

On the different forms of *Panulirus longipes femoristriga* (von Martens, 1872) (Crustacea: Decapoda: Palinuridae), with description of a new species

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Material previously identified as *Panulirus longipes femoristriga* (von Martens, 1872) is found to have two forms of coloration, namely the banded whisker form and the white whisker form. Careful comparisons of fresh lobsters reveal that the two forms differ in morphological characters. Data from allozyme analysis also shows that they are genetically distinct. To stabilize the confused taxonomy of these species, a neotype for *P. longipes femoristriga* is selected from a specimen of the banded whisker form from the type-locality Amboina. The white whisker form is shown to be a new species.

KEYWORDS: Spiny lobster, Palinuridae, *P. longipes femoristriga*, allozyme, new species.

Introduction

The spiny lobster *Panulirus longipes* (A. Milne Edwards, 1868) (type-locality: Mauritius) is generally considered to be widely distributed in the Indo-West-Pacific and to have two forms; the western spotted-legged form (here referred as the 'nominotypical form') in the Indian Ocean and the eastern striped-legged form in the West Pacific (George and Holthuis, 1965; George and Main, 1967; Sekiguchi, 1988, 1991; Holthuis, 1991). The two forms differ only in the colour pattern of the pereiopods. The subspecific name *Panulirus longipes femoristriga* (von Martens, 1872) (type-locality: Amboina, Indonesia) is often applied to the striped form. Recently, however, more than one kind of coloration has been observed in the striped form (George, 1972; Sekiguchi, 1991; Chan and Yu, 1993). The different striped-legged forms can generally be separated into two groups; those with the antennular flagella covered with pale cross-bands and those without cross-bands.

In Taiwan and the markets of Hong Kong, '*P. longipes femoristriga*' specimens of two very distinct colour patterns can be found (see photo in Chan and Yu, 1993). In one form the coloration, except the pereiopods, is almost identical with the nominotypical form (which is also present in Taiwan and Hong Kong) and with the antennular flagella conspicuously banded (here referred as the 'banded whisker form'). The other form has the colour of the carapace rather different from the nominotypical form and with the inner antennular flagella entirely whitish (referred here as the 'white whisker form'). However, the banded and white whisker forms are

uncommon in Taiwan and in the markets of Hong Kong they are imported, often from Indonesia. Other than having distinct colour patterns, careful comparisons of many fresh specimens reveal several slight but constant morphological differences between the banded and white whisker forms. Their distinct specific status is further confirmed by electrophoretic analysis of allozymes, which is widely used to distinguish cryptic or dubious species (Thorpe and Solé-Cava, 1994, for review), many of them crustaceans (e.g. Salmon *et al.*, 1979; Huber, 1985; Bert, 1986; Knowlton, 1986). The type material of *P. longipes femoristriga* is now lost (Holthuis, 1991) and the original description on the type provided by von Martens (1872) is too brief to determine which form it belongs to. Through neotype selection, *P. longipes femoristriga* is here fixed to the banded whisker form. The white whisker form is shown to be a new species.

Material and methods

Most of the lobsters were obtained from the fish markets of Taiwan and Hong Kong. Specimens used for morphological comparisons were retained and deposited at the National Taiwan Ocean University (NTOU). Furthermore, the collection of the Nationaal Natuurhistorisch Museum, Leiden (RMNH) and Muséum national d'Histoire naturelle, Paris (MNHN) were examined. The material listed for the two subspecies of *P. longipes* was limited to those with information on the coloration of the pereopods. The stated measurement is carapace length (cl) which is measured from the anterior to the posterior margins of the carapace along the dorsal midline. The above three institutions also have 52 specimens (13.2–90.1 mm cl) of *P. longipes longipes*: Taiwan, 36 spec. [NTOU]; Thailand, 1 spec. [RMNH D37937]; Ceylon, 1 spec. [RMNH D18691], Mauritius 4 spec. [MNHN Pall5, Pall6, Pa919, Pa1416], Zanzibar 1 spec. [MNHN 429-1864], La Réunion 3 spec. [MNHN Pa481, Pa920, Pa993] and Madagascar 7 spec. [MNHN Pa365, Pa370, Pa917, Pa918].

For morphological descriptions, the large tooth immediately behind the supraorbital horn is referred as the 'second anterior tooth'. The spine count at the ventral surfaces of the antennal peduncle does not include those spines on the margins. The bifurcate projection at the middle of the posterior margin of the thoracic sternite VIII is referred as the 'posterior fork' of the thoracic sternum. The synonymy provided here is limited to important works and those with clear colour illustrations which enable positive identification.

For allozyme analysis, samples of *P. longipes* (i.e. the spotted-legged form) and the new species obtained in Hong Kong were used. These samples originated from some unknown localities in Indonesia (part of the *P. longipes* samples might come from the Philippines). Specimens of *Panulirus japonicus* (von Siebold, 1824), used as an out group, were from Taiwan and transported on dry ice to Hong Kong. All specimens were frozen at -70°C in the Marine Science Laboratory of the Chinese University of Hong Kong until dissection. These specimens have a carapace length of 54–93 mm and body weight of 160–680 g. Hepatopancreas and abdominal muscle were separated and homogenized in 1 and 4 vol. cold buffer, respectively (0.01 M Tris-HCL, pH 7.5, with 1 mM EDTA, 1 mM 2-mercaptoethanol and 5 g l^{-1} NADP). Homogenates were centrifuged at 4°C for 20 min and supernatants were stored at -70°C until electrophoresis.

Starch gel electrophoresis was performed on a horizontal gel apparatus at 2°C with 12% (w/v) starch. Table 1 shows for which enzymes and tissue sources clear gel patterns were obtained under the specified electrophoretic conditions. Staining procedures were

Table 1. Enzymes assayed, tissue sources, electrophoretic systems used and loci scored in *Panulirus* species.

Enzyme	E.C. No.	Tissue used†	Electrophoretic system‡	Locus
Aspartate aminotransferase	2.6.1.1	H	EBT	<i>Aat</i>
Aldolase	4.1.2.13	M	TCE	<i>Ald</i>
Glucose phosphate isomerase	5.3.1.9	M	EBT	<i>Gpi</i>
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	M	TCE	<i>Gapdh</i>
Isocitrate dehydrogenase	1.1.1.42	M	TCE	<i>Idh</i>
Lactate dehydrogenase	1.1.1.27	M	TCE	<i>Ldh</i>
Malic enzyme	1.1.1.40	M	TCE	<i>Me</i>
Phosphoglucomutase	2.7.5.1	M	TCE	<i>Pgm</i>
6-Phosphogluconate dehydrogenase	1.1.1.44	M	TCE	<i>6-Pgdh</i>
Xanthine dehydrogenase	1.2.1.37	H	EBT	<i>Xdh</i>

† H: Hepatopancreas; M: Muscle.

