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## REDESCRIPTION OF *HYPOPTOPOMA INEXSPECTATA* (HOLMBERG, 1883), WITH NOTES ON ITS ANATOMY (SILURIFORMES: LORICARIIDAE)

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**RESUMEN:** Redescrición de *Hypoptopoma inexpectata* (Holmberg, 1883), con notas sobre su anatomía (Siluriformes: Loricariidae).

Se presenta una diagnosis y redescrición de *Hypoptopoma inexpectata* sobre la base del examen de material adicional y comparación con sus congéneres. Esta especie de *Hypoptopoma*, pobremente conocida, se distribuye en las cuencas de los ríos Paraná y Paraguay. *Hypoptopoma inexpectata* se diagnostica sobre la base de la autapomorfía ordenamiento bi-serial de los odontodes del margen rostral del hocico, extendiéndose lateralmente desde el extremo anterior hasta el límite entre los infraorbitales 2 y 3; la serie dorsalmente orientada se separa de la ventralmente orientada por un área angosta libre de odontodes. Esta especie se distingue además por la combinación (1) bajo número de la serie media de placas laterales (2022, típicamente 21), (2) presencia de placas prepectorales, (3) dos series de 3-5 placas abdominales, (4) distancia interorbital mínima 48-56 % longitud cabeza, (5) diámetro horizontal de la órbita 17-20% longitud cabeza, y (6) distancia mínima órbita-narina 8-12% longitud cabeza. Se reporta variación intraespecífica en relación con los huesos dérmicos de la cabeza, neuracráneo y suspensorio, placas dérmicas, y aleta adiposa.

**Palabras clave:** Siluriformes, Loricariidae, Hypoptopomatinae, Taxonomía, Anatomía.

**SUMMARY:** Redescription of *Hypoptopoma inexpectata* (Holmberg, 1883), with notes on its anatomy (Siluriformes: Loricariidae).

*Hypoptopoma inexpectata* is diagnosed and redescribed based on the examination of additional material and comparison with its congeners. This poorly known hypoptopomine species is distributed in the Paraguay and Paraná river drainages. *Hypoptopoma inexpectata* is diagnosable based on the autapomorphy biserial arrangement of anterior snout rostral margin odontodes, laterally extended to limit between second and third infraorbital plates, with dorsally directed dorsad series separated from ventrally directed ventrad series by a narrow odontode-free area, which at the level of first and second infraorbital plates is reduced to a dividing line of the series. The species can be further distinguished by the combination (1) low number of canal-bearing lateral plates (20-22, typically 21), (2) presence of a shield of prepectoral dermal plates, (3) arrangement of abdominal plates in one paired series of 3-5 plates, (4) shorter least interorbital distance 48-56% head length, (5) larger horizontal eye diameter 17-20% head length, and (6) least orbit-nare distance 8-12% head length. Intraspecific variation skull dermal bones, neuracranium and suspensorium bones, dermal plates, adipose fin is reported.

**Key words:** Siluriformes, Loricariidae, Hypoptopomatinae, Taxonomy, Anatomy.

### INTRODUCTION

The loricariid genus *Hypoptopoma* inhabits the drainage basins to the east of the Andes, except for river systems draining to the Atlantic between the mouth of the Amazon in Brazil and the Paraná in Argentina. The genus was established by Günther (1868: 234) for his new species *H. thorracatum*, on the basis of the «peculiar formation of the head, depressed, spatulate, the eyes being on the lateral edges of the head». Schaefer (1991) diagnosed *Hypoptopoma* by the presence of a canal on the preopercle forming a near semicircle and the fifth infraorbital bone bearing both mandibular and infraorbital canal branches. However, after the discovery and description of the genus *Nanno-*ptopoma** Schaefer, 1996, those characters were proposed as synapomorphies at

the level of the clade *Hypoptopoma* + *Nanno-*ptopoma** (Schaefer, 1996, 1998), a change that left *Hypoptopoma* with no recognized autapomorphies. For the present study, we follow the current definition of the genus proposed by Schaefer (1996: 915-916): *Hypoptopoma* + *Nanno-*ptopoma** can be distinguished from other hypoptopomines by the combination "adipose absent, head and snout greatly depressed and orbits visible from below, preopercle not exposed, trunk plate odontodes distributed along the posterior plate margin (versus an even distribution of odontodes on the posterior trunk plates)". *Hypoptopoma* can be distinguished from *Nanno-*ptopoma** by the presence of serrae along the posterior margin of the pectoral fin (versus absence of serrae) and paired series of abdominal plates composed by more than three plates each

*H. gulare* Cope, 1878; *H. joberti* (Vaillant, 1880); *H. psilogaster* Fowler, 1915; *H. thoracatum* Günther, 1868; and *H. steindachneri* Boulenger, 1895 -, of which the taxonomic revision is a project in progress of the first author in collaboration with S. Schaefer. Following Aquino (1997), *H. guentheri* is considered a junior synonym of *H. inexpectata*; following Eigenmann (1910), *H. carinatum* Steindachner, 1879, is considered a member of the genus *Oxyropsis* Eigenmann & Eigenmann, 1889.

For reasons of conciseness, in the anatomical account, only those features that have not been addressed in the literature are described in detail; otherwise, when the observation made on *Hypoptopoma inexpectata* confirms previous reports, only the reference to the corresponding source is indicated. In most cases, the particular condition observed for *H. inexpectata* is documented with self-explanatory figures.

Osteological preparations were made following Dingerkus & Uhler (1977). Abbreviations used: cs, cleared and stained material; HL, head length; SL, standard length. In the list of comparative material, the catalogue number is followed by the number of specimens examined, standard length between parentheses, if available, locality, and cleared, and stained specimens. Bone terminology

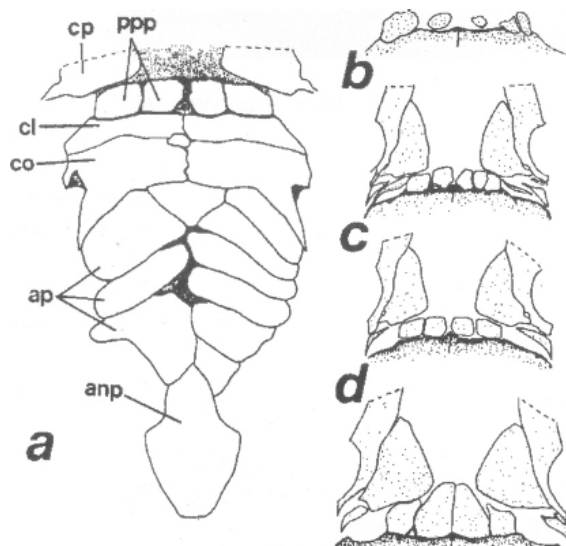
follows Schaefer (1987, 1991); muscle terminology follows Winterbottom (1974), Howes (1983), Schaefer & Lauder (1986), and Schaefer (1990).

#### Institutional abbreviations

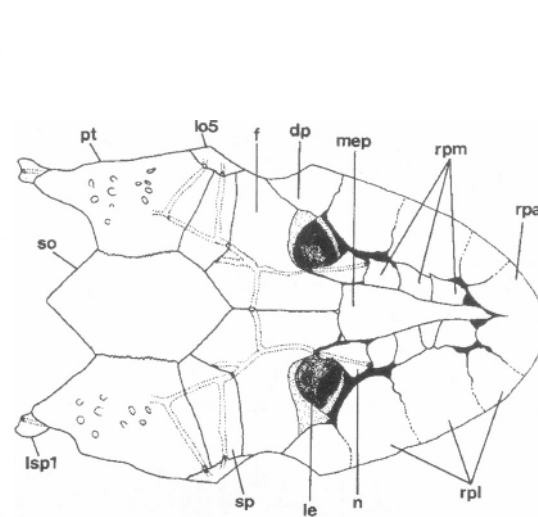
AMNH American Museum of Natural History, New York  
 ANSP Academy of Natural Sciences of Philadelphia  
 BMNH British Museum of Natural History, London  
 ILPLA Instituto de Limnología "Dr. Raúl A. Ringuélet", Buenos Aires  
 MACN Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires  
 MAS Museo Antonio Scasso, San Nicolás, Buenos Aires  
 MFA Museo Florentino Ameghino, Santa Fe  
 MNHN Muséum National d'Histoire Naturelle, Paris  
 BMNH Rijksmuseum van Natuurlijke Historie, Leiden, Holland

**Material examined:** All localities in Argentina unless noted otherwise.

*Ancistrus cirrhosus*. ILPLA 275, 3 cs (54.2-77.7), arroyo El Pescado, Buenos Aires.



**Fig. 2 a-e.-** Ventral dermal plates of *Hypoptopoma inexpectata*, anterior toward top. a: 51.2 mm SL, prepectoral, abdominal, and anal plates. b-e: ontogenetic series of the prepectoral plates; b: 41.7 mm SL; c: 51.2 mm SL; d: 53.0 mm SL, and e: 68.5 mm SL. anp: anal plate; ap: abdominal plates; cl: cleithrum; co: coracoid; cp: canal bearing ventral plate; ppp: prepectoral plates. Scale = 5 mm.



**Fig. 3.-** Dermal plates of the head of *Hypoptopoma inexpectata* (50.2 mm SL), dorsal view (dotted line = pathway of laterosensory canals); dp: dermal plate; f: frontal; io5: infraorbital 5; le: lateral ethmoid; lsp1: first laterosensory lateral line plate; mep: mesethmoid plate; n: nasal; pt: pterotic-supracleithrum-posttemporal complex; rpa: anterior rostral plate; rpl: lateral rostral plates; rpm: series of plates lateral to mesethmoid plate; so: supraoccipital; sp: sphenotic. Scale = 2 mm.

