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The squamation of "*Ctenacanthus*" *costellatus* (Chondrichthyes: Ctenacanthiformes) from the Carboniferous of Lublin area, south-eastern Poland

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ABSTRACT:

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A sample of late Viséan limestone from the Włodawa IG-4 borehole, east of Lublin, Poland, yielded a piece of a tooth and a few hundred well-preserved scales comparable to those of "*Ctenacanthus*" *costellatus* Traquair, 1884 from Glencartholm, Scotland, UK. Most of the scales are typical compound body scales of the ctenacanthid type. Their crowns are composed of several separate odontodes whose distal ends are turned backwards and bases are characterised by concave undersides. In the material, there are also sparse scales with similar crowns but with flat or convex bulbous bases, as well as ornamented plates and single, star-like denticles, probably from the head region. The taxonomic status of "*Ctenacanthus*" *costellatus* was analysed and a new generic name for that species, viz. *Glencartius* gen. nov., is proposed.

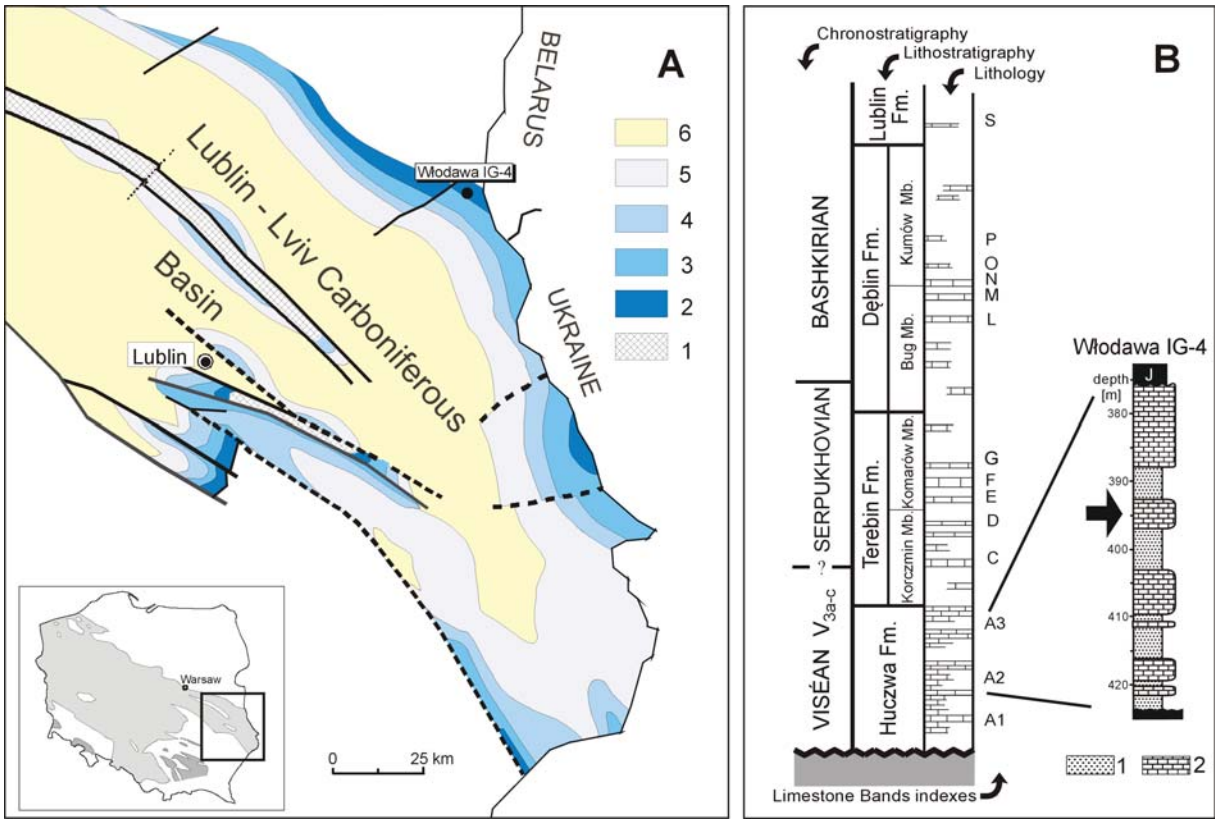
Key words: Ctenacanthiformes; Sharks; Dermal skeleton; Viséan; Lublin Coal Basin.

INTRODUCTION

In the early 1990s several limestone samples from the upper Viséan part of a borehole on the eastern margin of Lublin Coal Basin (Włodawa IG-4; Text-fig. 1) were dissolved in search of conodonts. The samples turned out to be rather poor in phosphatic microfossils, but one, from c. 395 m depth, was full of chondrichthyan scales which were easily observable even in thin sections (Text-fig. 2). In addition to a few hundred scales, one broken shark tooth was found. For several years the material remained unidentified, until the re-examination and the first precise description of the dentition of "*Ctenacanthus*" *costellatus* Traquair, 1884 from the Viséan of Scotland, UK (Ginter 2002; Ginter *et al.* 2010) and the subsequent identification of comparable teeth in Derbyshire (England, UK) and the Holy Cross Mountains (Poland; Ginter *et al.* 2015). Comparison of the scales and the tooth from the Włodawa IG-4 borehole to known specimens of "*C.*" *costellatus* showed that the former most probably also represent this species.

The main aim of this paper is to describe the diversity of scales from the new Polish material, to compare these scales to those from the articulated specimens of "*C.*" *costellatus*, and to propose a new generic name for this species, viz. *Glencartius* gen. nov., with a proper historical discussion supporting this proposal.

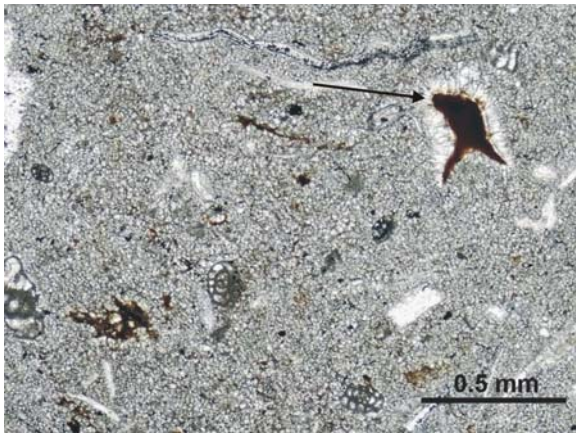
Institutional abbreviations: MWGUW, Stanisław Józef Thugutt Museum of the Faculty of Geology, University of Warsaw, Poland; NHMUK, The Natural History Museum, London, UK; ZPAL, Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.