‡ EBT: continuous Tris-borate-EDTA buffer, pH 9.0 (Redfield and Salini, 1980), 150 V, 17–22 h; TCE: Continuous Tris-citrate-EDTA buffer, pH 7.0 (Redfield and Salini, 1980), 50 V, 17–22 h.

derived from those of Redfield and Salini (1980) and Murphy *et al.* (1990). All chemicals were obtained from Sigma Chemical Co.

The commonest allele at each locus was termed 100, and the other alleles were designated by their percentage mobility relative to the 100 allele. The proportion of polymorphic loci and expected heterozygosity were calculated. Genetic distance, *D*, and genetic identity, *I*, between each pair were determined by the method of Nei (1978). A dendrogram was constructed from the *D* values, using the unweighted pair-group method with arithmetic means (UPGMA) (Sneath and Sokal, 1973).

Taxonomy

Family Palinuridae

Panulirus White, 1847

Panulirus longipes femoristriga (von Martens, 1872)

(Figs 1b, 2b, 3b, 4b, 5b, d)

Panulirus femoristriga von Martens, 1872: 125; Pfeffer, 1881: 35.

Senex femoristriga: Ortmann, 1891: 23.

Panulirus bispinosus Borradaile, 1899: 418; de Man, 1916: 33; Holthuis, 1946: 113.

Panulirus japonicus, var. *longipes*: de Man, 1916: 33 (part).

Panulirus japonicus: Holthuis, 1946: 123 (part). [*non* von Siebold, 1824].

Panulirus longipes: Kubo, 1954: 99, Figs 2–3, Pls 3, 4, 6E; 1971: 626, Fig. 1017; Utinomi, 1967: 61, Pl. 30–2; Harada, 1965: 37, 1966: 17; George and Holthuis, 1965: 21 (part); Chang, 1965: Fig. 34; George and Main, 1967: 812 (Part); George, 1968: 35; 1972: 12; Healy and Yaldwyn, 1971: 56, Pl. 25; Takeda, 1982: 39, Fig. 116; Miyake, 1982: 84, Pl. 28–4; Moosa and Aswandy, 1984: 26 (part); Williams, 1986: 20 (part); Sekiguchi, 1988: 161, Figs 1–2 (part); Hirata *et al.*, 1988: 61, unnumbered photo; Kamezaki *et al.*, 1988: 132, unnumbered photo; Holthuis, 1991: 145, Fig. 278 (part); Chan and Yu, 1993: 140 (part).

Panulirus longipes femoristriga: George, 1972: 3, 16, 19, 25, 31, 33; Phillips *et al.*, 1980: 67 (part); Sekiguchi, 1991: 18, Figs 2–3 ('Shirahige-ebi'); Junino *et al.*, 1991: 209; Chan and Yu, 1993: 140 lower Fig.

[not] *Panulirus longipes femoristriga*: George and Holthuis, 1965: Pl. 5a; George, 1972: 22; Holthuis, 1991: Fig. 277-left; Chan and Yu, 1993: 141 photo. [= new species].

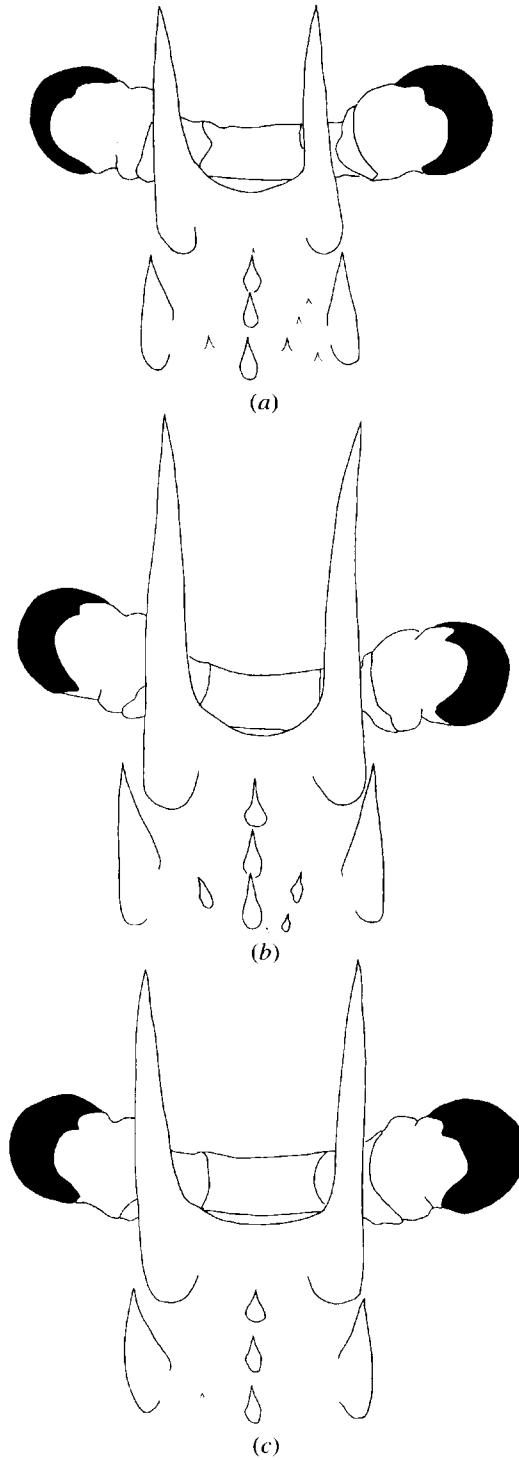
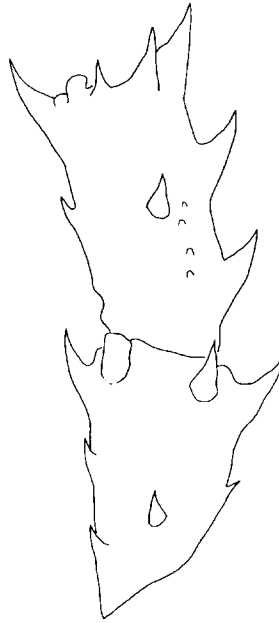


FIG. 1. Anterodorsal carapace: (a) *Panulirus longipes longipes* (A. Milne Edwards, 1868), male 67.1 mm cl, Taiwan; (b) *P. longipes femoristriga* (von Martens, 1872), neotype female 76.1 mm cl, Amboina, Indonesia; (c) *P. albiflagellum* sp. nov., paratype male, 77.5 mm cl, Indonesia.



