapace length with overall growth (see Table IV); there is complete overlap of Australian and New Zealand samples in this feature.

4. Cheliped. The relative growth of the merus of the cheliped is isometric (height 0.4–0.5 length) (see Table III and Fig. 5). There is again a very slight difference between Australian and New Zealand samples ($0.25 > P > 0.10$), New Zealand specimens having a slightly more slender merus, a feature more apparent in larger specimens.

The length of the chela changes isometrically in relation to carapace length in females and positively allometrically in males. There is no difference at the 5 percent level between samples in this feature ($P > 0.25$). The length of the chela increases very slightly in relation to height of the chela in males.

The relation between dactyl length and chela length is also isometric and the same in all samples (dactyl 0.6–0.8 chela).

5. Ambulatory dactyls. The width/length ratio of the second and third ambulatory dactyls remains constant with growth at about 0.4 in the second ambulatory leg and 0.2 in the third ambulatory leg respectively (see Table III). There are no differences at the 5 percent level between the samples in these features ($P > 0.25$ in both cases).

6. Abdomen. The length/width ratios of the fifth and sixth abdominal segments remains constant with growth but there is marked sexual dimorphism in the width/length ratio of the fifth segment and the relative lengths of the two segments (see Table IV); females have a broader fifth segment ($0.05 > P > 0.01$) and a longer sixth segment ($0.05 > P > 0.01$). There is, however, no difference at the 5 percent level between samples from eastern Australia and New Zealand in the relative dimensions of the abdominal segments ($P > 0.25$).

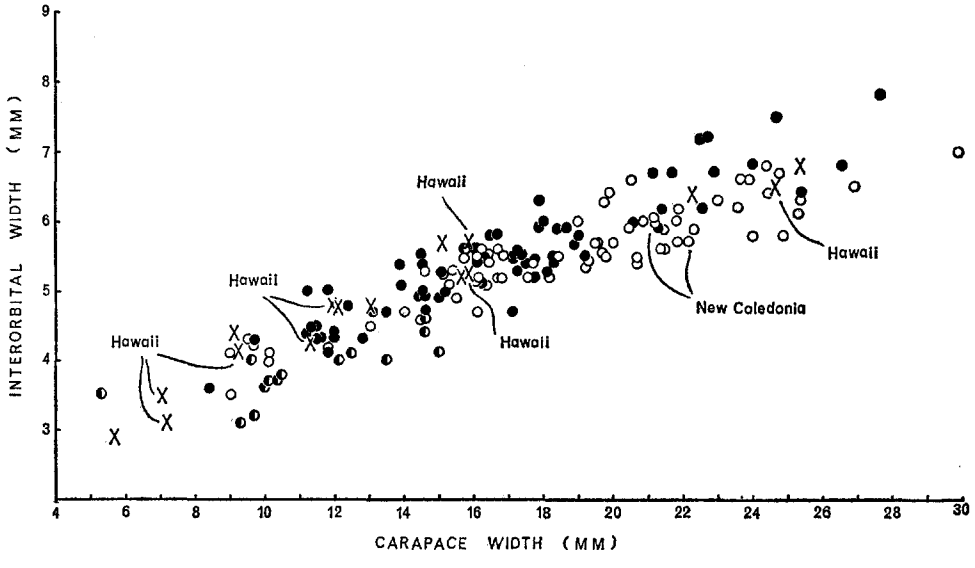
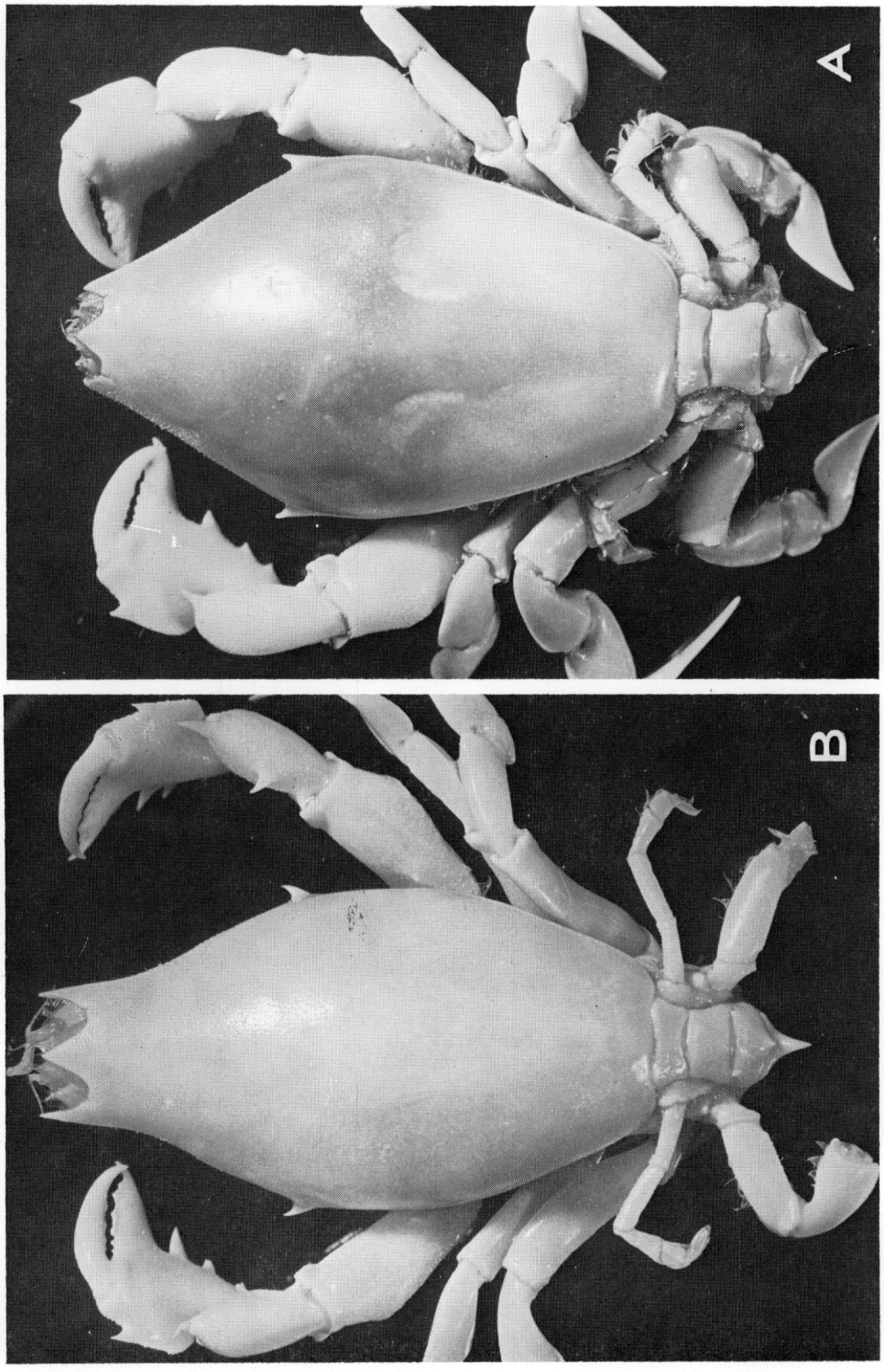


