Gaea
Journal of Geoscience
6(2):69-75, jul/dez 2010

Microstructure of paleoniscid fish scales from Irati Formation, Permian (Cisuralian) of Paraná Basin, Brazil

Eliseu Vieira Dias
Laboratório de Geologia e Paleontologia, Centro de Ciências Biológicas e da Saúde, Universidade Estadual do Oeste do Paraná. Rua Universitária, 2069, 85819-110, Cascavel, Paraná, Brasil. diaseliseu@yahoo.com.br

Cristina Silveira Vega
Departamento de Geologia, Centro Politécnico, Universidade Federal do Paraná, Jardim das Américas, Caixa Postal: 19001, 81531-980, Curitiba, PR, Brasil. cvega@ufpr.br

Marcus Vinicius Urbinatti Canhete
Programa de Pós-Graduação em Educação, Universidade Federal do Paraná. Rua Gal. Carneiro, 460, 1º andar, Reitoria da UFPR, Ed. D. Pedro I, 80060-150, Curitiba, PR, Brasil. urbinatti@gmail.com

ABSTRACT
The Permian paleoichthyofauna of Paraná Basin is poorly known, mainly due to lack of more complete specimens, especially in the levels from Irati Formation. Recently fossil specimens were collected on this unit, in a mine of pyrobetuminous shale on PETROBRAS-SIX Company, at São Mateus do Sul, Paraná State. The material is only composed by disarticulated scales and some parts of the fins. To histological studies the fish scales were included in resin, sectioned in thin sections and observed in petrographic microscope. The well-preserved histological material allows observing: an external layer, with the enamel type ganoine exhibiting an evident stratification and several pores, a middle layer, the dentine, with visible odontodes containing pulp cavity and dentinal tubules and an inner layer, the isopedine, with growth lines and spaces left by osteocytes and the blood vessels feeding the bone tissue. Sections were also displayed in the scale traces of growth tissue and show structures similar to that previously record in the group. The histology of the material and the structures of peg-and-socket type observed, allowed assigning this material to paleoniscids. The morphology and histological arrangement was also compared with other previous work made to the Paraná Basin and show a histological character similar to types P-1 and P-2 (*Elonichthys punctatus?*) firstly described.

Key words: histology, Actinopterygii, paleoniscid, ganoine, dentine, isopedine.

RESUMO
MICROESTRUTURA DAS ESCAMAS DE PEIXES PALEONISCÍDEOS DA FORMAÇÃO IRATI, PERMIANO (CISURALIANO) DA BACIA DO PARANÁ, BRASIL. A paleoictiofauna permiana da Bacia do Paraná é pouco conhecida devido à raridade de ocorrência de exemplares completos, especialmente na Formação Irati. O presente trabalho aborda novos materiais referentes a escamas desarticuladas que foram identificadas nesta unidade, acompanhadas de nadadeiras, para a mina de folhelho piro-betuminoso PETROBRAS-SIX, município de São Mateus do Sul, Paraná. Para o estudo histológico, as escamas foram inicialmente incluídas em resina, para a confecção de lâminas delgadas e observação em microscópio petrográfico. As escamas demonstraram uma boa preservação em seus aspectos histológicos e a identificação de uma camada mais externa, com o esmalte do tipo ganoína, uma camada de clara estratificação e diversos poros, uma mediana formada por dentina, com odontodes visíveis contendo cavidade pulpar e túbulos de dentina, uma camada interna, a isopedina, onde se observam linhas de crescimento com os espaços deixados pelos osteócitos e os vasos sanguíneos que nutriam o tecido ósseo. Nos cortes também foram visualizados resquícios do tecido de crescimento da escama, com estruturas similares àquelas previamente registradas em paleoniscídeos. Os caracteres histológicos das escamas e as estruturas do tipo *peg-and-socket* observadas, permitiram confirmar essa atribuição. A morfologia e o arranjo histológico foram comparados com trabalho prévio realizado na Bacia do Paraná, constatando-se que a histologia do peixe estudado se assemelha aos espécimes P-1 e P-2 (*Elonichthys punctatus?*) previamente descritos.

Palavras-chave: histologia, Actinopterygii, paleoniscídeos, ganoína, dentina, isopedina.

INTRODUCTION

The Paraná Basin is a depositional basin situated on the east-central portion of South America, with 1,600,000 km^2, being 1,000,000 located on Brazilian territory and the other areas are registered on Argentina, Paraguay and Uruguay (Schneider *et al.*, 1974).

The Passa Dois Group comprises Permian sediments of Paraná Basin, including Irati, Serra Alta, Terezina and Rio do Rasto formations (Schneider *et al.*, 1974). On recent works (Milani *et al.*, 2007), the group also covers part of Pirambóia and Sanga do Cabral formations. The Irati Formation extends almost throughout the entire Paraná Basin and has an average thickness of 40 m with peaks of about 70 m in the southern part of the basin (Holz *et al.,* 2010). The Irati Formation is correlated to Whitehill Formation from South Africa and both are nearly isochronous (Oelofsen and Araújo, 1983).

