

TAXONOMIC REVISION OF *LEIOSTRACUS ONAGER* AND *LEIOSTRACUS SUBTUSZONATUS* (GASTROPODA: PULMONATA: ORTHALICIDAE)

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Abstract *Leiostracus subtuszonatus* (Pilsbry 1899) was originally described as a colour variant of *L. onager* (Beck 1837). Here we conduct a taxonomic revision of these two species and regard them as separate taxa, distinguished by shell size, colour pattern, whorl convexity and protoconch sculpture. We also define a neotype for each species and offer updated descriptions, diagnosis and geographical ranges.

Key words Bahia state, Brazil, *Leiostracus*, *Bulimulinae*, land snails, *Stylommatophora*

INTRODUCTION

Leiostracus Albers 1850 is an endemic South American genus, occurring in Guyana, Surinam and Brazil, and being particularly diverse in the eastern and southeastern regions of the latter (Breure, 1979; Simone, 2006). The taxonomic status of two species from Bahia state, Brazil, has recently caught our attention: *Leiostracus onager* (Beck 1837) and *Leiostracus subtuszonatus* (Pilsbry 1899).

Beck (1837) named and defined *Bulimus onager* based on the description of the invalid *Bulimus zebra* by Spix (1827). Beck's description was lacking in detail, since Spix had already described the species. The species gained a better description and illustration in the work of Reeve (1848) and was finally better delimited by Pilsbry (1899), who allocated it in the genus *Drymaeus* Albers 1850 and, more specifically, in the subgenus *Leiostracus* Albers 1850. Pilsbry (1899) also described *D. onager subtuszonata* as a new colour variant (a variant already detected, but not named, by Küster & Pfeiffer, 1844, 1854). *Leiostracus* was afterwards elevated to genus level and *L. subtuszonatus* achieved the rank of a separate species from *L. onager* (Breure 1979), a decision followed by later authors (Salgado & Coelho, 2003; Simone, 2006).

Since *L. subtuszonatus* was first described as a subspecies of *L. onager* and specimens available in museum collections are almost always of the latter, we suspected that these species could in



Figure 1 Map of Bahia state showing the known occurrences of *Leiostracus onager* (Itabuna) and *L. subtuszonatus* (Ilhéus). Abbreviations of neighboring states: MA, Maranhão; PI, Piauí; PE, Pernambuco; AL, Alagoas; SE, Sergipe; TO, Tocantins; GO, Goiás; MG, Minas Gerais; ES, Espírito Santo.

fact be synonyms. The difference between them should be the colour pattern, as indicated by Pilsbry (1899), but these patterns are very variable in *Drymaeus* and in its former subgenus *Leiostracus*. Therefore, in order to investigate this matter more closely, we analyzed a large series of specimens of both species (stemming from

collections of many institutions) and conducted a throughout revision of the literature. We have contacted all major museums worldwide and were surprised at how few specimens of *L. onager* and *L. subtuszonatus* there are.

In our analysis, we have found striking conchological differences between these species besides the colour pattern, justifying the maintenance of two separate species. We also take this opportunity to provide updated descriptions, diagnosis and geographical ranges of the species, as well as to define a neotype for each.

MATERIALS AND METHODS

The analyzed material comes from the collections of the following institutions: ANSP, Academy of Natural Sciences of Philadelphia (Philadelphia, USA); LMD, Löbbecke Museum Düsseldorf (Düsseldorf, Germany); MNHN, Muséum National d'Histoire Naturelle (Paris, France); MZSP, Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil); SMF, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (Frankfurt am Main, Germany). Unfortunately, only dry shells were available in the collections and no living animal could be recovered in the field. A list of analyzed material follows each species description. The shell measurement abbreviations used through the text are: H = shell length; D = shell greatest width; S = spire length (excluding aperture); S' = spire length (excluding body whorl); h = aperture height; d = aperture width.

Since types were never defined for *L. onager* and *L. subtuszonatus* and there is much confusion in the literature regarding these species, we opted to designate neotypes for both, hoping to solve such problems with well-defined and figured type specimens. The chosen neotypes compare extraordinarily well to the original descriptions and stem from the type locality, Bahia state (unfortunately, the original collection localities of both species were never given more precisely than this in the previous literature).

