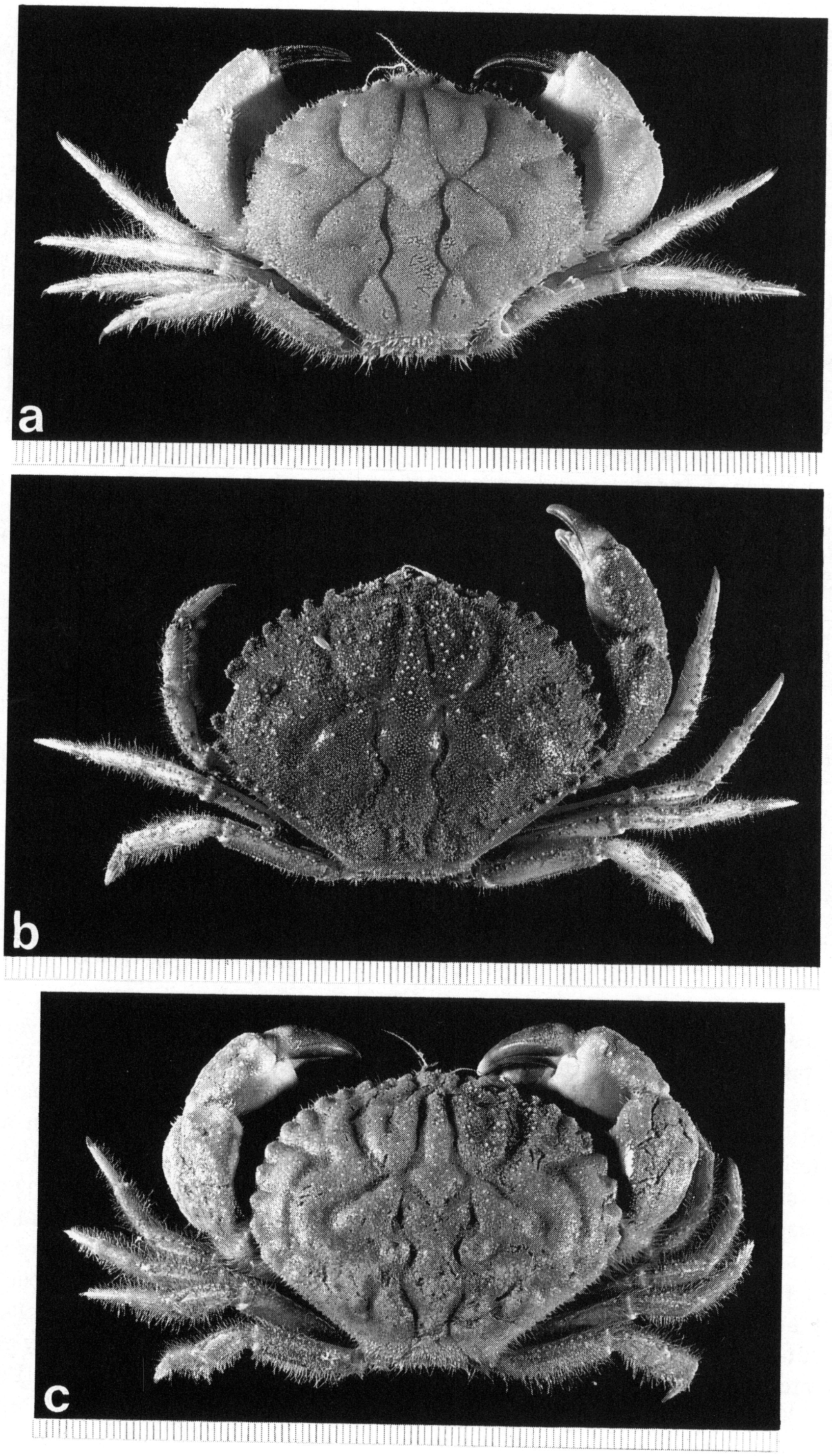

FIG. 6. — Dorsal views of : **a**, *Platepistoma balssii* (Zarenkov, 1990), ♂ 50.5 x 40.9 mm, Rurutu, Austral Islands, French Polynesia (MNHN-B 22211); **b**, *P. balssii* (Zarenkov, 1990), ♂ 58.4 x 44.9 mm, Eiao, Marquises Islands (MNHN-B 22215); **c**, *P. seychellense* sp. nov., holotype, ♂ 55.0 x 42.7 mm, Seychelles Archipelago (MNHN-B 19012).

