

New advances in understanding the heterohelcid planktic foraminifer early evolution

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Abstract. Three Late Cretaceous lineages of heterohelcid planktic foraminifera, which evolved in the proximity of the Cenomanian/Turonian boundary, bring new data in understanding the group evolutionary history. *Lunatriella* Eicher and Worstell, 1970a is a directional lineage of late Cenomanian-early Turonian age, which gradually develops peripheral backward extensions in the last-formed chambers. *Steineckia* Georgescu, 2009a of the Turonian is the earliest heterohelcid lineage that evolved ornamentation consisting of pore mounds; a gap spanning the latest Turonian-early Santonian separates it from *Laeviheterohelix* Nederbragt, 1991 of the late Santonian-Campanian, the second lineage that developed ornamentation consisting of pore mounds. *Pseudoplanoglobulina* Aliyulla, 1977 evolved in the early Turonian and is the first heterohelcid lineage that developed multichamber growth in the adult stage; it became extinct in the Santonian. The three directional lineages show that the iterative and convergent evolution patterns occur extensively in the early heterohelcid history.

Key words: planktic foraminifera, Late Cretaceous, evolutionary classification

INTRODUCTION

Heterohelcids represent a group of planktic foraminifera in which at least one growth stage consists of chambers alternately added with respect to the test growth axis resulting in biserial chamber arrangement. The earliest representatives of this group were completely biserial and the development of multichamber growth in the adult stage and/or early planispiral coil are later developments in the evolutionary history of the heterohelcids. Representatives of this group of planktic foraminifera are included in the family Heterohelcidae Cushman, 1927.

The earliest heterohelcids were described in the nineteenth century (Ehrenberg, 1839, 1843, 1844, 1854; Reuss, 1861; Rzehak, 1891, 1895) and significant advances in understanding the group taxonomy and stratigraphical distribution were made only in the twentieth century (Cushman, 1926, 1927, 1928, 1938; Loeblich, 1951; Brönnimann and Brown, 1953; Montanaro Gallitelli, 1957; Aliyulla, 1965; Pessagno, 1967; Brown, 1969). The use of the scanning electron microscope (SEM) in the study of Cretaceous planktics, which began in the late 1960s, increased the observation resolution and this has resulted in an increase of the number of species, genera and suprageneric categories (Eicher and Worstell, 1970a, b; Masters, 1976, 1977; Aliyulla, 1977; Nederbragt, 1989a, b, 1991, 1993; Georgescu, 2007a, b, 2009a, 2010). The first attempt to reconstruct the group's evolutionary history was made by Aliyulla (1965), who considered that the heterohelcids first occurred in the stratigraphic record in the late Early Cretaceous and underwent a significant diversification in the Coniacian-Santonian; the group continued its evolution in the Cenozoic despite an abrupt reduction in diversity at the

Cretaceous/Paleogene boundary (Aliyulla, 1965, p. 217-218). Subsequent studies showed relative agreement in regards to the heterohelcid first occurrence: late Albian (Brown, 1969; Masters, 1977; Aliyulla, 1977; Nederbragt, 1991; Georgescu, 2009b); two older first occurrences for the group were given by Fuchs (1973, 1975) in the Oxfordian and Pessagno (1967) in the Aptian. However, significant differences exist between various authors in estimating the group diversification: Turonian (Pessagno, 1967; Aliyulla, 1977; Nederbragt, 1991), Coniacian (Aliyulla, 1965; Brown, 1969) and Santonian (Masters, 1977).

New advances in understanding the heterohelcid evolutionary history became possible with the large-scale use of the scanning electron microscope and by considering the taxonomic significance of the test ultrastructure, ornamentation, pore characteristics, and high-detail morphological features (e.g., periapertural structures, position and shape of the backward projections of the last-formed chambers, etc.). Georgescu (2009b) demonstrated the benthic origins of the heterohelcid planktics, thereby showing that the planktic foraminifera represent a polyphyletic group rather than a unitary plexus; this evolutionary process happened in the late Albian (*Pseudothallmanninella ticinensis* Biozone) and *Protoheterohelix* Georgescu and Huber, 2009, the oldest heterohelcid genus, which is also the only genus in the late Albian-early Cenomanian, is characterized by asymmetrical tests and periapertural structures. The group gradually evolved in the middle and late Cenomanian and the earliest completely symmetrical test in edge view occurred in the middle Cenomanian: *Planoheterohelix* Georgescu and Huber, 2009. The oldest heterohelcid ornamented with thin costae

