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Not all spotted cats are leopards: evidence for a *Hemilienardia ocellata* species complex (Gastropoda: Conoidea: Raphitomidae)

Alexander E. FEDOSOV^{1,*}, Peter STAHLSCHMIDT², Nicolas PUILLANDRE³,
Laetitia AZNAR-CORMANO⁴ & Philippe BOUCHET⁵

¹A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Science,
119071, Leninsky prospect, 33, Moscow, Russia.

²Institute for Environmental Sciences, University of Koblenz-Landau,
Fortstr. 7, 76829 Landau, Germany.

^{3,4}Institut de Systématique, Évolution, Biodiversité ISYEB – UMR 7205 – CNRS,
MNHN, UPMC, EPHE, Muséum national d’Histoire naturelle, Sorbonne Universités,
43 rue Cuvier, CP26, F-75005, Paris, France.

⁵Institut de Systématique, Évolution, Biodiversité ISYEB – UMR 7205 – CNRS,
MNHN, UPMC, EPHE, Muséum national d’Histoire naturelle, Sorbonne Universités,
55 rue Buffon, CP26, F-75005, Paris, France.

* Corresponding author: fedosovalexander@gmail.com

² Email: stahlschmidt2@uni-landau.de

³ Email: puillandre@mnhn.fr

⁴ Email: aznar.laetitia@gmail.com

⁵ Email: pbouchet@mnhn.fr

¹ urn:lsid:zoobank.org:author:65A25D60-A36D-48E5-9A03-B21207A0FAE2

² urn:lsid:zoobank.org:author:4A571034-ECA3-455C-8DA3-7B12FD638AC0

³ urn:lsid:zoobank.org:author:00565F2A-C170-48A1-AAD9-16559C536E4F

⁴ urn:lsid:zoobank.org:author:C070F6C9-63C3-47B8-9C5B-683412F65E25

⁵ urn:lsid:zoobank.org:author:FC9098A4-8374-4A9A-AD34-475E3AAF963A

Abstract. The small conoidean *Hemilienardia ocellata* is one of the easily recognizable Indo-Pacific “turrids”, primarily because of its remarkable eyespot colour pattern. Morphological and molecular phylogenetic analyses revealed four species that share this “characteristic” colour pattern but demonstrate consistent differences in size and shell proportions. Three new species – *Hemilienardia acinonyx* sp. nov. from the Philippines, *H. lynx* sp. nov. from Papua New Guinea and *H. pardus* sp. nov. from the Society and Loyalty Islands – are described based on the results of phylogenetic analyses. Although the *H. ocellata* species complex clade falls in a monophyletic *Hemilienardia*, *H. ocellata* and *H. acinonyx* sp. nov. possess a radula with semi-enrolled or notably flattened triangular marginal teeth, a condition that diverges substantially from the standard radular morphology of *Hemilienardia* and other raphitomids.

Keywords. Integrative taxonomy, species delimitation, Indo-Pacific, COI, 16S.

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Introduction

Colour patterns with eyespots (ocellae) are widespread in the animal world and have obviously a great adaptive significance (Allen *et al.* 2011). Besides in various groups of seaslugs, ocellae may be present on the head-foot (as, e.g., in many ranellids and a few cancellariids) or mantle (as, e.g., in many ovulids and some eulimids) of shelled gastropods, or, alternatively, they may be part of the colour pattern of the shell (as, e.g., in various phasianellids, cowries, and columbellids). One of the iconic gastropod species with such a remarkable colour pattern is *Hemilienardia ocellata* (Jousseaume, 1884), a tiny shallow water Indo-Pacific raphitomid (Conoidea, Raphitomidae). The shell of this species is decorated with a bright yellow spiral line and regular olive green ovate spots fringed by brown, situated adapically of the yellow line in the interspaces between axial ribs, resembling a row of olives laid on a golden tray. This picturesque species, despite apparently being widely distributed in the tropical Indo-Pacific (Jousseaume 1884; Hedley 1922; B.J. Smith 2003; Tröndlé & Boutet 2005; Héros *et al.* 2007; Sysoev 2008), is, however, seldom encountered because of its minute size (its shell barely reaches a length of 5 mm), which helps it escape collecting by hand-picking.

Novel collecting techniques, that are routinely referred to as “brushing” and “air lifting”, have been developed to efficiently sample micro-molluscs associated with coral reefs at divable depths (Bouchet *et al.* 2002). They were first introduced in expedition routine in the 1990s in large scale surveys in New Caledonia and the Loyalty Islands in near-shore marine habitats and, later, in the Philippines, Papua New Guinea, Vanuatu and Madagascar. From one 30 000 hectare site in New Caledonia, 2738 morphospecies of molluscs were recovered, and a significant fraction (263 species) of this huge diversity belonged to the so-called turriform Conoidea. Among them, three distinct forms were referable to *Hemilienardia ocellata* which differed notably in shell proportions, but with these differences hidden under a remarkably similar eyespot colour pattern. However, in the absence of molecular data, the status of these forms remained uncertain. In more recent expeditions, the development of a new protocol for the separation of bodies and shells (Galindo *et al.* 2014) has allowed the building of large tissue collections for molecular analysis, and has allowed us to revisit the case of these divergent morphotypes of *Hemilienardia ocellata*.

Material and methods

Material

The material for the present study was collected at various Indo-Pacific localities in a series of shallow water expeditions to New Caledonia (Expedition Montrouzier – 1993), the Loyalty Islands (Atelier Lifou – 2000), Vanuatu (SANTO 2006) and Papua New Guinea (PAPUA NIUGINI 2012, KAVIENG 2014). This core dataset was supplemented by molecular-grade specimens obtained in 2008 in the Central Philippines (Cebu-Bohol area) from bulk lumun-lumun nets (Seronay *et al.* 2010), and in the Society Islands in the course of the Moorea Biocode Project (<http://mooreabiocode.org/>). Live specimens for molecular analysis collected before 2012 were anaesthetized in an isotonic solution of MgCl₂ and fixed in 96% ethanol. Specimens collected in later expeditions were processed with a microwave oven: the living mollusks in small volumes of sea water were exposed to microwaves for 7–12 seconds, depending on the specimen size. Bodies were immediately removed from shells and dropped in 96% ethanol; intact voucher shells are kept in MNHN. The collection data for sequenced specimens are summarized in Table 1. Despite the former having long been considered a subgenus of the latter, the genera

Table 1. Summary of the sequenced *Hemilienardia* specimens.

N° MNHN	Expedition	Station	Collection data	Genus	Species	BOLD ID	COI	16S
IM-2007-17861	PANGLAO_2004	B14	9°38.5'N - 123°49.2' E, 2–4 m	<i>Hemilienardia</i>	<i>calctincta</i>	CONO232-08	EU015683	HQ401684
IM-2009-18123	PANGLAO_2004	M18	9°33.0'N - 123°43.5' E, 1 m	<i>Hemilienardia</i>	<i>rubicunda</i>	CONO1855-16	KX233245	–
IM-2009-18134	SANTO_2006	DB63	15°26.9' S - 167°15.8' E, 21 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1853-16	–	KX233255
IM-2009-18135	SANTO_2006	DB20	15°30.5' S - 167°01.4' E, 22–25 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1852-16	–	KX233250
IM-2009-19139	SANTO_2006	DB69	15°24.4' S - 167°13.0' E, 38 m	<i>Hemilienardia</i>	<i>ocellata</i>	COCO1854-16	–	KX233263
IM-2009-33592	–	–	Philippines, Panglao Is., off Momo beach	<i>Hemilienardia</i>	<i>acinonyx</i> sp. nov.	CONO1856-16	KX233242	KX233261
IM-2009-33593	–	–	Philippines, Panglao Is., off Momo beach	<i>Hemilienardia</i>	<i>acinonyx</i> sp. nov.	CONO1857-16	KX233238	KX233249
IM-2013-4714	PAPUA_NIUGINI	PM38	05°11.8' S - 145°48.2' E, intertidal	<i>Hemilienardia</i>	aff. <i>rubicunda</i>	CONO1863-16	KX233246	–
IM-2013-4728	PAPUA_NIUGINI	PB28	05°11.9' S - 145°49.6' E, 10 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1858-16	–	KX233257
IM-2013-47788	KAVIENG	KS11	02°33.2' S - 150°48.2' E, 11 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1870-16	–	KX233262
IM-2013-47798	KAVIENG	KB08	02°33.2' S - 150°48.2' E, 13 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1871-16	KX233239	KX233251
IM-2013-50765	KAVIENG	KB16	02°34.6' S - 150°46.3' E, 13–14 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1872-16	KX233241	KX233256
IM-2013-51296	KAVIENG	KS29	02°41.7' S - 150°38.5' E, 3–9 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1873-16	–	KX233259
IM-2013-53768	KAVIENG	KS33	02°38.2' S - 150°38.7' E, 8–10 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1865-16	–	KX233252
IM-2013-53769	KAVIENG	KS33	02°38.2' S - 150°38.7' E, 8–10 m	<i>Hemilienardia</i>	<i>thyridota</i>	CONO1866-16	KX233247	–
IM-2013-53852	KAVIENG	KB40	02°36.6' S - 150°32.9' E, 2–7 m	<i>Hemilienardia</i>	aff. <i>rubicunda</i>	CONO1867-16	KX233244	–
IM-2013-54350	KAVIENG	KB42	02°38.3' S - 150°27.2' E, 6–12 m	<i>Hemilienardia</i>	sp.	CONO1868-16	KX233248	–
IM-2013-54351	KAVIENG	KS43	02°35.2' S - 150°29.1' E, 4–12 m	<i>Hemilienardia</i>	sp.	CONO1869-16	KX233243	–
IM-2013-5489	PAPUA_NIUGINI	PPI4	05°11.9' S - 145°49.6' E, 100–120 m	<i>Hemilienardia</i>	<i>lynx</i> sp. nov.	CONO1859-16	–	KX233260
IM-2013-5623	PAPUA_NIUGINI	PR159	05°07.1' S - 145°49.4' E, 15 m	<i>Hemilienardia</i>	<i>goubini</i>	CONO1860-16	KX233237	–
IM-2013-6175	PAPUA_NIUGINI	PB47	05°11.3' S - 145°49.6' E, 5 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1864-16	–	KX233258
IM-2013-6192	PAPUA_NIUGINI	PB47	05°11.3' S - 145°49.6' E, 5 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1861-16	KX233240	KX233254
IM-2013-6213	PAPUA_NIUGINI	PB47	05°11.3' S - 145°49.6' E, 5 m	<i>Hemilienardia</i>	<i>ocellata</i>	CONO1862-16	–	KX233253
BM00-17147	Moorea	–	17°33.15' S - 149°46.41' W, 73 m	<i>Hemilienardia</i>	<i>pardus</i> sp. nov.	–	KX296771	KX269877
BM00-10646	Moorea	–	17°35.85' S - 149°50.52' W, 1 m	<i>Hemilienardia</i>	<i>malleti</i>	–	–	KX269876