Text-fig. 1. A – Location of the Włodawa IG-4 borehole on the simplified geological map of the Carboniferous deposits in the Lublin region (without post-Carboniferous cover). Inset map of Poland shows the extent of the Carboniferous deposits. Map after Porzycki (1988), with modifications of Porzycki and Zdanowski (1995). 1 – Devonian rocks of the Kock Horst-Anticline and Trawniki Horst-Anticline; 2 – Huczwa Formation; 3 – Terebin Formation; 4 – Bug Member of the Dęblin Formation; 5 – Kumów Member of the Dęblin Formation; 6 – Lublin and Magnuszew Formations. B – Stratigraphic position of the Włodawa IG-4 borehole section against a stratigraphic scheme of the Lublin-Lviv Carboniferous succession (lithostratigraphy and limestone bands indexes A1, A2, A3 after Skompski 1996, C-S after J. Porzycki and A.M. Żelichowski *fide* Porzycki 1988). 1 – terrigenic sediments (sandstones to claystones, phytogenic sediments); 2 – limestones

THE HISTORY OF INVESTIGATIONS ON THE DERMAL SKELETON OF "*CTENACANTHUS*" *COSTELLATUS*

The first articulated specimen of "*Ctenacanthus*" *costellatus* was recovered from the famous outcrops of Mississippian (Viséan) Calciferous Sandstone within the Glencartholm Volcanic Beds, at Glencartholm in Eskdale, Dumfries and Galloway near the Scottish-English border (see Dineley and Metcalf 1999, pp. 286, 287), and described by Traquair (1884). He noted certain similarities of the two dorsal fin spines to Agassiz's (1837–1843) *Ctenacanthus major*, such as "a comparatively short implanted portion, obliquely marked off from the sculptured exposed surface; the nature of that sculpture, consisting of longitudinal ridges ornamented with tubercles; the evident presence of a posterior area with recurved denticles along the margins between it and each lateral surface" (Traquair 1884, p. 6), sufficient to include the new specimen in the genus *Ctenacanthus*. However, he noted that "the system of tuberculation of the ridges differs sufficiently from that in any hitherto described species" and assigned the specimen to a new species, *Ctenacanthus costellatus*. Traquair (1884) also suggested that the spines of *C. costellatus* "in general aspect ... perhaps approach most nearly" yet another Carboniferous shark described by Agassiz (1837–1843), viz. *Sphenacanthus serrulatus*, and that he could not "see any ground for the retention of *Sphenacanthus* as a separate genus." Thus, Traquair's (1884) understanding of the genus *Ctenacanthus* was very inclusive, comprising *C. major*, *C. costellatus*, *C. serrulatus* and a few other spine-based species referred to that genus before 1884.



Text-fig. 2. Neomorphised wackestone with rare endothyrid foraminifers and a section of a ctenacanthid scale (arrowed); Włodawa IG-4 borehole, depth 392–396 m

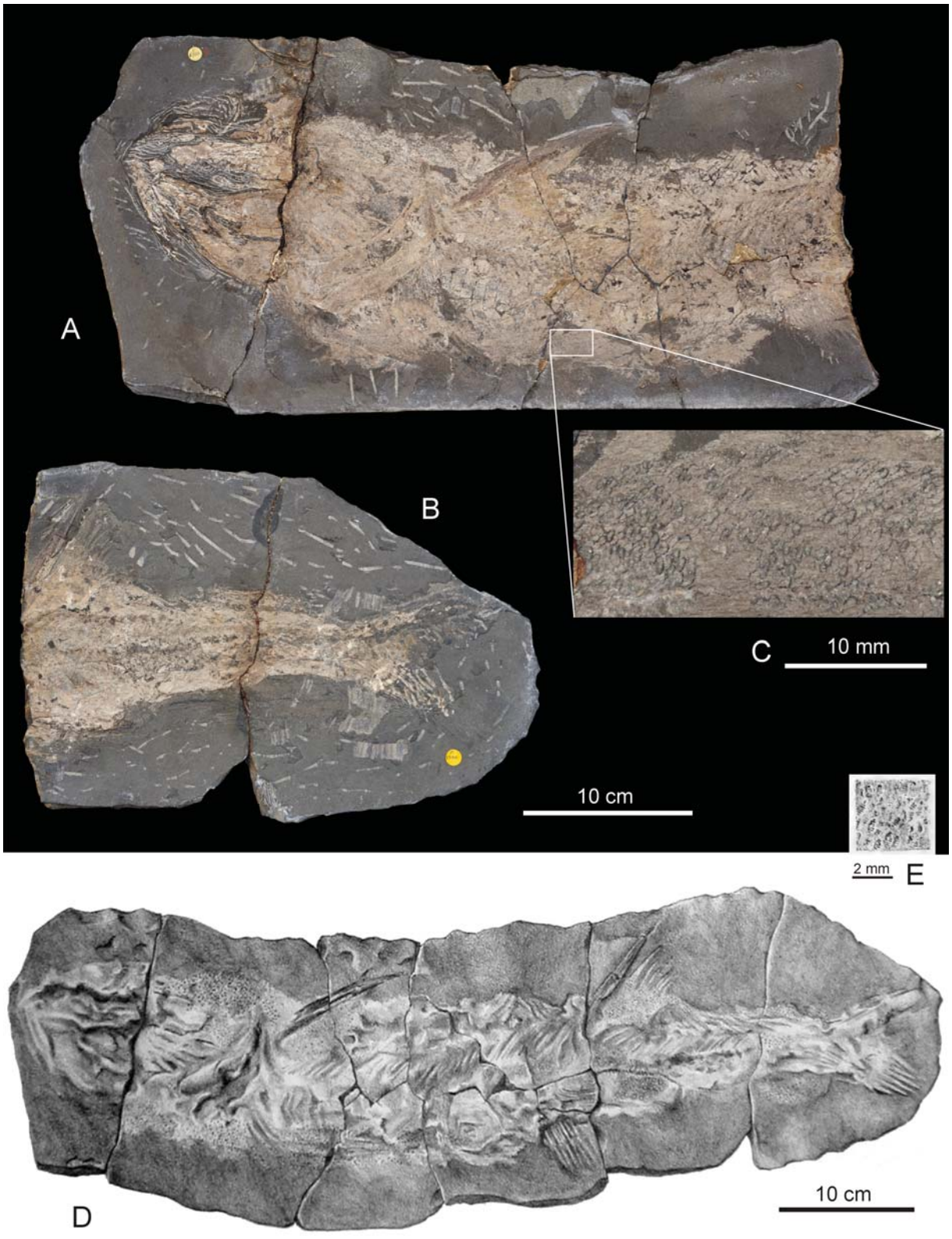
The holotype of "*C.*" *costellatus* (NHMUK PV P 5900, Text-fig. 3) is an almost complete specimen, composed of part and counterpart. Although the specimen includes an almost complete body outline, it is laterally flattened and bears numerous chisel marks. In addition to endoskeletal parts, preserved in rather poor condition, it exposes two dorsal fin spines, of which the anterior is better preserved (Traquair 1884, pl. 2, fig. 2), and large fragments of the body covered with a shagreen of scales which are "minute, 1/30 to 1/40 inch [0.6–0.8 mm] in diameter, mostly delicately ridged and pectinated, though sometimes they appear smooth" (Traquair 1884, p. 4; Text-fig. 3C, E). The scale crowns are rhomboidal in coronal (external) view. In some areas the crowns are removed and rounded basal pulp cavities can be observed. No extracted scale is available, so the lateral aspect of the scales cannot be observed. Unfortunately, there are almost no teeth. The only fragmentary tooth illustrated by Traquair (1884, pl. 2, fig. 6) consists of an abraded, conical cusp and a portion of a base, suggesting its 'cladodont nature'.

