

AN OVERVIEW OF THE SPECIFIC DIVERSITY IN THE GENUS *CYSTISCUS* STIMPSON, 1865 AND THE DESCRIPTION OF 27 NEW *CYSTISCUS* SPECIES (MURICOIDEA: CYSTISCIDAE) FROM THE WALTERS SHOAL, SOUTHWESTERN INDIAN OCEAN

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Abstract The *Cystiscus* fauna collected on the Walters Shoal by the 2017 MNHN/IRD Expedition is revised on the ground of shell morphology. Twenty-nine different species are recognized, 27 of them being formally described as *Cystiscus subcylindricus*, sp. nov., *C. triplicatus* sp. nov., *C. herberti* sp. nov., *C. inflatus* sp. nov., *C. stimpsoni* sp. nov., *C. pyriformis* sp. nov., *C. harpaeformis* sp. nov., *C. laurae* sp. nov., *C. robustus* sp. nov., *C. minimus* sp. nov., *C. ovooides* sp. nov., *C. mamillatus* sp. nov., *C. angustus* sp. nov., *C. profundus* sp. nov., *C. granum* sp. nov., *C. dentiferus* sp. nov., *C. alatus* sp. nov., *C. apertus* sp. nov., *C. contortus* sp. nov., *C. sinuosus* sp. nov., *C. pupoides* sp. nov., *C. lussii* sp. nov., *C. smithi* sp. nov., *C. serratus* sp. nov., *C. lachrymaformis* sp. nov., and *C. quinqueplicatus* sp. nov. Among the 27 described species, 25 of them are only known from their holotype, one paratype from the type station is reported for *C. subcylindricus*, and two conspecific specimens collected from a non-type station are reported for *C. lussii*. Eight morphs represented by one or two shells are tentatively ascribed to some of the 27 recognized species. Among the 29 recognized species, 28 of them are found at bathyal levels, and only one of them (*C. quinqueplicatus*) was collected at a reef level, so the *Cystiscus* fauna of the Walters Shoal is characterized as bathyal fauna. From the fact that any other *Cystiscus* assemblage was ever studied from the bathyal of the Indo-Pacific Province, no direct comparison is made with external items, and the *Cystiscus* species of the Walters Shoal are only compared to each other.

Key words *Cystiscidae*, *Cystiscus*, Walters Shoal, Southwest Indian Ocean, bathyal levels, shell morphology, phenetic disparity, species diversity, twin species.

INTRODUCTION

The benthic fauna of the Walters Shoal was subject to pioneer samplings in April-May 2017, through a campaign managed in the frame of the Tropical Deep-Sea Benthos Program. This MNHN/IRD Expedition (MD 208) embarked on the research vessel Marion-Dufresne and it lasted 23 days (from April 26th to May 18th). The Walters Shoal formation is located about 700km south of Madagascar and it peaks at 16m, most of its slopes belonging, however, to the bathyal field. Such a wide seamount (400 km² over the 500m isobath), discovered only in 1969, holds an original biogeographic status, being isolated at the southern tip of the Madagascar Plateau, far from the African continent and from the Mascarene Archipelago as well. The Shoal is situated at a subtropical/temperate latitude in the southwestern section of the Indian Ocean and it is excluded from the South African subprovince.

In such conditions, a high level of endemism was expected for the benthic fauna of the Walters Shoal. Scant prevalence of both biomass and

biodiversity was noted by the contents of the first samples taken, especially for the bathyal levels which constitute by far most of the Walters Shoal seabed. As a matter of fact, the real rate of endemism on the Walters Shoal as well as the figure of the local biodiversity prove to be more ambivalent in several respects. We tested for instance the occurrence of the widespread and much diversified molluscan group of the marginelliform gastropods, and the results were very asymmetric: at reef levels, some specimens of a *Hyalina* species (*Marginellidae*) matching closely *H. lucida* (Marrat, 1817), documented from South Africa, Southern Mozambique and Southern Madagascar; at reef and bathyal levels, some specimens of a *Gibberula* species (*Cystiscidae*) showing affinities with *G. elisae* Bozzetti & Cossignani, 2009, described from the southern tip of Madagascar; and about 37 separable morphospecies of tiny *Cystiscus* (*Cystiscidae*), all but one collected from bathyal levels and most often represented by only one specimen. Such a structure of the marginelliform fauna is deeply contrasting with the structure of the assemblages known from the neighbouring places at tropical

latitudes (Madagascar, Southern Mozambique and the Mascarene Archipelago) or at subtropical/temperate latitudes (South Africa): for example a great diversity of marginelliform genera is occurring at the reef levels of the Mascarenes (in the Marginellidae: no *Hyalina* species, but some species of *Volvarina*, *Closia*, *Marginella*, *Glabella*, *Dentimargo*, *Demissa*, *Serrata* and *Hydroginella*; in the Cystiscidae: a good number of *Gibberula* species and few *Cystiscus*; in the Granulinidae: some few *Granulina* species), whereas only some *Hydroginella* species were collected at bathyal level off La Réunion by the MD55 MNHN campaign [for these results, see Boyer (2004, 2014, 2015, 2016) and Boyer & Rosado (2019)]. Such a contrasting situation is not explained for now and it would deserve a special investigation by itself.

We focus here on the case of the *Cystiscus* assemblage collected on the Walters Shoal, studying the specific diversity and the phenetic disparity on the ground of the shell material conserved in the MNHN collection, and comparing the results as much as possible with other situations observed at different biogeographic scales (Indian Ocean, Southern Indo-Pacific, bathyal levels). The case of the population of *Hyalina* cf. *lucida* will be tackled in a separate review.

The *Cystiscus* fauna from the Pacific waters has been subject to three large scale revisions in the last 20 years. Boyer (2003) revised three species attributed to *Cystiscus* Stimpson, 1865 and described in the same genus 16 further species from the reef levels of the New Caledonia mainland. In 2005, Wakefield & McCleery described three new species from the reef levels of Tuamotu, and in 2006 they described eleven new species from reef levels of South Pacific sharing 'banded mantle patterns', from southern New Caledonia up to the Society Islands. Boyer (2003) established the importance of the study of soft parts chromatism for the identification at the species level in this group. The shells presented few diagnostic features by themselves and radiations of species sharing similar shells proved to be quite usual in *Cystiscus*, whereas the animal chromatism proved to be constant and most often well-characterized in each species. Through the study of a New Caledonia species clearly matching the animal features of *Plesiocystiscus* Coovert & Coovert, 1995, in addition Boyer discussed the high phenetic differences occurring between

the *Cystiscus* group and the *Plesiocystiscus* twin group, both for the morphology of the animal (red eyes and slitted head with no tentacles for *Cystiscus*, versus black eyes and unslitted head with long tentacles for *Plesiocystiscus*) and for the morphology of the radula (single rachidian plate for *Cystiscus*, versus rachidian plate and several laterals for *Plesiocystiscus*), despite their close similarity in the shell pattern. Boyer also underlined the scarce occurrence of *Plesiocystiscus* in the New Caledonia waters, evidencing in this genus only the new species *P. bavayi*, a large tear-shaped shelled species characterized by its animal features (black eyes and unslitted head with long tentacles), versus 19 *Cystiscus* species documented from the seas around the New Caledonia mainland on the ground of their animal features. The Boyer's tentative attribution of *Marginella tomlini* Bavay, 1917 to *Plesiocystiscus* on the simple ground of its shell features is less convincing. Wakefield & McCleery (2005 & 2006) documented the soft parts of the animals and tackled the point of the low variability of shell morphology and animal chromatism within the *Cystiscus* species under study. Despite his extensive samplings and observations of the live populations of cystiscids throughout the South Pacific waters, Tony McCleery did not observe any *Plesiocystiscus* species from this area (pers. comm.).

In the last 25 years, few authors have tackled the *Cystiscus* fauna from the southwestern Indian Ocean. Bozzetti (1997) did describe a narrow and slender shelled species from Zanzibar as *Hyalina gibberuliformis*, the generic attribution not being explained and the shell of the species matching the features found in species recognized by Boyer (2003) as belonging to *Cystiscus*. Lussi & Smith (1998) proposed a review of the Cystiscidae from the upper reef levels of South Africa (0–40m) based on the shell features, revising three species in *Cystiscus*, one in *Crithe*, Gould, 1860 and three in *Plesiocystiscus*, and describing six further species as new in these genera (two being proposed in *Cystiscus* and four in *Plesiocystiscus*). However, Lussi & Smith did not revise the elusive South African *Cystiscus capensis* Stimpson, 1865 (renamed as *Marginella cystiscus* Redfield, 1870), type species of the genus *Cystiscus* and revised by Coovert (1986 a) without reference to any living population. [The type species of *Cystiscus cystiscus* (Redfield, 1870) is lost. There

are no shells from the type locality of False Bay or indeed anywhere off South Africa that resemble the line-drawing of Coover & Coover (1995). It is possible that this shell never came from South Africa]. The generic attributions to *Plesiocystiscus* and to *Crithe* proposed by Lussi and Smith are not convincing, as any clear distinctive features are not evidenced at the genus level for the shell structure, and no documentation is given on the animal and radula features. Their placements in *Plesiocystiscus* are not explained and they look to be quite eclectic, the assigned shells presenting very contrasting outlines (from subtriangular to subcylindrical, ogival or heart-shaped) and ranging from 2 to 16 columellar plaits or lirations. The single placement in *Crithe* is also not explained and despite the superficial shell similarity of the considered species with the type species of *Crithe*, the point deserves to be deepened, as several species from New Caledonia look as intergrading between 'typical *Cystiscus*' and 'typical *Crithe*' for their shell shape, and their respective animal morphologies and chromatism looking to be often similar. As a matter of fact, despite a possible disparity in the shape of their rachidian plates, the separation of the genera *Crithe* and *Cystiscus* might prove to be artificial or more precisely these two generic assignments might encompass a more puzzling reality. In the wait for further investigation and on the ground of the similarity of their shell features with that of the species recognized as true *Cystiscus* species in New Caledonia, most of these South African species (if not all of them) seem to belong to the genus *Cystiscus*.

