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Keywords: Dermal scales, scale histology, Actinopterygii, Permian

Deep-scaled fish (Osteichthyes: Actinopterygii) from the lower Permian (Cisuralian) lacustrine deposits of the Parnaíba Basin, NE Brazil

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Abstract

The richly fossiliferous deposits of the Brazilian Pedra de Fogo Formation originated in an extensive aquatic system in tropical Pangaea, and grade from marginal lacustrine into marine deposits at the depocenter in the western part of the Parnaíba Basin. In addition to the well-known tetrapod and macrofloral records from these deposits, the Pedra de Fogo Formation yields extensive fish fossils indicating a diverse and abundant ichthyofauna. Among the actinopterygians, deep-bodied morphotypes are represented by whole fish as well as disarticulated dermal scales found at various localities in the states of Maranhão and Piauí. The gross morphology, ornamentation, and histology of some of these scales is highly distinctive, indicating the presence of a novel taxon (*Piratata rogersmithii* gen. et sp. nov.). The external surface of a *Piratata* scale is covered in multiple round-to-slightly elongated tubercles. The scale lacks a ganoin cover and is made up of cellular bone and odontocomplexes of orthodentine composing the tuberculated scale surface. The scale morphology and ornamentation most closely resemble that of *Cleithrolepis granulatus* from the Triassic of Australia and *Cleithrolepis extoni* from the Triassic Stormberg Beds of South Africa, but the new taxon differs from previously described species in several diagnostic morphological features. The use of scale characters in the taxonomy of ray-finned fishes and the palaeogeographic, palaeoenvironmental, and geochronological implications of the new taxon are discussed.

Keywords: Dermal scales, scale histology, Actinopterygii, Permian

(Introduction)

The vast majority of Palaeozoic and Early Triassic fishes can be divided into fusiform (e.g. Perleidiformes, see Mutter & Herzog, 2004) and 'deep-bodied' morphotypes bearing trunk scales much deeper (higher) than they are broad (e.g. Platysomidae). It is increasingly clear that species exhibiting the latter morphotype do not constitute a monophyletic unit, and deep-bodied fishes have been shown to have originated multiple times by the early Carboniferous Period at latest (Sallan and Coates, 2013, Wilson et al. 2021). Here we describe a new taxon, currently known only through its relatively large and deep scales, which are locally abundant in many lower Permian (Cisuralian) deposits of the Pedra de Fogo Formation in the states of Maranhão and Piauí, NE Brazil. Although squamation characters have long been utilised to complement the diagnosis of fossil species (e.g. Agassiz, 1833-43; Aldinger, 1937; Gardiner, 1967), detailed studies of the morphological variations along the body of fossil species are rare (e.g. Blot, 1966; Chen, 2012). This hinders the taxonomic identification of isolated (disarticulated) scales. Moreover, isolated scales of basal actinopterygian ('palaeoniscid') fishes have often been considered unreliable for identification at genus and species levels, because ornamentation can also vary along the body in many taxa (Gardiner, 1967). Proposals to improve and standardise the description of scales in ray-finned fishes have focused on fine details (e.g. distribution of microtubercles on the surface of the ganoin tissue and the ultrastructure of the ganoin tissue under the scanning electron microscope) in addition to general morphology and overall ornamentation patterns (Brito et al. 2000; Richter, 1995; Richter and Smith 1995, Sire, 1995; Schultze, 2016; Ørvig, 1978; Zilberberg et al. 2016 and others). However, such characters have not been described in enough taxa to be sufficiently informative to aid in character coding for cladistic analyses.

We investigated the surface ornamentation of scales of a number of Palaeozoic and early Mesozoic fishes, both from continental and marine deposits, and compared them to the new material described here. The Pedra de Fogo Formation has also yielded well-preserved skull and post-cranial remains of an additional new taxon of deep-bodied fish whose full description will be the subject of a future publication, although we discuss and figure some relevant details of its squamation here.

Geological setting

The richly fossiliferous Pedra de Fogo Formation (Plummer, 1946) comprises up to 100 m thick deposits situated within the Parnaíba Basin of northeast Brazil, which originated in a large lacustrine system in the middle of tropical Pangaea (Cisneros et al., 2015; 2020; Araújo et al. 2016; Iannuzzi et al, 2018; Marsicano et al. 2021). Its outcrops are distributed in an E-W direction, stretching for about 600 km within the Brazilian states of Tocantins, Maranhão and Piauí (Fig. 1A,B). Abrantes et al. (2016) describe the paleogeographic landscape of the region from the lower to middle Permian as 'coastal to continental sabkha' distantly linked to the Panthalassa Ocean to the west (Fig. 1E) and including lacustrine deposits with a rich community of temnospondyl amphibians, fish and flora (Cisneros et al. 2015; Iannuzzi et al. 2018).