The denomination of Irati Formation was proposed by White (1908) for strata registered on Irati city, Paraná State. This formation is characterized by pyrobetuminous black shales, presence of nodules and beds of dolomitic limestone. The mesosaurid reptiles are common vertebrate fossils of the unit (Mendes, 1967).

The Irati Formation was deposited predominantly on a shallow restrict marine paleoenvironment, with variable salinity and calm waters, sometimes disturbed by storm events (Lavina *et al.*, 1991). The Irati Formation is part of the Gondwana I Sequence of Milani *et al.* (2007), represented by carbonates and evaporites on the north part of the basin, and pyrobituminous black shales on the south part.

Santos *et al.* (2006), analyzing zircon crystals on a bentonite layer, dated the Irati Formation as 278.4 Ma, in accordance with the associated palinological data that suggested an Artinskian age to this unit. Joint those data to other biostratigraphic tools and the Sequence Stratigraphy, Holz *et al.* (2010) considered the Irati Formation as Late Artinskian.

The flora of Irati Formation is represented by leaves and silicified woods of gymnosperms, dominated by forms of *Glossopteris, Cordaites, Paracalamites* and *Pecopteris* (Guerra-Sommer and Cazzulo-Klepzig, 2000).

The fauna of Irati Formation includes mesosaur reptiles, fishes, foraminifers, brachiopods, sponges, crustaceans and insects (Schneider *et al.*, 1974; Adami-Rodrigues and Pinto, 2000; Würdig *et al.*, 2000; Pinto, 2000; Chahud and Fairchild, 2007), with the mesosaurs being its more typical element (Araújo-Barberena and Timm, 2000; Sedor and Ferigolo, 2001; Soares, 2003), also attested by ichnofossils (Sedor and Silva, 2004).

The known occurrence of paleoniscid fishes on Irati Formation are restricted to Rio Grande do Sul, Santa Catarina, Paraná and São Paulo states (Richter, 1985a, 1985b, 2000; Richter *et al.,* 1985; Chahud and Petri, 2008, 2010). Recently, almost complete paleoniscid fishes and isolated scales are discovered on Paraná State, at PETROBRAS-SIX quarry, at São Mateus do Sul municipality (Dias *et al.*, 2006).

According to Moy-Thomas and Miles (1971), the paleoniscids were actinopterygian fishes that appeared in Devonian period and were extinct on the Cretaceous, yet the terms "paleoniscids" and "paleoniscoids" are traditionally used to refer informally to a great variability of basal actinopterygians. Lund *et al.* (1995) used the term Paleoniscimorpha to include all basal actinopterygians non-neopterygians. Figueiredo and Gallo (2006) used the term paleopterygians to all basal non-neopterygians actinopterygians and even in some way with the same sense as paleoniscoids, but the restricted the use of paleoniscid to Paleoniscidae fishes included on a wider group, called Paleonisciformes. Considering the variety of distinct nomenclatures, to simplify, the term paleoniscids, as used in this work, follows Moy-Thomas and Miles (1971) and Richter *et al.* (1985).

The reconstructions show the paleoniscids with a usually fusiform body, triangular dorsal fin and a tightly heterocercal caudal fin and with a persistent notochord (Carroll, 1988; Colbert and Morales, 1991). They present conical teeth with a characteristic cap of acrodin (Moy-Thomas and Miles, 1971). The scales of these fishes are romboid with a *peg-and-socket* system, a dorsal process that articulates them in an internal ventral notch of the overlying scale (Carroll, 1988). The scales are composed by bone tissue, dentine and an enamel mineralized by hidroxiapatite $[Ca_{10}(PO_4)_6(OH)_2]$ (*e.g.* Hildebrand, 1995). Externally the enamel is shining and translucent, composed of ganoine layers from what arose its name (ganoid scales). According to Richter and Smith (1995), who revised the concept, there is no problem to call the multilamelar enamel that covers the scales of basal actinopterygians as ganoine. Internally to enamel is the dentine, followed by a layer of lamelar bone or isopedine (Hildebrand, 1995; Kent, 1987; Richter *et al.*, 2004).

MATERIAL AND METHODS

The studied specimen was collected on a mine at PETROBRAS-SIX Company, in the city of São Mateus do Sul, Paraná State, Brazil (Figure 1), and it is deposited on the paleontological collection of Museu de Ciências Naturais of Setor de Ciências Biológicas of the Universidade Federal do Paraná (MCN–SCB–UFPR) cataloged as MCN.P.909a and MCN.P.909b, corresponding to one of the samples cited by Dias *et al.* (2006) and that corresponds to a mass of disarticulated scales and bones preserved on siltic black shale.