*Hypoptopoma bilobatum*. ANSP 8280/81 (syntypes), 2 (59.5-74.8), Pebas (Perú).

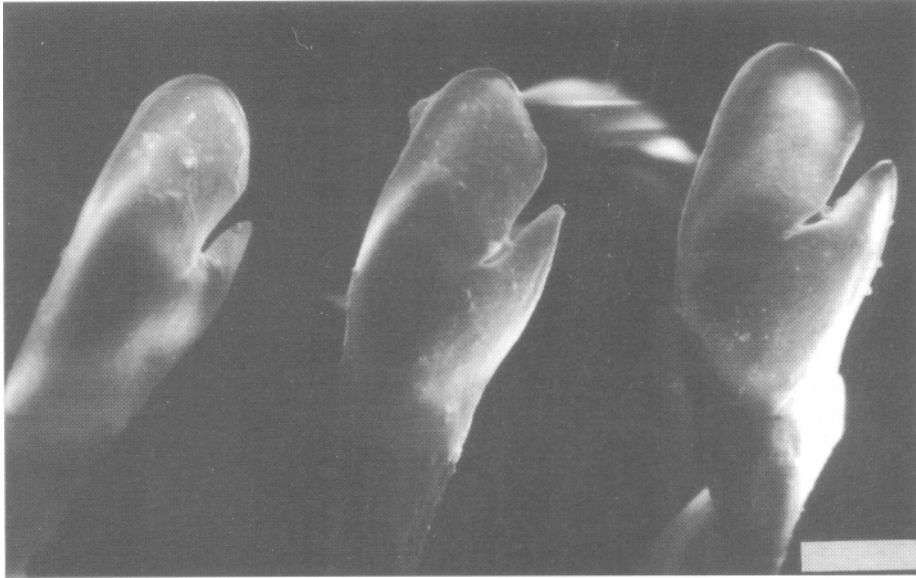
*Hypoptopoma guentheri*. BMNH 1895.5.17.77-82 (syntypes), 3 (43.0-55.0), Mato Grosso (Brazil).

*Hypoptopoma guianense*. BMNH 26922 (paratypes), 4 (47.0-56.0), Nickerie River. Below Blanche Marie Falls (Surinam).

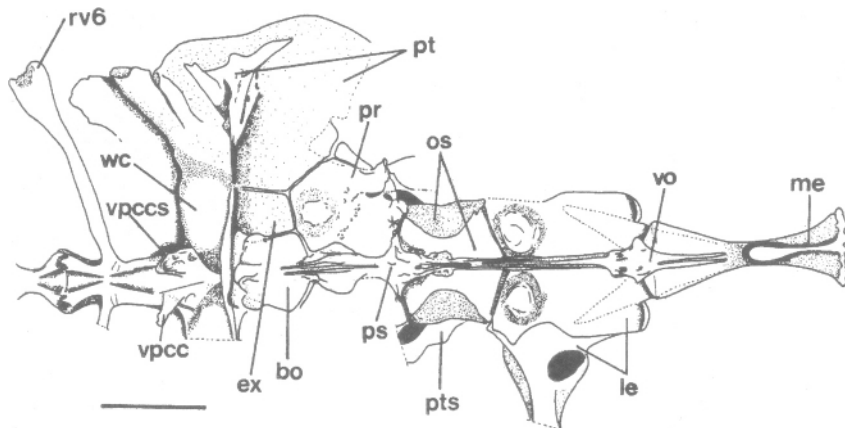
*Hypoptopoma gulare*. ANSP 21477 (holotype), (81.95), Peruvian Amazon: Río Marañón (Perú).

*Hypoptopoma inexpectata*. MACN 5164 (holotype), (53.6), Río Paraguay in Formosa. ILPLA 268, 2 (41.6-

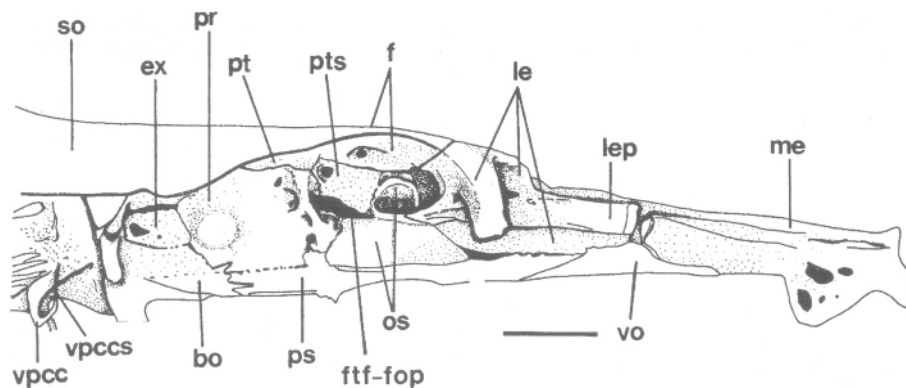
46.0), Isla Toro, Corrientes. ILPLA 269, 40 (34.0-68.4), 16 cs (33.0-69.0), Tuyutí, Corrientes. ILPLA 270, 4 cs (42.8-60.8), río Paraná, Corrientes. MFA-Z-VI.798, 2 (35.5-36.9), Riacho Santa Fe, Santa Fe. MAS (noncat.), (52.2), río Yaguarón, tributary of the Paraná, at San Nicolás, Buenos Aires. MACN 3244, 3, Río Formosa, Formosa. MACN 6547, Lago de Golf, Lago de Palermo in Buenos Aires. MACN 7013, 6, A° Cigüeña, Helvecia, Santa Fe. MACN 7014, 5, Río Santa Lucía, Corrientes. MACN 7015, 3, Helvecia, Santa Fe. MACN 7296; 100, Corsa-Cue, Río Paraná, Corrientes.



**Fig. 4.-** SEM of premaxillary teeth of *Hypoptopoma inexpectata*, right side, anterior view (58.4 mm SL). Scale = 100  $\mu$ m.



**Fig. 5.-** Neurocranium of *Hypoptopoma inexpectata* (41.7 mm SL), ventral view, anterior toward right. Only sixth-vertebra rib and swimbladder capsule of the right side are shown. bo: basioccipital; ex: exoccipital; le: lateral ethmoid; me: mesethmoid; os: orbitosphenoid; pr: prootic; ps: parasphenoid; pt: pterotic-supracleithrum-posttemporal complex; pts: pterosphenoid; rv6: sixth-vertebral rib; vo: vomer; vpcc: ventral process of vertebra complex centrum; vpccs: splint joining vpcc and wc; wc: swimbladder capsule. Scale = 2 mm.



**Fig. 6.-** Neurocranium of *Hypoptopoma inexpectata* (41.7 mm SL), right side, lateral view, anterior toward right. bo: basioccipital; ex: exoccipital; f: frontal; f+f - fop: compound foramen for the trigeminofacialis and optic nerves; le: lateral ethmoid; lep: anterior process of lateral ethmoid; me: mesethmoid; os: orbitosphenoid; ps: parasphenoid; pt: pterotic-supracleithrum-posttemporal complex; pts: pterosphenoid; so: supraoccipital; vo: vomer; vpcc: ventral process of vertebra complex centrum; vpccs: splint joining vpcc and wc. Scale = 2 mm.

*Hypoptopoma joberti*. MNHN A-1966 (holotype), (73.9), Calderón (Brazil).

*Hypoptopoma psilogaster*. ANSP 21922 (holotype), (51.0), Peruvian Amazon (Perú).

*Hypoptopoma thoracatum*. BMNH 1867-6:13-38 (holotype), (3 inches), Xeberos (Perú).

*Hypoptopoma* sp. "A". ANSP 166732, 5 (39.5-45.5), río Orinoco basin: Cabruta, L. Larga II, Venezuela. ANSP 128960, 7 (48.0-66.4), 1 cs (75.7), Río Negro, just downstream from main Villavicencio, Puerto López highway to La Balsa, Meta drainage (Colombia). ANSP 134007, 1 cs (61.1), Meta, Quebrada Venturosa, between La Balsa and Puerto López; Meta drainage

*Hypoptopoma* sp. "B". ANSP 138868, 2 (37.4-55.3), 1 cs (54.5), vicinity Iquitos, Río Nanay well above Morona coche, Loreto (Perú).

*Microlepidogaster maculipinnis*. BMNH 1909. 4.2.1922, 2 of 4 (26.4-27.4) (syntypes), La Plata, Buenos Aires. ILPLA 234, 2 cs (28.0-29.8), Bella Vista, Corrientes. ILPLA 235, 4 cs (23.9-28.1), arroyo Batel, Bella Vista, Corrientes.

*Otocinclus amoldi*. BMNH 1908, 12.5.13, 1 (44.1) (holotype), La Plata, Buenos Aires, Argentina.

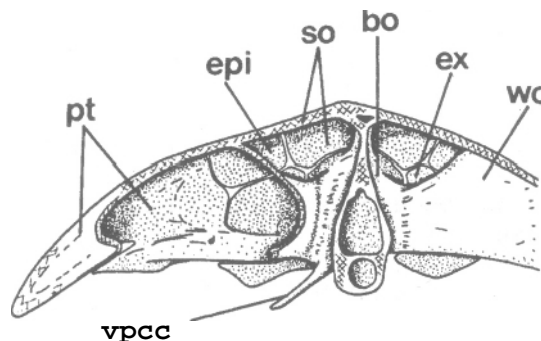
*Otocinclus fimbriatus*. ANSP 21585-21597, 8 (25.0-30.5) (syntype X-rays), Río Jacuí, Río Grande do Sul (Brazil).