Woodward, in his catalogue (1889, pp. 241, 242), separated "*C.*" *costellatus* from *Ctenacanthus sensu stricto* and included it in *Sphenacanthus*, together with *S. serrulatus* and *S. hybodoides* (Egerton, 1853). However, he did not give any anatomical reason for this decision (see the discussion in Maisey 1982) and, moreover, stated that "the dorsal finspines [of *Sphenacanthus*] are indistinguishable from those named *Ctenacanthus* by Agassiz" which is, at best, a very superficial observation. A few decades later, in his presidential address (Woodward 1921), he abandoned his earlier position and referred to this fish as *Ctenacanthus costellatus*.

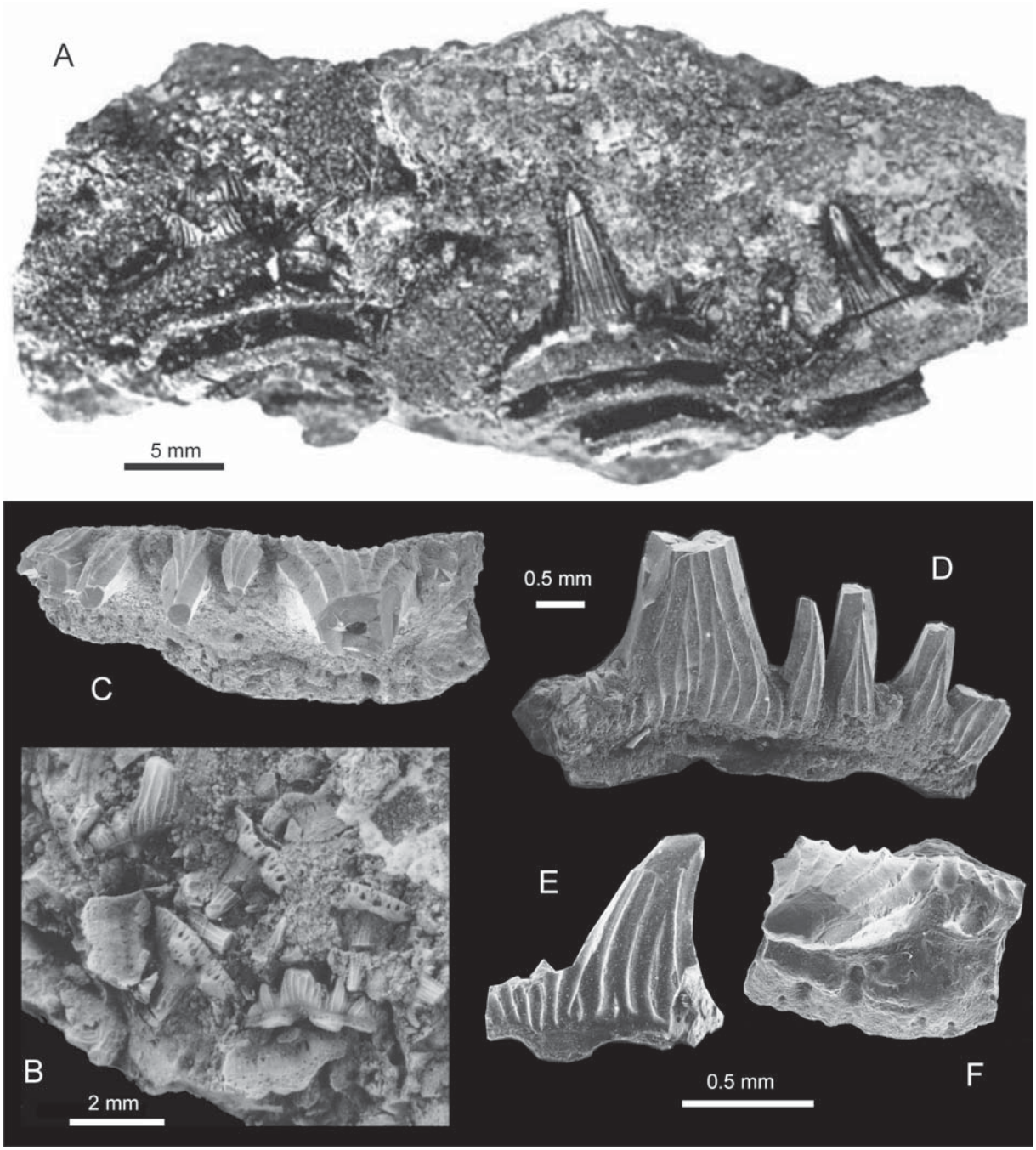
In his study on the ctenacanth sharks from the Cleveland Shale of Ohio, Dean (1909, p. 249) mentioned "*C.*" *costellatus* as a confirmation that sharks with ctenacanth spines are characterised by a cladodont dentition. He did not refer to the *Sphenacanthus–Ctenacanthus* problem at all and treated "*C.*" *costellatus* as a member of *Ctenacanthus sensu stricto*. Brough (1935) was the first to suggest that its pectoral fin is supported by three basal cartilages (pro-, meso- and metapterygium), as in Mesozoic and modern sharks. Concerning the dermal skeleton, Brough (1935, p. 42) only noted that "there is a mass of shagreen immediately of the ventral lobe of the caudal fin, and there is little doubt that this marks the position of the anal fin".

"*Ctenacanthus*" *costellatus* became relatively famous among palaeoichthyologists after the 1930s discovery of the second articulated specimen from the same locality at Glencartholm (Moy-Thomas 1936). This specimen (NHMUK PV P 20144/20145) consists of several pieces and is associated with numerous well-preserved teeth, some scattered and some organised in tooth families (Text-fig. 4A, B). Moy-Thomas (1936, text-figs 1, 2, pl. 1, figs a, b) provided several illustrations of teeth, and even a drawing of a thin section of a median cusp of one, but did not figure fin spines and scales. The only information provided about the spines is that "the anterior spine make[s] a very much smaller angle with the body than the posterior spine" and about the scales that "the covering of dermal denticles is exactly as has already been described by Traquair". The best-known restoration of a tooth (Moy-Thomas 1936, text-fig. 1), which influenced several future students of the ctenacanths (e.g., Glikman 1964b, fig. 18), is confusing, as it does not show crucial features of the base. It is worthwhile to note from the synonymy list (Moy-Thomas 1936, p. 762) that it is evident that Moy-Thomas knew of the *Sphenacanthus–Ctenacanthus* controversy and supported the ctenacanth affinity of "*C.*" *costellatus*.

Because the rock hosting the specimen easily crumbles, it was possible to extract loose teeth and scales and photograph them under the microscope. In the 1970s, Wolf-Ernst Reif obtained a few scales from Colin Patterson, who at that time was in charge of the collection at NHMUK. According to Reif (1978), the scales were taken from different parts of the body. Reif extracted them from the matrix using acetic acid and used them as examples for the definition of his 'ctenacanthid type' of growing scales in chondrichthyans. However, the scales illustrated (Reif 1978, fig.