Hemilienardia O. Boettger, 1895 and *Lienardia* Jousseau, 1884 are not closely related and not even confamilial (Bouchet *et al.* 2011), and comparisons here will be limited to other raphitomids.

DNA extraction and PCR

Total DNA was extracted from a piece of the foot using the Dneasy96 Tissue kit (Qiagen), following the manufacturer's recommendations. The barcode fragment of the COI gene (658 bp) and a 16S rRNA fragment were amplified using the universal primers LCO1490 and HCO2198 (Folmer *et al.* 1994) and a primer pair 16SH-16LC (Palumbi 1996), respectively. PCR reactions were performed in 25 μ l, containing 3 ng of DNA, 10 \times reaction buffer containing 15 mM MgCl₂, 0.26mM dNTP, 0.3 μ M of each primer, 5% DMSO, 1mg/ml BSA and 1 unit of QBIotaq (MPBiomedicals). Amplification of COI consisted of an initial denaturation step at 95°C for 5 min, followed by 35 cycles of denaturation at 95°C for 40 s, annealing at 50°C for 30 s, followed by extension at 72°C for 1 min. For 16S the annealing temperature was set to 50°C and the elongation phase to 50 s. The final extension was at 72°C for 5 min. PCR products were purified and sequenced by the Eurofins sequencing facility. Both directions were sequenced to confirm accuracy of each sequence.

The use of the barcode fragment of the COI sequence is preferable for purposes of species delimitation (Puillandre *et al.* 2012); however, amplification of COI encountered certain difficulties in many specimens, probably because of a mutation in the primer sequence. Thus, we mostly relied on the relationships inferred from the analysis of 16S to suggest hypotheses of species delimitation.

Species delimitation and phylogenetic analysis

We followed a two-step approach to propose species hypotheses. First, all specimens were separated into morphospecies based on shell characters. Then, the COI and 16S sequences were used to test (i) if the genetic distances between morphospecies were higher, than within morphospecies, and (ii) if each morphospecies corresponded to a clade (when represented by several sequenced specimens) or an independent lineage (when represented by a single sequenced specimen).

COI and 16S sequences were aligned using Muscle (Edgar 2004); the accuracy of each alignment was checked by eye and if needed modified using BioEdit v. 7.0.9.0 (Hall 1999). The best fit substitution model was estimated for each gene with Modelgenerator v. 85 (Keane *et al.* 2006). A set of COI and 16S raphitomid sequences accessed from GenBank was used to root the tree and assess affinities of the *Hemilienardia ocellata* species complex. Phylogenetic analyses were performed using MrBayes (Huelssenbeck *et al.* 2001), running two parallel analyses, each consisting of six Markov chains of 20 000 000 generations with a sampling frequency of one tree each 1000 generations, with a chain temperature of 0.02. Parameters of the substitution model were estimated during the analysis (6 substitution categories, a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites). A different model of substitution was applied for each codon position of the COI gene. Trees from the first 5 000 000 generations (25% of the total number of generations) were discarded as burn-in prior to the construction of consensus trees. Convergence of each analysis was evaluated using Tracer v. 1.4.1 (Rambaut *et al.* 2014) to check that ESS values were all greater than 200 (default burning). K2P genetic distances were calculated with MEGA v. 5.2.1 (Tamura *et al.* 2011).

Morphological studies

Radulae were extracted from specimens in which the body had been dried. The specimens were rehydrated over 2–3 hours, then a hole was drilled on the penultimate whorl of the shell, at about the place where the columellar muscle is attached, to ease extraction of the body. Rehydrated bodies were then dissected and buccal complexes treated by a solution of commercially available bleach until radulae were clean. Radulae were then rinsed in distilled water, mounted on a cover glass, air-dried,

gold coated and examined with a Hitachi CamScan scanning electron microscope. A Fei Quanto 250 environmental scanning electron microscope (ESEM) was used without preliminary coating to examine the fine morphology of protoconchs and shells, as it was essential to keep specimens uncoated (e.g., in case of examination of putative holotypes).

Abbreviations of museums and repositories:

MNHN = Muséum national d'Histoire naturelle, Paris, France
 PS = Peter Stahlschmidt collection, Rohrbach, Germany
 SMF = Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany
 UF = University of Florida, Gainesville, Florida, USA

Other abbreviations:

b/h = ratio of shell breadth to its height
 lw/h = ratio of last adult whorl length (measured along main shell axis) to total shell height
 a/h = ratio of aperture length (measured along main shell axis) to total shell height
 PI, PII = protoconch I and protoconch II
 dd = empty shell
 lv = live-collected specimen
 SD = standard deviation

Results

Species delimitation and phylogenetic analysis

GTR+I+G was selected as a best fit substitution model for the COI, and HKY+I+G for the 16S rRNA gene. The phylogenetic trees obtained after the analysis of COI and 16S were largely congruent, with no conflicting topologies highly supported (Fig. 1).

Four morphospecies were identified. The pairwise distances (p-distances) calculated for the COI sequences vary from 0 to 0.03 for within-morphospecies comparisons (mean = 0.016, SD = 0.0157) and from 0.157 to 0.169 for comparisons between morphospecies (mean = 0.162, SD = 0.0037). The p-distances calculated for the 16S sequences vary from 0 to 0.027 for within-morphospecies comparisons (mean = 0.012, SD = 0.0072) and from 0.069 to 0.104 for comparisons between morphospecies (mean = 0.082, SD = 0.0109). As the between-group genetic distances (especially for the COI gene) are greater than genetic distances between closely related species of conoideans found in our earlier studies (e.g., Puillandre *et al.* 2009, 2010; Fedosov & Puillandre 2012), the genetic differences found within the *H. ocellata* species complex support the species hypotheses based on the identified morphospecies.

Based on the results of both phylogenetic analyses, the *Hemilienardia ocellata* species complex forms a well supported clade (Posterior Probabilities (PP) = 1 and 0.99 for COI and 16S, respectively). Three distinct lineages are recognized on the COI based tree (marked as 1 to 3 on Fig. 1A), each corresponding to one morphospecies. One includes specimens MNHN IM-2013-6192, MNHN IM-2013-47798 and MNHN IM-2013-50675, all from Papua New Guinea (PP=1); the second clade includes two Philippine specimens, MNHN IM-2009-33592 and MNHN IM-2009-33593, sharing an identical COI haplotype (PP=1); specimen BMOO-17147 from Moorea constitutes the third lineage. The first and second clades cluster together with a high support (PP=0.99). The *Hemilienardia ocellata* species complex is nested within the unsupported *Hemilienardia* clade (PP=0.73).

Sixteen *Hemilienardia ocellata* specimens sequenced for 16S form four distinct groupings (Fig. 1B), once again each corresponding to one morphospecies. The largest of them combines 12 specimens from Papua New Guinea and Vanuatu, and is consistent with the first grouping on the COI based tree.

