

“*Ammodiscus*” *latus* Grzybowski, 1898: Its taxonomy, variability, and affinity to the genus *Trochamminoides* Cushman, 1910

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Abstract

Morphological analysis of the species „*Ammodiscus*” *latus* Grzybowski reveals that the initial part of its second chamber is not planispirally coiled, but has a glomospira-type coiling. In the studied material we observe different morphological forms of “*Ammodiscus*” *latus* that differ mainly in the size of the test, and whether the outline is circular, oval, or asymmetrically oval. We herein describe two forms of “*Ammodiscus*” *latus*: *A. latus* forma *latus*, and *A. latus* forma *ovoidalis*. In some specimens of *A. latus* forma *ovoidalis*, we observe that the interior of the second chamber possesses constrictions that subdivide the interior into elongated pseudochambers. This trend to establish pseudochambers in late ontogeny implies close connections to the genus *Trochamminoides* Cushman, 1910. At present it is not possible to firmly assign a generic designation to “*Ammodiscus*” *latus*, because none of the genera of ammodiscids currently recognised as valid possess the morphological features of “*Ammodiscus*” *latus*.

“*Ammodiscus*” *latus* first appears in the geological record in the Lower Eocene, during the Cenozoic climatic optimum. During the Eocene, the species successfully colonised the Boreal basins, where the species persisted until the Miocene. The migration of “*Ammodiscus*” *latus* and its successful colonisation of the Boreal shelves may be connected with the Eocene climatic cooling.

INTRODUCTION

“*Ammodiscus*” *latus* is one of the most characteristic forms in the Cenozoic flysch-type agglutinated foraminiferal assemblages. It was first recognised by Grzybowski (1898) in his pioneering micropalaeontological study of the submenilite Eocene claystones from the Polish Carpathians. The species has been subsequently identified in different parts of the western Tethys and Atlantic oceans, including the Caribbean (Cushman & Renz, 1948; Maslakova, 1955; Huss, 1966; Gradstein *et al.*, 1988; Kaminski *et al.*, 1989; Olszewska *et al.*, 1996; Bolli *et al.*, 1994; Gradstein & Bäckström, 1996; Osterman & Spiegler, 1996; Olszewska, 1997; Kaminski & Gradstein, 2005; Holbourn *et al.*, 2013; Waśkowska, 2015a and citations therein). The species is regarded to be cosmopolitan (Kaminski & Gradstein, 2005), with a wide geographical and stratigraphic range, and an isobathyal depth distribution (Kaminski & Austin, 1999).

In the course of stratigraphic studies of the Flysch Carpathians, the authors had the opportunity to observe numerous

specimens of “*Ammodiscus*” *latus* and discovered specimens that do not fit within the current definition of the species or the genus. Additionally, it appears that “*Ammodiscus*” *latus* developed and expanded during a period of Earth history that is marked by profound climatic changes, ending with the establishment of the Oligocene – Recent glacial climates. An interesting pattern can be seen in the geographical distribution of the species during this period of global change. With these observations in mind, our goal is to more accurately define the morphological variability of “*Ammodiscus*” *latus* and its geographical distribution.

MATERIALS AND METHODS

Our morphological observations are predominantly based on specimens from the Polish Carpathians, as well as from boreholes in the northern Atlantic basins. The Carpathian samples were mostly collected in the Subsilesian, Silesian,

Skole, Dukla, and Magura Units, while the Boreal specimens are from exploration wells in the Labrador Shelf and North Sea (Gradstein *et al.*, 1994), and from IODP Site 647 (Kaminski *et al.*, 1989).

The Carpathian samples were processed using standard laboratory techniques. Crushed samples were boiled with sodium sulphate, and then sieved over a 68 micron sieve. The IODP samples were boiled in a 1% Calgon solution and sieved over a 63 micron screen.

Selected specimens were cut in the Thin Section Lab at AGH. Analysis of the test ultrastructure and internal structure was carried out in reflected light and in the SEM. Specimens were ground down to half of their original thickness. Photos of the type specimens were used from the revision of the Grzybowski Collection by Kaminski & Geroch (1993). The *Ammodiscus latus* specimens have been deposited in the European Micropalaeontological Reference Center at Micropress Europe, Kraków, Poland.

