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A study on *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836) (Bivalvia, Pectinidae) from the Middle Miocene of Poland and Ukraine

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ABSTRACT:

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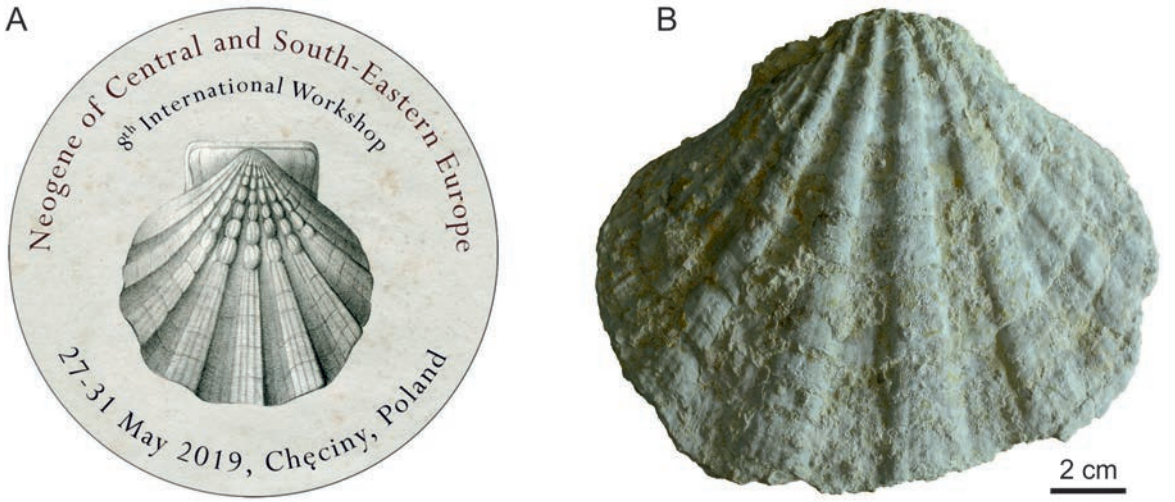
The year of publication and bibliographic reference of *Pecten nodosiformis* have been quoted incorrectly. It is concluded herein that the name was originally published in Pusch's *Geognostische Beschreibung von Polen*, and that the correct year is 1836. This highly distinctive pectinid species, with the left valve ornamented with nodules, and presently assigned to the genus *Gigantopecten* Rovereto, 1899, is a reliable guide to the Lower Badenian (upper Langhian, Middle Miocene) of Poland and Ukraine. Its occurrence in this area, restricted to carbonate deposits dated to the *Orbulina suturalis* planktonic foraminifera zone and the upper NN5 calcareous nannoplankton zone, help to refine the knowledge of palaeoclimatic changes during the Middle Miocene in individual Paratethyan basins. The comparison of many Polish, Ukrainian and Slovak specimens allows the demonstration of changes in the shape of the shell and its ornamentation during ontogeny. This was the reason for assigning herein numerous species as junior synonyms of *Gigantopecten nodosiformis*. Moreover, this paper presents a review of studies on the Middle Miocene sedimentary succession and its fossil content in Skotniki Quarry, the type locality of *Gigantopecten nodosiformis*, one of the most important geological exposures in the Holy Cross Mountains, studied already in the early 19th century by Pusch.

Key words: Pectinidae; Taxonomy; Coralline red algae limestones; Early Badenian (Middle Miocene, late Langhian); Palaeoclimate; Skotniki (Holy Cross Mountains); Central Paratethys.

INTRODUCTION

The 8th International Workshop on the Neogene of Central and South-Eastern Europe (NCSEE) was held in 2019 in Poland. As the logotype for this Biennale Workshop of the NCSEE, there was chosen the illustration of the left valve of *Pecten nodosiformis* (currently *Gigantopecten nodosiformis*) from Pusch's monograph (1837, pl. 5, fig. 9a) (Text-fig. 1A). This specimen, originally illustrated in an attractive lithograph by Mr. Blödner, was collected by Georg Gottlieb Pusch in Skotniki Quarry (50 km SSE of Kielce; 7 km SE of Busko-Zdrój).

Until recently, no other specimen representing this species has been found in this classical locality, visited every year by students since the 1970s, although the abandoned Skotniki Quarry is one of the best documented exposures of the transgressive Lower Badenian sequence (Dowgiałło and Nawrocka 1958; Radwański 1964, 1967, 1969; Małecki 1966; Radwański and Górka 2012, 2015; Górka *et al*. 2015). This is the reason why Skotniki Quarry was visited by the participants of the NCSEE Workshop in 2019 during a field session to observe a mosaic of Middle Miocene lithofacies in the northern marginal zone of the Central Paratethys (Górka 2019). In the outcrop,



Text-fig. 1. *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836). A – The species as the logotype of the 8th International Workshop on Neogene of Central and South-Eastern Europe. Designed by D. Nast; B – Exterior view of the right valve missing the anterior ear, from the Skotniki Quarry; specimen found in 2019 (MZ VII Ml 4133). Photograph by D. Nast.

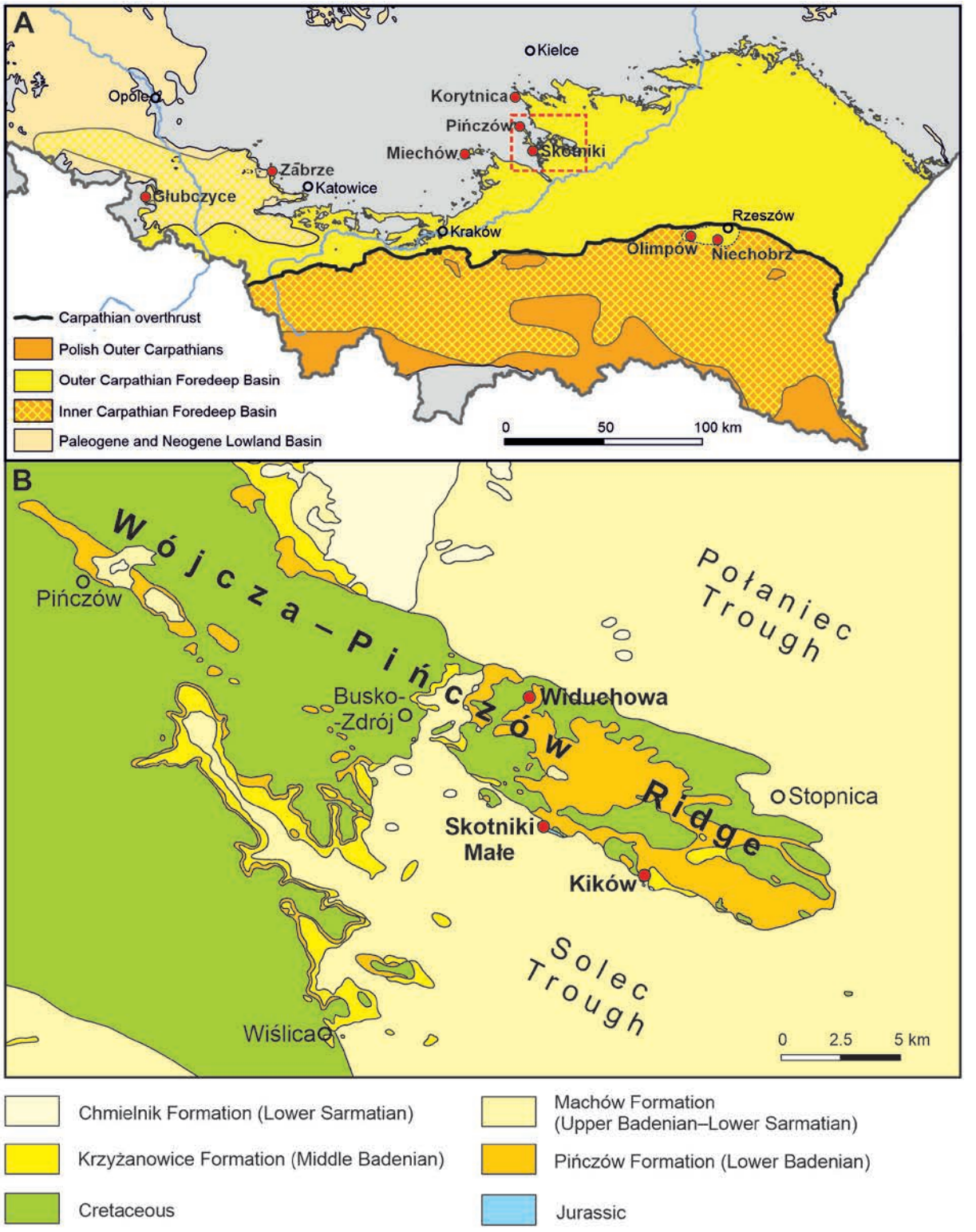
Dr. Samuel Rybár fortunately found the right valve of *Gigantopecten nodosiformis* (Text-fig. 1B). This finding, the first one in 200 years, in conjunction with the information by Švagrovský (1981, p. 58) that the Skotniki specimen, illustrated by Pusch (1837, pl. 5, fig. 9) and subsequently re-illustrated by Roger (1939, pl. 28, fig. 1), is housed in the Type Collection of the Faculty of Geosciences, Université Claude Bernard, Lyon, France (Mangold and Mongereau 1966, p. 16), led me to a thorough research on the Pusch Collection.

The results of these studies astonished me. Initially, I intended to present them in one article, however, after hearing the opinion of the journal reviewers on an earlier version of this manuscript, I decided to prepare three separate reports; the first one, presented herein, is a study of *Gigantopecten nodosiformis* from the Lower Badenian of Poland and Ukraine and its type locality – the abandoned Skotniki Quarry in the Holy Cross Mountains of Poland. The remaining two reports, one devoted to Pusch's research on the Tertiary deposits from the Kingdom of Poland and Eastern Galicia, and another – to Pusch's priceless collection of minerals and fossils, will be presented in the future issues of *Acta Geologica Polonica*.

DATE OF PUBLICATION OF *PECTEN NODOSIFORMIS*

So far, all researchers have unanimously dated the creation of the species *Pecten nodosiformis* to 1837, referring to the first monograph devoted to the fossil biota of the Kingdom of Poland, *Polens Paläontologie* by G.G. Pusch. The authorship of *Pecten nodosiformis* has been attributed in the past literature to de Serres in Pusch, 1837 (e.g., Glibert and van de Poel 1965; Švagrovský 1981; Studencka and Studencki 1988; Mandic 2004), de Serres, 1837 (e.g., Csepreghy-Meznerics 1960; Nicorici 1977), or Pusch, 1837 (e.g., Schultz 2001; Mandic 2003; Bongrain 2013; Studencka 2019). For unknown reasons, however, absolutely all of us who study pectinids have overlooked the fact that, in the second volume of the fundamental two-volume book entitled *Geognostische Beschreibung von Polen* which appeared in 1836, Pusch had already provided this name including a short diagnosis: "*Testa ovato-subrotunda, aequivalvis, transversim subtilissime undulatim striata, radiis novem vel decem crassis, latis longitudinaliter sulcatis, in parte superiori nodoso vesicularibus, interstitiis longitudinaliter plicatis, auriculis aequalibus perpendiculariter rugosis*" (Pusch 1836, p. 500).

Consequently, the authorship of the name *Pecten nodosiformis* must be credited to Pusch and de Serres, rather than de Serres in Pusch or Pusch as has been the practice (compare the selected synonymy in the Systematic account). The species was established on specimens collected in Poland, i.e., Skotniki Quarry, Widuchowa near Busko, and Kików near Stopnica (spelled by Pusch as *Stobnica*) from the "*pisolithenartiger Grobkalk*", presently termed as the red-algal limestones or coralline algal limestones. When introducing this species, Pusch noted that the well-preserved specimens come from Skotniki and



Text-fig. 2. Location maps. A – Geological sketch-map of the Middle Miocene deposits in southern Poland (after various sources) with the location of B (red insert) and sites yielding *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836) (red dots). Pre-Miocene basement marked in grey; B – Geological map of the Wójcza-Pińczów Ridge (southern slopes of the Holy Cross Mountains, northern part of Central Paratethys) without the Pliocene and Quaternary cover (adopted from Górka 2019). Red dots indicate sites where the specimens described by Pusch (1836, p. 500) came from.

Widuchowa, and described them as follows (Pusch 1836, p. 500, here translated): "shell ovate to suborbicular, equivalve, sculptured with slightly undulating commarginal striae, nine or ten prominent radial ribs longitudinally furrowed with well-developed hollow nodes in the upper part, interspace radially ribbed, almost equal ears vertically wrinkled."