Boyer (2004) described a new species from Mauritius as *Cystiscus viaderi* (Figs 1A–B), on the ground of its slender subtriangular shell outline, of the animal morphology and chromatism (slitted head and red eyes, alternated orange and black bands), and of the radula pattern (single rachidian plate with four heavy subequal rounded cusps), suggesting the occurrence of a widespread '*C. viaderi* species group' ranging in the Indo-Pacific waters and characterized by slender subtriangular shells and bicoloured banded animals with alternated black and orange/yellow bands. Cossignani (2009) described a tiny and squat heart-shaped shelled species from La Réunion as *Cystiscus mainardii*, the generic attribution looking to be right as the shell of *C. mainardii* is matching closely several

species from New Caledonia recognized by Boyer (2003) as belonging to *Cystiscus* on the ground of their animal morphology. Bozzetti, Da Costa & Cossignani (2010) did describe in *Plesiocystiscus* four new species from northern Mozambique (Pemba), with animal chromatism more or less visible through transparency of the shell: two of these species seem to have a creamy unicoloured animal and they closely match *Cystiscus mainardii* Cossignani, 2009 for their tiny size and their heart-shaped outline; the two other species look very similar to *Cystiscus viaderi* Boyer, 2003 for their slender subtriangular shell outline, but they seem to differ noticeably from each other with regards to the animal chromatism, one of them belonging clearly to the 'banded *C. viaderi* species group' with alternating orange and black bands, whereas the other species shows a uniform beige-brown colour. On the ground of these elements, we propose to provisionally place these four species described by Bozzetti *et al.* (2010) in the genus *Cystiscus* *sensu lato*.

As a matter of fact, the occurrence of real *Plesiocystiscus* species seems to be very uncommon in the Indo-Pacific province. Besides the single *Plesiocystiscus* species clearly attested from New Caledonia, we can only report for now with certainty an undescribed *Plesiocystiscus* species from Masirah Island (Eastern Oman: pers. obs.), quite similar to the massive tear-shaped shelled *P. bavayi* Boyer, 2003 from New Caledonia. From these observations, we are provisionally inferring that *Plesiocystiscus* is only represented with evidence in the Indo-Pacific province by a small species group of large tear-shaped species, dredged on soft bottoms at upper reef levels from Oman to New Caledonia, possibly as very localized relict species. Out of this small group, all similar white and smooth-shelled species from the Indo-Pacific deprived of outer margin, labial teeth and of siphonal notch must be provisionally considered as belonging to the genus *Cystiscus* or to its twin-group *Crithe* (the revision of the latter being under study by the author). On the ground of the present documentation about the animal morphology and of the radular pattern, the complex *Cystiscus/Crithe* seems to be restricted to the Indo-Pacific waters, whereas the genus *Plesiocystiscus* and sibling genera are mainly found in the Atlantic waters and in the Panamic province, with the exception of the elusive *P. bavayi* species group

restricted to small regions of the Indo-Pacific province.

The genus *Crithe* is mainly recognized on the ground of thick rounded shells with many columellar plaits and inner lirations, and of a distinctive asymmetrical radular plate (Covert, 1986 b & 1987), but any of the morphospecies studied from the Walters Shoal does not match the typical shell features of the genus *Crithe* (type species: *Crithe atomaria* Gould, 1860). On this ground and despite the absence of information about the animals and radulae features, we shall provisionally attribute to *Cystiscus* all the forms hereunder studied from the Walters Shoal.

MATERIAL & METHODS

Cystiscus lots were sampled at nine stations on the Walters Shoal, one lot from a reef level (40m) and eight other lots from bathyal levels (275m to 707m). All lots were composed of empty shells, collected in more or less worn condition, many of them resembling subfossil individuals. Only one morphospecies occurs at reef levels, whereas 2 to 10 morphospecies occur in each of the bathyal stations. Among 37 selected morphospecies, one is represented by 3 specimens (2 adults and 1 subadult), another one is represented by 2 adult shells, and a third morphospecies is represented by one fully preserved adult shell and one partially broken adult shell showing a more inflated outline. The 34 other morphospecies are represented by only one shell. Some shells or fragments were excluded from the study: one juvenile shell in good condition with a size of 1.10mm, was not assignable to any adult phenotype, five very damaged shells (deeply corroded shells, broken shells and shell fragments) were not taken into account for this study, not usable for an original description of a specific assignation. A tiny adult specimen, with narrow slender shell, quite produced spire and four plaits, clearly belonging to a distinctive species, was lost during laboratory manipulations. Eight morphospecies were considered as possibly conspecific with other forms described as good species and reported as '*Cystiscus* cf. X'. One morphospecies showed a distinctive cylindrical shell shape but was not described as a new species due to the damaged state of the shell and to the filling of the aperture by sediment.

Despite the poor state of the specimens, SEM photography did give pictures of use for a phenetic study and to proceed to a description. Great care was taken with the orientation of the body whorl and of the aperture in relation to the plane of the camera sensor, the slightest displacements of the axis or of the aperture orientation induced major changes in the perception of the features and in the comparability of individuals (Fig. 1C: *Cystiscus* shell photographed with the aperture and the body axis well-arranged in the photo plane; Fig. 1D: the same shell photographed with slight changes in the lateral orientation of the aperture and in the depth orientation of the body axis).

The diagnostic methods are inspired by previous large-scale works about *Cystiscus* faunas performed by Boyer (2003 & 2004) and by Wakefield & McCleery (2005 & 2006). For convenience of the shell comparisons, we shall dispatch the pictures and the descriptions according to three successive 'groups of form', namely the subpyriform, subtriangular and ovoid shapes. In fact, the shell of several species is intergrading between two or three of these shapes, and such a convenience grouping cannot be considered as reflecting closer phyletic affinities or as having any taxonomic value. The species will be compared to the closer congeners from the Walters Shoal, but not with species from other regions, those from southwestern Indian Ocean being all studied from the intertidal and infratidal zones and not comparable with a bathyal fauna, and those from the Australian region or from northern Indian Ocean as they are distant regions: in such cases, any kind of resemblance in shell morphology may come from a phenomenon of convergence or from chance as well as from a phyletic proximity.

In the description of the shell features, we shall use the term 'oblique' in reference to the horizontal plane. We shall use the term of 'sibling species' for the closely matching morphs, and the term of 'twin species' for undiscernable or about undiscernable morphs. The comparisons being made only on grounds of the shell morphology, the inferences drawn in our remarks are naturally only valid from the point of view of the shell morphology, without regard for other features which may change deeply our conclusions, such as the animal chromatism or the radula pattern for instance.

Abbreviations & Acronyms

MNHN:	Muséum national d'Histoire naturelle, Paris
NMW:	National Museum of Wales, Cardiff
IRD:	Institut de Recherche pour le Développement, Marseilles
ad:	adult
juv:	juvenile
sh:	shell
stn:	station
L:	shell length

SYSTEMATICS

Superfamily Muricoidea Rafinesque, 1815

Family Cystiscidae Stimpson, 1865

Subfamily Cystiscinae Stimpson, 1865

Genus *Cystiscus* Stimpson, 1865 (syn: *Euliginella* Laseron, 1957)

Type species: *Cystiscus capensis* Stimpson, 1865 (non-*Marginella capensis* Krauss, 1848)=*Marginella cystiscus* Redfield, 1870 (nom. nov.); by monotypy.

For the discussion about the Family status, refer to Covert & Covert (1995); for the discussion about the type species, refer to Covert (1986).

Cystiscus subcylindricus sp. nov. (Figs 1E–L)

urn:lsid:zoobank.org:act:7B0D0667-511C-4136-AE2A-FECAD4581C7F

Holotype 1 ad. sh. (Figs 1E–F, L=1.17mm); MNHN-IM-2000-38469; as sp. 20 in MNHN collection.

Paratype 1 ad. sh. (Figs 1G–H, L=1.07mm); MNHN-IM-2000-38496; as sp. 21 in MNHN collection.

Locality WALTERS SHOAL; Stn DW 4880: 33° 17' S -43° 51' E; depth 275–318m.

Other material As *Cystiscus* cf. *subcylindricus* sp. nov.: WALTERS SHOAL. 1 ad. sh. (Figs 1I–J), L=1.17mm); Stn DW4881: 33° 16' S - 43° 50' E; depth 377–382m; as sp. cf. 20 in MNHN collection. WALTERS SHOAL. 1 ad. sh. (Figs 1K–L, L=1.25mm); Stn DW 4887: 33° 17' S - 43° 57' E; depth 599–640m; as sp. 33 in MNHN collection.

Derivation of name The species name refers to the subcylindrical outline of the shell.

Description Shell morphology (Figs 1E–F): Subpyriform cylindrical outline, numerous thin vertical growth lines on the entire body whorl, flat top with the spire whorl making a distinct circular varicose pleat, tiny nipple-like protoconch, wide regular aperture, progressively widening in the lower part, subvertical labrum, thin labial lip, shoulder of the labrum quite angular and slightly elevating over the top, siphonal canal making a slight break on its left side, five well-spaced thin columellar plaits (the upper one only just visible), the basal one oblique and weakly bent, the three upper ones less oblique and decreasing in size.