SYSTEMATICS

“Ammodiscus” latus Grzybowski, 1898, forma *latus*
Plate 1, figs 1-12; Plate 2, fig. 1; Plate 3, figs 1-12

Ammodiscus latus Grzybowski, 1898, p. 282, pl. 10, figs. 27-28

Lituotuba eocenica Cushman & Renz, 1948, pl. 8, fig. 20, 21

Lituotuba navetensis Renz, 1950 (nomen novum)

Type reference. Grzybowski, J., 1898. Otwornice pokładów naftonośnych okolicy Krosna. Rozprawy Wydziału Matematyczno-Przyrodniczego, Akademia Umiejętności w Krakowie, ser. 2, vol. 33, p. 282, pl. 10, fig. 28.

Type level. Late Middle to Late Eocene of the Silesian Nappe of Polish Outer Carpathians.

Type locality. Krościenko Niżne, near Krosno, Poland. Red clays outcropping along the bank of the Wisłok River (Kaminski & Geroch, 1993).

Description. Test consisting of a globular proloculus and a spirally coiled second tubular chamber, often translucent. Wall thick, medium to coarsely agglutinated, consisting of quartz grains, with a somewhat rough surface. The coiled second chamber is relatively thick, of constant diameter or increasing in size very slowly. The initial stage is coiled glomospirally (the first whorl is inclined at a small angle to the subsequent whorl); later coiled in an evolute planispiral. The terminal stage has a tendency to uncoil, with a small straight rectilinear portion that bends away from the planispiral stage. The number of whorls varies from 2.5 to 4.5. Aperture simple, at the open end of the tube.

“Ammodiscus” latus Grzybowski, 1898, forma *ovoidalis*
Plate 2, figs 2, 4-10

Type level. Late Middle to Late Eocene Hieroglyphic beds of the Silesian Nappe of Polish Outer Carpathians.

Type locality. Krzesławice village, next to Szczyrzyc, Poland. Grey-green- grey shales outcropping along the banks of the Stradomka River (N49°48'14.33"; E20°10'25.23").

Reference sections

1. Lipie village at the Rożnów Lake, Poland, grey-green- grey shales outcropping along the banks of the Szczecinówka creek (N49°44'00.3"; E20°45'05.5").
2. Gorlice city, Poland. Grey-green- grey shales outcropping along the banks of the Sękówka River (N49°39'06.89"; E21°10'23.72").

Type Specimens. The holotype and paratypes are deposited in the collections of Micropress Europe, at AGH University of Science and Technology, Krakow.

Description. Test consisting of a globular proloculus and a spirally coiled second tubular chamber, often translucent. Wall thick, medium to coarsely agglutinated, consisting of quartz grains, with a somewhat rough surface. The coiled second chamber is relatively thick, of constant diameter or increasing in size very slowly. The initial stage is coiled glomospirally (the first whorl is inclined at a high angle to the subsequent whorl, as a result the outline of the test is oval); later coiled in an evolute planispiral. One or more constrictions may be present in the second chamber, forming pseudochambers. Often there is an indentation in the periphery of the test at the location of this constriction. The terminal stage has a tendency to uncoil, with a small straight rectilinear portion that bends away from the planispiral stage. The number of whorls varies from 2.5 to 4.5. Aperture simple, at the open end of the tube.

REMARKS AND DISCUSSION

“Ammodiscus” latus displays morphological variability in its test outline resulting from the nature of the coiling of the second chamber. We recognise two formae within the species: the typical *“Ammodiscus” latus* forma *latus*, as illustrated by Grzybowski with a circular outline, and *“Ammodiscus” latus* forma *ovoidalis*, which is elongated or oval in outline. Both forms have a tendency to uncoil. Among some specimens of *“Ammodiscus” latus* forma *ovoidalis*, there is often a slight break or constriction visible at the margin of the test. This break coincides with a constriction in the diameter of the last whorl of the coiled tubu-