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(leptocostae) evolved in the late Cenomanian: *Globoheterohelix* Georgescu and Huber, 2009; apparently the ornamented tests evolved independently in the *Planoheterohelix* lineage, namely in the species *P. postmoremani* Georgescu and Huber, 2009. Turonian heterohelcid assemblages worldwide show the development of elaborated morphological features, such as backward chamber peripheral extensions (e.g., *Lunatriella* Eicher and Worstell, 1970a), chamber backward extension (e.g., *Huberella* Georgescu, 2007a) and ornamentation consisting of pore mounds (e.g., *Steineckia* Georgescu, 2009a).

High resolution SEM-based studies provide a clearer view on the heterohelcid taxonomy and evolution when compared to those based on the observations made under the optical stereomicroscope. The advantage resides in the fact that observations of the wall ultrastructure, ornamentation features, porosity, as well as discrete morphological features (e.g., periapertural structures symmetry/asymmetry and characteristics, chamber backward extensions, etc) collected on well-preserved specimens and in stratigraphic context can be readily incorporated into a more accurate taxonomic and evolutionary framework. A SEM-based study in the proximity of the Cenomanian/Turonian boundary as part of the ongoing process of development of an evolutionary classification for the Cretaceous heterohelcids provides new insights on the group's early evolution. Three directional lineages are defined in evolutionary classification: *Lunatriella*, *Steineckia* and *Pseudoplanoglobulina*. Understanding the evolutionary developments in these three lineages is of paramount importance in understanding the early heterohelcid evolution and the morphological advances in the group history prior to the major Santonian diversification.

MATERIAL STUDIED AND METHODOLOGY

Collection specimens and new material collected from Deep Sea Drilling Project (DSDP)/Ocean Drilling Program (ODP) sites were used in this study (Fig. 1). Material provenance, quantity and preservation state are presented in Table 1. The SEM was extensively used in collecting morphological data; more than 400 micrographs were taken in order to make high resolution observations on the test wall ultrastructure, ornamentation, porosity and discrete test morphological features.

The collection specimens used in this study are deposited in the University of Colorado Museum in Boulder, Colorado (UCM), National Museum of Natural History in Washington, D.C. (USNM) and Naturkundemuseum in Berlin (ECO). Locality and sample labelling for the onshore material (Kansas and South Dakota, USA) is that used in the original articles

by Eicher and Worstell (1970a, b). The standard DSDP sample labelling system is used for the four sections offshore [DSDP Site 463 of the Mid-Pacific Mountains (Central Pacific Ocean), DSDP 511 of the Falkland Plateau (South Atlantic Ocean), ODP Hole 762C of the Exmouth Plateau (eastern Indian Ocean), and ODP Hole 1050C of the Blake Plateau (North Atlantic Ocean)]: leg number-site number-core number-section number, sample depth in centimetres.

SYSTEMATIC CLASSIFICATION

Higher categories are after Loeblich and Tappan (1987); evolutionary classification units are after Georgescu (2010, 2012). The concept of composite paleontological species (Georgescu and Huber, 2009) is followed throughout. The terminology for the transition from biserial to uniserial chamber arrangement is from Kaminski et al. (2011).

Directional Lineage *Lunatriella* Eicher and Worstell, 1970a – emended

Lunatriella gen. nov. Eicher and Worstell, 1970a, p. 117.

Lunatriella Eicher and Worstell, 1970. Loeblich and Tappan, 1987, p. 454.

Species included. Initiating species (IS): *L. fayose* (Petters, 1983), first descendant species (FDS): *L. digitata* (Masella, 1959) and second descendant species (SDS): *L. spinifera* Eicher and Worstell, 1970a.

Emended diagnosis. Late Cenomanian-early Turonian biserial to lax-uniserial planktics that gradually develop peripheral backward chamber extensions and leptoflanges.