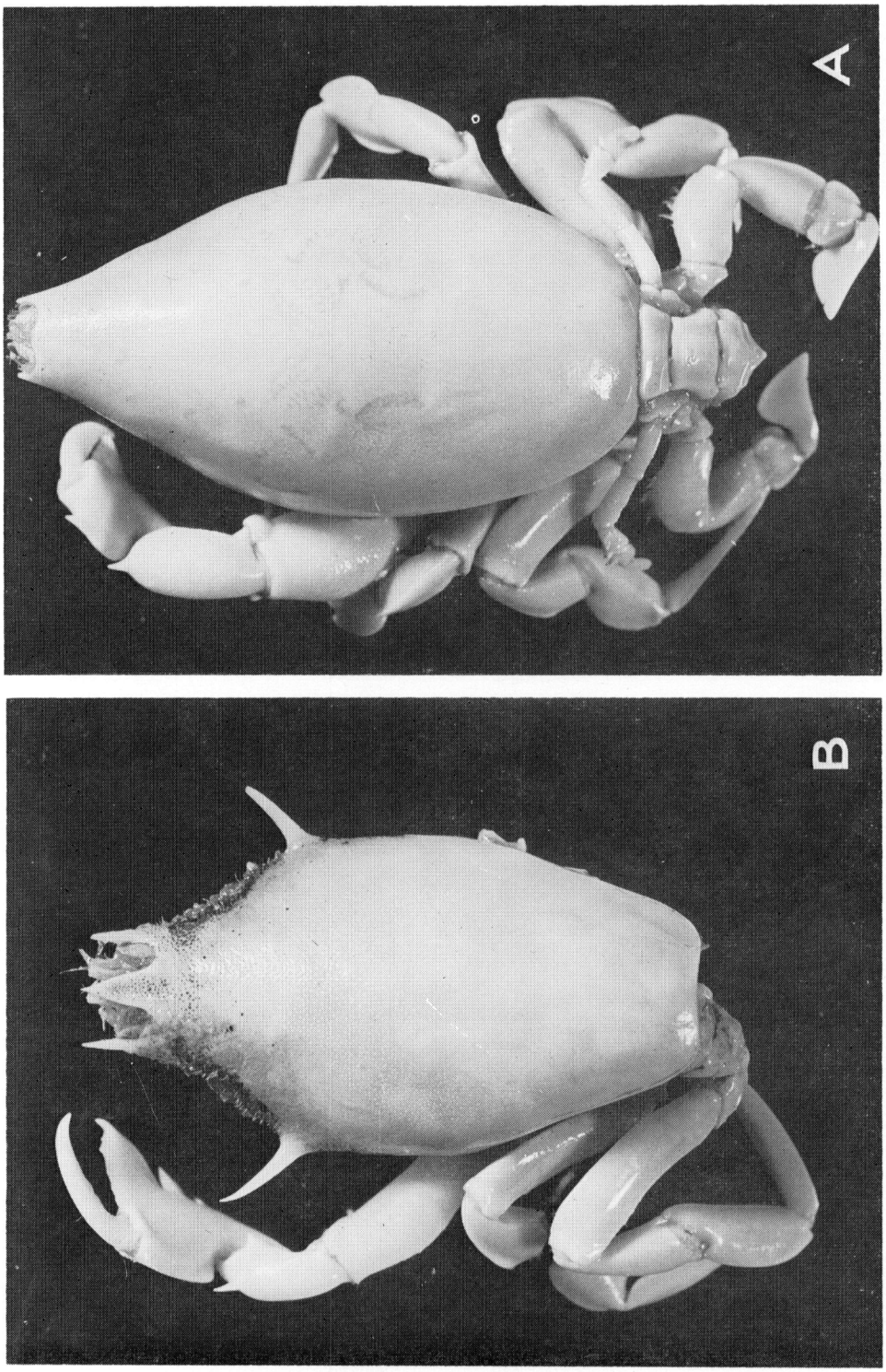
FIG. 4.—Relative growth in *Lyreidus tridentatus* (see Table IV). Symbols as in Fig. 2.

OTHER FEATURES

There is some marked variation with growth in the shape of the carapace. The anterolateral borders are weakly concavo-convex from front to back in most specimens; in small specimens (c.l. < 20mm) the concavity is typical whereas in



A, *Lyreidus tridentatus*, ♀, 48.0mm, outside Moreton Bay, Qld (AM P.15289). B, *Lyreidus brevifrons*, ♂, 30.5mm, south of Hainan (AM P.15782). (Photos — Anthony Healy.)



A, *Lyreidus stenops,* ♀, 37.4mm, south of Hong Kong (AM P.15780). B, *Lyreidus channeri,* ♂, 30.0mm, south of Hainan (AM P.15787). (Photos—Anthony Healy.)

some of the largest specimens from Australia and Japan (c.l. > 40mm) the antero-lateral margins are straight. The lateral spines, although usually straight and directed obliquely forwards, are often weakly curved and in small specimens are sometimes directed outwards. The lateral margins are straight and subparallel for a short distance immediately behind the lateral spines in specimens between about 20 and 40mm c.l. Ventrally, the external orbital spines sometimes reach forwards further than the first free segment of the antenna. The sternum is typically sub-truncate laterally and sometimes bluntly rounded but never acute.