Thin laminae of the specimen MCN.P.909b were made (Figure 2) on the Lamination Laboratory of Departamento de Geologia of UFPR. The sample was sectioned and the portions were included on epoxi resin. After polymerization, the blocks were abraded and polished. The polished face was pasted on lamina with Ester of Cianoacrilate (Super Bonder®). After dry on ambient temperature, it was abraded again until the exposition

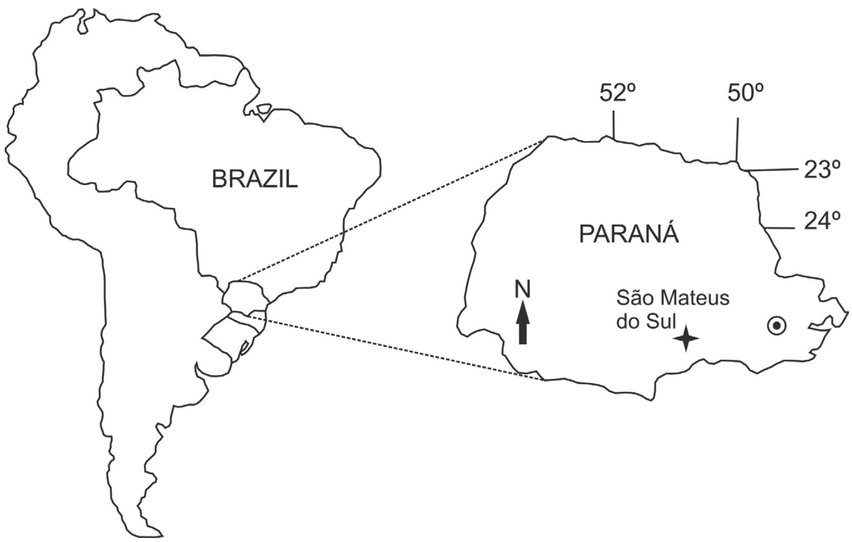

Figure 1. Location of São Mateus do Sul city, Paraná state, Brazil (black star), where the studied material was collected (modified from Leonardi *et al.*, 2002).

Figure 2. Sample MCN.P.909b, with disarticulated paleoniscid scales from Irati Formation. Scale bar: 3 cm.

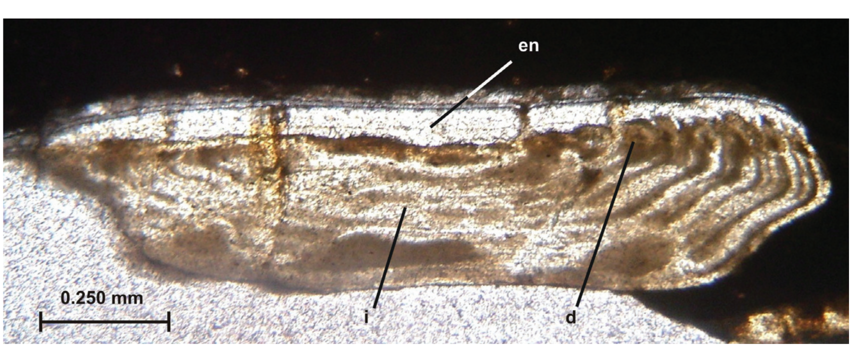

Figure 3. Paleoniscid scale from Irati Formation, in polarized light (MCN.P.909b, lam. 3). Abbreviations: **d**, dentine; **en**, enamel; **i**, isopedine.

of the scales. The final polishment was made manually on a glass surface with Carburundum® 800 abrasive and water.

The laminae were observed on petrographic microscope OLYMPUS BX60 with polarized light and the most relevant images were captured in a digital camera.

The laminae are deposited on the paleontological collection of MCN-SCB-UFPR numbered as follows: MCN.P.909b Lam. 1 to 6.

Abbreviations: **d**, dentine; **en**, enamel; **i**, isopedine; **o**, odontode; **pc,** pulpar cavity; **r.s.l.**, resorption line of the dentine and ganoine; **vc**, vascular channel.

RESULTS AND DISCUSSION

All scales are very well preserved considering the microstructure, and present the three typical layers of ganoid scales, as exemplified on Figure 3. The histological configuration of the three layers observed is typical of paleoniscids as proposed by several authors (Moy-Thomas and Miles, 1971; Carroll, 1988; Kent, 1987; Hildebrand, 1995). Flank scales and at least one fulcral were observed, with the first ones showing a peg-and-socket system of articulation.

The most external layer is composed by ganoine and was detected in all laminae. It presents a typical stratification that result of the superposition of several enamel layers during ontogenetic development (Francillon-Vieillot *et al.*, 1990). Channels cross the ganoine (Figure 4) and represent the place of the blood vessels that irrigate the epidermis.

The intermediate layer is composed by dentine and is more developed on the extremities of the analyzed scales. The dentine is formed by odontocytes that project their cytoplasm as a branched form on the mineralized matrix, forming the dentine tubules. This intermediate layer of dentine is organized in odontodes, according the definition proposed by Ørvig (1967). The odontodes are dentary dermic units formed by individual pulpar cavities (Francillon-Vieillot *et al.*, 1990), that when organized side by side, the series is definided as an odontocomplex (Ørvig, 1978a). The odontocomplexes were observed in the studied laminae and exemplified on Figure 5.

