



## *Moenkhausia lepidura* (Kner, 1858) (Characiformes, Characidae): osteology and relationships

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**Abstract:** Cladistic analysis of fishes are mostly based on osteological studies. Phylogenetic relationships within the family Characidae are poorly known in part due to the lack of anatomical studies of its members, including osteology. The present contribution aims to offer a detailed description of all bony complexes of *Moenkhausia lepidura*. Two remarkable morphological conditions present in the species are discussed: a bony lamella on the proximal portion of the ribs and a basal expansion of the gill rakers. A morphological survey of several species of Characidae along with available phylogenetic information of the family indicates the putative relationships of *Moenkhausia lepidura* with other small characids presenting bony lamella on ribs and a dark mark on the caudal fin.

**Keywords:** Osteology, *Moenkhausia lepidura*-group, ribs, gill rakers.

## *Moenkhausia lepidura* (Kner, 1858) (Characiformes, Characidae): osteologia e relações de parentesco

**Resumo:** Análises cladísticas morfológicas de peixes são, em grande parte, baseadas em estudos osteológicos. As relações filogenéticas em Characidae são pouco conhecidas, em parte devido à falta de estudos anatômicos de seus representantes, incluindo a osteologia. O presente estudo tem por objetivo oferecer uma descrição detalhada dos complexos ósseos de *Moenkhausia lepidura*. Duas condições morfológicas notáveis presentes na espécie são discutidas: uma lamela óssea na porção proximal das costelas e uma expansão basal dos rastros branquiais. Um estudo morfológico de diversas espécies de Characidae, juntamente com informações filogenéticas disponíveis na família, indica a possível relação de *M. lepidura* com pequenos caracídeos que apresentam lamelas ósseas nas costelas e marcas escuras na nadadeira caudal.

**Palavras-chave:** Osteologia, grupo *Moenkhausia lepidura*, costelas, rastros branquiais.

### Introduction

*Moenkhausia* Eigenmann is one of the species-richest genus in the Characidae, represented by currently 90 valid species (Soares et al. 2017, Eschmeyer, et al. 2018) widespread throughout South American drainages (Lima et al. 2003). Nearly a century ago (Eigenmann, 1917), a combination of morphological characters was proposed and it is still used to diagnose the genus: series of scales on the lateral line completely pored, premaxilla with two tooth rows, the inner row with five teeth and caudal-fin lobe partially covered by small scales. These characters, however, are not unique for *Moenkhausia*, genus that has long been considered polyphyletic (Fink, 1979, Costa, 1994, Weitzman & Palmer, 1997, Lucena & Lucena, 1999, Lima & Toledo-Piza, 2001, Malabarba & Weitzman, 2003, Benine et al. 2004, Bertaco & Lucinda, 2006, Lima & Birindelli, 2006, Lima et al. 2007, Mirande 2009, 2010, Mariguela et al. 2013). In the phylogenetic analysis of Characidae undertaken by Mirande (2010), the included species of *Moenkhausia* were not

recovered as monophyletic. This was confirmed by the molecular study by Mariguela et al. (2013), which obtained the genus distributed into five distinct clades along with species of other genera.

*Moenkhausia lepidura* is one of the oldest name in the genus, originally described in *Tetragonopterus* in 1858. Based on the presence of a black mark on the upper caudal-fin lobe Eigenmann (1908, 1910, 1917) recognized several subspecies of *M. lepidura* that were later raised to the species level and grouped by Géry (1977, 1992) into the “*Moenkhausia lepidura* group”. Marinho & Langeani (2016) considered *Gymnotichthys hildae* Fernández-Yépez, 1950 synonymous with *M. lepidura*. The osteology of the species of *Moenkhausia*, and in fact most characids, is poorly known given the morphological and taxonomic diversity of the group. The only osteological study within the genus is that of Walter (2013), in which the author performed a developmental study of the neurocranium of *Moenkhausia sanctafilomenae* Steindachner, 1907. However, no complete description of all bony complexes is available.

Given these scarce osteological information, the availability of a generic name associated with *M. lepidura*, the polyphyletic nature of *Moenkhausia* and the fact that *M. lepidura* bears a group name of probable related species, the osteological study and comments about its relationships are welcome. In this paper, the description of the skeleton of *Moenkhausia lepidura* is presented, and the relationships of the species are discussed.

## Material and Methods

The specimens were cleared and stained (c&s) following the method proposed by Taylor & Van Dyke (1985) and photographed with a ZEISS Discovery V20 stereomicroscope with ZEISS Axiocam ERc 5s digital camera attached. Standard length (SL) is given in millimeters. Dissection follows Weitzman (1974) and the models from figures of Weitzman (1962) with some adaptations: the infraorbital series, mandibular, hyoid, hyopalatine and branchial were removed from the skull; neurocranium was kept linked with vertebral column; pectoral and pelvic girdles were dissected from the body. Additionally, the third ribs from *Hemigrammus ulreyi*, *Moenkhausia lepidura*, *Moenkhausia pirauba*, and *Parecbasis cyclolepis* (see Material examined) were removed from body to photograph. Vertebrae of the Weberian ossicles were counted as four elements and the vertebrae of the compound caudal centra (PU1+U1) as a single element. Precaudal vertebrae include the Weberian ossicles and the vertebrae associated with ribs or haemal arches without haemal spine. The last two branched anal-fin rays fused on the base and supported by the last pterygiophore were counted as one single ray. The sclerotic bones, pelvic-fin radials and ear otoliths were not included in the description.

Osteological observations of *Moenkhausia lepidura* were taken from seven cleared and stained specimens from several river basins in Brazil (see Material examined). In the description, bony counts are followed by the number of specimens observed in parenthesis. Osteological terminology follows Weitzman (1962) with the following modifications suggested by subsequent authors (e.g., Vari 1979, 1995, Fink & Fink, 1981, 1996, Zanata & Vari, 2005, Carvalho et al., 2013): mesethmoid instead of ethmoid, vomer instead prevomer, epioccipital instead of

epiotic, endopterygoid instead mesopterygoid, anterior ceratohyal instead of ceratohyal, posterior ceratohyal instead epihyal, retroarticular instead articular, anguloarticular instead angular, accessory element of ceratobranchial four instead of epibranchial five. We use inner arm of the *os suspensorium* instead of *os suspensorium*, and outer arm of the *os suspensorium* instead of rib of fourth vertebra, following Conway & Britz (2007). Terminology of cartilaginous elements of caudal fin follows Fujita (1989) and terminology of the canals of cephalic lateral line system follow the unpublished master thesis of Pastana (2014). We used the classification of Characidae from the phylogenetic analysis of Mirande (2010) and Mariguela et al. (2013).

A total of 63 characids were analyzed herein. This number includes 36 species further analyzed by Benine (2004) and Mirande (2010) plus 27 species exclusively analyzed herein. Specimens examined for this study are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP).

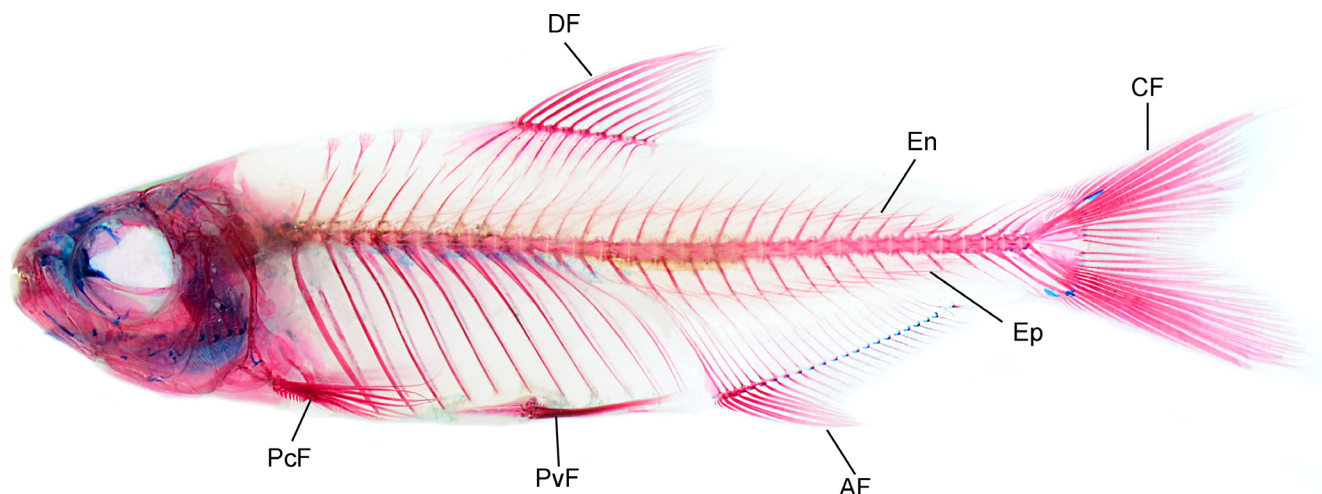
## Results

Overview of the entire body and fin positions in *Moenkhausia lepidura* (Figure 1).

