Descriptions of new species of Pacific *Cystiscus* Stimpson, 1865 (Gastropoda : Cystiscidae) Part 1: species with banded mantle patterns

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ABSTRACT. Eleven vividly coloured new species of banded Cystiscus are described from shallow subtidal habitats of the Pacific Ocean island groups of French Polynesia (Tuamotu's & Society Islands), Tonga, Fiji, Vanuatu, New Caledonia, and also Northeastern Australia (The Great Barrier Reef). The new species are: Cystiscus garretti n. sp., from French Polynesia and the Great Barrier Reef, C. vavauensis n. sp. and C. deeae n. sp. from Tonga, C. vitiensis n. sp., C. beqae n. sp., C. maloloensis n. sp., C. yasawaensis n. sp., and C. pusillus n. sp. from Fiji, C. maskelynensis n. sp. and C. havannensis n. sp. from Vanuatu, and C. matoensis n. sp. from New Caledonia. A possible new record of C. tricinctus Boyer, 2003, as C. cf. C. tricinctus, from the Loyalty Islands is also presented. The mantle roof of each species is shown to display different colours arranged in a banded pattern, which is made visible due to shell transparency. All of the new species are presented with reference to photographs of series of the living animals and their shells in order to demonstrate variability of shell morphology and mantle colour pattern within populations. Images of radulae are also included where their morphology has proved distinctive enough to assist with species separation. Species delimitations are based upon detailed analysis of differences in shell characters (in particular the morphology of the columella), the pattern of the mantle roof (in particular the colour, number, position and relative width of bands) and features of the radula.

INTRODUCTION. During 2000 and 2003 the second author made two transits of the Pacific Ocean on s/y 'Marina Em', from the Panama Canal to New Zealand and back again, visiting many isolated island localities en route, and during 2001 and 2002 seasonal visits were made to the island groups north of New Zealand. These included French Polynesia (Tuamotu's and Society Islands), several of the Cook Islands, American and Western Samoa, Tonga, Fiji, Vanuatu, and New Caledonia, where extensive intertidal to shallow subtidal sampling for micromolluscs was performed, in coral reef areas. The genus Cystiscus Stimpson, 1865 was found to be diverse (a total of 24 species were found) and formed a significant part of the marginelliform gastropod assemblage in many of these places. Almost 50% of the species discovered were 'banded', so-called because the mantle roof displays bands of vivid colour showing through the transparent shell.

The existence of populations of brightly coloured banded *Cystiscus* species across the Indo-Pacific Province have been known amongst workers for some years, but due to the lack of accurate field records they have not been seriously studied until relatively recently (Boyer, 2003 & 2004). A description of the shell and animal of a Pacific banded *Cystiscus* species, *C. tricinctus* Boyer, 2003 was made from five specimens collected at 15-20 metres depth off Touho, Northeast of the New Caledonian mainland, from samples taken during the intensive expeditions undertaken there in 1992-3 by the Paris Museum. The first Indian Ocean banded species, *C. viaderi* Boyer, 2004 was described with Mauritius as type locality.

The type species of the genus is the South African *Cystiscus capensis* Stimpson, 1865. A comparison of the type figure (Stimpson, 1865: 56, figs a, b) with our new species clearly establishes that they are congeneric but not conspecific. In the original description, the foot of the animal is described as being lemon yellow and since there is no mention of the colour of the mantle, it is unlikely to have been a banded species. In addition, unlike the ob-ovate profiles of our new species, the depicted type specimen of *C. capensis* has an inflated shell, which rapidly narrows towards the base of the columella, imparting a pyriform, truncated morphology to its anterior third.

The minute south Pacific species described from beach collected material by Bavay and other authors have been studied by us to determine if they could possibly represent *Cystiscus* species; The figured syntype of *M. micros* Bavay, 1922 is present in the MNHN. The length of its shell is similar to that of *C. garretti* n. sp., but there the similarity ends. The syntype of *M. micros* was examined and was found to be a poor specimen but it clearly has an elevated spire, rounded apex and a weakly emarginated, inflexed lip. These are a combination of characters not encountered in *Cystiscus* and we consider it to be a *Plesiocystiscus* Coovert & Coovert, 1995.

Marginella bougei Bavay, 1917 was described from Uvea [=Wallis Is., N.E. of Fiji] based upon an unspecified number of specimens. The original illustration (Bavay, 1917: pl. 2, fig. 3) was in error (Bavay, 1922: 58), and a new figure was published (Bavay, 1922: pl. 1, figs 6, 7). The specimen illustrated by Bavay in 1922 was listed by Fischer-Piette (1950: 178) as "exemplaire figuré", and by Roth & Clover (1973: 209) as "holotype". Under ICZN Art. 74.6, the latter pronouncement is to be interpreted as a lectotype designation. MNHN holds the lectotype and 7 paralectotypes (initially 8 paralectotypes but one was lost by Coovert during a loan). One of the paralectotypes measuring 1.39 x 0.99 mm is the specimen depicted in Boyer (2003: 259, fig. 58) as Cystiscus bougei. 43 additional specimens originating from Bavay were among material donated to MNHN by M. Desjardin in 1999 (Boyer, 2003: 21). The morphology of Marginella bougei is very similar to that of a subgroup of Granulina (see Wakefield & McCleery, 2004: 78). In our opinion the assignation of Marginella bougei to the genus Cystiscus is therefore doubtful, and we have excluded it from further consideration here.

In a handwritten note accompanying the original type lot of *Marginella bougei* in MNHN, Coovert explained that he had also separated out two specimens of *Cystiscus iota* Hedley, 1899. The holotype and paratypes of *C. iota* are in the Australian Museum, Sydney, with the type locality given as Funafuti Atoll (Tuvalu). We have examined these specimens and this species appears to be distinct, and at about 1.5 mm in length is smaller than all of the other ob-ovate species described herein. However, as we will explain, the shell morphology is not helpful in predicting whether it is a species with a banded mantle roof.

The generic assignments of the remainder of the region's other small historic cystiscids are rather more straightforward and clearly rule them out of inclusion; *M. goubini* Bavay, 1922 (*Crithe*), *M. tomlini* Bavay 1917 (*Plesiocystiscus*), *M. mariei* Crosse, 1807 and *M. montrouzieri* Bavay, 1922 (both *Granulina*), and *M. lifouana* Crosse, 1871, *M. hervieri* Bavay, 1922 and *M. sandwicensis* Pease, 1860 (all *Gibberula*).

Although many of the endemic Australian *Cystiscus* species have unusual morphologies with high flaring labial margins and submerged spires, several have morphologies similar to the ob-ovate and subtriangular profiles commonly found in banded *Cystiscus* species. These include *C. freycineti* May, 2

1916 a minute species from New South Wales to South Australia and the larger *C. connectans* May, 1911. Although there is some comment in the literature concerning the animal chromatism of several Australian species (May, 1920 for *C. obesula*; Laseron, 1948 for *C. angasi* Crosse 'var. *melania*'; Laseron, 1957 for *C. angasi* Crosse, 1870; Rudman, 2002 for *C: minutissimus* Tenison-Woods) so far none are reported as being banded. In fact the vast majority of the Australian *Cystiscus* fauna was described from New South Wales, South Australia and Tasmania and therefore are unlikely to be included in the ranges of the tropical species described in this paper.

The animal colour in Cystiscus is well established as an important species level character (Coovert & Coovert, 1995; Boyer, 2003 & 2004; Wakefield & McCleery, 2005) and we have therefore relied heavily upon it for our species determinations, and in our attempts to discover if it is appropriate to group similar species together. We have observed that although all of the species we are reporting upon are characterized by different patterns in various combinations of solid black, white, yellow, orange and red coloured bands, the brightness of these colours is also affected by the presence of groups of melanistic cells. The distribution of these cells can be clearly seen under adequate magnification (Figs 2-4) and their density controls the degree of melanism of the head, foot and mantle lobes. The appearance of the solid black banding of the mantle roof is in stark contrast to the much more diffuse melanistic effect produced by the scattering of melanistic cells in the remaining soft parts. It is possible that Laseron (1948: 46) was observing a particularly strong total melanistic effect when he considered a black 'variety' of the normally orange C. angasi Crosse, 1870 to be worthy of the name C. angasi var. melania Laseron, 1948.

Variation in the colouration of the bands within species was encountered in several species. In C. garretti n. sp. for example, the colour of the yelloworange banding of the mantle roof is subject to slight variations in intensity, and the foot can also be deeper orange in some individuals (compare Figs 13 & 15). Occasional specimens have a translucent crescent shaped posterior metapodium with two opaque white spots within, one on either side of the midline (Fig. 6). A similar observation has also been made in a specimen of a non-banded Cystiscus species from Vanuatu (Fig. 5). The incidence of this phenomenon has not been studied, but it probably falls within the normal variability range of the chromatism of the foot in this genus. It is also important to note that the Tongan C. vavauensis n. sp. was found to be polychromatic, with three different colour forms being found on neighbouring islands separated by only a few kilometres (Figs 25-33).

The extent of the intraspecific variability of shell morphology encountered in the species studied meant that we had to look very closely at shell morphology, focusing upon combinations of those shell characters which were unique to each species. The most stable character complex studied was the form and number of columella plications and lirae/denticles (Fig. 144). Their thickness, length, shape in cross section, extent of emergence from the aperture, their angulation, whether they were fused, separate or bifurcate, and their degree of excavation inside the aperture have all been considered important characters at the species level (Coovert & Coovert, 1995) and were heavily relied upon in our species determinations.

The shell morphologies encountered in the banded *Cystiscus* studied were ob-ovate, ovate and subtriangular. Interpreting the morphology of some species was made difficult by differences in the age and maturity of specimens, generally reflected in the degree of callus deposition and in the sites of that deposition, which is species specific in some cases.

Size was an important characteristic for many of the described species. Apart from occasional large examples of *C. yasawaensis* n. sp., all of the shells in the study were minute (L=<2.4mm). The size of the shell (except for the generally larger shelled *C. matoensis* n. sp.) was of limited value in separating the species in the ob-ovate group, most of which have similar shell sizes.

Their habitat (unless indicated otherwise) is in the interstices of coral rubble in shallow water of 1-2 metres depth with most specimens coming from just below the surface, and their abundance is generally greatest in zones of increased water flow such as the entrance to passes and in areas where water flows over the top of the reef.

Materials and methods

All live specimens were obtained by breaking apart dead coral pieces, subsequently sorted into four grades by screening. The two finest grades were placed in bowls of fresh seawater and covered. On emerging from the grit, the animals were seen to crawl up the side of the bowl and were easily collected.