Plate 1. *“Ammodiscus” latus* forma *latus* 1. sample 125 4 09 – Rożnów Lake section, Silesian Nappe; 2. sample 70 28 05, Stradomka section, Silesian Nappe; 3. sample 32 2 09, Janoska section, Silesian Nappe; 4. sample 70 22 07, Stradomka section, Silesian Nappe; 5. sample 64 58 05, Stradomka section, Silesian Nappe; 6. sample 65 46 05, Stradomka section, Silesian Nappe; 7. sample 7 21 06, Stradomka section, Silesian Nappe; 8. sample 32 10 6, Janoska section, Silesian Nappe; 9. sample 11/9/10, Poręby–Czarnotówki section, Skole Nappe; 10. sample 17/4/12, Sękówka section, Silesian Nappe; 11. sample 17/4/12, Sękówka section, Silesian Nappe; 12. sample 11/9/10, Poręby–Czarnotówki, section, Skole Nappe. Specimens from the Hieroglyphic beds. Scale bar = 100 μm.



Plate 2. 1–3 transitional forms “*Ammodiscus*” *latus* forma *ovoidalis* and “*Ammodiscus*” *latus*; 4–10 “*Ammodiscus*” *latus* forma *ovoidalis* 1. sample 5 19 05, Stradomka section, Silesian Nappe; 2. sample 17 4 12, Sękówka section, Silesian Nappe; 3. sample 83 17 09, Lipie section, Silesian Nappe; 4. sample 64 58 05, Stradomka section, Silesian Nappe; 5. sample 64 58 05, Stradomka section, Silesian Nappe; 6. sample 67 48 05, Stradomka section, Silesian Nappe; 7. sample 125 4 09, Rożnów Lake section, Silesian Nappe; 8. sample 64 58 05, Stradomka section, Silesian Nappe; 9. sample 17 4 12, Sękówka section, Silesian Nappe; 10. sample 27 7 12, Sękówka section, Silesian Nappe. Specimens from the Hieroglyphic beds. Scale bar = 100 μm.

lar chamber, which means the second chamber appears to be subdivided into long pseudochambers (Pl. 2, figs 7, 10). These pseudochambers affect the overall shape of the test. Thickenings in the test wall are observed at the beginning of the successive pseudochamber, and as a result the test margin may appear to be deformed.

“Ammodiscus” latus is a comparatively large species of *Ammodiscus*, with a test diameter typically reaching 0.8 mm in the Carpathian assemblages. On the boreal continental shelves, Kaminski & Gradstein (2005) report specimens with diameters up to 2 mm, more than twice the size of the Carpathian specimens.

In the original description of *Ammodiscus latus* by Grzybowski (1898), which is upheld by subsequent authors (e.g., Morgiel & Olszewska, 1981; Kaminski & Geroch, 1993; Olszewska *et al.*, 1996; Kaminski & Gradstein, 2005), the coiling of the second chamber is typically described as planispiral. Likewise this is the case with the species *Lituotuba eocenica* Cushman & Renz, 1948 (later renamed *Lituotuba navetensis* Cushman & Renz, 1950) from the Eocene Navet Formation of Trinidad. However, the illustrations of both species clearly show that the initial whorl of the coiled second chamber is not really planispiral, but coiled in a glomospiral manner. The initial whorl is offset at a small angle to the subsequent planispiral part of the test. This is particularly visible in the illustrations of the lectotype, paralectotype, and plesiotype specimens of *“Ammodiscus” latus* presented by Kaminski & Geroch (1993), and by Kaminski & Gradstein (2005). This feature is also observed in illustrations given by Cushman & Renz (1948); Geroch & Gradzinski (1955); Geroch (1960); Morgiel & Olszewska (1981); Geroch & Nowak (1984); Olszewska *et al.* (1996); Kaminski & Huang (1991); Neagu *et al.* (2011); Waśkowska (2014b), and by Waśkowska & Cieszkowski (2014) (Pl. 3).