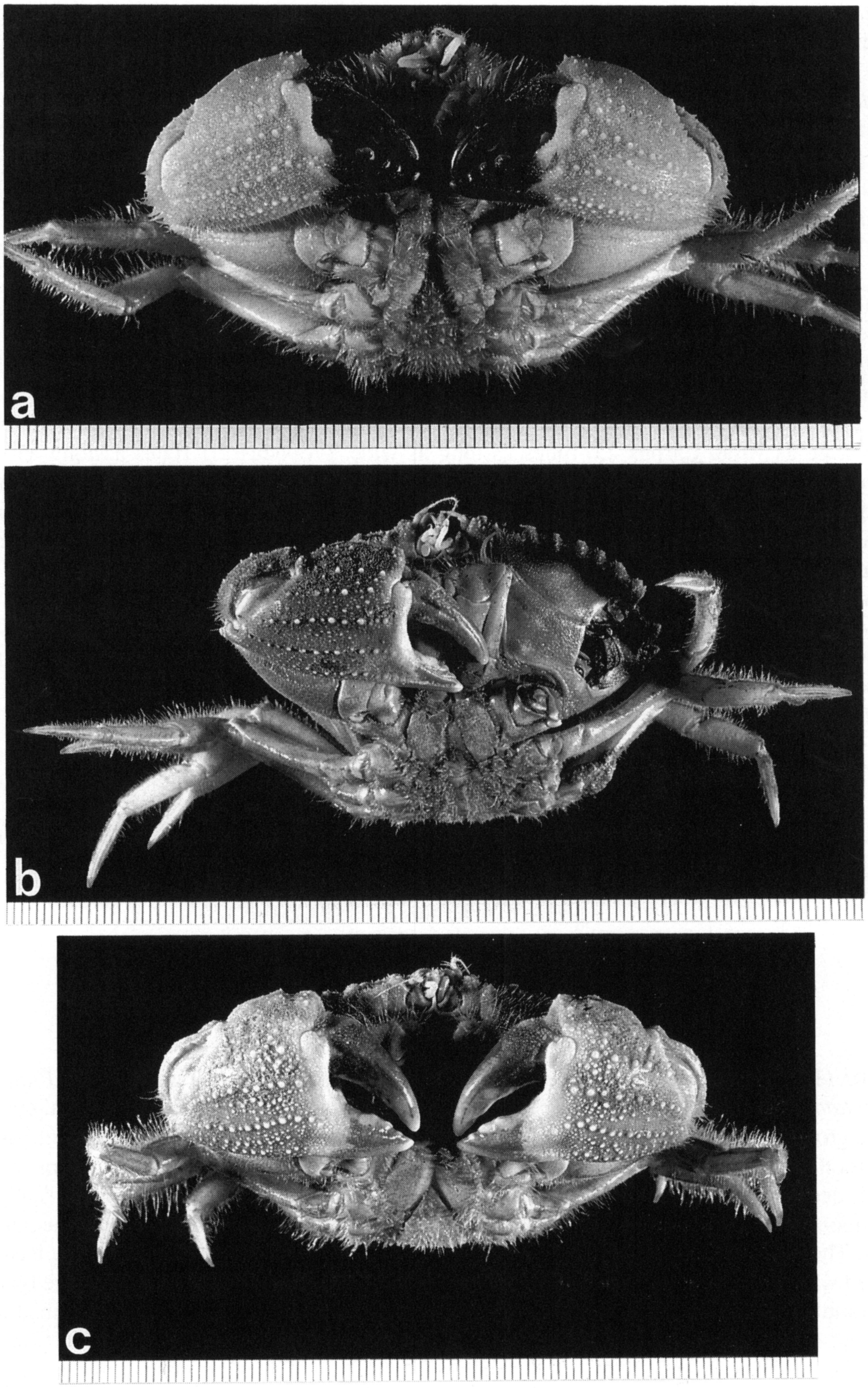

FIG. 7. — Frontal views of specimens in Fig. 6 : **a**, *Platepistoma balssii* (Zarenkov, 1990), ♂ (MNHN-B 22211); **b**, *P. balssii* (Zarenkov, 1990), ♂ (MNHN-B 2215); **c**, *P. seychellense* sp. nov., holotype, ♂.

Third maxilliped : Merus distinctly smaller than ischium. Merus quadrate; antero-external angle produced, rounded, bluntly pointed; inner margin with medial angle sharply pointed; 0.65 times length of ischium. Ischium rectangular, 1.9 times longer than wide; inner margin granular.

Chelipeds : Subequal; large and robust; merus with posterior border granulate; with distinct subdistal spine; lower border minutely granulate; anterior border minutely granulate; carpus with a broad tooth at inner angle; upper surface granular, granules just noticeable, most not projecting through tomentum; more-or-less in rows in proximal half; granules present on inner face of carpus just below inner angle, sharp, ending in a large swollen tubercle ventrally. Outer surface of palm coarsely granular, arranged in 3 distinct rows across medial and medioventral part behind gape, below these ventrally, granules smaller, more random, in 1 or 2 more-or-less distinct rows; upper outer face with well-separated blunt granules, with tips only just visible through thick tomentum; palm high, 0.67 times length of palm including fixed finger. Inner surface of palm microscopically granular. Immovable finger with a ventral and medial ridge; moderately