The merus of the cheliped bears a low spinule or, more often, a tubercle, 1/3 of the merus length from the base on the dorsal surface; there is no clear trend with growth in the size or sharpness of this tubercle. The two spines on the dorsal surface of the carpus of the cheliped are longer and more slender in smaller specimens but are equally sharp in all specimens. In small males and females the outer surface of the fixed finger of the chela is smooth whereas in large males (c.l. > 20mm) the outer surface is granular proximally or at least towards the cutting edge; the outer surface of the palm is granular in all specimens above 20mm c.l. The ventral edge of the palm typically possesses three broadly triangular flattened spines. However, there is small but important variation in this feature; thirteen of the specimens examined from eastern Australia and one from Japan (AM P.10500) have four spines, a small accessory spine being interposed between the central and the distal spine; one specimen, a 25.5mm female from off Port Stephens, N.S.W.

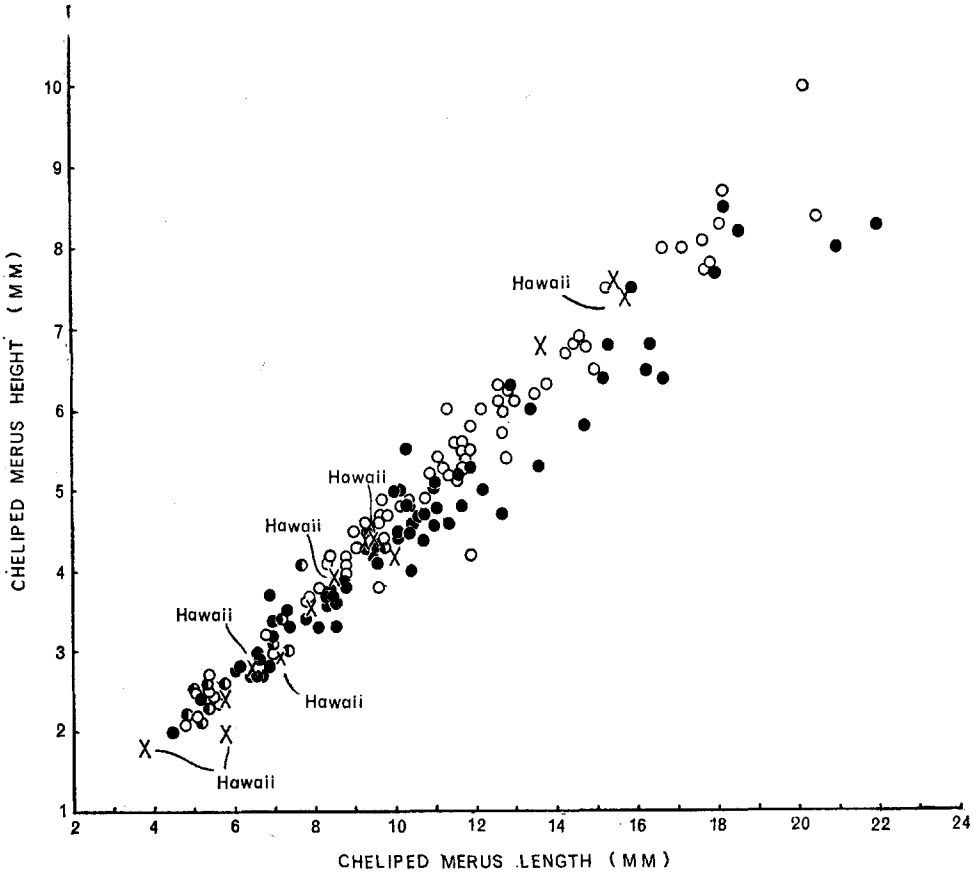
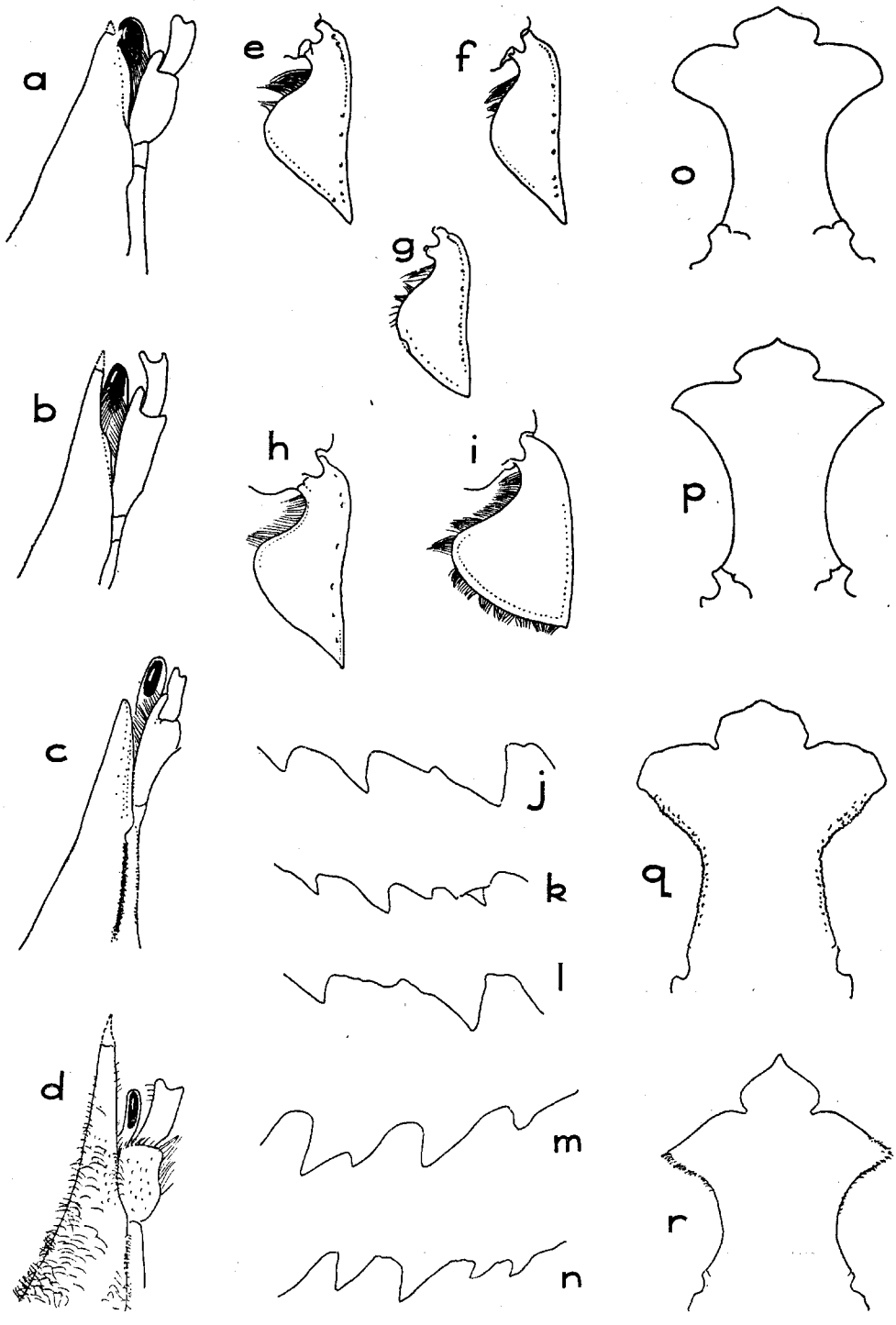