*Otocinclus flexilis*. ANSP 21622-21626 and 21756-21767, 8 (28.6-39.9) (syntype X-rays), Río Jacuí, Río Grande do Sul (Brazil). MFA-ZV-1.833, 2 (35.5-36.9), Porto Alegre, Vila Restinga, arroio Passo do Salso Río Grande do Sul (Brazil). ILPLA 207, 4 cs (28.9-40.7) and ILPLA 208, 2 cs (31.1-36.4), arroyo El Pescado, Buenos Aires.

*Otocinclus vittatus*. BMNH 1895.5.17.83 (29.7) (lectotype); BMNH 1895.5.17.86 -87, 2 (19.8-21.1) (paralectotypes), Descalvados (Brazil). ILPLA 261, 4 cs (22.0-27.7), Río Paraná, Nemesio Parma, Misiones. ILPLA 254, 4 cs (21.8-22.5), Río Paraná, Corrientes, Argentina. ILPLA 249, 1 cs (30.8), arroyo El Pescado, Buenos Aires.

*Hypoptopoma inexpectata* (Holmberg) (fig. 1)  
*Aristommata inexpectata* Holmberg, 1893a: 96; 1893b: 354. Type locality: Río Paraguay, al pie de Formosa.

*Hypoptopoma guentheri* Boulenger, 1895: 516. Type locality: Descalvados, Mato Grosso, Brazil. Boulenger, 1896: 31 (Río Paraguay). Regan, 1904: 264 (reference). Fowler, 1954: 125 (reference). Ringuélet & Arámburu, 1961: 52 (reference). Isbrücker, 1980: 88 (reference).



**Fig. 7.-** Cross section through fifth vertebral centrum (36.0 mm SL), posterior view showing swimbladder capsules; bones of posterior wall of left-side capsule removed, thus showing anterior wall. bo: basioccipital; epi: epiotic; ex: exoccipital; pt: pterotic-supracleithrum-posttemporal complex; so: supraoccipital; vpcc: ventral process of vertebra complex centrum; wc: swimbladder capsule. Scale = 1 mm.

**TABLE I- Morphometric data of the type specimens of *Hypoptopoma inexpectata* (A), *H. guentheri* (B), mean and standard deviation of two specimens of type series), *H. gulare* (C), and *H. joberti* (D).**

Character	A	Mean	<sup>B</sup> SD	C	D
Standard length (mm)	53.6	52.7	2.61	82.0	74.0
PERCENT OF STANDARD LENGTH					
Predorsal length	45.9	46.7	1.13	48.4	46.6
Head length	34.5	34.4	0.63	34.0	34.5
Body depth	16.4	17.4	0.34	19.4	18.8
Dorsal-fin spine length	25.5	29.9	2.65	-	-
Trunk length	44.4	44.8	0.57	43.4	42.5
Pectoral-fin spine length	27.1	29.2	0.79	28.6	29.1
Abdominal length	15.7	15.7	0.33	16.6	16.6
Caudal peduncle length	33.6	32.8	0.12	33.5	33.3
Caudal peduncle depth	9.9	8.9	0.31	8.6	8.2
PERCENT OF HEAD LENGTH					
Body depth	49.2	50.6	1.91	56.9	54.6
Head depth	47.8	46.4	0.63	52.4	47.9
Snout length	55.1	53.9	1.06	55.8	53.8
Horizontal eye diameter	18.6	17.9	1.22	16.9	16.
Orbit-nare least distance	11.2	11.5	0.04	16.3	15.
Least interorbital distance	54.9	56.3	0.63	60.8	58.7
Cleithral width	67.4	68.1	1.93	71.7	69.0
Head width	63.1	63.2	1.13	65.9	63.7

*H. inexpectatum*: Berg, 1898: 11 (taxonomy). Isbrücker, 1980: 88 (reference). López et al., 1987: 30. *Oxyropsis güntneri*: Eigenmann, 1910: 419 (reference).

*Oxyropsis inexpectatus*: Eigenmann, 1910: 412 (reference). Bertoni, 1914: 9 (Paraguay); Bertoni, 1939: 53 (Paraguay).

*Oxyropsis guentheri*: Pozzi, 1945: 263 and 275 (reference). Fowler, 1954: 110 (reference).

*O. inexpectata*: Pozzi, 1945: 263 and 275 (reference).

*H. inexpectata*: Ringuélet et al., 1967: 391 (reference). Boeseman, 1974: 265 (taxonomy); Aquino, 1997: 5 and 8 (taxonomy, distribution); Aquino, 1998: 233-235 (anatomy).

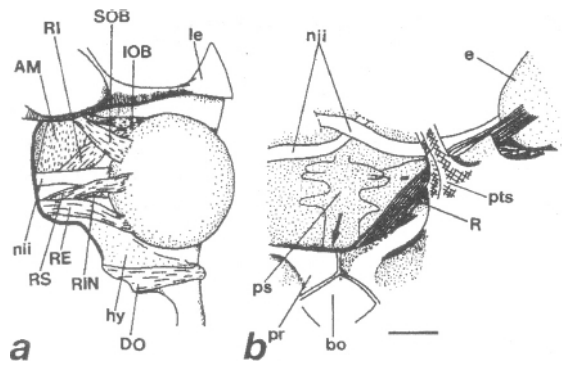
*H. inexpectata*: Braga & Azpelicueta, 1986: 86 (Río Paraná, Misiones, Argentina). Aquino & Miquelarena, 1994: 211-212 (anatomy).

*H. inexpectatum*: Weber et al., 1992: 11 (Río Negro, Paraguay)

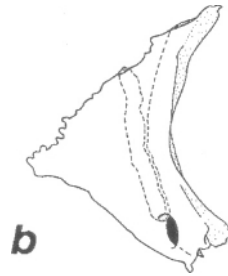
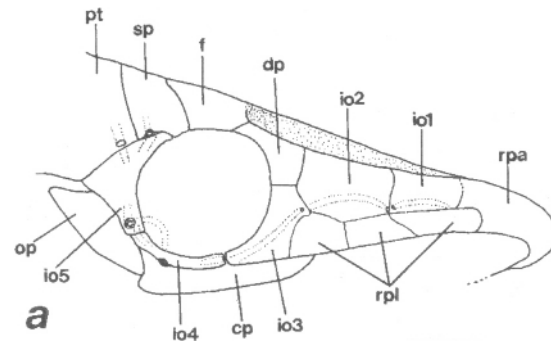
**Diagnosis.** *Hypoptopoma inexpectata* is diagnosed on the basis of the autapomorphic characters (1) odontodes of rostral margin of snout

arranged in dorsally up-turned and ventrally down-turned series laterally extended to limit between second and third infraorbital plates, and (2) presence of odontode-free narrow band between dorsal and ventral series, the band, at the level of first and second infraorbital plates, reduced to dividing line between series. In contrast, in other *Hypoptopoma* species, rostral margin snout odontodes not arranged in regular series, nor separated by odontode-free discontinuity. It can be further distinguished from its congeners by having a low number of canal-bearing lateral plates (20-22, typically 21, versus usually 22 or higher). (See the Discussion for a comparative analysis with other *Hypoptopoma* species).

**Description.** Morphometric data are given in table I. Body moderately elongate, dorsal profile of body smoothly ascending from tip of snout to origin of dorsal fin, trunk slightly tapering to base of caudal fin. Greatest body depth at dorsal-fin origin. Eyes relatively large (17.1-19.7 mm SL), laterally positioned on head, visible both in dorsal and ventral view.



**Fig. 8 a-b.-** Eye muscles of *Hypoptopoma inexpectata*. a: insertion of the eye muscles, right side, dorsal view, with fourth and fifth infraorbital bones, frontal, sphenotic, and pterotic-supracleithrum-posttemporal complex partially removed (47.4 mm SL); b: skull ventral wall, dorsal view, roof dorsal bones removed, showing the posterior myodome and the right-side recti muscles (40.2 mm SL); arrow indicating the myodome anterior opening. AM: *adductor mandibularis*; bo: basi-occipital; DO: *dilator operculi*; e: eye ball; hy: hyomandibula; IOB: *inferior obliquus*; le: lateral ethmoid; nii: optic nerve; pr: prootic; ps: parasphenoid; pts: pterosphenoid; R: *recti* muscles; RE: *rectus externo*; RI: *r. interno*; RIN: *r. inferior*; RS: *r. superior*; SOB, *superior obliquus*. Scale = 1 mm.



**Fig. 9 a-b.-** Head dermal plates of *Hypoptopoma inexpectata*, right side. a: 39.0 mm SL, ventrolateral view of head; b: 41.7 mm SL, fifth infraorbital, lateral view, right side. cp: canal-bearing ventral plate; dp: dermal plate; f: frontal; io1 to io5: first to fifth infraorbitals; op: opercure; pt: pterotic-supracleithrum-posttemporal complex; rpa: anterior rostral plate; rpl: lateral rostral plates; sp: sphenotic. Scale = 1 mm.

