New observations on the squamation patterns of articulated specimens of *Loganellia scotica* (Traquair, 1898) (Vertebrata: Thelodonti) from the Lower Silurian of Scotland

Živile ŽIGAITĖ
Université Lille 1, UFR Sciences de la Terre,
FRE 3298 du CNRS Géosystèmes,
F-59655 Villeneuve d'Ascq cedex (France)
and Uppsala University, Department of Organism Biology,
Subdepartment of Evolution and Development,
Norbyvägen 18A, 75236 Uppsala (Sweden)
zivile.zigaite@gmail.com

Daniel GOUJET
Muséum national d'Histoire naturelle, Département Histoire de la Terre,
Laboratoire de Paléontologie, UMR CNRS 7207,
case postale 39, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
goujet@mnhn.fr

Žigaitė Ž. & Goujet D. 2012. — New observations on the squamation patterns of articulated specimens of *Loganellia scotica* (Traquair, 1898) (Vertebrata: Thelodonti) from the Lower Silurian of Scotland. *Geodiversitas* 34 (2): 253-270. http://dx.doi.org/10.5252/g2012n2a1

ABSTRACT
Articulated squamations of *Loganellia scotica* (Traquair, 1898) from the Lower Silurian Lesmahagow inliers of southern Scotland have been studied. They include seven articulated specimens, three of them representing complete thelodont fossils, and four partially preserved postpectoral, precaudal and caudal parts of the exoskeleton. All the five main types of thelodont scales that is rostral, cephalo-pectoral, postpectoral, precaudal and pinnal sacles, as well as respective squamation patterns have been observed on articulated specimens. The specific orbital, branchial, and bucco-pharyngeal scales, characteristic of *L. scotica*, have not been found due to the poor or non-preservation of these particular areas within the specimens studied. Tail morphology and squamation pattern of the caudal fin have been studied with particular attention, and the constitution of the caudal fin rays has been analyzed. The rostral squamation pattern is argued to be characteristic to *L. scotica*.

KEY WORDS
Thelodonti,
articulated squamation,
thelodonts,
early vertebrates,
Lower Silurian,
Scotland.

RÉSUMÉ
Observations nouvelles sur la structure de la squamation sur des individus articulés de Loganellia scotica *(Traquair, 1898) (Vertebrata, Thelodonti) du Silurien inférieur d'Écosse.*
L'écaillure complète de plusieurs spécimens de *Loganellia scotica* (Traquair, 1898) du Silurien inférieur du gisement de Lesmahagow (sud de l'Écosse) est ici étudiée. Cette investigation porte sur sept individus articulés, trois d'entre eux représentant des spécimens de thélodontes fossiles complets et quatre, l'exosquelette correspondant à des régions partiellement conservées : postpectorale, précaudale et caudale. Les cinq types d'écailles présents chez les thélodontes, c'est-à-dire les types rostral, cephalopectoral, précaudal et pinnal ont été reconnus sur les spécimens complets. La squamation particulière des régions orbitaire, branchiale et bucco-pharyngienne, caractéristiques de *L. scotica*, n'a pu être observée compte-tenu de l'absence de préservation ou du mauvais état de conservation de ces régions sur les spécimens étudiés. La morphologie et le pattern de la squamation de la nageoire caudale ont été étudiés dans le détail et la constitution écailleuse des rayons caudaux a été analysée. Le pattern de la squamation rostrale est considéré comme représentatif de *L. scotica*.

MOTS CLÉS
Thelodonti,
squamation complète,
thélodontes,
vertébrés inférieurs,
Silurien inférieur,
Écosse.

INTRODUCTION

Loganellia scotica (Traquair, 1898) from the *Jamoytius* Horizon at the Birk Knowes site in southern Scotland is the earliest Scottish occurrence of complete articulated thelodonts. It is also the site of the first reported *Loganellia scotica* which was originally named and described as *Thelodus scoticus* by Traquair in 1898. The species has been regarded as marine, with a wide geographical range within the Euramerican province (Blieck *et al.* 1988; Märss *et al.* 2006, 2007).

Seven new articulated specimens of *L. scotica* have been studied in this work. The specimens possess quite well-preserved continuous squamations, or are preserved as natural moulds of exoskeleton, still having some areas with the continuous scale cover. The specimens come from the Lower Silurian, upper Llandovery beds of the Birk Knowes locality in Lesmahagow, southern Scotland. They have been purchased from a private collector on the initiative of the second author (DG), and are now stored in the Muséum national d'Histoire naturelle, Paris, Palaeontological collections of vertebrates (series numbers MNHN.F.GBP360, 361, 366, 367, 374, 376 and 381). The four of the specimens (numbers MNHN.F.GBP360, 361, 366 and 367) have already been attributed to the species by Van der Brugghen (1994), though squamations have not been studied in detail.

The articulated exoskeletons of thelodonts are not abundant, and most of the thelodont species have been described from disarticulated microremains (scales). Generally, the thelodont exoskeleton is a contiguous squamation of great complexity, composed approximately of 20 000 to 30 000 microscopic scales (Turner 1991), ranging from 0.1 mm to 3.7 mm in length (Märss *et al.* 2007). Each scale has a non-expanding, but centripetally thickening dentinous crown, and an expanding base of acellular bone tissue, aspidine (Märss *et al.* 2007). The structure of a particular thelodont scale depends both on its stage of ontogenetic development (age), and on its functions and place within exoskeleton, corresponding to different squamation areas. The scales could be referred to several different morphological types and different squamation patterns, respectively (Märss 1986a, b; Märss & Ritchie 1998; Märss *et al.* 2006, 2007). The five main types of the scales are: rostral (in earlier works referred to as oral), cephalo-pectoral, postpectoral, precaudal and pinnal. New observations of all of them have also been made on the *L. scotica* specimens studied, and are described and presented herein. In order to understand the intraspecific variability of thelodont microremains, studies of the scale diversity within

individual articulated specimens are necessary. They also serve as strong background in arguing the "artificial" palaeontological species to be sufficiently close to a natural palaeospecies. Thus detailed study of articulated fossils in this aspect is crucial for thelodont taxonomy.

This work is an attempt to analyse squamation patterns of *L. scotica* on the new articulated specimens of the species, in order to dertermine variability and arrangement of different scales types within the individual, and within the species. We do not intend to repeat the intraspecific morphological scale variation (morphological set) studies on the articulated squamations of *L. scotica*, which have already been presented in a number of previous works, most recently in appreciable detail by Märss & Ritchie (1998). Trying to avoid any recurrence, this study is concentrated on squamation patterns within the different parts of the body of *L. scotica.*

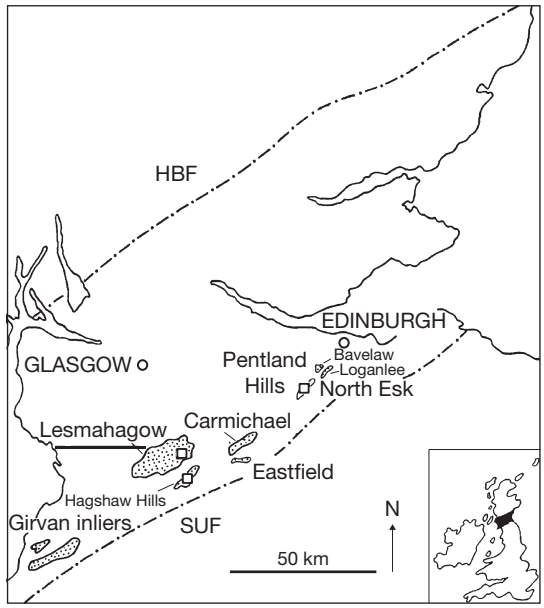

FIG. 1. — Main vertebrate localities (□) in the Silurian inliers (dotted areas) of southern Scotland (sketch map from Märss & Ritchie, drawn after Wellman & Richardson 1993). Abbreviations: **HBF**, Highland boundary fault; **SUF**, southern Uplands fault.

HISTORICAL ACCOUNT

Loganellia scotica first has been described by Traquair in 1898 and later years (Traquair 1899, 1905), then by Stetson (1931), and was originally named *Thelodus scoticus*. These descriptions and reconstructions have been used until recent time, and the initial concept of "conventional" thelodont body constitution is still strongly based on the Scottish articulated thelodont findings. Gross (1967) has established the new genus *Logania*, and splitted the previously described "*Thelodus scoticus*" into five species: *Logania scotica*, *L. kummerovi*, *L. ludlowiensis*, *L. martinssoni and Turinia pagei*. He was the first to divide scales of the thelodonts into different morphological types, as head, transitional and trunk scales (Gross 1967). He has figured the denticulated platelets of *Logania*, which later have been noticed by Ritchie (1968) as well. Subsequent reconstructions of *Loganellia scotica* were made by Turner (1970, 1991, 1992), including the correction of the genus name from former *Logania* to present *Loganellia*. The distribution patterns of denticles and denticle-bearing platelets inside the exoskeleton of *L. scotica* have been described by Van der Brugghen & Janvier (1993). Vergoossen (1992) has described scale sets of *L. scotica* from the *Jamoytius* Horizon, several scales from the branchial areas fused together, which indicates remaining problems in the interpretation of thelodont scale variations and patterns.