Moreover, specimens of related species such as *L. cinnamomeolineatus* (Moricand 1841), *L. clouei* (Pfeiffer 1856) and *L. vimineus* (Moricand 1833) were analyzed, coming from the collections of the museums listed above and also from: NHMUK, Natural History Museum (London, UK); ZMA, Zoological Museum Amsterdam (Amsterdam,

The Netherlands; now the NCB Naturalis); ZMB, Museum of Natural History History, Humboldt University Berlin (Berlin, Germany; formerly Zoologisches Museum Berlin). All type material of the above-mentioned species was analyzed: NHMUK 1975492 (*L. clouei*, lectotype); SMF 302126 (*L. cinnamomeolineatus*, syntypes, 3 shells) and 302131 (*L. vimineus*, syntype); ZMB 10316 (*L. vimineus*, syntype).

SYSTEMATICS

Family Orthalicidae

Subfamily Bulimulinae

Genus *Leiostracus* Albers 1850

Leiostracus onager (Beck 1837) (Figs 2–13)

Bulimus zebra Spix 1827 (*non* Bruguière 1789): 8, pl. 7, fig. 5

Bulimus (Bulimulus) onager Beck 1837: 64

Bulimus onager: Reeve, 1848: pl. 45, fig. 284; Küster & Pfeiffer, 1844: 167, pl. 16, fig. 16; Pfeiffer, 1853: 342; Küster & Pfeiffer, 1854: pl. 50, figs. 9–10

Liostracus onager: Albers, 1860: 213

Drymaeus (Leiostracus) onager: Pilsbry, 1899: 94, pl. 14, fig. 16; Morretes, 1949: 151

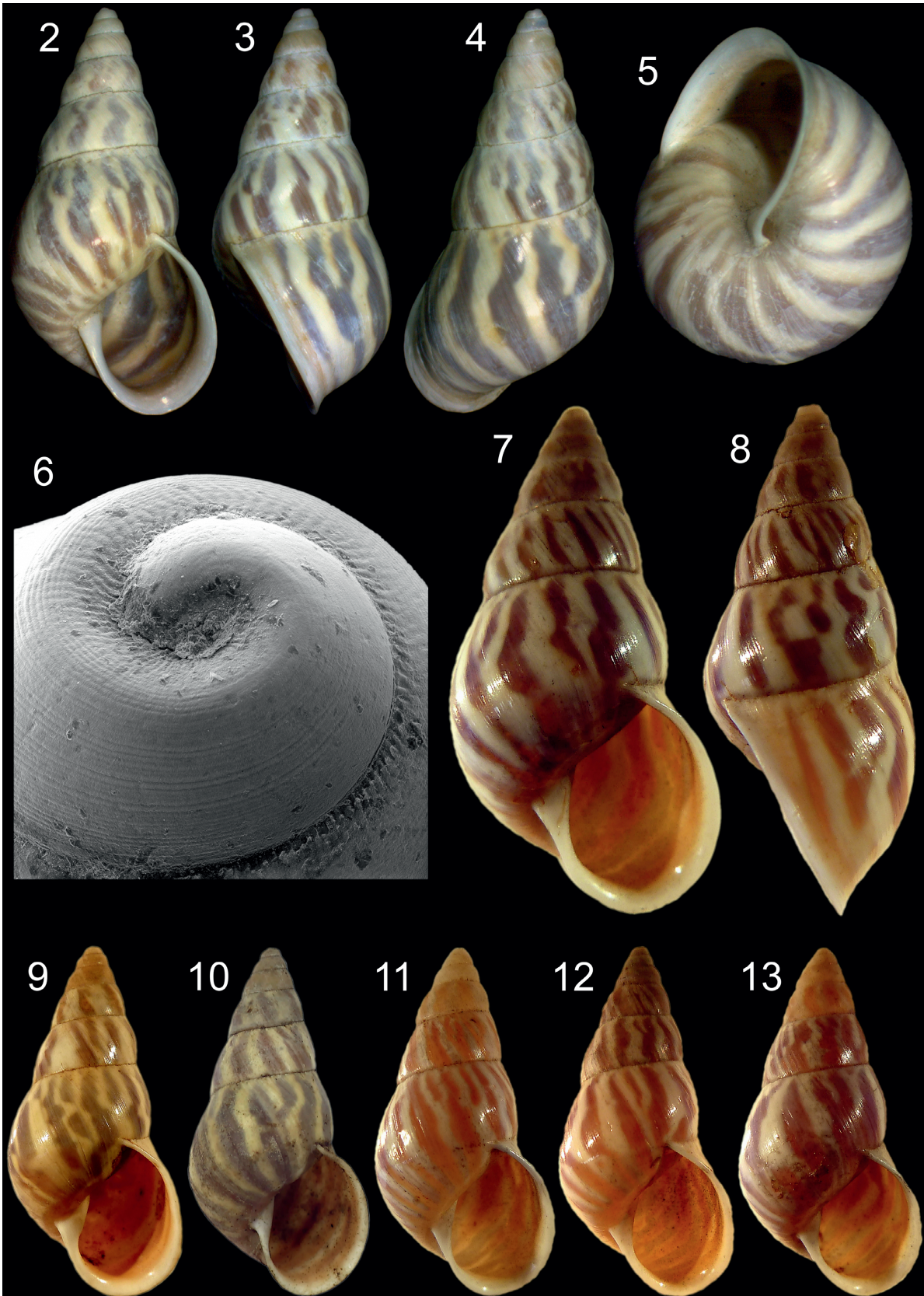
Leiostracus (Leiostracus) onager: Breure, 1979: 127

