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## A new species of *Otothyropsis* (Siluriformes: Loricariidae) from the upper Río Paraná basin, Paraguay, with a discussion of the limits between *Otothyropsis* and *Hisonotus*

BÁRBARA B. CALEGARI<sup>1,2</sup>, WALTER GILL MORLIS<sup>3</sup> & ROBERTO E. REIS<sup>1</sup>

<sup>1</sup>PUCRS, Pontifical Catholic University of Rio Grande do Sul, Laboratory of Vertebrate Systematics, Av. Ipiranga, 6681, 90619-900 Porto Alegre, RS, Brazil. E-mail: barbara.calegari@gmail.com (BBC); reis@pucrs.br (RER)

<sup>2</sup>Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, 20013-7012 Washington, DC, USA.

<sup>3</sup>Las Orquídeas c/ Las Acacias. A-1, D-1. Ciudad del Este, Paraguay. E-mail: wgilmor@gmail.com (WGM)

### Abstract

*Otothyropsis dialeukos* is described from Itá creek, tributary to the upper Río Paraná basin, Paraguay. The new species is distinguished from its congeners by having a unique caudal-fin coloration pattern composed of a brown to almost black background with roundish hyaline blotches in the middle of the outermost branched rays and a hyaline posterior border interrupted in middle rays; abdomen entirely covered by enlarged plates, without naked areas; longer pectoral- and dorsal-fin spines; absence of a raised crest of enlarged odontodes on the posterior portion of the parieto-supraoccipital, and other morphometric and meristic features. Morphological traits and geographic distributions of all species of *Otothyropsis* and *Hisonotus* are analyzed and a discussion on the limits between those genera is presented.

**Key words:** Biodiversity, Cascudinho, Neotropical, systematics, taxonomy

*Otothyropsis dialeukos* se describe del Arroyo Itá afluente del alto Río Paraná, Paraguay. La nueva especie se distingue de sus congéneres por presentar un patrón único de coloración en la aleta caudal, que consiste en un fondo de color marrón oscuro hasta casi negro, con dos manchas redondas hialinas en la parte media de los radios ramificados más externos, y el borde posterior hialino discontinuo en los rayos medios; abdomen completamente cubierto por placas grandes sin presentar áreas desnudas; espinas de las aletas pectorales y dorsales largas; ausencia de una cresta de odontódeos alargados en la parte posterior del parieto-supraoccipital, y otras características morfométricas y merísticas. Características morfológicas y distribución geográfica de todas las especies de *Otothyropsis* y *Hisonotus* son analizadas, y una discusión de los límites entre estos géneros es presentada.

**Palabras-claves:** Bagre, Biodiversidad, Neotropical, Sistemática, taxonomía

### Introduction

Hypoptopomatinae is a loricariid subfamily that includes 150 species distributed in 23 genera. Species of the Hypoptopomatinae are widely distributed in cis-Andean South America from Venezuela to Argentina (Schaefer, 2003). *Otothyropsis* was originally described by Ribeiro *et al.* (2005), and is currently diagnosed based on few characters: an elongated posterior extension of the compound pterotic, which forms the dorsal margin of an enlarged lateral opening of the swimbladder capsule; and the mid-dorsal series of lateral plates truncated posteriorly in the caudal peduncle, between the dorsal and the caudal fins (Ribeiro *et al.*, 2005; Calegari *et al.*, 2011, 2013). The genus currently includes five species: *Otothyropsis marapoama* Ribeiro, Carvalho & Melo, 2005, *O. piribebuy* Calegari, Lehmann & Reis, 2011, *O. polyodon* Calegari, Lehmann & Reis, 2013, *O. biamnicus* Calegari, Lehmann & Reis, 2013, and *O. alicula* Lippert, Calegari & Reis, 2014. Most species occur in the upper Río Paraná basin in Brazil, except for *O. piribebuy*, described from tributaries to the Río Paraguay in Paraguay.

The distinction between *Otothyropsis* and *Hisonotus*, however, has been controversial (Lippert *et al.*, 2014; Roxo *et al.*, 2016), in part because *Hisonotus*, as currently composed, is a mix of unrelated forms, and remains as one of the largest taxonomic problems in the Hypoptopomatinae. Despite these problems, Calegari *et al.* (2011) found *Otothyropsis* to be monophyletic and re-diagnosed the genus, but additional phylogenetic analyses, both morphological (Martins *et al.*, 2014) and molecular (Chiachio *et al.*, 2008; Cramer *et al.*, 2011), failed to demonstrate that *Hisonotus* and *Otothyropsis* are either monophyletic or closely related.

In order to properly allocate the new species, a comparison of morphological traits and geographic distribution was conducted with all valid species of *Otothyropsis* and *Hisonotus*. The limits between those genera is also discussed. As the new species unquestionably shares the features of *Otothyropsis*, it is herein allocated to this genus, and it is described from a small tributary to the upper Río Paraná basin in Paraguay.

## Material and methods

Morphological measurements were made point-to-point to the nearest 0.1 mm with digital calipers under a stereomicroscope. Counts of plates, rays, and oral teeth were also performed under the scope. Dermal-plate counts followed the schemes of serial homology and terminology proposed by Schaefer (1997) and the morphometric measurements are those described by Pereira *et al.* (2007) with the modifications introduced by Calegari *et al.* (2011; 2014). Morphometric data were expressed as percent of standard length (SL), except for subunits of the cephalic region, treated as percent of head length (HL). Vertebral counts include all vertebral centra, including the five centra that comprise the Weberian apparatus, and the caudal complex centrum (PU1 + U1) counted as a single element. The osteological examination was conducted on specimens cleared and double-stained (cs) for bone and cartilage according to the technique described by Taylor & Van Dyke (1985). Institutional abbreviations are those listed at <http://www.asih.org/codons.pdf>. The distribution map was created using shape and raster files from databases of IBGE (Instituto Brasileiro de Geografia e Estatística: <http://mapas.ibge.gov.br/bases-e-referenciais>), and ANA (Agência Nacional de Águas: <http://www.snhirh.gov.br/hidroweb>), and using the QGIS software (v. 2.14.5).

## Result

### *Otothyropsis dialeukos*, new species

Fig. 1; Tables 1, 2

**Holotype.** MNHNP 3880, female, 34.6 mm SL, Paraguay, Alto Paraná, Hernandarias, Arroyo Itá at Paso Itá, near to Embalse de Acaray, ca. 8 km from road between Hernandarias and Ciudad del Este, Río Paraná basin, 25°22'56.9"S 54°41'34.8"W, approx. 200 m asl, 21 January 2013, W. Gill Morlis and R. Torres.

**Paratypes.** All from Paraguay, MNHNP 3881, 4, 9.7–34.6 mm SL and MCP 49901, 5 + 1 cs, 9.6–35.8 mm SL, collected with the holotype; and MNHNP 3882, 1, 31.8 mm SL and MCP 49899, 1, 26.3 mm SL, same locality as the holotype, 16 February 2012, W. Gill Morlis and R. Torres.

**Diagnosis.** *Otothyropsis dialeukos* differs from congeners by its unique caudal-fin coloration pattern, composed of a brown to almost black background with roundish hyaline blotches in the middle of the outermost branched rays and a hyaline posterior border interrupted in middle rays (vs. various color patterns but never two isolated roundish hyalines blotches). The new species is also distinguished from all congeners, except *O. marapoama*, by having the abdomen entirely covered by enlarged plates (Fig. 2), without naked areas (vs. abdomen almost entirely naked or with naked areas among the plates). The new species further differs from all congeners, except *O. piribebuy* and *O. alicula*, by the absence of a raised crest of enlarged odontodes in the posterior portion of the parieto-supraoccipital (vs. presence of such crest). *Otothyropsis dialeukos* is further distinguished from *O. biamnicus*, *O. polyodon*, and *O. alicula* by having a longer prepelvic length (40.2–44.3%, vs. 36.7–39.3%, 35.8–39.5%, and 33.9–37.7% SL, respectively); longer pectoral-fin spine (26.7–30.9%, vs. 18.6–21.3%, 21.4–26.9%, and 16.5–20.0% SL, respectively); longer dorsal-fin spine (23.1–27.1%, vs. 19.4–22.9%, 18.2–22.0% and 19.1–22.3% SL, respectively); and shorter caudal peduncle (31.5–34.2%, vs. 41.3–45.1%, 40.0–45.1%, and 39.9–45.4%

SL, respectively). The new species differs from *O. biannicus* and *O. polyodon* by having fewer plates in the median lateral series (19–20 vs. 24–25 plates in both species). *Otothyropsis dialeukos* is distinguished from *O. marapoama* and *O. piribebuy* by having more numerous plates between the anal and the caudal fins (11–12 vs. 9–10 plates in both). It is further distinguished from *O. piribebuy* by having a higher number of premaxillary teeth (18–25 vs. 10–19), and by the larger orbital diameter (15.1–18.5, vs. 12.3–15.1% HL), and from *O. marapoama*, by having a smaller cleithral width (21.5–23.4 vs. 23.8–25.8% SL).