Text-fig. 3. Holotype of *Glencartius costellatus* (Traquair, 1884), NHMUK PV P 5900, from Glencartholm, Eskdale, Scotland, UK. A – Anterior part. B – Caudal part. C – Close-up of squamation on the ventral part. D – Drawing of a complete specimen. E – Drawing of a fragment of the scale cover. A-C, photographs by NHMUK photographers; D, E, from Traquair (1884)



Text-fig. 4. Teeth of *Glencartius costellatus* (Traquair, 1884). A, B – From Glencartholm, Eskdale, Scotland, UK, teeth associated with the articulated specimen NHMUK PV P 20144/20145; A – Two tooth families, from Moy-Thomas (1936); B – A cluster of teeth, photograph by NHMUK photographers. C, D – From Todowa Grząba, Holy Cross Mountains, Poland, ZPAL P.IV/256, in oral and labial views. E, F – From Włodawa IG-4 borehole, east of Lublin, Poland, MWGUW/Ps/12/1, in labial and oral views

1A, B) are quite unlike those covering the holotype and those observed in the specimen NHMUK PV P 20144/20145 by one of the authors of this paper (MG). Moreover, they also differ considerably from the other scales from the same figure (Reif 1978, fig. 1C–F), under the same caption "scales of the ctenacanthid type". The scales of "*C.*" *costellatus* figured by Reif are very small, thin and brittle and display only three

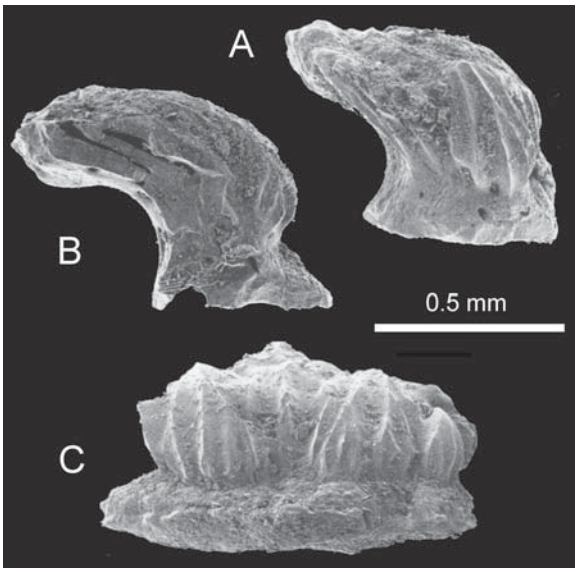
odontodes in the flat crown. This suggests that they were extracted from a special part of the body or represent a very early stage of development.

There is yet another problem with Reif's (1978) paper concerning the scales of "*C.*" *costellatus*. There exists an internal contradiction between his statements that "[t]he scales of *Ct. costellatus* differ from all other scales found in any other articulated shark remain" (Reif 1978, p. 111) and "*Goodrichthys eskdalensis* from the Lower Carboniferous has exactly the same type of scales as *Ct. costellatus*" (Reif 1978, p. 113). In light of this, his observation that " '*Ctenacanthus*' cf. *clarki*, Upper Devonian, has scales which have no similarity to *Ct. costellatus*" (Reif 1978, p. 113) should be treated with little confidence.

Despite the incompleteness of the existing descriptions of two Scottish specimens of "*C.*" *costellatus*, this fish became ubiquitous as an exemplar of 'ctenacanth' conditions in a series of authoritative, classic texts on vertebrate palaeontology (e.g., Moy-Thomas and Miles 1971, p. 216, fig. 9.8; Carroll 1988, p. 72, fig. 5.11A; Janvier 1996, p. 143, fig. 4.35 A1).

In his trilogy on the genus *Ctenacanthus*, Maisey (1981, 1982, 1984) analysed numerous fin spines referred to that genus in the past and provided a new, relatively narrow definition. He re-illustrated Traquair's (1884) drawings of "*C.*" *costellatus* spines (Maisey 1982, fig. 11B–E), but suggested that "*C. costellatus* is not referable to the genus *Ctenacanthus*, but may be allied to *Sphenacanthus*" because "the finspines are not covered by dense pectinations and are concave posteriorly" (Maisey 1981, pp. 17, 18). He provisionally placed the species in *Sphenacanthus* (Maisey 1982), despite his knowledge that Dick (1978) suggested *Sphenacanthus serrulatus* has teeth which differ from those referred to "*C.*" *costellatus* and are more similar to those of the euselachian *Tristychius arcuatus* Agassiz, 1837 (see also Dick 1998, fig. 3; Ginter *et al.* 2010, fig. 93). Maisey's taxonomic decision influenced the scientific community and is currently the most commonly cited on the internet (e.g., Wikipedia).

In the years 1996–2018 one of us (MG) had the opportunity to study both articulated specimens (NHMUK PV P 5900 and 20144/20145), and on his request several new photographs were taken by the NHMUK photographers. For the first time detailed images of "*C.*" *costellatus* teeth, demonstrating the features of both crown and base, were published by Ginter (2002, figs 4A, 5) and later re-illustrated in the Handbook of Paleoichthyology (Ginter *et al.* 2010, fig. 71; Text-fig. 4B). The teeth are clearly different from those of *Sphenacanthus*, but also are easily distinguishable from all known ctenacanths, in spite of a few ctenacanthiform traits (see the systematic section).



Text-fig. 5. Ctenacanthid-type scales of *Glencartius costellatus* (Traquair, 1884) from Glencartholm, Eskdale, Scotland, UK, associated with the articulated specimen NHMUK PV P 20144/20145

The majority of body scales are of a typical growing, compound, ctenacanthid form, with numerous, somewhat irregularly organised odontodes in the crown (Text-fig. 5). The odontodes' proximal parts are vertical, and then transition to horizontal, with the distal, sharp ends projecting backwards. The scale bases are concave or flat; the neck is rather short or absent. None of the observed scales could be called 'thin' or 'brittle'. They resemble the scale from the Triassic of Germany illustrated by Reif (1978, fig. 1C, D) and the scales of Late Devonian ctenacanths from Cleveland Shale of Ohio (Dean 1909), but not the scales supposedly extracted from NHMUK PV P 20144/20145 figured by Reif (1978, fig. 1A, B).

Because the fin spines of "*C.*" *costellatus* differ from both the spines of *Ctenacanthus* and *Sphenacanthus,* and the teeth have their own features, closer to those of the cladodontomorph ctenacanths than to the euselachian *Sphenacanthus*, we believe (in concordance with the suggestion made by Dick 1998, p. 21) that this species deserves a new generic name, *Glencartius* gen. nov.

Recognition of the complete set of dental characters of *G. costellatus* led to the identification of this species in collections of loose teeth from the Viséan outside of Scotland. Thus far, such teeth were

found in Derbyshire, UK (Ticknall Quarry) and the Holy Cross Mountains, Poland (Ostrówka Quarry) and published by Ginter *et al.* (2015, fig. 9D, E; Text-fig. 4C, D). A fragmentary tooth most probably belonging to this species and a few hundred scales have also been recovered from a borehole in the Lublin area of Poland, which is the main subject of the present paper.

