CLASSIFICATION AND EVOLUTIONARY INTERPRETATION OF LATE TURONIAN–EARLY CAMPANIAN GAVELINELLA AND STENSOEIENA (GAVELINELLIDAE, BENTHIC FORAMINIFERA) FROM WESTERN UKRAINE

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ABSTRACT

This paper discusses the classification and evolutionary trends of the late Turonian-early Campanian genera Gavelinella and Stensioeina from western Ukraine, including the definition of five Gavelinella lineages (G. ammonoides, G. stelligerarum, G. vombensis, G. pertusa, and G. clementiana) and two Stensioeina lineages (S. excelsa and S. perfecta). The latter two differ from each other in test shape, umbilical arrangement, and stratigraphic ranges. Older forms of S. excelsa possess an umbilicus partially covered by triangular flaps extending from the umbilical parts of the chambers (type-X ornamentation), whereas the umbilicus in younger forms is partially covered by undulating outgrowths extending from the surface of the test (type-Y ornamentation). Changes in the Stensioeina perfecta lineage include an increased test thickness and an umbilical area characterized by widening and joining of chamber flaps into an umbilical plug. Protostensioeina n. gen. is proposed to accommodate species characterized by the lack of features typically observed in Stensioeina, such as spiral-side ornamentation consisting of curved, limbate sutures, strongly elevated in somewhat irregular, curly ridges, resulting in a reticulose surface and a sharp, angular border.

INTRODUCTION

Gavelinella and Stensioeina, belonging to the family Gavelinellidae and the two subfamilies Gavelinellinae and Gyroidinoidinae, respectively, are very common and abundant genera of benthic foraminifera in the epicontinental Upper Cretaceous. They have a wide biogeographical distribution across the United Kingdom, northern France, Germany, Holland, Belgium, Denmark, southern Sweden, Poland, Ukraine, Belarus, Kazakhstan, and almost the entire NW European epicontinental shelf. Elements of the Gavelinellidae were also described from the Western Interior Seaway (Texas, U.S.A.; Frizzell, 1954), North Africa (Khalil, 1998), Western Australia (Belford, 1960), and the North Atlantic Ocean (Hart, 1987).

During the Late Cretaceous the Gavelinellinae suffered two faunal turnovers: the first one connected with the Coniacian-Turonian boundary event (CTBE) and the second with the Cretaceous-Paleogene boundary event (Schmitz et al., 1992; Paul et al., 1999; Culver, 2003; Hart et al., 2005). Gavelinellinae occurring in the mid-Cretaceous of the European epicontinental sea were a very common and abundant group of benthic foraminifera (Tyszka, 2006), which suffered a mass extinction during the CTBE, with only a very few surviving taxa (e.g., Gawor-Biedowa, 1972; Jarvis et al., 1988; Leary & Peryt, 1991; Peryt & Wyrwicka, 1993; Tronchetti & Grosheny, 1991; Hart et al., 1993; Peryt et al., 1994; Paul et al., 1999). Linguogavelinella globosa (Brotzen, 1945) and Gavelinella berthelini (Keller, 1935) are these survivors, and they possibly gave rise to younger lineages of Gavelinellinae within Gavelinella, Anguloavelinella, and Pseudogavelinella. Above the CTBE the Gavelinellinae evolved and diversified continuously without disturbance by any significant biogeographical crises until the end of Maastrichtian.

Stensioeinids appeared in the European epicontinental sea during the Turonian and became extinct at the end of Maastrichtian. During their evolution they suffered neither mass extinction nor significant faunal turnover. The lack of Stensioeina in the Turonian of our study area (Dubivtsi quarries) is probably connected with unfavorable environmental conditions (Dubicka & Peryt, 2012a).

Because of their widespread distribution and relatively fast evolution, these microfossils have been widely used in Upper Cretaceous biostratigraphy (e.g., Marie, 1941; Vasilenko, 1961; Koch, 1977; Rozumieko, 1978; Hart et al., 1989; King et al., 1989; Schönfeld, 1990; Gawor-Biedowa, 1992; Mortimore et al., 2001; Offerjev & Alekseyev, 2003; Hampton et al., 2007; Howe et al., 2007; Ogg & Ogg, 2008; Bailey et al., 2009; Wilkinson, 2011). Cretaceous smaller benthic foraminifera were also discussed as potential markers for Upper Cretaceous stage and substage boundaries (Hampton et al., 2007; Howe et al., 2007; Kopaevich et al., 2007). For example, at the Second International Symposium on Cretaceous Stage Boundaries, held in Brussels in 1995, the first occurrence of Stensioeina polonica Witwicka, 1958, was proposed as a secondary marker for the Coniacian/Santonian boundary (Lamolda & Hancock, 1996).

However, more than 150 years of investigation of these benthic foraminiferal groups has resulted in widely scattered, diffuse information and ambiguities concerning names and stratigraphical positions of taxa. The recorded occurrences of Gavelinella and Stensioeina species are poorly defined owing to the different morphological and nomenclatural interpretations proposed by various researchers. Benthic foraminifera of western Ukraine, which are the basis of this study, are rich in well-preserved specimens of Gavelinella and Stensioeina and come from a stratigraphically well-documented succession (Walaćczyk et al., in press), which is characterized by a substantially complete and expanded sedimentary record. Thus, taxonomic revision, evolutionary classification, and observation of progressive changes in morphology of species of the two genera were possible. The objectives of this study, therefore, are to facilitate identification of these foraminiferal groups.
and clarify the phylogenetic relationships of *Gavelinella* and *Stensioeina* during most of the Late Cretaceous.

**GEOLOGICAL SETTING**

The studied section is located ~120 km southeast of Lviv, at Dubivtsi village, near the town of Halych in western Ukraine (Fig. 1). The section is exposed in two huge quarries a few kilometers apart: an abandoned quarry (Dubivtsi 1) and a working quarry (Dubivtsi 2).

The strata exposed in the Dubivtsi succession record the sedimentary history of the south-central part of the European epicontinental sea, and belong to the Lviv-Styri part of the tectonic unit called the Border Synclinorium. The total thickness of the succession is ~100 m and is composed of alternating chalk, marls, limestones, and inoceramid limestones (Dubicka, 2012; Dubicka & Peryt, 2012b). Based on the inoceramid and belemnite fauna the succession represents an upper Turonian–lower Campanian interval (Walaszczyk et al., in press). The Dubivtsi 1 quarry contains a 31-m thick section divided into five lithological units: chalk, chalk-like limestones, hardgrounds, inoceramid limestones, and marls (Fig. 2). The Dubivtsi 2 quarry has ~60 m of carbonate rocks exposed in six exploitation levels (1–6 from bottom upward) and one partly quarried level (designated −1) at the base. The −1 level exposes inoceramid limestones and pelitic limestones, also occurring in level 1. Limestones in the middle of level 1 pass into gray marls, which continue almost to the top of level 3 in the western part of the quarry and to the lower part of level 4 in the eastern part. These marls are overlain by limestones to the top of the Dubivtsi outcrop (Fig. 2). Detailed description of the lithologic succession and the inoceramid, ammonite, and belemnite fauna will be published elsewhere (Walaszczyk et al., in press).

**SYSTEMATIC DESCRIPTIONS AND EVOLUTIONARY INTERPRETATION**

The suprageneric classification outlined below is based on Loeblich & Tappan (1987). Species descriptions within lineages are introduced in stratigraphic order.

Order FORAMINIFERIDA Eichwald, 1830
Suborder ROTALIINA Delage and Hérouard, 1896
Family GAVELINELLIDAE Hofker, 1956
Subfamily GAVELINELLINAE Hofker, 1956

Loeblich & Tappan (1987) described the Gavelinellinae as possessing a trochospirally coiled test, with an aperture as an interiomarginal equatorial arch that may continue on the umbilical side to the umbilicus where it is partially covered by distinctive flaps of successive chambers commonly visible in the umbilical area. The Cretaceous genera which are included in the Gavelinellinae are: *Angulogavelinella* Hofker, 1957 (Maastrichtian); *Berthelina* Malapris, 1965 (Albian); *Gavelinella* Brotzen, 1942 (Barremian–upper Paleocene); *Lingulogavelinella* Malapris, 1965 (Albian–Turonian); *Orithostella* Eicher & Worstell, 1970 (Cenomanian–Turonian); and *Pseudogavelinella* Voloshina in Subbotina succession, the first number of the sample indicates the exploitation level and the second one shows the sample sequence within each level.

All samples were disaggregated in Glauber’s salt and then were analyzed from the sieved 63–600-μm residues. The specimens were studied under a standard optical binocular microscope and scanning electron microscope in the Institute of Paleobiology, Polish Academy of Sciences. The illustrated specimens are stored in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (Collection ZPAL F. 63).

The systematic description of this work includes both previously published and new taxa. Because studied material comes from only one succession at one locality, we made a decision not to designate new species but left them in open nomenclature. These taxa are marked with the successive letters of the alphabet. The occurrences of these taxa need to be recorded elsewhere to formalize them as new species.

