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New histological information on *Holoptychius* Agassiz, 1839 (Sarcopterygii, Porolepiformes) provides insights into the palaeocological implications and evolution of the basal plate of the scales of osteichthyans

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Abstract

The porolepiform sarcopterygian *Holoptychius* Agassiz, 1839 from the Upper Devonian is one of the most widely found vertebrates in the Palaeozoic fossil record. *Holoptychius* is considered to display a more ubiquitous mode of life and a greater potential of dispersion than any other sarcopterygian taxon, consistent with its cosmopolitan distribution and profuse fossil record, mainly represented by scales. Previous histological studies on the squamation of *Holoptychius* have discussed the variable ornamentation of the superficial layer, however the basal plate has been less explored. Here we furnish new histological data on the scales of *Holoptychius*, focusing on the mineralization rate and organization of the lamellar bone. Ground sections show that the basal plate is made of a stacking of thick collagenous layers with a plywood-like structure. Collagenous fibres are parallel within layers, with two successive layers orthogonally arranged and with every second layer rotated by an angle of 36º. This condition, known as a double-twisted plywood-like organization, is similar to that of other sarcopterygians like *Eusthenopteron* and extant coelacanths and dipnoans. The new palaeohistological data provide insights into the morphofunctional, palaeoecological and phylogenetical implications of the microstructural characteristics of the scales, adding to our knowledge of the histological diversity of osteichthyans.

Running title: Palaeohistology of *Holoptychius* scales

Keywords: Devonian, *Holoptychius*, palaeohistology, scale, basal plate, twisted-plywood.

Word count: 6896

Introduction

The Porolepiformes are an exclusively Devonian clade of sarcopterygians, known from the early Lochkovian to the late Famennian, that populated near-shore and fresh water aquatic environments (Janvier 1996). They share a number of uniquely derived characters with lungfishes and are therefore regarded as their sister group within the Dipnomorpha (Ahlberg 1991). The order Porolepiformes is traditionally divided into two families: the Porolepidae (a possible paraphyletic assemblage of primitive porolepiforms including *Porolepis, Durialepis* and *Heimenia*) (Ørvig 1957, 1969; Clément 2004; Mondéjar-Fernández & Clément 2012; Mondéjar-Fernández et al. 2020) and the Holoptychiidae (comprising notably *Holoptychius, Glyptolepis* and *Laccognathus*, among others) (Ørvig 1957; Jarvik 1972; Ahlberg 1992a; Cloutier & Ahlberg 1996). A third family is now incorporated to the Porolepiformes: the Ventalepididae (Lebedev & Lukševičs 2018) that includes the enigmatic *Ventalepis ketleriensis* (Schultze 1980).

Porolepiform remains have been found worldwide, both in Euramerica (e.g., Jarvik 1972; Cloutier & Schultze 1996; Schultze 2000) and Gondwana (Johanson & Ritchie 2000; Young et al. 1992, 2010; Johanson et al. 2013). Holoptychiids became highly abundant in fresh water to marginal marine environments during the Middle to Upper Devonian as opposed to 'porolepids' found mainly in fully marine or near-shore environments during the Lower-Middle Devonian (Ahlberg 1992b). Among holoptychiids, *Holoptychius* is considered to have acquired the largest size, with certain species (e.g., *H. giganteus*) known from isolated scales and estimated to have reached several meters in length (Janvier 1996). The large size of the scales is coupled with a set of elongate fangs in the jaws, thus confirming that holoptychiids, and more particularly *Holoptychius,* were among the largest predators in any given Middle-Upper Devonian environment (e.g., Chevrinais et al. 2017). Moreover, given its cosmopolitan distribution and

profuse fossil record, *Holoptychius* is considered to display a more ubiquitous mode of life and a greater potential of dispersion than any other sarcopterygian taxon (Cloutier & Schultze 1996).

The evolutionary history of the Porolepiformes during the Devonian was marked by the transition from a squamation composed of thick and rhombic scales covered with cosmine in the 'porolepids', to thin and rounded imbricate scales lacking cosmine in the more derived holoptychiids (Ørvig 1957; Jarvik 1980; Mondéjar-Fernández & Clément 2012). The rise of the latter scale morphotype was mirrored by a similar type of ornamentation in the dermal bones of the skull and shoulder girdle displaying an irregular arrangement of tubercles and/or ridges. The rhombic scales of 'porolepids' possess the characteristic peg-and-socket articulation, an oblique articular ridge (or keel) on the internal (or visceral) surface, and reduced overlapped surfaces, whereas in holoptychiids the keel and the peg-and-socket articulation are lost, associated with the acquisition of a rounded outline with large overlapped surfaces. These characters used to be considered as mutually exclusive and characteristic of the two families within the Porolepiformes. However, the condition of *Heimenia*, displaying rhombic scales in the posterior region of the body and rounded scales anteriorly is informative on the evolutionary transformation of the squamation between 'porolepids' and holoptychiids (Mondéjar-Fernández & Clément 2012).

Histologically, the rounded scales of holoptychiids can be divided into two well-defined portions: a basal plate composed of lamellar bone overlaid by a superficial layer composed of vascular bone and usually associated with odontogenic components (i.e., dentine and enamel) responsible for the external ornamentation of the scales (Ørvig 1957; Francillon-Vieillot et al. 1990; Mondéjar-Fernández 2018). The scales of *Quebecius, Glyptolepis* and *Laccognathus* are ornamented by a combination of ridges and tubercles (Ørvig 1957; Schultze & Arsenault 1987; Cloutier & Schultze 1996). The ridges in *Glyptolepis* (and possibly in *Quebecius*) are made of dentine covered with enamel (Ørvig 1957). *Laccognathus* displays rounded dentine tubercles or

small ridges capped with enamel (Bystrow 1939; Ørvig 1957; Downs et al. 2011; Mondéjar-Fernández 2018). In *Ventalepis*, the exposed area of certain scales is ornamented by small tubercles made of dentine but no enamel has been identified (Schultze 1980). However, in *Holoptychius* the superficial ornamentations are reduced to various bony reliefs of the superficial layer of the posterior field; the scales are thus considered to have lost the odontogenic component, with the exception of a narrow anterior area covered with small, probably odontogenic, tubercles occurring in certain specimens (Ørvig 1957; Mondéjar-Fernández & Janvier 2014). Moreover, in *Holoptychius* the morphology and ornamentation of the scales varies throughout ontogeny (Ørvig 1957) and may even differ across the body. For instance, the scales of the ventral region in *H. jarviki* exhibit stout bony tubercles that are arranged in rows, whereas dorsal and flank scales display antero-posteriorly oriented bony ridges (Cloutier & Schultze 1996) (Fig. 1A-B).