Remarks The paratype of *Cystiscus subcylindricus* sp. nov. (Figs 1G–H) differs from the holotype by its slightly less widened aperture and by the faint break at the left of the siphonal canal. The two specimens associated as *C. cf. subcylindricus* (Figs 1I–L) differ respectively by their more pyriform or their more cylindrical outlines, and especially by their more narrowed aperture. These two species do not seem to be incompatible with *C. subcylindricus*, but from the fact that they were collected at deeper levels, we prefer to reserve the possibility that they may as well belong to a sibling species.

Cystiscus triplicatus sp. nov. (Figs 1M–P)

urn:lsid:zoobank.org:act:02BE33BE-579C-4700-BC66-6797C3A33D91

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 1M–N, L=1.24mm); Stn DW 4886: 33° 17' S - 43° 56' E; depth 573–582m; MNHN-IM-2000-38470; as sp. 16 in MNHN collection.

Other material WALTERS SHOAL. 1 ad. sh. (Figs 1O–P, L=1.17mm); Stn DW 4887: 33° 17' S - 43° 57' E; depth 599–640m; as sp. 10 in MNHN collection.

Derivation of name The species name refers to the presence of three plaits on the shell columella.

Description Shell morphology (Figs 1M–N): Moderately subpyriform outline, flat top with the spire whorl forming a poorly marked circular varix, protoconch minute and almost completely absorbed, aperture narrow and barely widening in its lower part, weakly oblique labrum, moderately thickened labial lip, shoulder of the labrum



Figs 1A–B *Cystiscus viaderi* Boyer, 2004, holotype MNHN-IM-2000-4551, L=1.5mm, Flic-en-Flac, Mauritius. **Figs 1C–D** *Cystiscus* sp. 15, L=1.06mm, Walters Shoal, Stn DW 4893, 623–629m. **Figs 1E–F** *Cystiscus cylindricus* sp. nov., holotype MNHN-IM-2000-38469, L=1.17mm, Walters Shoal, Stn DW 4880, 275–318m. **Figs 1G–H** *Cystiscus cylindricus* sp. nov., paratype MNHN-IM-2000-38496, L=1.07mm, Walters Shoal, Stn DW 4880, 275–318m. **Figs 1I–J** *Cystiscus* cf. *cylindricus* sp. nov., L=1.17mm, Walters Shoal, Stn DW 4881, 377–382m. **Figs 1K–L** *Cystiscus* cf. *cylindricus* sp. nov., L=1.25mm, Walters Shoal, Stn DW 4887, 599–640m. **Figs 1M–N** *Cystiscus triplicatus* sp. nov., holotype MNHN-IM-2000-38470, L=1.24mm, Walters Shoal, Stn DW 4886, 582–573m. **Figs 1O–P** *Cystiscus* cf. *triplicatus* sp. nov., L=1.17mm, Walters Shoal, Stn DW 4887, 599–640m.

quite angular and slightly elevating over the top, siphonal canal making a very slight break on its left side, three well-spaced columellar plaits, the basal one being thin, oblique and weakly bent, the second one short and slightly thicker, the third one much longer and thicker, and making an angled varix running in its upper part along the columellar edge.

Remarks *Cystiscus triplicatus* sp. nov. differs principally from *C. subcylindricus* by the presence of three columellar plaits instead of four, the third plait being noticeably longer and thicker than in *C. subcylindricus*. The narrow aperture, the thicker labial lip and the faint break at the left of the siphonal canal just can be considered as subsidiary discriminant features between both species. The specimen associated as *C. cf. triplicatus* (Figs 1 O–P) is roughly compatible with *C. triplicatus* for the general outline of its body whorl and for its narrow aperture, but it differs by its more produced spire and especially by the presence of four columellar plaits very similar to what is observed in *C. subcylindricus* (Figs 1 E–F). As far as the shell morphology is concerned, this morph looks more or less as intergrading between *C. triplicatus* and *C. subcylindricus*, and its specific status must be reserved in the present state.

Cystiscus herberti sp. nov. (2A–B)

urn:lsid:zoobank.org:act:86B6490D-ACC4-4ED5-BED8-8EB49972484F

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 2A–B, L=1.32mm); Stn DW 4887: 33° 17' S – 43° 57' E; depth 599–640m; MNHN-IM-2000-38471; as sp. 31 in MNHN collection.

Derivation of name The species is dedicated to David G. Herbert, Research Associate at NMW, for his contribution to the investigation of the molluscan collections from the Walters Shoal.

Description Shell morphology (Figs 2A–B): Oval and quite inflated outline, low spire, absorbed minute protoconch, aperture quite narrowed in its upper part but progressively widening towards the base, moderately arched labrum, more thickened in its peripheral part, weakly shouldered, siphonal canal wide with rounded base, columella with three well-spaced columellar plaits, the first one being moderately thickened, oblique and making a slight angle at its

upper third part, second plait thin and arched, third plait small, thin and sinuous, running along the columellar edge.

Remarks *Cystiscus herberti* sp. nov. differs mainly from the previous congeners by its more oval outline and by its sinuous and very oblique third plait.

Cystiscus inflatus sp. nov. (Figs 2C–F)

urn:lsid:zoobank.org:act:38FC4565-9D2F-46AF-8999-CCD97831C3FB

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 2C–D, L=1.22mm); Stn DW 4881: 33° 16' S – 43° 50' E; depth 377–382m; MNHN-IM-2000-38472; as sp. 24 in MNHN collection.

Other material As *Cystiscus cf. inflatus* sp. nov.: WALTERS SHOAL. 1 subad. sh. (Figs 2E–F, L=1.65mm); Stn DW4886: 33° 17' S – 43° 56' E; depth 573–582m; as sp. 1bis in MNHN collection.

Derivation of name The species name refers to the inflated shape of the shell.

Description Shell morphology (Figs 2C–D): Oval subpyriform outline, quite inflated, low spire with quite pointed small protoconch, aperture quite narrowed in its upper part and noticeably widened in its lower part, thin labrum, slightly sinuous, shoulder quite angular and slightly elevated, siphonal canal long and making a noticeable break on its left side, four columellar plaits quickly decreasing in size and in interspaces, the first one being thin, oblique and sinuous, the three upper ones quite packed and weakly oblique.

Remarks *Cystiscus inflatus* sp. nov. differs from *C. herberti* (Figs 2A–B) by its more pyriform outline, longer siphonal canal and by the presence of four columellar plaits instead of three, these plaits being moreover very different in their respective size, shape and place. The specimen presented as *C. cf. inflatus* (Figs 2E–F) looks like a subadult of *C. inflatus* for its shell outline and for its long siphonal canal, but its outline is more pyriform, the spire is higher and it has only three columellar plaits, the second and the third ones being slightly less oblique than in *C. inflatus*. Furthermore, this subadult shell is 1.65mm in size, whereas the type of *C. inflatus* is 1.22mm,

what leads to infer that the respective sizes at adult stage would be noticeably contrasted between the two morphs. On this background, the identity of *C. cf. inflatus* cannot be allocated to any known species.

Cystiscus stimpsoni sp. nov. (Figs 2G–J)

urn:lsid:zoobank.org:act:C230A1B4-4DC8-4A13-9A7B-0FA52B69186A

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 2G–H, L=1.21mm); Stn DW 4893: 33° 16' S – 43° 58' E; depth 623–629m; MNHN-IM-2000-38473; as sp. 14 in MNHN collection.

Other material As *Cystiscus cf. stimpsoni* sp. nov.: WALTERS SHOAL. 1 ad. sh. (Figs 2I–J, L=1.17mm); Stn DW4887: 33° 17' S – 43° 57' E; depth 599–640m; as sp. 34 in MNHN collection.

Derivation of name The species is dedicated to William Stimpson, who relevantly created the Family Cystiscidae and the genus *Cystiscus* in 1865.

Description Shell morphology (Figs 2G–H): Slender oval subpyriform outline, spire whorls level with low nipple-like protoconch, aperture quite narrowed in its upper part and moderately widened in its lower part, labrum thin and poorly arched, shoulder elevated and strongly angular, siphonal canal moderate, making a weak break on its left side, four spaced columellar plaits, basal plait thin, oblique and sinuous, three upper ones decreasing quickly in size.

Remarks *Cystiscus stimpsoni* sp. nov. differs from *C. subcylindricus* mainly (Figs 1E–F) by its more slender and oval outline, and by its more elevated and more angular labial shoulder. The columellar plaits of these two morphs are similar. The specimen presented as *C. cf. stimpsoni* (Figs 2I–J) is roughly comparable to *C. stimpsoni*, but its shell is more inflated, the labial shoulder is damaged and the columellar plaits are poorly visible due to the partial filling of the aperture. On this ground, the identity of this specimen cannot be allocated to any known species.

Cystiscus pyriformis sp. nov. (Figs 2K–L)

urn:lsid:zoobank.org:act:39F53958-7950-4F93-A7F0-79523C828A8F

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 2K–L, L=1.04mm); Stn DW 4887: 33° 17' S – 43° 57' E; depth 599–640m; MNHN-IM-2000-38474; as sp. 11 in MNHN collection.

Derivation of name The species name refers to the subpyriform outline of the shell.

Description Shell morphology (Figs 2K–L): Oval subpyriform outline, flat top with absorbed protoconch, aperture quite narrowed in its upper part and poorly widened in its lower part, thick labrum, moderately arched, shoulder elevated and much arched, siphonal canal long, making a noticeable break on its left side, four columellar plaits, the first one quite long, oblique and straight, the second one quite long, thin and arched, the two upper ones small and poorly distinct.