The most internal layer is composed by a lamelar bone called isopedine, presenting growth lines of the bone tissue (Figure 6).

The studied scale material presents vacuities secondarily filled by sediment, corresponding to the spaces of the osteocytes. Wide channels belonging to blood vessels are also present on the isopedine.

The lateral line system was also observed and it is represented by a large channel which occupies almost 2/3 of the total thickness of the scale, and is localized almost in the center of the lamelar bone, being or not filled by sediments (Figures 7 and 8).

There are some evidences that the growth process of scales were preserved on their borders (Figure 9). On MCN.P.909b Lam. 6, the isopedine presents a lateral projection that forms a thin floor with little mineralization. Externally, there are an odontode developing and a new layer of ganoine, still very thin, appears to cover the structure. This process represents a new growth line of isopedine which extends over the base of the scale.

Evidences of odontocomplexes growth by resorption zones of dentine and the formation of a new odontode were also observed (Figure 5). In this process, part of the oldest odontode is reabsorbed and a new odontode partially occupies its space, a process successively repeated when a new odontode is created (Francillon-Vieillot *et al.*, 1990).

Ørvig (1978a, 1978b, 1978c) described the microstructure and growth process of mineralized tissues in some basal actinopterygians and distinguish the growth patterns of mineralized dermal structures. Ørvig (1978a) pointed two basic patterns of growth, by lateral accretion, where the structure grows in area (*areal growth*), and by superficial accretion, where the structure grows in thickness by superposition of tissues to their external face (*superpositional growth*). In some cases those two kinds of growth could be combined. In many cases also occurs the apposition of new hard tissue to the basal face of the dermal elements, which may be connected to the areal or superpositional growth (Ørvig, 1978a).

On the studied laminae the growth pattern fits perfectly with lateral area accretion as well as the apposition on basal face (Figures 5 and 9).

The fossil material was compared with other paleoniscids previously described to the Irati Formation by

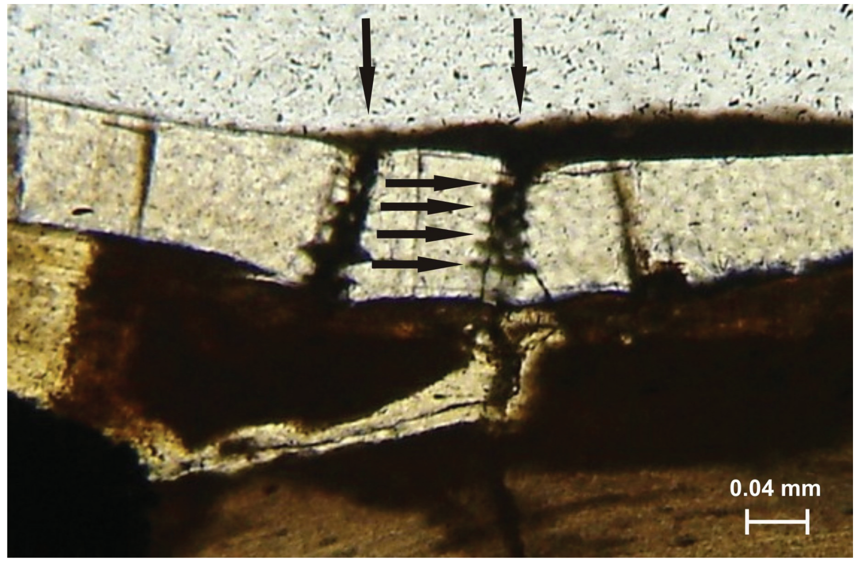

Figure 4. Detail of a paleoniscid scale from Irati Formation, in polarized light (MCN.P.909b, lam. 5). Horizontal arrows indicate enamel stratification (ganoine type) between two pores of the scale. Vertical arrows indicate the blood vassel channels.

