TAXONOMIC REASSESSMENT OF *MEGALOBULIMUS TORIII* (GASTROPODA, STROPHOCHEILIDAE)

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Abstract *The taxonomical status of* Megalobulimus toriii *Morretes, 1937 from southeastern Brazil is reassessed herein. A large series of shells of* M. toriii *and* M. yporanganus *(Ihering & Pilsbry, 1901) were analysed for conchological features and measured for a principal component analysis. The material included recent shells and sub-fossil specimens (no living specimens or ethanol-preserved specimens could be procured).* Megalobulimus toriii *falls within the spectrum of morphological variation of* M. yporanganus *and is thus considered its synonym.* Megalobulimus yporanganus *was originally described from the Ribeira Valley in São Paulo state and its present distribution includes only other localities in this valley. However, the species is also known from Holocene archaeological contexts (shell mounds) and karst outcrops, with the oldest records dating from circa 10,800–9,200 YBP. Its past distribution extended southwards to the coast of Santa Catarina state.*

Key words *Brazil,* Megalobulimus yporanganus*, principal component analysis, sambaqui, shell mounds, Stylommatophora.*

Introduction

The Strophocheilidae are an endemic South American family of typically bulky snails, containing the subfamilies Strophocheilinae and Megalobuliminae (Bouchet *et al*., 2017). The latter subfamily contains a single but reasonably diverse genus, *Megalobulimus* Miller, 1878 (Simone, 2006). These are the largest living land snails in South America, being colloquially known as "mega-snails". These animals are mostly nocturnal and have low-density populations, which contributes to them being scarcely studied in natural settings (Miranda & Fontenelle, 2015; Lima *et al*., 2017).

While analysing shells of *Megalobulimus* spp. for an ongoing project, we came across a pair of species that seemed to be potential synonyms: *Megalobulimus yporanganus* (Ihering & Pilsbry, 1901) and *M. toriii* Morretes, 1937. The former was originally described from a cavern in Iporanga municipality, while the latter was described from a shell mound ("sambaqui" in Portuguese, from the Tupi expression for shell mound) called Jipovura, in Iguape municipality (Sakai, 1981). Both locations belong to the Ribeira Valley ("Vale do Ribeira"), São Paulo state, SE Brazil, with the type locality of *M. toriii* being circa 200km downstream from that of *M. yporanganus*.

These two species differ only by shell size, with *M. toriii* being slightly smaller; Bequaert (1948) had already alluded to the similarity between them, classifying *M. toriii* as a subspecies of *M. yporanganus*. However, *M. toriii* and all subspecies rank taxa in Megalobuliminae were restored/elevated to species level by Leme (1971), in an unpublished thesis following largely the works of Morretes (1949, 1953), without giving a tangible rationale for each taxa concerned. This author followed this in his later published work (Leme, 1973), but with no specific mention to *M. toriii*. This classification was likewise adopted by later authors (Salgado & Coelho, 2003; Simone, 2006).

Therefore, herein we analysed a large series of shells of *M. yporanganus* and *M. toriii*, both recent and sub-fossil (from shell mounds or from karstic deposits). We intended to elucidate this matter through a study of conchological features supported by an analysis of shell shape (Principal Component Analysis). We also took the opportunity to better define the species' past and present distribution.

Material & Methods

All the adult dry shells of *M. yporanganus* and *M. toriii* in the malacological collection of the MZSP were analysed and measured, including the type material. See below for the full specimen list. Unfortunately, no living specimens or ethanol-preserved specimens could be procured.

