Thomasaria vs. *Pyramidalia* conundrum in Devonian brachiopod systematics solved: An argument to formalize epitypification under the ICZN

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Halamski, A.T. and Baliński, A. 2019. *Thomasaria* vs. *Pyramidalia* conundrum in Devonian brachiopod systematics solved: An argument to formalize epitypification under the ICZN. *Acta Palaeontologica Polonica* 64 (2): 399–408.

Pyramidalia is a brachiopod genus with *Spirifera simplex* as the type species. Imprecise diagnosis and misidentification of the material studied in the original description resulted in a plethora of interpretations (a valid genus belonging either to the order Spiriferida or to the Spiriferinida; synonym of the spiriferide *Thomasaria*; synonym of *Squamulariina* or *Cyrtinaella*, both spiriferinides). To address this problem we designated the specimen GSM 6915 from Wolborough quarry near Newton Abbot (Devon, England; Givetian) as the lectotype of *Spirifera simplex*. We examined microstructure and internal characters of a topotypic specimen and found out that *Spirifera simplex* has an impunctate shell and is thus a spiriferide, not a spiriferinide. No significant differences in morphology or internal characters of *Thomasaria* and *Pyramidalia* can be found, so the latter is interpreted as a junior subjective synonym of the former. The procedure used in the present analysis is equivalent to the epitypification provided for in the ICN; formalisation of a similar procedure under the ICZN is recommended.

Key words: Brachiopoda, *Pyramidalia*, *Thomasaria*, epitypification, ICZN, Devonian, UK, England.

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Received 1 February 2019, accepted 17 April 2019, available online 21 May 2019.

Introduction

The brachiopod genus *Pyramidalia* Nalivkin, 1947 was proposed with *Spirifera simplex* Phillips, 1841 as the type species. However, Nalivkin (1947) did not examine the type material of *S. simplex* from the Middle Devonian of south-western England, assuming instead that his material from the Frasnian of the Urals and central Asia was conspecific with the former. Moreover, the diagnosis included neither the shell microstructure nor a detailed description of internal characters. This resulted in a plethora of interpretations of *Pyramidalia*, the genus being considered as belonging either to the order Spiriferida or to the order Spiriferinida, and in each case either valid or synonymous with other previously established taxa. The only way of fixing the application of the generic name *Pyramidalia* is to investigate the type material of its type species. The necessity of examining the specimens described by Phillips (1841) has been stressed several times (Drot 1964: 79; Baliński 2006: 674; Mottequin 2008: 516; García-Alcalde 2010: 58; Halamski and Baliński 2013: 293) but never conducted heretofore; this is done herein.

The questions of the systematic position of *Pyramidalia* and of the correct application of the genus name are of considerable importance, insofar as brachiopods identified as *Spirifera simplex*, *Pyramidalia*, or *Thomasaria* (the two latter names are synonymous, as shown below) were reported from the Middle and Upper Devonian of several regions of four continents (see below) and sometimes even used as index fossils (Warren and Stelck 1956; Webby 1961: 538, 1964: 3; McLaren et al. 1962). However, the object of the present paper is solely *Spirifera simplex* from south-western England and the correct delimitation of the genus name *Pyramidalia*, whereas the revision of conspecific brachiopods from other regions and of other possibly congeneric species is postponed to a further study.

Institutional abbreviations.—GSM, Geological Society Museum (= Keyworth Biostratigraphy Museum), British Geological Survey, Keyworth, UK; NHMUK, British Museum (Natural History), now Natural History Museum, London, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; SM, Sedgwick Museum of Earth Sciences, Cambridge, UK; TCD, Trinity College, Dublin, Ireland.

Other abbreviations.—ICN, International Code of Nomenclature for algae, fungi, and plants; ICZN, International Code of Zoological Nomenclature.

Historical background

The original description and material of John Phillips.—The original description of *Spirifera simplex* was given by Phillips (1841: 71) on the basis of brachiopods from Plymouth and Newton in South Devon. Devonian rocks cropping out in Cornwall, Devon, and Somerset in south-western England (Fig. 1) belong to an upper Palaeozoic massif forming part of the Variscan orogen of western and central Europe (Leveridge and Hartley 2006; Shail and Leveridge 2009). More precisely, the discussed area belongs to the Rhenohercynian Zone that lay at or near the southern passive margin of the Eastern Avalonia plate (Franke 2000). In terms of palaeogeography this corresponds to a location south of the Old Red Sandstone Continent (Laurussia), more exactly south-western of its southern tip formed by the Welsh Massif and the London-Brabant massif (Ziegler 1982: map 7; Leveridge and Shail 2011 and references therein). The Givetian palaeolandscape may be reconstructed as a segmented marine shelf with limestone reefs on basement highs (Shail and Leveridge 2009: 143). Middle Devonian strata include slate facies cropping out mostly in Cornwall and limestone in South Devon (House and Selwood 1966).

The type series of *Spirifera simplex*, like always in the case of species established before 2000 (Art. 72.4.1 of the ICZN), consists of all specimens that can be proven to be known to the author earlier than the publication of the name (here 1841) and identified as the discussed taxon. Four specimens possibly referable to Phillips's collection could be traced in the GSM. No Phillips material could be traced in the NHMUK (Sarah Long, personal communication 2002) or in the OUMNH (Derek Siveter, personal communication 2002).

The specimens GSM 6915, GSM 6916, GSM 50930, and GSM 50931 are recorded as coming from Newton and "presented by R.A. Godwin-Austen Esq.", but any external evidence (i.e., documents) that they were used by Phillips is lacking. Such an regrettable situation is unfortunately by no means exceptional, as John Phillips (see biographical note by Bonne 1896) did not make "reference to precise localities. There has been much guess work on this subject, but nothing absolutely conclusive." (Howard Brunton, personal communication 2002).