Live animal photographs were taken using a Kodak DCS410 digital camera for earlier pictures and, later, a Kodak DCS760 camera mounted on an Olympus SZX12 stereo microscope over an aquarium measuring 50 mm x 75 mm and filled with seawater to a depth of 6-8 mm. For radula images, the same camera was mounted on an Olympus CX41 compound microscope with a x100 Plan Apo, oil-immersed lens. The structure of the columella of each species was determined by direct examination, facilitated in some species by the removal of the final quarter of the last adult whorl, including the lip. The cutting rig for this procedure consisted of a 22 mm dia. x 0.25 mm thick diamond coated disk rotating at a high r.p.m., with the motor and cutting disk mounted on a multi-axis stand. The specimen was mounted on a stub using a strong adhesive. It was then clamped to a simple multi-axis stand in order to present the desired shell surface to the cutting disk. The cutting procedure was performed under the SZX12 microscope, set to between X 10 and X 40 magnification. The cut specimen was then cleaned of dust debris, and examined in situ on the cutting rig. After removal of the specimen from the stub the morphology of the columella was recorded in detail by taking a wide range of photographic views from various angles and at different magnifications (e.g. Fig. 144).

All shells referred to in the text were from live taken adult specimens unless specified otherwise.

Radulae were extracted from dried specimens and from specimens preserved in denaturalised alcohol using KOH solution and were subsequently mounted either for scanning electron microscopy (*C. garretti* n. sp. only) or compound light microscopy. Analysis involved comparisons of various measurements and counts, the definitions of which are given here;

Measurements/Counts

Shell length (L): The length of the shell in mm.

Radula width (W): The width of the radula plate in μ m.

Pitch (P): This is the average distance from the centre of one plate to the centre of the next, measured axially along the length of the radula, in μ m. An average is taken between 8 to 30 radula plates depending on the length and condition of the radula after extraction.

Plate count: The length of the radula is difficult to measure because it is not straight and because fragmentation of radulae can occur during the extraction process. A simple count of the numbers of plates in those radulae which we considered to have been extracted whole has been included in the table.

Cusp count: The number of primary cusps per radula plate. The number of cusps per radula plate can increase from plate to plate due to the haphazard or ordered growth of extra cusps along a short series of plates. The reverse can also occur. In some cystiscid species the cusp count varies due to this phenomenon, whilst in others it is remains constant. Primary cusps are those which are normally present.

Cusps per mm: The number of cusps per millimetre of radula width. A way of expressing cusp density.

Indices

L: W index: Length of the shell (in mm), divided by the width of a plate (in μ m), multiplied by 1000. This index compares the width of the radula with the length of the shell.

 $P \times W$ index: The pitch is multiplied by the radula width. This index is related to the exposed surface area of each plate (it excludes the area of overlap of consecutive plates).

L: P index: Length of the shell (in mm), divided by the pitch of the plates (in μ m), multiplied by 100. This index compares the pitch of the radula plates with the length of the shell.

Note: Radula measurements/counts are not a substitute for visual examination of the radula. They do not

indicate chevron effects or the cusp arrangement and several other details, which would be impossible to quantify.

Terminology

In this paper, use is made of the same descriptive terminology originally introduced by Coovert & Coovert (1995) in their major taxonomic revision of marginelliform gastropods. This includes the following;

The cystiscid, type 3 animal: Coovert & Coovert (1995: 52) classified four types of marginelliform animal based upon anatomical features of the head, which in the genus Cystiscus is essentially a dorsomedially split tube which bifurcates anteriorly to form two short tentacles. It is termed a 'type 3 animal'. The eyes are always red and are on the side of the head some distance from the base of the tentacles (Figs 1, 4). We have observed a ciliated lower border of the head tube in one species (C. vavauensis n. sp.). It is not known if these are in fact present in all species, whether or not they are motile, or if they line the whole of the epithelial lining of the tube.

The cystiscid, type 2 radula: Coovert & Coovert (1995: 56) classified four types of cystiscid radula. The type 2 radula, typically found in the genus Cystiscus, is uniserial, and consists of a long narrow series of arched overlapping plates, each bearing 4-15 cusps (Figs 145, 146 & 148).

Internally reduced columellar plications: The abapical columella plication is termed the first plication. There are three columella plications in banded Cystiscus species. In contrast to the typical unmodified neogastropod internal whorls of the Marginellidae, the Cystiscidae modify their internal whorls by resorption. The effect of this process is that, in the case of Cystiscus which we are considering in this paper, the first and second plications (P1 and P2, Fig. 144) are reduced to a single sharp oblique columella edge within one full revolution (Fig. 143), with the third plication (P3, Fig. 144) appearing to end abruptly within approximately 3/8 of a revolution.

Parietal lirae and denticles: Posterior to the three columella plications are (when present) a series of gradually weakening parietal lirae (L, Fig. 144). These superficially appear to be smaller versions of the plications, but they differ in that they do not continue

Figures 1-12

into the aperture for any appreciable distance. They may be so short that they are as long as they are wide, and in this paper these are termed parietal denticles (d, Fig. 144). This row of lirae/denticles often runs parallel to a more internally positioned parietal callus ridge, the two being separated by an excavation which extends anteriorly to indent the third plication, flatten the second, but has no influence on the first.

The species are presented in an order emphasizing similarities in colouration and affinitics in morphology. Note that, with the exception of C. havannensis n. sp., living specimens illustrated on plates 1-4 cannot be linked to individual shells depicted on plates 5-10.

Abbreviations

MNHN: Muséum national d'Histoire naturelle, Paris, France.

AWC: Andrew Wakefield Collection. TMC: Tony McCleery Collection. GSC: Gerald Smith Collection. ad.: adult specimen. juv.: juvenile specimen. dd.: dead collected. lv.: live collected.

SYSTEMATICS

Family CYSTISCIDAE Stimpson, 1865 Subfamily CYSTISCINAE Stimpson, 1865 Genus Cystiscus Stimpson, 1865 Type species Cystiscus capensis Stimpson, 1865 (non Marginella capensis Krauss, 1848) = Marginella cystiscus Redfield, 1870 (nom. nov.)

> Cystiscus garretti n. sp Figs 6, 12-16, 65-72, 142-144

Type material. Society ls., Moorea, Vaiare, 17° 31.6'S 149° 45.9'W, in < 1m: 1 ad. lv., holotype (1.62 x 1.00 mm), MNHN ref. Moll 9395 (Figs 65, 68). Society Is., Moorea, Vaiare, I ad. lv., paratype 1 (1.75 x 1.06 mm), MNHN ref. Moll 9396; 2 ad. lv., paratypes 2 & 3 (1.68 x 1.02 mm, 1.64 x 0.98 mm), TMC (Figs 66, 67); 2 ad. lv., paratypes 4 & 5 (1.65 x 1.00 mm, 1.60 x 0.90 mm), AWC.

1. C. cf. C. tricinctus Boyer, 2003. Paguala, Ouvéa, Loyalty Islands. Head of live animal.; 2. C. vavauensis n. sp., Pau, Vava'u, Tonga; 3. C. havannensis n. sp., Port Havanna, Vanuatu. Left side of head under transillumination, demonstrating melanocytes; 4. C. maskelynensis n. sp., Sakao, Maskelyne Is., Vanuatu. Head of live animal (shell 1.5 x 1.0 mm); 5. Cystiscus sp. Vanuatu, live animal, unusual colouration of posterior metapodium; 6. C. garretti n. sp., live animal, Maeva Beach, Tahiti, Society Is., (shell L = 1.68 mm), unusual colouration of posterior metapodium; 7-8. C. yasawaensis n. sp. Wadigi, Yasawa Group, NW Fiji (shell 2.04 x 1.07 mm); 7. Live animal with external mantle extended; 8. Live animal in lateral view; 9-10. C. viaderi Boyer, 2004. Flic-en-Flac, W. Mauritius, (L = 1.5 mm); 9. Shell with dried animal within, ventral view; 10. Detail of columella, showing bifurcated third plication; 11. A sample of 23 specimens of C. deeae n. sp., Kenutu, Vava'u, Tonga; 12. A sample of 6 specimens of C. garretti n. sp., Raiatea, Society Is.



Type locality. Vaiare (17° 31.6'S 149° 45.9'W), Moorea, Society Islands.

Other material examined. Material collected in June 2001 and June 2003: Society Is., Tahiti, Maeva Beach, I ad. Iv. & I juv. Iv. in alcohol, AWC; 8 ad. Iv., TMC; Hitii, Ilot Nansouty, 6 ad. Iv., TMC; Huahine, Fare, 14 ad. Iv., TMC; 2 ad. Iv., AWC; Raiatea, West Lagoon, 14 ad. Iv. (Fig. 12), TMC; Moorea, Vaiare, 12 ad. Iv., TMC.

Tuamotu Archipelago, Fakarava South, 2 ad. dd. & 1 juv. dd., TMC; 1 ad. dd., AWC.

Opal Reef, Great Barrier Reef, Queensland, Australia, 3 ad. lvl, TMC (Figs 69-72).

Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, ob-ovate, tapering to base; Spire low, rounded, of 2 whorls including nucleus, suture smooth, indistinct (Fig. 142). Labial shoulder rounded, slightly elevated. Lip slightly thickened, straight internally, inflated externally in posterior half, posterior insertion at level of suture, just below apical level. External varix absent, siphonal and posterior notches absent. Aperture gently curving, narrow in posterior two-thirds, flaring slightly in anterior third. Three columella plications occupying anterior third of aperture. First plication continuous, strong, curving anteriorly around base to merge with lip. Second plication continuous, strong, widening from first plication as it emerges from aperture. Third plication abruptly discontinuous after entry into aperture. Often a small denticle between second and third plications, situated further out of aperture than parietal lirae and denticles. Middle third of aperture occupied by two long raised parietal lirae (L) and six shorter lirae or denticles (d). Sequence of this parietal morphology after the third plication is d/L/d/L/d/d/d. In line with the parietal lirae, the parietal surface of the posterior third of the aperture has a weak smooth callus ridge, which at its anterior end has a raised bump, then turns inwards at a 45° angle before gradually disappearing.

Anatomy (Figs 6, 12-16); Cystiscid type 3 animal. Head and tentacles opaque yellow-orange with a darker border then a very fine clear margin. Eyes small, red. Foot half width of shell, translucent yellow-orange, fringed with fine, more opaque yellow-orange. Propodium widened anteriorly into large left and right lobes. Mantle roof banded opaque yellow-orange (Y) alternating with black (B) in the order from anterior to posterior of Y/B/Y/B/Y/B including spire, where the colour change occurs at the suture. The central black band is the widest, the yellow-orange band at the suture the narrowest. Mantle lobes same colour and translucency as foot. All yellow and orange parts of the animal finely peppered with melanocytes, only visible under high magnification.

Radula: SEM examination of a radula (Fig. 148) from an adult specimen from the type locality; cystiscid type 2 radula, uniscrial, long (194 arched plates), narrow (10 µm in width), each plate bearing 9 primary cusps including the large centrally positioned cusp. Cusps immediately adjacent to the central one are smaller, with remaining side cusps gradually increasing in size and length (note: this radula is not included in Table 1). An examination of three further radulae from specimens from the type locality was performed with the compound microscope. The results are summarised in table 1. These show a cystiscid type 2 radula, 158-194 plates, each bearing 9 cusps. The pitch of the plates varied from 2.89 to 3.69 µm and the radula was 10.0 to 13.1µm in width.

