

Short communication

Cannibal predatory habits and their relationships with body shape and swimming pattern in the Cretaceous fish *Dastilbe crandalli* Jordan, 1910 from the Araripe Basin, Northeastern Brazil

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ABSTRACT

Dastilbe crandalli is a small to medium-sized fossil Chanidae species, between 65 mm and 180 mm in length, without dentition, feeding mainly on algae and small planktonic and benthic organisms. The fusiform and hydrodynamic body shape combined with the forked fin and elasmoid scales allow them to develop high speeds and less drag in the water, proving to be useful for escaping predators and predating on fish, including small specimens of *D. crandalli*. The presence of fossils showing predation among specimens of *D. crandalli* from the Cretaceous of Araripe Basin evidences cannibalism behavior in this species.

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1. Introduction

Gonorynchiformes fishes include the families Chanidae, Gonorynchidae and Kneriidae. This order together with the Otophysi (Cypriniformes, Characiformes, Gymnotiformes and Siluriformes) form the clade Ostariophysi (Nelson, 2016). The current species of this order are found in marine, brackish environments from Indo-Pacific region, rarely in the Atlantic, in the eastern Pacific portion and in freshwater environments (Nelson, 2016). Similarly fossil species were found in sediments from environments considered brackish and marine and less commonly in freshwater (Fara et al., 2010). Among these fossil species are those belonging to *Dastilbe* Jordan, 1910, an extinct genus belonging to the Chanidae family. This genus was originally composed of the species *D. batai* Gayet, 1989, *D. crandalli* Jordan, 1910 (Araripe Basin), *D. elongatus* Santos, 1947 (Parnaíba Basin, Codó Formation) and *D. moraesi* Santos, 1955 (Areado Formation). Currently, only *D. crandalli* remains valid, with the species *D. batai* (equatorial Africa) and *D. elongatus* considered

as junior-synonyms, while *D. moraesi* was renamed as *Franciscanos moraesi* (Santos, 1955) by Ribeiro et al., 2022, new and monotypic genus. There is also a supposed other species, "*Dastilbe minor*" (Tucano Basin, Marizal Formation), not formally described, and then it was considered as *nomen nudum*.

Dastilbe crandalli is a small to medium-sized species, reaching between 65 mm and 180 mm Standard Length (SL), without dentition, feeding mainly on algae and small planktonic and benthic organisms. Piscivory, according to the fossil record, and until the current article, seemed to occur only in fully developed specimens (from 150 mm SL) (Davis and Martill, 1999). Similarly, the only current species of its family, *Chanos chanos* (Fabricius, 1775), of equivalent size (from 50 mm to 180 mm SL) (Bagarinao, 1994; Gale Group, 2003), does not have dentition, feeding primarily on algae and small planktonic and benthic organisms. The piscivory (represented by the ingestion of small Clupeidae) would only be found in adult individuals (greater than 120 mm SL) (Bagarinao, 1991).

The presence of a fusiform body (Lagler et al., 1977), a furcated caudal fin in *D. crandalli*, and the presence of elasmoid scales, which promote a decrease in friction between the water and the body of the specimens (Bemvenuti and Fisher, 2010), indicate that