(a)



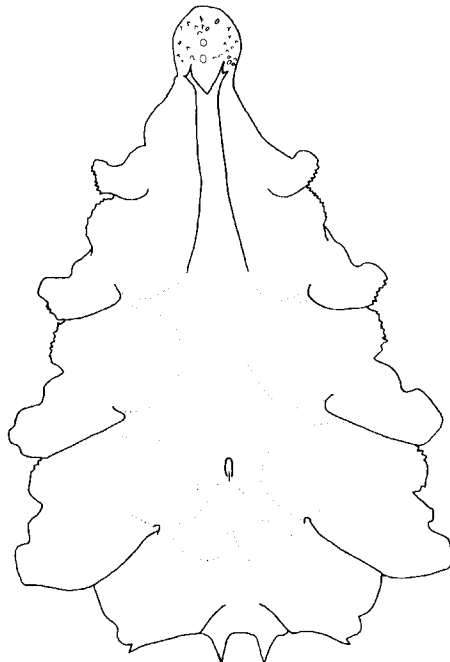
(b)



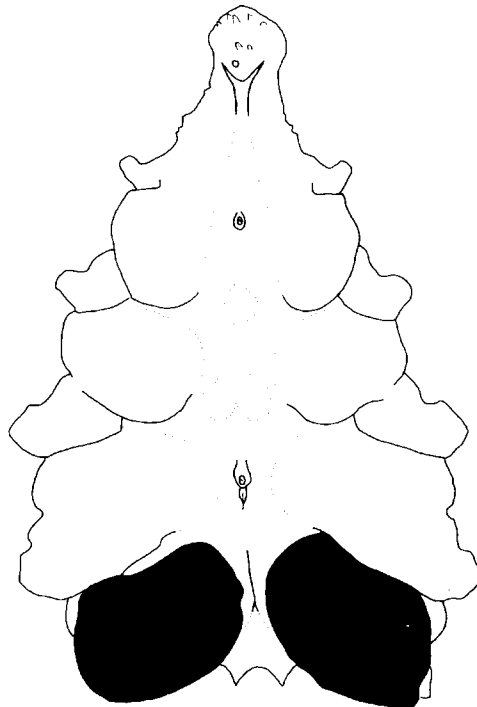
FIG. 2. Ventral view of distal two segments of antennal peduncle: (a) *Panulirus longipes longipes* (A. Milne Edwards, 1868), male 67.1 mm cl, Taiwan; (b) *P. longipes femoristriga* (von Martens, 1872), neotype female 76.1 mm cl, Amboina, Indonesia; (c) *P. albiflagellum* sp. nov., paratype male, 77.5 mm cl, Indonesia.

Material examined. **Indonesia.** Amboina, Moluccas, 1867, D. S. Hoedt coll., 1 ♀ 76.1 mm (neotype) [RMNH D1430] locality unknown (imported to Hong Kong market), 1991–1992, 7 ♂ 53.8–82.3 mm, 7 ovig. ♀ 54.8–76.3 mm, 3 ♀ 62.3–75.0 mm [NTOU R1001]. **New Caledonia.** Noumea, Nickel Bay, September 1979, 1 ♂ 39.7 mm, 3 ♀ 21.5–30.8 mm [MNHN Pa664]. **Loyalty Islands.** Lifu, Sandal Bay, 1896–1897, Willey coll., 1 juvenile 8.1 mm (type of *Panulirus bispinosus*) [University Museum of Zoology, Cambridge]. **Taiwan.** Northeastern coast, diving, 14 September 1984, 1 ♂ 63.3 mm [NTOU R1002]. Taitung County, 3 August 1988, 1 ♀ 49.7 mm [NTOU R1003]. No data, 1 ♀ 68.9 mm [NTOU R1004]. **Japan.** 1 spec. [RMNH D31993].

Diagnosis. Anteromedian carapace between supraorbital horns and second anterior teeth bearing 2–7 spines and/or spinules in addition to the longitudinal row of three large spines at middle (altogether five to ten and mostly about seven spines present). Antennular plate having three to twelve (mostly seven) spinules above and two to eight (mainly four) spinules below the two principal spines. Cervical groove more or less as wide as posterior marginal groove of carapace. Ventral surfaces of distal two segments of antennular peduncle armed with one large spine and often some other irregularly arranged smaller spines and spinules. Medial depression of thoracic sternum often bearing spine-like knob on anterior one third and sometimes also two weak protrusions near middle, posterior fork generally partly fused with thoracic sternum. Abdominal tergite I often provided with short dorsal carina. Well-developed transverse grooves present at abdominal tergites II–VI and joining corresponding pleural grooves. Anterior margin of abdominal pleuron II bearing 0–5 spinules.



(a)



(b)

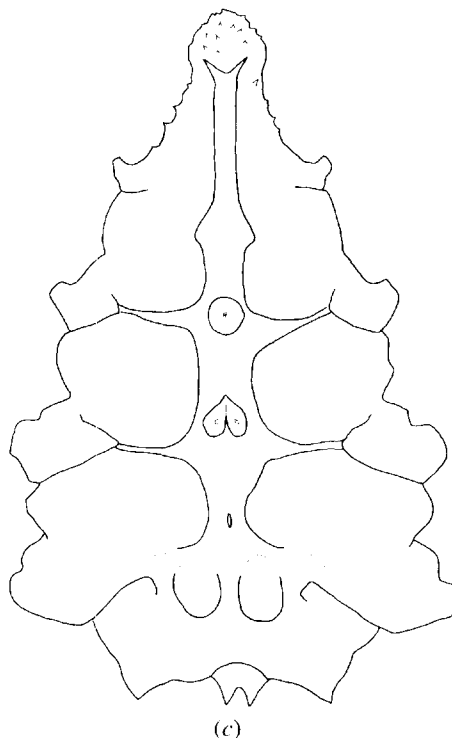


FIG. 3. Thoracic sternum: (a) *Panulirus longipes longipes* (A. Milne Edwards, 1868), male 67.1 mm cl, Taiwan; (b) *P. longipes femoristriga* (von Martens, 1872), neotype female 76.1 mm cl, Amboina, Indonesia; black areas represent dried spermatophore; (c) *P. albiflagellum* sp. nov., paratype male, 77.5 mm cl, Indonesia.