Interestingly, three specimens from Vanuatu form a rather distinct supported sub-clade (PP=0.98), although with a very short branch. The second clade contains two specimens from the Philippines and is consistent with the COI based tree. The third and fourth lineages include one specimen each, MNHN IM-2013-5489 from Papua New Guinea and BMOO 17147 from Moorea, respectively. These two lineages cluster together (PP=1) and show a supported affinity to the second clade (PP=0.97). The grouping of *Hemilienardia malleti* (Récluz, 1852) BMOO 10646 and *H. calcicincta* (Melvill & Standen, 1895) MNHN IM-2007-17861 is a sister-group to the entire *H. ocellata* species complex clade. *Hemilienardia* is recovered monophyletic and supported (PP=0.99) based on the analysis of 16S. The application of the name *Hemilienardia* to this clade is verified by the inclusion of *H. malleti*, the type species of the genus.

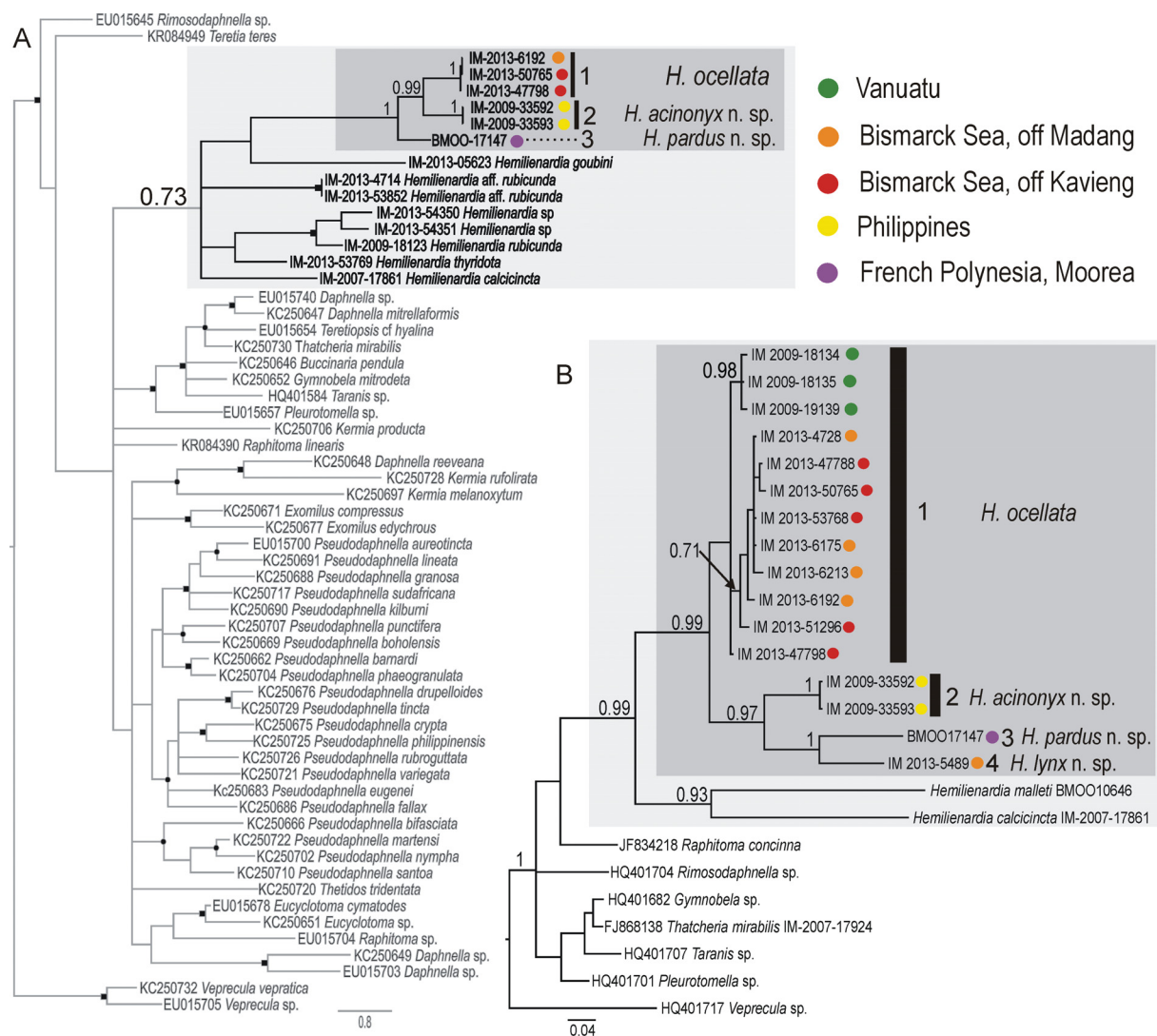


Fig. 1. Relationships of the *Hemilienardia ocellata* complex as inferred by the molecular phylogenetic analysis. **A.** Bayesian tree based on the analysis of 61 Raphitomidae COI sequences. Black circles indicate nodes with $0.9 < PP \leq 0.97$, squares nodes with $0.98 < PP \leq 1$. Light grey area marks the *Hemilienardia* segment of the tree, dark grey the *Hemilienardia ocellata* species complex. Localities indicated as explained in legend. **B.** Bayesian tree based on the analysis of 25 Raphitomidae 16S sequences. Support values (PP) indicated when > 0.7 .

Two Philippine specimens are remarkable in that they greatly (more than two times) exceed other sequenced specimens in size. Moreover, the specimens that form the first group are characterized by ovate spots, while these are squarish in specimens that form groups 2, 3 and 4 on the 16S based tree.

With both genes, identified morphospecies corresponded to independent lineages or clades (supported for most of them) when several specimens were included. It, thus, further reinforces the species hypotheses proposed with morphological data. There is only one species name available for this complex, *H. ocellata*, and, based on the comparison of shell vouchers and the *H. ocellata* type material, we conclude that this name should be applied to the first species hypothesis. Nevertheless, the type locality of *H. ocellata* is Mauritius, whereas all sequenced specimens were recovered from the Central Indo–West Pacific. Although *H. ocellata* occur throughout the Indo–Pacific, remaining seemingly invariant in morphology, the possibility exists that the sequenced material represents a separate species. However, to test this hypothesis molecular material from Mauritius is needed, and it remains inaccessible for the time being, and thus we adhere to a more parsimonious assumption of *H. ocellata* being a single species throughout Indo–Pacific.

Two other species that correspond to the groups 2 and 3 of our 16S based tree are here described as *Hemilienardia acinonyx* sp. nov. and *H. lynx* sp. nov., with holotypes selected from the sequenced vouchers. The specimen BMOO 17147, which constitutes the fourth species revealed by the molecular studies, is a subadult and it was unfortunately damaged while its tissue was clipped. In our opinion, this specimen would not constitute an adequate name-bearing type. Two additional *H. ocellata*-like empty shells from the Society Islands were found to be morphologically conspecific with the BMOO 17147 voucher. Similar specimens with rather biconic shells and a very long siphonal canal were collected in New Caledonia and the Loyalty Islands; however, none was available for sequencing. We assume that they belong to the same species as the specimens from the Society Islands (the fourth species hypothesis) and we describe it here as *H. pardus* sp. nov.

There is a conflict between the two studied markers with regard to the relationships between species in the *H. ocellata* complex. Based on the analysis of COI, *H. acinonyx* sp. nov. forms a sister group to *H. ocellata* (PP=0.99), whereas based on the analysis of 16S, *H. acinonyx* sp. nov. is closer to *H. lynx* sp. nov. and *H. pardus* sp. nov., although this result is not strongly supported. As relationships within the *H. ocellata* species complex are not specifically targeted in the present study, and the phylogenetic analysis was performed for the species delimitation purposes only, this conflict does not alter our conclusions.

Taxonomic account

Class Gastropoda Cuvier, 1795
Order Neogastropoda Wenz, 1938
Superfamily Conoidea Flemming, 1822
Family Raphitomidae Bellardi, 1875

Genus *Hemilienardia* O. Boettger, 1895

Type species

Pleurotoma malleti Récluz, 1852 (by original designation).

Hemilienardia ocellata (Jousseaume, 1884)
Figs 2A–D, 3A–C, 4B

Lienardia ocellata Jousseaume, 1884: 186, pl. 4, fig. 4.

Lienardia (*Hemilienardia*) *ocellata* – Powell 1966.

Hemilienardia ocellata – Hedley 1922: 297. — Loch 1992: 3, fig. 4. — B.J. Smith 2003: 257. — Sysoev 2008: 744, pl. 667, figs 5–6.

Material examined

Syntype

MAURITIUS: 4.0 mm (dd - Fig. 2A–B) (MNHN IM-2000-3128).

Other material

MALDIVES: Ari Atoll, Maagau Kandu, 25 m, private collection of S. Gori (1 dd, 3.1 mm - Fig. 3A).