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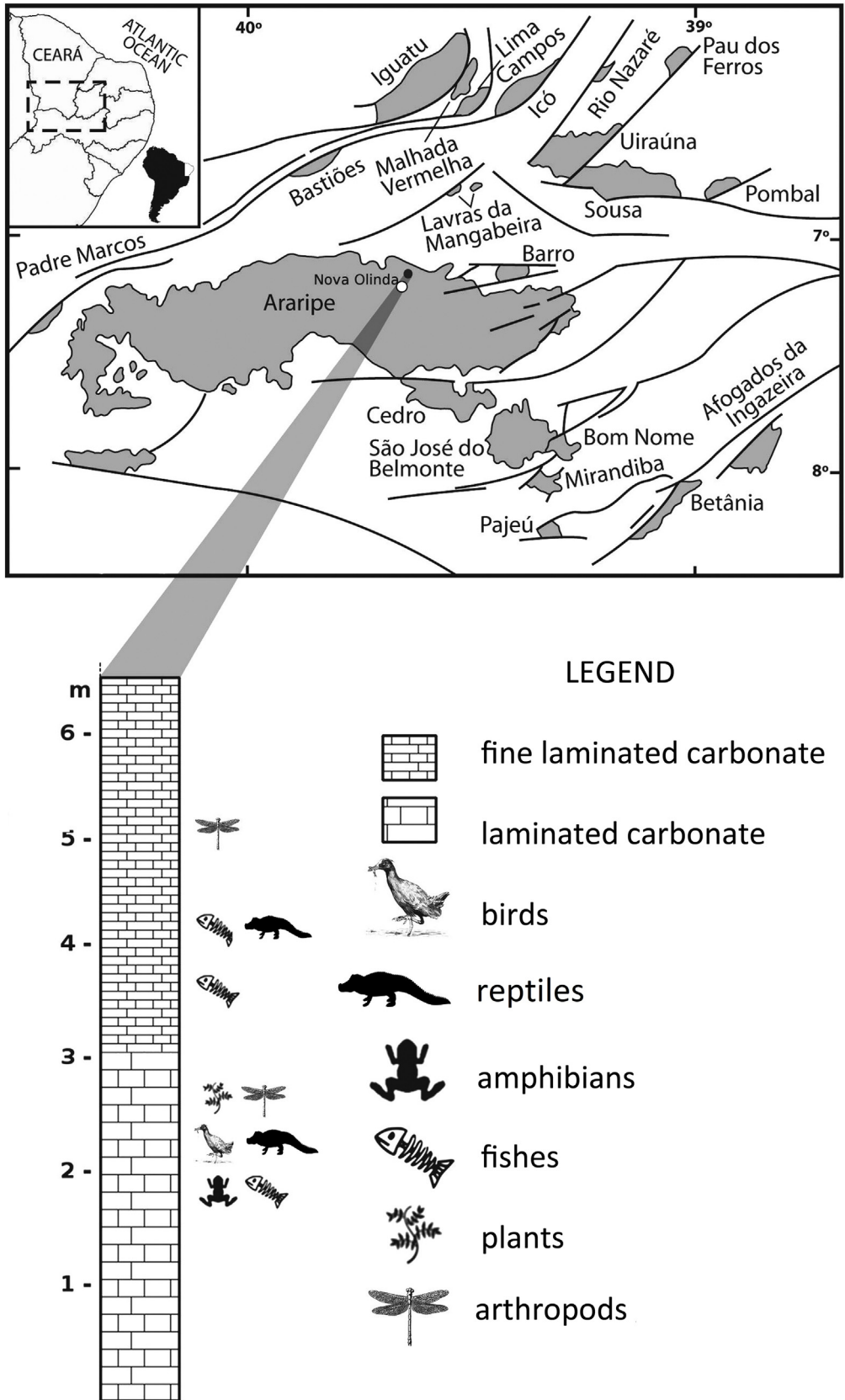


Fig. 1. White circle: Locality of specimens of *Dastilbe crandalli* Jordan, 1910 in cannibalism, UFRJ-DG-1909-P, Pedreira Mina Pedra Branca, Nova Olinda, Ceará, Brazil, 07°07'10"S 39°41'56"W. Horizon: Araripe Basin, Crato Formation. Map: modified from Degani et al. (2023).



Fig. 2. Specimens engaged in predation. *Dastilbe crandalli* Jordan, 1910, UFRJ-DG-1909-P, (larger: 95 mm SL, smaller: ±70 mm SL), Pedreira Mina Pedra Branca, Nova Olinda, Ceará, Brazil, 07°07'10"S 39°41'56"W. Horizon. Araripe Basin, Crato Formation. Scale bar: 2 mm.

D. crandalli were good swimmers using speed to run away from possible predators.

In this article is discussed predatory and cannibalistic behaviors found in specimens of *D. crandalli* from the Araripe Basin, Crato Formation (Aptian), Northeastern Brazil.

2. Geological background

The Araripe Basin is a northeastern Brazilian basin originated under complex tectonic history related with the Gondwana breakup and South Atlantic opening (Matos, 1992; Carvalho, 2000; Assine, 2007). It covers an area of 12,200 km² located in the south of the Ceará State, northwestern Pernambuco State and east of Piauí State. In surface area, the Araripe Basin include the Araripe Plateau (Chapada do Araripe), up to 900 m high and extending some 200 km from east to west (Maisey, 1991). The basin is filled with coarse and fine-grained clastic sediments and chemical deposits with many lithostratigraphic proposals (Beurlen, 1971; Machado et al., 1990; Ponte and Appi, 1990; Mabesoone et al., 2000; Neumann and Cabrera, 2002; Neumann et al., 2002; Heimhofer and Martill, 2007; Martill, 2007a, 2007b; Heimhofer et al., 2010; Paula-Freitas and Borghi, 2011; Rios-Netto et al., 2012; Assine et al., 2014; Araripe et al., 2022).