Remarks *Cystiscus pyriformis* sp. nov. differs from *C. stimpsoni* (Figs 2G–K) mainly by its thicker shell, its more pyriform outline and its highly arched upper labrum. The two morphs seem to be quite similar as far as their columellar plaits.

Cystiscus harpaeformis sp. nov. (Figs 2M–N)

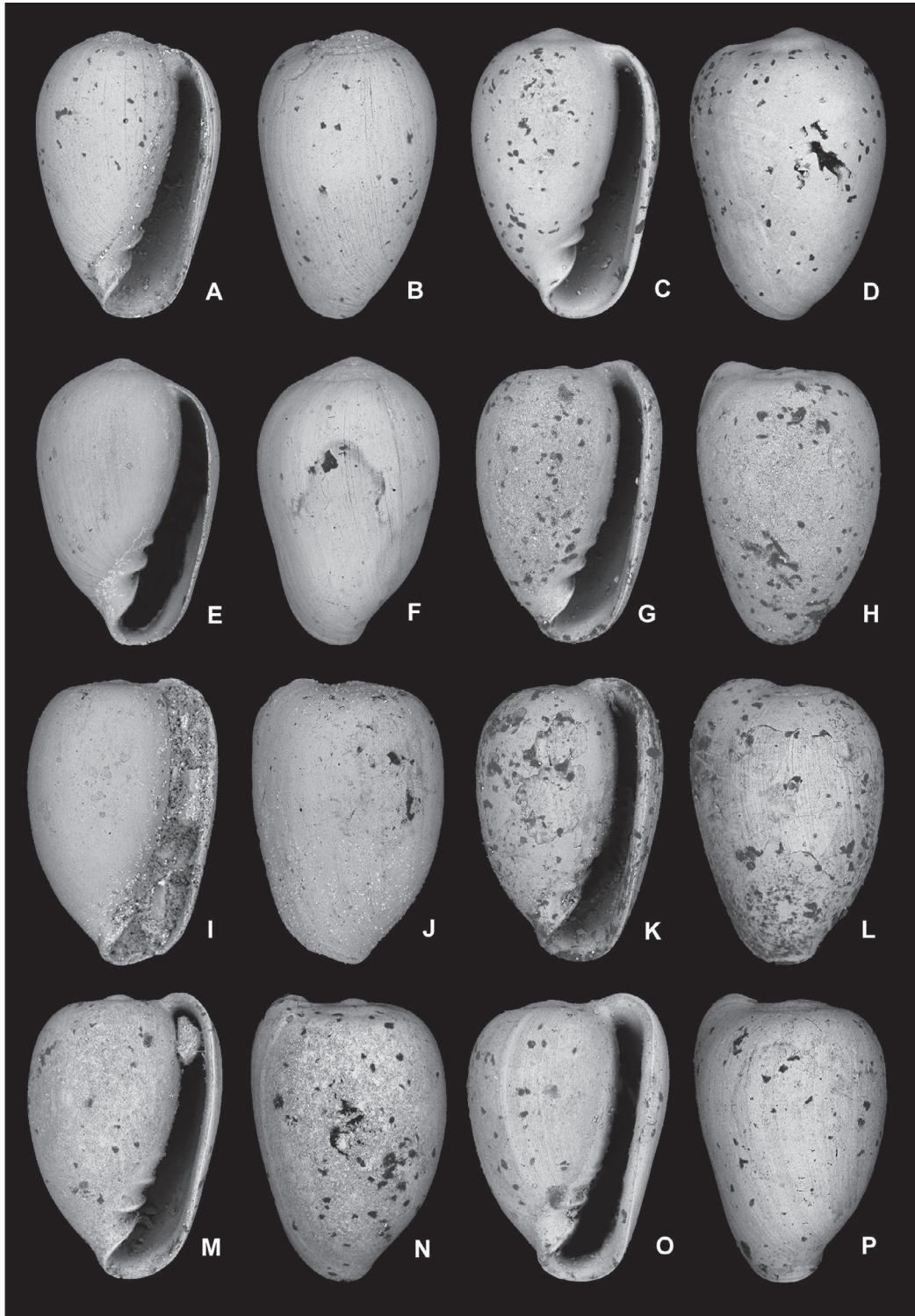
urn:lsid:zoobank.org:act:FEA66A24-E9F9-44F9-B904-E2C7BB50C1B7

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 2M–N, L=1.14mm); Stn DW 4881: 33° 16' S – 43° 50' E; depth 377–382m; MNHN-IM-2000-38475; as sp. 25 in MNHN collection.

Derivation of name The species name refers to the harp-shaped outline of the shell.

Description Shell morphology (Figs 2M–N): Inflated subpyriform outline, flat top with strong teat-like protoconch, aperture quite narrowed in its upper part and poorly widened in its lower part, thin labrum, shoulder much elevated and angular, siphonal canal long, making a noticeable break on its left side, four thin columellar plaits, well-spaced and decreasing regularly in size, the first basal plait being oblique and quite sinuous, the three upper ones being poorly oblique.

Remarks *Cystiscus harpaeformis* sp. nov. differs from *C. pyriformis* (Figs 2K–L) by its thinner shell, its more inflated outline, its strong protoconch and its sharp elevated upper labrum.



Figs 2A–B *Cystiscus herberti* sp. nov., holotype MNHN-IM-2000-38471, L=1.32mm, Walters Shoal, Stn DW 4887, 599–640m. **Figs 2C–D** *Cystiscus inflatus* sp. nov., holotype MNHN-IM-2000-38472, L=1.22mm, Walters Shoal, Stn DW 4881, 377–382m. **Figs 2E–F** *Cystiscus* cf. *inflatus* sp. nov., L=1.65mm, Walters Shoal, Stn DW 4886, 582–573m. **Figs 2G–H** *Cystiscus stimpsoni* sp. nov., holotype MNHN-IM-2000-38473, L=1.21mm, Walters Shoal, Stn DW 4893, 623–629m. **Figs 2I–J** *Cystiscus* cf. *stimpsoni* sp. nov., L=1.17, Walters Shoal, Stn DW 4887, 599–640m. **Figs 2K–L** *Cystiscus pyriformis* sp. nov., holotype MNHN-IM-2000-38474, L=1.04mm, Walters Shoal, Stn 4887, 599–640m. **Figs 2M–N** *Cystiscus harpaeformis* sp. nov., holotype MNHN-IM-2000-38475, L=1.14mm, Walters Shoal, Stn DW 4881, 377–382m. **Figs 2O–P** *Cystiscus laurae* sp. nov., holotype MNHN-IM-2000-38476, L=1.06mm, Walters Shoal, Stn DW 4881, 377–382m.

C. harpaeformis presents the same pattern of four spaced columellar plaits found in *C. stimpsoni* (Figs 2G–H), but with more arched and less oblique upper plaits.

Cystiscus laureae sp. nov. (Figs 2O–P)

urn:lsid:zoobank.org:act:20EAB9EA-182E-4637-BCBA-4A8BF22B6C30

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 2O–P, L=1.06mm); Stn DW 4881: 33° 16' S – 43° 50' E; depth 377–382m; MNHN-IM-2000-38476; as sp. 22 in MNHN collection.

Derivation of name The species is dedicated to Laure Corbari (MNHN/CNRS), who co-managed the Walters Shoal/MD208 Expedition.

Description Shell morphology (Figs 2O–P): Subtriangular pyriform outline, many thin vertical growth lines on the entire body whorl, weakly elevated spire with recessed minute protoconch, aperture strongly narrowing in its medium part, weakly widened in its lower part, thick and straight labrum, labial shoulder much elevated and sharply angular, siphonal canal long, making a noticeable break on its left side, indeterminate number of columellar plaits, the first basal plait being moderately thickened and straight, the second one making a short subhorizontal varix in shape of accent, and two or three blurred lirations seeming to occur on the rest of the columellar edge.

Remarks *Cystiscus laureae* sp. nov. is a distinctive species among its subpyriform congeners from the Walters Shoal, principally due to its triangular outline and its straight labrum.

Cystiscus robustus sp. nov. (Figs 3A–D)

urn:lsid:zoobank.org:act:9C42C690-D2CB-4CE0-95D9-369CCCE32CD7

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 3A–B, L=1.07mm); Stn DW 4881: 33° 16' S – 43° 50' E; depth 377–382m; MNHN-IM-2000-38477; as sp. 28 in MNHN collection.

Other material As *Cystiscus* cf. *robustus* sp. nov.: WALTERS SHOAL. 1 ad. sh. (Figs 3C–D, L=1.03mm); Stn DW 4887: 33° 17' S – 43° 57' E; depth 599–640m; as sp. 29 in MNHN collection.

Derivation of name The species name refers to the strong and thick appearance of the shell.

Description Shell morphology (Figs 3A–B): Squat rounded subpyriform outline, thick shell, spire damaged, supposed wide and low top, aperture quite narrow, moderately widening in its lower part, thick and arched labrum, labial shoulder strongly elevated and arched, siphonal canal wide and long, making a moderate break on its left side, four columellar plaits quickly decreasing in size and interspace, the first one thin, short, oblique and faintly arched, the second one much shorter and poorly arched, the two upper ones very short, thick and close-set.

Remarks Despite the spire having been damaged in the holotype, the species seems to have a wide and low top, almost flat (orientation of the shell curve in the upper body whorl). *Cystiscus robustus* sp. nov. differs from the other pyriform congeners by its squat outline, its very strong shell and its elevated and arched upper labrum. The specimen defined as *C. cf. robustus* (Figs 3C–D) is quite similar to *C. robustus* as for its squat pyriform outline and its quite narrow aperture, but its shell is less thick, its upper labrum is less elevated, and its two upper columellar plaits are not distinct and they seem to merge in a long vertical parietal varix running along the columellar edge. For these reasons the identity of this shell is reserved.