Distribution. Appears to be endemic to French Polynesia where it is widely distributed. It is most abundant in the Society Islands, but it appears to be rare in the Tuamotu Archipelago.

Remarks. There is noticeable variation in shell morphology in this species, with W/L ratios of between 62% and 66% in those specimens collected. The size also varies, with lengths ranging from 1.52 mm to 1.65 mm, which may possibly reflect differences between male and female specimens (females being larger) as reported in the case of C. viaderi by Boyer (2004). In the case of C. garretti n. sp., however, there are a full range of intermediate sizes with no particular trend towards either small or large morphs. The morphology of the columella is constant and very distinctive with alternating parietal lirae and denticles (Figs 68 & 144). Another important comparative shell feature is that the third plication is equidistant from the first two, only becoming remote from them as it emerges from deep within the aperture.

Gerald Smith (South Africa) sent us three preserved specimens of a banded species from the Great Barrier Reef. Their shells are indistinguishable from Polynesian *C. garretti* n. sp. but confirmation of the conspecificity of both populations requires more detailed comparative animal studies.

Figures 13-24

13-16. C. garretti n. sp., Raiatea, Society Is., (shell L = 1.60-1.75 mm). Dorsal views of 4 ad. lv.

17-18. *C. vitiensis* n. sp., 1 ad. lv., Beqa, South Viti Levu, Fiji (shell L = 1.66 mm); 17. Dorsal view; 18. Lateral view with mantle extended.

19-20. *C. matoensis* n. sp. dorsal views of 2 ad. lv., Mato Is., South Lagoon, New Caledonia (shell L = 1.90 & 2.10 mm).

21-24. *C. havannensis* n. sp. Port Havanna, Efate, Vanuatu, 2 ad. lv.; 21-23. holotype, MNHN ref. Moll 9358, (shell 1.73 x 1.11 mm), dorsal and lateral views; 24. paratype 1 (shell 1.80 x 1.15 mm), with algal growth.



Etymology. Named after Andrew Garrett (1823-87), a self-trained naturalist who became a professional collector of shells, fish, and other natural history objects from the South Paeific Islands. Most of the material described by Pease after 1860 was collected by Garrett (Thomas, 1979).

Cystiscus vitiensis n. sp. Figs 17, 18, 73-76

Type material. Fiji, South of Viti Levu, Beqa Is., 18° 24.2'S 178° 05.2'E, in 1 m, September 2001: 1 ad. lv., holotype (1.76 x 1.07 mm), MNHN rcf. Moll 9398 (Figs 73, 76); 1 ad. lv., paratype I (1.68 x 0.97 mm), MNHN rcf. Moll 9397; 2 ad. lv., paratypes 2, 3 (1.66 x 1.02 mm, 1.67 x 1.01 mm), TMC (Figs 74, 75), and 2 ad. lv., paratypes 4, 5 (1.75 x 1.00 mm, 1.66 x 1.01 mm), AWC.

Type locality. Beqa (Benga) Island (18° 24.2'S 178° 05.2'E), off South coast of Viti Levu, Fiji.

Other material examined. 3 ad spm, Beqa Island, Viti Levu, Fiji, TMC.

Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, ob-ovate, tapering to base. Spire low, rounded, of two whorls including nucleus, suture smooth, indistinct. Labial shoulder rounded, slightly elevated. Lip slightly thickened, straight internally, slightly inflated externally in posterior half, posterior insertion at level of suture, just below apical level. External varix absent, siphonal and posterior notches absent. Aperture gently curving, narrow in posterior two-thirds, flaring slightly in anterior third. Three columella plications occupying anterior third of aperture. First plication continuous, strong, curving anteriorly around base to merge with lip. Second plication continuous, strong, widening from first plication as it emerges from aperture. Third plication abruptly discontinuous after entry into aperture. Middle third of aperture occupied by ten long raised parietal lirae followed in the posterior third by a weak smooth callus ridge which at its anterior end has a raised bump, then turns inwards at a 45° angle before gradually disappearing.

Anatomy (Figs 17, 18); Cystiscid type 3 animal. Head and tentacles opaque yellow-orange with fine, clear margin. Eyes small, red. Foot half width of shell, translucent yellow-orange. Propodium widened anteriorly into large left and right lobes. Mantle roof banded opaque yellow-orange (Y) alternating with black (B) in the order from anterior to posterior of

Figures 25-36

Y/B/Y/B/Y/B including spire, where the colour change occurs at the suture. The yellow-orange bands are narrow and both of equal width. The central black band is the widest. Mantle lobes same colour and translucency as foot. All yellow and orange parts of the animal finely peppered with melanocytes, only visible under magnification.

Radula: The radula from an adult specimen (1.72 x 1.01 mm) from the type locality presents as a cystiscid type 2 radula, 183 plates, each bearing 9 cusps. The pitch was 4.06 μ m and the width 13.3 μ m.

Distribution. Only known from the type locality of Beqa ls, South Viti Levu, Fiji.

Remarks. *C. vitiensis* n. sp differs in several respects from *C. garretti* n. sp. From the point of view of shell morphology, *C. vitiensis* n. sp. is a slightly larger species with a generally much less inflated shell (W/L ratios of between 57% and 62% making it the most elongate of the species in the ob-ovate group). It has evenly sized parietal lirae (Fig. 75), rather than the alternating long and short ones of *C. garretti* n. sp., with the more anterior parietal lirae being more densely packed. The anterior part of the aperture is more flared than other members of the subgroup. The pattern shows consistent differences to that of *C. garretti* n. sp. as the black bands of the internal mantle are consistently wider and the yellow-orange bands correspondingly narrower (Figs 17, 18).

C. vitiensis n. sp. occurs sympatrically with the much smaller *C. beqae* n. sp.

Etymology. Named after the main Fiji island of Viti Levu, close to the type locality of the species.

Cystiscus matoetisis n. sp. Figs 19, 20, 81-88

Type material. New Caledonia, Mato Is., 22° 33.5'S 166° 47.4'E, central South Lagoon, in 1 m, September 2002: 1 ad. lv., holotype (1.94 x 1.21 mm), MNHN ref. Moll 9394 (Figs 81-84); 2 ad. lv., paratypes 1-2 (2.08 x 1.18 mm, 2.10 x 1.23 mm), MNHN ref. Moll 9357 & Moll 9393 (Figs 85, 86); 2 ad. lv., paratypes 3, 4 (1.80 x 1.10 mm, 1.92 x 1.15 mm), AWC (Figs 87, 88); 3 ad. lv., paratypes 5-7 (2.13 x 1.30 mm, 2.03 x 1.22 mm, 2.04 x 1.28 mm), TMC.

Type locality. Mato Island (22° 33.5'S 166° 47.4'E), New Caledonia.

25-33. *C. vavauensis* n. sp. Dorsal views of 9 ad. lv., from 3 Tongan localities, demonstrating subtle colour variations (shell L = 1.62-1.64 mm); 25-27. Orange bands and orange animal, Pau, Vava'u; 28. White bands and reddish animal, Mala, Vava'u; 29-33. Pale pinkish bands and orange animal, Kenutu, Vava'u.
34-35. *C. maskelynensis* n. sp. Dorsal views of 2 ad. lv., Sakao, Maskelyne ls., Vanuatu (shell L = 1.60 & 1.70 mm); 36. *C. maloloensis* n. sp. Dorsal view of 1 ad. lv., Musket Reef, Southwest Viti Levu, Fiji (shell L= 1.62 mm).



Other material examined. No further material was available for study.

Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, ob-ovate, tapering to base. Spire low, rounded, of two whorls including nucleus, suture smooth, indistinct. Labial shoulder rounded, slightly elevated. Lip slightly thickened, straight internally, slightly inflated externally in posterior half, posterior insertion at level of suture, just below apical level. External varix absent, siphonal and posterior notches absent. Aperture gently curving, narrow in posterior two-thirds, flaring in anterior third. Three columella plications occupying anterior third of aperture. First plication continuous, strong, curving anteriorly around base to merge with lip. Second plication continuous, strong, widening from first plication as it emerges from aperture. Strong concavity in columella between first and second plications. Third plication weak, discontinuous.

Distance between second and third plications greater than distance between first and second. Middle third of aperture occupied by a weak short parietal lira, then a weaker long one then another barely visible short one, all being equidistant from each other.

Anatomy (Figs 19, 20); Cystiscid type 3 animal. Head and tentacles opaque yellow-orange with fine, clear margin. Eyes small, red. Foot half width of shell, translucent yellow-orange. Propodium widened anteriorly into large left and right lobes. Mantle roof banded opaque yellow-orange (Y) alternating with black (B) in the order from anterior to posterior of Y/B/Y/B/Y/B including spire, where the colour change occurs at the suture. The yellow-orange bands are narrow and both of equal width. The central black band is as wide as the anterior black band. Mantle lobes darker translucent yellow-orange. All yellow and orange parts of the animal finely peppered with melanocytes, only visible under high magnification. Radula: The radula was not extracted for this species.

Habitat. Shallow water, in dead coral on the lagoon side of the reef.

Distribution. Only known from the middle part of the South Lagoon on the West Coast of New Caledonia.

Remarks. The mantle lobes of C. matoensis n. sp are blacker than those of C. garretti n. sp. but in other respects the animal colouration is practically indistinguishable. There are, however, notable differences in shell morphology between both species: C. matoensis n. sp. is generally larger, at slightly over 2 mm in length. It tends to be narrower, with a W/Lratio of 57-63% (C. garretti n. sp. is 62-66%). The concave columella axis between the first and second plications enhances the anterior flare of the aperture and imparts a noticeable bend in the base of the columella in an apertural direction. The third plication is remote from the first two along the whole of its length whereas in C. garretti n. sp. it is equidistant within the depths of the aperture, only becoming remote as it emerges. Finally, the parietal lirae of C. matoensis n. sp. are much less evident than in C. garretti n. sp. to the point of being barely discernable at all in the majority of specimens, and those that are present only reach to mid-apertural level beyond which there is no parietal callus.

Etymology. Named after the type locality of Mato Island, New Caledonia.

Cystiscus havannensis n. sp. Figs 3, 21-24, 89-92

Type material. Vanuatu, Efate, Port Havannah, 17° 31.5'S 166° 18.5'E, in 1-2 m, August 2002: 1 ad. lv., holotype (1.73 x 1.11 mm), MNHN ref. Moll 9358 (Figs 21, 22, 89, 90).

Type locality. Port Havannah, Efate (17° 31.5'S 166° 18.5'E), Vanuatu.

Other material Examined. Vanuatu, Efate, Port Havannah, 1 ad. lv. (1.80 x 1.15 mm), (Figs 23, 24, 91, 92). Shell disintegrated during radula extraction.

Figures 37-53

37-41. *C. yasawaensis* n. sp. Dorsal views of 5 ad. lv., Yasawa Group, Northwest Fiji; 37-38. 2 ad. lv., Wadigi (shell L = 2.10 & 2.27 mm); 39-41. 3 ad. lv., Nanuya-Sewa (shell L = 2.04-2.07 mm).