First specialized publication on thelodont squamation patterns has been made by Turner (1994). The most recent detailed study of articulated squamations and revised diagnosis of *L. scotica* have been made by Märss & Ritchie (1998), which allowed more detailed subdivision of the scales into five scale types, viz. orbital, cephalo-pectoral (including the rostral area of the body, as *L. scotica* was supposed not to possess any typical rostral squamation: Märss & Ritchie 1998; further arguments on this topic is considered in discussion below), postpectoral, precaudal and pinnal scales (Märss & Ritchie 1998; Märss *et al.* 2006, 2007), and the squamation patterns respectively. This classification of different squamation patterns was first elaborated on *Phlebolepis elegans* Pander, 1856 articulated specimens by Märss (1986a). It has also

been revealed in the same work (Märss 1986a), that not only morphology, but also histology of the scales varies between the scales from different squamation types. For example, the rostral (previously oral) and most of anterior cephalo-pectoral scales do not possess any pulp canal, while it is present in the scales from the other squamation areas (Märss 1986a). Later some more scale types of thelodonts have been described by Turner (2000). Finally, combining data of thelodont scale morphology, histology and squamation patterns, a refined scheme of scale associations has been presented as a tool to deal with disarticulated microremains (Märss 1986a, b).

Scales and denticles of the bucco-pharyngeal and branchial areas of *L. scotica* have been studied in detail by Märss & Ritchie (1998). Several post-pectoral squamation features have been presented in the same paper, illustrating both the dorsal and ventral sides; some characteristics elicited in latex casts. Presence of distinct rostral squamation pattern in *L. scotica* has been declined, and the cephalo-pectoral squamation type has been regarded as the main of the body, starting from rostrum up to the end of the base of pectoral fins (Märss & Ritchie 1998). The intraspecific scale variety of *L. scotica* has also been studied in this work.

According to the previous studies, *Loganellia scotica* is widely distributed in the Llandovery of Eurasia (Turner 1973; Aldridge & Turner 1975; Karatajūtė-Talimaa 1978; Märss 1989; Turner *et al.* 1994), and also known in late Llandovery and Wenlock of North America (Turner & Nowlan 1995; Märss *et al.* 1997, 1998a, 2006) and Greenland (Blom 1999), and is used for biostratigraphic correlation between these areas and Britain.

GEOLOGICAL SETTING

The articulated specimens presented in this study come from the Silurian locality of Lesmahagow, 30 km south of Glasgow, in Lanarkshire, southern Scotland (Fig. 1). Lesmahagow locality is world-renowned, as many important collections of Silurian vertebrates have been made there since the mid to late 1800's. The campus named "Camp Siluria" has been set up near Lesmahagow in 1890's by the Geological Society of Glasgow to signify its geological importance. It is now very difficult to obtain permission to collect from these rocks as a result of inappropriate collecting. Birk Knowes SSI – site of special scientific interest having special protection under the law in Scotland – is also known as the *Jamoytius* Horizon named by Ritchie (1960, 1968) after the rare soft-bodied fish found from this locality. This site has been made off-limits to all collecting for the time being.

The Lesmahagow Inlier is a block of Silurian sediments surrounded by sediments of Carboniferous age. The inlier consists of shales and sandstones with occasional pebble conglomerates of a lagoon or lake. The articulated squamations and imprints have been collected in the *Jamoytius* Horizon outcrops at Birk Knowes, which are three small exposures on Logan Water, in the Lesmahagow inlier. The vertebrates from these fish-bearing horizons are amongst the oldest in Britain (see Aldridge & Turner 1975; Turner 2000; Märss & Miller 2004), and have been attributed to two species, *Loganellia scotica* and *Jamoytius kerwoodi* White, 1946. The possible third one, *Thelodus planus* Traquair, 1898, has been recorded by Traquair (1898), but then regarded as dubious by Ritchie (1968), and synonymized with *L. scotica* by Märss & Ritchie (1998).

The *Jamoytius* Horizon lies within the Patrick Burn Formation at the base of the Priesthill Group. The Patrick Burn Formation consists of at least 400 m of greywackes and shales which may be divided into two types: dark, finely laminated siltstones and non-laminated olive mudstones. Vertebrates, together with crustacean fossils, occur in the laminated siltstones. Recent evidence indicates a late Llandoverian age of the Horizon (Cocks *et al.* 1992: fig. 2.8; Wellman & Richardson 1993: 158).

The *Jamoytius* Horizon is 10 m thick, consisting of alternating grey-black finely laminated carbonaceous siltstones and non-laminated olive to greyish green mudstones. Macroscopic remains are almost entirely confined to the organic-rich laminated siltstones. The sequence within the

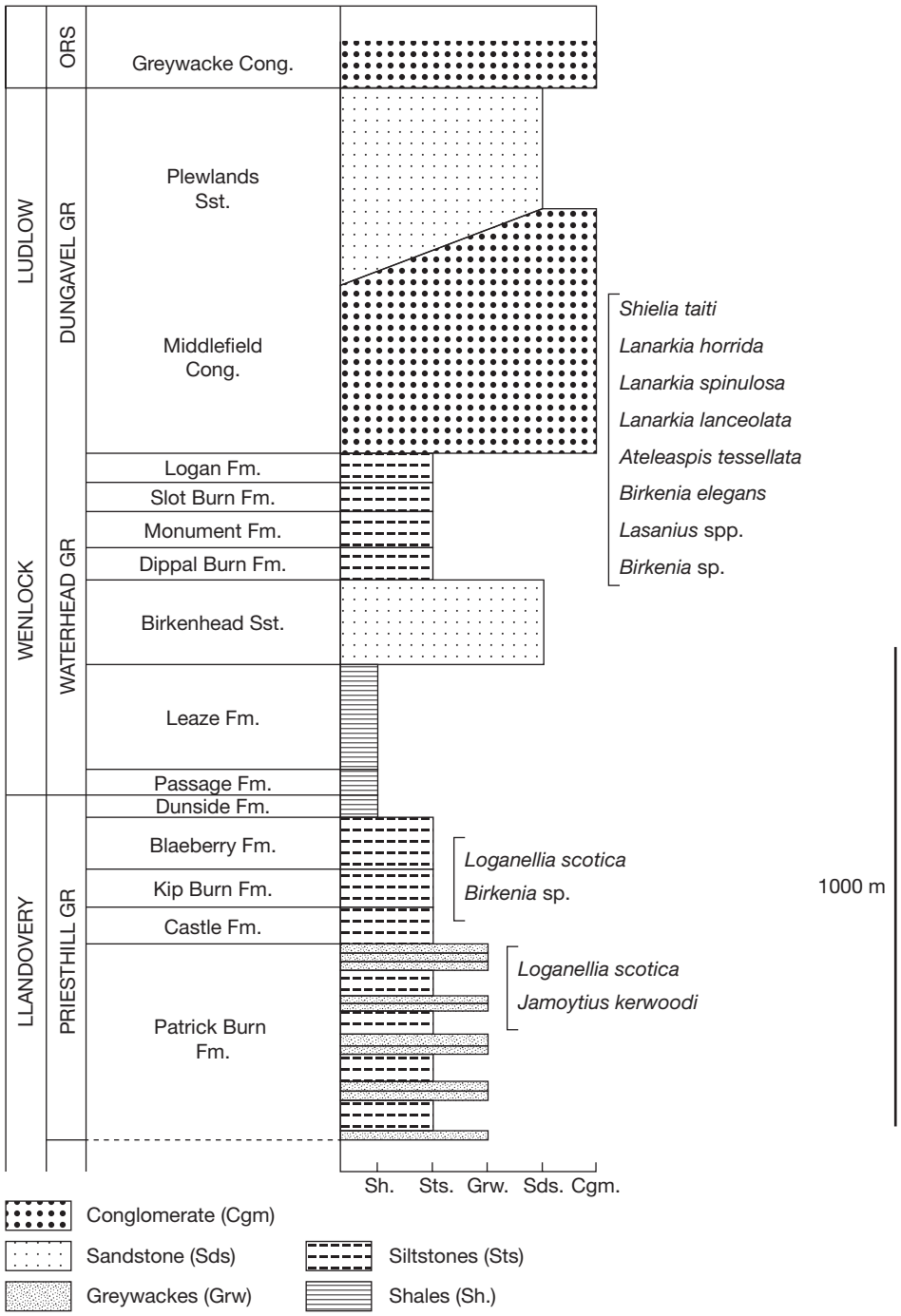

FIG. 2. — Vertebrate bearing horizons in the sections of the Silurian inlier of the Lesmahagow locality (modified after Märss & Ritchie 1998). Abbreviations: **cong.**, conglomerate; **SSt**, Sandstone; **Fm**, Formation.

Priesthill Group represents a transition from marine to fluvial and deltaic conditions (Ritchie 1985), though the *Jamoytius* Horizon corresponds to truly marine sediments. Both the greywackes and shales of the Patrick Burn Formation have slump structures reflecting unstable bottom conditions. Ripple marks indicate current directions towards the north-north-east for the formation as a whole. Equivalents of the Lesmahagow rocks in the Baltic area range through a variety of facies with vertebrates in clearly marine conditions as well (Blieck *et al.* 1988).

The fossils occur throughout the *Jamoytius* Horizon but are noticeably more abundant and better preserved in the middle 7 m. Calcareous concretions occur throughout; those found within the mudstone nearly always enclose fossils. The concretions also contain thelodont remains, either as articulated individuals, patches of exoskeleton or, more commonly, as coprolitic layers of denticles (Ritchie 1968). The *Jamoytius* Horizon is the only unit in the Patrick Burn Formation in which articulated thelodonts occur. According to the most recent stratigraphy of the Silurian inliers at Lesmahagow (Walton & Oliver 1991; Rolfe 1992; Wellman & Richardson 1993), the *Jamoytius* Horizon of the Birkenhead Burn outcrop fish beds are treated as belonging to the upper Llandovery (Fig. 2). This study provides a new additional record of *L. scotica* in the *Jamoytius* Horizon at the Birk Knowes locality of the Lesmahagow Inlier.

