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KYRTATRYPA PAULI SP. NOV., A KEY BRACHIOPOD SPECIES OF POST-TAGHANIC RECOVERY FAUNAS IN THE MIDDLE DEVONIAN (GIVETIAN) OF THE HOLY CROSS MOUNTAINS, POLAND

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Abstract: *Kyrtatrypa pauli* Halamski and Baliński, sp. nov. is described from two late Middle to Late Givetian (Middle Devonian) localities in the Holy Cross Mountains, Poland. The type locality is at Błonia Sierżawskie, near Świętomarz, in the Northern (Łysogóry) Region, whereas the other locality is at Laskowa, in the Kostomłoty Transitional Zone. The internal features of the new species, investigated by the method of serial sections, are fully concordant with those of *K. culminigera* Struve, 1966 (the type species); *K. pauli* sp. nov. differs in the overall smaller convexity of its shell. New palynological data on the type locality of Błonia Sierżawskie indicate that it belongs to the Ex3 subzone of the Ex Miospore Zone. In contrast to the currently accepted schemes, these strata therefore belong to the Nieczulice Beds and not to the Skały Formation; accordingly, their rich fauna represents a post-Taghanic recovery biota, of which *K. pauli* sp. nov. is a key element.

Key words: Rhynchonelliformea, Atrypida, Taghanic Event, palaeoecology, ecosystem recovery, palynostratigraphy.

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INTRODUCTION

General context and purpose of the present work

Brachiopods were a major group of Devonian marine life, so the study of them is a paramount part of the investigation of geological events affecting the biosphere. The replacement of brachiopod faunas in the later part of the Givetian age was among the first observations that led to the recognition of the Taghanic event of worldwide significance (e.g., Johnson, 1970; Aboussalam, 2003; Zambito *et al.*, 2012, 2016). Preliminary observations (Halamski, 2018) indicated major differences between the successions of brachiopod faunas in the classical area of New York State and in the Holy Cross Mountains (Central Poland; Fig. 1A), which led to proposing a long-term research programme on the Taghanic Event in the Polish part of the Laurussian shelf. The systematic palaeontology and palaeoecology of pre-Taghanic faunas were investigated in detail in the Miłoszów section (Halamski, 2022; Halamski *et al.*, 2022a; Baliński and Halamski, 2023), whereas the present contribution is the first to deal with post-Taghanic faunas. The aims are as follows: (i) to describe formally a new species, belonging to the genus *Kyrtatrypa* Struve, 1966; (ii) to overview its palaeoecology in the context of post-Taghanic recovery faunas; (iii) to analyse its stratigraphic distribution, including in particular (iv) the new palynological dating of an important Givetian succession at Błonia Sierżawskie, near Świętomarz, modifying its currently accepted age.

Institutional abbreviations. GIUS – Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia, Sosnowiec, Poland; L – Natural History Museum, National Academy of Sciences of Ukraine, Lviv (formerly Dzieduszycki Museum, Lwów), Ukraine; ZPAL – Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland. The conventions for inventory numbers follow Halamski (2009, p. 48) and Baliński and Halamski (2023, p. 6).

History of research

Devonian outcrops along the Psarka River, between Świętomarz and Śniadka, were first noted in print by Schneider (1829) and Pusch (1833, p. 100), and the earliest lithostratigraphic scheme was given by Zeuschner (1866;

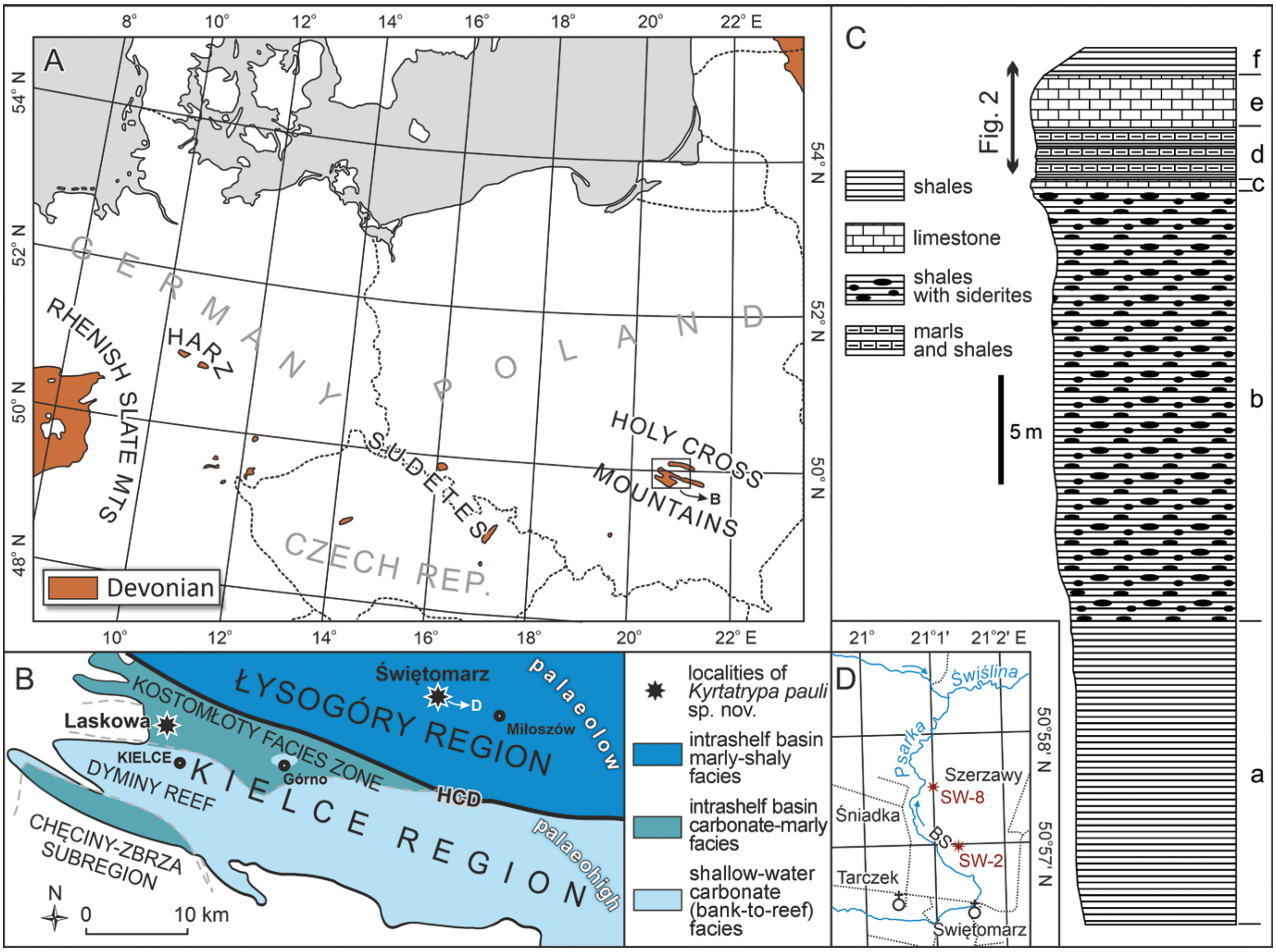

Fig. 1. Geographical and geological context of the present study. **A.** Map of Central Europe showing political boundaries and Devonian outcrops (after Asch, 2005). **B.** Palaeogeography of the Holy Cross Mountains in the Givetian (after Racki, 1993 and Baliński *et al.*, 2016; modified from Halamski *et al.*, 2022) with the presumed locations of the sites of *Kyrtatrypa pauli* sp. nov. and other sites mentioned in the text. **C.** Lithostratigraphy of the type outcrop of *Kyrtatrypa pauli* sp. nov. (SW-2, Świętomarz–Śniadka section). Based in part on the data by Kłossowski (1976), redrawn from Halamski (2004). **D.** Topographic map of the Psarka valley between Świętomarz and Śniadka, showing main rivers, villages (with churches, if present), the Błonia Sierżawskie meadow (abridged BS), main roads, and the two outcrops mentioned in the text.