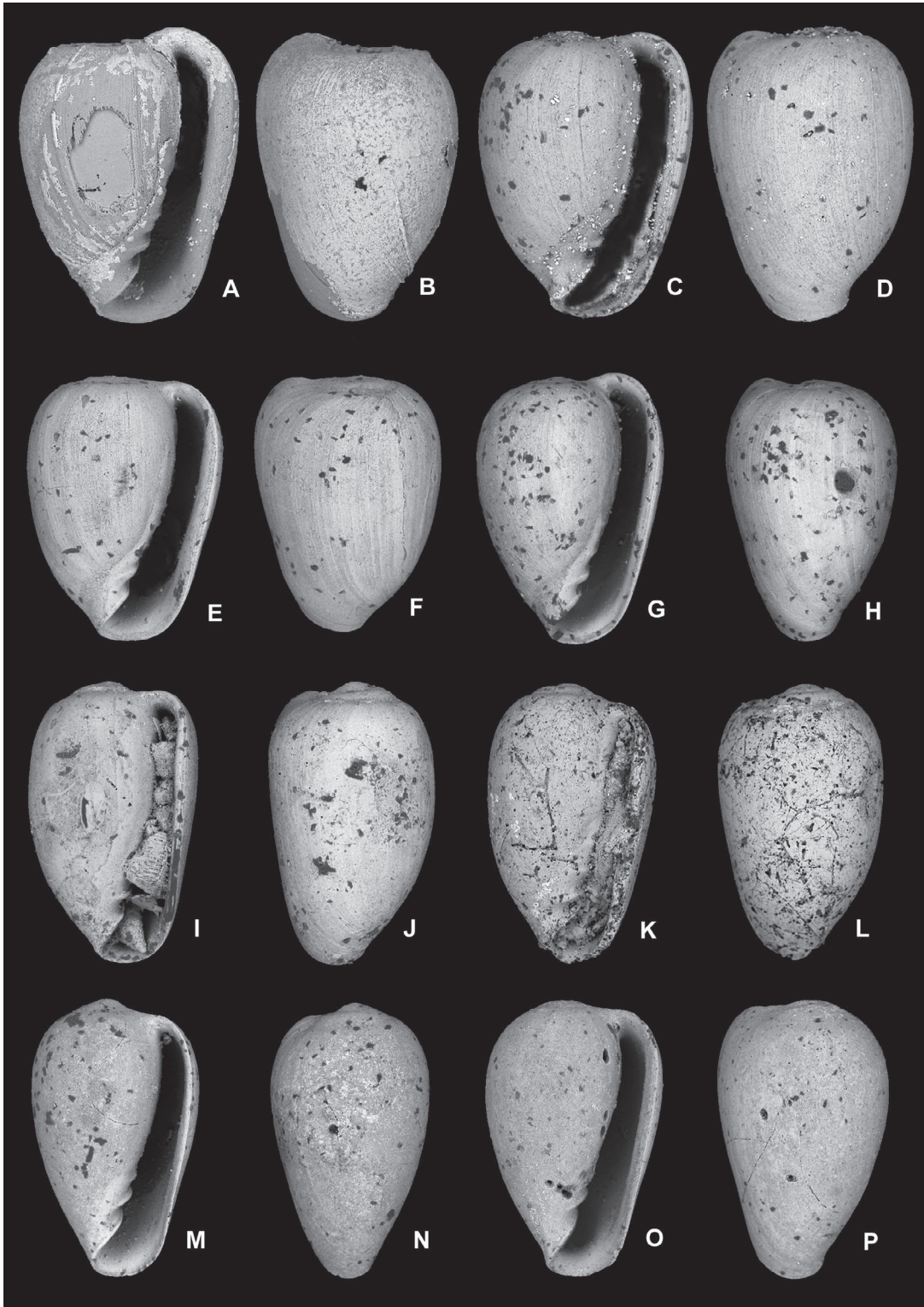
Cystiscus minimus sp. nov. (Figs 3E–F)

urn:lsid:zoobank.org:act:DBB61ADA-B3D7-43FE-BA2C-385DF0C6439D

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 3E–F, L=0.97mm); Stn DW 4899: 33° 09' S – 43° 58' E; depth 353–465m; MNHN-IM-2000-38478; as sp. 35 in MNHN collection.

Derivation of name The species name refers to the tiny size of the shell.

Description Shell morphology (Figs 3E–F): Short and quadrate, subpyriform outline, numerous thin growth lines giving an iridescent appearance to the surface of the body whorl, very low spire, almost level, minute absorbed protoconch, aperture moderate, weakly widening in its lower part, oblique, straight and moderate labrum, thinner and poorly elevated at its shoulder, siphonal



Figs 3A–B *Cystiscus robustus* sp. nov., holotype MNHN-IM-2000-38477, L=1.07mm, Walters Shoal, Stn DW 4881, 377–2382m. **Figs 3C–D** *Cystiscus* cf. *robustus* sp. nov., L=1.03mm, Walters Shoal, Stn DW 4887, 599–640m. **Figs 3E–F** *Cystiscus minimus* sp. nov., holotype MNHN-IM-2000-38478, L=0.97mm, Walters Shoal, Stn DW 4899, 707–720m. **Figs 3G–H** *Cystiscus ovoides* sp. nov., holotype MNHN-IM-2000-38479, L=1.06mm, Walters Shoal, Stn DW 4893, 623–629m. **Figs 3I–J** *Cystiscus mamillatus* sp. nov., holotype MNHN-IM-2000-38480, L= 1.34mm, Walters Shoal, Stn DW 4887, 599–640m. **Figs 3K–L** *Cystiscus* cf. *mamillatus* sp. nov., L=1.20mm, Walters Shoal, Stn DW 4879, 288–300m. **Figs 3M–N** *Cystiscus angustus* sp. nov., holotype MNHN-IM-2000-38481, L=1.32mm, Walters Shoal, Stn DW 4880, 275–318m. **Figs 3O–P** *Cystiscus* cf. *angustus* sp. nov., L=1.39mm, Walters Shoal, Stn DW 4890, 492–588m.

canal short and quite wide, with a weak break on its left side, six regularly spaced columellar plaits, the two lower ones being short, straight and oblique, the four upper ones being very short and quite obese, looking better as simple lirations on the columellar edge.

Remarks *Cystiscus minimus* sp. nov. differs from its subpyriform congeners by its quadrate outline, its much smaller size of 0.97mm and the occurrence of six regularly spaced columellar plaits, the four upper ones looking like simple lirations. *Cystiscus minimus* presents the smallest size observed in the *Cystiscus* fauna from the Walters Shoal.

Cystiscus ovoides sp. nov. (Figs 3G–H)

urn:lsid:zoobank.org:act:14069082-FE9E-44E2-9871-BFF2ABBBAA4C

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 3G–H, L=1.06mm); Stn DW 4893: 33° 16' S – 43° 58' E; depth 623–629m; MNHN-IM-2000-38479; as sp. 15 in MNHN collection.

Derivation of name The species name refers to the egg-shaped outline of the shell.

Description Shell morphology (Figs 3G–H): Egg-shaped outline with tapered base, numerous growth lines on, the body whorl, low and narrow spire, absorbed protoconch, medium sized, quite narrow aperture, moderately widening in its lower part, quite thin labrum, thinner and sharply elevated at its shoulder, siphonal canal long, with a weak break on its left side, three regularly spaced columellar plaits, the lower one quite straight and moderately thickened, the second one short, thicker, and quite angular, the upper one very short, thick and oblique, almost merging into the columellar callus.

Remarks *Cystiscus ovoides* sp. nov. differs from its oval-shaped congeners mainly by its elevated labrum and the organization and shape of its three columellar plaits.

Cystiscus mamillatus sp. nov. (Figs 3I–L)

urn:lsid:zoobank.org:act:BAB67205-B3B1-40BC-BFF5-EC0A5213469E

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 3I–J, L=1.34mm); Stn DW 4887: 33° 17' S – 43° 57' E;

depth 599–640m; MNHN-IM-2000-38480; as sp. 30 in MNHN collection.

Other material As *Cystiscus* cf. *mamillatus* sp. nov.: WALTERS SHOAL. 1 ad. sh. (Figs 3K–L, L=1.20mm); Stn DW4879: 33° 17' S – 43° 52' E; depth 288–300m; as 'Franck' in MNHN collection.

Derivation of name The species name refers to the mamillate top of the shell.

Description Shell morphology (Figs 3I–J): Narrow subcylindrical outline, mamillate spire with quite large and produced protoconch, narrow aperture, slightly widening in its lower part, labrum moderately thickened in its upper part and thinner in its lower part, moderately elevated, the two lower columellar plaits are visible, the first one being very thin and straight, the second one very short, thin and faintly oblique.

Remarks *Cystiscus mamillatus* sp. nov. differs from its congeners by its narrow cylindrical outline and its mamillated spire. Some gravel material is filling the aperture and possibly hiding upper columellar plaits, so their real number remains unclear. The specimen defined as *C. cf. mamillatus* (Figs 3K–L) is much damaged but it seems to match the general features of *C. mamillatus*, except for its lower labial shoulder. A third plait is also visible in this specimen, being quite short, thick and well-spaced from the second plait. Such variability of the height of the labial shoulder is often observed in *Cystiscus* (Boyer, 2003) and this specimen must be considered as being probably conspecific with *C. mamillatus*.