MATERIAL AND METHODS

The material studied comprises 11 articulated squamations of thelodont *Loganellia scotica*, with complete or partially preserved scale cover. The specimens are stored in the Muséum national d'Histoire naturelle, Paris, Palaeontological collections of vertebrates, series MNHN.F.GBP and collection numbers: MNHN.F.GBP360, 361, 366, 367, 374, 376, and 381.

Articulated squamations were photographed using a Nikon Coolpix 4500 digital camera; details of the squamations and close-ups were studied and imagined by high resolution optical microscope Zeiss Axioplan2 with digital image processing, with a Canon PowerShot G5 digital camera. Contrast enhancing technique has been used for macroimaging: specimens have been whitened by MgO dust. SEM imaging within the premises of MNHN has not been possible because of the oversize of the samples.

In descriptions of the articulated squamations of *L. scotica*, scale size has been ascribed referring to the classification presented by Märss *et al.* (2006), which is as follows: very small, up to 5 cm in lengh; small, up to 10 cm; medium, up to 20 cm; and large, up to 40 cm or more. The size of scales is subdivided as follows: very small, 0.1-0.5 mm; small, 0.5-1.0 mm; medium, 1-2 mm; and large, 2-3.7 mm. In order to estimate the size of articulated specimens with creased or insufficiently preserved anterior parts, the total body length of the exoskeletons has been approximated, deriving a relationship from the known evident total body length of fully preserved exoskeletons. The width of caudal peduncle has been used as a reference and indication of an approximate total body length of the thelodont. We have assumed the width of caudal peduncle as the most evident and presumably most adequate measurement in relation to the total body length of the animal, and also as the best preserved feature in all the studied squamations, considered for this calculation. Therefore, in addition to our material, the ratios of body lengths and caudal peduncle widths of 8 more articulated specimens of *L. scotica* have been taken from the work of Märss & Ritchie (1998: 150, table 2), collection numbers: NMS.G.1967.65.18B, BMNH.P.10137, GSE1137, AM.F.89434A, AM.F.89433B, NMS.G.1905.3.5, AM.F.89432, and NMS.G.1905.3.4. From our new material, the measurements of three fully preserved thelodont exoskeletons have been considered in the same manner (specimens MNHN.F.GBP361, 374 and 376). Summarizing all the data available, a mean ratio coefficient for the total body length approximation on the width of the caudal peduncle, has been obtained. The equations used are as follows:

$$TL_{app} = P \times C$$

Where TL_{app} = approximate total body length; P = known width of the caudal peduncle and C = mean ratio coefficient.

$$R = L/P$$

Where R = ratio of the total body length to the width of caudal peduncle; L = actual body length; P = width of the caudal peduncle.

$$C = 9.826$$

Where R = ratio of the total body length to the width of caudal peduncle; n = number of specimens (11 complete fossils of *L. scotica* have been measured); C = mean ratio coefficient, which has been derived and used in this work as C = 9.826, to approximate total body lengths of incomplete specimens. However, this approximation must be taken into account considering the post-mortem deformation of the exoskeleton, which very often results in a twisted caudal fin and altered real width of caudal peduncle (see also Mark-Kurik & Botella 2009).

The terminology of scale types corresponds to the five main categories of body regions of *L. scotica*, according to those first distinguished in the exoskeleton of *Phlebolepis elegans* (Märss 1986a), which represent distinct scale morphologies as well as specific functions. They are as follows: rostral, cephalo-pectoral, postpectoral and precaudal, and pinnal body areas, and scale types respectively (Fig. 3).

In the synonymy of species, only publications containing illustrations have been considered.

ABBREVIATIONS

AM	American Museum, New York;
BMNH	The Natural History Museum, London;
GSE	Geological Survey of Scotland, Edinburgh;
MNHN	Muséum national d'Histoire naturelle, Paris;
NMS	National Museum of Scotland, Edinburgh.

SYSTEMATICS

Subclass THELODONTI Kiaer, 1932
Order LOGANELLIIFORMES Turner, 1991
Family LOGANELLIIDAE

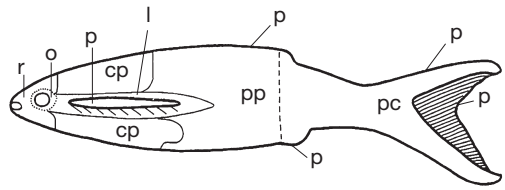

FIG. 3. — Squamation patterns in the *Loganellia scotica* (Traquair, 1898) exoskeleton. Abbreviations: **cp**, cephalo-pectoral squamation; **l**, lateral squamation; **o**, orbital squamation; **p**, pinnal squamation; **pc**, precaudal squamation; **pp**, postpectoral squamation; **r**, rostral squamation (modified after Märss & Ritchie 1998).

Märss, Wilson & Thorsteinsson, 2002

Genus *Loganellia* Fredholm, 1990

TYPE SPECIES. — *Loganellia scotica* (Traquair, 1898).

Complemented synonymy list after Märss *et al.* (2006, 2007).

Thelodus scoticus Traquair, 1898: 72; 1899: 829, *partim*, pl. 1, figs 1, 2, 5-10; *non* pl. 1, figs 3, 4; 1905: 880, pl. 1, figs 1-4. — Stetson 1931: 141, fig. 1a, b. — Stensiö 1958: 417, fig. 218; 1964: 371, fig. 124a.

Thelodus planus Traquair, 1899: 831, pl. 2, figs 1-3.

Logania taiti – (Stetson) Gross 1967: 33, pl. 5, figs 26-42, text-fig. 13N-Q.

Katoporus? sp. – Gross 1967. — Aldridge & Turner 1975: 419-420, pl. 1, figs 4-6.

Logania scotica – (Traquair) Gross 1967: 32, pl. 5, figs 12-25, text-fig. 13c-f. — Aldridge & Turner: 419, 420, pl. 1, figs 1-3, 7-9. — Turner 1991: fig. 1f; 1992: 26, text-fig. 2. — Vergoosen 1992: 51, figs 2, 3, 5-24. — Van der Brugghen 1993: 88, figs 1-3; 1994: figs 2, 3, 5-8. — Turner & Van der Brugghen 1993: 132, fig. 2. — Märss & Ritchie 1998: 147, figs 7-21, 33e. — Märss *et al.* 1998a: 56, 60, figs 2, 3; 1998b: 37, fig. 1; 2006: 17-20, pl. 1, figs 1-5, 7-17, text-fig. 7A-Z; 2007: 49-52, fig. 42a, b. — Blom 1999: 98, fig. 2.

LECTOTYPE. — Traquair (1899: pl. 1, fig. 1) specimen GSE5996 from the British Geological Survey Museum, Keyworth, stored in NMS.

TYPE LOCALITY AND HORIZON. — Patrick Burn Formation, Priesthill Group, upper Llandovery; Logan Water, Lesmahagow Inlier, southern Scotland.

DIAGNOSIS. — (modified after Märss *et al.* 2007): medium to large thelodonts with fusiform body, with dorsoventrally