42-43. *C. cf. C. tricinctus* Boyer, 2003. Paguala, Ouvea, Loyalty Is.; 42. ad. lv. with split posterior black band (shell L = 1.38 mm); 43. juv. lv.(unmeasured); **44-45.** *C. pusillus* n. sp. Beqa, South Viti Levu, Fiji. Dorsal and ventral views of ad. lv. (shell L = 1.12 mm); **46-51.** *C. deeae* n. sp. Vava'u, Tonga; 46-49. Pau, Dorsal and lateral views of 3 ad. lv. (shell L = 1.16-1.21 mm); 50-51. Kenutu, dorsal view of 2 ad. lv. (shell L = 1.16 & 1.20 mm); **52-53.** *C. beqae* n. sp. South Viti Levu, Fiji; 52. Dorsal view, ad. lv., from Beqa (shell L = 1.40 mm); 53. Dorsal view, live animal from Vomo (shell L = 1.53 mm).



Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, ob-ovate, tapering to base; Spire low, rounded, of 2 whorls including nucleus, suture smooth, indistinct. Labial shoulder rounded, slightly elevated. Lip slightly thickened, straight internally, inflated externally in posterior half, posterior insertion at level of suture, just below apical level. Bead of callus externally on labial edge. Siphonal and posterior notches absent. Aperture gently eurving, narrow in posterior two-thirds, flaring slightly in anterior third. Three columella plications occupying anterior third of aperture. First plication continuous, strong, curving anteriorly around base to merge with lip. Second plication continuous, strong, widening from first plication as it emerges from aperture. Third plication abruptly discontinuous after entry into aperture. Often a small denticle between second and third plications, situated further out of aperture than parietal lirae and denticles. Middle third of aperture occupied by two long raised parietal lirae (L) and four shorter lirae (S) which reduce to denticles on progressing posteriorly. Sequence of this parietal morphology after the third plication is S/L/S/L/S/S. In line with the parietal lirae, the parietal surface of the posterior third of the aperture has a weak smooth callus ridge, which at its anterior end has a raised bump, then turns inwards at a 45° angle before gradually disappearing.

Anatomy (Figs 21-24); Cystiscid type 3 animal. Head and tentacles opaque orange with fine, clear margin. Eyes small, red. Foot half width of shell, translucent reddish-orange, fringed with fine, more opaque dark red. Whole of animal intensely peppered with melanocytes (Fig. 3). Propodium widened anteriorly into large left and right lobes. Mantle roof banded opaque yellow-orange (Y) alternating with black (B) in the order from anterior to posterior of Y/B/Y/B/Y/B including spire, where the colour change occurs at the suture. The central black band is the widest, both yellow-orange bands the narrowest. Both anterior black bands fusing dorso-laterally, reducing central yellow line to a dorsal streak. Mantle lobes black.

Radula: Extracted from an adult specimen (L = 1.80 mm) from Port Havannah, Efate, Vanuatu. Cystiscid type 2 radula, 194 plates, each bearing 9 cusps, pitch 3.79μ m, 15.3μ m in width.

Habitat. Unlike the usual habitat, this species was found in a very shallow, dirty, muddy pass, with much algal growth on the dead coral.

Distribution. Only known from Port Havannah (north coast of Efate), Vanuatu. This species was not

collected in the nearby Maskelyne Islands (southern Efate), despite extensive sampling on two occasions.

Remarks. Only two specimens of this species were discovered. Unlike other *Cystiscus* they appeared sluggish *in vitro*. One of the specimens had algal growth dorsally (Fig. 24), likely to be the result of a deficient mantle. We have conferred separate species status on this population in view of the fact that the yellow banding of the internal mantle is greatly reduced in favour of an increase in size of the black zones, and because the external mantle is black compared to shades of yellow and orange found in other similar species. The shell morphology including the parietal structure is indistinguishable from *C. garretti* n. sp., and *C. havannensis* n. sp. is obviously a very similar species.

Etymology. Named after the type locality; Port Havannah, Efate, Vanuatu.

Cystiscus vavauensis n. sp. Figs 2, 25-33, 77-80

Type material. Tonga, Vava'u, Pau, 18° 45.3'S 174° 01.0'E, in 2 m, September 2001: 1 ad. lv., holotype (1.77 x 1.22 mm), MNHN ref. Moll 9392(Fig. 77); 1 ad. lv., paratype 1 (1.62 x 1.06 mm), MNHN ref. Moll 9391 (Figs 78, 80); 2 ad. lv., paratypes 2 & 3 (1.64 x 1.04 mm, 1.73 x 1.12 mm (Fig. 78)), AWC; 2 ad. lv., paratypes 4 & 5 (1.66 x 1.04 mm, 1.61 x 1.03 mm), TMC.

Type locality. Pau (18° 45.3'S 174° 01.0'E), Vava'u, Tonga.

Other material examined. Pau, Vava'u, Tonga: 7 ad. lv., and 1 juv. lv., TMC; pass reef area, Vava'u, Tonga, 41 ad. lv., and 10 juv. lv., TMC; Kenutu, Vava'u, Tonga, 27 ad. lv., and 3 juv. lv., TMC; Malo, Vava'u, Tonga, 8 ad. lv., and 2 juv. lv., TMC.

Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, ob-ovate, tapering to base; Spire low, rounded, of two whorls including nucleus, suture smooth, indistinct. Labial shoulder rounded, slightly elevated. Lip slightly thickened, straight internally, inflated externally in posterior half, posterior insertion at level of suture, just below apical level. External varix absent, siphonal and posterior notches absent. Aperture gently curving, narrow in posterior two-thirds, flaring slightly in anterior third.

Figures 54-64

54-64. *C. yasawaensis* n. sp., Nanuya-Sewa, Yasawa Group, NW Fiji; 54-57. ad. lv., holotype (2.27 x 1.21 mm), MNHN ref. Moll 9369; 58-61. ad. lv., paratype 1 (2.04 x 1.07 mm), MNHN ref. Moll 9368; 62. ad. lv., paratype 2 (2.07 x 1.04 mm), TMC; 63. ad. lv., paratype 3 (2.41 x 1.14 mm), TMC. 64. ad. lv., paratype 4 (22.0 x 1.24 mm), TMC.



Three columella plications occupying anterior third of aperture. First plication continuous, strong, curving anteriorly around base to merge with lip. Second plication continuous, strong, widening from first plication as it emerges from aperture, flattened as it enters aperture, indented in line with antero-posterior, parietal excavation. Third plication strong, discontinuous, more deeply indented than second plication. Weak denticle between second and third plications just below external termination of third plication. Middle and postcrior thirds of aperturc occupied by uniformly sized parietal lirae separated into an inner and outer series by an antero-posterior

excavation which extends anteriorly to indent second and third plications. Outer series of lirae shorter in length than inner series, both series remaining reasonably strong along the entire length of the parictal surface, only diminishing at its posterior end.

Anatomy (Figs 2, 25-33); Cystiscid type 3 animal. Head and tentacles opaque orange with clear margin. Eyes small, red. Foot half width of shell, translucent orange to reddish. Mantle roof banded with either white, pale pinkish or orange, alternating with black in the order from anterior to posterior of W/B/W/B/W/B (in, for example, a white banded specimen). The bands vary in width and the black bands become narrow dorsally. Mantle lobes a darker shade than the foot. All coloured parts except mantle roof peppered with melanocytes.

Radula; Nine radulae were extracted from adult specimens from the type locality and all were found to have similar characteristics. Cystiscid type 2 radula, 173 plates, each with 9 cusps, pitch 4.20 μ m, width 15.2 μ m (mean result).

Distribution. Only found in Vava'u, Tonga (Mala, Kenutu, Pau and Foelifuka).

Remarks. There are differences in shell morphology between *C. garretti* n. sp. and *C. vavauensis* n. sp. In *C. vavauensis* n. sp., the spire is taller, the shell more inflated with a weaker shoulder. The columella structure also differs, with the alternating long and short parietal lirae of *C. garretti* n. sp. being replaced in *C. vavauensis* n. sp. by evenly sized lirae not weakening to any marked degree, and divided into an inner and outer series by an antero-posterior excavation or groove (probably more accurately described as an area where the parietal callus is absent) which strongly indents the third and to a lesser extent the second plication (Fig. 80). The structure of the columella is similar to that of *C. vitiensis* n. sp., but the flatter spire and less bulbous morphology of *C. vitiensis* n. sp. helps separate the two species (compare Figs 73-76, with Figs 77-80).

In Vava'u, Tonga, C. vavauensis n. sp. was discovered abundantly at four localities (Mala, Kenutu, Pau and Foelifuka, Fig. 147) each separated by only a few kilometres of water, and each population having identical shell morphologies but displaying three subtly different colour forms in which other colours as well as the usual orange bands (as exemplified by C. garretti n. sp.) were represented; Specimens from Mala have pure white bands and a reddish animal (Fig. 28), not unlike C. maloloensis n. sp. described hereunder. Those from Kenutu have pale pinkish bands and an orange animal (Figs 29-33), and those from the Pau and Foelifuka area have the normal orange bands and orange animal (Figs 2, 25-27), with some variation expressed in the intensity of the orange hue.

Etymology. Named for the type locality of Vava'u, Tonga.

Cystiscus maskelynensis n. sp. Figs 4, 34, 35, 93-100

Type material. Vanuatu, Maskelyne Is, Sakao, 16° 29.9'S 167° 47.9'E, 1-2 m., July 2002: 1 ad. lv., holotype (1.66 x 1.06 mm), MNHN ref. Moll 9390 (Fig. 93); 1 ad. lv., paratype 1 (1.66 x 1.08 mm), MNHN ref. Moll 9372 (Fig. 94); 2 ad. lv., paratypes 2 & 3 (1.72 x 1.14 mm, 1.59 x 1.05 mm), AWC (Figs 95, 96).

Type locality. Maskelyne Islands (16° 29.9'S 167° 47.9'E), Vanuatu.

Other material examined. Vanuatu, Maskelyne Is. numerous ad. lv., $(1.55 \times 1.00 \text{ mm}, \text{ to } 1.70 \times 1.15 \text{ mm})$, 2 examples shown in Figs 97-100.

Figures 65-80

65-68. *C. garretti* n. sp., Vaiare, Moorea, Society Is; 65, 68. ad. lv., holotype (1.62 x 1.00 mm), MNHN ref. Moll 9395; 66. ad. lv., paratype 2 (1.68 x 1.02 mm), TMC; 67. ad. lv., paratype 3 (1.64 x 0.98 mm), TMC; **69-72.** *C. garretti* n. sp., Opal Reef, Great Barrier Reef, Queensland, Australia; 69-70. ad. lv., (1.69 x 1.01 mm), GSC; 71. ad. lv., (1.65 x 1.06 mm), GSC; 72. ad. lv., (1.73 x 1.07 mm), GSC; **73-76.** *C. vitiensis* n. sp., Beqa Is, South Viti Levu, Fiji; 73, 76. ad. lv., holotype (1.76 x 1.07 mm), MNHN ref. Moll 9398; 74. ad. lv., paratype 2 (1.75 x 1.00 mm), TMC; 75. ad. lv., paratype 3 (1.66 x 1.01 mm), TMC; **77-80.** *C vavauensis* n. sp., Pau, Vava'u, Tonga; 77. ad. lv., holotype (1.77 x 1.22 mm), MNHN ref. Moll 9392; 78, 80. ad. lv., paratype 1 (1.62 x 1.06 mm), MNHN ref. Moll 9391; 79. ad. lv., paratype 3 (1.73 x 1.12 mm), TMC.



Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, sub-triangular to ob-ovate, tapering to base. Spire low, rounded, of 2 whorls including nucleus, suture smooth, indistinct. Labial shoulder inflated, rounded, slightly elevated. Lip slightly thickened, straight internally, inflated externally in posterior half, posterior insertion at level of suture, just below apical level. External varix absent, siphonal and posterior notches usually absent but posterior notch present in callused specimens. Aperture gently curving, narrow in posterior twothirds, flaring slightly in anterior third. Three columella plications occupying anterior third of aperture. First plication continuous, strong, curving anteriorly around base to merge with lip. Second plication continuous, strong, weakly excavated, widening from first plication as it emerges from aperture, its distal end terminating well outside aperture. Third plication strong, strongly excavated, short. Middle and posterior thirds of aperture occupied by parietal lira and denticles. Sequence of this parietal morphology after the third plication is d/L/d/d/d. The single parietal lira is strong, remote from third plication, separated from it by a small denticle level with distal end of first lira. Subsequent parietal anatomy comprising lirae that are excavated in such a way as to create a double series of gradually weakening denticles. Wide ridge of strong parietal callus merges with denticles (distal series) in posterior half of aperture.

Anatomy (Figs 4, 34, 35); Cystiscid type 3 animal. Head and tentacles translucent bright greenishyellow. Eyes small, red. Foot half width of shell, translucent bright greenish-yellow. Mantle roof banded bright opaque white (W) alternating with black (B) in the order from anterior to posterior of W/B/W/B/W/B including spire, where the colour change occurs at the suture. The black bands usually narrow mid-dorsally. Mantle lobes same colour and translucency as foot. All greenish-yellow parts of the animal finely peppered with melanocytes, only visible under high magnification.

Radula (Fig. 146): The radulae of five adult specimens (L = 1.64 mm to 1.70 mm) from the type locality were examined and found to have cystiscid type 2 radulae, with 218-255 plates, each bearing 11-13 cusps. The pitch varied from 2.21-2.76 μ m and the width from 12.5-14.2 μ m.

Distribution. Found only in the Maskelyne 1s., Vanuatu.

Remarks. The animal colour of this species is very striking, but other identifying features are worthy of note. The morphology is variable, ranging from obovate specimens (Figs 97, 98), which are weakly callused, through to sub-triangular, heavily callused shells (Figs 99, 100). In these heavily callused specimens the parietal callus forms a thick ridge (Fig. 100). This species has perhaps the most distinctive radula of all of the species studied herein, in that there is a regular and repeating cuspal pattern which results in a chevronned appearance to the radula (Fig. 146). C. maskelynensis n. sp., is perhaps most similar to C. maloloensis n. sp., because the stark black and white bands, shell size, and the variability in shell morphology are common to both. The principal characters which serve to separate the two species are the difference in the colour of the head, foot and mantle lobes (yellow for C. maskelynensis n. sp. and crimson for C. maloloensis n. sp., Figs 34-36) and the consistently chevronned radula of C. maskelynensis n. sp.

Etymology. Named for the Maskelyne Is., the type locality of the species.

Cystiscus maloloensis n. sp. Figs 36, 101-108

Type material. Fiji, Malolo Is (Mamanuca Group), Musket reef, 17° 46.5'S 177° 09.8'E, 2 m., October 2001: 1 ad. lv., holotype (1.62 x 1.08 mm), MNHN ref. Moll 9371 (Figs 101-104); 1 ad. lv., paratype 1 (1.53 x 1.06 mm), MNHN ref. Moll 9370 (Fig. 105); 2 ad. lv., paratypes 2, 3 (1.62 x1.02 mm, 1.62 x 1.09 mm (Fig. 106)), AWC; 3 ad. lv., paratypes 4-6 (1.62 x 1.08 mm (Fig. 107), 1.74 x 1.18 mm (Fig. 108), 1.64 x 1.13 mm), TMC.

Type locality. Musket reefs (17° 46.5'S 177° 09.8'E), Southwest of Viti Levu, Fiji.

Other material examined. Fiji, Malolo Is (Mamanuca Group), Musket reef, approx. 50 ad. lv., (L = 1.55 - 1.70 mm), TMC.

Figures 81-92

81-88. *C. matoensis* n. sp., Central South Lagoon, New Caledonia; 81-84. ad. lv., holotype (1.94 x 1.21 mm), MNHN ref. Moll 9394; 85. ad. lv., paratype 1 (2.08 x 1.18 mm), MNHN ref. Moll 9357; 86. ad. lv. paratype 2 (2.10 x 1.23 mm), MNHN ref. Moll 9393; 87. ad. lv., paratype 3 (1.80 x 1.10 mm), TMC; 88. ad. lv., paratype 4 (1.92 x 1.15 mm), AWC; **89-92.** *C. havannensis* n. sp. Port Havanna, Efate, Vanuatu; 89-90. ad. lv., holotype (1.73 x 1.11 mm), MNHN ref. Moll 9358; 91-92. ad. lv., (1.80 x 1.15 mm), disintegrated during process of radular extraction.



Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, sub triangular to ob-ovate, tapering to base. Spire low, rounded, of 2 whorls including nucleus, suture smooth, indistinct. Labial shoulder inflated, rounded, slightly elevated. Lip thickened, straight internally, inflated slightly externally in posterior half, posterior insertion at level of suture, just below apical level. External varix absent, siphonal and posterior notches absent. Aperture gently curving, narrow in posterior twothirds, flaring slightly in anterior third. Three columella plications occupying anterior third of aperture. First plication continuous, strong, curving anteriorly around base to merge with lip. Second plication continuous, strong, weakly excavated, widening from first plication as it emerges from aperture, its distal end terminating well outside aperture. Third plication strong, strongly excavated, short. Middle and posterior thirds of aperture occupied by parietal lira and denticles. Sequence of this parietal anatomy after the third plication is d/L/d/d/d. First parietal lira strong, remote from third plication, separated from it by a small denticle level with distal end of first lira. Subsequent parietal morphology comprising lirae that are excavated in such a way as to create a double series of gradually weakening denticles. Wide ridge of strong parietal callus merges with denticles (distal end of lirae) in posterior half of aperture.

Anatomy (Fig. 36): Cystiscid type 3 animal. Head and tentacles translucent red. Eyes small, red. Foot half width of shell, translucent red. Mantle roof banded bright opaque white (W) alternating with black (B) in the order from anterior to posterior of W/B/W/B/W/B including spire, where the colour change occurs at the suture. The black bands usually narrow considerably mid-dorsally. Mantle lobes same colour and translucency as foot. All red parts of the animal finely peppered with melanocytes, only visible under high magnification.

Radula: The radulae of nine adult specimens (L = 1.53 mm to 1.65 mm) from the type locality were examined and found to have cystiscid type 2 radulae, with 238-269 plates, each bearing 11 cusps. The pitch varied from 2.55-3.00 µm and the width from 11.2-15.9 µm.

Distribution. Known only from the reefs and Islands to the West of Viti Levu, Fiji, including Musket.

Remarks. The similarities and differences between *C. maloloensis* n. sp. and *C. maskelynensis* n. sp. have been discussed in remarks on the latter species.

Due to the similarity in appearance of C. maloloensis n. sp. to the black and white banded form of C. vavauensis n. sp., a series of specimens of both were examined in great detail to determine their differences. Nine radulae were extracted from specimens of each species and it was discovered that the cusp count was constant for each species, at nine cusps per plate in C. vavauensis n. sp., and eleven per plate for C. maloloensis n. sp. There are also other significant radula differences: C. maloloensis n. sp. has a much higher average number of plates than C. vavauensis n. sp., and they are also narrower. Further measurements indicate that the plates of C. *maloloensis* n. sp. are more closely spaced than those of C. vavauensis n. sp. (see P x W index averages for both species in table 1).

In both *C. maskelynensis* n. sp. and *C. maloloensis* n. sp., obovate and subtriangular shells are regularly encountered. However, the shoulder of the shell of *C. maloloensis* n. sp. is more raised and angular than that of *C. vavauensis* n. sp. Furthermore, comparisons of the head of the animal of each species reveals that there is a noticeable medial bulge at the base of each tentacle in *C. maloloensis* n. sp. (*C. maskelynensis* n. sp. also shares this character but it is absent in *C. garretti* n. sp., *C. matoensis* n. sp., *C. vitiensis* n. sp. and *C. havannensis* n. sp., their tentacles appearing much finer as a result). The final difference between the two species is that *C. vavauensis* n. sp. is a polychromatic species whereas no colour variation was encountered in *C. maloloensis* n. sp.

Etymology. Named for Malolo Is, Mamanuca Group, West of Viti Levu.

Cystiscus yasawaensis n. sp. Figs 7, 8, 37-41, 54-64

Type material. Northwest Fiji, Yasawa Group, Nanuya-sewa, 16° 56.45'S 177° 22.55'E, in 1 m, September 2001: 1 ad. lv., holotype, (2.27 x 1.21 mm), MNHN ref. Moll 9369 (Figs 54-57).

Northwest Fiji, Yasawa Group, Nanuya-sewa: 1 ad. lv., paratype 1 (2.04 x 1.07 mm), MNHN ref. Moll 9368 (Figs 58-61); 3 ad. lv., paratypes 2-4, (2.07 x 1.04 mm (Fig. 62), 2.41 x 1.14 mm (Fig. 63), 2.20 x 1.24 mm (Fig 64), TMC.

Figures 93-108

93-100. *C. maskelynensis* n. sp., Sakao, Maskelyne Is., Vanuatu; 93. ad. lv., holotype (1.66 x 1.06 mm), MNHN ref. Moll 9390; 94. ad. lv., paratype 1 (1.66 x 1.08 mm), MNHN ref. Moll 9372; 95. ad. lv., paratype 2 (1.72 x 1.14 mm), TMC; 96. ad. lv., paratype 3 (1.59 x 1.05 mm), TMC; 97-98. ad. lv., (1.50 x 0.0394 in), TMC; 99-100. ad. lv., unusually inflated (1.74 x 1.27 mm), TMC; **101-108.** *C. maloloensis* n. sp., Musket reef, Southwest Viti Levu, Fiji; 101-104. ad. lv., holotype (1.62 x 1.08 mm), MNHN ref. Moll 9371; 105. ad. lv., paratype 1 (1.53 x 1.06 mm), MNHN ref. Moll 9370; 106. ad. lv., paratype 3 (1.62 x 1.02 mm), TMC; 107. ad. lv., paratype 4 (1.62 x 1.08 mm), AWC; 108. ad. lv., paratype 5 (1.74 x 1.18 mm), AWC.