**MATERIAL AND METHODS**

This study is based on the analysis of *Gavelinella* and *Stensioeina* specimens identified in samples newly collected from the Dubivtsi quarries. Samples were taken from fresh quarry walls at ~0.5-m intervals. In the Dubivtsi 2
Figure 2. Lithologic column of the Dubivtsi 1 and Dubivtsi 2 composite section, inoceramid stratigraphy, and the ranges of Gavelinellidae in western Ukraine.
et al., 1981 (Campanian), a genus we consider synonymous with Gavelinella.

According to Loeblich & Tappan (1987) Berthelina with type species Anomalina intermedia Berthelin, 1880, occurs in the Albain. During the mid-Cretaceous Berthelina was one of the most widespread and abundant group of benthic foraminifiers (Carter & Hart, 1977; Tyszka, 2006). The most common species are Berthelina baltica (Brotzen, 1942), B. belorusssica (Akimets, 1961), B. intermedia (Berthelin, 1880), B. kaptarenkae (Plotnikova, 1962), and B. varsoviensis (Gawor-Biedowa, 1972). They became extinct during the CTBE (Carter & Hart, 1977; Koutsoukos et al., 1990; Leary and Peryt, 1991; Peryt & Wyrwicka, 1993; Peryt et al., 1994; Peryt & Lamolda, 1996; Paul et al., 1999).

On the other hand, Revets (2001) reassigned to Berthelina six post-Cenomanian species previously classified as Gavelinella. They are: B. ammonoides (Reuss, 1845) and B. moniliformis (Reuss, 1844) (Turonian), B. tenissima (Gawor-Biedowa, 1992) and B. sibirica (Dain in Vasilenko, 1954) (Campanian), B. incerta (Hofker, 1957) (Maastrichtian), and B. umbilicata (Brotzen, 1948) (Paleocene). Typical Berthelina has no clearly defined differences between the spiral and umbilical sides that are very similar (Malapris, 1965; Revets, 1996), and possesses a covered umbilicus and perumbilical ridges (Revets, 2001). These features set the genus apart from other gavelinellids. Berthelina tenissima and B. incerta have these characteristics, while some of the other four only partially meet the definition. Berthelina ammonoides does not have a visible umbilicus and perumbilical ridge, and B. moniliformis, B. umbilicata, and B. sibirica possess a spiral side easily distinguishable from the umbilical side without a perumbilical ridge. Revets (2001) studied only the morphology of holotypes or other types specimens and did not analyze the variability of species and their evolution. In our opinion, these six post-Cenomanian species of Berthelina do not represent the same mid-Cretaceous group of foraminifera which suffered mass extinction during the CTBE. Moreover, Berthelina can be related only to the mid-Cretaceous small benthic foraminifera as defined originally by Malapris, 1965 (see also Loeblich & Tappan, 1987).

Genus Gavelinella Brotzen, 1942
Type species: Discorhina pertusa Marsson, 1878

According to Revets (2001) the genus Gavelinella has a low trochospiral and biconvex test, with evolute spiral and partially involute umbilical sides. The umbilicus is open and deep. The interiomarginal aperture may extend to become almost equatorial, and extends toward and along the umbilicus over the entire length of the chamber. An apertural lip borders the aperture and continues toward the umbilicus, where it becomes a folium, shielding the umbilical part of the aperture.


In light of our detailed study of the Gavelinella morphology and distribution in the Dubivtsi succession, we recognized several separate groups. Representatives of each group are probably closely related with readily visible, gradual, and successive morphological changes through time, and probably constitute five evolutionary lineages: G. ammonoides, G. clementiana, G. pertusa, G. stelligera, and G. vombensis.

The Gavelinella ammonoides Lineage

The G. ammonoides lineage includes G. ammonoides, G. lorneiana, and G. costulata. They possess very low trochospiral, nearly planispiral, and slightly asymmetrically biconvex tests; a small umbilicus almost entirely covered by the umbilical folium; a rounded or slightly narrowed, prominent periphery in younger specimens; and broad, raised, prominent septal-ridge elements on the umbilical side. Foraminifers of this lineage appear in the Turonian, with the oldest representative G. ammonoides giving rise successively to the phyletic line of G. ammonoides/G. lorneiana, G. lorneiana, and G. costulata. The close relationship between G. ammonoides and G. lorneiana was recognized by previous authors (Brotzen, 1942; Vap’tzarova, 1972, 1973; Edwards, 1981).

The evolutionary changes involved in the transition from G. ammonoides to G. costulata are: 1) the broadening and enhancement of umbilical septal-ridge elements around the umbilicus, largely shielding the umbilical aperture; increasing number of chambers; narrowing of the test periphery; and development of a “keel-like” structure (the transition from G. ammonoides to G. lorneiana); and 2) the appearance of test asymmetry and a shift of the aperture and “keel-like structure” from the equatorial to the umbilical position (the transition from G. lorneiana to G. costulata).

Interestingly, the G. stelligera lineage developed an asymmetrical test within the Santonian, simultaneously with the similar morphological changes present in the G. ammonoides lineage (Fig. 3). The development of a similar trait in these two lineages can be defined as parallel evolution, which is the development of similar traits occurring in related, but distinct, species that descended from the same ancestor but within different clades (Zhang & Kumar, 1997).

Gavelinella ammonoides (Reuss, 1845)
Figs. 4.1, 4.2
Rosalina ammonoides Reuss, 1845, p. 36, pl. 4, figs. 2a–c.
Anomalina (Gavelinella) ammonoides (Reuss). Vasilenko, 1954, p. 77, pl. 7, fig. 3; Akimets, 1961, p. 138, pl. 13, fig. 5.
not Anomalina ammonoides (Reuss). Rozumeko, 1978, p. 103, 104, pl. 13, fig. 2.
Gavelinella ammonoides (Reuss). Kaptarenko-Chernousova et al., 1979, p. 126, pl. 47, fig. 6; Hradecká, 1996, p. 89, 90, pl. 3, figs. 7–9; Dubicka & Peryt, 2012b, pl. 7, figs. 1a–c, Ka, c.
Berthelina ammonoides (Reuss). Revets, 2001, p. 18, pl. 5, figs. 10–12.

Material. Over 100 specimens.

Description. Test low trochospiral, nearly planispiral, symmetrically biconvex, oval in outline, and with a flush margin; test outline faintly incised; typically 9 chambers in
the last whorl. Periphery bluntly rounded. The oldest whorls on the spiral side strongly depressed, forming a big central depression which constitutes \(3/4\) of the test diameter. Sutures on the spiral side slightly arcuate and depressed, on the umbilical side gently arcuate and also depressed. In the middle of the test on the umbilical side, broad and convex septal-ridge elements start to form, gradually turning into small triangular apertural flaps partly covering the aperture and umbilicus.

**Remarks.** *Gavelinella ammonoides* seems to be the ancestor of *G. lorneiana*, from which it differs in having a more rounded periphery, fewer chambers in the last whorl, and the absence of broad, elevated, and distinctive septal-ridge elements in the central umbilical area. Transitional forms are presented on Figure 4.3a–c.

**Stratigraphic range and geographic distribution.** The stratigraphic distribution of *G. ammonoides* in eastern and western Europe is Turonian, although its complete range is
unknown. In our study area, *G. ammonoides* occurs in upper Turonian deposits.

_Gavelinella lorneiana* (d’Orbigny, 1840)

_Figs. 4.4–4.6_ Rosalina lorneiana d’Orbigny, 1840, p. 36, pl. 3, figs. 20–22.


**Material.** Over 100 specimens.

**Description.** *Gavelinella lorneiana* has a large, robust and symmetrically biconvex, low trochospiral test with a subcircular periphery and flush margin outline. There are 10–11 chambers in the final whorl. One third of the initial part of the spiral side is depressed, forming a large round depression. The periphery is imperforate, slightly narrowed, and subcircular in contrast to the coarsely perforate umbilical and spiral surface of the test. Sutures on the umbilical and spiral sides are gently curved and depressed. On the umbilical side there are prominent septal-ridge elements that are gently curved, broad, raised, and imperforate and project into the umbilicus.

**Remarks.** It is highly possible that *G. lorneiana* evolved during the Coniacian from *G. ammonoides* by acquisition of broader, distinctive, and partially conjoined septal-ridge elements.
elements on the umbilical side. The final chamber varies in the shape and degree of its inflation.

**Stratigraphic range and geographic distribution.** *Gavelinella lorneiana* is known from Coniacian and Santonian beds of the European epicontinental basin. In the studied sections, it ranges from the middle Coniacian–lower upper Santonian.

*Gavelinella costulata* (Marie, 1941)  
Figs. 4.7, 4.8

*Discorbis lorneana* var. *costulata* Marie, 1941, p. 216, pl. 34, fig. 315.

*Gavelinella costulata* (Marie). Rozumeko, 1978, p.104, pl. 13, fig. 3; Kaptarenko-Chernousova et al., 1979, p. 126, pl. 48, fig. 3; Hart et al., 1989, p. 336, pl. 7.11, figs. 10–12; Gawor-Biedowa, 1992, p. 166, pl. 35, figs. 4–6.