FIG. 5.—Relative growth in *Lyreidus tridentatus* (see Table III). Symbols as in Fig. 2.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(AM P.14787), has only two ventral spines on the chela. Miers' *L. elongatus* is based on a specimen with four ventral spines on the chela (A. L. Rice, pers. comm.) and Richardson and Krefft figure a similar specimen from New Zealand.

The medial tubercle on the third segment of the abdomen is never large; it is seldom sharp and is often only a very low swelling not obvious in lateral view.

The first pleopod of the male shows little variation in shape and typically bears a short, flattened, apically rounded lobe extending medially at right angles from the shaft not far from the tip which continues as a longer and more slender, bluntly pointed lobe. In one specimen from Japan (AM P.10499) this process is short and the terminal opening large.

In summary, there is considerable variation in morphological features in all populations of this species. Differences between Australian and New Zealand animals are slight and confined to but a few features; in no case are the differences statistically significant at the 5 percent level. Japanese populations appear to vary to a slightly greater extent than others and their range of variation generally encompasses that of most other populations.

TABLE IV.—Growth and sexually dimorphic differences in ratio of some dimensions of *Lyreidus tridentatus*. The category column specifies the size and/or sex of the specimens (n is the number of specimens, s is the standard deviation).

Ratio	Category	Mean	s	n
exorbital spine length / carapace length	c.l. < 20mm	0.073	0.0934	8
	c.l. 21–40mm	0.067	0.0115	50
	c.l. > 41mm	0.067	0.0030	12
inter-orbital width / carapace width	c.l. < 20mm	0.42	0.436	13
	c.l. 21–40mm	0.31	0.058	121
	c.l. > 41mm	0.25	0.073	16
abdominal segment 5 width / length	males	1.02	0.116	32
	females	1.11	0.139	35
abdominal segment 6 length / abdominal segment 5 length	males	1.05	0.103	32
	females	1.13	0.130	35

The incomplete specimen from north of Bunguran, South China Sea (AM P.15783), possesses very small, conical, lateral spines on the carapace, the rostrum is 1.46 times as broad at the base as long, the fronto-orbital border is 0.36 times the carapace width, the anterolateral borders are only minutely granular and concavo-convex from front to back, the external orbital spines are laterally divergent and are no longer than the rostrum and the sternum is anterolaterally rounded. This

FIG. 6.—Ventral view of anterior part of right side of carapace (a-d), posterior view of dactyl of third ambulatory leg (e-i), ventral edge of palm of chela (j-n) and anterior portion of sternum (o-r) of *Lyreidus* species. *L. tridentatus*: a, o, ♂, 39.9mm, Japan (AM P.10499); e, ♂, 43.0mm, off Castlepoint, New Zealand (DM Z.Cr.615); f-n, off Port Stephens, N.S.W. (AM P.14787)—f, ♂, 31.8mm, j, ♀, 28.1mm, k, ♀, 24.4mm, l, ♀, 25.5mm, m, ♀, 27.0mm, n, ♂, 26.1mm. *L. brevifrons*: b, g, p, ♂, 32.2mm, off Honshu, Japan (USNM 57687). *L. stenops*: c, h, q, ♀, 41.6mm, south of Hong Kong (AM P.15778). *L. channeri*: d, i, r, ♂, 30.0mm, south of Hainan (AM P.15787).

specimen is therefore assigned to *L. tridentatus;* it is the southernmost record for the genus in the South China Sea and is an isolated locality for this species.

GEOGRAPHIC DISTRIBUTION: Western Pacific: South-eastern and western Japan, South China Sea near Hong Kong, central and south-eastern coast of Australia; Fiji; New Caledonia; northern New Zealand. Central Pacific Ocean: Hawaii. Eastern Indian Ocean: South-western coast of Australia.

BATHYMETRIC DISTRIBUTION: Continental shelf and slope from 15 to 210 fms.

Lyreidus brevifrons Sakai, Figs. 1; 6b, g, f; 7c, d; 8c. Pl. 1B.

Lyreidus brevifrons Sakai, 1937: 171, text-figs. 38b, 41b, 42a, b, pl. 16 fig. 6 (type locality: Mimase, Tosa Bay, Japan; type probably not extant—T. Sakai, pers. comm.); 1965: 6, pl. 2 fig. 4.

Lyreidus tridentatus; Doflein, 1904: 52.
(non) *Lyreidus tridentatus* De Haan, 1841.

LOCALITIES PREVIOUSLY REPORTED: Japan: Tosa Bay (Sakai, 1937). Amadaiba, Aoyama-dshi and west of Jogashima, Sagami Bay, 65–80 m. (Sakai, 1965).

Western Indian Ocean: Off Dar-es-Salaam, 400 m., "Valdivia" Sta. 242 (Doflein, 1904—as *Lyreidus tridentatus*).