The fossils analyzed in this study occur in the lower carbonate succession of upper Aptian age (Crato Formation), one of the most important Cretaceous Lagerstätten from the Gondwana (Fig. 1). Large numbers of fossils from the Crato Lagerstätte show exquisite soft tissue preservation (Martill et al., 2007a; Barling et al., 2015; Carvalho et al., 2015a, 2015b; Catto et al., 2016; Maldanis et al.,

2016; Warren et al., 2017; Carvalho et al., 2019; Varejão et al., 2019; Agnolin et al., 2020; Dias and Carvalho, 2020; Santos et al., 2020; Santos et al., 2021; Santos et al., 2021; Santos et al., 2023; Carvalho and Leonardi, 2021; Carvalho et al., 2021; Gomes et al., 2021; Ribeiro et al., 2021; Cincotta et al., 2022; Batista et al., 2023; Degani-Schmidt et al., 2023; Gúsman et al., 2023).

The deposition of Crato Formation occurred during a phase of tectonic quiescence, consisting of laminated limestone which indicate periods of low and high concentration of sulfite related to relatively anoxic water conditions (Varejão et al., 2020; Gomes et al., 2021; Guerra-Sommer et al., 2021; Iniesto et al., 2021; Dias and Carvalho, 2022). The general growth pattern of the Araucariaceae *Agathoxylon* Hartig, 1848, found in this succession was interpreted by Santos et al. (2021) as the resulted of temporary water stress, a limiting factor for favorable growing.

3. Material and methods

3.1. Specimens

Two specimens of *D. crandalli*, between 70 and 95 mm SL, housed in the Macrofossil Collection, Geology Department, Rio de Janeiro Federal University (UFRJ-DG-1909-P).

3.2. Measures, counts and proportions

The specimens were measured using a 200 mm Marberg digital caliper, the measurements being presented in millimeters. Counts were made under stereomicroscopes. Proportions were calculated



Fig. 3. *Dastilbe crandalli* Jordan, 1910 preoperculum, in detail, in, UFRJ-DG-1909-P (95 mm SL), Pedreira Mina Pedra Branca, Nova Olinda, Ceará, Brazil, 07°07'10"S 39°41'56"W. Horizon. Araripe Basin, Crato Formation. Scale bar: 2 mm.

using the Excel program. All data are organized in tables of this same program. Digital photographs were obtained and edited using a Zeiss Plan Apo S1x FWD 60 mm SyCOP 3 stereomicroscope coupled to an Axio Cam MRC 5 digital camera, using the AxioVision Release 4.8 program.

4. Results

4.1. Systematic paleontology

Ostariophysi Sagemehl, 1885.
 Anotophysii Rosen and Greenwood, 1970.
 Gonorynchiformes Greenwood, Rosen, Weitzman and Myers, 1966.
 Chanidae Jordan, 1887.
Dastilbe Jordan, 1910.

Dastilbe crandalli Jordan, 1910.

Examined Material. *Dastilbe crandalli*. UFRJ-DG-1909-P – two specimens: one with 95 mm SL and other with 70 mm SL (estimate). Locality and Horizon: Pedreira Mina Pedra Branca, Nova

Olinda, Ceará, Brazil, 07°07'10"S 39°41'56"W. Araripe Basin, Crato Formation. Upper Aptian.