The absence of stenohaline marine fossils (corals, cephalopods, trilobites) in the Pedra de Fogo Formation is noteworthy, although their absence is not an infallible guide to depositional environments with periodic or seasonal marine influence (Gray, 1988; Cunningham, 1993; Schultze, 2009).

Fig 1 hereabout

Material and Methods

Photographs of the new fish material are provided on Figures 2 and 3. Specimen MAP PV1031 (an isolated dermal scale), has been thin-sectioned for histological study, and two polished slides were made utilising established methods (Chimsamy & Raath, 1992; Richter and Smith, 1995).

The fossil scales were collected during four fieldwork seasons between 2012–2018 at quarries of the Pedra de Fogo Formation in the states of Maranhão and Piauí.

Institutional abbreviations: MAP, Museu de Arqueologia e Paleontologia, Universidade Federal do Piauí, Teresina, Brazil; PB, Parnaíba Basin locality number at MAP catalogue (see Table 1 for geographic locations).

Systematic Palaeontology

OSTEICHTHYES Huxley, 1880

ACTINOPTERYGII Woodward, 1891

Piratata gen. nov.

urn:lsid:zoobank.org:pub:C388ACBD-9C33-40CC-A382-739F9AA60435

Type and only species. *Piratata rogersmithii* sp. nov. (**Figs. 2, 4I**)

urn:lsid:zoobank.org:pub:C388ACBD-9C33-40CC-A382-739F9AA60435

Etymology. The genus name is a combination of the Guarani indigenous language epithets *pira* (fish) and *tata* (fire), meaning ‘fire fish’ in reference to its provenance from the Pedra de Fogo Formation. The species name is in honour of geologist and Distinguished Professor Roger Malcolm Harris Smith who has greatly contributed to palaeontological expeditions in this region.

Materials: Isolated dermal scales: MAP PV1031 (holotype)**;** MAP PV069.1 (paratype), from PB12, Pastos Bons. Referred specimens: MAP PV1015; MAP PV369.2; MAP PV468a; MAP PV468b;

MAP PV630.10 (; MAP PV690.5; MAP PV690.6; MAP PV703.2; MAP PV840.1; MAP PV 630.7; MAP PV 630.3; PV 630.1; PV 630.4. The provenance of the material is given on Fig. 1 and Table 1.

Table 1 hereabout

Horizon and Type Locality. Pedra de Fogo Formation, Cisuralian. The holotype, MAP PV1031 was collected at locality PB42 (Fig. 1C), within the JG de A Ferreira limestone quarry, in the municipality of Pastos Bons, Maranhão State. PV069.1 (paratype) was collected at locality PB12 (Fig. 1C), only 50 m southeast of PB42, within the same quarry (see Table 1). This area is also the type locality of the actinopterygian *Brazilichthys macrognathus* Cox and Hutchinson 1991 and the temnospondyl *Prionosuchus plummeri* Cox and Hutchinson 1991. Most of the referred specimens were found at quarries in the municipality of Nazária in Piauí State, some 45 km south of the city of Teresina. The geological setting of these fossil sites, including the sedimentology and stratigraphic position of fossils found at PB133 locality, is addressed in Cisneros et al. (2020, fig. 1). Isolated scales of this new taxon are relatively common in other outcrops and quarries of the Pedra de Fogo Formation in both states.

Diagnosis as for type and only species. Actinopterygian fishes with rhombic, deep dermal scales. Height of flank scales including the dorsal peg is approximately three times the length of the scale. Dorsal peg broad-based and stout, making up a third of the scale height. External exposed area of the scale rectangular; scale external surface covered in blister-like, round and slightly elongated tubercles histologically made up of odontocomplexes, with odontodes composed of metadentine. Odontodes devoid of any enameloid or ganoin cover. Basal lamellar bone layer cellular, occupying up to two thirds of the scale's thickness. Internal side of the scale smooth, with an anteriorly positioned, narrow vertical crest; elongated socket for the articulation of the peg of the scale originally positioned in the row below.