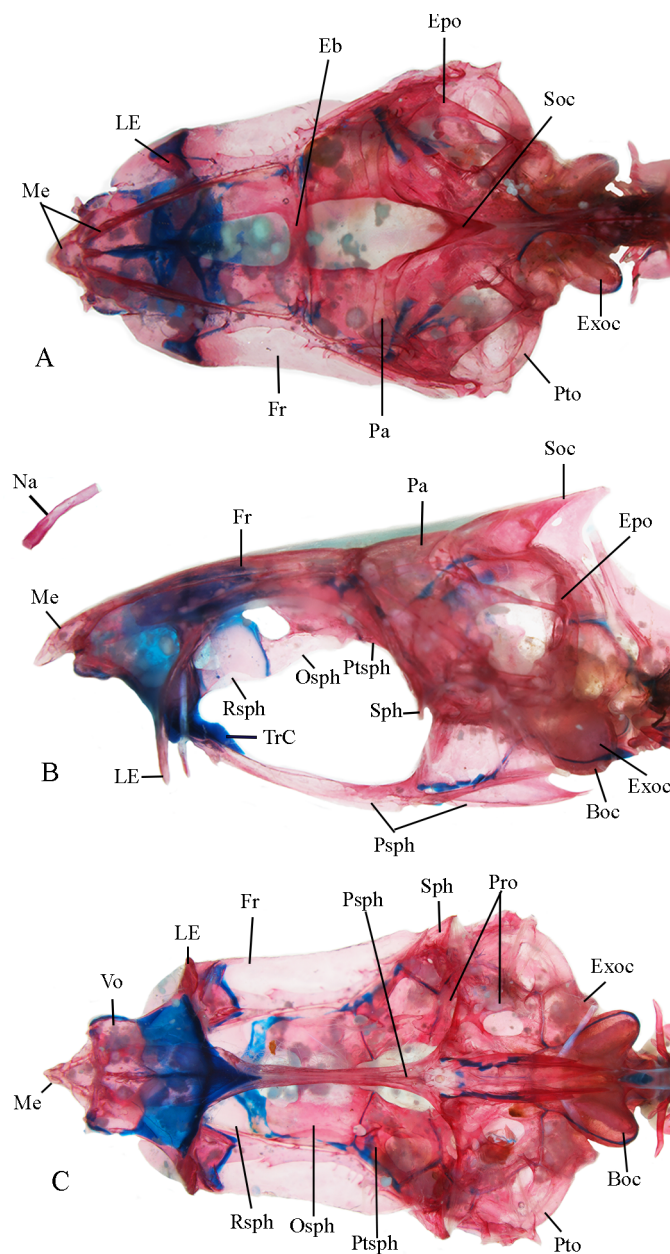
### 1. Neurocranium

1.1. **Olfactory region** (Figure 2): Anterior tip of mesethmoid triangular shaped, slightly sloped anteroventrally, in between bases of ascending processes of the premaxillae. Lateral wing of mesethmoid pointed distally and directed straight laterally. Vomer T-shaped, pointed posteriorly, limited anterolaterally by the mesethmoid and posteriorly by the anteriormost portion of the parasphenoid. Lateral ethmoid well developed, its anterior process slender, leaving a broad space between this portion and the lateral margin of posterior portion of the vomer. Nasal in form of an elongate bony tube and containing the anteriormost portion of the supraorbital canal lacking bony lamellae (Fig. 2B).

1.2. **Orbital region** (Figure 2): Frontal large and relatively long, bordering the upper portion of orbit, with the supraorbital lateral-line canal starting at the nasal and running along the lateral margin of frontal. Frontals connected by the epiphyseal bar, limiting the frontal and parietal fontanels. Frontal fontanel two-thirds length of parietal fontanel.



**Figure 1.** *Moenkhausia lepidura*, lateral view of entire skeleton, MZUSP 8181, 64.1 mm SL. AF, Anal fin, CF, caudal fin, DF, dorsal fin, En, epineural, Ep, epipleural, PcF, pectoral fin, PvF, pelvic fin.



**Figure 2.** *Moenkhausia lepidura*, neurocranium, MZUSP 37458, 66 mm SL, **A:** dorsal view. **B:** lateral view. **C:** ventral view. **Boc**, basioccipital, **Eb**, epiphyseal bar, **Epo**, epioccipital, **Exoc**, exoccipital, **Fr**, frontal, **LE**, lateral ethmoid, **Me**, mesethmoid, **Na**, nasal, **Osph**, orbitosphenoid, **Pa**, parietal, **Pro**, prootic, **Pto**, pterotic, **Pspsh**, parasphenoid, **Ptsph**, pterosphenoid, **Rspsh**, rhinosphenoid, **Soc**, supraoccipital, **Sph**, sphenotic, **TrC**, trabecula communis, **Vo**, vomer. Scale bar: 2 mm.

Orbitosphenoid in contact with frontal dorsally and pterosphenoid posteriorly, with median, slender horizontal process projecting anteriorly toward rhinosphenoid. Rhinosphenoid expanded posterodorsally, limited dorsally by posteroventral portion of mesethmoid cartilage anteriorly by trabecula communis cartilage and posteriorly by the orbitosphenoid. Pterosphenoid flat, anterior margin contacting the posterior margin of orbitosphenoid synchondrally, leaving a small foramen for the passage of trochlear nerve. Parasphenoid long, and narrow, wider on posterior

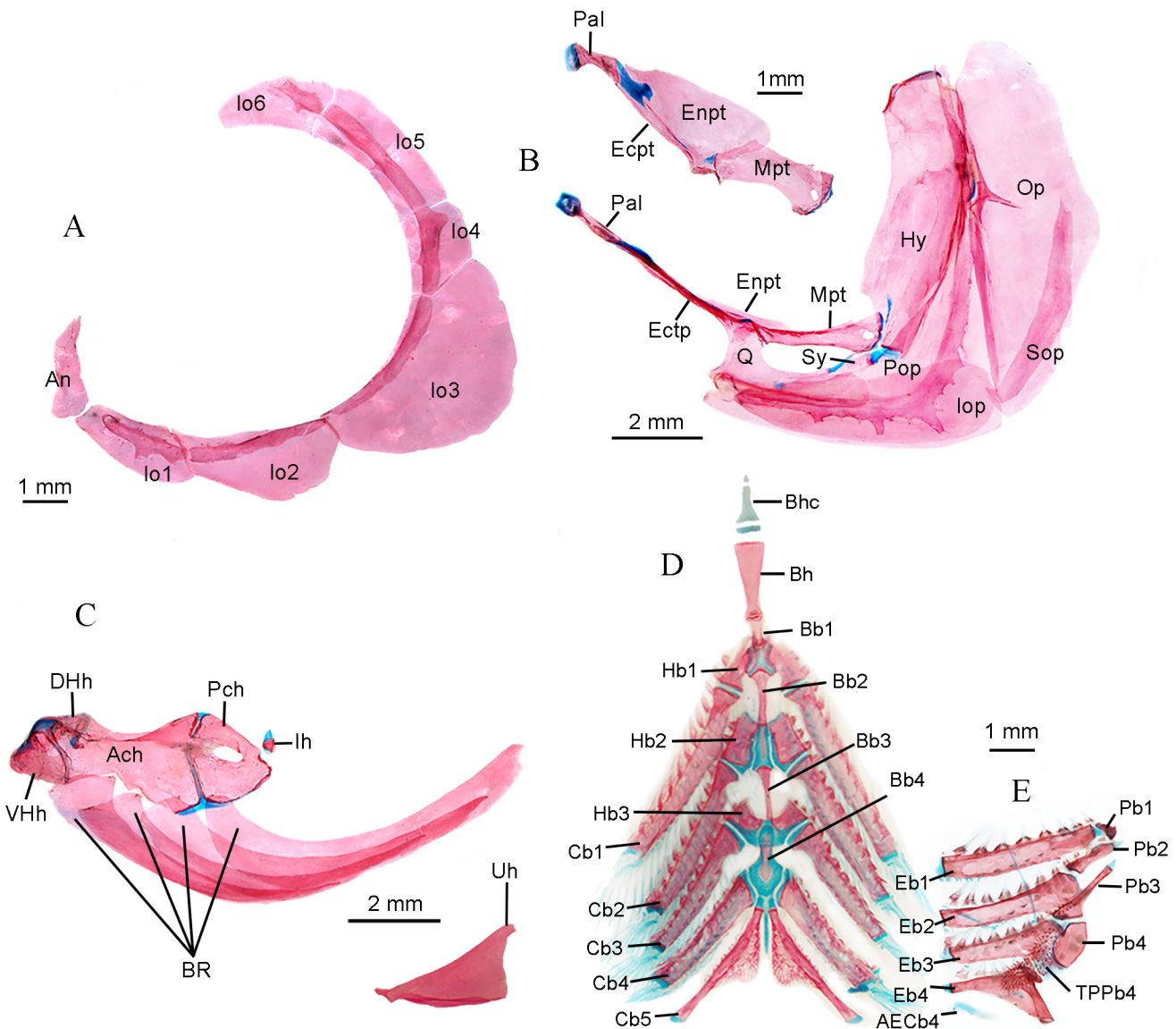
portion, with a pair of ascending processes extending to approximately the vertical through the midlength of basioccipital.

**1.3. Otic region** (Figure 2): Prootic with two foramina, facial foramen and trigemino-facial foramen, displaced anteriorly to the large auditory foramen covering more than one-half of its posterior surface. Prootic in contact with pterosphenoid and sphenotic anteriorly and with pterotic, exoccipital and basioccipital posteriorly. Supraoccipital limiting the posterior margin of posterior cranial fontanel. Parietal branch of supraorbital canal over the posterior portion of frontal and spread along the anteroposterior extension of the parietal bone. Supratemporal canal bordering the posterior portion of parietal. Sphenotic small, with a conspicuous lateral sphenotic spine. Pterotic limited anteriorly by sphenotic, ventrally by prootic and posteriorly by exoccipital, articulating to the hyomandibula ventrally. Posterior spiniform projection present. The otic and postotic canals are associated to the pterotic anterior and posteriorly, respectively.

**1.4. Occipital region** (Figure 2): Main portion of epioccipital roughly rectangular, contacting supraoccipital dorsally and exoccipital ventrally. Epioccipital bridge cylindrical, located over the posttemporal fossa, expanded anteriorly and contacting parietal. Anterior margin of supraoccipital slightly concave forming the posterior margin of cranial fontanel. Supraoccipital spine short, extending posteriorly approximately one half extent of neural complex. Exoccipital large, its ventral region forming the dorsal surface of the lagenar capsule. Basioccipital large, forming the ventral surface of the lagenar capsule. Intercalar absent.

**2. Infraorbital series** (Figure 3A): Antorbital roughly rectangular, pointed dorsoposteriorly, with expanded base. No laterosensory canal ossifications on antorbital. Six infraorbital bones, all bearing ossifications of the laterosensory canals. Infraorbitals one to five with laterosensory canal located near to inner margin of the infraorbital bones. Posterior portion of canal of infraorbital two and middle-anterior portion of canal of infraorbital three contacting the inner margin its respective bones. Infraorbital six with laterosensory canal located on its posterior margin, in contact with frontal dorsally. Ventral portion of infraorbital one overlapping the posterodorsal portion of maxilla. Infraorbital two elongated, with developed posteroventral margin. Infraorbital three largest, with posteroventral margin bordering dorsally the angle of preopercle. Infraorbital four approximately square and bordered dorsally by infraorbital five. Infraorbital five rectangular. Infraorbital six with the anterodorsal portion slightly pointed. Supraorbital absent.