THE NEW MATERIAL FROM POLAND

Geological setting

The investigated palaeontological material was found in the Viséan (V3a–c) limestones of the Włodawa IG-4 borehole section (Text-fig. 1A) of the Lublin-Lviv Basin (eastern Poland). Here, the Carboniferous paralic succession started in the late Viséan and was preceded by a volcanic episode (Skompski 1986; Waksmundzka 2010). A shallow sea invaded the marginal part of the Laurussia continent, probably opening a connection with the epeiric seas of the Moscow and Dneper-Donets Basins. Regular sedimentary cyclicity, corresponding to a deltaic regime of Yoredale-type deposition (Skompski 1996; Waksmundzka 2013), is a characteristic feature of this part of the succession (Text-fig. 1B), especially during the late Viséan and early Serpukhovian. The Carboniferous part of the Włodawa IG-4 borehole section is relatively thin due to the marginal (in the context of the entire basin) position of this area and post-Carboniferous erosion.

The investigated limestones represent shallow water sedimentary environments, generally dominated by algal populations. The most characteristic calcareous algae found here are the codiacean taxon *Calcifolium okense* Shvetsov and Birina, 1935, the dasycladacean genera *Nanopora* Wood, 1964 and *Kulikia* Golubtsov, 1961, and different red algal palaeoberesellids and stachaeiinids (Skompski 1986, 1996). The sediments were probably deposited in quiet, lagoonal areas, separated from the open sea by shoals formed by crinoid and bioclastic banks. Sporadically found fish remains are relatively rare in the investigated Viséan limestones, and therefore the assemblage collected – where the frequency of fish remains is greater than 200 specimens/1 kg of rock – is absolutely exceptional for the entire Lublin-Lviv Basin. The investigated sample is characterised by a wackestone microfacies with a neomorphically recrystallised matrix and sporadic endothyrid forams, productid spines, ostracods, and gastropods.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880
Order Ctenacanthiformes Glikman, 1964
Family indet.
Genus *Glencartius* gen. nov.

TYPE SPECIES: *Ctenacanthus costellatus* Traquair, 1884. Carboniferous, Mississippian, Viséan, Calciferous Sandstone, bottom of the Upper Border Group, Glencartholm Volcanic beds; Glencartholm, Dumphries and Galloway, Scotland, UK.

ETYMOLOGY: From the locality Glencartholm in Scotland, which yielded the first two articulated specimens of this genus.

DIAGNOSIS: The following diagnosis is based exclusively on the dermal skeleton – teeth, scales and fin spines – because usually only such elements can be compared with the fossil material outside the type locality. The precise description of the available endoskeletal parts was given by Moy-Thomas (1936).

Teeth. The teeth of *Glencartius* gen. nov. are cladodont, symmetrical mesio-distally. The median cusp is wide, slightly compressed at the base and rounded in cross-section at the tip. Two to three lateral cusps are developed on each side. The outermost cusps are always the highest, but the difference in size between them and the intermediate ones is quite small. All cusps are ornamented on both sides with rather coarse, often slightly wavy cristae. Some of the cristae bifurcate at the base. On the labial side of the base there is a shallow depression, framed by thick basolabial projections, and there are two pad-like, rounded buttons on the orolingual surface, either completely separated from each other or connected by means of a low ridge.

The teeth differ from those of *Ctenacanthus* Agassiz, 1837, *Cladodus* Agassiz, 1843 and *Goodrichthys* Moy-Thomas, 1951, by the presence of two separate orolingual buttons instead of a continuous ridge; from those of *Heslerodus* Ginter, 2002, by the prominent median cusp; and from *Glikmanius* Ginter, Ivanov and Lebedev, 2005, by the coarse, bifurcating cristae on the labial side of the median cusp and the arrangement of lateral cusps.

Scales. Most of the body scales are compound, growing elements of the ctenacanthid type. The crown is composed of numerous, closely placed odontodes whose proximal parts are vertical and distal parts horizontal, projecting backwards and forming a rough, rhomboidal surface. Each odontode

bears a few longitudinal ridges, often bifurcating at the base. The scale crowns are packed in a shagreen manner, forming a continuous body cover. The bases are usually concave or flat; the necks are rather short.

In addition to the most common type, there occur slightly different scales – such as minute plates with a few vertically directed odontodes – which probably represent special regions.

Fin spines. There are two dorsal fin spines, sharp and slightly recurved, with a concave posterior face. The proximal, unornamented part is relatively short. The ornamentation of the distal part is composed of longitudinal, tuberculated ridges. On the few anterior ridges the tubercles are situated more densely (about two tubercles per 1 mm) than in the postero-lateral region of the spine. There are two rows of minute hook-like denticles along the posterior edges of the spine.

OCCURRENCE: Carboniferous, Mississippian, Viséan; Scotland (Dumphries and Galloway, Glencartholm) and England (Derbyshire, Ticknall) in the UK, Holy Cross Mountains (Todowa Grząba) and Lublin area (Włodawa) in Poland.

Glencartius costellatus (Traquair, 1884)
(Text-figs 3–7)

1884. *Ctenacanthus costellatus*; Traquair, pp. 3–8, pl. 2.
1889. *Sphenacanthus costellatus*; Woodward, pp. 241, 242.
1921. *Ctenacanthus costellatus*; Woodward, p. 32, fig. 2.
1935. *Ctenacanthus costellatus*; Brough, pp. 41, 42, pl. 3, fig. 1.
1936. *Ctenacanthus costellatus* Traquair; Moy-Thomas, pp. 762–771, text-figs 1, 2, pl. 1a, b.
1978. *Ctenacanthus costellatus* Traquair; Reif, pp. 111–113, fig. 1A, B.
1982. *Sphenacanthus costellatus* (Traquair); Maisey, p. 20, fig. 11B–E.
1984. *Sphenacanthus costellatus*; Maisey, p. 15.
2002. "*Ctenacanthus*" *costellatus* Traquair; Ginter, figs 4A, 5.
2010. "*Ctenacanthus*" *costellatus* Traquair; Ginter *et al.*, pp. 77, 78, fig. 71.
2015. "*Ctenacanthus*" *costellatus* Traquair; Ginter *et al*., pp. 914, 915, fig. 9D, E.

MATERIAL: One broken tooth (MWGUW/Ps/12/1) and over 200 scales (illustrated specimens: MWGUW/Ps/12/2–15).