PHILIPPINES: PANGLAO 2004: stn B1, Panglao Island, Alona Reef, 9°33.0' N, 123°46.5' E, 8–14 m (2 lv, 3.3 mm, 3.4 mm); stn B2, Panglao Island, Alona Reef, 9°33.0' N, 123°46.5' E, 5 m (1 lv, 2.8 mm); stn B10, Panglao Island, Momo Beach, 9°36.5' N, 123°45.6' E, 3–14 m (1 lv, 2.8 mm); stn B13, Bohol Island, Baclayon Takot, 9°37.1' N, 123°52.6' E, 3–5 m (2 lv, 2.8 mm, 3.2 mm); stn B17, Panglao Island, Bingag, 9°37.5' N, 123°46.9' E, 3–21 m (1 lv, 2.9 mm); stn B20, Bohol Island, Ubajan, 9°41.5' N, 123°51.0' E, 2–8 m (1 lv, 2.9 mm); stn B38, Balicasag Island, 9°30.9' N, 123°40.8' E, 17–18 m (1 lv, 2.7 mm); stn L69-73, Balicasag Island, 9°30.7' N, 123°40.9' E, 90–98 m (1 dd); stn L74-75, Balicasag Island, 9°30.7' N, 123°40.9' E, 120–139 m (1 lv, 3.4 mm); stn S1, Panglao Island, Biking, 9°35.3' N, 123°50.5' E, 5 m (1 lv, 2.9 mm); stn S7, Panglao Island, Sungcolan Bay, 9°38.5' N, 123°49.2' E, 1–4 m (3 lv, 2.8 mm, 3.2 mm, 3.2 mm); stn S13, Bohol Island, Baclayon Takot, 9°37.1' N, 123°52.6' E, 8–15 m (1 lv, 2.7 mm); stn S14, Pamilacan Island, 9°29.3' N, 123°55.1' E, 5–12 m (1 lv, 3.1 mm); stn S16, Panglao Island, Bingag, 9°37.6' N, 123°47.3' E, 15–18 m (1 lv, 3.0 mm).

INDONESIA: Togian Islands: stn Tog13, Batudaka Island, 0°29.8' S, 121°36.9' E, 36–39 m (1 dd, 3.6 mm; PS-020554); stn Tog14, Batudaka Island, 0°29.8' S, 121°36.9' E, 21–25 m (1 dd); stn Tog22, Batudaka Island, 0°31.0' S, 121°37.1' E, 20–22 m (1 dd, SMF); stn Tog34, Pasir Tengah Atoll, 0°25.0' S, 121°38.9' E, 23–26 m (1 dd, SMF).

PAPUA NEW GUINEA: KAVIENG 2014: stn KB04, NW point of Nusa Island, 2°33.9' S, 150°46.7' E, 15–17 m (1 dd); stn KB08, E of N Cape, 2°33.2' S, 150°48.2' E, 13 m (3 dd); stn KB16, between Big Nusa and Little Nusa, 2°34.6' S, 150°46.3' E, 13–14 m (2 dd); stn KB26, entrance of Albatross Passage, 2°44.6' S, 150°43' E, 9–15 m (3 dd); stn KB28, S side of Baudisson Island, 2°43.7' S, 150°38.4' E, 15–26 m (1 dd); stn KB36, N side of Wadei Island, 2°38.8' S, 150°38.4' E, 3–8 m (1 lv); stn KB38, S side of Patio Island, 2°36.2' S, 150°31.6' E, 6–8 m (4 lv); stn KB58, N point of Nusalomon Island, 2°34.1' S, 150°37.5' E, 12 m (3 lv); stn KB64, New Ireland mainland, N coast, 2°33.5' S, 150°48.8' E, 19 m (1 dd); stn KPS09, Baudisson Island, 2°41.6' S, 150°37.2' E, 18–27 m (2 dd, 3.3 mm, 3.4 mm; PS-020555); stn KPS10, Baudisson Island, 2°41.6' S, 150°37.2' E, 12–14 m (3 dd, 2.7 mm, 2.8 mm, 3.5 mm); stn KPS11, Lemus Island, 2°38.3' S, 150°37.4' E, 8–19 m (2 dd, 2.5 mm, 2.9 mm); stn KS09, W of Nago Island, 2°36.1' S, 150°45.9' E, 15–16 m (2 dd); stn KS33, E of Nusaum Island, 2°38.2' S, 150°38.7' E, 8–10 m (2 lv); stn KS51, E side of Anelaua Island, 2°35.2' S, 150°30.5' E, 2–4 m (1 dd).

MARSHALL ISLANDS: Kwajalein Atoll, ocean side of reef, shell grit, 70 feet, leg. W. Blacketer, 2007 (1 dd, 3.3 mm; PS-020491).

VANUATU: Expedition SANTO 2006: stn DB80, 15°37.1' S, 167°07.5' E, 18 m (2 lv, 2.5 mm, 2.8 mm); stn FB 43, 15°28.4' S, 167°14.9' E, 19 m (1 lv, 2.6 mm); stn FB 56, 15°35.2' S, 167°02.1' E, 3–18 m (2 lv, 2.7 mm, 3.0 mm); stn ZB06, 15°36.8' S, 167°01.3' E, 30 m (4 lv, 2.3 mm, 2.4 mm, 2.5 mm, 2.7 mm); stn ZB20, 15°36.31' S, 167°05.4' E, 15–20 m (3 lv, 2.7 mm, 3.2 mm, 3.9 mm).

NEW CALEDONIA: Expedition MONTROUZIER: Secteur de Koumac, stn 1319, 20°44.7' S, 164°15.5' E, 15–20 m (1 lv, 3.6 mm - Figs 2D, 3B–C); Secteur de Koumac, stn 1357, 20°30.2' S, 166°26.4' E, 25–35 m (1 lv, 3.3 mm); Secteur de Nouméa, stn 1318, 20°41.4' S, 164°14.8' E, 20–30 m (1 lv, 3.6 mm).

LOYALTY ISLANDS: Lifou, Baie du Santal, Atelier LIFOU 2000: stn 1423, 20°54.0' S, 167°07.3' E, 12 m (2 lv, 3.5 mm, 3.6 mm); stn 1424, 20°54.9' S, 167°03.0' E, 4 m (1 lv, 3.7 mm); stn 1429, 20°47.5' S, 167°07.1' E, 8–18 m (2 lv, 3.3 mm, 4.4 mm - Fig. 2 C); stn 1432, 20°53.5' S, 167°02.7' E, 8–18 m (1 lv, 3.2 mm); stn 1436, 20°55.5' S, 167°04.2' E, 10–20 m (1 lv, 3.6 mm); stn 1457, 20°46.8' S, 167°02.75' E, 5–10 m (1 lv, 3.1 mm).

FIJI: MUSORSTOM 10: stn CP1334, 16°51' S, 178°14' E, 251–257 m (1 dd, 4.8 mm).

Description

SHELL. Very small (3.0–4.5 mm), ovate to fusiform (b/h 0.47–0.5; lw/h 0.65–0.67; a/h 0.48–0.5), pointed at its tip. Teleoconch usually of 3–3.5, up to 5 whorls. Suture incised, undulating. Early 1–1.5 teleoconch whorls almost cylindrical, with distinct shoulder; later whorls strongly convex in outline, with narrower concave subsutural ramp delineating adjacent whorls. Sculpture of strong and wide rounded axial ribs (10 on last whorl), well pronounced on whorls periphery and vanishing adapically. Axial ribs overridden by evenly interspaced, low and rounded spiral cords with shallow interstices. Late spire whorls sculptured with three spiral cords, adapical one much weaker, than succeeding. Microsculpture of dense microtubercles covering entire teleoconch surface. Last adult whorl and shell base with 6–7 subequal spiral cords followed by 3–5 oblique rows of tubercles on fasciole. Siphonal canal stout, moderately long, notably notched at its tip. Aperture narrow, elongated, contorted due to strong denticles of outer lip directed inwards. Adapicalmost of four denticles strongest. Inner lip strong, with distinct varix. Anal sinus subsutural, rounded, moderately deep and slightly constricted by callous subsutural tubercle.

PROTOCONCH. White, conical, of 3.3–3.5 whorls, PI whorls evenly rounded with fine sculpture of spiral cords and weak axial riblets. Late ~1.5 whorls with slightly flattened subsutural area and convex periphery, sculptured with subsutural row of fine, evenly interspaced axial riblets and with somewhat “crumpled” diagonally cancellate sculpture on periphery. Protoconch-teleoconch transition distinct, with moderately deep subsutural notch.

COLOUR. Background colour white, spire whorls with one row of large, oval, dark-olive spots encircled by a fine darker line, situated in interspaces between axial ribs above whorl periphery. Shell base with another row of dark olive spots and smaller regular spots on siphonal canal. Periphery of last adult whorl with bright yellow spiral line in interspace between third and fourth spiral cords, this line also visible on spire whorls, right above suture. Protoconch off-white.

RADULA. Small, of 7 transversal rows, consisting of narrowly triangular, pointed, marginal teeth, with slightly convex dorsal side (Fig. 4B–C). Tooth length 130–140 µm (about 7.3% of aperture height), tooth width about 40 µm.

Distribution and habitat

Distributed throughout the Indo-Pacific from Mauritius and the Maldives to the Philippines, Guam, Marshall Islands, Indonesia, Papua New Guinea, Queensland, Vanuatu, New Caledonia and Fiji, in shallow water.