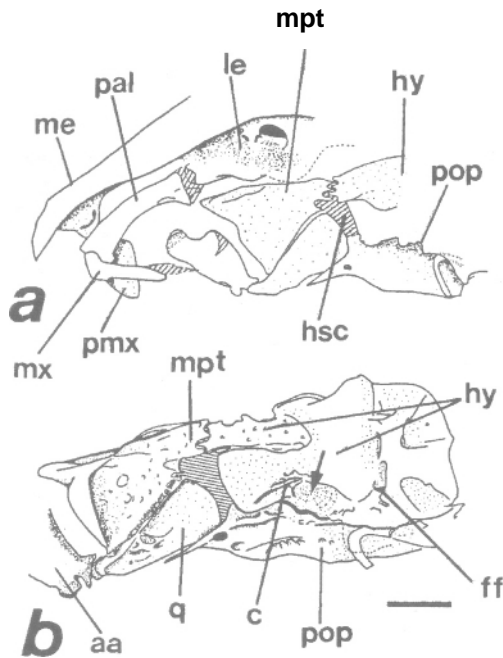
Adults with body entirely covered by plates, except ventral surface of head, area around anus, and base of dorsal, anal, pectoral, and pelvic fins. Odontodes on rostral plates and ventral side of pectoral -and pelvic- fin unbranched rays bearing slightly enlarged odontodes. In adult stages, surface of trunk plates smooth, only bearing a row of odontodes along posterior margin. Body and head without crests. Coracoid and cleithrum ventral laminar projections covered ventrally by a thin layer of skin, and directly supporting odontodes. One paired series of 3-6 abdominal plates, which in adults meet at midline, and one anterior median plate (fig. 2a). Large anal plate between pelvic fins, covering tips of ventrolateral trunk plates. Two pairs of prepectoral plates, in adults forming together a relatively large shield (fig. 2a, b, c, d, e). Large paired canal-bearing cheek plates ventrally positioned on head. Snout covered dorsally by plates (fig. 3). Anterior and lateral rostral plates large and few in number, dorsally and ventrally reflected.

Lips wide. Maxillary barbels short. Premaxillary teeth 17-20, mandibular teeth 13-18. Teeth slender and bifid (fig. 4); major cusp broad, with parallel margins and roundish tip; minor cusp pointed.

Dorsal fin 1,7; dorsal-fin origin slightly behind pelvic-fin origin; first dorsal-fin spine (spinelet) absent. Pectoral fin 1,6; when depressed reaching to anus; pectoral-fin spine with serrae along posterior margin. Pelvic fin 1,5; short, unbranched and first branched rays equal in length, when depressed reaching to anus. Anal fin 1,5; caudal fin 1,14,1, posterior margin concave, upper and lower lobes equal. Adipose fin variably present.

Color in alcohol. Ground color tan brown, lighter on ventral region of head and trunk. Darker longitudinal stripes anterior to nares. Variably defined darker bands along sides of trunk and posterior to dorsal-fin base. All fins with brown bands, more pronounced along unbranched rays. Branched rays distally hyaline. Caudal fin with larger dark blotch at base of lower lobe.

**Distribution.** Río Paraguay and río Paraná drainage basin. There are no records for the up-



**Fig. 10 a-b.-** Suspensorium and mandibular arch of *Hypoptopoma inexpectata*. a: 50.2 mm SL, left side, lateral view, in relation to the neurocranium; b: 41.7 mm SL, right side, mesial, view. The arrow points to the articulation site for the posterohyal. aa: anguloarticular; c: crest; hsc: hyosimplectic cartilage; hy: hyomandibular; le: lateral ethmoid; me: mesethmoid; mpt: metapterygoid; mx: maxilla; pal: palatine; pmx: premaxilla; pop: preopercle; q: quadrate. Scales: a = 1 mm; b = 2 mm.

per Paraná upstream Salto das Sete Quedas (Brazil).

## ANATOMY

**Neurocranium.** Condition described for genus (Howes, 1983; Schaefer, 1991) confirmed in *Hypoptopoma inexpectata* (figs. 5, 6, 7). Aquino (1998) reported that this species, while sharing the presence of functional posterior myodome with other loriciariids examined, *H. inexpectata* is distinguished for not presenting an anteriomyodome-like cavity for the origin of the obliquii-eye muscles, which in contrast occurs from a ridge on the posterior wall of the lateral ethmoid lateral process (fig. 8a, b). The significance of this character state will be assessed in the scope of the revision of the genus (Aquino & Schaefer, in prep.).

**Infraorbital series and laterosensory canal system.** Condition at genus level (Schaefer, 1991) confirmed in *Hypoptopoma inexpectata*

(fig. 9a, b). The character fifth infraorbital bone bearing botín mandibular (preopercular) and infraorbital canals (fig. 9b), a character state originally indicated as derived at genus level (Schaefer, 1991), after a re-analysis of the character evidence has been proposed as synapomorphic of the clade *Hypoptopoma* + *Nannoptopoma* (Schaefer, 1996).

**Suspensorium and mandibular arch.** Osteological and myological characters at subfamily and family levels (Howes, 1983; Schaefer, 1990, 1991) confirmed in *Hypoptopoma inexpectata* (osteology figs. 10a, b; 12a, b, c, d; 13a, b, c, d; myology fig. 11 a, b).

**Opercular series.** Osteological and myological characters at genus level (Howes, 1983; Schaefer, 1991) confirmed in the present work (fig. 15a).

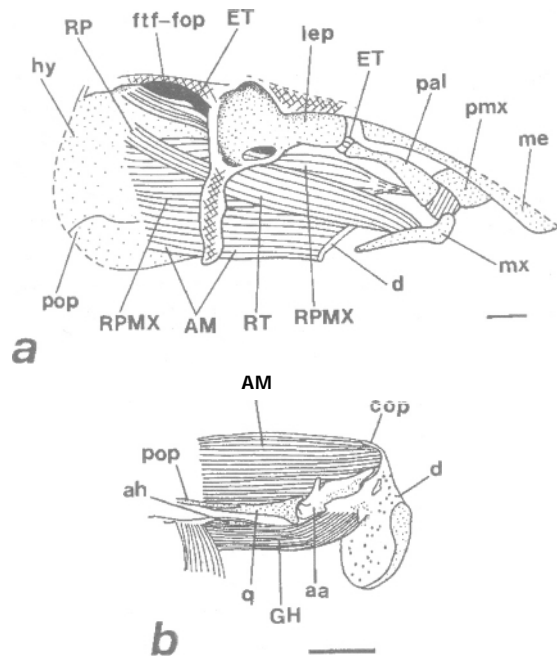
**Hyoid and branchial arches.** Osteology described at genus level (Schaefer, 1991) confirmed in *H. inexpectata* (fig. 14). Both the characters anterior margin of anterohyal greatly expanded and presence of ridge on ventral side of anterohyal, proposed as synapomorphies of the clade *Hypoptopoma* + *Oxyropsis* + *Acestridium* (Schaefer, 1991), are here confirmed in *H. inexpectata*. Hyoid-arch myology (fig. 15a, b) congruent with previous descriptions made at genus, subfamily and family levels (Howes, 1983; Schaefer, 1990, 1991).

**Weberian apparatus and axial skeleton.** Bony capsule of swimbladder laterally elongate, slightly tubular in shape (fig. 5, 7), similar to condition described for *Hypostomus plecostomus* (Schaefer, 1987) and different from the usually globous shape of the swimbladder capsule of other hypoptopomines (Schaefer, 1991). General osteology of the Weberian apparatus similar to that described at family level (Chranilov, 1929; Alexander, 1964; Chardon, 1968). In *Hypoptopoma inexpectata* (figs. 16a, b), scaphium discoidal and mesially concave in shape, tripus curving at approximately one-third from anterior tip, with a small mesial process for connection with the dorsoanterior portion of the weberian-complex centrum via connective tissue.

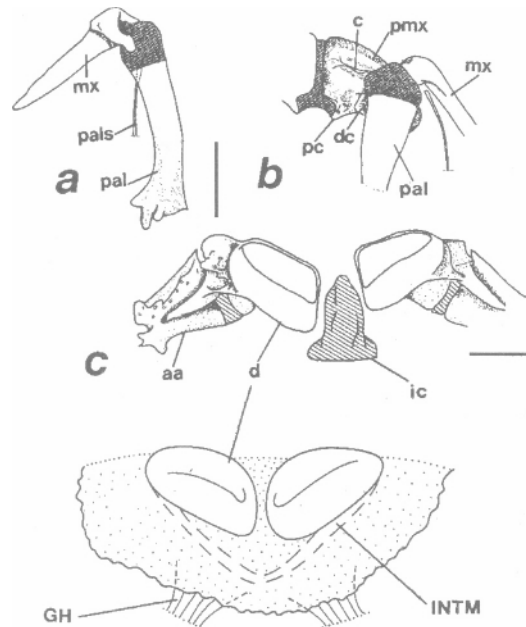
Total vertebrae 25 (including first five incorporated into Weberian complex and fused with skull, and single centrum incorporated into ural complex). Connection among vertebrae, supraoccipital bone, dermal plates, supraneural, and dorsal-fin pterigiophores (fig. 17) congruent with condition described at genus and tribe levels (Schaefer, 1991).