Zejszner, 1867). The Świętomarz–Śniadka section was investigated in detail by Gürich (1896), Sobolew (1904, 1909), and Czarnocki (1950; see Racki *et al.*, 2022, pp. 428–430 for a comprehensive historical account). The atrypide brachiopod, commonly occurring at Błonia Sierżawskie (outcrop SW-2 *sensu* Halamski, 2004; see below), was described under the catch-all name *Atrypa reticularis* Linnaeus, 1758 (Sobolew, 1909, p. 115). This name in fact refers to a Silurian (Gorstian, Ludlow) species (Alexander, 1949; Copper, 2004), but for many years was used indiscriminately for Silurian to Devonian atrypides, belonging to many genera and even several families (Copper, 2004). Later on, the Świętomarz–Śniadka section was investigated by Bednarczyk (1955), Kłossowski (1976, 1981, 1985), Malec (1988), and Halamski (1999, 2004), but most of their results remained unpublished. Filonowicz (1963, 1965, 1968) drew up a geological map. The only published paper to deal with the outcrop at Błonia Sierżawskie in some detail was a short contribution by Halamski and Segit (2006), who reported the discovery of a stringocephalid brachiopod. On that basis, they recognised the Givetian age of the strata. This had been uncertain, owing to their presumed assignment to the Eifelian–Givetian Skały Formation.

Devonian outcrops at Laskowa (Fig. 1B) were first described in detail by Racki *et al.* (1985), who included a cursory survey of the brachiopod fauna. Several studies, based in part on material from the Laskowa Quarry, have been published since that time, for example, on conodonts (Racki, 1985; Racki and Bultynck, 1993), trilobites (Chlupáč, 1993), tentaculites (Hajłasz, 1993), bryozoans (Morozova *et al.*, 2002), and mesophotic coral reefs (Zapalski *et al.*, 2017; Zatoń *et al.*, 2018). Individual brachiopod species were described separately (Godefroid and Racki, 1990; Sartenaer and Racki, 1992; Baliński, 1995), as in the present contribution; a comprehensive study of the brachiopods from Laskowa is at present in progress.

The palynology of the Middle Devonian of the Łysogóry Region (Fig. 1B) is insufficiently recognised. Fijałkowska-Mader and Malec (2011) and Filipiak (2011) studied the deposits of ages, ranging from the Pragian (Lower Devonian) to the Eifelian. The detailed palynostratigraphical description of the Skały Formation and the lower part of the Nieczulice Beds was carried out by Malec and Turnau (1997). A study that involved also palynofacies was conducted by Turnau and Racki (1999). The latest documentation of the Givetian palynology of the northern part of the Holy Cross Mountains was carried out by Kondas *et al.* (2022) and Kondas and Filipiak (2022a).

Initial modified stratigraphic conclusions from preliminary analyses of the strata, cropping out at Błonia Sierżawskie, were reported in advance by Halamski *et al.* (2022a) and Racki *et al.* (2022). The present paper comprises the analytical part and detailed palynostratigraphic analysis of the study.

GEOLOGY

The Holy Cross Mountains (further abridged HCM; in Polish: Góry Świętokrzyskie) are a range of hills, made up of Palaeozoic sediments and situated in central Poland (Fig. 1A). The Palaeozoic inlier of the HCM is divided into two major tectonic and facies regions (Szulczewski, 1995; Lamarche *et al.*, 1999), the Łysogóry Region or Northern HCM (NHCM) and the Kielce Region or Southern HCM (SCHM; Niezabitowska and Szaniawski, 2023; see Fig. 1B). The latter corresponds to generally shallower depositional environments, whereas the rocks of the former originated in deeper parts of the Rheic Ocean. In the Devonian, the area discussed was located on the southern shelf of Euramerica (Laurussia; see e.g., Golonka *et al.*, 2019). The material described here was found in two localities, Błonia Sierżawskie in NHCM and Laskowa in the Kostomłoty Zone (part of the SCHM, transitional with respect to the NHCM; see Fig. 1B).

Following Becker *et al.* (2020) and Halamski *et al.* (2022a), the Givetian substages are spelt with capital letters (Early/Lower Givetian and so on).

Błonia Sierżawskie is a toponym, referring to a meadow, situated in the Psarka valley, north of the village of Świętomarz and south-east of the village of Śniadka (Fig. 1D, abridged BS). The outcrop at Błonia Sierżawskie (SW-2 *sensu* Halamski 2004, 2009), located at about 50°56′59″N, 21°1′2″E, consists of a low cliff (up to 2 m high) and exposures along a dirt road, leading to Szerzawy (formerly Sierżawy). Starting in the 2000s, the area has become partly forested, so outcrop quality has significantly decreased; the present description is based in part on the data, collected by Kłossowski (1976), with minor additions by Halamski (1999, 2004) and Halamski and Segit (2006). The brachiopod material was collected by the late Andrzej Piotrowski in the 1970s and by A. T. Halamski, mostly between 1997 and 2003, with minor additions up to 2023. Samples for palynology were collected by M. Kondas in 2021 and 2022.

The lithological sequence at Błonia Sierżawskie (Figs 1C, 2), transected both below and above by faults (Kłossowski, 1976), is over 25 m thick, with shales both at the base (units a, b *sensu* Halamski and Segit, 2006, fig. 1D) and at the top (unit f). However, only the package of marls (unit d) and limestone (unit c, lower; unit e, upper, cliff-forming) in the middle part of the succession contains a rich fauna, with over 25 species of brachiopods, including in particular *Kyrtatrypa pauli* sp. nov. (Sobolew, 1909; Bednarczyk, 1955; Kłossowski, 1976; Halamski, 2004).

Owing to the lack of conodonts (Kłossowski, 1976), the dating of this outcrop was contentious. On account of the rich fauna, the exposed strata were considered to belong to the Skały Formation (Filonowicz, 1968). Halamski and Segit (2006) proved their Givetian age, owing to the occurrence of Stringocephalinae gen. et sp. indet. Only recently, the palynological data allowed these strata to be dated to the Ex3 subzone and thus to interpret them as the Nieczulice Beds; the details of this dating are provided in the present paper.

Laskowa was formerly a village in its own right and now forms a part of Kostomłoty Drugie (Rymut, 2005, p. 21). The large active Laskowa (also called Laskowa Góra or Laskowa Hill) Quarry provides outcrops of Givetian limestone, marls, and dolomite (Racki *et al.*, 1985). The brachiopod and conodont material studied was collected by G. Racki and collaborators in the 1980s (see Racki *et al.*, 1985, p. 161 and fig. 2 for detailed location) and by A.T. Halamski and A. Baliński in 2022 (from the south-western part of the quarry, about 50°55′32″N, 20°32′16″E).

Kyrtatrypa pauli sp. nov. occurs in the Laskowa Góra Beds, a ca. 4–5 m a thick horizon of limestone with numerous marl intercalations, containing a rich assemblage of brachiopods, including, among others, representatives of the genera *Spinatrypina*, *Warrenella*, and *Echinocoelia* (A. T. Halamski, A. Baliński, G. Racki unpublished data). The Laskowa Góra Beds can be dated as the *varcus* to *disparilis* conodont zones (Racki *et al.*, 1985), with the diversified B-3 brachiopod assemblage (with *Kyrtatrypa*) being more precisely dated as the undivided *hermanni* to *disparilis* chrones (Racki, 1985).