While the superficial layer and the various types of odontogenic or osteogenic ornamentations have been widely illustrated and discussed (e.g., Gross 1956; Ørvig 1957), the basal plate of the scales of holoptychiids has been less explored. Here we furnish new histological data on the organization of the basal plate of the scales of *Holoptychius*, focusing on the mineralization rate and arrangement of the collagen plies of the lamellar bone. Comparison with fossil and extant taxa will shed more light on the morphofunctional, paleoecological and evolutionary implications of the peculiar organization of the lamellar bone of the basal plate of the scales of holoptychiids, sarcopterygians, and osteichthyans more broadly.

Material and methods

Material

The fossil scale material consists of trunk scales of *Holoptychius* sp. found free (MNHN, URSS 5075) from the Frasnian of Latvia ("Nadmeshi beds"), or enclosed in sediment (donated by the late Pr. T. Ørvig) from the Frasnian-Famennian of Greenland, and isolated scales of *Holoptychius* cf. *nobilissimus* (MB.f. 1994.1) from the Givetian-Frasnian of Latvia (Fig. 1). All the fossil material is housed at the Muséum national d'Histoire naturelle (MNHN) in Paris, France.

Methods

The fossil material was embedded in polyester resin (GBS 1; Brot) and sectioned for study. The various sections were ground and polished to a thickness of 60-80 μm and observed under transmitted natural light with an Olympus BX51 microscope. Pictures were taken with a digital camera Olympus Camedia C-5060 and finalized in Adobe Photoshop.

Ground sections are registered in the histological collection of the MNHN: MNHN-F-HISTOS 2736 (T. Ørvig's specimens of *Holoptychius* sp. from Greenland), MNHN-F-HISTOS 2737 to 2739 (*Holoptychius* sp. from Latvia) and MNHN-F-HISTOS 2740 (*Holoptychius* cf. *nobilissimus* from Latvia).

Remarks

The scales of *Holoptychius* were initially described by Agassiz (1833-44) as rounded, ornamented by undulating furrows or ridges and small associated tubercles. Such description has turned out to be too broad and matches the general morphology of the scales of many other sarcopterygian taxa (e.g., Janvier 1996; Johanson & Ritchie 2000). However, in depth observations and the combined occurrence of diagnostic features from the external and internal (or visceral) surface of the scales now allows to confidently assign isolated material to *Holoptychius* (e.g., Miller & Brazeau 2007; Mondéjar-Fernández & Janvier 2014). In contrast to other round-scaled Devonian sarcopterygians, the scales of *Holoptychius* are characterized by an

external ornamentation composed of undulating stout bony ridges, that could be associated with a fan of small tubercles anteriorly, and by the lack of any ornamentation of the internal surface (Fig. 1D,F), as opposed to other taxa that display narrower and straighter ridges in the exposed area (e.g., Devonian actinistians) (Forey 1998) or a drop-shaped boss in the internal surface (e.g, rhizodonts and tristichopterids) (Jarvik 1980).

During the 19th century, the case of systematic attribution of any given similar scale (either isolated or in articulation) to *Holoptychius* resulted in the publication of a myriad of *Holoptychius* species. Cloutier & Schultze (1996) critically reviewed the taxonomy of the genus and noted that only three among the twenty-four known species of *Holoptychius* were known from cranial material (*H. nobilissimus* Agassiz 1839, *H. flemingi* Agassiz 1843, and *H. jarviki* Cloutier & Schultze 1996); for ten of the remaining twenty-one, the species name was erected based on a single scale. Since then, systematic attribution of fossil remains to *Holoptychius* has been more careful and relies more on non-scale-based characters, such as cranial and postcranial skeletal features (e.g., *H. bergmanni,* Downs et al. 2013). It is thus currently difficult to reliably assign isolated scales to a given *Holoptychius* species and as such our description of the material will remain limited to the generic level.

Histological description

The scales of *Holoptychius* are round and imbricate (Fig. 1). Each scale shows an anterior field (or overlapped area), overlaid by the neighbour anterior, dorsal and ventral scales, and a posterior field (or exposed area) with an external ornamented surface (Fig. 1B,C,E). The ground sections (Figs 2, 3) confirm that the scales are constituted of two superimposed portions: *i*) a relatively thick basal plate formed of stacked and parallelly-aligned collagenous lamellae (bp, Figs 2, 3),

and *ii*) an overlaying superficial bony layer with numerous vascular canals (sl, Figs 2, 3). This superficial layer totally lacks odontogenic structures in our material, the ornamentation being solely represented by bony longitudinal ridges (Figs 1B, 2B,C, 3). The lower surface of the scales is smooth and regular (Fig. 1D,F).

Superficial layer

The superficial layer is constituted of a vascularised cellular bony tissue (vb, Figs 2, 3). Numerous vascular canals and cavities are seen, especially in the region close to the basal plate (vc, Figs 3, 4A). Certain vascular canals and cavities can result from remodelling processes (Fig. 4B). Numerous star-shaped osteocytic lacunae (Fig. 4B) with ramified cytoplasmic extensions (i.e., osteocytic canalicles) are present (Fig. 4C). The external surface of this osseous layer is irregular as a result of the bony reliefs (Figs 1C,E,G, 2B-C, 3).

Basal plate

The basal plate is constituted of a thick staked lamellar bone (lb, Figs 2A-B, 3) histologically and topologically called isopedine (Pander 1856; Gross 1956; Meunier 1987; Francillon-Vieillot et al. 1990). The basal plate is crossed by several more or less parallel ascending vascular canals (Figs 3, 4D) that originate from the lower surface of the scale (Fig. 2A). Some of these vascular canals can merge with the vascular network of the superficial bony layer (Fig. 3).

Vertical sections reveal that the basal plate is made of lamellar bone composed of relatively thick layers of horizontal collagen fibres with the existence of a pattern repeating every five layers (Fig. 5B, C). The average thickness of each layer is about 18-23 μm. Elongate osteocytes (elasmocytes *sensu* Meunier 1984; Francillon-Vieillot et al. 1990), are inserted between the collagenous layers, with their cytoplasmic processes extending along the collagen

fibres (Fig. 4E, 5C). The collagen fibres are arranged as bundles composed of collagenous fibrils. Seen in cross sections, these bundles form small rectangles with round angles (Fig. 5A).