**Material.** Over 100 specimens.

**Description.** *Gavelinella costulata* has a large, robust, low trochospiral test with a subcircular periphery and flush margin outline. Test is asymmetrically biconvex with an almost flat spiral side and moderately convex umbilical side. There are 10–11 chambers in the final whorl. One third of the initial part of the spiral side is depressed, forming a large round depression. The slightly narrowed, subcircular, and imperforate periphery moves toward the spiral side. Except for the periphery, the test surface is coarsely perforate on the spiral and umbilical sides. Sutures are depressed and gently arcuate on both sides of the test.

**Remarks.** *Gavelinella costulata* evolved from *G. lorneiana*, from which it differs in its more asymmetric test with flattened spiral and convex umbilical sides. The edge of the peripheral margin and aperture move toward the umbilical side.

**Stratigraphic range and geographic distribution.** *Gavelinella costulata* was described from beds in northwestern and eastern Europe; however, its precise stratigraphic distribution is not defined. In the studied material, it occurs from the middle upper Santonian–lower Campanian.

**THE GAVELINELLA STELLIGERA LINEAGE**

*Gavelinella* sp. A, G. sp. B, and *G. stelligera* seem to be closely related, and they probably constitute an evolutionary lineage named after *G. stelligera*. Specimens of this lineage possess a very low trochospiral to nearly planispiral test, small umbilicus almost entirely covered by an umbilical folium, and a blunt or sharply angled peripheral edge. The lack of broad, raised and prominent septal-ridge elements on the umbilical side distinguish this lineage from the *G. ammonoides* lineage. Species within the *G. stelligera* lineage differ mainly from each other in test symmetry. In the Dubivtsi succession the lineage appears in the lower Campanian. A transition from *G. sp. B* to *G. stelligera* occurs within the middle Santonian. The morphological changes involved in this transition are a continuous decrease in test thickness, increasing acuteness of the peripheral margin, and the appearance of test asymmetry (i.e., the shift of the aperture and “keel-like” structure from an equatorial to umbilical position). This asymmetry is also observed in the same stratigraphic interval within the *G. ammonoides* lineage in the transition from *G. lorneiana* to *G. costulata*. The development of a similar trait in related, but distinct, lineages of foraminifera is interpreted as parallel evolution (Fig. 2).

*Gavelinella* sp. A  
Figs. 5.1, 5.2

*Gavelinella stelligera* (Marie). Hradecka, 1996, p. 91, 92, pl. 6, figs. 7–9.

**Material.** Thirteen specimens.

**Description.** Test is very low trochospiral, almost planispiral, symmetrical, slightly biconvex with a flush margin outline and sharply angular periphery. Approximately 11–13 crescent-shaped and inflated chambers occur in the last whorl, enlarging gradually and separated by depressed, arcuate sutures on both sides of the test. Test surface smooth, with coarse pores on the umbilical side. The inner sections of chambers on the umbilical side gradually turn into triangular apertural flaps covering the aperture and umbilicus.

**Remarks.** *Gavelinella* sp. A differs from *G. sp. B* in possessing a sharply angular periphery and from *G. stelligera* in its biconvex and symmetrical test.

**Stratigraphic range and geographic distribution.** In the Dubivtsi succession, the taxon occurs in the lower–middle Santonian.

*Gavelinella* sp. B  
Figs. 5.3, 5.4

**Material.** Over 40 specimens.

**Description.** Test is very low trochospiral, almost planispiral, slightly biconvex with a flush margin outline and rounded periphery. There are ~11–13 crescent-shaped, inflated chambers, elongated in the direction of coiling in the last whorl, increasing slowly in size, and separated by depressed, gently arcuate sutures on both sides of the test. The test surface is smooth, unornamented with coarse pores on the umbilical side. Inner sections of chambers on the umbilical side gradually turn into triangular apertural flaps covering the aperture and umbilicus.

**Remarks.** *Gavelinella* sp. B differs from *G. stelligera* in its asymmetrically biconvex test with rounded periphery.

**Stratigraphic range and geographic distribution.** In the Dubivtsi succession, the species is limited to the middle Santonian.

*Gavelinella stelligera* (Marie, 1941)  
Figs. 5.5, 5.6

*Planulina stelligera* Marie, 1941, p. 245, pl. 37, fig. 344.


*Gavelinella stelligera* (Marie). Rozumeko, 1978, p. 109, pl. 15, fig. 1; Kaptarenko-Chernousova et al., 1979, p. 128, pl. 48, fig. 7; Hart et al., 1989, p. 338, pl. 7.12, figs. 10–12; Gawor-Biedowa, 1992, p. 171, pl. 36, figs. 3–5.

**Material.** Over 100 specimens.

**Description.** Test is very low trochospiral, almost planispiral, compressed with a flush margin outline, and asymmetrical with an almost flat spiral side and slightly convex umbilical side. Approximately 14 chambers occur in the last whorl, increasing slowly in size and separated by
depressed, gently arcuate sutures on both sides of the test. A sharply angular periphery, which constitutes the “keel-like” structure, is moved toward the spiral side. On the umbilical side, the inner parts of chambers gradually turn into triangular apertural flaps covering the aperture and umbilicus. Test surface is smooth, unornamented with coarse pores on the umbilical side.

Remarks. *G. stelligera* differs from its ancestor *G. sp. B* in possessing a more flattened, compressed, and asymmetrical test and much more acute angular periphery. In the middle–upper Santonian interval *G. sp. B* gradually evolves into *G. stelligera*, and there are many transitional forms.

Stratigraphic range and geographic distribution. The species is widely recorded in Santonian and Campanian epicontinental beds in Europe. In the Dubivtsi succession *G. stelligera* appears close to the lower boundary of the upper Santonian defined by the first occurrence of the inoceramid bivalve *Cordiceramus muelleri* (Petrascheck) (Walszczczyk et al., in press) and persists to the top of the section in the lower Campanian. It appears to be a similar interval in southern England, where Hart et al. (1989) first recorded the species in south Kent in the highest part of the *Micraster coranguinum* Zone slightly below the lower boundary of the *Uintacrinus socialis* Zone, i.e., in the higher middle Santonian (see also Edwards, 1981). Thus the first appearance of *G. stelligera* seems to be a useful marker for the middle/upper Santonian boundary interval in eastern and western Europe.

**THE GAVELINELLA VOMBENSIS LINEAGE**

The closely related species *Gavelinella vesca*, *G. praefrasantonica*, and *G. vombensis* constitute the *G. vombensis* lineage. The evolutionary changes within this lineage were related to the formation of biconvex tests and the increasing prominence of the umbilical septal ridges (Fig. 6).

*Gavelinella vesca* (Bykova, 1939)

Figs. 7.1, 7.2

*Discorbis vescus* Bykova, 1939, p. 28, pl. 3, figs 1–6.


*Gavelinella vesca* (Bykova). Dubicka & Peryt, 2012b, pl. 7, figs. Da–c.

**Material.** Over 50 specimens.

**Description.** Test is low trochospiral, with a slightly convex spiral side and almost flat umbilical side; margin outline flush, and periphery rounded to slightly angular. On
the spiral side, the inner whorls are covered by a smooth, convex boss of variable size. On the umbilical side, inner parts of chambers gradually turn into triangular apertural flaps covering the aperture and umbilicus. Test surface smooth, unornamented with pores on umbilical side.

Remarks. Gavelinella vesca is ancestral to G. praeinfrasantonica within the G. vombensis lineage. It differs from G. praeinfrasantonica in lacking an umbilical stellate pattern of thread-like depressions and prominent ridge elements and in possessing a plano-convex instead of a biconvex test.

Stratigraphic range and geographic distribution. The species is known from the Turonian of the Mangyshlak Peninsula, Kazakhstan (Vasilenko, 1961). In the Dubivtsi succession, G. vesca occurs in the upper Turonian–lower Coniacian.

Gavelinella praeinfrasantonica (Mjatliuk, 1947)
Figs. 7.3, 7.4
Anomalina praeinfrasantonica Mjatliuk in Vasilenko & Mjatliuk, 1947, p. 211, pl. 3, figs. 8a–c.
Anomalina (Pseudovalvulineria) praeinfrasantonica (Mjatliuk). Vasilenko, 1954, p. 101, pl. 13, fig. 5; Vasilenko, 1961, p. 121, pl. 22, fig. 1.
Pseudovalvulineria praeinfrasantonica (Mjatliuk). Rozumeiko, 1978, p. 112, pl. 16, fig. 2; Kaptarenko-Chernousova et al., 1979, p. 130, pl. 49, fig. 6.


Material. Over 20 specimens.

Description. Test is low trochospiral, biconvex, with a flush margin outline and rounded periphery. There are ~11 crescent-shaped, inflated, and narrow chambers, elongated in the direction of coiling in the final whorl, enlarging gradually, and separated by depressed, gently arcuate sutures on the both sides of the test. On the spiral side, the inner whorls are covered by a smooth, convex boss of variable size. In the central part of the umbilical side, there is a stellate pattern of thread-like depressions and broad, raised, imperforate, and prominent ridge elements of varying length encircling the umbilicus. Test surface is smooth with coarse pores located only on the umbilical side.

Remarks. Gavelinella praeinfrasantonica is transitional between G. vesca and G. vombensis. Differences with G. vesca are given in the remarks about that species. It differs from G. vombensis in having a less enhanced umbilical stellate pattern.