On the other hand, in the original description of *Spirifera simplex* (Phillips, 1841) five specimens are illustrated (Phillips 1841: pl. 29: 124αa–d; pl. 60: 124α) and thus belong undoubtedly to the type series. The last specimen (i.e., Phillips 1841: pl. 60: 124α) can be identified with GSM 6915, whereas the other ones could not be found in any existing collections.

The provenance of GSM 6915 is described in some detail: "Mr. Austen has furnished me with more perfect specimens, one of which is represented on pl. 60, fig. 124" (Phillips 1841: 71). House and Selwood (1966: 85), when re-illustrating the discussed specimen, supposed erroneously that it had originated "probably from the Plymouth limestone". However, the English geologist Robert Alfred Cloyne Godwin-Austen (see biographical note by Boase 1890) collected the Devonian fauna in Newton Bushel (Phillips 1841: 203; Davidson 1864: 9).

The specimen GSM 6915, coming thus in all probability from Newton Bushel, is chosen herein as the lectotype of *Spirifera simplex* Phillips, 1841. It might be objected that the second specimen is said to come to Phillips "since the figures were drawn" (Phillips 1841: 71), this is why it is figured on the last plate. However, it must be stressed that the entire book was printed simultaneously (August 1841 according to Sherborn 1922: lxiii; the date 1839 given ibid. p. cii is a lapsus calami), so both specimens belong to the type series and have equal status.

According to House and Selwood (1966: 57), Phillips's "Newton Bushel" corresponds to Wolborough quarry (SX 850706; spelt Woolborough by Davidson 1864: 46) near Newton Abbot in Devon. The Wolborough quarry is an outcrop of coarse, subordinately dolomitised limestone belonging to a local stratigraphic unit called East Ogwell Limestone (Selwood et al. 1984: 30). Descriptions of the quarry are given by Scrutton (1968: 185–186), Selwood et al. (1984: 49–50) and House (2002: 281–282). According to Selwood et al. (1984: 174), conodonts allow dating the strata cropping out in the quarry to the *Polygnathus varcus* Zone, but in this case a better dating may be obtained on the basis of a rich goniatite fauna (*Maenioceras molarium* Zone; House 2002: 288–289). Brachiopods from Wolborough were included in the monograph by Whidborne (1893). Fossil fauna from this locality is summarised by Ussher (1913: 22–24); 53 brachiopod taxa are listed along with numerous molluscs, arthropods, crinoids and less diverse corals and bryozoans. The only newer treatment of brachiopods is that of *Mimatrypa* by Copper (1965).

History of the name Pyramidalia *Nalivkin, 1947*.—The genus *Pyramidalia* was introduced by Nalivkin (1947: 124) as a representative of the (then widely understood) family Spiriferidae King, 1846 closest to "*Reticularia* Martin" (recte: *Reticularia* M'Coy, 1844) and *Eoreticularia* Nalivkin in Fredericks, 1924. The type species of the new genus was given as *Spirifer simplex* Phillips, 1841 (lapsus calami pro *Spirifera simplex*). However, the material on which the description was based was not topotypic (i.e., not from the Middle Devonian of south-western England), but came from the Frasnian (Upper Devonian) of the Urals, central Asia, and Kuznetsk Basin (Nalivkin 1947: 125). According to Oleneva (2006: 421), the only shell illustrated by Nalivkin (1947: pl. 31: 4; copy of Nalivkin 1930: pl. 10: 5) as *Pyramidalia simplex* comes from the Frasnian of the Alai Ridge and represents another species, namely *Thomasaria rotunda* Oleneva, 2006.

Vandercammen (1957) correctly interpreted *Spirifera simplex* as a reticularioid, but misapplied the generic name *Plectospirifer* Grabau, 1931 thereto. As a matter of fact, *Plectospirifer* is an athyridide (a junior subjective synonym of *Athyrisina* Hayasaka in Yabe and Hayasaka, 1920; Hou 1959: 457; Alvarez and Rong 2002: 1507; Hou et al. 2017: 433). It may also be noted that, according to Mottequin (2008: 512), the material described by Vandercammen (1957) as *Plectospirifer simplex* partly represents *Thomasaria* cf. *altumbona* and partly another more distantly related species.

Baliński (1979: 71; 2006: 674), Brice (1985: 145), Oleneva (2006: 419), Halamski and Baliński (2013: 293), and Alekseeva et al. (2018) considered *Pyramidalia* (with various degrees of confidence) as a junior subjective synonym of *Thomasaria* Stainbrook, 1945, the latter a representative of the superfamily Reticularioidea Waagen, 1883 either within the Reticulariidae Waagen, 1883 or Thomasariidae Cooper and Dutro, 1982. It might be of interest to note that Vandercammen (1956) misinterpreted *Thomasaria* as an ambocoelioid.

Drot (1964: 78–79) and García-Alcalde (2010: 58) considered *Pyramidalia* as a valid genus within the family Reticulariidae Waagen, 1883.

A very different line of interpretation of *Pyramidalia* started with Ivanova (1959: 62) who included the discussed genus into the family Cyrtinidae Fredericks, 1911 (in a synoptic classification, without any comment). Such a classification was adopted by Ivanova in further works (Ivanova 1960: 279; 1962: 119; 1972: 37). Also Biernat (1966: 136) treated *Pyramidalia* as a valid genus within the family Cyrtinidae.

