

## The Neotropical catfish genus *Epapterus* Cope (Siluriformes: Auchenipteridae): a reappraisal

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*Abstract.*—The Neotropical auchenipterid catfish genus *Epapterus* Cope is reviewed. *Epapterus* was found to share synapomorphies with *Auchenipterus* Valenciennes and *Pseudepapterus* Steindachner and within that clade it is the sister-group to *Pseudepapterus*. *Epapterus* lacks an adipose dorsal fin, a derived reductive feature unique to the genus within the clade consisting of *Epapterus*, *Auchenipterus*, and *Pseudepapterus* and which is hypothesized to be a synapomorphy for the genus. The extension of the interradial membrane to join the contralateral pelvic fins is identified as an additional possible synapomorphy for *Epapterus*. Contrary to recent practice, *Epapterus* is considered to consist of only two species, *E. dispilurus* Cope (1878) and *E. blohmi* Vari et al. (1984). Examination of *Epapterus* samples from a number of localities in the Rio Amazonas and Río Paraguay basins failed to reveal differences between the populations of the genus in those drainage systems. As a consequence *Epapterus chaquensis* Risso & Risso (1962), described from the Río Paraguay system, is placed as a synonym of *E. dispilurus* originally described from the western portion of the Amazon basin. *Euanemus longipinnis* Steindachner (1881) is retained as a synonym of *Epapterus dispilurus* as proposed by Steindachner (1882) and Eigenmann & Eigenmann (1888). *Epapterus dispilurus* is found to have a broad distribution in the central and western portions of the Rio Amazonas system and the Río Paraguay basin. The distribution of *E. blohmi* is extended from the state of Guarico, Venezuela to include other portions of the Río Orinoco basin and the Río Tuy of the Caribbean coast of Venezuela.

*Resumo.*—O gênero de bagres neotropicais *Epapterus* Cope é revisado. *Epapterus* compartilha várias sinapomorfias com *Auchenipterus* Valenciennes e *Pseudepapterus* Steindachner, e dentro deste grupo é o grupo irmão de *Pseudepapterus*. *Epapterus* não possui nadadeira adiposa, uma característica reductiva derivada única para o gênero dentro do grupo composto por *Epapterus*, *Auchenipterus* e *Pseudepapterus*, e proposta como sinapomórfica para o gênero. A extensão da membrana inter-radial que une as duas nadadeiras pélvicas é uma outra possível sinapomorfia para *Epapterus*. Contrariamente à opinião corrente, *Epapterus* é composto de apenas duas espécies, *E. dispilurus* Cope (1878) e *E. blohmi* Vari et al. (1984). O exame de amostras de *Epapterus* provenientes de várias localidades no rio Amazonas e Río Paraguay não revelou nenhuma diferença entre as populações daquelas duas drenagens. Conseqüentemente, *E. chaquensis* Risso & Risso (1962), descrito da bacia do Río Paraguay, é colocado como sinônimo de *E. dispilurus*, originalmente descrito da porção ocidental da bacia amazônica. *Euanemus longipinnis* Steindachner (1881) é mantido como sinônimo de *E. dispilurus* conforme proposto por Steindachner (1882) e Eigenmann & Eigenmann (1888). *Epapterus dispilurus* possui

ampla distribuição nas porções central e ocidental do sistema do rio Amazonas, assim como na bacia do Río Paraguay. A distribuição geográfica de *E. blohmi* é ampliada do estado de Guarico, Venezuela, para outras porções da bacia do rio Orinoco e ao norte para o Río Tuy na costa caribenha de Venezuela.

In his original description of the auchenipterid catfish genus *Epapterus* from the Peruvian Amazon, Cope (1878:677) distinguished the genus and its single species from the other then-known genera now assigned to the Auchenipteridae by a combination of characters, most notably the lack of the adipose fin, the reduced dorsal fin, and the absence of jaw teeth. Soon thereafter Steindachner (1881) described another auchenipterid, *Euanemus longipinnis*, from specimens collected in the western Amazon along the present Peru-Brazil border. Steindachner (1882:31) noted that the two nominal species were apparently identical and Eigenmann & Eigenmann (1888:152) formally proposed that *Euanemus longipinnis* was a synonym of *Epapterus dispilurus*. Soon thereafter Eigenmann & Eigenmann (1890) redescribed *E. dispilurus* on the basis of specimens that they considered to be syntypes of *Euanemus longipinnis* (see, however, under "Remarks" for *Epapterus dispilurus*). The seven decades following this series of publications saw only one citation of *Epapterus* based on additional material, that of Fowler (1940) of a single specimen of *E. dispilurus* collected in the Río Ucayali in Amazonian Peru. This hiatus ended when Risso & Risso (1962) described *E. chaquensis* from five specimens collected in the Río Paraguay basin of Argentina. Risso & Risso distinguished their nominal species from *E. dispilurus* on the basis of purported differences in the number of pectoral- and anal-fin rays, relative eye size, and details of body and fin pigmentation. In the absence of available samples of *E. dispilurus*, Risso & Risso compared *E. chaquensis* to data in the original description of *E. dispilurus* by Cope (1878) and a relatively simple drawing of the lec-

totype of the latter species published twice by Fowler (1941:468, fig. 26; 1945:66, fig. 26).

Vari et al. (1984) described another species, *E. blohmi*, from samples originating in the central portions of the Río Orinoco system. *Epapterus blohmi* is readily differentiated from nominal congeners by its distinct caudal-fin pigmentation pattern, a difference supplemented by other features. In their discussion of *E. blohmi* Vari et al. (1984) also commented on the pronounced sexual dimorphism in the species of *Epapterus* and noted a series of characters potentially informative as to the phylogenetic position of the genus within the Auchenipteridae. Those authors noted, however, that definitive statements on the questions of the monophyly and relationships of *Epapterus* necessitated an encompassing phylogenetic analysis of the Auchenipteridae, an effort which was beyond the scope of their study. Vari et al. (1984) also briefly reported on new locality records for the two other *Epapterus* species (*E. dispilurus* and *E. chaquensis*) generally recognized as valid at that time, but lacked the population samples necessary to address the utility of the purported distinguishing features of those species.