The basal plate is thus made of isopedine with superimposed layers of parallel fibres arranged in a relatively complicated network. An oblique section shows the varying orientations of the fibres, resulting in arciform patterns (Fig. 5C). Combined with the observations in vertical section (Fig. 5B), these patterns allow us to infer the three-dimensional organization of the basal plate. The fibres of each pair of successive layers (odd and even) are roughly orthogonal. However, every second layer rotates by discrete steps with a small angle (approximately 36°) around a vertical axis perpendicular to the superimposed layers (Fig. 5E). This structural arrangement results in a right-handed helicoidal structure with a repetitive pattern every five layers (Fig. 5B, F). The intersection of the arciform motifs (Fig. 5D) thus highlights the occurrence of a double system of layers intermingled with one another known as a double-twisted plywood organization (Giraud et al. 1978a,b). Some relatively thin ascending fibrillary structures (most probably collagenous fibrils) perpendicular to the layers of the basal plate (Fig. 4D) can also occur, filling the space between the horizontal layers.

The lower surface of the basal plate is regular and straight (Fig. 2), which indicates that the collagenous layers of the isopedine were completely and homogenously mineralized throughout their whole thickness.

Discussion

On elasmoid scales

Bertin (1944) introduced the term elasmoid scale to describe the round scales of osteichthyans. Elasmoid scales (from the Greek ἔλασμα or *elasma* meaning lamella or plate-like) are flexible and relatively thin imbricated scales in which the anterior region is deeply embedded in the

dermis and the posterior region widely overlaps the lateral and anterior fields of the neighbouring scales. Histologically, elasmoid scales are composed of two parts: *i*) a relatively thin, mineralized, and ornamented superficial layer and *ii*) a thick basal plate made of collagen lamellae with different orientations of the fibres in successive layers (e.g., Williamson 1851; Goodrich 1907; Francillon-Vieillot et al. 1990). Elasmoid scales occur mainly in teleosts and amiids but they are not restricted to the Actinopterygii since the scales of extant sarcopterygians (e.g., *Latimeria*, lungfishes, and gymnophionan tetrapods) are also considered elasmoid scales (Smith et al. 1972; Castanet et al. 1975; Miller 1979; Meunier & François 1980; Zylberberg et al. 1980; Zylberberg 1988; Meunier & Zylberberg 1999; Zylberberg & Wake 1990; Hadiaty & Rachmatika 2003; Meunier et al. 2008). An elasmoid scale is thus a scale morpho- and histotype that is widely spread and convergently acquired in osteichthyans (e.g., Francillon-Vieillot et al. 1990; Schultze 1977, 2015) (Fig. 6).

Microstructurally, the rounded scales of *Holoptychius* with their superficial bony layer overlaying a basal plate with a lamellar organization of its collagen fibres can thus be ascribed to the elasmoid type. However, elasmoid scales have been traditionally characterized by a reduced thickness and mineralization rate, since the basal plate of all extant taxa displaying elasmoid scales is either totally or greatly unmineralized (e.g., teleosts). Nevertheless, elasmoid scales are also known to occur among extinct taxa and, in these cases, the basal plate is generally fully mineralized. Fossil osteichthyans with rounded scales that match the elasmoid type include both actinopterygians (e.g., the amiid *Amia robusta*, Meunier & Poplin 1995; the teleosts *Pachycormus*, *Leptolepis*, *Laelichthys*, Meunier & Brito 2004) and sarcopterygians (e.g., the onychodont *Selenodus*, Mondéjar-Fernández 2020; the actinistian *Miguashaia,* J. Mondéjar-Fernández et al. in prep; the porolepiforms *Holoptychius, Laccognathus* and *Glyptolepis,* Gross 1956; Ørvig 1957, this study; the dipnoans *Phaneropleuron* and *Scaumenacia,* Ørvig 1957; the rhizodont *Barameda,* Long 1989; the 'osteolepiform' *Eusthenopteron,* Zylberberg et al. 2010).

The mineralized basal plate of these taxa represents the primitive state from which the unmineralized condition of their closely-related extant forms (e.g., amiids, teleosts, coelacanths and dipnoans) certainly evolved. Moreover, in certain elasmoid scales, such as in coelacanths, the superficial layer can be ornamented by odontogenic tubercles or ridges, regardless of the mineralization state of the basal plate. Elasmoid scales are thus no longer limited to the largely unmineralized scales of extant osteichthyans lacking odontogenic components but should rather describe round, imbricated scales with a lamellar structure of the basal plate, irrespective of its mineralization state.

Isopedine versus elasmodine

The term isopedine was coined by Pander (1856) to describe the lamellar bone from the base of the scales and bones of sarcopterygians and 'agnathans'. The term was reprised by Gross (1956) who clearly illustrated that isopedine is made of osseous lamellae composed of collagen bundles whose direction change from layer to layer. The mineralized collagen fibres cross at a right angle or at slightly acute angles and bone cells are present between the bundles but very rarely within them. This arrangement of the collagen plies constitutes a plywood-like structure (Meunier & Géraudie 1980). Isopedine is considered osteogenic in nature and thus synonym to lamellar bone (Francillon-Vieillot et al. 1990; Sire 1990).

Elasmodine was introduced by Schultze (1996) to characterize the basal plate of the elasmoid scales of actinopterygians (including the amioid scales of amiids and the cycloid/ ctenoid scales of teleosts). Schultze justified his claim stating that the partially mineralized elasmodine of derived actinopterygians was different from the fully mineralized isopedine of basal actinopterygians ('palaeonisciforms') and sarcopterygians, and that the modalities and role of Mandl's corpuscles in the mineralization of the elasmoid scales were not equivalent to that of ganoid and cosmoid scales with isopedine. Sire (1989, 1990) reported that in *Polypterus*, a

relatively thin plywood-like structure occurs between the overlying dentine layer and the underlying bony basal plate. This structure was called 'elasmodine' and was considered to be of odontogenic originSire & Huysseune (2003) and Sire et al. (2009) then used 'elasmodine' to describe the poorly mineralized basal plate of extant sarcopterygians (coelacanths and dipnoans), thus considering that the plywood-like tissue of these taxa was derived from a putative layer of lamellar dentine present in the common ancestor of osteichthyans (Sire et al. 2009). However, it has been shown that the 'elasmodine' of *Polypterus* forms before the dentine and mineralizes slowly with the help of Mandl-like corpuscles (Daget et al. 2001, fig. 6) as in amiids and teleosts (Meunier 1981; Schönbörner et al. 1981; Zylberberg et al. 1992; Meunier & Poplin 1995), refuting its odontogenic origin.