Stratigraphic range and geographic distribution. The taxon was described from the Coniacian of eastern and northwestern Europe. In the Dubivtsi succession, the species occurs in the lower–middle Coniacian.
**Gavelinella vombensis** (Brotzen, 1945)
Figs. 7.5, 7.6

*Pseudovalvulineria vombensis* Brotzen 1945, p. 50, 51, tab. 1, fig. 13, not fig. 12, text-fig. 9.

*Anomalina (Pseudovalvulineria) infrasantonica* Balakhmatova. Vasilenko, 1954, p. 102, pl. 13, fig. 6.

*Anomalina infrasantonica* Balakhmatova. Akimets, 1961, p. 154, pl. 15, fig. 5.

*Pseudovalvulineria infrasantonica* (Balakhmatova). Rozumeiko, 1978, p. 113, pl. 16, fig. 3; Kaptarenko-Chernousova et al., 1979, p. 130, pl. 50, fig. 1.

*Gavelinella vombensis* (Brotzen). Gawor-Biedowa, 1980, p. 44, pl. 9, figs. 9–11, pl. 9, figs. 8, 9; Edwards, 1981, p. 404, 405, pl. 56, figs. 16–18, pl. 57, figs. 1–3; Gawor-Biedowa et al., 1984, p. 303, pl. 49, figs. 4–6; Schönfeld, 1990, p. 108, pl. 6, figs. 4, 5; Hradecká, 1996, p. 91, pl. 6, figs. 1–6.

*Gavelinella arnagerensis* Solakius. Watkins & Veltkamp, 1994, pl. 2, figs. 1, 2.

*Lingulogavelinella cf. vombensis* (Brotzen). Howe et al., 2007, figs. 6S–U.

**Material.** Over 100 specimens.

**Description.** Test is low trochospiral, biconvex, with a flush margin outline and rounded periphery. There are ~11 crescent-shaped, inflated, and narrow chambers, elongated in the direction of coiling in the final whorl, increasing slowly in size, and separated by depressed, gently arcuate sutures on both sides of the test. The spiral-side inner whorls are covered by a smooth, convex boss of variable size in the majority of examined specimens. In the central part of the umbilical side, there is a stellate pattern of thread-like depressions and broad, raised, imperforate, and prominent ridge elements of varying length encircling the umbilicus. Test surface smooth with coarse pores only on umbilical side.

**Remarks.** *Anomalina infrasantonica* is a junior synonym of *G. vombensis*. The species probably evolved from *G. praeinfrasantonica* during the Coniacian and differs from the latter in having a much more enhanced umbilical stellate pattern as suggested by previous workers (Vasilenko, 1954; Edwards, 1981). Vasilenko (1954) proposed that her *G. praeinfrasantonica*–*G. santonica* lineage evolved from *G. kelleri* (Vasilenko & Mjatliuk, 1947). The convexity of the test and the size and presence of the spiral boss are highly variable within *G. vombensis*.

**Stratigraphic range and geographic distribution.** The species is widely known from the Coniacian and lower Santonian in Europe. In the Dubivtsi succession, it appears in the middle Santonian (*Volviceramus involutus* Zone) and disappears close to the lower/middle Santonian boundary defined as the LAD of *Cladoceramus undulatoplicatus* (Roemer). Its age has also been precisely documented in many other sections. For example, at Lägerdorf in N
Germany *G. vombensis* appears within the Praebulimina ovulum Zone and disappears close to the upper boundary of the Gavelinopsis eriksdalensis/Gavelinella vombensis Zone (Schoenfeld, 1990). This corresponds to an interval from the higher part of the Volviceras koeneni Zone to the boundary between the coranguinum/westfalica and rogalae/westfalica zones (sensu Ernst & Schulz, 1974; Schulz et al., 1984; Schulz, 1985). This interval is placed close to the lower boundary of the Cordiceramus cordiformis Zone, i.e., the inoceramid lower/middle Santonian boundary. In southern England at Seaford Head, *Gavelinella arnagerensis*, which is a synonym of *G. vombensis*, disappears 1 m above the last occurrence of *Cladoceramus* and below the last occurrence of *Stenioeina polonica* (Hampton et al., 2007), and in southeastern Kent *G. vombensis* disappears within the Micraster coranguinum Zone, below the last occurrence of *S. polonica* (Hart et al., 1989). Consequently, at all these localities *G. vombensis* disappears within a similar interval, i.e., close to the lower/middle Santonian boundary; thus this event seems to be a useful stratigraphical indicator for proximity to this boundary in eastern and western Europe.

**Figure 8.** Foraminifera of the *Gavelinella pertusa* lineage; scale bars = 100 μm. 1, 2 *Gavelinella tumida* Brotzen: 1, Dubivtsi 1, sample 47, ZPAL F63/10/21; 2, Dubivtsi 1, sample 49, ZPAL F63/10/17. 3, 4 *Gavelinella pertusa* (Marsson): 3, Dubivtsi 2, sample 4.22, ZPAL F63/19/14; 4, Dubivtsi 2, sample 4.22; ZPAL F63/19/20. 5, 6 *Gavelinella* sp. aff. *G. tumida* Brotzen: 5, Dubivtsi 2, sample 2.1, ZPAL F63/19/29; 6, Dubivtsi 2, sample 2.15, ZPAL F63/19/30.

**The Gavelinella pertusa Lineage**

The *Gavelinella pertusa* lineage comprises the following species: *G. tumida*, *G*. sp. aff. *G. tumida*, and *G. pertusa*. They have a plano-convex test with an almost flat spiral side and convex umbilical side, and a deep and wide umbilicus. Edwards (1981) proposed that *G. pertusa* evolved from *G. lorneiana* by reduction in the degree of umbilical perforation and deepening of the umbilicus.

*Gavelinella tumida* Brotzen, 1942

Figs. 8.1, 8.2

*Anomalina lorneiana* (d’Orbigny). Brotzen, 1936, p. 178–181, text-fig. tab. 64.

*Gavelinella tumida* Brotzen, 1942, p. 47, fig. 15; Hradecká, 1996, p. 92, pl. 9, figs. 3–6; Revets, 2001, p. 70, pl. 4, figs. 10–12.

**Material.** Over 100 specimens.

**Description.** Test plano-convex with moderately convex umbilical side and flattened spiral side; periphery broadly rounded. Margin outline flush in the older part of the last whorl and slightly lobulate in the youngest part. Unornamented central depression on the spiral side constitutes 1/3–1/4 of the test diameter. Large umbilicus is ≥ half the chamber.

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width in depth, only partially covered by umbilical folia. The ~10–11 chambers are crescent shaped and inflated, elongated in the direction of coiling in the last whorl, increasing rapidly in size, and separated by depressed, gently arcuate sutures on the both side of the test. The last chamber is much larger than the older ones and strongly inflated on the umbilical side. Test surface is smooth, unornamented with coarse pores, which are located on both sides except in the spiral-side central depression.

Remarks. Gavelinella tumida differs from G. pertusa in its bulged, tightly coiled test, much larger and inflated last chamber, and less open umbilical area. Specimens resembling G. tumida, but differing in their considerably smaller size (Figs. 8.5, 8.6) and more tightly coiled test, are named herein G. sp. aff. G. tumida.

Stratigraphic range and geographic distribution. Gavelinella tumida have been recorded from the upper Coniacian–lower Santonian of Sweden, France, and Bohemia. In the Dubivtsi succession, it spans the Volviceras involutus and Magadiceramus subquadratus zones (middle–upper Coniacian), whereas G. sp. aff. G. tumida is limited to the lower Santonian–lower middle Santonian.

Gavelinella pertusa (Marsson, 1878)

Figs. 8.3, 8.4

Discorbina pertusa Marsson, 1878, p. 166, pl. 4, figs. 35 a–e.
Gavelinella giedroyci Grigelis, 1966, p. 386–388, pl. 4, figs. a–v, tab. 2, figs. 1–2.

Gavelinella pertusa (Marsson). Edwards, 1981, p. 397, 398, pl. 56, figs. 7–9; Hart et al., 1989, p. 338, pl. 7.12, figs. 4–6; Gawor-Biedowa, 1992, p. 169, pl. 36, figs. 6, 7.

Material. Over 40 specimens.

Description. Test plano-convex with a convex umbilical side and flattened spiral side; periphery rounded. The ~10–11 crescent-shaped and inflated chambers are elongated in the direction of coiling in the last whorl, increasing moderately in size, and separated by depressed, gently arcuate sutures on both sides of the test. The deep and wide umbilicus exposes 2½ whorls on the umbilical side. Test surface smooth, unornamented, with coarse pores that are located on both sides except in the spiral-side central depression.

Remarks. Gavelinella pertusa differs from G. tumida in having a wide, open, shallow umbilicus, smaller last chamber in comparison to the older ones, and less inflated umbilical side. The upper Campanian and Maastrichtian forms described, for example, by Gawor-Biedowa (1990) and Hart et al. (1989) differ from Santonian and lower Campanian individuals in their thicker test and deeper umbilicus.

Stratigraphic range and geographic distribution. The species is widely recorded in epicontinental beds in Great Britain, France, Germany, Poland, Ukraine, and Kazakhstan, dated roughly as Santonian–Maastrichtian. In the Dubivtsi succession, the species ranges from the middle Santonian to the top of the section (lower Campanian).