In the course of our ongoing studies within the Auchenipterinae (Ferraris & Vari 1999) we have been able to examine numerous specimens of *Epapterus* in addition to those available to previous authors. This additional material led to a reappraisal of the distinctiveness of *E. dispilurus* and *E. chaquensis*. We address that problem herein, discuss the phylogenetic information pertinent to the monophyly of *Epapterus*, note broader meristic variation within *E. blohmi* revealed by the examination of ad-

ditional specimens, and report extensions of the known distribution of *E. blohmi*.

### Materials and Methods

Materials are listed alphabetically by country and within country by district, state, or province, and then repository abbreviation. Specimen sizes are reported in standard length (SL). Localities of specimens, other than type-localities, are translated into English when listed originally in another language. Coordinates are either taken from labels associated with specimens, or from publications, information provided by collectors, or from gazetteers when the locality is sufficiently precise.

Institutional abbreviations used are as follows: ANSP, Academy of Natural Sciences of Philadelphia; MCNG, Museu de Ciencias Naturales, Guanare; MCZ, Museum of Comparative Zoology, Cambridge; MHNG, Muséum d'Histoire naturelle, Geneva; MLP, Museo de La Plata; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; MZUSP, Museu de Zoologia, Universidade de São Paulo; NMW, Naturhistorisches Museum Wien, Vienna; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Vertebrae and unpaired fin rays were counted, when possible, from radiographs. Comparative counts made directly from specimens often failed to discern the anterior most anal-fin ray(s) and the posterior most dorsal- and anal-fin rays in small specimens. Vertebral counts were separated into precaudal and caudal elements. The anterior most caudal vertebra is the element possessing an elongate hemal spine that extended just anterior to the first basal radial of the anal fin. Usually, the last precaudal vertebra possesses a markedly shorter hemal spine than does the first caudal vertebra, and is the anterior most vertebra with a closed hemal arch. The ural complex is counted as one element. Precaudal and total vertebral counts assume that the Weberian

complex is composed of four centra. The fifth centrum is suturally united to the complex and lacks articulated ribs. The first rib-bearing centrum is the sixth vertebra.

Fin-ray counts include all elements and treat the two posterior most dorsal- and anal-fin rays that articulate on the last distal radial as separate rays. The last pelvic-fin ray is often branched at its base, which is hidden beneath thick skin. Dissection was sometimes performed to verify the pelvic-fin ray count. Caudal-fin ray counts include only the branched principal rays. Anal-fin ray counts from sexually mature, transformed males assume that the gonopodium consists of one unbranched and one branched ray in the few instances in which separate elements could not be discerned from radiographs. The posterior most anal-fin rays are recorded as branched, although many were too small and/or fine to discern whether they actually branch. Rudimentary anal-fin rays occur irregularly. Rudiments that appear to possess a base that articulates with a basal radial element were included in counts, even if the rays do not extend distally to the fin margin. The first two rays posterior to the gonopodium in males often exhibit this rudimentary development. Rudiments suspended in the fin margin and fully formed rays that do not appear to articulate with a radial element were not counted.

Gill rakers were counted on the first gill bar on the right side of the specimen. Counts included all rakers, including anterior rudiments.

Measurements were made with digital calipers and were point-to-point, as follows: body depth was taken at the anal-fin origin; head length was measured parallel to the body axis, from the posterior tip of the bony operculum to the snout tip; length of anal-fin base was measured from the posterior edge of the anus to the insertion of the last anal-fin ray; orbital width was taken as the horizontal measure across the middle of the eye, bounded by the infraorbital bones; pelvic-fin length represents the distance from

the attachment of the first branched ray to the fin tip; pectoral-fin spine length is from the anterior (or lateral) spine base to the tip of the bony spine not including the fleshy or flexible bony terminal parts; snout length is from the snout tip to the anterior margin of the eye.

Proportional measurements are presented as percentages of standard length (SL) or head length (HL). Values for the lectotype of *Epapterus dispilurus* are indicated in brackets in the description.

Nuptial males are those individuals demonstrating the transitory sexually dimorphic features of the maxillary barbels and dorsal-fin spine.

### *Epapterus* Cope

*Epapterus* Cope, 1878:677 (type species: *Epapterus dispilurus* Cope, 1878, by monotypy).—Eigenmann & Eigenmann, 1888:152 [citation].—Eigenmann & Eigenmann, 1890:292 [citation].—Eigenmann, 1910:396 [citation].—Fowler 1951:465 [citation].—Vari et al., 1984:468 [discussion of relationships and potential synapomorphies].

*Diagnosis.*—*Epapterus* along with *Auchenipterus* Valenciennes, in Cuvier and Valenciennes (1840) and *Pseudepapterus* Steindachner (1915) form a monophyletic assemblage within the Auchenipteridae defined by various synapomorphies (Ferraris 1988, Ferraris & Vari 1999). The combination of the absence of jaw teeth and the possession of a reduced dorsal fin with only two to four short rays and a poorly developed spine (other than in nuptial males) delimits a clade formed by *Epapterus* and *Pseudepapterus* within the Auchenipteridae. The lack of an adipose fin is a synapomorphy for the species of *Epapterus* within that lineage. *Epapterus* species also have the pelvic fins joined to each other across the ventral midline by extensions of the interradiial membrane; an additional potential synapomorphy for the members of the genus (see comments under “Phyloge-

netic relationships and monophyly of *Epapterus*” below).