Grzybowski (1898) described the species *Ammodiscus umbonatus* alongside *Ammodiscus latus*, noting that the two species are very similar to one another. In his original description of *Ammodiscus latus*, Grzybowski noted that the species has few whorls, which are thick and distinct, and that the second chamber finally uncoils. *Ammodiscus umbonatus* was described by Grzybowski as possessing a larger number of whorls as well as a large round proloculus. The forms with a large proloculus were regarded by Kaminski & Geroch (1993) to be megalospheric forms of *Ammodiscus latus*. Jurkiewicz (1967) in his observations of the Grzybowski collection noted that some of the specimens labeled *Ammodiscus latus* better correspond to the description of *Ammodiscus umbonatus*. Jurkiewicz proposed that specimens possessing a small number of whorls in which

the second chamber has a constant diameter should be placed in the species *latus* (Jurkiewicz assigned the species to *Lituotuba*), whereas specimens with a greater number of whorls that increase in diameter with ontogeny and lack a terminal uncoiled stage should be assigned to the species *umbonatus*. We observe this *umbonatus* sensu Jurkiewicz in our material from the Carpathians and the boreal Atlantic seas. In the umbilical region of the test, the second chamber increases in diameter and is coiled in a convolute planispire in which subsequent whorls slightly overlap the previous ones, which allows a greater number of whorls to be present. The increase in chamber diameter with ontogeny means that the test is bowl-shaped, with a depressed umbilical area. Such forms are consistent with the descriptions given by Jurkiewicz (1967) and by Grzybowski (1898). The initial whorl, similar to *“Ammodiscus” latus*, is coiled in a glomospiral manner.

A form that displays close morphological affinity to *“Ammodiscus” latus* is the species *Ammodiscus pennyi* Cushman & Jarvis, 1928, originally described from the lower Paleocene of Trinidad. This species has been reported from Upper Cretaceous and Paleocene localities by Cushman & Jarvis (1932), Bolli *et al.* (1994), Kaminski & Gradstein (2005), and Holbourn *et al.* (2013). The main difference between the two species is seen in the larger dimensions of *Ammodiscus pennyi*, which may possess as many as 6 whorls, and in the fact that the species sometimes displays irregular coiling in the final one or two whorls. Like *“Ammodiscus” latus*, the initial stage of *Ammodiscus pennyi* is not planispiral, but glomospiral. The glomospiral stage of *A. pennyi* may be even better developed than *“Ammodiscus” latus*, and may encompass the first two whorls. However, *Ammodiscus pennyi* does not display a tendency to uncoil. The obvious morphological similarities between two species suggests that they are closely related.

Geographical and Stratigraphic Range

“Ammodiscus” latus is known from the Paleogene and lower Neogene from the Northern Hemisphere. Bolli *et al.* (1994) reports it from the lower Eocene of the Caribbean region, where it is recorded as occurring rarely in the Morozovella subbotinae to the Morozovella formosa formosa Zones. In the Celebes Sea it was found in the lower Eocene (Kaminski & Huang, 1991) (Fig. 1). It is also recorded as *Lituotuba eocenica* from the Middle Eocene in Trinidad (Cushman & Renz, 1948). The specimens identified as *Ammodiscus latus* from the Upper Cretaceous and Paleocene of northeastern Mexico (Alegret & Thomas, 2001), which would be the oldest report of the species, likely belong to another species.

In the Carpathian basins, the first occurrence of “*Ammodiscus*” *latus* is correlated to the Lutetian/Bartonian boundary. It is a widely-occurring form that continues until the end of the Eocene (e.g., Pokorný, 1953; Maslakova, 1955; Huss, 1966; Jurkiewicz, 1967; Morgiel & Olszewska, 1981; Geroch & Nowak, 1984; Olszewska *et al.*, 1996; Olszewska 1997; Kaminski & Gradstein, 2005; Neagu *et al.*, 2011; Waśkowska, 2015a and citations therein). “*Ammodiscus*” *latus* is regarded as a stratigraphic index taxon in the Outer Flysch Carpathians, a marker species for the Bartonian stage. The *Ammodiscus latus* partial range zone is defined as the interval between the FO of “*Ammodiscus*” *latus* and the FO of *Reticulophragmium gerochi* Neagu *et al.* 2011 (which in the older literature corresponds to the older morphotype of *Reticulophragmium rotundidorsatum* (Hantken, 1875)). “*Ammodiscus*” *latus* displays an optimum or acme in the upper Eocene.