*Otothyropsis dialeukos* can be also distinguished from the species of *Hisonotus* inhabiting the upper Paraná River system by the deeper caudal peduncle 9.5–11.0% SL (vs. 7.2–8.5% in *H. alberti*, 7.9–9.4% in *H. depressicauda*, 6.6–7.9% in *H. depressinotus*, 6.9–8.3% in *H. francirochai*) and São Francisco basin (6.8–8.2% in *H. vespuccii*), or by the plated abdomen (vs. abdomen naked in *H. pachysarkos*).

**TABLE 1.** Morphometric data for *Otothyropsis dialeukos*. Holotype (Hol) and five paratypes; ranges include holotype. SD = standard deviation.

Character	Hol	N	Low	High	Mean	SD
Standard length (mm)	34.6	6	26.3	35.8	31.8	-
% SL						
Head length	35.3	6	33.8	35.4	34.8	0.6
Predorsal length	46.3	6	44.2	48.7	45.6	1.7
Postdorsal length	44.9	6	40.9	44.9	42.8	1.4
Prepectoral length	26.6	6	26.6	27.8	27.1	0.5
Prepelvic length	42.9	6	40.2	44.3	42.3	1.4
Preanal length	62.4	6	58.1	63.2	61.5	2.0
Cleithral width	23.4	6	21.5	23.4	22.7	0.8
Snout-opercle distance	26.6	6	26.5	27.8	27.1	0.5
Pectoral-pelvic-fins distance	17.5	6	14.5	17.5	16.2	1.2
Pelvic-anal-fins distance	21.3	6	19.0	22.0	20.6	1.1
Dorsal-fin spine length	24.9	6	23.1	27.1	24.7	1.4
Dorsal-fin base length	12.3	6	11.4	12.8	12.2	0.5
Pectoral-fin spine length	29.8	6	26.7	30.9	29.2	1.8
First pelvic-fin unbranched ray length	17.0	6	15.2	20.0	17.2	1.8
First anal-fin unbranched ray length	17.4	6	13.4	18.3	16.6	1.8
Caudal-peduncle length	34.2	6	31.5	34.2	32.6	1.0
Caudal-peduncle depth	11.1	6	9.6	11.1	10.4	0.5
Caudal-peduncle width	4.1	6	3.6	5.5	4.5	0.8
Body depth at dorsal-fin origin	17.6	6	14.2	17.6	16.1	1.2
Body width at dorsal-fin origin	19.5	6	16.9	19.5	18.2	1.1
% HL						
Head depth	40.3	6	38.4	45.9	42.4	2.7
Snout length	52.0	6	50.3	53.7	52.1	1.2
Orbital diameter	15.3	6	15.1	18.5	16.7	1.4
Interorbital distance	40.4	6	38.2	41.3	40.0	1.1
Internareal width	10.7	6	8.1	10.7	9.4	1.0
Nares diameter	7.7	6	7.5	13.3	10.0	2.6
Prenasal length	37.4	6	35.2	38.8	37.5	1.3
Suborbital depth	16.4	6	14.6	17.1	15.9	0.9
Barbel length	10.6	6	7.0	10.6	9.0	1.7

**TABLE 2.** Meristic data for *Otothyropsis dialeukos*. Holotype included in range. n = number of specimens.

Character	n	Holotype	Range
Right premaxillary teeth	6	19	18-25
Left premaxillary teeth	6	19	18-24
Right dentary teeth	6	17	15-20
Left dentary teeth	6	17	14-21
Plates in dorsal lateral series	6	20	18-20
Plates in mid-dorsal lateral series	6	17	17
Plates in median lateral series	6	20	19-20
Plates in mid-ventral lateral series	6	18	16-18
Plates in ventral lateral series	6	19	17-19
Plates between anal and caudal fins	6	11	11-12
Plates at dorsal-fin base	6	5	5
Plates at anal-fin base	6	2	2-3
Predorsal plates	6	3	3

**Description.** Morphometrics in Table 1 and meristics in Table 2. Body in dorsal perspective progressively tapering from operculum to end of caudal peduncle. Dorsal profile of head straight to slightly convex from snout tip to middle of parieto-supraoccipital, and straight to slightly concave from that point to dorsal-fin spinelet. Dorsal profile of body sloped and descending from origin of dorsal fin to few plates before end of caudal peduncle. Ventral profile of body relatively straight from head to tail. Greatest body width at cleithrum. Body deepest at dorsal-fin origin and shallowest right before end of caudal-fin peduncle. Trunk and caudal peduncle oval in cross-section and laterally compressed. Adipose fin absent. Head and snout rounded in dorsal view. Snout long with region anterior to nares depressed. Mid-portion of head from end of rostral plates to posterior margin of nares raised. Dorsal margin of orbit slightly elevated. Eye dorsolaterally placed. Iris operculum present. Oral disk round; lower lip relatively short, reaching midway to pectoral girdle.

Lips papillose with small fleshy ridge immediately behind dentary. Lower lip with minute papillae except for naked area at median portion of lip just posterior to dentary. Barbel short and laterally positioned, distal portion free from lip margin. Posterior border of lower lip crenulate. Tooth series in premaxilla and dentary forming overall angle of approximately 90 degrees. Teeth bifid, elongated and slender, with large blade-like medial cusp and small lateral cusp. Accessory teeth lacking on premaxilla and dentary in adult and juvenile specimens.

Body almost entirely covered by plates, except for ventral surface prior to pectoral girdle, anterior to urogenital opening, around dorsal-fin base, and region from posterior margin of median rostral plate to posterior margin of naris. Abdomen completely covered by enlarged plates (Fig. 2). Four or five large plates in lateral series of abdominal plates ( $n = 6$ ), wider than long. Plates in median series of abdominal plates comparatively smaller, forming single regular series. Plates in preanal abdominal series large and irregularly distributed, somewhat quadrangular in shape. All abdominal plates bearing small odontodes, except for pair of posterior most preanal abdominal plates which bear larger odontodes on posterior border.

Head mostly smooth, lacking odontode crests; odontodes on body uniform in size and distribution, except for augmented odontodes on ventral margin of snout tip. Infraorbital sensory canal entering infraorbital series via compound pterotic. Median series of lateral plates with 19–20 plates, incomplete, ending two plates before the end of the caudal peduncle, but continuously perforated. Mid-dorsal and mid-ventral series of lateral plates with 17 and 16–18 plates, respectively, truncated posteriorly, near to caudal fin. Three irregular transverse rows of predorsal plates, in addition to nuchal plate. Cleithrum and coracoid entirely exposed on ventral surface and covered with odontodes. Arrector fossa open in restricted portion medially, covered by bone shelves from both coracoid and cleithrum laterally. Pectoral fin I,6. Pectoral-fin spine long and somewhat slender. Tip of adpressed pectoral-fin spine almost reaching to end of first pelvic-fin ray; approximately of same width along its length. Odontodes on pectoral-fin spine distributed only on lateral border of spine and slightly increasing in size gradually towards tip. Pectoral-fin branched rays becoming progressively shorter posteriorly. Pectoral-fin axillary slit present in adults

and juveniles. Pelvic fin i,5. Pelvic-fin unbranched ray thick and shorter than branched rays. Interradial membrane of pelvic fin fringed distally. Dorsal fin II,7, its origin slightly posterior to vertical through end pelvic-fin base. Dorsal-fin spinelet plate-like, oval to triangular in shape. Anal-fin i,5, its unbranched ray thicker and slightly shorter than remaining branched rays. First unbranched anal-fin ray covered with odontodes; odontodes increasing in size towards ray tip. Caudal-fin I,14,I (1 specimen with I,15,I). Caudal fin weakly forked. Total vertebrae 28 (in 1 cs specimen).



