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Middle Devonian thelodont *Australolepis* sp. (Thelodonti) from the Skały Formation, Holy Cross Mountains, Poland

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ABSTRACT:

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Sparse fish microremains have been found in marine limestones from the Middle Devonian (Givetian) Skały Formation (Sitka Coral-Crinoid Limestone Member and Sierżawy Member), Świętomarz–Śniadka section, Bodzentyn Syncline, Łysogóry Region, northern Holy Cross Mountains, associated with conodonts of the *hemiansatus* to *ansatus* zones. Thelodont scales referred here to *Australolepis* sp. cf. *A. seddoni* come from near Śniadka village, from samples dated as *hemiansatus* to *rhenanus/varcus* zones. This increases the known range for the genus from its original find in Western Australia. The presence of a thelodont in the late Middle Devonian in Poland extends the known distribution of turiniids around the peri-Gondwana shorelines of Palaeotethys.

Key words: Vertebrate palaeontology; Taxonomy; Biostratigraphy; Thelodonti; Turiniidae; Givetian; Northern Gondwana; Poland.

INTRODUCTION

There are relatively few records of mid to later Devonian thelodonts, the longest-lived Palaeozoic agnathans and most come from North and East Gondwana (NG, EG); *Australolepis seddoni* Turner and Dring, 1981 was first found in the late Givetian to early Frasnian Gneudna Formation of the Canning Basin, Western Australia and then appeared in further localities in Australia as well as in central Iran (Märss *et al*. 2007). The youngest thelodonts, therefore, belong to the turiniid clade with recent finds of scales of *Australolepis* species, *Neoturinia* and *Arianalepis* extending their range into the later Famennian (Hairapetian *et al*. 2015, 2016).

Various agnathans remains, including thelodont scales, are known from older rocks in Poland including a Silurian erratic and 14 core samples from the north and east (Halstead and Turner 1970; Märss 1997). Halstead and Turner's (1970) few scales are now identified as late Silurian *Thelodus laevis* and *Th. admirabilis* or *Th. sculptilis*; Märss (1997, pl. 4) found latest Silurian (Pridoli) thelodonts *Th. parvidens* including costatus and trilobatus forms, *Th. sculptilis*, *Th. traquairi*, *Goniporus alatus*(?), *Loganellia cuneata*, "*Loganellia*" *kummerowi*(?) and *Loganellia* sp. from the Miastko-1 borehole. Bremer *et al*. (2017a, b) introduced the first Late Silurian vertebrate microfossils from the Holy Cross Mountains, including a *Thelodus parvidens* fauna (*sensu* Gross 1967; Turner 2000) including *Th. trilobatus* and *Paralogania ludlowiensis*, typical of late Ludlow to early Pridoli elsewhere in Europe (Märss *et al*. 2007).

Younger Devonian microvertebrates of gnathostomes from Poland were noted by Liszkowski and Racki; they (1993, fig. 6A–F) described scales from the Givetian of the Holy Cross Mountains, which they assigned to *Acanthoides*? *dublinensis* Stauffer,

