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NEW COLLECTIONS OF *CILIOPAGURUS* FROM FRENCH POLYNESIA, WITH THE DESCRIPTION OF A NEW SPECIES FROM THE MARQUESAS ISLANDS (CRUSTACEA: DECAPODA: ANOMURA: DIOGENIDAE)

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ABSTRACT. – The present paper reports on the collections of hermit crabs of the genus *Ciliopagurus* from French Polynesia, most of which were collected during the MUSORSTOM 9 cruise in the Marquesas Islands between August and September 1997. These include *Ciliopagurus vakovako*, new species, *C. strigatus* (Herbst, 1804), and *C. krempfi* (Forest, 1952). In its gross morphology *C. vakovako* is most similar to *C. strigatus*, widespread in the Indo-West Pacific, and *C. tricolor* Forest, 1995, restricted to the western Indian Ocean, a species formerly confused with *C. strigatus*. In its coloration, *C. vakovako* is closest to *C. liui* Forest, 1995, known from the Gulf of Tonkin (Vietnam) and southern Japan, and to *C. krempfi*, common in the Indo-West Pacific. Affinities among these species are discussed.

KEY WORDS. – Diogenidae, *Ciliopagurus*, Systematic, Sibling species; Marquesas.

INTRODUCTION

During the Marquesas MUSORSTOM 9 cruise, August 18th to September 11th, 1997, several hermit crabs of the genus *Ciliopagurus* were collected using dredges or when diving around Islands. The most interesting specimen was collected by myself while snorkeling along the seashore of Eiao Island. Its walking legs were banded red and white, and it was preliminary attributed to the similarly colored *Ciliopagurus strigatus* (Herbst, 1804), a species widespread in the Indo-West Pacific and already reported from French Polynesia (Forest, 1995; Poupin, 1996). Later, when sorting color slides of the species collected during the cruise, it became apparent that the coloration of the Eiao specimen was in fact slightly different from that of typical *C. strigatus*. This observation suggested that it might in fact belong to a new species. To establish this, more specimens were examined in the collections of the Muséum national d'Histoire naturelle, Paris, where the crustacean material of the cruise is deposited. Fortunately, several other specimens with a similar coloration to the Eiao specimen were found. Four had been collected while diving at Nuku Hiva; two had been dredged around Ua Pou, at a depth of 53 to 57 m, and eight had been collected at Ua Huka, between the seashore and 34 m. The diagnostic coloration of these specimens, as well as some subtle morphological differences, confirm that they belonged to a new species. The species is here described and named *Ciliopagurus vakovako*, new species.

Additional specimens of *Ciliopagurus* also included in this work were dredged between 75 to 252 m, during the same cruise, and all belong to *Ciliopagurus krempfi* (Forest, 1952). In order to be compared with the new species, several specimens of *Ciliopagurus strigatus*, collected in French Polynesia and deposited in Paris, are also included in this work.

MATERIAL AND METHODS

Shield length, from the tip of rostrum to posterior edge of the shield, is used as standard measurement for all specimens. As the arrangement of striae on the outer faces of the chelae is useful to separate the species, the following convention has been adopted (Fig. 3): stria n°1 is the first main stria behind the articulation of the movable fingers and subsequent striae are numbered from n°2 to n°4. Most of the station numbers mentioned in the 'Material examined' section refer to the MUSORSTOM 9 cruise. A report of that cruise with full list of stations, including those of a stay at Ua Huka (September 16th - October 19th, 1997), is given in Richer de Forges et al. (1999). Few stations refer to the cruises of the fishing research vessel *Marara*, between 1986 and 1996. A full list of *Marara* stations is given in Poupin (1996). All

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these specimens are deposited in the collections of the Muséum national d'Histoire naturelle, Paris. The shells were determined by R. Von Cosel and J. Tröndlé of the museum. The following abbreviations are used throughout the manuscript: coll., collector of specimens examined; CP, beam trawl; D, dredge; DW, Waren dredge; Frv, Fishing research vessel; IRD, Institut de Recherche pour le Développement (formerly ORSTOM); MNHN, Muséum national d'Histoire naturelle, Paris; MS, Natur-Museum Senckenberg, Frankfurt-am-Main; P2, P3, second pereopod, third pereopod; stn, station; WAM, Western Australian Museum, Perth; and ZRC, Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore.

TAXONOMY

FAMILY DIOGENIDAE ORTMANN, 1892

Ciliopagurus vakovako, new species
(Figs. 1a, 2a-d, 3b, 4)

Ciliopagurus krempfi - Forest, 1995: 59 (in part, only specimens from Marquesas). [Not *Ciliopagurus krempfi* (Forest, 1952)].
Ciliopagurus strigatus - Forest, 1995: 50 (in part, only specimens from Marquesas). [Not *Ciliopagurus strigatus* (Herbst, 1804)].

Material examined. – Marquesas Islands, 19 specimens (from MUSORSTOM 9 cruise if not stated). Holotype – male (4.3 mm) (MNHN Pg 5896), Eiao Island, coll. J. Poupin, snorkeling 1-2 m, 7 Sep. 1997.

Paratypes – 3 males (3.4-6.2 mm), 1 female (2.8 mm) (MNHN Pg 5897), Nuku Hiva Island, Anao bay, coll. P. Laboute, scuba diving at night, 21 Sep.1997; 2 females (1.6, 7.3 mm) (MNHN Pg 5898), Ua Huka Island, Teuahia bay, coll. R. Von Cosel, J. Tardy & J. Tröndlé, stn 25, 8°55.7'S, 139°36.7'W, dredge 6-15 m, 16 Sep.-19 Oct.1997; 1 female (3.7 mm) (WAM), Ua Huka Island, Hane bay, coll. Von Cosel et al., stn 29, 8°55.7'S, 139°32.0'W, dredge, 7-11 m, 16 Sep.-19 Oct.1997; 2 males (1.2, 1.9 mm), 2 females (2.3, 3.8 mm), 1 additional specimen in shell (ZRC), Ua Huka Island, Haavei bay, Tenoni point, 'île aux Oiseaux' (Teuaua islet), coll. Von Cosel et al., stn. 34, ca. 8°56.8'S, 139°35.7'W, dredge 10-15 m, 16 Sep.-19 Oct.1997; 2 males (3.2, 3.5 mm) (MNHN Pg 5901), Ua Pou Island, stn CP1264, 9°21.3'S, 140°07.7'W, 53-57 m, 3 Sep.1997.

Others – 1 male (5.3 mm), 1 female (5.5 mm) (WAM C 25048), Nuku Hiva Island, Marquesas Expedition, stn STA-NH-III, west side of Taiohae Bay, 1-3 m, 16 Sep.1967; 2 females (1.4, 2.3 mm) (MNHN Pg 5439), Tahuata Island, Frv Marara, stn D47, 9°54.3'S, 139°06.5'W, dredge 48 m, 31 Aug.1990.