*Phylogenetic relationships and monophyly of Epapterus.*—In his original description of *Epapterus*, Cope (1878:677) listed a series of “Char. Gen.,” presumably the diagnostic features for the genus. These features largely consisted of what would now be regarded as various plesiomorphic characters, at least at the level of the Auchenipteridae. Nonetheless, three features cited by Cope as distinguishing *Epapterus* from *Euanemus* (= *Auchenipterus*), the lack of an adipose fin, the reduced number of dorsal-fin rays, and the absence of teeth on the jaw and palate, are considered derived within the Auchenipteridae under the context of an encompassing phylogenetic analysis (Ferraris 1988). Steindachner (1915) subsequently described *Pseudepapterus* as a subgenus of *Auchenipterus*. *Pseudepapterus* shares with *Epapterus* a lack of jaw dentition and a reduced dorsal fin but was distinguished from the latter genus on the basis of the possession of an adipose fin. Mees (1974:112) commented briefly on the similarities between *Auchenipterus*, *Epapterus*, and *Pseudepapterus*. Vari et al. (1984:467–468) identified a number of features in *Epapterus* of potential phylogenetic importance. Those authors were unable to make definitive statements on these questions in the absence of comparative specimens of *Pseudepapterus*, and as a consequence of the lack, at that time, of a rigorous hypotheses of higher level groupings within the Auchenipteridae.

*Auchenipterus*, *Epapterus*, and *Pseudepapterus* comprise a monophyletic group within the Auchenipteridae united by various characters summarized by Ferraris (1988) and Ferraris & Vari (1999). The reduced dorsal fin with only two to four short rays and a poorly-developed spine other than in nuptial males, along with the lack of dentition on both the jaws and palate, are derived features within the Auchenipteridae uniting *Pseudepapterus* and *Epapterus* as sister-taxa. *Epapterus* has been traditionally

distinguished by its lack of an adipose dorsal fin. An adipose fin is also absent elsewhere in the Auchenipteridae in *Trachelyopterus Valenciennes*, *Trachelyopterychthys* Bleeker, and *Trachelyichthys* Mees (the reported absence of the fin in *Ceratocheilus* by Miranda-Ribeiro (1918) was in error; see comments in Ferraris & Vari (1999). The lack of an adipose fin is considered synapomorphic for the species of *Epapterus* in the clade consisting of *Auchenipterus*, *Epapterus*, and *Pseudepapterus* under the overall most parsimonious hypothesis of intrafamilial relationships for the Auchenipteridae (Ferraris 1988).

*Epapterus* species also have the pelvic fins joined to each other across the ventral midline by extensions of the interradial membrane. Such continuity of the contralateral pelvic fins is hypothesized as derived within the Auchenipteridae given the absence of a comparable union of the fins in most auchenipterids and in proximate outgroups to the family. A continuity between the contralateral pelvic fins also occurs elsewhere within the clade consisting of *Auchenipterus*, *Epapterus*, and *Pseudepapterus* in *Auchenipterus fordicei* Eigenmann & Eigenmann (Ferraris & Vari 1999). *Auchenipterus fordicei*, a poorly known species, shares with its congeners the presence of grooves on the ventral surface of the head that accommodate adducted mental barbels, a synapomorphy for the species of *Auchenipterus* (Ferraris & Vari 1999). Nuptial males of *A. fordicei* are unknown and it is uncertain whether *A. fordicei* has the second potential synapomorphy for *Auchenipterus*, the presence of papillae on the dorsal and medial surfaces of the ossified maxillary barbel of nuptial males (Ferraris & Vari 1999). *Auchenipterus fordicei*, nonetheless, lacks the derived features considered synapomorphic for *Epapterus* and *Pseudepapterus* and retains a relatively large dorsal fin and an adipose fin, contrary to the derived reduction and absence, respectively, of those structures in *Epapterus*. Thus, the common possession of pelvic fins joined to

each other across the ventral midline by extensions of the interradial membrane in *Auchenipterus fordicei* and *Epapterus* is most parsimoniously considered a result of convergence.

Key to the species of *Epapterus*

- 1. Dorsal lobe of caudal fin with irregularly rounded patch of dark pigmentation in central portion of lobe, pigmentation not forming distinct transverse bar; ventral lobe of caudal fin with distinct patch of dark pigmentation in middle of lobe; pectoral-fin rays 11 to 13, typically 12 or 13 ..... *E. dispilurus*
- Dorsal lobe of caudal fin with a dark transverse bar extending from upper anterodorsal margin to posterior margin of middle rays of dorsal lobe; ventral lobe of caudal fin without a distinct patch of dark pigmentation; pectoral-fin rays 9 to 11 ..... *E. blohmi*

*Epapterus dispilurus* Cope, 1878  
Figs. 1–3, Table 1

*Epapterus dispilurus* Cope, 1878:677 (type locality: Peruvian Amazon).—Steindachner, 1882:31 [*Euanemus longipinnis* Steindachner, 1881:17 equated with *Epapterus dispilurus*].—Eigenmann & Eigenmann, 1888:152 [citation].—Eigenmann & Eigenmann, 1890:292 [redescription based on specimens erroneously thought to be syntypes of *Euanemus longipinnis*].—Eigenmann, 1910:397 [citation].—Fowler, 1915:222 [citation; original Cope specimens cited as cotypes].—Fowler, 1940:231 [Peru, Río Ucayali].—Fowler, 1941:468, fig. 26 [lectotype designation].—Fowler, 1945:66, fig. 26 [reproduction of Fowler, 1941].—Fowler, 1951:465 [citation].—Böhlke, 1984:24 [type holdings at ANSP].—Vari et al., 1984:470, fig. 2 [Brazil, Iha da Marchantaria; Peru, Río Ucayali basin; comparison with *Epapterus blohmi*].—Ortega & Vari, 1986:14 [as component of Peruvian freshwater fish fauna].

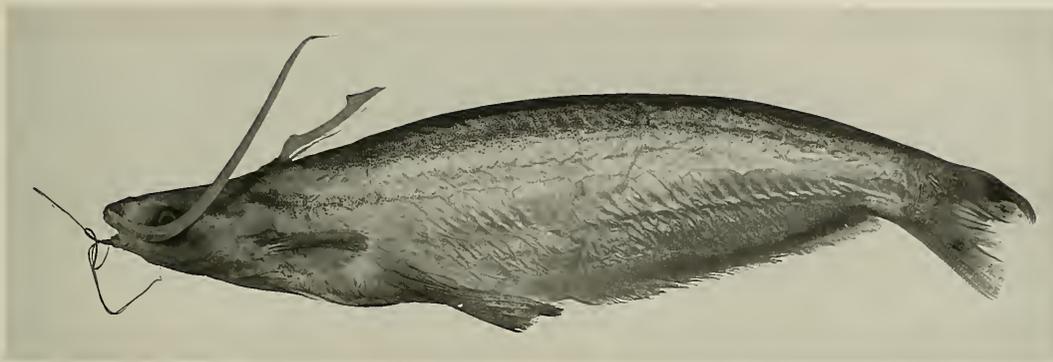


Fig. 1. *Epapterus dispilurus*, nuptial male, USNM 273591, 106 mm SL; showing pronounced development of dorsal-fin spine and maxillary barbel.