The size of one of the specimens, without specifying its exact location, was reported as "*Meine Exemplare sind 6 Zoll lang, 5 Zoll breit*", i.e., about 15.2 cm in height and 12.7 cm in length. This size is different, however, from the Skotniki specimen of which excellent illustrations appeared in the *Polens Paläontologie* (Pusch 1837, pl. 5, fig. 9a, b).

As indicated by Pusch (1836, pp. 500–502), the specific name *nodosiformis* reflects the similarity to the present-day pectinid species *nodosus* Linnæus, 1758 (designated in 1898 by Dall as the type-species of the new genus *Nodipecten*). Pusch also noted that it is highly probable that a pectinid specimen from the south of France identified by de Serres (1829, p. 130) as *Pecten* sp. represents the same species. This view was influenced by the opinion of de Serres, who first noticed the similarity of the French specimen to *nodosus* (incorrectly assigning the authorship of this species to Lamarck) but did not introduce a specific name for it. In the opinion of Pusch, the new created species *nodosiformis* displays some affinities to other large pectinids, such as *Pectinites gigas* Schlotheim, 1813 (currently *Gigantopecten gigas*), *Pecten grandis* Sowerby, 1828 and *Pecten jacobaeus* (Linnæus, 1758). Importantly, *Ostrea latissima* Brocchi, 1814 (currently *Gigantopecten latissimus*), was not listed among those species, although Pusch was familiar with Brocchi's monograph (1814) and believed that the molluscan fauna of the Kingdom of Poland resembled the fauna of the Vienna Basin in Austria and the Tertiary Basin of Piedmont in north-western Italy more than that of the Paris and Aquitaine basins in France (Pusch 1829, p. 41).

GEOLOGICAL FRAMEWORK, LITHOLOGY AND FAUNAL CONTENT OF THE SKOTNIKI SITE

The syntype series of *Pecten nodosiformis* includes specimens collected during field seasons in the summer of 1817 and the spring of 1819 in Skotniki, Widuchowa and Kików (Pusch 1831[1], pp. 1–3). All specimens originated from carbonate deposits characterized by coralline algae, bryozoans and bivalves (known as the Pińczów Limestones), which crop out widely along the Wójcza-Pińczów Ridge (Text-fig. 2). These sediments, known in the literature as the *Heterostegina* limestones (Polish *wapień heterosteginowy*; Zejszner 1861), the *Nullipora* marls and the Leitha-limestones (Polish *margiel nulliporowy i wapień leitański*; Kontkiewicz 1882; Siemiradzki 1888), lithothamnian and organodetrital limestones (Polish *wapienie litotamniowe i organodetryczne*; e.g., Krach 1955; Radwański 1967, 1969), the Leitha-limestones (Polish *wapienie litawskie*; Kontkiewicz 1881; Krach 1947; Radwański 1964, 1965a), and the Pińczów Limestones (Studencki 1988) correspond to the main Badenian transgressive pulse of Central Paratethys, dated as the latest Early Badenian (correlating with the late Langhian) based on the calcareous nannoplankton Zone NN5 (Studencka and Studencki 1988) and the foraminiferal Zone *Orbulina suturalis* (Alexandrowicz and Parachoniak 1956; Chruszcz 2002). They were deposited in a temperate shallow-marine environment within an elongated carbonate platform, and they largely accumulated under moderate to strong water-energy conditions (Studencki 1988, 1999). In terms of palaeogeography, the study area is located in the southern foreland of the Holy Cross Mountains, which during the latest Early Badenian marked the northern margin of Central Paratethys.

The Lower Badenian sediments (Pińczów Formation) exhibit great facies variations and developed mainly as highly variable littoral lithofacies with structures such as abrasion surfaces and cliff conglomerates (Radwański 1969). One of the best documented nearshore settings is the largest cliff conglomerate exposed in Skotniki Quarry located about 7 km to the south-west of Busko-Zdrój (N 50º25'30.24", E 20º39'17.49"), on a hill called Zajęcza Góra (Dowgiałło and Nawrocka 1958; Radwański 1964, 1967, 1969; Małecki 1966; Radwański and Górka 2012, 2015; Górka *et al*. 2015; Górka 2019) that represents the oldest evidence of the Early Badenian transgressive phase in the northern part of the Fore-Carpathian Basin.

The cliff conglomerate at Skotniki Quarry was first mentioned by Dowgiałło and Nawrocka (1958) who briefly reported that transgressive Lower Badenian deposits unconformably cover Upper Cretaceous strata (Cenomanian sandstones and Turonian

[1] The date of publication of the first volume of *Geognostische Beschreibung von Polen* is imprecisely specified. Pągowski (1847, p. 288) gave 1831 as the date of publication. The same year was also given by Kleczkowski (1977, pp. 59–60), adding that the first volume was already printed in 1830, but could not be distributed due to the November Uprising in 1830. Therefore, almost all copies of *Geognostische Beschreibung von Polen* were issued with the date 1833 and this date is usually cited.

thinly laminated biogenic limestones with cherts) exposed in the northern wall of the quarry. As observed in 1957, the Lower Badenian succession began with about 0.2–1.2 m of transgressive basal conglomerates covered with sandy limestones (0.7–1.5 m; thickness increasing towards the east) with common, more or less fragmented unattached coralline branches, numerous large benthic foraminifera and molluscan remains. The upper 4 m of the exposed section (with the top destroyed by present-day erosion) was referred originally to the 'upper conglomerate' composed primarily of Jurassic (Kimmeridgian) limestone boulders, cobbles and pebbles, very variable in size (mostly between 10 and 40 cm) and bearing traces of a pitting structure (Dowgiałło and Nawrocka 1958; Radwański 1965b).

Further intensive exploitation of the quarry made it possible to observe a 10-m-thick section of Lower Badenian transgressive deposits that filled a large WNW-ESE-oriented trough with a lens-geometry (up to 100 m long and 35–40 m wide) eroded in lithologically heterogenous Jurassic and Upper Cretaceous sediments (Radwański 1964, 1967, 1969). The thickness of the cliff conglomerates observed in 1963 was 9.5–9.7 m in the axial part of the trough. Carbonate cobbles and boulders (mostly 10–20 cm, occasionally almost 70 cm in size) have been found heavily bored and occasionally encrusted with coralline algae, bryozoans, polychaetes and vermetid gastropods (Radwański 1967). Studies by Radwański (1964, 1965a, 1967, 1969) focused mainly on the identification of the organisms inhabiting the hard substrates and description of the bioerosion structures. Their morphological analysis revealed an assemblage consisting of the following boring organisms: endolithic bivalves represented by *Lithophaga lithophaga* (Linnæus, 1758), *Jouannetia semicaudata* Des Moulins, 1828, and *Aspidopholas rugosa* (Brocchi, 1814); demosponges: *Cliona celata* Grant, 1826, *Cliona vastifica* Hancock, 1849 (currently *Piona vastifica*) and *Cliona viridis* (Schmidt, 1862); and polychaetes: *Potamilla reniformis* (O.F. Müller, 1771) [currently *Pseudopotamilla reniformis* (Bruguière, 1789)], *Polydora ciliata* (Johnston, 1838) and *Polydora hoplura* Claparède, 1868. The same list of trace-producing organisms was provided by Radwański and Górka (2012, 2015).

Surprisingly, despite the opinion expressed by Radwański (1969) that the Skotniki assemblage is the richest among the Badenian rocky-shore assemblages of Poland, he made no attempt to deal with the trace fossils in a systematic way. However, based on the descriptions and illustrated material presented by Radwański (1964, 1965a, 1969) and comments by Kelly and Bromley (1984), Mayarol (1987), and Rajchel and Uchman (1999) it was possible to recognize five ichnogenera: *Gastrochaenolites* Leymarie, 1842 produced by several mytilid and pholadid boring bivalves, *Entobia* Bronn, 1837, i.e., structures made by clionid sponges, *Trypanites* Mägdefrau, 1932, and *Caulostrepsis* Clarke, 1908, which are the result of the boring activity of polychaetes (mainly by representatives of the genus *Polydora* Bosc, 1802), and *Renichnus* Mayoral, 1987, corresponding to the etching activity of vermetid gastropods.

The most conspicuous is *Gastrochaenolites*, a typical colonizer of hard substrates, represented by three ichnospecies, i.e., *torpedo* Kelly and Bromley, 1984, *dijugus* Kelly and Bromley, 1984, and *orbicularis* Kelly and Bromley, 1984. The producers of such borings are likely to be the bivalve species *Lithophaga lithophaga*, *Aspidopholas rugosa* and *Jouannetia semicaudata*, respectively, of which external moulds of shells were found in living position inside *Gastrochaenolites*. Other bioerosion traces include sponge boring systems (*Entobia* isp.) that have been mostly seen together with *Gastrochaenolites*, and polychaete dwellings: *Trypanites* isp. and *Caulostrepsis taeniola* Clarke, 1908, which occur abundantly.

The walls of *Gastrochaenolites* borings were locally encrusted with rich and diversified bryozoan assemblages which have been extensively studied by Małecki (1966), who identified 51 species of cheilostome and cyclostome bryozoans. Various colonies of bryozoans have been observed occasionally on the surface of pebbles together with coralline algae, numerous serpulid polychaetes *Serpula subpacta* Rovereto, 1904 and *Spirobranchus* sp., and a sessile gastropod species *Petaloconchus intortus* (Lamarck, 1818) with its sparse trace fossil *Renichnus arcuatus* Mayarol, 1987. This ichnological assemblage has been attributed by Górka (2019) to the *Trypanites* ichnofacies.

While in 1963 the cliff conglomerates were exposed in the almost 100-m long trough, its south-eastern part ceased to exist due to intensive exploitation of the quarry in the 1960s and 1970s. Recently, only a small western part can be observed (Text-fig. 3). The extremely fortunate finding of the second specimen of *Gigantopecten nodosiformis* after 200 years happened right there.

Radwański (1969, p. 45, figs 15 and 16) reported the presence of an unconformity within the Badenian sequence, which could then be observed in the southwestern part of the trough. An erosive surface separated both the cliff and the sandy limestones from the overlying red algal limestones con-

Text-fig. 3. View of the north-eastern wall of Skotniki Quarry, the type locality of *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836). Note the basal unconformity between the transgressive Lower Badenian deposits and the Cretaceous basement observed on the northern wall. Photograph taken in May 2019 by B. Studencka.

taining large benthic foraminifera *Amphistegina* sp. and *Heterostegina* sp., bivalves (including pectinids) and gastropods, echinoid test remains (isolated plates and spines) and fish remains (teeth). Although Dowgiałło and Nawrocka (1958) and Radwański (1969) gave a brief account on the presence of bivalves in both sandy limestones (below the cliff conglomerate) and red-algal limestones (above the cliff conglomerate), little attention has been paid to their taxonomic content. Only Radwański (1969, p. 46) stated that the pectinids are an important element, the largest of which, incorrectly identified as *Chlamys latissima* (Brocchi, 1814), is already known from the Pusch Collection, as reported by Friedberg (1936, p. 217).

However, none of the authors ever mentioned that Pusch was the first to describe the Miocene sediments in Skotniki Quarry. Dowgiałło and Nawrocka (1958) and Radwański (1969) were apparently unaware of the work by Pusch (1836) and its Polish abridged edition (Pusch 1903), containing a detailed description of the Miocene succession in the Skotniki Quarry.

According to Pusch (1836, p. 458), the Tertiary deposits discovered at the foot of Zajęcza Góra hill, covering Cretaceous marls with black cherts, were composed of as follows:

– sandy limestones ("*sandiger Grobkalk*") in the basal part of the section;
– a clay horizon;
– sandy limestones above the clay horizon, intercalated with red-algal limestones ("*pisolithenartiger Grobkalk*"), which passed upwards into marly limestones yielding large pectinid shells;
– rhodolith pavement facies ("*kugelig abgesonderter mürber Grobkalk*").

Unfortunately, the exact location and thickness of the individual units have remained obscure. Exploitation of Skotniki Quarry, which began in the 19th century and lasted until the 1990s, completely destroyed its western part, the most likely site of the sediments examined by Pusch in the 1820s. Samples

of limestones collected by Pusch from Skotniki Quarry together with those from Górki near Pińczów, Pińczów, Stopnica, and Ossówka near Szydłów were stored until the outbreak of the Second World War in September 1939 (Małkowski 1948, pp. 5, 26) in the Mineralogical Cabinet of the former Royal University of Warsaw under the catalogue numbers 1962–1969 (Morozewicz 1900, p. 668).