Pitrat (in Boucot et al. 1965: H678) proposed to treat *Pyramidalia* as a synonym of *Cyrtinaella* Fredericks, 1916 (family Cyrtinidae). This was followed by Sapelnikov and Mizens (2000: 125), although it should be noted that, according to Oleneva (2006), *Cyrtinaella simplex* sensu Sapelnikov and Mizens (2000) represents *Pyramina oskolensis* Ljaschenko, 1969 (family Ambocoeliidae George, 1931). Carter et al. (1994) and Johnson (2006: 1882) considered *Pyramidalia* as a junior subjective synonym of *Squamulariina* Fredericks, 1916 (family Cyrtinidae).

To sum up, excluding obvious nomenclatural misapplications (*Plectospirifer*) and attributions to genera formerly treated more widely than at present (*Spirifer*, *Reticularia*, *Eoreticularia*, *Cyrtia*; see the synonymy in Vandercammen 1957: 12), *Pyramidalia* was considered: (i) a valid genus within the order Spiriferida (Drot 1964; García-Alcalde 2010); (ii) a valid genus within the order Spiriferinida as presently circumscribed (Ivanova 1959, 1960, 1962, 1972; Hou 1963; Biernat 1966); (iii) a synonym of *Thomasaria* within the Spiriferida (Baliński 1979; Brice 1985; Oleneva 2006; Halamski and Baliński 2013; Alekseeva et al. 2018); (iv) a synonym of either *Squamulariina* (Carter et al. 1994; Johnson 2006) or *Cyrtinaella* (Pitrat in Boucot et al. 1965; Sapelnikov and Mizens 2000) within the Spiriferinida as presently circumscribed.

Material and methods

The quarry at Wolborough has been inactive for several years (already inaccessible to Copper 1965: 360). Brachiopods coming from this quarry were traced in two collections, in GSM and in NHMUK. The collection of the GSM is very small and includes only historical specimens than cannot be sectioned. Specimens in the NHM have thus been the only ones that could be chosen for the purpose of the present study.

The specimen NHMUK PI B 2807 (Newton, coll. J.E. Lee, presented to the Museum in October 1885) has been chosen for serial sections because: (i) its origin from Wolborough (Newton Bushel) is undoubted (not always so in 19th century collections); (ii) it is neither a type nor a figured specimen. The internal structures of this shell were investigated using the standard technique of serial sections and acetate peels. Due to the pyramidal shape of the shell, each valve was sectioned separately. The acetate peels were mounted between microscope slides and photographed under a binocular microscope. The photographs were imported to CorelDRAW software and internal details were drawn using a digital drawing tablet.

Systematic palaeontology

Phylum Brachiopoda Duméril, 1805

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer, and Popov, 1996

Class Rhynchonellata Williams, Carlson, Brunton, Holmer, and Popov, 1996

Order Spiriferida Waagen, 1883

Family Thomasariidae Cooper and Dutro, 1982

Stratigraphic and geographic range.—Middle to Late Devonian, Eifelian?, Givetian to Frasnian (corrected herein).

Genus *Thomasaria* Stainbrook, 1945

= *Pyramidalia* Nalivkin, 1947

Type species: *Thomasaria altumbona* Stainbrook, 1945; Iowa, USA; Independence Shale, upper Frasnian (after Day and Witzke 2017), Upper Devonian.

Remarks.—*Pyramidalia* Nalivkin, 1947 with type species *Spirifera simplex* Phillips, 1841 is a synonym of *Thomasaria*. As shown below, the shell of *Spirifera simplex* is impunctate (Fig. $2E_6$), *Pyramidalia* is thus a spiriferide, not a spiriferinide (contrary to, among others, Ivanova 1959; Pitrat in Boucot et al. 1965; Johnson 2006). Morphology and internal structures of *Spirifera simplex* and *Thomasaria* are very similar. More precisely, *Spirifera simplex* is in accordance with the diagnosis of *Thomasaria* given by Johnson (2006: 1864), except for the cardinal angles that may be either acute (Fig. $2C_1$) or rounded (Fig. $2D_1$). It should be noted, however, that the cardinal process was not observed due to preserva-