Cystiscus angustus sp. nov. (Figs 3M–P, 4A–B)

urn:lsid:zoobank.org:act:A8D0FF1B-B986-4A4E-9AAE-2B475EB79330

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 3M–N, L=1.32mm); Stn DW 4880: 33° 17' S – 43° 51' E; depth 275–318m; MNHN-IM-2000-38481; as sp. 5 in MNHN collection.

Other material As *Cystiscus* cf. *angustus* sp. nov. WALTERS SHOAL. 1 ad. sh. (Figs 3O–P, L=1.39mm); Stn DW4890: 33° 09' S – 43° 59' E; depth 492–588m; as sp. 6 in MNHN collection. WALTERS SHOAL. 1 ad. sh., partially broken (Figs 4A–B, L=1.24mm); Stn DW4879: 33° 17' S –

43° 52' E; depth 288–300m; as sp. 18 in MNHN collection.

Derivation of name The species name refers to the narrow outline of the shell.

Description Shell morphology (Figs 3M–P): Narrow and slender oval-shaped outline with tapered base, short conical spire, fairly wide and low protoconch, narrow aperture, moderately widening in its lower part, thin labrum, slightly sinuous in its lower part, rounded shoulder, siphonal canal long, no break on its left side, three thin columellar plaits, the two lower ones long and arched and quite distant, the upper one very short and oblique.

Remarks *Cystiscus angustus* sp. nov. differs from its oval-shaped congeners by its narrower and more slender outline, its short conical spire, its long siphonal canal and its long and arched lower columellar plait. The two specimens referred as *C. cf. angustus* (Figs 3O–P, Figs 4A–B) are closely allied to the holotype of *C. angustus*: the first one differs mainly from its quite domed spire, and the second one by a more pointing spire. Such variations in the spire height and shape being previously observed in *Cystiscus* species (Boyer, 2003), these two specimens can be considered as probably conspecific with *C. angustus*.

Cystiscus profundus sp. nov. (Figs 4C–F)

urn:lsid:zoobank.org:act:C021E29D-FB15-4FBD-B9B0-BD286FCF1F71

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 4C–D, L=1.13mm); Stn DW 4899: 33° 09' S – 43° 58' E; depth 353–465m; MNHN-IM-2000-38482; as sp. 2 in MNHN collection.

Other material As *Cystiscus cf. profundus* sp. nov.: WALTERS SHOAL. 2 ad. sh. (Figs 4E–F, L=1.68mm); Stn DW 4886: 33° 17' S – 43° 56' E; depth 573–582m; as sp. 9 in MNHN collection.

Derivation of name The species name refers to the deep level of the sampling station.

Description Shell morphology (Figs 4C–D): Conical outline with poorly tapered base, very short conical spire, quite wide and bulging protoconch, moderate aperture, widening in its lower part, thin labrum, slightly sinuous in its lower

part, rounded shoulder, siphonal canal short and wide, no break on its left side, four regularly spaced columellar plaits, decreasing regularly in size, the first plait moderately long, thin and poorly arched, the three upper plaits very thin and moderately oblique.

Remarks *Cystiscus profundus* sp. nov. differs from *C. ovooides* (Figs 3G–H) and from *C. angustus* (Figs 3M–N) by the presence of four instead of three plaits. It differs also from *C. ovooides* by its more rounded and less elevated labial shoulder, and from *C. angustus* by its less narrow and less slender outline. The specimen referred as *C. cf. profundus* differs from the holotype of *C. profundus* principally by its more sinuous first columellar plait and by its straighter labrum. The two shells differ also noticeably in size (1.13mm for the holotype of *C. profundus*, versus 1.68mm for *C. cf. profundus*), but they seem however to be conspecific. Among the two shells from Stn DW 4886 reported as *C. cf. profundus*, one of them is broken and its outline is more inflated than that of the type, so despite the resemblance of some features, the tentative attribution to the nominal species is poorly supported.

Cystiscus granum sp. nov. (Figs 4G–H)

urn:lsid:zoobank.org:act:66D9AA07-2516-46B5-B13A-B02EA9BD9B71

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 4G–H, L=1.75mm); Stn DW 4881: 33° 16' S – 43° 50' E; depth 377–382m; MNHN-IM-2000-38483; as sp. 26 in MNHN collection.

Derivation of name The species name refers to grain-shaped outline of the shell.

Description Shell morphology (Figs 4G–H): Outline conical with convex sides and poorly tapered base, slightly upturned on its left side, very short conical spire, wide and low protoconch, moderate aperture, widening in its lower part, thin labrum, slightly sinuous in its lower part, rounded shoulder, siphonal canal short and wide, three thin and regularly spaced columellar plaits, decreasing regularly in size, the first basal plait moderately long, very oblique and quite straight.

Remarks *Cystiscus granum* sp. nov. is similar to *C. ovooides* (Figs 3G–H) for its three columellar plaits,



Figs 4A–B *Cystiscus* cf. *angustus* sp. nov., L=1.24mm, Walters Shoal, Stn DW 4879, 288–300m. **Figs 4C–D** *Cystiscus profundus* sp. nov., holotype MNHN-IM-2000-38482, L=1.13mm, Walters Shoal, Stn DW 4899, 707–720m. **Figs 4E–F** *Cystiscus* cf. *profundus* sp. nov., L=1.68mm, Walters Shoal, Stn DW 4886, 573–582m. **Figs 4G–H** *Cystiscus granum* sp. nov., holotype MNHN-IM-2000-38483, L=1.75mm, Walters Shoal, Stn DW 4881, 377–382m. **Figs 4I–J** *Cystiscus dentiferus* sp. nov., holotype MNHN-IM-2000-38484, L=1.44mm, Walters Shoal, Stn DW 4887, 599–640. **Figs 4K–L** *Cystiscus alatus* sp. nov., holotype MNHN-IM-2000-38485, L=1.42mm, Walters Shoal, Stn DW 4879, 288–300m. **Figs 4M–N** *Cystiscus apertus* sp. nov., holotype MNHN-IM-2000-38486, L=1.28mm, Walters Shoal, Stn DW 4881, 377–382m. **Figs 4O–P** *Cystiscus contortus* sp. nov., holotype MNHN-IM-2000-38487, L=1.37mm, Walters Shoal, Stn DW 4887, 599–640m.

but it differs in its less rounded outline, its more rounded and less elevated labial shoulder, and its very oblique lower columellar plait. *C. granum* differs from *C. profundus* (Figs 4C–D) mainly by the presence of three columellar plaits instead of four, by its flat protoconch and by the very oblique orientation of the lower plait. However, these two morphs look as very similar, and the specific separation that we are proposing here is quite hypothetical, as an intraspecific variation in the number of columellar plaits is sometime observed in *Cystiscus* species, even if uncommon.

Cystiscus dentiferus sp. nov. (Figs 4I–J)

urn:lsid:zoobank.org:act:D0913C64-D540-4AE3-AD19-F1561E29E76E

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 4I–J, L=1.44mm); Stn DW 4887: 33° 17' S – 43° 57' E; depth 599–640m; MNHN-IM-2000-38484; as sp. 13 in MNHN collection.

Derivation of name The species name refers to the strong and produced lower columellar plait of the shell.

Description Shell morphology (Figs 4I–J): Outline conical with convex sides and weakly tapered base, very short conical spire, wide and low protoconch, moderate aperture, widening significantly in its lower part, labrum thickened in its upper part, faintly sinuous in its lower part, rounded shoulder, siphonal canal short and wide, three thin and regularly spaced columellar plaits, decreasing regularly in size, the lower plait extended and deeply arched.

Remarks Despite its stockier outline and its quite thicker shell, *Cystiscus dentiferus* sp. nov. differs overall from *C. granum* (Figs 4G–H) by its strongly arched first columellar plait deeply produced in the aperture, versus very oblique and quite straight lower plait in *C. granum*. Even if single, this kind of morphologic disparity generally reveals a specific separation.

Cystiscus alatus sp. nov. (Figs 4K–L)

urn:lsid:zoobank.org:act:3DE82EC3-8838-4764-AB5C-CAAABFE1C091

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 4K–L, L=1.42mm); Stn DW 4879: 33° 17' S –

43° 52' E; depth 288–300m; MNHN-IM-2000-38485; as sp. 17 in MNHN collection.

Derivation of name The species name refers to the elevated and enfolding upper labrum of the shell, resembling a bird wing.

Description Shell morphology (Figs 4K–L): Outline conical with tapered base, slightly upturned on its left side, very low spire with slightly inflated ante-penultimate whorl, wide and low protoconch, quite narrow aperture, widening significantly in its lower part, labrum sinuous, moderately thickened in its upper part, shoulder elevated and angular, siphonal canal short, base slightly truncated, three thin and regularly spaced columellar plaits, decreasing in size, the first basal plait extended and straight.

Remarks *Cystiscus alatus* sp. nov. is comparable to *C. ovooides* (Figs 3G–H) for its elevated sharp labial shoulder, but it differs by a less rounded and more angular outline and by its sinuous labrum.

Cystiscus apertus sp. nov. (Figs 4M–N)

urn:lsid:zoobank.org:act:8FED4114-207D-4F69-96EA-478C15339614

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 4M–N, L=1.28mm); Stn DW 4881: 33° 16' S – 43° 50' E; depth 377–382m; MNHN-IM-2000-38486; as sp. 23 in MNHN collection.

Derivation of name The species name refers to the aperture, which is of equal width along its length.