From Skotniki Quarry, in addition to the newly created pectinid species *nodosiformi*s, Pusch (1836, pp. 502, 542) also reported two bivalve species *Pecten* ?*tournali* de Serres, 1829 (currently *Gigantopecten tournali*), *Mytilus brardii* Brongniart, 1823 (currently *Coelogonia brardii*), and the sole gastropod species *Turritella terebralis* Lamarck, 1822.

However, Serres' species *tournali* was not mentioned in the list of Tertiary bivalves appended to the monograph (Pusch 1837, pp. 181–184). Moreover, Pusch (1837, p. 42) pointed out that this species exhibits an affinity to *nodosiformis*. Hence, it is highly likely that specimens attributed by Pusch (1836, p. 502) to *tournali* represent the right valve of *nodosiformis* without the node series on the rib tops. Up to now, no specimen of *Gigantopecten tournali* has been documented in the Badenian deposits of Poland. In the opinion of Bongrain (1992), the range of this species is restricted to the middle–late Burdigalian. It certainly existed in the Burdigalian of southern France (Rhône Basin), Algeria (Oran Province), Tunisia, Italy (Sardinia and Turin Hills), Montenegro and Turkey (Roger 1939; Blondel and Demarcq 1990). Paratethyan records of *Gigantopecten tournali*, apart from the findings in Croatia (Bošnjak *et al*. 2024), were nearly exclusively limited to the upper Ottnangian–lowermost Badenian (middle–uppermost Burdigalian) of the Alpine-Carpathian Foredeep Basin (Mandic 2004), the Karpatian (upper Burdigalian) of the Central Hungarian Várpalota Basin (Mandic 2003), and to the lowermost Badenian of the Fâget Basin in Romania (Studencka *et al*. 1998). Moreover, *Turritella terebralis* was also not mentioned by Pusch (1837, pp. 104–105) in the *Polens Paläontologie* among the seven turritellid species recognized. It is most probably that Pusch referred the Skotniki specimens to *Turritella subangulata* Brocchi, 1814, especially since it is unlikely that specimens determined by Pusch as *Turritella terebralis* are clearly related to the very characteristic Lamarck's species *terebralis* restricted to the Aquitanian–Burdigalian of the eastern Atlantic and the Burdigalian of the Proto-Mediterranean, and unknown from the Paratethys (Harzhauser and Landau 2019, pp. 19, 20). On the other hand, Pusch pointed to the similarity of the Skotniki specimens with *Turritella turris* Basterot, 1825. According to Hörnes (1855, pp. 423, 424), specimens identified by Pusch (1837) as *Turritella subangulata* [now accepted as *Oligodia spirata* (Brocchi, 1814)] indeed represent *Turritella turris*, whereas Bałuk (1975, pp. 105–107) determined them as *Turritella* (*Haustator*) *badensis* Sacco, 1895. More recently, Landau *et al*. (2013, pp. 58–61) recognized that, when introducing *Turritella badensis* as a replacement name for *Turritella turris sensu* Hörnes (1855), Sacco (1895, p. 3) overlooked that Handmann (1882, p. 15) had already provided the name *Turritella vindobonensis* for the same Austrian turritellid specimens. Hence, it is highly likely that the turritellid specimens from Skotniki represent the extraordinarily variable *Ptychidia vindobonensis* (Handmann, 1882), which is the most abundant species in the Polish Badenian deposits known as *Turritella* (*Haustator*) *badensis* (see Bałuk 1975).

In turn, the accuracy of the proper identification of specimens recognized by Pusch (1836, p. 402) as *Mytilus brardii* will probably never be confirmed. Pusch (1837, p. 182) reported *brardii* from both sandy limestones in Skotniki, Kików, and Staszów (southern slopes of the Holy Cross Mountains), and the rich-fossiliferous sands in Biały Kamień, Zabłotówka and Żukowce in Eastern Galicia, presently in the Ukraine (Ukrainian spelling Bilyy Kamin', Zabolotivka and Zhukivtsi). It is hardly likely that they represent Brogniart's species *brardii*, which was designated by Bronn (1837, pp. 164, 166) as a species representing the new genus *Coelogonia*, known from Oligocene freshwater setting of the Mainz Basin (Germany).

GIGANTOPECTEN NODOSIFORMIS – DATA FROM POLAND AND UKRAINE

The examined material comes from the Lower Badenian (upper Langhian) sites in Poland and Ukraine (Table 1). Except for a very fine surface abrasion they are well preserved. The present study is mostly based on the collection stored in the Museum of the Earth, Polish Academy of Sciences in Warsaw. Additional studied material is stored in the collections of the Geological Museum of the Polish Geological Institute – National Research Institute, Warsaw, Poland (collected by J. Czarnocki and K. Kowalewski), Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Kraków, Poland (Friedberg Collection), State

Locality	Repository and inventory number	Length [mm]	Height [mm]	Apical angle [º]	Illustrated herein
Skotniki	shell illustrated in Pusch (1837, pl. 5, fig. 9a, b); inventory number unknown, originally probably housed in the Mineralogical Cabinet of the University of Warsaw	126	130	100	Text-fig. 4A, B
	shell illustrated in Roger (1939, pl. 28, figs 1, 1a); inventory number and repository unknown	126	130	100	Text-fig. 5A, B
	cast of shell illustrated in Roger (1939, pl. 28, figs 1, 1a), UCBL-FSL 29270	126	130	100	Text-fig. 5C, D
	right valve, MZ VIII Ml 4133	125	109	109	Text-fig. 1B
Kików	shell, MZ VIII Ml 2603/1	98	90	103	Text-fig. 6A, B
Widuchowa	shell, MZ VIII Ml 4147	114	112	106	Text-fig. 6C
	right valve, MZ VIII Ml 4149/MG	106	96	109	Text-fig. 6D
Pińczów	shell, MUZ PIG 27.II.430a	40	38	93	Text-fig. 7A–C
	shell, MZ VIII Ml 4322	116	133	101	Text-fig. 8A, B
	shell, MZ VIII Ml 4146	138	122	107	Text-fig. 8C, D
Niechobrz	left valve, MZ VIII Ml 2872	28	30	95	Text-fig. 7D
	left valve, ZNG PAN A-I-73/973	202	155	*120*	Text-fig. 10A, B
Zebegény	left valve, MZ VIII Ml 4138	58	54	101	Text-fig. 7E
Khorosno	left valve, MZ VIII Ml 4139	155	136	110	Text-fig. 9A
Mohylnitsia	right valve, SMNH-PZ-N-1104	190	160	110	Text-fig. 9B

Table 1. Lengths, heights and apical angles of illustrated specimens of *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836) with repository numbers and localities. The value of the apical angle of the largest specimen from Niechobrz is in italics due to its extremely oblique outline with the posterior margin almost twice as long as the anterior margin, unusual for the examined specimens.

Museum of Natural History, National Academy of Sciences of Ukraine, Lviv, Ukraine (material from the former Dzieduszycki Natural History Museum collections; names of sites are given in their present-day spelling, whereas the originally used names are given in brackets) and the Henryk Teisseyre Geological Museum, University of Wrocław, Poland (material from Boguchwałów, formerly Hohndorf). In total, 22 shells, 64 valves and fragments of 14 valves of *Gigantopecten nodosiformis* from the Lower Badenian of Poland, and two shells, 11 valves and fragments of three valves from the Lower Badenian of Ukraine were examined. In addition, complementary studies were carried out on material from the Upper Badenian (lower Serravallian) carbonate deposits of Slovakia stored in the Natural History Museum in Bratislava, Slovakia (Švagrovský Collection).

Institutional abbreviations

MGUWr – Henryk Teisseyre Geological Museum, University of Wrocław, Poland; MUZ PIG – Museum of the Polish Geological Institute – National Research Institute, Warsaw, Poland; MWGUW – Stanisław J. Thugutt Geological Museum of the Faculty of Geology, University of Warsaw, Poland; MZ – Polish Academy of Sciences, Museum of the Earth in Warsaw, Poland; NHM – Natural History Museum, Bratislava, Slovakia; SMNH – State Museum of Natural History, National Academy of Sciences of Ukraine, Lviv, Ukraine; UCBL-FSL – Faculty of Geosciences, Université Claude Bernard, Lyon, France; ZNG PAN – Geological Museum of the Institute of the Geological Sciences, Polish Academy of Sciences, Kraków, Poland.

SYSTEMATIC ACCOUNT

Order Pectinida J. Gray, 1854
Suborder Pectinidina J. Gray, 1854
Superfamily Pectinoidea Rafinesque, 1815
[emend. Waller, 1978]
Family Pectinidae Rafinesque, 1815
[emend. Waller, 1978]
Subfamily Pectininae Rafinesque, 1815
[emend. Waller, 1978]
Genus *Gigantopecten* Rovereto, 1899
(ICZN Opinion 2203, 2008)
[a replacement name for *Macrochlamys* Sacco, 1897b; = *Grandipecten* Cossmann, 1914 in Cossmann and Peyrot, 1914; non *Macrochlamys* Benson, 1832]

TYPE SPECIES: *Ostrea latissima* Brocchi, 1814, by subsequent designation of Sacco (1897). Pliocene; northern Italy.

Gigantopecten nodosiformis (Pusch and de Serres in Pusch, 1836)
(Text-figs 1B, 4–10)