**Media fins.** Osteology of caudal skeleton (fig. 18a, b) responding to condition described





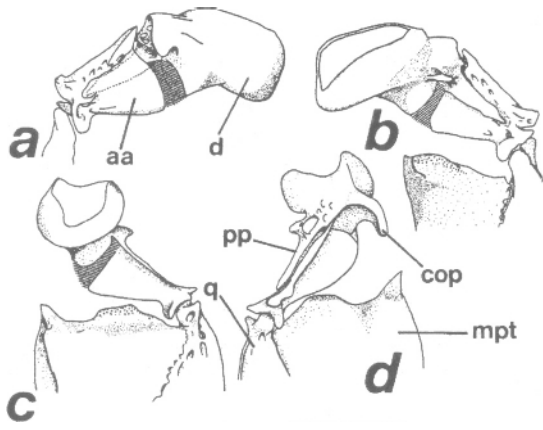
**Fig. 11 a-b.-** Jaw-palatine muscles of *Hypoptopoma inexpectata* (43.6 mm SL), right side. a: dorsolateral view, part of snout plates, frontal and sphenotic removed; b: insertion of muscle b and *protractor hyoideus* a, ventrolateral view. Cross-hatched areas = partially removed bones. aa: anguloarticular; ah: anterohyal; AM: *adductor mandibularis*; cop: coronoid process; d: dentary; ET: *extensor tentaculi*; ftf-fop: compound foramen for the trigemino-facialis and optic nerves; GH: *genohyoideus*; hy: hyomandibula; lep: anterior process of lateral ethmoid; me: mesethmoid; mx: maxilla; pal: palatine; pmx: premaxilla; pop: preopercle; q: quadrate; RP: *retractor palatini*; RPMX: *retractor premaxillae*; RT: *retractor tentaculi*. Scale = 1 mm.



**Fig. 12 a-d.-** Mandibular arch of *Hypoptopoma inexpectata*. a: palatine and maxilla, left side, ventral view (41.7 mm SL); b: palatine, maxilla, and premaxilla, right side, dorsal view (41.7 mm SL); c: left and right mandibles and intermandibular cartilage, ventral view, and d: position of the *intermandibularis* (dotted line) below the inferior lip. aa: anguloarticular; d: dentary; dc: dorsal condyle for insertion of interpremaxillary cartilage; GH: *genohyoideus*; ic: intermandibular cartilage; INTM: *intermandibularis*; mx: maxilla; pal: palatine; pals: palatine spine; pc: posterior condyle for insertion of the interpremaxillary cartilage; pmx: premaxilla. Scales = a, b = 5 mm; c = 1 mm.

at family level (Lundberg & Baskin, 1969; López, 1986; Schaefer, 1987, 1991; López & Miquelarena, 1991). The caudal endoskeleton myology, not addressed in the literature at the genus, subfamily nor family levels, includes body muscles -with insertion point on caudalskeleton related elements- and intrinsic caudal muscles. The body-muscle group includes: *epiaxialis* and *hypaxialis*, forming distinct bundles of fibers inserting on the dorsal and ventral marginal principal caudal-fin rays, respectively (EPAX, HYPAX; fig. 19a); *infracarinalis inferioris*, with origin from the last anal-fin ray and inserting onto lower branched caudal-fin ray (ICARP; fig. 19a, b), and *supracarinalis posterior*, with origin from last dorsal-fin ray and inserting onto upper branched principal caudal-fin ray (SCARP; fig. 19a). The in-

trinsic caudal muscles include: *interradialis*, extended between branched caudal-fin rays 2-3 of each lobe and base of central rays (INT; fig. 19a, b); *flexor dorsalis*, with origin along longitudinal line close to level of second preural centrum, and insertion point on both marginal and branched rays of upper caudal lobe (FD; fig. 19b); *flexor ventralis*, symmetrical to *flexor dorsalis* (FV; fig. 19b); *flexor ventralis inferioris*, with origin from second preural centrum as a distinct bundle of fibers, then intermingling with fibers of the *flexor ventralis* along posterior third of its length, and inserting together onto lower marginal principal ray (FVI; fig. 19b); and *hypochordal longitudinalis*, with origin from the hypurapophysis and insertion onto upper-caudal lobe first branched caudal-fin rays, its fibers intermingling with the *flexor dorsalis*.



**Fig. 13 a-d.-** Left mandible of *Hypoptopoma inexpectata* (41.7 mm SL). a: dorsal view; b: ventral view; c: mesial view and d: lateral view. aa: anguloarticular. cop: coronoid process; d: dentary; mpt: metapterygoid; pp: posterior process; q: quadrate. Scale = 1 mm.

Osteology of dorsal and anal fins (figs. 20, 21) congruent with observations at genus and sub-family level (Schaefer, 1991). Adipose fin variably present (See Ontogeny non-dependant variation section).

**Paired fins.** Osteology of pectoral girdle (fig. 22) similar to that described at genus level (Schaefer, 1991). Serrae along posterior margin of pectoral-fin spine well developed (fig. 22a). Two pectoral-fin radials (versus presence of three radials in other loriciariids), small first one supporting first branched ray, elongate second one straddling the coracoid bony column and supporting remaining branched rays (fig. 22c, d). Regarding the myology of the pectoral girdle, the identified muscles are the *abductor superficialis*, its fibers originating in part from the coracoid vertical lamina, and the *arrector ventralis superficialis*, issuing through lateral opening of coracoid (fig. 22b).

Osteology of the pelvic girdle (fig. 23a, b) not differing from condition described at family level (Shelden, 1937; Howes, 1983; López, 1986). Basipterygium fossa muscularis with ventral transverse ridge orthogonal to girdle longitudinal axis (fig. 23a) (versus ridge oblique in most loriciariids). Pelvic-girdle muscles include: *adductor profundus*, inserted on ventral transversal ridge; *adductor superficialis*, and the *arrector dorsalis*, both inserted on the basipterygium lateral anterior process.

### Morphological intraespecific variation

#### Ontogeny-dependant variation:

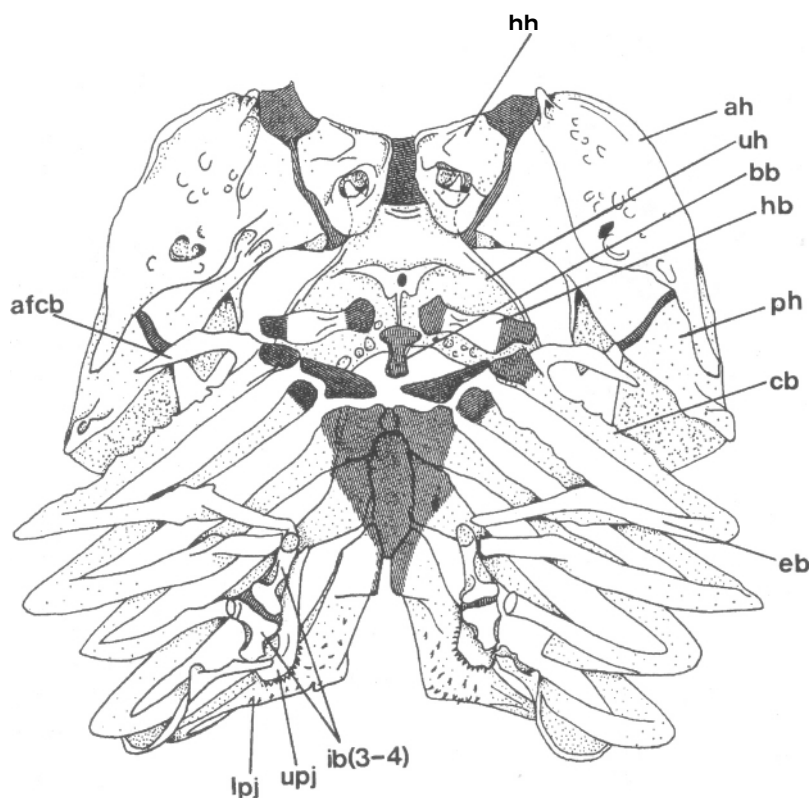
1. Dorsal rim of the orbit with increasing participation of fifth infraorbital along with decreasing participation of both sphenotic and frontal bones. The exclusion of the frontal from the orbit rim, proposed as a character unique of the genus *Hypoptopoma* by Gosline (1948), here is confirmed only for the largest individuals.
2. Gradual increment in the area covered by dermal plates with increasing individual size. This is particularly noticeable in abdominal plates, pre-pectoral plates, anal plate, plate series anterior to nares, and rostral plates. Trunk plates first in being fully developed. This growth pattern is similar to that described for other hypoptopomines (e.g. *Otocinclus*; Schaefer, 1997).
3. Increasing reduction in size and number of surface odontodes of trunk plates. The largest specimens with plate surface smooth, keeping only a line of odontodes along posterior border.

#### Ontogeny non-dependant variation:

4. Lateral ethmoid completely to partially encapsulating the nasal organ from below. The character nasal organ partially to entirely open from below was reported as derived state for the hypoptopomines (Schaefer, 1991).
5. Interdigitating joint between metapterygoid and hyomandibula variable in length. A restricted interdigitating joint and not elongated had been proposed as derived for *Hypoptopoma*, *Oxyropsis*, among other hypoptopomine genera (Schaefer, 1991).
6. Adipose fin variably present. When present, it can be represented by a patch of odontodes closely arranged, by an odontode-covered spiny axis supporting a delicate membrane, or only by a delicate membrane. Adipose fin absent had been indicated as synapomorphic for the clade *Hypoptopoma* + *Nannoptopoma* (Schaefer, 1996).