Description: A number of isolated, thick scales that are at least three times as high as they are long have been recovered from various outcrops of the Pedra de Fogo Formation (Fig.1). Three of the scales belong to the type series (Fig. 2) and others are referred materials (Fig. 3). All presumably come from the flanks of the fish bodies rather than other regions and represent a new taxon of ray-finned fishes with rectangular-shaped scales that are higher than they are long. The scales are known to reach up to 7.5 cm in height, including the dorsal articulation peg. They show a well-developed peg-and-socket articulation system, with the stout peg making up a third of the height of the scale. The two specimens shown in external view are ornamented with small, round and sometimes slightly elongated tubercles that resemble blisters. The holotype (Fig. 2C-G) was vertically sectioned and two polished thin sections were made to investigate its histological features. The scale is composed of a basal layer of cellular lamellar bone making up to two thirds of the scale thickness. Overlaying the bone there is a layer of odontocomplexes (see Ørvig, 1967;1977; Fraser et al. 2010) whose component odontodes are composed entirely of metadentine (Smith and Hall, 1993). There is no hyper-mineralised tissue such as ganoin (see Richter and Smith, 1995) covering the odontodes, which make up the round tubercles on the surface of the scale. The absence of ganoin is also indicated by the matte (not shiny) aspect of the scale and its ornamental tubercles. Many reversal lines are observed within the odontocomplexes (Fig. 2F,G), which indicate intensive resorption and redeposition of dentinal tissue during scale growth. This accounts for the individual shapes of the tubercles observed on the surface of the scale. It is worth noting that this represents the first South American record of scales of Palaeozoic fishes ornamented with round tubercles composed of odontocomplexes but devoid of ganoin.

Figure 2 hereabout

Figure 3 hereabout

Flank Scale external ornamentation of selected Palaeozoic deep-bodied fishes

The flank scales of selected deep-bodied fishes are represented schematically in Figure 4. Six main types of external ornamentation were identified, independent of the presence or absence of a ganoin cover: *i*. very fine, numerous and parallel striations along the longest (vertical) axis of the scale, which has a smooth posterior margin (Fig 4 A-G). *ii*. Multiple small, round or very slightly elongated tubercles and a smooth posterior margin (Fig. 4 H-K). *iii*. A mix of longitudinally elongated and round tubercles and a smooth posterior margin (Fig. 4 L-M). *iv*. Fine, antero-posterior striations and surface punctuations with a slightly serrated posterior margin (Fig. 4 N). *v*. Elongated tubercles of various sizes that are approximately anteroposteriorly aligned and form a complex vermicular scale surface in some cases stretching over the scale margin and giving it a roughly serrated posterior margin (Fig. 4 O-P). *vi*. Longitudinal ridges varying in length and thickness, often transitioning into serrations at the posterior margin of the scale (Fig. 4 Q-S).

The flank scales of the majority of species that have been ascribed either to Platysomidae or Guildaichthyformes (Lund 2000) belong to type *i*. (Fig. 4A-F). However, it is uncertain whether all platysomids as a possible monophyletic clade possess this type of ornamentation (Sallan and Coates, 2013). For instance, the putative platysomid *Soetendalichthys cromptoni* Gardiner 1969 from the Upper Witteberg beds of South Africa (Mississipian) has tuberculated scales with serrated posterior margins. Ornamentation type *ii* is found with variation in tubercle distribution and shape on the deep-bodied fish *Platysomus bashkirus* Minikh 1992 from the Permian of Russia; *Piratata rogersmithii* gen. et sp. nov.; *Cleithrolepis granulatus* Egerton 1863 from the Triassic of Australia, *Cleithrolepis extoni* Woodward, 1888 from the Triassic of South Africa and *Amphicentrum granulosum* Young 1866 from the Pennsylvanian of Great Britain. Type *iii* is found in *Adroichthys tuberculatus* Gardiner, 1969 from the Carboniferous of South Africa and *Hemicalypterus weiri* Schaeffer, 1967 from the Late Triassic of the USA. (Figs 4H-M). Type *iv* is represented by *Eurynotus crenatus* Agassiz 1835, ascribed by Sallan and Coates (2013) to a distinct order, Eurynotiformes, which is characterised by the bones around the mouth developing a thick cover of ganoin and forming a 'beak' associated with the first crushing dentitions for actinopterygians in the geologic record. Type *v* is presented by two genera from the Cisuralian of Russia (*Ufalepis magnificus* and *Kargalichthys efremovi,* Fig. 4 O,P). Type *vi* is a variety of miscellaneous of taxa with longitudinally directed ridges of ganoin and serrated posterior margins (Fig. 4Q-S).