Remarks

Hemilienardia ocellata can be distinguished from other eyespot-patterned *Hemilienardia* species by the ovate outline of the teleoconch and a proportionally very large protoconch. *Hemilienardia*

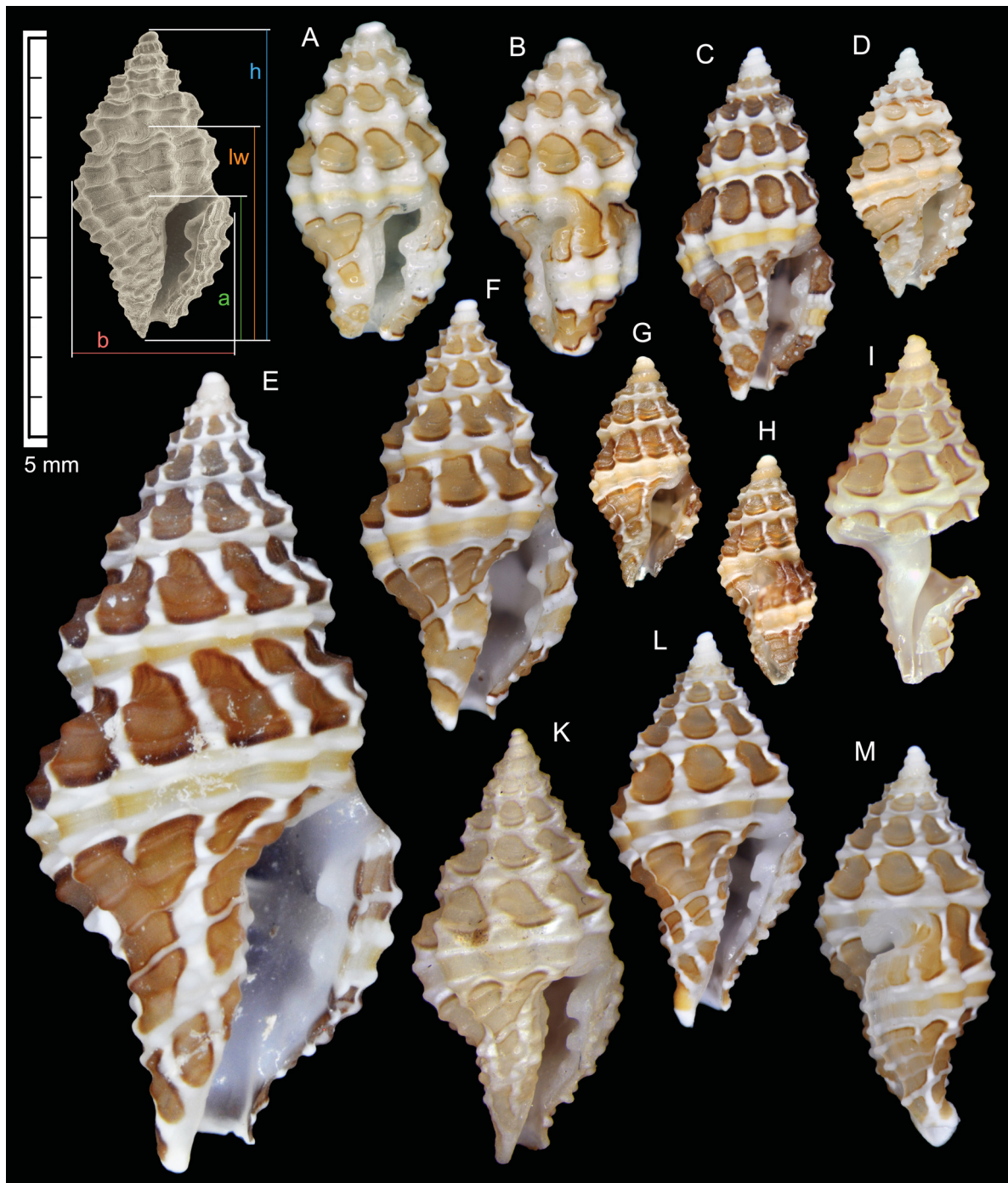


Fig. 2. Species of the *Hemilienardia ocellata* complex. The SEM image with no letter denoted shows standard measurements. **A–D.** *Hemilienardia ocellata* (Jousseaume, 1884). **A–B.** Syntype, MNHN IM-2000-3128, Mauritius, 4.0 mm. **C.** Loyalty Islands, Lifou, Baie du Santal, Atelier Lifou 2000, stn 1429, 20°47.5' S, 167°07.1' E, 8–18 m, 4.4 mm. **D.** New Caledonia, Secteur de Koumac, Expedition Montrouzier, stn 1319, 20°44.7' S, 164°15.5' E, 15–20 m, 3.6 mm. **E–F.** *Hemilienardia acinonyx* sp. nov. **E.** Holotype, MNHN IM-2013-33593, Philippines, 8.1 mm. **F.** Loyalty Islands, Lifou, Baie du Santal, Atelier Lifou 2000, stn 1441, 20°46.4' S, 167°02.0' E, 20 m, 5.4 mm. **G–H.** *Hemilienardia lynx* sp. nov., holotype, MNHN IM-2013-5489, Papua New Guinea, 2.75 mm. **I–M.** *Hemilienardia pardus* sp. nov. **I.** BMOO 17147, Society Islands, Moorea. **K.** Holotype, MNHN IM-2000-31661, 5.8 mm. **L–M.** Loyalty Islands, Lifou, Baie du Santal, Atelier Lifou 2000, stn 1454, 20°56.65' S, 167°02.0' E, 15–18 m, 5.2 mm.

lynx sp. nov. is undoubtedly the closest species in terms of size and shell shape. However, the two species differ in the number of protoconch whorls and the shape of the ocellae; these are ovate in *H. ocellata* and more “squarish” in *H. lynx* sp. nov. *Hemilienardia acinonyx* sp. nov. differs from *H. ocellata* by its orthoconoid spire, smaller protoconch and larger adult size; in addition, specimens of *H. acinonyx* sp. nov. have a characteristic spiral thread in the interval between the third and fourth spiral cords, while the second spiral cord is often strongly pronounced, giving a somewhat shouldered appearance to the late teleoconch whorls. Finally, *H. pardus* sp. nov. may be easily separated from *H. ocellata* by its broad biconical shell with very narrow aperture and long siphonal canal.

***Hemilienardia acinonyx* sp. nov.**

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Figs 2E–F, 3D–E, 4C

Etymology

The epithet refers to the genus *Acinonyx* (family Felidae) and its graceful member, the cheetah. Used as a noun in apposition.

Type material

Holotype

PHILIPPINES: Panglao Island, off Momo Beach, lumun-lumun net, 60–80 m (lv, 8.1 mm - Fig. 2E) (MNHN IM-2013-33593).

Paratypes

PHILIPPINES: paratype 1, same locality as holotype (lv, 5.5 mm) (MNHN IM-2013-33592); paratype 2, same locality as holotype (lv, 7.6 mm) (MNHN IM-2013-33594); paratype 3, Balicasag Island, lumun-lumun net, 70–80 m (lv, 7.0 mm) (PS-020556).

Other material examined

PAPUA NEW GUINEA: KAVIENG 2014, stn KB20, S coast of Baudisson Island, 2°45.2' S, 150°41.7' E, 8 m (1 dd, 6.8 mm).

LOYALTY ISLANDS: Lifou, Atelier LIFOU 2000: stn 1441, Baie du Santal, 20°46.4' S, 167°02.0' E, 20 m (1 lv, 5.4 mm - Fig. 2F); stn 1448, Baie du Santal, 20°45.8' S, 167°01.65' E, 20 m (1 lv, 5.0 mm - Fig. 3D–E).

PHILIPPINES: same locality as holotype (juveniles, 4 lv, 2.9 mm, 2.8 mm, 2.7 mm, 2.5 mm).

NEW CALEDONIA: LAGON Secteur de Poindimié, stn DW 830, 20°49' S, 165°19' E, 105–110 m (1 dd, 3.3 mm).

FIJI: MUSORSTOM 10, stn CP1363, 18°12' S, 178°33' E, 144–150 m (1 dd, 4.4 mm).

Description

SHELL. Small, broadly fusiform to biconical (b/h 0.47; lw/h 0.67–0.69; a/h 0.48–0.5), with rather long and slightly recurved siphonal canal. Spire orthoconoid, teleoconch of 3.5–5 whorls. Suture incised, undulating. Adapical portion of teleoconch whorls forming wide concave depression, basal portion strongly convex, with periphery shifted towards lower suture. Sculpture of very strong, widely interspaced axial ribs (9–10 on last whorl), vanishing on adapical areas of whorls. Axial ribs overridden by rounded spiral cords, slightly thickened where intersecting axials. Interspaces shallow. Microsculpture of dense tubercles covering entire teleoconch surface and fine arcuate growth lines in adapical depression. Spire

whorls sculptured with three spiral cords, adapical one weaker, than two succeeding; second spiral cord strongly elevated, giving spire whorls indistinctly shouldered appearance. Last adult whorl with 6 major spiral cords, and distinct thread situated in interspace between third and fourth major cords. Siphonal canal long, recurved abaxially, deeply notched at its tip, sculptured with oblique rows of tubercles. Aperture elongate, slightly contorted. Outer apertural lip with moderately developed varix, its inside with four denticles, of which the adapicalmost is strongest. Inner lip contorted below its mid-height, with oblique cords sculpturing fasciole, continuing inside aperture. Anal sinus rounded, deep and rather narrow, slightly constricted by subsutural callous tubercle.