Etymology. – The species name is derived from the Marquesan '*vakovako*' for striped, alluding to the transverse rings on the legs. The name is used as a noun in apposition.

Diagnosis. – Ocular peduncles 0.70 as long as shield. Ocular acicles with 4 terminal spines. Chelipeds similar; merus without prominent tubercle on ventral surface; outer face of chela with 3 complete transverse striae, and 1 additional less regular, proximal stria; striae smooth or with minute spines, but not tuberculated. Two posterior lobes of telson subequal, each with 2-4 minute spines on terminal margins. Coloration: ocular, antennular, and antennal peduncles reddish-orange; chelipeds and ambulatory legs with bright red rings alternated with narrower yellow rings; red rings absent on fixed and movable fingers of chelae and on dactyls of ambulatory legs; propodi of ambulatory legs yellow along distal margins, each with 6 main red rings; abdomen red with a pattern of undulating yellow lines.

Description. – Shield approximately as long as wide. Rostrum rounded, slightly overreaching level of obtusely triangular lateral projections; anterior margins between rostrum and lateral projections somewhat concave; anterolateral margins strongly convex.

Ocular peduncles 0.60-0.77 times as long as shield (average 0.70), slightly constricted medially, occasionally right longer than left. Cornea little if at all dilated, diameter included 3.62-5.72 times in length of ocular peduncles (average 4.61). Ocular acicles well developed, subtriangular, distally truncated, armed with 3-5 terminal spines (mode 4). Antennular peduncle reaching to distal one-third of ocular peduncle. Ultimate segment 0.21-0.31 times as long as shield. Antennal peduncle slightly shorter than antennular peduncle, reaching between middle and distal one-third of ocular peduncle. Fifth segment unarmed. Fourth segment with dorsodistal spine, sometime with additional smaller spine. Third segment with strong spine at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in bifid spine, sometimes with additional strong spine on dorsolateral surface. First segment unarmed. Antennal acicle long, reaching well beyond proximal margin of ultimate peduncular segment, with strong terminal spine, and 2 rows of 2-4 spines on dorsolateral and dorsomesial margins, obscured by tufts of long setae. Antennal flagellum overreaching outstrectched chelipeds.

Chelipeds equal, distal margins of carpi almost reaching distal margins of corneae. Chela 0.77-0.94 times as long as shield, 1.02-1.67 times as long as wide. Cutting edges of dactyl and fixed finger with few large calcareous teeth. Dactyl 0.44-0.63 as long as chela; outer face with 3-4 transverse striae each bearing stiff setae and minute corneous spinules. Fixed finger usually with 2 similar transverse striae. Outer face of palm with several transverse striae set with stiff setae (Figs. 2c, 3b). When chela fully extended, following striae are observed: 3 main transverse striae (n°1, 2, 3, on Fig. 3b), 1 additional proximal striae, irregular and fragmented (n°4 on Fig. 3b), and some intermediate shorter striae (Fig. 3b). An extra stria, hidden behind anterior margin of carpus, is noticeable only when chela bent. Dorsomesial surface of palm with stridulating apparatus in distal half including 4 main areas composed of parallel corneous crests (Fig. 2b). Largest distal area with 8-11 crests oriented obliquely to longitudinal axis of palm, distally rounded or occasionally acute; dorsal crest often reduced to denticle, length of crests increasing subsequently to the 6th-8th crest, longest being about 0.5 length of this stridulating area. Second area with only 3-4 short crests near dorsal margin of palm. Third and fourth areas as long as first area but with much shorter crests: third area with 8-10 crests, dorsally

reduced to thorny tubercles; fourth area with 8-9 short crests, some of them reduced to granules. A fifth area sometimes distinct but limited to few corneous denticles. Carpus slightly shorter than palm, with striae set with stiff setae. Outer face with 2 main striae behind distal margin and 1 additional incomplete stria on proximodorsal area. Merus usually with 2 complete striae on outer face behind distal margin and 4-6 additional posterior striae which are somewhat fragmentary; ventral area depressed, without prominent tubercle; ventromesial margin with 2-3 distal spines.

Ambulatory legs similar from left to right, over-reaching outstretched chelipeds by length of dactyls. Relative length of segments and arrangement of striae, setae, and spines similar between second and third pereopods. Dactyl 0.90-1.16 times as long as propodus, with strong terminal claw; ventral margin with 7-10 corneous spines (mode 9), decreasing in size posteriorly, obscured by tufts of long setae; outer face with 7-9 transverse striae (mode 7), some medially interrupted; dorsal margin with pattern of imbricated scales set with setae. Propodus 0.74-0.96 times as long as shield, with 6-7 complete transverse striae and some additional shorter striae; distal margin and striae set with stiff setae, much longer near ventral margin. Carpus 0.48-0.65 times as long as propodus, with 4 main complete striae and few additional shorter striae, all set with short setae; distal margin with setae that are remarkably long near distolateral angle. Merus 0.84-1.01 times as long as propodus, with 5-7 complete transverse striae and few shorter striae; outer face convex, inner face flattened, dorsal margin with a sharp corner; setae much longer near dorsal and ventral margins.

Fourth pereopod semichelate; dactyl with long setae on dorsal margin; propodus with broad rasp composed of many rows of corneous scales, dorsodistal margin with long setae; carpus with acute dorsodistal spine and long setae on dorsal margin; merus with few squamous striae on outer face, dorsal and ventral margins with long setae. Fifth pereopod chelate; merus with few squamous striae on outer face.

Abdomen with four unpaired biramous pleopods, on left side in both sexes. First pleopod shortest, other 3 subequal in length. Sixth abdominal tergite with longitudinal median furrow, weakly marked on anterior lobe, forming deep depression on posterior lobe; transverse median furrow anteriorly bordered by setae.

Telson with distinct lateral indentations. Posterior lobes subequal to moderately asymmetrical, terminal margins with long setae at external angles. Left lobe rounded, only slightly longer than right, lateral margin unarmed, terminal margin with 2-4 spinules (sometimes missing or indistinct); right lobe rounded, terminal margin armed with 2-4 spinules.

Color in life (Fig. 1a). – Distal half of shield and rostrum cream; proximal half of shield and posterior carapace cream with mottling of light orange. Ocular peduncles and ocular acicles reddish-orange. Antennular and antennal peduncles reddish-orange, flagella cream coloured.