The scales of *Piratata rogersmithii* (Fig. 4I) resemble those in Fig. 4J, K, which represent marine and freshwater fishes confined to the Lower Triassic of Australia, Middle Triassic of South Africa, the Late Triassic of Germany and England and the Triassic of Libya (Gardiner, 1967, 1988). They also superficially resemble those of *Platysomus bashkirus* Minikh ~~et al.~~ 1992 (illustrated in Minikh & Minikh, 2009, p. 178, Pl. 46, fig. 2), which occurs in the middle Permian of Orenburg in European Russia (see Fig. 4H), but it is worth noting that the ornamentation of the Russian species differs from the 'typical' platysomid type *i* (Fig.4A-G). Further studies are needed to establish the systematic interrelationships between fishes ascribed to Platysomidae, which are currently considered a paraphyletic group (Sallan and Coates 2013). Although the scale ornamentation of lower actinopterygian fishes is generally considered of limited taxonomic value (Mickle, 2017; Stamberg, 2018) due to the fact that there can be substantial variations in the same individual, we argue that in the case of Palaeozoic and early Mesozoic deep-bodied fishes there seems to be retention of certain discrete patterns (e.g. Fig 4A-G) that could be indicative of close phylogenetic interrelationships. This hypothesis requires further investigation, as none of the published cladistic analyses utilise scale ornamentation as a character.

Figure 4 hereabout

Scale histology of deep-bodied fishes

An overview of the main histological features of dermal scales of osteichthyan fishes, including the distribution of tissues such as dentine, ganoin and bone is provided by Schultze (2016).
However, the histological features of the scales of most deep-bodied fishes are poorly known. Williamson (1849) pioneered the histological investigation of 'ganoid' scales. He described and figured a sectioned scale of *Platysomus parvulus* Agassiz 1835 (in Williamson, 1849, pl xvi, figs. 12-14) from the Carboniferous of England. Although the terminology he utilised is (understandably) not a modern one, he demonstrated that there is a basal layer of lamellar, cellular bone overlain by odontocomplexes (his 'arches'). It would be worth reinvestigating the histology of the scales of this species utilising modern optical microscopes, because he wrote that '*no appreciable layer of ganoin covers these*

arches' (Williamson, 1849, p.450) and the illustration provided does not clarify the matter. However, Aldinger (1937) found that scales of *Platysomus* sp. from the late Permian of Greenland lack ganoine and dentine, the 'hollow ridges' making up the most superficial layer of the scales consist instead of cellular lamellar bone, whereas *Kargalichthys efremovi* Minikh 1986 (in Bakaev et al., 2020) possesses a ganoin cover (Ivanov et al. 2021).

Traquair (1879) provided one of the first detailed accounts of the differences and similarities between various deep-bodied fossil fishes, noting that the resemblances between the platysomids, *Dapedium* and pycnodonts are mere resemblances of analogy, and not of real affinity" (p. 389). Also, "*in the majority of Platysomidae the scales of the body have the keel of the internal surface, which passes above into the articular spine, coincident with, or close to the anterior margin. This is, however, not the case in Eurynotus*" (p. 388).

Schultze (1985), who '*tend[ed] to assign scales without ganoin but with bone sculpture to platysomoids*' (Schultze, 1985, p.9), figured isolated teeth and scales from the Lower Permian of Kansas, mostly from marine sequences, but none are similar to *Piratata*. The fact that *Piratata* presents a previously unknown ornamentation histology (rounded tubercles composed of odontocomplexes but lacking ganoin) underscores that significant unexplored histological variation exists among the scales of Paleozoic deep-bodied fishes. A more comprehensive assessment of this variation is needed as a first step to synthesizing histology, gross scale morphology and ornamentation, and morphological characters from other parts of the skeleton (where available) in a modern phylogenetic context.

Conclusions

For the first time, deep-bodied fish scales ornamented with round tubercles composed of odontocomplexes but devoid of ganoin are reported from the Palaeozoic of South America.

Piratata rogersmithii is also one of the few Palaeozoic fish with a presumed deep-bodied morphology whose scale histology is now known. The other deep-bodied fish from the Permian of Brazil, namely *Paranaichthys longianalis* Dias, 2012 from the late Permian of the Paraná Basin in southern Brazil differs from *P. rogersmithii* in possessing scales covered with ganoin layers and flank scales approximately as long as they are deep.

There is a noteworthy range of morphological variation in flank scales among the better known deep-bodied fishes, including their proportions, surface ornamentation, morphology of their posterior margin and articulation features, that have not been added to cladistic analyses to our knowledge.

