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A New Genus and Species of †Cladocyclidae (Teleostei: †Ichthyodectiformes) from the Lower Cretaceous "Batateira Beds", Barbalha Formation, Araripe Basin: The First Vertebrate Record in a Still Poorly Explored Fossil Site

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Abstract: The Mesozoic Teleostei †Ichthyodectiformes presents a widespread distribution in marine brackish and freshwater deposits worldwide. The Brazilian fossil record of this group is represented by five nominal genera distributed exclusively in the sedimentary basins of Northeast Brazil (cf. Parnaíba, Sergipe-Alagoas, Recôncavo, Tucano, and Araripe). In the Araripe basin, the unique representative of the order is †*Cladocyclus gardneri*, restricted to the Crato and Romualdo Formations. Recent collecting efforts carried out in the Araripe Basin led to the discovery of two specimens of †Cladocyclidae. Based on the comparison with the known Brazilian taxa, we conclude that this new record represents a new genus and species of this clade. †*Cladocynodon araripensis* represents the first vertebrate described from the dark shales of the "Batateira Beds" of the Barbalha Formation and differs from the other †Cladocyclidae by the presence of hypertrophied bony fangs at the anterior region of the dentary, with other relatively small true teeth abruptly reduced posteriorly, and by presenting premaxillary and maxillary teeth significantly reduced in size. †*Cladocynodon araripensis* increases the anatomic diversity and temporal range of †Cladocyclidae in Gondwana.

Keywords: Teleostei; †Cladocyclidae; anatomy; taxonomy; mid-Cretaceous; Batateira Beds; Barbalha Formation; Araripe basin

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1. Introduction

The order †Ichthyodectiformes Bardack and Sprinkle [1] comprises an extinct lineage of stem Teleostei whose fossil record ranges from the Middle Jurassic (Bathonian) to Upper Cretaceous (Maastrichtian), with a widespread distribution in marine estuarine and freshwater sediments from Australia, North and South America, Antarctica, Europe, Middle East, Africa, and East Asia [2–17].

According to Patterson and Rosen [18], this clade is compounded by the suborders †Allothrissopoidei and †Ichthyodectoidei, being well supported by five synapomorphies (cf. paired ethmopalatine ossification in the floor of the nasal capsule, articulating with the palatine; six or seven uroneurals, the first three or four extending anteroventrally to cover the entire lateral surface of the first, second, or third preural centra; teeth in a single series in the jaws; coracoid enlarged ventrally, meeting its fellow in a mid-ventral coracoid symphysis; anal fin long, falcate, opposed by a short, remote dorsal fin). The suborder †Allothrissopoidei, erected by these authors, is supported by three synapomorphies: the absence of the suborbital bone; an infraorbital canal with few canaliculi, ending blindly in lachrymal without reaching antorbital; and, the hemal arches fused with centra in most of the caudal region. †Ichthyodectoidei [19] is supported by five synapomorphies: a supraoccipital crest high and triangular; parietals located far from the posterior border of the skull; a large intercalar forming the posterior edge of the hyomandibular facet; ethmopalatine with membranous outgrowths separating and suturing with the rostrodermethmoid and lateral ethmoid; and a palatine head modified into a disc-like malleolus. Originally the clade was positioned at the base of crown-group teleosts [18,20], and later, considered closely related to basal extant teleosts [21,22], a well-supported hypothesis [12,17].

Nowadays, the †Ichthyodectiformes are represented by more than 30 species [12]; however, the skulls and caudal skeleton are not frequently completely preserved, and the unquestionable synapomorphies for the group are very often hard to be identified or even homoplastic through the various lineages of teleosts. For instance, it concerns the definition of what should be classed as ethmopalatines, which are bones with a high variability in each fish group where they are found, e.g. in [23–29] and the composition of the caudal skeleton (cf. compound of six or seven hypurals in this group), and which represent a problematic state of character through basal Teleostei [21] (see discussion).

Previous authors [9,12,17] have already realized the problem of identifying these synapomorphies in new species of †Ichthyodectiformes—the case we face in this new taxon herein described—and pointed out a combination of useful characteristic features to identify this group: the peculiar *bauplan* of this group characterized by its bulldog-like head; a moderate-to-very-elongated trunk; expanded first rays of the pectoral and pelvic fin; large and expanded coracoids with a longitudinal symphysis; paired fins located posteriorly in the body; and finally a reduced dorsal fin. Unquestionably, †Ichthyodectiformes are predatory fishes with fusiform and elongated shapes [12] and with high plasticity in their shape of teeth. Patterson and Rosen [18] pointed out that all †Ichthyodectiformes present short premaxilla, long maxilla, and dentary, all bearing a single row of teeth varying from minute (cf. †*Allothrissops*, †*Gillicus*, some †*Thrissops* spp.) to larger and uniform (†*Ichthyodectes*, †*Cladocyclus*, †*Thrissops sensu stricto*, †*Eubiodectes*, †*Spathodactylus*, †*Saurodon*, †*Saurocephalus*) and much enlarged (†*Xiphactinus*, †*Chirocentrites*).

The current Brazilian fossil record of †Ichthyodectiformes is represented by five nominal genera (†*Saurocephalus*, †*Chiromystus*, †*Itaparica*, †*Ogunichthys,* and †*Cladocyclus*) with a temporal range from the Aptian to the Maastrichian distributed exclusively in the sedimentary basins of NE Brazil (cf. Parnaíba, Sergipe-Alagoas, Recôncavo, Tucano, and Araripe basins) [7,10]. In the Araripe basin, the exclusively former representative of the order is the †Cladocyclidae species †*Cladocyclus gardneri*, restricted to the laminated limestones of the Crato Formation and the carbonate concretions of the Romualdo Formation, both from Santana Group [5,30].

The family †Cladocyclidae Maisey [5] consists of a clade originally diagnosed by the presence of a supraoccipital crest overhanging the occiput. The family contents have been subsequently rearranged [12] and are currently composed of the genera †*Chirocentrites*, †*Cladocyclus*, †*Chiromystus*, and †*Eubiodectes*—all being a group of mid-Cretaceous †Ichthyodectiformes [12].

Wenz and Campos [31], for the first time, cited, without any description, the presence of some fishes closely related to the genus †*Cladocyclus* in the bituminous shales from the upper border of the "Missão Velha" Formation. This sequence has been also previously assigned as the "Fundão Member" of the "Rio da Batateira Formation" according to Ponte and Appi [32] and Rios-Netto et al. [33]. According to Assine et al. [34], the so-called "Rio da Batateira" interval consists of a lower sequence of the Barbalha Formation and comprises a vertical facies succession of fluvial channels, culminating with lacustrine shales that exhibit great lateral extension and thicknesses up to 10 m. This black shale interval is known as the "Batateira Beds" and constitutes an important stratigraphic mark in the basin because they record the establishment of a large lake characterized by severe water level fluctuations and anoxic events.

Recent collecting efforts carried out in the "Batateira Beds" [34] led to the discovery of additional †Ichthyodectiformes specimens. Based on the comparison with the known taxa currently assigned to this order, we conclude that this new record represents a new genus and species of †Cladocyclidae (Figure 1A–C). These new records represent the first formal description of a vertebrate in this locality, whose vertebrate fossil record is restricted to dinosaur trampling probably associated with sauropod tracks [35].