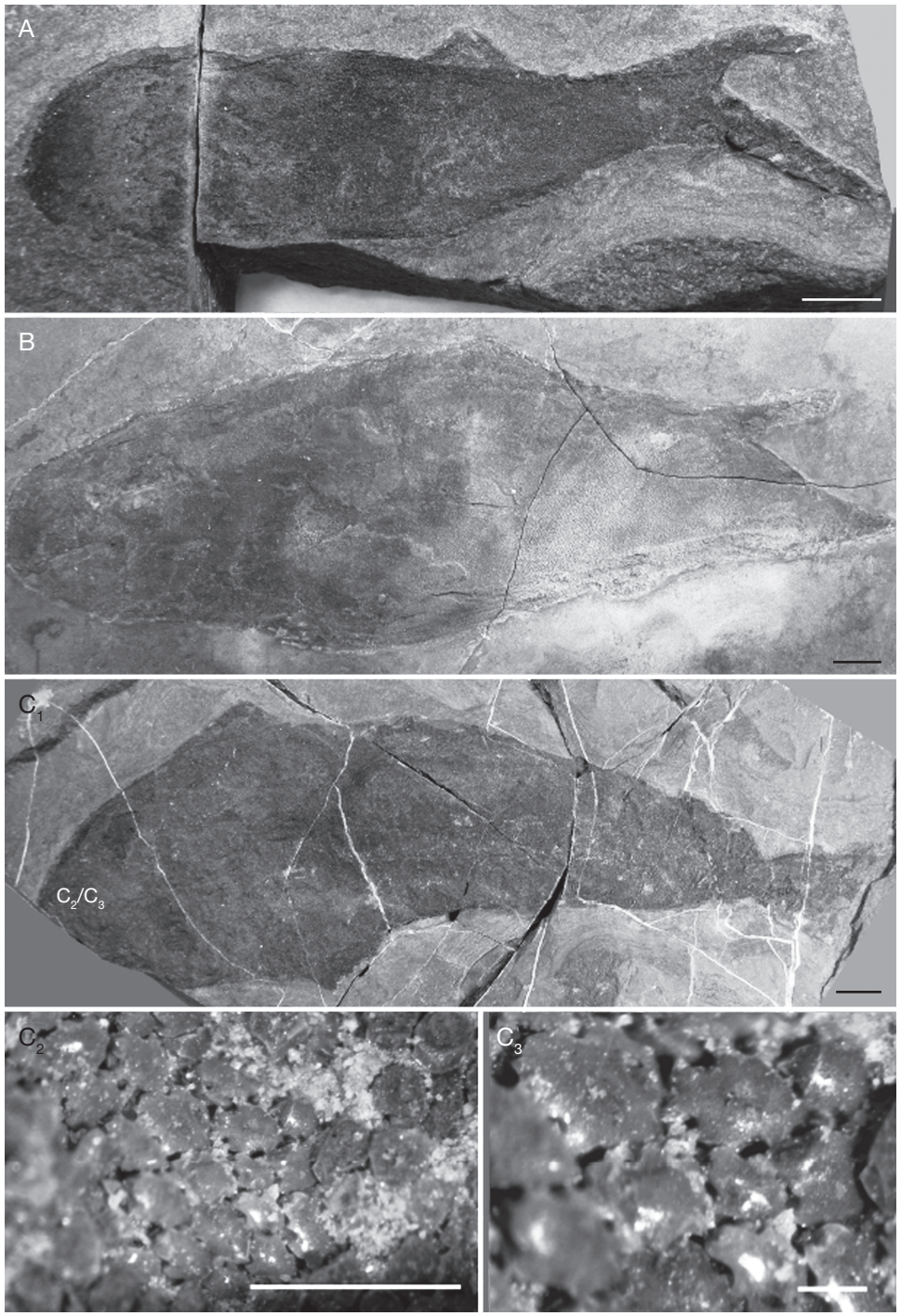

Fig. 4. — Articulated specimens of *Loganellia scotica* (Traquair, 1898): **A**, MNHN.F.GBP374; **B**, MNHN.F.GBP361; **C_1**, MNHN.F.GBP376; **C_2**, **C_3**, rostral squamation pattern in MNHN.F.GBP376. Scale bars: A-C_1, 1 cm; C_2, 1 mm; C_3, 0.2 mm.

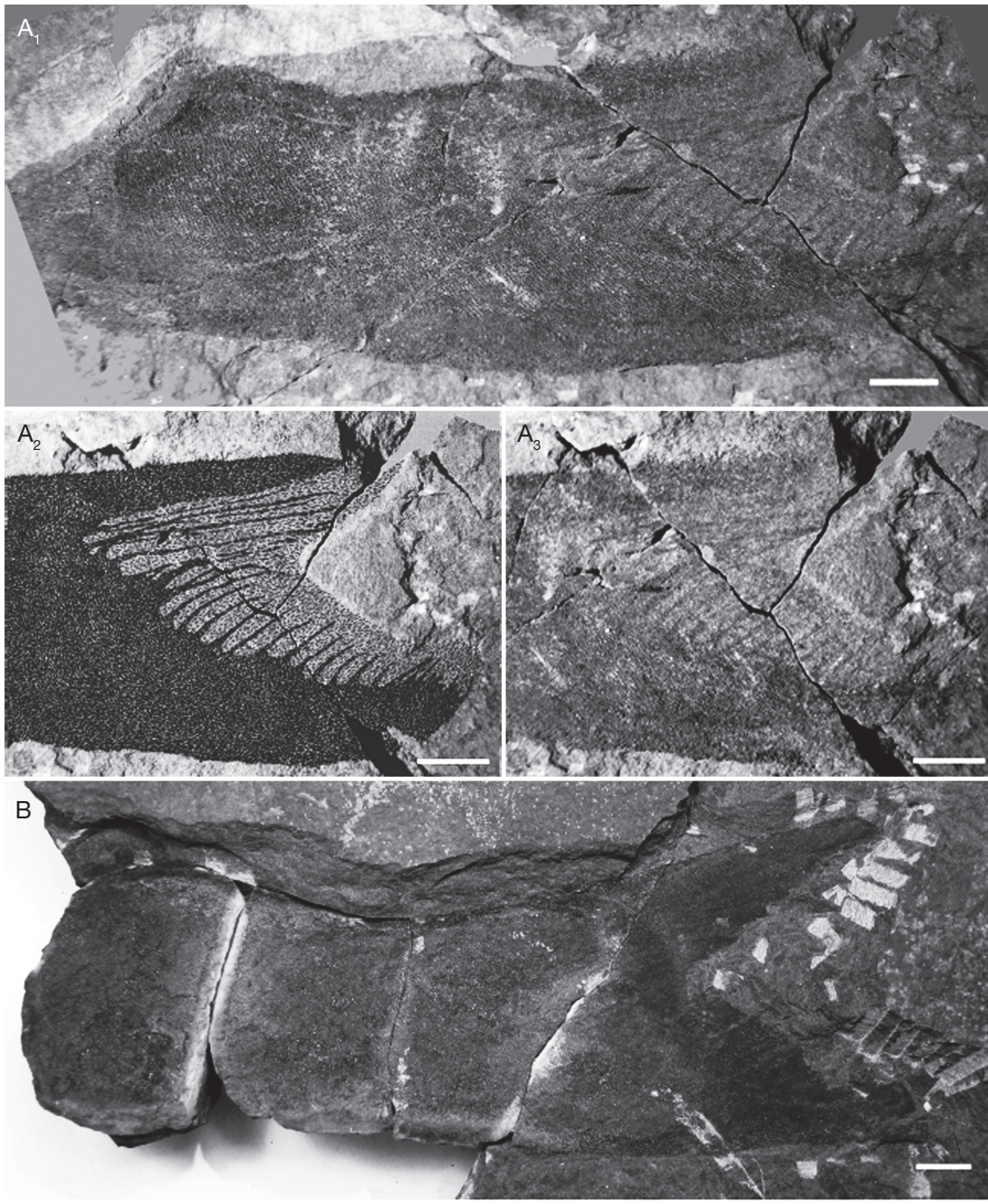

Fig. 5. — Caudal and precaudal parts of articulated squamations (tails) of *Loganellia scotica* (Traquair, 1898) : **A1**, **A2**, **A3**, MNHN.F.GBP367; **B**, MNHN.F.GBP366. Scale bars: 1 cm.

TABLE 1. — Body length and width (in mm) of *L. scotica* (Traquair, 1898) articulated squamations studied in this paper.

Specimen	Length of the part of the body	Length of the caudal fin	Width of the caudal peduncle	Width of the caudal fin	Body length (derived lengths)
MNHN.F.GBP360	192	41	20	59	(197)
MNHN.F.GBP361	190	35	27	29	190
MNHN.F.GBP366	175	85	45	67	(442)
MNHN.F.GBP367	141	84	33	40	(324)
MNHN.F.GBP374	107	30	8	20	107
MNHN.F.GBP376	201	35	11	32	201
MNHN.F.GBP381	195	116	40	54	(393)

flattened anterior part, and strongly rounded rostral part. The scale cover is comparatively uniform. Postpectoral and precaudal scales are elongate, wedge-shaped, elliptical and sometimes carinate; raised median rhombic area of the crown is common; base tending to bulge anteriorly in older scales and an anterior process is common. The pulp cavity is deep and open in young scales, reduced to a slit-like groove in older scales, which leads to a single pulp canal opening being located at the distal end of the scale. Possess specialized branchial denticles.

OCCURRENCE. — Lower Silurian, Upper Llandovery, lower fish beds (articulated), Patrick Burn, Kip Burn & Blaeberry formations, Lesmahagow, Scotland; upper Llandovery, Wych Formation, *Pentamerus* beds, Purple Shale Formation, Welsh Borderland; Upper Llandovery, Kilbride Formation, Ireland (in part); Upper Llandovery, Lafayette Bugt Formation, Hall Land, northern Greenland; Upper Llandovery, Wulff Land Formation, Thors Fjord Member, *Monograptus spiralis* Biozone, Greenland; Upper Llandovery, Rumba Formation, Raikkula Stage, Estonia; Upper Llandovery, Lower Visby Formation, Gotland, Sweden; Lower Llandovery, Clemville and Weir formations, Quebec, eastern Canada; Upper Llandovery, Limestone Point Formation, New Brunswick, eastern Canada; Upper Llandovery, Anse Cascon and Anse a la Pierre Loiselle formations, Quebec, eastern Canada; Cape Phillips Formation, Devon Island, Canadian Arctic; Upper Llandovery, Baillie-Hamilton Island, Canadian Arctic, Avalanche Lake, Mackenzie Mountains, northern Canada (Märss *et al.* 2007).

MATERIAL STUDIED. — MNHN.F.GBP360, 361, 366, 367, 374, 376, and 381; see Material and methods.

LOCALITY AND HORIZON OF THE STUDIED MATERIAL. — *Jamoytius* Horizon, Patrick Burn Formation, Priesthill Group, upper Llandovery; Birk Knowes, Lesmahagow Inlier, southern Scotland.