The distribution of scale ornamentation and histological characters remains underexploited and may be taxonomically significant in many cases. The similar, strongly rugose scales of *Ufalepis magnificus* and *Kargalichthys efremovi* (Fig. 4 O-P) seems in this case to indicate close affinity between the two genera. The vertical delicate ridges covering the scales of most of the platysomids included on Fig. 4 seems to support a hypothesis that this is indeed 'typical' of platysomids scales. However, it would be inadvisable to base phylogetic conclusions on shared squamation characters alone, because

Platysomus striatus and the bobasatraniiform *Ebenaqua ritchiei* (Fig. 4 F-G) show some slight deviation from a similar pattern. Deep-bodied fishes with scales ornamented with a variety of round tubercles, as is the case of *Platysomus bashkirus*, *Piratata rogersmithii*, *Cleithrolepis extoni, Cleithrolepis granulatus, Amphicentrum granulosum*, *Adroichthys tuberculatus* and *Hemicalypterus weiri* (Fig. 4 H-M) obviously do not form a monophyletic group and therefore utilising their squamation characters in phylogenetic studies requires substantial attention to detail. Scales covered in nearly smooth ganoine showing only punctuations such as in *Eurynotus crenatus* (Fig. 4N) seem to represent the plesiomorphic condition based on studies of the early bone fish *Psarolepis romeri* Qu et al., 2013 and the same pattern is found in many palaeoniscid fishes. Lower actinopterygian scales such as those of *Blourugia seeleyi, Paranaichthys longianales* and *Proceramala montanensis* (Fig. 4 Q-S), which are covered in ganoine forming parallel or subparallel costae are also widely distributed among the lower actinoperygian fishes, for instance, in the Devonian species *Donnrosenia schaefferi* Long et al. 2008. Clearly, one cannot utilise scale ornamentation morphology alone in phylogenetic analyses, but they may provide useful character information as part of more holistic sampling of actinopterygian morphology.

The palaeogeographic significance of the (partial) morphological similarities between the dermal scales of the material described herein and those of taxa known from the Palaeozoic and early Mesozoic of the Northern and the Southern Hemispheres remains elusive. However, scale ornamentation and morphology suggest possible close affinity between *Piratata rogersmithii* and cleithrolepidids from the Triassic of the Southern Hemisphere. Further detailed studies of the squamation in association with more complete skeletal remains are required to resolve the phylogenetic interrelationships between extinct deep-bodied fishes. Since *P. rogersmithii* is only known by its dermal scales at present, it would be premature to include the species in a cladistic analysis together with taxa represented by more complete fossils.