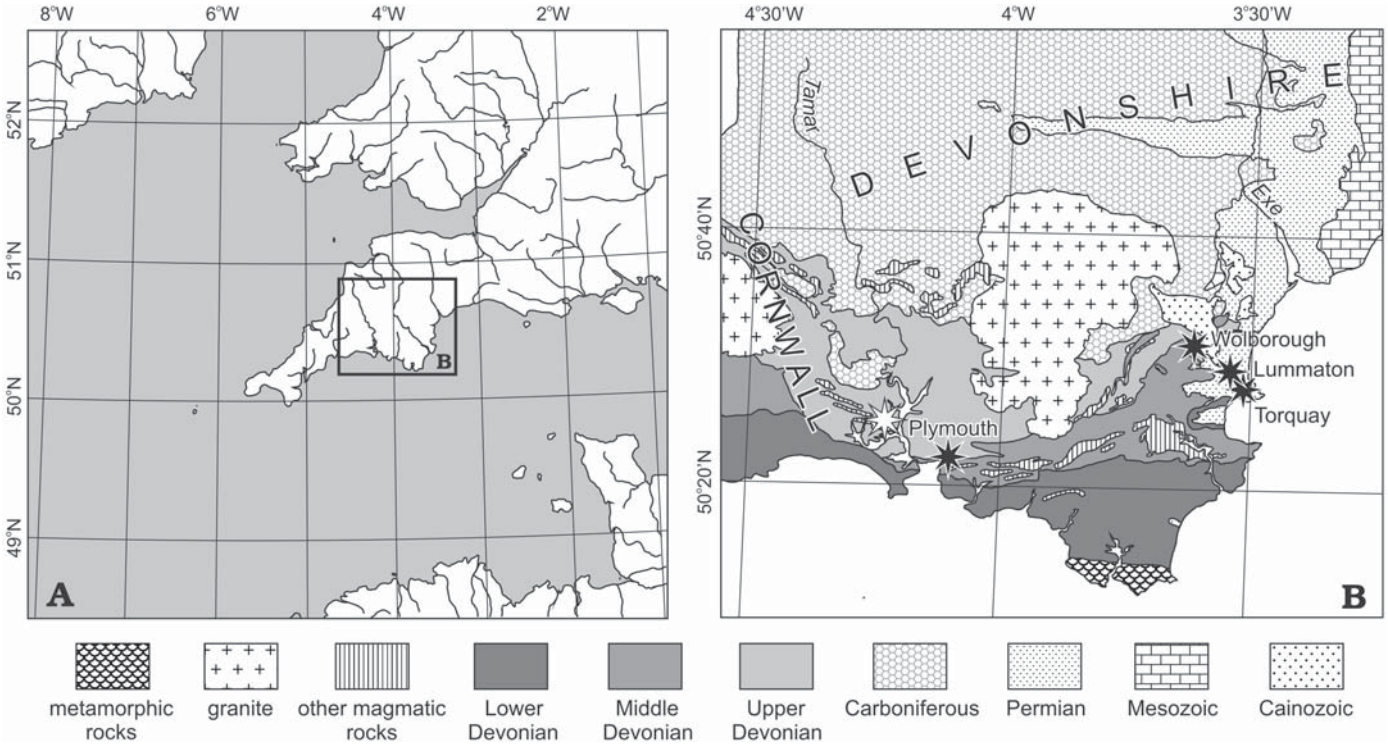

Fig. 1. **A**. Geographical location of the study area in north-western Europe. **B**. Geological map of eastern Cornwall and southern Devon (Devonian after House and Selwood 1966, otherwise simplified and modified after British Geological Survey 1957). Black asterisks show fossil localities mentioned in the text. The white asterisk shows the presumed position of "Port Stephens" (see text for further explanation).

tional condition of the sectioned specimen of *Spirifera simplex*. Moreover, the internal morphology of the dorsal valve is known solely for *Thomasaria warreni* Cooper and Dutro, 1982 from the Frasnian of New Mexico (Cooper and Dutro 1982: pl. 40: 26–27; pl. 43: 1–9) and for *Thomasaria* cf. *altumbona* from the Frasnian of Belgium (Mottequin 2008: fig. 56). The dorsal valve of *T. altumbona* has been sectioned neither by Stainbrook (1945) nor by Pitrat (1965), Johnson (2006), or any subsequent author. Notwithstanding these minor issues, the most satisfying solution is clearly treating *Pyramidalia* as a junior subjective synonym of *Thomasaria*, following Baliński (1979), Brice (1985), Oleneva (2006), Halamski and Baliński (2013), and Alekseeva et al. (2018).

García-Alcalde (2010: 58) suggested the following differences between *Pyramidalia* and *Thomasaria* warrant distinction at genus level: (i) symphytium lacking in *Thomasaria*, present in *Pyramidalia*; (ii) crural plates lacking in *Thomasaria*, present in *Pyramidalia*; (iii) cardinal angles acute or right-angled in *Thomasaria*, rounded in *Pyramidalia*; (iv) dental plates in *Thomasaria* longer than in *Pyramidalia*.

As a matter of fact, the above-mentioned differences are either nonexistent or insufficient for distinction at genus level.

(i) A pair of conjunct apical plates fused with the bases of the dental plates umbonally and extending below the level of interarea is present in *Thomasaria altumbona* (Johnson 2006). Cooper and Dutro (1982: pl. 35: 2–3) showed that in *T. altumbona* there is also a pair of convex plates rising from lateral edges of the delthyrium. This strongly suggests that a convex pseudodeltidium (symphytium sensu García-Alcalde 2010) covering the delthyrial opening was present at least in adult-gerontic shells.

(ii) Inner socket ridges are present in both *Thomasaria* and *Pyramidalia* (see Fig. 3B for the former and Cooper and Dutro 1982: pl. 43: 6–7 for the latter). García-Alcalde (2010) misinterpreted the inner socket ridges in *Pyramidalia palentina* García-Alcade, 2010 from the Givetian of the Asturias as crural plates (crural plates are defined as being in contact with the valve floor, which is not the case in any of the referred brachiopods).

(iii) The position of the maximal width and, in consequence, the form of postero-lateral extremities are subject to ontogenetic (compare Halamski and Baliński 2013: fig. 36A, C, H) and intraspecific (compare Fig. $2A_1$–D_1) variability.

(iv) Such a difference is not significant for a distinction at genus level (compare Stainbrook 1945: fig. 2.14A–C; Fig. 3A).

Brachiopods presumably belonging to *Thomasaria* were reported under various generic names (including *Pyramidalia*) from Europe: south-western England (Phillips 1841; Webby 1964); Eifel, Germany (Schnur 1853–1854); Montagne Noire, France (Bergeron 1889; Brice 1985); Pyrenees, France (Joseph et al. 1980); Ardennes, Belgium (Mottequin 2008); Holy Cross Mountains and Dębnik Anticline, Poland (Gürich 1896; Sobolew 1909; Biernat 1966; Baliński 1979, 2006); Cantabrian Mountains, Spain (van Loevezijn 1986; García-Alcalde 2010); Asia: central Asia (Nalivkin 1930); China (Hou 1963); Urals (Tschernyschew 1887; Skompski et al. 2001); Timan (Oleneva 2006); Caucasus (Alekseeva et al. 2018); Afghanistan (Brice 1971); Iran (Brock and Yazdi 2000); North