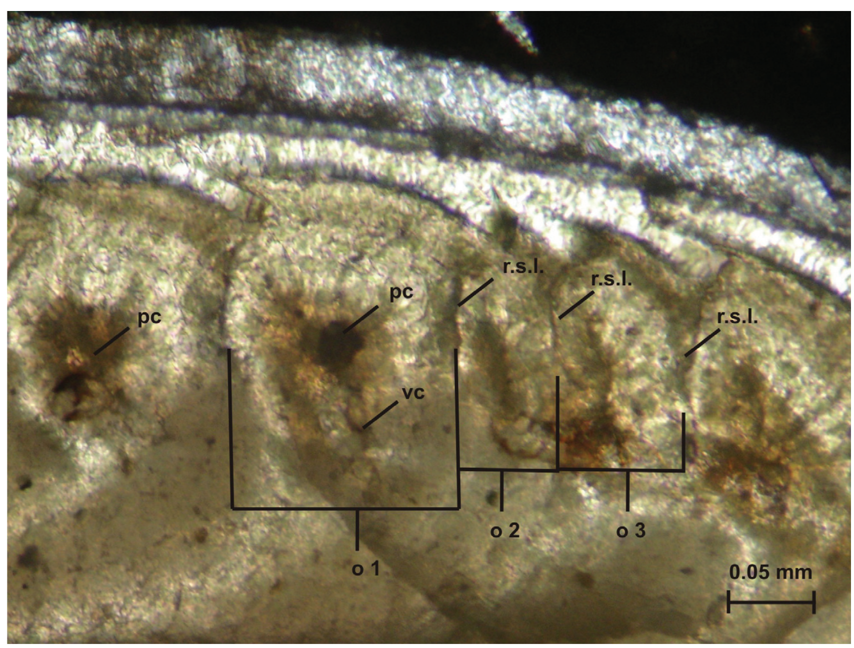

Figure 5. Microstructure of the paleoniscid scale in polarized light (MCN.P.909b, lam. 1). Abbreviations: **o**, odontode; **pc**, pulpar cavity; **r.s.l.**, resorption line of the dentine and ganoine; **vc**, vascular channel.

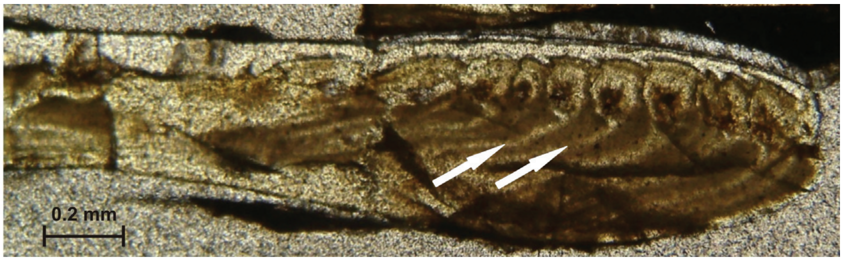

Figure 6. Detail of a paleoniscid fulcral scale from Irati Formation in polarized light (MCN.P.909b, lam. 1). Arrows indicate growth lines of bone tissue.

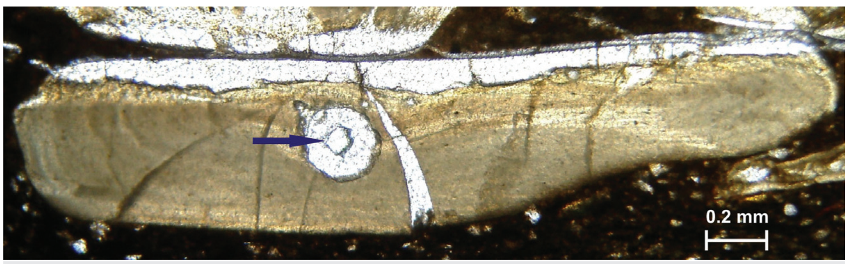

Figure 7. Lateral line channel (arrow) from the paleoniscid scale, under polarized light (MCN.P.909b, lam. 2).

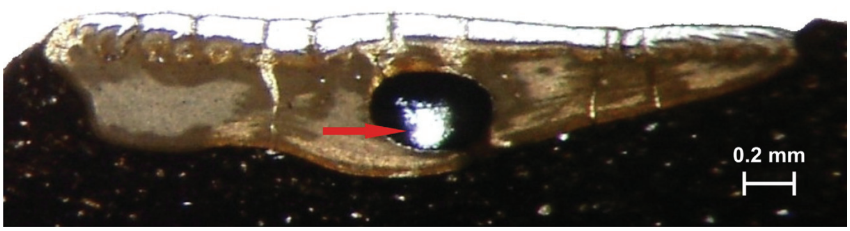

Figure 8. Transversal section of the lateral line channel (arrow) under polarized light (MCN.P.909b, lam. 6).

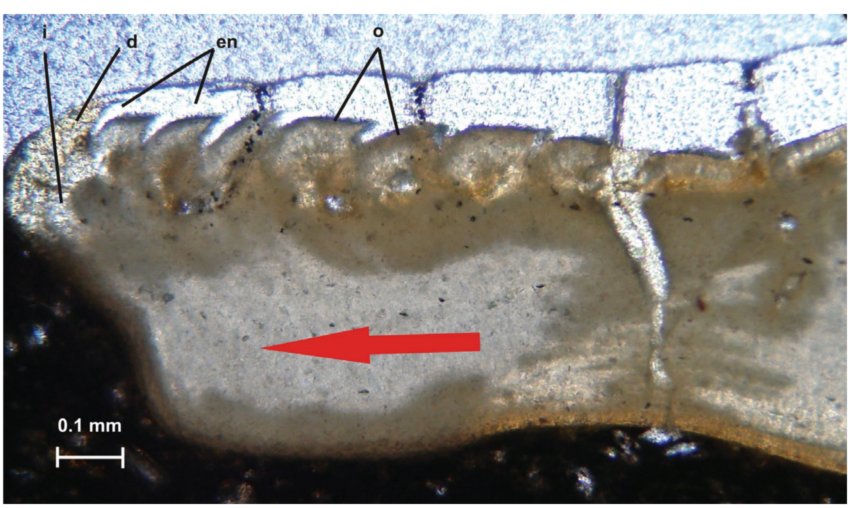

Figure 9. Odontodes (**o**) in a single layer with curved teeth format and extremities turned medially, similar to the P-1 pattern of Richter *et al.* (1985), identified in the sample MCN.P.909b, lam. 6. Arrow indicates the way of scale growth. Other abbreviations: **d**, dentine; **en**, enamel; **i**, isopedine.