The proposed homology between the unmineralized basal plate of extant sarcopterygians with the thin 'elasmodine' of polypterids is problematic and fossil evidence does not confirm this bold prediction. Palaeohistological data (e.g., Mondéjar-Fernández & Clément 2012; Qu et al. 2013) and phylogenetic reconstructions (e.g., Giles et al. 2017; Clement et al. 2018) (Fig. 6) do not allow to claim that the unmineralized basal plate of extant coelacanths (*Latimeria*) and lungfishes (*Neoceratodus, Protopterus* and *Lepidosiren*) corresponds to 'elasmodine' as described in *Polypterus*. In these taxa, the basal plate consists of an irregularly mineralized lamellar bone (e.g., Smith et al. 1972; Castanet et al. 1975; Meunier and François, 1980; Meunier, 1980), topologically and structurally similar to the isopedine found in fossil taxa (e.g., early actinistians like *Miguashaia*, dipnomorphs like *Porolepis* and *Dipterus,* and tetrapodomorphs like *Eusthenopteron*). We thus consider that the introduction of 'elasmodine' is an unnecessary complexification and confusing terminology. We favor the use of the term isopedine to describe the lamellar tissues of the scales of osteichthyans, composed of variably mineralized lamellar bone with a plywood-like structure of the collagen plies.

Evolutionary significance of the plywood-like structures in the dermal skeleton of vertebrates

Many of the plywood-like structures occurring in the dermal skeleton of vertebrates have been characterized as isopedine. Structurally, isopedine is thus one of the oldest histological features of the vertebrate dermal skeleton, forming the lowest layer of the primitive bipartite skeleton consisting of a superficial layer ornamented with odontogenic products (i.e., odontodes made of dentine and enamel) overlying an osteogenic laminated basal layer (Keating & Donoghue 2016). However, the structure of the isopedine varies across taxa displaying more or less important specializations of the plywood-like organization (e.g., orthogonal or twisted plywood), a lack of incorporated cells (cellular or acellular isopedine), and regression or even lack of a mineral component (partially or unmineralized isopedine) (Francillon-Vieillot et al. 1990) (Fig. 6).

The evolutionary history of isopedine can be traced back to the earliest vertebrates. Pteraspidomorphs (including the arandaspids, astraspids and heterostracans) possess an acellular isopedine composed of an orthogonal arrangement of collagen plies anchored to the dermis by Sharpey's fibres (Donoghue & Sansom, 2002; Sansom et al. 2005; Donoghue et al. 2006; Sire et al. 2009; Keating et al. 2015; O'Shea et al. 2019). The small scales of anaspids present a basal layer of vascularized, acellular lamellar bone, usually identified as 'aspidine' (Gross 1938, 1958), but bearing more similarities with isopedine (Gross 1958; Blom et al. 2001; Donoghue & Samson 2002; Donoghue et al. 2006; Keating & Donoghue 2016). Thelodont scales do not possess isopedine and solely retain a superficial layer of odontodes with associated bone of attachment (Märss et al. 2007; Sire et al. 2009; Keating et al. 2015). The dermal skeleton of galeaspids is also greatly reduced, lacking odontogenic components, and displays a type of lamellar bone with an orthogonal plywood-like arrangement of thin collagen fibrils termed galeaspidin (Wang et al. 2005; Donoghue et al. 2006; Qu et al. 2013) that is comparable to isopedine (Gross 1968a; Keating et al. 2015). In osteostracans, the isopedine lacks cells (O'Shea

et al. 2019) and forms a homogenous basal layer with an orthogonal arrangement of thick collagen bundles (Gross 1935, 1961; Denison 1947, 1951).

In gnathosthomes, a lamellar structure can be found in the basal-most layer of the dermal bones and scales of 'placoderms' (Gross 1973; Burrow & Turner 1999; Giles et al. 2013) but it is not clear whether it can be considered isopedine or not. A plywood-like tissue forms the base of the scales referred to some 'acanthodians' (Gross 1947, 1971) and putative early chondrichthyans (Ørvig 1966). Otherwise, the dermal skeleton of stem and crown chondrichthyans is characterized by a significant reduction of its osteogenic components, including a basal layer of lamellar bone, and the sole retention of the superficial odontodes with associated bone of attachment forming the characteristic placoid scales of extant chondrichthyans (Agassiz 1833-44, Williamson 1849; Goodrich 1907).

Homologies of organization of the basal plate of the scales of osteichthyans

The histological variability and evolution of the basal plate of the scales of osteichthyans have been difficult to decipher. The main source of problems originates in a partial understanding of the different types of lamellar structures in the scales resulting in an oversimplification of the histological nature of the basal plate. Thus, in osteichthyans, the occurrence and distribution of isopedine is puzzling and its evolutionary history might be more complex than previously expected.

Many stem-osteichthyans from the Late Silurian-Early Devonian (e.g., *Andreolepis, Dialipina, Ligulalepis, Lophosteus, Naxilepis, Orvikuina,* and *Terenolepis*) (Friedman & Brazeau 2010; Burrow & Turner 2012) (Fig. 6) are known mainly from isolated scale material that has been histologically surveyed, providing key information on the early establishment of the osteichthyan squamation. In the scales of *Andreolepis, Lophosteus, Ligulalepis, Naxilepis* and *Terenolepis* the basal-most layer is made of a homogenous cellular lamellated bone, with

numerous Sharpey's fibres (Gross 1968b, 1969; Schultze 1968; Wang & Dong 1989; Burrow 1995; Jerve et al. 2016) but no distinctive plywood-like organization appears to be present. *Orvikuina* and *Dialipina* display a basal plate composed of an acellular lamellated bone (Schultze 1968, 1977) but whereas in *Orvikuina* it is poorly preserved, in *Dialipina* a plywood-like organization might have been present (Schultze 1968, pl.4). In the lower jaw of *Guiyu* (Zhu et al. 2009) a thick layer of lamellated bone occurs underneath the dentine, but its structure is unclear.

The earliest undisputed account of a plywood-like structure in a stem-osteichthyan is found in *Psarolepis,* however not in the basal plate but in the keel of its rhombic scales, which is composed of isopedine with an orthogonal arrangement of collagen bundles composed of small fibrils (Qu et al. 2013). The rest of the scale base consists of cellular pseudo-lamellar bone or parallel-fibred bone penetrated by Sharpey's fibres. Therefore, with the exception of *Psarolepis,* it is difficult to ascertain whether isopedine occurred in stem-osteichthyans without better imagery and more detailed histological information. In taxa described as presenting 'lamellar bone' in their scales, the absence of a clear plywood-like structure might indicate that the lamellated bone was rather a type of pseudo-lamellar bone or parallel-fibred bone, different from isopedine (*sensu* Francillon-Vieillot et al. 1990).