DESCRIPTION

Size of the articulated specimens studied varies from 107 to 450 mm in length. According to Turner (1991: 89; 1992: text-fig. 3B) the body of *L. scotica* usually is 275 mm in length, but may reach 300-400 mm (Märss & Ritchie 1998). The material studied in this work comprises one small thelodont specimen (MNHN.F.GBP374), three medium sized ones (MNHN.F.GBP360, 361 and 376), and three very large exoskeletons (MNHN.F.GBP366, 367 and 381). Though only postpectoral, precaudal and caudal parts of the large specimens have been preserved. The total body length estimations based on the width of caudal peduncle of the specimen enables us to consider that the maximum total body length of *L. scotica* may have exceeded 40 cm (Fig. 5B). The measurements of the specimens studied, as well as their derived total body lengths on the basis of the length ratio of caudal peduncle, are given in Table 1. Three of the seven articulated specimens are partly incomplete exoskeletons of large animals; the smaller ones are complete animal fossils, even if the best parts are preserved as natural moulds, lacking the bulk of their squamation (Fig. 4A-C). Tails of all specimens possess a clearly hypocercal asymmetrical caudal fin with a very wide ventral lobe, best contrasted on the tail of MNHN.F.GBP361 (Fig. 4B), with numerous narrow fin rays branching off from it. The ventral lobe is longer, thicker and much more massive than the dorsal lobe. This wide ventral lobe has already been noticed in its first description by Van der Brugghen (1994).

Scales are small to medium in size. The rostral, cephalo-pectoral, postpectoral, precaudal and pinnal squamation types (Fig. 3) have been observed and studied on the specimens. The pinnal squamation pattern is particularly well preserved on several

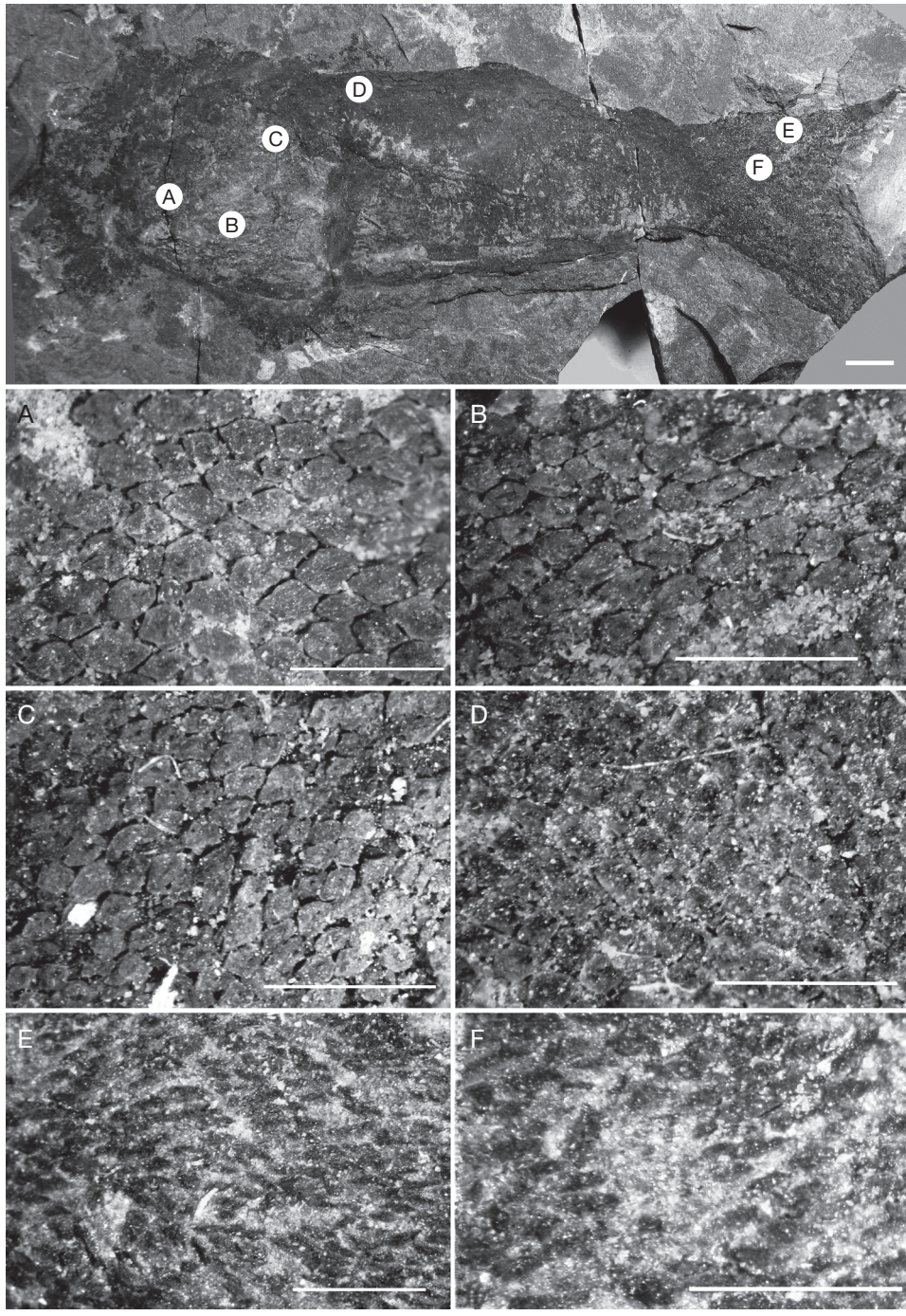

FIG. 6. — Squamation patterns of *Loganellia scotica* (Traquair, 1898), specimen MNHN.F.GBP360 with details of: **A**, cephalo-pectoral squamation pattern; **B**-**D**, postpectoral squamation pattern; **E**, pinnal squamation pattern of caudal fin. Scale bars: articulated exoskeleton, 1 cm; A-F, 1 mm.

articulated caudal fins (Fig. 5A$_1$, A$_3$). Pinnal squamation of pectoral fins or pectoral flaps (Märss *et al.* 2007), of dorsal and anal fins are less clearly preserved within the specimens studied. Neither scale cover of bucco-pharyngeal area, with its specific denticles, well described by Märss & Ritchie in 1998, and named lateral squamation, nor orbital squamation patterns have been observed within the material studied (see Märss & Ritchie 1998: figs 9, 10).

Rostral squamation pattern
This, or an anterior cephalo-pectoral squamation, according to Märss & Ritchie (1998), has been observed within the specimens MNHN.F.GBP361 and 374. A clear rostral squamation type is present on the anterior bucco-lateral sides of the head of the complete articulated specimen MNHN.F.GBP376 (Fig. 4C$_1$). The rostral scales are round to oval in shape, very small, 0.2-0.4 mm in diameter; the crown is of a symmetrical oak-leaf-like shape, with a smooth and slightly bulging surface, and crenulations on the margins (Fig. 4C$_2$). Natural moulds of rostral squamation have been observed on the specimens MNHN.F.GBP361 and 374.

Cephalo-pectoral squamation pattern
It is particularly well preserved within the exoskeleton of the specimen MNHN.F.GBP361 (Fig. 4B), and it has also been observed as natural moulds within the specimens MNHN.F.GBP374 (Fig. 4A) and 376 (Fig. 4C$_1$). Cephalo-pectoral scales are rhomboidal in shape, with comparatively dim surface sculpture, and one or two lateral areas which are rather indistinct, expressed as shallow grooves on the anterior part of the crown. In average they are 0.3 to 0.4 mm long. The cephalo-pectoral scales cover the anterior (but rostral) and middle parts of the body, and may also be found on the pectoral flap (pectoral fin), which is the case in the specimen MNHN.F.GBP360 (Fig. 6A).

Postpectoral squamation pattern
It is the main squamation type of thelodonts (see the discussion below), and it comprises the best part of the articulated specimens studied. It is very well preserved within the specimens MNHN.F.GBP360 (Fig. 6B-D), 361, 366, 367 and 381 (Fig. 7A, B). Natural moulds of postpectoral squamation have also been observed within the specimens MNHN.F.GBP374, and 376, with an exception of few patches of postpectoral scale cover on the latter one. Postpectoral scales are rhomboidal to wedge-shaped, 0.25 to 0.45 mm in length. The crown is elongated, with relatively wide anterior part and sharp posterior apex of the crown. It is clearly divided into elevated median area with oblong shallow furrow, and two lower lateral ridges, separated by sharp longitudinal grooves, which meet at the posterior apex of the crown.

Precaudal squamation pattern
It is characterized by very thin and elongated scales, and covers the zone of the tail up to the caudal fin. Precaudal scales have general morphology quite similar to the postpectoral ones, however they are comparatively smaller (0.15-0.35 mm long), more narrow and elongated. Referring to the specimens observed it is necessary to admit that the change of squamation pattern going from postpectoral to precaudal is very gradual.

Pinnal squamation pattern
It is the most peculiar. Pinnal scales of the caudal fin are tiny (0.1-0.25 mm in diameter) and very narrow (less than 0.01 mm in width). Scales are strongly elongated, less rhomboidal and more bubbin-shaped. Their general crown sclupture is similar to that of postpectoral and precaudal scales, only the median areas are narrower, as well as are the lateral ridges. Being much smaller and more elongate compared to precaudal ones, they cover continuously the flexible ray area of the caudal fin. The caudal fin squamation is exceptionally well preserved on the specimen MNHN.F.GBP367, possessing fully articulated continuous pinnal squamation, with caudal rays as distinct accentuated lines of more compact scale cover (Fig. 5A$_{1-3}$). The scale cover is significantly denser in the area of the rays forming arch-shaped ramifications, wider proximally near the base of the caudal lobes, and narrowing distally towards the posterior end of caudal fin (Fig. 5A$_2$). At least 20 caudal fin rays can be observed on the ventral lobe of the specimen MNHN.F.GBP367.