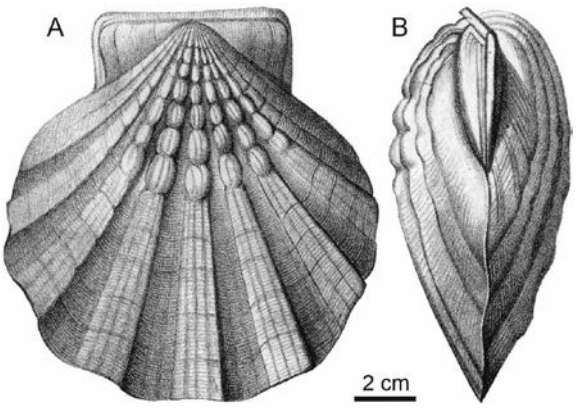
*1836. *Pecten nodosiformis nob. et* Serres.; Pusch, pp. 500, 501.
1836. *P.*[*ecten*] *laticostatus* Lam.; Pusch, p. 501.
1837. *Pecten nodosiformis* M. de Serres; Pusch, p. 42, pl. 5, fig. 9a–c.
1845. [*Pecten*] *nodosiformis* Serres; Zeuschner, p. 85.
1861. *P.*[*ecten*] *nodosiformis* Marc. de Serres; Zejszner, p. 731.
1867. *Pecten latissimus* (Brocchi, 1814); Hörnes, pp. 395–397, pl. 56, figs 1–4, pl. 57, figs 1–4.
1870. *Chlamys latissimus* Defrance [sic!]; Roemer, pp. 396, 397, pl. 46, figs 1–3.
1881. *Pecten latissimus*; Kontkiewicz, p. 169.
1881. *Pecten Ponzii*; Meli, p. 117, pl. 1, figs 1–3.
1882. *Pecten latissimus* (Brocc.); Kontkiewicz, p. 192.
1883. *Pecten latissimus* Br.; Uhlig, p. 481.
1884. *Pecten latissimus*; Kosiński, p. 73.
1884. *Pecten latissimus* Defr. [sic!]; Michalski, p. 98.
1903. *Pecten latissimus* Brocchi; Friedberg, pp. 17, 21, 22.
1904. *Pecten latissimus* Brocc.; Łomnicki, p. 338.
1904. *Pecten latissimus* Brocc.; Zuber, p. 419.
1905. *P.* [*ecten*] *Melii* Ugol.; Ugolini, p. 117 [a replacement name for *Pecten Ponzii* Meli, 1881]
1906. *Chlamys* (*Flexopecten*) *sardous*; Ugolini, pp. 180, 181, pl. 10, fig. 5, pl. 12, fig. 1.
1906. *Chlamys* (*Lyropecten*) *Melii* Ugol.; Ugolini, pp. 181–184, pl. 10, fig. 6a–d.
1906. *Chlamys* (*Lyropecten*) *nodosiformis* Serr.; Ugolini, pp. 184–186, pl. 10, fig. 7a–c.
1906. *Chlamys* (*Lyropecten*) *nodosiformis* var. *miocostulata* n. var.; Ugolini, pp. 186, 187, pl. 10, fig. 8.
1928. *Pecten* (*Oopecten*) *latissimus* Brocch. var. *austriaca* nov. var.; Kautsky, pp. 246, 252, 253.
1930. *Pecten latissimus* Lam. [sic!]; Kowalewski, p. 31.
1932. *Pecten latissimus* Brocchi; Gołąb, p. 30.
1932. *Pecten* (*Grandipecten*) *latissimus* Brocc.; Friedberg, p. 50.
1936. *Pecten* (*Grandipecten*) *latissimus* Brocc.; Friedberg, pp. 215–217, pl. 35, fig. 1, pl. 36, figs 1, 2.
1938. *Pecten latissimus* Brocc.; Friedberg, p. 10.
1939. *Chlamys latissima* Br. var. *nodosiformis* Pusch; Roger, pp. 42, 43, pl. 28, figs 1, 1a.
1939. *Chlamys Melii* Ugolini; Roger, pp. 44–46, text-fig. 18, pl. 19, figs 2, 2a, pl. 27, fig. 6.
1939. *Chlamys sardoa* Ugolini; Roger, pp. 46, 47, text-fig. 19, pl. 19, figs 3, 3a.
1947. *Pecten latissimus* Brocc.; Krach, p. 44.
1952. *Pecten* (?) *latissimus* Brocchi, 1814; Kazakova, pp. 216, 217, pl. 3, fig. 1.
1952. *Pecten latissimus* Brocc. var. *nodosiformis* de Serres (Pusch); Kazakova, p. 217, pl. 4, fig. 1.
1955. *Pecten latissimus*; Krach, p. 112.
1955. *Chlamys sardoa* Ugolini; da Veiga Ferreira, p. 21, pl. 4, fig. 20.
1960. *Chlamys latissima nodosiformis* (de Serres); Csepreghy-Meznerics, p. 33, pl. 26, figs 1–5, pl. 27, figs 1, 2, pl. 28, figs 1, 2, pl. 29, figs 1, 2, pl. 32, figs 1, 2.
1965. *Oopecten* (*Gigantopecten*) *latissimus nodosiformis* (De Serres in Pusch, 1837); Glibert and van de Poel, p. 17.
1977. *Chlamys latissima nodosiformis* (De Serres); Nicorici, pp. 132, 133, pl. 13, fig. 1, pl. 14, figs 1a, 1b, pl. 15, figs 1–4.
1978. *Chlamys* (*Macrochlamys*) [sic!] *latissima nodosiformis* (de Serres, 1829); Steininger *et al*., p. 345, pl. 10, figs 2, 3.
1981. *Chlamys* (*Macrochlamys*) [sic!] *latissima nodosiformis* (M. Serres in G. Pusch, 1837); Švagrovský, pp. 57, 58, pl. 13, figs 1–3, pl. 14, fig. 1, pl. 15, fig. 1.
1986. *Chlamys latissimus*; Urbaniak, pp. 28–30.
1988. *Chlamys* (*Macrochlamis*) *latissima nodosiformis* (de Serres in Pusch, 1837); Studencka and Studencki, pp. 26, 27, text-fig. 4, pl. 5, figs 1a, b.
1994. *Gigantopecten nodosiformis* (de Serres); Studencka, pp. 141, 144.
1996. *Pecten* (*Gigantopecten*) *latissimus nodosiformis* (de Serres in Pusch, 1837); Jakubowski in Jakubowski *et al*., pp. 678, 679, pl. 196, fig. 6, pl. 197, fig. 6, pl. 198, fig. 8.
1998. *Gigantopecten nodosiformis* (de Serres); Studencka *et al*., pp. 296, 297, 314, 315.
2001. *Gigantopecten nodosiformis* (Pusch, 1837); Schultz, pp. 249–254, pl. 36, fig. 3a, c, pl. 37, figs 1a, b, 2, pl. 38, fig. 2, pl. 39.
2004. *Macrochlamis nodosiformis* (de Serres in Pusch, 1837); Mandic, pp. 141, 142, fig. 6. 1a–c, 2a–c.
2010. *Pecten latissimus* (Brocchi); Krzeszowska and Machłajewska, pl. 7, fig. 13.
2012. *Macrochlamis nodosiformis* (de Serres in Pusch, 1837); Wysocka *et al*., pp. 479, 488.
2019. *Gigantopecten nodosiformis* (Pusch, 1837); Studencka, pp. 11–16, figs 2–4.

COMMENTS ON THE SYNONYMY: Although Pusch (1837) attributed *Pecten nodosiformis* to de Serres, this specific name was never published by that author. De Serres (1829, p. 130) in the work on the Tertiary fauna of southern France, in addition to *Pecten laticostatus* Lamarck, 1819 (currently *Gigantopecten latissimus*), also mentioned a single specimen with ornamentation similar to the extant *Pecten nodosus* (Linnæus, 1758) (currently *Nodipecten nodosus*), probably representing a related species.

Bronn had no doubt (Pusch 1837, p. 42, footnote) that *Pecten* sp. mentioned by de Serres (1829) and *Pecten nodosiformis* relate to the same species, which he amalgamated with *Ostrea latissima* Brocchi, 1814, a species created on the basis of Pliocene material from Italy. The opinion concerning the status of *nodosiformis*, restated by Bronn (1848, p. 926), became the basis for the statement that *nodosiformis* is conspecific with Brocchi's species *latissima*. This position had great influence on the opinions of many researchers, starting with Hörnes (1867), who previously considered *nodosiformis* and *latissima* as two separate species, but who uncritically accepted it as correct (Hörnes 1850, p. 667). Following the authority of Hörnes, researchers of the Polish Miocene at that time (e.g., Roemer 1870; Friedberg 1903, 1932, 1936, 1938) considered *Pecten nodosiformis* as a junior synonym of *Pecten latissimus*.

A different opinion was expressed by Meli (1899), who referred Miocene specimens from the Viennese collections to *Pecten laticostatus* Lamarck, which Hörnes (1867) identified as *Pecten latissimus*, concluding that they were certainly closer to Fonntanes' species *restitutensis* originally described from the Lower Miocene of southern France (Rhône Basin), than to the Brocchi's species *latissima*. Furthermore, Meli (1899) discovered that the Viennese and Budapest collections contained Miocene specimens undoubtedly identical with his species *Ponzii*, introduced on the basis of Pliocene (Zanclean) specimens from Civitavecchia near Rome, Italy (Meli 1881). Importantly, according to Meli (1881), the aforementioned Pliocene species is also similar to the Miocene *Pecten nodosiformis* presented by Pusch (1837).

In 1897, Sacco designated Brocchi's species *latissima* as a type species for the newly created subgenus of *Chlamys* Röding, 1798. The name of this taxon was first published in June 1897 as *Macrochlamis*, without any illustration or description (Sacco 1897a, p. 101). It was simply a note announcing the contents of the next two parts of the monograph on the Tertiary fauna of Piedmont and Liguria, i.e., part 23 concerning the Ostreidae, Anomidae and Dimyidae, and part 24 devoted to the Pectinidae. The latter, published in December 1897, contained an adequate description and illustrations of *Macrochlamys* and its type species *latissima* (Sacco 1897b, pp. 32, 33, pl. 9, figs 5a, b, pl. 10, figs 1–5). The species *nodosiformis*, however, was treated by Sacco (1897b, p. 33) as a separate entity. In the synonymy of *Pecten latissimus*, this author included only the note given by Bronn in Pusch (1837, p. 44), omitting the original Pusch's description and illustrations.

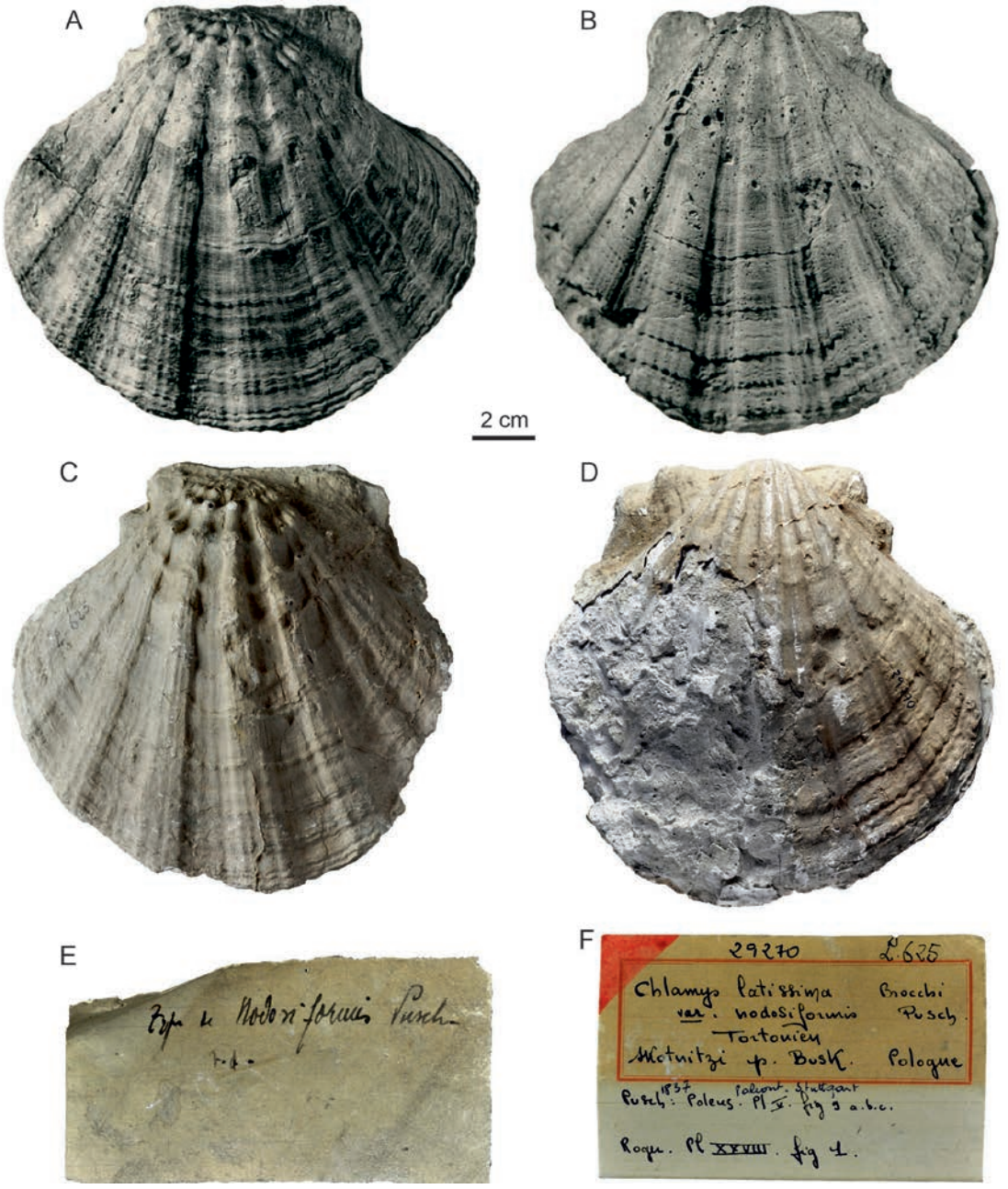


Text-fig. 4. *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836), lectotype, Skotniki, Poland. A – Left valve of articulated shell; B – Postero-lateral view of the same specimen. Copies from Pusch (1837, pl. 5, fig. 9a, b).

On the other hand, Sacco considered that both the Miocene specimens from the Vienna Basin illustrated by Hörnes (1867, pl. 56, figs 1–4) as *Pecten latissimus* and the Angevin specimen named by Dollfus and Dautzenberg (1896, pl. 1) as *Chlamys* (*Pallium*) *Apollo* represent a variety of *Macrochlamys latissima*, which he called *gibboplana* (Sacco 1897b, p. 33, pl. 10, fig. 6). However, a different opinion was expressed by Dollfus and Dautzenberg (1920, p. 407), who stated that due to the lack of sufficient material, *apollo* could only be considered a subspecies of *latissima*, and not a separate species.

Since the name *Macrochlamys* was already preoccupied by *Macrochlamys* Benson, 1832, Rovereto (1899) introduced a new replacement name – *Gigantopecten*. This action was accepted by Sacco as clearly evidenced by the note in part 30 of the monograph (Sacco 1904, p. 143), reading as follows: "*Gigantopecten* Rover. 1899 (= *Macrochlamys* Sacco 1897, non Benson 1832)."