THE GAVELINELLA CLEMENTIANA LINEAGE

All foraminifera belonging to the G. clementiana lineage are characterized by specific and easily recognizable ornamentation that occurs on both sides of the test. The ornamentation forms numerous nodules and ridges on the septal sutures and spiral suture. These foraminifera are widely recorded in the upper part of the Santonian and Campanian epicontinental beds of Europe. Some authors have described their earliest occurrence in the middle/upper Santonian boundary interval (e.g., Schönfeld, 1990, from the Lägeordorf section, N Germany) and others much higher in the lower Campanian (e.g., Hampton et al., 2007, from the Seaford Head section, S England). Watkins & Veltkamp (1994) also noticed that the first appearance of a representative of this group—G. pseudoexcolata (Kalinin, 1937)—is diachronous across the Anglo-Paris Basin, ranging from the basal Santonian in Cangery (Touraine, France) to the base of the Uintacrinus socialis Zone at Seaford Head, S. England.

In the studied succession the Gavelinella clementiana lineage appears in the middle part of level 4 which corresponds to the lower part of the Cordiceramus muelleri Zone (upper Santonian). In the upper Santonian, these forms occur occasionally and have poorly developed ornamentation (Figs. 9.1, 9.2). It is not until the middle part of level 6 (lower Campanian) that specimens of the Gavelinella clementiana lineage become numerous and constitute a significant part of the benthic foraminiferal assemblages. Moreover, in the lower Campanian these forms are clearly differentiated into two separate taxa: G. clementiana and G. costata.

Gavelinella clementiana (d’Orbigny, 1840)

Figs 9.3, 9.4

Rosalina clementiana d’Orbigny, 1840, p. 37, pl. 3, figs. 23–25.
Discorbis clementiana f. typica Marie, 1941, p. 213, pl. 33, fig. 312.
Anomalina (Pseudovalvulineria) clementiana var. pseudoexcolata Kalinin. Vasilenko, 1954, p. 91, pl. 9, fig. 1.
Anomalina (Pseudovalvulineria) clementiana var. clementiana (d’Orbigny). Vasilenko, 1961, p. 121, pl. 22, fig. 4.
Pseudovalvulineria clementiana (d’Orbigny). Rozumeiko, 1978, p. 110, pl. 15, fig. 2.
Pseudovalvulineria clementiana var. pseudoexcolata (Kalinin). Kaptarenko-Chernousova et al., 1979, p. 130, pl. 49, fig. 3.
Gavelinella clementiana (d’Orbigny). Hart et al., 1989, p. 336, pl. 7.11, figs. 1–3.

Material. Over 40 specimens.

Description. Test large, robust, very low trochospiral, plano-convex with convex umbilical side and flattened or slightly concave spiral side, oval in outline, and with a flush margin outline. Periphery broad and bluntly rounded. Typically 11 chambers are in the last whorl, increasing moderately in size. Sutures on spiral side arcuate, raised, forming irregular ridges; sutures on umbilical side radial, slightly depressed in the youngest part of the last whorl, raised in the older part forming irregular ridges. Umbilical ends of sutures thicken and coalesce into a ridge partly covering the umbilicus. Test surface smooth with coarse pores on the umbilical side. Ornamentation in the form of tubercles and short, corrugated ribs, which occur along the spiral suture and chamber sutures on both sides of the test.

Remarks. Rosalina clementiana is the type species of the genus Pseudogavelinella Voloshina in Subbotina et al., 1981,
that we consider synonymous with *Gavelinella*. *Gavelinella clementiana* is very similar to other species of the genus, especially those of the *G. ammonoides* lineage from which it differs in possessing characteristic ornamentation on both sides of the test. It differs from *G. costata* in its plano-convex test.

**Stratigraphic range and geographic distribution.** At Dubivtsi *G. clementiana* appears in the lower Campanian.

*Gavelinella costata* (Marie, 1941)

Figs. 9.5, 9.6


**Material.** Over 30 specimens.

**Description.** Test large, robust, very low trochospiral, nearly planispiral, and biconvex. Test has a smooth surface with coarse, oval pores on the umbilical side and a flush margin outline. Periphery broad and bluntly rounded. Typically 11 chambers are in the last whorl, increasing moderately in size. Sutures on spiral side arcuate, raised, forming irregular ridges; those on umbilical side radial, slightly depressed in the youngest part of the last whorl, raised in the older part, forming irregular ridges. Umbilical ends of sutures thicken and coalesce into a ridge partly covering the umbilicus. On both sides of the test there is a very distinctive ornamentation in the form of tubercles and short, corrugated ribs occurring at the sutures and in the central part of spiral side.

**Remarks.** *Gavelinella costata* differs from *G. clementiana* in possessing a biconvex test and more distinctive ornamentation on the umbilical side.

**Stratigraphic range and geographic distribution.** In the studied succession, *Gavelinella clementiana* appears in the lower Campanian.

Subfamily *GYROIDINOIDINAE* Saidova, 1981

**STENSIOEINIDS**

According to Loeblich & Tappan (1987), the main characteristics of *Stensioeina* are: a low trochospiral test with a flattened or slightly convex and evolute spiral side and bluntly convex umbilical side; gradually enlarging chambers on the spiral side, separated by curved, limbate sutures,
strongly elevated in somewhat irregular ridges, resulting in a reticulose surface; and the aperture a low interiomarginal opening between the umbilicus and periphery.

Hofker (1957), Trümper (1968), Koch (1977), Gawor-Biedowa et al. (1984), Hart et al. (1989), King et al. (1989), Mortimore et al. (2001), and Hampton et al. (2007) described and documented the stratigraphic distribution of Stensioeina. However, the evolutionary relationships within the genus are still poorly recognized, and there are only a few papers dealing with its evolution. Koch (1977) gave the most comprehensive description on the classification, evolutionary relationships, and stratigraphic distribution of Stensioeina. He placed S. pokornyi Scheinbernová, 1963, at the beginning of the Stensioeina lineage, while Mjatliuk (1953) and Vasilenko (1961) were of the opinion that S. praeexsculpta (Keller, 1935) began the lineage. According to Bailey et al. (2009), there are two quite distinct, parallel trends within the genus from the latest Cenomanian to the Maastrichtian. One involves the degree of ornamentation on the spiral side of the test, which was also described by Sadekov et al. (2006), and the other being the increasing thickness of the test. Sadekov et al. (2006) recognized close affinities among S. excelsa, S. incondita, and S. pommerana. According to these authors, the species constitute one lineage, showing evolutionary changes within the umbilical area.

Based on results of the present study we split all Stensioeina into two distinct groups. Representatives of each group differ significantly in morphology, evolutionary changes, and stratigraphic ranges. Moreover, Loeblich & Tappan’s (1987) definition of Stensioeina clearly fits the description of only one of the two groups. Herein we distinguish two separate genera: Stensioeina as defined by Loeblich & Tappan (1987) and Protostensioeina n. gen.

Genus Protostensioeina n. gen.
Type species: Rotalia excelsa granulata Olbertz, 1942

Diagnosis. Test plano-convex; flush margin outline; spiral side of the test varies significantly from smooth and without ornamentation to covered by irregularly scattered tubercles and short, irregular ridges resulting in a rough surface; on the umbilical side inner sections of chambers gradually grow into small triangular flaps covering the umbilicus, which in some species or specimens merge into a round plug.

Description. Protostensioeina has a plano-convex test with a flattened spiral side and convex umbilical side slightly flattened in the center, and a rounded or only slightly compressed periphery. Sutures on the umbilical side are wide, imperforate, gently curved, and raised. On the umbilical side the inner sections of chambers gradually grow into small triangular flaps covering the umbilicus. In some species or specimens these flaps merge into a round plug. Test surface on the umbilical side smooth with coarse pores. Spiral side of the test varies significantly in ornamentation, on which the taxonomy of this group is based. Aperture a low interiomarginal opening between the umbilicus and periphery.

Remarks. The evolutionary development of the genus is difficult to determine because the interval containing the oldest species (upper Turonian–middle Coniacian) is incomplete in the studied section. During that interval the pattern of ornamentation on the spiral side—a primary species characteristic—changes within successively younger representatives. The final stage of evolution is related to the reduction of ornamentation, and the last species (Protostensioeina polonica) of this group possesses a smooth spiral side. Bailey et al. (2009) also mentioned changes in spiral-side ornamentation as a distinct trend in the evolution of Stensioeina. Protostensioeina spp. are known from the Turonian–mid-Santonian of the European epicontinental basin.

Protostensioeina bohemica (Jirová, 1958)
Figs. 10.1–10.3

Stensioeina bohemica Jirová, 1958, p. 224, pl. 1, fig. 2.
Stensioeina granulata granulata (Olbertz). Howe et al., 2007, pl. 6, figs. Y–AA.

Material. Over 30 specimens.