Richter *et al.* (1985); unfortunately, the photos and drawings presented by these authors are not so evident, what limits more detailed comparisons. To Richter *et al.* (1985) there are five patterns of fish scales from Irati Formation, designed to P-1 to P-5 scales.

The scale P-1 was attributed to *Elonichthys punctatus*?, and present a punctuated surface with short furrows on the ganoine. The odontodes are in a single horizontal layer along all the scale, on curved teeth format with extremities turned medially (Richter *et al.*, 1985). The specimen MCN.P.909b presents odontodes on curved teeth format (Figures 3, 5, 6, 8 and 9), and punctuations (Figures 4, 8 and 9) very similar to that of P-1 scale. The same occurs by the presence of a similar thick ganoine layer. Some evident punctuation in the smaller scales was observed under stereomicroscope.

The P-2 pattern, also attributed to *Elonichthys punctatus*?, is characterized by sharp ribs on the external surface of the scale. Histologically this morphotype is marked by ondulations on the ganoine layer that corresponds to the ribs beyond odontodes on a lozenge shape (Richter *et al.*, 1985). This pattern differs from that observed here, even under stereomicroscope, those scales of intermediate sizes can show a variation from elongated punctuations, short furrows to elongated sulcus and crest of ganoine, while bigger scales show less punctuation and more crests and sulcus in the ganoine layer. Even not observed on laminae, the bigger scales of MNC.P.909b are externally similar to the P-2 type of Richter *et al.* (1985).

The scales pattern P-3 and P-4 (the last one also attributed to *Elonichthys gondwanus*?) from Richter *et al.* (1985), although present some ribs on the surface, histologically show a partial or total superposition of the odontodes, forming a superposition of odonto-complexes. This pattern differs from our material, where the surface is smooth and the growth pattern corresponds to lateral area accretion, as proposed by Ørvig (1978a).

Finally, the scale pattern P-5, attributed to *Acrolepis*?, presents external low ribs, "diverging from an axis that divides the scale into two halves equivalent" (Richter *et al.*, 1985). The authors do not present the histological description of this scale, but in comparison with the scales here described, it is possible to observe that low ribs occurs, without dividing the scale in dorsal and ventral portions.

CONCLUSION

The scales are organized in clusters due to a taphonomic scenario of decay of a single fish associated to the action of scavenger invertebrates. Considering the studied scales as probably belonging to a single disarticulated fish this configuration points to a variation in the size of the scales which is predictable.

The studied material is tentatively assigned to a form similar to that presenting the P-1 and P-2 scale patterns and could also be related to *Elonichthys punctatus*?. New collects looking for more complete materials could confirm this hypothesis.

ACKNOWLEDGMENTS

The authors would like to thank MsC. Fernando Sedor and PhD. José Eduardo Figueiredo Dornelles who collected the fossil samples, and to Museu de Ciências Naturais, from Departamento de Biologia, Universidade Federal do Paraná, for allowing the access to the material for this study. To Adilson Antônio Dalagassa thanks for the laminae preparation and to PhD. José Manoel dos Reis Neto for the use of the microscope from the Laboratório Analítico de Minerais e Rochas (LAMIR).

REFERENCES

ADAMI-RODRIGUES, K.; PINTO, I.D. 2000. Os crustáceos, Ordem Pygocephalomorpha. *In*: M. HOLZ; L.F. de ROS (eds.), *Paleontologia do Rio Grande do Sul.* Porto Alegre, UFRGS/CIGO, p. 141-147.

ARAÚJO-BARBERENA, D.; TIMM, L.L. 2000. Características estruturais dos mesossauros e suas adaptações ao meio aquático. *In:* M. HOLZ; L.F. de ROS (eds.), *Paleontologia do Rio Grande do Sul.* Porto Alegre, UFRGS/CIGO, p. 194-209.

CARROLL, R.L. 1988. *Vertebrate Paleontology and Evolution*. 6th ed., New York, W.H. Freeman and Company, xiv + 698 p.

CHAHUD, A.; FAIRCHILD, T.R. 2007. Levantamento preliminar do potencial paleontológico da transição Tautí-Irati no centro-leste do Estado de São Paulo. *Paleontologia em Destaque*, **57**:41.

CHAHUD, A.; PETRI, S. 2008. Registro de paleoniscóides na base do Membro Taquaral, Formação Irati, Permiano da Bacia do Paraná. *Revista do Instituto Geológico*, **29**(1/2):33-40.