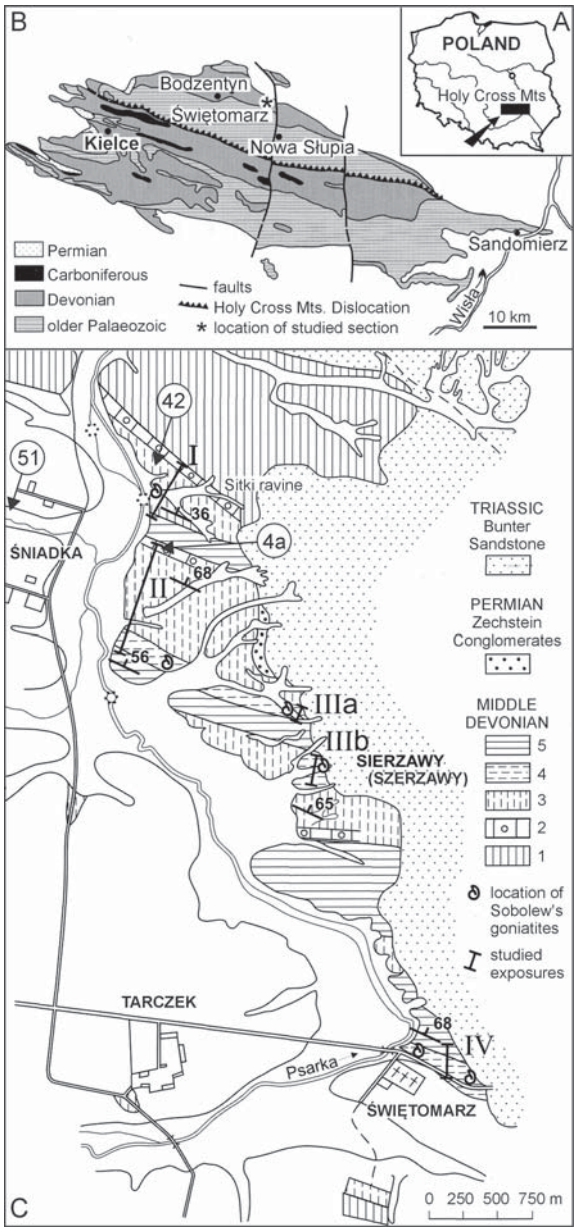
1938 and *Cheiracanthoides comptus* Wells, 1944. J. Kłossowski collected Middle Devonian samples from the Świętomarz–Śniadka section, Łysogóry Region, northern Holy Cross Mountains in 1976; he prepared rocks for conodonts, also finding fish remains (Kłossowski 1976, 1985). This material was later given by Professor M. Szulczewski to one of us (Ginter 1994), and examples were later shown to the senior author (ST), who identified the thelodont scales. Woroncowa-Marcinowska (2012) later re-studied this section and found further sparse fish microremains, from which we also identified a thelodont scale.

The aim of this paper is to give the first formal description of the thelodont scales found in these Middle Devonian rocks from Poland.