**3. Jaws:** Premaxillary teeth in two rows, both aligned in a straight line. Outer row with four tricuspid teeth (seven), inner row with five teeth (seven), in which the symphyseal and the posteriormost teeth are tetracuspid, remaining teeth pentacuspid. Maxilla elongated, with one (four) or two (three) conical or tricuspid teeth. Ascending portion of maxilla slender, with pointed tip, reaching the posterodorsal portion of premaxilla. Posterior portion of maxilla expanded, its tip almost reaching the vertical through the middle of infraorbital two. Posterior tip of maxilla reaching posterior end of Meckelian cartilage. Dentary slightly elongate, with four large pentacuspid teeth (seven) followed by a small tricuspid tooth and by a row of six or eight small conical teeth. Mandibular canal long, starting slightly below the base of first large pentacuspid teeth extending horizontally along the entire dentary and anguloarticular, ventral to Meckel's cartilage. Anterior portion



**Figure 3.** *Moenkhausia lepidura*, infraorbital and opercular series, branchial, hyopalatine and hyoid arches. **A:** infraorbital series, lateral view, left side, MZUSP 8181, 62.7 mm SL. **B:** hyopalatine arch and opercular series, lateral view, left side **C:** lateral view of hyoid arch, left side, MZUSP 6247, 61 mm SL. **D:** upper portion of branchial arch, right side, ventral view, MZUSP 109841, 60.2 mm SL. **E:** lower portion of branchial arch, dorsal view, MZUSP 6247, 61 mm SL. **ACh**, anterior ceratohyal, **AECb4**, accessory element of ceratobranchial 4, **An**, antorbital, **Bb1-4**, basibranchial 1-4, **Bh**, basihyal, **Bhc**, basihyal cartilage, **BR**, branchiostegal rays, **Cb1-5**, ceratobranchial 1-5, **DHh**, dorsal hypohyal, **Eb1-4**, epibranchial 1-4, **Ecpt**, ectopterygoid, **Enpt**, endopterygoid, **Hb1-3**, hypobranchial 1-3, **Hy**, hyomandibular, **Ih**, interhyal, **Io1-6**, infraorbital 1-6, **Iop**, interopercle, **Mpt**, metapterygoid, **Op**, opercle, **Pal**, palatine, **Pb1-4**, pharyngobranchial, **PCh**, posterior ceratohyal, **Pop**, preopercle, **Q**, quadrate, **Sop**, subopercle, **Sy**, symplectic, **TPPb4**, tooth plate of pharyngobranchial 4, **Uh**, urohyal, **VHh**, ventral hypohyal.

of dentary aligned vertically with the anterior portion of premaxilla. Posterior tip of dentary at vertical through the middle of infraorbital two. Bony interdigitations between dentaries, disposed horizontally and parallel to each other. Anguloarticular with vertical arm extending laterally on the posterodorsal portion of dentary and with horizontal arm extending on its medial surface. Meckelian cartilage along the medial portion of dentary, contacting the anguloarticular posteriorly in medial view. Coronomeckelian bone ovate, situated mainly lateral to the Meckelian cartilage. Retroarticular small and roughly triangular (see Marinho & Langeani, 2016: Figure 4).

**4. Hyopalatine arch** (Figure 3B): Hyomandibular large, elongate, with wide thin bony lamellae developed anteriorly. Hyomandibular

fossa bordered by sphenotic and prootic anteriorly and pterotic dorsally. Hyomandibular with a condylar articulation posteriorly with opercle. Symplectic thin and elongated. Metapterygoid horizontally elongate, approximately rectangular. Posterior portion larger than anterior, slightly overlapping laterally a small portion of hyomandibular lamellae, with the foramen for afferent pseudobranchial artery completely encircled by metapterygoid. Quadrate contacting the anterior and posterior portions of metapterygoid by a cartilage. Anterodorsal portion of quadrate synchondrally articulated with metapterygoid. Posterior tip of quadrate reaching approximately the vertical through middle of symplectic, its tip separated from posteroventral portion of metapterygoid by remnants of palatoquadrate cartilage. Metapterygoid-quadrate fenestra

large and horizontally ovate. Endopterygoid lamellar, wide, tapering anteriorly. Posterior portion of endopterygoid slightly overlapping the anterodorsal margin of metapterygoid and quadrate, with a pointed lateroventral projection, directed to quadrate. Ectopterygoid elongate, narrow posteriorly, bordered laterally by the endopterygoid. Anterior portion of ectopterygoid wider, articulating synchondrally with palatine. Posterior portion of ectopterygoid in contact with the anterodorsal region of quadrate. Palatine roughly rectangular in dorsal view, shorter than a half-length of ectopterygoid. Palatine located lateroventrally to vomer.

**5. Opercular series** (Figure 3B): Opercle laminar, large, slightly concave posterodorsally, extending beyond the vertical through dorsal margin of hyomandibular dorsally, and reaching the horizontal through the ventral margin of quadrate ventrally. Preopercle large, inverted L-shaped, round on its anterior corner, bordering posteriorly and ventrally the hyomandibular arch. Well-developed preopercular laterosensory canal running along the central portion of preopercle. Dorsal portion of preopercle represented solely by the ossified preopercular canal tube, lacking bony lamellae, reaching the horizontal through the dorsal margin of hyomandibula. Interopercle elongated anteroposteriorly. Anterior portion narrow, extending slightly beyond the anterior end of preopercle. Subopercle elongated and slightly arched.

**6. Hyoid arch** (Figure 3C): Anterior ceratohyal slightly narrow at its medial portion, connected anteriorly with the hypohyals and posteriorly with the posterior ceratohyal. Ventral margin of anterior ceratohyal with two or three notches, for articulation of the anteriormost branchiostegal rays. A large canal containing the hyoid artery is present on the dorsal portion of the anterior and posterior ceratohyal. The hyoid canal opens on anterior portion of the anterior ceratohyal, continuing as a canal on posterior ceratohyal. Posterior ceratohyal triangular, with a central foramen through which the hyoid artery enters. Interhyal short, its tips cartilaginous connecting to the posterior margin of posterior ceratohyal to the suspensorium at the cartilaginous connection between hyomandibula and symplectic. Dorsal hypohyal with two arms, connecting with anterodorsal portion of anterior ceratohyal, forming a foramen dorsally. Ventral hypohyal triangular shaped, separated from dorsal hypohyal by a cartilage. Basihyal elongated (Figure 3D) with anterior portion wider. Urohyal triangular shaped, with small lateral bony lamellae on ventral portion (Figure 3E). Anterodorsal projection of urohyal short at insertion of ligaments connecting to ventral hypohyal. Four branchiostegal rays, anteriormost three articulated with anterior ceratohyal and posteriormost ray articulating laterally on ventral portion of posterior ceratohyal.

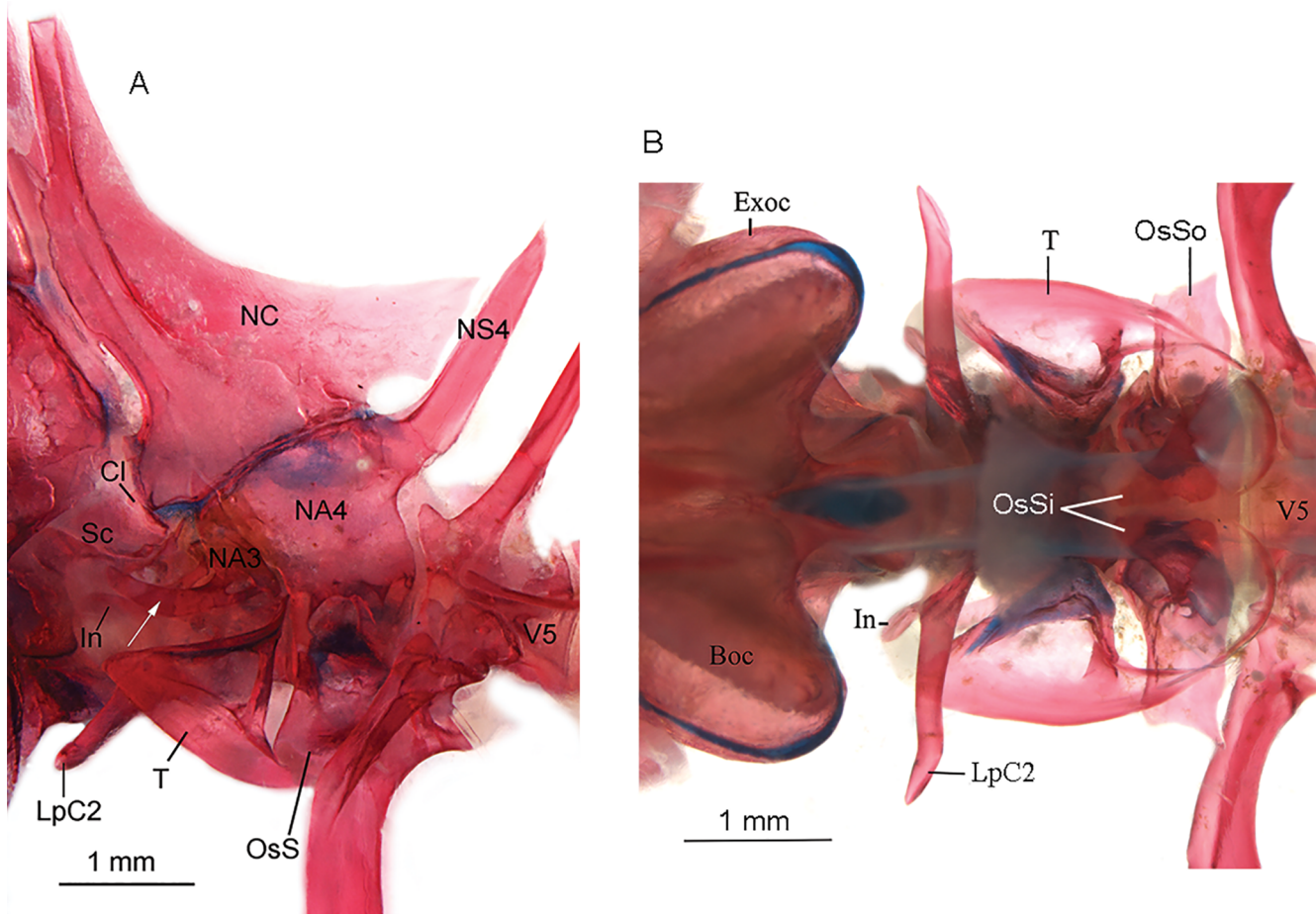
**7. Branchial arches** (Figure 3D–E): Three (four) or four (three) ossified basibranchials, separated by cartilages, each situated medial to hypobranchials. Anterior portion of basihyal with three blocks of cartilage. Anterior margin of first basibranchial articulating with the posterior margin of basihyal. Three hypobranchials with cartilaginous margins. Each hypobranchial bearing one to three gill rakers, basally expanded, completely covered with small denticles. Five well-developed ceratobranchials, decreasing in length from first to last ceratobranchial, all covered with gill rakers. Ceratobranchial one with nine or 10 elongated gill rakers in one series, situated anteriorly, with few small spines scattered on its surface. Ceratobranchial two to five with shorter gill rakers, each with a basal extension forming a lateral plate full of small denticles. Ceratobranchial two with nine gill rakers in one series

located on its anterior margin. Ceratobranchial three and four with gill rakers in two distinct series. Anterior series with seven, eight or nine and posterior with six, seven or eight gill rakers. Ceratobranchial four with eight gill rakers on anterior series and six or nine gill rakers on posterior series. Accessory element of ceratobranchial four cartilaginous, small and slightly elongate. Four small pharyngobranchials with cartilaginous edges. Ceratobranchial five with seven gill rakers in a single anterior series, posterior margin of ceratobranchial five with a triangular tooth plate. Five epibranchials, first four ossified and the last one cartilaginous. Epibranchial one to three with two series of gill rakers and epibranchial four with only one series of gill rakers. Epibranchial one to four with small triangular gill rakers. Their basal and lateral expansions covered with small spines. Epibranchial one with eight gill rakers on anterior series and seven or eight gill rakers on posterior ones. Epibranchial two with six, eight or nine gill rakers on anterior series and seven on posterior ones. Epibranchial three forked dorsally, with seven gill rakers on anterior series and six on posterior ones. Epibranchial four wider and triangular shaped with five gill rakers on the anterior series. Pharyngobranchial one slightly round. Pharyngobranchial two elongate, some specimens with denticles on its base. Pharyngobranchial three mostly slender, wider on its base, bearing small denticles. Pharyngobranchial four cartilaginous (six) or ossified (one) (see Figure 3 E), with a tooth plate well developed connected with the tip of fourth epibranchial.