4.2. Description of the fossil

UFRJ-DG-1909-P (Fig. 2): larger specimen (95 mm SL) with fusiform body (hidrodinamycis characteristic), presence of pectoral, dorsal, pelvic, anal and caudal fins, the last one being furcated. In the larger specimen is observed: pre-operculum with branches forming right angles to each other (Fig. 3). Edentulous maxillomandibular apparatus, consisting of premaxillary, maxillary and dentary, with the supramaxillary absent (Fig. 4). Smaller specimen (estimate – 70 mm SL) with forked caudal fin (characteristic of carangiform swimming pattern), supported by six hypurals (Fig. 5). By comparison with other specimens of *D. crandalli*, of equivalent sizes, it is correct to state that the sample with the two specimens belong to this species. As similarities in the larger specimen, the bones of the skull and of the caudal skeleton stand out, equivalent in shape and number. In the smaller specimen, the number and shape of the bones of the caudal skeleton stand out, especially the hypurals. This sample

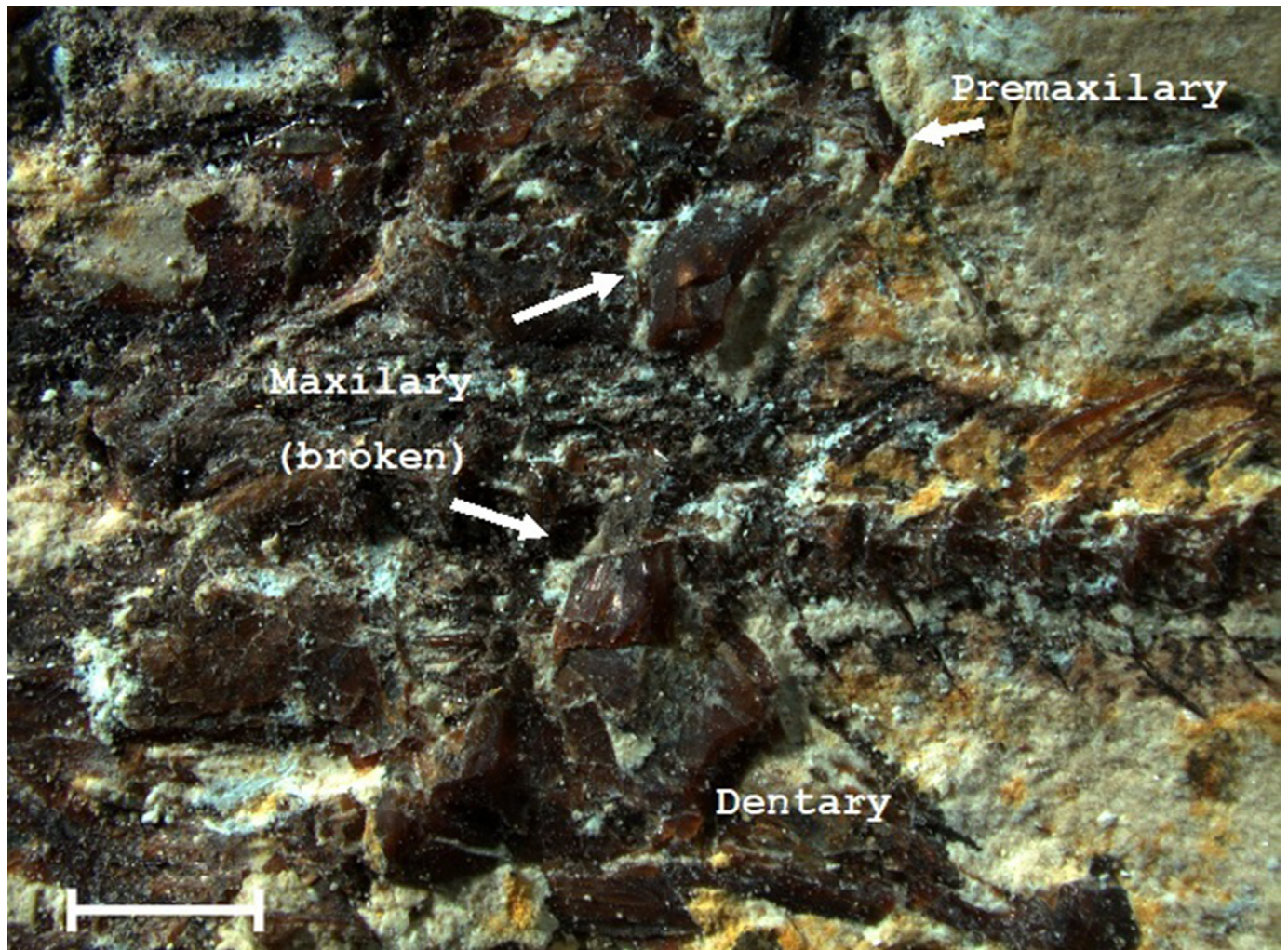


Fig. 4. Oral region of *Dastilbe crandalli* Jordan, 1910, specimen UFRJ-DG-1909-P (95 mm SL), Pedreira Mina Pedra Branca, Nova Olinda, Ceará, Brazil, 07°07'10"S 39°41'56"W. Horizon. Araripe Basin, Crato Formation. Scale bar: 2 mm.

record the cannibalism practiced by a specimen of 95 mm SL on a smaller specimen (see Fig. 6).