Coloration. Body dark brown to indigo and covered with numerous white spots and markings. Eyes black brown. Cardiac area of carapace having a small 'V'-shaped white marking and median part of cervical groove somewhat whitish. Lateral carapace bearing one short and one long longitudinal white stripes; dorsal stripe starting anteriorly below orbit and ended before reaching cervical groove, ventral stripe extending along entire lateral surface from area below antennal peduncle to posterolateral carapace. Antennular plate brown to purple and with large white triangular posteromedian spot. Mesial surface of antennal peduncle also brown to purple and with stridulating pad bright blue. Antennal flagella brownish, with ventral surfaces lighter in colour. Antennules (both peduncles and flagella) dark brown and alternated with conspicuous white bands. Pereiopods striped with white or pale lines. Abdomen covered with numerous small to medium sized white spots and bearing pair of larger spots near hinges of each somite. Middle of depressed area on abdominal tergite I with short but broad white band. Non-calcified part of tailfan orange brown and with distal margin whitish. Pleopods somewhat greenish and white margined. Eggs orange.

Size. Largest male 82.3 mm cl and largest female 76.1 mm cl in the present study (largest body length 350 mm in Kamezake *et al.*, 1988).

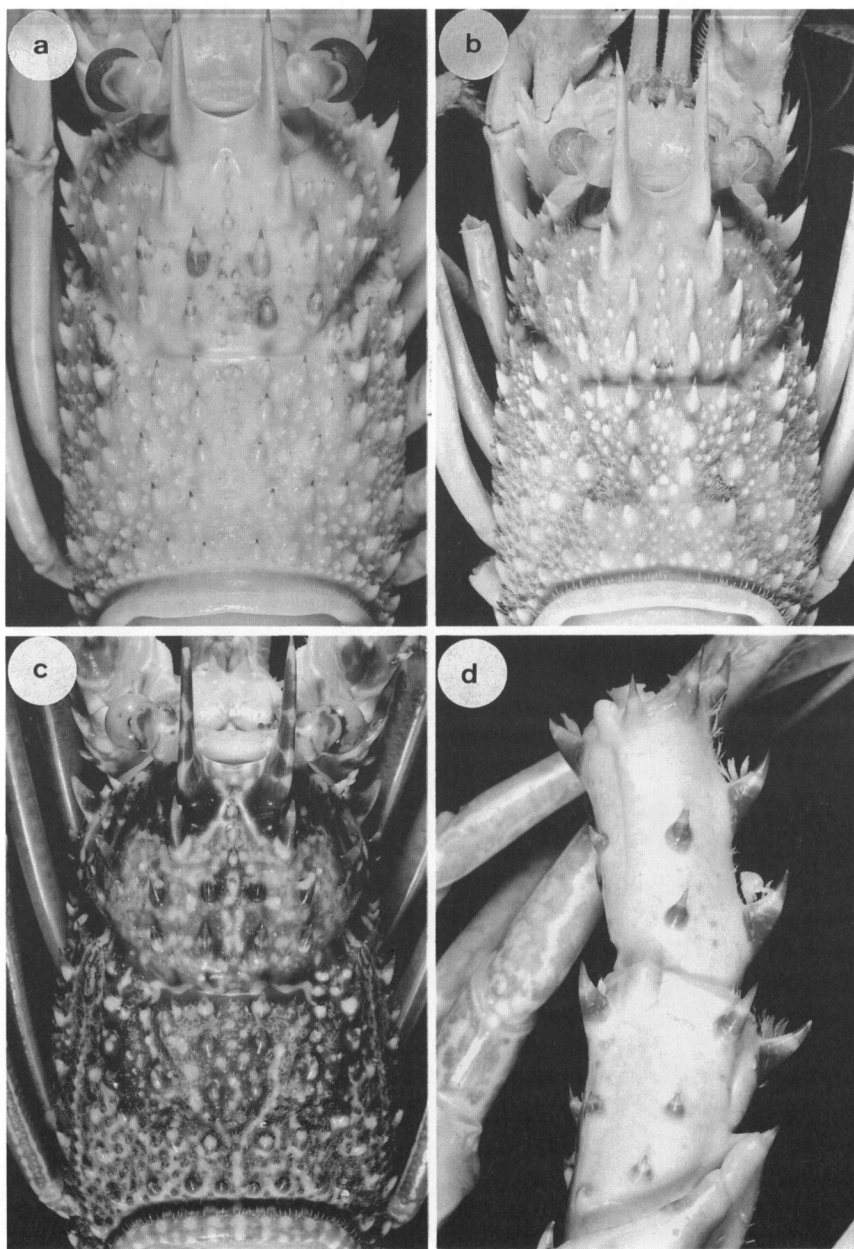


FIG. 4. (a–c) Dorsal carapace; (d) ventral view of distal two segments of antennal peduncle. (a) *Panulirus longipes longipes* (A. Milne Edwards, 1868), male 67.1 mm cl, Taiwan; (b) *P. longipes femoristriga* (von Martens, 1872), neotype female 76.1 mm cl, Amboina, Indonesia; (c–d) *P. albiflagellum* sp. nov., paratype male, 77.5 mm cl, Indonesia.