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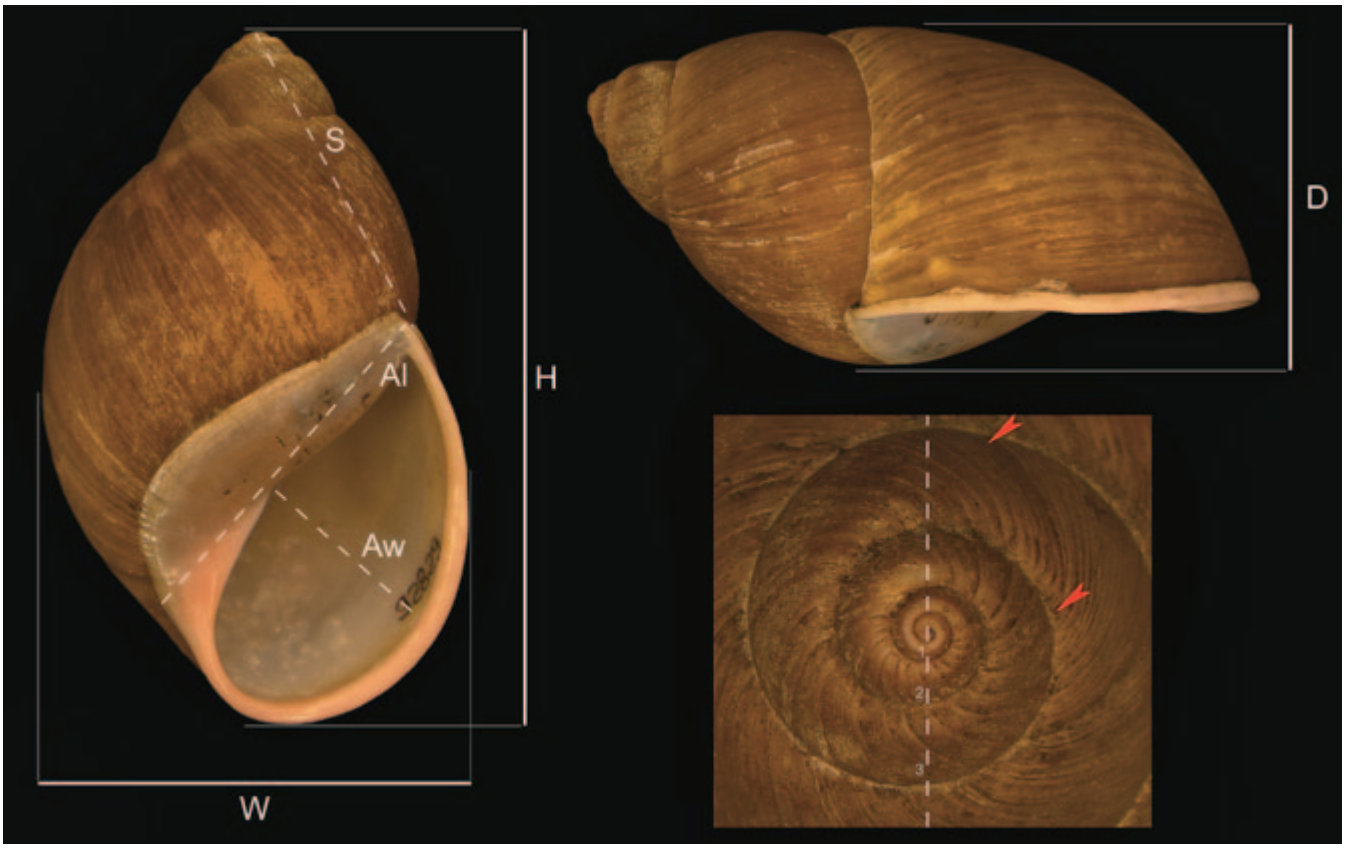

Figure 1 Shell of *Megalobulimus yporanganus* (MZSP 92829) in apertural and lateral views, showing the measurements taken. The close-up of the apical view of the shell shows the method of whorl counting; the arrow indicates the boundary between proto- and teleoconch.

To avoid biasing the analysis (by shell size, for instance), we used the identification given on the museum labels, not assigning the specimens to either species ourselves. We did, however, check the identification to make sure the specimens did not actually belong to another species of *Megalobulimus* or Strophocheilidae.

A series of eight measurements (Fig. 1) was taken per shell by a single person (JHF): the six measures were taken with a digital caliper and the two whorl counts were done with the aid of a handheld magnifier loupe.

Statistical analyses were performed in R version 3.4.3 (R Core Team, 2017). We conducted a Principal Component Analysis on the standardised values of all measurements (mean centered at 0, standard error at 1). Missing values, when present, were replaced by zeros after the standardisation (thus replaced by the mean value). Principal components 1 and 2 explained 86% of the variation, with PC1 alone explaining 73%; thus, both were retained for subsequent analyses. We conducted two analyses: a multivariate analysis of variance (MANOVA) with both PC1 and PC2 as response variables and two separate regressions for PC1 and PC2 separately. Because some specimens of *M. yporanganus* date from the early Holocene (Capelinha shell mound, 10,560–9,293 YBP) and are extremely abundant (127 specimens), we also performed two tests: the first including all specimens, and the second with only the present and more recent archaeological material (i.e., excluding the specimens from the Capelinha shell mound).

Abbreviations

Institutions: AMNH, American Museum of Natural History (New York, USA); MZSP, Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil).

Localities: PR, Paraná state; SC, Santa Catarina state; SP, São Paulo state.

Shell measurements: Al, aperture length; Aw, aperture width; D, greatest shell depth (perpendicular to H); H, shell length (parallel to columellar axis); Np, number of whorls of

protoconch; Nt, total number of whorls; S, spire length; W, greatest shell diameter (perpendicular to H).

Analyses: PCA, principal component analysis; PC1, first component; PC2, second component; spm, specimen(s).

Material analysed

The adult specimens used in the PCA are as follows: MZSP 5662 (**paratype** of *M. yporanganus*, SP, Iporanga, Caverna do Lambari); MZSP 14108 (**paratype** of *M. toriii*, SP, Iguape, Jipovura, Sambaqui Morro do Bernardes); MZSP 15604 (6 spm, SP, Iporanga); MZSP 15714 (1 spm, PR, Adrianópolis); MZSP 15593 (22 spm, SP, Iporanga); MZSP 16474 (14 spm, PR, Adrianópolis); MZSP 16552 (1 spm, SP, Iporanga, Gruta da Areia); MZSP 16606 (11 spm, SP, Iguape, Sambaqui Morro do Bernardes); MZSP 16649 (**holotype** of *M. toriii*, SP, Iguape, Jipovura, Sambaqui Morro do Bernardes); MZSP 16650 (**paratypes** of *M. toriii*, 3 spm, SP, Iguape, Jipovura, Sambaqui Morro do Bernardes); MZSP 16574 (5 spm, PR, Antonina, Itapema); MZSP 29299 (1 spm, SP, Registro); MZSP 29301 (1 spm, SP, Iguape, Serrote); MZSP 29303 (2 spm, SP, Guapiara); MZSP 42549 (2 spm, SC, Araquari, Sambaqui Pinheiros I); MZSP 64144 (**holotype** of *M. yporanganus*, SP, Iporanga); MZSP 92822 (1 spc, SP, Miracatu, Sambaqui Moraes); MZSP 92817 (5 spm, SP, Eldorado Paulista, sambaqui); MZSP 136429 (127 spm, SP, Cajati, Sambaqui Capelinha).

The following additional lots, consisting of juvenile or fragmented shells, were used for morphological comparison and geographic distribution, but not included in the PCA: AMNH 24244 (**holotype** of *M. iguapensis*, SP, Iporanga); MZSP 15025 (7 spm, SP, Capão Bonito, Caverna do Sumidouro); MZSP 29304 (1 spm, SP, Iporanga, Vale do Bethari); MZSP 29306 (1 spm, SP, Iporanga, Caverna de Santaninha); MZSP 29376 (1 spm, SP, Guapiara); MZSP 43683 (1 spm, SP, Iporanga, Abismo da Flecha); MZSP 43685 (1 spm, SP, Iporanga, Abismo da Flecha); MZSP 43694 (1 spm, SP, Iporanga, Abismo da Flecha); MZSP 92821 (5 spm, SP, Iguape, Sambaqui Barranco Alto); MZSP 92825 (1 spm, SP, Juquiá); MZSP 92829 (1 spm, SP, Rio Claro); MZSP 92830 (1 spm, SP, Juquiá); MZSP 92427 (1 spm, SP, São Sebastião); MZSP 122720 (2 spm, SP, Iguape).

RESULTS

In total, 210 specimens were measured in the present work. When all specimens were used (i.e., including those from the Capelinha shell mound), *M. yporanganus* and *M. toriii* do not significantly differ in morphology, regardless of using PC1 (*M. yporanganus*=0.08 ±0.17, *M. toriii*=-1.09 ±0.17, $F_{1,228}$=3.60, p=0.06), PC2 (*M. yporanganus*=0.02 ±0.07, *M. toriii*=-2.23 ±0.15, $F_{1,228}$=0.89, p=0.36) or both PCs ($F_{2,227}$=2.25, p=0.11) as response variables (Fig. 2a–b). However, when the Capelinha shell mound specimens were excluded from the analyses (Fig. 2c–d), the two taxa differ significantly in PC1 (*M. yporanganus*=-2.34 ±0.20, *M. toriii*=-1.09 ±0.17, $F_{1,101}$= 6.91, p=0.01) and when both PCs were used ($F_{1,100}$=3.66, p=0.03), but not in PC2 alone (*M. yporanganus*=-0.13 ±0.14, *M. toriii*=-0.23 ±0.15, $F_{1,101}$=0.09, p=0.76). This suggests that recent specimens (including younger archaeological material) of *M. yporanganus* are larger than *M. toriii* in all characters measured.

DISCUSSION

Shell morphology

The results of the PCA (Fig. 3) reveal that the specimens of *M. toriii* are well inside the distribution of *M. yporanganus*, clearly not forming a separate cluster (which would be expected in case of distinct species). Nevertheless, when comparing PC1 (excluding the oldest specimens from Capelinha shell mound), the values of *M. toriii* are statistically different from *M. yporanganus*. This echoes the diagnosis of Bequaert (1948), which stated that *M. toriii* could be distinguished only by its smaller size. Nevertheless, this author did not have access to a large series of specimens such as the present one, nor to an ample archaeological record such as the one from Capelinha shell mound. The shell height range of *M. toriii* (7.1 to 8.1cm) is well within the range of *M. yporanganus* (5.7 to 9.3 cm). The same is valid for whorl count: *M. toriii* has 5 to 5⅓ whorls, while *M. yporanganus* has 3¼ to 5¾ whorls. Likely, small specimens have artificially been identified as *M. toriii* in the MZSP collection (which is something also hinted at by the reduced number of specimens identified as *M. toriii*). We conclude that the difference in the PC1 values is an artifact of the small variation within specimens of *M. toriii* (of which one third are type specimens) when compared to *M. yporanganus*, which encompasses

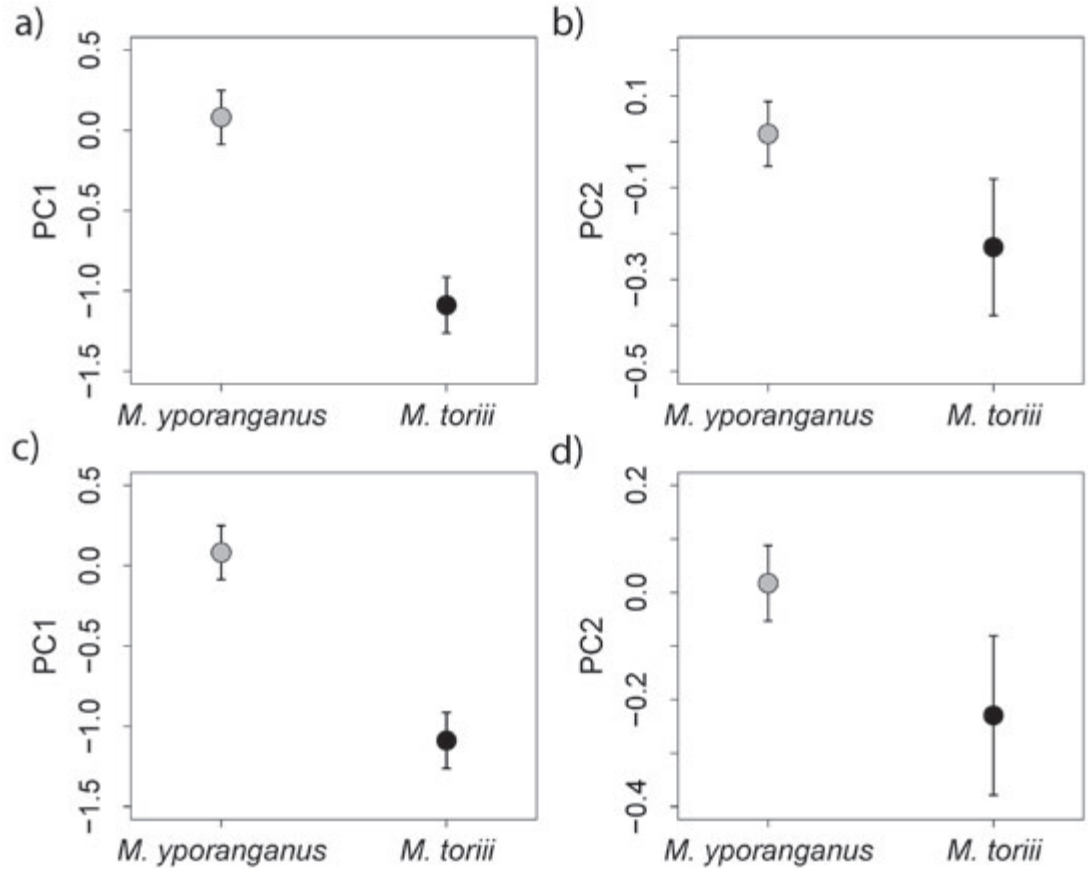

Figure 2 Results of the analysis testing for the differences in PC1 and PC2 between the two taxa. **a.** PC1 comparison using all specimens, **b.** PC2 comparison using all specimens, **c.** PC1 comparison excluding the *M. yporanganus* specimens from the Capelinha shell mound, **d.** PC2 comparison excluding the *M. yporanganus* specimens from the Capelinha shell mound.

a large variation in shell dimensions (especially when including the archaeological material from Capelinha shell mound, which is largely composed of smaller specimens).

Furthermore, there are no other conchological features that might distinguish these two supposed species (Fig. 4): the shell shape, aperture shape, proto- and teleoconch sculpture are all the same, as already argued by Bequaert (1948). This author also alluded to a broader and thicker peristome in *M. toriii*, but this is also found in *M. yporanganus* and depends on the age of the individual. Since all supposed specimens of *M. toriii* are either empty shells or sub-fossils from young shell mounds, it is presently not possible to know whether any anatomical or genetic differences would be observed.

Therefore, given our finds, we conclude that *M. toriii* is synonymous with *M. yporanganus*. A further synonym of *M. yporanganus* is *M. ovatus iguapensis* (Maury, 1935), described from the limestone caves of Iporanga, São Paulo, based on recent fragmentary specimens mistakenly considered of Pleistocene age (Bequaert, 1948). This subspecies was placed in synonymy of *M. yporanganus* by Bequaert (1948). We follow this decision here, as the holotype of *M. iguapensis* (Fig. 4g) bears the diagnostic features of *M. yporanganus*.

Distribution

The main occurrences of *M. yporanganus* are in archaeological contexts (riverine shell mounds) and as sub-fossils in karst outcrops (typically in caves). Comparatively few recent records are known.

Unfortunately, most of the shell mounds in southern Brazil were never properly dated and several have been destroyed since the first studies. Therefore, it is not possible to assess with any reasonable confidence if and how the species distribution changed through the Holocene.

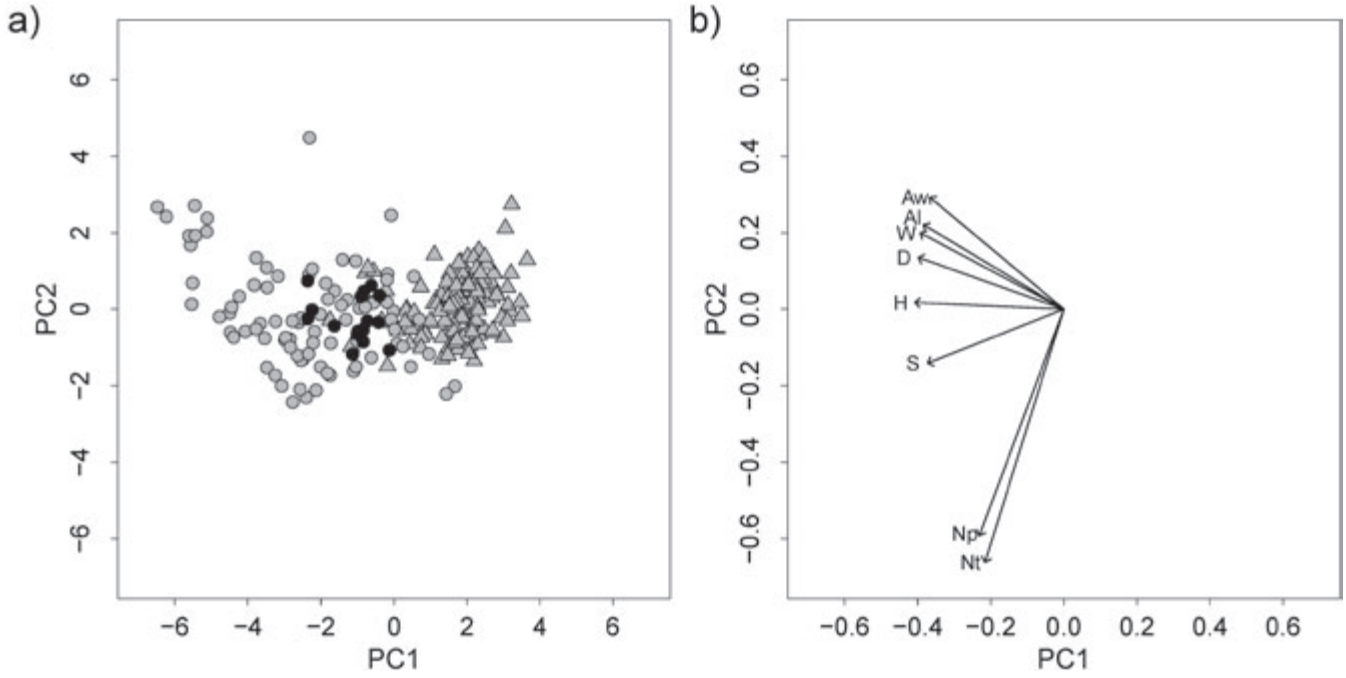

Figure 3 **a** Scatterplot of the two first components obtained from the PCA. Light gray: *M. yporanganus*; Black: *M. toriii*; Circles: recent specimens (including young archaeological material); Triangles: old archaeological specimens from the Capelinha shell mound. **b** Loadings plot of the two first components obtained from the PCA.

Specimens of *M. yporanganus* were found in the Capelinha shell mound, which is the oldest mound known in Brazil, dating from circa 10,560–9,293 YBP (calibrated age; Figuti *et al*., 2013; Figuti & Plens, 2014). All the other shell mounds where *M. yporanganus* can be found are likely much younger than that.

Taking the whole Holocene record together, the past distribution of the species ranged from southern São Paulo state to the northern portion of Santa Catarina state (Fig. 5). The majority of records are from the Ribeira Valley region in São Paulo state, but this extended through coastal Atlantic Forest settings to the Babitonga Bay ("Baía da Babitonga") area in Santa Catarina.

Presently, *M. yporanganus* is only known from the Ribeira Valley in São Paulo, with some dubious further occurrences in this state (see Systematics section). Therefore, it is clear that this species had a much wider distribution in the past. Its presence in riverine shell mounds indicates that these animals were used by paleoindians as food (including funerary feasts; Figuti *et al*., 2013). In fact, Figuti & Plens (2014) consider that land snails were the only type of prey intensively gathered by the Ribeira Valley paleoindians. It is likely, although presently not possible to define, that this intensive gathering has contributed to the contraction in the geographic distribution of the species. Naturally, climatic changes during the Holocene could likewise have impacted distribution. Such matters shall remain unsettled for the moment, but future genetic studies with living specimens of *M. yporanganus* might give us clues about the past population dynamics of the species. Moreover, recent advances in ancient DNA analysis are starting to access the genetic material entrapped within shell carbonate, as der Sarkissian *et al*. (2017) have demonstrated with seashells from archaeological settings.

SYSTEMATICS

STYLOMMATOPHORA
Family Strophocheilidae
Genus *Megalobulimus* K. Miller, 1878
Megalobulimus yporanganus (Ihering & Pilsbry, 1901)
(Fig. 4)

Strophocheilus (*Strophocheilus*) *yporanganus* Ihering & Pilsbry, 1901: 120, pl. 19, figs. 56–57.
Strophocheilus yporanganus: Clench & Archer, 1930: 77; Morretes, 1949: 143; Clench & Turner, 1962: 163; Sawaya & Petersen, 1962: 35.
Strophocheilus ovatus iguapensis Maury, 1935: 12, figs. 12–13.

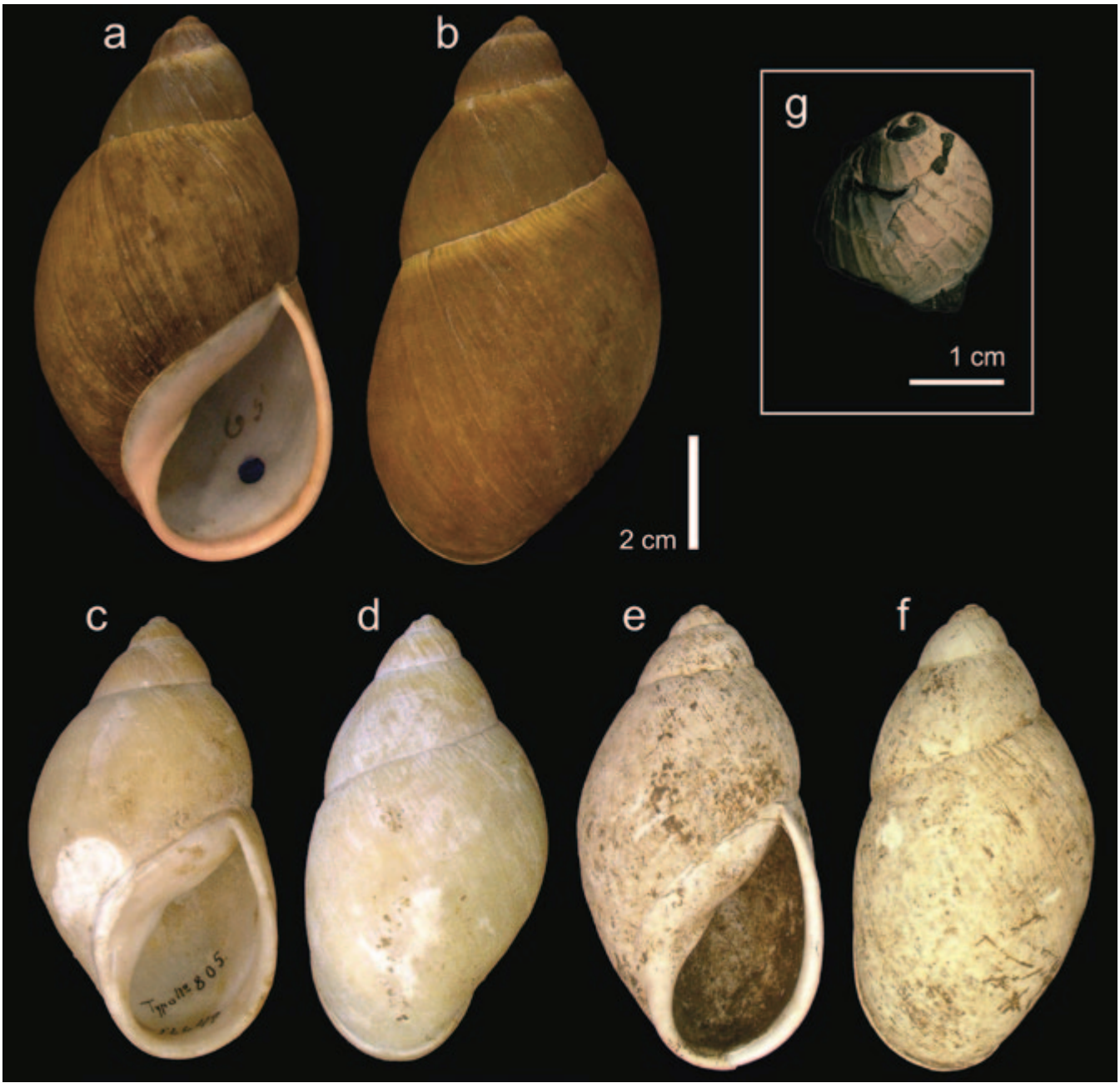

Figure 4 *Megalobulimus yporanganus* **a–b** MZSP 64144, holotype. **c–d** MZSP 16649, holotype of *M. toriii*. **e–f** MZSP 136429-A, from Capelinha shell mound. **g** AMNH 24244, holotype of *M. iguapensis*.

Megalobulimus toriii Morretes, 1937: 301, pl. 1, figs. 1–5; Salgado & Coelho, 2003: 158; Agudo-Padrón, 2008: 161; Dornellas & Simone, 2011: 40; Fontenelle *et al*., 2014: 34, fig. 21.
Strophocheilus iporanganus [sic]: Mezzalira, 1946: 280.
Strophocheilus (*Megalobulimus*) *yporanganus*: Bequaert, 1948: 139, pl. 13, fig. 14.
Strophocheilus yporanganus toriii: Bequaert, 1948: 141, pl. 25, fig. 4.
Strophocheilus toriii: Morretes, 1949: 142.
Megalobulimus (*Phaiopharus*) *yporanganus*: Morretes, 1952: 113; Morretes, 1953: 66.
Megalobulimus (Phaiopharus) torii [sic]: Morretes, 1952: 113.
Megalobulimus (*Phaiopharus*) *toriii*: Morretes, 1953: 66.
Megalobulimus yporanganus: Leme, 1975: 174; Vieira & Simone, 1990: 57; Salgado & Coelho, 2003: 159; Simone, 2006: 222, fig. 840; Dornellas & Simone, 2011: 42.
Strophocheilus yporanganus torii [sic]: Atay, 1978: 190.

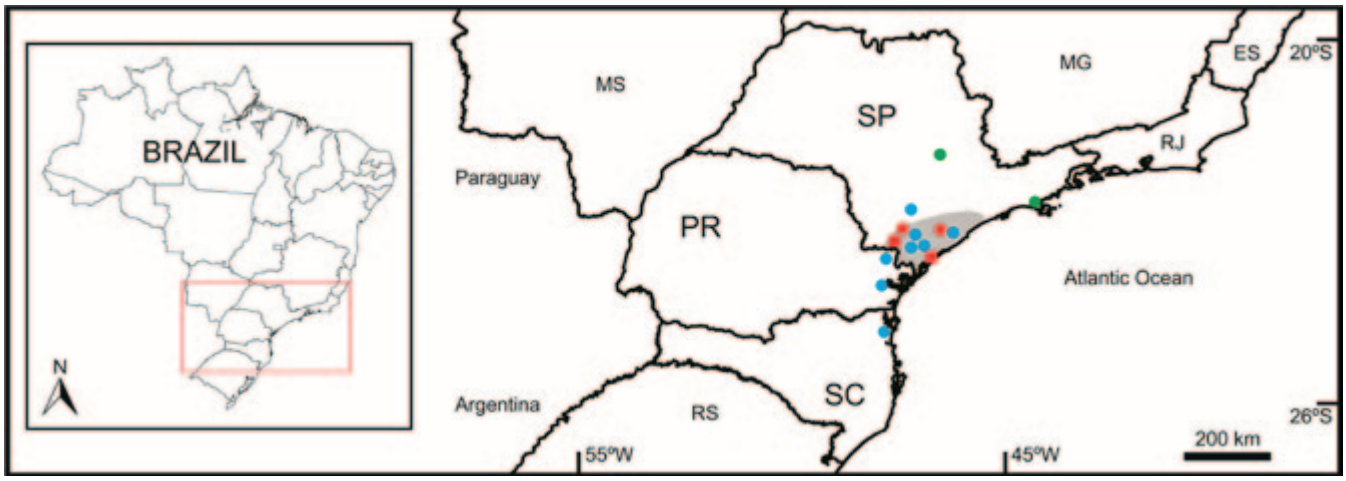

Figure 5 Map showing the present (red circles) and past (blue circles) distribution of *Megalobulimus yporanganus*. Localities with both recent and archaeological records are shown as red squares. Dubious recent records (see text) are shown as green circles. The shaded area represents the Ribeira Valley in São Paulo state.

Megalobulimus torii [sic]: Simone, 2006: 221, fig. 835.

Type locality Brazil, SP, Iporanga ("Yporanga").

Type material MZSP 64144 (holotype); MZSP 5662 (paratype; Brazil, SP, Iporanga, Caverna do Lambari).

Diagnosis Coarse nepionic sculpture of widely-spaced prosocline axial ribs; shell (especially teleoconch) marked by spirally arranged granulation.

Description Shell large overall, but of medium size for genus; shell fusiform, slightly compressed dorsoventrally, imperforate. Penultimate whorl tall and narrow; body whorl more inflated than penultimate whorl. Suture shallow. Periostracum of uniform yellowish brown colouration, with a lighter coloured subsutural spiral band. Protoconch lightly flattened; first whorl smooth; following whorls sculptured by widely-spaced prosocline axial rib; microgranular markings present. Teleoconch marked by strong growth-lines and spirally arranged granulation. Aperture drop-shaped, with round basal area; about half shell length. Oblique columellar area, with fold extending to parietal region. Peristome lightly reflected and thickened, of light pink colour. Parietal callus large, distinctly marked.

Measurements H=70.9±8.17mm (max 93.5, min 57.5); D=39.8±3.82mm (max 53.0, min 33.5); Np=3¼–3½ (max 3¾, min 2¾); Nt=4¾–5¼ (max 5¾, min 3½).

Present distribution Known only from the Ribeira Valley ("Vale do Ribeira"), in São Paulo state (Fig. 5). Specific occurrences: **SP:** Guapiara, Iguape, Iporanga, Juquiá, Rio Claro, São Sebastião. The latter two records (São Sebastião and Rio Claro municipalities), outside the Ribeira Valley, should be regarded with caution, as they come from private collections acquired by the MZSP and thus, could have erroneous or misleading locality data.

Holocene record From São Paulo to northern Santa Catarina (Fig. 5), being the earliest record from the Capelinha shell mound (10,560–9,293 YBP). Specific occurrences: **SP:** Cajati (Capelinha shell mound, 10,560–9,293 YBP; Figuti & Plens, 2014), Capão Bonito (caves), Eldorado Paulista (unspecified riverine shell mound), Iguape (Barranco Alto shell mound, Morro do Bernardes shell mound), Iporanga (caves), Miracatu (Moraes shell mound, 6,777–5,048 YBP; Figuti & Plens, 2014), Registro. **PR:** Adrianópolis, Antonina. **SC:** Araquari (Pinheiros I shell mound). A further record, from São Francisco do Sul municipality (SC, Linguado shell mound), reported by Morretes (1949) could not be confirmed.

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