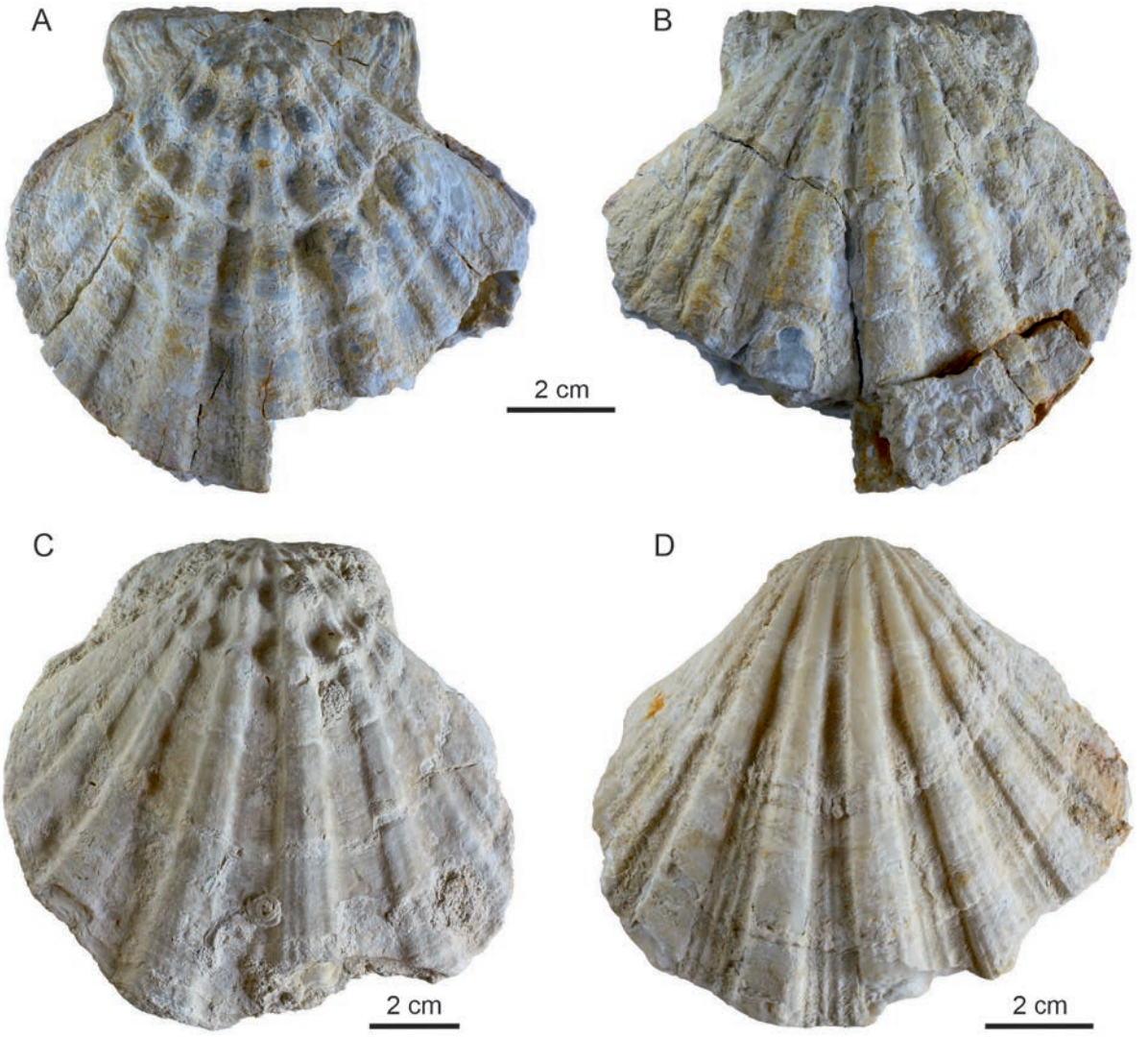
According to Ugolini (1906), although Sacco (1897b, p. 33) united *P. nodosiformis* with *P. latissimus*, the first one should nevertheless be completely separated from the latter. Ugolini (1906) considered *latissimus* and *nodosiformis* not only as distinct species, but also placed them into separate subgenera of the genus *Chlamys* Röding, 1798: *latissimus* to *Gigantopecten*, and *nodosiformis* to *Lyropecten* Conrad, 1862. Furthermore, Ugolini (1906, p. 186) stated that the Austrian specimens attributed by Hörnes (1867, pl. 56, figs 3, 4 and pl. 57, figs 3, 4) to *Pecten latissimus* can be considered perfectly similar to the specimen presented by Pusch (1837, pl. 5, fig.



Text-fig. 5. *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836), lectotype, Skotniki, Poland. A – Left valve of articulated shell; B – Right valve of the same specimen. Copies from Roger (1939, pl. 28, figs 1, 1a; as *Chlamys latissima* var. *nodosiformis*); C, D – Overcast (UCBL-FSL 29270) of the first plaster cast (No. 29270 in Mangold and Mongereau 1966) of the specimen presented by Roger (1939): C – Left valve; D – The same cast, right valve missing a large portion of the disc. E, F – Museum labels of the first plaster cast with inventory number 29270 (F) and the facsimile of the original label with Pusch's hand writing (E). Photographs by E. Robert.

9a, b) and should therefore be assigned to the species *nodosiformis*, whereas the others (Hörnes 1867, pl. 56, figs 1, 2 and pl. 57, figs 1, 2) certainly belong to Fontannes' species *restitutensis* and not to Brocchi's species *latissima*.

A similar opinion was expressed by Kautsky (1928, pp. 252, 253), who stated that the specimens in the Natural History Museum in Vienna, designated by Hörnes as *Pecten latissimus* (which also included specimens from Upper Silesia), seem to be appar-



Text-fig. 6. *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836) from Kików (A, B) and Widuchowa (C and D) in Poland, two other localities from which Pusch (1836) reported the species. A, B – Articulated shell with fragmented ventral disc portion (MZ VIII Ml 2603/1): A – Exterior of left valve; B – Exterior of right valve; C – Left valve of articulated shell with abraded margins (MZ VIII Ml 4147); D – Exterior of right valve missing ears with well visible secondary riblets developed on both primary ribs and interspaces (MZ VIII Ml 4149/MG). Photographs by D. Nast.

ently more related to *restitutensis* than to *latissimus*. However, he decided to distinguish a new variety of Brocchi's species *latissima* which he called *austriaca*, ignoring Pusch's work (1837) and the earlier specific name *nodosiformis.*

The name *Macrochlamis* fell completely into oblivion and was not mentioned again until the publication of the *Genera of Bivalvia: Systematic and bibliographic catalogue* by Vokes (1967, p. 177), who stated it as an error of the name *Macrochlamys*, and accepted *Gigantopecten* Rovereto, 1899 as the substitute name for *Macrochlamys*. However, in mentioning the name *Grandipecten* Cossmann, 1914 as an alternative name for *Macrochlamys*, a junior synonym of *Gigantopecten*, he himself made a mistake and the latter was published with an error as *Gifandopecten* Rovereto.

Shortly thereafter, Hertlein (1969, p. *N*358) in the *Treatise on Invertebrate Paleontology* recognized the priority of *Macrochlamis* over *Macrochlamys*, and therefore also over *Gigantopecten,* without any discussion. Conversely, Malatesta (1974, p. 52) consid-

ered the name *Macrochlamis* to be a misprint of the name *Macrochlamys*.

The correctness of the latter position may be confirmed by the fact that the name *Macrochlamis*, after its first appearance in June 1897, was apparently never mentioned except by Dall (1898, p. 729), and was completely ignored by Rovereto (1899), Sacco (1904), Ugolini (1906), Cossmann (1914), Roger (1939), and Glibert and van de Poel (1965), all of whom confirmed the validity of the name *Gigantopecten* instead of *Macrochlamys.*

It should also be remembered that part 24 of Sacco's monograph (containing the diagnosis of *Macrochlamys*) must have been written and submitted for printing much earlier than the short advertisement for its contents in which the name *Macrochlamis* appeared. After all, according to the rule for translating Greek names into the Latin alphabet, the correct spelling is *Macrochlamys*.

Unfortunately, Hertlein's opinion was accepted by Vokes (1980, p. 229), who had previously considered the name *Macrochlamys* to have priority (Vokes 1967, p. 177), and later by other researchers, including myself (see Waller and Bongrain 2006, pp. 158–162). However, it can be assumed that this opinion resulted from the fact that the *Treatise on Invertebrate Paleontology* was a kind of bible for palaeomalacologists.

On the other hand, the opinion expressed by Malatesta (1974) was accepted by Freneix *et al.* (1987, p. 32), who raised *Gigantopecten* to generic rank but at the same time emphasized the distinction of the Miocene forms known as *nodosiformis* from the typical Pliocene form *latissima*, recognizing the former as a subspecies of the latter. However, they did not confirm Malatesta's opinion regarding Fontannes' species *restitutensis*. According to Malatesta (1974), the differences between *restitutensis* and *latissimus* given by Fontannes (1884) were considered negligible and consequently *restitutensis* was considered as a junior synonym of *latissimus*.

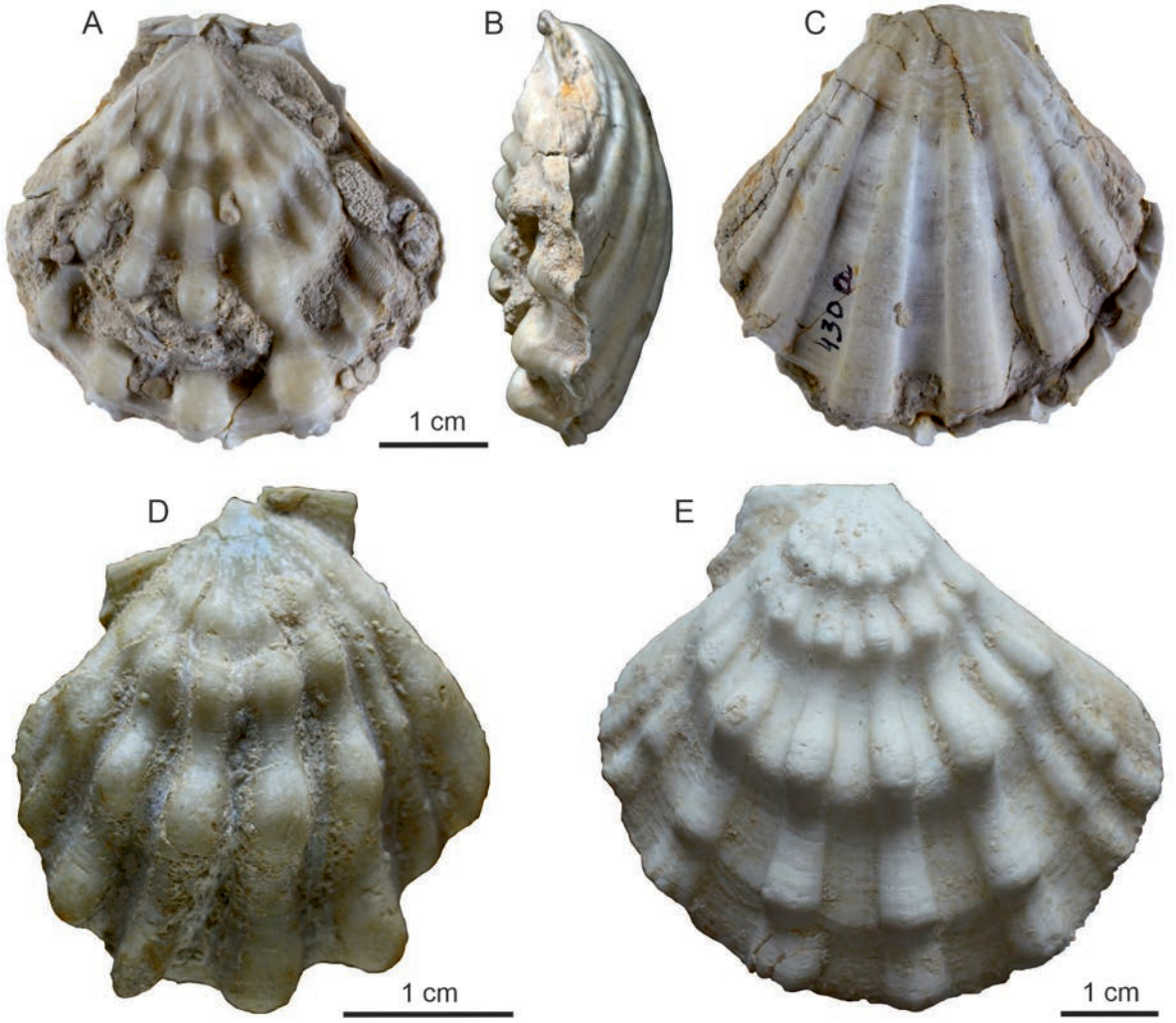
Bongrain (1992) was the first to recognize all three taxa as separate species within the Neogene representatives of the genus *Gigantopecten*, i.e., *latissima* (in her opinion the species probably occurs in the Serravallian and certainly ranges from the late Tortonian to the Early Pliocene), *nodosiformis* (known to occur from the middle Burdigalian to the middle Tortonian), and *restitutensis* (restricted to the late Burdigalian of the Mediterranean).