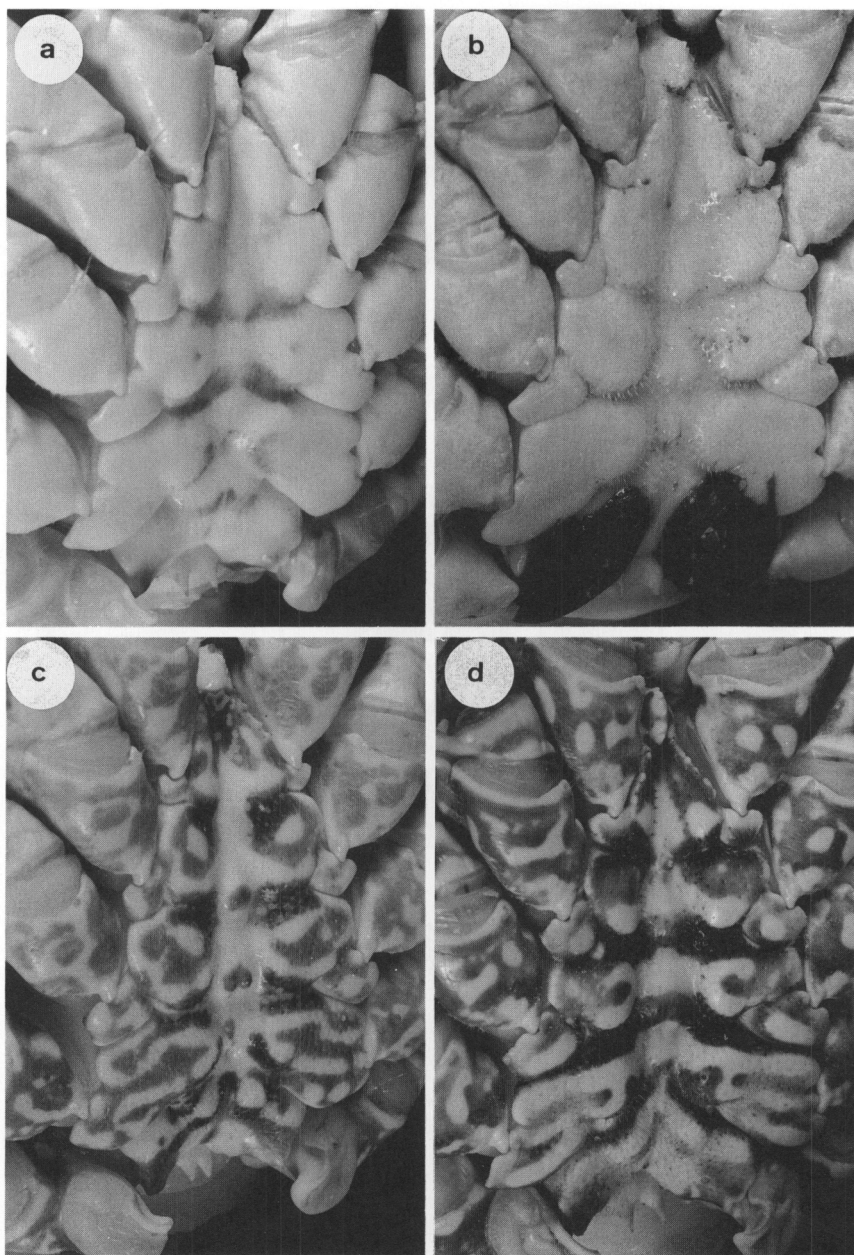


FIG. 5. Thoracic sternum: (a) *Panulirus longipes longipes* (A. Milne Edwards, 1868), male 67.1 mm cl, Taiwan; (b) *P. longipes femoristriga* (von Martens, 1872), neotype female 76.1 mm cl (with dried spermatophore), Amboina, Indonesia. (c) *P. albiflagellum* sp. nov., paratype male, 77.5 mm cl, Indonesia; (d) *P. longipes femoristriga* (von Martens, 1872), male 81.5 mm cl, Indonesia.

Distribution. West and South Pacific from Japan to the Bonin Is., Taiwan, the Philippines, Indonesia [type-locality], Australia, New Caledonia, Loyalty Is., New Hebrides, Fiji and likely also in Micronesia, Papua New Guinea, Tonga, Cook Is. In shallow reef areas to 130 m deep (under *P. longipes* in George and Holthuis, 1965; George, 1968).

Remarks. The present banded whisker form has both the morphological characteristics and coloration almost identical with the nominotypical form of *P. longipes* except the pereopods are striped instead of spotted. The subspecific name *P. longipes femoristriga* is generally used for the striped-legged form of *P. longipes* (George and Holthuis, 1965; George, 1972; Holthuis, 1991; Sekiguchi, 1991; Chan and Yu, 1993). However, more than one striped-legged forms are now found in the western Pacific. Nevertheless, the type of *P. femoristriga* from Amboina is now lost (Holthuis, 1991) and the original description of the type given by von Marten (1872) is too brief for determining the distinguishing characters (see 'Remarks' of next species). Since *Panulirus* is an important commercial genus, a neotype should be fixed for *P. femoristriga* to ensure that the taxonomy of the various forms is stable. Although both the banded whisker and white whisker forms are present in Indonesia and probably also in Amboina, the only striped-legged specimen (RMNH D1430) obtained from Amboina in the present study is chosen as the neotype of *P. femoristriga*. This Amboinan specimen was collected by D. S. Hoedt more than one century ago and with the colour faded (but assigned by George and Holthuis (1965) as *P. longipes femoristriga*). Nevertheless, it shows all the characteristics of the banded whisker form but not the white whisker form (Figs 1b, 2b, 3b, 4b, 5b). Von Marten's name *femoristriga* is hence restricted to the banded whisker form even though both George and Holthuis (1965: Pl. 5a) and Holthuis (1991: Fig. 277 left) used the white whisker form for the illustrations of '*P. longipes femoristriga*'.

The species *Panulirus bispinosus* described by Borradaile (1899) from the Loyalty Is. (type-locality) is generally considered to be a synonym of *P. femoristriga* (Borradaile, 1899; de Man, 1916; Holthuis, 1946; 1991; George and Holthuis, 1965). A re-examination of Borradaile's specimen (1899) shows that it is very small (8.1 mm cl) and bears all the juvenile characteristics (e.g. with abdominal furrows medially interrupted and posterior fork of thoracic sternum not yet developed). Furthermore, its body has been slightly squashed (both the abdomen and thoracic sternum are slightly carinate but these are probably due to the specimen has been folded) and turns black. Nevertheless, it has five spinules on the anteromedian carapace between the supraorbital horns and 2nd anterior teeth, and the antennal peduncle bears only one large spine on the ventral surface of each of the distal two segments. Thus, Borradaile's specimen (1899) clearly belongs to the banded whisker form and *P. bispinosus* should then be treated as a junior synonym of *P. femoristriga s.st.*

After comparing a large amount of material from different localities, it is found that a distinct protrusion or tooth (more pronounced in males) is often present at the anterior one third of the medial depression of the thoracic sternum in the banded whisker form (Figs 3b, 5b, d). Although the medial depression of the thoracic sternum is generally smooth in the nominotypical form (Figs 3a, 5a), a distinct tubercle is sometimes present at the anterior one third of the sternum particularly in specimens from the western Indian Ocean and in young specimens (i.e. < 40 mm cl). The presence of a short dorsal carina on the abdominal tergite I also appears to be variable. This carina is generally distinct in the material from Japan to Indonesia but usually absent in specimens from the South

Pacific and western Indian Ocean. Since no satisfactory morphological character has been found to separate the nominotypical and banded whisker forms, and biochemical analysis also showed that intermediate forms are present (Juinio *et al.*, 1991), the subspecific name *P. longipes femoristriga* is used for the banded whisker form.