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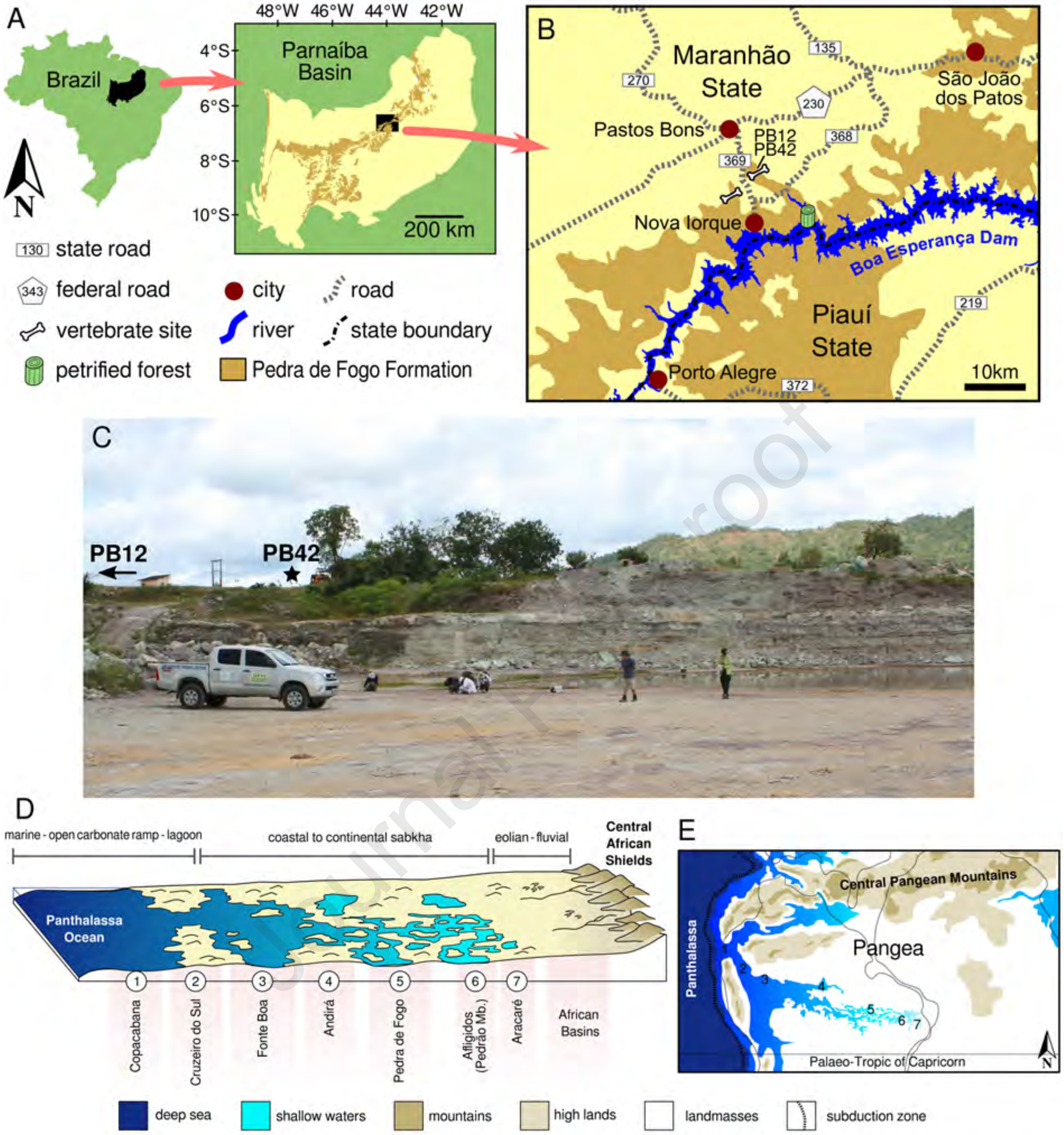
Table 1: Location of fossil sites mentioned in the text. *holotype **paratype