Chelipeds and ambulatory legs banded with pattern of bright red rings, each ring associated with a setiferous stria; surfaces situated beneath the setae light yellow. This arrangement gives a pattern of alternating narrow yellow and large red rings. Chelipeds with red rings on palms, carpi and meri, but not on fixed and movable fingers. Palms each with 4-5 main red rings (Fig. 2c). Carpi each with 3 main red rings. Meri each with 3 main distal red rings and 3-4 irregular proximal rings.

Second and third pereopods almost similarly colored, with red rings on propodi, carpi and meri, but not on dactyls. Propodi each with yellow distal area, 6 main red rings, a 7th narrower red ring (almost reduced to a simple line), and a yellow proximal area; the 6 main rings are often divided by intermediate incomplete striae, chiefly on dorsal margin where up to 8-10 red bands can be counted. Carpi each with 4 main red rings and a 5th narrower proximal ring. Meri each with 7-8 (on P2) or 6-7 (on P3) main rings.

Fourth and fifth pereopods with red specks on meri. Abdomen red, striped with undulating transverse yellow lines, almost parallel.

It has been shown that none of the *C. strigatus* illustrated in color from other Indo-Pacific localities (see references under *C. strigatus*) possess the characteristic coloration of *C. vakovako*.

Color in preservative (75%, ethanol). – After three years in preservative, ocular, antennular, and antennal peduncles, light orange. Red rings on chelipeds and ambulatory legs still clear, although the bright red has faded into reddish-orange. Coloration of shield, posterior carapace, and abdomen, has totally disappeared, these parts being white.

Shells. – This species was found to use narrow-mouthed shells: *Conus tessulatus* Born (Conidae) and *Oliva* sp. (Olividae).

Remarks. – In its coloration, *Ciliopagurus vakovako*, new species, is related to *C. liui* Forest, 1995, and to *C. krempfi* (Forest, 1952). The coloration of *C. liui*, as figured by Miyake (1982: Pl. 35, Fig. 2, left, as *Trizopagurus krempfi*), and *C. vakovako* are very similar. However, *C. liui* differs in having a few red rings on the proximal half of the dactyls of the ambulatory legs whereas this part is uniformly yellow in *C. vakovako*. The coloration of *C. krempfi* is also very close to that of *C. vakovako* (cf. Fig. 1a and 1c) but differs by the following points: a) coloration of ocular peduncle, yellowish-orange in *C. krempfi*, reddish-orange in *C. vakovako*; b) the propodi of ambulatory legs usually with five red rings in *C. krempfi*, instead of usually six in *C. vakovako*; and c) abdomen not colored in *C. krempfi*, red with yellow lines in *C. vakovako*. Despite similarities in coloration, *C. liui* and *C. krempfi* can easily be differentiated from *C. vakovako* by several morphological and ecological characteristics. The following morphological differences were observed: a) the ocular scale has a single terminal spine in *C. liui* and *C. krempfi* whereas in *C. vakovako* there are 3-5 terminal spines

(mode 4); b) the ocular peduncle is usually longer in *C. krempfi* and *C. liui* than in *C. vakovako*, its mean length being 0.85 times as long as shield in *C. krempfi* (range 0.73-0.94; calculated from material examined in this study), 0.86 in *C. liui* (a single specimen, in Forest, 1995), and only 0.70 (range 0.60-0.77) in *C. vakovako*; c) the dactyls of the ambulatory legs are slightly longer in *C. krempfi* and *C. liui*: the left P3 dactyl is usually 1.18 (range 0.84-1.46) times as long as the propodus in *C. krempfi*, 1.5 in *C. liui*, and only 1.07 (range 0.90-1.16) in *C. vakovako*. Furthermore, *C. krempfi* is a deeper water species, usually collected between 80-200 m, and it can use shells with large apertures such as *Tritonoranella* (see Miyake, 1982), *Ancillaria* (see Forest, 1952), or *Bursa*, *Chicoreus*, *Distorsio*, *Latiaxis*, and *Terebra* (this study) (*C. liui* has been described from only a single specimen collected at 53 m, without a shell). On the contrary, *C. vakovako* appears to be a mostly littoral species and it uses only shells with narrow apertures, such as *Conus* and *Oliva*.

On the basis of the morphology *C. vakovako* is much closer to *C. strigatus* (Herbst, 1804) and *C. tricolor* Forest, 1995. These three sibling species are all intertidal. Although easily differentiated by their distinct color patterns, the three species of this group are morphologically nearly indistinguishable without careful examination. Among the 17 species now included in the genus *Ciliopagurus*, these three species can be recognized at once by the ocular acicle possessing four or five terminal spines (against usually with only one or two terminal spines, occasionally three spines, in the remaining 14 species). Species of this group are also distinct in having: a) relatively short ocular peduncles, about 0.7 shield length;