5. Discussion

Predation between fish specimens are described in the fossil record related to different species. Maisey (1994) reported cases of predation involving ichthyofauna species from the Araripe Basin, elucidating local trophic networks. Remains of specimens of *Rhacolepis* Agassiz, 1841 were found in the stomach of *Notelops* Woodward, 1901 Specimen. Remains of *Santanichthys* Santos, 1995 were also found in the stomach of *Racholepis*. Predation of specimens of *Cladocyclus* Agassiz, 1841 on *Rhacolepis* and *Calamopleurus* Agassiz, 1841 on *Vinctifer* Jordan, 1919 were also recorded. In Wilby and Martill (1992) also a disarticulated fish was found in the gut region of a single specimen of *Vinctifer*. Specimens of *Santanaclupea* Maisey, 1993 containing remains of small Gonorynchiformes were evidenced in Maisey (1994). Robertson et al. (2019) also reported cases of predation involving a specimen of *Diplomystus* Cope, 1877 (Clupeiformes, Eocene), from freshwater environments. Ebert et al. (2015) described in deposits from southern Germany (Late Jurassic), a fossil of *Belonostomus* cf. *kochi* Münster, 1836 (Aspidorhynchiformes) containing in its mouth, pharynx and esophagus a specimen of *Orthogonikleithrus hoelli* Arratia 1997 (Teleostei).

Specimens of *O. hoelli* were found involved in cannibalism: remains of other individuals present in the digestive tract, including the mouth opening with smaller fish inside (Ebert et al., 2015). These researchers recorded 20 specimens with small fish in their mouths and 39 individuals with specimens in their stomachs (Ebert et al., 2015). Regarding South American species, in Maisey (1994) were registered cannibalism cases involving specimens of *Calamopleurus* (probably), *Notelops* and *Racholepis*. In Maisey (1994) was registered the first record involving predation and cannibalism in *D. crandalli*. This researcher found remains of a specimen (± 35 mm SL) in the stomach of a larger specimen (135 mm SL), concluding that cannibalism in *D. crandalli* is a rare event, given the eating habits and morphology of the mouth in this species, similarly to that was reported by Ribeiro et al. (2020). The second record of the cannibalism in *D. crandalli* was registered in Davis and Martill (1999), in specimens with 150 mm SL on smaller specimens in *D. crandalli*. In the present study, predation and cannibalism of smaller specimens (95 mm SL) of *Dastilbe crandalli* on other specimens were found for the first time, constituting the third record involving specimens of *D. crandalli* in this type of intraspecific interaction. Maisey (1994) and Davis and Martill (1999) found cannibalism only in greater specimens (135 mm SL and bigger than 150 mm SL, respectively) under smaller ones, not finding evidence of predation (in this case, cannibalism) in smaller specimens,