long; length cutting edge 0.38 times length propodus. Ventral border of chela concave at base of fixed finger. Dorsal surface of dactyl granular near base, becoming smooth distally. Fingers pointed; a moderate gape between cutting margins.

Walking legs : Relatively long; cylindrical; slender; first three pairs all of similar length. Merus of third leg 3.2 times as long as wide. Carpus 2.6 times as long as wide. Propodus 2.1 times as long as wide. Dactyli 1.4 times length of propodus. Dactyli slender and straight; terminating in an acute chitinous recurved tip. Merus anterior margin terminating in an acute spine, and with a series of small erect spines along upper margin, longer distally, continuing along carpus and with a few spines proximally on propodus, especially on anterior legs; posterior margin minutely granular. Dactyli with two deep longitudinal grooves laterally. Setae stiff, of medium length, covering entire surface, longer marginally.

Male abdomen : First segment 0.8 times width third segment. Segments three-six tapering. Segment six 1.7 times wider than long. Telson longer than preceding segments; 1.2 times longer than wide; bluntly pointed, reaching about half distance towards suture between sternites 3 and 4.

Gonopods : First and second gonopods of male as figured.

ETYMOLOGY. — Named in reference to the type locality.

DISTRIBUTION. — Known only from the type locality, Seychelles Archipelago, southwestern Indian Ocean. Bathymetric range : 420-430 m.