### DISCUSSION

The taxonomic status of *Hypoptopoma inexpectata* has been variable along its nomenclature history. The species has been alternatively considered a valid taxon (Berg, 1898; Eigenmann, 1910; Ringuelet et al., 1967; Aquino, 1997) or junior synonym (Gosline, 1945; Fowler, 1954). Aquino (1997) redescribed the species but without being able to provide a phylogenetic diagnosis. Based on this taxonomic background, and on the basis of availability of additional material and consideration of new character evidence, in the

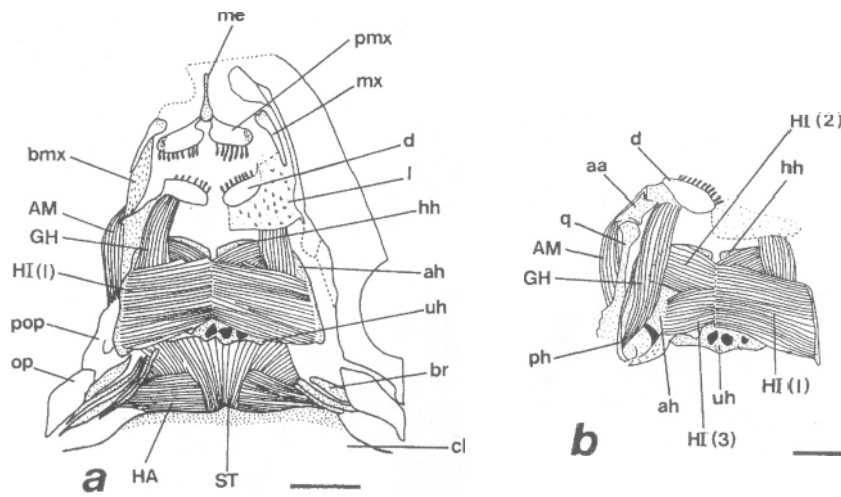


**Fig. 14.-** Hyoid and branchial arches of *Hypoptopoma inexpectata* (41.7 mm SL), dorsal view. afcb: accessory flange of first ceratobranchial; ah: anterohyal; bb: basibranchial; cb: ceratobranchial; eb: epibranchial; hb: hypobranchial; hh: hypohyal; ib(3-4): third and fourth infrapharyngobranchials; lpj: lower pharyngeal tooth plate; ph: posterohyal; uh: urohyal; upj: upper pharyngeal tooth plate. Scale = 1 mm.

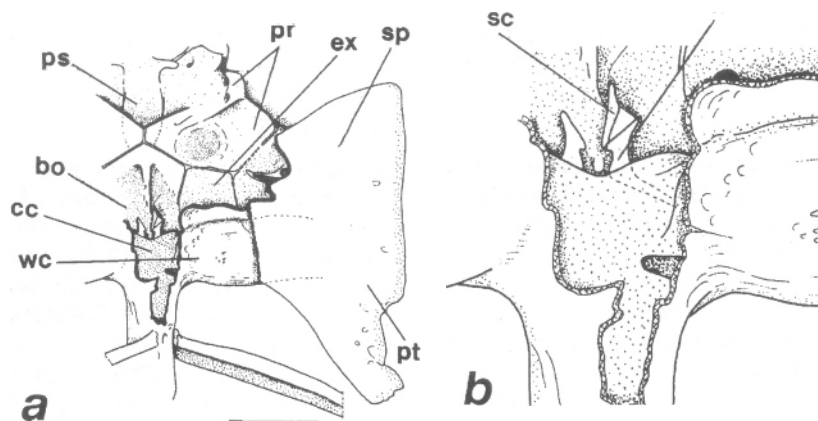
present paper we reviewed the taxonomic status of the species. *Hypoptopoma inexpectata* is diagnosable based on the autapomorphy bi-serial arrangement of anterior snout rostral margin odontodes, with dorsally directed dorsad series separated from ventrally directed ventrad series by a narrow odontode-free area. This character has not been reported for any other nominal species of *Hypoptopoma*, nor for any other genus of the tribe Hypoptopomatini. Eventually, individuals of other taxa can be found with a slightly similar arrangement of dorsally -and ventrally-directed odontode series on the rostral margin, however, without exhibiting the associated odontode-free gap or naked space between odontode series. Among the Otothyriini, the presence of a similar snout odontode discontinuity was reported for species of *Hisonotus* Eigenmann & Eigenmann 1889 (pers. obs.), *Pseudotocinclus* Nichols, 1919 (Schaefer, 1991), and *Otothyris* Myers, 1927

(Garavello *et al.*, 1998). However, in those species, the dorsoventral arrangement is limited to the rostral plate, not being laterally extended to the limit between second and third infraorbital plates as observed in *H. inexpectata*. Furthermore, since the genera *Hisonotus*, *Pseudotocinclus* and *Otothyris* are well supported taxa within the Otothyriini (Schaefer, 1998), this suggests that the presence of an odontode-free narrow gap between dorsally- and ventrally-directed odontode series was independently derived in *H. inexpectata*.

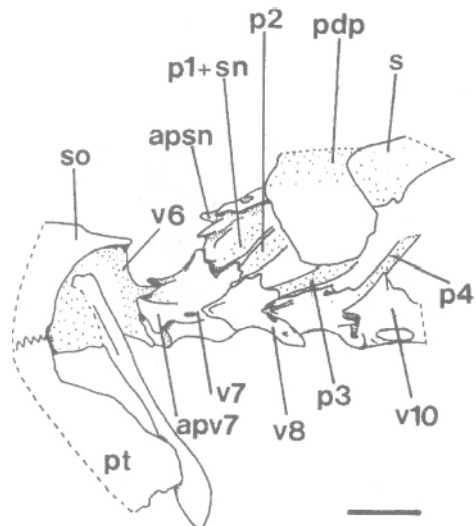
This species can be further distinguished, with the exception of *H. gulare*, *H. joberti*, and *H. steindachneri*, by the combination (1) presence of a shield of prepectoral dermal plates (*versus* absence of prepectoral plates), and (2) arrangement of abdominal plates in one paired series of 3-5 plates, which in adults meet at midline, plus an anterior mediaj plate (*versus* arrangement in one paired series plus a complete median series).



**Fig. 15 a-b.-** Hyoid muscles of *Hypoptopoma inexpectata* (43.2 mm SL). a: adductor muscle b and hyoid muscles in relation to right mandibular arch and pectoral girdle bones; ventral view, a portion of the right-side posterior lip removed, and b: hyoid muscles in relation to right mandibular arch; ventral view, with the posterior division of the *hyohyoideus inferioris* and the *protractor hyoideus* b of the right side removed. aa: anguloarticular; ah: anterohyal; AM: adductor mandibularis; bmx: cartilaginous axis of maxillary barbel; br: branchiostegal rays; cl: cleithrum; d: dentary; GH: genohyoideus, HA: hyohyoideus adductor; hh: hypohyal; HI: *hyohyoideus inferioris*; HI(1), HI(2), HI(3): posterior, anterior and inferior; l: lip; me: mesethmoid; mx: maxilla; op: opercle; ph: posterohyal; pmx: premaxilla; pop: preopercle; q: quadrate; ST: sternohyoideus; uh: urohyal. Scale = 1 mm.



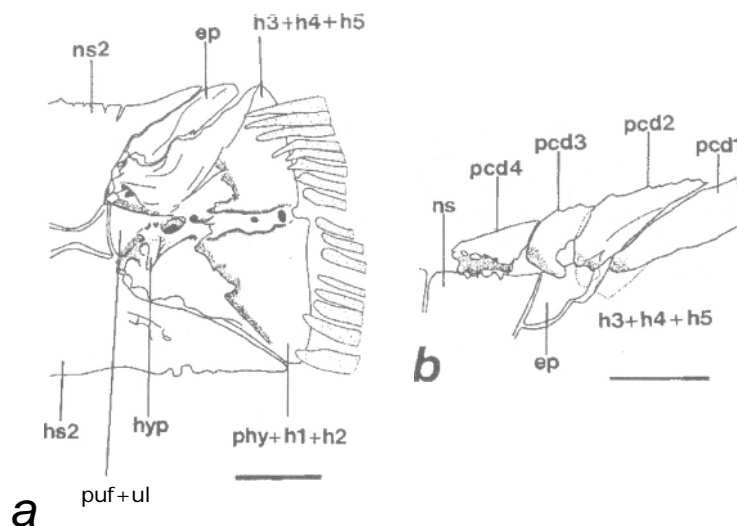
**Fig. 16 a-b.-** Ventral wall of cranium posterior portion, Weberian-complex centrum and sixth vertebra of *Hypoptopoma inexpectata*, dorsal view, anterior towards top. a: general view, supraoccipital, sphenotic and part of the pterotic-supracleithrum-posttemporal complex of the right side removed; right side swimbladder capsule and sixth centrum rib only shown, and b: detail of the Weberian ossicles, left-side scaphium removed. bo: basioccipital; cc: Weberian-complex centrum; ex: exoccipital; pr: prootic; ps: parasphenoid; pt: pterotic-supracleithrum-posttemporal complex; sc: scaphium; sp: sphenotic; tr: tripus; wc: swimbladder capsule. Scale = 2 mm.