Lamellar bone is widespread and homogenously distributed among sarcopterygians and isopedine has been widely used to label the osseous basal plate of their scales (e.g., onychodonts, actinistians, porolepiforms, dipnoans, 'osteolepiforms' and 'elpistostegalians') (Gross 1956; Ørvig 1956; Forey 1998; Witzmann 2011) (Fig. 6). The occurrence of cells located between the isopedine layers is also common, however the arrangement of the plywood-like structure is variable across taxa. In the porolepiform *Heimenia*, the rounded scales from the anterior region of the body display a twisted plywood, whereas the rhombic scales from the posterior region show a more orthogonal arrangement of the collagen plies (Mondéjar-Fernández & Clément

2012). When compared with the cosmoid scales of *Porolepis*, *Osteolepis* and *Megalichthys* (Gross 1956, 1966) and the rhombic scales of *Panderichthys* (Witzmann 2011), it appears that an orthogonal arrangement is more commonly found in rhombic scales. On the other hand, a twisted arrangement occurs in the rounded scales of the onychodont *Selenodus* (Mondéjar-Fernández 2020), the 'osteolepiform' *Eusthenopteron* (Zylberberg et al. 2010), the porolepiform *Holoptychius* (Fig. 5), and probably the dipnoan *Dipterus* (Gross 1956), which indicates that a twisted plywood might be more frequently correlated with a rounded scale morphotype, irrespective of the retention of cosmine (Fig. 6). An orthogonal arrangement of isopedine can thus be considered primitive in sarcopterygians relative to the derived twisted condition.

In the case of actinopterygians, the depiction of the basal plate of the scales has been somewhat overlooked and poorly illustrated in many fossil specimens; consequently much of the paleohistological information is either confusing or unreliable. Scales are unknown in *Meemannia* (Zhu et al. 2006, 2010) but in the dermal bones the basal-most layer was described and illustrated as 'lamellar bone', however it does not display a clear plywood-like structure (Qu et al. 2013). In *Moythomasia* and *Mimipiscis*, the scale base was illustrated as a homogenous cellular lamellated bone penetrated by Sharpey's fibres, but its microstructure was not figured (Jessen 1968; Gardiner 1984). The 'lamellar bone' in these taxa does not clearly show a plywood-like structure and is probably pseudo-lamellar bone instead (Francillon-Vieillot et al. 1990). *Cheirolepis* is one of the few examples where the bony base is certainly not made of a plywood-like structure and thus isopedine can be confidently considered absent (Gross 1966; Zylberberg et al. 2015). In *Polypterus*, the bony base of the scales has been described as constructed by homogenous pseudo-lamellar bone (Goodrich 1907; Sire et al. 2009). The only plywood-like structure present is the thin isopedine layer underneath the dentine (Sire 1989), which has also been identified in a variety of fossil polypterids: *Dagetella* (Gayet & Meunier, 1992), *Latinopollia* (Meunier & Gayet, 1996; Meunier & Gayet, 1998), and *Bawitius* (Meunier et

al. 2016). A twisted plywood-like structure with an irregular mineralization rate has been described in the basal plate of the scales of the holostean *Amia* (Meunier 1981; Meunier & Poplin 1995), probably the caturid *Caturus* (Schultze 1966), and numerous teleosts (Meunier & Géraudie 1980; Meunier 1984; Neville 1993; Meunier & Brito 2004) with a left-handed rotation, whereas as in the pleuronectiform *Pleuronectes microcephalus* a right-handed rotation has been observed (Darke 1986).

The disjunct phylogenetic distribution of isopedine in osteichthyans and the variable orientation of the collagen layers across taxa clearly point towards a convergence between plywood-like structures in sarcopterygians and actinopterygians (Fig. 6). Sarcopterygian fishes display a consistently well-developed lamellar bone layer in all surveyed taxa; isopedine can thus be considered a primitive shared feature of the Sarcopterygii. However, the paleohistological data suggest that the occurrence of isopedine is irregular in actinopterygians, complicating its use as a reliable phylogenetic character. Isopedine may thus not be a shared feature of actinopterygians since its disappearance from the basal plate might have occurred early on in their evolutionary history (e.g., *Meemannia* and *Cheirolepis*). As seen in the scales of several primitive actinopterygians (e.g., *Moythomasia*, *Mimipiscis*, *Polypterus*), other types of bony tissues replaced the lamellar bone from the basal plate but these can hardly be considered isopedine. A lamellar organization of the basal plate might then have been acquired convergently in amiids and teleosts but whether these plywood-like structures are derived from those of polypterids or represent a convergent acquisition is still unclear.

Histology of the basal plate of* Holoptychius *and comparisons

The basal plate of the scales of holoptychiids has only been briefly histologically surveyed in *Holoptychius, Glyptolepis* and *Laccognathus*. In *Laccognathus,* the arrangement of the collagen plies appears orthogonal as illustrated by Gross (1956, fig. 57). For *Glyptolepis*, Ørvig (1957, p.

389) stated that the organization of the isopedine layer is 'indistinguishable' from that of *Holoptychius*, without further descriptions. The basal plate of *Ventalepis* was also illustrated by Schultze (1980, fig. 13) but its structure was not described. Moreover, it has been noted that the thickness of the basal plate relative to the superficial layer increased during the transition from the rhombic scales of 'porolepids' (e.g., *Porolepis, Heimenia*) (Mondéjar-Fernández & Clément 2012) to the rounded scales of holoptychiids, in which the basal plate of *Laccognathus* is relatively thinner to that of *Holoptychius* (Ørvig 1957; Mondéjar-Fernández 2018, fig. 3). The increase in the thickness of the isopedine layer relative to the rest of the scale can be explained in *Holoptychius* by the disappearance of the odontogenic component of the superficial layer compared with the cosmoid scales of 'porolepids'. This evolutionary trend in holoptychiids has palaeocological implications (see below) and might be explained by the capacity of the plywood-like structure of the basal plate to be both flexible and resistant, as opposed to thick superficial layers with well-developed osseous and odontogenic components.

Our new data reveal that in *Holoptychius* the collagen fibrils are gathered into bundles (or fibres) forming layers which cross at an angle of roughly 90º and every second layer is rotated of approximately 36º, with a pattern repeating every five layers. This peculiar arrangement of the collagen plies is not simply orthogonal but it can rather be described as a double-twisted plywood (Fig. 5). To our knowledge, this is the second example of such an elaborate network described in the scales of a extinct osteichthyan. A double-twisted plywood organization of the basal plate was first described in the scales of the 'osteolepiform' *Eusthenopteron* (Zylberberg et al. 2010). A repetitive pattern every five layers can also be observed in the scales of the dipnoan *Dipterus* (Gross 1956, fig. 71D), suggesting a twisted condition, similar to that revealed in *Holoptychius*. Similarly, this three-dimensional organization of the scales of *Holoptychius* recalls the double-twisted plywood organization found in the scales of the extant coelacanths *Latimeria chalumnae* (Giraud et al. 1978a,b) and *L. menadoensis* (Meunier et al. 2008); the sole difference

is the rotation angle that is about 36° in *Holoptychius* instead of 27° in *L. chalumnae* (Giraud et al. 1978a,b), which has a repetitive pattern every seven layers. A double-twisted plywood has also been described in the basal plate of living lungfishes but with a mean rotation angle of 30° in *Neoceratodus forsteri* and 35-36° in *Protopterus annectens* and *Lepidosiren paradoxa* (Meunier & François 1980).