*Euanemus longipinnis* Steindachner, 1881: 17 (type locality: Hyavary [=Brazil, Amazonas, Rio Javari]).—Steindachner, 1882:31 [equated with *Epapterus dispilurus*].—Eigenmann & Eigenmann, 1888:152 [citation, as synonym of *Epapterus dispilurus*].—Eigenmann & Eigenmann, 1890:292 [citation, as synonym of *Epapterus dispilurus*].—Eigenmann, 1910:397 [citation, as synonym of *Epapterus dispilurus*].—Fowler, 1951:466 [citation, as synonym of *Epapterus dispilurus*].

*Epapterus chaquensis* Risso & Risso, 1962: 5, figs. 1–3 (type locality: Argentina, Chaco, Resistencia).—Risso & Risso, 1964:5 [citation].—Vari et al., 1984:470, fig. 3 [Paraguay, Río Negro of Río Paraguay].—[not Burgess, 1989, pl. 113, unnumbered figure].

*Auchenipterus nuchalis*, Sands, 1984:24, unnumbered photo.—Burgess, 1989; pl. 13.

*Auchenipterus demerarae*, Sands, 1986:43, unnumbered photos.

**Diagnosis.**—*Epapterus dispilurus* is diagnosed by, and is readily distinguished from its single congener, *E. blohmi*, by having a distinct, irregularly-shaped, patch of dark pigmentation on each caudal-fin lobe which contrasts with the dark transverse bar extending from the upper anterodorsal margin of the dorsal lobe of the caudal fin to the posterior margin of the middle rays of

the dorsal lobe, and by the lack of a distinct patch of dark pigmentation on the ventral lobe of the caudal fin in *E. blohmi*. The two species also differ in the number of pectoral-fin rays (11 to 13, typically 12 or 13, in *E. dispilurus* versus 9 to 11 in *E. blohmi*), and in differences, other than for nuptial males of *E. dispilurus*, in the relative length of the maxillary barbel (166–194% of HL in *E. blohmi* versus 122–163% of HL in *E. dispilurus*). *Epapterus dispilurus* nuptial males also have a highly developed dorsal spine with well developed basal and distal anterior projections, modifications which are unknown in *E. blohmi*.

**Description.**—Body elongate, distinctly compressed, head depressed (Figs. 1, 2). Dorsal profile of head flat or barely convex. Dorsal profile of body from rear of head to end of caudal peduncle slightly to distinctly convex. Ventral profile of head slightly convex. Ventral profile of body gently curved to anal-fin origin. Intromittent organ of males extending along entire anterior margin of third anal-fin ray. Anal-fin base gently convex to caudal peduncle.

Greatest body depth 19.3–25.6 [19.6] of SL; snout tip to dorsal-fin origin 19.3–22.5 [19.7] of SL; snout tip to pelvic-fin origin 33.2–37.1 [34.0] of SL; snout tip to anal-fin origin 39.0–45.6 [39.6] of SL.

Head depressed. Snout viewed from dorsal view somewhat more truncate in mature males than in females in which snout mar-

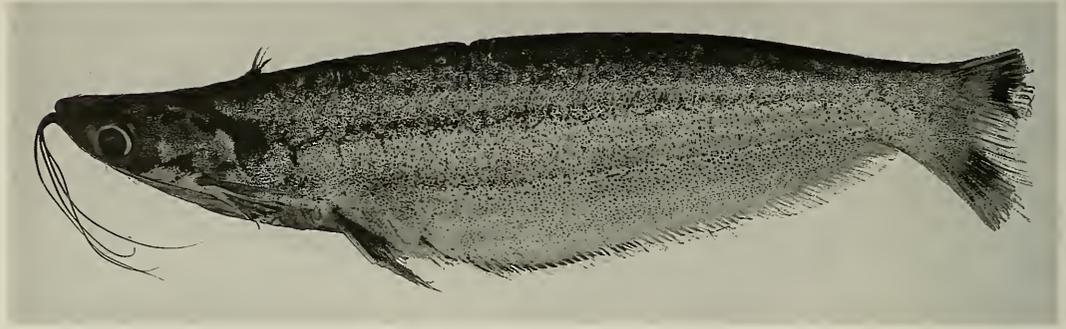


Fig. 2. *Epapterus dispilurus*, female, USNM 305651, 102 mm SL; showing form of dorsal-fin spine and maxillary barbel in females and immature individuals.

gin distinctly rounded from that view. Head length 18.3–21.6 [18.9] of SL. Lower jaw slightly shorter than upper jaw in females and immature specimens, difference in jaw lengths slightly more pronounced in mature males; no teeth present on premaxillae, dentaries, vomer, and palatines. Lower pharyngeal tooth plates large and round with short conical teeth; convex fourth upper pharyngeal tooth plate with short conical teeth. Snout length 36.2–40.9 [40.7] of HL. Orbital margin not free, horizontal width of orbit 26.7–30.2 [29.2] of HL. Length of postorbital portion of head 41.5–46.7 [41.5] of HL. Interorbital region gently convex. Nares of each side of head separated by distance approximately equal to 4.5–5.0 times diameter of posterior nostril; anterior nostril somewhat tubular, located on anterodorsal surface of snout, above lip; posterior nostril larger, oval.