Description. Test low trochospiral, oval, with flush margin outline, flattened and evolve spiral side, and bluntly convex and involute umbilical side. There are 9–11 chambers in the final whorl. Central part of umbilical side slightly flattened. A large and shallow depression on the spiral side makes up the bulk of the test and is bordered by a thickened peripheral rim. The internal edge of the depression is irregular, sinusous, and slightly thickened. The surface inside the depression is covered by prominent, wavy ridge elements and tubercles. On the umbilical side, sutures are raised, forming wide ridges. Umbilical ends of chambers grow into small triangular apertural flaps covering the umbilicus. Test surface on the umbilical side smooth with coarse pores. Periphery subangular to rounded.

Remarks. Protostensioeina bohemica is distinguishable by the spiral-side ornamentation described above and by the barely visible sutures on the spiral side.

Stratigraphic range and geographic distribution. In the Seaford Head section, Howe et al. (2007) illustrated specimens of P. bohemica (identified as Stensioeina granulata granulata) in the Coniacian/Santonian boundary interval. In our study area, P. bohemica occurs in the middle of level 1, representing the same stratigraphic position.

Protostensioeina granulata (Olbertz, 1942)
Figs. 10.4–10.6

Rotalia excelsa granulata Olbertz, 1942, p. 132, pl. 5, figs. 2a–c.
Valvulineria undulata Belford, 1960, p. 76, pl. 20, figs. 19–24.
Stensioeina praeexsculpta var. praeexsculpta Akimets, 1961, p. 120, pl. 11, fig. 1.
Stensioeina granulata granulata (Olbertz). Teisseyre, 1975, p. 114, 115, pl. 1, fig. 6; Koch, 1977, p. 35, pl. 9, figs. 1–3; Gawor-Biedowa et al., 1984, p. 306, pl. 111, figs. 3–5; Peryt, 1988, pl. 2, figs. 18, 19; Hart et al., 1989, p. 362, pl. 7.24, figs. 4–6.

Material. 19 specimens.

Description. Test low trochospiral, oval, with flush margin outline, flattened and evolve spiral side, and bluntly convex and involute umbilical side. There are 9–11 chambers in the final whorl. Central part of umbilical side slightly flattened. Spiral side covered by irregularly scattered tubercles and short, irregular ridges resulting in a rough surface. On the umbilical side, sutures are raised, forming wide ridges. Umbilical ends of chambers turn into small triangular apertural flaps, of which the three youngest
conjoin to form a circular plug over the umbilicus. Test surface on the umbilical side smooth with coarse pores. Periphery subangular to rounded.

Remarks. Protostensioeina granulata is distinguishable by its ornamentation on the spiral side, a circular plug covering the umbilicus, and lack of visible sutures on the spiral side.

Stratigraphic range and geographic distribution. The species is widely recorded in Coniacian epicontinental beds in Great Britain, France, Germany, Poland, Ukraine, and Kazakhstan. According to Koch (1977) the first appearance of Protostensioeina granulata in northwestern Germany is placed close to the Cremnoceramus deformis and Volviceramus koeneni zonal boundary (lower/middle Coniacian). Its first appearance datum in southern England was found at the Micraster cortestudinarium/Micraster coranguinum zonal boundary (Bailey et al., 1983; Hart et al., 1989). In the Dubivtsi succession the species was found within the Volviceramus involutus Zone (middle Coniacian).

Protostensioeina polonica (Witwicka, 1958)
Figs. 10.7, 10.8
Stensioina praeexsculpta var. laevigata Akimets, 1961, p. 121, 122, pl. 11, fig. 2.
Protostensioeina granulata polonica

Description. Test low trochospiral, oval, with flush margin outline, flat and evolute spiral side, and bluntly convex and involute umbilical side. There are 9–11 chambers in the final whorl. Central part of umbilical side slightly flattened. Spiral-side sutures curved, thickened, and strongly elevated. Umbilical-side sutures raised, forming wide ridges. Umbilical ends of chambers grow into small triangular apertural flaps covering the umbilicus. Test surface on the umbilical side smooth with coarse pores; spiral side smooth and without ornamentation. Periphery subangular to rounded.

Remarks. Protostensioeina sp. A differs from P. bohemicana in having strongly elevated sutures on the spiral side. It closely resembles P. sp. B in spiral-side ornamentation. However, its sutures are arcuate instead of the irregular, undulating ridges in P. sp. B.

Stratigraphic range and geographic distribution. In the Dubivtsi succession the species is limited to the middle–upper Coniacian.

Protostensioeina sp. B

Material. 21 specimens.

Description. Test low trochospiral, oval, with flush margin outline, flat and evolute spiral side, and bluntly convex and involute umbilical side. There are 9–11 chambers in the final whorl. Central part of umbilical side slightly flattened. Spiral-side sutures curved, thickened, and strongly elevated. Umbilical-side sutures raised, forming wide ridges. Umbilical ends of chambers grow into small triangular apertural flaps covering the umbilicus. Test surface on the umbilical side smooth with coarse pores; spiral side smooth and without ornamentation. Periphery subangular to rounded.

Remarks. Protostensioeina sp. B probably originated from P. granulata, from which it differs in possessing irregular, wavy, and undulating sutures elevated into ridges, irregularly scattered tubercles, and short ridges resulting in a rough surface. Umbilical-side sutures are raised, forming wide ridges. Umbilical ends of chambers grow into small triangular apertural flaps covering the umbilicus. Test surface on the umbilical side smooth with coarse pores; spiral side smooth and without ornamentation. Periphery subangular to rounded.

Protostensioeina sp. C

Material. Ten specimens.

Description. Test low trochospiral, oval, with delicately lobate margin outline, flat and evolute spiral side, and bluntly convex and involute umbilical side. There are 9–11 chambers in the final whorl. Central part of umbilical side slightly flattened. Spiral-side chambers are crescent shaped. Sutures arcuate, raised, and widest in the peripheral part. Central part of the spiral side covered by irregularly developed ridges. On the umbilical side sutures are raised, forming wide ridges. Umbilical ends of chambers grow into small triangular apertural flaps covering the umbilicus. Test surface on the umbilical side smooth with coarse pores; spiral side smooth and without ornamentation. Periphery subangular to rounded.

Remarks. Protostensioeina sp. C differs from other representatives of the genus in possessing a lobate margin.
Stratigraphic range and geographic distribution. In the Dubivtsi succession it occurs in the middle Coniacian.

**Protostensioeina** sp. D
Figs. 10.10, 11.6

*Stensioeina granulata polonica* Witwicka. Hart et al., 1989, p. 362, pl. 7.24, figs. 7–9.

**Material.** 20 specimens.

**Description.** Test low trochospiral, oval, with flush margin outline, flat and evolute spiral side, and bluntly convex and involute umbilical side. There are 9–11 chambers in the final whorl. Central part of umbilical side slightly flattened. Spiral side sutures curved, raised, visible only in the last whorl. Central part of test flush and slightly elevated. Umbilical-side sutures are raised, forming wide ridges. Umbilical ends of chambers grow into small triangular apertural flaps covering the umbilicus. Test surface on the umbilical side smooth with coarse pores; spiral side smooth and without ornamentation. Periphery subangular to rounded.

**Remarks.** *Protostensioeina* sp. D differs from *P. polonica* in possessing distinct, raised, and curved sutures in the peripheral part of the spiral side.

Stratigraphic range and geographic distribution. In the Dubivtsi succession, the species ranges from middle Coniacian–middle lower Santonian.

**Protostensioeina** sp. E
Figs. 11.7, 11.8


*Stensioeina granulata incondita* Koch. Howe et al., 2007, pl. 6, figs. BB-DD.

**Material.** 35 specimens.

**Description.** Test low trochospiral, oval, with flush margin outline, flat and evolute spiral side, and bluntly convex and involute umbilical side. There are 9–11 chambers in the final whorl. Central part of umbilical side slightly flattened. Spiral side sutures distinct, elevated and curved sutures and short wavy ridges, resulting in a reticulose surface in the central part of the test. Umbilical-side sutures are raised, forming wide ridges. Umbilical ends of chambers grow into small triangular apertural flaps covering the umbilicus. Test surface on the umbilical side smooth with coarse pores; spiral side smooth and without ornamentation. Periphery subangular to rounded.
Remarks. Protostensioeina sp. E differs from P. bohemica in having a flat, instead of depressed, central spiral side.

Stratigraphic range and geographic distribution. In the Dubivtsi succession Protostensioeina sp. E ranges from upper Coniacian–lower lower Santonian (lower part of the Cladoceramus undulatoplicatus Zone). In the Seaford Head sections (S England), the species also occurs in the Coniacian/Santonian boundary interval (Howe et al., 2007).

Genus Stensioeina Brotzen, 1936
Type species: Rotalia exsculpta Reuss, 1860

The main characteristic of Stensioeina is the spiral-side ornamentation that includes curved, limbate, and elevated sutures and a suture ridge forming a highly irregular, reticulate network and a sharp, angular border. During its evolution the spiral-side ornamentation remained stable while that on the umbilical side changed through time. Also of importance are the shape and thickness of the test which show distinct changes. Stensioeina is known from middle Coniacian–upper Maastrichtian. We distinguished two separate lineages, S. exsculpta and S. perfecta, which followed different courses of evolution. The S. perfecta lineage evolved during the early Santonian from the S. exsculpta lineage, from which it differs in possessing a thicker test in axial view; hence the lineage S. exsculpta is called “thin Stensioeina,” whereas the lineage S. perfecta is called “thick Stensioeina.” The main evolutionary changes in both groups focus on the umbilical area, which is modified in a slightly different way in each lineage.