The tail itself is strongly asymmetrical, referring to a rather young age of the thelodont animal. The maximum width of the ventral lobe reaches 2.5 cm, while the dorsal lobe is less than 1.0 cm in width. The ventral lobe still retains rather postpectoral-like squamation. These well expressed caudal fin rays have also been observed within the specimens MNHN.F.GBP366 and 381, though their scale cover is much less well preserved. Distinct squamation patterns have been observed on the leading edges of caudal fins (specimens MNHN.F.GBP366 and 381), present as denser linear structures of particular pinnal scales, ontop of the precaudal squamation pattern (Fig. 7C, G).

The squamation pattern of the dorsal fin has been observed with the specimens MNHN.F.GBP360 and 361, and that of the anal fin is rather well preserved in the specimen MNHN.F.GBP381 (Fig. 7D). The shape of the dorsal fin of a young *L. scotica* is well preserved as a natural mould in the specimen MNHN.F.GBP374 (Fig. 4A). The anal fin has been observed only as a natural mould on the specimen MNHN.F.GBP361 (Fig. 4B), and as an incomplete articulated squamation on the specimen MNHN.F.GBP381 (Fig. 7A-D).

DISCUSSION

The rostral squamation pattern of the *L. scotica* articulated specimens studied are sufficiently distinct when compared with the crown sculpture of the cephalo-pectoral scales, which tend to be elongated, with clearly discernible pointy and shorter anterior part, and wider obtuse posterior part of the crown (Fig. 6A). Referring to the previous studies, *L. scotica* possesses more squamation varieties than the five main ones of Märss & Ritchie (1998), though it has been argued it does not possess any typical rostral scales (Märss & Ritchie 1998: 152), and reference comparison with the *Phlebolepis elegans* has been made (Märss 1986a). In our opinion, *P. elegans*, being a representative of the family Phlebolepididae Berg, 1940, is quite different group of thelodont by means of scale morphology and general body structure. Referring to the intraspecific scale varieties (morphological sets) within the different species of loganiid thelodonts (Karatajūtė-Talimaa 1978; 1991; Žigaitė 2004; Märss *et al.* 2007), and to our study of the articulated squamations described above, we suggest the rostral squamation pattern to be present in *L. scotica*. The best examples could be the rostral squamations of the specimens MNHN.F.GBP361 and 374. The scale cover on the most anterior parts of the blunt head, and on the sides of the branchial (or lateral, according to Märss & Ritchie 1998) area within these speciments (Fig. $4C_{1-3}$) we consider as the rostral squamation pattern. Moreover, rostral scales of *L. scotica* have been clearly figured by Märss *et al.* (2007: fig. 42A[a], B[a]). We have also observed that in some cases, the precaudal scale cover, especially if considering older and larger specimens (Fig. 7E, F), may resemble the postpectoral squamation type of younger individuals of *L. scotica* (Fig. 6B). The squamation of the tail in larger specimens becomes completely typical precaudal and narrow-scaled just on the forefront of caudal fin (Fig. 7H). Although the characteristic narrow and pointy shape of precaudal scales, compare to the wider and rhombic postpectoral ones, is being kept through all the squamations observed. Distinct pinnal scale coverings are present on the leading edges of caudal fins, which consist of denser pinnal scale web ontop of the precaudal squamation pattern, and are typical for the leading edges of thelodont fins. The particular attention shall be given to the squamation pattern of the caudal fin. Stetson (1931) was the first to recognize a hypocercal tail fin in thelodonts, and the thin film of scales, covering continuously the flexible intra-posterior part of the caudal fin, as well as presumable fin rays. He described a tail of a large specimen of *L. scotica* with caudal finweb and up to 18 possible internal cartilaginous fin rays (Stetson 1931). We have observed at least 20 long fin rays within the pinnal scale cover of the caudal fin on the specimen MNHN.F.GBP367 (Fig. $5A_{1-3}$). All of them do clearly branch off from the ventral lobe (Fig. $5A_2$). Van der Brugghen (1994: fig. 8E) has already mentioned and drew these caudal rays in the first description of the specimen, implying them to reflect traces of the former cartilaginous caudal rays. Considering our recent observation of the fossil, the caudal fin rays

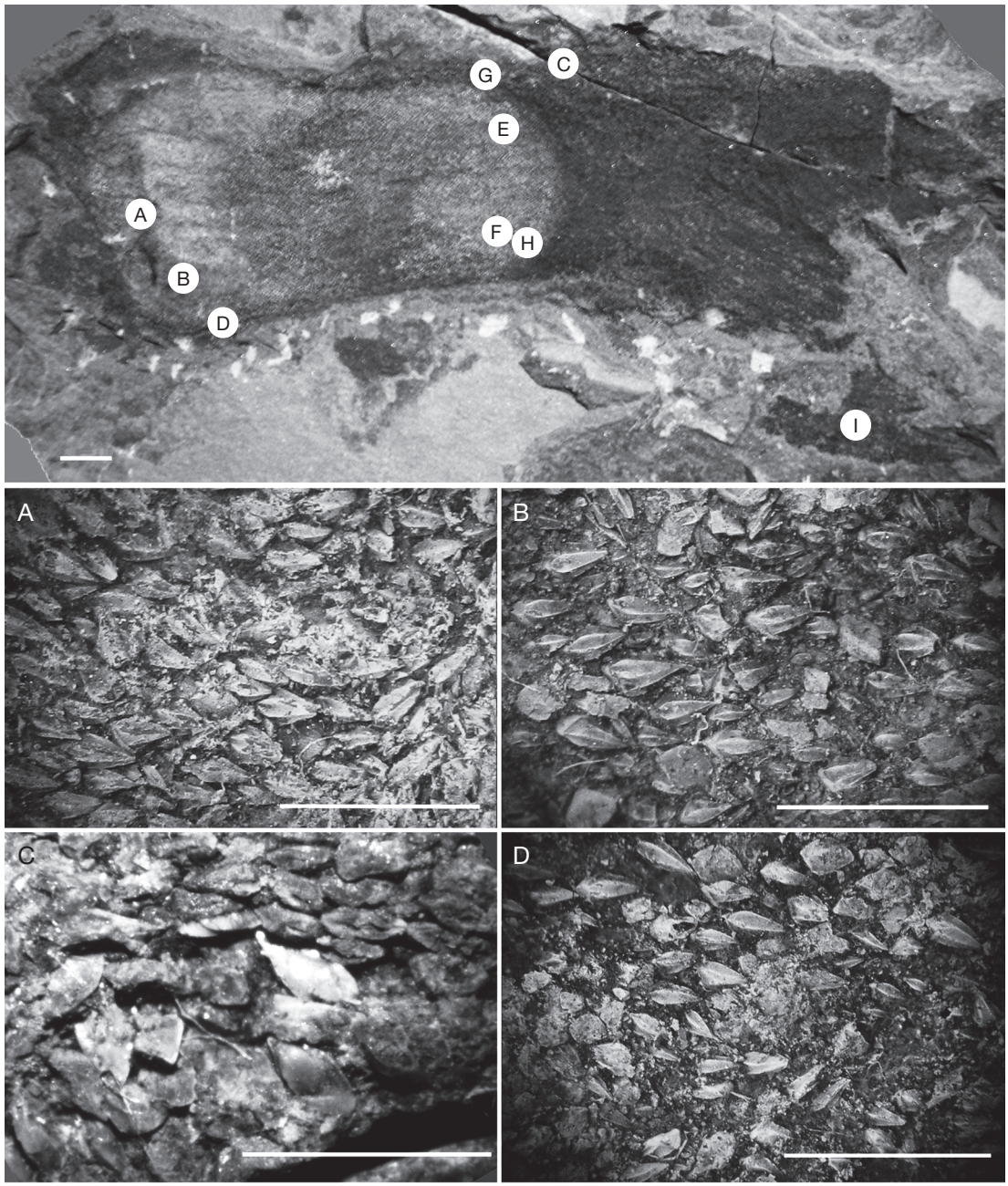

Fig. 7. — Squamation patterns of *Loganellia scotica* (Traquair, 1898), specimen MNHN.F.GBP381, with details of the postpectoral squamation pattern (**A**, **B**), the squamation pattern of the leading edge of caudal fin (**C**), the squamation pattern of anal fin (**D**), the precaudal squamation pattern (**E**, **F**, **H**), the squamation pattern of the leading edge of caudal fin (**G**) and the pinnal squamation pattern of caudal fin (**I**). Scale bars: articulated exoskeleton, 1 cm; A-I, 1 mm. Arrows on element G indicate orientation of the scales.