DISCUSSION

Generic status

As TAKEDA (1977) states, it is difficult to find a single definitive character that will separate *Platepistoma* from *Cancer sensu lato*. There are however a number of characters, which when taken in combination, point to a natural monophyletic group worthy of generic status. **1**. The lateral teeth are all widely separated and not basally fused. **2**. The median tooth of the front is pointed, and placed ventral to the lateral teeth, and the ventral surface of each lateral tooth is deeply excavated to form the antennular fossa. In *Cancer* the frontal teeth are typically on the same plane from side-to-side, although as TAKEDA (1977) points out some species do have the medial tooth a little depressed. **3**. The walking legs of all the species considered here to belong to *Platepistoma*, have the anterior margins armed with a row of erect spines. In *Cancer* the anterior margins of the walking legs are typically smooth or slightly granular, although on *Cancer* (*Romaleon*) *nadaensis* Sakai, 1969, they are described as "obscurely spinulated", and on *Cancer luzonensis* Sakai, 1983, there are also some spinules. **4**. The anterolateral margin of the merus of the third maxilliped is noticeably produced laterally, and angular; this is not a typical condition in *Cancer* although a few species have developed this to a greater or lesser extent (notably *C. oregonensis*, *C. amphioetus* and *C. luzonensis*). **5**. The posterolateral margins are not obviously defined by a smooth or granulate ridge as in *Cancer*, which, in *Cancer*, continues as a strong ridge above the hind margin. In *Platepistoma* there may be a series of spines more-or-less defining the posterolateral border but even when they are strongly developed they do not continue medially above the hind margin.

I disagree with the conclusions of NATIONS (1975, 1979) and TAKEDA (1977) that *Cancer oregonensis* Rathbun, 1898, and *C. amphioetus* Rathbun, 1898, are closely related to *Platepistoma sakaii* (= *P. anaglyptum* Balss, 1922) and thus to the other species of *Platepistoma* discussed here. RATHBUN (1930) showed that *C. oregonensis* is a remarkably variable species, but nevertheless, in none of its forms does it closely resemble the species of *Platepistoma* described here. As NATIONS (1975) made *Cancer oregonensis* the type of his subgenus *Glebocarcinus*, I consider *Glebocarcinus* must remain a valid taxon and not be placed into the synonymy of *Platepistoma* as TAKEDA (1977) suggests. Therefore *Cancer* (*Glebocarcinus*) Nations, 1975, is here considered to contain only two certain extant species, *viz. Cancer oregonensis* Rathbun, 1898, and *C. amphioetus* Rathbun, 1898. I agree with TAKEDA'S (1977) doubts about the position of *Cancer tumifrons* Yokoya, 1933. It was included by NATIONS (1975) in *Glebocarcinus*, and perhaps should remain for the present in that subgenus; it certainly cannot be included in *Platepistoma* as it is here defined.

Glebocarcinus differs from *Platepistoma* by : **1.** The carapace not covered in thick tomentum; **2.** The development of the carapace regions is different, 2M is not divided, and other regions are more uneven and projecting, not broad and flat and moderately to well defined; **3.** The walking legs are comparatively shorter; **4.** The meri of the walking legs are without erect spines on their anterior margins; **5.** The medial tooth of the rostrum is in more-or-less the same plane as the lateral teeth, not markedly displaced ventrally; **6.** The posterolateral margins are strongly indicated and terminate in a strong ridge distinctly medial to the lateral edge of the hind costate margin.

I have examined the holotype female of *Cancer luzonensis* Sakai, 1983, and feel that its systematic position is problematical. It resembles *Platepistoma* in having strong carapace regions, in the shape of the third maxillipeds, and in the form of the posterolateral margins. It is however very different in lacking the dorsal tomentum on the carapace; by lacking the strong granulation of the carapace; and in having the lateral teeth fused over their basal half and then evenly triangular. SAKAI (1983) compared it most closely with *Cancer* (*Romaleon*) *nadaensis* Sakai, 1969, and it does indeed seem most closely related to that species, although I have not examined specimens of *C. nadaensis* in the present study. A larger more comprehensive study is needed of the species of *Romaleon* to determine if *C. luzonensis* and *C. nadaensis* are proper members of that subgenus.

I have also examined the fossil cancrid from Kerguelen Islands mentioned in the preliminary article of NOËL and LEMAIRE (1990) and don't believe it can be placed in the present genus as the carapace does not show the characteristic regional development and has a smooth, non-granulated surface.