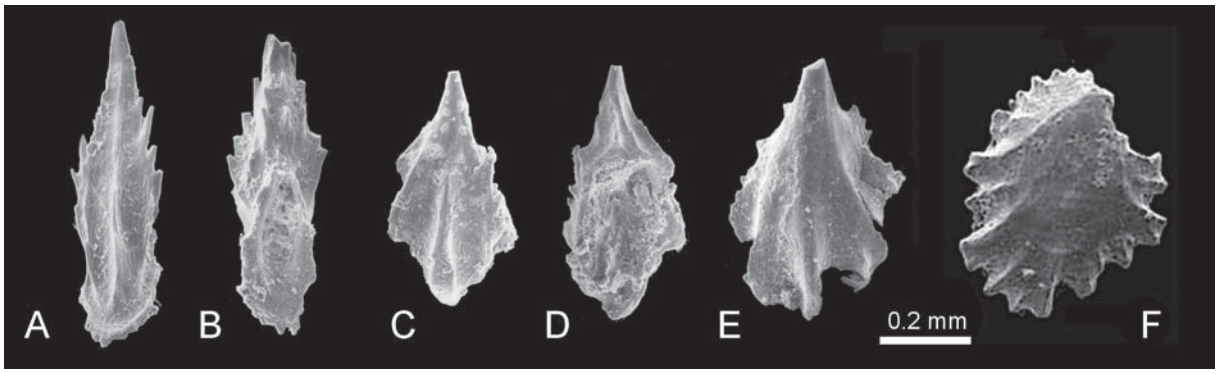
GEOLOGY AND MATERIAL

Six thelodont scales were found in limestones from the Middle Devonian (Upper Givetian) Skały Formation of the Świętomarz–Śniadka section, Bodzentyn Syncline in the Łysogóry Region, northern Holy Cross Mountains (Text-fig. 1), by J. Kłossowski (1976, samples 42/38 and 51/55). The scales come from the Sierżawy Member, most probably from a marine black, thin-bedded micritic limestone. According to Kłossowski (1976), sample 42/38 was collected in the northern part of the section, near Śniadka village, north of the Sitki gorge, and contained conodonts *Icriodus regularicrescens* and *I. obliquimarginatus*, the co-occurrence of which indicates the early Givetian (*hemiansatus–rhenanus/varcus* Conodont zones; see, e.g., Bultynck 2003; Liao and Valenzuela-Ríos 2008). However, Woroncowa-Marcinowska (2012), based on her recent re-examination of the section, placed almost all the lower part of the Sierżawy Member, including the dark-coloured limestones, in the *rhenanus/varcus* Zone, so it is reasonable to conclude that sample 42/38 also represents this zone. Sample 51/55 comes from a small section on the northern side of the valley of a western tributary of the Psarka river, between Śniadka II and III. Kłossowski (1976) reported conodonts with rather long ranges from the same section, comprising *Polygnathus linguiformis linguiformis*, *Icriodus* aff. *obliquimarginatus* and *I. curvatus*. However, as in the former case, the lithology also suggests the *rhenanus/varcus* age.

The work by Kłossowski (1976) is an unpublished M.Sc. thesis and, although it is available in the archives of the Faculty of Geology, University of Warsaw, the locality maps attached to it are missing, so the detailed positions of his collected outcrops (given herein 42 and 51, Text-fig. 1C) are only tentative, based on Kłossowski's descriptions in the text.



Text-fig. 1. Maps to show localities of finds. A, B – position of the Holy Cross Mts and the Świętomarz–Śniadka section. C – schematic geological map of Świętomarz–Śniadka section; 1 – Wojciechowice Formation, dolostones; 2-4 – Skały Formation: 2 – Sitka Coral-Crinoid Limestone Member; 3-4 – Sierżawy Member: 3 – marly and clayey shales with organodetritic and dark micritic limestone; 4 – clayey and marly shales with *Maenioceras terebratum*, 5 – Świętomarz Formation, shales and sandstones (after Woroncowa-Marcinowska 2012, modified). 42, 51 – numbers of Kłossowski's (1976) outcrops; 4a: number of Woroncowa-Marcinowska's (2012) sample which yielded thelodont scales



Text-fig. 2. **A-E** – *Australolepis* sp. cf. *A. seddoni*, possible trunk scales, Świętomarz village, Bodzentyn Syncline, northern Holy Cross Mountains, Poland, sample 42/38. A – dorsal crown view of MWGUW/Ps/1/245; B – basal view of MWGUW/Ps/1/245; C – dorsal crown view of MWGUW/Ps/1/246; D – basal view of MWGUW/Ps/1/246; E – dorsal crown view of MWGUW/Ps/1/251. **F** – *Australolepis* sp. cf. *A. seddoni*, possible cephalopectoral scale in dorsal crown view from the Świętomarz–Śniadka section, Sitka Coral-Crinoid Limestone Member, Poland (MUZ PIG 1818.II.24, from Woroncowa-Marcinowska, 2012, fig. 8H). Posterior to top

These descriptions do not indicate precisely from which part of an outcrop a particular sample was collected, and so there is a slight possibility that sample 42/38 does not come from the black limestones, but from the underlying grey shales with limestone intercalations. This placement would still date the sample from the same, *rhenanus/varcus* Zone.

Further new evidence of thelodonts was found by Woroncowa-Marcinowska (2012) in the Skały Formation of Świętomarz–Śniadka section. A single scale was reported by her from the Sitka Coral-Crinoid Limestone Member, *hemiansatus* Conodont Zone, cropping out near Śniadka village (Text-fig. 1C, section II, sample 4a). Woroncowa-Marcinowska (2012) gave full details of the stratigraphy and sedimentology of the Skały Formation in that area and, in addition to the thelodont scale, which she did not identify beyond 'fish remains' (her fig. 8H; re-illustrated by us in Text-fig. 2F), she figured several ichthyoliths, which we note here comprise acanthodian scales (figs 8F, I, L–N), a gnathostome spinelet?, teeth? (fig. 8G, J), and an osteichthyan lepidotrichium (fig. 8O). The residue of these Middle Givetian samples also contained semi-spherical problematic forms, sponge spicules, scleroform elements, tentaculite fragments and leiospheres.