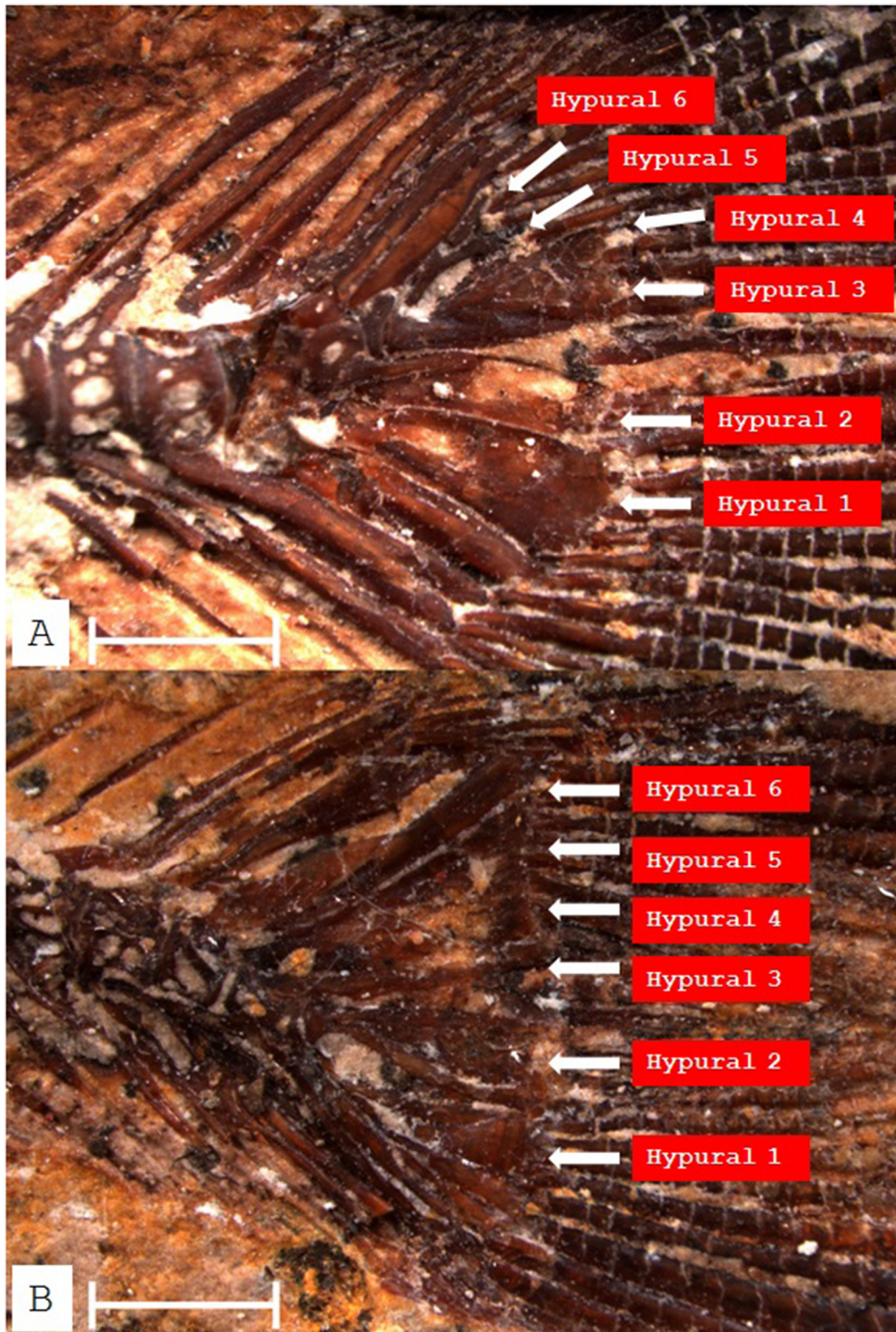


Fig. 5. Caudal skeletons, in detail, in *Dastilbe crandalli* Jordan, 1910, specimen UFRJ-DG-1909-P, A. larger specimen (95 mm SL), and B. smaller specimen (± 70 mm SL), Pedreira Mina Pedra Branca, Nova Olinda, Ceará, Brazil, 07°07'10"S 39°41'56"W. Horizon. Araripe Basin, Crato Formation. Scale bar: 2 mm.



Fig. 6. Reconstitution scenery of the cannibalism among *Dastilbe crandalli* Jordan, 1910, from the Araripe Basin (Art by Deverson Silva, Pepi).

measuring between 65 and 92 mm SL. The size of the cannibal specimen described in this study is 95 mm SL, enlarging the size range in which this cannibalism is possible. In addition, by the shape of the specimens and their caudal fins, it can be deduced that they were specimens capable of sudden increases in speed (carangiform swimming). The presence of a terminal mouth suggests the use of different levels at half water. For the first time, body and fin shape and eating and swimming habits were related in *Dastilbe crandalli*.