MÜLLER (1984) and JANSSEN and MÜLLER (1985) described a new fossil genus of cancrid, *Tasadia* Janssen and Müller, 1985, with a single species *T. carniolica* (Bittner, 1884) which had previously been questionably assigned to *Cancer*. In most of the characters observable from the figures it seems very close to *Platepistoma* Rathbun, 1906, such that its separate generic status must be in doubt. *Tasadia carniolica* has stronger tuberculation on the dorsal margin of the finger than extant species; and the lateral carapace regions seem to differ slightly in having the hepatic region separated from the branchial region, whereas in *Platepistoma* these regions are connected in a more-or-less distinct, laterally rotated, V-shape.

The close relationship of *Tasadia* with the subgenus *Glebocarcinus* has already been noted by KARASAWA (1990) who felt that *Tasadia* should be considered a junior synonym of *Glebocarcinus* Nations, 1975. KARASAWA (1990, Addenda : 34) also believed that TAKEDA'S (1977) decision to make *Glebocarcinus* a junior synonym of *Platepistoma* was wrong because he doubted the correctness of TAKEDA'S identification of his adult material of *P. macrophthalmus*. I am convinced that TAKEDA's identification was correct as one of my specimens of *P. nanum* was juvenile like the type of *P. macrophthalmus* and showed the same pattern of alternating large and small lateral spines which RATHBUN (1906) had used as a generic character. Nevertheless as discussed in this paper I elect to maintain *Glebocarcinus* as a separate taxon from *Platepistoma* and, for the present, as a subgenus of *Cancer*. It seems possible that the Japanese Miocene species *Cancer* (*Glebocarcinus*) *kaedei* Karasawa, 1990, is referable to *Platepistoma* as KARASAWA (1990) considers *C. kaedei* to be closely related to *Cancer sakaii* (= *Platepistoma anaglyptum* Balss, 1922).

Species differentiation

As now recognized *Platepistoma* contains the following species :

- *P. macrophthalmus* Rathbun, 1906 — Hawaii; 370-465 m.
- *P. anaglyptum* Balss, 1922 — Japan; 50-120 m.
- *P. guezei* (Crosnier, 1976) — Réunion Is., and Madagascar; 350-720 m.
- *P. balssii* (Zarenkov, 1990) — Sala-y-Gomez Ridge, southeastern Pacific, and french Polynesia ; 295-550 m.
- *P. kiribatiense* sp. nov. — Kiribati, West Pacific; 400 m.
- *P. nanum* sp. nov. — South-west Pacific from New Caledonia into the Tasman Sea; 425-560 m.
- *P. seychellense* sp. nov. — Seychelles, Indian Ocean; 420-430 m.

The majority of the species occur in rather deep water, between about 300-720 m, with only one species *P. anaglyptum* from Japan occurring in water as shallow as 50 m, and this is probably related to cooler water temperatures.

All the species of *Platepistoma* have extremely similar facies and the major features to readily separate them are : density, coverage, and sharpness of the dorsal tubercles. Some other features are important for diagnosing particular species and are discussed in the following. The relatively small differences between some of the species beg the question as to whether sub-specific rank may be more suitable, i.e., are they just geographic variants. I consider full specific status should be given because although the differences in most cases are small, they are nevertheless very consistent within a restricted area of occurrence; this suggests that the gene pools are discrete and there is no evidence of the clinal variation that one might expect from simple geographic varieties. It is unclear what isolating factors would have operated to allow such speciation as there are no significant differences in bathymetric ranges.

The male first gonopods of all the species examined in this study (Fig. 3) are very similar but have some small differences. *Platepistoma nanum* (Fig. 3b) has the apex tapering quite evenly to an acute tip, whereas the other species have the tip comparatively more flanged and blunter. *P. seychellense* has the aperture broadly open (Fig. 3e) while on *P. balssii* it is longer and more slit-like (Fig. 3d), which is more like it is for *P. guezei* (see fig. 8e, in CROSNIER, 1976). The sub-apical flange on *P. kiribati* and *P. balssii* is very similar but on *P. seychellense* it is comparatively longer and a little less prominent. The second gonopod is very similar for all the species (Fig. 3c, f).