**8. Weberian ossicles** (Figure 4): Vertebral centrum one shorter than the remaining ones. Centrum two presenting well-developed lateral process, extending beyond the ventral anterior portion of tripus. Claustrum small, situated dorsally to scaphium. Scaphium rectangular shaped, located dorsally to vertebral centrum one. Intercalarium elongate. Tripus well developed, triangular shaped, displaced lateroventrally to neural arch three, with posterior pointed projection reaching the *os suspensorium* inner arm. Neural arch pedicle of centrum three elongate, well developed. *Os suspensorium* outer arm arched ventrally, robust and flattened, and inner arm projecting ventrally, with expanded anterior tip almost meeting its counterpart in ventral midline. Neural complex well developed, roughly triangular and concave on its dorsal surface. Neural spine of fourth vertebrae well developed, reaching approximately one half-length of neural spine of centrum five.

**9. Post-Weberian axial skeleton** (Figure 1): Total of 31(1), 32(3) or 33(3) vertebrae consisting of 16(7) precaudal vertebrae and 15(1), 16(3) or 17(3) caudal vertebrae. Vertebral centra slightly longer than deep. Neural pre and postzygapophyses present in all vertebrae except the posteriormost three caudal vertebrae. Haemal pre and postzygapophyses present in all caudal vertebrae. Four (seven) supraneurals with expanded dorsal portion. Usually, the first supraneural displaced between neural spines of fourth and fifth vertebrae (Figure 5A). Parapophysis well developed on ventral portions of five–10 precaudal vertebrae. Ribs associated with fifth to 14<sup>th</sup> (three), 15<sup>th</sup> (three) or 16<sup>th</sup> (one) precaudal vertebrae. All ribs similar in size. Posterior ribs thinner. Second to eighth (one) or ninth (six) ribs with a dorsal triangular shaped lamellae expansion (Figure 1 and 8 C, see details in Discussion). Neural arch and spines present in all vertebrae posterior to the Weberian apparatus.

**9.1 Intermuscular bones** (Figure 1): 26(one), 27(four) or 28(two) epineurals and 16(one) or 17(six) epipleurals along body. Epineurals and epipleurals forked proximally from the first to eighth caudal vertebrae.



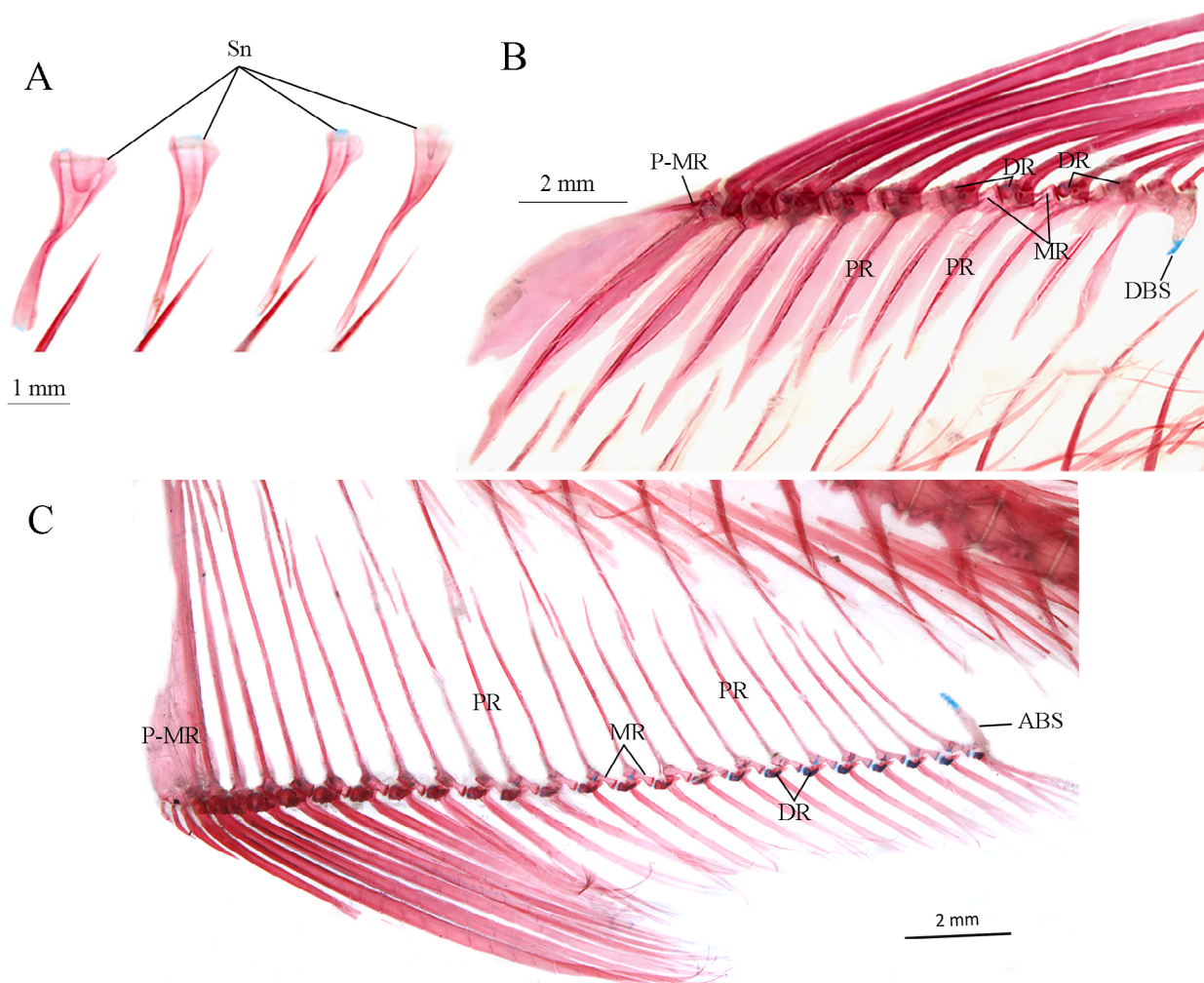
**Figure 4.** *Moenkhausia lepidura*, Weberian ossicles. **A:** Left lateral view, MZUSP 37458, 40 mm SL. White arrow indicates the transverse process of neural arch pedicle of third vertebra. **B:** Ventral view, MZUSP 37458, 66 mm SL; **Boc**, basioccipital, **Cl**, claustrum, **Exoc**, exoccipital, **In**, intercalarium, **LpC2**, lateral process of centrum 2, **NA3-4**, neural arch 3-4, **NC**, neural complex, **NS4**, neural spine 4, **OsSo**, *os suspensorium* outer arm, **OsSi**, *os suspensorium* inner arm, **Sc**, scaphium, **T**, tripus, **V5**, vertebrae 5.

10. **Dorsalfin** (Figure 5B): Ten pterygiophores supporting the dorsal-fin rays (seven). Anteriormost five proximal and middle radials are fused into one single structure and the remaining with proximal and middle radials separated by cartilage. First proximal-middle radial the longest, its tip extending frontward between the neural spine of ninth and 10<sup>th</sup> vertebrae (seven), with well-developed lateral flanges, supporting two unbranched dorsal-fin rays in supernumerary association (seven). All analyzed specimens with a small bony spine under skin anterior to first dorsal-fin ray, associated with the first proximal-middle radial. Laterally flattened bony lamellae associated to the anterior and posterior surface of all proximal radials, decreasing in size posteriorly. Last two(one), three(one) or four(one) dorsal-fin proximal radial presenting a small foramen distally. Bony stay L-shaped, vertically aligned with 17<sup>th</sup> neural spine (seven). Ventral tip of bony stay cartilaginous. Anteriormost unbranched dorsal-fin ray approximately half-length of second unbranched ray, which is the longest, followed by nine (seven) branched rays decreasing in length.

11. **Anal fin** (Figure 5C): Anal-fin rays supported by 22(two), 23(two), 24(two) or 25(one) pterygiophores. First to fifth pterygiophores with proximal and middle radials fused into a single bone (proximal-middle radials). Remaining pterygiophores with proximal and middle radials separated by cartilage. Distal radial present as separate bone

in all pterygiophores. Pterygiophores decreasing in size posteriorly. Anteriormost proximal-middle radial larger at base, longer, reaching the haemal spine of first caudal vertebrae, and supporting three(one) or four(six) supernumerary unbranched rays. Anteriormost supernumerary unbranched ray shortest. Anal fin falcate. Last unbranched anal-fin ray the longest. Rays decreasing in size posteriorly from sixth branched ray. Remaining rays smaller, and similar in size. Bony stay variable in shape: vertically elongate, its dorsal tip cartilaginous, reaching approximately half-length of posteriormost proximal-radial (five) or short and wide, its dorsal tip reaching approximately one-fourth length of posteriormost proximal-radial (two).