Leiostracus onager: Parkinson, Hemmen & Groh, 1987: 132, pl. 12, fig. 9; Salgado & Coelho, 2003: 163; Simone, 2006: 122, fig. 383.

Neotype Since no type specimen was defined either by Spix (1827) or Beck (1837), we designate here the following specimen as neotype: MZSP 29794 (Figs 2–5).

Neotype locality Itabuna (Bahia state, Brazil; Fig. 1); city center coordinates 14°47'09"S 39°16'48"W, ~54 m of elevation (E. Garbe col., viii/1900).

Material analyzed **Brazil.** *Precise locality undetermined*: LMD 115401b (1 sh; Scheepmaker col.); LMD 115401d (1 sh; Scheepmaker col.); MNHN IM-2012–2008 (1 sh; Denis collection, 1945). **Bahia.** *Itabuna*: MZSP 29794 (neotype; E. Garbe col., viii/1900); MZSP 110834 (1 sh; E. Garbe col., viii/1900). *Precise locality undetermined*: MNHN IM-2012–2003 (1 sh; M. Dugrivet col., 1841); MNHN IM-2012–2004 (3 sh); MNHN IM-2012–2006 (3 sh; Letellier collection, 1949).



Figures 2–13 *Leiostracus onager*. 2–5. Neotype (MZSP 29794; H = 25.6 mm). 6. SEM image of protoconch, MNHN IM-2012–2004. 7–8. MNHN IM-2012–2003; H = 21.5 mm. 9. MNHN IM-2012–2006; H = 23 mm. 10. LMD 115401b; H = 24 mm. 11. MNHN IM-2012–2003; H = 22 mm. 12. MNHN IM-2012–2003; H = 23 mm. 13. MNHN IM-2012–2003; H = 22.5 mm.

Measurements (in mm) Neotype: $6\frac{3}{4}$ whorls; H = 25.6; D = 11.8; S = 15.7; S' = 9.5; h = 10.8; d = 8.0. Mean (n = 10): $6\frac{1}{4}$ to $6\frac{1}{2}$ whorls (rarely 6 or 7); H = 22.7 ± 1.0 (max 24.4; min 21.3); D = 10.5 ± 0.3 (max 1.0; min 10.2); S = 13.0 ± 0.6 (max 14.0; min 12.5); S' = 9.4 ± 0.3 (max 9.9; min 8.9); h = 10.3 ± 0.5 (max 10.9; min 9.5); d = 7.3 ± 0.4 (max 8.0; min 6.8).