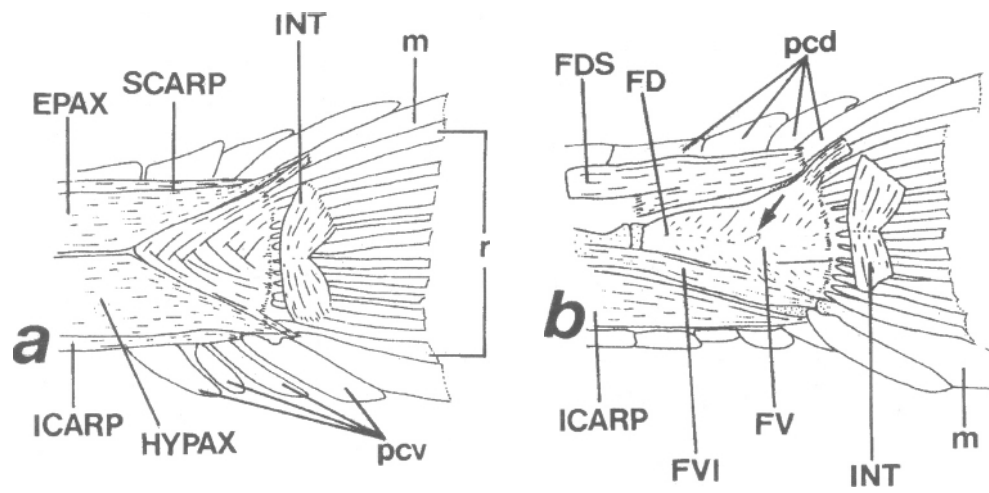
**Fig. 17.-** Vertebrae 6-10 of *Hypoptopoma inexpectata* in relation to the neurocranium and dorsal-fin supports, left side, lateral view (41.7 mm SL). apsn: anterior processes of supraneural; apv7: anterior processes of seventh vertebra; pi+sn: fused first dorsal-fin pterygiophore and supraneural; p2, p3, etc.: second, third dorsal-fin pterygiophores, etc.; pdp: predorsal plate; pt: pterotic-supracleithrum-posttemporal complex; s: spine; so: supraoccipital; v6, v7, etc.: sixth, seventh vertebra, etc. Scale = 2 mm.

*Hypoptopoma inexpectata* can be further distinguished from *H. gulare*, *H. joberti*, and *H. steindachneri* by the combination (1) shorter least interorbital distance 48-56% HL (versus 55-63 and 63-72, respectively), (2) larger horizontal eye diameter 17-20% HL (versus 15-18), and (3) least orbit-nare distance 8-12% HL (versus 15-18 and 18-22, respectively).

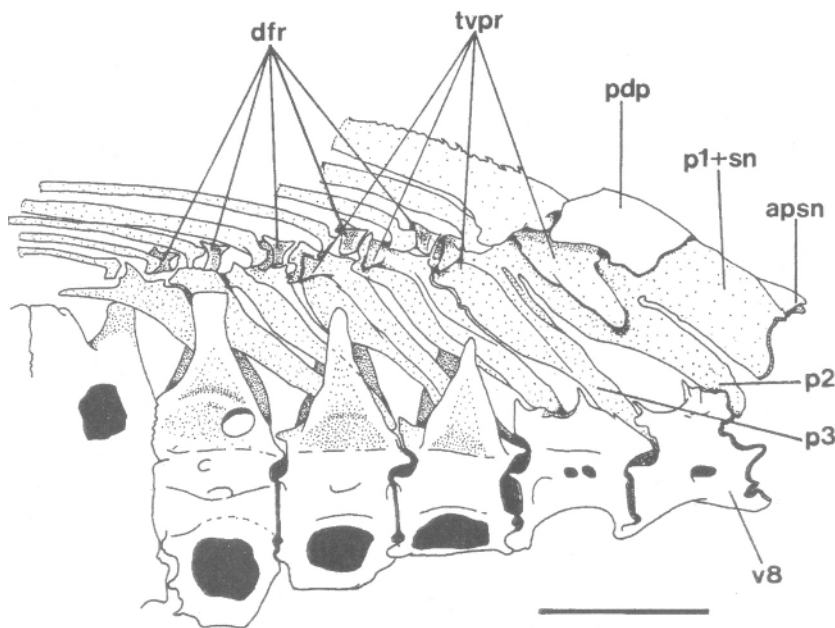
As far as we can determine from available material, the distribution of *Hypoptopoma inexpectata* is restricted to the Paraguay-Paraná river drainage. No other species of the genus- excepting *H. guentheri*, here considered a junior synonym of *H. inexpectata*- has been reported for that drainage. The northern limits of the distribution of *H. inexpectata* are the headwaters of the Paraguay river in Mato Grosso, and the Parana river, up to Sete Quedas in southern Brazil. This distribution is partially congruent with the "Río Paraguay endemic region" proposed by Vari (1988). This area of endemism -mostly based on curimatid distribution- includes in addition to the Paraguay and the Parana rivers, the Uruguay river and coastal streams of central Argentina, Uruguay and southern Brazil. There are no records of *H. inexpectata* for the latter drainages, which suggests a distribution pattern similar to



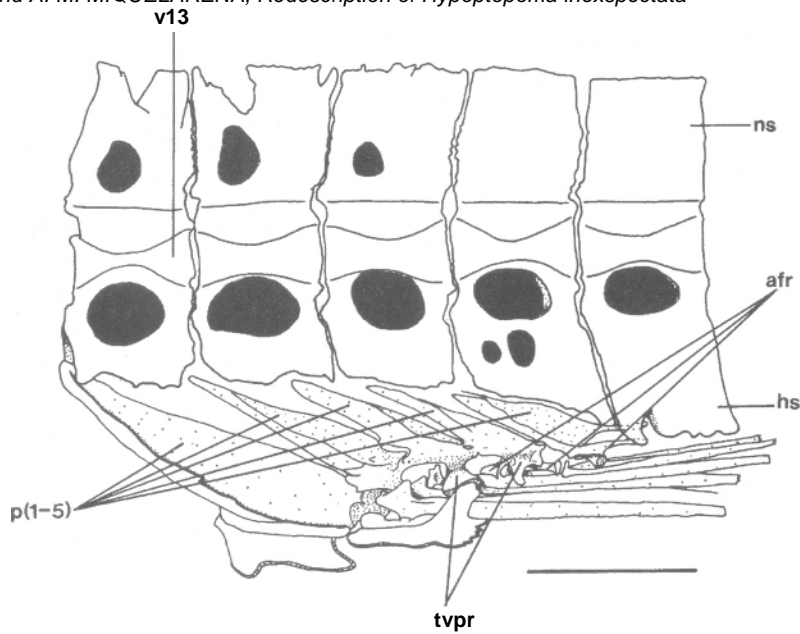
**Fig. 18 a-b.-** Caudal skeleton of *Hypoptopoma inexpectata* (41.7 mm SL), left side. a: lateral view including the last two preural central and proximal portions of the principal rays, and b: dorsal procurent rays, left side, lateral view. ep: epural; h3+h4+h5: fused third, fourth and fifth hypurals; hs2: hemal spine of the second preural centrum; hyp: hypurapophysis; ns: neural spine; ns2: neural spine of second preural centrum; phy+h1+h2: fused parhypural, first and second hypurals; pcd1, pcd2, etc.: first and second dorsal procurent caudal-fin rays, etc.; pu1+u1: fused first preural and first ural centra. Scale = 1 mm.



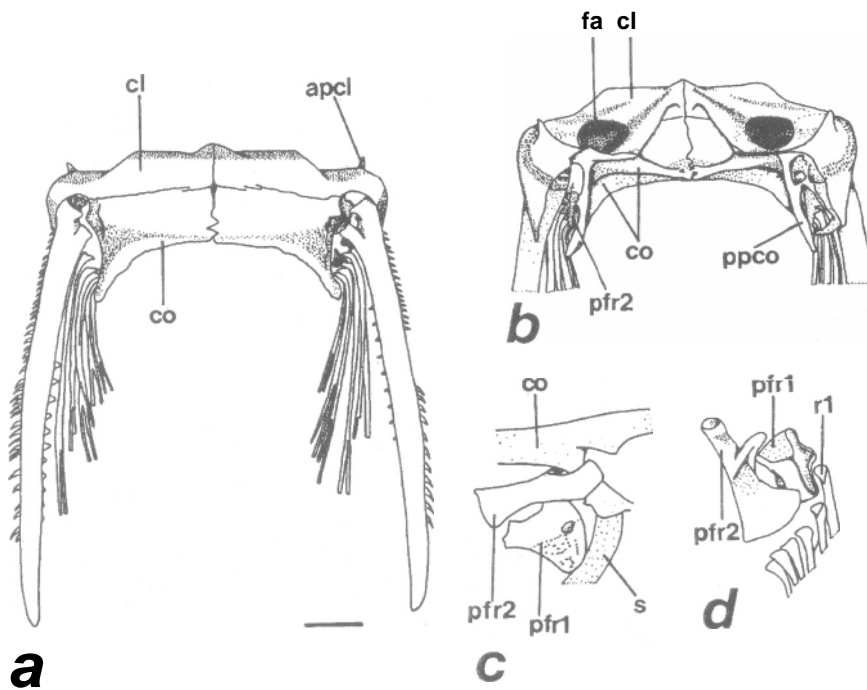
**Fig. 19 a-b.-** Caudal skeleton muscles of *Hypoptopoma inexpectata*; procurrent caudal-fin rays and proximal portions of principal rays are included. a: superficial muscles, left side, lateral view, and b: deeper muscles, left side, lateral view, *epaxialis* e *hypaxialis* removed; the arrow points to the position of the hypurapophysis (light dotted line). EPAX: *epaxialis*; FD: *flexor dorsalis*; FDS: *flexor dorsalis superior*, FV: *flexor ventralis*; FVI: *flexor ventralis inferior*, HYPAX: *hypaxialis*; ICARP: *infracarinalis posterior*, INT: *interradialis*; m: marginal caudal-fin ray; pcd: dorsal procurrent caudal-fin rays; pcv: ventral procurrent caudal-fin rays; SCARP: *supracarinalis posterior*. Scale = 1 mm.