The produced anterolateral corner of the third maxilliped has been seen as an important generic character, but as has already been noted, it is not unique to *Platepistoma* among the cancrids. The precise form of the third maxilliped is however remarkably consistent within the genus with the species showing only minor differences. For example *P. kiribatiense* (Fig. 4a) differs from *P. seychellense* (Fig. 4b) by having the inner medial tooth of the merus more acute and armed with accessory granules; and by having the anterior margin of the merus flatter, and the anterolateral corner more angular. *P. nanum* is intermediate between the two forms, while *P. balssii* is almost identical with *P. kiribatiense*.

The male abdomens are also very similar and show only relatively minor differences — for example the telson of *P. nanum* (Fig. 4c) is slightly longer and more pointed than for *P. seychellense* (Fig. 4d). The slightly shorter telson of *P. seychellense*, and more especially its position on the sternum, is shared with *P. guezei*, and splits off the two Indian Ocean species from all the Pacific species examined in this study. On *P. guezei* and *P. seychellense* the telson only reaches about half the length of sternite 4, such that the anteromedial part of sternite 4 is not as deeply and broadly grooved, almost to the third sternite, as it is for *P. balssii* and *P. kiribatiense* (compare Fig. 5a and b). *P. nanum* is intermediate in this regard having a telson a little longer than the Indian Ocean species pair, but not as long as the other Pacific species.

P. nanum is clearly separated from all the other species by its small size (maximum c.b. = < 30 mm); poor regional definition; dorsal carapace tubercles not protruding through the tomentum, and only barely visible without denudation; the relative shape and length of the telson and sternal segments; the posterolateral margins with a marked row of granules terminating in a moderately large tubercle laterally above hind margin (a similar but smaller granule is also present on *P. guezei* and *P. seychellense*); and a deep concavity on the distal half of the superior margin of the chela.

P. seychellense is only easily separated from *P. guezei* by the much stronger definition of carapace regions, the inter-regional furrows being in all cases relatively broader, deeper, and more sharply defined. This is particularly marked in the case of the deep longitudinal groove over the anterior two-thirds of 2M; the strong grooves almost splitting 3M from 4M; the strong definition of the triangular region on the inner part of the mesobranchial area lateral to gastro-cardiac region which is strongly demarcated posteriorly by a broad deep groove; and the strong curved mediolateral groove on the branchial region. The first impression of the carapace of *P. seychellense* is one of a strongly defined meandrine regional pattern, whereas the carapace of *P. guezei* presents a much less obvious impression of the regions. Despite having only a single specimen of *P. seychellense* I am convinced this difference is significant because a good series of *P. guezei*, from quite small to large, shows an identical bland regional pattern. Also the Pacific species are remarkably consistent within themselves in this character.

P. kiribatiense most closely resembles *P. macrophthalmus* in its strong regional definition and obvious granulation — it differs obviously in only having granules across the anterior two-thirds of the carapace, and not having them continue evenly across the whole surface to the posterior margin (see TAKEDA, 1977, fig. 4B). *P. balssii* is also similar to *P. kiribatiense* but the regions are not separated by such broad deep furrows, and the granules do not typically protrude through the tomentum.

P. anaglyptum most closely resembles *P. macrophthalmus* in having both strong regional definition and an entire covering of granules. In *P. anaglyptum* however the granules are larger and rounder, and according to TAKEDA (1977) the legs are also much more slender.

Key to the Indo-west Pacific species of *Platepistoma*

1. Small species (carapace breadth < 30 mm); posterolateral margins with a marked row of granules terminating in a moderately large tubercle laterally above hind margin; a deep concavity on distal half of superior margin of chela .... ***P. nanum*** sp. nov.

