



Comment on “A Saharan fossil and the dawn of Neotropical armoured catfishes in Gondwana” by Brito et al.

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1. Introduction

Fossils have become indispensable for molecular phylogenetic studies aiming to provide a temporal framework for origin, diversification and biogeographic scenarios for virtually any kind of organism. Relying on the correct assignment of a given fossil to a clade, a time tree calibrated by key fossils can be a powerful tool to address questions about timing of evolutionary events. The oldest fossil of a given clade holds a special place in evolutionary studies, as it provides factual evidence of the minimum age that the clade it belongs to is in existence. Assigning a fossil to a clade is therefore a crucial step and due to frequent lack of genetic information for fossils, assigning it to a clade usually relies entirely on morphological characters. With decreasing levels of completeness of a fossil and of the quality of its preservation its phylogenetic assignment will usually become more problematical.

A recent paper by Brito et al. (2024) described a new fossil genus and species, *Afroscascudo saharensis*, of what the authors considered to represent a member of the highly diverse catfish family Loricariidae. This African fossil then also becomes the oldest fossil of this family, a group restricted otherwise to Central and South America (Reis et al., 2003). *Afroscascudo saharensis* was discovered from the Kem Kem formation in Morocco, a well-known fossil site of the Upper Cretaceous, which has previously yielded a multitude of important fossils, especially vertebrates (see Ibrahim et al., 2020).

2. Material and methods

We downloaded the high resolution images accompanying Brito et al. (2024) from <https://zenodo.org/records/10019045> and their Synchrotron CT scan data from <https://doi.org/10.6084/m9.figshare.23669274.v1> and studied them in detail. The latter were visualized and saved as images in ORS Dragonfly[®]. Images were further studied and labeled in Adobe Photoshop[®].

3. Results and discussion

While reading Brito et al. (2024), we initially discovered a small error in the data matrix they used to analyze the phylogenetic position of their putative loricariid (Supplementary file: 1-s2.0-S1342937X24000947-mmc2: Character 2 *Danio* is coded with state 0, i.e. having “usually eight or more” branchiostegal rays, when it should have been coded with state 1, “four or fewer”, as cypriniforms have just three branchiostegals; Conway, 2011). We also noted that the “reconstruction” of *Afroscascudo* presented in Brito et al.’s (2024) Fig. 3 did not appear to closely match the fossilized remains of that taxon presented in other figures. Though an anal fin is illustrated in the “reconstruction” of *Afroscascudo* by Brito et al. (2024), there is no sign of this structure in the fossilized remains presented in their figures. And the position of the fin they identified as the dorsal fin is “reconstructed” in the same position as in other loricariids. However, the dorsal fin should have been illustrated much more posteriorly on the body in the reconstruction of *Afroscascudo*, because in this fossil it is separated from the head/Weberian apparatus by at least seven post-Weberian vertebrae (Brito et al., 2024: Supplementary Data Fig. S3) while it inserts right behind the Weberian vertebrae in loricariids.

This short list of inconsistencies led us to scrutinize their paper more thoroughly and we conclude that the fossil *Afroscascudo* is not a loricariid but a juvenile lepisosteiform, most likely of the fossil gar genus *Obaichthys* (Wenz and Brito, 1992). Along with other gar species (Cavin and Brito, 2001; Grande, 2010), *Obaichthys* fossils are already known from the Kem Kem formation (Grande, 2010). The arguments for our conclusion are presented and discussed here.

Brito et al. (2024) did not discuss in detail why they thought *Afroscascudo* is a loricariid, but provided the majority of arguments for this conclusion (without further discussion) in their introduction stating that “the structure of the caudal fin, including division of hypurals into dorsal and ventral groups . . . , clearly indicates that it is a teleost fish.” They pointed out that the “most notable feature of this new taxon is the presence of bony plates on the surface of the body”, which they concluded are only known from “gasterosteiforms, siluriforms, syngnathiforms, and some scorpaeniforms, beryciforms, and cottiforms” and a fossil aulopiform

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amongst teleosts. They then argued that the “presence in the new taxon of a single dorsal fin positioned anteriorly on the body, with a spine on its anterior part” is unknown in any of the aforementioned groups of teleosts except catfishes, “thus leaving the possibility of it being a siluriform” and concluded that such “bony plates on the body surface occur in families of the Loricarioidei... and the Doradidae... and the Amphiliidae...” Based on “the presence of dermal plates covering the entire flank and dorsum and the presence of odontodes on the body...” they further concluded that these characters support “its inclusion among Loricarioidei, possibly among loricariids, the only group possessing three longitudinal series of dermal plates.” With the conclusion arrived at in the Introduction that *Afroscascudo* can only be a siluriform and most likely a loricarioid, the skeletal anatomy of *Afroscascudo* was then described in the Results section of Brito et al. (2024) with the loricarioid skeleton in mind. As a further consequence of their conclusion, the phylogenetic analysis in Brito et al. (2024) was restricted to only 12 ostariophysan taxa (one gonorynchiform, one cypriniform, one characiform, one non-loricarioid catfish and eight loricarioids) and *Afroscascudo* scored for a total of 15 morphological characters and molecular sequence data (3015 base pairs derived from one mitochondrial and two nuclear genes). It resulted in *Afroscascudo*, which could not be scored for molecular data, being recovered as a member of Loricariidae (Brito et al., 2024; Fig. 3).

Their entire argument thus presents a hierarchical tower of hypotheses that crumbles if the initial hypothesis is incorrect. This initial hypothesis is that *Afroscascudo* is a teleost evidenced by “the structure of the caudal fin, including division of hypurals into dorsal and ventral groups.” Identification of caudal-fin bones by Brito et al. (2024) was based on a tomographic study of *Afroscascudo*, for which we downloaded the original data (<https://doi.org/10.6084/m9.figshare.23669274.v1>). In the main body of their paper, Brito et al.'s (2024) Fig. 2e already presented the final rendering according to their interpretation that it is a loricariid catfish. Checking their actual tomography files it is, however, unclear how the authors arrived at their rendering, as large areas around what they consider to be hypurals/parhypural/neural spine of second preural centrum have the same density and seem to us impossible to separate from the matrix or the body of the thick scales (compare Fig. 1a and 1b). The entire fossil is heavily compressed and the thickness of the region, for which Brito et al. (2024) identify hypurals, measures less than 1 mm. We thus doubt the accuracy of their rendering of the caudal-fin skeleton (which we suggest also has the dorsal and ventral sides reversed in their Fig. 1e, 2d,e) and as a consequence the validity of the only character they presented to exclude non-teleosts as potential taxa for their *Afroscascudo*.

In the following paragraphs we will lay out our arguments that demonstrate *Afroscascudo* is not a loricariid teleost but actually a gar of the genus *Obaichthys*.

A highly unusual character of *Afroscascudo*, as Brito et al. (2024) point out is the presence of odontodes on the skull bones, which they confirm in their Supplementary Data Fig. S6. Among teleosts such odontodes covering several skull bones are indeed only known from loricarioids, the clupeomorph *Denticeps*, and the atherinomorph *Atherion* (Sire and Huysseune, 1996; Sire et al., 1998; Sire and Allizard, 2001). However, among recent non-teleostean actinopterygians, odontodes are also known from polypterids and lepisosteids (Sewertzoff, 1932; Nickerson, 1893; Grande, 2010). Among fossil actinopterygians they are especially numerous on the head and body of the fossil gar genera *Obaichthys* and *Dentilepisosteus*, both with members from the Kem Kem fossil site in Morocco (Grande, 2010). We find that comparing the figures in Brito et al. (2024) with those of *Obaichthys decoratus* in Grande (2010) provides a close match, especially once bones are identified without a loricariid bodyplan in mind. We think the bone labeled pt (pterotoc-supracleithrum) in Brito et al.'s (2024) Fig. 1a,c and S1,S3 is actually the opercle, the unlabeled bone in their Fig. 1a and S1 in front of it the preopercle, which in turn is separated from the orbit by infraorbitals, and the bone behind the operculum is the supracleithrum (compare Supplementary Data Fig. S1 in Brito et al., 2024 with Figs. 471–477 in Grande, 2010).

Once it is accepted that *Afroscascudo* is actually an *Obaichthys*, other puzzling characters start to make more sense. *Obaichthys* has five rows of large rhombic ganoid scales with a long, pointed median and posteriorly directed spine-like projection, a unique character, which Grande (2010) used to define the family Obaichthyidae. This type of scales in *Obaichthys* matches the structure and appearance of the scales of *Afroscascudo* perfectly. Another perfect match is that of these five rows of scales only the middle three reach the level of the dorsal, anal and caudal fins. These three series in *Obaichthys* (Grande, 2010: Fig. 471, 473A–B, 479C) are exactly positioned on the body as the three series of scales with the large posterior projections illustrated in Fig. 1–2 and Supplementary Data Figs. S4–5 for *Afroscascudo* by Brito et al. (2024).

As a consequence of this close match we are convinced that in the image of the body and caudal fin in Brito et al., (2024: Fig. 1e), dorsal and ventral sides are reversed and the fin labeled the dorsal fin by Brito et al., (2024: Fig. 1e) is actually the anal fin and the fin labeled as both the pelvic fin (their Fig. 1e) and anal fin (their Supplementary Data Fig. S5a) is actually the dorsal fin. Our conclusion about the reversed dorsal and ventral sides in Brito et al.'s (2024) Fig. 1e and S5a is based on the fact that it is

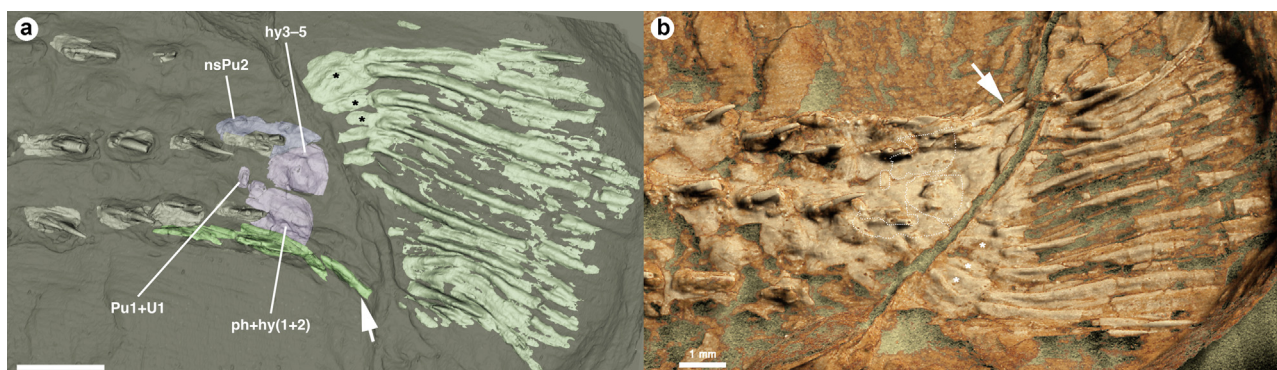


Fig. 1. Comparison of the rendered caudal-fin illustration (a) by Brito et al., (2024: Fig. 1e) and our illustration (b) with dorsal and ventral sides reversed. The areas limited by dotted lines in b are those identified as parhypural + hypurals1 + 2, hypurals 3–5, neural spine of preural centrum 2 and preural centrum1 + ural centrum 1 by Brito et al. (2024). The asterisks mark the structures we identify as the actual hypurals and the arrows one of the fringing fulcra.

the lowermost row of scales with the spine-like projection that ends in advance of the other two, just like the series that is now on the part of the fossil that is considered by Brito et al. (2024) to represent the dorsal side. This reversion of dorsal and ventral sides allows us to identify the dense areas at the base of the ventralmost caudal-fin rays as some of the actual hypurals (Fig. 1, marked with asterisks). The position of the dorsal and anal fins in relation to the caudal fin and the overall arrangement of caudal-fin rays and their shape closely matches the shape of the caudal area of gars with their typical abbreviated heterocercal tail (Fig. 1b).

Our conclusion of reversed dorsal and ventral sides also solves the identity of the series of structures along the “ventral” margin of the caudal peduncle and caudal-fin base, which are highlighted in darker green in Fig. 2e and Supplementary Data Fig. S4a–b, but were not further considered in Brito et al. (2024). These are dorsal fringing fulcra of the caudal fin (see our Fig. 1 and Fig. 479B in Grande, 2010), structures typical for the leading edges of fins of many basal actinopterygians (Arratia, 2008). Also the elements considered odontodes in Brito et al.’s (2024) Supplementary Data Fig. S5b–c are fringing fulcra of what we are convinced is the anal fin (and not the dorsal fin). Our reinterpretation of the dorsal fin as the anal fin and the pelvic fin as the dorsal fin also raises questions about the structure identified in the text (though not indicated in any figure) as the anal fin by Brito et al., (2024:109): “Although the anal fin is not preserved, we can see the impression of four rays in the resin.” Without access to the resin prepared by Brito et al. (2024), we are unable to comment further.