**FIGURE 1.** *Otothyropsis dialeukos*, holotype, MNHNP 3880, female, 34.6 mm SL, Paraguay, Alto Paraná, Hernandarias, Itá creek at Paso Itá, Rio Paraná basin.

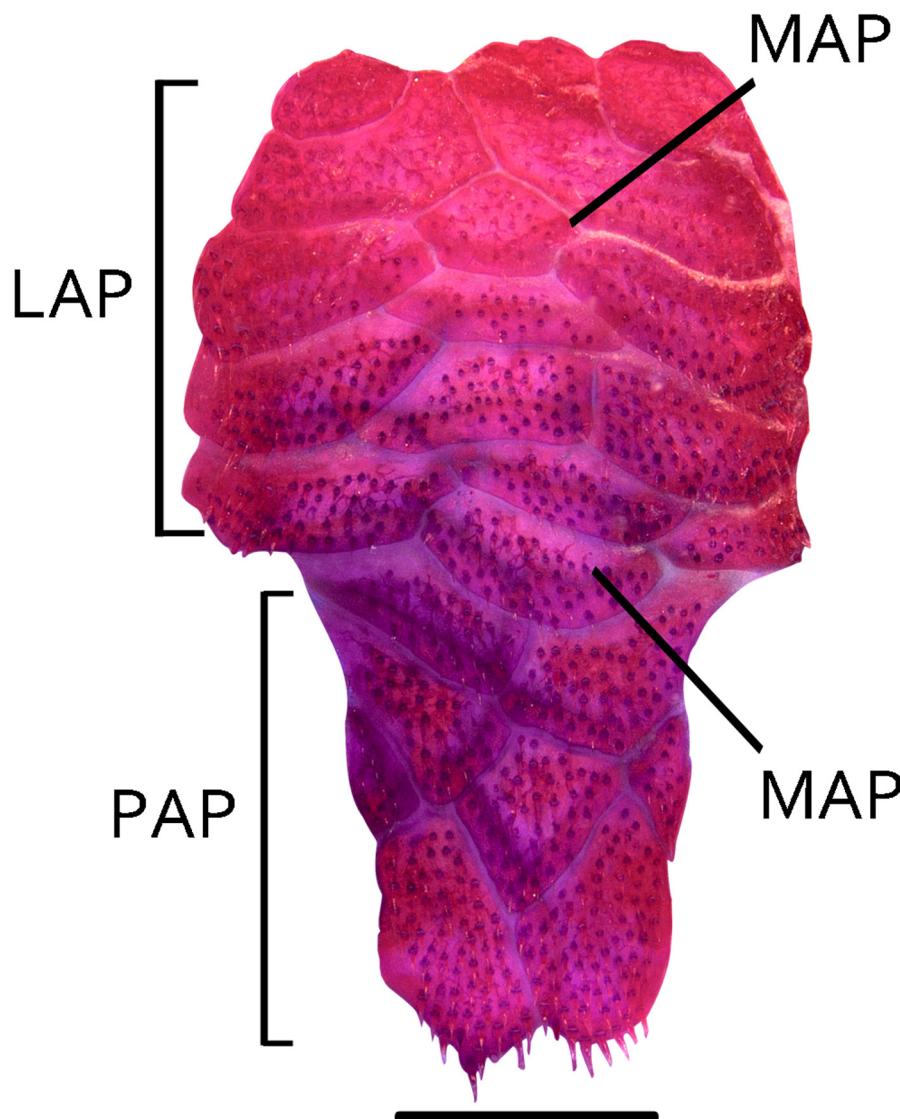
**Color in alcohol.** Ground color of dorsal surface of head dark brown with lighter stripe in front of each nostril. Posterior process of parieto-supraoccipital and dorsal surface of trunk medium brown with dark chromatophores uniformly distributed. Inconspicuous longitudinal dark brown stripe from snout, crossing orbit and opercle, and continuing to end of caudal peduncle. Postrostral plates, opercle, and lateral portion of cleithrum light cream, with many dark chromatophores unevenly sprinkled, forming conspicuous light cream to white cheek. Ventral surface mostly pale yellow, with dark chromatophores unevenly scattered on lower surface of head, lateral portions of

abdomen and more heavily concentrated on caudal peduncle. Fin membranes mostly hyaline, with series of small dark dots arranged in irregular transverse bands in all fins except caudal fin. Caudal fin with both rays and membrane mostly dark brown, with roundish hyaline blotches in middle of outermost branched rays, and hyaline posterior border disconnected in middle rays (Fig. 1).

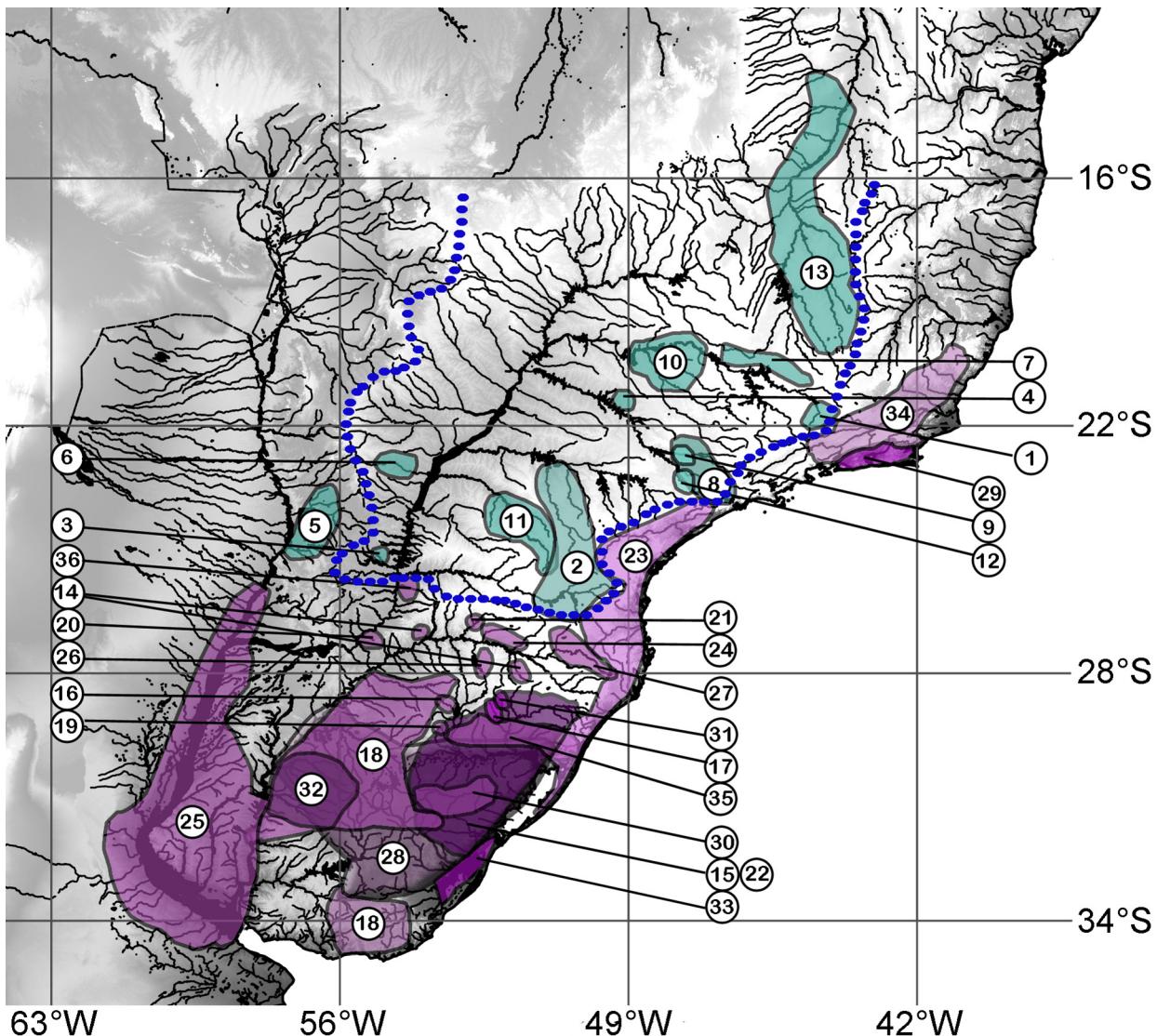
**Sexual dimorphism.** Sexual dimorphism characterized by the possession of a small, conical urogenital papilla immediately posterior to the anal opening in males, which also possess a fleshy flap along the dorsal margin of the first pelvic-fin ray. In addition, males have longer first unbranched pelvic-fin ray (18.8–20.0 vs. 15.2–17.0% SL in females). As usual in *Otothyropsis* species, males have markedly wider nares than females (13.1–13.3 vs. 7.5–9.4% HL in females), and smaller internareal width (8.1–8.4 vs. 9.2–10.7% HL in females).