Diagnosis Distinctive striped colour pattern. Umbilicus region brown (as axial marks). Whorls profile slightly convex. Protoconch sculptured by fine parallel axial wrinkles only on the topmost portion of whorls, but this sculpture soon stops and gives place to numerous very fine parallel spiral lines.

Re-description Shell medium-sized, sub-conical; width $\sim 1/2$ shell length. Spire top colour ($\sim 2\frac{3}{4}$ whorls, including protoconch) whitish to light brownish yellow; remaining whorls white with thick brown axial bands, sometimes forked above. Colour pattern visible from the inside of shell; peristome white; region surrounding umbilicus brown (same colour as axial marks). Spire angle $\sim 40^\circ$. Protoconch ($\sim 1\frac{1}{2}$ whorls) sculptured by fine parallel axial wrinkles only on the topmost portion of whorls, but this sculpture soon stops and gives place to numerous very fine parallel spiral lines; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Whorls profile slightly convex. Suture well-marked, slightly oblique (diagonal) to columellar axis. Aperture large, oval, slightly prosocline ($\sim 15^\circ$ with columellar axis); $\sim 1/2$ shell length, $\sim 2/3$ shell width. Peristome reflected, especially on columellar region, partially covering umbilicus. Body whorl $\sim 2/3$ shell length. Umbilicus rimate.

Etymology From the Latin *onager*, meaning "wild ass"; probably referring to the stripes on the shell, as some wild asses show black stripes on their legs (also remembering that the species described by Spix was named "zebra").

Habitat Atlantic rainforest. Supposedly lives on trees, as usual for the genus. Silva (1985) mentions some snails, identified by Dr. R.T. Abbott, which occur on cacao trees (*Theobroma cacao*; Malvaceae) in the municipalities of Buerarema, Coaraci, Itamari, Uruçuca and Una, all in Bahia state; *L. onager* is listed among them.

Geographic range Known only from Bahia state. Unfortunately, the greatest part of the museum specimens (collected before the 1950's) and the literature does not provide specific localities, simply stating that the species occurs in Bahia (or, in the worst cases, they indicate only "Brazil"). Up to now, the only determined locality is the municipality of Itabuna (Fig. 1).

Leiostracus subtuszonatus (Pilsbry 1899)
(Figs 14–24)

Drymaeus (Leiostracus) onager var. *subtuszonata* Pilsbry 1899: 95, pl. 14, fig. 17