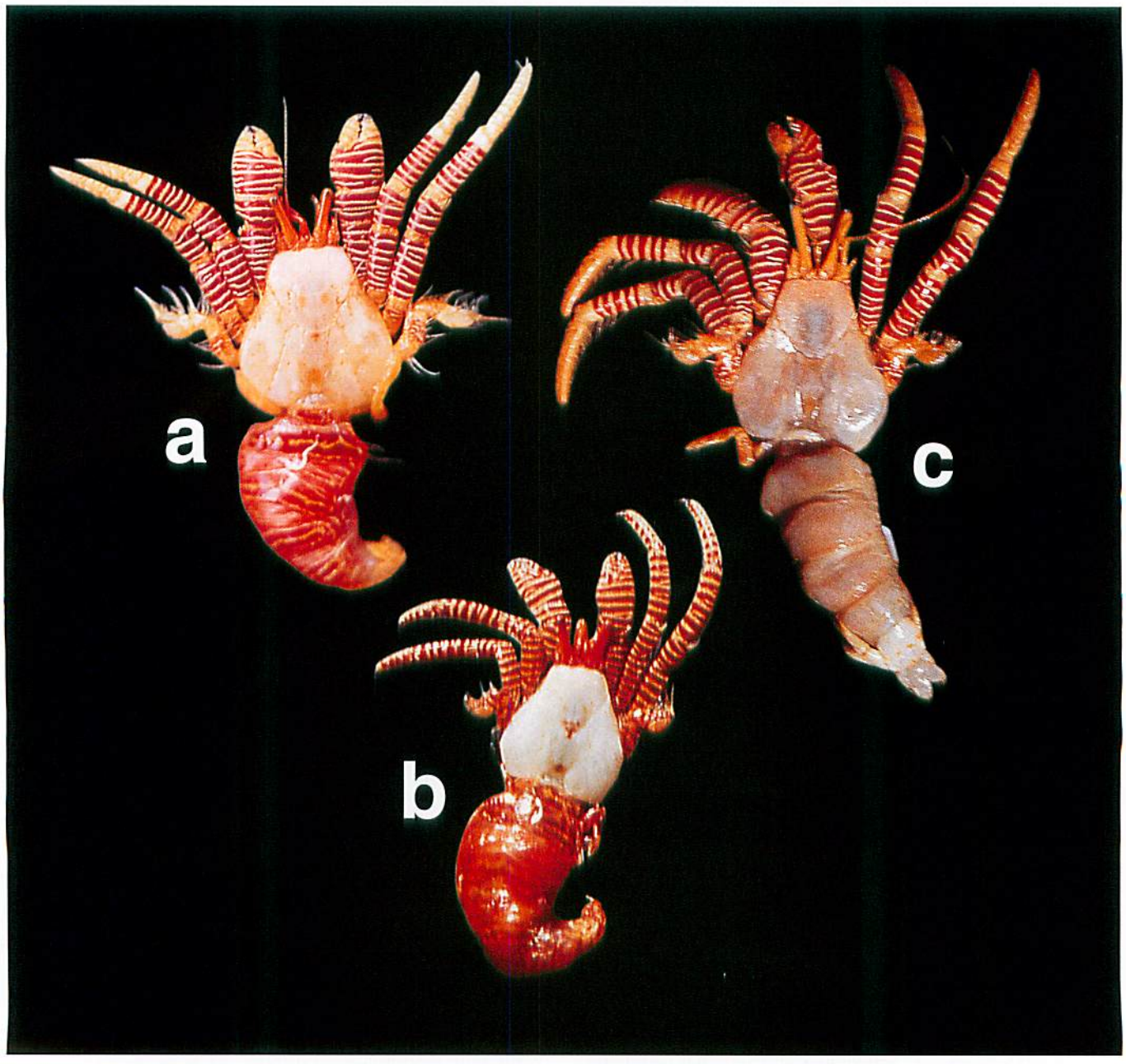

Fig. 1. Live colorations - a) *Ciliopagurus vakovako,* new species, holotype male, 4.3 mm (MNHN Pg 5896), Marquesas Islands, Eiao, 1-2 m deep; b) *C. strigatus* (Herbst, 1804), male, 2.8 mm (MNHN Pg 5919), Society Islands, Tahiti, seashore; c) *C. krempfi* (Forest, 1952), male 7.9 mm (MNHN Pg 5908), Marquesas Islands, Hiva Oa, 125-135 m.

b) relatively short distal segments of antennular peduncles, about 0.25 shield length; c) their use of narrow apertures shells (e.g. Conidae or Olividae), which results in having a more flattened cephalothorax; and d) living in the intertidal habitat, whereas all other *Ciliopagurus* species occur in deeper habitats: *C. vakovako* occurs from the intertidal zone to 53-57 m, *C. strigatus* is mostly intertidal (see below), and all known specimens of *C. tricolor* are intertidal, except for a single individual collected at 30 m.

When fresh specimens are considered, members of the 'intertidal group' are easily differentiated by their coloration. *Ciliopagurus vakovako* and *C. strigatus* are at once separated by coloration of fingers of chelae and dactyls of ambulatory legs. These parts are uniformly yellow without red rings in *C. vakovako*, whereas, in *C. strigatus* they show the same pattern of alternating red and yellow rings that ornament the remaining parts of chelipeds and ambulatory legs (cf. Figs. 1a, b). Additionally, the propodi of the ambulatory legs of *C. vakovako* have large yellow rings at the distal and proximal parts, while these extremities appear red in *C. strigatus*. The coloration of the ocular and antennular peduncles is also slightly different between the two species, reddish-orange in *C. vakovako*, dark red in *C. strigatus*. *Ciliopagurus vakovako* and *C. tricolor* are similarly colored in having light yellow or orange on the fingers of the chelae and dactyls of ambulatory legs, but the coloration of the remaining parts of these appendages is very different. In *C. vakovako*, there is a simple pattern of alternating red and yellow rings, while in *C. tricolor*, each 'ring' consists of a median blue ring plus two lateral red rings, these mixed rings being disposed on a light orange background.

In the case of preserved specimens which have lost their coloration, it is much more difficult to separate the three species. In most cases, *C. vakovako* and *C. strigatus* can be differentiated by the arrangement of striae on the outer face of chela. The two patterns are illustrated in Figs. 3a, b. The outer face of the chela has four main striae in *C. vakovako*, stria n°4 being less regular and interrupted near the ventral margin, but there are only three in *C. strigatus* (in both species, there is an additional proximal stria, hidden behind the anterior margin of the carpus and not noticeable when the chela is fully extended, see Fig. 3). This character was useful to determine the old discolored specimens examined in this study: two specimens collected during the 1967 Marquesas Expedition (WAM C 25048), attributed to *C. vakovako*; and six specimens collected between 1890 and 1982 in the Society Islands, attributed to *C. strigatus* (see below). This character, however, is size related and useless in the case of two small specimens collected during the 1990 Frv *Marara* cruise (MNHN Pg 5439). These two juveniles have lost all traces of their coloration and have only three main striae on the outer face of the chela and therefore could be assigned to *C. strigatus*. Nevertheless, they should belong to *C. vakovako* because Forest (1995), who examined their fresh coloration, referred them to *C. krempfi*, the closest species to *C. vakovako* in terms of the coloration. In addition, these two juvenile specimens cannot belong to *C. krempfi* because their ocular acicles are armed with three to four terminal spines, instead of only one in *C. krempfi*. On the basis of the structure of their ocular acicles and arrangement of the striae on the outer face of chela, they might perhaps be referable to *C. strigatus*, although this is unlikely as there are no clear records of this species from the Marquesas Islands.

Aside from the striation of the outer face of the chela, there are no significant differences between *C. vakovako* and *C. strigatus*. Certain characters used by Forest (1995) to separate *Ciliopagurus* species were ineffective here. For example, the following proportions were calculated in *C. vakovako* and *C. strigatus*, respectively (for *C. strigatus*, proportions are from Society Islands specimens examined below): relative length of ocular peduncle to length of shield 0.60-0.77 (average 0.70) versus 0.61-0.73 (average 0.68); relative length of fingers of chela to length of entire chela 0.44-0.63 (average 0.54) versus 0.48-0.61 (average 0.54); and relative length of dactyls to length of propodi of ambulatory legs 0.90-1.16 (average 1.07) versus 0.88-1.09 (average 1.03).