Description Shell morphology (Figs 4M–N): Roughly conical outline with tapered base, short triangular spire, wide and low protoconch, moderate aperture, which is of equal width along its length, thin and straight sided labrum, shoulder rounded, siphonal canal short with a slight notch on its left side, base slightly truncated, three very thin, very oblique and quite short columellar plaits, regularly spaced columellar plaits, decreasing regularly in size and poorly produced, the first basal plait being angled at its mid-part.

Remarks *Cystiscus apertus* sp. nov. differs from its ovoid shelled relatives mainly by the combination

of a straight labrum, a regular aperture and very thin subvertical columellar plaits, the basal plait being noticeably angled at its mid-part.

Cystiscus contortus sp. nov. (Figs 4O–P)

urn:lsid:zoobank.org:act:4A18C05F-3936-4E80-9792-19695B882050

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 4O–P, L=1.37mm); Stn DW 4887: 33° 17' S – 43° 57' E; depth 599–640m; MNHN-IM-2000-38487; as sp. 12 in MNHN collection.

Derivation of name The species name refers to the twisted orientation of the base of the shell.

Description Shell morphology (Figs 4O–P): Outline conical with convex sides and tapered base, slightly upturned on its left side, short triangular spire, wide and low protoconch, quite narrow aperture, slightly widening in its lower part, labrum slightly sinuous, weakly thickened in its upper part, shoulder poorly elevated and quite angular, siphonal canal short, slightly twisted inward, weak notch at its left side, three thin and regularly spaced columellar plaits, decreasing in size, the basal plait not very long, quite oblique and sinuous.

Remarks *Cystiscus contortus* sp. nov. is mainly comparable to *C. alatus* (Figs 4K–L) for its quite angular outline, but *C. contortus* has a less elevated and less angled labial shoulder, its basal outline is more upturned on the left side, and its lower columellar plait is more oblique and more sinuous.

Cystiscus sinuosus sp. nov. (Figs 5A–B)

urn:lsid:zoobank.org:act:0676EB19-7280-43BD-93E4-AE2988B47DAC

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 5A–B, L=1.86mm); Stn DW 4893: 33° 16' S – 43° 58' E; depth 623–629m; MNHN-IM-2000-38488; as sp. 8 in MNHN collection.

Derivation of name The species name refers to the sinuous anterior part of the labrum.

Description Shell morphology (Figs 5A–B): Outline conical with convex sides and tapered base, short triangular spire, moderate and low protoconch, moderate aperture, widening in its

lower part, labrum thin and sinuous, shoulder rounded, siphonal canal relatively long, weak notch on its left side, three thin and regularly spaced columellar plaits, decreasing regularly in size, the basal plait relatively short, very oblique and almost straight.

Remarks *Cystiscus sinuosus* sp. nov. differs from *C. apertus* (Figs 4M–N) mainly by its moderately widening aperture towards the base, versus regular aperture in *S. apertus*, its sinuous labrum versus straight labrum in *C. apertus*, and its quite straight basal columellar plait versus angled plait in *C. apertus*. *Cystiscus sinuosus* differs also by its large size of 1.86mm, the largest size observed in the *Cystiscus* fauna from the Walters Shoal.

Cystiscus pupoides sp. nov. (Figs 5C–D)

urn:lsid:zoobank.org:act:D0717F33-3D6A-4F49-9AA0-C3BA647D76C7

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 5C–D, L=1.25mm); Stn DW 4887: 33° 17' S – 43° 57' E; depth 599–640m; MNHN-IM-2000-38489; as sp. 32 in MNHN collection.

Derivation of name The species name refers to the shell outline which resembles the casing of an insect pupa.

Description Shell morphology (Figs 5C–D): Outline elongate-oval with faintly tapered base, slightly upturned on its left side, short triangular spire, wide and low protoconch, aperture of equal width along its length, and quite narrow, labrum thin and faintly sinuous, shoulder rounded, siphonal canal short, no notch on its left side, three thin and regularly spaced columellar plaits, decreasing regularly in size, the lower plait quite long and arched.

Remarks *Cystiscus pupoides* sp. nov. differs from its congeners mainly by its more oval outline, associated to an aperture which is of equal width along its length and a long arched basal columellar plait.

Cystiscus lussii sp. nov. (Figs 5E–F)

urn:lsid:zoobank.org:act:4F297214-5982-4D16-9682-10CFD5B0D6B9

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 5E–F, L=1.55mm); Stn DW 4880: 33° 17' S –



Figs 5A–B *Cystiscus sinuosus* sp. nov., holotype MNHN-IM-2000-38488, L=1.86mm, Walters Shoal, Stn DW 4893, 623–629m. **Figs 5C–D** *Cystiscus pupoides* sp. nov., holotype MNHN-IM-2000-38489, L=1.25mm, Walters Shoal, Stn DW 4887, 599–640m. **Figs 5E–F** *Cystiscus lussii* sp. nov., holotype MNHN-IM-2000-38490, L=1.55mm, Walters Shoal, Stn DW 4880, 275–318m. **Figs 5G–H** *Cystiscus smithi* sp. nov., holotype MNHN-IM-2000-38492, L=1.53mm, Walters Shoal, Stn DW 4880, 275–318m. **Figs 5I–J** *Cystiscus serratus* sp. nov., holotype MNHN-IM-2000-38493, L=1.46mm, Walters Shoal, Stn DW 4893, 623–629m. **Figs 5K–L** *Cystiscus lachrymaformis* sp. nov., holotype MNHN-IM-2000-38494, L=1.65mm, Walters Shoal, Stn DW 4881, 377–382m. **Figs 5M–N** *Cystiscus quinqueplicatus* sp. nov., holotype MNHN-IM-2000-38495, L=1.67mm, Walters Shoal, Stn WS 04, 40m. **Figs 5O–P** *Cystiscus* sp. A, L=1.25mm, Walters Shoal, Stn 4879, 288–300m.

43° 51' E; depth 275–318 m; MNHN-IM-2000-38490; as sp. 1 in MNHN collection.

Other material WALTERS SHOAL. 1 ad. sh. & 1 subad sh; Stn DW 4886: 33° 17' S - 43° 56' E; depth 573–582 m.

Derivation of name The species is dedicated to Markus Lussi, who co-authored a revision of the Cystiscidae from South Africa.

Description Shell morphology (Figs 5E–F): Egg-shaped outline with weakly tapered base, slightly upturned on its left side, short domed spire, minute low protoconch, narrow aperture, weakly widening in its lower part, relatively thick labrum in its mid-part, faintly sinuous in its lower part, rounded shoulder, siphonal canal short and wide, very faint notch on its left side, five thin and regularly spaced columellar plaits, decreasing regularly in size, the basal plait being quite long, oblique and quite concave, the second plait proportionally very thin and short, the three tiny upper plaits subhorizontal, very short and decreasing gently in size.

Remarks *Cystiscus lussii* sp. nov. differs from *C. granum* (Figs 4G–H) mainly by its thicker and more oval shell, and by the presence of five plaits with the three upper ones very short, subequal and subhorizontal.

Cystiscus smithi sp. nov. (Figs 5G–H)

urn:lsid:zoobank.org:act:84846288-6494-43CB-86E6-711D1BF2678B

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 5G–H, L=1.53 mm); Stn DW 4880: 33° 17' S - 43° 51' E; depth 275–318 m; MNHN-IM-2000-38492; as sp. 4 in MNHN collection.

Derivation of name The species is dedicated to Gerald Smith, who co-authored a revision of the Cystiscidae from South Africa.

Description Shell morphology (Figs 5G–H): Outline roughly conical with rounded top, minute low protoconch, relatively narrow aperture, weakly widening in its lower part, labrum thickened in its mid-part, faintly sinuous in its lower part, shoulder rounded, siphonal canal short and wide, three thin and regularly spaced columellar plaits decreasing regularly in size, the

basal plait being moderately long, oblique and quite straight, the second plait proportionally very thin and short, the third plait very short and forming a sinuous varicose pleat on the columellar edge, three upper lirations, very short, subhorizontal and well-spaced from the three lower plaits.

Remarks *Cystiscus smithi* sp. nov. differs slightly from *C. lussii* (Figs 5E–F) by its more rounded top, and especially by the three upper lirations well-spaced from the three lower columellar plaits. The two morphs look very similar, they were collected at the same sampling station, and the size of the two holotypes are more or less the same, so the differences between the two types of columellar pleats could be considered as accidental or as belonging to the natural range of variability of a single species. However, this kind of natural discontinuity for the organization of the columellar pleats is unusual, and any 'accidental discontinuity of organization between the columellar lower plaits and the upper lirations' was never observed among the *Cystiscus* species (Boyer, 2003; Wakefield and McCleery, 2006). So, the cohabitation of two twin species is here considered as the most probable occurrence.

Cystiscus serratus sp. nov. (Figs 5I–J)

urn:lsid:zoobank.org:act:37DEA1C1-C040-40F0-B319-CC88E37ED2FC

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 5I–J, L=1.46 mm); Stn DW 4893: 33° 16' S - 43° 58' E; depth 623–629 m; MNHN-IM-2000-38493; as sp. 7 in MNHN collection.

Derivation of name The species name refers to the saw-like shape of the plaits series on the columellar edge.

Description Shell morphology (Figs 5I–J): Thick and squat shell, conical outline with convex sides and low rounded top, minute low protoconch, truncated base, fairly narrow aperture, noticeably widening in its lower part, thick and straight labrum, rounded shoulder, siphonal canal short and wide, four regularly spaced columellar plaits, decreasing regularly in size from the first to the fourth, the basal plait being moderately long, oblique and slightly concave, the second plait quite oblique and straight, the third plait very short and forming a sinuous varicose pleat

on the columellar edge, the fourth plait very sub-horizontal, short and thick, two upper short and thick lirations, regularly spaced from the fourth plait.