Leiostracus (Leiostracus) subtuszonata [sic]: Breure, 1979: 127

Leiostracus subtuszonatus: Salgado & Coelho, 2003: 163

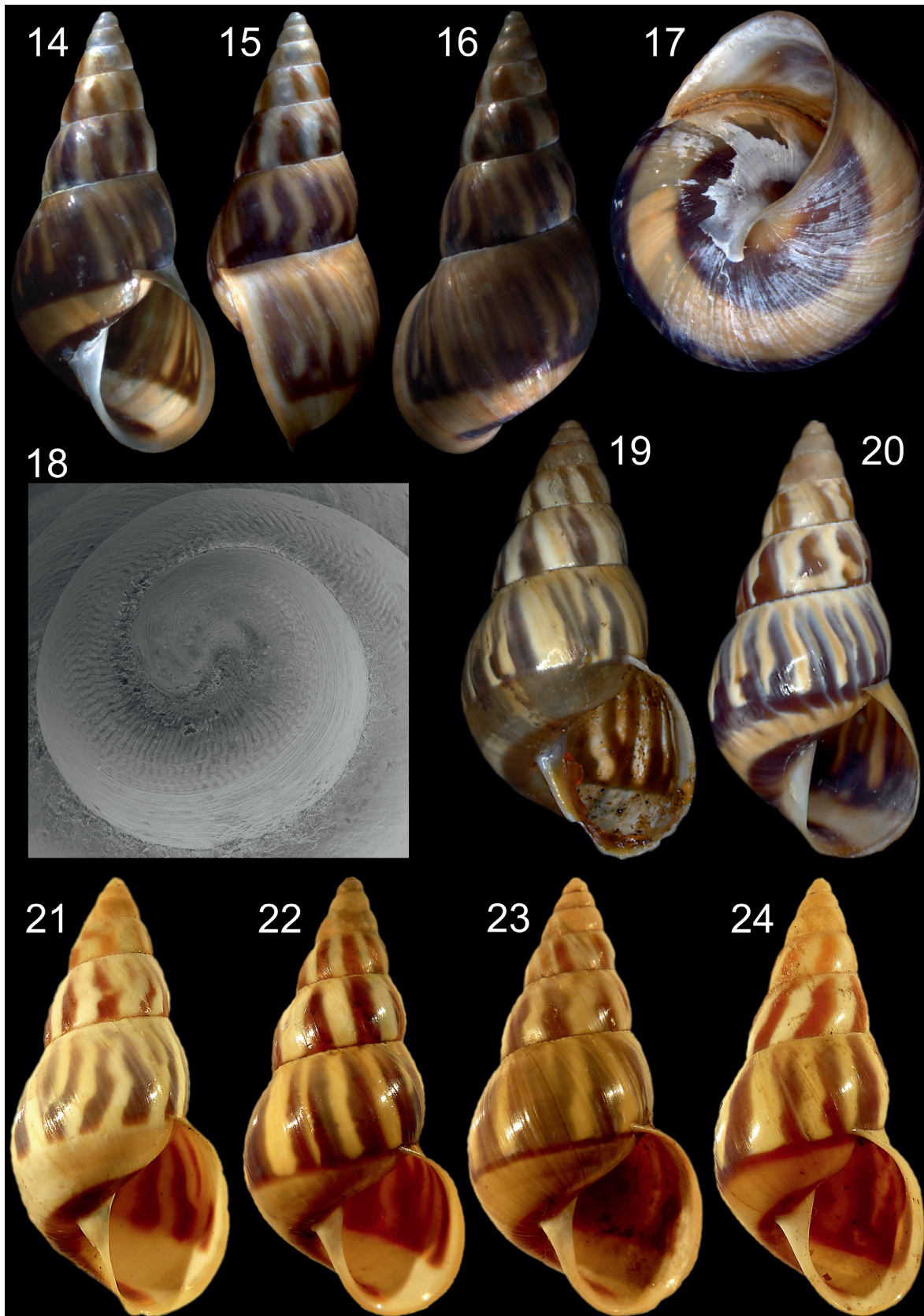
Leiostracus subtuszonatus [sic]: Simone, 2006: 123, fig. 387

Neotype No type specimen was defined by Pilsbry, since he was just describing a colour variant. Therefore, here we designate the following specimen as neotype for this species: MZSP 108040 (Figs 14–17).

Neotype locality Ilhéus (Bahia state, Brazil; Fig. 1); city center coordinates $14^\circ 47' 20''$ S $39^\circ 02' 56''$ W, ~ 52 m of elevation.

Material analyzed **Brazil.** *Precise locality undetermined:* LMD 115401a (1 shell; Scheepmaker col.); LMD 115401c (1 shell; Scheepmaker col.); LMD 115633 (1 shell; Lischke? col.); MNHN IM-2012–2007 (4 shells; Jousseume collection); MNHN IM-2012–2009 (1 shell; Denis collection, 1945); SMF 284391 (1 shell; G. Naegele collection). **Bahia.** *Ilhéus:* MZSP 29796 (Bela Vista farm, Rio do Braço district; 2 shells, MZSP personnel col., 08/ii/1964); MZSP 30302 (1 shell; CEPLAC personnel col., iv/1998); MZSP 86781 (1 shell; $14^\circ 45'$ S $39^\circ 13'$ W; CEPLAC personnel col.); MZSP 108040 (neotype; 1 shell, J.F. Vaz col., v/1995); MZSP 110707 (1 shell, J.F. Vaz col., v/1995). *Precise locality undetermined:* ANSP 25963 (1 shell, T.B. Wilson col.); MNHN IM-2012–2005 (1 shell); MZSP 27650 (1 shell; Bander col., 1921); SMF 284019 (2 shells; Bronn collection, ex. H. Rolle).