12. **Pectoral girdle** (Figure 6A-B): Extrascapular well developed and square shaped. Sensory canal contained in the extrascapula connecting to supratemporal canal dorsally, and to postotic canal anteriorly and posteroventrally. Posttemporal pointed dorsally, enlarged and rounded ventrally, with medial well-developed pointed projection. Sensory canal on its anteroventral portion. Supracleithrum elongate, aligned with posttemporal, thinner ventrally, overlapping the dorsal tip of cleithrum and dorsal portion of postcleithrum one. Postotic canal bypass the supracleithrum from its lateral to medial face and follows to the first pored lateral line. Cleithrum tapered dorsally, enlarged posteroventrally. Cleithrum contacting the coracoid anteriorly by

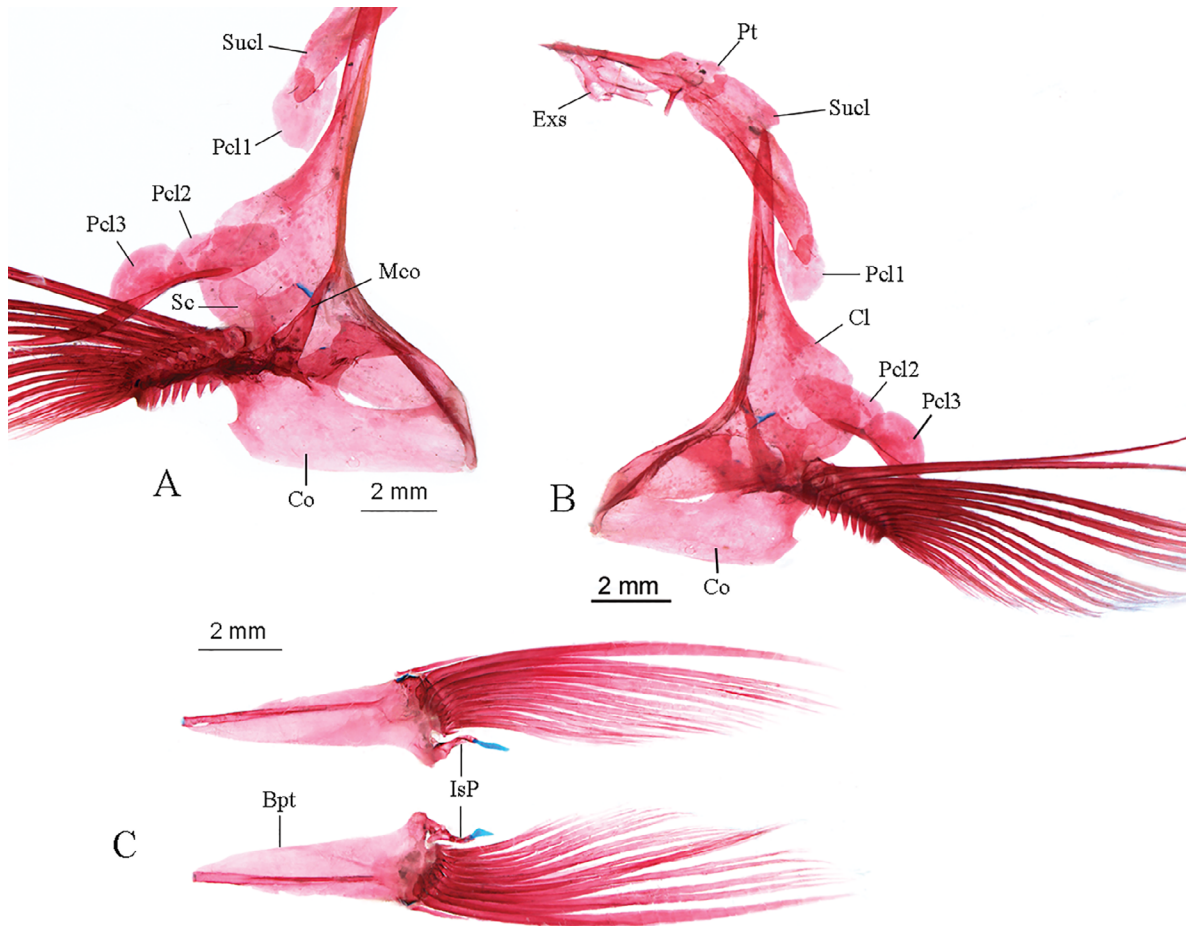


**Figure 5.** *Moenkhausia lepidura*, supraneurals, dorsal and anal fins. **A:** supraneurals, MZUSP 37458, 66 mm SL. **B:** dorsal fin and **C:** anal fin, MZUSP 8181, 62.7 mm SL. **ABS**, anal-fin bony stay, **DR**, distal radial of pterygiophore, **DBS**, dorsal-fin bony stay, **MR**, middle radial, **P-MR**, proximal middle radial, **PR**, proximal radial, **Sn**, supraneural.

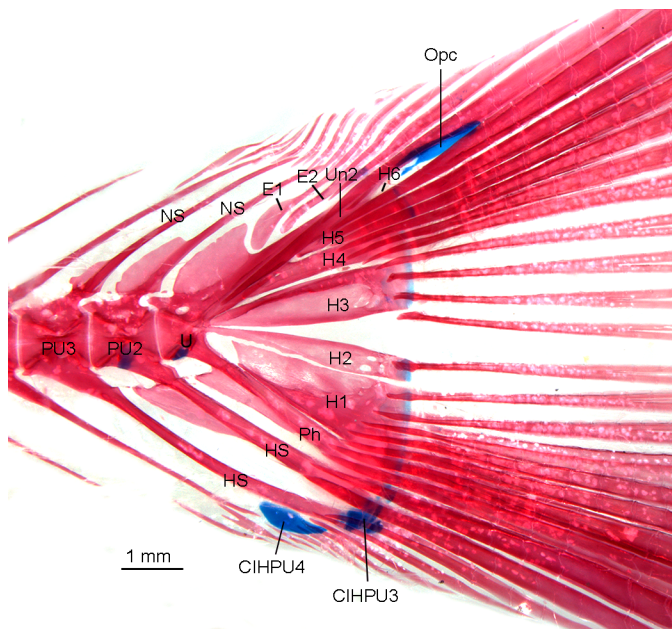
interdigitating sutures, the scapula and mesocoracoid medially, pectoral-fin rays ventrally and postcleithrum two posteriorly. Postcleithrum one rounded, located ventral to the tip of supracleithrum. Postcleithrum two ovate, located medially to posterior tip of cleithrum, slightly overlapping anterodorsal tip of postcleithrum three. Postcleithrum three thin, elongated, with ovate, posterior bony lamella. Coracoid flat, located medially to cleithrum, connected to it anteriorly and laterally to the medial lamellae of cleithrum (cleithrum-coracoid bridge) to form the interosseous space. Coracoid connected with scapula and mesocoracoid posterodorsally. Round opening delimited by cleithrum-coracoid bridge anteriorly and scapula posteriorly. Mesocoracoid thin, elongate, enlarged basally, its dorsal tip contacting the anterior portion of cleithrum and its ventral tip the posterior portion of coracoid. Scapula located medially to the posteroventral portion of cleithrum. Dorsal portion of scapula bifurcated, with anterior and posterior projection. Rays on pectoral-fin i(seven), 12(four) or 13(three). Four proximal radials. Four distal radials partially ossified distally.

**13. Pelvic girdle** (Figure 6C): Basipterygium roughly triangular in shape, its tip situated posterior to vertical through ribs of sixth (three) or seventh (four) vertebrae. Ischiatic process with a posteriorly directed process, with cartilaginous tip.

**14. Caudal fin** (Figure 7): Dorsal procurent caudal-fin rays 10 (two), 11 (three) or 12 (two) contacting the last three neural spines, two epurals and a pair of uroneurals. Ventral procurent caudal-fin ray eight (two), nine (two), 10 (one) or 11 (two) contacting the last three haemal spines and parhypural. Principal caudal-fin rays i,9,8,i (seven). Compound centrum with dorsal specialized neural process well developed. First hypural not connected to the compound centrum. Second hypural thin, always connected with the compound centrum. First and second hypurals and parhypural supporting the ventral caudal-fin lobe. Third, fourth, fifth and sixth hypurals supporting the upper caudal-fin lobe. Relatively wide, distal gap between second and third hypurals. One specimen presenting the first and second hypurals fused, possibly representing an abnormal condition. Distal portions of hypurals, haemal spines of preural centra two and three and parhypural cartilaginous. Two ventral caudal radial cartilages; anterior one (inter-haemal spine cartilage of preural centrum four: CIHPU4) situated anterior to tip of haemal spine of preural centrum three, posterior one (inter-haemal spine cartilage of preural centrum three: CIHPU3) situated between tips of haemal spines of preural centra two and three. CIHPU3 smaller than anterior cartilage. Dorsal caudal radial cartilages absent. Opisthural cartilage present in all specimens at posterior tip of notochord.



**Figure 6.** *Moenkhausia lepidura*, pectoral and pelvic fins. **A:** pectoral girdle, medial view and **B:** pectoral girdle, lateral view, MZUSP 37458, 66 mm SL. **C:** pelvic girdle, ventral view, MZUSP 8181, 62.7 mm SL. **Bpt**, basipterygium, **Cl**, cleithrum, **Co**, coracoid, **Exs**, extrascapular, **IsP**, ischiatic process, **Mco**, mesocoracoid, **Pcl1-3**, postcleithrum 1-3, **Pt**, posttemporal, **Sucl**, supracleithrum, **Sc**, scapula.



**Figure 7.** Caudal fin of *Moenkhausia lepidura*, MZUSP 8181, 64.1 mm SL. **CIHPU3-4**, inter-haemal spine cartilage of preural centrum 3 and 4, **E1-2**, epural 1 and 2, **H1-6**, hypural 1-6, **HS**, haemal spines, **NS**, neural spines, **Opc**, opisthural cartilage, **Ph**, parhypural, **PU2-3**, preural centrum 2 and 3, **U**, compound ural centrum, **Un2**, uroneural 2.

## Discussion

A comparative survey with several other characids was performed in addition to the osteological description of *Moenkhausia lepidura* (see Material examined) in order to search for possibly informative phylogenetic characters. Extensive descriptions and illustrations of morphological conditions in the Characidae were investigated (e.g. Benine, 2004, Miranda, 2010, Mattox et al. 2014). The comparative analysis undertaken herein revealed two remarkable characters present in *Moenkhausia lepidura* that deserve further attention due its restricted distribution within the family.