**Distribution.** *Otothyropsis dialeukos* is known only from its type locality, the Arroyo Itá, a tributary to the Embalse de Acaray, upper Río Paraná basin in Paraguay (Fig. 3).

**Etymology.** From the Greek *dialeukos*, meaning marked with white, in reference to the white or light cream color of the cheek. A noun in apposition.



**FIGURE 2.** Abdominal plate series of *Otothyropsis dialeukos*, MCP 49901, 34.0 mm SL. LAP, lateral abdominal plate series; MAP, median abdominal plate series; PAP, preanal abdominal plate series. Scale bar = 2 mm.



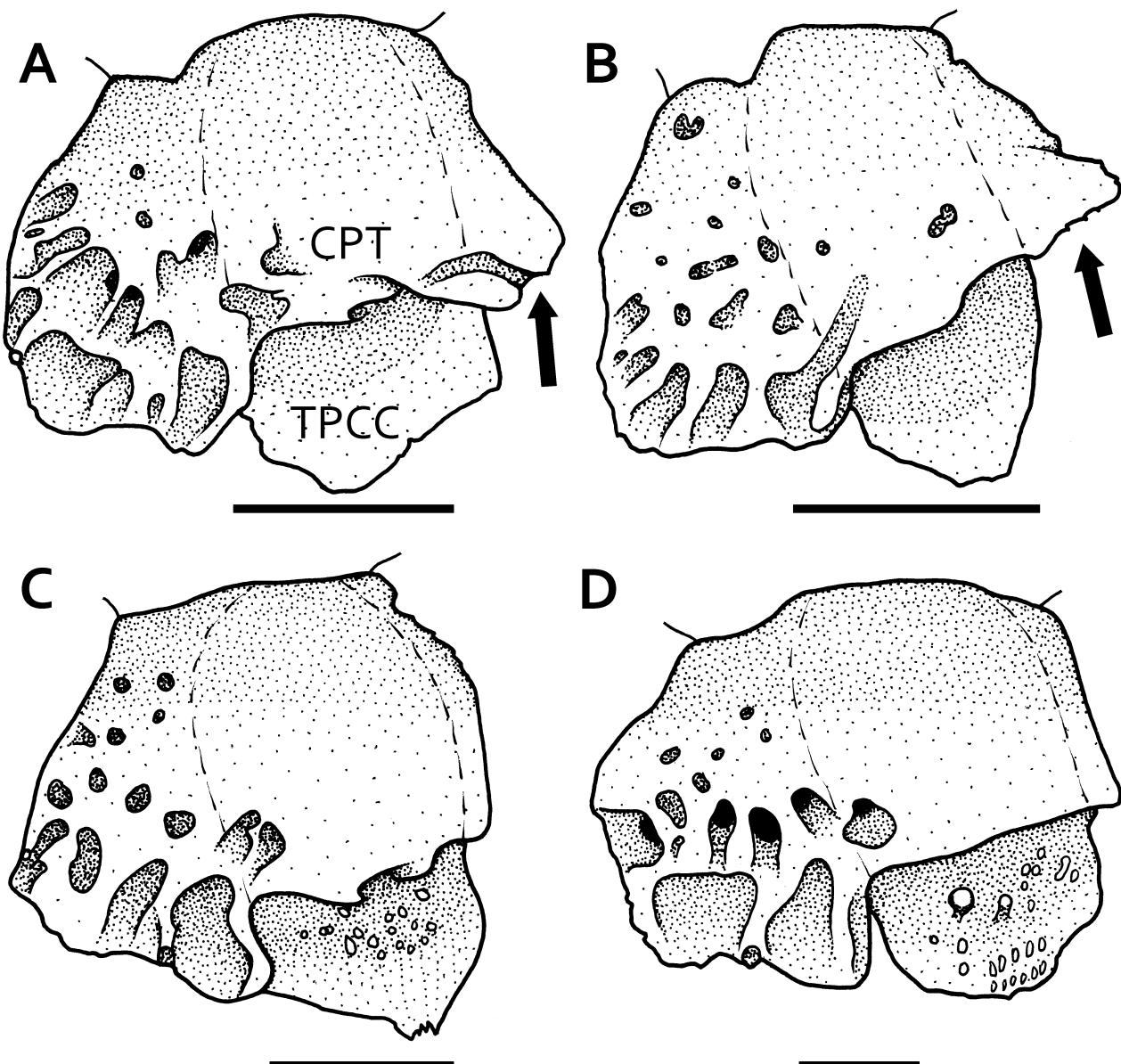
**FIGURE 3.** Map of southeastern South America depicting generalized distributions of species currently assigned to *Otothyropsis* and *Hisonotus*. **Green:** 1. *Otothyropsis alicula*; 2. *Otothyropsis biamanicus*; 3. *Otothyropsis dialeukos*; 4. *Otothyropsis marapoama*; 5. *Otothyropsis piribebuy*; 6. *Otothyropsis polyodon*; 7. *Hisonotus alberti*; 8. *Hisonotus depressicauda*; 9. *Hisonotus depressinotus*; 10. *Hisonotus francirochai*; 11. *Hisonotus pachysarkos*; 12. *Hisonotus paulinus*; 13. *Hisonotus vespucii*. **Purple:** 14. *Hisonotus aky*; 15. *Hisonotus armatus*; 16. *Hisonotus brunneus*; 17. *Hisonotus carreiroi*; 18. *Hisonotus charrua*; 19. *Hisonotus heterogaster*; 20. *Hisonotus hungry*; 21. *Hisonotus iota*; 22. *Hisonotus laevior*; 23. *Hisonotus leucofrenatus*; 24. *Hisonotus leucophrys*; 25. *Hisonotus maculipinnis*; 26. *Hisonotus megaloplax*; 27. *Hisonotus montanus*; 28. *Hisonotus nigricauda*; 29. *Hisonotus notatus*; 30. *Hisonotus notopagis*; 31. *Hisonotus prata*; 32. *Hisonotus ringueleti*; 33. *Hisonotus taimensis*; 34. *Hisonotus thayeri*; 35. *Hisonotus vireo*; 36. *Hisonotus yasi*. Distribution patches based on comparative material examined and on literature. Dotted blue line represents the limit between Pattern A and Pattern B areas of distribution.

## Discussion

The monophyly of *Otothyropsis* and *Hisonotus*, as well as the position of these genera within the Hypoptopomatinae, remain uncertain. Of the three morphology-based phylogenetic studies including *Otothyropsis* (Ribeiro *et al.*, 2005, Calegari *et al.*, 2011; and Martins *et al.*, 2014), only Ribeiro *et al.* (2005) recovered a close relationship of *Otothyropsis* with a clade formed by *Pseudotothyris* + *Otothyris*. The remaining two studies could not definitively place the position of *Otothyropsis* within the Hypoptopomatinae, although Calegari *et al.* (2011) found support for the monophyly of the genus. On the other hand, *Hisonotus* has repeatedly been found to be

polyphyletic (Cramer *et al.*, 2011; Martins *et al.*, 2014; and Roxo *et al.*, 2014; 2015) and some species of *Hisonotus* are considered morphologically similar to *Otothyropsis* (see Calegari *et al.*, 2011, 2013) or *Curculionichthys*. Some of those species (*H. insperatus*, *H. luteofrenatus*, *H. oliveirai*, *H. paresi* and *H. piracanjuba*) have recently been reallocated to the latter genus by Roxo *et al.* (2015).