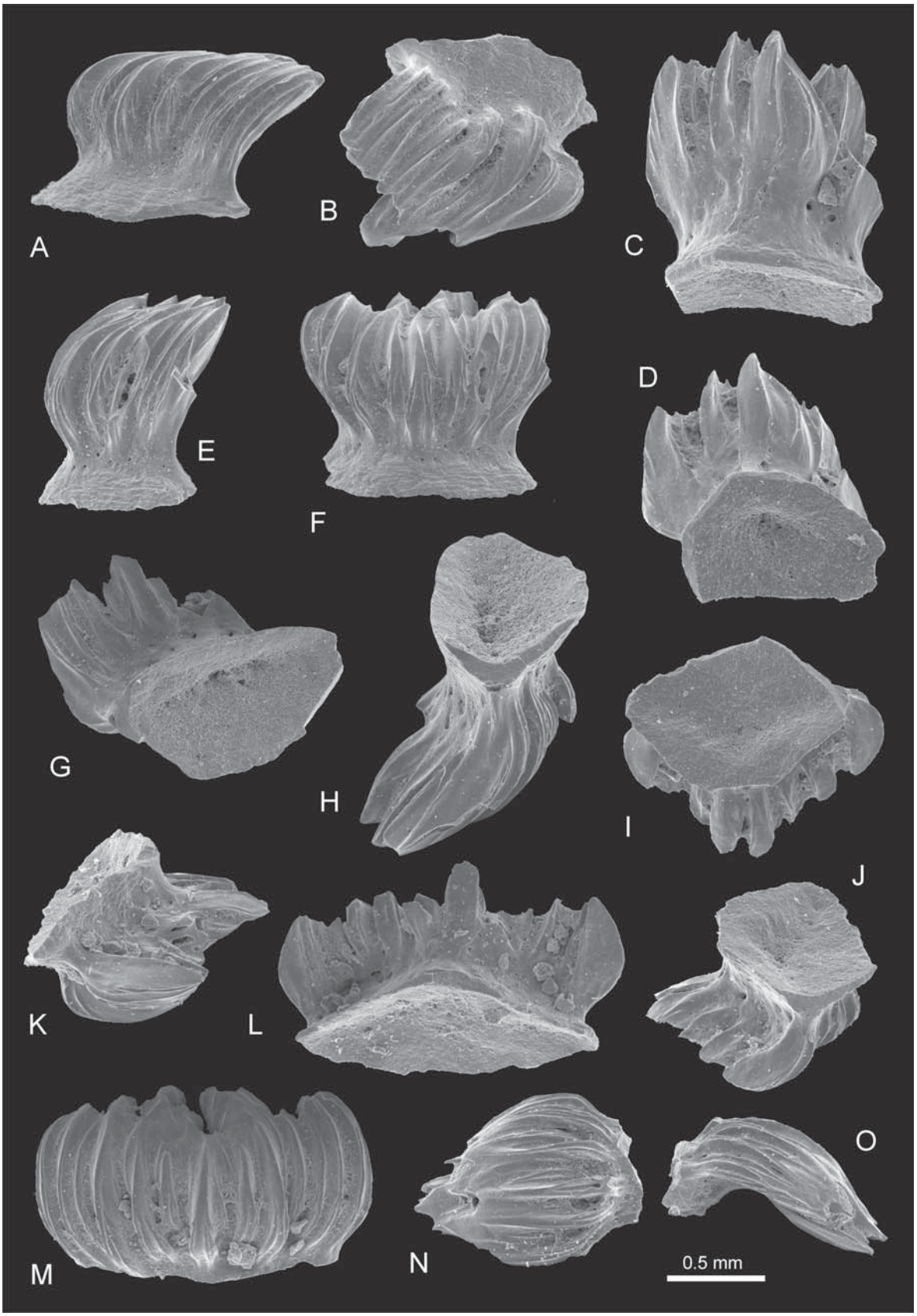
DESCRIPTION:

Tooth. Only a piece of the median part of a tooth is preserved. It comprises the lower two thirds of the median cusp, the basal part of a lateral cusp and a portion of the base. The median cusp is somewhat compressed labio-lingually and its labial side is covered with strong cristae, two of which bifurcate at the base. Similar ornamentation continues on the lateral cusp. The cristae on the lingual side are weaker. The mesio-distal dimension of the preserved part of the tooth is 1 mm.

Body scales. The crowns of the most common, fully grown body scales (Text-fig. 6; compare Text-fig. 5A, B) usually measure between 1 and 1.5 mm transversally to the body axis. The difference in size corresponds to the number of odontodes, usually between 8 (Text-fig. 6N) and 15 (Text-fig. 6M). The shape and structure of the crown are described in the diagnosis of the genus (see above). The base forms a shallow cup, the outline of which in basal view is trapezoidal (Text-fig. 6G) or rhomboidal (Text-fig. 6I). In the centre there occurs one major foramen, probably leading to the remnants of pulp cavities of the primary, most central, odontodes. It is usually associated with a few smaller openings. The neck is well defined but rather short. It also often bears minute foramina (Text-fig. 6E, F), in this case probably leading to the pulp cavities of marginal odontodes.

Other scales. There are a few rarer types of scales that can also be attributed to this fish. The first type ('bulbous'; Text-fig. 7I–K) is relatively similar to the body scales described above as far as the crown is concerned, but the base is different: it lacks the basal concavity, and is either basally flat or even bulbous, resembling the scales of the euselachian shark *Protacrodus vetustus* (Gross, 1938) or the acanthodian scales. The base of the second, very rare type ('brittle'; Text-fig. 7G, H) is similar to that of the body scales, but the crown is very thin and compact. It is somewhat similar to Reif's (1978) figure 1B. The crown of the third type looks like a star in the coronal view ('star'; Text-fig. 7A) and like a closed flower in the lateral view. The odontodes are directed vertically with no side deflection. The base is very small and rounded. Such scales probably represent the oral region; they are similar to the scales covering the area of jaws of *Ctenacanthus concinnus* (Newberry, 1875)