Measurements (in mm) Neotype: 7 whorls; H = 28.5; D = 13.1; S = 17.1; S' = 10.6; h = 12.8; d = 8.8. Mean (n = 14): $6\frac{3}{4}$ to 7 whorls (rarely $6\frac{1}{2}$); H = 25.5 ± 2.2 (max 28.2; min 21.3); D = $12.6 \pm$



Figures 14–24 *Leiostracus subtuszonatus*. 14–17. Neotype, MZSP 108040; H = 28.5 mm. 18. SEM image of protoconch, MNHN IM-2012–2007. 19. MZSP 27650; H = 21.5 mm. 20. Juvenile, MZSP 110707; H = 24 mm. 21. SMF 284019; H = 28 mm. 22. SMF 284019; H = 25.5 mm. 23. MNHN IM-2012–2007; H = 25.5 mm. 24. MNHN IM-2012–2007; H = 28 mm.

1.0 (max 14.0; min 10.6); $S = 14.9 \pm 1.8$ (max 17.7; min 12.0); $S' = 10.7 \pm 1.3$ (max 12.3; min 8.0); $h = 11.4 \pm 1.0$ (max 12.8; min 9.0); $d = 8.5 \pm 0.6$ (max 9.4; min 7.1).

Diagnosis Body whorl with a wide yellow or white spiral band flanked by brown bands (upper band may be absent). Umbilicus region white to light yellowish brown. Protoconch sculptured by fine parallel axial wrinkles on the upper portion of whorls, and by very fine parallel spiral lines on the remaining surface. Whorls profile convex.

Re-description Shell medium-sized, sub-conical; width $\sim 1/2$ shell length. Spire top colour (~ 3 whorls, including protoconch) whitish to yellowish brown; remaining whorls whitish with thick brown axial bands, sometimes forked. On body whorl, these axial bands are interrupted by a broad yellow or whitish spiral band flanked by brown bands (the upper brown band, usually much narrower, may not be present on some specimens). Colour pattern visible from the inside of shell; peristome and umbilical region white to light yellowish brown. Spire angle $\sim 45^\circ$. Protoconch ($\sim 1\frac{1}{2}$ whorls) sculptured by fine parallel axial wrinkles on the upper portion of whorls, but this sculpture stops in the middle portion and gives place to very fine parallel spiral lines; transition to teleoconch unclear. Teleoconch smooth, except for growth lines. Whorls profile convex. Suture well-marked, slightly oblique (diagonal) to columellar axis. Aperture large, oval, slightly prosocline ($\sim 15^\circ$ with columellar axis); $\sim 2/5$ shell length, $\sim 2/3$ shell width. Peristome reflected, especially on columellar region, partially covering umbilicus. Body whorl $\sim 3/5$ shell length. Umbilicus rimate.

Etymology The epithet "*subtuszonatus*" indicates that the "typical" colour pattern of axial bands is suddenly interrupted by a spiral band, a useful diagnostic feature of this species.

Habitat Atlantic Forest. Remarks on some specimens' labels point towards a tree-dwelling species, many mentioning their occurrence on Cacao tree leaves. Notably, the city of Ilhéus, the locality of the neotype and some other specimens, is known in Brazil as "the Cacao Capital". This agrees with the report of Silva (1985) mentioned above, especially if some of his specimens of *L. subtuszonatus* were identified as *L. onager*.

Geographic range Known only from Bahia state. Unfortunately, the greatest part of the museum specimens (collected before the 1950's) and the literature does not provide specific localities, simply stating that the species occurs in Bahia (or, in the worst cases, they indicate only "Brazil"). Up to now, the only determined locality is the municipality of Ilhéus (Fig. 1).

DISCUSSION

Pilsbry (1899) defined the spiral band-bearing shells as the variety *L. onager subtuszonata*, a feature already detected, but not named, by Küster & Pfeiffer (1844, 1854). Pilsbry (1899) also stated that this variety was slightly larger. The variety later achieved species rank (Breure, 1979), but with no formal definition or diagnosis. Here it is maintained as a separate species, for there are many conchological features distinguishing it from *L. onager*.