The distinction between *C. vakovako* and *C. tricolor*, which appears to be restricted to the western Indian Ocean, is even more difficult than between *C. vakovako* and *C. strigatus*. For comparison, several specimens of *C. tricolor* were examined (Madagascar, Tuléar: holotype ovigerous female, 6.9 mm, MNHN Pg 4663; female, 4.2 mm, MNHN Pg 5427; paratype male, 8.0 mm, MNHN Pg 3637, male, 4.9 mm, MNHN uncatalogued, coll. Thomassin. - Tanzania, two males, 6.5, 7.3 mm, MNHN Pg 5426. - Europa Island, male, 10.1 mm, MNHN Pg 620). Examination of the outer face of the chela shows that it is usually similar to *C. vakovako* with four main striae, the proximal stria (n°4 in Fig. 3b) being irregular and interrupted near the ventral margin as in *C. vakovako* (this pattern is illustrated by Forest, 1995: 57, Fig. 10b, for the holotype of *C. tricolor*). The two small differences observed are: a) the armature of the posterior margins of both lobes of the telson, usually unarmed in *C. tricolor* bearing at most 1-2 obscure spines, whereas these margins usually have 2-4 minutes spines in *C. vakovako*; and b) the proportions of the ocular peduncle, being slightly shorter and thinner in *C. tricolor*, its length to the length of shield being 0.57-0.69 (mean 0.62), versus 0.60-0.77 (mean 0.70) in *C. vakovako*, and the diameter of the cornea being included 4.48-6.36 (mean 5.17) in the length of the ocular peduncle versus 3.62-4.72 (mean 4.61) in *C. vakovako*. These differences are, however, not fully satisfactory because the two samples are of different sizes (mean shield length is 6.8 mm for *C. tricolor*, and only 3.6 mm for *C. vakovako*), which may account for the slight differences observed. The smaller size of ocular peduncle in *C. tricolor* could also be attributed to the shrinkage of this soft appendage which has been kept 10-30 years in preservative, instead of only three years for *C. vakovako*. For the hard appendages (chelipeds and ambulatory legs), the proportions are similar in the two sets of specimens. In fact, careful examination of the holotype of *C. vakovako* (4.3 mm) and a specimen of *C. tricolor* of almost the same size (a male 4.9 mm, Tuléar, coll. Thomassin, MNHN Pg uncatalogued) does not show any significant morphological differences, although their geographical

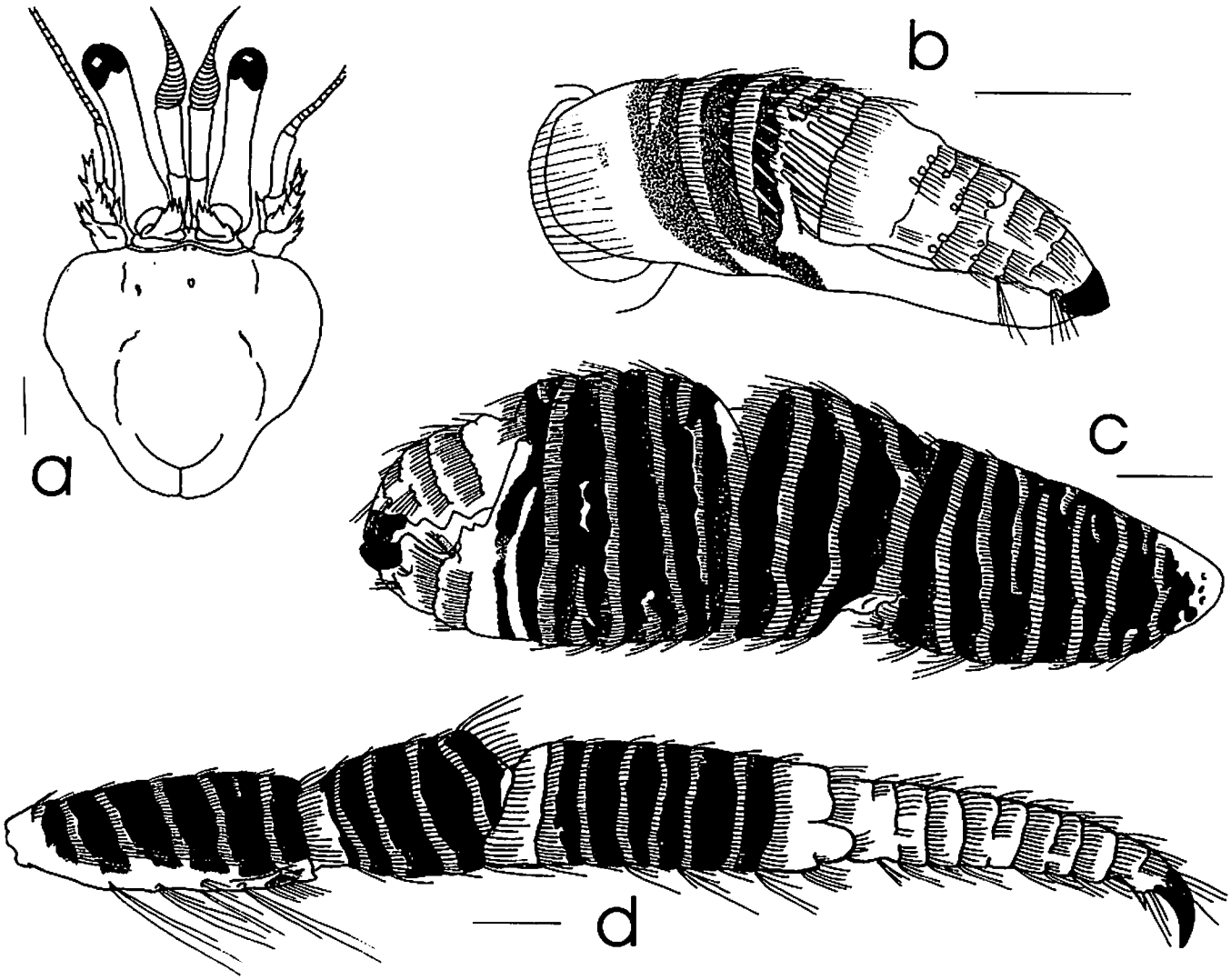

Fig. 2. *Ciliopagurus vakovako*, new species, holotype, male, 4.3 mm (MNHN Pg 5896): a) shield and cephalic appendages; b) left chela, dorsomesial face, arrangement of stridulating apparatus; c) left cheliped, outer face; d) left third pereopod, dorsomesial face. Scale bar = 1.0 mm.

Fig. 3. Pattern of striae on outer face of left chela: a) *Ciliopagurus strigatus*, male, 2.8 mm (MNHN Pg 5919), Tahiti; b) *C. vakovako*, new species, holotype, male, 4.3 mm (MNHN Pg 5896), Eiao. Setae omitted for clarity; note that, in both species, there is an additional proximal stria, hidden behind anterior margin of carpus and not noticeable when chela is fully extended.

distributions (Fig. 4) and color patterns are very distinct.