PROTOCONCH. White, narrowly conical, of 2.3 evenly convex whorls. PI whorls with sharp spiral cords on its abapical portion, intersected by short axial strokes to form elevated, cross-shaped tubercles. PII sculptured with subsutural row of fine, evenly spaced, axial riblets and bearing somewhat “crumpled” diagonally cancellate sculpture on periphery.

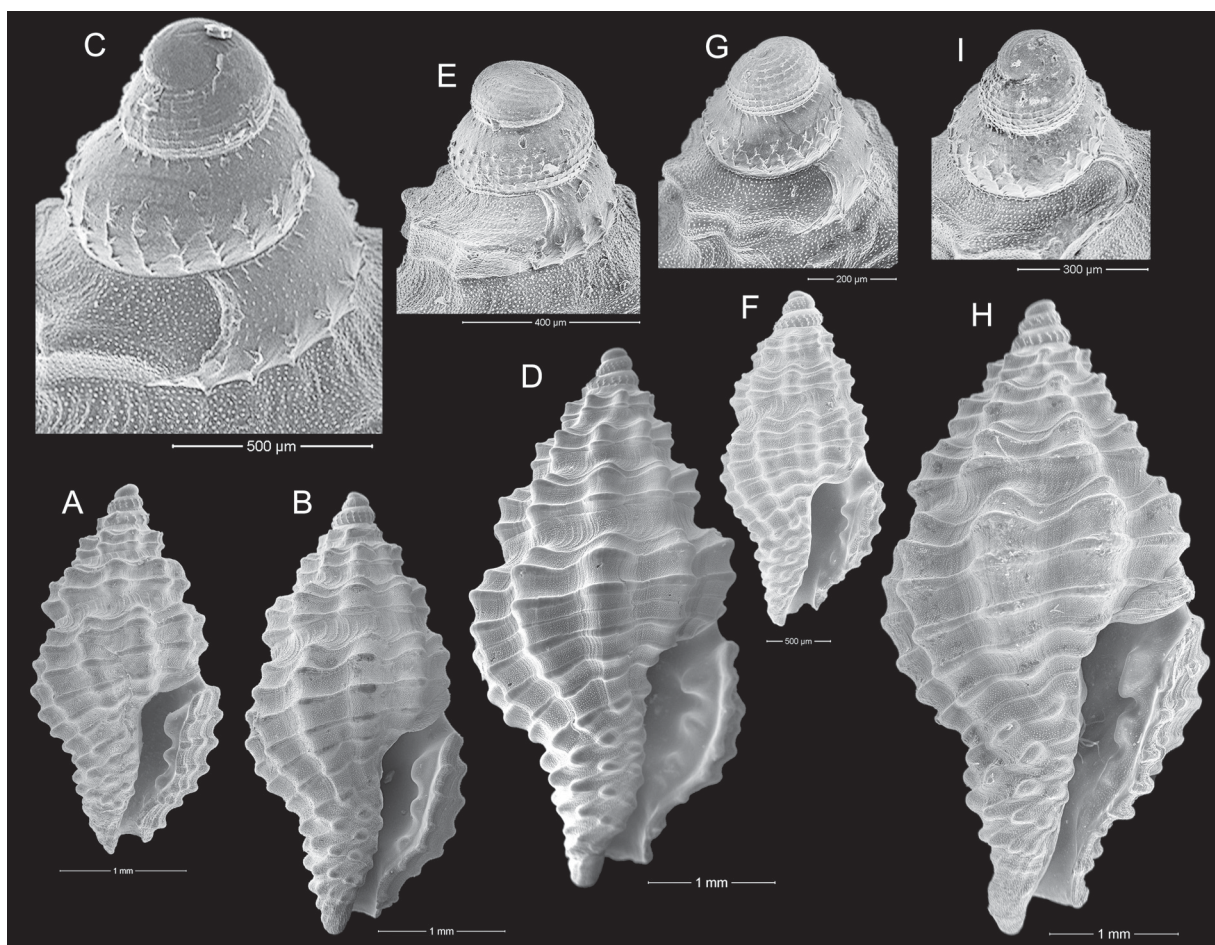


Fig. 3. Protoconch and shell morphology in the *Hemilienardia ocellata* complex. **A–C.** *H. ocellata* (Jousseaume, 1884). **A.** Specimen from the Maldives, Ari Atoll, Maagau Kandu, 25 m, 3.1 mm long. **B–C.** Specimen from New Caledonia, Expedition MONTROUZIER, stn 1319, 20°44.7' S, 164°15.5' E, 15–20 m, 3.6 mm long. **D–E.** *H. acinonyx* sp. nov. Specimen from the Loyalty Islands, Lifou, Baie du Santal, Atelier Lifou 2000, stn 1448, 20°45.8' S, 167°01.65' E, 20 m, 5.0 mm long. **F–G.** *H. lynx* sp. nov. Holotype, MNHN IM-2013-5489, Madang District, off Kranket Island, PAPUA NIUGINI stn PP14, 05°12' S, 145°50' E, 100–120 m, 2.75 mm long. **H–I.** *H. pardus* sp. nov. Specimen from the Loyalty Islands, Lifou, Baie du Santal, Atelier LIFOU 2000, stn 1454, 20°56.65' S, 167°02.0' E, 15–18 m, 5.2 mm long.

COLOUR. Background colour white with yellow line in interspace between third and fourth spiral cords, and regular triangular or squarish olive blotches encircled by darker line, situated above third spiral cord in interspaces between axial folds. Similar blotches covering shell base and siphonal canal.

RADULA. Very small, consisting of less than 10 rows of marginal teeth that are triangular, flat, with slightly thickened margins (Fig. 4D). Tooth width about 24 μm , length about 35 μm (about 1.5% of aperture height).

DIMENSIONS. Holotype 8.1 \times 3.8 mm.

Distribution and habitat

Recorded from the Philippines, Papua New Guinea, New Caledonia and Fiji, living at depths of 20–70 m.

Remarks

Hemilienardia acinonyx sp. nov. can be distinguished from other eye-spotted species of *Hemilienardia* by its orthoconoid spire with rather small protoconch, and the presence of the diagnostic spiral thread in the interspace between the third and fourth spiral cords. The ocellae decorating shell of *H. acinonyx* sp. nov. are usually triangular or squarish, which easily tells it apart from the more common *H. ocellata*. Specimens of *H. acinonyx* sp. nov. from the type locality notably exceed other ocellated species of *Hemilienardia* in size, as they may reach a height of 10–12 mm. Besides, the radula teeth in studied specimens of *H. acinonyx* sp. nov. are about three times shorter compared to the marginals of *H. ocellata*, and are flattened, broadly triangular in shape.

Hemilienardia lynx sp. nov.

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Figs 2G–H, 3F–G

Etymology

The epithet of this species refers to a smaller spotted cat, the lynx. Used as a noun in apposition.

Type material

Holotype

PAPUA NEW GUINEA: PAPUA NIUGINI 2012 stn PP 14, Bismarck Sea, Madang District, off Kranket Island, 5°12' S, 145°50' E, 100–120 m (lv, 2.75 mm - Figs 2G–H, 3F–G) (MNHN IM-2013-5489).

Other material examined (*Hemilienardia* cf. *lynx*)

PHILIPPINES: PANGLAO 2004: stns L69–73, Balicasag Island, 9°30.7' N, 123°40.9' E, 90–98 m (1 dd); stn 76, off Momo Beach, 9°36.5' N, 123°45.3' E, ca 80 m (1 lv, 2 dd; 1 dd, PS-020572).

Description

SHELL. Very small, ovate to fusiform (b/h 0.49; lw/h 0.67; a/h 0.5), pointed at its tip. Teleoconch of 3.2 whorls. Suture incised, undulating. Early 1–1.5 teleoconch whorls almost cylindrical, with distinct shoulder; later whorls strongly convex in outline, with narrower concave subsutural ramp, delineating adjacent whorls. Sculpture of strong, wide and rounded axial ribs (10 per whorl), well pronounced on periphery of whorls and vanishing adapically. Axial ribs overridden by evenly spaced, low and rounded spiral cords with shallow interspaces. Late spire whorls sculptured with three spiral cords, adapical one much weaker, than succeeding. Microsculpture of dense micro-tubercles covering entire teleoconch surface. Last adult whorl and shell base with 8 subequal spiral cords followed by 3 oblique rows of

tubercles on fasciole. Siphonal canal stout, moderately long, notably notched at its tip. Aperture narrow, elongated, with four denticles, the adapicalmost strongest. Outer lip strong, with distinct varix. Anal sinus rounded, moderately deep and slightly constricted by callous subsutural tubercle.

PROTOCONCH. Conical, of slightly less than 3.0 whorls, PI white, evenly rounded with fine sculpture of spiral cords and weak axial riblets. Late ~1.5 PII whorls light brown, with slightly flattened subsutural area and convex periphery, sculptured with subsutural row of fine evenly spaced axial riblets and with diagonally cancellate sculpture on periphery. Protoconch-teleoconch transition distinct, with moderately deep subsutural notch.