The exact distribution and relative abundance of *P. longipes femoristriga* in the West and South Pacific is not fully understood because most of the previous reports on '*P. longipes*' and '*P. longipes femoristriga*' have not mentioned any of the distinguishing characters used in the present study to separate the white and banded whisker forms. Clear colour photographs of the present subspecies have been given by Utinomi (1967), Healy and Yaldwyn (1971), Miyake (1982), Friese (1984: 70), Hirata *et al.* (1988), Kamezaki *et al.* (1988) and Chan and Yu (1993). In Japan *P. longipes femoristriga* is very rare in the mainland but is the commonest spiny lobster in the Ryukyu Is. (Sekiguchi 1988; pers. comm.). In the Bonin Is. *P. longipes femoristriga* (referred as the 'Shirahige-ebi' in Sekiguchi, 1991) is not as common as the 'Aki-ebi' form. In Taiwan (Chan and Yu, 1993) and the Philippines (Juinio *et al.*, 1991) it is less common than *P. longipes longipes*. In the South Pacific only Australia (Healy and Yaldwyn, 1971) and Richer de Forges and Laboute (in press) from New Caledonia, have published photographs of *P. longipes femoristriga*. Nevertheless, the survey of George (1972) indicated that the present form probably also occurs in the Micronesia, the Papua New Guinea, the New Hebrides, Fiji, Tonga and the Cook Islands but nowhere is this species abundant and in some localities it is considered to be very rare.

Panulirus albiflagellum sp. nov.

(Figs 1c, 2c, 3c, 4c–d, 5c)

Panulirus longipes: George and Holthuis, 1965: 21 (part); George and Main, 1967: 812 (part); George, 1972: 25, 28; Mossa and Aswandy, 1984: 26 (part); Williams, 1986: 20 (part); Sekiguchi, 1988: 161, Figs 1–2 (part); Holthuis, 1991: 145, Fig. 278 (part); Chan and Yu, 1993: 140 (part). [non A. Milne Edwards, 1868]

Panulirus longipes femoristriga: George and Holthuis, 1965: Pl. 5a; George, 1972: 22; Phillips *et al.*, 1980: 67 (part); Holthuis, 1991: Fig. 277-left; Chan and Yu, 1993: 141 photo. [non von Martens, 1872]

Panulirus jenicillatus: Baensch and Debelius, 1992: 571 lower photo. [erroneous spelling and not *Panulirus penicillatus* (Olivier, 1791)]

Material examined. HOLOTYPE: **Taiwan**. Keelung, diving, 20 m, 14 September 1984, 1♂ 58.5 mm [NTOU H-1984-9-14].

PARATYPES: **Taiwan**. Pei-Kuan, I-Lan County, 22 November 1991, 1♂ 63.2 mm [NTOU P-1991-11-22]. Taitung County, 1990, 1♂ 49.6 mm [NTOU 1990]; December 1990, 1♂ 44.3 mm, 1♀ 43.9 mm [NTOU P-1990-12]; August 1991, 1♂ 42.8 mm [NTOU P-1991-8]; 26 October 1992, 1♂ 63.8 [NTOU P-1992-10-26]. **Indonesia** (imported to Hong Kong), 1991–1992, 10♂ 71.4–90.8 mm, 3 ovig. ♀ 75.3–84.6 mm, 2♀ 69.7–77.6 mm [NTOU P-1991-1992, one specimen donated to MNHN]. **West New Guinea**. Sorido, Biak Is., 4.2.1955, 1♀ 69 mm (specimen of Pl. 5a in George and Holthuis, 1965) [RMNH D17447].

Diagnosis. Anteromedian carapace between supraorbital horns and second anterior teeth generally bearing longitudinal row of three large spines only (rarely with one or two additional spinules). Antennular plate having 0–5 (mean 2.9) spinules above and two to five (mean 2.9) spinules below the two principal spines. Cervical groove distinctly wider than posterior marginal groove of carapace. Ventral surfaces of distal

two segments of antennular peduncle each only bearing a row of two equal sized large spines. Medial depression of thoracic sternum having two distinct knobs near middle, posterior fork generally separated from sternum. Abdominal tergite I completely lacking dorsal carina. Well-developed transverse grooves present on abdominal tergites II to VI and joining corresponding pleural grooves. Anterior margin of abdominal pleuron II bearing 0–3 spinules or tubercles.

Coloration. Body dark brown to indigo and covered with numerous white spots and markings. Eyes black brown. Cardiac area of carapace bearing large 'V'-shaped white marking and middle of cervical groove also having transverse white line. Lateral carapace having two longitudinal white stripes extending along entire carapace; anteriorly the two stripes starting above and below antennal peduncle but posteriorly both stripes joining together near posterolateral carapace. Antennular plate, stridulating pad and mesial surfaces of antennal peduncles pink. Posteromedian part of antennular plate also having large white triangular spot. Antennal flagella dorsally brown but ventrally whitish to pink. Antennular peduncles dark brown but laterally white; with outer flagella dark brown and inner flagella entirely whitish. Pereiopods striped with conspicuous white lines. Abdomen covered with numerous medium sized white spots and bearing pair of larger spots near hinges on each somite. Middle of depressed area on abdominal tergite I having short but broad white band. Non-calcified part of tailfan orange brown and with distal margin whitish. Pleopods somewhat greenish and white margined. Eggs orange.

Size. Largest male 90.8 mm cl and largest female 77.6 mm cl in the present study.

Distribution. Indo-West-Pacific and only known with certainties from Japan, Taiwan, Indonesia, West New Guinea, Vietnam and Maldives. Likely also occurs in the Solomon Is., New Hebrides and French Polynesia (see 'Remarks'). In shallow reef areas to about 20 m deep.