— Large species (carapace attains breadth > 40mm); posterolateral margins with granules or small spines anteriorly, but not continuing as a marked row; sometimes with a small tubercle laterally above hind margin. **2**

2. Strong granulation visible over entire dorsal surface of carapace................................ **3**

— Granulation confined primarily to the anterior two-thirds, or hidden by tomentum posteriorly **4**

3. Carapace granules relatively large, rounded and set closely together, walking legs relatively slender.. ***P. anaglyptum*** Balss, 1922

— Carapace granules pointed, not set closely together.. ....***P. macrophthalmus*** Rathbun, 1906

4. Telson of male abdomen relatively short, reaching only about half distance towards suture between sternites 3 and 4 (Fig. 5b)... **5**

— Telson of male abdomen relatively longer, reaching half to three-quarters distance towards sternite 3 (Fig. 5a).. **6**

5. Carapace regions relatively poorly defined, 2M without obvious subdivision over anterior two-thirds.. ***P. guezei*** (Crosnier, 1976)

— Carapace with strongly defined, meandrine regional pattern, 2M obviously subdivided over anterior two-thirds.. ***P. seychellense*** sp. nov.

6. Regions strongly developed, separated by broad deep furrows; granules strongly evident over anterior two-thirds, protruding through tomentum......... ***P. kiribatiense*** sp. nov.

— Regions present but not separated by such broad deep furrows; granules not typically protruding through tomentum...................................... ***P. balssii*** (Zarenkov, 1990).

Biogeography

Until now biogeographers have treated *Cancer* as the only modern genus to represent the Cancridae, *Platepistoma* having been poorly known and ignored. The biogeography of *Cancer* has been thoroughly discussed and a North Pacific origin for *Cancer* has been postulated by EKMAN (1953), NATIONS (1975, 1979) and CARVACHO (1989). NATIONS suggested coastal migration routes to account for the present distribution. As NEWMAN (1991) outlines the theory — *Cancer* originated in the Miocene of the North Pacific where most species are found today. Radiation followed : **1**) up and over the pole into the Atlantic; **2**) down the East Pacific to South America; and hence, **3**) to Australia and New Zealand via Antarctica (against the West Wind Drift). NEWMAN (1991) remarks that there are a number of difficulties with accepting this view; and they are well discussed in his paper. The Cancridae had a tropical/subtropical history in the Paleocene, before the tropics began to narrow in the Oligocene and to warm in the Miocene. This, along with other evidence, supports the idea of reliction of a previously wide ranging Tethyan complex. As NEWMAN also remarks, the record of a cancrid (not *Platepistoma*, as already discussed in this paper) in the Mio-Pliocene of Kerguelen, in the southern Indian Ocean (NOËL & LEMAIRE, 1990) is not compatible with a North Pacific radiation hypothesis. KARASAWA (1990) also reasons that *Glebocarcinus* (*sensu* NATIONS, 1975, 1979) had its origin in the Indo-West Pacific Ocean during the Early Miocene, and agrees with NEWMAN (1991) that *Cancer* evolved in the Tethys Sea during the Eocene to Oligocene.

Prior to NEWMAN (1991) biogeographers had not mentioned CROSNIER's (1976) description of *Cancer guezei* from Madagascar and Réunion Island, and only KARASAWA (1990) had briefly mentioned TAKEDA's (1977) report of *Cancer* (*Platepistoma*) from deep water off Hawaii. As NEWMAN (1991) points out, the latter could fit into a North Pacific origin and radiation hypothesis but the former does not. With the discovery of the three new species described in this paper from the tropical and sub-tropical Indo-West Pacific it is clear that at least for *Platepistoma* the distribution of species is compatible with a Tethyan rather than a North Pacific origin hypothesis. Caution must be exercised in generating hypotheses because it is clear that the species of *Platepistoma* have had a separate evolutionary history from the mainstream group of shallow water *Cancer* species, and it is potentially dangerous to look at the modern distribution patterns of both groups and expect them to reflect the same pattern of radiation and/or reliction. *Platepistoma* in particular appears to have been subject to a retreat into deep water as GLAESSNER (1969 : 425) states has been the case for a number of bathyal decapod groups that "have fossil representatives in assemblages which indicate shallow-water conditions".

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