Text-fig. 6. Ctenacanthid-type body scales of *Glencartius costellatus* (Traquair, 1884) from the upper Viséan of the Włodawa IG-4 borehole, east of Lublin, Poland. A, B – MWGUW/Ps/12/2 in anterior/lateral and coronal views. C, D – MWGUW/Ps/12/3 in posterior and basal views. E, F – MWGUW/Ps/12/4 in anterior/lateral and anterior views. G, H – MWGUW/Ps/12/5 in oblique basal and lateral views. I, J – MWGUW/Ps/12/6 in basal and lateral views. K, L – MWGUW/Ps/12/7 in lateral and basal/posterior views; M – MWGUW/Ps/12/8 in coronal view. N, O – MWGUW/Ps/12/9 in coronal and lateral views →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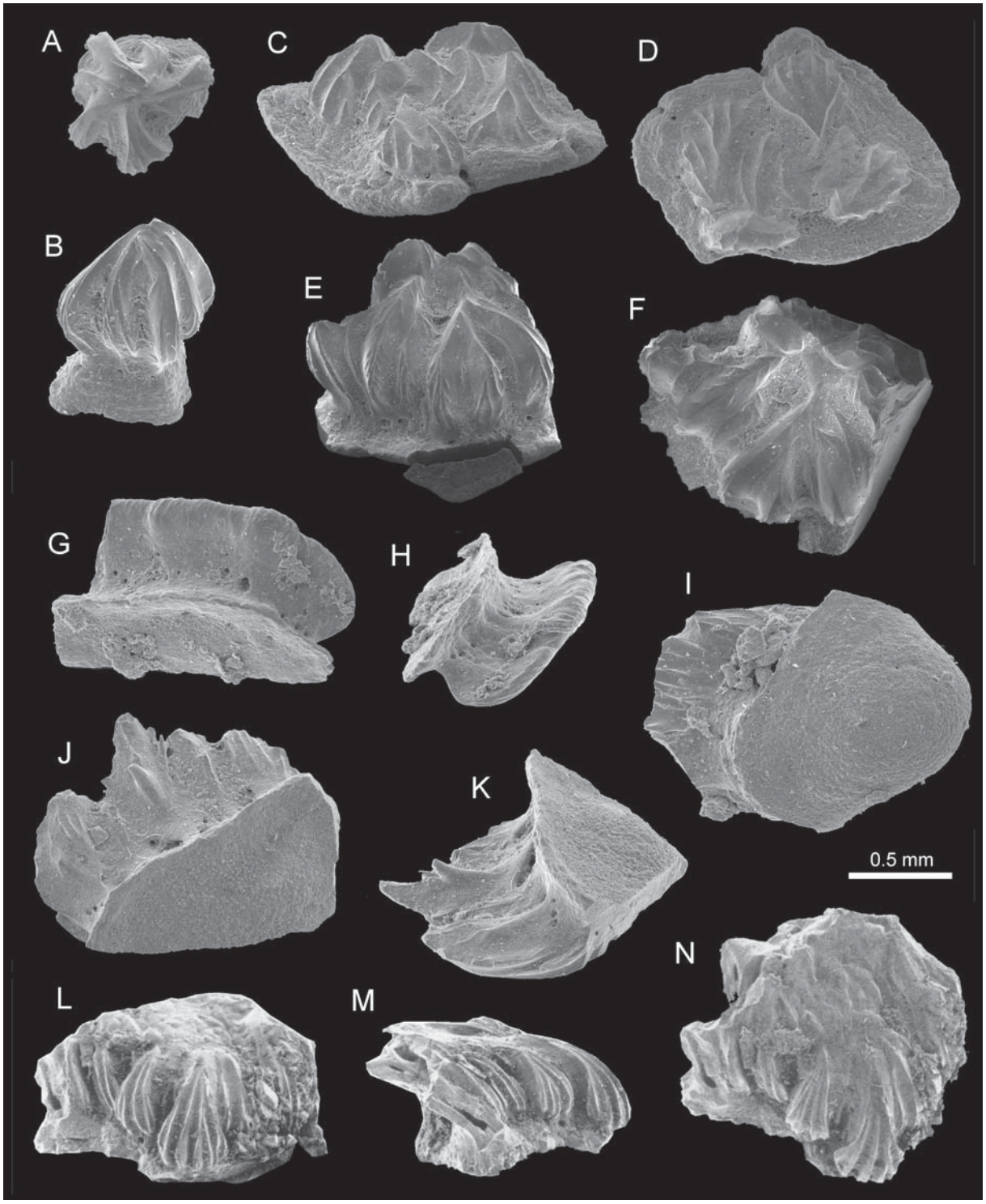

Text-fig. 7. **A-K** – Various scales, probably of *Glencartius costellatus* (Traquair, 1884), from the upper Viséan of the Włodawa IG-4 borehole, east of Lublin, Poland. A, B – star-like denticle, probably from the head region, MWGUW/Ps/12/10 in coronal and lateral views; C, D – a complete ornamented plate, MWGUW/Ps/12/11 in lateral and coronal views; E, F – fragment of a similar plate, MWGUW/Ps/12/12 in anterior? and coronal views; G, H – body scale with a thin crown, MWGUW/Ps/12/13 in posterior/basal and lateral views; I – body scale with a bulbous base, MWGUW/Ps/12/14 in basal view; J, K – body scale with a slightly convex base, MWGUW/Ps/12/15 in basal and lateral views. **L-N** – Ornamented plate associated with the articulated specimen of *G. costellatus*, NHMUK PV P 20144/20145, from Glencartholm, Eskdale, Scotland, UK, in anterior?, lateral and coronal views

from the Cleveland Shale of Ohio (CMNH 9440, Ginter 2010, fig. 1J). The last, but relatively common, type is represented by a rhomboidal to squarish plate with a few short, pyramidal, ornamented odontodes, standing upright or inclined in one direction ('plate'; Text-fig. 7C–F; compare Text-fig. 7L–N).

REMARKS: The proportion of the scale types in the studied sample: numerous body scales, a few head scales and a single broken tooth, suggests that the borehole captured the anterior part of the fish (or a cluster of ichthyoliths from that part), but not the head itself. The discovery of the tooth was very fortunate, as otherwise the identification of the shark would be impossible, since the morphology of Palaeozoic shark scales is very conservative. Very similar scales to those described here occur not only among the ctenacanthiforms, but also in the other orders of primitive chondrichthyans, such as Devonian phoebodontiforms (compare Ginter and Turner 1999, fig. 6; Liao *et al.* 2007, fig. 4).

OCCURRENCE: Carboniferous, Viséan. Hitherto reported from Scotland (Glencartholm, lower Viséan, two articulated specimens), England (Derbyshire, Ticknall Quarry, Brigantian, one tooth) and Poland (Holy Cross Mountains, Todowa Grząba, Asbian or Brigantian, one tooth). The material described herein comes from Poland, Lublin area, Włodawa IG-4 borehole section, upper Viséan (V3a–c).

CONCLUSIONS

Examination of the dermal skeleton of *Glencartius costellatus* (Traquair, 1884) once again shows that whereas the teeth of primitive Palaeozoic sharks can be diagnostic at the specific level and helpful in phylogenetic analysis, the dorsal fin spines give only general information. The scales, because of their diversity on a single shark body and conservative morphology, cannot be used in taxonomy without association with other skeletal parts. Reif's (1978) ctenacanthid type of body scales occurs without any significant change at least from the Givetian through to the Triassic and the shapes of two Devonian phoebodont scales can differ more between each other than each of these scales compared to corresponding elements of a Carboniferous ctenacanth. Therefore, recognising *Ctenacanthus* in the fossil material based on the scales only, as was the common practice in the past (e.g., Derycke *et al.* 1995), has no meaning and can be confusing to the reader.

We hope that the erection of the new generic name for the former "*Ctenacanthus*" *costellatus* will be helpful for the future students of this interesting species, and particularly for those who undertake the long awaited revision of its endoskeleton.

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REFERENCES

Agassiz, L.J.R. 1837–1843. Recherches sur les poissons fossiles, 3, viii + 390 p. Petitpierre; Neuchâtel et Soleure.

Brough, J. 1935. On the structure and relationships of the Hybodont sharks. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society*, **79**, 35–49.

Carroll, R.L. 1988. Vertebrate palaeontology and evolution, x + 698 p. Freeman; New York.

Dean, B. 1909. Studies on fossil fishes (sharks, chimaeroids and arthrodires). *Memoir of the American Museum of Natural History*, **9**, 211–287.

Derycke, C., Brice, D., Blieck, A. and Mouravieff, N. 1995. Upper Givetian and Frasnian ichthyoliths from Bas-Boulonnais (Pas-de-Calais, France): preliminary records. *Bulletin du Muséum national d'Histoire naturelle*, **17**, 487–511.

Dick, J.R.F. 1978. On the Carboniferous shark *Tristychius arcuatus* Agassiz from Scotland. *Transactions of the Royal Society of Edinburgh*, **70**, 63–109.

Dick, J.R.F. 1998. *Sphenacanthus*, a Palaeozoic freshwater shark. In: Norman, D.B., Milner, A.R. and Milner, A.C. (Eds), A study of fossil vertebrates. *Zoological Journal of the Linnean Society*, **122**, 9–25.

Dineley, D.L. and Metcalf, S.J. 1999. Fossil fishes of Great Britain, xxi + 675 p. Joint Nature Conservation Committee; Peterborough.