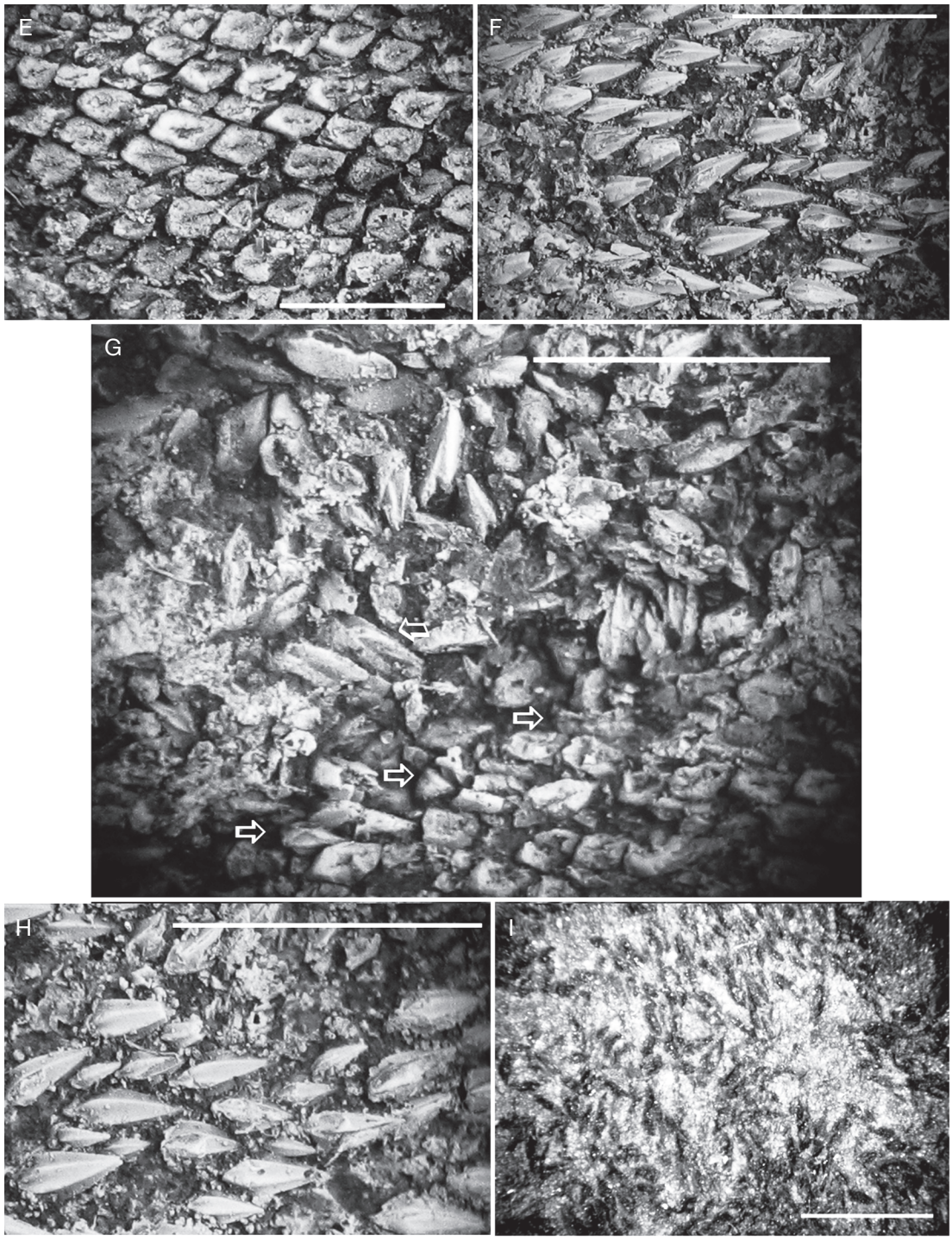

FIG. 7. — Continuation.

represent the denser squamation lines within the articulated film of pinnal (caudal fin) squamation pattern (Fig. $5A_2$). The very similar organisation of caudal fin squamation also can be observed in the heterostracan *Errivaspis* (White, 1935), only with fewer (three) and thicker intermediate fin rays (Mark-Kurik & Botella 2009). Nevertheless, their function shall be similar in both *L. scotica* and *Errivaspis* (Mark-Kurik & Botella 2009), which consists of supporting the web between the dorsal and the ventral lobes. However, the number and thickeness of fin rays must have played a certain role in flexibility and navigation properties of the caudal fin. The longer and much wider ventral lobe of the caudal fin presumably could have housed the notochord in both animals.

The majority of caudal fins of *L. scotica* studied in this work are strongly hypocercal, but the biggest specimen, MNHN.F.GBP366, has caudal fin lobes of a similar size (Fig. 5B). This provides additional evidence to S. Turner's idea that large specimens of *L. scotica* might have more symmetrical tails, reflecting a change of their life habit with age (Turner 1991; Märss & Ritchie 1998; Märss *et al.* 2007). The symmetrical tails are also described as common for heterostracans (e.g., Pernègre 2002; Purnell 2002; Pradel *et al.* 2007).

CONCLUSIONS

Seven articulated exoskeletons of *L. scotica* have been studied, revealing new data on different patterns of thelodont squamation. The mean ratio coefficient, permitting estimation of the total body length of the *L. scotica* specimens with creased or insufficiently preserved anterior parts, has been derived from the measurements of caudal peduncles of 11 articulated specimens. The total body length of the largest specimen studied in this work, which is preserved as an articulated squamation of precaudal and caudal parts of the exoskeleton (MNHN.F.GBP366), has been estimated to reach at least 450 mm in length, which exceeds the so far considered maximum length of the species (Turner 1992; Märss *et al.* 2007). The former maximum body length of *L. scotica* had been estimated to go up to 400 mm, but this also has been inferred from detached caudal fins (Turner 1992). Rostral squamation pattern has been suggested to be present within the exoskeleton of *L. scotica*, contrary to the descriptions of the articulated squamations of this species (Märss & Ritchie 1998), later re-evaluated on better material (Märss *et al.* 2006, 2007). This is an important information regarding further studies of the taxonomy of disarticulated thelodonts. The pinnal squamation pattern of the caudal fin of *L. scotica* has been studied and described reflecting its complex structure, and certain morphological and functional affinities with the caudal fins of heterostracans. Therefore, appending to the previous interpretations of the caudal fin rays of *L. scotica* as internal cartilaginous outgrowth (Stetson 1931), we conclude that the caudal fin rays consist of ray-like rows of accentuated scale cover within the contiguous web of pinnal (caudal fin) squamation pattern.

This work is a contribution to our understanding of the organization of micrometric thelodont exoskeleton, particularly as concerns structure and squamation pattern of their caudal fin, and estimation of the total body length from partly preserved articulated specimens.

Acknowledgements
We are grateful to Didier Geffard-Kuriyama (MNHN, Département Histoire de la Terre, Unité de Paléontologie, CNRS, UMR 7207) for the supervision of the high resolution optical imaging of the specimens; to Dr Vincent Dupret (University of Lille 1, CNRS, UMR 8157 Géosystèmes, Villeneuve d'Ascq, France) for the appreciable contribution during the work with the collections in the MNHN and to Dr Alain Blieck (University of Lille 1, CNRS, UMR 8157 Géosystèmes, Villeneuve d'Ascq, France) for valuable comments.

We are particularly thankful to the reviewers, Dr Tiiu Märss (Tallinn University of Technology, Institute of Geology, Tallinn, Estonia), Dr Henning Blom (Uppsala University, Department of Organism Biology, Uppsala, Sweden), and Annemarie Ohler (MNHN) for the detailed, professional and highly valuable comments.

REFERENCES

ALDRIDGE R. J. & TURNER S. 1975. — Britains's oldest agnathans. *Geological Magazine* 112: 419-20.

BERG L. S. 1940. — [Classification of fish-like animals and fishes, recent and fossil.] *Proceedings of the Zoological Institute, Academy of Sciences of the USSR* 5: 87-517 (in Russian).

BLIECK A., MARK-KURIK E. & MÄRSS T. 1988. — Biostratigraphical correlations between Siluro-Devonian invertebrate-dominated and vertebrate-dominated sequences: the East Baltic example, *in* MCMILLAN N. J., EMBRY A. F. & GLASS D. J. (eds), *Devonian of the World*. III. Canadian Society of Petroleum Geosciences, Memoir 14: 579-587.

BLOM H. 1999. — *Loganellia* (Thelodonti, Agnatha) from the Lower Silurian of North Greenland. *Acta Geologica Polonica* 49 (2): 97-104.

COCKS L. R. M., HOLLAND C. H. & RICKARDS R. B. 1992. — A revised correlation of Silurian rocks in the British isles. The Geological Society of London, *Special Report* 21.

FREDHOLM D. 1990. — Agnathan vertebrates in the Lower Silurian of Gotland, Sweden. Geol. Foren. *Stockholm Forhandl* 112: 61-84.

GROSS W. 1967. — Über Theledontier-Schuppen. *Palaeontographica* 127A: 1-67.

KARATAJŪTĖ-TALIMAA V. N. 1978. — [*Silurian and Devonian Thelodonts of the USSR and Spitsbergen*]. Mokslas, Vilnius, 334 p., 42 figs, 55 pls (in Russian).

KARATAJŪTĖ-TALIMAA V. N. 1991. — Taxonomy of loganiid thelodonts. *Modern Geology* 21: 1-15.

KIAER J. 1932. — New coelolepids from the Upper Silurian on Oesel (Estonia), *in* Heinz A. (ed.), Eesti Loodust Archives. *Publications of the Geological Institution of Tartu University* 27 (10): 1-8.

MARK-KURIK E. & BOTELLA H. 2009. — On the tail of *Errivaspis* and the condition of the caudal fin in heterostracans. *Acta Zoologica (Stockholm)* 90 (1): 44-51.

MÄRSS T. 1986a. — Squamation of the thelodont agnathan *Phlebolepis*. *Journal of Vertebrate Plaaeontology* 6: 1-11.

MÄRSS T. 1986b. — *Silurian Vertebrates of Estonia and West Latvia.* Volume 1. *Fosilia Baltica*. Valgus, Tallinn, 104 p.