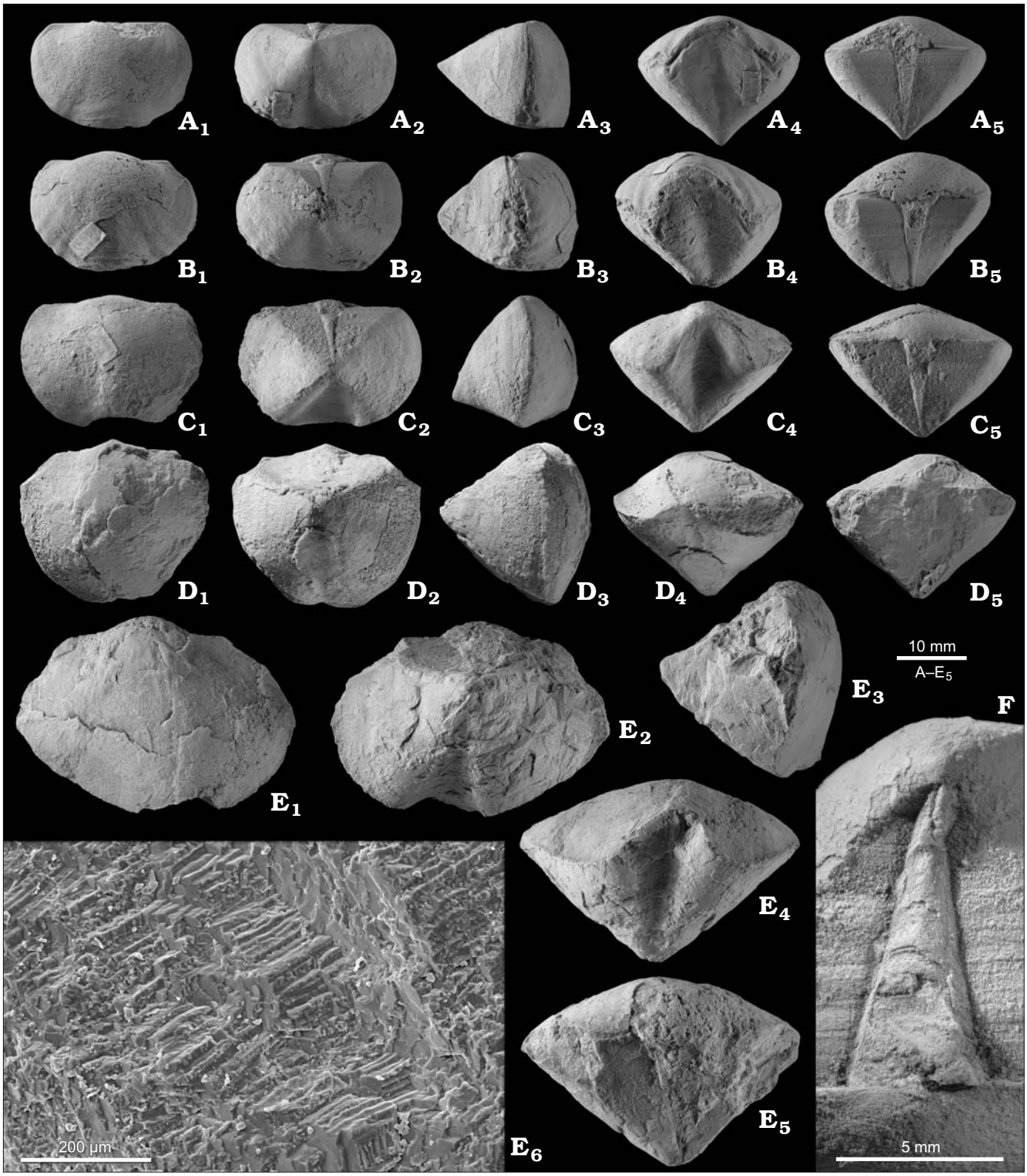

Fig. 2. Spiriferide brachiopod *Thomasaria simplex* (Phillips, 1841) from the Middle Devonian of south-western England, UK (type region). **A**–**C**. Articulated shells (TCD 16991c, **A**; TCD 16991b, **B**; TCD 16991a, **C**) from Port Stephens, in dorsal (A_1–C_1), ventral (A_2–C_2), lateral (A_3–C_3), anterior (A_4–C_4), and posterior (A_5–C_5) views. **D**. Lectotype, articulated shell GSM 6915 from Wolborough, in dorsal (D_1), ventral (D_2), lateral (D_3), anterior (D_4), and posterior (D_5) views. Reproduced with the permission of the British Geological Survey ©UKRI. All rights reserved. **E**. Topotype, articulated shell NHMUK PI B 2807 (specimen serially sectioned, see Fig. 3) from Wolborough, in dorsal (E_1), ventral (E_2), lateral (E_3), anterior (E_4), and posterior (E_5) views, enlargement (SEM micrograph) of the secondary shell layer showing impunctate condition (E_6). **F**. Articulated shell TCD 16991d from Port Stephens, fragmentary posterior view showing the delthyrium partially closed by a convex pseudodeltidium.

America: Iowa, USA (Stainbrook 1945); New Mexico, USA (Cooper and Dutro 1982), Alaska, USA (Nilsen et al. 1980); Alberta, Canada (Warren and Stelck 1956; MacKenzie 1965); District of Mackenzie, Canada (McLaren et al. 1962); and Africa: Anti-Atlas, Morocco (Halamski and Baliński 2013).