Gill rakers on first arch 33 to 42. Branchiostegal rays 6. Gill membranes broadly attached to isthmus. Maxillary barbels rounded in cross section, elongate, length 122–163% of HL in females, immature specimens, and males without fully developed ossification of barbel; barbel length 191% of HL in single available nuptial male; tip of barbel reaching posteriorly to, nearly or to, end of pectoral fin in females, immature specimens, and males without fully developed ossification of the barbel, extending distinctly beyond tip of pectoral fin in fully nuptial male; degree of ossifi-

cation of barbel highly sexually dimorphic (see “Sexual dimorphism” below). Mental barbels four, transversely rounded, arranged in arc along ventral surface of jaw, barbels reaching posteriorly approximately to line through middle of pectoral fin.

Lateral line complete, dendritic, with short side branches at irregular intervals, divided on caudal fin into 2 or 3 branches that run in some individuals through slightly ossified tubes.

Dorsal fin greatly reduced, with 1 spine and 2 or 3 rays (2 rays present in 1 of 43 specimens examined for this feature). Dorsal-fin spine non-serrate and sexually dimorphic, relatively short and slender, length 2.8–3.6 of SL in females, immatures, and males not in reproductive condition. Dorsal fin proportionally much thicker and distinctly elongate in one available nuptial male, length 16.4 of SL (see “Sexual dimorphism” below for detailed description of spine). First dorsal-fin ray typically slightly longer than dorsal-fin spine in females and immature specimens. Single available nuptial male with first dorsal-fin ray distinctly longer proportional to SL than in females, immature specimens, and males not in reproductive condition, but with lengthened ray extending only about three-quarters of length of greatly enlarged dorsal-fin spine. Adipose dorsal fin absent.

Pectoral fin with 1 spine and 11 to 13, most often 12 [12], rays; pectoral-spine length 12.3–14.0 [13.0] of SL; medial mar-

gin of pectoral spine with series of serrations, serrations absent basally and sometimes along distal one-fifth of spine; rayed portion of fin pointed, longest pectoral-fin rays ranging from approximately same length as, to somewhat longer than, pectoral spine; length of longest pectoral-fin rays 12.3–14.4 of SL; tip of pectoral fin not reaching to pelvic-fin origin.

Pelvic-fin margin pointed, fin with 14 to 16 rays [15], lateral most rays longest, length of longest pelvic-fin rays 16.0–19.3 of SL; pelvic fin with broad, posteroventrally sloping base with interradiation membrane continuing across midline of body to join interradiation membrane of contralateral pelvic fin; insertion of pelvic fin situated distinctly dorsal of ventral margin of body.

Anal-fin margin in females smoothly convex anteriorly, straight for much of its length and convex posteriorly; last unbranched and first branched anal-fin rays in males greatly developed and conjoined for support of intromittent organ (see “Sexual dimorphism” below for details); remainder of anal fin of males as in females; length of anal-fin base 51.4–56.0 [55.5] of SL. Anal-fin rays 54 to 61 [59]. Caudal fin distinctly emarginate.

Precaudal vertebrae 14 to 16, typically 15 [15], caudal vertebrae 33 to 36 [35], total vertebrae 48 to 50 [50].

*Color in life.*—Sands (1986:43, unnumbered photos) published two photographs of what is apparently the same individual of *Epapterus dispilurus* (identified by that author as *Auchenipterus demerarae*). These illustrations were later reproduced by Burgess (1989, pl. 113, unnumbered photographs) who identified the species as *Auchenipterus nuchalis*. Overall dark pigmentation on the head and body in specimen in the photos is as described below for preserved specimens, but with more lightly pigmented portions of body having a silvery sheen which also extends onto the basal portions of the caudal and anal fins. The anterior margin of the pectoral fin white. Barbels with white tips. Neither the

silvery pigmentation nor the white margin to the pectoral fin is apparent in the aquarium specimen of *E. dispilurus* published by Sands (1984:24, photo; identified therein as *Auchenipterus nuchalis*).

*Color in alcohol.*—Overall ground coloration ranging from tan to light purplish brown, overall pigmentation tending to increase with increasing body size, but with population samples of similar size individuals from different sites in the Río Ucayali basin showing notable difference in overall intensity of pigmentation.

Dorsal surface of head in lighter colored specimens with scattered chromatophores more concentrated lateral to, and particularly posterior to, fronto-parietal fontanel. Margin of upper lip in region anterior to orbit with distinct patch of dark pigmentation. With increasing intensity of overall head and body pigmentation, chromatophore field on dorsal surface of head expands laterally and anteriorly to contact orbit laterally and patch of pigmentation on upper lip anteriorly. In very dark individuals entire dorsal portion of head dark, other than for light anterior margin of upper lip. Lateral surface of head with scattered dark chromatophores in light specimens; darker specimens with patches of dark pigmentation anterior and posterior to orbit continuous dorsally with dark pigmentation on dorsal portion of head.

Dorsal portion of body with scattered dark chromatophores in lighter specimens, but with nearly solid purplish pigmentation in darker individuals. Distinct, dark humeral spot present in all individuals; spot slightly horizontally elongate in some smaller, lighter-colored specimens, more rounded in larger specimens, with posterior portion of spot continuous in some individuals with variably developed zigzag pattern of dark chromatophores overlying lateral line. Darker individuals with ventral and sometimes midlateral portions of body with dusky purplish pigmentation.

Caudal fin with irregular patch of dark pigmentation on dorsal lobe; vertical extent

of patch usually greater than its horizontal length. Ventral lobe of caudal fin with irregular patch of dark pigmentation on center of lobe; shape of patch ranging from somewhat rotund to vertically elongate. Caudal pigmentation more intense in specimens with overall darker coloration. Anal fin nearly unpigmented in some specimens, with distal margin darker in most examined specimens. Dark pigmentation on distal portions of fin limited to anterior one-half to two-thirds of fin in some specimens whereas other individuals have field of pigmentation along distal region of fin more elongate, occasionally with fin margin quite dark along its entire length. Basal portions of anal fin purplish in very dark individuals. Extent of dark pelvic fin pigmentation variable among specimens with differences in degree of development correlated with overall intensity of dark pigmentation of specimen. Distal margin of pelvic fin dusky in all specimens, more so in dark individuals. Lateral margin and basal portions of pelvic fin in less intensely pigmented individuals with scattered dark chromatophores. Pelvic fin with dark patch of pigmentation in more intensely pigmented specimens. Pectoral fin with scattered dark chromatophores more concentrated along distal margin; more intensely pigmented individuals with varyingly developed basal patch of dark pigmentation.