General Biology. – *Ciliopagurus vakovako* usually inhabits cone shells and occurs on coral grounds, from the intertidal zone to 53-57 m, but mainly between 10-20 m. Its distribution is presently restricted to the Marquesas Islands where it seems to be a vicariant of *C. strigatus*.

Ciliopagurus strigatus (Herbst, 1804)
(Figs. 1b, 3a, 4)

Trizopagurus strigatus - Allen & Steene, 1994: 151; Debelius & Baensch, 1994: 610; Tudge, 1995: 30; Takeda, 1994: 197; Yu & Fo, 1991: 57.

Ciliopagurus strigatus - Hoover, 1998: 252; McLaughlin, 1997: 221; Minemizu, 2000: 132. [Not *Ciliopagurus strigatus* - Forest, 1995: 50 (in part, only specimens from the Marquesas) = *C. vakovako* new species (see above)].

[Full synonymy is given by Forest (1995: 49); see also remarks below about Sakai (1999). References not included in Forest's (1995) synonymy but with color figures listed above].

Material examined. – 7 specimens, all from the Society Islands. Tahiti Island: 1 male, 2.8 mm (MNHN Pg 5919), Lafayette reef, seashore, coll. J. Poupin, 17 Oct.1996; 1 male, 5.3 mm (MNHN Pg 5920), ? Tahiti; 1 male, 5.9 mm (MNHN Pg 1745), Papeete reef, coll. abbé Cullieret, Aug.1890; 1 female, 5.3 mm (MNHN Pg 1746), 1 male, 5.5 mm, 1 female, 5.9 mm (MS 5013), Bredin Expedition, 8 May.1957; Moorea Island: 1 male, 4.1 mm (MNHN 5425), Tiahura reef, coll. M. Monteforte, 26 Jun.1982.

Diagnosis – Ocular peduncles 0.61-0.73 times as long as shield (average 0.68). Distal segment of antennular peduncle 0.21-0.24 times as long as shield (average 0.28). Ocular acicles with 3-4 terminal spines. Chelipeds equal; outer face of chela with 3 complete transverse striae, smooth or with minute spinules. Chela 0.70-1.03 times as long as shield (average 0.88); ratio of height to length 0.61-0.75 (average 0.68); fingers 0.48-0.61 times as long as chela (average 0.54). Main stridulating area with 9-11 parallel corneous crests, distally rounded or acute; 6th to 8th crest longest, 0.33-0.50 times as long as stridulating area. Merus of cheliped without prominent tubercle on ventral face. Dactyl of third ambulatory leg 0.88-1.09 times as long as propodus (average 1.03). Posterior lobes of telson subequal, unarmed or with 1-2 inconspicuous spines on terminal margins.

Coloration. – Antennular and antennal peduncles orangish-red; ocular peduncles red. Chelipeds and ambulatory legs with bright red rings, alternating with narrower yellow rings; red rings present on chelae (including fingers), dactyls, propodi, carpi and meri. Propodi of ambulatory legs each with a distal red ring along anterior margin and 5 subsequent rings (sometimes divided by yellow lines). Abdomen red with a pattern of undulating yellow lines, almost parallel (Fig. 1b).

Shells. – No shells on material examined. According to literature this species is typically found in shells of the Conidae.

Remarks. – The exact status of *Ciliopagurus strigatus* is unclear since Sakai (1999: 10) has stated that the holotype of *C. strigatus* in Herbst's collection in the Berlin Zoological Museum differs from specimens identified as this species by Forest (1995). According to Sakai (1999), a reappraisal of the identity of *C. strigatus* will be undertaken by J. Forest, and Indo-West Pacific species currently assigned to '*C. strigatus*' will receive a new name after this revision. This point, however, is beyond the scope of the present work and the status of *C. strigatus* is left here as it is usually admitted. In any case, it is clear from Sakai's (1999) figures and comments, and Herbst's original color plate that the real *C. strigatus* (sensu Herbst, 1804) is not conspecific with the present new species, *C. vakovako*.

Within the genus, *C. strigatus* is the oldest and the most often recorded species. Forest (1995) has shown that it is essentially a littoral species and that records of *C. strigatus* deeper than 60-90 m are in fact *C. krempfi*. He has also indicated that specimens from the southwestern Indian Ocean (Somalia, Mozambique, Madagascar) have a distinct color pattern and belong to a new species, *C. tricolor* Forest, 1995. The discovery of *C. vakovako* new species is interesting. The distribution of these three species is shown on Fig. 4. According to the typical hypothesis that the East Indies is the center of evolutionary radiation (see for example Briggs, 1995), it can be speculated that *C. strigatus* is the parent species, and that *C. tricolor* and *C. vakovako* are two peripheral species that have arisen from vicariant events.

Abdominal coloration has rarely been reported for this species because it quickly vanishes in preservative and is no longer visible when preserved specimens are studied. A similar coloration is observed in *C. liui*, as illustrated by Miyake (1982: Pl. 35, Fig. 2, left, as *Trizopagurus krempfi*) and in *C. vakovako*, new species (cf. Fig. 1a). Other *Ciliopagurus* species with colored abdomens, but with different patterns are: *C. shebae* (Lewinsohn, 1969), *C. major* Forest, 1995, and *C. babai* Forest, 1995. Abdomens might also be colored in *C. carpati* (Forest, 1952), *C. alcocki* Forest, 1995 (cf. Forest, 1995: Fig. 42a) and *C. tricolor* Forest, 1995. Unfortunately, although this character might be helpful in recognizing the species, it is usually not recorded when hermit crabs are collected and many photographs illustrate them with the abdomens hidden in the shells.

General Biology. – Widely distributed in the Indo-West Pacific, from Red Sea, North Indian Ocean, Indonesia, North and East Australia, Vietnam, Philippines, Japan, to French Polynesia (Society Islands). It is mainly an intertidal species. In Indonesia, Haig & Ball (1988) indicate a usual depth range of 3-15 m; in southern Japan, Miyake (1982) indicates that most of the specimens are found shallower that 20-30 m; in Hawaii, Hoover (1998) states that the species occurs most frequently at depths of 6 m or more.