Type locality. Northwest Fiji, Yasawa Group, Nanuya-Sewa (16° 56.45'S 177° 22.55'E).

Other material examined. Fiji, Yasawa Group, Nanuya-sewa, 4 ad. lv., and 2 juv. lv., TMC; Wadigi, 3 ad. lv., and 1 ju.v lv., TMC.

Description. Shell small, thin, hyaline, translucent white, smooth, glossy, elongate ob-ovate, tapering to base; Spire involute, concealed by last adult whorl, suture not visible, cap of callus present in highly callused specimens. Labial shoulder rounded, highly elevated. Lip slightly thickened, straight, slightly inflexed or curved internally. External lip straight or inflated at mid-body, posterior insertion just to the right of, and well above, apical level. External varix absent, siphonal notch absent. Deep posterior notch present especially in highly callused specimens. Aperture gently curving along most of its length, severe curvature at posterior end onto spire, narrow in posterior two-thirds, flaring slightly in anterior third. Three columella plications occupying anterior third of aperture. First plication continuous, strong, curving anteriorly around truncated base to merge with lip.

Second plication continuous, strong, widening from first plication as it emerges from aperture. Third plication discontinuous after entry into aperture. Often a small denticle between second and third plications, situated further out of aperture than parietal lirae and denticles (see paratype 1, Fig. 61). Middle to posterior thirds of aperture occupied by five long raised parietal lirae (L) and five shorter lirae (S) which gradually weaken on progressing posteriorly but always remain distinct. Sequence of this parietal morphology after the third plication is S/L/S/L/S/L/S/L. Short lirae weaker than the long lirae and situated further out of the aperture.

Anatomy (Figs 7, 8, 37-41); Cystiscid type 3 animal. Head and tentacles opaque black. Eyes small, red. Foot half width of shell, black with more opaque black median line. Propodium widened anteriorly into left and right lobes. Mantle roof banded opaque yellow (Y) alternating with black (B) in the order from anterior to posterior of Y/B/Y/B/Y/B including spire, where the colour change occurs at the suture. The posterior black band is the widest, the yellow-orange band at the suture the narrowest. Mantle lobes black.

Radula: Radulae of two specimens from the type locality (one ad. and one juv.) were examined. The radula from the adult specimen (shell L = 2.2 mm)

was found to have cystiscid type 2 radula, with 199 plates, each bearing 13 cusps. The pitch was $3.22 \ \mu m$ and the width $23.5 \ \mu m$.

Habitat. This species was discovered amongst the reefs to the Northwest of Nanuya-sewa, one creating the point forming the bay, the other 100 metres further out to sea. It was more common on this shallow outer reef, which was composed of very worn hard coral pieces scattered amongst soft coral and sponges.

Distribution. Only encountered at two localities, Nanuya-sewa, in the remote Yasawa group in Northwestern Fiji, and at Wadigi, on the Southwest end of Malolo Island, Southwest of Viti Levu.

Remarks. In *C. yasawaensis* n. sp., callus deposition appears to be concentrated in three locations towards the posterior end of the shell. Deposition at the posterior end of the lip and parietal surface results in the formation of a deep, curved notch between these zones. Deposition on the spire results in an apical dome of callus and an overall opaque callus wash extending to the top of the shoulder region (Fig. 63). The effect of callus deposition on the overall morphology of the shell is to change its profile from elongate-ovate to a more cylindrical form. The curved posterior extension of the lip and the characterization of the columella and parietal lirae, however, remain constant in all specimens.

This is the only banded Pacific species so far discovered which has an animal with a black head, foot and mantle lobes (Figs 7, 8). It shares this colour scheme with the Indian Ocean *C. viaderi*, but there the similarity ends. The banding pattern is reasonably stable, with any variation presenting as irregular edges to the black bands (Fig. 39) and occasional inclusions of yellow in the black bands (Fig. 41).

Etymology. Named for the type locality of the Yasawa Islands, Northwestern Fiji.

Cystiscus cf. *C. tricinctus* Boyer, 2003 Figs 1, 42, 43, 109-115

Voucher material. Loyalty Islands, Ouvéa, Paguala, 20° 26.4'S 166° 28.6'E, in 3 m., September 2002 : 1 ad. lv., (1.28 x 0.83 mm), MNHN ref. Moll 9379 (Figs 109-112, 115); 1 ad. lv., (1.38 x 0.86 mm), MNHN ref. Moll 9377.

Figures 109-123

109-115. *C. cf. C. tricinctus* Boyer, 2003, Paguala Is, Ouvea, Loyalty Is; 109-112. ad. lv., (1.28 x 0.83 mm), MNHN ref. Moll 9379; 113. ad. lv., (1.30 x 0.85 mm), AWC; 114. ad. lv., (1.32 x 0.83 mm), AWC; 115. Columella detail; **116-123.** *C. beqae* n. sp. Beqa Is., South Viti Levu, Fiji; 116-119. ad. lv., holotype (1.46 x 1.02 mm), MNHN ref. Moll 9384; 120. ad. lv., paratype 1 (1.48 x 1.03 mm), MNHN ref. Moll 9383; 121. ad. lv., paratype 3 (1.39 x 0.96 mm), TMC; 122. ad. lv., paratype 4 (1.50 x 1.06 mm), AWC; 123. ad. lv., paratype 5 (1.56 x 1.06 mm), AWC.



Other material examined. Loyalty Islands, Ouvéa, Paguala, 1 ad. lv., (1.40 x 0.89 mm), TMC; 1 ad. lv., (1.30 x 0.85 mm), AWC (Fig. 113); 1 ad. lv. (1.38 x 0.88 mm), TMC; 1 ad. lv., (1.32 x 0.83 mm), AWC (Fig. 114), 3 juv. lv., TMC.

Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, ovate, tapering to base. Spire low, of two whorls, rounded, with a callus glaze extending over sutural areas. Anterior and posterior notches absent. Aperture almost straight, narrow in posterior two-thirds, flaring slightly in anterior third. Insertion of labial shoulder at level of last suture, with callus curving round posteriorly to thicken the labrum. Lip raised centrally and slightly inflexed. Labial thickening in central third of lip not on the edge but slightly back from it. From dorsal aspect, slight bead or varix visible at anterior extremity and central lip concave due to labial inflexion. Three columella plications; First plication slightly excavated, widening and thickening as it emerges, then stops abruptly resulting in an axial step. Second plication strong, top flattened, more excavated than first, oblique, outer edge merging with callus which extends from first plication. Third plication medium strong, excavated, merging into parietal callus, not as strong as frst two plications. Parietal callus ridge weak in middle and posterior apertural thirds. Posterior to third plication is first parietal denticle which is prominent, followed by a lira which ends deep inside aperture, followed by 2 to 4 gradually weakening lirae, the last two being extremely weak.

Anatomy (Figs 1, 42, 43); Cystiscid type 3 animal. Head and tentacles opaque bright yellow within, with fine, translucent margin. Eyes small, red. Foot half width of shell, translucent, with a well defined opaque yellow median line occupying central third of the width of the foot, terminating short of the posterior edge of the metapodium. Mantle roof banded opaque pale yellow (Y) alternating with black (B) in the order from anterior to posterior of Y/B/Y/B/Y/B including spire, where the colour change between last yellow and black zones occurs at the suture. The anterior black band is the thinnest and does not pass around the whorl evenly like the second black band, but is formed into an inverted 'u' shape (when viewed dorsally with the animals head downwards). The 'u' shape is distorted so it lies at an angle (from the 1 o'clock to

Figures 124-141

the 7 o'clock position) to the central axis of the shell. Mantle lobes translucent. Radula not examined.

Habitat. The type material of *C. tricinctus* was collected from the outer reef slope in 15-20 metres, whereas *C. cf C. tricinctus* was recorded from 3 metres.

Distribution. The type locality of *C. tricinctus* is Touho, Northeast New Caledonia. *C. cf. C. tricinctus* was found approximately 100 km further east in Ouvéa, Loyalty Islands.

Remarks. This little species is more heavily callused than most, although as always, more mature specimens are the ones which develop more callus. Its spire is lower than the other small species, and its shoulders more rounded and therefore less prominent. One of the specimens examined had a dorso-medial division of the second black band (Fig. 42), indicating that the pattern may be unstable in this species.

The banding pattern and shell morphology in both Loyalty Island and New Caledonian populations are similar. At the type locality, *C. tricinctus* does not have the yellow median line in the foot and is on average 17.5% larger than *C. cf C. tricinctus*. Its head is described as light green whereas that of *C. cf. C tricinctus* is yellow. We are cautiously treating them here as one species, but the Loyalty Island population may ultimately turn out to be a distinct species when its molecular characters are examined.

Cystiscus beqae n. sp. Figs 52, 53, 116-123

Type material. Fiji, South of Viti Levu, Beqa Island, 18° 24.2'S 178° 05.2'E, in 1 m., September 2001: 1 ad. lv., holotype (1.46 x 1.02 mm), MNHN ref. Moll 9384 (Figs 116-119); 1 ad. lv., paratype 1 (1.46 x 1.03 mm), MNHN ref. Moll 9383 (Fig. 120); 2 ad. lv., paratypes 2, 3 (1.38 x 1.06 mm, 1.62 x 1.02 mm (Fig 121)), AWC; 2 ad. lv., paratypes 4, 5 (1.50 x 1.06 mm, 1.56 x 1.06 mm), TMC (Figs 122, 123).

Type locality. Beqa Island (18° 24.2'S 178° 05.2'E), South Viti Levu, Fiji.

Other material examined. Fiji, Viti Levu, Malalola, 12 ad. lv., L = 1.4 mm to 1.55 mm, and 3 juv. lv., TMC; Mamanuca Is, 2 ad. lv., L = 1.4 mm and 1.53 mm, TMC; Vomo, 2 ad. lv., L = 1.53 mm, TMC.

124-131. *C. deeae* n. sp., Kenutu, Vava'u, Tonga; 124-127. ad. lv., holotype (1.23 x 0.86 mm), MNHN ref. Moll. 9382; 128. ad. lv., paratype 1 (1.20 x 0.86 mm), MNHN ref. Moll 9381; 129-131. ad. lv., paratype 3 (1.29 x 0.90 mm), TMC; **132-141.** *C. pusillus* n. sp., Beqa Is, South Viti Levu, Fiji; 132-136. ad. lv., holotype (1.18 x 0.81 mm). MNHN ref. Moll 9380; 137. ad. lv., paratype 1 (1.19 x 0.82 mm), MNHN ref. Moll 9378; 138. ad. lv., paratype 2 (1.19 x 0.82 mm), TMC; 139-141. ad. lv., paratype 3 (1.15 x 0.81 mm), AWC.



Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, subtriangular, tapering to base. Spire slightly elevated, of two whorls, rounded, with a callus glaze extending over suture area. Anterior and posterior notches absent. Aperture almost straight, narrow in posterior two-thirds, flaring slightly in anterior third. Insertion of strong labial shoulder slightly above or level with last suture, with callus eurving round posteriorly to thicken posterior lip.

Thick external labial callus, especially posteriorly, occasionally with a beading of callus on leading edge externally. Posterior end of lip indented. Three equidistant columella plications. Columella concave in region of plications, spaces between plications deeply excavated; First plication strong, oblique, rounded, passing round anterior extremity to join labial callus. Second plication strong, tending to square in cross section, flat or slightly excavated, less oblique than first, distal end terminating abruptly. Third plication medium strong, excavated, tending to square in cros section, distal end abruptly terminating closer to aperture than terminus of second plication. merging into parietal callus, not as strong as first two Parietal lirae/denticles evident along plications. remaining apertural length, becoming weaker from anterior to posterior. Parietal callus ridge present on apertural side of lirae/denticles, separated from them by an excavated zone running length of aperture to indent third plication, and flatten second plication. Posterior to third plication, short and long lira alternating along aperture, gradually weakening to posterior labial insertion.

Anatomy (Figs 52, 53); Cystiscid type 3 animal. Head and tentacles opaque bright yellow-orange within, with fine, translucent margin. Eyes small, red. Foot half width of shell, translucent orange, becoming gradually more opaque centrally. Mantle roof banded yellow (Y) alternating with black (B) in the order from anterior to posterior of Y/B/Y/B including spire, where the colour change between last yellow and black zones occurs at the suture. The anterior black band is positioned mid-body, is thin compared to the wide yellow bands and its edges are irregular and fringed with a hazy orange colouration. There is no such orange colour at the yellow and black transition at level of the suture. Mantle lobes translucent orange. Radula; The radulae of three adult specimens (shell L = 1.44 - 1.47 mm) from the type locality were

extracted. Cystiscus type 2 radula, with 180 plates, 10 cusps per plate, a pitch of $3.70 \ \mu m$ and a width of $14.1 \ \mu m$.

Distribution. Only known from the type locality and Southwest Viti Levu, Fiji.

Remarks. The central black band has an irregular border on both sides and this irregularity varies from specimen to specimen (see two examples Figs 52 & 53).

This species has a similar shell morphology to the three species of *Cystiscus* recently described from the Tuamotu's (Wakefield & McCleery, 2005), none of which exhibit a banded pattern. *C. beqae* n. sp. differs from *C. deeae* n. sp. in that the shell of the former is approximately 20% larger, the central black band is bordered by a diffuse orange line, and the colouration of the head of the animal is more intense with a much thinner translucent border. The species share the features of a posterior labial indentation, sub-triangular shell shape, plication configuration, and same basic pattern style, and they come from neighbouring island groups (Fiji and Tonga respectively).

Etymology. Named for the Island of Beqa off the south coast of Viti Levu, the type locality of this species.

Cystiscus deeae n. sp. Figs 11, 46-51, 124-131

Type material. Tonga, Vava'u, Kenutu Island, 18° 41.4'S 173° 55.8'W, in 1-2 m., September 2001: 1 ad. lv., holotype (1.23 x 0.86 mm), MNHN ref. Moll 9382 (Figs 124-127); 1 ad. lv., paratype 1 (1.20 x 0.80 mm), MNHN ref. Moll 9381 (Fig. 128); 2 ad. lv., paratypes 2 & 3 (1.21 x 0.81 mm, 1.29 x 0.90 mm (Figs 129-131), AWC; 1 ad. lv., paratype 4 (1.16 x 0.81 mm).

Type locality. Kenutu Is. (18° 41.4'S 173° 55.8'W), Vava'u, Tonga.

Other material examined. Tonga, Vava'u, Kenutu Island, 35 ad. lv., L = 1.15 to 1.30 mm; Mala Island, 20 ad. lv., L = 1.20 to 1.30 mm; Pau Island, 21 ad. lv., L = 1.20 to 1.30 mm. TMC.

Figures 142-148

142-144. *C. garretti* n. sp. 142. Spire and suture; 143. Columellar structure (P1-P3 = columella plications 1-3, d = denticle, L = lira); 144. Modified cystiscid internal whorls visible through semi-transparent shell; **145.** Radula of *C. viaderi* Boyer, 2004 (see table 1 for details); **146.** Radula of *C. maskelynensis* n. sp. showing chevron effect (see table 1 for details); **147.** Map of Vava'u, Tonga; **148.** *C. garretti* n. sp., Moorea, Society Is. SEM of radula of ad. lv. (shell L = 1.6 mm). 194 plates, 8 cusps per plate, width 10 μ m.



Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, subtriangular, tapering to base. Spire slightly elevated, of two whorls, rounded, with a callus glaze extending over suture areas. Anterior and posterior notches absent. Aperture almost straight, narrow in posterior two-thirds, flaring slightly in anterior third. Insertion of strong labial shoulder slightly above or level with last suture, with callus curving round posteriorly to thicken posterior lip.

Thick external labial callus, especially posteriorly, occasionally with a beading of eallus on leading cdge externally. Posterior end of lip indented. Three equidistant columella plications. First plication strong, oblique, rounded, passing round anterior extremity to join labial callus. Second plication strong, tending to square in cross section, flat or slightly excavated, less oblique than first, distal end terminating abruptly. Third plication slightly more remote from second plication, excavated, distal end abruptly terminating closer to aperture than terminus of second plication. merging into parietal callus, not as strong as first two plications. 6-7 crowded parietal lirae/denticles evident along remaining apertural length, becoming weaker from anterior to posterior. Parietal callus ridge present on apertural side of lirae/denticles, separated from them by an excavated zone running length of aperture to indent third plication, and flatten second plication. Posterior to third plication, short and long lira alternating along aperture, gradually weakening to posterior labial insertion.

Anatomy; Cystiscid type 3 animal. Head and tentacles opaque bright yellow within, with wide, translucent margin. Eyes small, red. Foot half width of shell, translucent yellow, becoming slightly more opaque centrally. Mantle roof banded yellow (Y) alternating with black (B) in the order from anterior to posterior of Y/B/Y/B including spire, where the colour change between last yellow and black zones occurs at the suture. The anterior black band is positioned midbody, is very thin (in some specimens almost to the point of division) compared to the wider yellow bands and its edges are regular to very irregular. Mantle lobes translucent yellow-orange.

Radula; The radulae of three adult specimens (shell L = 1.19 - 1.29 mm) from the type locality were extracted. Cystiscus type 2 radula, with 201 plates, 7 cusps per plate, a pitch of 2.81 µm and a width of 8.43 µm.

Distribution. Found at several localities in Vava'u, Tonga (Pau and Kenutu Islands).

Remarks. The shell of this species is similar to that of *C. pusillus* n. sp., but *C. deeae* n. sp. is generally larger and has a more angular shoulder. The structure of the columella in both species is very similar. The colour pattern is, however, very different and there is no doubt that even though they occur on adjacent island groups, they represent distinctly separate

species. This species was found to be locally common (Fig. 11).

Etymology.

Named for Dee McClccry, wife of the second author, who participated in the Pacific transits of S.Y. 'Marina Em'.

• *Cystiscus pusillus* n. sp. Figs 44, 45, 132-141

Type material. Fiji, South of Viti Levu, Beqa Island, 18° 24.2'S 178° 05.2'E, in 1 m, September 2001: 1 ad. lv., holotype (1.18 x 0.81 mm), MNHN ref. Moll 9380 (Figs 132-135); 1 ad. lv., paratype 1 (1.19 x 0.82 mm), MNHN ref. Moll 9378 (Fig. 137); 2 ad. lv., paratypes 2, 3 (1.19 x 0.82 mm, 1.15 x 0.81 mm), AWC (Figs 138-141); 3 ad. lv., paratypes 4 - 6 (1.11 x 0.78 mm, 1.15 x 0.79 mm, 1.12 x 0.78 mm), TMC.

Type locality. Beqa Island (18° 24.2'S 178° 05.2'E), South of Viti Levu, Fiji.

Description. Shell minute, thin, hyaline, translucent white, smooth, glossy, ovate, tapering to base; Spire slightly elevated, pointed, of 2 whorls including nucleus, suture smooth, indistinct due to callus wash. Labial shoulder strong and raised almost to level of top of spire. Lip slightly thickened, straight internally, inflated externally in posterior half, posterior insertion at level of last suture. External varix absent, siphonal and posterior notches absent. Aperture almost straight, narrow in posterior two-thirds, flaring slightly in anterior third. Parietal callus ridge present as a continuous sinuous line from posterior aperture to step at first plication in mature callused specimens.

Three columella plications; all strong, equidistant from each other. First plication extending outwards to form a 'keel', merging into a heavy callus and forming a step at its end, before sweeping around anterior extremity. Second plication also strongly emergent from aperture, slightly excavated. Third plication shorter than first two, slightly excavated. Small denticle between third plication and first parietal lira in callused mature specimens. First parietal lira strong, followed by a short lira then several more small denticles with an adjacent parietal callus ridge.

Anatomy (Figs 44, 45); Cystiscid type 3 animal. Head and tentacles translucent yellow-orange at the periphery becoming progressively deeper orange centrally within each tentacle. Eyes small, red. Foot half width of shell, translucent yellow-orange, colour becoming deeper medially. Mantle roof banded opaque yellow-orange (Y) alternating with black (B) in the order from anterior to posterior of Y/B/Y/B/Y/B including spire, where the colour change between last yellow and black zones occurs at the suture. The anterior black band is completely divided dorsomedially (when the animal is fully extended) by an antero-posterior extension of the central (second) yellow band. This extension appears to drag the first black band with it anteriorly, not only dividing it in two but making the remaining portion to the right of the yellow extension into an inverted 'u' shape (when viewed dorsally with the animals head downwards).

Ventrally, the anterior divided black band and the shoulder black band coalesce. Mantle lobes same colour and translucency as foot, gradually becoming a deeper orange as margin is approached. Radula not examined.

Distribution. Only known from the type locality.

Remarks. In some immature specimens there is no denticle between the third plication and first lira. This and the sinuous parietal callus ridge are really only apparent in occasional specimens with more than usual callus formation. Compared to *C. cf. C. tricinctus*, however, *C. pusillus* n. sp. is not heavily callused.

This species is very close to *C. tricinctus* and *C. cf. C. tricinctus* by virtue of the appearance of the first (anterior) black band or zone, which resembles a distorted, inverted 'u' shape to the right of the central axis of the shell. This peculiarity of the anterior black band was encountered in all of the specimens collected and examined.

C. pusillus n. sp. was found to occur sympatrically with *C. beqae* n. sp.

Etymology. From the Latin; *pusillus* – 'tiny' or 'puny'.