I agree with the supposition expressed by Bongrain (1993) that *Pecten nodosiformis* and *Pecten melii* (a replacement name for *Pecten Ponzii* Meli, 1881 introduced by Ugolini in 1905) are synonyms. This view is supported by both the Middle Miocene specimens from Poland and Slovakia, and from Hungary described by Csepreghy-Meznerics (1960). In the work on the family Pectinidae from Hungary she clearly stated the presence of specimens exactly comparable to *Chlamys melii* (Csepreghy-Meznerics 1960, p. 33, pl. 26, fig. 1; a specimen from Mátraverebély-Szupatak), which was also reported earlier by Meli (1889).

In addition, the examined material and the available information and illustrations concerning Ugolini's species *sardous*, established on the basis of a partially preserved small right valve, confirm Bongrain's assumption regarding its taxonomic status. The upper Burdigalian articulated shell from Gabel Geneffe in Egypt presented by Roger (1939, pl. 19, figs 3, 3a as *Chlamys sardoa* Ugolini) and Bongrain [1993, pl. 2, figs 4a, b as *Chlamys sardoa* Ugolini (= *G. nodosiformis*, *morph melii*)], and the left valve from Santa Maria Island in the Azores, illustrated by da Veiga Ferreira (1955, pl. 4, fig. 20 as *Chlamys sardoa* Ugolini) unequivocally convince me that these specimens are indistinguishable from both the Lower Badenian juvenile specimens of *Gigantopecten nodosiformis* of Poland (Text-fig. 7A–C) and Hungary (Csepreghy-Meznerics 1960, pl. 26, fig. 4), and from the Upper Badenian specimen of Romania (Nicorici 1977, pl. 15, fig. 3). The hollow nodules decorating the ribs of the left valve not exceeding 50 mm in height, occur along their entire length, and closely match the ornamentation of Linnæus' present-day species *nodosus*, so that even the Portuguese specimen had previously been so identified (see da Veiga Ferreira 1955, p. 51). Therefore, I am of the opinion that *Chlamys* (*Flexopecten*) *sardous* Ugolini, 1906 should be treated as a junior synonym of *Pecten nodosiformis.*

The over 50-year-old dispute regarding the priority of *Macrochlamis* Sacco, 1897a and *Macrochlamys* Sacco, 1897b was resolved by the International Commission on Zoological Nomenclature in 2008 (Opinion no. 2203). The Commission retained the generic name *Gigantopecten* Rovereto, 1899 (a replacement name for *Macrochlamys* Sacco 1897b), stating that the name *Macrochlamis* Sacco, 1897a is an incorrect original spelling of the name *Macrochlamys*. However, despite this decision, the name *Macrochlamis* was still used by Wysocka *et al*. (2012).

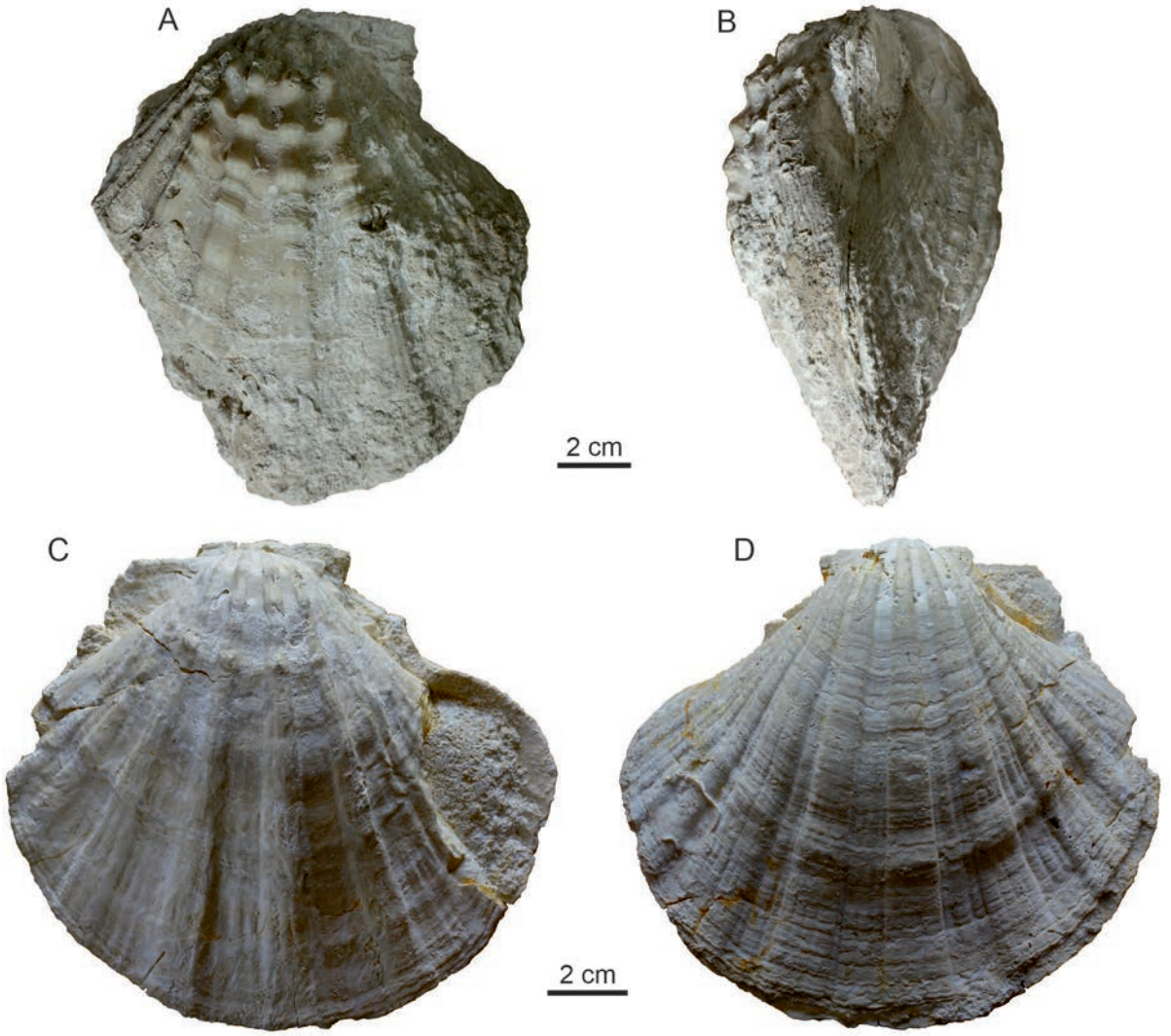
TYPE MATERIAL: The holotype was not designated. The type series was collected in Skotniki, Kików near Stopnica, and Widuchowa near Busko (Pusch 1836, p. 500). However, the number of *Pecten nodosiformia* specimens found at that time remains unknown. It



Text-fig. 7. Juvenile specimens of *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836) from Pińczów (A–C) and Niechobrz (D) in Poland, and Zebegény, Börzsöny Mountains, Hungary (E). A–C – Articulated shell (MUZ PIG 27.II.430a); A – Exterior of left valve; B – Posterolateral view of the same shell; C – Exterior of right valve. D – Exterior of left valve with partly damaged anterior ear (MZ VIII Ml 2872). E – Exterior of left valve missing the posterior ear (MZ VIII Ml 4138). Photographs by D. Nast.

can only be assumed that the syntype series contained at least 7 specimens (Pusch 1836, pp. 500, 501; 1837, p. 42). In addition to his own material collected in Skotniki, Widuchowa, and Kików, Pusch also had specimens found by Zeuschner in Korytnica, which he initially designated as *Pecten laticostatus* Lamarck, 1819 (Pusch 1836, p. 501), then recognized and illustrated under the name *Pecten nodosiformis* var. β (Pusch 1837, pl. 5, fig. 9c). As reported by Friedberg (1936, p. 217) in the early 1930s, there was only one syntype remaining in the Pusch Collection at that time.

The lectotype, designated by Švagrovský (1981, p. 58) as an articulated shell from Skotniki, figured by Pusch (1837, pl. 5, fig. 9a, b) and re-illustrated by Roger (1939, pp. 42, 43, pl. 28, fig. 1, 1a), is shown in Text-figs 4 and 5A, B herein. Its current repository remains unknown. In Roger's monograph devoted to the European representatives of the genus *Chlamys*, it is the only specimen out of the 370 illustrated on 28 plates without any precise location of its original repository. Currently, only its plaster cast is available (Text-fig. 5C, D), housed in the Type Collection of the Faculty of Geosciences, Université Claude Bernard, Lyon, France under the inventory number UCBL-FSL 29270 (no. 29270 in Mangold and Mongereau 1966, p. 16, incorrectly designated as the holotype, with the type locality spelled as *Skotnitzi* and age as Tortonian; Text-fig. 5E, F).



Text-fig. 8. *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836) from Pińczów, Poland. A, B – Articulated shell (MZ VIII Ml 4322) missing the anterior ear and a portion of the anteroventral disc region; A – Exterior of left valve; B – Posterolateral view of the same shell. C, D – Articulated shell (MZ VIII Ml 4146); C – Exterior of left valve with fragmented anteroventral disc portion; D – Exterior of right valve. Photographs by D. Nast.

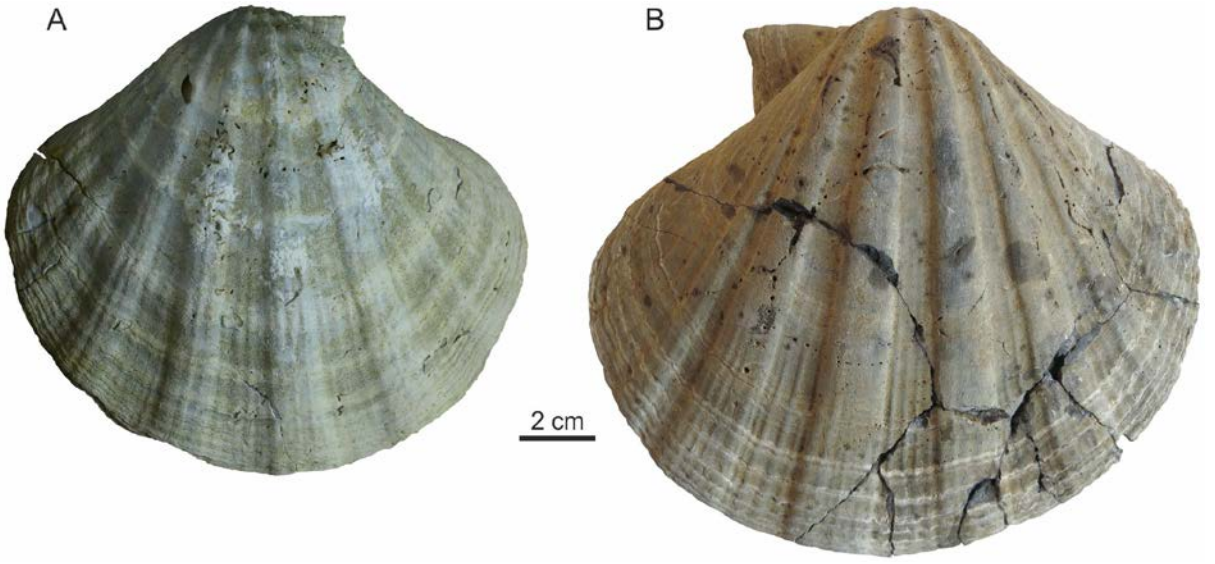
TYPE LOCALITY: Skotniki, Wójcza-Pińczów Ridge, Central Poland, northern marginal part of Central Paratethys.

TYPE STRATUM: Coralline red algae limestones of the Pińczów Formation.

AGE: Middle Miocene, Early Badenian (late Langhian).

ORIGINAL DIAGNOSIS: The original diagnosis given by Pusch (1836, p. 500) is repeated herein in this work (p. 3) along with its English translation. A year later, Pusch (1837, p. 42) presented a slightly emended diagnosis along with an illustration of the specimen from Skotniki.