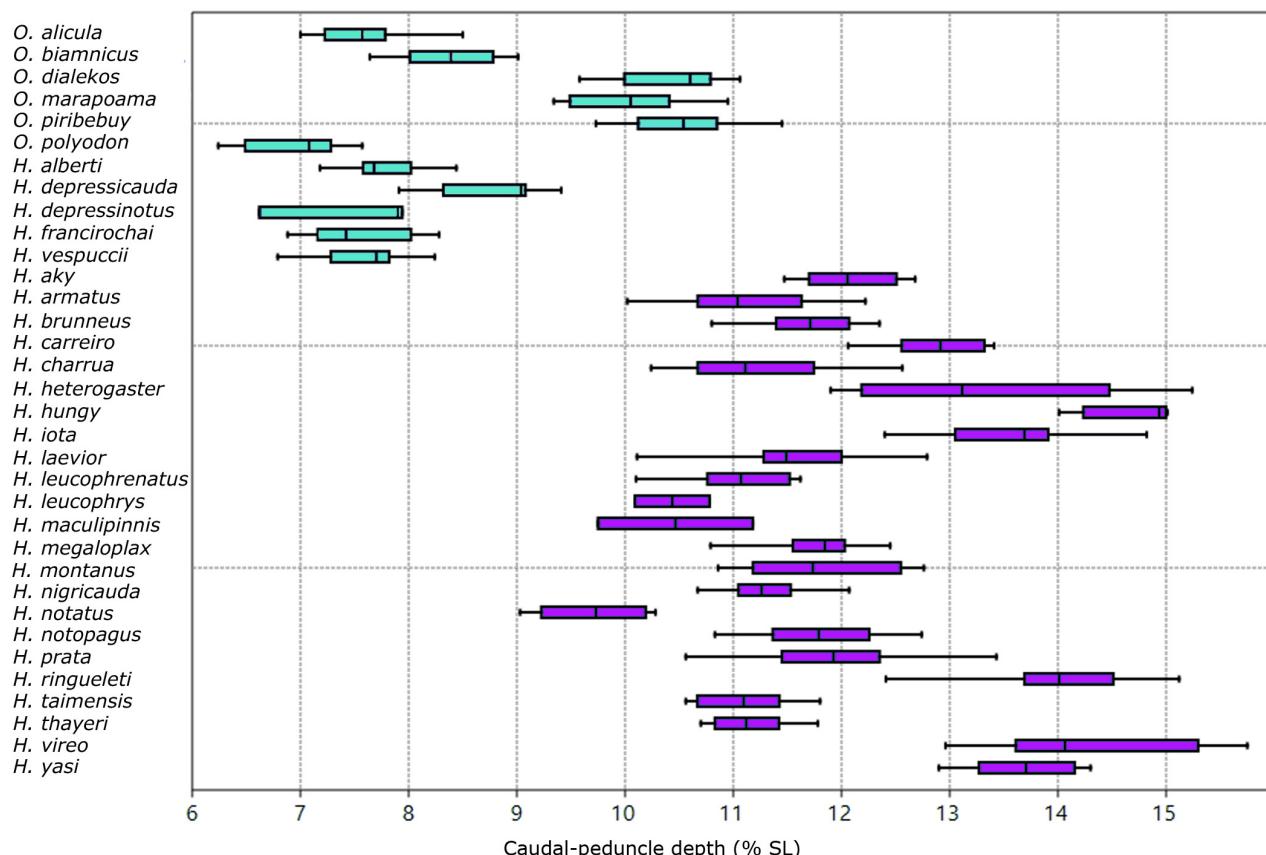
In order to properly classify the new species, an analysis of relevant morphological traits and geographic distribution was performed including all currently valid species of *Otothyropsis* and *Hisonotus*. Characters used in this analysis (Table 3) include: (1) the extension of the posterior margin of the compound pterotic, (2) the depth of the caudal peduncle, (3) the position of the truncation of the mid-dorsal series of lateral plates, and (4) the functionality of the dorsal-fin locking mechanism. In addition to the morphological features, the geographic distribution of all species has also been mapped (Fig. 3). Pattern A represents the geographic distribution in the upper Rio Paraná/Rio São Francisco basins, while Pattern B represents the occurrence in the lower Rio Paraná, and all its lowland tributaries below the mouth of the Rio Iguaçu, lower Río Paraguay, Rio Uruguay, Laguna dos Patos system, and all coastal drainages from Uruguay to the Espírito Santo State, in Brazil (Fig. 3; Table 3).



**FIGURE 4.** Posterolateral region of head of *Otothyropsis* and *Hisonotus*. (A) *O. marapoama*, MCP 42119; (B) *O. biannicus*, MCP 37164; (C) *H. charrua*, MCP 27539; (D) *H. nigricauda*, MCP 26865. Dashed lines indicate position of swimbladder capsule; CPT, compound pterotic; TPCC, transverse process of the complex centrum; arrows indicate extension of compound pterotic. Scale bar = 2 mm.

A posterior extension of the compound pterotic (Fig. 4), that forms the dorsal margin of an enlarged lateral opening of the swimbladder capsule, is shared by all *Otothyropsis* and the species of *Hisonotus* with Pattern A distribution. Among the *Hisonotus* with Pattern B distribution, only *H. notopagios* have this posterior extension, and *H. heterogaster* and *H. megaloplax* are variable for this feature. The condition is unknown to *H. packysarkos* and *H. paulinus*.

Additionally, the caudal peduncle is deep in all species of *Hisonotus* with Pattern B distribution, varying from 9 to 16% of the standard length, contrary to most *Otothyropsis* and all species of *Hisonotus* with Pattern A distribution, in which caudal-peduncle depth varies from 6 to 9% SL (but condition unknown to *H. paulinus*). Exceptions for the latter condition are *O. dialekos*, *O. marapoama*, and *O. piribebuy*, which have a slightly deeper caudal peduncle compared to its congeners, but still in the lower range of the variation presented by the species of *Hisonotus* with Pattern B distribution (Fig. 5).



**FIGURE 5.** Boxplot of caudal-peduncle depth as percent of standard length of species currently assigned to *Otothyropsis* and *Hisonotus*. *Hisonotus packysarkos* and *H. paulinus* not examined.

The truncation of the mid-dorsal series of lateral plates is located posteriorly on the caudal peduncle, between the end of dorsal-fin base and the caudal fin, in *Otothyropsis* and all species of *Hisonotus* with Pattern A distribution, with a range of 15–25 plates (except *O. marapoama* with 8–16). Conversely, most *Hisonotus* with Pattern B distribution have the mid-dorsal plate series short, with 4–8 plates, truncated usually before the dorsal-fin origin or sometimes up to the end of the dorsal-fin base (Fig. 6). Exceptions for this condition are *H. maculipinnis* (18 plates), *H. nigricauda* (14–18 plates), *H. notopagios* (18 plates), *H. ringueleti* (16–19 plates), *H. thayeri* (16 plates), and *H. yasi* (17–19 plates). Despite the fact that these species of *Hisonotus* have the mid-dorsal series of plates surpassing the dorsal-fin base, they share other traits that distinguish them from *Otothyropsis*, such as a deep caudal peduncle and, except for *H. notopagios*, the lack of a posterior extension of the compound pterotic.

Finally, all *Otothyropsis* and *Hisonotus* species have the dorsal-fin spinelet plate-like and the associated dorsal-fin locking mechanism non-functional, except for *H. acuen*, *H. bocaiva*, *H. bockmanni*, *H. chromodontus*, and *H. vespuccii* (but feature unknown in *H. paulinus*). The first four species inhabit the upper portion of the Xingu, Tapajós, or São Francisco basins, and their general morphology and the V-shaped dorsal-fin spinelet with a functional locking mechanism suggest that they are not closely related to *Otothyropsis* and *Hisonotus*, but to *Curculionichthys*.