PALYNOSTRATIGRAPHY

The palynoflora assemblage obtained is similar to the microflora of Eastern Europe to some extent, but nonetheless with a few distinctive characteristics. For that reason, the most precise zonation for the palynostratigraphy of the study area is that of Avkhimovitch *et al.* (1993), with a modified variant proposed by Turnau (1996, 2008). The zonation by Turnau (1996, 2008) has been successfully applied for the investigation of the Middle and Upper Devonian deposits of the HCM, Radom-Lublin Area and Western Pomerania (e.g., Turnau, 1996, 2007, 2008, 2011; Malec and Turnau, 1997; Turnau and Racki, 1999; Kondas and Filipiak, 2021, 2022a).

The lower and upper boundaries of the "*Geminospora*" *extensa* Miospore Zone (Ex) by Avkhimovitch *et al.* (1993)

and Turnau (1996, 2008) correspond, but the divisions of the zone into subzones differ. The local Ex Zone *sensu* Turnau (1996, 2008) consists of three subzones: Ex1, Ex2 and Ex3. The base of the Ex1 subzone is defined by the first appearance of *Geminospora lemurata*. This palynological event indicates the approximate position of the Eifelian–Givetian boundary (Loboziak *et al*., 1991). The base of the Ex2 subzone is marked by the first appearance of *Chelinospora concinna*. The lower boundary of the uppermost Ex3 subzone of Ex Zone is determined by the first appearance of *Samarisporites triangulatus*. A typical feature of this zone is the presence of *Kraeuselisporites spinutissimus* and *Geminospora decora* (Turnau, 2007, 2008, 2011). The Ex2–Ex3 boundary is located within the *ansatus* conodont Zone (Turnau and Narkiewicz, 2011). The last appearance of *Aneurospora extensa* indicates the lower boundary of the local *Geminospora aurita* Miospore Zone (abridged Aur; Turnau, 2007). According to Turnau (2007), other significant taxa that disappear on this boundary are: *Chelinospora concinna*, *Densosporites devonicus*,

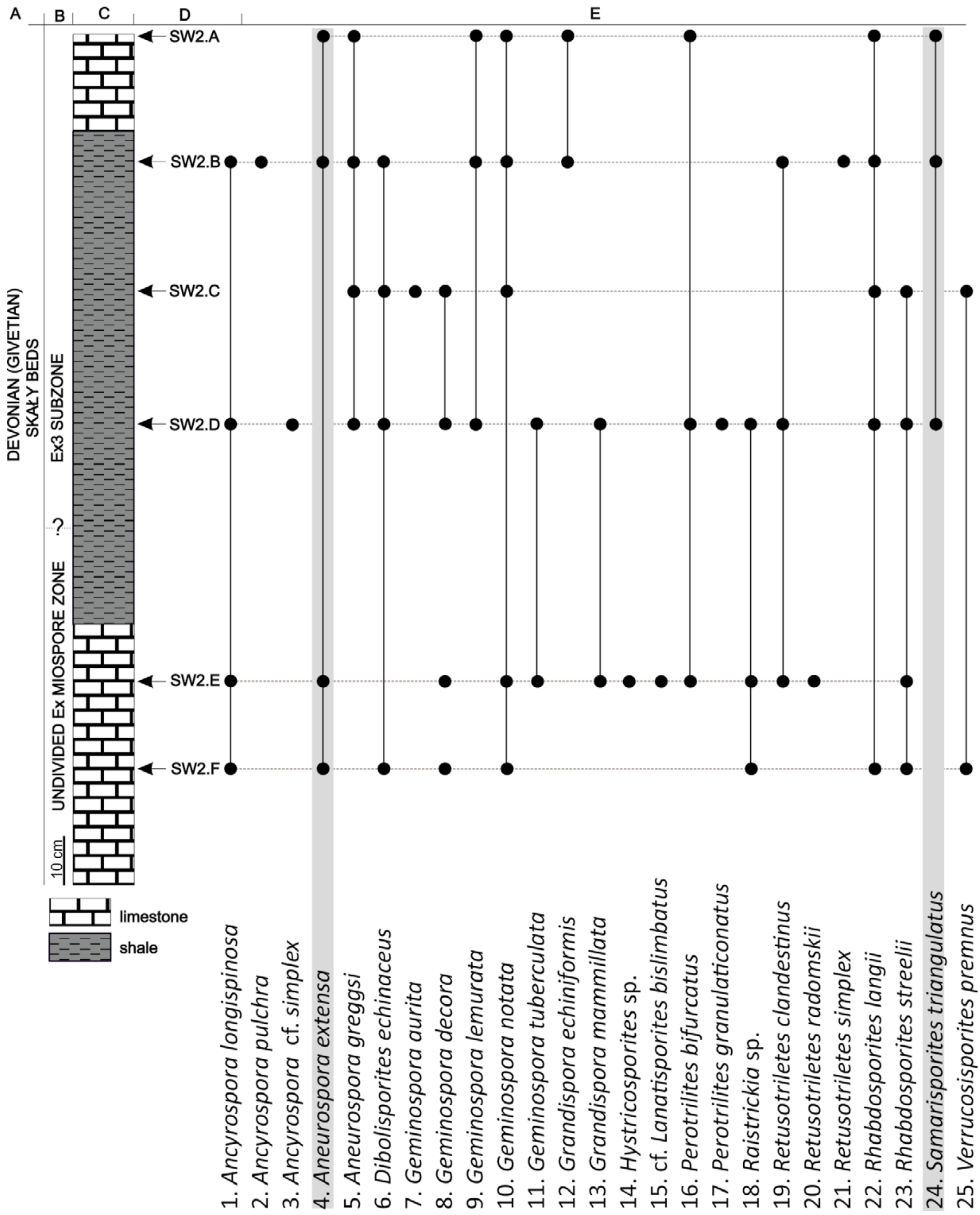

Fig. 2. Lithostratigraphy of the currently cropping out part of the section at Błonia Sierżawskie, near Świętomarz (SW-2 *sensu* Halamski, 2004, 2009; lithostratigraphic units c–e *sensu* Halamski and Segit, 2006; compare Fig. 1C) and occurrences of selected miospore taxa. A – lithostratigraphy, B – miospore zones, C – lithology, D – samples, E – miospore taxa. Index taxa are marked with grey colour.