COLOUR. Background colour white, spire whorls with one row of large, oval, dark-olive squarish blotches encircled by a fine and slightly darker line, situated in interspaces between axial ribs above whorl periphery. Shell base with another row of dark olive blotches reaching tip of siphonal canal. Periphery of last whorl with a yellow spiral line in interspace between third and fourth spiral cords; this line can also be seen on spire whorls, right above the suture.

RADULA. No data.

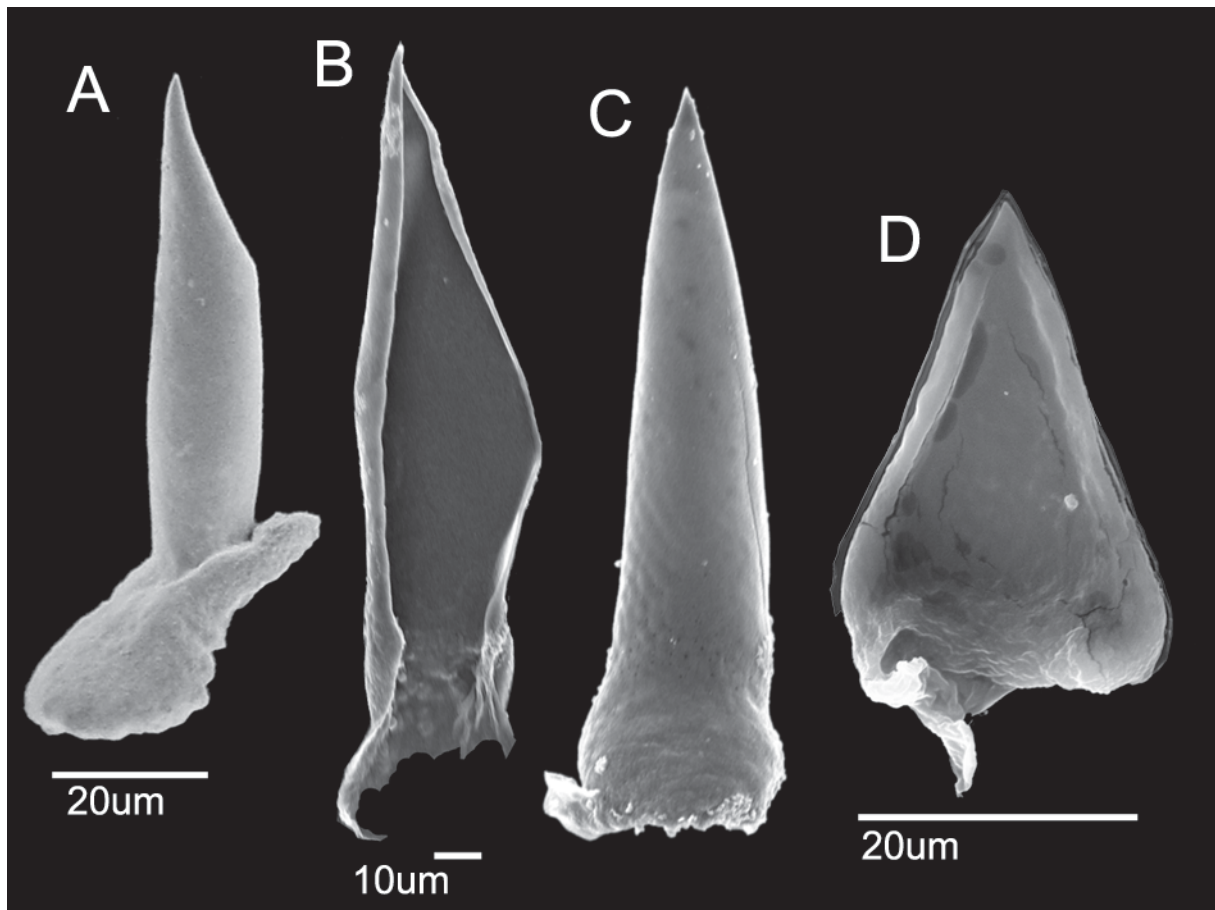


Fig. 4. Marginal radular teeth of some species of *Hemilienardia*. **A.** *H. malleti* (Récluz, 1852) (from Kantor & Taylor 2002). **B–C.** *H. ocellata* (Jousseau, 1884). Specimen from the Loyalty Islands, Lifou, Baie du Santal, Atelier LIFOU 2000, stn 1429, 20°47.5' S, 167°07.1' E, 8–18 m, 4.4 mm long. **D.** *H. acinonyx* sp. nov. Specimen from the Loyalty Islands, Lifou, Baie du Santal, Atelier LIFOU 2000, stn 1448, 20°45.8' S, 167°01.65' E, 20 m, 5.0 mm long.

DIMENSIONS. 2.75 × 1.35 mm.

Distribution and habitat

Papua New Guinea, Bismarck Sea, off Madang, 100–120 m; possibly Central Philippines, Balicasag Island, 80 m.

Remarks

This small ocellate *Hemilienardia* species is closest to *H. ocellata* in dimensions and shell shape. However, *H. lynx* sp. nov. can be distinguished from *H. ocellata* by the smaller and slightly shorter protoconch, the less narrow aperture, the less convex teleoconch whorls and the larger and more squarish ocellae. The holotype of *H. lynx* sp. nov. has an adult apertural morphology and appears to be mature. At 2.75 mm, it seems to be the smallest ocellate *Hemilienardia* species, notably smaller, than the otherwise similar *H. acinonyx* sp. nov. Based on the preliminary records of *H. lynx* sp. nov. from the Philippines, it does co-occur there with *H. acinonyx* sp. nov., and the two species were sampled together from deep lumun-lumun nets. The two species are identical regarding coloration; however, specimens of *H. acinonyx* sp. nov. of a shell size below 8 mm retain a thin and fragile juvenile outer lip, whereas specimens of *H. lynx* sp. nov. display an adult morphology of the aperture, although their size does not exceed 3 mm. The other character allowing separation of these two species is the shell shape, being rather fusiform in *H. lynx* sp. nov. and biconical with an orthoconoid spire in *H. acinonyx* sp. nov.

Hemilienardia pardus sp. nov.

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Figs 2I–M, 3H–I

Hemilienardia cf. *ocellata* – Tröndlé & Boutet 2009: 39.

Etymology

The species epithet refers to a well known spotted cat, the leopard. Used as a noun in apposition.

Type material

Holotype

SOCIETY ISLANDS: Tahiti, faille d'Arue, 20 m (1 dd, 5.8 mm - Fig. 2K) (MNHN IM-2000-31661).

Paratypes

SOCIETY ISLANDS: paratype 1, Tahiti, faille d'Arue, Mateval Bay, in front of Radisson Hotel, 20 m (1 dd, 5.4 mm) (MNHN IM-2000-31662); paratype 2, Moorea, off Motu Ahi, 17°33.15' S, 149°46.41' W, 73 m, deep reef slope (1 lv, 4.05 mm - Fig. 2I) (UF4565454, sequenced as BMOO 17147).

Other material examined

LOYALTY ISLANDS: Lifou, Baie du Santal, Atelier LIFOU 2000, stn 1434, 20°52.5' S, 167°08.1' E, 5–20 m (1 dd, 5.0 mm); stn 1451, Baie du Santal, 20°47.3' S, 167°06.8' E, 10–21 m (2 dd, 5.2 mm, 4.8 mm); stn 1454, 20°56.65' S, 167°02.0' E, 15–18 m (1 lv, 5.2 mm - Figs 2L–M, 3H–I).

NEW CALEDONIA: Touho, Récif man, Expedition MONTROUZIER, stn 1269, 20°35.1' S, 165°08.1' E, 15–20 m (1 lv, 5.6 mm).

Description

SHELL. Small, widely biconical (b/h 0.5; lw/h 0.71; a/h 0.51), with rather low spire and very long recurved siphonal canal. Teleoconch of 4.5 whorls; early 1–1.5 spire whorls distinctly shouldered, with angulate outline, later with concave subsutural depression and convex below; periphery shifted abapically. Suture

indistinct. Axial sculpture of strong and wide rounded axial ribs (8 on last whorl), best pronounced at whorl periphery and indistinct in subsutural ramp. Axial folds overridden by spiral cords, slightly widened where intersecting axials. Microsculpture of dense tubercles covering entire teleoconch surface. Spire whorls with three spiral cords below subsutural ramp. Adapical cord weaker than two succeeding ones, abapical spiral cord, marking whorl periphery, strongest. Peripheral cord bordered by suture of succeeding whorl. Last adult whorl and shell base with 8 spiral cords, adapical and abapical slightly weaker, than others. Siphonal canal long, recurved abaxially and slightly widened and notched at its tip. Fasciole sculptured with three distinct, oblique, gemmate cords. Aperture very narrow. Outer lip thick, with strong varix; inside of outer lip with three very strong, broad denticles with flattened crests, adapicalmost strongest. Inner lip recurved abaxially below mid-height, with three indistinct rounded plicae facing denticles of outer lip. Anal sinus rounded, deep and narrow, constricted by callous tubercle.