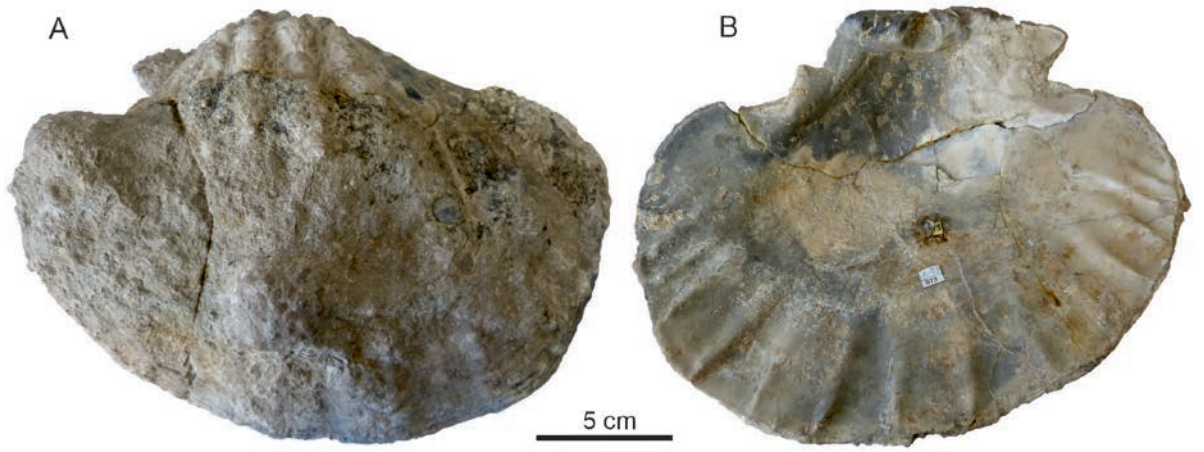
MATERIAL EXAMINED: Poland: 1 valve (SMNH-PZ-N-726) from Biskupice near Zabrze; 1 valve (MZ VIII Ml 4288) from Boczkowice; 2 valves (MGUWr 1889s, 1880s) from Boguchwałów near Głubczyce; 2 valves (MZ VIII Ml 2603/8–9) from Bogucice; 1 shell (MGUWr 1887s/1/l), fragment of 1 valve (MUZ PIG 24.II.5) from Chańcza; 13 valves (MZ VIII Ml 718;



Text-fig. 9. *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836) from Khorosno (A) and Mohylnytsia near Trembovlya (B), Ukraine. A – Exterior of left valve missing the anterior ear and with fragmented posterior ear (MZ VIII Ml 4139). B – Exterior of right valve missing the anterior ear (SMNH-PZ-N-1104). Photographs by D. Nast (A) and S. Bakayeva (B).

specimen MZ VIII Ml 718/1 illustrated in Jakubowski *et al*. 1996, pl. 197, fig. 6 and pl. 198, fig. 8), 1 valve (MUZ PIG 28.II.59), 1 valve (ZNG PAN A-I-73/970 illustrated in Friedberg 1936, pl. 35, fig.1) and fragments of 2 valves (ZNG PAN A-I-73/972) from Chomentów; 1 valve (MZ VIII Ml 4134), fragments of 3 valves (MZ VIII Ml 4146) from Gołuchów; 1 valve (MZ VIII Ml 4145) from Grobie; 1 shell (MZ VIII Ml 2603/10) from Kapturów near Szczaworyż; 1 shell (MZ VIII Ml 2603/1; illustrated in Studencka and Studencki 1988, text-fig. 5, fig. 1a, b and in Jakubowski *et al*. 1995, pl. 196, fig. 6) from Kików (Text-fig. 6A, B); 1 shell (MUZ PIG.28.II.328) from Konradów near Pińczów; 1 valve (MZ VIII Ml 4031), 1 valve (MWGUW 001974), fragment of 1 valve (SMNH-PZ-N-2514), 1 shell (private coll. of Edward Noniewicz) from Korytnica; 2 shells, 15 valves (MZ VIII Ml 2872), 1 valve (MZ VIII Ml 4333), 1 shell (ZNG PAN A-I-73/972 illustrated in Friedberg 1936, pl. 36, fig. 2a, b), 1 valve (ZNG PAN A-I-73/971 illustrated in Friedberg 1936, fig. 2a, b) and 8 valves (ZNG PAN A-I-73/973) from Niechobrz (Text-figs 7D and 10); fragment of 1 valve (MZ VIII Ml 4135), fragments of 9 valves (MUZ PIG 24.II.180) from Osówka Stara (formerly Ossówka); 1 shell, 5 valves (MZ VIII Ml 2603/2-7; MZ VIII Ml 2603/2 illustrated in Studencka and Studencki 1988, text-pl. 4), 1 valve (MZ VIII Ml 3665), fragment of 1 valve (MZ VIII Ml 4137), 1 shell (MZ VIII Ml 4146), 1 shell (MZ VIII Ml 4322), 1 valve (MUZ PIG 27.II. 430), 1 shell (MWGUW 002006), 1 shell (MWGUW 003940), 1 shell (MUZ PIG 27.II.430a), 1 shell (MUZ PIG 28.II. 327), 1 shell (MUZ PIG 28.II. 563), 6 valves (ZNG PAN A-I-73/975–978) from Pińczów (Text-figs 7A–C, 8); 1 valve (MZ VIII Ml 4133) from Skotniki (Text-fig. 1B); fragments of 2 valves (MZ VIII Ml 4332) from Skowronno; fragment of 1 valve (MUZ PIG 32.II.169), 1 shell (SMNH-PZ-N-755) from Szczaworyż; 1 shell (MUZ PIG 28.II.565) from Szczecno; 1 shell (MZ VIII Ml 4147), 3 shells, 4 valves (MZ VIII Ml 4149) from Widuchowa (Text-fig. 6C, D); 1 shell (MZ VIII Ml 4147), 1 shell (MZ VIII Ml 4141) from Zabelin; 1 shell (MZ VIII Ml 2603/11) from Żerniki. Ukraine: 1 valve (MZ VIII Ml 4139), 1 shell, 4 valves (MZ VIII Ml 4140) from Khorosno (formerly Chrusno) (Text-fig. 9A); 3 valves (ZNG PAN A-I-73/974.1–3) from Kuriany (formerly Kurzany); 1 valve (SMNH-PZ-N-1104) from Mohylnytsia (formerly Mogielnica) (Text-fig. 9B); fragments of 2 valves (SMNH-PZ-N-63) from Nadrichne (formerly Dryszczów);1 valve (SMNH-PZ-N-340) from Pidhaytsi (formerly Podhajce); 1 valve (SMNH-PZ-N-787), 1 shell (SMNH-PZ-N-2868) from Pustomity (formerly Pustomyty); fragment of 1 valve (SMNH-PZ-N-2282) from Zboriv (formerly Zborów).

DESCRIPTION: Shell up to 160 mm high and 202 mm long; massive, sometimes strongly thickened; inequivalve; nearly orbicular in outline sometimes more or less oblique; both valves moderately convex,



Text-fig. 10. *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836) from Niechobrz, Poland. A – Exterior of left valve partly encrusted with coralline algae (ZNG PAN A-I-73/973), the largest specimen from Poland, missing the posterior ear; B – Interior of the same specimen showing interspaces wider than the primary ribs decorating its external surface. Photographs by B. Studencka.

the right a little more so; auricles very large (almost 2/3 length of shell), subequal; umbonal angle c. 110º; growth stages clearly distinct.

The right valve sculptured with 8 (less often 10) obvious, unevenly spaced wide, low rectangular primary ribs, sometimes five central ones are stronger than the others. Interspaces narrower than ribs, sometimes with 1–3 weak, narrow riblets that appear slightly earlier than 3–5 weakly or strongly developed secondary riblets on the primary ribs. Commarginal lamellae closely spaced on radial ribs and interspaces, somewhat coarser near ventral margin than elsewhere. Small, orthogyrate beak projects farther beyond hinge line than the left beak. Auricles sculptured by fine growth lines more prominent on anterior one; byssal notch weak.

The left valve sculptured with 8 obvious primary ribs, which near the umbonal area are decorated with strongly developed hollow nodes, ordinarly arranged in 5 very distinct commarginal rows. In this part of the shell, delicate commarginal lines only in the interspaces, narrower than the ribs, then they also decorate the primary ribs, on which 3 secondary riblets appear. The commarginal lines vary in spacing from very closely to more widely set.

REMARKS: The specimens of *Gigantopecten nodosiformis* examined are considerably variable in the shell size, outline and radial ornamentation. It can be assumed that for this reason several names were given to this species: *Pecten Ponzii* by Meli (1881), *Macrochlamys latissima* var. *gibboplana* by Sacco (1897b), *Pecten Melii* by Ugolini (1905), *Chlamys* (*Flexopecten*) *sardous* by Ugolini (1906), *Chlamys* (*Lyropecten*) *nodosiformis* var. *miocostulata* by Ugolini (1906) and *Pecten* (*Oopecten*) *latissimus* Brocch. var. *austriaca* by Kautsky (1928).

The smallest examined specimen (NHM 1982/10102, Z-17270) comes from the Upper Badenian in Devinská Nová Ves, Slovakia. This flat left valve is 27 mm long and 27 mm high, with the apical angle 89º and is decorated with 8 rounded ribs on which the hollow nodules form only 3 rows (see Švagrovský 1981, pl. 13, fig. 3). The rounded interspaces are as wide as the ribs lacking any secondary riblets. The entire surface is decorated with dense commarginal lines, slightly stronger in the interspaces. The largest examined specimen (ZNG PAN A-I-73/973) from the Lower Badenian in Niechobrz, Poland, attains a length of 202 mm and a height of 155 mm, and is characterized by a clearly oblique outline, with the posterior part being significantly larger than the anterior one (Text-fig. 10), which causes the apical angle to reach as much as 120º, which is unique for this species. Its outline is the same as that of the Serravallian specimen from Omo Morto in the Central Apennines in Italy (Bongrain 1993, pl. 1, fig. 4) and the Zanclean specimen from Monte Mario near Rome (Bongrain 1993, pl. 1, fig. 5) defined by that author as *Gigantopecten nodosiformis* morph *melii.*

The outline of shell changes in the ontogeny: from oval with an umbonal angle of about 90º in juvenile forms to almost circular with an umbonal angle of up to 110º in adults. Changes also concern the convexity of the valves. In juvenile forms, the left valve is very slightly convex or almost flat (Text-fig. 7B;

Csepreghy-Meznerics 1960, pl. 26, fig. 4; Nicorici 1977, pl. 15, fig 3b), whilst the right valve is convex with the maximum convexity halfway up its height. In the adult forms, both valves are convex, the right one is more convex, and its maximum convexity is located at 1/3 of its height (Text-fig. 8B).

The examined specimens exhibit a highly variable and irregular secondary radial sculpture, which concerns both the left and right valve. In juvenile forms the primary ribs have a rounded outline (Text-fig. 7; Csepreghy-Meznerics 1960, pl. 26, figs 2, 4, 5), whereas at a later growth stage they become rectangular. Subsequently, secondary riblets may emerge in the interspaces (usually earlier than on the primary ribs). Concerning the concentric sculpture of dense lines, sometimes sharp lirations are equally developed on both radial elements. In some adult specimens, near the ventral margin, a cancellate sculpture is visible that developed by interrupting the dense prominent lirations, and numerous secondary riblets spread over the primary ribs and in the interspaces.

Gigantopecten nodosiformis differs from the closely related species *G. latissimus*, with which it has been often confused, in the outline of the shell, the size of the ears, the number of ribs, and the type of ornamentation. The confusion associated with this species in fact stems from Bronn's note in the *Polens Paläontologie* by Pusch (1837, p. 42). This error was exacerbated by Hörnes' (1867, p. 396) who wrongly included *Pecten nodosiformis* into the synonymy of *Pecten latissimus*.

In contrast to the nearly equilateral to almost circular, fan-shape shell of *Gigantopecten latissimus*, with an umbonal angle ranging from 120º (holotype, right valve; Rossi Ronchetti 1951, pp. 26–29, figs 8a, b), 125º in the Messinian specimens from Algeria (Freneix *et al*. 1987, pp. 32, 33), up to 135º in the Badenian specimens from Hungary (Csepreghy-Meznerics 1960, pls 30 and 31), the shell of adult *Gigantopecten nodosiformis* is less circular with an umbonal angle not exceeding 110º. Both valves in the adult forms are convex, however, unlike *G. latissimus*, which is characterized by a greater convexity of the left valve compared to the right, in *G. nodosiformis* the left valve is less convex than the right one.

The greatest differences, however, concern the ornamentation. The number of primary ribs in *nodosiformis* is much greater (8, less often 10) than in *latissimus*, the right valve of which is decorated with only 3 to 4 wide, low primary ribs disappearing towards the ventral margin, separated by wider interspaces, while the left valve is adorned with 3 wide ribs of the same width as the interspaces. Roger (1939, p. 41) reported that the primary ribs of the left valve are adorned with hollow nodes arranged in 3–4 commarginal rows, while in *nodosiformis* the primary ribs are decorated with strongly developed hollow nodes, usually arranged in 5 very distinct commarginal rows (as previously pointed out by Nicorici 1977, p. 133), but there may be as many as 8 of them (Text-fig. 8A, B).