MATERIAL EXAMINED: A total of six specimens, as follows: Japan: Off Honshu, 5/5/1900, "Albatross" Sta. 3698, 1 ♂, 32.2mm (USNM 57687).

South China Sea: S.E. of Hainan, 16°20'N., 114°39' to 114°39.5'E., 216–214 fms, fine calcerous sand, Agassiz trawl, 15/8/1965, FHK Sta. 57, 2 ♂♂, 26.7, 33.5mm, 1 ♀ (fragments) (AM P.15781). S. of Hainan, 16°47.5'N., 109°49.5'E to 16°45'N., 109°52'E., 200–290 fms, find mud, Agassiz trawl, 5/3/1965, FHK Sta. 17, 2 ♂♂ (1 with sacculina), 28.9, 30.5mm (AM P.15782).

Western Indian Ocean: Off Dar-es-Salaam, 400 m., "Valdivia" Sta. 242, 1 ♂, 31.3mm (ZMB 13656—photographs and drawings only).

REMARKS: Sakai (1937) listed nine features in which *L. brevifrons* differed from *L. tridentatus.*

1. "The spine on the anterolateral borders is more prominent and curved forward at the tip." This feature provides a difference from most adults of *L. tridentatus* but some large specimens of that species have the lateral spines forwardly curved and small specimens often do.

2. "The carapace is markedly constricted immediately behind the external orbital spines." In *L. brevifrons* the anterior part of the anterolateral borders of the carapace are parallel, rather than convergent posteriorly; this feature is found only in very small *L. tridentatus*—in large specimens of the latter these borders are markedly divergent even anteriorly.

3. "The external orbital spines are much more prominent . . . they are very slender and parallel . . . and project outwards at the tips; the lower edge . . . is not concave and not angled below the eyes." These features are a corollary for 2 above and provide a similarly good distinction between the two species.

4. "The tip of the second antenna projects far beyond the tip of the external orbital spine, while in *L. tridentatus* the former falls much short of the latter." Sakai presumably meant the basal article of the second antenna and his sentence should be changed by substituting *L. brevifrons* for *L. tridentatus* (see Sakai, 1937: figs. 38a and b) but the distinction is difficult to make.

5. "The tips of the external orbital spines project beyond the tip of the rostrum, the distance between both spines being more than one-third the extreme width of the carapace." The narrowness of the carapace anteriorly in *L. brevifrons* is a reliable distinction from *L. tridentatus,* despite changes with growth, but the length of the external orbital spines does not appear to be—in both species the tip of the rostrum is almost on the same level as the tips of the external orbital spines and the differences are small. However, the rostrum and the external orbital spines are more slender in *L. brevifrons* giving the orbits a deeper appearance in dorsal view than in *L. tridentatus.* Sakai (1965) figures a specimen of *L. brevifrons* in which the external orbital spines project forwards very much further than in specimens previously recorded.

6. "Abdomen (male) as in *L. tridentatus,* but the median tubercle on the third tergum is rudimentary. The long spine on the fourth tergum is projecting backward and then upward at the tip." These characters provide no distinction between the two species because of the wide variation in *L. tridentatus.*

7. There are no differences between *L. brevifrons* and *L. tridentatus* in the characters of the cheliped except for slightly longer spines on the carpus in the former. Sakai's (1937) figure (42a) of the chela of *L. brevifrons* suggests a major difference, in relation to the number of spines on the ventral edge which, however, is swamped by the wide variation in *L. tridentatus;* it can be seen from Sakai's (1937) figure of this species (pl. XVI fig. 6) that only the left chela possesses four ventral spines.