SYSTEMATIC PALAEONTOLOGY

Class Thelodonti Jaekel, 1911
Order Thelodontiformes Kiaer, in Kiaer and Heintz 1932
Family Turiniidae Obruchev, 1964

Genus *Australolepis* Turner and Dring, 1981

TYPE SPECIES: Type and only species *Australolepis seddoni* Turner and Dring, 1981.

Australolepis sp. cf. *A. seddoni* Turner and Dring, 1981
(Text-fig. 2)

MATERIAL EXAMINED: Six scales from samples 42/38 and 51/55, Middle Devonian (Upper Givetian: *rhenanus/varcus* Conodont Zone), Skały Formation, Sierżawy Member, Świętomarz–Śniadka section at Śniadka village, Bodzentyn Syncline, Łysogóry Region, Holy Cross Mountains, Poland. The specimens are housed at the Museum of the Faculty of Geology, University of Warsaw, Poland (MWGUW).

ADDITIONAL MATERIAL: One possible head or cephalopectoral scale figured by Woroncowa-Marcinowska (2012, fig. 8H) from sample 4a, Middle Devonian (Upper Givetian: *hemiansatus* Conodont Zones), Skały Formation, Sitka Coral-Crinoid Limestone Member, Świętomarz–Śniadka section, Śniadka village, Bodzentyn Syncline, Łysogóry Region, Holy Cross Mountains, Poland. The specimen is housed at the Geological Museum of the Polish Geological Institute – National Research Institute, Warsaw, Poland (MUZ PIG 1818.II.24).

DESCRIPTION: The six scales from samples 42/38 and 51/55 (Text-fig. 2A–E) each have fragile elongate crowns with raised ridges. There are four to six ridges at the rim and small spines can developed along the

lateral ridges. One scale has some six spinelets on the lateral rim (Text-fig. 2A). Spinelets can also be found on the underside of the posterior crown (Text-fig. 2B); all crowns end in a long posterior point. The crown-base interface is very shallow and narrow in all (e.g. Text-fig. 2A, B, D). The scale from sample 4a (Text-fig. 2F) has a thin crown that rises to a high point towards the posterior with around 15–20 ridges, some bi- or trifurcated at the rim.

The bases are thin, which can have many small tuberosities (e.g. Text-fig. 2A, B). All have open pulp cavities. The basal view of the scale from sample 4a has not been seen but appears to be an open pulp cavity.

There are no details of histology as there are too few scales. However, the general thinness of the crowns and wide-open pulp cavities (Text-fig. 2B, D) and the thin bases with tuberose thickenings concur with the turiniid type seen in the genus *Australolepis*.

REMARKS: For now, we are comparing the Polish scales to those of the type species, particularly the scale figured by Woroncowa-Marcinowska (2012; Text-fig. 2F).

DISCUSSION: Based on the fragile elongate crowns with spinelets and thin bases with small tuberosities, the few thelodont scales so far discovered in the Holy Cross Mountains are referred to the genus *Australolepis* Turner and Dring, 1981 and probably represent trunk scales, as seen in most thelodonts (Märss *et al*. 2007) and those in the type and other *A. seddoni* scales (e.g., Trinajstic 2001). One of the scales (Text-fig. 2A, B) is more elongate and spiny than those of the late Givetian to Frasnian type species *A. seddoni* and in general they have more crown ridges and so a new species is possible but more material is needed to see the variation. Alternatively, this spinose form might be a special scale related for instance to the leading edge of fins (Märss *et al*. 2007). The spiny Polish scales resemble one referred to *Australolepis seddoni* from Horse Spring, Western Australia from the later Frasnian (Roelofs *et al*. 2015, text-fig. 3A). A recent study by Ferrón and Botella (2017) looked at the relationship between thelodont squamation and palaeoecology and in general spinyness in scales was considered an attribute to muddy or rocky substrates.

The genus *Australolepis* was first found from several beds of the Gneudna Formation in the Carnarvon Range of mid-west Western Australia, when it was given a span of late Givetian to early Frasnian (Turner and Dring 1981). When first Dring sent scales collected during his thesis work, ST thought they were all immature scales, i.e. they all had wide open concave pulp cavities with extremely thin bases and almost no neck; this became a main character of the genus and may well relate to the paedomorphic nature of these scales, retaining the first stage of morphogenesis in their bases.