Remarks *Cystiscus serratus* sp. nov. differs mainly from *C. smithi* (Figs 5G–H) by its more triangular and thicker shell, but it is very similar for the pattern of its columellar pleats, the single difference from this point of view being the fact that in *C. smithi* the three upper lirations are separated from the three lower plaits by a relatively wide gap. The similar pattern of the pleats in *C. serratus* and in *C. smithi* allows one to believe that such a pattern has a diagnostic value at the specific rank in this fauna. So, it can be taken as an additional argument in favour of the distinct specific status of *C. smithi* beside its twin *C. lussii*.

Cystiscus lachrymaformis sp. nov. (Figs 5K–L)

urn:lsid:zoobank.org:act:8FAF7248-9F02-4F8E-BC35-DA24F4763887

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 5K–L, L=1.65mm); Stn DW 4881: 33° 16' S – 43° 50' E; depth 377–382m; MNHN-IM-2000-38494; as sp. 27 in MNHN collection.

Derivation of name The species name refers to the tear-drop shape of the shell outline.

Description Shell morphology (Figs 5K–L): Outline conical with convex sides and tapered base, very short conical spire, wide and low protoconch, moderate and aperture of equal width along its length, quite thin and straight labrum, rounded shoulder slightly elevated at the level of the spire, with a sharp top making a narrow notch over the anal canal, siphonal canal short and moderate, no break on its left side, three thin and regularly spaced columellar plaits, decreasing regularly in size, the lower plait quite short, straight and oblique.

Remarks *Cystiscus lachrymaformis* sp. nov. differs from *C. granum* (Figs 4G–H) by its more ovoid outline, not hooked profile on its left side, by its straighter labrum, its aperture, which is of equal width along its length and its much shorter and less oblique first columellar plait. *C. lachrymaformis* differs from *C. apertus* (Figs 4M–N) mainly by its shorter and not angled first columellar plait, and by its much larger third plait. As far as

the shell characters are concerned, *C. lachrymaformis* and *C. apertus* can be considered as twin species.

Cystiscus quinqueplicatus sp. nov. (Figs 5M–N)

urn:lsid:zoobank.org:act:D612E31B-CDE1-40DB-A571-832B3E09FCAA

Holotype WALTERS SHOAL. 1 ad. sh. (Figs 5M–N, L=1.67mm); Stn WS 04: 33° 12.2' S – 43° 50.8' E; depth 40m; MNHN-IM-2000-38495; as sp. 3 in MNHN collection.

Derivation of name The species name refers to five plaits on the columellar edge.

Description Shell morphology (Figs 5M–N): Outline conical with rounded sides and weakly tapered base, strongly truncated base, very short conical spire, wide and low protoconch, moderate and regular aperture, thin labrum, quite sinuous in its lower part, rounded shoulder slightly elevated over the apex, with a sharp top and a long oblique anal canal, siphonal canal short and wide, five moderate columellar plaits, regularly spaced and decreasing regularly in size, the first basal plait being long, oblique and sinuous, the fourth plait being very oblique and thinner by comparison with the four other plaits, including by comparison with the fifth one.

Remarks *Cystiscus quinqueplicatus* sp. nov. is comparable to *C. pupoides* (Figs 5C–D) for its oval outline and its aperture, which is of equal width along its length, but it differs by a more inflated and stockier look, and especially by its five columellar plaits instead of three in *C. pupoides*, its first plait being concave whereas it is convex in *C. pupoides*. The discontinuity in thickness and orientation presented by the thinner and more oblique fourth columellar plait of *C. quinqueplicatus* is remarkable and unambiguous. It is confirming that discontinuity in the organisation of the plaits can be a diagnostic feature at the specific rank (see above, under Remarks for *C. smithi* and *C. serratus*).

Cystiscus sp. A (Figs 5O–P)

Material examined WALTERS SHOAL. 1 ad. sh. (Figs 5O–P, L=1.25mm); Stn 4879: 33° 17' S – 43° 52' E; depth 288–300m; as sp. 19 in MNHN collection.

Remarks This very cylindrical shell with narrow, long and regular aperture belongs clearly to a distinctive *Cystiscus* species, but the hard sediment filling the aperture does not allow to describe it in reliable conditions, so we just report this morph as additional clue of the high specific diversity displayed by the genus *Cystiscus* on the Walters Shoal.

DISCUSSION

Shell disparity

The disparity of the shell morphologies at work in the *Cystiscus* fauna from the Walters Shoal seems to be more diverse than what is observed in documented reefal fauna from South Africa (Lussi & Smith, 1998) and from New Caledonia (Boyer, 2003), where the shell shapes are all matching more or less an ovoid pattern, whereas subpyriform or cylindrical shapes are undocumented. Oversimplifying the situation, we could characterize the disparity at work in the *Cystiscus* fauna from the Walters Shoal as mainly divided between subpyriform and ovoid patterns. As a matter of fact, even these two categories are subject to intense plasticity, from heavily subpyriform (*C. laurae*: Figs 2O-P; *C. robustus*: Figs 3A-B) to slightly subpyriform (*C. stimpsoni*: Figs 2G-H), and from ovoid-subtriangular (*C. angustus*: Figs 3M-N; *C. alatus*: Figs 4K-L) to ovoid-pupoid (*C. pupoides*: Figs 5C-D). Furthermore, the shell morphology of some species more or less intergrades between the two dominant patterns, for example with *C. inflatus* (Figs 2C-D) presenting an ovoid but slightly pyriform outline, or with *C. mamillatus* (Figs 3I-J) presenting an ovoid-pupoid outline with a slightly subpyriform base. Few morphs look as marginal compared to the dominant morphological series, such as *C. serratus* (Figs 5I-J) which looks quite similar to the type of the genus *Crithe* due to its quite thick, squat and rounded shell with many columellar plaits, or *Cystiscus* sp. A (Figs 5O-P) with its narrow cylindrical outline. Such a higher disparity of the shell morphologies in the *Cystiscus* species on the Walters Shoal could be the clue of an older assemblage evolving in an isolated bathyal hotbed, and the closely matching forms occurring in the shell series could be the clue of a high degree of conservation of the disbranching lineages, what would be coherent with the more stable conditions generally prevailing at bathyal levels.

Another field of explanation of these high morphological disparity and species diversity could however be that in the absence of competitors from other cystiscids genera, the simultaneous occurrence of numerous species and shapes and absence of *Gibberula* species constitutes a striking and original situation. The study of comparable situations in Indo-Pacific waters may result in testing these different hypothesis.

Specific diversity

Twenty-eight *Cystiscus* species are formally recognized from the Walters Shoal, all but one from bathyal levels, and 27 of them are described as new, the cylindrical shelled *Cystiscus* sp. A remaining undescribed due to the bad condition of the shell. Such a degree of diversity was unreported, as the most important *Cystiscus* assemblages ever studied did amount to 13 species for South Africa in Lussi & Smith (including the species they indicated as '*Plesiocystiscus*' and as '*Crithe*') and to 19 species for the New Caledonia mainland in Boyer [including the species he indicated as '*Crithe*' and the dubious case of '*Plesiocystiscus tomlini* (Bavay, 1917)']. Furthermore, 11 specimens are associated as '*Cystiscus* cf. X' with 8 nominal species, from the fact that despite their great resemblance with the nominal species the formal attribution to that one is not totally convincing, and that cases of twin species may occur. This situation comes from the very limited material at hand, implying almost zero knowledge of the specific variability at work in each case. Among the 28 morphs recognized as good species, 8 of them have 1 or 2 specimens associated as *Cystiscus* cf. X, only one species (*C. lussii*) is formally recognized through 3 specimens (one being subadult and less evident), one species (*C. subcylindricus*) is formally recognized through two specimens, and 18 species (64% of the 28 recognized species) are only known from a single specimen, with no matching form associated with it. In other words, each random sampling at bathyal levels on the Walters Shoal frequently elicits new *Cystiscus* species. From this we can infer that the knowledge of the real *Cystiscus* diversity occurring at bathyal levels of the Walters Shoal is far from being documented, and our results lead to a better understanding that many other *Cystiscus* species are probably living in this area. As a matter of fact, we cannot consider in the present state to have a good view on the *Cystiscus* radiation(s)

ranging on the Walters Shoal: possibly other species are intergrading among what we already know, as suggested by our striking series of closely matching forms, but possibly also undocumented divergent lineages may occur, as suggested by the occurrence of our 'marginal forms'.

Biogeography

Among the 28 recognized *Cystiscus* species, 27 of them occur at bathyal levels, and only one of them (*C. quinqueplicatus*) was collected at a reef level, so the *Cystiscus* fauna of the Walters Shoal must be characterized typically as bathyal fauna. To compare this fauna with the *Cystiscus* assemblages from other bathyal places of the Indo-Pacific Province would be naturally of interest. The point would be in particular to verify if *Cystiscus* is widely represented by intense radiations at bathyal levels in Indo-Pacific waters or if the situation prevailing on the Walters Shoal is exceptional. Further investigations in this direction are recommended, for example through the study of the public collections conserved at MNHNH for the Southwest Pacific fauna, as well as those conserved in South Africa, Australia and New Zealand.

ACKNOWLEDGEMENTS

I am hugely indebted to Philippe Maestrati (MNHN) for the skilful SEM-photography and plate mounting. I am also grateful to Virginie Héros (MNHN) for her tireless help with the type material and for her precious support on Latin idioms. Walter Renda (Amantea, Italy) corrected flaws in the first proof with usual sagacity. Special thanks to Anna Holmes, editor of the *Journal of Conchology*, for her kind, welcome and tactful mastering.

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