Type-locality. Taiwan

Remarks. Although the colour pattern of the abdomen is more or less the same, the coloration of the carapace and anterior appendages of the white whisker form is very different from that of the banded whisker form. The white 'V'-shaped mark on the posterodorsal carapace is considerably larger and the dorsal white stripe on the lateral carapace is extending posteriorly along the entire carapace instead of terminated at the cervical groove in the white whisker form. The most conspicuous difference is the colour of the antennules. Both the antennular peduncles and flagella of the banded whisker form are brown and alternated with many conspicuous white bands. In the present form, however, the antennular peduncles and the outer flagella are brown but the inner flagella are entirely whitish. Furthermore, the antennular plate and the mesial surfaces of the antennal peduncles (including the stridulating pads) are pinkish in the white whisker form. On the other hand, the mesial surfaces of the antennal peduncles and the antennular plate are mostly brown (or orange brown) and with the stridulating pads conspicuously bright blue in the banded whisker form.

Morphologically, the white whisker form shows several differences from the banded whisker form. The carapace is relatively less spiny in the former and with the area between the supraorbital horns and the 2nd anterior teeth usually only having a

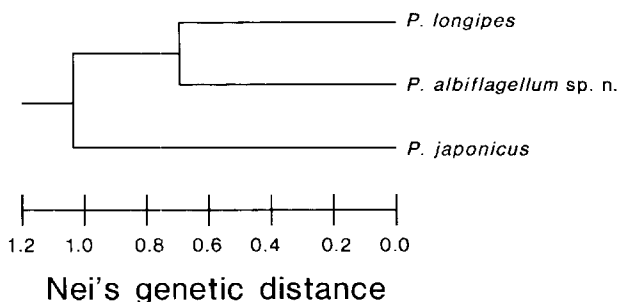


FIG. 6. Phenetic dendrogram of *Panulirus* species based upon UPGMA analysis of genetic distances given in Table 3.

longitudinal row of three large spines along the midline. Occasionally one (rarely two) additional spinule(s) may be present in front of the row or next to the posteriormost spine. In the banded whisker form, however, there are always five or more (as many as 10, and in *P. longipes longipes* 4–16, mostly about 7, Fig. 1a) spines and spinules present within the area between the supraorbital horns and the 2nd anterior teeth. The ventral surface of each of the distal two segments of the antennal peduncle in the white whisker form generally bears only a row of two equal sized large spines (those of the second segment were occasionally almost equal). Only in four of the 23 specimens examined there is one more or one less spine present in one side of either the distal or the 2nd segment of the antennal peduncle. On the other hand, the distal two segments of the antennal peduncle usually each bears one large ventral spine which sometimes accompanied by some other irregularly arranged spines and spinules in the banded whisker form as well as in *P. longipes longipes* (Fig. 2a, only five of the 79 specimens of these two subspecies examined have two ventral teeth on the 2nd segment). The cervical groove of the white whisker form is distinctly wider than the posterior marginal groove (Fig. 4a–c) and making the median white line along the cervical groove very prominent. Moreover, the present form always has the medial depression of the thoracic sternum bearing two distinct knobs near the middle (a slight protrusion is also present at the anterior one third of the thoracic sternum in some young specimens). In contrast, a well-developed spine or tooth is often present at the anterior one third of the medial depression of the thoracic sternum while the two submedian knobs, if present, are generally weak and lower than the anterior spine in the banded whisker form (in *P. longipes longipes* the medial depression of thoracic sternum is generally smooth).

Although the above differences are slight, they are rather constant and can be used to separate the white whisker and banded whisker forms very well even for preserved colourless specimens. Data from allozyme analysis (see later) also shows that the white whisker form is genetically distinct from *P. longipes* (Table 3, Fig. 6). Thus, the white whisker form should warrant a distinct specific status. Since the name *P. longipes femoristriga* is now fixed to the banded whisker form and Borradaile's (1899) *P. bispinosus* is also shown to represent the banded whisker form, no other suitable name is available for the white whisker form. A new name, *P. albiflagellum* sp. nov., is hence used for the present species.

Some authors (George and Holthuis, 1965; Juinio *et al.*, 1991; Holthuis, 1991) mentioned that intermediate coloration on the pereopods could be found in the overlapping areas between the spotted-legged and striped-legged forms. Careful comparisons of fresh specimens show that the white (or pale) stripes on the pereopods

are more often broken into short sections (sometimes somewhat circular) at the ending of each segment and on the ventral surfaces in the banded whisker form than in the white whisker form. The intermediate form referred by the above authors likely represents these broken white stripes of the banded whisker form, e.g. no white whisker form has yet been found in the Philippine waters (Junio, personal communication).

Similar to *P. longipes femoristriga*, the exact distribution of *P. albiflagellum* is not clear. Nevertheless, it is interesting that the present species is also found in the Indian Ocean (from the photograph of a Maldive specimen in Baensh and Debelius, 1992). Moreover, clear colour illustrations of this form from west New Guinea (George and Holthuis, 1965) and Taiwan (Chan and Yu, 1993) have been provided. Some colour photographs of the spiny lobsters from Sulawesi (= Celebes), Indonesia and Vietnam also show the present white whisker form. Dr H. Sekiguchi kindly informed us that one *P. albiflagellum* specimen has been found from the southern tip of the Ryukyu chain islands and this species likely also occurs in mainland Japan (but very rare). The '*P. longipes femoristriga*' without cross-banded flagella reported from the Bonin Is. by Sekiguchi (1991, referred as 'Aka-ebi') has a coloration almost identical to that of *P. longipes femoristriga s. str.* and only differs in both the outer and inner antennular flagella being entirely brownish. Therefore, the coloration of 'Aki-ebi' differs considerably from that of *P. albiflagellum*. More careful comparisons will be necessary to ascertain the exact identity of the 'Aki-ebi'. On the other hand, the '*P. longipes*' and '*P. longipes femoristriga*' without cross-bands on the antennular flagella reported by George (1972) from the Solomon Is., New Hebrides (those from Malekula and west coast of Espiritu Santo) and French Polynesia have the colour of the anterior carapace and the feelers very similar to those of the present species. Nevertheless, their exact identities also need to be verified.

Etymology. The latin *albiflagellum* refers to the white inner antennular flagella of this lobster.