The Stensioeina exsculpta Lineage—“Thin Stensioeina”

The Stensioeina exsculpta lineage includes S. exsculpta, S. gracilis, S. sp. A, and S. sp. B. This group is characterized by a relatively low test and open umbilicus that is not covered or only partially covered by chamber flaps. The main species differences are in the test shape and/or arrangement of the umbilical chamber sections on the umbilical side (Fig. 12).

Stensioeina exsculpta begins the lineage, and although it could have arisen from Protostensioeina, its origin is uncertain. The evolutionary changes of the S. exsculpta lineage or “thin Stensioeina” mainly concern test shape and umbilical ornamentation. As in most Gavelinellidae, S. exsculpta possesses small triangular apertural flaps, partially covering the umbilicus, which constitute direct extensions of the chambers. This ornamentation is herein named “type X.” In contrast, S. sp. A, S. gracilis, and S. sp. B possess undulating outgrowths that extend from the surface of the test and are separated by grooves. This type of ornamentation, herein named “type Y,” is found in all specimens of the S. exsculpta lineage within upper Santonian and younger beds. Thus, one evolutionary trend is observed within the whole S. exsculpta lineage, which reflects a progressive change in the arrangement of umbilical chamber extensions. Stensioeina gracilis and Stensioeina sp. B probably evolved from a S. exsculpta/B. sp. A ancestor.

Stensioeina exsculpta (Reuss, 1860)
Figs. 13.1, 13.2

Rotalia exsculpta Reuss, 1860, p. 222, pl. 11, figs. 4a–c.
Stensioeina exsculpta (Reuss). Brotzen, 1936, p. 165, 166, pl. 11, figs. 8 a–c; Pozaryska 1954, p. 264, pl. 22; Witwicka, 1958, p. 205, pl. 11, fig. 19; Vasilenko, 1961, p. 65, pl. 11, fig. 4; Heller, 1975, pl. 4, fig. 6; Koch, 1977, p. 40, pl. 11, figs. 9–11; Rozumeiko, 1978, p. 97, pl. 16, fig. 1; Howe et al., 2007, pl. 6, figs. V–X.
Stensioeina mursataiensis Vasilenko, 1961, p. 66, pl. 11, fig. 5.
Stensioeina exsculpta exsculpta Teissérye, 1975, p. 115, pl. 1, fig. 7; Hart, 1989, p. 360, pl. 7.23, figs. 11–13.

Material. Over 40 specimens.

Description. Test plano-convex with spiral side flat; umbilical side slightly convex and flattened in central part, giving trapezoidal shape in axial section. Umbilicus slightly depressed, open or covered by triangular flaps. Test margin acute. Approximately 9–11 chambers in the final whorl enlarge gradually. Spiral-side chambers separated by curved, sharply raised, spiral sutures forming irregular, elevated septal ridges. Umbilical-side sutures flush to slightly depressed; periphery broadly rounded. Umbilical side smooth with coarse pores.

Remarks. The recently used concept of Protostensioeina and Stensioeina sp. B probably evolved from a Reuss, 1860
S. gracilis S. S. exsculpta S. S. perfecta, Brotzen, 1936, p. 165, 166, pl. 11, figs. 8 a–c; Pozaryska 1954, p. 264, pl. 22; Witwicka, 1958, p. 205, pl. 11, fig. 19; Vasilenko, 1961, p. 65, pl. 11, fig. 4; Heller, 1975, pl. 4, fig. 6; Koch, 1977, p. 40, pl. 11, figs. 9–11; Rozumeiko, 1978, p. 97, pl. 16, fig. 1; Howe et al., 2007, pl. 6, figs. V–X.
Stensioeina mursataiensis Vasilenko, 1961, p. 66, pl. 11, fig. 5.
Stensioeina exsculpta exsculpta Teissérye, 1975, p. 115, pl. 1, fig. 7; Hart, 1989, p. 360, pl. 7.23, figs. 11–13.

Material. Over 40 specimens.

Description. Test plano-convex with spiral side flat; umbilical side slightly convex and flattened in central part, giving trapezoidal shape in axial section. Umbilicus slightly depressed, open or covered by triangular flaps. Test margin acute. Approximately 9–11 chambers in the final whorl enlarge gradually. Spiral-side chambers separated by curved, sharply raised, spiral sutures forming irregular, elevated septal ridges. Umbilical-side sutures flush to slightly depressed; periphery broadly rounded. Umbilical side smooth with coarse pores.

Remarks. Stensioeina sp. A differs from S. exsculpta in possessing type-Y umbilical-side ornamentation, and from S. gracilis and S. sp. B in its trapezoidal shape in axial section.
Stratigraphic range and geographic distribution. In the studied section it ranges from upper Santonian (within the Cordiceramus muelleri Zone)–lower Campanian [identified on the occurrence of Bolivinoides culverensis Barr, 1967 (Dubicka, 2012; Hampton et al., 2007)].

\[\text{Stensioeina gracilis} \text{ Brotzen, 1945} \]
\[\text{Figs 13.5, 13.6}\]

\[\text{Stensioeina exsculpta} \text{ var. gracili} \text{ Brotzen, 1945, p. 52, pl. 1, fig. 15; Bieda 1958, p. 50, fig. 18.}\]

\[\text{Stensioeina exsculpta} \text{ var. aspera} \text{ Hofker, 1957, p. 349, 350, text-figs. 401, 402.}\]

\[\text{Stensioeina exsculpta gracilis} \text{ Brotzen. Koch, 1977, pl. 11, figs 5–8; Peryt, 1988, pl. 2, figs. 25, 26; Hart et al.,1989, p. 362, pl. 7.24, figs. 1–3.}\]

\[\text{Stensioeina gracilis} \text{ Brotzen. Gawor-Biedowa, 1984, p. 404, 405, tab. 110, figs. 7–9.}\]

Material. Over 30 specimens.

Description. Test biconvex, sharply keeled with a raised and irregularly ragged periphery. Approximately 11–12 chambers in the final whorl enlarge gradually. Umbilical-side sutures nearly radial and the youngest may be slightly depressed. Spiral-side chambers are separated by curved, sharply raised sutures, which form irregular elevated septal ridges. These chamber sutures together with the spiral suture result in a reticulate network. Umbilical side smooth with coarse pores. Umbilicus small, covered by undulating outgrowths extending from the umbilical part of the test. Chamber flaps and umbilical plug are absent.

Figure 12. Evolution of the Stensioeina exsculpta lineage.
Remarks. *Stensioeina gracilis* differs from all other *Stensioeina* in its raised trochospiral coil on the spiral side and in its thin, irregular, sharply keeled test margin. The convexity of the spiral side is variable.

Stratigraphic range and geographic distribution. The species is widely recorded from the upper Santonian and Campanian in European epicontinental facies. In southern England (Hart et al., 1989) and northern Germany (Koch, 1977; Niebuhr et al., 1999), it appears close to the middle/upper Santonian boundary and thus may be a useful marker to indicate proximity to that boundary. At the Dubivtsi sections it appears close to the middle/upper Santonian boundary, slightly below the boundary between the *Sphenoceramus pinniformis* and *Cordiceramus muelleri* inoceramid zones.

Material. Over 20 specimens.

Description. Test plano-convex with flattened spiral side and convex umbilical side; semi-oval in axial section. Umbilicus partially covered by undulating outgrowths extending from the umbilical part of the test. Test margin acutely angular. Approximately 11–12 distinct chambers in the final whorl enlarge gradually. Spiral-side chambers are separated by curved, sharply raised sutures which form irregular elevated septal ridges. These chamber sutures together with the spiral suture produce a reticulate network.
Umbilical-side sutures are nearly radial and later ones may be depressed. Umbilical side smooth with coarse pores.

Remarks. Stensioeina sp. B differs from S. sp. A in its semi-oval shape in axial section and from S. gracilis in its flat spiral side and lack of a sharply keeled and irregular margin.

Stratigraphic range and geographic distribution. In the studied section Stensioeina sp. B occurs in the lower Campanian.

The Stensioeina perfecta Lineage—“Thick Stensioeina”

The Stensioeina perfecta lineage includes S. perfecta, S. pommerana, and S. sp. C (Fig. 14) that probably constitute one evolutionary stock according to Sadekov et al. (2006). These taxa have a relatively thick test and an umbilicus partially or completely covered by chamber flaps or an umbilical plug. Because of its significant test thickness, this lineage is herein named “thick Stensioeina.”

It is highly probable that the “thick Stensioeina” evolved during the early Santonian from ancestral S. exsculpta from which it differs in possessing a thicker test and different arrangement of the umbilical area. The first appearance of the “thick Stensioeina” in the Dubivtsi succession is represented by S. perfecta in the lower Santonian. The first appearances of S. granulata perfecta and S. granulata incondita—both regarded herein as synonymous—were reported earlier in N Germany in the middle Santonian (Koch, 1977; Schöpf, 1990). These two subspecies have a relatively thick test with highly variable convexity of the umbilical side.

The transition from S. perfecta to S. pommerana through S. cf. S. pommerana is easily discernible in the studied succession. The oldest specimens of S. perfecta possess very narrow umbilical flaps partially covering the umbilicus. Specimens with much broader umbilical flaps appear up section. The evolution of S. perfecta to S. pommerana throughout the Santonian and lower Campanian reflects progressive changes in the umbilical area, including a gradual broadening of the umbilical flaps and their accretion into an umbilical plug in the middle Santonian. Stensioeina sp. C appears in the upper Santonian, displaying a different chamber shape on the umbilical side that probably evolved from the S. perfecta-S. pommerana lineage. Through time S. sp. C also shows a progressive covering of the umbilical area and accretion of the flaps into an umbilical plug.

Stensioeina perfecta Koch, 1977

Figs. 15.1–15.3

Stensioeina granulata perfecta Koch, 1977, p. 37, pl. 10, figs. 4–6; Schöpf, 1990, pl. 6, figs. 10–12.

Stensioeina granulata incondita Koch, 1977, p. 38, pl. 10, figs. 1–3; Schöpf, 1990, pl. 6, figs. 6–9.

Material. Over 100 specimens.

Description. Test relatively high, plano-convex with flattened spiral side and convex umbilical side, bowl-shaped in axial section with flush margin outline. The central part of the spiral side may be slightly elevated. Approximately 11 chambers in the final whorl enlarge gradually, separated on the umbilical side by curved, nearly radial sutures, slightly depressed in the youngest part of the test. Spiral-side sutures are wavy, limbate, and strongly elevated into somewhat irregular ridges, forming a reticulose pattern. Test margin is acutely angular. Umbilicus covered by thin
apertural flaps extending from the chambers. Umbilical side smooth with coarse pores.

Remarks. *Stensioeina perfecta* is the oldest form within the lineage. It differs from all other lineage species by the very narrow flaps incompletely covering the umbilicus. Koch (1977) distinguished two subspecies of *S. granulata* (see synonymy) based on morphological differences in the inflation of the inner whorls on the spiral side. Because these two species show the same stratigraphic range and the convexity of their inner spiral-side whorls is highly variable, we regard them as synonymous.

Stratigraphic range and geographic distribution. The first appearance of *S. perfecta* in northwestern Germany is from the middle Santonian *rogala*/westfalica Zone (Koch, 1977) and, thus, later than in western Ukraine. The species appears in the Dubivtsi succession in the middle of the lower Santonian. It is difficult to determine its upper limit because of its gradual change to *S. ex. gr. S. pommerana*.

*Stensioeina pommerana* Brotzen, 1936

Figs. 15.4, 15.5

*S. pommerana* Brotzen, 1936, p. 164–167; Pożaryska, 1954, p. 263, 264, text-fig. 21; Holker, 1957, p. 352, 353, text-fig. 407; Vasilyenko, 1961, p. 67–69, pl. 11, figs. 6a–c; Koch, 1977, p. 51, pl. 11, figs. 1–4; Peryt, 1988, pl. 2, figs. 27, 28; Hart et al., 1989, p. 362, pl. 7.24, figs. 10–12; Schönfeld, 1990, p. 101, 102, pl. 6, figs. 13–15;
Overview of the Cretaceous Gavelinellidae of Ukraine

**Description.** Test thick, plano-convex with flattened spiral side and strongly convex umbilical side, bowl-shaped in axial section with flush margin outline. The central part of the umbilical side slightly flattened. Approximately 11 chambers in the final whorl enlarge gradually, separated on the umbilical side by curved, nearly radial sutures, slightly depressed in the youngest part of the test. Spiral side sutures are wavy, limbate, and strongly elevated into somewhat irregular ridges, forming a reticulose pattern. Margin of the test acutely angular. Umbilicus completely covered by wide flaps or plug. Umbilical side smooth with coarse pores.

**Remarks.** Specimens found in the upper Santonian–lower Campanian in the Dubivtsi succession closely resemble those described from the middle Campanian–Maastrichtian (e.g., Gawor-Biedowa, 1992); however, they slightly differ in the thinner test and smaller umbilical area. Forms transitional from *S. perfecta* to *S. pommerana* are herein identified as *S. cf. S. pommerana* (Figs. 14, 15.6). They show an increasingly thicker test as Bailey et al. (2009) previously noticed.

**Stratigraphic range and geographic distribution.** *Stensioeina pommerana* is known from the Campanian and Maastrichtian of Europe, North Africa and the northwest Atlantic. A few papers record it from the Santonian. The first appearance of *Stensioeina* ex. gr. *S. pommerana* in the Dubivtsi succession is recorded in the upper Santonian, whereas *Stensioeina pommerana* is present in the highest Santonian–lower Campanian strata.

*Stensioeina sp. C*

Figs. 15.7, 15.8


**Material.** Over 50 specimens.

**Description.** Test relatively thick, lobate, plano-convex with flattened spiral side and convex umbilical side. Approximately 11 distinctly inflated petaloid chambers are separated by thick, curved, and raised sutures on the umbilical side. Spiral-side sutures wavy, limbate, and strongly elevated in somewhat irregular ridges which, together with the spiral suture, form a reticulose pattern. Umbilicus completely covered by wide, irregular flaps or a plug. Umbilical side smooth with coarse pores.

**Remarks.** It differs from other *Stensioeina* species in the spiral-side petaloid chambers, lobate periphery, and more curved sutures on the umbilical side.

**Stratigraphic range and geographic distribution.** In the studied section, *S. sp. C* appears in the upper Santonian (within the *Cordiceramus muelleri* Zone) and ranges to the top of the section (lower Campanian).

**SUMMARY**

Our research on *Gavelinella* and *Stensioeina* from the Turonian–lower Campanian interval at the Dubivtsi quarries (western Ukraine) led to a taxonomic revision and evolutionary classification through recognition of progressive changes in their morphology. Within *Gavelinella* we distinguished five distinct lineages:

1. The *Gavelinella ammonoides* lineage comprises *G. ammonoides* (Reuss), *G. lorneiana* (d’Orbigny), and *G. costulata* (Marie). Its main evolutionary changes are: broadening and thickening of the septal-ridge elements around and over the shielding umbilicus; increasing the number of chambers in the last whorl; narrowing of the test periphery and development of a “keel-like” structure (the *G. ammonoides-G. lorneiana* transition); and the appearance of test asymmetry from *G. lorneiana* to *G. costulata.*

2. The *Gavelinella stelligera* lineage comprises *G. stelligera* (Marie), *G. sp. A*, and *G. sp. B.* During its evolution, the species show a continuous decrease in test thickness, a more angular peripheral margin, and the appearance of test asymmetry. The gradual development of asymmetry occurs at the same time in the *G. lorneiana-G. costulata* transition within the *G. ammonoides* lineage. We attribute these simultaneous changes to parallel evolution.

3. The *Gavelinella pertusa* lineage comprises *G. tumida* Brotzen, *G. sp. A*, *G. tumida Brotzen*, and *G. pertusa* (Marsson). Within this lineage the main morphological changes are the appearance of a widely open and shallow umbilicus and reduced inflation of the last chamber on umbilical side.

4. The *Gavelinella vombensis* lineage comprises *G. vesca* (Bykova), *G. praevinfrasantonica* (Mjaltuk), and *G. vombensis* (Brotzen). The evolutionary changes here are the appearance of test biconvexity and increasingly prominent umbilical septal ridges.

5. The *Gavelinella clementiana* lineage comprises foraminifera which are characterized by specific and easily recognizable ornamentation that occurs on both sides of the test (numerous nodules and ridges on the septal sutures and spiral suture). In the studied succession, the *G. clementiana* lineage is represented by *G. ex. gr. G. clementiana* (d’Orbigny), *G. clementiana* (d’Orbigny), and *G. costata* (Marie). The appearance of representatives of the *G. clementiana* lineage is diachronous across Europe and is probably significantly related to palaeoenvironmental factors.

We introduced a new genus *Protostensioeina* to accommodate species characterized by a plano-convex test, flush margin outline, variable spiral-side ornamentation (from smooth to irregularly scattered tubercles and short, irregular ridges, resulting in a rough surface), and small triangular flaps covering the umbilicus, which in some species or specimens merge into a round plug. *Protostensioeina* also lacks the stable *Stensioeina* curved, limbate, and elevated spiral-side sutures that produce a highly irregular, reticulate network of ridges and a sharp, right-angled margin. On the contrary, the spiral-side morphology of *Protostensioeina* evolved significantly over time and is pivotal for their classification.

*Stensioeina* species are divided into the “thin *Stensioeina*” lineage and the “thick *Stensioeina*” lineage that differ in test shape, arrangement of the umbilical area, and stratigraphic ranges. The *S. exsulcata* lineage, of uncertain origin,
appears in the middle Coniacian and probably gave rise to the *S. perfecta* lineage in the early Santonian.

The main evolutionary changes in the *S. exsculpta* lineage are within the umbilical area. Older forms possess an umbilicus partially covered by triangular flaps extending from the umbilical sections of the chambers (type-X ornamentation). Younger forms have an umbilicus partially covered by undulating outgrowths extending from the surface of the test (type-Y ornamentation). Species of the *S. perfecta* lineage increase in test thickness, and the chamber flaps widen and merge into an umbilical plug.

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