The basal plate of the scales of *Holoptychius* is fully mineralized, as in many other extinct sarcopterygians (e.g., *Porolepis, Heimenia, Dipterus, Osteolepis, Megalichthys, Eusthenopteron, Panderichthys*) (Goodrich 1907; Gross 1956; Zylberberg et al. 2010; Witzmann 2011; Mondéjar-Fernández & Clément 2012), but contrary to the basal plate of the scales of living coelacanths and lungfishes (Smith et al. 1972; Kemp et al. 2015). In *Latimeria,* the basal plate remains widely unmineralized (Castanet et al. 1975; Meunier et al. 2008), except at its contact with the superficial layer as thin mineralized globules (Meunier & Zylberberg 1999). In dipnoans, the basal plate is completely unmineralized (*Neoceratodus*) or partly mineralized (*Lepidosiren* and *Protopterus*) (Günther 1871; Brien 1962; Castanet et al. 1975; Meunier & François 1980). Lack of mineralization was also hypothesized to explain the absence of preserved isopedine in the fossil scales of the early tetrapod *Tulerpeton* (Mondéjar-Fernández et al. 2014). Incompletely mineralized basal plates with a plywood-like structure are thus common among sarcopterygians and also occur in actinopterygians, such as the amiids *Amia calva* (Meunier 1981) and *Amia robusta* (Meunier & Poplin 1995) (Fig. 6). These evolutionary changes of the mineralization rate of the isopedine might be due to convergent heterochronous processes (e.g., paedomorphosis) in osteichthyans (Meunier 1987) linked to a general trend of reduction of the ossification of the dermal skeleton in vertebrates since the Palaeozoic (e.g., Smith & Hall 1990; Donoghue & Samson 2002).

The presence of cells in the isopedine has also been confirmed in *Holoptychius* (Figs 4, 5). These cells are flat, elongated, spindle-shaped osteocytes (elasmocytes *sensu* Meunier 1984;

Francillon-Vieillot et al. 1990), with cellular expansions localized essentially in their extremities (Castanet et al., 1975, fig. 12; Zylberberg et al., 2010, fig. 3E). Elongate osteocytes occur between the collagen layers in the basal plate of rounded scales, like in *Latimeria* (Géraudie & Meunier 1981), *Dipterus* (Gross 1956), and *Laccognathus* (Mondéjar-Fernández 2018). In elasmoid scales, the direction of the cellular expansions of the osteocytes is mainly parallel to the collagen bundles and as such they differ from the osteocytes found in other bony tissues, which typically display star-shaped cellular processes distributed all around the cell lacunae.

Thin ascending collagenous fibrils perpendicular to the remaining large collagenous layers of the basal plate have been found in *Holoptychius* (Figs 4D). These anchoring fibrils may represent Sharpey's fibres but also bear similarities with the so-called TC fibres described in the scales of several actinopterygian teleosts (e.g., *Carassius*) (Onozato & Watabe 1979; Zylberberg & Nicolas 1982, fig. 1; Zylberberg et al. 1992, fig. 3). In teleosts, TC fibres appear to be involved in the first stage of mineralization (Schönborner et al. 1979; Zylberberg & Nicolas 1982). Thin ascending fibrils have also been described in the scales of *Latimeria chalumnae* (Giraud et al. 1978a,b) where they constitute a binding material that strengthen the cohesion of the plywood, similar to the role of Sharpey's fibres. We propose that in the scales of *Holoptychius*, these fibrils could have assumed both functions.

***Palaeocological implications for* Holoptychius**

Thin and flexible rounded scales have been morphofunctionally interpreted as an evolutionary answer to the problem of lightening of the body and as an improvement of the swimming capacities in fishes (e.g., Burdak 1979; Belles-Isles 1992; Gemballa & Bartsch 2002). In the case of porolepiforms, the rounded scales of holoptychiids (e.g., *Holoptychius, Laccognathus, Glyptolepis*) contrast with the thick and densely mineralized rhombic scales of 'porolepids' (e.g., *Porolepis*, *Heimenia*) and other primitive sarcopterygians, usually reconstructed as almost

exclusively benthonic fishes with reduced abilities to reach high swimming speeds (Clément 2004). However, irrespective of the scale morphology, the fusiform body of porolepiforms, the posteriorly displaced median fins, and the heterocercal caudal fin are congruent with a predatory behaviour, both in 'porolepids' and holoptychiids (Ahlberg 1992b; Clément 2004).

The proposed general body outline, swimming style, and size range of *Holoptychius* allow us to clearly identify this taxon as an ambush predatory fish capable of performing speed bursts (Ahlberg 1989; Belles-Isles 1992; Clément 2004; Mondéjar-Fernández & Clément 2012) (Fig. 1A). A modern analogue to this behavioural and anatomical profile can be found in the extant osteoglossomorph actinopterygian *Arapaima gigas* (Pirarucú), one of the largest fresh water fish in the world (up to 3 meters in length) from the Amazon Basin in South America (Nelson 2006). The head morphology, relative position of the eyes and mouth, and the general proportions of the body are similar to those of *Holoptychius* (Fig. 1A). The large elasmoid scales of *A. gigas* are rounded and display a well-developed basal plate with a lamellar organization (Meunier 1984; Sherman et al. 2017) (Fig. 6). A similar configuration of imbricate rounded scales can be found in large extant sarcopterygians (reaching more than 1.5 meters in length) like the coelacanth *Latimeria* found in the deep waters of the eastern coast of South Africa and the Mozambique Channel (*L. chalumnae*) and Indonesia (*L. menadoensis*) (Roux 1942; Smith et al. 1972; Castanet et al. 1975; Giraud et al. 1978a,b; Meunier et al. 2008) and the dipnoan *Neoceratodus forsteri* found in the freshwaters of the coastal rivers of Queensland, Australia (Kerr 1955; Meunier & François 1980; Kind 2011).