Genetic analysis

Results. A total of 10 loci could be scored consistently in the lobsters studied (Table 1). All staining activities were observed in the anodal area. Allelic frequencies of the loci are listed in Table 2. Three loci (*6Pgdh*, *Ldh*, *Pgm*) were monomorphic in all specimens. *Panulirus japonicus* shared one additional fixed allele in the locus *Xdh* with *P. longipes*, but no more fixed alleles with *P. albiflagellum*. In the loci *Aat* and *Idh*, *P. longipes* and *P. albiflagellum* shared the same fixed alleles as distinct from the ones in *P. japonicus*. In the loci *Ald*, *Gapdh*, *Gpi* and *Me*, the fixed alleles in each species were different from one another. The only polymorphic locus was *Gpi*, detected in *P. japonicus*, and the observed phenotypic frequencies did not depart from Hardy-Weinberg equilibrium distribution ($P > 0.05$, chi-square goodness of fit). The proportion of polymorphic loci ($P_{0.95}$) is thus 0.1 for this species and 0 of the other two. The average expected heterozygosity values of *P. japonicus* is 0.045.

The estimates of genetic identity, *I*, and genetic distance, *D*, between the species are presented in Table 3. The highest *I* value of 0.500 was found between *P. longipes* and *P. albiflagellum*. Accordingly, the phenetic dendrogram of the lobsters (Fig. 6) showed that the two species are more closely related to one another than either is to *P. japonicus*.

Table 2. Allelic frequencies for 10 loci in species of *Panulirus*. N = number of individuals; H_o = observed heterozygosity. Proportion of polymorphic loci and average heterozygosity of individual species were given at the bottom of the table.

Locus	Allele	<i>P. longipes</i>	<i>P. albiflagellum</i> sp. n.	<i>P. japonicus</i>
<i>Aat</i>	N	15	15	19
	140	0.00	0.00	1.00
	100	1.00	1.00	0.00
<i>Ald</i>	N	11	10	18
	120	0.00	1.00	0.00
	100	1.00	0.00	0.00
<i>Gapdh</i>	N	14	15	19
	125	0.00	1.00	0.00
	100	1.00	0.00	0.00
<i>6Gpdh</i>	N	13	15	19
	100	1.00	1.00	1.00
	N	15	15	19
<i>Gpi</i>	114	0.00	1.00	0.00
	100	1.00	0.00	0.00
	57	0.00	0.00	0.66
	31	0.00	0.00	0.34
	H_o	0.00	0.00	0.37
<i>Idh</i>	N	13	15	19
	114	0.00	0.00	1.00
	100	1.00	1.00	0.00
<i>Ldh</i>	N	14	15	19
	100	1.00	1.00	1.00
<i>Me</i>	N	14	14	19
	100	1.00	0.00	0.00
	94	0.00	0.00	1.00
	90	0.00	1.00	0.00
<i>Pgm</i>	N	14	15	19
	100	1.00	1.00	1.00
<i>Xdh</i>	N	15	15	19
	100	1.00	0.00	1.00
	90	0.00	1.00	0.00

Table 3. Nei's genetic distance, D (below diagonal), and genetic identity, I (above diagonal) of *Panulirus* species. Calculation followed Nei's correction (1978) for small size.

	<i>P. longipes</i>	<i>P. albiflagellum</i> sp. n.	<i>P. japonicus</i>
<i>P. longipes</i>		0.500	0.409
<i>P. albiflagellum</i> sp. n.	0.693		0.307
<i>P. japonicus</i>	0.893	1.180	

Discussion. Nelson and Hedgecock (1980) reported the proportion of polymorphic loci ($P_{0.95}$) in *Panulirus interruptus* (Randall, 1840) and *Panulirus cygnus* George, 1962 to be 0.143 and 0.172 respectively. The corresponding values for average heterozygosity (H) are 0.039 and 0.066. Shaklee and Samollow (1984) reported $P_{0.99}$ and H in *Panulirus marginatus* (Quoy and Gaimard, 1825) to be 0.152 and 0.021 respectively. These values are not very different to those reported for *P. japonicus* ($P_{0.95} = 0.1$; $H = 0.045$). The only polymorphic locus, glucose phosphate isomerase is frequently variable in decapod crustaceans (Shaklee and Samollow, 1984). Apparently, the lack of genetic diversity found in *P. longipes* and *P. albiflagellum* can at least partially be attributed to the small number of loci and animals sampled. Yet low genetic diversity appears to be a phenomenon common to decapod crustaceans (Redfield *et al.*, 1980; Hedgecock *et al.*, 1982; Busack, 1988; Chu *et al.*, 1990, Tam and Chu, 1993). The absence of polymorphic loci has been reported in populations of some species (Gooch, 1977; Nelson and Hedgecock, 1980; Attard and Vianet, 1985) and low heterozygosity of < 0.05 was documented in many studies (Hedgecock *et al.*, 1982 and Tam and Chu, 1993 for reviews).

Panulirus albiflagellum have five (*Ald*, *Gapdh*, *Gpi*, *Me* and *Xdh*) loci studied which display fixed alleles different from those of *P. longipes*, i.e., 50% of the loci studied are diagnostic between these two forms. Therefore the two forms are genetically distinct. Based on a survey of Nie's genetic identity (1978) of a wide variety of organisms (I), Thorpe (1982) suggested that allopatric populations which have I values below 0.85 probably represent separate species (see also Thorpe and Sole-Cava, 1984). The I value of 0.50 between *P. longipes* and *P. albiflagellum* which also falls within the range of 0.36–0.92 (mean = 0.66) reported for congeneric species of decapod crustaceans (Hedgecock *et al.*, 1982), thus indicated that the two forms are distinct species. Stewart (1993) suggested in amphipods that pairs of populations with I values above 0.85 probably represent intraspecific populations, whereas pairs of populations below about 0.45 probably represent different species, and if I values fall between 0.45 and 0.85, additional taxonomic factors should be considered. If this suggestion can be applied to decapods, the I values of 0.50 between *P. longipes* and *P. albiflagellum*, together with their concordant morphological differences documented, would support their status as separate species.

The phenetic diagram (Fig. 6) shows that *P. longipes* and *P. albiflagellum* are more closely related with each other than they are with *P. japonicus*. An average Nei's genetic distance (D) value of 0.92 between the three species of *Panulirus* gives an estimate of the time of divergence (Nei, 1978), $t = 4.6 \times 10^6$ years, suggesting that speciation of *Panulirus* has occurred during that late Pliocene, instead of Pleistocene as suggested by George and Main (1967). This result has to be accepted with caution as estimates of divergence time has very large errors and no other D values from *Panulirus* are available. Menzies *et al.* (1979) studied the genetic relatedness of three *Panulirus* species from the west Atlantic but the genetic distance values were not presented. To clarify the phylogeny of *Panulirus*, the genetic polymorphism of more species has to be examined.

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