*Sexual dimorphism.*—Females attain a greater maximum size than do males. The largest specimen examined by us was a 124 mm female and a number of females exceeded 110 mm. The largest identifiable male was 107 mm and the smallest was 97 mm. The snout in nuptial males is somewhat more truncate when viewed from a dorsal view than that in females in which the snout margin is distinctly rounded. Females have the bony core of the maxillary barbel relatively short with the remainder of the barbel flexible, thin, and extending posteriorly to the middle of, or to the posterior margin of, the pectoral fin. In the single examined nuptial male the barbel is greatly

thickened, distinctly curved (Fig. 1), and somewhat lengthened relative to the condition in females. When adducted the barbel of the nuptial male reaches distinctly beyond the posterior tip of the pectoral fin.

The dorsal-fin spine in the single available nuptial male is distinctly thicker and more notably is distinctly longer than the spines of immature individuals, females, and males not in reproductive condition (compare Figs. 1 and 2). The spine in nuptial males is somewhat sinusoidal in lateral view, with a distinct anterior process toward its base and a well developed anterior process toward its tip which gives the distal portion of the spine a harpoon-like shape in lateral view (Fig. 1). The first dorsal-fin ray is also distinctly longer in the nuptial male than in immature specimens, females, and males not in reproductive condition. The dorsal-fin spine of males can be hyperextended anteriorly to an approximately 75° angle relative to the predorsal profile, instead of the vertical or slightly posterodorsal fully adducted position of the spine in females and juveniles. Mature males have an anal fin with the last unbranched and the first branched anal-fin rays distinctly thickened and more elongate than those in females and conjoined to form the structural support of an intromittent organ. The genital pore of males is at the end of an elongate tube that extends along, and is bound to, the anterior margin of the anal fin. The tube terminates slightly beyond the end of the tip of the conjoined last unbranched and first branched anal-fin rays.

*Distribution.*—Central and western portions of the Amazon basin along and south of the main channel of the Rio Amazonas, and the Río Paraguay system in Paraguay, northern Argentina, and southern Brazil (Fig. 3).

*Remarks.*—*Epaeterus dispilurus* Cope (1878) was described on the basis of two specimens which originated in the upper Amazon basin of Peru. These specimens were cited as "cotypes" by Fowler (1915: 222). Some years later, and without any dis-



Fig. 3. Map of central portions of South America showing known distribution of *Epapterus dispilurus* (type locality of *E. dispilurus* inexact = Peruvian Amazon; 1 = type locality of *Euanemus longipinnis*; 2 = type locality of *Epapterus chaquensis*; some symbols represent more than one locality or lot of specimens).

cussion, that author (Fowler 1941:468, fig. 26 repeated in Fowler 1945:66, fig. 26) provided a cryptic, but valid, lectotype designation by the statement "tipo, largo 125 mm" which accompanied his line drawing of the species. The cited length corresponds with the total length of the larger of the two syntypes of *E. dispilurus* which we consequently consider to be the lectotype (ANSP 21353). This obscure lectotype designation was overlooked in Böhlke (1984).

The name *Euanemus longipinnis* is generally cited as being published in 1882 with the author credited as being Agassiz in a Steindachner paper. Both this date and author are questionable. The name was published as the first article of the Denkschriften der Akademie der Wissenschaften,

Mathematisch-Naturwissenschaftliche Klasse for 1882, but Troschel (1882) listed the paper as having been published in 1881. Barbara Hertzog (NMW, in litt.) indicated that separate copies of the publication were available, and probably distributed, in 1881, which would account for the date cited in Troschel's account. On the basis of this evidence, we use the year 1881 as the date of description of *E. longipinnis*.

Steindachner (1881:17) indicated that the specimens on which he based his description of the species were sent to him by Agassiz with the name "*Euanemus longipinnis* Agass." Agassiz's contribution appears to be limited to the creation of the name and sending the specimens to Steindachner given that the format of the species description

is typical for Steindachner's other publications of the period. As such, we consider Steindachner as the author of the name and only the specimens examined by Steindachner can be considered as constituting the type series. Steindachner (1881:18) noted in the original description of the species that he examined four specimens, a number matching the identified syntypes in the NMW holdings (NMW 46682:1-4). We have examined two of the four syntypes catalogued as NMW 46682:1-4 and select the larger of those specimens (NMW 46682:1, 93 mm SL) as the lectotype of *Euanemus longipinnis*.

Four specimens deposited in MCZ (originally MCZ 9834 (4 specimens), now divided between MCZ 9834 (3 specimens) and MCZ 33450 (1 specimen)) were identified as syntypes of *Euanemus longipinnis* by Eigenmann & Eigenmann (1890:292) in their redescription of *Epapterus dispilurus*. However, given that all specimens cited as syntypes in the original description of *Euanemus longipinnis* are accounted for in the NMW holdings, we do not consider the MCZ material to be part of the type series.

#### Status of *Epapterus chaquensis*

In the abstract of their original description of *Epapterus chaquensis*, Risso & Risso (1962:4) noted that their nominal species differed from *E. dispilurus* in the form of the dark humeral spot and in the presence of dark pigmentation of the ventral (=pelvic) fin. Within the main body of the text Risso & Risso (1962:6) cited, however, a more extensive series of characters discriminating the two species, proposing that *E. chaquensis* differed from *E. dispilurus* "principally in the dark coloration of the anal fin and basal and distal regions of the ventrals [=pelvic fins]. The humeral mark is not rounded but obliquely lengthened. Lesser number of rays in the anal and pectoral. Head and eyes smaller, etc." (our translation).