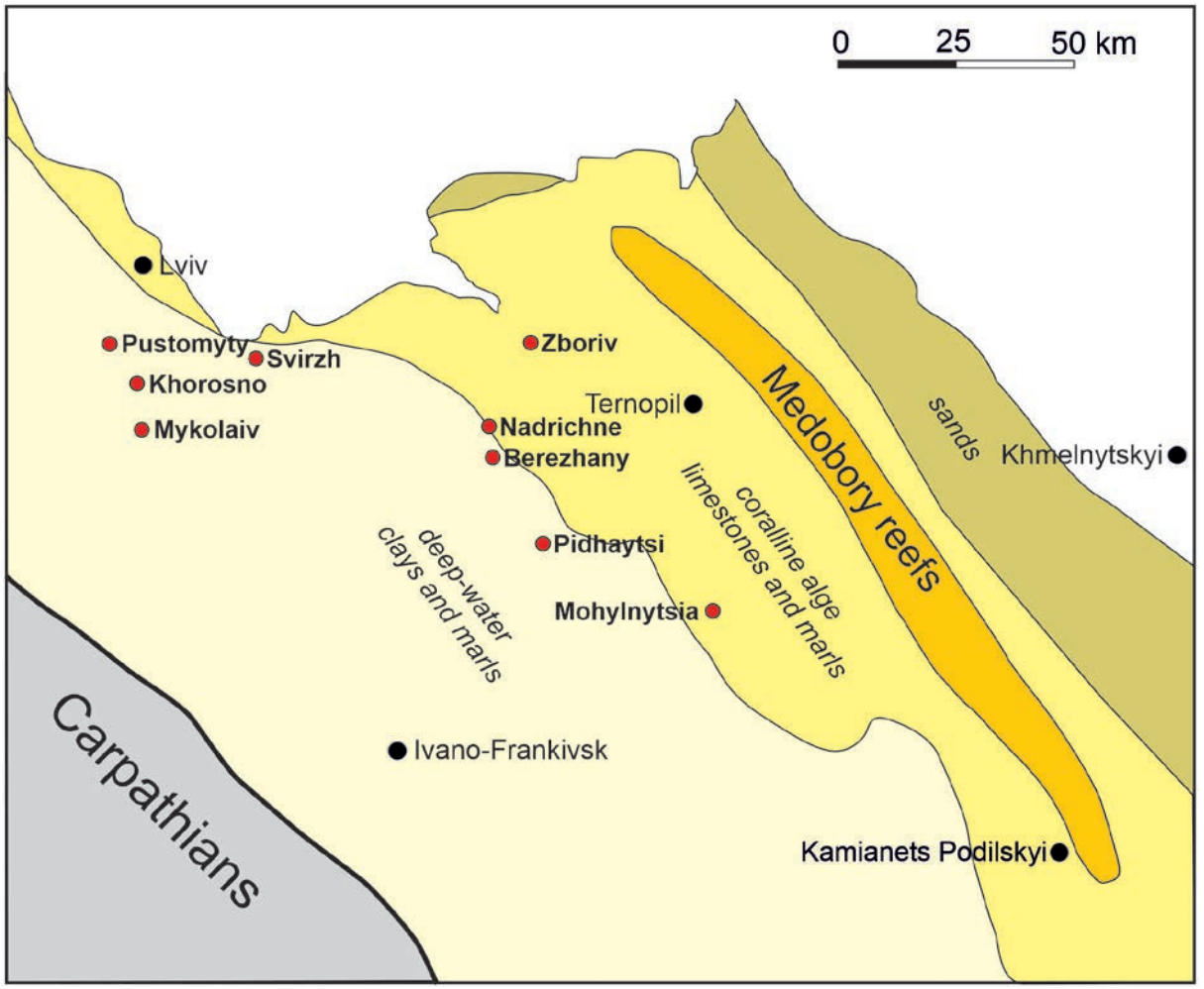
STRATIGRAPHIC AND GEOGRAPHIC RANGE

The species first appeared in the Early Miocene (middle Burdigalian) of the Lower Tagus Basin (da Veiga Ferreira 1961), and later its area embraced the northeastern Atlantic and the Mediterranean Sea. In the Central Paratethys it appeared in the Karpatian (late Burdigalian) of the North-Alpine-Carpathian Foredeep and became extinct in the Late Badenian (early Serravallian). In the Middle Miocene, *Gigantopecten nodosiformis* was widespread, extending along the Atlantic coast of Portugal to the Mediterranean (Italy, Sardinia, Syria and Turkey) and the Central Paratethys. During the Langhian (Early Badenian), *G. nodosiformis* reached its greatest distribution in Europe, when the prevailing climatic conditions allowed it to inhabit the areas of the highest latitude, around 50º N, in the northern part of Central Paratethys. The northernmost occurrence of this species is Chomentów (N 50º68'57.33", E 20º51'99.67"), located on the southern slopes of the Holy Cross Mountains. Schultz (2001, pp. 253, 254) summarized its records from the Miocene of the Atlantic, Mediterranean, and Central Paratethys. According to Bongrain (1993), in the Mediterranean *G. nodosiformis* is known with certainty until the Zanclean (Pliocene) of Italy.

DISTRIBUTION IN POLAND AND UKRAINE

In Poland – the northernmost part of Central Paratethys – the occurrence of *G. nodosiformis* is limited to the Lower Badenian (corresponding to the upper Langhian; Middle Miocene) of the:

– Silesian Upland: Boguchwałów near Głubczyce (formerly Hohndorf bei Leobschütz) (Roemer 1870), Bytom-Bobrek (Roemer 1870), Bytom-Miechowice (formerly Miechowitz) (Roemer 1870; Krzeszowska and Machłajewska 2010), Dzierżysław near Kitrz (formerly Dirschel bei Katscher) (Roemer 1870), Zabrze-Mikulczyce (formerly Mikultschütz) (Roemer 1870);



Text-fig. 11. Map of western Ukraine showing the distribution of Badenian deposits during the maximum phase of the Late Badenian transgression. Red dots indicate sites yielding the specimens of *Gigantopecten nodosiformis* (Pusch and de Serres in Pusch, 1836). Modified after Maslov and Utrobin (1958).

– Miechów Upland: Boczkowice (this paper), Małoszów (Krach 1947), Trzonów (Michalski 1884);
– Wójcza-Pińczów Ridge: Bogucice (Studencka and Studencki 1988), Chańcza (Kowalewski 1930), Gołuchów (this paper), Grobie (this paper), Kików near Stopnica (Pusch 1836, 1837; Studencka and Studencki 1988), Osówka Stara (this paper), Piestrzec (Kosiński 1884), Pińczów (Kontkiewicz 1882; Friedberg 1932, 1936; Studencka and Studencki 1988), Skotniki near Busko (Pusch 1836, 1837; this paper), Skowronno (this paper), Smogorzowice near Stopnica (Friedberg 1932, 1936), Stawiany Pińczowskie (Krach 1967), Suchowola (Kosiński 1884), Szczaworyż (Studencka and Studencki 1988), Widuchowa near Busko (Pusch 1836, 1837; this paper), Zabelin (this paper), Żerniki (Studencka and Studencki 1988; this paper);
– southern slopes of the Holy Cross Mountains: Chomentów (Friedberg 1932, 1936; Jakubowski in Jakubowski *et al.* 1996), Korytnica (Pusch 1837; Friedberg 1932, 1936);
– marginal part of the Carpathians: Głobikowa near Pilzno (Zeuschner 1845), Niechobrz (Uhlig 1883; Friedberg 1903, 1932, 1936; Gołąb 1932; Urbaniak 1986), Olimpów (Uhlig 1883; Friedberg 1903, 1932, 1936; Urbaniak 1986), Siedliska (Uhlig 1883), Tarnów (Zeuschner 1845), Wola Zgłobieńska (Uhlig 1883).

In Ukraine, *Gigantopecten nodosiformis* is known exclusively from the Lower Badenian of Opillia (formerly Opole), southwestern part of Podolia (Text-fig. 11):

Berezhany (formerly Brzeżany) (Zuber 1904), Khorosno (formerly Chrusno) (Wysocka *et al.* 2012;

this paper), Kuriantsi (formerly Kurzany) (Friedberg 1936; Kazakova 1952), Mohylnytsia near Trembovlya (formerly Mogielnica near Trembowla) (Łomnicki 1904), Mykolaiv (formerly Mikołajów), Nadrichne (formerly Dryszczów) (Zuber 1904), Pidhaytsi (formerly Podhajce) (this paper), Pustomity (formerly Pustomyty) (Łomnicki 1904), Swirzh near Peremyshliany (formerly Świrz near Przemyślany) (Kazakova 1952), Welika Wola (formerly Wola Wielka) (Kazakova 1952) and Zboriv (formerly Zborów) (this paper). The species is very rare in all the above-mentioned localities.

PALAEOENVIRONMENT

Gigantopecten nodosiformis, especially in its advanced evolutionary stage, is a common species in the Lower Badenian carbonate deposits of Poland. The heavy, massive shells of this species, preferentially adapted to high-energy, shallow-water environments, occupied fully marine, bioclastic carbonate seafloors. It was collected by Pusch (1836, 1837) from deposits exposed along the top part of the Wójcza-Pińczów Ridge, distinguished as the Pińczów Limestones (Studencki 1988). These limestones were formed under strong to moderate water agitation, at depths estimated as 30–80 m, on an eastward deepening, elongated carbonate platform, located several kilometres from the shoreline. According to Studencki (1988), the Pińczów Limestones are comparable to the Mediterranean coralligenous facies (maërl, prâlines and coralligenous plateau) and its closest analogue may be the Adventure Bank, off southwestern Sicily.

It should be noted that no specimens of *G. nodosiformis* have been detected in the Upper Badenian deposits of Poland (Studencka 1999, 2024). On the other hand, its occurrence in the Central Paratethys during the Late Badenian (early Serravallian) has been confirmed in various inner Carpathian basins (see Csepreghy-Meznerics 1960; Nicorici 1977; Švagrovský 1981 and Schultz 2001), where it became extinct during the Badenian–Sarmatian Extinction Event. The reasons for the extinction of *G. nodosiformis* in the Late Badenian in Poland and Ukraine should be sought in the progressive cooling of waters in the Fore-Carpathian basins compared to the inner Carpathian basins of Central Paratethys during the Middle Miocene Climatic Transition phase about 13.82 Ma (e.g., Harzhauser *et al*. 2010) due to significant changes in the palaeogeography of the Paratethys which induced different directions of sea currents that took place at that time.

CONCLUSIONS

- The description of *Pecten nodosiformis* was first published in the *Geognostische Beschreibung von Polen* by Pusch (1836), the first original book on the geology of the Kingdom of Poland. Until the present study was conducted, this extremely important work had been omitted by all researchers of Neogene pectinids.
- *Gigantopecten nodosiformis* occurs in Poland and Ukraine exclusively in Lower Badenian carbonates. This species, occurring together with large benthic foraminifera *Amphistegina* sp. and *Heterostegina* sp., became extinct at the end of the Early Badenian in the northern Paratethys, but both foraminiferal genera and *G. nodosiformis* still inhabited the remaining areas of the Paratethys in the Late Badenian. Therefore, it can be considered a good indicator of the progressive cooling of the sea-water in the northern part of the Paratethys during the Badenian.
- It has been shown that specimens of *Gigantopecten nodosiformis* are considerably variable in shell outline and radial ornamentation, therefore the names *Pecten Ponzii* by Meli (1881), *Macrochlamys latissima* var. *gibboplana* by Sacco (1897b), *Pecten Melii* by Ugolini (1905), *Chlamys* (*Flexopecten*) *sardous* by Ugolini (1906), *Chlamys* (*Lyropecten*) *nodosiformis* var. *miocostulata* by Ugolini (1906), and *Pecten* (*Oopecten*) *latissimus* Brocch. var. *austriaca* by Kautsky (1928) should be treated as junior synonyms of *G. nodosiformis*, for which a lectotype was designated by Švagrovský (1981).
- The location of the specimen designated as the lectotype remains unknown and is presumed to have been lost. Only its plaster cast is available, housed in the Type Collection of the Faculty of Geosciences, Université Claude Bernard, Lyon, France.
- The description of Skotniki Quarry, from which the illustrated specimen of *Gigantopecten nodosiformis* originated (Pusch 1837, pl. 5, fig. 9a, b), was published by Pusch (1836, p. 458) and then repeated in an abridged Polish edition of the *Geognostische Beschreibung von Polen* (Pusch 1903, p. 202). Unfortunately, subsequent researchers of the Miocene deposits from Skotniki never referred to Pusch's achievements. The present article includes an English translation of the description of the Skotniki Quarry succession along with information about the molluscan fauna collected there by Pusch.

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