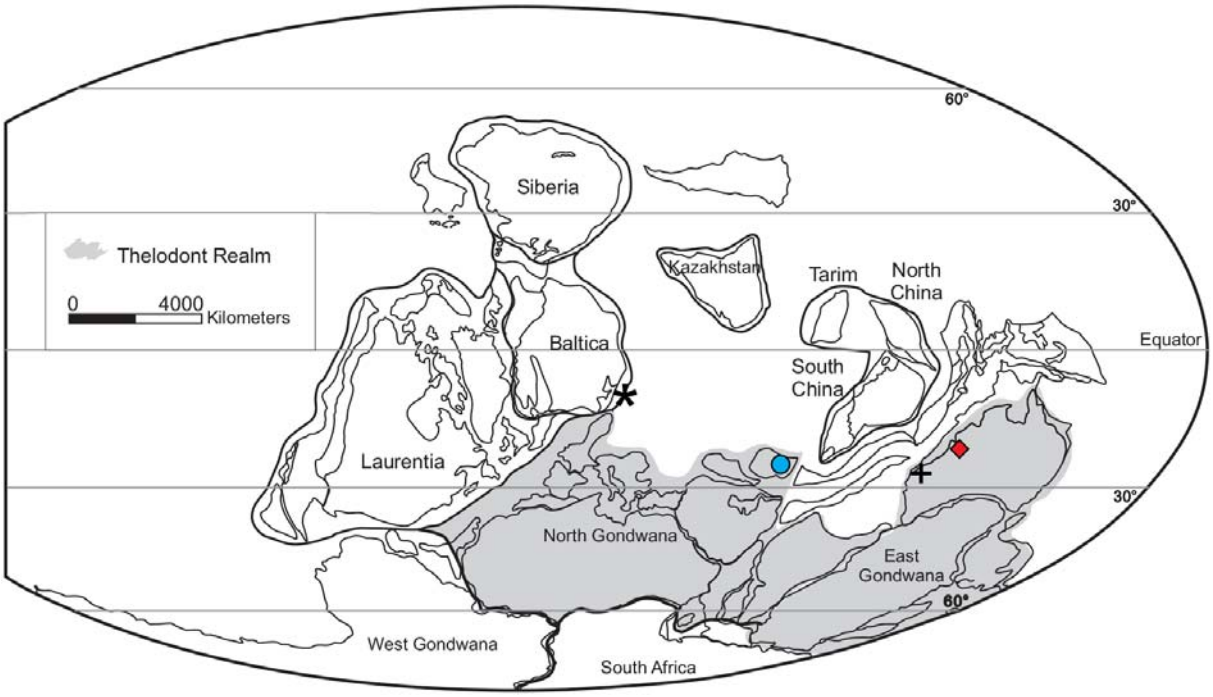
Later detailed work on *Australolepis seddoni* revealed the scale variation and extent to Iran (Trinajstic 2001; Turner 1997; Turner *et al*. 2002). As in Poland, only rare *Australolepis* scales have so far been discovered in Iran, in the Late Devonian (early Frasnian: Middle *falsiovalis–hassi* Conodont zones) mixed carbonate–siliciclastic succession exposed in the Chariseh section, Kaftari Mountains, north-east of Esfahan and Sanadaj Sirjan (Turner *et al*. 2002; Hairapetian *et al*. 2015).

Recent work in the Canning Basin has further widened the stratigraphic and geographic distribution of *Australolepis seddoni* in Australia (e.g. Trinajstic and George 2009; Chow *et al*. 2013; Trinajstic *et al*. 2014; Roelofs *et al*. 2015, see their text-fig. 1 for localities). *Australolepis* is now known to extend its range into the later Devonian in Western Australia and Iran (Hairapetian *et al*. 2015, 2016).