CHAHUD, A.; PETRI, S. 2010. Anfíbio e Palaeonisciformes da Porção Basal do Membro Taquaral, Formação Irati (Permiano), Estado de São Paulo, Brasil. *Revista do Instituto de Geociências - USP, Série Científica,* **10**(1):29-37.

COLBERT, E.H.; MORALES, M. 1991. *Evolution of the Vertebrates,* 4th ed., New York, Wiley-Liss, Inc., 470 p.

DIAS, E.V.; SEDOR, F.; DORNELLES, J.E.F. 2006. New remains of Paleoniscoid fishes from the Irati Formation (Upper Permian, Paraná Basin) in São Mateus do Sul, Paraná, Brazil. *Ciência e Natura,* edição especial:19.

FIGUEIREDO, F.J.; GALLO, V. 2006. Actinopterígios paleopterígios: morfologia e taxonomia. *In*: V. GALLO; P.M. BRITO; H.M. SILVA; F.J. FIGUEIREDO (eds.), *Paleontologia de Vertebrados: grandes temas e contribuições científicas*. Rio de Janeiro, Interciência, p. 1-29.

FRANCILLON-VIEILLOT, H.; BUFFRENIL, V.; CASTANET, J.; GÉRAUDIE, J.; MEUNIER, F.J.; SIRE, J.Y.; ZYLBERBERG, L.; RICQLÈS, A. 1990. A. Microstructure and mineralization of vertebrate skeletal tissues. *In*: J.G. CARTER (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends*. 1st ed., New York, Van Nostrand Reinhold, vol. I, p. 471-530.

GUERRA-SOMMER, M.; CAZZULO-KLEPZIG, M. 2000. As floras gonduânicas do Paleozóico Superior do Rio Grande do Sul. *In:* M. HOLZ; L.F. de ROS, (eds.), *Paleontologia do Rio Grande do Sul.* Porto Alegre, UFRGS/CIGO, p. 67-84.

HILDEBRAND, M. 1995. *Análise da Estrutura dos Vertebrados*. 3rd Ed., São Paulo, Atheneu, 700 p.

HOLZ, M.; FRANÇA, A.B.; SOUZA, P.A.; IANNUZZI, R.; ROHN, R. 2010. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Paraná Basin, Brazil, South America. *Journal of South American Earth Sciences*, **29**:381-399. http://dx.doi.org/10.1016/j.jsames.2009.04.004

KENT, G.C. 1987. *Comparative anatomy of the vertebrates*. 7th ed., Dubuque, C. Brown, p. 164-168.

LAVINA, E.L.; ARAÚJO-BARBERENA, D.C.; AZEVEDO, S.A.K. 1991. Tempestades de inverno e altas taxas de mortalidade de répteis mesossauros: um exemplo a partir do afloramento Passo São Borja, RS. *Pesquisas*, **18**(1):64-70.

LEONARDI, G.; SEDOR, F.A.; COSTA, R. 2002. Pegadas de répteis terrestres na Formação Rio do Rasto (Permiano Superior da Bacia do Paraná), Estado do Paraná, Brasil. *Arquivos do Museu Nacional,* **60**(3):213-216.

LUND, R.; POPLIN, C.; McCARTHY, K. 1995. Preliminary analysis of the interrelationships of some Paleozoic Actinopterygii. *Geobios Memoire Special,* **19**:215-220. http://dx.doi.org/10.1016/S0016-6995(95)80117-0

MENDES, J.C. 1967. The Passa Dois Group (The Brazilian portion of the Paraná Basin). *In*: J.J. BIGARELLA; G.D. BECKER; I.D. PINTO (eds.), *Problems in Brazilian Gondwana Geology*. Curitiba, Instituto de Geologia, p. 119-166.

MILANI, E.J.; DE MELO, J.H.G.; DE SOUZA, P.A.; FERNANDES, L.A.; FRANÇA, A.B. 2007. Bacia do Paraná. *Boletim de Geociências da PETROBRAS*, **15**(2):265-287.

MOY-THOMAS J.A.; MILES, R.S. 1971. *Paleozoic Fishes.* 2nd ed., London, Chapman and Hall, 259 p.

OELOFSEN, B.; ARAÚJO, D.C. 1983. Paleoecological implications of the distribution of mesosaurid reptiles in the Permian Irati sea (Paraná Basin), South America. *Revista Brasileira de Geociências,* **13**(1):1-6.

ØRVIG, T. 1967. Phylogeny of tooth tissues: Evolution of some calcified tissues in early vertebrates. *In:* A.E.W. MILES (ed.), *Structural and chemical organization of teeth*. New York & London, Academic Press, p. 45-110.