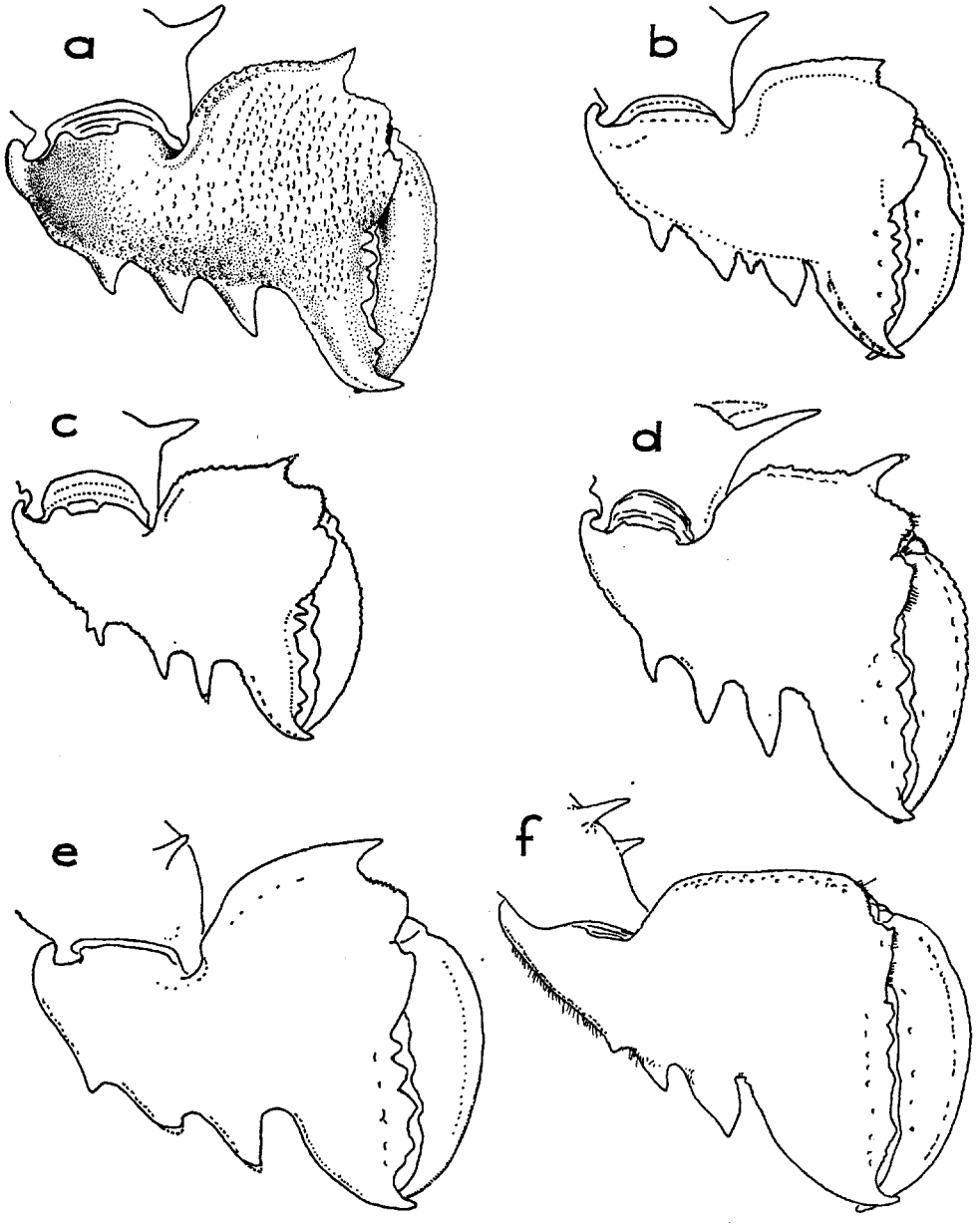

FIG. 7.—Outer face of right chela of *Lyreidus* species. a, *L. tridentatus,* ♂, 39.9mm, Japan (AM P.10499); b, *L. tridentatus,* ♀, 41.7mm, Japan (AM P.10500); c, *L. brevifrons,* ♂, 32.2mm, off Honshu, Japan (USNM 57687); d, *L. brevifrons,* ♂, 30.5mm, South of Hainan (AM P.15782); e, *L. stenops,* ♀ 41.6mm, south of Hong Kong (AM P.15778); f, *L. channeri,* ♂, 30.0mm, south of Hainan (AM P.15787).

8. "The sternum is more strongly constricted between the bases of the chelipeds than in *L. tridentatus*." This is rather difficult to discern: whereas the shape of the lateral wings of the first sternite—truncate or rounded in *L. tridentatus*, acute in *L. brevifrons*—is obvious in Japanese specimens; in specimens of *L. brevifrons* from the South China Sea the lateral wings of the sternum are rounded.

9. "The form of the apex of the male first pleopod is quite different in the two species." The present study confirms this.

Thus the most reliable features differentiating these two very similar species are the width between the tips of the external orbital spines relative to the greatest carapace width, the shape of the external orbital spines, rostrum and anterolateral borders and the form of the apex of the first pleopod in the male. In addition, the anterolateral border of the carapace, the dorsal border of the palm of the chela and dactyl of the cheliped are more distinctly granular in *L. brevifrons*. This is particularly well borne out by a specimen of *Lyreidus* from Japan in the Australian Museum's collections (AM P.10500) which has strongly curved lateral spines and four distinct teeth on the ventral edge of one of the chelae but is clearly *L. tridentatus* because of the shape of the carapace, and the shortness and broadness of the external orbital spines and rostrum.

Examination of photographs and drawings of the specimen recorded from off Dar-es-Salaam by Doflein (1904) (kindly sent by Dr H. E. Grüner) shows that this specimen is actually *L. brevifrons*. It possesses a narrow front, strongly concave anterolateral borders of the carapace, the outer margins of the slender external orbital spines being subparallel, slender rostrum, strongly curved lateral spines, greatest carapace width well behind these and exceeding the width between the tips of the lateral spines, and the sternum is laterally subacute anteriorly.

GEOGRAPHIC DISTRIBUTION: Western Indian Ocean: Dar-es-Salaam. Western Pacific Ocean: South eastern Japan, South China Sea near Hong Kong and west of the Philippines.

BATHYMETRIC DISTRIBUTION: Continental slope from 103 to 216 fms.

Lyreidus stenops Wood-Mason, 1887, Figs. 1; 6c, h, g; 7e; 8d. Pl. 2A.

Lyreidus stenops Wood-Mason, 1887: 209, pl. 1 figs. 7, 8 (type locality: Hong Kong; holotype (female) in collections of Zoological Survey of India, Calcutta—reg. no. 8467/6).

Lyreidus integra Terazaki, 1902: 217, text-fig. (type locality: Japan; location of types unknown—probably not extant—T. Sakai, pers. comm.). Sakai, 1965: 5, pl. 2 fig. 2.

Lyreidus integer (sic); Utinomi, 1958: 73, pl. 37 fig. 3.

Lyreidus politus Parisi, 1914: 311, pl. 13 fig. 5 (type locality: Enoshima, Sagami Bay, Japan; holotype (male) in Museo Civico di Storia Naturale, Milan—reg. no. 1286). Gordon, 1931: 532. Yokoya, 1933: 112. Sakai, 1934: 283, pl. 18 fig. 5; 1936: 68, pl. 13 fig. 4; 1937: 172, text-fig. 43.

LOCALITIES PREVIOUSLY REPORTED: Japan: "Japan" (Terazaki). Manazuru, Sagami Bay (Sakai, 1934, 1937). Enoshima, Sagami Bay (Parisi). Off Enoshima and west of Jogashima, Sagami Bay, 85 m. (Sakai, 1965). Simoda, Kii Peninsula; Seto (Sakai, 1934, 1937). Tosa Bay (Sakai, 1937). Kagoshima (Yokoya).

South China Sea: Hong Kong (Wood-Mason, Gordon).

MATERIAL EXAMINED: A total of seven specimens, as follows:—Locality unknown: "Chile", 1 ♂, 34.0mm (det. "*Lyreidus inermis* A. Milne Edwards"—MP unreg.).

Japan: Japanese Seas, before April 1934, pres. T. Sakai, 1 ♂, 30.8mm (AM P.10501).

South China Sea: Hong Kong, 30–40 fms, mud, before 1930, Barney, 1 ♂, 37.0mm (BM 1930.12.263–66). S. of Hong Kong, 21°20′N., 114°25.6′E., 46 fms, Agassiz trawl, 24/4/1965, FHK Sta. 15, 1 ♀, 41.6mm (AM P.15778). S. of Hong Kong, 21°11.3′ to 21°10.7′N., 114°26′E., 44–45 fms, mud and coarse sand, Agassiz trawl, 24/7/1965, FHK Sta. 9, 1 ♂, 31.4mm (AM P.15779). S. of Hong Kong, 21°17.5′N., 11°28.5′E., to 21°20′N., 114°25.6′E., 46 fms, mud, Granton trawl, 24/4/1965, FHK Sta. 13, 1 ♀, 37.4mm (AM P.15780).

Philippines: S. of Panglao Is, off Bohol, 40–77 fms, sand, "Pele", Mary E. King, 8/2/1964, 1 ♀, 11.0mm (WAM 350–67).

REMARKS: This species has been best known as *L. politus*. Recently Sakai has pointed out that Terazaki (1902) had earlier described this species as *L. integra;* Terazaki's paper had been overlooked by later carcinologists. However, the species was first described by Wood-Mason as *Lyreidus stenops*. Wood-Mason's remarks on this species come at the end of the explanation of pl. 1 in his 1887 paper. "This species may at once be distinguished from its congeners by its narrow metope, its unarmed carapace and its decumbent abdominal spine. A single specimen of it, with a male and two females of another species identical with the specimen from Japan referred in the above description [of *L. channeri*] to *L. 3-dentatus* [sic], has been received by me from Hong Kong from Brigade-Surgeon Hungerford, since this paper was written". Wood-Mason's figures show the abdomen in dorsal and (of segments 3–5) in lateral view (Fig. 7) and the carapace (Fig. 8) of this female specimen. This species, according to Wood-Mason's figures, agrees with descriptions and figures of *L. politus* given by Parisi (1914) and by Sakai (1934, 1937) in all features of the carapace and abdomen, except that the distance between the external orbital spines is slightly greater in Wood-Mason's figure of *L. stenops* than in published figures of *L. politus*. In my opinion, therefore, *Lyreidus stenops* is the oldest available name for the species up to now variously known as *Lyreidus politus* and *Lyreidus integra.*

There is a dry specimen of a species of *Lyreidus* in the collections of the Muséum National d'Histoire Naturelle, Paris, labelled "*Lyreidus inermis* A. Edw. Chili." This specimen is referrable to *L. stenops*. It possesses a narrow front, unarmed carapace and the carpus of the cheliped possesses a single spine. No species of *Lyreidus* has ever been reported from the east Pacific and all other eastern Pacific raninids (see Rathbun, 1937) are quite different from species of *Lyreidus*. The locality given on the label of this Paris Museum specimen therefore, can only be regarded at the present time as erroneous.

GEOGRAPHIC DISTRIBUTION: Western Pacific Ocean: South-eastern Japan; South China Sea near Hong Kong, Philippines.

BATHYMETRIC DISTRIBUTION: Continental shelf from 30 to 77 fms.

Lyreidus channeri Wood-Mason, 1885, Figs. 6d, i, r; 7f; 8e. Pl. 2B.

Lyreidus channeri Wood-Mason, 1885: 104 (type locality: Bay of Bengal, 21°6′30″N., 89°20′E., 405–285 fms, dredged in trawl; holotype (male) in collections of Zoological Survey of India, Calcutta—reg. no. 8468/6); 1887: 206–208, pl. i figs. 1–6. Alcock, 1896: 294–5. Kemp and Sewell, 1912: 29.

Lyreidus gracilis Wood-Mason, 1888: 376 (type locality: off Port Blair, Andaman Sea, 271 fms; holotype (female) in collections of Zoological Survey of India, Calcutta—reg. no. 8567/6).

LOCALITIES PREVIOUSLY REPORTED: Bay of Bengal, 200–405 fms; Andaman Sea, 220–271fms (Wood-Mason 1885, 1887, 1888; Alcock). Arabian Sea, off Trivandrum, 237 fms, "Investigator" Sta. 391 (Kemp and Sewell, 1912).

MATERIAL EXAMINED: One specimen, as follows:—South China Sea: S. of Hainan, 16°47.5′N., 109°49.5′E., to 16°45′N., 109°52′E., 200–290 fms, fine mud, Agassiz trawl, 5/3/1965, FHK Sta. 17, 1 ♂, 30.0mm (AM P.15787).

REMARKS: The single specimen agrees fairly well with Wood-Mason's description (Wood-Mason, 1887) but the anterior of the two lateral spines is represented by a small, blunt lobe on the right side and an obscure bump on the left side. The external orbital spines are parallel and level with the acuminate rostrum. The eyestalks are compressed and the pigment is equally well developed in both eyes although the cornea is difficult to see in dorsal view. The distal tooth on the ventral edge of the chela is about three times the size of the proximal and there is a very small blunt tooth near the base making three teeth in all. The inner edge of each dactyl is obscurely tridentate, not bidentate. The merus of each cheliped has a