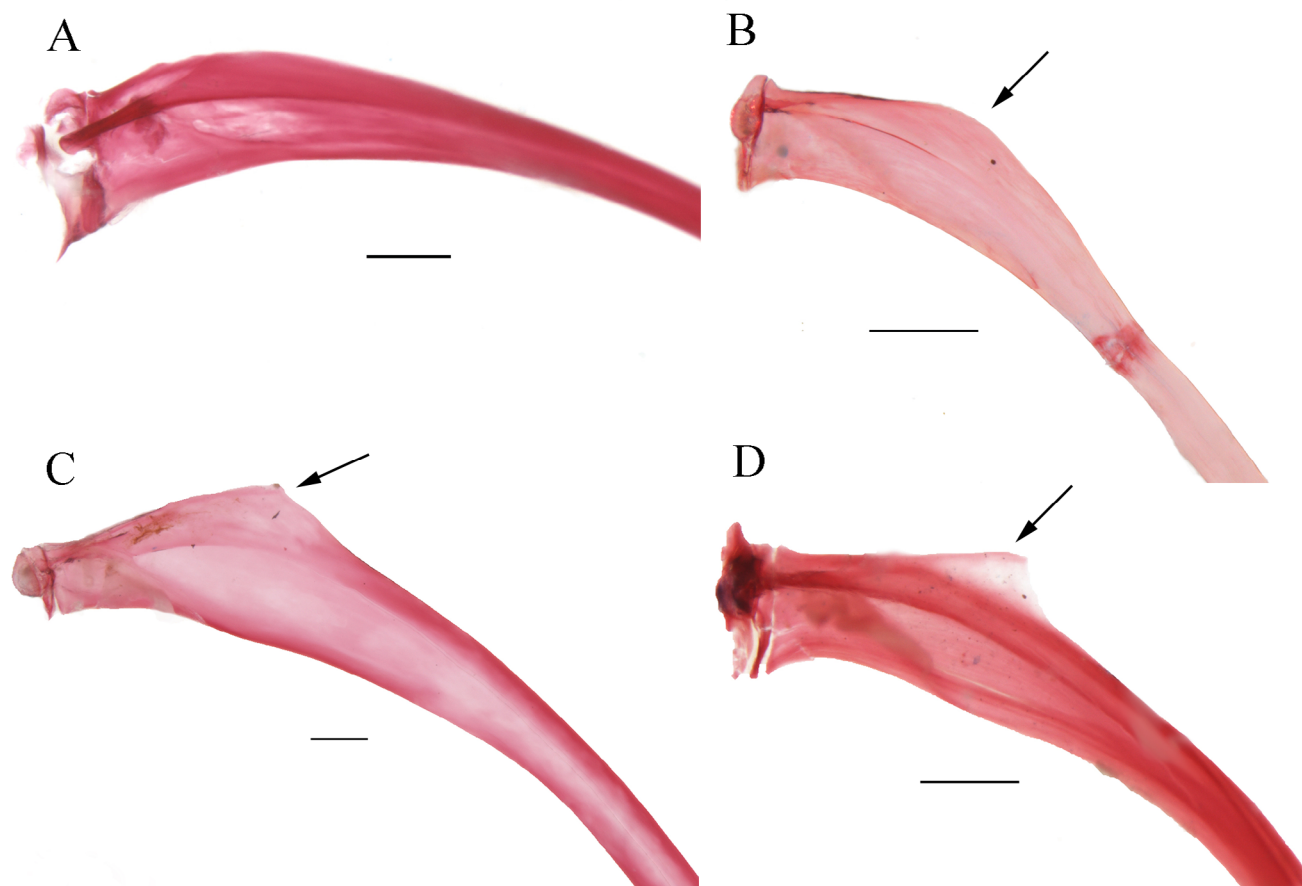
In *Moenkhausia lepidura* there is a triangular shaped bony lamella on the dorsal margin of the ribs, directed slightly posteriorly along its distal portion (Figure 8C). These bony lamellae are located from the second to eighth (one) or ninth (six) ribs, and serves as the attachment site for fibers of the *obliquus superioris* muscle. In the present study, a total of 63 species of Characidae were analyzed, of which 36 were also analyzed by Benine (2004) and Miranda (2010), and the remaining 27 species were exclusively examined herein, which provided a deep and detailed view about the variation of this character in closely related species. In the material examined, the dorsal portion of the ribs exhibited the following morphological variations: (0) bony lamellae absent (Figure 8A), found in most characids, (1) bony lamellae present and small, with smooth surface along the dorsal margin of the ribs (Figure 8B), as



observed in *Hemigrammus durbinae* Ota, Lima & Pavanelli, 2015, *H. ulreyi* (Boulenger, 1895), *H. unilineatus* (Gill, 1858) and *M. phaenota*, (2) bony lamellae triangular in shape, slightly pointed posteriorly on the distal portion, present in *Astyanax multidentis* Eigenmann, 1908, *Hemigrammus marginatus*, *Hyphessobrycon diancistrus* Weitzman, 1977, *H. hebertaxelrodi* Géry, 1961, *M. aurantia* Bertaco, Jerep & Carvalho, 2011, *M. bonita*, *M. collettii*, *M. costae*, *M. dichroua*, *M. intermedia*, *M. jamesi* Eigenmann, 1908, *M. lopesi* Britski & de Silimon, 2001, all species assigned to the *M. lepidura* group *sensu* Géry (1992), *Moenkhausia abyss* Oliveira & Marinho, 2016, *M. celibela* Marinho & Langeani, 2010, *M. gracilima*, *M. hasemani* Eigenmann, 1917, *M. hysterozticia* Lucinda, Malabarba & Benine, 2007, *M. icae* Eigenmann, 1908, *M. inrai* Géry, 1992, *M. megalops* (Eigenmann, 1907), *M. lata* Eigenmann, 1908, *M. lepidura*, *M. loweae* Géry, 1992, *M. mikia* Marinho & Langeani, 2010 and *Thayeria obliqua* Eigenmann, 1908, (3) very thin lamellae present, connected to a thin elongated bony projection on the proximal portion of the ribs, present only in *Parecbasis cyclolepis* (Figure 8D).

According to the distribution of the conditions of ‘bony lamellae on the ribs’ herein observed and the results of phylogenetic studies discussed below, it seems condition 1 is homologous to condition 2, but not condition 3, presented by *Parecbasis cyclolepis*. Lucena (1993) mentioned the presence of bony lamellae on the ribs as parallel

autapomorphy of *M. lepidura* and *Parecbasis cyclolepis* Eigenmann, 1914. Benine (2004) also noticed similar condition in *Hemigrammus marginatus* Ellis, 1911, *Moenkhausia barbouri* Eigenmann, 1908, *M. bonita* Benine, Castro & Sabino, 2004, *M. browni* Eigenmann, 1909, *M. ceros* Eigenmann, 1908, *M. collettii* (Steindachner, 1882), *M. copei* (Steindachner, 1882), *M. costae* (Steindachner, 1907), *M. dichroua* (Kner, 1858), *M. gracilima* (Eigenmann, 1908), *M. intermedia* Eigenmann, 1908, *M. justae* Eigenmann, 1908, *M. lepidura*, *M. phaenota* Fink, 1979, *M. shideleri* Eigenmann, 1909 and *Stichonodon insignis* (Steindachner, 1876) and proposed the presence of such bony lamellae as one of the three synapomorphies for a clade including all abovementioned species (Benine, 2004: fig. 62, Clade 42) with exception of *M. barbouri* and *S. insignis*. In a phylogenetic analysis of the Characidae based on morphological data, Miranda (2010) observed these lamellae in the ribs of *Moenkhausia intermedia*, *M. dichroua*, *Parecbasis cyclolepis* and *Stichonodon insignis* (character 224:1, synapomorphy for node 297 and paralleled in *P. cyclolepis* and *S. insignis*). In the molecular phylogeny of *Moenkhausia* species by Mariguela et al. (2013), a “*M. lepidura*” was recovered as closely related to *M. copei* (Clade 2), but it is a misidentification of *M. copei* (Petrolli et al. 2016). Although not including *M. lepidura*, most species (14 of 17) of clade 4 of Mariguela et al. (2013) present bony lamella in the ribs. Of which, 12 present the condition described for *M. lepidura* (condition 2)



**Figure 8.** Lateral view, left side of proximal portion of third rib of **A:** *Moenkhausia pirauba*, MZUSP 73467, 40.8 mm SL. **B:** *Hemigrammus ulreyi*, MZUSP 59538, 29.3 mm SL. **C:** *Moenkhausia lepidura*, MZUSP 37458, 66 mm SL. **D:** *Parecbasis cyclolepis*, MZUSP 25942, 41.7 mm SL. Arrow indicates the distinct conditions found in bony rib lamella of characids. Scale bar: 0.5 mm.

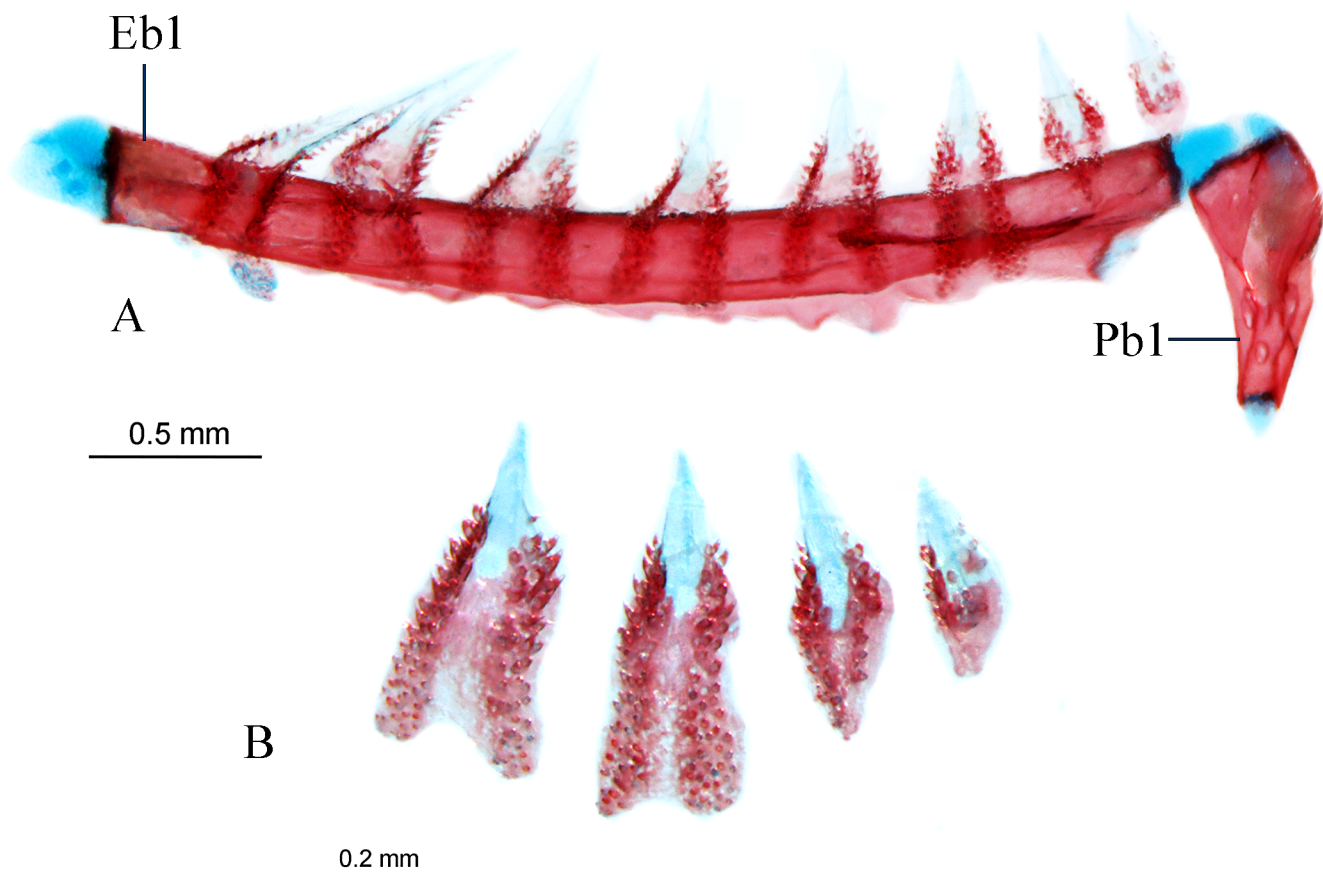
and two present the condition describe for the type species of the genus, *M. xinguensis* (condition 1). Therefore, all aforementioned phylogenetic analysis indicate that there is a monophyletic assemblage within the Characidae sharing the presence of bony lamellae dorsally to the ribs.