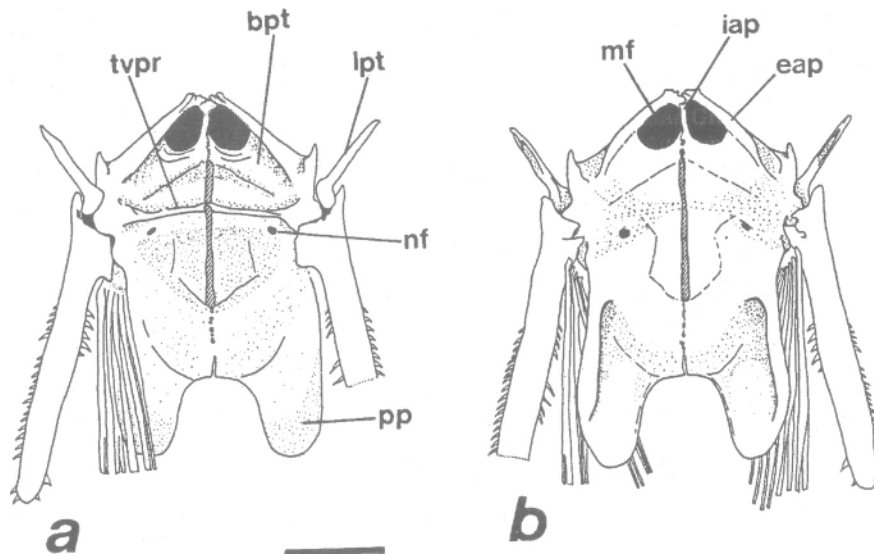
**Fig. 20.-** Vertebrae 8-13 of *Hypoptopoma inexpectata* in relation to the dorsal fin, right side, lateral view (41.7 mm SL). aspn: anterior processes of supraneural; dfr: dorsal-fin radials; p1+sn: fused first dorsal-fin pterygiophore and supraneural; p2, p3: second, third dorsal-fin pterygiophores; pdp: predorsal plate; tvpr: transverse process; v8: eighth vertebra. Scale 2 mm.



**Fig. 21.-** Vertebrae 13-17 in relation to anal-fin supports, left side, lateral view (41.7 mm SL). afr: anal-fin radials; hs: hemal spine; ns: neural spine; p(1-5): first to fifth anal-fin pterygiophores; tvpr: transverse process; v13: thirteenth vertebra. Scale = 2 mm.



**Fig. 22 a-d.-** Pectoral skeleton and fin rays of *Hypoptopoma inexpectata* (41.7 mm SL), anterior towards top. a: ventral view; b: dorsal view; c: pectoral-fin radials in relation to the coracoid in ventral view, and d: in dorsal view. apcl: anterior process of cleithrum; cl: cleithrum; co: coracoid; fa: fossa arrector; pfr1, pfr2: first and second pectoral-fin radials; ppco: posterior process of coracoid; r1: first pectoral-fin branched ray; s: spine. Scales: a, b = 2 mm; c, d = 0.5 mm.



**Fig. 23 a-b.-** Pelvic skeleton of *Hypoptopoma inexpectata* (41.7 mm SL). a: ventral view, and b: dorsal view. bpt: basipterygium; eap: externa; anterior process; iap: inner anterior process; lpt: lateropterygium; mf: marginal foramen; nf: neural foramen; pp: posterior process; tvpr: transverse process. Scale = 2 mm.

that observed in *Otocinclus* Cope, 1872 (Schaefer, 1997), a basal genus within the clade Hypoptopomatini. In contrast, recent biogeographical considerations made on the richness in endemic species in the upper Parana upstream Sete Quedas, Uruguay and Jacui river drainages (Reis & Schaefer, 1998; Wimberger *et al.*, 1998) is suggesting a differential history among drainages within the "Río Paraguay endemic region" sensu Vari (1988). On going work focusing on phylogeny and biogeography of different neotropical groups will provide the opportunity to test that hypothesis.

#### ACKNOWLEDGMENTS

We thank the following individuals and institutions for loan of material, W. Saul (ANSP), O. Crimmer, D. Siebert and P. Campbell (BMNH), L. Protogino (ILPLA), L. Braga (MACN), J. Liotta (MAS), C. Virasoro (MFA) J.-C. Hureau (MNHN), G. Mees (RMNH). We are indebted to L. Protogino and H. López for their comments made on first drafts of the MS, and to J. Liotta and his team, who provided material and organized a field trip to the lower Paraná. G. Arratia, S. Schaefer and anonymous reviewer for their comments and suggestions. This research, part of

the PinD Thesis of AEA (Aquino, 1994), has been possible thanks to financial support received from CONICET (Argentina). Adriana Aquino was also supported by a Starr Fellowship and Axelrod Fund of the American Museum of Natural History fellowship and by CONICET while in residence at the American Museum of Natural History. This paper is Contribution No. 692 of the Instituto de Limnología "Dr. Raúl A. Ringuelet" (ILPLA).

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(versus series composed by one plate) (Schaefer, 1996).

Holmberg (1893b) proposed the genus *Aristommata* for his new species *A. inexpectata*, based on a single specimen from the Paraguay river collected in Formosa, Argentina. While the synonymy of *Aristommata* and *Hypoptopoma* was promptly recognized by Berg (1898), the taxonomic status of *H. inexpectata* remained unsettled. Considered a valid species in several checklists and fauna studies, it was suggested by Berg (1898) as a putative junior synonym of both *H. joberti* (Vaillant, 1880), as a junior synonym of *H. guentheri* Boulenger, 1895 and *H. gulare* Cope, 1878, by Fowler (1915) and Gosline (1945), respectively, and proposed as a senior synonym of *H. guentheri* by Berg (1898), Eigenmann (1910), Ringuélet et al. (1967), and Aquino (1997). As further indication of the dubious taxonomic situation of *H. inexpectata*, Regan (1904) did not include the species in the first extensive monograph on loricariids, and Boeseman (1974) included it among the "obscure species" of the loricariid subfamily Hypoptopomatinae. Aquino (1997), in a revision of the hypoptopomine species reported for Argentina, did not provide a phylogenetic-based diagnosis of *H. inexpectata*. On account of this background, herein we provide a diagnosis and redescription of *H. inexpectata* on the basis of availability of additional material and new character evidence that support the taxonomic status of the species.

Morphological variation across populations of widespread Neotropical species is a cause of major concern in cases in which there's no cut demarcation between geographic units (e.g. different species versus different populations of a single species) (e.g. *Pygocentrus nattereri*-Fink, 1993; *Pimelodella chagresi*-Martin & Bermingham, 2000; *Otocinclus vittatus*-Schaefer, 1997). The factors generally precluding a one-way decision are both insufficient sample size and intra-population variation. Since this has been an issue also

in the framework of the revision of the genus *Hypoptopoma* (Aquino & Schaefer, in prep.), the inclusion in the present paper of data on intraspecific variation of *H. inexpectata* will represent a precedent for decision-taking situations involving species demarcation.

The osteology and myology of *Hypoptopoma inexpectata* was studied by Aquino (1994, unpubl.). A summary is presented in Aquino & Miquelarena (1994). The results of that study were basically congruent with descriptions of other species of *Hypoptopoma* as well as with statements made at higher taxonomic levels (Regan, 1904, 1911; Gosline, 1948; Howes, 1983; Schaefer, 1987, 1990, 1991, 1998). Herein, we present an overview of the anatomy of *H. inexpectata*, an account we consider of particular interest as a basis for a comparative analysis within the ongoing revisionary work of the genus (Aquino & Schaefer, in prep.).

On this basis, the purpose of the present study is (1) to diagnose *Hypoptopoma inexpectata* on a phylogenetic basis, (2) to re-describe the species, and (3) to describe anatomical features and cases of intraspecific variation not previously reported for the genus.

## MATERIAL AND METHODS

Counts and measurements were mostly taken following Boeseman (1968). Total lateral plates counted along median series (*sensu* Schaefer, 1997) to posteriormost canal-bearing plate: first two segments of canal at the entrance to bony swimbladder capsule (below pterotic lateral margin) excluded, since they are only plated in adult stages. A Wild M-5 stereomicroscope and a caliper to the nearest 0.1 mm were used.

In the evaluation of the taxonomic validity of *Hypoptopoma inexpectata*, seven other nominal species of the genus are considered - *H. bilobatum* Cope, 1870; *H. guianense* Boeseman, 1974;

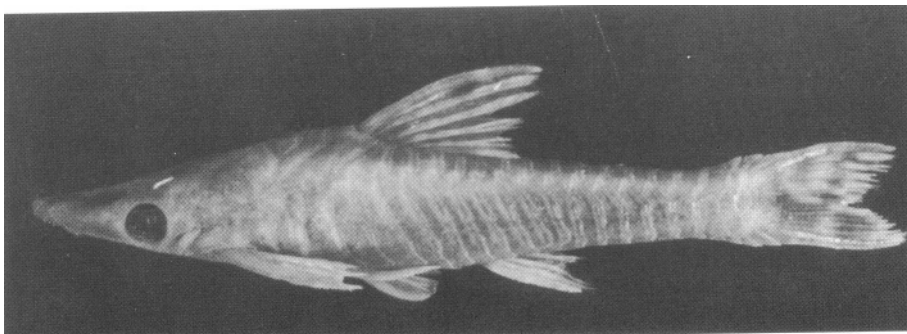


Fig. 1.- *Hypoptopoma inexpectata*. ILPLA 269, female 67.0 mm specimen.

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Recibido: 19-07-99  
 Aceptado: 30-11-00  
 Fecha de distribución: 27-12-01

Versión Electrónica

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