Risso & Risso gave no indication that

they examined comparative specimens of *E. dispilurus*, rather their literature cited and introductory remarks indicate that their comparisons were based on literature information, in particular the original description of *E. dispilurus* (Cope, 1878:677) and the line drawing of the lectotype of that species included in Fowler's listing of the fishes of Peru (1941, 1945). Cope (1878), in his original description of *E. dispilurus* (1878), commented neither on the form of the humeral spot nor made mention of any pigmentation of the pectoral, pelvic, and anal fins. Fowler's relatively simple line drawing (1941:468, fig. 26; 1945:66, fig. 26) was based on the lectotype of *E. dispilurus*, a specimen which is now in very poor condition and which may not have been in a much better state at the time that Fowler prepared the figure. Specimens of other species cited by Cope (1878) were already in poor condition less than two decades later when reported on in 1906 by Fowler (Vari 1992:117-118). More recently collected specimens of *E. dispilurus* from the Peruvian Amazon, the type region of that species, have a humeral spot which is much more horizontally elongate than that shown in Fowler's figure of the species. The humeral pigmentation pattern in *E. dispilurus* specimens from the Peruvian Amazon is comparable to that in population samples of *Epapterus* from the Río Paraguay, the type-region for *E. chaquensis*. Similarly, Fowler's drawing (1941, 1945) does not include the dark anal-, pelvic-, and pectoral-fin pigmentation which is typical for Amazonian *Epapterus* populations samples and which also occurs in population samples of the genus from the Río Paraguay basin as noted by Risso & Risso. The incomplete representation of the dark body and fin pigmentation in Fowler's figures (1941, 1945) presumably lead Risso & Risso to erroneously propose that the Amazonian and Paraguayan populations differed in details of dark pigmentation. Our comparisons of population samples from the two basins have, in contrast, failed to reveal any consistent dif-

Table 1.—Ranges in population samples of *Epapterus* from the Río Paraguay and Río Amazonas basins for meristic and morphometric features cited by Risso & Risso (1962) as distinguishing *E. dispilurus* (Río Amazonas) from *E. chaquensis* (Río Paraguay).

Feature	Basin	
	Río Amazonas	Río Paraguay
Anal-fin rays	52–62	53–61
Pectoral fin rays	11–13	12–13
Head length in SL	18.3–21.9	18.5–20.9
Eye diameter in HL	25.0–33.1	26.7–29.8

ference in these or any other pigmentation patterns.

Risso & Risso (1962:6) also cited purported differences in the numbers of anal and pectoral-fin rays and relative sizes of the head and eye as distinguishing *Epapterus chaquensis* from *E. dispilurus*. Presumably their comparative data for the latter species was taken from the original description by Cope (1878) which was based on only two specimens. Similarly, Risso & Risso had only five specimens of *E. chaquensis* available for their analysis. A comparison of larger population samples from the Amazon and Paraguay basins (see “Material Examined”) has shown that the degree of variation in the number of anal and pectoral-fin rays and in the range in the relative size of the head and eyes in the population samples from the Amazon and Paraguay basin is significantly greater than indicated by the limited type-series of *E. dispilurus* and *E. chaquensis*. As a consequence there is broad, or complete, overlap between the samples from the two basins in all features proposed by Risso & Risso (1962:6) to distinguish the nominal species (Table 1). We have been unable to identify any meristic, morphometric, or color pattern differences that would justify the continued recognition of *E. chaquensis* and we consequently place that species into the synonymy of *E. dispilurus*.

*Material examined*.—Total specimens: 75. Specimens from which counts and measurements were taken: 50, 59–123 mm SL.

Argentina: Chaco: Resistencia, Laguna along side of the Río Salado (27°27'S, 58°59'W), MLP 8017, 1 (124). Río Negro, Resistencia (27°27'S, 58°59'W), MZUSP 10252–53, 2 (88–93).

Bolivia: El Beni: Canal San Gregório, Trinidad (14°47'S, 64°47'W), MZUSP 27816, 2 (63–72). Trinidad (14°47'S, 64°47'W), USNM 278586, 3 (59–92). Río Itenez, Londra, USNM 278563, 2 (78–100). Río Matos, 48 km E San Borja, below road crossing (14°55'S, 66°17'W), USNM 305651, 2 (79–102).

Brazil: Amazonas: Rio Javari of Rio Solimões (4°21'S, 70°02'W), MCZ 9834, 3 (75–107; erroneously identified as syntypes of *Euanemus longipinnis* by Eigenmann & Eigenmann 1888:292); MCZ 33450, 1 (78; erroneously identified as syntype of *Euanemus longipinnis* by Eigenmann & Eigenmann 1888:292). Humaitá, Igarapé Joari (7°31'S, 63°02'W), MZUSP 27912, 2 (88–95). Rio Aripuaná, Igarapé on Ilha do Castanhal (~5°07'S, 60°24'W), MZUSP 48866, 1 (73). Hyavary [=Rio Javari] (4°21'S, 70°02'W), NMW 46682:1, 1 (93, lectotype of *Euanemus longipinnis*); NMW 46682:2 (79, paralectotype of *Euanemus longipinnis*). Lago Terra Preta, Januari (3°12'S, 60°05'W), USNM 261422, 2 (73–86). Mato Grosso: Lagoa on Fazenda Onça Magra, Município de Cáceres (~16°04'S, 57°41'W), MZUSP 38172, 1 (90). Mato Grosso do Sul: Rio Aquidauana, Baía da Onça or Jatobá, Fazenda Alegrete (~19°44'S, 56°50'W), MZUSP 40084, 4 (98–122).

Paraguay: Cordillera: Río Piribebuy, 5 km N of Emboscada (~25°29'S, 57°03'W), MHNG 2212.27, 1 (123). Presidente Hayes: Río Negro, 6 km S of Chaco-I (~25°15'S, 57°38'W), MHNG 2212.30, 1 (116). Río Paraguay at San Antonio, MHNG 2213.25, 1 (119). Río Aguaray-guazu, at km 117 of Transchaco Road (24°47'S, 57°19'W), MHNG 2213.26, 1 (123). Río Negro at Trans-Chaco Highway crossing (~25°10'S, 58°30'W), USNM 232304, 1 (87).