Cases of cannibalism are common among current fish species (Hancock, 1852), although some studies considered a mechanism without evolutionary bias (Dawkins, 1976; Nesbit and Meffe, 1993). In other studies (Fox, 1975; Polis, 1981; Smith and Reay, 1991; Manica, 2002) the cannibalism is evaluated as an important survival mechanism, reducing the number of competing specimens and energy costs in its capture. Berg et al. (2010), Bjørnstad et al. (1999), Claessen et al. (2000), Huss et al. (2010), Persson et al. (2003) and Polis (1981) showed the emergence of a bimodality of body size in cannibals and non-cannibals from the same population. Cannibal specimens would become much larger than non-cannibal ones, which would feed only on invertebrates, as demonstrated in *Salvelinus alpinus* (Linnaeus, 1758) – Arctic trout – (Berg et al., 2010).

In the Ostarioclupeomorpha (clade where *Dastilbe* is inserted), cannibalism involving some species of Clupeiformes, such as *Clupea harengus* Linnaeus, 1758 (family Clupeidae), on its larvae (Balfoort, 1984) and *Engraulis ringens* Jenyns, 1842 (Engraulidae), on their eggs (Santander, 1987) and Cypriniformes such as *Cyprinus carpio* Linnaeus, 1758 on their larvae (Damme et al., 1989), have also been reported.

In Neotropical species, cannibalism has been widely recorded in *Hoplias malabaricus* (Bloch, 1794), on their juveniles (Winemiller, 1989; Luz-Agostinho et al., 2008; Bozza and Hahn, 2010), in *Brycon moorei* Steindachner 1878 and *Salminus*

brasiliensis (Cuvier 1816) on their larvae (Santos et al., 1993; Baras et al., 2000; Baras and Jobling, 2002; Schütz and Nüner, 2007) based on artificial environments with high number of individuals. It is present in other Characiformes such as *Acestrorhynchus lacustris* (Lütken 1875) (Rocha et al., 2011) and *A. pantaneiro* Menezes, 1992, on its juveniles (Krinski, 2010), *B. cephalus* (Günther 1869) and *S. hilarii* Valenciennes, 1850, on its larvae (Leonardo et al., 2008; Honji et al., 2011). Cannibalism has even been verified in the only living species of Chanidae, *Chanos chanos*, on its eggs (Toledo and Gaitan, 1992). It is interesting to note that the vast majority of these species that practice cannibalism have an invertivore diet, and some do not have dentition (*C. chanos*, *Cl. harengus*, *E. ringens*), similarly to *Dastilbe*, to which a supensivore-detritivore diet is assigned. Bagarinao (1991) found that larger specimens of *C. chanos* (same diet) eventually prey on juveniles of Clupeiformes, similarly to larger specimens of *Dastilbe* on smaller individuals.

Regarding the hydrodynamic body shape in *D. crandalli*, it seems to be useful both for escaping predators and as a facilitator in the capture of other fish. All the aforementioned species show a fusiform (Lagler et al., 1977) and hydrodynamic body, a furcated caudal fin (with the exception of *H. malabaricus*) and elasmoid scales, which reduce friction with water (Bemvenuti and Fisher, 2010). The fusiform shape facilitates reaching high speeds, body and caudal peduncle heights favor greater stability and dissipation of opposite kinetic energy originating in the anterior part of the body and dissipated by the peduncle (Breda et al., 2005).

The fusiform shape is usually found in fish that swim in the middle regions of the water column (Lopes, 2019; Lopes and Barreto, 2019). Its association with a terminal mouth (Fuentes, 2011; Fuentes and Quiroga, 2012) characterizes this behavior even more, as it facilitates the apprehension of other individuals in the water column (Rotta, 2003), turning these species generalists in relation to the exploration of food items (Gatz, 1979).

Regarding to swimming mode, species with a fusiform body have a type of BCF (Body and/or Caudal Fin) locomotion (Valdivia and Alvarado et al., 2006) of carangiform subtype (Lindsay, 1978). It is defined by undulations of the posterior half of the body, with the forked caudal fin (Bemvenuti and Fisher, 2010) as the main propulsive organ.

6. Conclusion

The fact that specimens of *D. crandalli* have a terminal mouth, a fusiform and hydrodynamic body and a furcated caudal fin (characters found in UFRG-DG-1909), characterize this species as a carangiform swimmer, an explorer of different depths in the water column and able of high speeds. It was a generalist fish, feeding on different food items, such algae, planktonic and benthic faunas. The presence of a smaller specimen in the initial portion of the digestive system of a larger one, as in UFRG-DG-1909, demonstrates the cannibalism habits in *D. crandalli*.

Data availability

Data will be made available on request.

Acknowledgments

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