Stratigraphic and geographic range.—Middle to Late Devonian (Eifelian?, Givetian to Frasnian). The presence of *Thomasaria* in the Eifelian stage of its type region is probable, but has not been proved conclusively. Data provided by Schnur (1851, 1853–1854) are equivocal due to imprecise stratigraphy and uncertain taxonomy (the identification of *Spirifer simplex* given by Schnur 1851: 12 was considered doubtful by Schnur 1853–1854: 208; *Spirifer pyramidalis* is from the Frasnian of Büdesheim, see e.g., Korn et al. 2013 for the age; the identification of *Spirifer nudus* is considered uncertain by Schnur 1853–1854). The report from the upper Eifelian of Skały in the Holy Cross Mountains by Halamski and Zapalski (2006: 147) is based on a misquotation of Biernat's material coming from the Givetian of Miłoszów and should be excluded. The age of *Pyramidalia paoshanensis* Hou, 1963 from South China is given as "Eifelian (?)" (Hou 1963: 425).

Thomasaria simplex (Phillips, 1841)

Figs. 2, 3.

1841 *Spirifera simplex*; Phillips 1841: 71; pl. 29: 124αa–d; pl. 60: 124α.
1864 *Spirifera simplex*, Phillips; Davidson 1864: 46; pl. 6: 18–22.
1893 *Spirifera simplex*, Phillips; Whidborne 1893: 109.
1913 *Spirifera simplex* Phill.; Ussher 1913: 22.
non 1930 *Reticularia* (*Eoreticularia*) *simplex* Phillips; Nalivkin 1930: 133–134; pl. 10: 5 [= *Thomasaria rotunda* Oleneva, 2006].
non 1947 *Pyramidalia simplex* Phillips, 1841; Nalivkin 1947: 124–125; pl. 31: 4 [= *Thomasaria rotunda* Oleneva, 2006].
1966 *Pyramidalia simplex* (Phillips); House and Selwood 1966: 54; pl. 2: 8–9.

Lectotype (selected herein): Articulated shell GSM 6915 (coll. Austen), illustrated by Phillips (1841: pl. 60: 124α), re-illustrated by House and Selwood (1966: pl. 2: 8, 9) and herein (Fig. 2D).

Type locality: Wolborough quarry (SX 8522 7047), on the east side of the A381, east of Wolborough church, on the southwest outskirts of Newton Abbot, Devon, England, UK (House 2002: 281).

Type horizon: East Ogwell Limestone; Givetian, *Maenioceras molarium* Zone (House 2002: 288–289).

Material.—Wolborough: GSM 6916, GSM 50930, GSM 50931 (possible paralectotypes; coll. Austen), NHMUK PI B 2807 (coll. Lee), B 22089 (coll. Vicary). Lummaton: NHMUK PI B 9144 (coll. Pengelly), SM H2521–2525 (coll. Whidborne). Torquay: NHMUK PI B 7320 (coll. Davidson). Port Stephens: TCD 16991a–e (collector unknown). Probably all Givetian, England, UK.

Description.—Shell pyramidal, (thickness-to-length ratio usually about 0.9–1.1), strongly ventribiconvex (ventral valve ca. 2.5–4 times as thick as the dorsal one), variably transverse (width-to-length ratio 1.15 in the lectotype, but 1.79 in the topotypic specimen GSM 6916; Table 1). Maximal observed width ca. 44 mm (estimated on the basis of the subcomplete ventral valve GSM 6916). Hinge line straight. Cardinal extremities most often feebly angular forming a wide angle with rounded lateral margins. Anterior margin straight to indented. Maximal width usually slightly anteriorly to the mid-length of the dorsal valve. Dorsal valve weakly to distinctly convex; fold none to distinct; interarea very low, approximately orthocline. Ventral valve strongly convex, subpyramidal, rarely with slightly twisted umbo; interarea very high, laterally bordered by delicate but sharp extremities, narrower than the total shell width, attaining about three quarters of the latter, most often procline, more seldom apsacline, concave, flat or weakly convex (Fig. $2C_3$), with growth striation parallel to the hinge line; delthyrium well developed, with delthyrial angle 15–19°, its width up to about one fifth of that of the shell; four of six investigated shells show delthyrium closed for most of its height by a convex pseudodeltidium (Fig. $2A_5$, B_5, C_5, F). Anterior commissure uniplicate to weakly parasulcate. Ornamentation either none or consisting of low, rounded, often hardly discernible costae, 1–2(–3) per valve. Micro-ornamentation poorly preserved, consisting of regularly spaced faint concentric growth lines with density 10 lines per 1 mm.

Interior of the shell was studied by serial sections of a single, slightly incomplete and deformed topotypic shell NHMUK PI B 2807 shown in Fig. 2E.

Ventral valve (Fig. 3A): dental plates strongly divergent at about 80° toward the floor of the valve and in contact with the valve floor on a length of 2.8 mm, then extending

Table 1. Measurements (in mm) of selected specimens. [1] lectotype, [2] specimens from the restricted type locality and stratum, [3] specimens from south-western England.

	Shell			Width of			Thickness of valve	
	width	length	thickness	tongue	delthyrium (maximum)	interarea	dorsal	ventral
GSM 6915[1]	26.7	23.2	20.9	12.4	6.2	–	4.0	16.9
GSM 6916[2]	≈44	26.0	–	?	8.9	≈30	–	15.8
GSM 50931[2]	23.2	12.9	13.9	12.7	–	–	–	–
NHM B.2807[2]	≈41	–	26.5	13.3	–	30.4	7.0	19.5
NHM B.22089[2]	22.2	15.6	14.8	–	–	–	–	–
NHM B.7320[3]	18.5	12.7	10.4	–	–	–	–	–
NHM B.9144[3]	28.4	17.5	22.0	–	–	–	–	–
TCD 16991a[3]	26.1	24.2	18.9	11.9	3.9	20.2	5.9	13.0
TCD 16991b[3]	23.9	15.8	19.0	13.2	4.8	18.5	4.0	15.0
TCD 16991c[3]	23.0	15.3	17.9	12.8	2.7	15.8	4.0	13.9