Locality number	Specimens	Latitude	Longitude	Municipality	State
PB12	MAP PV069.1**	6° 38.064' S	44° 3.868' W	Pastos Bons	Maranhão
PB42	MAP PV1031*	6° 38.066' S	44° 3.892' W	Pastos Bons	Maranhão
PB101	MAP PV369.2	6° 37.925' S	44° 3.954' W	Pastos Bons	Maranhão
PB133	MAP PV468a MAP PV468b	5° 29.238' S	42° 57.978' W	Nazária	Piauí
PB137	MAP PV840.1	5° 29.128' S	42° 58.090' W	Nazária	Piauí
PB170	MAP PV703.2	6º 38.255' S	44º 04.025' W	Nazária	Piauí
PB175	MAP PV630.10	5° 28.481' S	42° 54.125' W	Nazária	Piauí
PB181	MAP PV 630.1 MAP PV 630.3 MAP PV 630.4 MAP PV690.5 MAP PV690.6 MAP PV 630.7	5° 28.869' S	42° 54.242' W	Nazária	Piauí
PB196	MAP PV1015	5° 28.611' S	42° 55.321' W	Nazária	Piauí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48°W
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42°W
4°S
6°S
8°S
10°S
Parnaíba Basin
200 km
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130 state road
343 federal road
vertebrate site
petrified forest
city
river
road
state boundary
Pedra de Fogo Formation
B
Maranhão State
São João dos Patos
Pastos Bons
PB12
PB42
Nova Iorque
Boa Esperança Dam
Piauí State
Porto Alegre
135
270
230
368
369
219
372
10km
C
PB12
PB42
D
marine - open carbonate ramp - lagoon
coastal to continental sabkha
eolian - fluvial
Central African Shields
Panthalassa Ocean
1 Copacabana