DISCUSSION

The bands on the mantle roof of C. viaderi are deep orange and are fewer in number than in the more yellowish banded Pacific species. As far as shell characters are concerned, the third plication of C. viaderi is bifurcated (Fig. 10) whereas it does not divide in Pacific species, and there is a lack of parietal anatomy in contrast to the multiplicate Pacific species. Radula differences are more subtle; C. viaderi has a typical Cystiscid type 2 uniserial radula, with 168 arched plates each bearing 9 cusps (Fig. 145 and table 1). For a proportionally shorter shell, the pitch of the plates in the radula of C. viaderi was slightly greater than that of C. garretti n. sp. (for example) but otherwise there was little difference between the two. Nevertheless, it can be concluded that the Pacific banded species have more in common with each other than they do with C. viaderi.

Our studies show a tendency towards three pattern types in banded *Cystiscus*. The most frequently occurring of these is the multiple transverse banding pattern. The species which fall into this category are *C. viaderi*, *C. garretti* n. sp., *C. vitiensis* n. sp., *C. matoensis* n. sp., *C. havannensis* n. sp., *C. vavauensis* n. sp., *C. yasawaensis* n. sp., *C. maskelynensis* n. sp. *and C. maloloensis* n. sp. The second pattern type presents with a very distorted first (anterior) transverse band, which is often divided dorso-medially. *C.* *tricinctus*, *C. cf. C. tricinctus* and *C. pusillus* n. sp. are examples. The third pattern type, seen in *C. deeae* n. sp. and *C. beqae* n. sp. takes the form of a single, narrow transverse black band situated centrally. Whether these three groups represent phyletic groupings remains to be tested.

Since all of the historic type specimens of small South Pacific Cystiscus are dead, empty, beached shells, it would be particularly useful to know if there is any correlation between shell morphology and animal colour and pattern type, and if so, would shell morphology lend itself to accurate predictions of anatomical characters? Our results show that most, but by no means all species exhibiting the transverse banding pattern type have an ob-ovate morphology. Unfortunately, since this correlation is unreliable, it would be unwise to rely on it for taxonomic purposes. Furthermore, it is important to note that the various shell morphologies seen in banded Cystiscus are not exclusive to species with banded patterns. Other colour patterns such as solid colours, reticulated patterns and irregular multicoloured patterns have also been encountered in the same morphologies as the banded species [for published examples, see Boyer (2003) and Wakefield & McCleery (2005)].

Distribution Patterns. The Pacific Island groups where banded *Cystiscus* were encountered are isolated and yet these molluscs which have non-planktonic, benthic egg and juvenile stages have somehow reached remote locations, perhaps via rafting of egg capsules or juveniles from source areas. Many of the new species described herein were only encountered in their type localities, and are possibly endemic to those areas.

No live specimens were collected in the central atolls of the Tuamotu's, the only part of this archipelago searched, but several dead shells of C. garretti n. sp. were found in South Fakarava. Banded Cystiscus were widespread in the Society Islands. Extensive collecting was done in Penrhyn and Suwarrow (the Northern Cook Islands), limited collecting was done in Atutaki and no Cystiscus were found at these localities. Extensive collecting was done at Beveridge reef (Southeast of Niue, between the Southern Cook ls. and Tonga) and only small non-banded Cystiscus were found. In American Samoa, limited collecting was done and in Western Samoa extensive collecting was done along the north and east shores, with no Cystiscus being found. Vava'u in Tonga, and the Western Islands of Fiji were found to be a hotspot for banded (5 species) and non-banded Cystiscus. Many of the islands of Vanuatu were not prospected, although superficial collecting was done in Port Havannah (Efate). In the Maskelyne Islands (South of Malekula, Vanuatu) however, extensive sampling was performed. As a result only two species of banded Cystiscus were found in Vanuatu amongst other, nonbanded species. In the Loyalty Islands (Ouvéa), only one species was found after extensive collecting, but other islands to the south were not visited. In New

The most significant negative sites were Penhryn and Suwarrow (Northern Cook Is.) and Western Samoa – these are relatively small areas and were reasonably well searched. Having said that, the limitations of our methods must be borne in mind when interpreting distribution patterns and population densities. In addition, any one sampling site covered only a very small percentage of the total area of any locality, so sampling saturation has by no means been reached at any of the locations mentioned in this study. It is therefore impossible to state with any degree of certainty that banded *Cystiscus* are absent from any of the negative places mentioned above.

The largest 'group' of similar species, *C. garretti* n. sp., *C. vitiensis* n. sp., *C, matoensis* n. sp., *C. havannensis* n. sp., *C. vavauensis* n. sp. and *C. yasawaensis* n. sp. have a wide Pacific distribution from the Barrier Reef and then on each major island group to the Society Islands. Their occurrence in the smaller Pacific island groups at more northerly latitudes is unknown, but a banded species with an unusual morphology has been discovered in Panglao, Philippines (P. Bouchet, pers. comm.). [The authors will be studying and reporting upon this sample in a future issue of Novapex].

Similar species show a tendency to be found on adjacent island groups; *C. maskelynensis* n. sp. and *C. maloloensis* n. sp. were found on the adjacent Vanuatu and Fiji. *C. tricinctus* from New Caledonia, is certainly very close to *C. cf. tricinctus* from the nearby Loyalty Islands (the latter may eventually turn out to be a distinct species). The similar *C. beqae* n. sp. and *C. deeae* n. sp. are from the adjacent island groups of Fiji and Tonga respectively.

CONCLUSION

Evidence continues to mount which demonstrates a high degree of diversity of banded *Cystiscus* (in terms of species numbers) in the South Pacific, and that Western Fiji seems to be a hotspot. In terms of abundance, French Polynesia (the Society Islands), Tonga (Vava'u) and Vanuatu (Maskelyne Islands) were notable for the size of their populations.

Some species are so similar to each other that conventional shell and animal characters may be inadequate for certainty in species separation, and for these, research at molecular level will ultimately be required. For the time being, species have to be recognised according to their columella and parietal morphology, and animal colour and pattern, and we have demonstrated that these are good characters to use at the species level. We have also demonstrated that the overall shell morphology of each species is variable due mainly to callus deposition, and that the prediction of animal colour from empty shells is not possible at present.

Finally, our radula studies suggest that there are specific characters present in the radulae of several of the banded *Cystiscus* described herein, which can be considered useful for taxonomic purposes at the species level.

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Species	Shell	.d.	Plate	Cusp	Pitch	W	sps /mm	L:W	L:P	PxW
sawaonsis	2 2()	JJUV.	199	13	(μm) 3 22	(µm) 25.0	520	88	68 3	81
540 401515	4.040			15	J. 20 20 20		520	00	00.5	01
viaderi*	1.5	A	168	9	3.96	10.9	825.7	137	37.8	43
garretti	1.56	A	189	9	3.55	11.8	762	132	43.9	42
garretti	1.56	A	174	9	3.60	13.1	687	119	43.3	47
garretti	1.66	A	158	9	3.69	12.4	125	133	44.9	46
garretti	1.70	A	192	9	3.70	15.1	594	112	45.9	48
(mean)	1.62		178	9	3.64	13.1	692	124	44.5	46
vitiensis	1.72	A	183	9	4.06	13.3	677	129	42.3	54
111011313	1.72		105			10.0	011	12)		
vavauensis	1.65	A	177	9	3.50	13.9	647	118	47.1	49
vavauensis	1.71	A	190	9	3.72	14.6	616	117	46.0	54
vavauensis	1.63	A	177	9	3.77	14.8	608	110	43.2	56
vavauensis	1.61	A	183	9	3.95	14.1	638	114	40.7	56
vavauensis	1.73	A	178	9	4.29	13.9	647	124	40.3	60
vavauensis	1.72	A	176	9	4.40	15.5	580	110	39.0	68
vavauensis	1.60	A	165	9	4.45	15.1	596	106	36.0	67
vavauensis	1.73	A	155	9	4.75	17.8	505	97	36.4	85
vavauensis	1.57	A	152	9	4.95	16.9	532	93	31.7	84
vavauensis	1.66		173	Q	4 20	15.2	597	110	40.0	64
(mean)	1.00		175	,	4.20	1.5.2	571	mo	40.0	04
mataonsis	no data									
matochata	no data				- man a serie son a fair a Braker			-4.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1.1		
havannensis	1.80	A	194	9	3.79	15.3	588	118	48.0	60
maskelynensis	1.70	A	218	11	2.21	12.5	880	136	76.9	28
maskelynensis	1.64	A	255	11	2.41	14.1	780	116	68.0	34
maskelvnensis	1.68	A	278	10	2.43	13.1	763	128	69.1	32
maskelynensis	1.70	<u>A</u>	230		2.44	13.4	821	126	69.6	33
maskelvnensis*	1.58	A	230	9	2.46	13.9	647	114	64.2	34
maskelynensis	1.60	A	218	11	2.65	13.6	809	117	60.3	36
maskelynensis	1.66	A	240	13	2.76	14.2	915	116	60.1	39
maskelynensis	1.65		238	11	2.48	13.5	802	122	66.9	34
(mean)	1.02				2.10	10.0	002			
malalamain	1.64	A	240	11	2.55	11.2	002	146	64.2	20
maloloensis	1.64	A	249	11	2.55	11.2	982	140	64.3	29
maloloensis	1.05	A	264	11	2.55	12.4	057	133	61.7	32
maloloensis	1.60	A	262	11	2.39	11.5	951	139	58.1	30
malologusis	1.55	A	235		2.07	12.7	000	122	60.2	34
malolognsis	1.05	A	240	11	2.74	12.4	602	103	50.2	44
maloloensis	1.03	A	244		2.79	13.9	720	105	50.2	44
maloloonsis	1.02	A	255	11	2.75	14.9	897	122	60.0	3/
malologneis	1.05	A	209	11	3.00	14.0	786	117	55.0	42
maloloansis	1.05	A	230	11	5.00	14.0	780	11/	55.0	72
(mean)	1.63		254	11	2.71	13.0	854	126	60.3	36

Table 1 (1). Radula characters and indices (* denotes radula figured on Figs 145-146).

Species	Shell L(mm)	Ad. /Juv	Plate Count	Cusp	Pitch	W (um)	Cusps /mm	L:W	L:P index	PxW index
	L(IIIII)	7047.	Count	Count	(µm)	(µm)	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	mucx	mucx	Index
cf. C. tricinctus	no data									
begae	1.47	A	186	9	3.30	12.9	698	113	44.5	43
begae	1.46	A	164	11	3.85	14.9	759	100	37.9	56
begae	1.44	A	191	9	3.96	14.4	625	100	36.3	57
beqae	1.46		180	10	3.70	14.1	694	104	39.6	52
(mean)										
deeae	1.29	A	231	7	2.54	8.70	805	148	50.7	22
deeae	1.19	A	194	7	2.90	8.00	875	148	41.0	23
deeae	1.19	A	177	7	3.00	8.60	814	138	39.6	26
deeae	1.22		201	7	2.81	8.43	831	145	43.8	24
(mean)										
pusillus	no data			100	1000		1000		1000	-

Table 1 (II). Radula characters and indices (* denotes radula figured on Figs 145-146, 148).