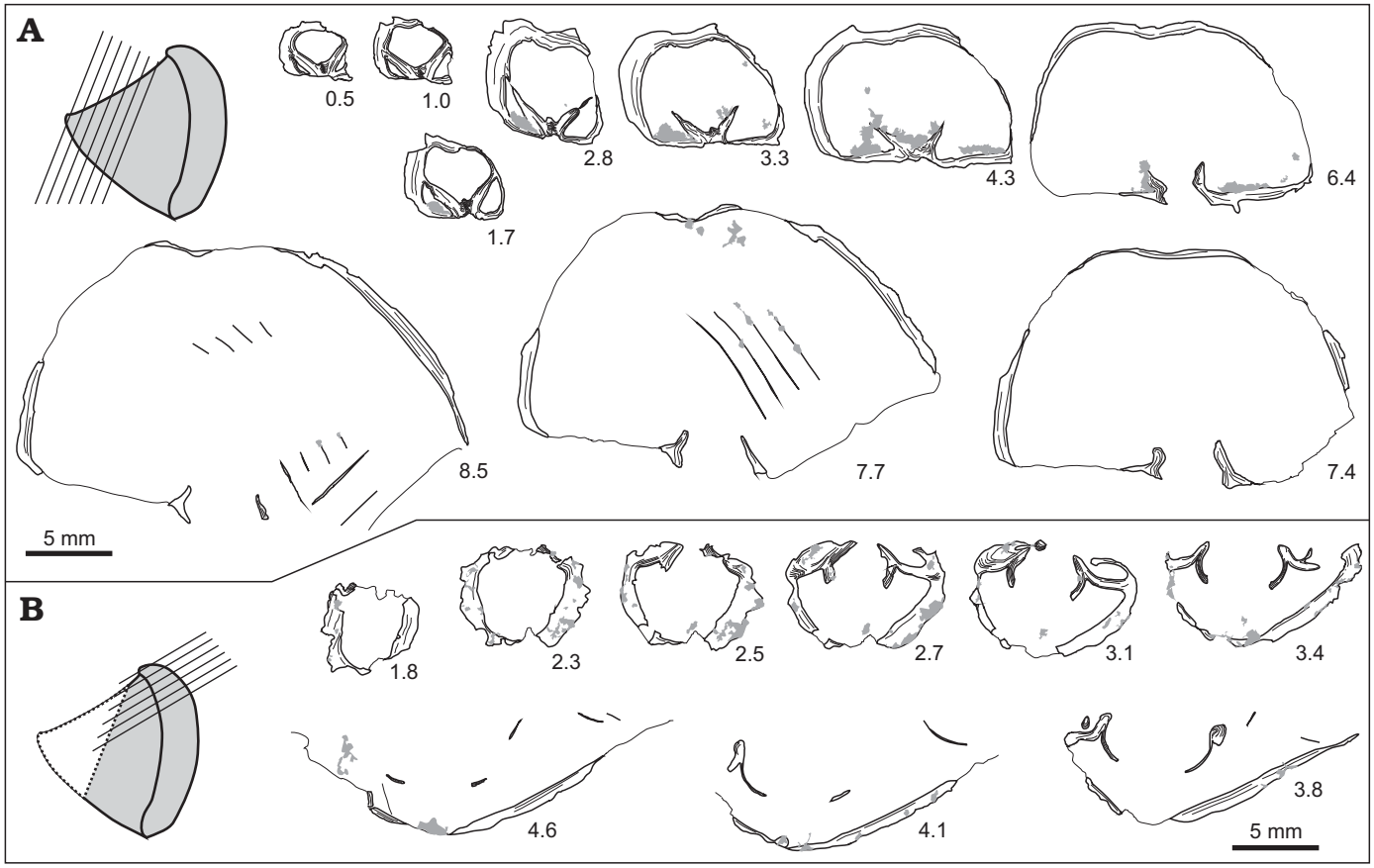

Fig. 3. Transverse serial sections of spiriferide brachiopod *Thomasaria simplex* (Phillips, 1841) through shell NHMUK PI B 2807 (topotype) from the Givetian of Wolborough, England, UK. Sections through ventral (**A**) and dorsal (**B**) valves. The schematic drawings on the left of each section describe the direction of sectioning (see text). Distances measured in millimetres from the tip of the ventral and dorsal umbos, respectively. Gray areas denote local silicification.

anteriorly as high dental ridges on the inner edges of the delthyrium; in the umbo bases of the dental plates fused and thus occluding the apical region of the delthyrium; other features of the internal structure of the valve not preserved.

Dorsal valve (Fig. 3B): cardinal process not preserved in the sectioned specimen; sockets bordered by inner socket ridges coalescent with crural bases and thus forming concave, subvertical plates; crural blades slightly concave ventrally and subparallel to the valve floor; crural plates not developed; spiralium broken and displaced, so only some of the whorls are visible on the serial sections.

Shell substance impunctate (see SEM micrograph on Fig. $2E_6$ taken from a fragment of the shell NHMUK PI B 2807).

Remarks.—The type locality and horizon of *Spirifera simplex* were originally given as "[i]n South Devon: Plymouth; Newton" (Phillips 1841: 71) and "Plymouth Group" (Phillips 1841: 147), this unit being more inclusive than the Plymouth Limestone sensu House and Selwood (1966: 54, fig. 2). However, according to the Art. 76.2 of the ICZN, "the place of origin of the lectotype becomes the type locality of the nominal species-group taxon, despite any previously published statement of the type locality", so the type locality and horizon of the discussed species are given as above as a consequence of the lectotype designation effectuated herein.