2 Cruzeiro do Sul
3 Fonte Boa
4 Andirá
5 Pedra de Fogo
6 Afligidos (Pedrão Mb.)
7 Aracaré
African Basins
E
Central Pangean Mountains
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Panthalassa
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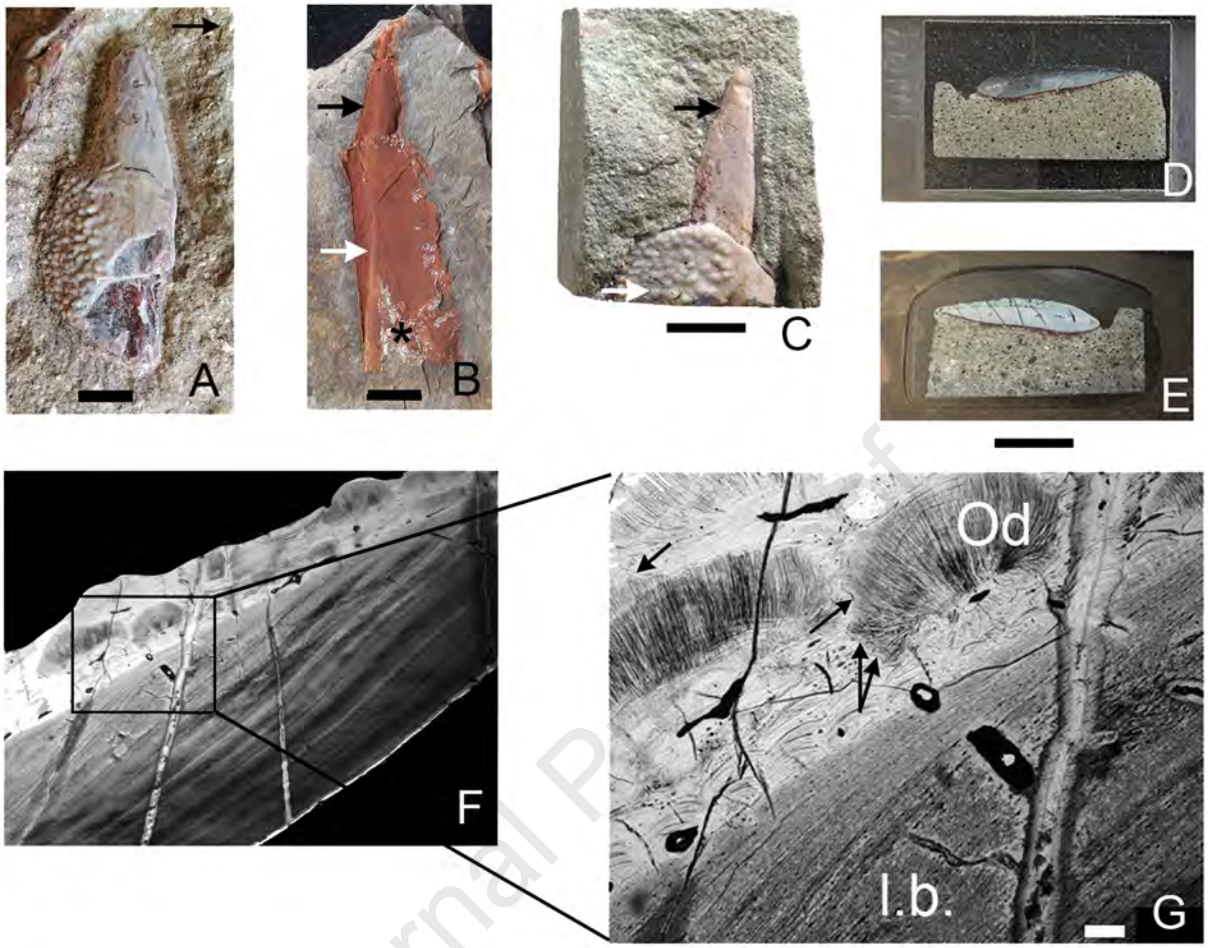
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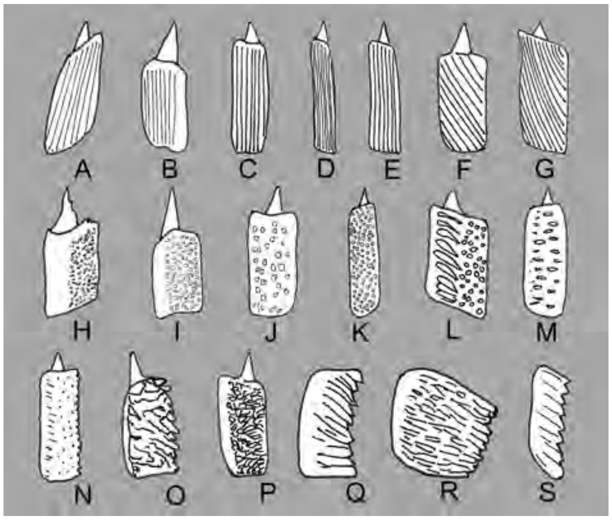
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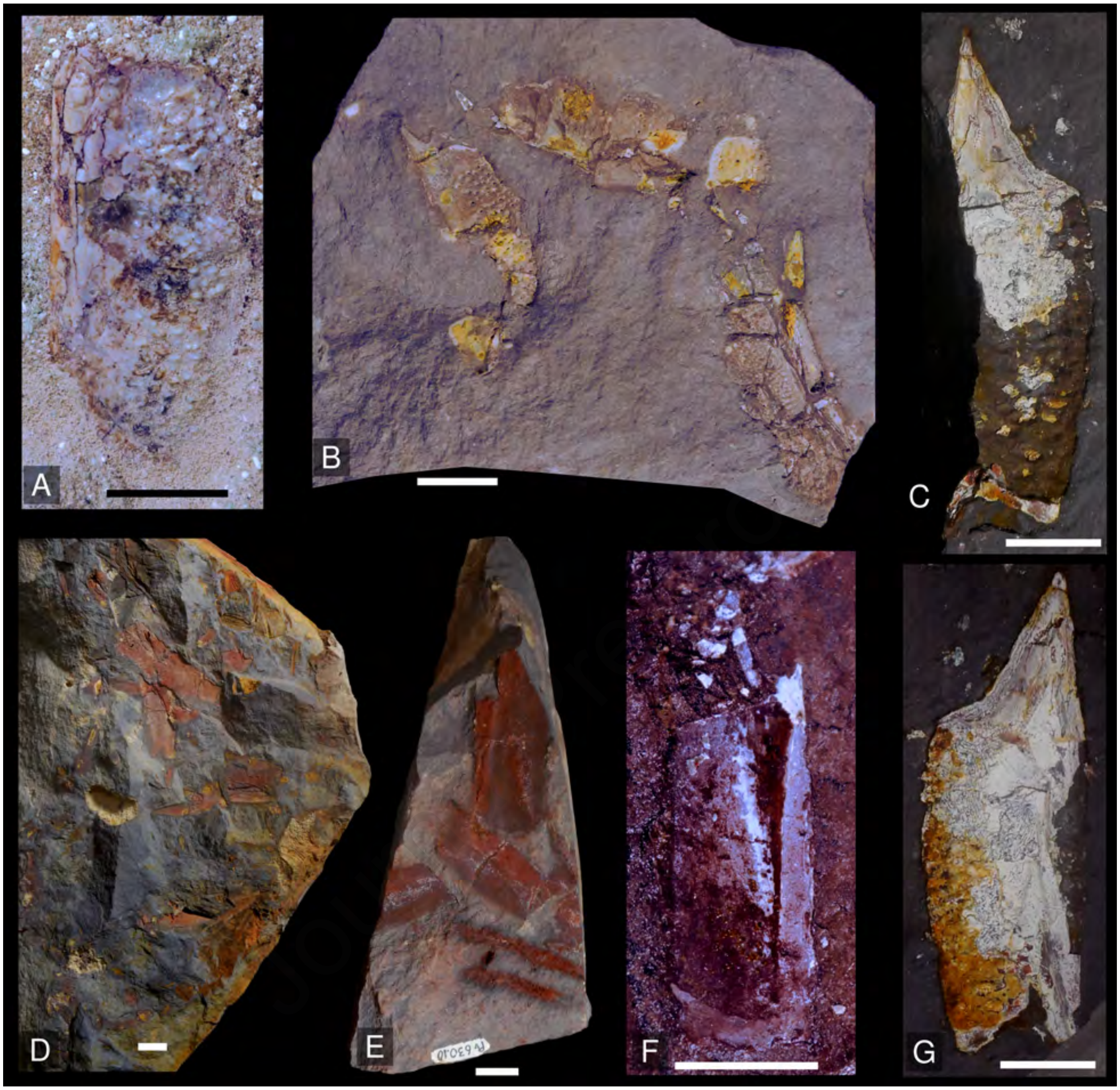
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A new deep-bodied fish from the Permian of Brazil is reported. *Piratata rogersmithii* gen. et sp. nov. is only known by isolated dermal scales. The external surface of *Piratata* dermal scales is covered in multiple round-to-slightly elongated tubercles. The scale lacks a ganoin cover and is made up of cellular bone and odontocomplexes of orthodentine composing the tuberculated scale surface. It is the first time this scale morphology was found in South America and it most closely resemble that of *Cleithrolepis granulatus* from the Triassic of Australia and *Cleithrolepis extoni* from the Triassic Stormberg Beds of South Africa.

Declaration of interests

☒ 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.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: