Distribution of the agglutinated foraminifer *Ammolagena clavata* (Jones and Parker) in Western Tethyan Upper Cretaceous and Paleogene deep-water deposits (Outer Carpathians, Poland)

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ABSTRACT: *Ammolagena clavata* (Jones *et* Parker) – a cosmopolitan agglutinated foraminifera – is present as an accessory taxon in assemblages of the Outer Carpathians. This species has been found in deep water settings, exclusively in rich and diversified assemblages, among taxa representing various strategies of life from epifauna to deep infauna. *Ammolagena clavata* is one of the most common of attached forms in flysch foraminiferal assemblages and inhabits as a substrate other agglutinated foraminiferal tests. In the Outer Carpathian basins this species was more abundant in middle Eocene successions above the carbonate compensation depth (CCD), dominated by mudstones deposited under reduced clastic supply conditions. *Ammolagena clavata* can be regarded as an indicator of an environment with a low supply of clastic material.

KEY WORDS: Deep-water agglutinated foraminifera, attached foraminifera, paleoecology, Cretaceous-Paleogene, Outer Carpathian Basins

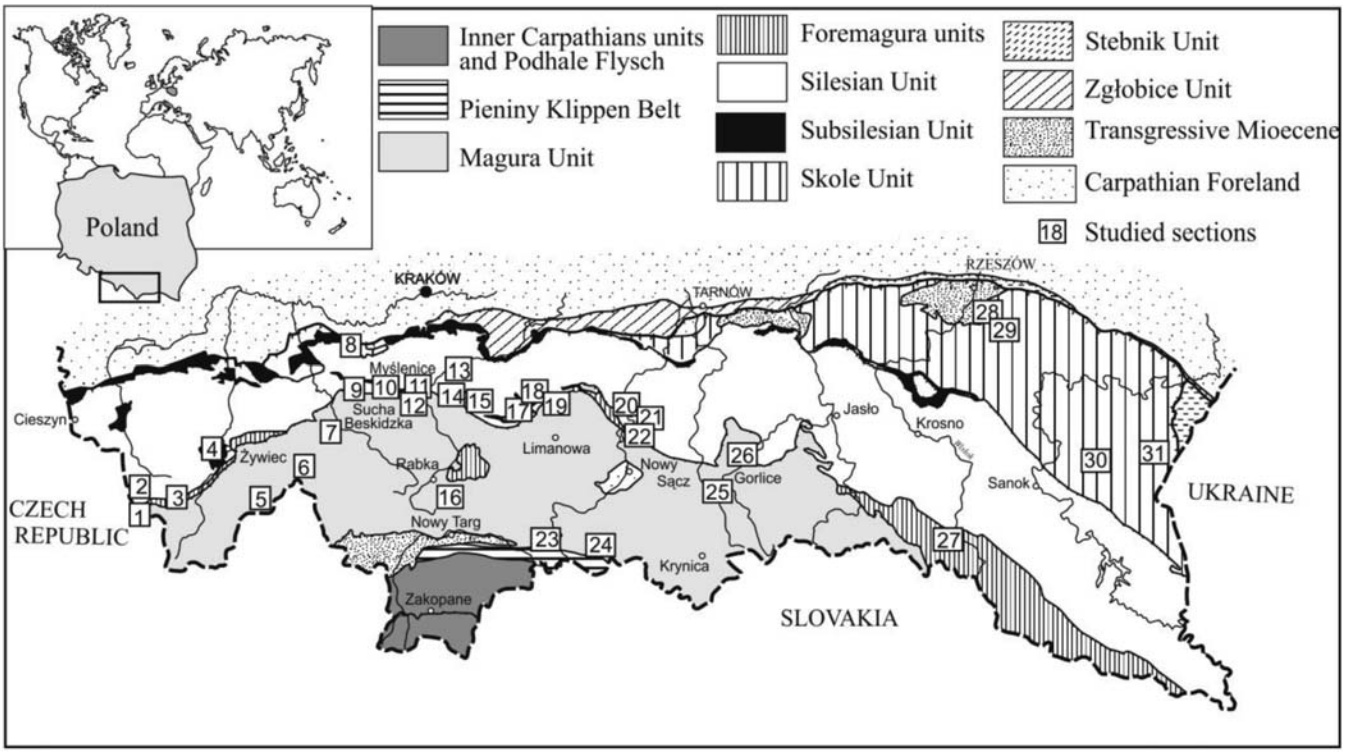
INTRODUCTION

The deep-water environment dominated by flysch type sedimentation creates a specific environment for the development and preservation of foraminiferal assemblages. Assemblages dominated by agglutinated foraminifera inhabiting the surface and subsurface of the sediment, are the most common among them. Representatives of various epi- and infaunal feeding strategies are present, but foraminifera with an attached lifestyle are quite rare. *Ammolagena clavata* (Jones and Parker), a long living and cosmopolitan species (Cushman 1918; Kaminski and Gradstein 2005), is the most common species with such a lifestyle. *Ammolagena clavata* is present in slope as well as abyssal environments, listed currently from various depths from a few hundred meters to about 5000m (e.g., Benhard et al. 2008; Herb 1971; Lukina 1980; Schröder 1986; Schönfeld 1997; 2001), and different values of oxygen saturation and a few degrees temperatures of water (e.g., Cushman 1918; Fontanier et al. 2008; Harloff and Mackensen 1997; Hess and Kuhnt 1996; Nigam et al. 2004; Schönfeld 2001). The wide range of ecological tolerance that *Ammolagena clavata* displays also favoured its geographical dispersal in the modern oceans and over geological time. Observations of deep modern environments suggest that *Ammolagena clavata* is most common in the middle and lower parts of the slope, where it forms a characteristic part of the assemblage (Alve et al. 2011; Kuhnt et al. 2000; Fontanier et al. 2008; Rosso et al. 2010). In such areas *Ammolagena clavata* may comprise more than 10% of the foraminiferal fauna (Fontanier et al. 2008; Kuhnt et al. 2000). Other studies show that *Ammolagena clavata* is irregularly distributed in basinal sediments, and constitutes an accessory component of assemblages (Duros et al. 2012; Nigam et al. 2004).

Its first occurrence is known from the Early Cretaceous (Kaminski et al. 1992; Holbourn and Kaminski 1997). This species is relatively common in younger (e.g. Kaminski and Austin 1999; Kaminski et al. 2009; Morlotti and Kuhnt 1992; Mullen and McNeil 1995; Olszewska et al. 1996) and recent assemblages from deep-water environments (e.g., Bernhard et al. 2008; Burch and Burch 1995; Duros et al. 2012; Fontanier et al. 2008; Harloff and Mackensen 1997; Hess and Kuhnt 1996; Jones and Parker 1860; Kaminski and Gradstein 2005; Kuhnt et al. 2000; Nigam et al. 2004; Schönfeld 1997, 2001), only occasionally being found in shallower environments (e.g. Milker and Schmiedl 2012; Murray and Alve 2011; Pflum and Frerichs 1976; Schröder-Adams and McNeil 1994). The geographical distribution of this species is very wide, including all the modern oceans (Nigam et al. 2004). *Ammolagena clavata* is commonly known from the Upper Cretaceous and Paleogene deposits of the Carpathian Tethys (e.g. Bąk 2004; Blaicher 1958; Bubík 1995; Bubík et al. 1999; Cieszkowski et al. 2007; Cieszkowski et al. 2011; Geroch and Gradziński 1955; Geroch et al. 1967; Jednorowska 1966; 1968; Jurkiewicz 1967; Kaminski and Gradstein 2005; Olszewska et al. 1996; Waśkowska-Oliwa 2008; 2005). The paleontological record of this species in deep-water Outer Carpathian deposits of various environments and ages is here reviewed in detail.

METHODOLOGY

A total of 601 samples were studied from deep-water deposits of the Outer Carpathians in Poland, including 160 samples coming from upper Cretaceous and 441 samples from lower Paleogene rocks. The material was collected from 31 sections of flysch-type deposits, cropping out in natural exposures (text-figs. 1, 2).



TEXT-FIGURE 1
Sampled section on the background tectonic-skech map of Polish Carpathians (with litostratigraphical divisions): 1 - Jaworzynka area (Jaworzynka Fm.), 2 - Istebna-Jasnowice area (Istebna beds, Ciężkowice sandstones, Hieroglyphic beds), 3 - Kamesznica-Szare area (Jaworzynka Fm., Istebna beds, Ciężkowice sandstones, Hieroglyphic beds), 4 - Żywiec-Leśna area (Paleogene Subsilesian deposits), 5 - Jeleśnia-Mutne area (Jaworzynka Fm.), 6 - Zawoja area (Jaworzynka Fm., Beloveza Fm.), 7 - Sucha Beskidzka area (Łabowa Fm.), 8 - Wadowice area (Cretaceous-Paleogene Subsilesian deposits), 9 - Harbutowice area (Beloveza Fm., Zembrzyce Mb.), 10 - Sułkowice-Gościbia area (Cretaceous-Paleogene Subsilesian deposits), 11 - Myślenice area (Łabowa Fm.), 12 - Stróża area (Beloveza Fm.), 13 - Szczyrzyc-Stardomka area (Istebna beds, Ciężkowice sandstones, Hieroglyphic beds), 14 - Czerwin area (Cretaceous-Paleogene Subsilesian deposits), 15 - Wiœniowa area (Cretaceous-Paleogene Subsilesian deposits), 16 - Rabka area, 17 - Nowe Rybie-Pluskawaka area (Cretaceous-Paleogene Subsilesian deposits), 18 - Rajbrot area (Cretaceous-Paleogene Subsilesian deposits), 19 - Żegocina area (Cretaceous-Paleogene Subsilesian deposits), 20 - Czchów area (Istebna beds, Ciężkowice sandstones), 21 - Lipie area (Ciężkowice sandstones, Hieroglyphic beds), 22 - Gródek- Rożnów Lake area (Ciężkowice sandstones, Hieroglyphic beds), 23 - Frydman area (Eocene deposits), 24 - Krościenko area (Szczawnica, Życzanów Fm.), 25 - Klimkówka area (Łabowa Fm., Beloveza beds), 26 - Gorlice area (Istebna beds, Ciężkowice sandstones, Hieroglyphic beds), 27 - Dukla-Jasiółka area (Cisna beds, Majdan beds, Hieroglyphic beds), 28 - Zabratówka area (variegated shales, Hieroglyphic beds), 29 - Błażowa-Poręby Czarnotówki area (Hieroglyphic beds, Menilitic beds), 30 - Leszczawa area (variegated shales, Hieroglyphic beds, Menilitic beds), 31- Makowa area (variegated shales, Hieroglyphic beds).

For preparation were used 0.5 kg mudstone and claystone, coming from deposits representing part of the slope of Carpathian basins forming now the Magura, Silesian, Skole, Dukla and Subsilesian nappes. The material was prepared using standard micropalaeontological procedures, including: maceration in Glauber's salt mixed with water, washing with use of 0.068mm – 3mm sieves, and separation of the all foraminiferal tests from the psammitic residue. Biogenic material, including agglutinated foraminifera, comprised from 5% to 30% of the residue. The rest of the components comprised very fine-grained material (< 0.068mm), mostly clay and silt fractions that were sieved in the laboratory. Microfossils were taxonomically determined with separation of *Ammolagena clavata*. 594 specimens of *Ammolagena clavata* were obtained from the analyzed material (Supplementary Table 1, available online). Many of the *Ammolagena clavata* specimens were damaged and incomplete. *Ammolagena clavata* was assessed in relation to their number, size and distribution on the background of the stratigraphical and structural units within Outer Carpathians. SEM images were made in the Scanning Microscopy Laboratory of the Faculty of Geology, Geophysics and Environmental Protection, AGH (plates 1, 2). Specimens of *Ammolagena clavata* are housed in the Department of General Geology and Geotourism AGH, in the author's collection.

GEOLOGICAL BACKGROUND

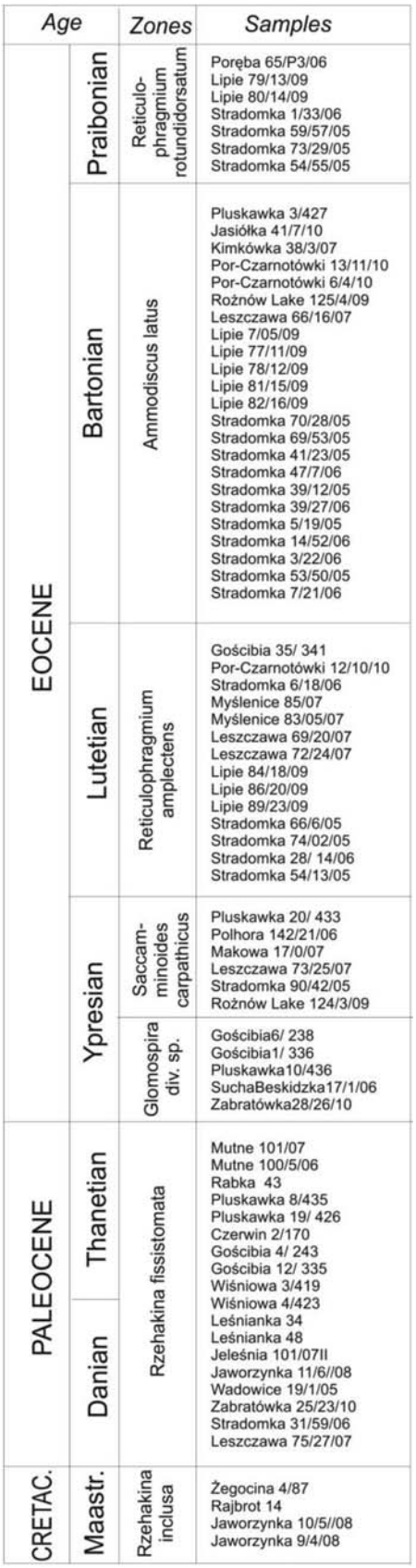
The Outer Carpathians belong to the Alpine orogeny structures (text-fig. 1) and consist of a series of overthrust nappes. These deposits, originally formed in the Carpathian basins (Golonka 2011; Golonka et al. 2011; Golonka and Waśkowska-Oliwa 2007; Golonka et al. 2006; 2008), are represented by various lithotypes, from typical medium- to fine-bedded sandstone-mudstones and mudstone-sandstones complexes, to thick-bedded complexes of sandstones and grainstones, or homogenous mudstone-siltstones deposits. Shallow water facies are poorly represented in the Outer Carpathians. The Carpathian basins reached their largest extent during the Cretaceous-early Paleogene, when four basins were present in the Carpathian part

of the Tethys (text-fig 3). These were the Magura, Silesian, Skole and Fore-Magura basins, which were separated by interbasinal elevations.

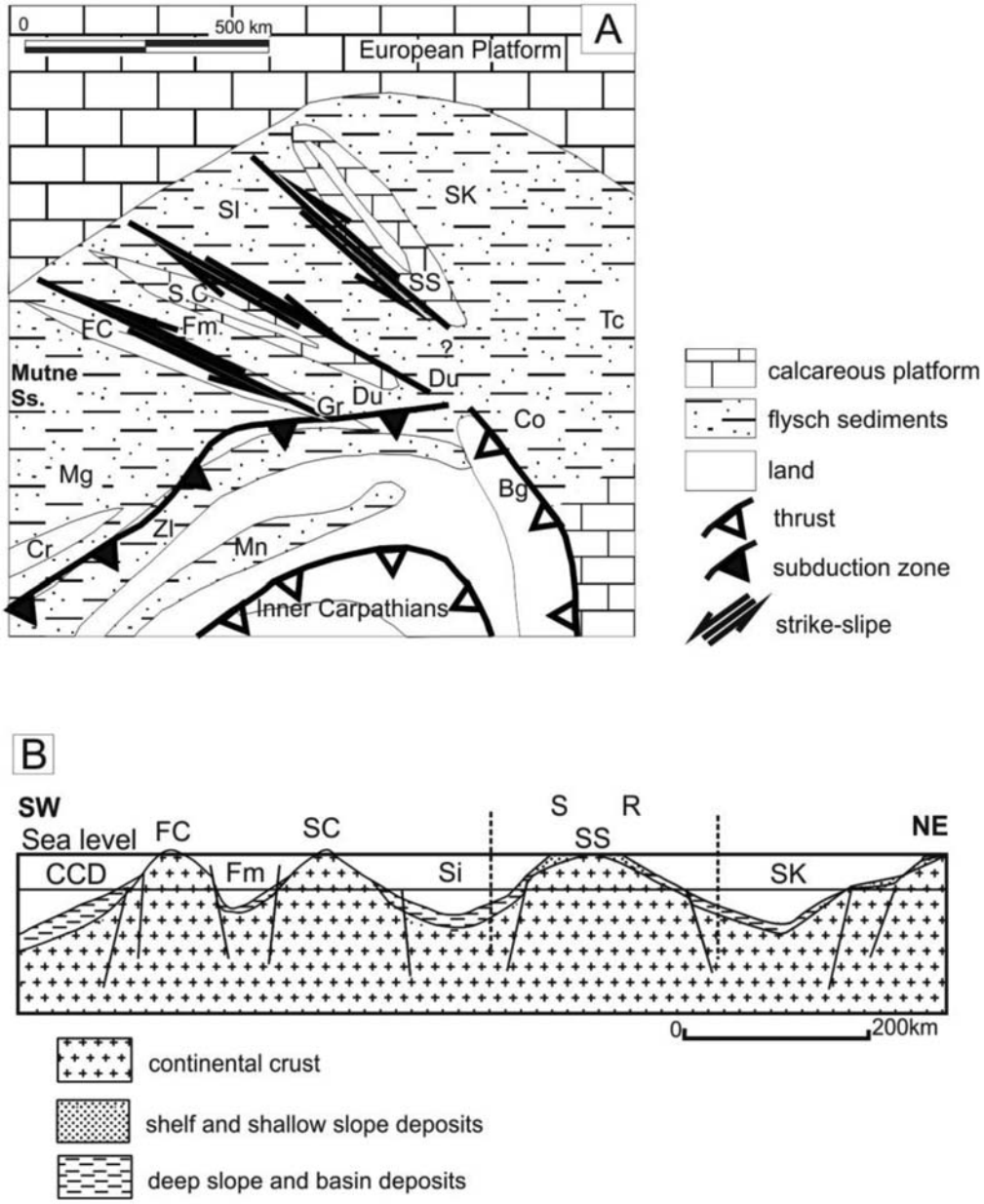
MATERIAL AND RESULTS

Ammolagena clavata (Jones and Parker) was described in 1860 from Recent Mediterranean deposits as *Trochammina irregularis* (d'Orbigny) var. *clavata*. *Ammolagena clavata* belongs to the superfamily Hormosinellacea Rauser and Reitlinger 1986, Family Ammolagenidae Kaminski et al. 2009. The presence of pseudo-chambers is characteristic for this family. *Ammolagena clavata* usually possesses a large ovoid proloculus followed by a tubular chamber that may be several times longer. A double aperture is typical, the main one is at the open end of the tubular part of the test, and a smaller one located at the free end of the oval chamber (Kaminski et al. 2009). The smaller aperture could be a scar after the tubular part of the chamber. In many fossil specimens from the Carpathians, the edge of the opening is uneven and ragged, more of a scar character than of an original apertural lip. Two tubular parts extending out from both ends were observed only in one specimen of *Ammolagena clavata*. The wall of the test is very finely agglutinated, with a smooth surface. Modern forms are comprised of agglutinated grains of very fine quartz cemented together by organic matter, which is replaced by silica in fossil specimens (Bender 1995). The color of recent tests is brown, while in fossil forms the color changes to grey or white because of diagenesis, or it may become red when tests are fossilized in reddish mudstones. Specimens from the Carpathians are of various sizes, some larger forms are more than three times the size of the lectotype. The oval parts ranges to 0.8-0.65mm in width. Tubular parts are rarely preserved in the fossil stage as an intact test, these are usually mechanically damaged. The longest recovered incomplete test exceeded 1.5mm in length. *Ammolagena clavata* is usually attached to abiotic or organic objects lying on the sea floor.

Foraminiferal assemblages were obtained from the upper Cretaceous and lower Paleogene deposits of the flysch-type sediments from the Polish Outer Carpathians. *Ammolagena clavata* was present in 25 within 31 analyzed sections (text-fig. 1). It occurs in 16.8% of Paleogene samples (total 74 samples) and in 3.12 % of the Cretaceous ones (5 samples), mostly as a single specimen (text-fig. 2). Samples with abundant representatives of *Ammolagena clavata* are rare (max. 41 specimens per sample in middle Eocene deposits of the Skole Nappe – sample Poręby Czarnotówki 17/15/10). It occurs irregularly, as an ephemeral, accessory form. It usually makes only 0.01% - 0.4% of the benthic assemblages, rarely exceeding 1% of the assemblage (text-fig. 4). The maximum percentages fluctuate between 6.1% (sample Poręby-Czarnotówki 7/15/10), 7.05% (Mutne 1010/07), 7.1% (Poręba 65/P3/06) and 7.50% (Jeleśnia 101/07II). *Ammolagena clavata* is more common in Paleogene than in Cretaceous assemblages, being most common in the middle Eocene assemblages of Hieroglyphic beds of the Skole and Silesian nappes, and in variegated shales of the Łabowa Shale Formation of the Magura Nappe. Sampling was carried out in profiles containing continuous sedimentary sequences. *Ammolagena clavata* occurs irregularly across the sequences, appearing only in high-diversity assemblages. The typical assemblage with *Ammolagena clavata* includes: e.g., *Psammosiphonella*, *Bathysiphon*, *Ammodiscus*, *Annectina*, *Glomospira*, *Reophax*, *Subreophax*, *Placentammina*, and *Paratrochamminoides*. Average generic diversity is about 19 (ranging from 15–23), and



TEXT-FIGURE 2
Biostratigraphical age of sampled deposits with *Ammolagena clavata*; foraminiferal zones after Olszewska 1997.



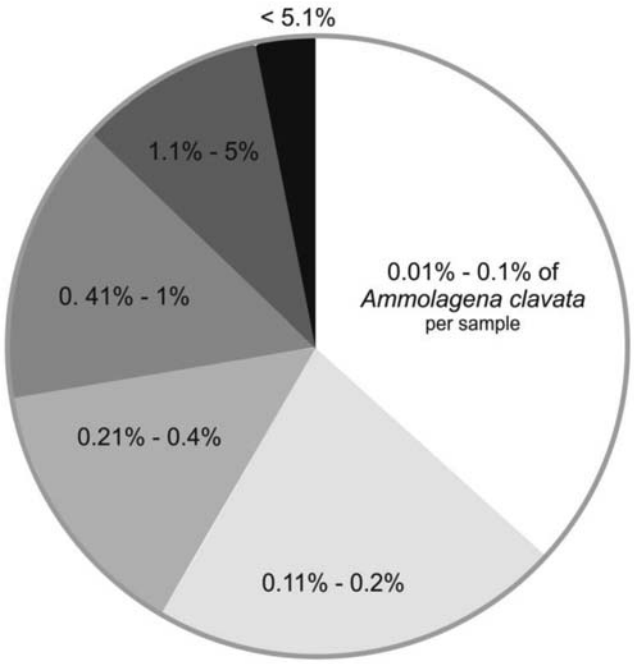
TEXT-FIGURE 3A
Paleogeography of the Outer Carpathian basins during the Late Cretaceous. BG - Bucovinian-Getic, Co - Chornohora, Porkulec, Audia, Teleajen, Cr - Czorsztyn Ridge, Du - Dukla, FC - Fore-Magura Ridge, FM - Fore-Magura Basin, Gr - Grybów, Mg - Magura, Mn - Manin, Si - Silesian Basin, SK - Skole, SC - Silesian Ridge, SS - Sub-Silesian Ridge, Tc - Tarcau, Zl - Zlatna (from Cieszkowski et al. 2006 – modified).

TEXT-FIGURE 3B
Palinspastic cross-section showing the Outer Carpathian basins during the Paleocene. Abbreviations: FC - Fore-Magura Ridge, Fm - Fore-Magura Basin, Si - Silesian Basin, SK - Skole Basin, SC - Silesian Ridge, SS - Subsilesian Ridge, SR -Subsilesian Sedimentary Area (after Waśkowska et al. 2009).

species diversity is about 32 (ranging from 26–36). *Ammolagena clavata* is absent in assemblages with reduced taxonomic diversity. Subsequently, it may be inferred that *Ammolagena clavata* is a component of assemblages with a complex trophic structure, in which all feeding ecogroups from epifaunal mobile to sessile and deep infaunal deep are well represented (text-fig. 5). *Ammolagena clavata* was found not only in assemblages with a majority of suspension feeders (mainly *Psammosiphonella*), but also in assemblages that are dominated by infaunal (e.g., *Reophax*, *Recurvoides*) or epifaunal taxa (e.g., *Paratrochamminoides, Trochamminoides*) (text-fig. 5).

Ammolagena clavata is an attached form, living on foraminiferal tests or on other elements available at the seafloor. In the studied samples from the flysch Carpathians, *Ammolagena clavata* is usually found on the surface of the tests of other agglutinated foraminifera (plates 1, 2). These are illustrated in text-fig. 6. The result is based on more than 300 specimens of

Ammolagena clavata. This species was found usually as a single specimen on a particular foraminiferal substrate, and only rarely as several specimens (but not more than 6) on one foraminiferal substrate (pl. 1, fig. 10). Foraminiferal substrates are of various sizes, and usually correspond to larger tests with various-sized grains. These substrates are sometimes of the size of, or even smaller than the size of the oval chamber of *Ammolagena clavata* (pl. 1, fig.1, 2, pl. 2, fig. 11). Tests of *Ammolagena clavata* have different sizes, with larger ones being found in mudstone/claystone deposits, while significantly smaller tests have been observed in sandy mudstones.



TEXT-FIGURE 4
Relative contribution of *Ammolagena clavata* to the total foraminiferal assemblage in the studied samples. Note that *Ammolagena clavata* makes up less than 0.1% and 0.2% of the assemblages in more than half of the studied samples.

DISCUSSION

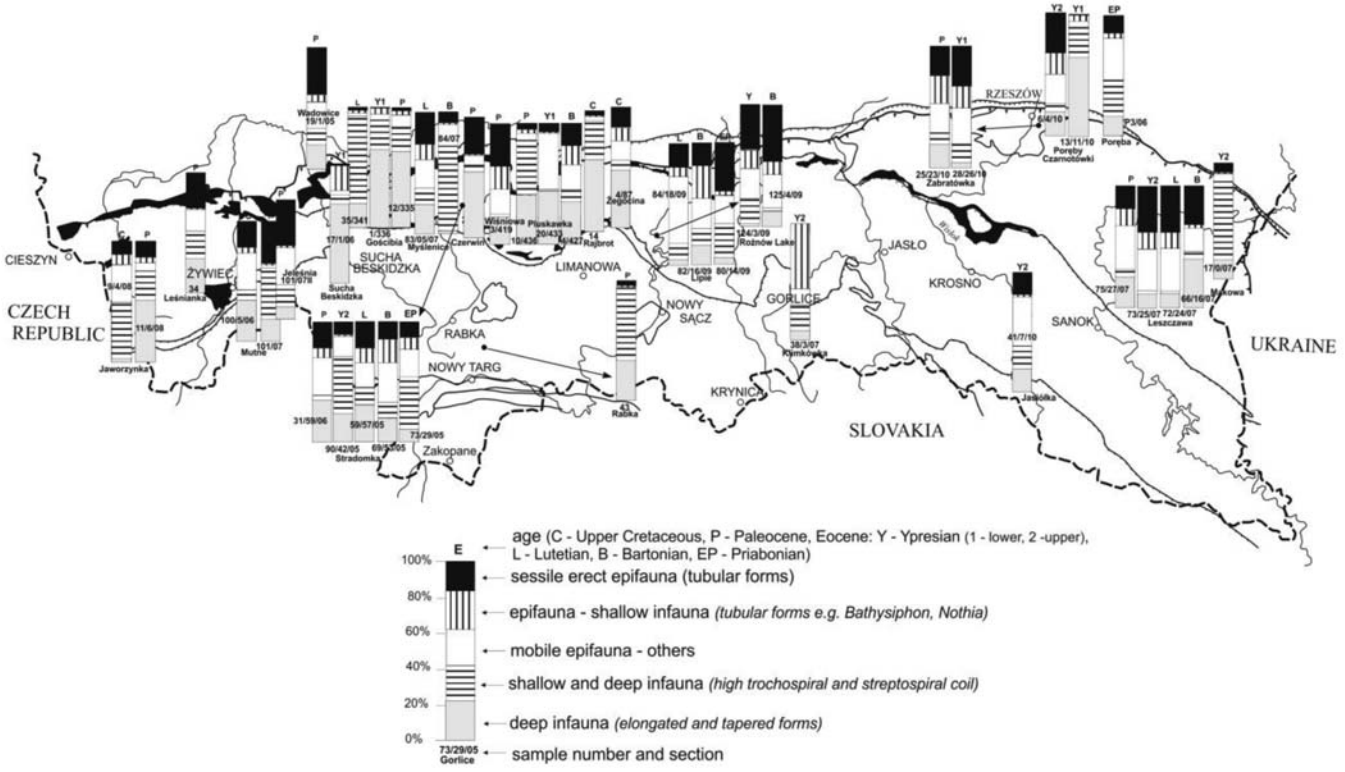
Ammolagena clavata is rare in the Carpathians, although it makes up 7% of the assemblages in the Jaworzynka Formation, Magura Nappe and Hieroglyphic beds, Skole Nappe. *Ammolagena clavata* prefers environments inhabited by foraminiferal assemblages of various feeding strategies, belonging to infauna and epifaunal (text-fig. 5). *Ammolagena clavata* is present exclusively in high diversity assemblages. These assemblages of flysch-type of sedimentation are known as being indicators of favourable environmental conditions i.e., a high supply of organic matter, well oxygenated bottom sediment, and low-energy water conditions that occur between turbiditic flows. The high numbers of foraminifera (usually several hundred to a few thousand specimens per sample) are considered to be the result of test condensation. *Ammolagena clavata* is present in samples typical for environments with a low terrigenous supply. For example, the variegated shales, developed as mudstones with altered tuffites, are enriched in *Ammolagena clavata*. The deposition of bentonites is highlighted by the very low supply of clastic material, so pyroclastics have not been mixed with terrigenous material (Cieszkowski et al. 2011).

Ammolagena clavata is more common in deep-water settings (middle and lower parts of the slope; Alve et al. 2011; Kuhnt *et al.* 2000; Fontanier et al. 2008; Rossoet al. 2010), where it is part of relatively stable assemblages. It is less common in deeper environments, and its occurrence is limited by adverse conditions. Its occurrence, together with clastic material, in the deeper parts of the basin may have been favoured by gravity. The abundance data show that *Ammolagena clavata* is most common in the middle Eocene deposits of the Carpathians. This was a time period when hemipelagic deposition prevailed in many parts of the Carpathian Basin. The activity of high-energy turbidity currents is reduced in this interval, and the main lithology is marly shale with very thin sandstones layers. In the Magura Basin, the middle Eocene is developed as the Variegated Shales of the Łabowa Formation (sequences of green-red mudstones). In the Skole, Silesian and Magura basins, they are known as the Hieroglyphic beds (thin-bedded flysch with dominant mudstone) or variegated shales (mudstone complexes).

Ammolagena clavata is regarded as an epifaunal (e.g. Bąk 2004, Kaminski and Gradstein, 2005), or shallow infaunal form (Fontanier et al. 2008). Under changing conditions, attached forms may migrate to the subsurface of the sediment (Diz et al. 2004). *Ammolagena clavata* is an attached foraminifer and lives connected to hard substrates on the sea floor. Usually it is found on the free grains of clastic material (e.g., Burch and Burch 1995; Cole 1981; Heron-Allen 1915; Kaminski et al. 2005; Kaminski and Austin 1999), on macrofaunal shells, mainly molluscs (e.g. Burch and Burch 1995; Gradstein and Geroch 1992; Heron-Allen 1915; Holbourn and Kaminski 1997; Rosso et al. 2010), fish otoliths (e.g., Burch and Burch 1995; Cita and Zoechi 1978; Kaminski et al. 2009) and on agglutinated foraminiferal tests (e.g., Cieszkowski et al. 2011; Jurkiewicz 1967). Fewer occurrences have been noted on planktonic foraminiferal tests (Kuhnt et al. 2000; Schröder 1986). In recent environments, Nigam et al. (2004) reported *Ammolagena clavata* from planktonic and agglutinated foraminiferal tests, but not from co-ocurring benthic calcareous foraminiferal tests.

In the deeper parts of the Carpathian basins, *Ammolagena clavata* occupies agglutinated foraminiferal tests only. Less than 9% of the specimens were found without a substrate, or only with a residually preserved one. Analysis of these elements reveals that they correspond to fragments of agglutinated foraminiferal tests. Foraminiferal tests of autochthonous fauna are a relatively stable component of muddy and clayey sediments in deep-water settings, and they are convenient objects to settle. Calcareous bioclasts commonly settled by *Ammolagena clavata* (e.g., Burch and Burch 1995; Gradstein and Geroch 1992; Heron-Allen 1915; Holbourn and Kaminski 1997; Rosso et al. 2010) are rare in flysch environments. Some of them – especially macrofaunal hard elements – are supplied from shallower parts of basin and destroyed during turbiditic transport. Occurrences of calcareous planktonic foraminiferal tests are limited by physico-chemical conditions in the water column and they are dissolved at depths below and near the foraminiferal lysocline.

Ammolagena clavata was not found on inorganic clasts in the studied material (text-fig. 6); in flysch environments, detrital grains are generally much more common than foraminiferal tests. *Ammolagena clavata* attaches itself to species with a

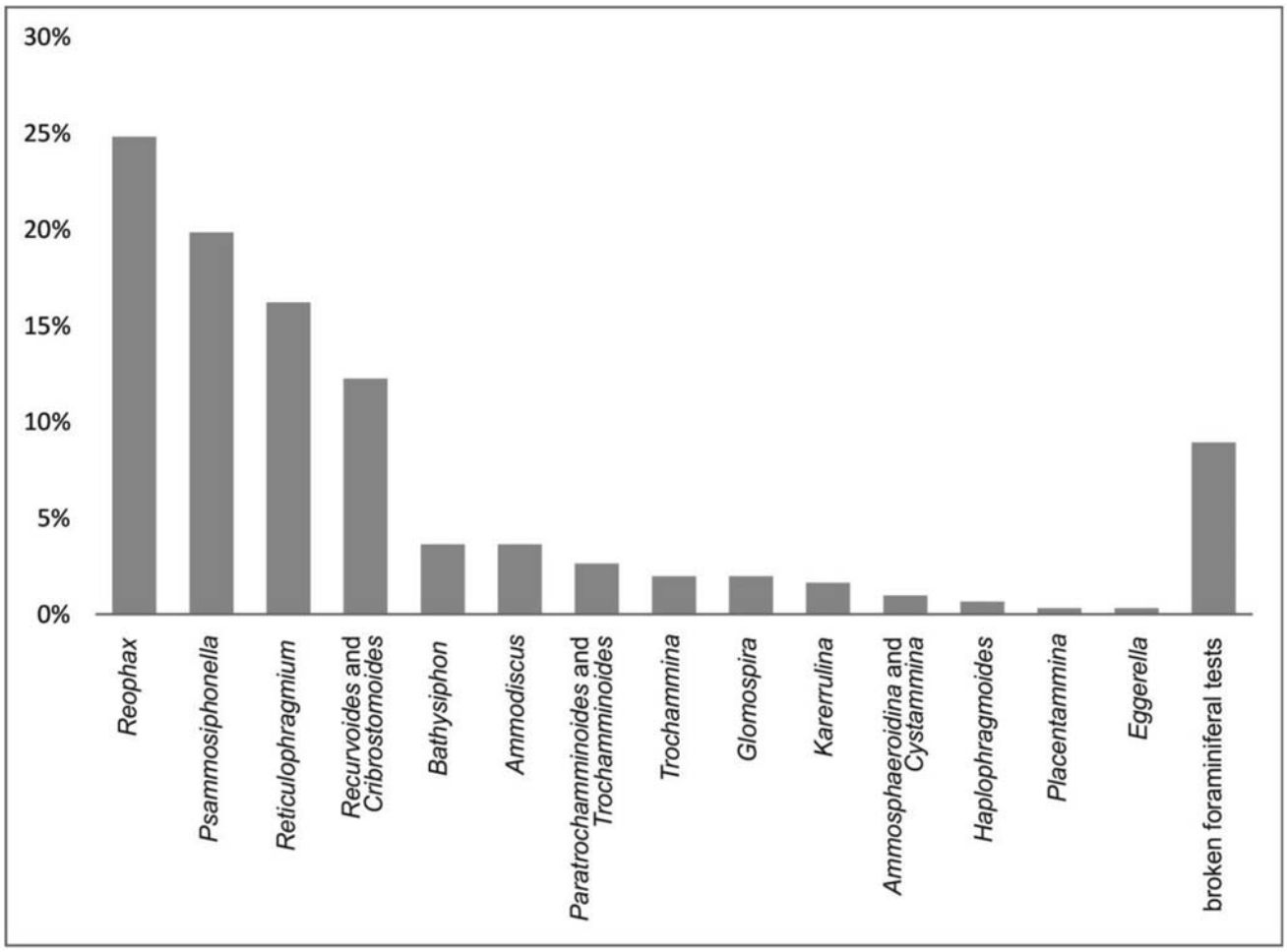


TEXT-FIGURE 5
Morphogroup distribution in formainiferal assemblages with *Ammolagena clavata.*

smooth test, such as *Ammodiscus incertus* (d'Orbigny), *Ammodiscus latus* Grzybowski or *Reticulophragmium amplectens* (Grzybowski), but it is also often found on coarse-grained agglutinated foraminifera, such as *Reophax pilulifer* (Brady), *Karrerulina conversa* (Grzybowski), *Psammosiphonella cylindrica* (Glaessner), *Recurvoides* or *Cribrostomoides* (text-fig. 6, plates 1, 2). It may be concluded that it does not show any preferences for attachment to the substrates of smooth foraminiferal tests, which was suggested by Burch and Burch (1995), Jurkiewicz (1967) and Nigam et al. (2004).

It should also be noted that inhabited foraminifera belong to different groups according to feeding strategy and position in/on the sea floor. The inhabited substrates belong to sessile epifauna (e.g., *Psammosiphonella*), mobile epifauna (e.g., *Ammodiscus, Trochammina*, *Trochamminoides* and *Paratrochamminoides*), as well as shallow infauna (e.g., *Reticulophragmimum*, *Recurvoides*) and deep migrating forms (i.e., *Reophax* or *Karrerulina*) (plates 1, 2). It also seems doubtful that *Ammolagena clavata* would occupy the tests of infaunal forms during their lifetime. It rather inhabited lifeless forms (Kaminski et al. 2009), which were exhumed due to bioturbation of the sediment. They could also be removed from the loose sediment by the accumulation of gases inside the tests, due to the cytoplasmic degradation process, which was possible in the environment with decreased supply of the clastic material.

From the oval proloculus of *Ammolagena clavata* at least one long tube is developed, which most often surrounds the test of the inhabited foraminifera. In bilaterally flattened forms, the oval part is usually placed close to the umbilicus, and the tubular chamber extends to the other part of the foraminifer (e.g. *Ammodiscus*, *Reticulophragmium*, *Trochammina*). On the tubular forms (*Bathysiphon*, *Psammosiphonella*) or enlarged ones (e.g. *Karrerulina*), *Ammolagena clavata* runs along most of the length of the test. On the spherical forms (e.g. *Recurvoides*, or fragments of *Reophax*) the tubular chamber surrounds the basic form, and in case of morphologically variable forms (e.g. *Reophax*), the oval part of *Ammolagena clavata* is very often located in the inter-chamber suture of settled test, and the tubular part extends along the test. A substrate grain may be colonized by more than one individual of *Ammolagena clavata.* The tubular chamber is often directed towards the aperture of the inhabited form. It can spread over various parts of substrate test, usually covering the main aperture of the inhabited foraminifera and blocking it (pl. 1, fig. 5). In the Carpathian deposits, *Ammolagena clavata* is found on certain parts of the agglutinated foraminifera – these are mainly single chambers of *Reophax*, on which the tubular chamber of *Ammolagena* extends across the sutures between the chambers – which were not exposed during the lifetime of the inhabited foraminifera. Similarly, specimens of *Ammolagena clavata* are attached to a damaged part of the test of *Ammodiscus latus*. This supports the idea that *Ammolagena clavata* at least partly inhabited dead parts of the other foraminifera. After the death of the foraminifera there is a certain amount of residual organic matter, which can be used for the next generation. In an oligotrophic environment be-



TEXT-FIGURE 6
Foraminiferal tests substrate settled by *Ammolagena clavata* – taxonomic distribution.

low the CCD, this resource could be used by such forms like *Ammolagena clavata*, which prefers tests of agglutinated foraminifera as a substrate. *Ammolagena clavata* did not use abiotic material even though this was available on the sea floor. Observations were carried out concerning the preference of the inhabited substrate. Shells with a large surface (e.g., *Reophax pilulifer*, *Psammosiphonella cylindrica*, *Reticulophragmium amplectens,* and *Recurvoides*; plates 1, 2, text-fig. 3) are the most common ones. These forms are common components of the assemblages, but some of them are only a minor component of the assemblages containing *Ammolagena clavata. Reophax pilulifer* and *Reticulophragmium amplectens* are among such taxa, usually comprising only a few percent of the whole foraminiferal assemblage. The abundant tests of *Bathysiphon* were only used rarely as a substrate (text-fig. 2). Similarly, *Ammodiscus*, *Trochamminoides* and *Paratrochamminoides*, which are assumed to be epifaunal forms that are largely exposed at the seafloor, were very rarely colonized by *Ammolagena clavata*.

In recent environments, Nigam et al. (2004) reported *Ammolagena clavata* from planktonic and agglutinated foraminiferal tests, but not from co-ocurring benthic calcareous foraminiferal tests. It is also common in shallower environments where it uses fish otoliths (Burch and Burch 1995; Cita and Zoechi 1978; Kaminski et al. 2009).

CONCLUSIONS

In the deep-water deposits of the flysch Outer Carpathians *Ammolagena clavata* is found as an accessory form in the foraminiferal assemblages. It very rarely exceeds 0.4% of the assemblages, exceptionally making up to 7.5% of the benthic assemblages. *Ammolagena clavata* is most common in deposits sedimented above the CCD, represented by the Hieroglyphic beds of the Skole Nappe. *Ammolagena clavata* occurs only in rich and diversified assemblages with a well-developed ecological structure consisting of all morphogroups, developing in favorable conditions with a low supply of clastic material. Poorly diversified assemblages do not contain *Ammolagena clavata*.

In the Outer Carpathians, *Ammolagena clavata* is most common in middle Eocene, hemipelagic mudstones. *Ammolagena clavata* preferred an epibenthic lifestyle, selecting the tests of other agglutinated foraminifera as a substrate for settlement. Abiotic grains were not chosen for substrates. The most commonly occupied tests are *Reophax pilulifer*, *Psammosiphonella*

cylindrica, and *Reticulophragmium amplectens*. These taxa are common in the assemblages, but not dominant.

The colonization of tests of exhumed infaunal taxa by *Ammolagena clavata* is here described. This species may have fed on organic matter still present in lifeless tests.

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PLATE 1

SEM photographs. Scale bar = 100μm.

Ammolagena clavata attached to:

1–5, 9 *Ammolagena clavata* attached to tubular forms, mainly *Psammosiphonella* sp.,

7, 10, 11, 13, 14 *Ammolagena clavata* attached to *Reophax* tests,

6, 12, 15 *Ammolagena clavata* attached to single *Reophax* chamber,

16 Three specimens of *Ammolagena clavata* attached to *Arthrodendron,*

10 Six specimens of *Ammolagena clavata* attached to *Reophax* test – in this projection five specimens are visible, the next is attached behind.

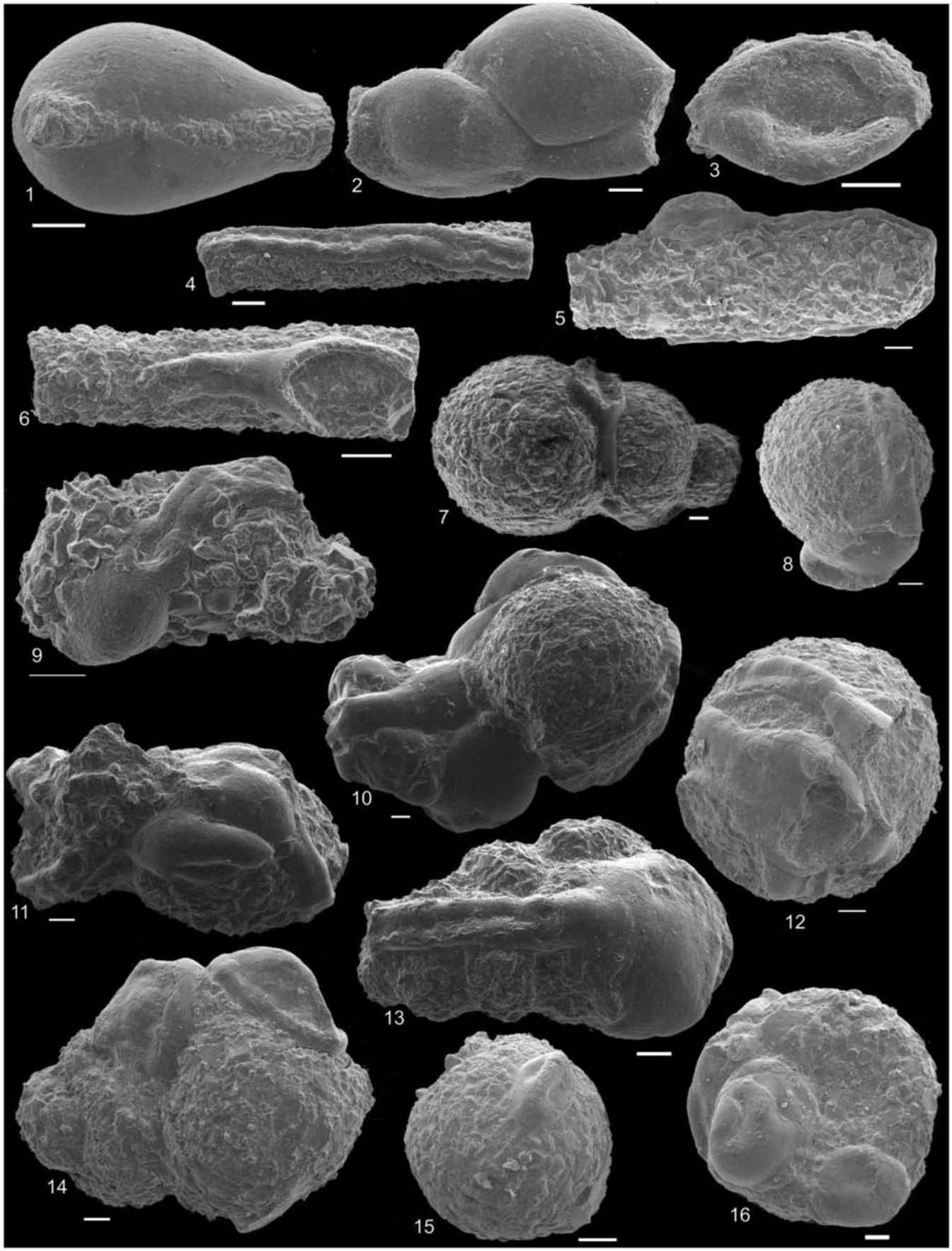
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PLATE 2

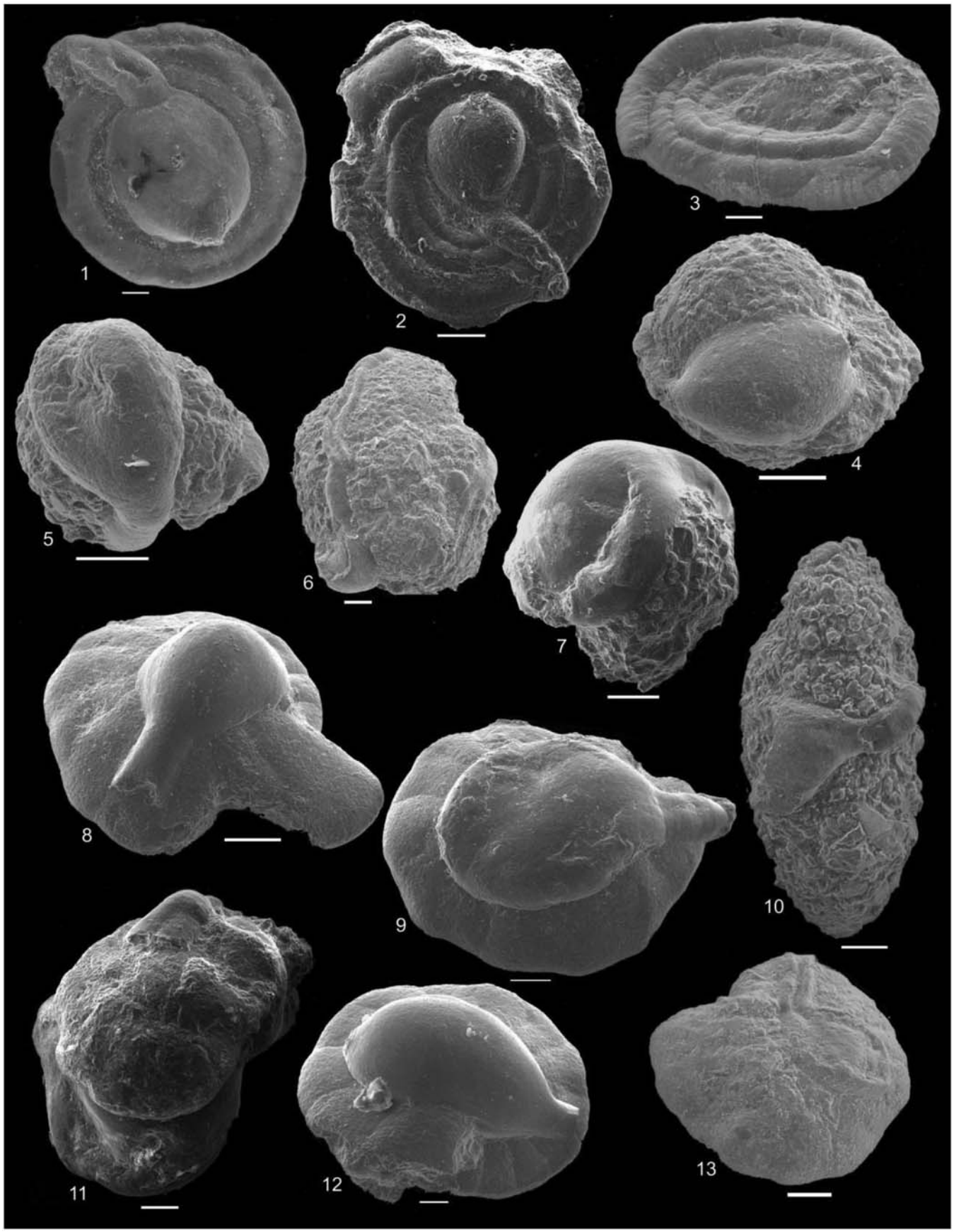
SEM photographs. Scale bar = 100μm.

1–3 *Ammolagena clavata* attached to *Ammodiscus* tests,

4–7 *Ammolagena clavata* attached to *Recurvoides* test,

10 *Ammolagena clavata* attached to *Karrerulina* test,

8, 9, 11–13 *Ammolagena clavata* attached to *Reticulophragmium* tests.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