In the Newfoundland region, the range of “*Ammodiscus*” *latus* is similar to its range in the Carpathians. It is recorded from the upper part of the Middle Eocene until the upper Eocene (Thomas, 1994a,b; 2001). In the deep Labrador Sea at IODP Site 647, an “*Ammodiscus latus* – *Turrilina alsatica* assemblage” was defined based on the common occurrence of these two species in the Lower Oligocene (Kaminski *et al.*, 1989; Kaminski & Ortiz, 2014). In the North Sea, the species is recorded from the Upper Eocene and Oligocene (Gradstein *et al.*, 1988; Charnock & Jones, 1990; Gradstein & Bäckström, 1996). In the northern Atlantic and Arctic basins, the species is recorded until the Late Miocene (Osterman & Spiegler, 1996; Kaminski *et al.*, 2005; Kaminski & Gradstein, 2005; Holbourn *et al.*, 2013) (Fig. 1). At lower latitudes in the Western Tethys, “*Ammodiscus*” *latus* has been reported to occur until the Upper Eocene (e.g., Geroch & Nowak, 1984; Kaminski & Huang, 1991; Bolli *et al.* 1994; Morlotti & Kuhnt, 1992; 1994, Olszewska *et al.*, 1996; Waśkowska, 2014). The specimens illustrated by Kender *et al.* (2008) from the Upper Oligocene of offshore Angola display more convolute coiling, and likely belong to a different species.

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In the Paleogene, we observe geographical differences in the stratigraphic range of “*Ammodiscus*” *latus*. This form, which first appears in the Early Eocene at low latitudes progressively expands its range in the Middle to Late Eocene and colonises the middle and high latitudes, where it finds it optimal living conditions. It becomes a cosmopolitan form in deep-water assemblages, and achieves its maximum abundance and size. Such features displayed by a primitive agglutinated foraminifer are an indicator of optimal palaeoecological conditions. The Eocene was a time of intense and rapid climatic and oceanographic changes, which left their imprint on the deep sea environment. During the Early Eocene, the highest deep-ocean temperatures were recorded during the greenhouse conditions of the Early Eocene Climatic Optimum (Zachos *et al.*, 2001). From this point, temperatures progressively cooled, sometimes in a step-wise manner, culminating in the massive glaciation of Antarctica during the Early Oligocene (e.g., Miller *et al.*, 1987; 2005; Ortiz & Thomas, 2006; Zachos *et al.*, 2001; Coxall *et al.*, 2005; Lear *et al.*, 2008; Galazzo *et al.*, 2013). Concurrently, in the deep ocean basins a succession of faunal turnovers took place, which were certainly linked to periods of rapid climatic change (e.g., Keller, 1983a, 1986; Corliss, 1981; Miller *et al.* 1987; Kaminski *et al.*, 1989; Milner, 1992; Ortiz & Thomas, 2006; Kaminski & Ortiz, 2014). Additionally, widespread acmes of certain agglutinated foraminiferal species are observed in the deep ocean at this time (Kaminski & Gradstein, 2005), reflecting changes in the trophic conditions at the sea floor. Periods of rapid climatic cooling continue to occur throughout the Neogene (Miller *et al.*, 1987; Zachos *et al.*, 2001), culminating in the onset of northern hemisphere glaciation, but the link between Miocene-Pliocene climatic change and the benthic and especially agglutinated assemblages is less widely known. In any case, during the cool period of the Early Oligocene, “*Ammodiscus*” *latus* colonised the cooler regions of the northern Atlantic, becoming especially common on the Newfoundland margin and in the Central North Sea, and at the same time reaches its maximum size.

Taxonomic implications: “*Ammodiscus*” *latus* – *Ammodiscus umbonatus*

The generic affiliation of “*Ammodiscus*” *latus* is still not

resolved. The widely-accepted definition of the genus *Ammodiscus* given by Loeblich & Tappan (1964, 1988) clearly states that the coiling of the second chamber is planispiral. No mention is made of a glomospirally-coiled initial stage. In 1993 Reitlinger (in Vdovenko *et al.*, 1993) distinguished the subgenus *Rectoammodiscus*, in which the second chamber bends away from the planispiral portion at a right angle, and becomes rectilinear. This subgenus was elevated to genus rank by Kaminski (2004). The coiling of the second chamber in *“Ammodiscus” latus* does not fit within the current definition of either *Ammodiscus* or *Rectoammodiscus*. Because of its non-planispiral (glomospiral) initial stage, *“Ammodiscus” latus* is therefore only tentatively assigned by us to the genus *Ammodiscus*, pending a more formal revision of the family Ammodiscidae.