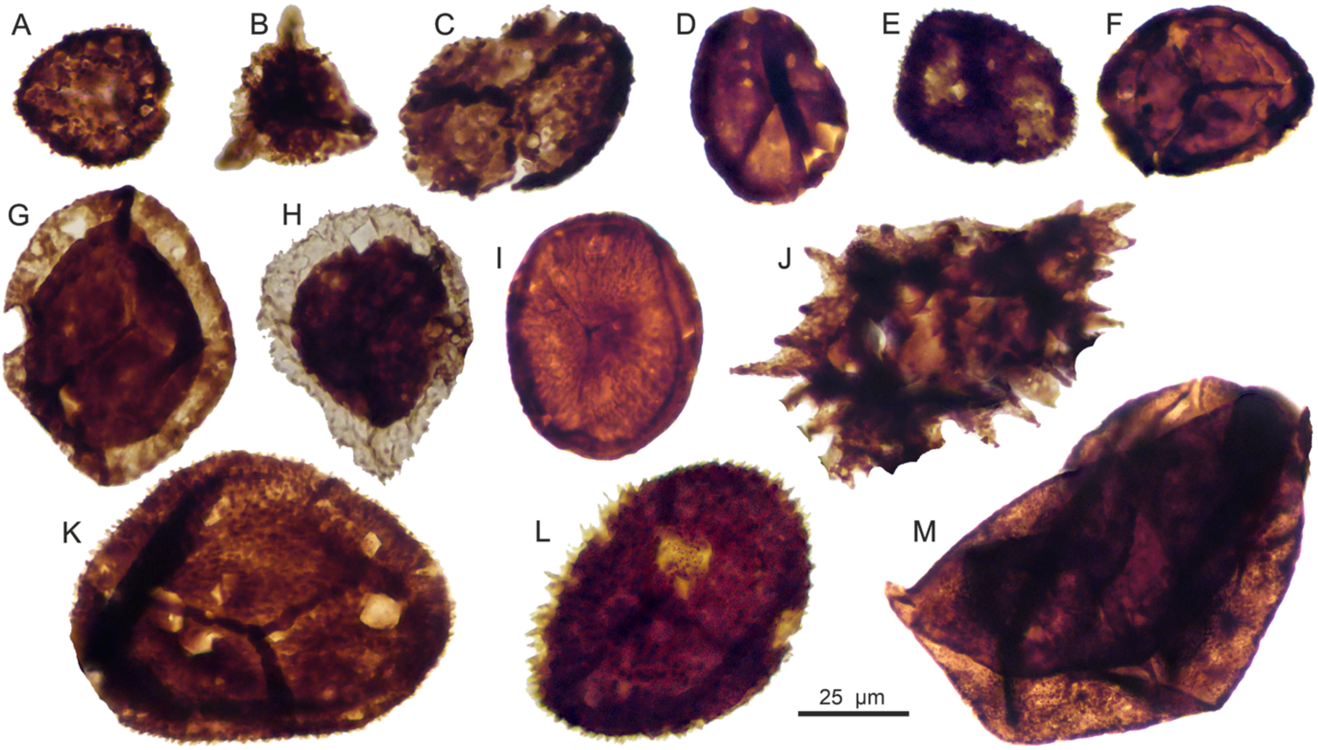

Fig. 3. Miospores obtained from the section SW-2 at Błonia Sierżawskie. **A.** *Aneurospora extensa* (Naumova) Turnau, 1986*,* sample SW2.A (EF: 35J1). **B.** *Samarisporites triangulatus* Allen, 1965*,* sample SW2.A (EF: 32N3). **C.** *Geminospora obtusispinosa* Turnau in Turnau & Racki, 1999, sample SW2.B (EF: 6T2). **D.** *Geminospora notata* (Naumova) Obukhovskaya in Avkhimovitch *et al.*, 1993*,* sample SW2.E (EF: 7M). **E.** *Geminospora decora* (Naumova) emend. Arkhangelskaya, 1985, sample SW2.E (EF: 7M1). **F.** *Geminospora aurita* Arkhangelskaya, 1987, sample SW2.A (EF: 37K2). **G.** *Rhabdosporites streelii* Marshall, 1996, sample SW2.C (EF: 8U1). **H.** *Grandispora echiniformis* Kedo, 1955, sample SW2.A (EF: 7D1). **I.** Unidentified miospore, sample SW2C (EF: 15X). **J.** *Ancyrospora* cf. *simplex* Guennel, 1963, sample SW2.D (EF: 31V2). **K, L.** *Dibolisporites echinaceus* (Eisenack) Richardson, 1965; samples SW2.B (EF: Q32) [K] and SW2.C (EF: 46R) [L]. **M.** *Rhabdosporites langii* (Eisenack) Richardson, 1960, sample SW2.B (EF: 8F2).

Geminospora decora, *G. tuberculata*, *Lanatisporites bislimbatus*, *Kraeuselisporites spinutissimus*, and *Rhabdosporites langii*.

During the present study, a currently accessible part of the section at Błonia Sierżawskie (SW-2 *sensu* Halamski, 2004) was studied for palynostratigraphy (Fig. 2). Six samples, taken from the lower limestone (unit c, two samples), marls (unit d, three samples), and the upper limestone (unit e, one sample), were macerated, using the standard palynological procedure with an HCl-HF-HCl acids combination (Wood *et al*., 1996; Riding, 2021). Each miospore specimen was tagged with England Finder (EF) coordinates. Slides and residues are housed at the Faculty of Natural Sciences, in Sosnowiec, Poland. The land microflora obtained was numerically abundant but relatively poorly diversified taxonomically (Fig. 3). The whole miospore assemblage was enriched in species of *Geminospora* and *Aneurospora*. *Aneurospora extensa*, a taxon important for biostratigraphy, was documented in all of the samples studied, except SW2.D (Fig. 2). The assemblage was characterised also by the presence of other Givetian taxa, such as *Geminospora decora*, *G. notata*, *G. tuberculata*, *Lanatisporites bislimbatus*, *Rhabdosporites langii*, and, according to Avkhimovitch *et al*. (1993), the first four taxa mentioned are typical for the Ex Miospore Zone (see Appendix I for the full list of taxa). Samples SW2.A, SW2.B, and SW2.D contained specimens of *Samarisporites triangulatus*, the index miospore for the Ex3 subzone. Thus, the age of the rock interval studied is established as Ex, and its upper part (samples SW2.A–SW2.D) is included in the Ex3 subzone.

In the study area, the Ex2–Ex3 boundary is placed within the basal part of the Nieczulice Beds (Turnau and Racki, 1999). For that reason, the rock interval analysed should be considered as belonging to the Nieczulice Beds.

BRACHIOPOD SYSTEMATIC PALAEONTOLOGY

Order Atrypida Rzhonsnitskaya, 1960
Suborder Atrypidina Moore, 1952
Family Atrypidae Gill, 1871
Subfamily Atrypinae Gill, 1871
Genus *Kyrtatrypa* Struve, 1966

Type species: *Atrypa* (*Kyrtatrypa*) *culminigera* Struve, 1966; Hillesheim, Eifel; Junkerberg Formation, middle Eifelian.

Species assigned: The following species are or were considered to be representatives of *Kyrtatrypa*. If the taxonomic interpretation is based on previous authors' conclusions and the published descriptions and illustrations are insufficient to confirm such a conclusion, this is commented on as '*fide*…' (Latin: following the authority of…). The species are listed below in stratigraphic order.

Atrypa thomsonensis Talent, 1955; Victoria; Ludlow–Gedinnian [*fide* Struve, 1966];

Anulatrypa anulata Havlíček, 1987; Bohemia; Lochkovian [*fide* Copper, 2004];

Anulatrypa hyperanulata Havlíček, 1987; Bohemia; Zlichovian [*fide* Copper, 2004];

Atrypa exquisita Johnson, 1975; Arctic Canada; Gedinnian [*fide* Copper, 1978];

Kyrtatrypa balda Havlíček, 1987; Bohemia; Pragian;

Kyrtatrypa cf. *balda sensu* Halamski & Baliński, 2018; Morocco; Emsian;

Kyrtatrypa canalibalda Havlíček, 1987; Bohemia and Carnic Alps (Latz, 1992); Pragian;

Kyrtatrypa sp. *sensu* Havlíček, 1987; Bohemia; Eifelian;

Kyrtatrypa sp. nov., Skały; Upper Eifelian;

Kyrtatrypa? sp. *sensu* Halamski *et al.*, 2022b; Jbel Issoumour, Anti-Atlas, Morocco; upper Eifelian to Givetian;

Kyrtatrypa pauli sp. n.; Świętomarz; upper Middle Givetian (here described);

Atrypa bentonensis Stainbrook, 1938; USA; Frasnian? [*fide* Struve, 1966];

Atrypa teicherti Coleman, 1951; Australia; Frasnian [assigned to *Kyrtatrypa* by Grey (1978, p. 13), by Ma *et al.* (2006, p. 798), and by Halamski and Baliński (2018, p. 139); tentatively to *Kyrtatrypa* by Halamski (2013, p. 295)];

Kyrtatrypa barnimi Halamski, 2013; Sudetes; upper Frasnian.

Kyrtatrypa pauli Halamski and Baliński sp. nov.
(Figs 4–7)

p	1872	*Atrypa reticularis* Dalman – Trejdosevič, p. 35.
p	1875	*Atrypa reticularis* Dalman – Trejdosiewicz, p. 19.
p	1904	*Atrypa reticularis* L. – Sobolew, p. 68.
p	1909	*Atrypa reticularis* L. – Sobolew, p. 115.
vp	1909	*Atrypa reticularis* L. – Siemiradzki, p. 85.
vp	1922	*Atrypa reticularis* L. – Siemiradzki, p. 21.
	1985	*Atryparia* (?) – Racki *et al.*, p. 166, pl. 8, fig. 4.
v.	2004	*Kyrtatrypa pauli* sp. n. – Halamski, pp. 169–172, text-figs 31–33, pl. 6, fig. 8, pl. 7, figs 1–4 [unpublished work].
v.	2005	*Kyrtatrypa* sp. – Zapalski, pp. 677, 680, 682, figs 3, 4.
v.	2008	*Kyrtatrypa* sp. n. 2 – Halamski, p. 90.
v.	2013	*Kyrtatrypa* n. sp. (*K. pauli*, *nomen nudum*, Halamski 2004) – Halamski, p. 295.
v.	2018	*Kyrtatrypa* sp. n. 2 (= *Kyrtatrypa pauli* nomen nudum sensu Halamski 2004) – Halamski and Baliński, p. 139

Type material: Holotype ZPAL Bp 48/32/1/1 (leg. A. Piotrowski), illustrated herein (Figs 4U–Y; 5C, E, F). Over sixty variously preserved articulated shells from the outcrop SW-2, ZPAL Bp 48/32/1 (topotypic paratypes). Eight specimens from Sitka (possibly outcrop SW-8c *sensu* Halamski, 2004; L PZ-D.959, *olim* 696; L PZ-D.926, *olim* 696; non-topotypic paratypes). Over forty variously preserved shells and single dorsal and ventral valves from Laskowa (GIUS 4-296/Bp; ZPAL 86/1; non-topotypic paratypes).

Nomenclatural act: The nomenclatural act has been registered in ZooBank under urn:lsid:zoobank.org:act:047C594C-40AB-41D1-AD45-5D1B8047F94E.

Locus typicus: Błonia Sierżawskie, near Świętomarz, outcrop SW-2 *sensu* Halamski (2004, 2009).

Stratum typicum: Nieczulice beds, upper Middle Givetian.

Etymology: In honour of Paul Copper (formerly Laurentian University, Sudbury, Canada), in recognition of his contribution to the study of the atrypide brachiopods.

Diagnosis: Moderately large to large atrypine, possessing a weakly convex ventral valve, solid teeth, uniplicate anterior commissure, with moderately broad but often relatively high tongue, frills, and rather coarse radial ornamentation.

Description: Shell shield-shaped to rounded in outline, strongly dorsibiconvex, typically about 20–26 mm long, 19–26 mm wide, and 10–16 mm thick at Świętomarz, 28–39 mm long (up to over 50 mm long if frills are preserved), 26–40 mm wide, and 17–24 mm thick at Laskowa; approximately as long as wide [width-to-length ratio (0.87–)0.96–1.05(–1.13), mean 1.00, $N = 49$], usually markedly convex [thickness-to-length ratio (0.36–)0.54–0.66(–0.79), mean 0.60; $N = 46$]. Maximum width about the posterior margin (Fig. 4Z), about mid-length (Fig. 4A) or between them. Anterior commissure mostly uniplicate, more rarely rectimarginate (often so in small specimens, rarely in larger ones); tongue moderately wide, making about half of the width of the shell, but often high, sometimes as high as wide, approximately subtrapezoidal. Ventral valve moderately convex in umbonal region, nearly flat on flanks; frills (Figs 4H, 5D; Racki *et al.*, 1985, pl. 8, fig. 4), if preserved, up to 15 mm long, bent outwards, so the ventral valve peripherally acquires a concave appearance; beak small, hypercline, appressed to the dorsal umbo (Fig. 5A–C, E). Dorsal valve arched in anterior view, quite frequently high; beak hidden by the ventral valve (Fig. 5C).

Ornament (Fig. 5F) of radial ribs, at Laskowa (4–)5–6(–7) per 5 mm at anterior margin, ca. 4 per 5 mm on frills, at Świętomarz 5–7(–8) per 5 mm at anterior margin and ca. 6 per 5 mm on frills. New ribs arising mostly by bifurcation on the ventral valve and by intercalation on the dorsal one.

Internally, shell wall thick umbonally. Interior of ventral valve with thick pedicle callist well developed, in the sectioned subadult shell with tendency to form pedicle collar (Fig. 7A, section at 0.55 mm); dental nuclei barely noticeable in the sectioned subadult shell and absent in the larger specimens (Fig. 7B, C); teeth thick, solid, dorso-medial in direction, with long accessory lateral lobes. Ventral muscle field: large, flabellate diductor scars and smaller, more posteriorly located, narrowly lanceolate adductor scars (Fig. 5I, J).

Dorsal interior with a small cardinal process lining the cardinal pit and partly also the inner socket ridges; sockets with low middle socket ridge (*sensu* Copper, 1967b, pp. 1176, 1180, text-fig. 1, pl. 155, fig. 4; 2002, p. 1382, figs 932, 933); hinge plates strong; median myophragm low

Fig. 4. General external morphology of the upper Middle to Upper Givetian atrypine *Kyrtatrypa pauli* Halamski and Baliński, sp. nov. Articulated shells from the type locality at Błonia Sierżawskie (A–O, U–Y) and Laskowa (P–T, Z–DD) in dorsal, ventral, lateral, anterior, and posterior views. **A–E, F–J, K–O.** Paratypes ZPAL 48/32/1/28, 36, 37 (36 = 5A,D; 37 = 5B). **P–T.** Paratype GIUS 4-296/Bp-9. **U–Y.** Holotype ZPAL 48/32/1/1 (see also Fig. 5C, E, F). **Z–DD.** Paratype GIUS 4-296/Bp-2.

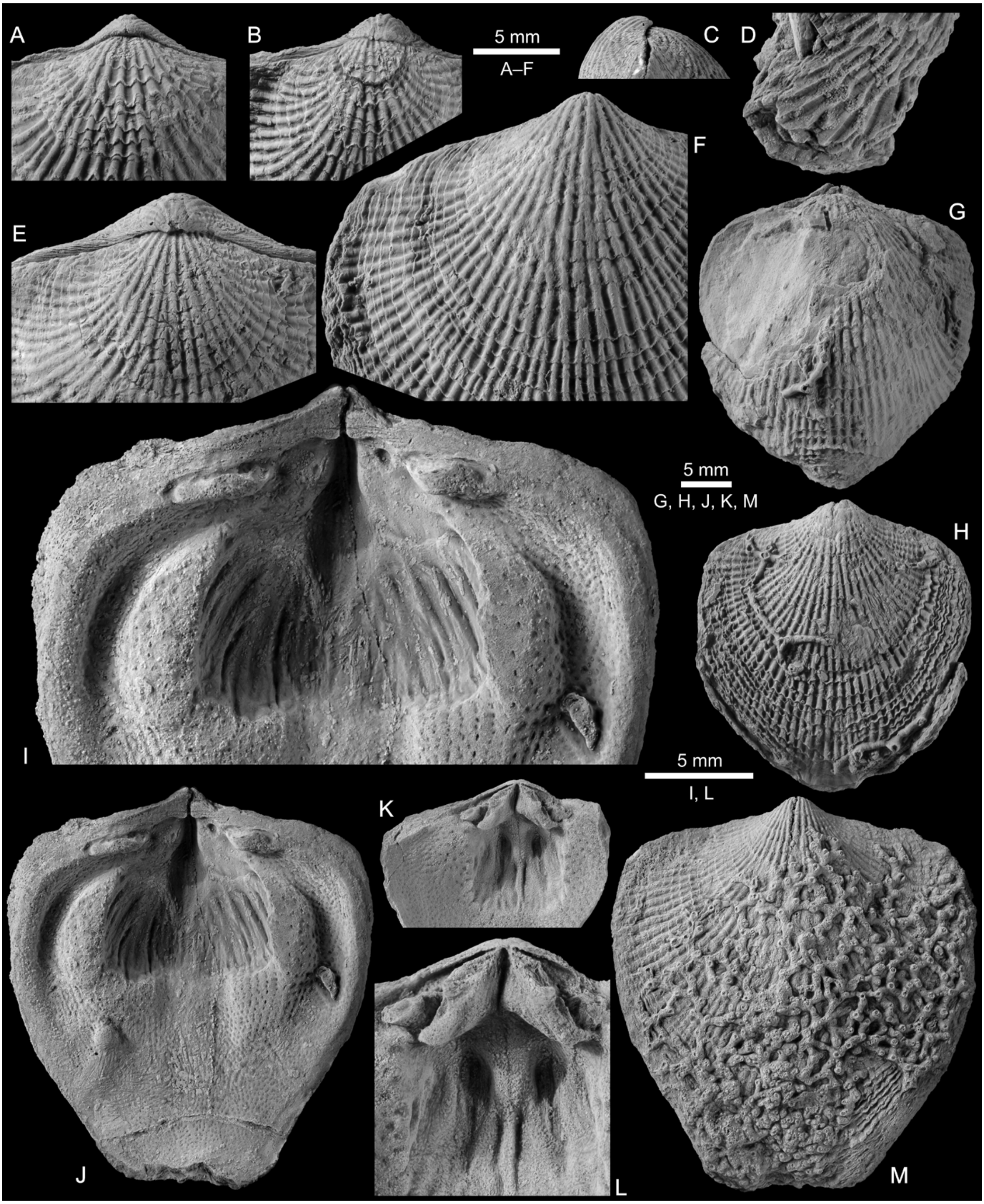

Fig. 5. Morphological details of the upper Middle to Upper Givetian atrypine *Kyrtatrypa pauli* Halamski and Baliński, sp. nov. from the type locality at Błonia Sierżawskie (A–H) and Laskowa (I–M). **A, B.** Articulated shells ZPAL 48/32/1/36, 37, enlargements of the ventral umbo in postero-dorsal view (see also Fig. 4F, K). **C, E, F.** Articulated shell ZPAL 48/32/1/1 (holotype; see also Fig. 4U–Y): enlargements of the umbones in lateral view (C), of the ventral umbo in postero-dorsal view (E), and of ventral ornamentation (F). **D.** Enlargement of frills in lateral view of the shell ZPAL 48/32/1/36 (see also Fig. 4F–J). **G, H.** Articulated shell ZPAL 48/32/1/38, overgrown by auloporid tabulate corals on both dorsal (G) and ventral (H) valves. **I, J, M.** Ventral valve GIUS 4-296/Bp-1: exterior, overgrown by auloporid tabulate corals (M), interior (J), enlargement of muscle scars (I). **K, L.** Fragmentary dorsal interior GIUS 4-296/Bp-8: partial view (L) and enlargement of muscle scars (K).

to high posteriorly, wide; small crural bases; crura laterally directed, fibrous; spiralia and jugal processes not preserved. Dorsal muscle field: deeply impressed adductor scars medially separated by a wide median ridge (Fig. 5 K, L).

Remarks: *Kyrtatrypa pauli* was first described by Halamski (2004) in an unpublished Ph.D.; as a consequence, no nomenclatural act was proposed at that time. However, this name was cited twice as a *nomen nudum* (Halamski, 2013; Halamski and Baliński, 2018). In the present paper this name is made available for the first time.

The two samples sufficiently numerous for biometric analysis, from the type locality near Świętomarz and from Laskowa, are quite different, if absolute sizes are considered: the former sample contains much smaller shells. Conversely, their relative proportions are nearly identical (Fig. 6). A detailed comparison is given in Table 1. The ornamentation of the Świętomarz sample is also slightly finer (see above), which may be related to the generally smaller sizes of the shells.

This species is included within *Kyrtatrypa* Struve, 1966, on the basis of internal characteristics, the uniplicate anterior commissure, and the presence of frills. However, it markedly differs from the type species of the genus *Kyrtatrypa*, namely *K. culminigera* (Struve, 1966), in the much smaller convexity of the ventral valve.

As far as the external form is concerned, the nearest form in the studied material is *Atrypa subtrigonalis* Biernat, 1964, from which the new species differs in its larger size and coarser ornamentation (see Baliński and Halamski, 2023). *Atryparia agricolae* Halamski and Baliński in Baliński *et al.*, 2016 is also similar in its strongly dorsibiconvex to convexoplane shell form and coarse ornamentation. Internal characteristics of both species preclude their assignment to the same genus as *K. pauli* sp. nov.

In none of the sectioned shells is the spiralium preserved; only the crura are left. Generally speaking, such a situation is not exceptional (for atrypides see, e.g., Halamski and Baliński, 2013, figs 20, 22, 24; 2018, figs 6, 10), insofar as these delicate structures are easily damaged or destroyed during the early stages of the preservation process (shell infill with sediment) or during diagenesis (Yuan *et al.*, 2021, p. 554).

Zejszner's collection from Sitka (L PZ-D.926, *olim* 696) includes *Kyrtatrypa pauli* sp. n. and *Spinatrypa*? sp.

Distribution: Holy Cross Mountains, Łysogóry Region, Świętomarz-Śniadka section, type outcrop SW-2 at Błonia Sierżawskie; Sitka (possibly outcrop SW-8c). Kostomłoty Zone: Laskowa.

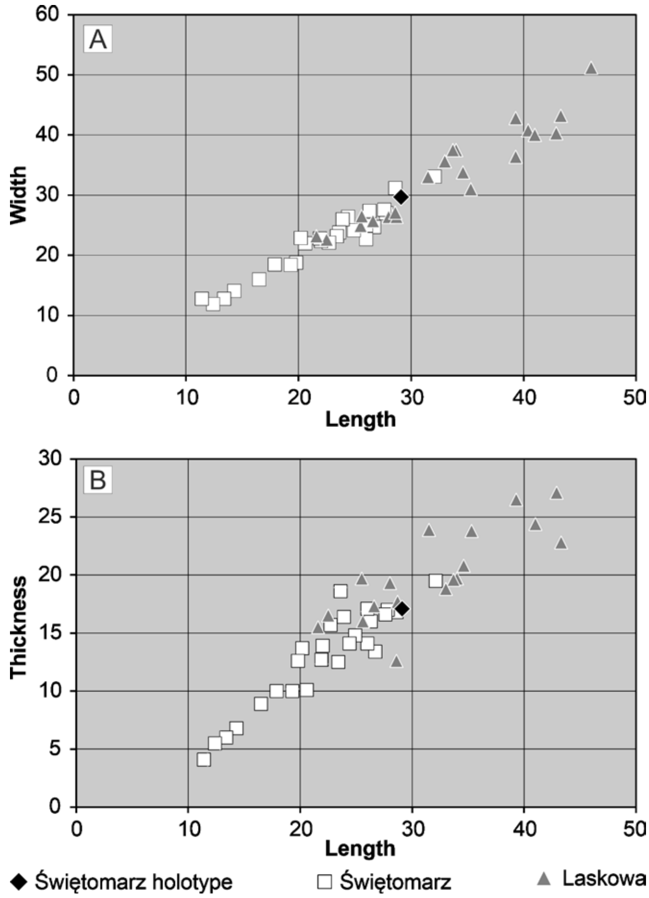

Fig. 6. Comparison of biometric characters of *Kyrtatrypa pauli* Halamski and Baliński, sp. nov. from the two studied samples (Błonia Sierżawskie and Laskowa). **A.** Width-to-length ratio. **B.** Thickness-to-length ratio.

Atrypa, *Planatrypa*, and *Kyrtatrypa*

Kyrtatrypa pauli sp. nov. is included into the genus *Kyrtatrypa* on account of frills, commissure, and internal characteristics, but on the other hand, its strong external similarity to the slightly older *Atrypa subtrigonalis* is noted (see above). The latter species was tentatively included

Table 1

Biometric comparison of samples of *Kyrtatrypa pauli* sp. nov. from Świętomarz and Laskowa.

Sample Measurements or ratios		Świętomarz		Laskowa	
		Value	*N*	Value	*N*
Measurements in mm	Width	(12–)19–26(–33)	28	(22–)26–40(–51)	21
	Length	(11–)20–26(–32)		(21–)28–39(–46)	
	Thickness	(4–)10–16(–20)		(12–)17–24(–27)	18
Ratios	Width-to-length	(0.87–)0.97–1.04(–1.13)		(0.88–)0.95–1.07(–1.11)	21
	Thickness-to-length	(0.36–)0.53–0.62(–0.79)		(0.44–)0.58–0.69(–0.77)	18
	Tongue width-to-width	0–0.8		(0–)0.34–0.55(–0.70)	16

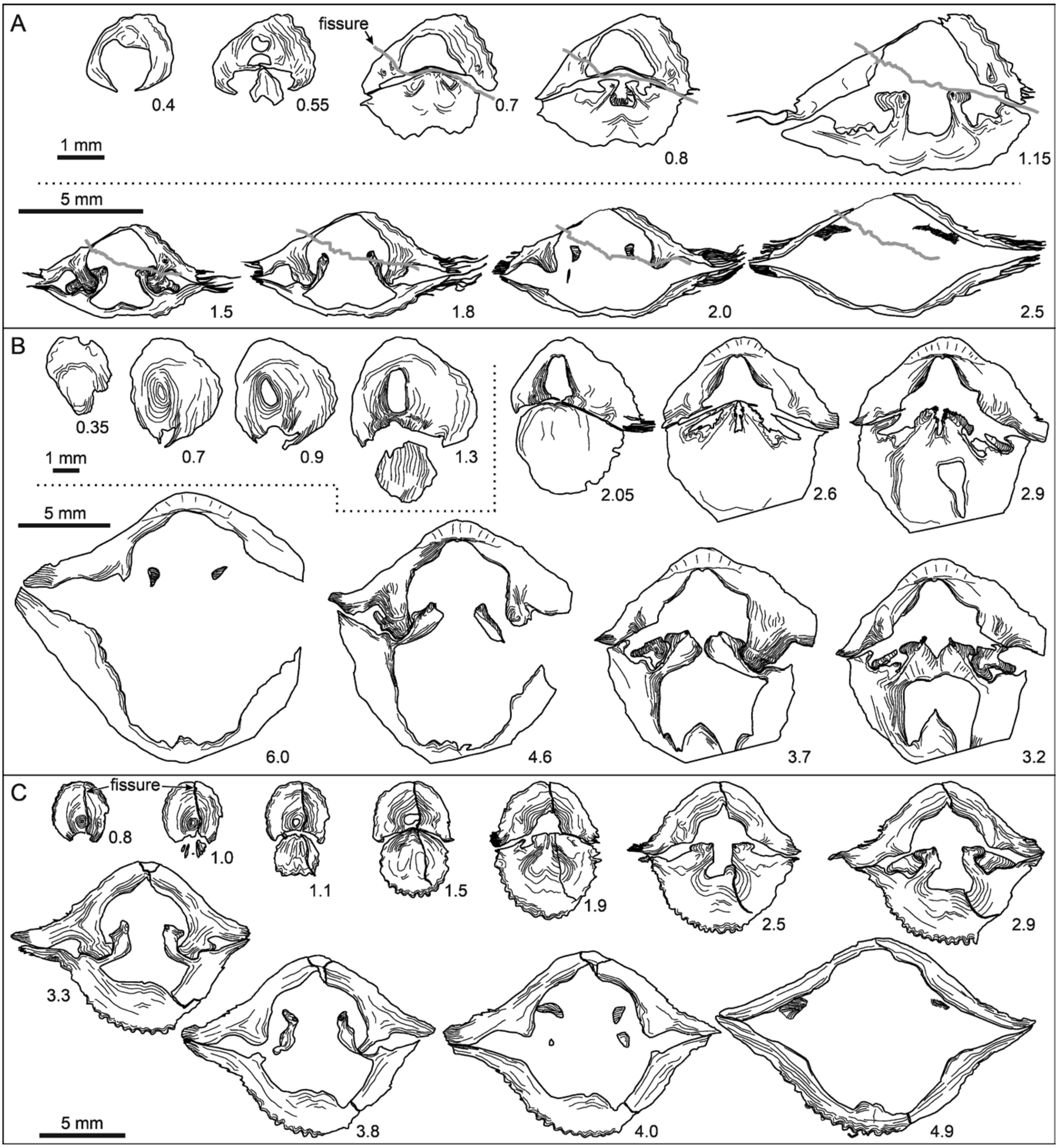

Fig. 7. Transverse serial sections of *Kyrtatrypa pauli* Halamski and Baliński, sp. nov. through the shells ZPAL 48/32/1/39 (A) and 48/32/1/40 (B) from the type locality at Błonia Sierżawskie, near Świętomarz, and GIUS 4-296/Bp-3 from Laskowa (C). Distances measured in millimetres from the tip of the ventral umbo.

in *Atrypa* (*Kyrtatrypa*), then treated as a subgenus, by Struve (1966). Recently Baliński and Halamski (2023, p. 40) included this species in *Atrypa*, noting its similarity to *Atrypa* (*Planatrypa*) *tirocinia* Copper, 1967 (see Copper, 1967a), but refraining from using any generic subdivisions of *Atrypa*, either *A.* (*Atrypa*) or *A.* (*Planatrypa*). Such a situation makes a few comments on the mutual relationships of a few closely related atrypid genera or subgenera desirable. The taxa concerned are *Atrypa* (considered as a genus by all modern authors), *Planatrypa* (subgenus in Struve, 1966; Copper, 2002, 2004; genus in Havlíček, 1987; Struve, 1992), and *Kyrtatrypa* (genus in Havlíček, 1987; Copper, 2002, 2004; subgenus in Struve, 1966; Copper, 1978). *Atryparia* Copper, 1966 is more different, with flattened costae and dental nuclei (Copper, 2002, pp. 1391–1392).

The most thorough discussion of the evolutionary relationships of Silurian and, to a lesser extent, Devonian representatives of the subfamily Atrypinae was given by Copper (2004, pp. 34–35), supplementing a necessarily condensed corresponding part of the *Treatise on Invertebrate Paleontology* (Copper, 2002, pp. 1389–1402). The above-mentioned results can be summarised as follows. The three taxa can be distinguished by their external and internal characteristics (Copper, 2002):

- *Atrypa* (*Atrypa*): pedicle valve with a weakly convex umbo, anterior commissure plicate, frills numerous, dental nuclei present;
- *Atrypa* (*Planatrypa*): pedicle valve flat, anterior commissure rectimarginate to weakly plicate, frills not known to be present, dental nuclei lacking;
- *Kyrtatrypa*: pedicle valve convex, anterior commissure plicate, wide frills, teeth solid.

An evolutionary interpretation is given by Copper (2004). *Atrypa* and *Kyrtatrypa* are considered to have evolved independently from either *Gotatrypa* or *Oglupes*. However, somewhat paradoxically, *Kyrtatrypa* (but neither *Gotatrypa* nor *Oglupes*) is listed among the genera that "could arguably be assigned as subgenera of *Atrypa*, if a much broader definition of the genus is used" (Copper, 2004, p. 35).

The type species of *A.* (*Atrypa*), *A.* (*Planatrypa*) and of *Kyrtatrypa*, namely *A.* (*A.*) *reticularis* s.s., *A.* (*P.*) *collega*, and *K. culminigera*, respectively, are indeed very different in external form and can be distinguished at the first view. However, *Atrypa confusa* and *Atrypa subtrigonalis* have the characteristics of both subgenera of *Atrypa* (Halamski and Baliński, 2013; Baliński and Halamski, 2023). *Kyrtatrypa pauli* resembles (*A.*) *Planatrypa* on account of its weakly convex pedicle valve and moderate plication of the commissure. Given the existence of such intermediate species, the question may be asked whether it is useful to retain these subdivisions or rather to admit a "broader definition" of the genus *Atrypa*, perhaps even without any subgenera. The situation in the Middle Devonian, with no clear distinction between *A.* (*Atrypa*), *A.* (*Planatrypa*), and *Kyrtatrypa*,would be an argument for the latter approach. On the contrary, the study of large Silurian material by Copper (2004) led him to opt for the former.

To sum up, a conservative approach is followed. *Kyrtatrypa* is retained as a separate genus, on the basis of its postulated independent evolutionary origin from *Gotatrypa* or *Oglupes* (*fide* Copper, 2004). It can be distinguished from *Atrypa* on the basis of internal characteristics, but as far as the external morphology is concerned, there can be almost complete overlap between *Atrypa* and *Kyrtatrypa* (see below for the discussion of the possible meaning of this observation). *Atrypa* (*Planatrypa*) is provisionally retained for a group of closely related species with a flat ventral valve, for example *A.* (*P.*) *depressa* Sobolew, 1904. *A. confusa* and *A. subtrigonalis* are considered as *incerti subgeneris* representatives of the genus *Atrypa*.

KYRTATRYPA PAULI WITHIN POST-TAGHANIC RECOVERY FAUNAS

Kyrtatrypa pauli sp. nov. occurs in two localities that are estimated to be approximately coeval on the basis of a synthesis of regional and local conodont and miospore biostratigraphic data as well as lithostratigraphy and event stratigraphy. This can be summarised as follows.

- In the Łysogóry Region, the investigated part of the section at Błonia Sierżawskie, near Świętomarz (SW-2 *sensu* Halamski, 2004), is dated to the Ex3 miospore subzone and belongs to the Nieczulice Beds, a lithostratigraphic unit underlain either by the Pokrzywianka Beds or the Skały Formation (eastern and western parts of the region, respectively; see Racki *et al.*, 2022, fig. 9).
- In the Kielce Region, and more precisely in the Kostomłoty Transitional Zone, which is its northernmost subregion, the assemblage B-4 at Laskowa belongs to the middle or – questionably – the upper part of the Laskowa Góra Beds, a lithostratigraphic unit, partly equivalent to the lower parts of the Nieczulice Beds (Racki, 1985; see also Racki *et al.*, 2022, fig. 9). The lower-lying B-3 assemblage (see below) is evidently older, even if precise biostratigraphic data are lacking.

Middle Givetian brachiopod faunas consisting almost exclusively of minute species, either protorthides at Laskowa (B-3 assemblage; Racki *et al.*, 1985), or chonetidines at Pokrzywianka (Pokrzywianka Beds; Turnau and Racki, 1996, 1999; see also Halamski *et al.*, 2022a, p. 365), are tentatively interpreted as corresponding to a period of significant environmental perturbations, more precisely, on account of the dating, the Taghanic Bioevent (Halamski *et al.*, 2022a, p. 365). If so, the slightly younger, rich and diversified assemblages at Laskowa, Błonia Sierżawskie and, to a lesser extent, at Włochy, represent the post-Taghanic recovery faunas. At both Laskowa and Błonia Sierżawskie *Kyrtatrypa pauli* sp. nov. co-occurs with numerous (over twenty) brachiopod species that dominate the assemblage in terms of both individuals and taxa. Other animal groups present include mostly cnidarians and echinoderms (crinoids), and to a lesser extent bryozoans (at both Świętomarz and Laskowa) and rare trilobites and gastropods (Świętomarz). In particular, the presence of *Levenea polonica* (Sobolew, 1909), an orthide known exclusively from Błonia Sierżawskie (Sobolew, 1909; Halamski, 2009) and from Laskowa (A. T. Halamski, A. Baliński, unpublished data), should be emphasised. Also noteworthy are similar epizoan assemblages with auloporid tabulate corals (Fig. 5G, H from Świętomarz; Fig. 5M from Laskowa).

Another point to be noted is a strong external similarity among three atrypide brachiopods, belonging to different lineages: Early to early Middle Givetian *Atrypa trigonalis*, late Middle Givetian *Kyrtatrypa pauli*, and early Frasnian *Atryparia agricolae*. Nearly identical morphologies are likely to indicate very close ecological preferences (ecological niches). Their presence in successive brachiopod faunas (Miłoszów, Świętomarz, Radlin) can be explained by replacement through immigration. Thus, even if broadly similar animal communities re-appeared after the Taghanic crisis, some lineages died out, at least locally, and were replaced by ecological equivalents, coming from elsewhere.

CONCLUSIONS

1. Palynological investigation of the Middle Devonian strata, cropping out at Błonia Sierżawskie, near Świętomarz (outcrop SW-2 *sensu* Halamski, 2004, 2009), allowed dating of them confidently as the Ex3 subzone. They are thus considered to belong to the Nieczulice Beds and not to the Skały Beds, as previously supposed.
2. *Kyrtatrypa pauli* Halamski and Baliński sp. nov. is described from Błonia Sierżawskie as the type locality and from Laskowa. It is indistinguishable from the type species of the genus internally but has a distinctly flatter ventral valve.
3. In both localities, *Kyrtatrypa pauli* Halamski and Baliński sp. nov. co-occurs with rich faunas, interpreted as post-Taghanic recovery biota.
4. Late Middle Givetian *Kyrtatrypa pauli* Halamski and Baliński sp. nov. is externally very similar to the slightly older (early Middle Givetian) *Atrypa trigonalis* Biernat, 1964 and the younger (early Frasnian) *Atryparia agricolae* Halamski and Baliński in Baliński *et al.*, 2016. These three species are considered ecological equivalents, so the same ecological niche was occupied by three separate lineages, each younger species replacing the precedent one when the latter died out, at least locally .

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Appendix I

List of miospore taxa found in the outcrop SW-2 at Błonia Sierżawskie, near Świętomarz (SW-2, units c–e *sensu* Halamski, 2004, 2009, Halamski and Segit, 2006).

Ancyrospora longispinosa Richardson, 1962

Ancyrospora pulchra Owens, 1971

Ancyrospora cf. *simplex* Guennel, 1963

Aneurospora extensa (Naumova) Turnau, 1986

Aneurospora greggsii (McGregor) Streel in Becker *et al*., 1974

Dibolisporites echinaceus (Eisenack) Richardson, 1965

Geminospora aurita Arkhangelskaya, 1987

Geminospora decora (Naumova) emend. Arkhangelskaya, 1985

Geminospora lemurata Balme emend. Playford, 1983

Geminospora notata (Naumova) Obukhovskaya in Avkhimovitch *et al.*, 1993

Geminospora obtusispinosa Turnau in Turnau and Racki, 1999

Geminospora tuberculata (Kedo) Allen, 1965

Grandispora echiniformis Kedo, 1955

Grandispora parvula Turnau in Turnau and Racki, 1999

Grandispora mammillata Owens, 1971

Hystricosporites sp.

Lanatisporites bislimbatus (Tchibrikova) Arkhangelskaya, 1985

Perotrilites bifurcatus Richardson, 1962

Perotrilites granulaticonatus Turnau in Turnau and Racki, 1999

Raistrickia sp.

Retusotriletes clandestinus Tchibrikova, 1972

Retusotriletes radomskii Kondas and Filipiak, 2022b

Retusotriletes simplex Naumova, 1953

Rhabdosporites langii (Eisenack) Richardson, 1960

Rhabdosporites streelii Marshall, 1996

Samarisporites triangulatus Allen, 1965

Verrucosporites premnus Richardson, 1965