ØRVIG, T. 1978a. Microstructure and growth of the dermal skeleton in fossil Actinopterygian fishes: *Birgeria* and *Scanilepis*. *Zoologica Scripta*, **7**:33-56. http://dx.doi.org/10.1111/j.1463-6409.1978.tb00587.x

ØRVIG, T. 1978b. Microstructure and growth of the dermal skeleton in fossil Actinopterygian fishes: *Boreosomus, Plegmolepis* and *Gyrolepis. Zoologica Scripta*, **7**:125-144. http://dx.doi.org/10.1111/j.1463-6409.1978.tb00596.x

ØRVIG, T. 1978c. Microstructure and growth of the dermal skeleton in fossil Actinopterygian fishes: *Nephrotus* and *Colobodus*, with remarks on the dentition in other forms. *Zoologica Scripta*, **7**:297-326. http://dx.doi.org/10.1111/j.1463-6409.1978.tb00613.x

PINTO, I.D. 2000. Insetos fósseis. *In:* M. HOLZ; L.F. de ROS (eds.), *Paleontologia do Rio Grande do Sul*. Porto Alegre, UFRGS/CIGO, p. 132-140.

RICHTER M. 1985a. Situação da Pesquisa Paleoictiológica no Paleozóico Brasileiro. *In:* Congresso Brasileiro de Paleontologia, 8, 1983, Brasília, MME-DNPM, Setor de Geologia *Anais*, **27**:105-110.

RICHTER, M. 1985b. Paleoictiologia no Estado do Rio Grande do Sul, Brasil: características da tafofauna e afloramentos fossilíferos. *Iheringia. Série Geologia*, **10**:29-45.

RICHTER, M. 2000. Peixes fósseis do Rio Grande do Sul. *In:* M. HOLZ; L.F. de ROS (eds.), *Paleontologia do Rio Grande do Sul.* Porto Alegre, UFRGS/CIGO, p. 162-175.

RICHTER, M.; SMITH, M. 1995. A microstructural study of the ganoine tissue of selected lower vertebrates. *Zoological Journal of the Linnean Society*, **114**:173-212. http://dx.doi.org/10.1006/zjls.1995.0023

RICHTER M.; PICCOLI A. E.M.; LIMA M.C.F.S. 1985. Variação Morfológica de Restos de Paleoniscídeos (Pisces) no Permiano da Bacia do Paraná. *In:* Congresso Brasileiro de Paleontologia, 8, 1983, Brasília, MME-DNPM, Setor de Geologia, *Anais*, **27**:111-122.

RICHTER, M.; VIANA, M.S.S.; MALABARBA, M.C.S.L. 2004. Agnatos e Peixes. *In:* CARVALHO, I.S. (ed.), *Paleontologia.* 2nd ed., Rio de Janeiro, Interciência, p. 733-761.

SANTOS, R.V.; SOUZA, P.A.; ALVARENGA, C.J.S.; DANTAS, E.L.; PIMENTEL, M.M.; OLIVEIRA, C.G.; ARAÚJO, L.M. 2006. Shrimp U-Pb Zircon sating and palynology of bentonitic layers from the Permian Irati Formation Parana Basin, Brazil. *Gondwana Research*, **9**(4):456-463. http://dx.doi.org/10.1016/j.gr.2005.12.001

SCHNEIDER, R.L.; MUHLMANN, H.; TOMMASI, E. 1974. Revisão Estratigráfica da Bacia do Paraná. *In*: Congresso Brasileiro de Geologia, 28, Porto Alegre, *Anais*, SBG, p. 41-65.

SEDOR, F.A.; FERIGOLO, J. 2001. A coluna vertebral de *Brazilosaurus sampauloensis* Shikama & Ozaki, 1966 da Formação Irati, Permiano da Bacia do Paraná (Brasil) (Proganosauria, Mesosauridae). *Acta Biologica Paranaense*, **30**(1-4):151-173.

SEDOR, F.A.; SILVA, R.C. 2004. Primeiro registro de pegadas de Mesosauridae (Proganosauria) na Formação Irati (Permiano Superior da Bacia do Paraná) do Estado de Goiás, Brasil. *Revista Brasileira de Paleontologia,* **7**(2):269-274. http://dx.doi.org/10.4072/rbp.2004.2.21

SOARES, M.B. 2003. A taphonomic model for the Mesosauridae assemblage of the Irati Formation (Paraná Basin, Brazil). *Geologica Acta*, **1**(4):349-361.

WHITE, I.C. 1908. Relatório sobre as Coal Measures e rochas associadas do sul do Brasil. *In*: I.C. WHITE; J.H. MAC GREGOR; D. WHITE, *Relatório Final Comissão de Estudos Minas de Carvão de Pedra do Brasil*. Rio de Janeiro, Imprensa Nacional, pt 1, 617 p. + XIV estampas.

WÜRDIG, N.L.; PINTO, I.D.; COIMBRA, J.C. 2000. Ostracoda, um microcrustáceo. *In:* M. HOLZ; L.F. de ROS (eds.), *Paleontologia do Rio Grande do Sul.* Porto Alegre, UFRGS/CIGO, p. 148-161.

Submetido em: 10/06/2010
Aceito em: 09/11/2010