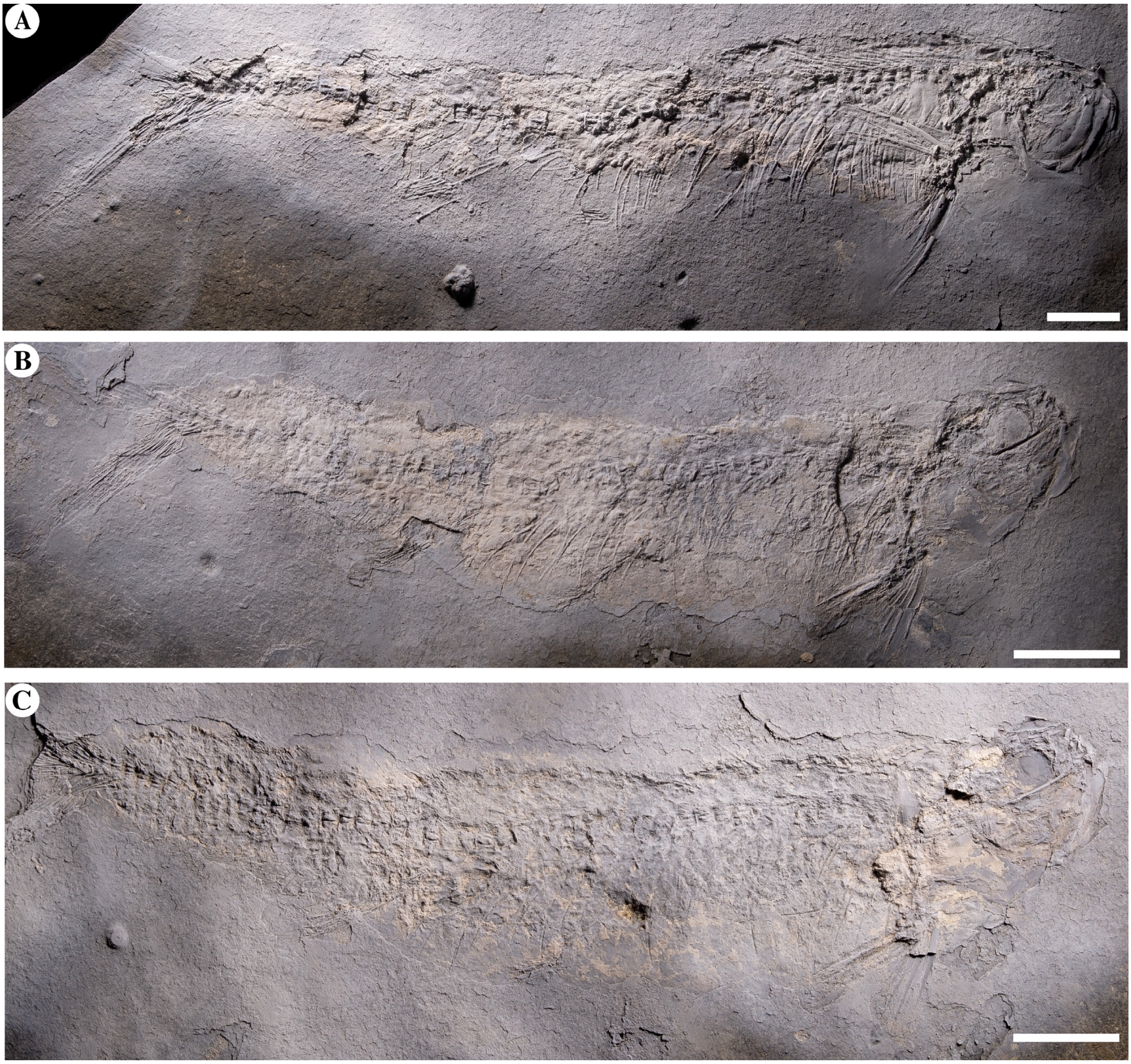

Figure 1. †*Cladocynodon araripensis* gen. et sp. nov.: (**A**) CFUFMT 139, 231 mm SL. Holotype. Batateira Beds, Barbalha Formation, Araripe basin; (**B**) CFUFMT 432A; (**C**) CFUFMT 432B, part and counterpart of the paratype, 178 mm SL, collected together with the holotype. Ribbon magnesium preparation. Scale bar = 2 cm.

2. Materials and Methods

Type specimens are from Coleção de Fósseis do Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Mato Grosso, Brazil (CFUFMT) (Figure 1). Comparative specimens are from CFUFMT and Coleção de Paleontologia, Universidade do Estado do Rio de Janeiro, Brazil (UERJ-PMB). Type specimens were prepared mechanically with needles under the stereomicroscope. The comparative material from the Crato and Romualdo Formations was acid, mechanically prepared following the methods of Toombs and Rixon [36]. None of these specimens have been prepared via the transfer method. The exemplars are flattened, preserved, and reveal a typical †Ichthyodectiformes *bauplan* with the characteristic bulldog-like head, preopercular sensorial canal with numerous posterior branches, pectoral girdle positioned anteroventrally, with well-developed first pectoral fin rays, and imprints of numerous epineural intermuscular bones along the column. The skull roof and braincase are not completely preserved in both exemplars. The caudal skeleton is badly preserved, as well as the anal and dorsal fins.

Photographs were made under low-angle light using a Sony α-57 digital camera with a Tamron (NY, USA) 60-mm F2.8 objective macro lens, and drawings were made directly on the photographs. For better observation of certain anatomical pieces, precisely because of the low contrast between the sediment and the fossil, ribbon magnesium was used to enhance such details.

2.1. Institutional Abbreviations

CFUFMT: Coleção de Fósseis da Universidade Federal do Mato Grosso. **UERJ-PMB**: Coleção de Paleontologia da Universidade do Estado do Rio de Janeiro.

2.2. Anatomical Abbreviations

The anatomical abbreviations modified from Cavin et al. [12] and Patterson and Rosen [18]. **Ang**: angular; **Art**: articular; **b.pop.s.c**: posteroventral branches of the preopercular sensorial canal; **Boc**: basioccipital; **Bsp**: basisphenoid; **Bspt**: basipterygoid process; **Cor**: coracoid; **DBF**: dentary bone fang; **Den.l**: left dentary; **Den.r**: right dentary; **EDT**: enlarged dentary teeth; **En**: epineural muscular bones; **Enpt**: entopterygoid; **Ep**: epural; **Eth.pal**: ethmopalatines; **f.VII.hm**: foramen for the hyomandibular trunk of the facial nerve; **H.s**: hemal spines; **Hy**: hypural (numbered) **Fr**: frontal; **L.e**: lateral ethmoid; **Mpt**: metapterygoid **Mx**: maxilla; **N.s**: neural spine; **Op**: opercle; **Op.p**: opercular process of the hyomandibular; **P.g**: pectoral girdle; **p.r** (numbered): pectoral rays; **Pal**: palatine; **Pal.mal**: palatine with developed malleolar head; **paro**: parapophysis; **Ph**: parhypural; **Pmx**: premaxilla; **Pop**: preopercle; **pro.r**: procurrent rays; **Psp**: paresphenoid; **Pu**: preural centrum (numbered); **Qu**: quadrate; **Qu.pv.p**: posteroventral process of the quadrate; **R**: ribs; **ra**: radials; **Retr**: retroarticular; **Rode**: rostrodermethmoid; **S.r**: skull roof; **Sca**: scapula; **Scl**: supracleitrum; **Smx.a**: anterior supramaxilla; **Smx.p**: posterior supramxilla; **Soc.c**: supraoccipital crest; **Sop**: subopercle; **U**: ural centrum (numbered); **Un**: uroneural.

2.3. Measurements Abbreviations

The measurements abbreviations follow Cavin et al. [12]: **HD**: head depth (measured from the tip of supraoccipital to the ventral limit of the skull); **HL**: head length (horizontal distance between the tip of the premaxilla and the posterior limit of the opercle); **SL**: standard length (horizontal distance between the tip of the premaxilla and the posteriormost limit of the hypurals); **TL**: total length, measured as the horizontal distance between the tip of the premaxilla and the posterior limit of the caudal fin lobe); **1PL**: pectoral fin length (length of the first principal pectoral fin ray) (Figure 2).

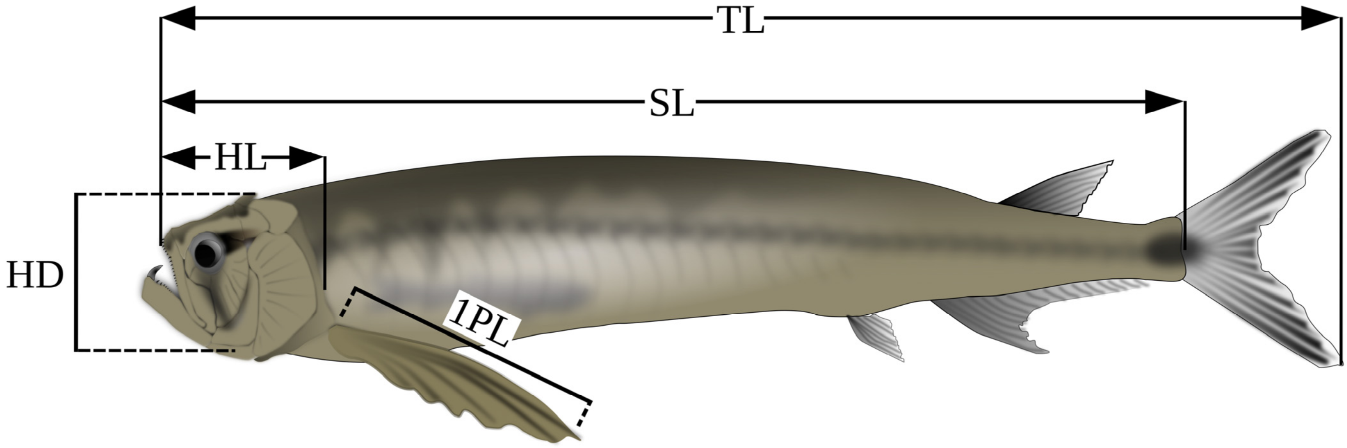

Figure 2. Diagram of anatomical measurements: **HD**: head depth; **HL**: head length; **SL**: standard length; **TL**: total length; **1PL**: pectoral fin length.

3. Geological Settings

The Araripe basin is an interior sedimentary basin located in Northeastern Brazil, covering an area of almost 8000 km^2 wedged between the states of Ceará, Pernambuco, and Piauí e.g., [34,37–39] (Figure 3). The geological history of this basin is closely related to the rifting process between South America and Africa continents together with the opening of the South Atlantic Ocean [40]. The Araripe basin comprises a thick siliciclastic succession of fluvial and lacustrine strata with no fully marine strata (cf. absence of ammonites, brachiopods, bryozoans, and corals), even though it presents some brief traces of marine incursions in specific strata indicated by the records of echinoids, marine mollusks, foraminifera, and dinoflagellates [41,42]. It was installed on Archaean and Proterozoic rocks of the Borborema Province and Paleozoic units from the Cariri sub-basin in the Vale do Cariri depression and is bounded to the north by the Patos Lineament [43,44]. The reactivation of the Precambrian shear zones during the South America and Africa break-up was responsible for the origin and generation of distinct subsidence cycles in the basin [39], as such: one—the continental pre-rift phase; two—the lacustrine syn-rift phase, and three—the transitional post-rift phase. In the Araripe basin, the post-rift Aptian sequence corresponds to the Santana Group, which is composed, in upward succession, of mostly clastic continental and rare carbonate layers of the Barbalha, Crato, Ipubi, and Romualdo Formations [45].

According to Souza et al. [46], based on Assine [38,39] and Ponte and Ponte Filho [47], the Araripe basin is compounded by four super sequences. The first one is pre-Jurassic and is the Mauriti Formation with fluvial sediments and without a fossil record; the second one is the Late Jurassic Brejo Santo and Missão Velha Formations, characterized by fluvio-lacustrine sediments, whose fossil record is marked by the presence of ostracods; the third one is the Early Cretaceous Abaiara Formation, with fluvial sandstones and shales and also with ostracods in the fossil record; and finally the fourth topmost Aptian–Cenomanian is the Santana Group (Crato and Romualdo Formations) and the Batateira Beds of the Barbalha Formation. Despite being treated in the same supersequence and the Santana Group being known as one of the most important fossiliferous units worldwide, especially recognized by the vertebrate and invertebrate fossil record on its Romualdo and Crato Formations [42,48], the Barbalha Formation does not have the same paleontological importance.

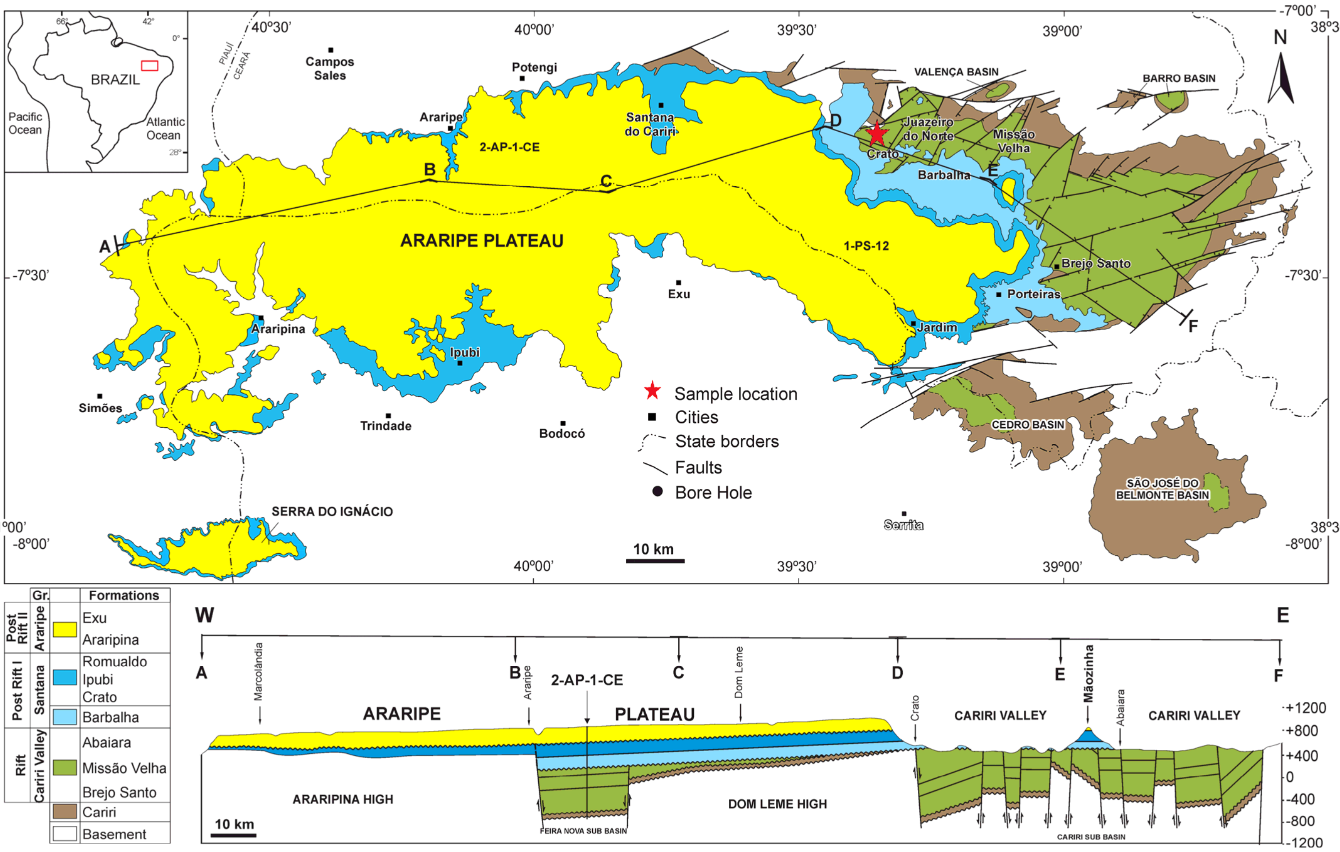

Figure 3. Geological map of Araripe basin. The red star indicates the sample location where the exemplars were collected.

The Barbalha Formation is usually classified as the first post-rift basin record. It includes a vertical facies succession of fluvial channels that culminate with lacustrine shales with great lateral extension up to 10-m thick [34]. The sequence is recognized as Aptian in the age-local Alagoas stage [35]. This unit is characterized by dark shale with a decametric layer of limestone and represents the first episode of lake deposition [33,46]. It is marked by the absence of vertebrate fossil records except for the presence of dinosaur tracks [35]. However, the previous author [31] pointed out the presence of some fossil fishes in what was once called the upper border of the Missão Velha Formation, as already pointed out. Despite being constituted predominantly by sandstone, the Barbalha Formation includes important pelitic intervals known as Batateira layers (or "Beds") consisting of dark shales [34], from where this new fossil record has been collected (Figure 4).

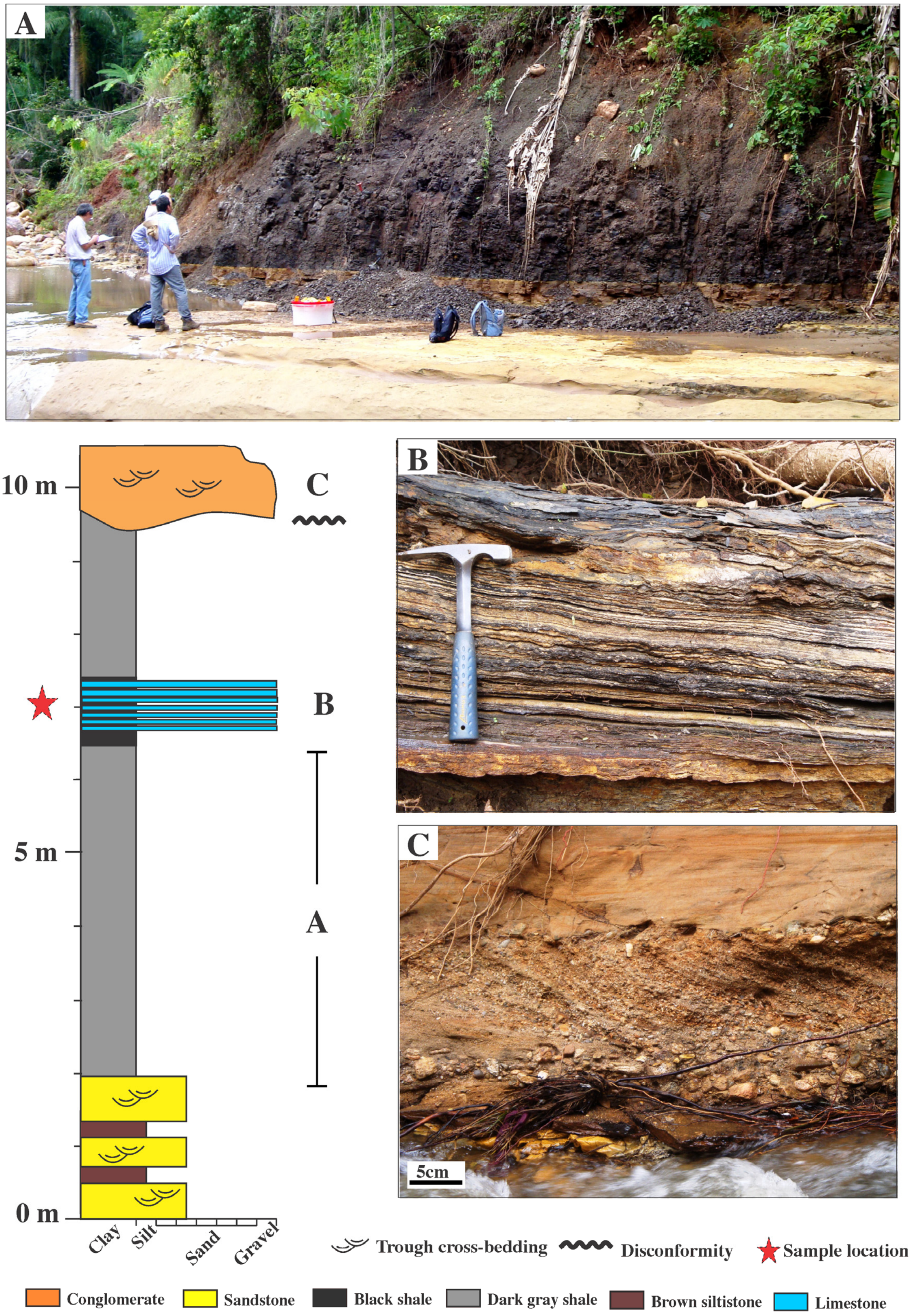

Figure 4. "Batateira Beds" in the Rio de Batateira section. (**A**) Contact between dark shales from the Batateira layers and the underlying fluvial sandstones of the Barbalha Formation (riverbed); (**B**) organic-rich dark shales interbedded with thin limestone laminae; (**C**) basal conglomerate and cross-bedded sandstones overlying shales (based on Assine et al. [34]).

4. Results

4.1. Systematic Palaeontology

Teleostei Müller, 1846 [49]
Order †Ichythyodectiformes Bardack and Sprinkle, 1969 [1]
Suborder †Ichthyodectoidei Romer, 1966 [19]
Family †Cladocyclidae Maisey, 1991 [5]
†*Cladocynodon* gen. nov.
Type species †*Cladocynodon araripensis* sp. nov.
Zoobank LSID. urn:lsid:zoobank.org:act:3D7833AD-294A-4897-9496-F0220BCAAB1E

Derivation name: Composite epithet. The first part of the generic name, *Clado*, comes from "†Cladocyclidae", the family to which the new taxon belongs. The second part, *cynodon*, is a noun in apposition derived from the Neotropical fish *Cynodon*, an extant neotropical fish with similar general convergent morphology predatory fish. The specific epithet "*araripensis*" refers to the Araripe basin, the place where the new species specimens were collected.

Holotype: CFUFMT 139 (Figures 1, 5, 6C, 7A and 8A).

Paratypes: CFUFMT 432A (Figures 1 and 6A); CFUFMT 432B (Figures 1, 6B and 8B). Part and counterpart.

Comparative material observed: †*Cladocylcus gardneri* from Romualdo Formation, Santana Group (thirty-three specimens UERJ-PMB 501-533); and †*Ogunichthys triangularis* from Marizal Formation, Tucano Basin (seven specimens, UERJ-PMB 93, 94, 95, 97, 98, 99, and 100).

Horizon and Age: Organic-rich dark shales interbedded with thin limestone laminae from the Earlier Cretaceous (Aptian) of Batateira layers; Barbalha Formation, Araripe basin [34].

Diagnosis: †Cladocyclidae fish differ from others by the following exclusive combination of characters: hypertrophied bony fangs (without evidence of enamel) at the anterior region of the dentary, with other relatively small true teeth abruptly reduced in size posteriorly; premaxillary and maxillary teeth significantly reduced in size compared to the hypertrophied teeth; dental arrangement in the premaxilla, maxillar, and dentary bones, with areas of overlapping teeth along all their alveolar surfaces in a single row; two supramaxillar bones, the anterior one bigger than the posterior; angular, articular, and retroarticular forming the articular facet for the quadrate; retroarticular forming the posterior edge of the quadrate facet; the presence of basipterygoid process angled downward; preopercle with the vertical and horizontal limbs equal in size; preopercular sensorial canal with seven posteroventral branches; vertebral column with 46–54 total centra.

4.2. Anatomical Description

4.2.1. General Aspect, Morphometrics, and Meristics

Incomplete preserved †Cladocyclidae with a total length (TL) reaching 278 mm and standard length (SL) of about 231 mm. Head length (HL) consists of 14.6% of SL. Head depth (HD) is about 14.2% of SL. Pectoral fin length (1PL) consists of about 17.8 % of SL. Five to eight pectoral fin rays are discernible on both pectoral fins. The number of anal fin rays is not discernible. The caudal fin with only the ventral lob is completely preserved through the complete fin length. The axial skeleton is badly preserved in the abdominal region, with only over-imposed impressions of vertebrae. Ribs and supraneurals are only partially preserved. Well-developed epineurals are present in the anterior region of the trunk. Total vertebrae count around 46–54. The exemplars present many parts of the body preserved as imprints in the matrix, and thus some details about biometric parameters and measurements cannot be precisely ascertained because of the absence of many bony pieces that are used as landmarks for these purposes. These measurements (Figure 2) were obtained from the holotype, in which such measures are more clearly observed.

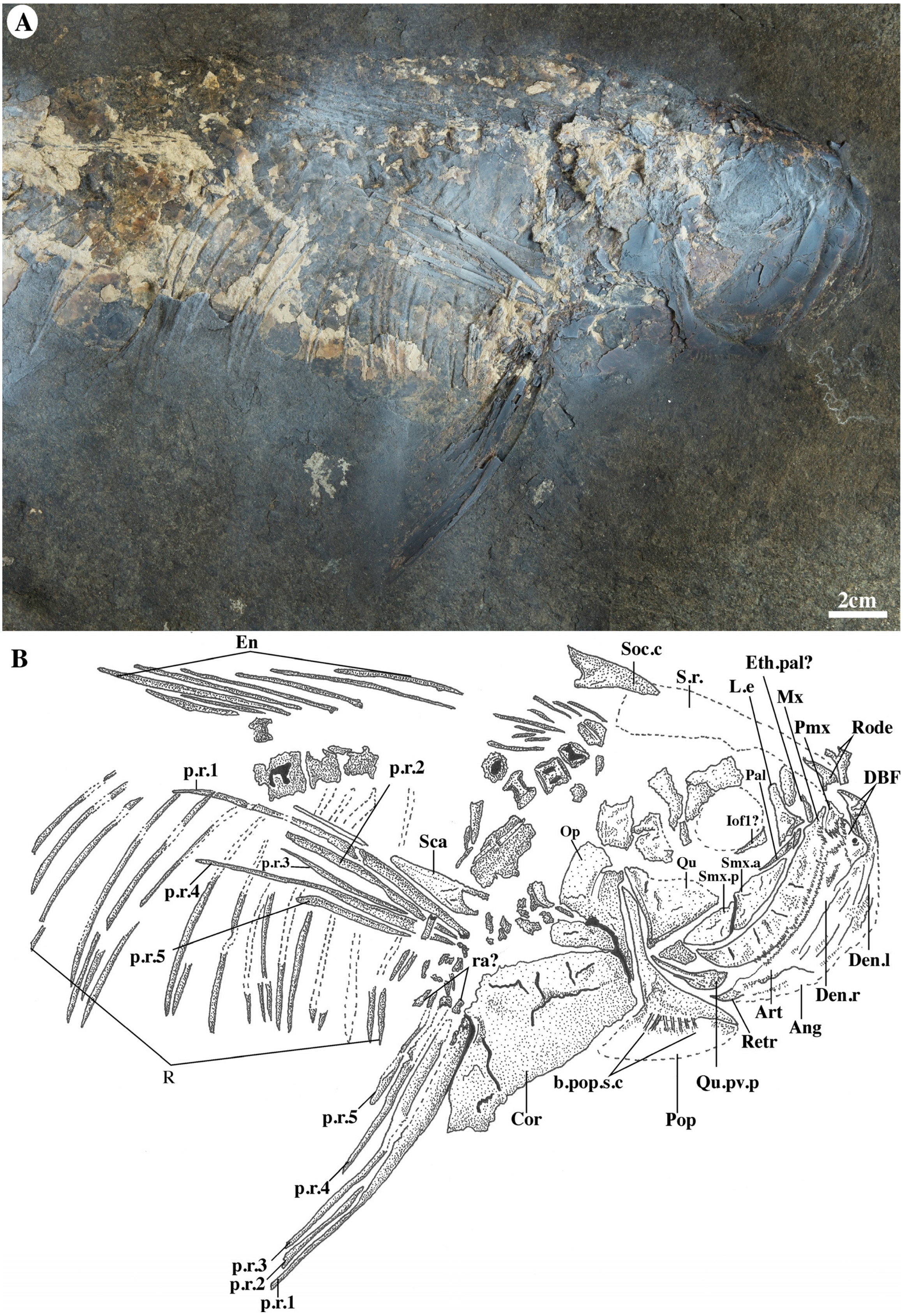

Figure 5. †*Cladocynodon araripensis* gen. et sp. nov. (**A**) Photo and (**B**) interpretative draw of the holotype CFUFMT 139.

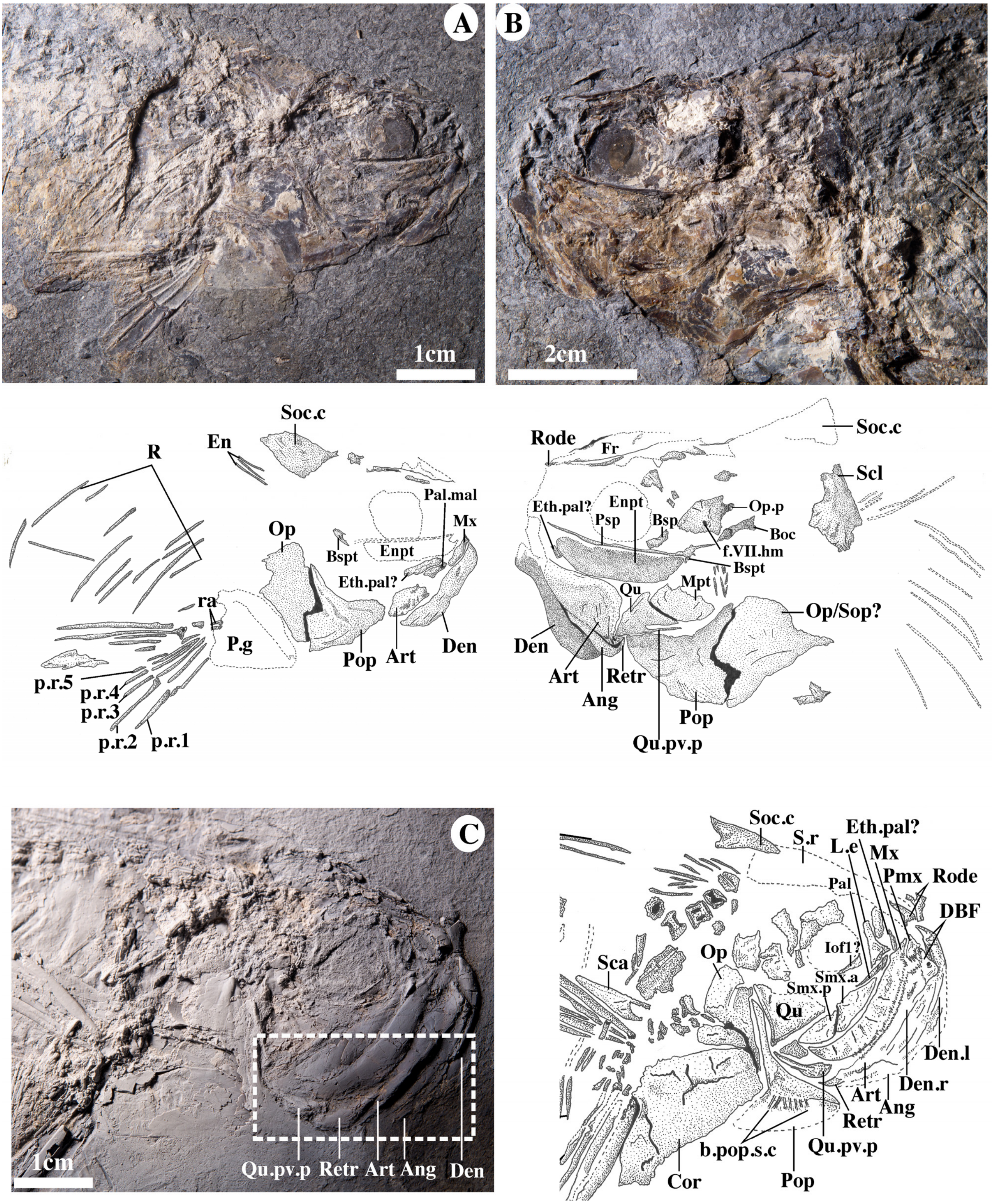

Figure 6. Photo and interpretative of head details of the holotype and paratype of †*Cladocynodon araripensis* gen. et sp. nov. (**A**) photo and interpretative draw of the exemplar CFUFMT 432A (part). (**B**) Photo and interpretative draw of the exemplar CFUFMT 432B (counterpart). (**C**) photo with a demarcated area (to enhance the contrast in this specific region, the specimen was treated with ribbon magnesium, which made it possible to detail the specific bone pieces related to the quadrate facet) and interpretative drawing of the holotype CFUFMT 139, highlighting the mandibular joint.

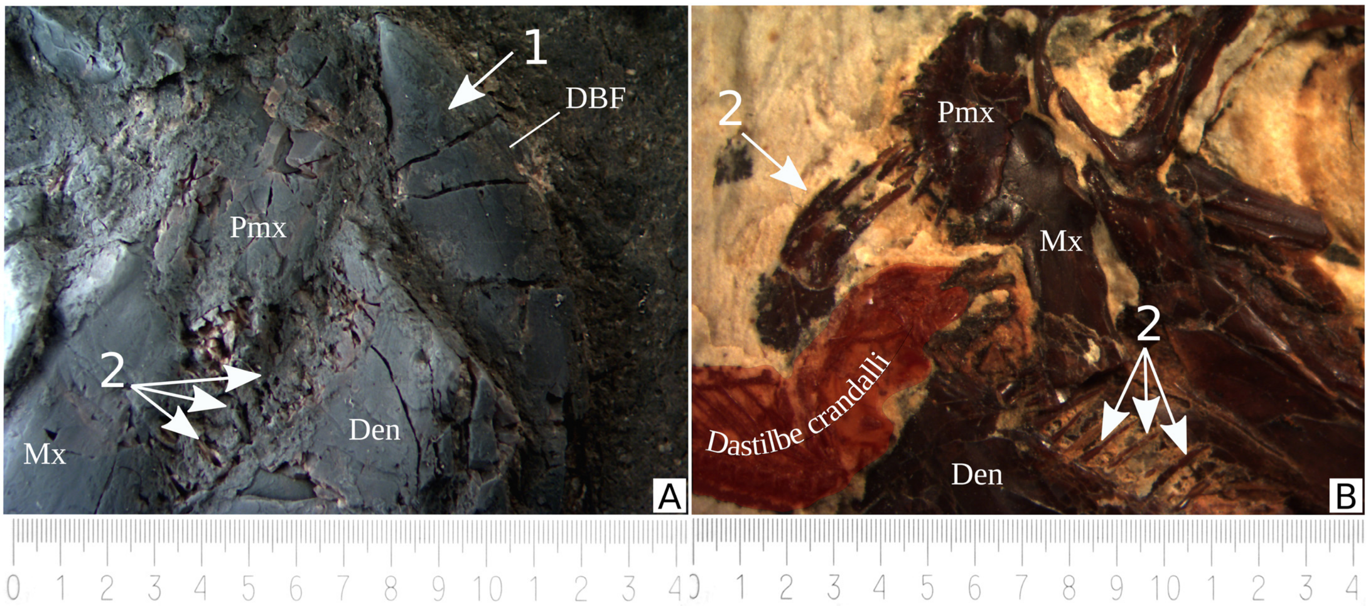

Figure 7. Anterior jaw area in †*Cladocynodon araripensis* sp. nov. (**A**) (CFUFMT 139; holotype, anterior to right) and (**B**) †*Cladocyclus gardnerii* (CFUFMT 87, Crato Formation, anterior to left). Arrows indicate anterior enlarged dentary bone fang (**DBF**) (1), followed by smaller posterior true teeth (2). †*Cladocyclus gardnerii* has only typical teeth of similar size (2). A small †*Dastilbe crandalli* is observed in the mouth of †*Cladocyclus gardnerii*, but it is not possible to conclude that it is due to predation or represents an aleatoric association.

4.2.2. Neurocranium

Most of the skull roof is not preserved, except by the holotype CFUFMT 139 (Figure 1). †*Cladocynodon araripensis* presents, posteriorly, a well-developed supraoccipital crest (Figures 5 and 6), similar to †*Cladocyclus* and all other †Cladocyclidae. The crest is high, triangular, and thickened and the dorsal margin exposes an ellipse outline [5,9,18,27], but the characteristic leading edge angled outward from the profile of the orbitotemporal region [5] found in this group cannot be evaluated in the former species. All other bones of the occipital and optic regions are not preserved. In the paratype CFUFMT 432B (Figure 6B) is observed dorsally and partially dislocated an elongated and smooth frontal above the orbital region, with a triangular rostrodermethmoid sutured on its anterior border. In the medial ventrolateral portion of this frontal section, fragments of the autosphenotic with a small ventral projection are present, as also are some bony pieces that are probably the remaining dermopterotic. The rostrodermethmoid, observed in the lateral view in the holotype, presents a ventrolateral projection to articulate with the premaxilla.

The parasphenoid is better preserved in the paratypes CFUFMT 432A (Figure 6A) and CFUFMT 432B (Figure 6B). It is an edentulous bar extending all along the neurocranial length with a triangular basipterygoid process projected anteroventrally, immediately below the otic region. Anteriorly it is sutured with the vomer and posteriorly it is not preserved. The basisphenoid is L-shaped in the lateral view (Figure 6B).

4.2.3. Hyopalatine and Circumorbital Series

Most of the hyopalatine bones are not preserved. In the holotype, anteriorly the palatine is preserved with its robust malleolar head (Figure 5) and the presence of contact with the posterolateral condyle of the maxilla is clear. Between the anterior edge of the palatine and the posteromedial surface of the maxilla there is a small bone occupying the position of an ethmopalatine, but due to the poor state of preservation it is not possible to confirm its presence. In the paratype CFUFMT 432B (Figure 6B), there is also a broken stick-shape bone in a similar position where the ethmopalatines are normally found in

†Ichthyodectiformes, but because of the poor state of preservation it is not possible to confidently specify its identification. Nevertheless, it is important to point out that whether this bone represents an ethmopalatine in †*Cladocynodon* or not, it probably has the same shape and position that is found in primitive †Ichthyodectiformes (see discussion).

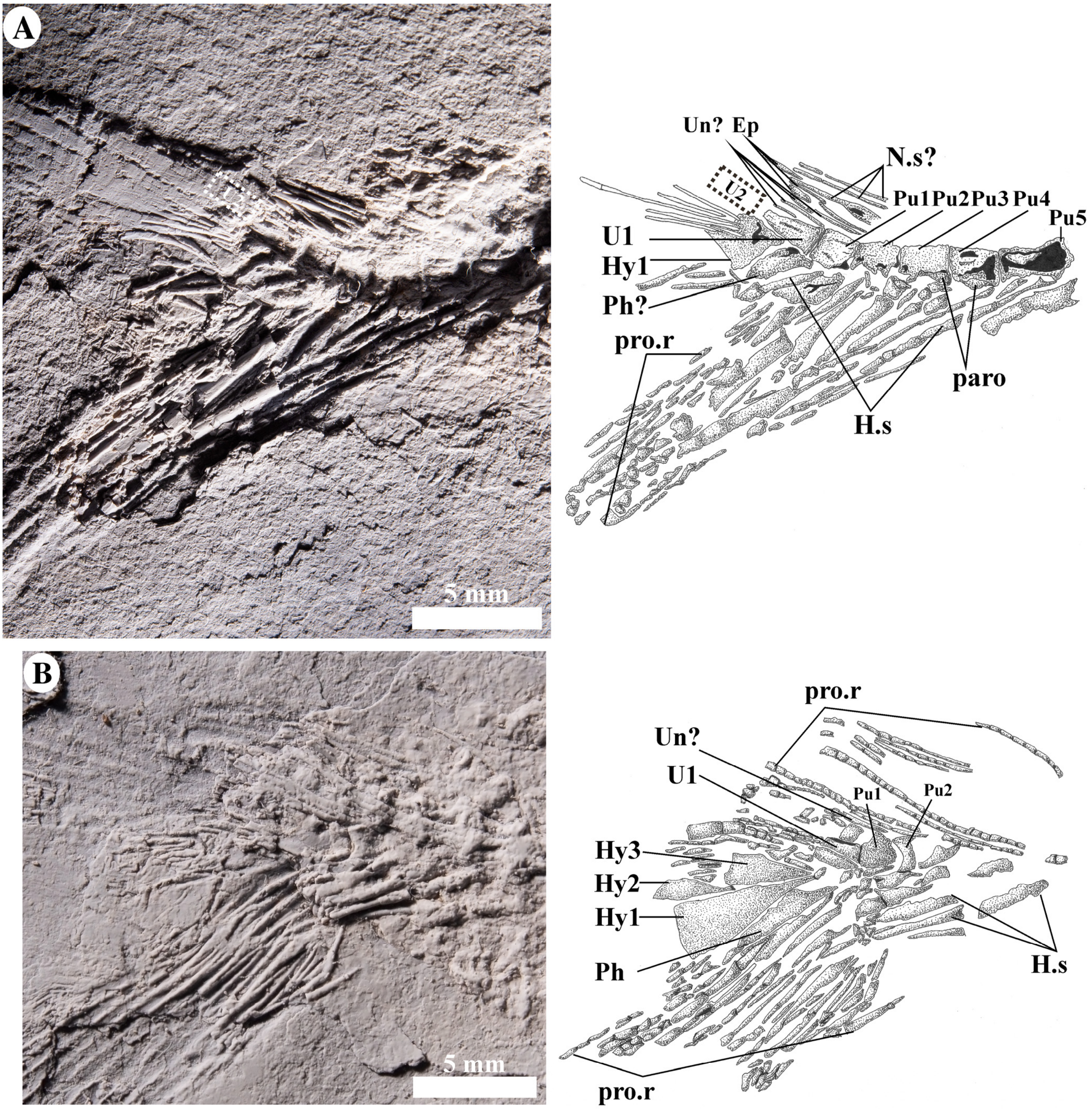

Figure 8. Caudal skeleton of †*Cladocynodon araripensis* gen. et sp. nov. (**A**) Photo and interpretative drawing of the exemplar CFUFMT 139 (holotype). (**B**) Photo and interpretative draw of the exemplar CFUFMT 432B (paratype).

The quadrate presents a massive posteroventral process (Figures 5 and 6B) as it is seen in the holotype with some parts partially preserved. In the paratype CFUFMT 432B (Figure 6B), the dorsal portion of the hyomandibula with both condyles is observed—the posterior one articulating with the pterotic and anterior one articulating with the autosphenotic—as is the foramen for the hyomandibular trunk of the facial nerve (f.VII.hm) (Figure 6B). Posteriorly the rounded opercular process is observed.

The pterygoid series is not complete and only the entopterygoid is preserved as a concave edentulous bone beneath the parasphenoid, extending anteriorly until it reaches the posterior border of the vomer (Figure 5). The circumorbial series is badly preserved to allow for a precise description, albeit in the holotype (Figure 5) there is probably a fragment of the Infraorbital 1(?) posterodorsally to the palatine.

4.2.4. Jaws

The upper jaw is composed of the premaxilla, maxilla, and two supramaxillae. The premaxilla is slightly curved with a triangular shape. The premaxillary alveolar border is badly preserved and thus the precise arrangement and number of teeth cannot be ascertained. The maxilla presents the typical shape of †Ichthyodectiformes—saber-shaped maxilla—as already pointed out by Bardack [2]. The lateral surface of the bone does not present any sort of ornamentation and reveals areas of small-sized teeth in a single row along all its extension. These teeth are small, caniniform, and regular in size. There are two well-developed supramaxillae, and the posterior one is with no dorsal process, a typical synapomorphy of Cretaceous †Ichthyodectiformes [12].

The lower jaw is composed of the dentary, angular, articular, and retroarticular. The dentary is a massive bone, and the maxilla likely presents teeth in a single row along all its extension (Figures 5 and 6). The anterior region of the dentary is marked by the presence of wide hypertrophied bony fangs, with other relatively small caniniform true teeth abruptly reduced in size posteriorly (Figure 7). In †*Cladocynodon araripensis*, the mandibular joint is composed of the angular, articular, and retroarticular, a pattern only known in †*Cladocyclus* [5], †*Gillicus*, †*Africathrissops*, and †*Furloichthys* [5,12,50,51] within †Ichthyodectoidei, due to the state of preservation of almost all species of the group. However, differently from all the other species of †Ichthyodectiformes, only in †*Cladocynodon* does the retroarticular form the posterior part of the articular facet for the quadrate (Figures 5 and 6B,C).

4.2.5. Opercular Series

Except for the preopercle and part of the opercle, all bones of the opercular series are not preserved (Figure 5). Partially preserved, the preopercle is L-shaped with a straight vertical limb and a blunt horizontal border (Figures 5 and 6). It is not possible to ascertain the shape of the posterior margin of the preopercle in †*Cladocynodon*, which is an important feature to distinguish some taxa of †Ichthyodectiformes—indented or not. The number of branches of the preopercular sensorial canal is highly variable within †Cladocyclidae, especially in the lower part. †*Cladocynodon araripensis* presents seven branches on its ventral border, the lowest number within the whole group (cf. †*Cladocyclus gardneri* presents twenty-five branches; †*Eubiodectes libancus* presents nine; †*Chiromystus mawsoni* fifteen; and †*Chirocentrites coroninii* twelve) [5,10,12,18].

4.2.6. Pectoral Fin and Girdle

The pectoral fin and girdle are not completely preserved in †*Cladocynodon.* The best-preserved pectoral fin and girdle are observed in the holotype CFUFMT 139 and paratype CFUFMT 432A (Figures 5 and 6A). The pectoral girdle was flattened and preserved. The coracoid is large and plate-like. In the dorsal surface of the expanded first right fin ray, it is possible to see the scapula and its anterior edge forming two condyles, probably the remaining scapular foramen. In the exemplar CFUFMT 432 B (Figure 6B), it is possible to observe a massive supracleithrum.

A well-developed first ray marks the pectoral fin. The exact number of rays is not possible to confirm, but it seems to be around five, which are unsegmented and unbranched. The poor state of preservation with many fin elements dislocated or hidden by sediments does not allow for precisely the exact number of radials, albeit there seems to be at least three.

4.2.7. Vertebral Column

The exact number of vertebrae centra is uncertain due to the poor preservation of the whole body (cf. part preserved as imprints, part dislocated, or partly covered by sediments). From what can be observed, †*Cladocynodon araripensis* presents around 46–54 vertebrae centra. Like all other †Ichthyodectiformes, prominent longitudinal ridges separating the deep dorsal and ventral pit mark the lateral surface of the centra. The anterior ribs are big and enclose the abdominal area (Figure 1), and thin longer epineurals are present and associated with abdominal neural arches (Figures 1, 5 and 6).

4.2.8. Pelvic, Anal, and Dorsal Fins

These fins are badly preserved and most of the details, such as the number of rays and pterygiophores, cannot be ascertained. However, it is important to notice that the dorsal fin is remote and opposed to a falcate and long anal one, revealing a typical †Ichthyodectiformes type (Figure 1).

4.2.9. Caudal Skeleton

Most of the caudal skeleton is not completely preserved. In the holotype CFUFMT 139 (Figure 8A), there are two ural centra and at least four preural centra and all hemal spines are autogenous. The first ural centrum is elongated with an acuminate posterior extremity and the second ural centrum is preserved as an imprint (Figure 8A). The exact number of hypurals is uncertain, albeit the first three are preserved (Figure 8B), with the first two presenting a triangular shape and articulate to the first ural centrum. The exact number of uroneurals (Figure 8A,B) is unknown. There are at least three epurals (Figure 8A). The exact number of principal and procurrent rays is unknown, and the remaining pieces of them are segmented and branched.

5. Discussion and Conclusions

According to Patterson and Rosen [18], the clade †Ichthyodectiformes is supported by five synapomorphies (cf. paired ethmopalatine ossification in the floor of the nasal capsule, articulating with the palatine; six or seven uroneurals, the first three or four extending anteroventrally to cover the entire lateral surface of the first, second, or third preural centra; teeth in a single series in the jaws; coracoid enlarged ventrally, meeting its fellow in a mid-ventral coracoid symphysis; anal fin long, falcate, opposed by a short, remote dorsal fin). Within these characters, †*Cladocynodon araripensis* certainly shares with this group, despite the uncertain number of bony pieces; the presence of uroneurals covering the lateral surface of the first preural centra (it is not possible to specify how far anteriorly they extend, Pu3 or Pu4); the teeth arrangement in the premaxilla, maxilla, and dentary bones in a single row; the pectoral girdle marked by coracoids enlarged ventrally, meeting each other in a mid-ventral symphysis; and a long, falcate anal fin positioned opposed to a remote dorsal fin. More recently, Cavin et al. [12] in a huge phylogenetic analysis proposed 10 characters to support the node "Cretaceous †Ichthyodectiformes", two of them being synapomorphic for the group (cf. presence of two supramaxillae, the posterior one with no dorsal process; the typical bulldog shape of the mandible). Taking into account this last hypothesis, †*Cladocynodon araripensis* also shares both characters with the †Ichthyodectiformes from the Cretaceous period.

Notwithstanding, several fossil taxa aligned to †Ichthyodectiformes are often badly or incompletely preserved which prevents a precise identification of some characters—a problem we face with †*Cladocynodon*. This problem has already been highlighted by some authors, e.g., [9,12,17], who proposed a combination of useful general features for this group (cf. peculiar *bauplan* characterized by its bulldog-like head; moderate to very elongated trunk; expanded first rays of the pectoral and pelvic fin; paired fins located posteriorly in the body; reduced dorsal fin). Besides the synapomorphies pointed out above, †*Cladocynodon araripensis* also shares with †Ichthyodectiformes this character combination, which doubtlessly corroborates its inclusion within this order.

Patterson and Rosen [18] subdivided †Ichthyodectiformes into two suborders: †Allothrissopoidei and †Ichthyodectoidei. According to them, †Allothrissopoidei is supported by three synapomorphies (cf. absence of suborbital bone; infraorbital canal with few canaliculi, ending blindly in lachrymal without reaching antorbital; and, hemal arches fused with centra in most of the caudal region). In †*Cladocynodon araripensis*, the suborbital bone and infraorbital canal are not preserved, and the hemal arches are autogenous in the caudal region. Patterson and Rosen [18], followed by Alvarado-Ortega and Brito [10] and Cavin et al. [12], proposed five synapomorphies to support the suborder †Ichthyodectoidei (cf. supraoccipital crest high and triangular; parietals located far from the posterior border of the skull; large intercalar forming the posterior edge of the hyomandibular facet; ethmopalatine with membranous outgrowths separating and suturing with the rostrodermethmoid and lateral ethmoid; and palatine head modified into a disc-like malleolus). Within these characters, †*Cladocynodon araripensis* shares with †Ichthyodectoidei a high supraoccipital crest and the palatine head modified into a disc-like malleolus. Conversely, most of its skull roof is not preserved, and thus the parietals and intercalar are not observable. The ethmopalatines cannot be confidently identified in †*Cladocynodon araripensis*, something directly related to the definition/interpretation of what these bones should be. The typical supraoccipital crest and the condition observed in the palatine bone, together with the typical *bauplan* body plan, corroborates the inclusion of †*Cladocynodon araripensis* within the †Ichthyodectoidei.

The ethmopalatines bones vary in shape, number, and composition in Teleostei. Despite this, there is a consensus, e.g., in [23–29], that these bones are always positioned between the anterior edge of the palatine and the posteromedial process of the maxilla, something extremely hard to observe in the †Ichthyodectiformes fossil fishes, especially those flattened and preserved (most of the species with preserved skulls).

According to Forey and Cavin [9], for example, based on a unique braincase, the ethmopalatine of †*Cladocyclus pankowskii* (Cenomanian of Morocco)—recently considered synonymous of †*Aidachar paludalis* from Uzbekistan [52]—is well-developed and forms the floor and the inner and posterior walls of the nasal capsule; anteriorly it contacts the rostrodermethmoid and is sutured to the vomer, forming a cup-shaped articulatory facet for the head of the maxilla; posteriorly it overlies the lateral ethmoid. This pattern is quite different from the former identification of these bones. They also pointed out that in primitive †Ichthyodectiformes, the ethmopalatine is very small and lies beneath the lateral ethmoid and rostrodermethmoid without direct contact with the maxilla. Cavin et al. [12] detailed in distinct †Ichthyodectiformes, especially in †Cladocyclidae species, the relationship between the ethmopalatines and maxilla to form such an anatomic complex. Within †Cladocyclidae [12], the ethmopalatines are not observed in †*Chirocentrites coroninii*, being large without membranous outgrowth in †*Chiromystus mawsoni* and †*Eubiodectes libanicus* and large with membranous outgrowths separating and suturing with the rostrodermethmoid and lateral ethmoid of the articular facet in †*Cladocyclus gardneri*. According to [12], in †*Eubiodectes libanicus*, the ethmopalatines is sutured only with the rostrodermethmoid that is responsible for the articulation with the maxilla. †*Cladocyclus gardneri* shares with other †Ichthyodectiformes (cf. †*Thrissops formosus*; †*Heckelichthys vexillifer*) the ethmopalatines articulated to the posteromedial process of the maxilla without the participation of the rostrodermethmoid. In all †Ichthyodectiformes species, the ethmopalatines present a high variability in shape, size, and relationship with the maxilla that deserves further attention in future phylogenic analysis. Finally, if the bone present in †*Cladocynodon* represents an ethmopalatine (Figures 5 and 6B), it probably has the same pattern found in primitive †Ichthyodectiformes (cf. small bone positioned beneath the lateral ethmoid and rostrodermethmoid and without contact with the maxilla).

Maisey [5] erected the family †Cladocyclidae to encompass the genera †*Cladocyclus*, †*Chiromystus*, and †*Chirocentrites*, based on one synapomorphy—the presence of a high supraoccipital crest overhanging the occiput. Later, Alvarado-Ortega and Brito [10] and Alvarado-Ortega [53] considered this family an unnatural group. According to [10,53], this pattern on the supraoccipital crest is also found in some other non-†Cladocyclidae (cf. †*Thrissops* and †*Xiphactinus*), and almost all other †Ichthyodectiformes or this region are badly preserved or covered with plates of the pectoral girdle, preventing a more precise observation. †*Cladocynodon araripensis* presents a high supraoccipital crest preserved as an imprint, and consequently, its relationship with the occiput cannot be detailed.

Cavin et al. [12], obtained a different hypothesis for †Cladocyclidae. According to them, this family encompasses the species †*Cladocyclus gardneri*, †*Chiromystus mawsoni*, †*Chirocentrites coroninii,* and †*Eubiodectes libanicus*, being well-supported by five synapomorphies: the presence of a prominent basipterygoid process projected upward (character 8 (state 2)); the presence of large ethmopalatines without no membranous outgrowth (character 13 (state 2)); retroarticular contributes to the articular facet (character 32 (state 0)); well defined and rounded opercular process on the hyomandibula (character 37 (state 0)); the first uroneural extends forwards to preural centrum 2 (character 65 (state 3)). †*Cladocynodon araripensis* certainly with them the characters 32 and 37, which justify its inclusion within this family.

Concerning the presence and shape of the basipterygoid process in †Cladocyclidae, it deserves further observations in more exemplars. According to Cavin et al. [12], in their data matrix, this character is considered unknown (coded "?") for †*Chiromystus mawsoni* and †*Chirocentrites coroninii*, and presents as described in the respective state only in †*Cladocyclus gardneri* and †*Eubiodectes libanicus*. †*Cladocynodon araripensis* presents a dislocated basipterygoid process angled downward (character 8 state [1]), which could represent a reversion in this taxon.

†*Cladocynodon araripensis* differs from the other †Cladocyclidae by the presence of hypertrophied bony fangs (no evidence of enamel has been identified) at the anterior region of the dentary with other relatively small true teeth, regular in size, abruptly reduced posteriorly (Figure 7); by the presence of reduced premaxillary and maxillary teeth; by presenting a mandibular joint composed by the angular, articular, and retroarticular (pattern only known in †*Cladocyclus* [5], †*Gillicus*, †*Africathrissops*, and †*Furloichthys* [5,12,50,51] within †Ichthyodectoidei) but differently from all other species; only in †*Cladocynodon* does the retroarticular form the posterior part of the articular facet for the quadrate (Figures 5 and 6).

The description of †*Cladocynodon araripensis* from the Aptian of the Batateira Beds, Barbalha Formation, and the Araripe basin represents the first record of a vertebrate in this unit. It also raises questions about the key †Ichthyodectiformes synapomorphies, due to their weak support in almost all taxa, which is probably linked to their badly/poor/incomplete preservation. †*Cladocynodon* also represents the first †Cladocyclidae known outside of the Crato and Romualdo Formation, Santana Group, and increases the anatomic diversity and paleoenvironment of †Cladocyclidae in the Mesozoic. The occurrence of †*Cladocynodon araripensis*, a predator at the top of the food chain (Figure 9), requires the co-occurrence of an as-yet-unknown fish community.

Figure 9. †*Cladocynodon araripensis* gen. et sp. nov. Reconstruction of lifestyle (illustration by Vitor Silva).

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