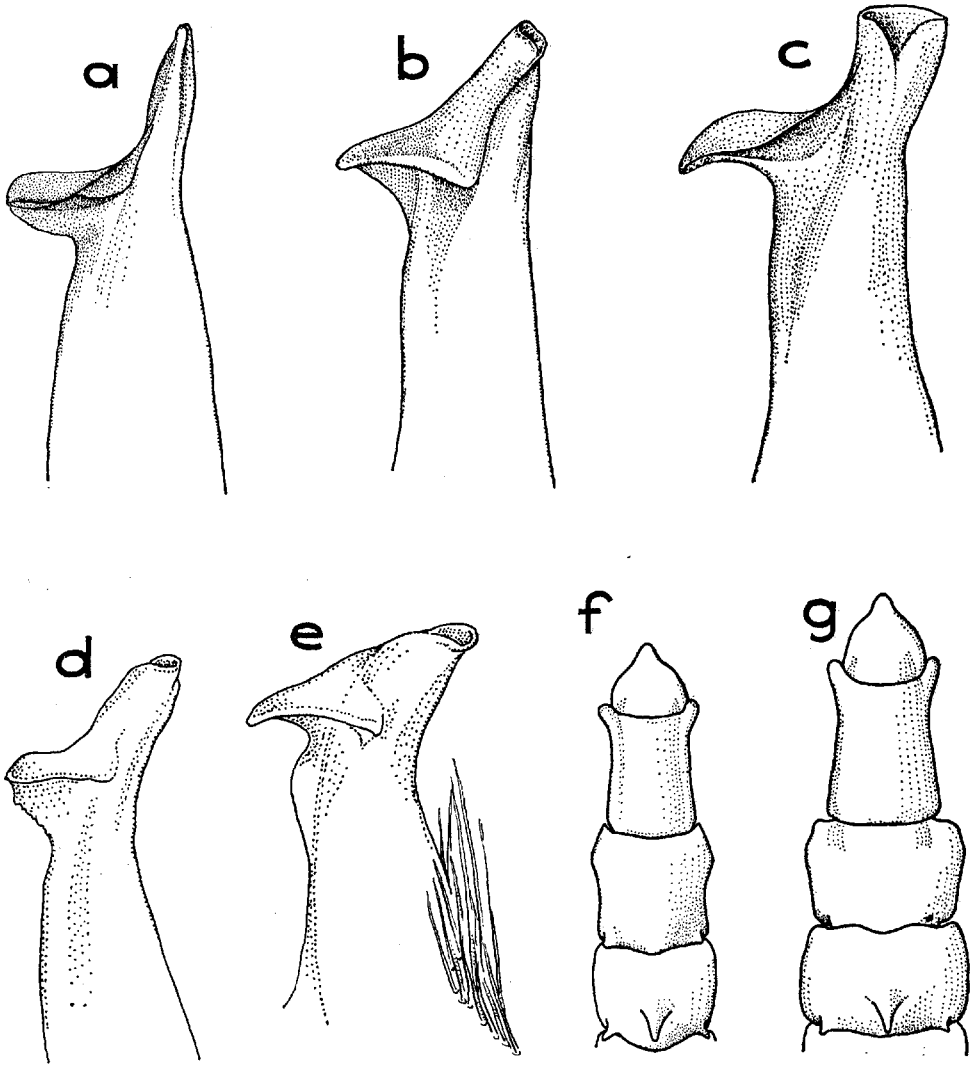

FIG. 8.—Male left first pleopods, tip, medio-abdominal aspect, of *Lyreidus* species (a-e) and abdomen, segments 4–7, of *L. tridentatus* (f, g). a, *L. tridentatus,* 28.3mm, Misaki, Japan (USNM 63689); b, *L. tridentatus,* 39.9mm, Japan (AM P.10499); c, *L. brevifrons,* 32.2mm, off Honshu, Japan (USNM 57687); d, *L. stenops,* 31.4mm, south of Hong Kong (AM P.15779); e, *L. channeri,* 30.0mm, south of Hainan (AM P.15787); f, *L. tridentatus,* ♂, 43.0mm, off Castlepoint, New Zealand (DM Z.Cr.615); g, *L. tridentatus,* ♀, 38.2mm, off Castlepoint, New Zealand (DM Cr.1058).

enough to warrant specific separation for this single specimen. The lack of a strong anterolateral spine in front of the long slender one not far from the widest part of the carapace in this specimen may be due to breakage during life whilst the difference in the shape of the rostrum (Wood-Mason describes and figures it as apically rounded) is due to breakage during life in Wood-Mason's specimen as noted by Alcock (1896: 295). The carapace features described by Wood-Mason—ridges and depressions—are obscure but the coarser granulations of the surface anteriorly are obvious.

low, blunt, dorsal spine proximally. Finally, the central spines on the third and fourth abdominal segments are short and blunt. These differences are not important

GEOGRAPHIC DISTRIBUTION: Northern Indian Ocean: Bay of Bengal and Andaman Sea near Ceylon. Western Pacific Ocean: South China Sea west of the Philippines.

BATHYMETRIC DISTRIBUTION: Continental slope from 200 to 405 fms.

DISCUSSION

Examination of the specimens on which this report is based has shown clearly that there is wide variation in all four Recent Indo-west Pacific species of *Lyreidus*. This variation concerns almost all features—carapace shape, prominence of spines and granules, shape of chelae and ambulatory dactyls and shape of sternum. These changes are correlated with growth or are differences due to sex. Such variation makes discrimination between species very difficult.

Within any group of similar species differences of three kinds may exist. The species may differ from each other: 1, in the range of variation, in which case statistical tests would show the mean values to be significantly different although the variances would be approximately the same; 2, in the extent to which they varied, i.e., the mean values would be similar but the variances would differ significantly; or 3, there may be differences in gross structure such as number of spines, tubercles, ridges, etc. It is this third kind of difference which immediately separates the four Indo-Pacific species of *Lyreidus* into three groups—*channeri, stenops* and *tridentatus-brevifrons*. *L. tridentatus* and *L. brevifrons* are distinguished by differences of the first kind—both show changes of the same kind with growth and possess generally the same number of spines and tubercles although there are a very small number of differences in relative proportions of some spines. Within this framework, if variation in any adequate population sample is wide, or narrow but correlated with growth, then only rigorous analysis can provide data which would allow distinctions both valid taxonomically and likely to represent any reasonable approach to reality. Historically, descriptions of new species of animals have been in general based on differences of the third kind—structural differences; these are the much more obvious ones. Presumably, it is for this reason that both Ward's and Bennett's species have been regarded with suspicion: their "species" were based on differences of the first kind but were supported by inadequate data.

It is also evident from the present study that within *Lyreidus* only two species could be distinguished which possess a single spine at about the middle of the lateral margin of the carapace, and the other features common to *L. tridentatus* and *L. brevifrons*. Thus it seems doubtful that Glaessner's *L. elegans,* from the New Zealand Miocene, is a species distinct from *L. tridentatus;* the stated differences between the two include the position of the lateral spines, relative width of the front and shape of the anterolateral margins. However, it appears clear that in certain features New Zealand populations of *Lyreidus* differ slightly but in a constant manner from Australian ones and are therefore probably in the course of becoming a species distinct from those to which the Australian populations belong. The small number of Japanese specimens examined suggests that variation is slightly greater in Japanese populations than in Australian and New Zealand ones.

The present zoogeography of the genus—three species distributed throughout the northern Indo-west Pacific and one in the western Pacific and south-eastern Indian Ocean provides no precise evidence as to areas of evolution of the genus. It is obvious only that the genus was at one time much more widely distributed than at present. Fossil species are known from the Oligocene of Europe but the precise relations of these to Recent species is quite unclear as in most cases the fossil remains are only fragmentary.

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