The elasmoid scales of osteichthyans display large overlapping surfaces and are flexible in all directions, increasing the whole mobility of the fish during swimming, as opposed to ganoid (e.g., 'paleonisciforms', *Lepisosteus* and *Polypterus*) or cosmoid (e.g., primitive sarcopterygians) scales with reduced overlapping surfaces, increasing lateral curvature but diminishing vertical flexion (Gemballa & Barstch 2002). However, trunk flexibility is not only

linked to the presence of rounded scales but also to a lesser degree of overlapping and to a lower body thickness invested by scales in transverse section. Many lungfishes, either extinct (e.g., *Dipterus, Chirodipterus, Griphognathus*) or extant (e.g., *Neoceratodus*), present an extensive overlapping pattern of the scales (Kerr 1955; Pridmore & Brawick 1993) in which the trunk is protected by up to eight layers of rounded scales. Moreover, scales from the anterior portion of the trunk are slightly more elongate and quadrangular (e.g., *Neoceratodus*) and thus constrain the lateral bending of the body more than small scales, resulting in a limited lateral flexibility. In other sarcopterygians like *Latimeria* (Millot & Anthony 1958, 1978) and *Holoptychius* (Jarvik 1980; Mondéjar-Fernández & Clément 2012), as well as in *Arapaima* and many other actinopterygians (Burdak 1979), the mean number of protective layers is only three and the scales are relatively less elongate than in dipnoans, thus suggesting a higher degree of lateral torsion of the trunk.

The squamation also has a crucial protective role in vertebrates and its study reveals different strategies developed to cope with potential predators. In fishes adapted to escape from predators, the structure of the scales will be correlated with an enhancement in flexibility and lightness, whereas in armoured, more protected fishes the scales will have higher resistance to fracture and average bending stiffness (Burdak 1979; Bruet et al. 2008; Song et al. 2011; Zimmerman et al. 2013; Sherman et al. 2017). A comparison of *Holoptychius* with *Arapaima* and *Latimeria* reveals that all these taxa possess a plywood-like structure of the basal plates of their scales. Mechanical experiments (Yang et al. 2013; Zimmermann et al. 2013; Sherman et al. 2017) have demonstrated that a plywood-like arrangement of the collagen fibres in the scales of *Arapaima* and *Latimeria* is highly resistant to crack propagation caused by the attack of predators. In the case of *Arapaima*, the mineralized external layer resists the penetration of teeth from its main predator, the piranha, while the plywood-like structure of the basal plate provides strength and stiffness to accommodate the deformation. An external ornamentation of

longitudinal ridges and/or tubercules, either bony as in *Holoptychius,* or odontogenic as in *Latimeria*, has also been proven to actively contribute to flexion of the body during swimming or in case of an attack, minimizing the tensile stresses acting on the scales (Song et al. 2011; Sherman et al. 2017).

The organization of the basal plate in extant osteichthyans has revealed its role in the protection against predators. Histological structure thus mirrors ecological behaviour and allows us to confidently propose palaeoecological strategies in extinct taxa based on features from the squamation. Shark bite marks found on *L. chalumnae* suggest that sharks may be one possible predator of *Latimeria* (Fricke et al. 1991; Forey 1998; Fricke & Hissmann 2000), making the squamation of coelacanths suitable to successfully defend them from many small sharks, but not optimal to cope with more powerful bites from larger ones. In the case of *Holoptychius,* bite marks have been found in several large scales from the Middle to Upper Devonian of the Baltic States and Russia (Lebedev et al. 2009). The marks correspond to gaps left by the teeth of predatory sarcopterygians co-occurrying in the same palaeoenvironment, such as 'osteolepiforms' (e.g., *Jarvikina*) but also other holoptychiids (probably *Holoptychius*), thus indicating that sarcopterygian fishes were the main predators of *Holoptychius* and that intrageneric predation might also have occurred at different stages of development of certain *Holoptychius* species (Lebedev et al. 2009). Our new data suggests that the plywood-like organization of the basal plates of the scales of *Holoptychius,* similar to those of *Latimeria* and *Arapaima,* might have provided both resistance and flexibility to the scales in the case of an attack while the bony superficial layer was capable of resisting the penetration of the teeth from predators (e.g., Song et al. 2011). The scales of *Holoptychius* might have thus been suited for protection from small Devonian predators (e.g., chondrichthyans, 'acanthodians', smaller sarcopterygian fishes or early tetrapods), but not from the powerful bites of larger predators (e.g., 'placoderms' like *Dunkleosteus*) (Janvier 1996; Young 2010).

Conclusions

Our new data on the organization of the basal plate of the scales of the holoptychiid porolepiform *Holoptychius* completes previous descriptions of the superficial layer and ornamentation patterns of the exposed area of the scales, adding to our knowledge on the histological diversity of the squamation in sarcopterygians. The basal plate of the scales of *Holoptychius* is composed of a fully mineralized isopedine in which the collagen layers display a double-twisted plywood arrangement. Among sarcopterygians, this peculiar organization was previously only known in the 'osteolepiform' *Eusthenopteron* (Zylberberg et al. 2010) but is common in extant forms like the coelacanth *Latimeria* (Giraud et al. 1978a,b) and the dipnoans *Neoceratodus, Lepidosiren and Protopterus* (Meunier & François 1980). Comparisons with modern analogues like *Arapaima* and *Latimeria* suggest that the scales of *Holoptychius* with large overlapped regions and a low degree of imbrication might have been adapted against predators with sharp teeth (small tip radius) (Sherman et al. 2017). The combined occurrence of protective yet flexible scales, with a double-twisted plywood arrangement of the basal plate, coupled with the acquisition of a large size in certain species might have facilitated the cosmopolitanism and versatility of the genus *Holoptychius* and its establishment as a main predator of coastal and freshwaters environments during the second half of the Devonian period.

The occurrence of elasmoid scales in *Holoptychius* further confirms that the elasmoid morpho- and histotype appeared convergently in various osteichthyan lineages, including both sarcopterygians (e.g., actinistians, derived dipnomorphs and tetrapodomorphs) and actinopterygians (amiids and teleosts). Our new data on *Holoptychius* support the idea that the isopedine from the basal plate of extant coelacanths and dipnoans cannot be considered

homologous to the thin isopedine layer in *Polypterus* and strongly suggest that the occurrence of a basal plate with a plywood-like structure in *Latimeria, Neoceratodus, Protopterus* and *Lepidosiren* corresponds to a retained primitive feature of sarcopterygians. Finally, new palaeohistological data highlight that the importance of the basal plate in the evolution of the osteichthyan squamation has been neglected, mainly based on inaccurate observations, incomplete descriptions, and terminological incoherence, stressing the necessity of in-depth new studies on the evolutionary history of isopedine in vertebrates.

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FIGURES

Figure captions

Figure 1. The scales of the holoptychiid porolepiform *Holoptychius*. **A**. Reconstruction of *Holoptychius* sp. (modified after Jarvik 1980). **B.** Detail of the squamation of *Holoptychius jarviki* from the Escuminac Formation of Miguasha (Québec) (modified from Ørvig 1957). Note the imbricate scales and the variability of the superficial ornamentations of the exposed area (from tubercles to ridges). Anterior to the left. Scale bar = 10 mm. **C-D.** Isolated scales of *Holoptychius* sp. (MNHN, URSS, 5075) from the Frasnian of Latvia in external view (**C**) and internal view (**D**). **E-F.** Isolated scales of *Holoptychius* cf. *nobilissimus* (MB.f. 1994.1) from the Givetian-Frasnian of Latvia in external view (**E**) and internal view (**F**). Arrows point anteriorly. Scale bar = 10 mm. **G.** Scales of *Holoptychius* sp. (MNHN-F-HISTOS 2736) from the Frasnian-Famennian of Greenland still embedded in sediment. Arrow points to the selected scale detailed in Fig. 2C. Scale bar = 10 mm.