Egerton, P. 1853. Palichthyologic notes. No. 5. On two new species of placoid fishes from the Coal Measures. *Quarterly Journal of the Geological Society of London*, **9**, 280–282.

Ginter, M. 2002. Taxonomic notes on "*Phoebodus heslerorum*" and *Symmorium reniforme* (Chondrichthyes, Elasmobranchii). *Acta Palaeontologica Polonica*, **47**, 547–555.

Ginter, M. 2010. Teeth of Late Famennian ctenacanth sharks from the Cleveland Shale. In: Elliott, D.K., Maisey, J.G.,

Yu, X. and Miao, D. (Eds), Morphology, phylogeny and paleobiogeography of fossil fishes, pp. 145–158. Friedrich Pfeil; München.

Ginter, M., Duffin, C.J., Dean, M.T. and Korn, D. 2015. Late Viséan pelagic chondrichthyans from northern Europe. *Acta Palaeontologica Polonica*, **60**, 899–922.

Ginter, M., Hampe, O. and Duffin, C.J. 2010. Chondrichthyes. Paleozoic Elasmobranchii. Teeth. In: Schultze, H.-P. (Ed.), Handbook of Paleoichthyology, vol. 3D, 168 p. Friedrich Pfeil; München.

Ginter, M., Ivanov, A. and Lebedev, O. 2005. The revision of "*Cladodus*" *occidentalis*, a Late Palaeozoic ctenacanthiform shark. *Acta Palaeontologica Polonica*, **50**, 623–631.

Ginter, M. and Turner, S. 1999. The early Famennian recovery of phoebodont sharks. *Acta Geologica Polonica*, **49**, 105–117.

Glikman, L.S. 1964a. Paleogene sharks and their stratigraphic meaning, 228 p. Nauka; Moscow. [In Russian]

Glikman, L.S. 1964b. Subclass Elasmobranchii. Sharks. In: Obruchev, D.V. (Ed.), Osnovy paleontologii. XI. Beschelustnye, ryby, pp. 196–237. Nauka; Moscow. [In Russian]

Golubtsov, V.K. 1961. *Kulikia*: a new genus of calcareous alga from the Visean. *Akademiya Nauk Byelorusskoi SSR, Institut Geologicheskich Nauk, Minsk, Sbornik*, **3 (1961)**, 348–353. [In Russian]

Gross, W. 1938. Das Kopfskelett von *Cladodus wildungensis* Jaekel. 2. Teil: Der Kieferbogen. Anhang: *Protacrodus vetustus* Jaekel. *Senckenbergiana*, **20**, 123–145.

Huxley, T. 1880. A manual of the anatomy of vertebrated animals, 431 p. D. Appleton & Co.; New York.

Janvier, P. 1996. Early vertebrates, 393 p. Clarendon Press; Oxford.

Liao, J.-C., Ginter, M. and Valenzuela-Ríos, J.-I. 2007. Chondrichthyan microremains from the Givetian of the Aragonian Pyrenees (Spain). *Bulletin de la Société Géologique de France*, **178**, 171–178.

Maisey, J.G. 1981. Studies on the Paleozoic selachian genus *Ctenacanthus* Agassiz: No. 1. Historical review and revised diagnosis of *Ctenacanthus*, with a list of referred taxa. *American Museum Novitates*, **2718**, 1–26.

Maisey, J.G. 1982. Studies on the Paleozoic selachian genus *Ctenacanthus* Agassiz: No. 2. *Bythiacanthus* St. John and Worthen, *Amelacanthus*, new genus, *Eunemacanthus* St. John and Worthen, *Sphenacanthus* Agassiz, and *Wodnika* Münster. *American Museum Novitates*, **2722**, 1–24.

Maisey, J.G. 1984. Studies on the Paleozoic Selachian Genus *Ctenacanthus* Agassiz. No. 3. Nominal species referred to *Ctenacanthus*. *American Museum Novitates*, **2774**, 1–20.

Moy-Thomas, J.A. 1936. The structure and affinities of the fossil elasmobranch fishes from the Lower Carboniferous rocks of Glencartholm, Eskdale. *Proceedings of the Zoological Society of London*, **1936**, 761–788.

Moy-Thomas, J.A. 1951. On the name of the fossil shark *Goodrichia*. *Annals and Magazine of the Natural History*, **4**, 304.

Moy-Thomas, J.A. and Miles, R.S. 1971. Palaeozoic fishes, 259 p. Chapman and Hall; London.

Newberry, J.S. 1875. Descriptions of fossil fishes. *Geological Survey of Ohio*, **2**, 1–64.

Porzycki, J. 1988. Lithologic and sedimentologic characteristics of Carboniferous deposits. In: Dembowski, Z. and Porzycki, J. (Eds), Carboniferous of the Lublin Coal Basin. *Prace Instytutu Geologicznego*, **122**, 40–76. [In Polish with English summary]

Porzycki, J. and Zdanowski, A. 1995. Lithostratigraphy and sedimentologic-paleogeographic development: southeastern Poland (Lublin Carboniferous Basin). In: Zdanowski, A. and Żakowa, H. (Eds), The Carboniferous system in Poland. *Prace Państwowego Instytutu Geologicznego*, **148**, 102–109.

Reif, W.-E. 1978. Types of morphogenesis of the dermal skeleton in fossil sharks. *Paläontologische Zeitschrift*, **52**, 110–128.

Shvetsov, M.S. and Birina, L.M. 1935. On the petrology and origin of the Oka Limestone in the Mikhailov-Aleksin region. *Trudy Moskovskogo Geologicheskogo Tresta*, **10**, 1–86. [In Russian]

Skompski, S. 1986. Upper Viséan calcareous algae from the Lublin Coal Basin (Poland). *Acta Geologica Polonica*, **36**, 251–280.

Skompski, S. 1996. Stratigraphic position and facies significance of the limestone bands in the subsurface Carboniferous succession of the Lublin Upland. *Acta Geologica Polonica*, **46**, 171–268.

Traquair, R.H. 1884. Description of a fossil shark (*Ctenacanthus costellatus*) from the Lower Carboniferous rocks of Eskdale, Dumfrieshire. *Geological Magazine*, (3), **1**, 3–8.

Waksmundzka, M.I. 2010. Sequence stratigraphy of Carboniferous paralic deposits in the Lublin Basin (SE Poland). *Acta Geologica Polonica*, **60**, 557–597.

Waksmundzka, M.I. 2013. Carboniferous coarsening-upward and non-gradational cyclothems in the Lublin Basin (SE Poland): Palaeoclimatic implications. *Geological Society Special Publication*, **376**, 141–175.

Wood, A. 1964. A new dasycladacean alga, *Nanopora*, from the Lower Carboniferous of England and Kazakhstan. *Palaeontology*, **7**, 181–185.

Woodward, A.S. 1889. Catalogue of the fossil fishes in the British Museum (Natural History), Part 1, xlvii + 474 p. British Museum (Natural History); London.

Woodward, A.S. 1921. Presidential address, 1921. Observations on some extinct elasmobranch fishes. *Proceedings of the Linnean Society of London*, **133**, 29–39.

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