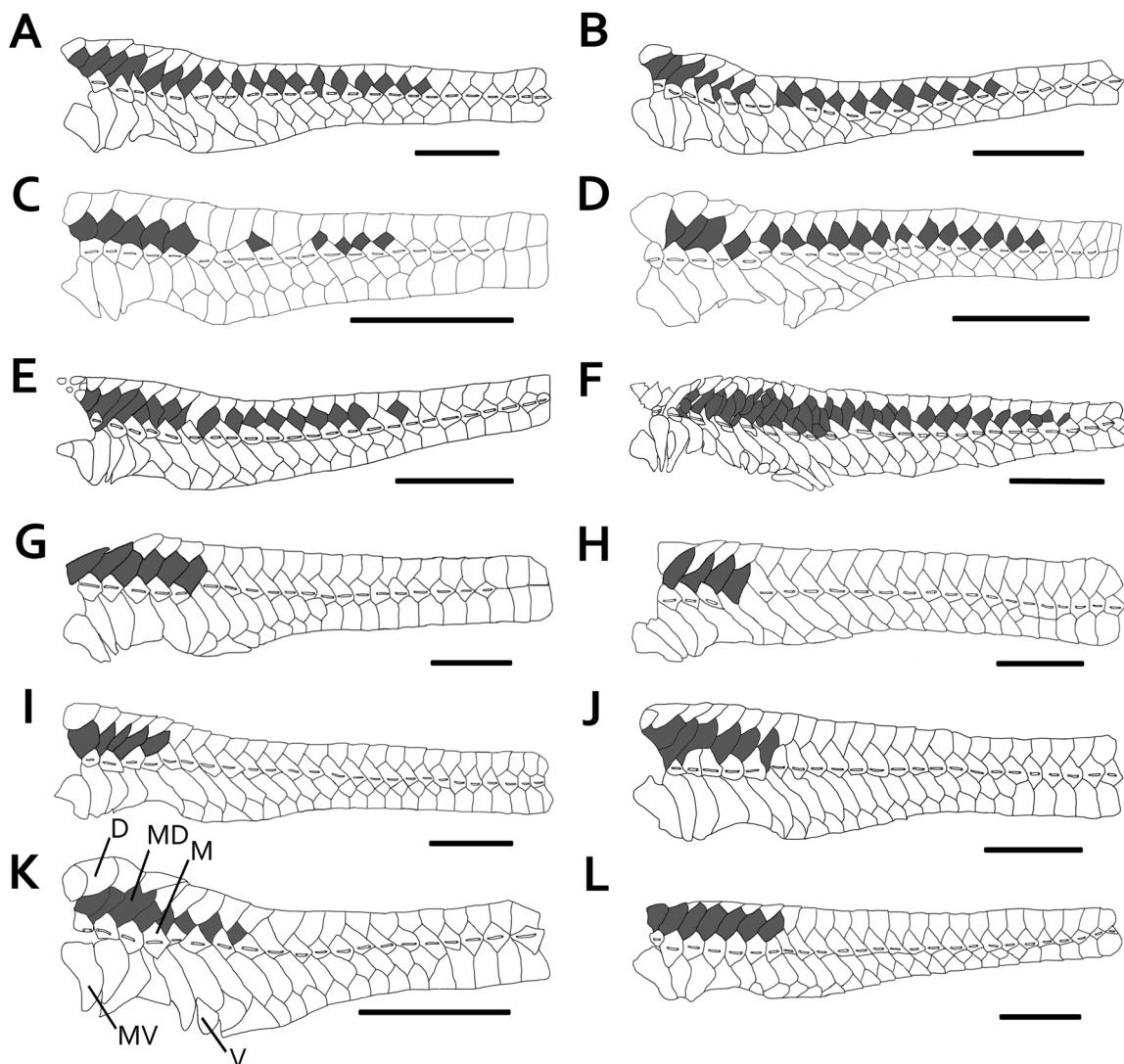
**TABLE 3.** Species currently assigned to *Otothyropsis* and *Hisonotus* arranged by generalized distribution pattern, and their morphological traits. Variations of the expected pattern are highlighted. Under Distribution, Pattern A includes the upper Rio Paraná and upper Rio São Francisco drainages; Pattern B includes the lower Rio Paraná, lower Rio Paraguay, Rio Uruguay, lagunas dos Patos system and coastal drainages from Uruguay to the Brazilian State of Espírito Santo. Under Truncation of mid-dorsal series of plates, anterior and posterior are relative to the end of the dorsal-fin base. \* Plates somewhat fractioned in smaller platelets. \*\* Condition estimated from the illustration in original description.

Nominal species	Distribution (Fig. 3)	Extension of compound pterotic	Depth of caudal peduncle	Truncation of mid-dorsal series of plates	Number of mid-dorsal plates	Dorsal-fin locking mechanism
<i>Otothyropsis alicula</i>	Pattern A	present	low	posterior	21–25*	non-functional
<i>Otothyropsis biaminicu</i>	Pattern A	present	low	posterior	18–19	non-functional
<i>Otothyropsis dialeucus</i>	Pattern A	present	deep	posterior	17	non-functional
<i>Otothyropsis marapoama</i>	Pattern A	present	deep	posterior	8–16	non-functional
<i>Otothyropsis piribebuy</i>	Pattern B	present	deep	posterior	17–18	non-functional
<i>Otothyropsis polyodon</i>	Pattern A	present	low	posterior	17–21	non-functional
<i>Hisonotus albertii</i>	Pattern A	present	low	posterior	17–18	non-functional
<i>Hisonotus depressicauda</i>	Pattern A	present	low	posterior	17–18	non-functional
<i>Hisonotus depressinotus</i>	Pattern A	present	low	posterior	18	non-functional
<i>Hisonotus francirochai</i>	Pattern A	present	low	posterior	17–18	non-functional
<i>Hisonotus pachysarkos</i>	Pattern A	?	low**	posterior	17	non-functional
<i>Hisonotus paulinus</i>	Pattern A	?	?	posterior	15**	?
<i>Hisonotus vespucii</i>	Pattern A	present	low	posterior	16–18	functional
<i>Hisonotus akv</i>	Pattern B	absent	deep	anterior	4–6	non-functional
<i>Hisonotus armatus</i>	Pattern B	absent	deep	anterior	5–6	non-functional
<i>Hisonotus brunneus</i>	Pattern B	absent	deep	anterior	5	non-functional
<i>Hisonotus carreiro</i>	Pattern B	absent	deep	anterior	4–5	non-functional
<i>Hisonotus charrua</i>	Pattern B	absent	deep	anterior	6–7	non-functional
<i>Hisonotus heterogaster</i>	Pattern B	absent/present	deep	anterior	5–6	non-functional
<i>Hisonotus hungy</i>	Pattern B	absent	deep	anterior	5	non-functional

.....continued on the next page

TABLE 3. (Continued)

Nominal species	Distribution (Fig. 3)	Extension of compound pterotic	Depth of caudal peduncle	Truncation of mid-dorsal series of plates	Number of mid-dorsal plates	Dorsal-fin locking mechanism
<i>Hisonotus iota</i>	Pattern B	absent	deep	anterior	6–8	non-functional
<i>Hisonotus laevior</i>	Pattern B	absent	deep	anterior	6–7	non-functional
<i>Hisonotus leucofrenatus</i>	Pattern B	absent	deep	anterior	4–6	non-functional
<i>Hisonotus leucophrys</i>	Pattern B	absent	deep	anterior	6–7	non-functional
<i>Hisonotus maculipinnis</i>	Pattern B	absent	deep	posterior	18	non-functional
<i>Hisonotus megaloplax</i>	Pattern B	absent/present	deep	anterior	5	non-functional
<i>Hisonotus montanus</i>	Pattern B	absent	deep	anterior	5	non-functional
<i>Hisonotus nigricauda</i>	Pattern B	absent	deep	posterior	14–18	non-functional
<i>Hisonotus notatus</i>	Pattern B	absent	deep	anterior	5–7	non-functional
<i>Hisonotus notopagos</i>	Pattern B	present	deep	posterior	18	non-functional
<i>Hisonotus prata</i>	Pattern B	absent	deep	anterior	5–6	non-functional
<i>Hisonotus ringuelei</i>	Pattern B	absent	deep	posterior	16–19	non-functional
<i>Hisonotus taimensis</i>	Pattern B	absent	deep	anterior	5–7	non-functional
<i>Hisonotus thayeri</i>	Pattern B	absent	deep	posterior	16	non-functional
<i>Hisonotus viro</i>	Pattern B	absent	deep	anterior	4	non-functional
<i>Hisonotus yasi</i>	Pattern B	absent	deep	posterior	17–19	non-functional
<i>Hisonotus acuen</i>	Xingu	present	low	anterior	6–7	functional
<i>Hisonotus bocaina</i>	São Francisco	absent	low	posterior	14–17	functional
<i>Hisonotus bockmanni</i>	Tapajós	absent	low	anterior	8–11	functional
<i>Hisonotus chromodonius</i>	Tapajós	absent	low	anterior	6	functional



**FIGURE 6.** Position of truncation of mid-dorsal series of lateral plates of *Otothyropsis* and *Hisonotus* species in lateral view: (A) *Otothyropsis biamanicus*, MCP 37164, paratype; (B) *O. polyodon*, paratype, MCP 45756; (C) *O. marapoama*, MCP 38303, paratype; (D) *O. piribebuy*, MCP 44394, paratype; (E) *H. francirochai*, MCP 34630; (F) *O. alicula*, MCP 23957, paratype; (G) *H. megaloplax*, MCP 31779, paratype; (H) *Hisonotus vireo*, MCP 14619, paratype; (I) *H. laevior*, MCP 23854; (J) *H. heterogaster*, MCP 41073, paratype; (K) *H. iota*, MCP 40029, paratype; (L) *H. leucophrys*, MCP 41354, paratype. D, dorsal series of lateral plates; MD, mid-dorsal series of lateral plates; M, median series of lateral plates; MV, mid-ventral series of lateral plates; V, ventral series of lateral plates. Odontodes not shown. Scale bar = 5 mm.