Interestingly, most species of the assemblage of Clade 4 (Mariguela et al. 2013) bearing bony lamellae described as condition 2 (bony lamellae triangular, slightly pointed posteriorly on the distal portion), similar to *M. lepidura*, have pigmented caudal-fin lobes. They are *M. celibela*, *M. gracilima*, *M. lata*, *M. costae*, in which the upper caudal-fin lobe is dark as in *M. lepidura*, and *Hemigrammus marginatus*, *M. bonita*, *M. dichrourea*, and *M. intermedia* in which both lobes are black marked. Other species sharing both characters herein examined are *Moenkhausia abyss*, *M. hasemani*, *M. hysterostricta*, *M. icae*, *M. inrai*, *M. megalops*, *M. loweae*, *M. mikia*, all pertaining to the *Moenkhausia lepidura* group (*sensu* Géry, 1992), which may indicate that they are closely related. However, all these assumptions must be tested in a broad phylogeny encompassing all species.

Another remarkable feature of *M. lepidura* is the presence of well-developed gill rakers with a basal expansion covered with small denticles (Figure 9), which were used by Marinho & Langeani (2016) as one of the diagnostic features of the species (*vs.* all the other species herein analyzed have gill rakers slender, with no basal expansions and with few spines scattered along its surface). Herein, we observed that these well-developed gill rakers are present in all

branchial arches, except in ceratobranchial of the first arch. Such unique morphological condition is most likely an autapomorphy of *M. lepidura*. Toledo-Piza (2007) reported similar condition, but in the first branchial arch, in *Acestrohynchus* (Agassiz, 1829) and Cynodontinae as a synapomorphy uniting both taxa (character 65:1). Mirande (2010, character 197:2) also reported “short, broad and strongly denticulated gill rakers”, but in the first branchial arch (specifically in first ceratobranchial) of *Acestrorhynchus pantaneiro* Menezes, 1992 and *Rhaphiodon vulpinus* Spix & Agassiz, 1829. Furthermore, Mirande (2010, character 199:1) coded “broad and laminar lateral base of gill rakers on first ceratobranchial” for *Acestrorhynchus pantaneiro*, *Brycon* spp., *Rhaphiodon vulpinus*, *Salminus brasiliensis* (Cuvier, 1816) and *Triporthus* spp. These are all piscivorous species considered basal lineages in Characidae (Malabarba & Weitzman, 2003; Calcagnotto et al., 2005; Mirande, 2010). Although they also present basal expansion on gill rakers similar to *M. lepidura*, such structures are not located in the same branchial elements and seems not to be homologous.

As observed, the comparative morphological analysis presented herein, along with the molecular and morphological based phylogeny of the Characidae available (e.g. Benine, 2004, Mirande, 2010, Mariguela et al. 2013) suggest the relationships of *M. lepidura* are among the species of *Moenkhausia* (and related small characids such as *Hemigrammus marginatus*) with the caudal fin black marked and bony lamella on the ribs, such as those belonging to the *M. lepidura*



**Figure 9.** Gill rakers of *Moenkhausia lepidura* showing distinct basal expansions full of spines, MZUSP 109841, 60.2 mm SL. **A:** epibranchial and pharyngobranchial of first branchial arch, right side, ventral view. **B:** close up of the gill rakers of epibranchial 1 showing the presence of a basal expansion full of small spines. **Eb1**, epibranchial 1, **Pb1**, pharyngobranchial 1.

group. Considering the vast diversity of the Characidae, such hypothesis still needs to be tested through a cladistics analysis, but the features highlighted will certainly be useful in future phylogenetic studies of the Characidae.

**Material examined.** *Acestrocephalus sardina*: MZUSP 29241 (1 c&s, 64.1 mm SL), rio Negro basin, rio Marauí, near to mouth, Amazonas State, 0°24'S 65°12'W, Brazil. *Agoniatès halecinus*: MZUSP 34332 (1 c&s, 119.2 mm SL), rio Xingu basin, Belo Monte, Pará State, 3°7'S 51°42'W, Brazil. MZUSP 103245 (1 dry skeleton, 134.8 mm SL), rio Jari basin, rio Iratapuru, tributary of left margin of rio Jari on community of Iratapuru, Amapá State, 0°33'59"S 52°34'43"W, Brazil. MZUSP 94366 (1 dry skeleton, 164.65 mm SL), rio Xingu basin, Miriam Lake, right margin of rio Culuene, Mato Grosso State, 13°25'48"S 53°2'24"W, Brazil. *Astyanax guianensis*: MZUSP 109674 (4 c&s, 31.5–33.7 mm SL), rio Negro basin, right margin of downstream of rio Jurubaxi, Amazonas State, 0°30'6"S 64°49'11"W, Brazil. MZUSP 104823, (2 c&s, 36.8–38.4 mm SL), left margin of rio Jari, at pier of Santo Antônio community, Amapá State, 0°38'22"S 52°30'33"W, Brazil. *Astyanax multidentis*: MZUSP 96726 (2 c&s, 34.4–34.8 mm SL), rio Tapajós basin, rio Teles Pires near to float of MT-416 road, Mato Grosso State, 9°27'7"S 56°30'46"W, Brazil. *Brycon nattereri*: MZUSP 59623 (1 c&s, 130.0 mm SL), rio Tocantins basin, tributary stream of rio Tocantinzinho, Goiás State, 14°2'27"S 48°12'22"W, Brazil. *Bryconops caudomaculatus*: MZUSP 84978 (1 c&s, 74.8 mm SL), rio Tiqué, between waterfall of Pedra Curta and village of São Pedro, Amazonas State, 0°16'S 69°58'W, Brazil. *Coptobrycon bilineatus*: MZUSP 87723 (2 c&s, 31.9–33.5 mm SL), Ribeirão Venerando, rio Tietê drainage, São Paulo State, 23°39'8"S 45°53'21"W, Brazil. *Charax stenopterus*: MZUSP 9616 (1 c&s, 69.4 mm SL), rio Patos, Pelotas, Rio Grande do Sul State, 31°46'S 52°20'W, Brazil. *Cynopotamus gouldingi*: MZUSP 77268 (1 c&s, 113.2 mm SL), rio Madeira basin, rio Roosevelt, above the waterfall, Mato Grosso State, 9°11'29"S 60°44'9"W, Brazil. *Galeocharax goeldii*: MZUSP 92436 (1 c&s, 35.8 mm SL), rio Madeira basin, Igarapé Karipuna, upper rio Madeira, Rondônia State, 9°15'10"S 64°38'31"W, Brazil. *Hemigrammus bleheri*: MZUSP 29435 (3, 24.4 – 26.7 mm SL), rio Negro basin, confluence with rio Urubaxi, Amazonas State, 0°31'S 64°50'W, Brazil. *Hemigrammus durbinae*: MZUSP 50074 (1 c&s, 20.5 mm SL), rio Solimões basin, Januacá lake, Amazonas State, 3°25'S 60°17'W, Brazil. *Hemigrammus marginatus*: MZUSP 113913 (1 c&s, 26.3 mm SL), rio São Francisco basin, Rio Porto Alegre, tributary of rio Grande, Bahia State, 12°47'49"S 44°67'54"W, Brazil. *Hemigrammus ulreyi*: MZUSP 59538 (1 c&s, 29.3 mm SL), rio Verde of Mato Grosso, Mato Grosso do Sul State, 19°9'67"S 55°17'86"W, Brazil. *Hemigrammus unilineatus*: MZUSP 38713 (1, 34.8 mm SL), first north tributary of rio Tarapuy, rio Negro basin, Napo, Ecuador. *Hyphessobrycon bifasciatus*: MZUSP 55159 (6 c&s, 21.6–42.2 mm SL), Ribeira de Iguape, São Paulo State, 24°18'42"S 42°35'50"W, Brazil. *Hyphessobrycon compressus*: MZUSP 28535 (1 c&s, 22.1 mm SL), Orangewalk District, Baba Creek near New River Lagoon, Belize State, 17°46'44"S 88°38'29"W, Mexico. *Hyphessobrycon diancistrus*: MZUSP 29846 (2 c&s, 27.0–29.7 mm SL), MZUSP 29847 (1 c&s, 29.6 mm SL), rio Negro basin, island of Tamanquaré, 0°30'S 64°55'W, Brazil. *Hyphessobrycon elachys*: MZUSP 59415 (9 c&s, 15.5–19.5 mm SL), lower rio Negro, rio Paraguai basin, Mato Grosso do Sul State, 19°20'29"S 56°58'10"W, Brazil. *Hyphessobrycon eques*: MZUSP