MÄRSS T. 1989. — Vertebrates, *in* HOLLAND C. H. & BASSETT M. G. (eds), *A Global Standard of the Silurian System*. National Museum of Wales, Geological Series 9: 284-289.

MÄRSS T. & RITCHIE A. 1998. — Articulated thelodonts (Agnatha) of Scotland. *Transactions of the Royal Society of Edinburgh*: *Earth Sciences* 88 (3): 143-195.

MÄRSS T., WILSON M. V. H. & THORSTEINSSON R. 2002. — New thelodont (Agnatha) and possible chondrichthyan (Gnathostomata) taxa established in the Silurian and Lower Devonian of Arctic Canada. *Proceedings of the Estonian Academy of Sciences, Geology*: 51 (2): 88-120.

MÄRSS T. & MILLER G. 2004. — Thelodonts and distribution of associated conodonts from the Llandoverylowermost Lochkovian of the Welsh Borderland. *Palaeontology* 47: 1211-1265.

MÄRSS T., MÄNNIK P., MARTMA T., WILSON M., CALDWELL M., GAGNIER P.-Y., GOUJET D. & THORSTEINSSON R. 1997. — Distribution of Silurian vertebrate microremains in the Baillie Hamilton and Cornwallis Island sections, Arctic Canada, *in* WILSON M. (ed.), Circum-Arctic palaeozoic vertebrates: biological and geological significance. *Ichthyolith Issues,* Special Publication 2: 20-2.

MÄRSS T., CALDWELL M., GAGNIER P.-Y., GOUJET D., MARTMA T., MÄNNIK P. & WILSON M. 1998a. — Distribution of Silurian and Lower Devonian vertebrate microremains and conodonts in the Baillie-Hamilton and Cornwallis Island sections, Arctic Canada. *Proceedings of the Estonian Academy of Sciences, Geology* 47: 51-76.

MÄRSS TIIU., CALDWELL M., GAGNIER P.-Y., GOUJET D., MÄNNIK P., MARTMA T. & WILSON M. 1998b. — Results of the expedition to Baillie-Hamilton and Cornwallis Island in 1994, *in* GUTIERRES-MARCO J. C. & ROBANO I. (eds), *Proceedings of the Sixth International Graptolite Conference of the GWG (IPA) and the SW Iberia Field Meeting 1998 of the International Subcommission on Silurian Stratigraphy*. ICS-IUGS, Madrid, 337 p.

MÄRSS T., WILSON M. V. H. & THORSTEINSSON R. 2006. — Silurian and Lower Devonian thelodonts and putative chondrichthyans from the Canadian Arctic Archipelago (Cornwallis, Baillie-Hamilton, Devon, and Prince of Wales Islands). *Special Papers in Palaeontology* 75: 1-140.

MÄRSS T., TURNER S. & KARATAJŪTĖ-TALIMAA V. N. 2007. — Agnatha II*, in* SCHULTZE H.-P. (ed.), *Handbook of Palaeoichthyology*. Volume 1B. Verlag Dr. Friedrich Pfeil, Munchen, 143 p.

PANDER C. H. 1856. — *Monographie der fossilen Fische des silurischen Systems der russisch-baltischen Gouvernments. Obersilurische Fische.* Bruchdruckerei der Kaiserlichen Academie des Wissenschaften, St. Petersburg, 91 p.

PERNÈGRE V. N. 2002. — The genus *Doryaspis* White (Heterostraci) from the Lower Devonian of Vestspitsbergen, Svalbard. *Journal of Vertebrate Paleontology* 22: 735-746.

PRADEL A., SANSOM I. J., GAGNIER P.-Y., CESPEDES R. & JANVIER P. 2007. — The tail of Ordovician fish *Sacabambaspis. Biology Letters* 3: 72-75.

PURNELL M. A. 2002. — Feeding in extinct jawless heterostracan fishes and testing scenarios of early vertebrate evolution. *Proceedings of the Royal Society of London* B, 269: 83-88.

RITCHIE A. 1960. — A new interpretation of *Jamoytius kerwoodi* White. *Nature* 188: 647-649.

RITCHIE A. 1968. — New evidence on *Jamoytius kerwoodi* White, an important ostracoderm from the Silurian of Lanarkshire, Scotland. *Palaeontology* 11: 21-39.

RITCHIE A. 1985. — *Ainiktozoon loganense* Scourfield, a protochordate? from the Silurian of Scotland. *Alcheringa* 9: 117-42.
ROLFE W. D. 1992. — Excursion 22. Lesmahagow, *in* LAWSON J. D. & WEEDON D. S. (eds), *Geological Excursion around Glasgow and Girvan*. The Geological Society of Glasgow: 280-287.
STETSON H. C. 1931. — Studies on the morphology of the Heterostraci. *Journal of Geology* 39: 141-154.
STENSIÖ E. A. 1958. — Sous-Classe Thelodonti, *in* GRASSÉ P. P. (ed.), Traité de zoologie. Agnathes et poissons. *Anatomie, Éthologie, Systématique* 13 (1): 414-419.
STENSIÖ E. A. 1964. — Turiniida, turiniiformes, Thélodontes, *in* PIVETEAU J. (ed.), Traité de paléontologie, l'origine des vertébrés, leur expansion dans les eaux douces et le milieu marin. *Vertébrés (Généralités), Agnathes* IV (1): 271-273, 369-382.
TRAQUAIR R. H. 1898. — Report on fossils fishes. *Summary of Progress of the Geological Survey of the United Kingdom for 1897*: 72-76.
TRAQUAIR R. H. 1899. — Report on fossil fishes collected by the Geological Survey of Scotland in the Silurian rocks of the south of Scotland. *Transactions of the Royal society of Edinburgh* 39: 827-864.
TRAQUAIR R. H. 1905. — Supplementary report on fossil fishes collected by the Geological Survey of Scotland in Upper Silurian rocks of Scotland. *Transactions of the Royal Society of Edinburgh* 40: 879-888.
TURNER S. 1970. — Fish help to trace continental movements. *Spectrum, Bulletin of the Center for Official Information* 79: 8-10.
TURNER S. 1973. — Siluro-Devonian thelodonts from the Welsh Borderland. *Journal of the Geological Society* 129: 557-584.
TURNER S. 1991. — Monophyly and interrelationships of the Thelodonti, *in* CHANG M.- M., LIU Y.-H. & ZHANG G.-R. (eds), *Early Vertebrates and Related Problems of Evolutionary Biology*. Beijing Science Press, Beijing: 87-119.
TURNER S. 1992. — Thelodont lifestyles, *in* KURIK E. (ed.), *Fossil Fishes as Living Animals. Academia* 1. Academy of Sciences of Estonia, Tallinn: 21-40.
TURNER S. 1994. — Thelodont squamation. *Ichthyolith Issues* 13: 12-15.
TURNER S. 2000. — New Llandovery to Early Pridoli microvertebrates including Early Silurian zone fossil, *Loganellia avonia* nov. sp., from Britain, *in* BLIECK A. & TURNER S. (eds), Palaeozoic vertebrate biochronology and global marine/non-marine correlation. *Final Report of IGCP 328 (1991-1996), Courier ForschungsInstitut Senckenberg* 223: 91-127.
TURNER S. & VAN DER BRUGGHEN W. 1993. — The Thelodonti, an important but enigmatic group of Palaeozoic fishes. *Modern Geology* 18: 125-140.
TURNER S. & NOWLAN G. S. 1995. — Early Silurian microvertebrates of eastern Canada. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 4e sér., section C, n°17: 513-29.
TURNER S., ALDRIDGE R. J., JONES G. L. & HARPER D. A. T. 1994. — The Llandovery microvertebrates from the Kilbridge Formation, Co. Galway, western Ireland. *Abstracts Volume of the Annual Irish Geology Research Meeting, 25th-27th February, 1994*.
VAN DER BRUGGHEN W. 1993. — Thelodonten binnenste buiten gekeerd. *Grondboor en Hamer* 3: 88-91 (in Dutch).
VAN DER BRUGGHEN W. 1994. — Over magen en staarten van thelodonten. *Grondboor en Hamer* 4/5: 87-93 (in Dutch).
VAN DER BRUGGHEN W. & JANVIER P. 1993. — Denticles in thelodonts. *Nature* 364: 107.
VERGOOSSEN J. M. 1992. — On complex dermal elements in Loganellia species (Agnatha, thelodonti) from the Upper Llandovery of Scotland. *Geologie en Mijnbouw* 71: 51-64.
WALTON E. K. & OLIVER G. J. H. 1991. — Lower Palaeozoic stratigraphy, *in* CRAIG G. Y. (ed.), *Geology of Scotland*. 3rd ed. Scottish Academic Press, Edinburgh: 161-193.
WELLMAN C. H. & RICHARDSON J. B. 1993. — Terrestrial plant microfossils from Silurian inliers of the Midland Valley of Scotland. *Palaeontology* 36: 155-193.
WHITE E. I. 1935. — The ostracoderm Pteraspis Kner and the relationships of the agnathous vertebrates. *Philosophical Transactions of the Royal Society of London*, B 225: 381-457.
WHITE E. I. 1946. — Jamoytius kerwoodi, a new chordate from the Silurian of Lanarkshire. *Geological Magazine* 83: 89-97.
ŽIGAITĖ Ž. 2004. — A new thelodont from Lower Silurian of Tuva and north-west Mongolia. *Acta Universitatis Latviensis* 679: 158-165.

Submitted on 8 February 2010;
accepted on 22 February 2011.