Figure 2. Vertical cross sections of the scales of *Holoptychius*. **A**. Longitudinal cross section of MNHN-F-HISTOS 2737. Note that the laminated basal plate is crossed by vascular canals that are perpendicular to the collagenous layers. Arrow points anteriorly. **B**. Transversal cross section of MNHN-F-HISTOS 2740. Note that the surface of the superficial bony layer displays round reliefs that correspond to the antero-posterior ridges ornamenting the exposed area (see Fig. 1E). **C**. Transversal cross section of MNHN-F-HISTOS 2736. Square inset detailed in Fig. 3. Arrow heads indicate the occurrence of post-mortem cracks separating the superficial layer and the basal plate. **Abbreviations**: **bp**, basal plate; **lb**, lamellar bone; **vb**, vascular bone; **sl**, superficial layer; **vc**, vascular canal. Scale bar = 5 mm.

Figure 3. Vertical cross section of the scales of *Holoptychius*. Detail of the transversal cross section of the posterior field of *Holoptychius* sp. (MNHN-F-HISTOS 2736) showing the stratified basal plate overlaid by the ornamented superficial layer. Note that the bony layer is abundantly vascularised and numerous osteocytes can be seen. Black arrow-heads in the basal plate point to ascending vascular canals that merge with the vascular canals of the superficial bony layer. Abbreviations as in Fig. 2. Scale bar = 100 μm.

Figure 4. Histological organization of the scales of *Holoptychius* in vertical cross section. **A**. Detail of the superficial layer and basal plate showing the organization of the bony tissue (MNHN-F-HISTOS 2736). Numerous vascular cavities (vc) and star-shaped osteocytes (pointed by arrow heads) occur in the vascular bone of the superficial layer. The basal plate is formed by lamellar bone in which the collagen plies (pointed by asterisks) are arranged in parallel. Scale bar = 50 μm. **B**. Detail of the superficial layer showing a secondary vascular canal (the asterisk indicates the light of the vascular canal) with osteocytes (pointed by black arrow heads) occurring in its bony walls (MNHN-F-HISTOS 2739). Scale bar = 50 μm. **C**. Detail of the osteocytes from the vascular bone of the superficial layer and their ramified osteocytic canalicles (MNHN-F-HISTOS 2736). Scale bar = 20 μm. **D**. Detail of the basal plate showing four ascending vascular canals that cross the successive collagenous layers (indicated by black arrows) in which many thin parallel ascending collagenous fibres (pointed by white arrow heads) are also seen (MNHN-F-HISTOS 2736). Scale bar = 50 μm. Inset, detail of an ascending vascular canal (MNHN-F-HISTOS 2737). Scale bar = 25 μm. **E**. Detail of the elongate osteocytes (elasmocytes) from the basal plate embedded between the lamellae of the isopedine (MNHN-F-HISTOS 2737). Scale bar = 50 μm.

Figure 5. Organization of the basal plate of the scales of *Holoptychius*. **A.** Detail of three compound collagenous fibres (MNHN-F-HISTOS 2737). Each fibre is constituted of several collagenous units (fibrils) forming a bundle. Scale bar = 5 μm. **B.** Vertical cross section of the posterior field of a scale showing the successive layers of the isopedine (MNHN-F-HISTOS 2736). The arrows point to layers where the thick collagenous fibres are cut at a right angle. These specific layers occur every five layers. Scale bar = 50 μm. **C.** Schematic representation of an oblique cross section through the isopedine of the basal plate. Numbers correspond to the arrangement of the layers from top (earliest deposited layers) to bottom (latest deposited layers). Note that the black arrows from B match the fibres cut perpendicularly. The grey and black fibres represent the even and odd system of layers respectively, resulting in arciform patterns in cross section evidencing a double-twisted plywood arrangement of the collagen layers (cf). Cellular spaces (bp.c, basal plate cells) occur between the layers. **D**. Oblique section of the basal plate (MNHN-F-HISTOS 2738). Note that the direction of the collagenous layers changes from one layer to the next. The resulting rods form arciform patterns (dashed lines) that characterise a double-twisted plywood-like organization. The asterisks point to ascending vascular canals. Arrow points towards the external surface (top) of the scale. Scale bar = 500 μm. **E.** Model of an oblique section through the isopedine of the basal plate. Each pair of layers (1/2, 3/4, etc.) form successive roughly orthogonal plies and their orientation progressively rotates of approximately 36º in the direction of the arrows (clockwise from top to bottom). The grey and black lines correspond to the even and odd systems respectively and match the arciform patterns in C. **F.** Model of an oblique section in which the even and odd systems of layers have been separated. Note the progressive rotation of the fibres in each system and the resulting intermingled arched patterns. **Abbreviations**: **bp.c**, basal plate cell; **cf**, collagen fibre.

Figure 6. Simplified phylogeny of selected osteichthyans highlighting the evolution of the scale shape and microstructural features related to the basal plate (as discussed in the text). Phylogenetic hypotheses after Friedman & Brazeau 2010 and Clement et al. 2018. Drawings not to scale, modified after Kerr 1955 (*Neoceratodus*); Schultze 1968 (*Dialipina*, *Ligulalepis*, *Orvikuina*), 2018 (*Lophosteus*, *Amia, Holoptychius*); Jarvik 1980 (*Eusthenopteron, Osteolepis, Porolepis*); Pearson 1982 (*Cheirolepis*); Gardiner 1984 (*Moythomasia*); Janvier 1996 (*Dipterus*); Witzmann 2011 (*Panderichthys*); Qu et al. 2013 (*Andreolepis, Psarolepis*); Mondéjar-Fernández et al. 2014 (*Tulerpeton*); Mondéjar-Fernández 2020 (*Selenodus*). Asterisks indicate taxa displaying the elasmoid scale morpho-histotype. **Abbreviations**: **-min**, partially mineralized isopedine; **A**, actinopterygians; **D,** dipnomorphs; **dt**, double-twisted arrangement of the layers; **i**, isopedine (i.e., lamellar tissue with a plywood-like arrangement of the collagen layers); **o**, orthogonal arrangement of the layers; **S**, sarcopterygians; **t**, twisted arrangement of the layers; **T,** tetrapodomorphs.