Regarding geographic distribution, all species of *Otothyropsis* are confined to the upper Paraná (Pattern A), except for *O. piribebuy*, which occurs in tributaries to the lower Río Paraguay basin in Paraguay (Fig. 3). Some of the Río Paraguay tributaries in that region have their headwaters on the upper Paraná plateau and very close to the headwaters of the Rio Paraná tributaries. For this reason, a headwater capture event between those basins is very likely (Ribeiro *et al.*, 2013) and could explain the current distribution of *O. piribebuy*. On the other hand, species of *Hisonotus* inhabiting the upper Paraná and São Francisco basins (Pattern A; *H. alberti*, *H. depressicauda*, *H. depressinotus*, *H. francirochai*, *H. pachysarkos*, *H. paulinus*, and *H. vespucci*) are morphologically more similar to *Otothyropsis* (Fig. 3, green shaded areas) and might be more closely related to that genus than to the remaining *Hisonotus* (Fig. 3, purple shaded areas).

The differences outlined above show the existence of a phenotypic pattern that distinguishes *Otothyropsis* plus some species of *Hisonotus* from most species of *Hisonotus*, and is corroborated by their respective geographic distributions. Nevertheless, a detailed phylogenetic study with wide taxon sampling in both genera and remaining representatives of the subfamily is still needed to test this arrangement and properly establish their phylogenetic relationships.

## Comparative material examined

*Hisonotus acuen*: MCP 32673 (10 + 1 cs), creek tributary to Rio da Saudade on road MT-423 ca. 38 km SE of Marcelândia, Analândia do Norte, Mato Grosso. MCP 32684 (1 cs), creek tributary to Rio Tartaruga on road from Vera to Feliz Natal, ca. 5 km E of Vera, Mato Grosso. *Hisonotus aky*: MCP 41474 (33), Rio forquilha at Balneário Espraiado, on secondary road between Maximiliano de Almeida and Paim Filho, Rio Grande do Sul. *Hisonotus alberti*: MCP 33942 (3), Rio Peruaçu, at Fabião I district, Januária, Minas Gerais. UFRGS 9848 (17), Córrego Doce at road BR-364, between Buritizeiro and João Pinheiro, Buritizeiro, Minas Gerais. LBP 19477 (31), Córrego Doce, São Francisco basin, Buritizeiro, Minas Gerais. *Hisonotus armatus*: MCP 25458 (3 cs), Arroio Corupá on road between Agudo and the Dona Francisca Hydroelectric plant, Agudo, Rio Grande do Sul. MCP 34776 (31 paratypes), Arroio Arambaré on road from Pedro Osório to Herval, Herval, Rio Grande do Sul. *Hisonotus bocaiuva*: MCP 16740 (18), creek 45 km S of Montes Claros on road BR-135 towards Bocaiuva, Minas Gerais. MCP 36851 (16), Córrego Sumidouro, ca. 6 km W of Francisco Dumont on road to Jequitai, Francisco Dumont, Minas Gerais. *Hisonotus bockmanni*: MCP 46046 (3 paratypes), sand bank on Rio Cururu, tributary to Rio Teles Pires, Jacareacanga, Pará. *Hisonotus brunneus*: MCP 41072 (13 paratypes), Rio Passo Novo on road from Cruz Alta to Ibiruba, Cruz Alta, Rio Grande do Sul. *Hisonotus carreiro*: MCP 44515 (holotype), Rio Carreiro downstream from Balneário Carreiro, Serafina Correa, Rio Grande do Sul. MCP 41548 (1 paratype), Rio Carreiro downstream from Corsan Reservoir, Guaporé, Rio Grande do Sul. MCP 40945 (2 paratypes), Rio Carreiro downstream from Balneário Carreiro, Serafina Correa, Rio Grande do Sul. MCP 40943 (3 paratypes), Arroio Guabiju, tributary to Rio Carreiro on secondary road between Guabiju and Vila São Jorge, Guabiju, Rio Grande do Sul. *Hisonotus charrua*: MCP 27539 (2 cs), Arroio do Tigre, tributary to Rio Jaguarí, on secondary road between road BR-453 and Ijucapirama, ca. 2.5 km NE of BR-453, Jaguari, Rio Grande do Sul. MCP 35337 (4), Arroio Albino, right bank tributary to Rio Ijuí, São Pedro do Butiá, Rio Grande do Sul. MCP 34876 (1), Arroio Albino, right bank tributary to Rio Ijuí, São Pedro do Butiá, Rio Grande do Sul. MCP 27611 (23), Arroio Caraí-Passo, on road from São Francisco de Assis to Manuel Viana, São Francisco de Assis, Rio Grande do Sul. *Hisonotus chromodontus*: MCP 37636 (5 paratypes), Rio Sumidouro Grande, tributary to Rio Arinos at Fazenda Arrossensal, Nortelândia, Mato Grosso. MCP 44413 (16), creek on road MT-235 between Nova Mutum and Santa Rita do Trivelato, Nova Mutum, Mato Grosso. MCP 32659 (4), creek at Fazenda Esplanada Arinos, on dust road between road MT-010 and ferry to Nova Mutum, São José do Rio Claro, Mato Grosso. MCP 35873 (189 + 10 cs), Rio Saue-Una downstream from reservoir on road BR-364 towards Sapezal, Mato Grosso. MCP 32675 (5 cs), Rio Celeste ca. 9 km W of Nova Ubiratã, on road to Sorriso, Nova Ubiratã, Mato Grosso. MCP 32678 (2 cs), Córrego Maria or Córrego Quinze, on road BR-163 ca. 23 km N of Sinop, Mato Grosso. MCP 32677 (1 cs), creek tributary to Rio Celeste ca. 47 km NW of Nova Ubiratã, on road to Sorriso, Mato Grosso. *Hisonotus depressicauda*: MZUSP 86986 (3 of 4), Rio Pardo, tributary to Rio Grande, at road from Campo Grande to Paranapiacaba, Santo André, São Paulo. MZUSP 103693 (3 of 5), Rio Grande on road between Araçauva and Campo Grande, Santo André, São Paulo. MCP 25553 (3), Rio Paraítinga, upstream from Salesópolis, São Paulo. MCP 25554 (6), Rio Paraítinga, at Salesópolis, São Paulo. *Hisonotus depressinotus*: MZUSP 88431 (3 of 5), Ribeirão Passa Cinco, tributary to Rio Corumbataí, Ipeúna, São Paulo. *Hisonotus francirochae*: MCP 34630 (1 cs), Córrego José Mendes, tributary to Rio São João, Fortaleza de Minas, Minas Gerais. MCP 47017 (10), Córrego 15 de Janeiro, tributary to Rio Aguapeí at Fazenda Paturi Queixada, Valparaíso, São Paulo. MCP 47018 (9 + 1 cs), Rio Pardo, Rio Grande basin, Bebedouro, São Paulo. *Hisonotus heterogaster*: MCP 44514 (holotype), Arroio Felício on road from Nova Palma to Júlio de Castilhos, Júlio de Castilhos, Rio Grande do Sul. MCP 41073 (5 + 2 cs paratypes), Arroio Felício on road from Nova Palma to Júlio de Castilhos, Júlio de Castilhos, Rio Grande do Sul. MCP 26802 (1 paratype), Arroio Felício, ca. 10 km SSE of Júlio de Castilhos, Rio Grande do Sul. *Hisonotus hungi*: MCP 47176 (5), Misiones, Argentina. *Hisonotus iota*: MCP 40029 (18 + 3 cs paratypes), Rio Chapecó, Vila São Miguel, Coronel de Freitas, Santa Catarina. *Hisonotus laevior*: MCP 11521 (2 cs), rio Jacui, Rio Grande do Sul. MCP 23008 (6), Arroio Bom Jardim on access road to the III Polo Petroquímico, Triunfo, Rio Grande do Sul. MCP 23854 (1 cs), creek tributary to Arroio Santa Isabel on road BR-116, ca. 17 km S of Cristal, Rio Grande do Sul. MCP 34779 (8), Arroio Mata Olho on road between Pedro Osorio and Basílio, Pedro Osório, Rio Grande do Sul. MCP 34781 (1), Arroio Arambari on road between Pedro Osorio and Basílio, Pedro Osório, Rio Grande do Sul. *Hisonotus leucoxanthus*: MCP 11540 (2 cs), Rio Cubatão near road BR-101, Joinville, Santa Catarina. MCP 32202 (24), creek tributary to Rio Itapocuzinho by the road to Santa Luiza, Jaraguá do Sul, Santa Catarina. *Hisonotus leucophrys*: MCP 42576 (holotype), Rio

Ariranhas at road SC-466, Xavantina, Santa Catarina. MCP 41354 (3 + 2 cs paratypes), Rio Ariranhas at road SC-466, Xavantina, Santa Catarina. *Hisonotus maculipinnis*: MCP 48067 (2 cs), Laguna El Rey, Río Salado basin, Santa Fé, Argentina. *Hisonotus megaloplax*: MCP 42577 (holotype), Arroio Caragoata on secondary road near BR-153, between Passo Fundo and Ipiranga, Passo Fundo, Rio Grande do Sul. MCP 31779 (9 + 3 cs paratypes), Rio Passo Fundo downstream to Corsan Reservoir, Passo Fundo, Rio Grande do Sul. MCP 41352 (6 paratypes), Arroio Caragoata on secondary road near BR-153, between Passo Fundo and Ipiranga, Passo Fundo, Rio Grande do Sul. *Hisonotus montanus*: MCP 42578 (holotype), Rio Rufino on road SC-427, Rio Rufino, Santa Catarina. MCP 22369 (1 paratype), creek tributary to Rio João Paulo on road inside Fazenda Jair Philippe, Bom Retiro, Santa Catarina. MCP 41459 (16 + 3 cs paratypes), Rio Rufino on road SC-427, Rio Rufino, Santa Catarina. *Hisonotus nigricauda*: MCP 26865 (3 cs), Arroio do Salso, tributary to Rio Ibicui Da Armada, on road BR-158, Rosário do Sul, Rio Grande do Sul. MCP 28986 (11), Arroio Passo dos Carros, Eldorado do Sul, Rio Grande do Sul. MCP 40761 (10 + 3 cs), Arroio Banhado Grande on road BR-153 from Bagé to Caçapava do Sul, Bagé, Rio Grande do Sul. *Hisonotus notatus*: MCP 20822 (3), Rio Macacu ca. 1.5 km SE of Cachoeiras de Macacu on road RJ-116, Cachoeiras de Macacu, Rio de Janeiro. *Hisonotus notopagis*: MCP 44517 (holotype), creek tributary to Arroio das Lavras on road from Lavras do Sul to Bagé, Lavras do Sul, Rio Grande do Sul. MCP 46510, Arroio Canguçu, ca. 4 km N of Canguçu, Camaquã, Rio Grande do Sul. MCP 25924 (2 cs paratypes), Arroio da Mantiqueira, Lavras do Sul, Rio Grande do Sul. MCP 44504 (9 paratypes), Arroio Maria Santa, Encruzilhada do Sul, Rio Grande do Sul. *Hisonotus prata*: MCP 44513 (holotype), Rio da Prata at Passo do Despraiado, between Guabiju and André da Rocha, Nova Prata, Rio Grande do Sul. MCP 22204 (9 paratypes), Rio da Prata at Passo do Despraiado, between Guabiju and André da Rocha, Nova Prata, Rio Grande do Sul. MCP 40942 (18 paratypes), Rio da Prata at Passo do Despraiado, between Guabiju and André da Rocha, Nova Prata, Rio Grande do Sul. *Hisonotus ringueleti*: MCP 26154 (3 + 1 cs paratypes), bog near road to Rivera, Rivera, Uruguay. MCP 11215 (128 + 2 cs), Arroio Quaraí-Mirim on road from Quaraí to Alegrete, Quaraí, Rio Grande do Sul. *Hisonotus taimensis*: MCP 17417 (29 + 3 cs), Arroio Taim, Taim Ecological Station, Rio Grande, Rio Grande do Sul. MCP 45828 (7), Arroio Corrientes, Pelotas, Rio Grande do Sul. *Hisonotus thayeri*: MCP 35692 (6), Rio do Ouro, tributary to Rio Macaé, near Córrego do Ouro, Macaé, Rio de Janeiro. MCP 44806 (65), Arroio Santo Antonio, tributary to Rio Itapemirim, on road towards Menino Jesus, Espírito Santo. *Hisonotus vireo*: MCP 14619 (3 cs paratypes), Rio dos Sinos, ca. 5 km upstream Caraá, Rio Grande do Sul. MCP 17643 (6 paratypes), Rio dos Sinos 7 km N of Caraá, on road to Fundo Quente, Caraá, Rio Grande do Sul. MCP 26568 (6), Arroio Caemborá near Caemborá, Nova Palma, Rio Grande do Sul. MCP 38766 (15 + 3 cs), Arroio Sarauá, near botanical garden, Lageado, Rio Grande do Sul. *Hisonotus vespuccii*: MCP 17034 (5), Rio Carinhanha at Juvenília, ca. 30 km NE of Montalvânia, Minas Gerais. MCP 17153 (113 + 1 cs), creek at São João das Missões, on road between Itacarambi and Manga, Manga, Minas Gerais. MCP 23521 (6), Rio Paraopeba downstream from Igarapé Hydroelectric plant, Juatuba, Minas Gerais. MCP 28340 (25 + 1 cs), creek on road BR-040 from Paracatu to João Pinheiro, Paracatu, Minas Gerais. MCP 29019 (4), Rio Peruaçu, Januária, Minas Gerais. MCP 49061 (12), Rio Cipó, tributary to Rio das Velhas, Cardeal Mota, Minas Gerais. *Hisonotus yasi*: MCP 47824 (16), Rio Siemens, between Planalto and Sagrada Família, Planalto, Paraná. NUP 790 (2 cs), Caxias Reservoir, Capitão Leonidas Marques, Paraná. *Otothyropsis alicula*: MNRJ 23957 (1 of 4 cs paratypes), Rio Santo Antônio at Água Limpa, near mouth of Ribeirão do Salto, Rio Grande basin, Delfim Moreira, Minas Gerais. MCP 23500 (10 + 2 cs paratypes), Rio Santo Antônio, tributary to Rio Sapucaí, Delfim Moreira, Minas Gerais. *Otothyropsis biannicus*: MCP 39531 (3 + 2 cs paratypes), Rio Água Verde, tributary to Rio Canoinhas, Canoinhas, Santa Catarina. MCP 37164 (1 cs paratype), Rio dos Patos on road PR-427 between Lapa and Campo do Tenente, Lapa, Paraná. UFRGS 11495 (6 + 1 cs, paratypes), Rio Tibagi at Uvaia, approx. 100 m from highway, Ponta Grossa, Paraná. MCP 47713 (1 cs), Riacho Médio, tributary to Rio Tibaji, Telêmaco Borba, Paraná. *Otothyropsis marapoama*: MCP 38303 (9 + 1 cs paratypes), LIRP 5641 (3 of 48 paratypes), and MZUSP 87893 (3 + 1 cs paratypes), Córrego Cubatão at Sítio Cubatão, Catanduva, São Paulo. MCP 42119 (1 cs paratype), Rio Boa Esperança, left margin tributary to Rio Jacaré Guaçu near its mouth, Gavião Peixoto, São Paulo. LIRP 5640, holotype, and LIRP 4621 (2 of 3 paratypes), Ribeirão Cubatão, Marapoama, São Paulo. *Otothyropsis piribebuy*: MCP 44394 (25 + 3 cs paratypes), Arroyo Piribebuy, Cordillera, Eusébio Ayala, Paraguay. MCP 45754, (2 paratypes) Río Aguilar at Lima, tributary to Río Jejui, Río Paraguay basin, Departamento San Pedro, Paraguay. *Otothyropsis polyodon*: MCP 45756 (4 + 1 cs paratypes), Rio Verde at mouth of Ribeirão Tamanduá, Água Clara, Mato Grosso do Sul. MCP 47038 (7 + 1 cs paratypes), creek tributary to Rio Verde on road between Mutum and São Domingos Hydroelectric plant, Água Clara, Mato Grosso do Sul.

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