According to the original description, "the specimens, both at Plymouth and Newton, are entirely devoid of lateral radiating plaits" (Phillips 1841: 71). A similar observation was made by Whidborne (1893: 109): "there is no indication [of ribs] in any English specimens". However, three faint rounded costae may be observed in NHMUK PI B 9144 and one or two faint costae in NHMUK PI B 7320. Moreover, smooth and costate individuals occur within a single sample (compare TCD 16991b, Fig. 2B and TCD 16991a, Fig. 2C). Variability in dorsal valve convexity, presence or absence of the fold, and the form and position of the interarea has been noted in the description.

Detailed comparison of *Thomasaria simplex* with other representatives of the genus is out of the scope of the present paper, but it may be briefly noted that *T. altumbona* (the type species of the genus) is much smaller in size and its dorsal fold is more distinct (Stainbrook 1945).

Stratigraphic and geographic range.—The synonymy of *Spirifera simplex* given above is limited to the type area sensu lato (south-western England) and to the works related to the problem of the genus *Pyramidalia*. The following discussion of localities is also limited to south-western England. Both Phillips (1841) and Davidson (1864) quote this species solely from Newton Bushel (= Wolborough) and Plymouth.

According to museum labels, other localities include Torquay, Lummaton near Torquay, and "Port Stephens". As there is no such place name as Port Stephens in south-western England, one may suppose it refers to St Stephens by Saltash situated just opposite Plymouth on the western side of the Tamar; St Stephen-in-Brannel near St Austell, and St Stephen-by-Launceston are less likely. Probably the age of all the above-mentioned localities is Givetian. Whidborne (1893) seems right in qualifying this species as "rather rare".

Methodological comments

Schrödl and Haszprunar (2016) proposed an amendment of the rules of the zoological nomenclature consisting in adopting a procedure similar to epitypification of the botanical nomenclature (ICN, Art. 9.8). An epitype (notion introduced in the botanical nomenclature by Greuter et al. 1994) is an additional specimen (i.e., not belonging to the original material; not necessarily topotypic) that can be introduced when "all original material associated with a (…) name is demonstrably ambiguous and cannot be critically identified for purposes of the precise application of the name to a taxon" (Turland 2013: 61). Problems related to epitypification were discussed by Hyde and Zhang (2008) who concluded advantages of this procedure were greater than disadvantages.

It is worth noting that the method adopted in the present work is much alike epitypification. The diagnostic characters of a brachiopod genus (anatomy, microstructure of the shell) could not be checked on specimens belonging to the type series, so a specimen which is most probably (but not beyond all doubts) topotypic has been selected and studied according to standard modern methods. It has thus become a de facto epitype. A comparable procedure is not unusual in palaeontology, so formalisation of such an approach by the ICZN seems desirable.

An example of a problem that might be easily solved if the notion of epitypes were inserted into the ICZN is the long-standing controversy on the well-known and widely reported Devonian brachiopod *Athyris concentrica* (von Buch, 1834). The type series of this species consists of brachiopods belonging to several genera, so Alvarez et al. (1996) selected a "neotype" conforming to the original description and possessing precise locality data. Grunt and Weyer (2002) were right in pointing out that a neotype cannot be selected unless any specimen belonging to the type series is unavailable (ICZN, Art. 75.1). However, Alvarez and Brunton (2005) responded that Grunt and Weyer (2002), when selecting a lectotype for the discussed species differing from the original description, acted against the Recommendation 74A of the ICZN in failing to "act consistently with (...) previously accepted taxonomic restrictions". A detailed reply by Grunt and Weyer (2016) ended with the sentence "Finally this problem could be solved by the plenary power of the Commission of ICZN" (Grunt and Weyer 2016: 620). As of 2019, no consensus on this matter seems to have been reached. The possibility of designating the alleged neotype of *Athyris concentrica* as the interpretative epitype would be a simple solution satisfying both the formal requirements and the necessity of having a precisely localised reference specimen in order to restrict the application of the name. A universal solution probably does not exist, but epitypification may be recommended at least in some cases.

Conclusions

Spirifera simplex Phillips, 1841 is lectotypified with GSM 6915 as the lectotype. This specimen comes from the Givetian (upper Middle Devonian; *Maenioceras molarium* Zone) of Wolborough quarry near Newton Abbot (Devon). Internal characters and microstructure of the shell are studied on the specimen NHMUK PI B 2807 from the same quarry.

Spirifera simplex, the type species of *Pyramidalia* Nalivkin, 1947, has an impunctate shell, next to other diagnostic characters of the order, wherefore it belongs to the order Spiriferida. The interpretation of *Pyramidalia* as a spiriferinide given in both editions of the *Treatise of Invertebrate Paleontology—Brachiopoda*, must thus be rejected.

Morphology and internal structures of *Spirifera simplex* do not show any significant differences from those of *Thomasaria* Stainbrook, 1945. *Pyramidalia* is confirmed as a junior subjective synonym of *Thomasaria*, as proposed first by Baliński (1979).

The procedure adopted in the present work is equivalent to epitypification in use under the ICN. Such a modus operandi is not rare in palaeontology, so formalisation of this procedure under the ICZN seems desirable.

Acknowledgements

This study could not be completed without help of several collection curators and staff of the following institutions: Louise Neep, Paul J. Shepherd, and Simon J. Harris (all GSM); the late Howard Brunton, Sarah Long and Zoë Hughes (NHMUK); Patrick N. Wyse Jackson (TCD); Derek Siveter (OUMNH); Matt Riley (SM). Ulrich Jansen (Senckenberg, Frankfurt am Main, Germany) and an anonymous reviewer commented on an earlier version of the paper. The research was supported by the National Science Centre, Poland (grant 2016/23/B/ST10/02744 to AB).

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