PROTOCONCH. White, narrowly conical, of about 3 whorls. PI evenly rounded, with fine sculpture of spiral cords and weak axial riblets. Late ~1.5 PII whorls with slightly flattened subsutural area and convex periphery, sculptured with subsutural row of fine, evenly spaced axial riblets and with somewhat “crumpled” diagonally cancellate sculpture on periphery. Protoconch-teleoconch transition distinct, with moderately deep subsutural notch.

COLOUR. Background colour white, spire whorls with regular, ovate, dark-olive spots encircled by a fine darker line in interspaces between axial ribs above whorl periphery. Shell base and siphonal canal with similar blotches, though less regular, often merged together. Periphery of last adult whorls with bright yellow spiral line in interspace between third and fourth spiral cords.

RADULA. No data.

DIMENSIONS. Holotype 5.8 × 2.85 mm.

Distribution and habitat

Known from the Society Islands, living at a depth of 73 m, and from the Loyalty Islands and New Caledonia, living at depths of 15–20 m (Fig. 5).

Remarks

Even though there are no molecular data available for *H. pardus* sp. nov. from New Caledonia and the Loyalty Islands, we assume that it is conspecific with specimens from the Society Islands based on shell characters. This species can easily be distinguished from other members of this group by its widely biconical shell, with a very long and recurved siphonal canal and proportionally low spire. Apart from that, *H. pardus* sp. nov. is characterized by having only eight axial ribs on the last adult whorl, while there are typically ten in *H. ocellata* and *H. acinonyx* sp. nov.

Discussion

Despite the fact that the recognition of species in the *Hemilienardia ocellata* complex is complicated by the shared ocellate colour pattern, they demonstrate stable differences in shell morphology, which become clear in SEM images. Moreover, the material shows notable differences in size and number of whorls of the protoconch. The latter character is known to vary notably among closely related conoidean species (Bouchet 1990; Puillandre *et al.* 2010), and particularly in the family Raphitomidae (Fedosov & Puillandre 2012; Fedosov & Stahlschmidt 2014). Thus, the species treated in the present study are not cryptic. Their ranges overlap in the western Pacific (the Philippines, Papua New Guinea, New Caledonia, Fiji), but there is evidence of distinct bathymetrical preferences: while *H. ocellata* occurs in shallow water, from the intertidal to 20–25 meters, both *H. acinonyx* sp. nov. and *H. lynx* sp. nov. were sampled from greater depths, about 70–100 m. *Hemilienardia ocellata*, *H. acinonyx* sp. nov. and *H. pardus* sp. nov. all occur – but do not co-occur – in the Loyalty Islands at depths of 5–20 m.

The continuous geographic range of *Hemilienardia ocellata* is still to be confirmed. Only specimens from the Bismarck Sea were sequenced for COI, and low inferred genetic distances cannot be extrapolated to broader geographic scales. On the contrary, there is a clear, although rather weak, genetic structuring in *H. ocellata* revealed in the analysis of 16S: specimens from Vanuatu form a distinct clade, separate from most sequenced specimens from the adjacent Bismarck Sea. Better geographic coverage in future studies may result in either a continuous range of genetic distances, where such differences between local populations will vanish, or in a set of separate clades corresponding to local, more or less distinctive, populations, depending likely on the presence of natural barriers decreasing the efficiency of dispersal. It should be noted that the protoconch of *H. ocellata* is notably larger, than in the other ‘spotted cats’, suggestive of the increased dispersal abilities of this species (Jablonski & Lutz 1983). Nevertheless, the examination of specimens of *H. ocellata* from multiple localities from Mauritius and the Maldives to New Caledonia and Vanuatu revealed no consistent differences in shell morphology. Thus, if future work would demonstrate the existence of several molecular species referable to *H. ocellata* as circumscribed herein, this would truly be a case of cryptic species.

The *Hemilienardia ocellata* species complex is undoubtedly one of the most distinctive lineages among Conoidea. The purpose of their shell pattern remains unclear. Spotted colour patterns are common in the gastropod families Ovulidae and Eulimidae (Schiaparelli *et al.* 2005; Dgebuadze *et al.* 2012) and may be associated with their sedentary, symbiotic lifestyle; by adjusting shell and soft tissue colouration to their host species, ovulids and eulimids generate remarkable defensive camouflages or, on the contrary their ocellate mantle may be aposematic as is known in different lineages of nudibranchs, in particular chromodorids (Rudman 1991). These models, however, do not seem to apply to the ‘spotted cat’ raphitomids, as no conoideans are known to live symbiotic lifestyles. It is still likely, however, that the major role of the pattern is defense: visual recognition of the snails by predators may be hampered by the breaking of a recognizable shell outline into a set of separate bright blotches. Overall, owing to the minute size of many conoideans, very little is known about their biology and the spectrum of their

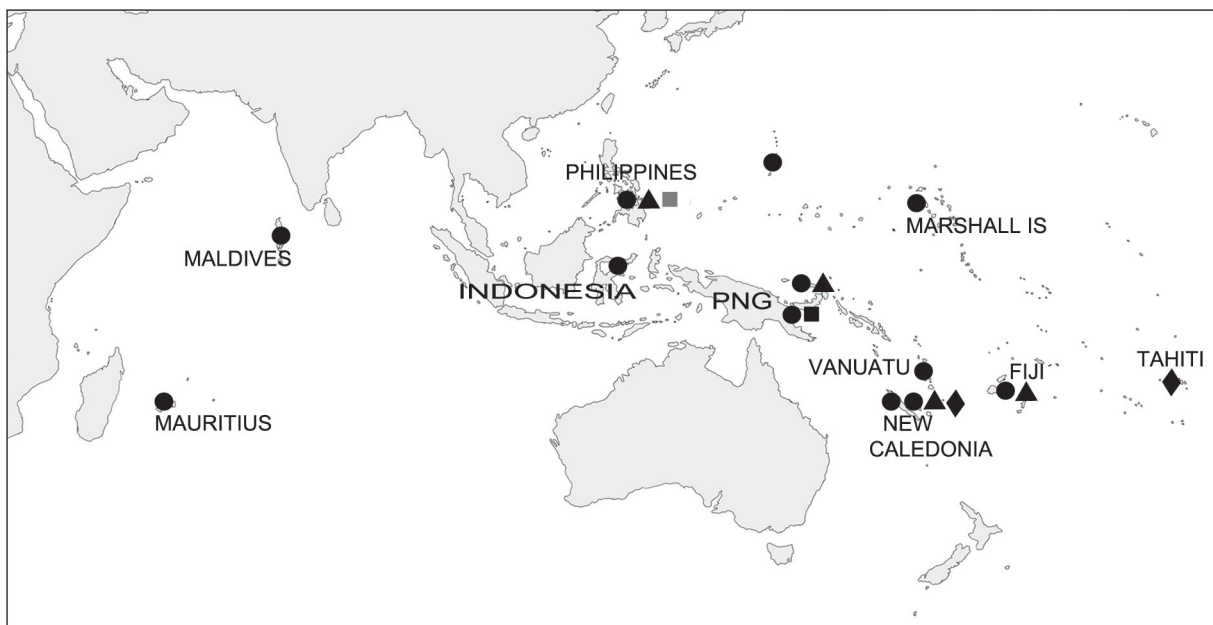


Fig. 5. Records of the *Hemilienardia ocellata* species complex, based on material examined in the present paper. Filled circles = *H. ocellata* (Jousseume, 1884); triangles = *H. acinonyx* sp. nov.; black square = *H. lynx* sp. nov.; grey square = *H. cf. lynx* sp. nov.; diamonds = *H. pardus* sp. nov.

biological interactions, which would be a prerequisite to suggest reasonable hypotheses on the role of colour pattern for these molluscs.

‘Spotted cats’ are distinctive not only because of their remarkable colour pattern: their flat or semi-enrolled radulae teeth are unique for the family Raphitomidae, all members of which that have been studied so far possess hypodermic teeth (Kantor & Taylor 2002; Bouchet *et al.* 2011), excepting several species that were proven to be radula-less (Kantor & Sysoev 1989; Kantor & Taylor 2002; Fedosov 2007). According to Kantor & Puillandre (2012), hypodermic marginal teeth are a key morphological determinant of the major conid conoidean clade, which comprises Borsoniidae, Conidae, Conorbidae, Clathurellidae, Mangeliidae, Mitromorphidae and Raphitomidae. Thus, the unusual morphology of marginals in the *Hemilienardia ocellata* complex is most likely a result of secondary simplification. This simplification of the radula is becoming further obvious from the relative dimensions of the radular teeth: whereas the marginal teeth attain about 7% of the aperture height in *H. ocellata*, the marginals only reach 1.5% of the aperture height in *H. acinonyx* sp. nov. Semi-enrolled, simplified radular teeth were also found in some species of *Mangelia* (Bouchet *et al.* 2011), and the appearance of such teeth in *Hemilienardia* species can be attributed to the general tendency towards morphological simplification recorded in minute members of Raphitomidae and Mangeliidae (Kantor & Taylor 2002).

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