Peru: Peruvian Amazon, ANSP 21353, 1

(107; lectotype of *Epapterus dispilurus*), ANSP 21354, 1 (96, paralectotype of *Epapterus dispilurus*). Loreto: Río Ucayali basin, Contamana (7°20'S, 75°01'W), ANSP 103412, 1. Reserva Natural Pacaya-Samiria, Caño Ungurahue of Río Pacaya (4°13'S, 74°24'W), MUSM 2524, 1 (66). Ucayali: Río Ucayali, Provincia Coronel Portillo, Bagazan, MZUSP 26183, 4 (96–110). Provincia Coronel Portillo, Pucallpa, Cashibococha (7°33'S, 74°53'W), MZUSP 26318, 6 (100–109). Provincia Coronel Portillo, Pucallpa, Río Ucayali (8°23'S, 74°32'W), MZUSP 26410, 7 (51–63). Provincia Coronel Portillo, Río Aguaytia, Nueva Requena (8°20'S, 74°34'W), USNM 261388, 6 (59–106). Provincia Coronel Portillo, Río Ucayali at Pucallpa (8°23'S, 74°32'W), USNM 263114, 1 (59). Provincia Coronel Portillo, Río Ucayali, Utuquinia (8°15'S, 74°33'W), USNM 263115, 4 (83–89); USNM 273591, 5 (103–115); USNM 273615, 4 (115–128).

*Epapterus blohmi* Vari et al., 1984

*Epapterus blohmi* Vari et al., 1984:463, fig. 1 (type locality: Venezuela, Guarico State, Fundo Pecuario Masagural, Laguna Los Guácimos).—Machado-Allison & Moreno, 1993:87 (Venezuela, Guarico State, Río Orituco).—Machado-Allison et al., 1993:130 (Venezuela, lower Ilanos).—Lasso et al., 1995:4, 7, 8 (Venezuela, flooded Ilanos; ecology).—Taphorn et al., 1997:83 (Venezuela).

Publications dealing with aspects of the distribution and ecology of *Epapterus blohmi* which appeared subsequent to its original description are cited in the synonymy for the species.

*Remarks.*—Vari et al. (1984) provide a detailed description of *Epapterus blohmi* and there is no need to repeat that account in its entirety. Nonetheless, in the course of this study we had the opportunity to examine a greater number of specimens of *E. blohmi* from a wider geographic range (see "Distribution" below) than were available

to Vari et al. (1984). This increased sample, not unexpectedly, revealed that the following meristic values were found to demonstrate a broader range in this study than reported in the original description of *E. blohmi*: dorsal-fin rays 2 or 3; pectoral-fin rays 9 to 11; pelvic-fin rays 13 to 16; anal-fin rays 49 to 61; gill-rakers 29 to 40; precaudal vertebrae 14 or 15; caudal vertebrae 34 to 36; total vertebrae 49 to 51 (note: vertebral counts presented in original account did not include consolidated elements in Weberian apparatus). Vari et al. (1984) reported that teeth were absent on the lower pharyngeal tooth-plate of *E. blohmi*. Examination of additional cleared and stained specimens has revealed that the cited absence was an individual variant in a smaller specimen and that dentition on the lower pharyngeal tooth-plate is typically present in the species.

*Distribution.*—Vari et al. (1984) described *Epapterus blohmi* on the basis of a series of specimens collected from Guarico State, Venezuela, in the central portions of the Río Orinoco basin. Subsequent collecting efforts elsewhere in that river system have shown that the species is widespread in Apure State and occurs in the Portuguesa State, both of which are located to the west of the type-locality. These efforts have also revealed that the range of the species extends east into the Anzoategui State. More unexpected was the discovery of *E. blohmi* in the Río Tuy system, a Caribbean versant basin along the northern coast of Venezuela, a distinct range extension to the north of the type locality of the species and the first reported occurrence of *E. blohmi* outside of the Río Orinoco basin. A single lot of *E. blohmi* examined during this study originated in Quebrada Caraballo within the Río Tuy system, Miranda state.

The fishes of the Río Tuy basin are still poorly known, a problem exacerbated by the large scale pollution of the main channel of the river. Nonetheless, a pattern has become apparent in recently revised groups in which species are found to be common

to the Río Tuy and Río Orinoco basins. In addition to *Epapterus blohmi*, these include the characiform species *Creagrutus melasma* (Vari et al. 1994:95) and *Steindachnerina argentea* (Vari 1991:41). Although the phylogenetic relationships of most species endemic to the Río Tuy basin remain uncertain, there is some indication of sister-group relationships between species in that basin and those of the Río Orinoco system (e.g., *Serrasalmus neveriensis* Machado-Allison et al., 1993:53; Machado-Allison & Fink, 1996:113). The distribution data from *Epapterus blohmi* is congruent with the hypothesis of a once continuous ichthyofauna between the Río Tuy and Río Orinoco basins which was disrupted by the uprise of the Serranía de la Costa as proposed by Machado-Allison et al. (1993:53).

*Material examined* (in addition to that cited in Vari et al. 1984).—Venezuela: Anzoátegui. Río Zuata, near Zuata (8°22'N, 65°22'W), USNM 316822, 4. Apure. Módulo UNELLEZ, near Caño Caicara, MCNG 3599, 8. Módulo UNELLEZ, east dyke, MCNG 2435 1; MCNG 3932, 1. Módulo de Mantecal, MCNG 19593, 1. Hato El Frio (7°49'N, 68°54'W), MCNG 5963, 1; MCNG 9914, 1; MCNG 9668, 10. Laguna El Pozon, MCNG 24075, 1. Miranda. Quebrada Caraballo, along highway between Caracas and Caucagua, parcela Yaguara (Río Tuy basin), MCNG 27358, 7 (of 44). Portuguesa. Caño Maraca (8°47'N, 69°05'W), MCNG 8637, 1. Distrito Turen, Caño Salado ~5 km S of Nueva Florida (latter locality at 8°57'N, 69°01'W), MCNG 12679, 1.

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