In the first place, both characters used by Pilsbry (1899), colour and size, are indeed diagnostic. Intra-specific colour variation is commonly found in the related genus *Drymaeus*, but seem to be less marked in *Leiostracus*. In any case, the difference in colour pattern between *L. onager* and *L. subtuszonatus* is constant and in accordance with the other conchological diagnostic features. Furthermore, here we add yet another one: the region surrounding the umbilicus in *L. onager* is brown, of the same colour as the axial bands, while the same region in *L. subtuszonatus* is white, like the peristome. This feature is constant in all analyzed specimens. Still, both *L. onager* and *L. subtuszonatus* display some variation in colour pattern when considering the axial bands, which can be fine to very broad and sometimes forked on their upper portion. Moreover, in *L. subtuszonatus*, the upper brown spiral band may or may not be present (compare, for instance, Figs 21 and 24). As for the colour *per se*, there is some common variation in colour tone in both species, with the bands going from light to dark brown and the base colour of the shell from dirty white to a more creamy tone. Additionally, *L. subtuszonatus* sometimes shows some very fine yellowish marks accompanying the axial bands, giving it a "fiery" appearance (Fig. 20). As such, overall *L. subtuszonatus* shows more colour variation than *L. onager*.

Regarding shell size, *L. subtuszonatus* is indeed larger than *L. onager*, and usually has about

half a whorl more. There is some intraspecific variation in size, of course, with rare smaller *L. subtuszonatus* and not-so-rare larger *L. onager* specimens that make the size range of the two species overlap. Nevertheless, *L. subtuszonatus* indeed tends to be larger than *L. onager*. Other diagnostic features include more convex whorls and a broader shell in *L. subtuszonatus*; *L. onager* has a more acuminate profile. Moreover, a curious difference can be found in the protoconch sculpture. In *L. subtuszonatus*, the entire upper portion of the whorls is sculptured by fine parallel axial wrinkles and it only changes to the fine spiral lines on the median portion of the whorl (Fig. 18). However, in *L. onager* only the very topmost portion of the whorls shows the axial wrinkles; this sculpture very soon stops and gives place to numerous very fine parallel spiral lines (Fig. 6).

Some other Brazilian species that resemble *L. onager* are *L. vimineus* (considered by Pilsbry, 1899, as a closely related species), *L. clouei* and *L. cinnamomeolineatus*. At first glance, these species display a similar colour pattern to *L. onager*, but many features can distinguish them. *L. vimineus* has a more pronounced keel on the body whorl, a more diagonally positioned aperture, a distinct fold in the basal region of the aperture and, usually, fewer and darker axial bands. *L. clouei* has a more conical profile, with a smaller and more rounded aperture; it also has fewer and fainter axial bands, sometimes with diminutive brown spots scattered through the white regions of the shell. *L. cinnamomeolineatus* has a broader shell and a broader and more rounded aperture; it is white with numerous very fine yellowish light brown axial bands and the region surrounding the umbilicus is always white. The conchological features cited above also apply for distinguishing *L. subtuszonatus*. Anyway, this species is also easily distinguishable from the other by its spiral bands on the body whorl and usually also by its larger size and more convex whorls.

Finally, in order to avoid future confusion, a remark should be made here regarding the compendium of Brazilian land and freshwater molluscs by Simone (2006), since it is a reference work for all researchers dealing with the Brazilian fauna. Simone (2006) figures specimens of *L. subtuszonatus* for the following species' entries: *L. subtuszonatus* (p. 123, fig. 387), naturally; *L. onager* (p. 122, fig. 383), which likely reflects the difficulty of finding actual *L. onager* specimens in

museum collections; and *L. cinnamomeolineatus* (p. 121, fig. 376). Moreover, one of the specimens figured by Simone (2006) as *L. vimineus* (p. 124, fig. 388B; Figs 2–5 here) is actually *L. onager*.

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