Waśkowska (2014, 2015a,b) as well as Bubik (2016) mistakenly assigned the species to the genus *Dolgenia* Kemper, 1995, which was defined as possessing a planispirally coiled second chamber that later becomes irregular and may uncoil. *Dolgenia* also possesses a thick medium to coarsely agglutinated wall. Within the family Ammodiscidae there is a number of genera that are planispirally coiled with the exception of the initial stage. The genus *Glomospirella* (type species *Glomospira umbilicata* Cushman & Waters, 1927) sensu Plummer (1945) is characterised by a planispiral later stage, but has an initial stage that is described as streptospiral. This species from the Pennsylvanian of Texas appears to be quite irregular, and the illustration of the holotype by Loeblich & Tappan (1964) shows a glomospirally-coiled specimen with what appear to be constrictions in the final two whorls of the tubular chamber. This species needs to be revised in light of our new observations of *Ammodiscus latus*. The genus *Ammodiscoides* sensu Cushman (1909) possesses an early trochospiral stage, later changing to planispiral coiling. Of the existing genera in the family Ammodiscidae, the coiling pattern observed in *“Ammodiscus” latus* is most similar to the genus *Spirillinoides* sensu Rhumbler (1938), in which the proteinaceous early portion of the test is composed of a planispiral or slightly trochospiral coil. The generic assignment of *“Ammodiscus” latus* is therefore problematical. The transition from glomospiral to planispiral coiling is not embraced by any existing genus within the family Ammodiscidae Reuss, 1862. A revision of the family is therefore a necessity.

The appearance of constrictions or pseudochambers in the final whorl of *“Ammodiscus” latus* forma *ovoidalis* has further taxonomical implications, especially its relationship to the genus *Trochamminoides*. Grzybowski (1898) described the species *Ammodiscus septatus*, which is now assigned to the genus *Trochamminoides*. The new form

ovoidalis with its final whorl pseudochamber appears to be transitional to the genus *Trochamminoides*. Its evolutionary relationship to *T. septatus* requires further investigation.

CONCLUSIONS

“Ammodiscus” latus Grzybowski is a cosmopolitan deep-water agglutinated foraminifera known from Eocene to Miocene deposits in the Western Tethys and Atlantic. Its test is comprised of two chambers, a globular proloculus and a tubular second chamber that is initially coiled glomospirally, later planispirally, and has a tendency to uncoil in its terminal part. The combination of characters in *“Ammodiscus” latus* do not fit into any previously described ammodiscid genus.

Within the variability of *“Ammodiscus” latus*, we recognise two forms. The typical form described by Grzybowski has a circular outline, and is here named *“Ammodiscus” latus* forma *latus*. A second morphotype with an oval or slightly irregular outline and displaying constrictions in the chamber lumen that appear as pseudochambers is here described as *“Ammodiscus” latus* forma *ovoidalis*. This form is transitional to the genus *Trochamminoides*, and may be related to the species *Trochamminoides septatus* Grzybowski.

“Ammodiscus” latus first appeared in low latitudes during the Early Eocene, and during the Middle Eocene progressively colonised the European Tethyan basins and the northern high latitudes. Because it is common on the boreal shelled, *“Ammodiscus” latus* is regarded to be a cold-adapted form. Its colonisation of the boreal shelves coincides with the Eocene period of global cooling. Its disappearance from the low latitude basins and its abundance acme in the boreal basins suggests that it found its optimum ecological conditions in the cooler high latitudes, where it persisted until the Miocene.

ACKNOWLEDGEMENTS

We thank Teresa Wójcik for picking samples from the Polish Flysch Carpathians. We also thank Mirek Bubík for useful discussion. MAK thanks Stanisław Geroch for access to the Grzybowski Collection, and for making photos of the type specimens. This study was supported by AGH grant no 11.11.140.173 (AW) and the Micropress Europe Foundation.