Rare *Australolepis*-like scales also occur with *Jesslepis* in the Givetian Papilio Formation (*varcus–hermanni* Conodont zones) of the Broken River 'embayment' or terrane, northern Queensland (Turner 1997; Turner *et al*. 2000). A detailed search in all potential Givetian to Famennian limestones around the Paleotethyan shoreline is now necessary to confirm more regarding the taxonomy.

As yet, however, there are no known articulated remains of turiniid thelodonts from Gondwana and so as yet it is difficult to judge the range of variation. For this reason, we leave the Polish scales as an undetermined species of *Australolepis*.

PALAEOGEOGRAPHIC SIGNIFICANCE: The Polish *Australolepis* scales are found in limestones with associated marine fauna such as sponges, tentaculites, conodonts, acanthodians, and osteichthyans and this supports the known palaeoenvironmental setting of other *Australolepis* scales from continental shelf locales. Liszkowski and Racki (1993) pointed the similar presence of microvertebrates in offshore. open shelf carbonate (peri-reef) settings. They (Liszkowski and Racki 1993) also noted a large mid-Givetian deepening pulse (base of T-R Cycle IIa) that probably resulted in colonization of the Holy Cross Mountains carbonate banks by diverse benthic communities. There are strong cosmopoli-



Text-fig. 3. General palaeogeographic setting for *Australolepis* distribution in the Gondwana–Laurussian shorelines of Palaeotethys during the mid- to Late Devonian. Asterisk – Holy Cross Mountains, Poland; circle – Chariseh and Hodjedk, Iran; cross – type locality of *A. seddoni* Carnarvon Range, Western Australia; diamond – Canning Basin, Western Australia. The map shows the situation of continents in the Famennian (base map after Golonka 2007, modified by Lebedev and Zakharenko 2010) and the "Thelodont Realm" *sensu* Hairapetian *et al.* (2015)

tan ranges for many chondrichthyans and gnathostomes around Palaeotethys at this time (e.g. Burrow *et al*. 2010; Klug *et al*. 2010; Young *et al*. 2010) and new thelodont occurrences in Morocco, Turkey and Pakistan (Turner 2017). This Givetian event would also have allowed expansion of the thelodont range, as seen in other taxa such as *Neoturinia* (e.g. Turner 1997; Hairapetian *et al*. 2016). Interestingly, as the Polish example is the oldest record of the genus, we need to determine if *Australolepis* occurs elsewhere at this time in Laurussian terranes or whether it appears first in Gondwana.

From their now wider-known distribution it seems that these turiniid thelodonts were inhabiting and crossing or at least moving around the Palaeotethyan waterway. They have now been found in peri-Gondwanan Poland, in a region that is close to the northern shore of Palaeotethys, in Iran, along the southern NG shoreline, and in the Carnarvon and Canning basins of Western Australia in EG (Text-fig. 3). This area constitutes what Hairapetian *et al*. (2015) termed the later Devonian 'Thelodont Realm', from where we might expect further new evidence of thelodont diversification before their final demise in the later Famennian (Hairapetian *et al*. 2016).

We provide here a general palaeogeographic setting showing *Australolepis* distribution during the mid- to late Devonian (Text-fig. 3).

CONCLUSION

This is the first record of a mid-Devonian thelodont from Poland and the first, and earliest, of *Australolepis* scales within current European borders from an area that might have been close to the northern NG shoreline, where other younger records of *Australolepis* are known. There are now *Australolepis* species known from three main regions: EG (Western Australia) where they were first found; the NG southern shoreline (localities in central Iran); and the material described here from the Łysogóry Region (Skały), Holy Cross Mountains (presumed Palaeotethys northwestern shoreline). The Polish *Australolepis* sp. cf. *A. seddoni* indicates that the Holy Cross Mountains should be included within

Hairapetian *et al*.'s (2015) Late Devonian Thelodont Realm and thus far extends the temporal range of the genus further back in time.

The find extends the geographic range of *Australolepis* from East Gondwana (western Australia) and the northern Gondwana shoreline (in Iran) further around Palaeotethys (Text-fig. 3). Consideration of this general palaeogeography indicates that a more determined search for thelodont scales is needed in these respective regions, especially in Poland.

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