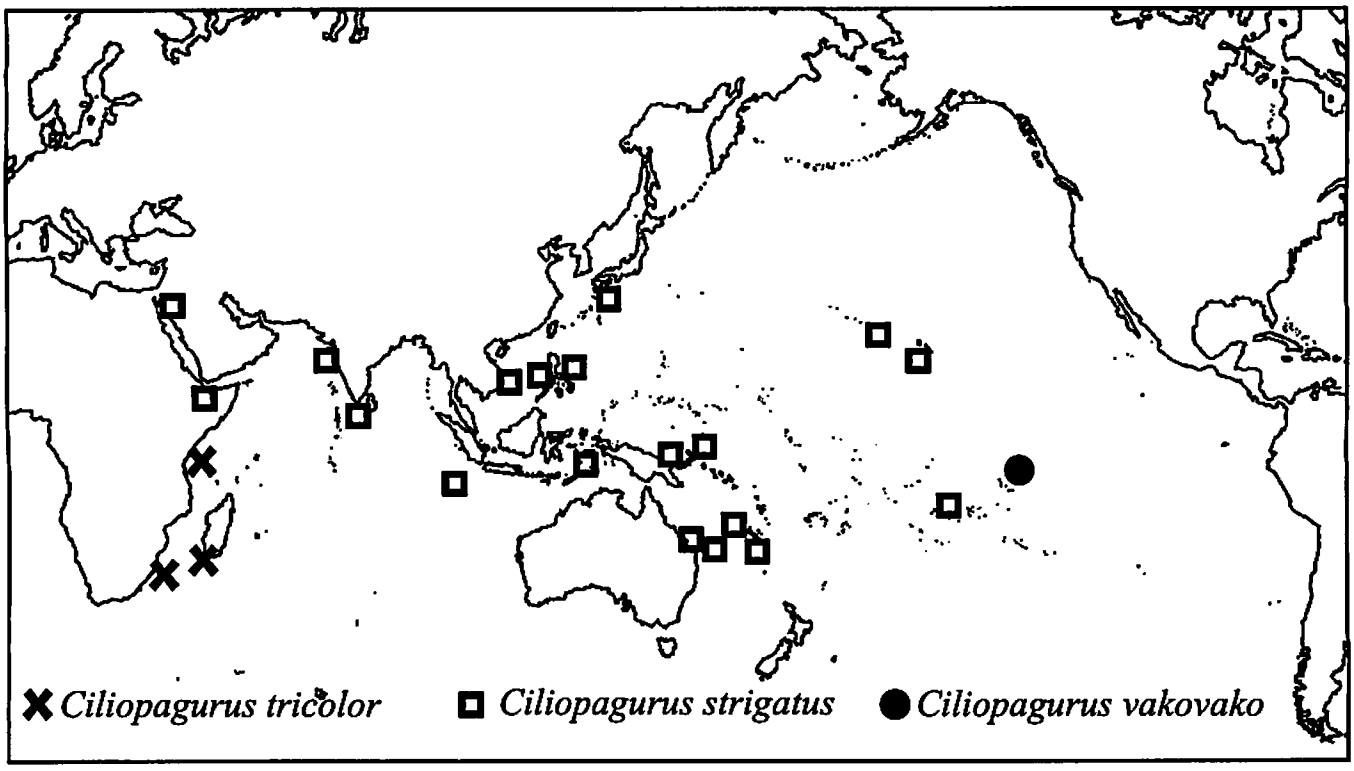

Fig. 4. Indo-West Pacific distribution for the intertidal *Ciliopagurus* species: *C. tricolor* Forest, 1995; *C. strigatus* (Herbst, 1804); *C. vakovako*, new species (adapted from Forest, 1995: Fig. 29).

Ciliopagurus krempfi (Forest, 1952)
(Fig. 1c)

Ciliopagurus krempfi - Minemizu, 2000: 132. [Not *Ciliopagurus krempfi* - Forest, 1995: 59 (in part, only specimens from the Marquesas) = *C. vakovako* new species (see above)].

[Full synonymy is given by Forest (1995: 59). Reference not included in Forest's (1995) synonymy and with color illustration indicated above].

Material examined. – Marquesas Islands, 17 adults specimens, all from MUSORSTOM 9 cruise. 2 males, 4.5, 5.7 mm (MNHN Pg 5910), Eiao Island, stn CP1159, 7°58.3'S, 140°43.7'W, 145 m, 23 Aug.1997; 1 male, 6.4 mm (ZRC), Eiao Island, stn DW1274, 7°54.6'S, 140°40.1'W, 100-120 m, 5 Sep.1997; 1 male, 5.1 mm, 1 juvenile (MNHN Pg 5916), Eiao Island, stn DW1154, 7°58.5'S, 140°43.7'W, 102 m, 23 Aug.1997; 3 males, 3.1-7.9 mm, 1 female, 5.3 mm, 1 ovigerous female, 4.5 mm, several additional juveniles (MNHN Pg 5908), Hiva Oa Island, stn DW1218, 9°44.5'S, 138°50.9'W, 125-135 m, 30 Aug.1997; 2 juveniles, 1 specimen in shell (MNHN Pg 5912), Hiva Oa Island, stn DW1224, 9°44.6'S, 138°51.1'W, 115-120 m, 30 Aug.1997; 3 juveniles (MNHN Pg 5914), Hiva Oa Island, stn DW1208, 9°48.9'S, 139°09.5'W, 117 m, 28 Aug.1997; 1 female, 2.9 mm (MNHN Pg 5909), Ua Huka Island, stn DW1288 (with a doubt), 8°53.9'S, 139°38.0'W, 200-220m, 8 Sep.1997; 1 male, 2.9 mm, 1 ovigerous female, 3.5 mm, several additional specimens, juveniles or in shells (MNHN Pg 5911), Nuku Hiva Island, stn DW1170, 8°45.1'S, 140°13.1'W, 104-109 m, 25 Aug.1997; 1 male, 3.1 mm, 1 female, 3.4 mm, 1 ovigerous female, 2.9 mm, several other small or broken specimens (MNHN Pg 5917), Nuku Hiva Island, stn DW1171, 8°44.9'S, 140°19.9'W, 248-252 m, 25 Aug.1997; 1 male, 4.0 mm, 1 juvenile (MNHN Pg 5918), Nuku Hiva Island, stn CP1178, 8°46.1'S, 140°14.5'W, 74-75 m, 25 Aug.1997; 1 male, 8.2 mm, 1 juvenile in shell (WAM), Fatu Hiva Island, stn DW1242, 10°28.1'S, 138°41.1'W, 119-122 m, 1 Sep.1977.

Diagnosis. – Ocular peduncles 0.73-0.94 times as long as shield (average 0.85). Diameter of cornea included 4.36-7.47 times in peduncular length (average 5.59). Distal segment of antennular peduncle 0.26-0.40 times as long as shield (average 0.33). Ocular acicles with single terminal spine (sometimes with 1-2 additional spinules). Chelipeds equal, with 4 main striae on outer faces of palms. Chela 0.82-1.12 times as long as shield (average 0.93) and 1.19-1.52 longer than wide (average 1.37); fingers 0.47-0.59 times as long as chela (average 0.54). Main stridulating area with 15 corneous crests, largest crest (6th to 8th), 0.4 times as long as main area. Merus of cheliped without distal tubercle on ventral face. Dactyl of third ambulatory leg 1.01-1.46 times as long as propodus (average 1.20; proportion only 0.86 for single unusual specimen, female 2.9 mm, MNHN Pg 5909). Posterior lobes of telson each armed with 0-4 small spines on terminal margin.

Coloration. – Ocular peduncles pale yellow. Shield and posterior carapace white. Chelipeds and ambulatory legs with a pattern of alternating red and yellow rings on palms of chelae, propodi, carpi, and meri. Red rings absent on fingers of chelae and dactyls of ambulatory legs, these parts being uniformly yellow. Propodi of ambulatory legs yellow on distal and proximal areas, each with 5 main red rings (sometimes divided by yellow lines). Abdomen white.

Shells. – This species has previously been found in shells with large apertures, such as *Tritonoranella* (Miyake, 1982) and *Ancillaria* (Forest, 1952) and in shells with narrower apertures such as *Conus*, *Mitra*, and *Cassis* (Japan, cf. Miyake, 1978, as *C. strigatus*). This is also the case in French Polynesia where *C. krempfi* uses both shells with narrow apertures (Conidae: *Conus quercinus* (Lightfoot), *C.*

moluccensis marielae Rehder & Wilson, *C. tessulatus* Born; and undetermined Cypraeidae), and shells with large apertures (Fasciolariidae: *Cyrtulus serotinus* Hinds; Muricidae: *Chicoreus thomasi* (Crosse), *Chicoreus* sp.; Personidae: *Distorsio* sp.; Coralliophillidae: *Latiaxis* sp.; undetermined Buccinidae; Bursidae: *Bursa* sp.; and Terebridae: *Terebra* sp.).

Remarks. – The apparent first record of this species in French Polynesia is from Forest (1995) who mentioned two juveniles trapped at Frv *Marara* stn D47 (Aug. 1990, Tahuata Island, 48 m). Reexamination of these specimens show that they actually belong to *C. vakovako*, new species. Despite this earlier confusion, the presence of *C. krempfi* around the Marquesas Islands is now confirmed by the specimens collected during the MUSORSTOM 9 campaign. The species was found in almost all the islands investigated, and therefore must be common in the archipelago. It is clearly not littoral, as it has been collected only between 74 to 252 m. In shallow waters, it seems to be replaced by the related *C. vakovako* (0-57 m), which has a similar coloration. However, around 60-70 m, it is to be expected that vertical distributions of these two species may overlap.

Affinities between *C. krempfi* and *C. vakovako* have already been discussed under *C. vakovako*. Their coloration patterns are similar (Figs. 1a, c), the most striking similarity being the absence of red rings on the fingers of the chelae and dactyls of the ambulatory legs. The two main differences are: a) number of red rings on propodi of ambulatory legs, usually five in *C. krempfi* versus six in *C. vakovako*; and b) abdomen coloration, white in *C. krempfi*, red with a pattern of yellow lines in *C. vakovako*. In the case of preserved specimens that have lost their coloration, the two species are easily separated by the form of the ocular scales: a single terminal spine is present in *C. krempfi*, versus three to five spines in *C. vakovako*. Moreover, in complement to differences already stated under *C. vakovako*, it has been observed that the outer face of the palm has four regular striae in *C. krempfi*, whereas only three striae are regular in *C. vakovako*, the proximal stria (stria n°4 on Fig. 3b) being irregular and interrupted near the ventral margin.

General Biology. – Large Indo-West Pacific distribution, East Indian Ocean, Kenya to south of Arabia, Réunion Island, South China Sea, Indonesia, Philippines, Japan, New Caledonia, and Marquesas (Eiao, Hiva Oa, Nuku Hiva, Ua Huka, and Fatu Hiva), mainly between 80-300 m. Records between 10-38 m (cf. Forest, 1995: 59) appear now questionable in the view of the deep distribution observed around the Marquesas Islands: a lot of specimens captured between 74-252 m, and absence of the species in shallower waters, despite several investigations at these depths.

DISCUSSION

With this work, six representatives of the genus *Ciliopagurus* are now reported from French Polynesia. Not surprisingly, the oldest record is *C. strigatus*, littoral and ubiquitous in the Indo-West Pacific. It was first recorded from Tahiti by Ortmann (1892), and later by Monteforte (1984, 1987). Three subsequent species are recorded in the revision of the genus *Trizopagurus* by Forest (1995), all deep water species trapped or dredged between 120-480 m during the Frv *Marara* cruises (Poupin, 1996): *C. major* Forest, 1995 (Tuamotu Islands, 240-280 m); *C. pacificus* Forest, 1995 (Austral and Tuamotu Islands, 120-480 m and possibly 800 m; also Marquesas Islands, 104-140m, pers. observ.); and *C. plessisi* Forest, 1995 (Tuamotu Islands, 160-240 m; also Austral Islands, 110 m, pers. observ.). Two additional species, *C. krempfi* (Forest, 1952) and *C. vakovako*, new species, are included in the present work. Only two of these six *Ciliopagurus* are still unrecorded outside French Polynesia. They are, *C. vakovako*, littoral and possibly endemic to the Marquesas Islands where it might represent a vicariant of *C. strigatus*, and the deep-water *C. plessisi* (110-240 m) that may well be found in other regions when more deep-water explorations are undertaken.

Among the 17 species now included in the genus *Ciliopagurus*, *C. strigatus* was for a long time considered as the only intertidal species. New collections in the Indo-West Pacific with more attention paid to color patterns, have revealed the existence of two other sibling species that were previously confused with *C. strigatus*: *C. tricolor* Forest, 1995, from the southwestern Indian Ocean, and *C. vakovako*, a new species described here from the Marquesas archipelago. These three intertidal species cannot always be confidently separated on the basis of morphology and can be best recognized by color differences. This trait is mostly lost with preservation, thus explaining the previous confusions in the literature. Such sibling species, although they are a source of debate among taxonomists about their validity, are nevertheless increasingly recognized in the Decapoda (Knowlton, 1986, 1993). Other examples of species mainly separated by the use of color pattern have also been given by Castro (1996) for brachyuran crabs (*Trapezia*), and Poupin (1997) and Poupin & McLaughlin (1998) for hermit crabs (*Calcinus*). In this last genus, the pair *Calcinus elegans* (H. Milne Edwards, 1836)/*C. orchidae* Poupin, 1997, is very similar to *Cilopagurus strigatus*/*C. vakovako* which are studied here. In both pairs, the first species is widespread across the Indo-West Pacific, while the second occurs allopatrically in the Marquesas Islands and, in both cases, is mainly distinguished by the color pattern. The geographical isolation of the two color morphs reinforces the existence of separate species as well as it distinguishes the Marquesas Islands as a separate area within French Polynesia and Indo-West Pacific. These results underscore the critical importance of color in alpha-taxonomy.

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