The head skeleton of *Afroscascudo* as labeled by Brito et al. (2024) would also need reinterpretation of almost all skull bones, but this is beyond the scope of this comment.

4. Conclusion

There is no solid evidence to suggest that *Afroscascudo* is a loricariid catfish and we are convinced that it is a juvenile specimen of a species of the gar genus *Obaichthys*. *Afroscascudo* should therefore be considered a junior synonym of *Obaichthys* (urn:lsid:zoo-bank.org:pub:CF44182D-5633-4D45-ADD3-7239B3E3F08A). Our conclusion has major consequences for the biogeographic history of loricariids and loricarioids (as outlined by Brito et al., 2024) and any calibration of molecular trees, which would have used the fossil *Afroscascudo* as a calibration point.

CRediT authorship contribution statement

Ralf Britz: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Formal analysis, Data curation, Conceptualization. **Amanda K. Pinion:** Writing – review & editing, Writing – original draft, Visualization, Validation, Conceptualization. **Kole M. Kubicek:** Writing – review & editing, Writing – original draft, Visualization, Validation, Conceptualization. **Kevin W. Conway:** Writing – review & editing,

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Arratia, G., 2008. Actinopterygian postcranial skeleton with special reference to the diversity of fin ray elements, and the problem of identifying homologies. In: Arratia G., Schultze H.-P., Wilson M.V.H. (Eds.), Mesozoic Fishes 4 – Homology and Phylogeny, Verlag Dr. Friedrich Pfeil, München, pp. 49–10.
- Brito, P.M., Dutheil, D.B., Gueriau, P., Keith, P., Carnevale, G., Britto, M., Meunier, F.J., Khalloufi, B., King, A., de Amorim, P.F., Costa, W.J., 2024. A Saharan fossil and the dawn of Neotropical armoured catfishes in Gondwana. *Gondwana Res.* 132, 103–112.
- Cavin, L., Brito, P.M., 2001. A new Lepisosteidae (Actinopterygii, Ginglymodi) from the Cretaceous of the Kem Kem Beds, southern Morocco. *Bull. Soc. Géol. France* 172, 661–670.
- Conway, K.W., 2011. Osteology of the South Asian Genus *Psilorhynchus* McClelland, 1839 (Teleostei: Ostariophysi: Psilorhynchidae) with investigation of its phylogenetic relationships within the order Cypriniformes. *Zool. J. Linn. Soc.* 163, 50–154.
- Grande, L., 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *Amer. Soc. Ichthyol. Herpetol. Spec. Publ.* 6, 1–871.
- Ibrahim, N., Sereno, P.C., Varricchio, D.J., Martill, D.M., Dutheil, D.B., Unwin, D.M., Baidder, L., Larsson, H.C., Zouhri, S., Kaoukaya, A., 2020. Geology and paleontology of the Upper Cretaceous Kem Kem group of eastern Morocco. *ZooKeys* 928, 1–216.
- Nickerson, W.S., 1893. The development of the scales of *Lepidosteus*. *Bull. Mus. Comp. Zool.* 24, 115–139.
- Reis, R.E., Kullander, S.O., Ferraris, C.J., Jr. (Eds.), 2003. Check List of the Freshwater Fishes of South and Central America. EDIPUCRS, Porto Alegre.
- Sewertzoff, A.N., 1932. Die Entwicklung der Knochenschuppen von *Polypterus delhesi*. *Jenaische Ztschr. Naturkde.* 47, 232–314.
- Sire, J.Y., Allizard, F., 2001. A fourth teleost lineage possessing extra-oral teeth: the genus *Atherion* (Teleostei: Atheriniformes). *European J. Morphol.* 39, 295–305.
- Sire, J.Y., Huysseune, A., 1996. Structure and development of the odontodes in an armoured catfish, *Corydoras aeneus* (Siluriformes, Callichthyidae). *Acta Zool.* 77, 51–72.
- Sire, J.Y., Marin, S., Allizard, F., 1998. Comparison of teeth and dermal denticles (odontodes) in the teleost *Denticiceps clupeioides* (Clupeomorpha). *J. Morphol.* 237, 237–255.
- Wenz, S., Brito, P.M., 1992. Première découverte de Lepisosteidae (Pisces, Actinopterygii) dans le Crétacé inférieur de la Chapada do Araripe (N-E du Brésil). Conséquences sur la phylogénie des Ginglymodi. *Compt. Rend. Acad. Sci., Ser. 2.* 314, 1519–1525.

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