102973 (3 c&s, 15.8–22.8 mm SL), rio Solimões basin, Lago do Castanho, Amazonas State, Brazil. *Hyphessobrycon hebertaxelrodi*: MZUSP 103764 (3 c&s, 20.6–28.8 mm SL), rio Paraguai basin, Mato Grosso do Sul State, 18°28'50"S 54°40'37"W, Brazil. *Hyphessobrycon luettenii*: MZUSP 19021 (4 c&s, 24.5–44.9 mm SL), road to Grande/Cassino, rio Patos drainage, Rio Grande do Sul State, 32°5'S 52°12'W, Brazil. *Hyphessobrycon megalopterus*: MZUSP 96690 (6 c&s, 12.8–17.1 mm SL), rio Paraguai basin, rio Mutum, between Mimoso Village and Joselândia, Mato Grosso State, 16°19'30"S 55°49'59"W, Brazil. *Hyphessobrycon pulchripinnis*: MZUSP 92682 (6 c&s, 25.1–31.9 mm SL), igarapé afluente do rio Tapajós, rio Amazonas basin, Pará State, 4°33'48"S 56°15'40"W, Brazil. *Hyphessobrycon socolofi*: INPA 32626 (1 c&s, 33 mm SL), rio Negro basin, Roraima State, Brazil. *Moenkhausia abyss*: MZUSP 29422 (2 c&s, 34.0–36.7 mm SL), rio Negro basin, Brazil. *Moenkhausia aurantia*: MZUSP 113875 (1 c&s, 30.1 mm SL), rio Tocantins basin, rio Arraias above bridge of road TO-050, Tocantins State, 12°81'94"S 47°6'36"W, Brazil. *Moenkhausia bonita*: MZUSP 38086 (1 c&s, 34.9 mm SL), rio Paraguai basin, Ponte e Lacerda Farm, rio Jauru, Mato Grosso State, 16°8'S 58°1'W, Brazil. *Moenkhausia celibela*: MZUSP 30309 (1 c&s, 35.0 mm SL), rio Tapajós basin, Jacareacanga-Itaituba road, Pará State, Brazil. MZUSP 97629 (3 c&s, 27.7–31.3 mm SL), rio Xingu basin, flood at BR163 bridge, near Castelo dos Sonhos, Pará State, 8°15'17"S 55°6'40"W, Brazil. *Moenkhausia colletii*: MZUSP 109450 (1 c&s, 30.9 mm SL), rio Negro basin, Igarapé on tributary of rio Jaradi, near to joint of rio Jaradi and rio Marauí, Amazonas State, 0°22'44"S 65°12'39"W, Brazil. *Moenkhausia cosmops*: MZUSP 93556 (3 c&s, 26.1–28.1 mm SL), rio Juruena, rio Tapajós basin, Mato Grosso State, 13°14'47"S 59°0'52"W, Brazil. *Moenkhausia costae*: MZUSP 90893 (1 c&s, 29.5 mm SL), Itapicurú basin, rio Itapicurú on city of Queimadas, below to Barragem Grande, Bahia State, 10°59'2"S 39°40'9"W, Brazil. *Moenkhausia cotinho*: MZUSP 55125 (3 c&s, 29.5–39 mm SL), rio Negro basin, Igarapé in São João, near Tapurucuara, Amazonas State, 0°24'S 65°2'W, Brazil. *Moenkhausia dichroua*: MZUSP 90191 (1 c&s, 28.1 mm SL), rio Paraguai basin, rio Sepotuba, Mato Grosso State, 15°47'33"S 57°39'20"W, Brazil. *Moenkhausia gracilima*: MZUSP 5447 (2 c&s, 44.9–46.4 mm SL) rio Trombetas basin, Oriximiná, Pará State, 1°46'S 55°52'W, Brazil. *Moenkhausia hasemani*: MZUSP 99015 (2 c&s, 64.3–70.2 mm SL), rio Tefê, tributary of rio Amazonas, Juruapari, Amazonas State, 3°22'S 64°43'W, Brazil. *Moenkhausia hysterostricta*: MCP 32561 (4 c&s, 40.5–47.5 mm SL), rio Tocantins basin, Legeado, Funil, Tocantins State, 9°45'2"S 48°21'56"W, Brazil. *Moenkhausia icæ*: MZUSP 104338 (1 c&s, 33.9 mm SL) rio Japurá basin, Paraná da Jacintara, Amazonas State, 1°57'S 65°10'W, Brazil. *Moenkhausia* cf. *intermedia*: MZUSP 40918 (1 c&s, 35.7 mm CP), rio Tocantins basin, Poço do Gandaia, marginal lake of rio Paranã, Olho d'água farm, Goiás State, 14°26'S 47°3'W, Brazil. *Moenkhausia jamesi*: MZUSP 17352 (1 c&s, 53.8 mm SL), Sorubim Island, above Coari, rio Solimões basin, Amazonas State, 3°55'S 63°20'W, Brazil. *Moenkhausia lata*: MZUSP 7921 (2 c&s, 53.2–55.3 mm SL), rio Amazonas basin, Igarapé of rio Jamari, above Terra Santa, Pará State, 2°7'S 56°29'W, Brazil. MZUSP 18047 (1 c&s, 49.4 mm SL), Igarapé Inó, Furo de Panaquera, Pará State, Brazil. *Moenkhausia lepidura*: MZUSP 6247 (1 c&s, 61 mm SL), rio Negro basin, above Manaus, Amazonas State, 3°10'S 60°W, Brazil. MZUSP 8181 (2 c&s, 62.7–64.1 mm SL), rio Trombetas, Jacuapá Lake, Oriximiná, Pará State, 1°46'S 55°54'W, Brazil. MZUSP

37458 (2 c&s, 66–70 mm SL), rio Madeira basin, rio Alegre, tributary of rio Guaporé, approximately 30 km from Vila Bela da Santíssima Trindade, Mato Grosso State, 15°30'S 59°20'W, Brazil. MZUSP 109841 (2 c&s, 60.2–64.2 mm SL), rio Amazonas basin, rio Tefé, tributary of rio Amazonas, Juruapari, Amazonas State, 3°22'S 64°43'W, Brazil. *Moenkhausia lopesi*: MZUSP 82057 (1 c&s, 33.7 mm SL), tributary of rio Culuene, upper rio Taquari, Sonora, Mato Grosso do Sul State, Brazil. *Moenkhausia loweae*: MZUSP 91869 (2 c&s, 47.4–45.5 mm SL), stream of farm of Lício, tributary of rio Culuene, city of Paranatinga, Mato Grosso State, 13°49'S 53°15'W, Brazil. *Moenkhausia megalops*: MZUSP 97314 (1 c&s, 46.2 mm SL), rio Tapajós basin, rio Jamanxim, near Vila Mil, Pará State, 7°43'51"S 55°16'36"W, Brazil. *Moenkhausia mikia*: MZUSP 81198 (1 c&s, 46.7 mm SL), rio Tiquié, sand beaches downstream waterfall, Caruru village, Amazonas State, 0°16'29"S 69°54'54"W, Brazil. MZUSP 81219 (2 c&s, 33.7–37 mm SL), rio Tiquié, port between São Domingos Sávio and Jabuti village, Amazonas State, 0°4'59"S 68°25'W, Brazil. *Moenkhausia nigromarginata*: MZUSP 118180 (1 c&s, 39.7 mm SL), rio Papagaio, after rio Sacre, Mato Grosso State, 13°37'32.6"S 58°17'38.7"W, Brazil. *Moenkhausia oligolepis*: MZUSP 092942 (2 c&s, 41.9–56 mm SL), rio Negro basin, Igarapé Castanha tributary of rio Tiquié, Sítio Belém, slightly below of community of Santa Rosa, Amazonas State, 0°5'23"S 69°39'57"W, Brazil. *Moenkhausia phaenota*: MZUSP 45301 (2 c&s, 30.1–35.9 mm SL), headwater of rio Preto, Cuiabá-Santarém road, rio Tapajós basin, Mato Grosso State, 14°20'S 56°13'W, Brazil. *Moenkhausia pirauba*: MZUSP 73467 (3 c&s, 40.8–50.9 mm SL), rio Tapajós basin, Arinos river, Igarapé about 30 Km above Ponte dos Gaúchos, Mato Grosso State, Brazil. *Moenkhausia sanctaeofilomenae*: MZUSP 96038 (3 c&s, 29.6–38.3 mm SL), rio São Francisco basin, Bahia State, Brazil. *Moenkhausia tergimacula*: MZUSP 97940 (1 c&s, 57.1 mm SL), rio do Sono, Tocantins State, 10°15'40"S 46° 53'3"W, Brazil. *Moenkhausia xinguensis*: MZUSP 111531 (1 c&s, 44.8 mm SL), rio Xingu, in Cachoeira do Espelho, Pará state, 3°39'5"S 52°22'42"W, Brazil. *Nematocharax venustus*: MZUSP 102635 (2 c&s, 36.8–46.8 mm SL), rio Água Preta do Mocambo, rio Almada drainage, Bahia State, 14°34'53"S 39°17'56"W, Brazil. *Parecbasis cyclolepis*: MZUSP 25942 (1 c&s, 41.7 mm SL), Rio Ucayali, Coronel Portillo, Perú. *Phenacogaster tegatus*: MZUSP 35889 (1 c&s, 35.5 mm SL), rio Paraguai basin, Piquiri river mouth, Santo Antônio do Paraíso, Mato Grosso State, 17°12'S 54°9'W, Brazil. *Poptella paraguensis*: MZUSP 59914 (1 c&s, 49.64 mm SL), rio Negro, road between Nhecolândia and road BR-262, Mato Grosso do Sul State, 19°17'16"S 57°3'39"W, Brazil. *Rhaphiodon vulpinus*: MZUSP 92008 (1 dry skeleton, 306–385.6 mm SL), rio Tocantins basin, hidroelétric, Serra da Mesa, Brazil. *Roeboides paranensis*: MZUSP 19830 (1 c&s, 35 mm SL), rio Paraguai basin, rio Cuiabá, mouth of rio Croará, 20km from Barão de Melgaço, Mato Grosso State, 16°11'S 55°57'W, Brazil. *Roeboides xenodon*: MZUSP 54684 (1 c&s, 56.7 mm SL), rio São Francisco basin, Santana stream, 31 km Southern from Jesus da Lapa, at road to Malhada, Bahia State, 13°31'13"S 43°21'28"W, Brazil. *Salminus brasiliensis*: MZUSP 19439 (1 c&s, 132.2 mm SL), rio Grande basin, rio Mogi Guaçu, Emas, São Paulo State, 21°55'S 47°23'W, Brazil. *Thayeria obliqua*: MZUSP 29391 (1 c&s, 32.2 mm SL), rio Negro basin, joint with rio Urubaxi, Amazonas State, 0°31'S 64°50'W, Brazil. *Triportheus nematurus*: MZUSP 85808 (1 c&s, 116.6 mm SL), rio Paraguai basin, Taimã island, rio Paraguai, Mato Grosso do Sul State, Brazil.

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## Authors' Contributions

Gustavo Darlim: Description of the bony complexes of the species; contributions to the photographs and laboratory preparations of cleared and stained specimens; contributions to data collection; contributions to data analysis and interpretation; contribution to manuscript preparation, concept and design of the study; contribution to critical revision, adding intellectual content.

Manoela Maria Ferreira Marinho: Support for orientation methodology and scientific theoretical contributions; contributions in the manuscript preparation, concept and design of the study; contributions to the photographs of the bones and laboratory preparation of cleared and stained specimens; contribution to data analysis and interpretation; contributions adding intellectual content; contribution to critical revision and intellectual content.

## Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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