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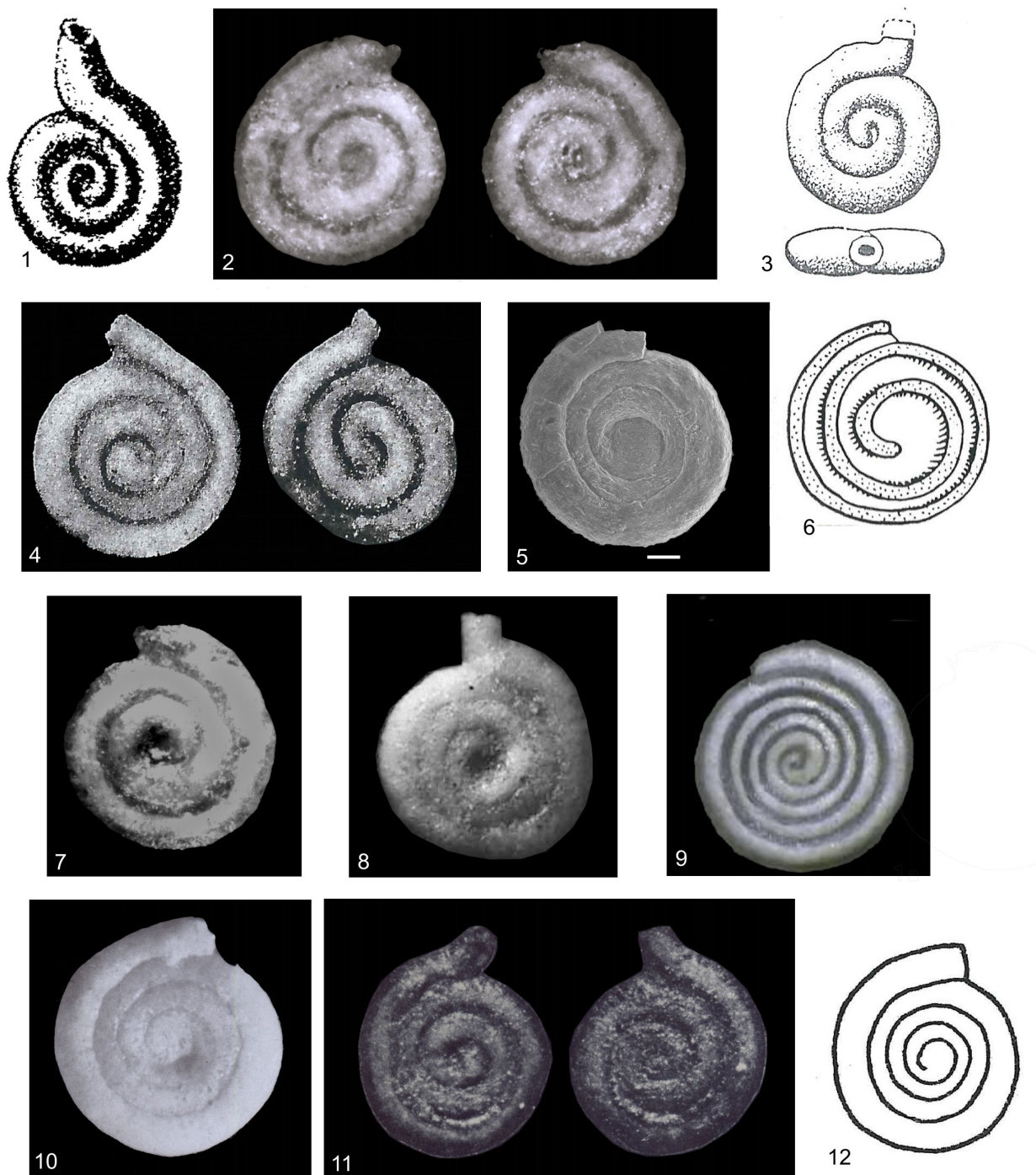


Plate 3. Published photos *Ammodiscus latus* forma *latus* with glomospiral initial whorl of the coiled second chamber, after: 1. Grzybowski, 1898; 2. Geroch *et al.*, 1993; 3. Geroch, 1960; 4. Cushman & Renz, 1948; 5. Wałkowska, 2014b; 6. Huss, 1966; 7. Kaminski & Gradstein, 2005; 8. Morgiel & Olszewska, 1981; 9. Holbourn *et al.*, 2013; 10. Olszewska *et al.*, 1996; 11. Geroch & Gradziński, 1955; 12. Geroch & Nowak, 1984.