Emended description. Test with chambers added alternating to the test growth axis resulting in a biserial arrangement, which may become loosely biserial and finally lax uniserial in later chambers. Earlier chambers are subglobular, those of the adult stage reniform. One peripheral backward chamber extension occurs in the first descendant and second descendant species, but is absent in the initiating species. Sutures are distinct and depressed, straight to curved and oblique to the test growth axis. Test is compressed and symmetrical in edge view; periphery is rounded and simple, lacking peripheral structures. Aperture is a high arch at the base of the last-formed chamber. Symmetrically developed orthoflanges border it on each side in the initiating and first descendant species; leptoflanges are developed in the second descendant species. Chamber surface is smooth. Test wall is calcitic, hyaline and perforate; pores are simple and circular, with a diameter of 0.4–1.2 µm.

Remarks. *Lunatriella* is emended to accommodate a lineage of late Cenomanian-early Turonian age. The evolution in this lineage led to the development of chambers with peripheral backward extensions, which is in the incipient stage in the first descendant species and well developed in the second descendant species, and terminally lax-uniserial chamber arrangement and aperture bordered by leptoflanges in the second descendant species. The species included in *Lunatriella* have a smooth chamber surface and simple and circular pores (0.4–1.0 µm); additional well-preserved specimens are necessary to study the pore size evolution along the lineage. *Lunatriella* evolved from the smooth species of *Planoheterohelix* in the late Cenomanian; the lineage initiation happened with the development of reniform chambers in the adult stage in *L. fayose*.

Age. Late Cenomanian-Early Turonian.

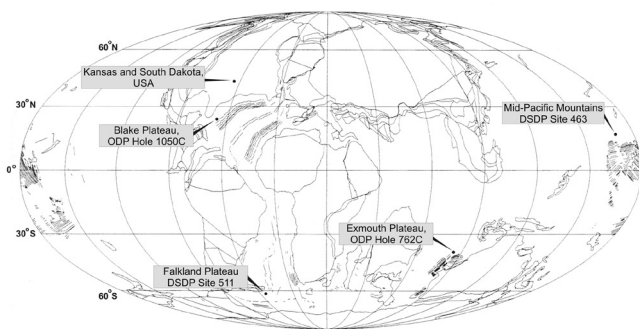


Fig. 1. Geographic locations of the sites that provided the foraminiferal material used in this study. Base map after Hay et al. (1999).

Table 1. Foraminiferal material used in this study: provenance, quantity and preservation state.

	Site/age	Species	Specimen number	Preservation
Eicher and Worstell (1970a) localities	Locality 2 - Fall River County, South Dakota - early Turonian	<i>Lunatriella fayose</i>	2	excellent
		<i>L. digitata</i>	1	excellent
		<i>L. spinifera</i>	3	excellent
	Locality 5 - Hamilton County, Kansas - early Turonian	<i>Lunatriella fayose</i>	23	excellent
		<i>L. digitata</i>	6	excellent
		<i>L. spinifera</i>	12	excellent
		<i>Steineckia</i> sp.	4	excellent
	Locality 6 - Hamilton County, Kansas - early Turonian	<i>Lunatriella fayose</i>	9	excellent
		<i>Steineckia</i> sp.	3	excellent
DSDP and ODP drillings	DSDP Site 463 - Mid-Pacific Mountains, Central Pacific Ocean - Turonian to early Santonian	<i>Pseudoplanoglobulina directa</i>	circa 100	very good
	DSDP Site 511 - Falkland Plateau, South Atlantic Ocean - late Turonian	<i>Pseudoplanoglobulina directa</i>	14	excellent
	ODP Hole 762C - Exmouth Plateau, eastern Indian Ocean - Turonian-Santonian	<i>Pseudoplanoglobulina directa</i>	circa 60	very good
	ODP Hole 1050C - Blake Plateau, North Atlantic Ocean - early Turonian	<i>Pseudoplanoglobulina directa</i>	18	very good
Other	Upper Missouri, Ehrenberg Collection, samples 1595b and 1595f - late Santonian	<i>Pseudoplanoglobulina directa</i>	11	excellent

Legend - Preservation

excellent	pristine tests; original calcite is often preserved
very good	test recrystallized but detail morphological features (including ultrastructure) can be adequately observed

Geographic distribution. Europe (Italy), USA (Colorado, Kansas, South Dakota, Utah, Wyoming), western Africa (Senegal) and western Central Atlantic Ocean (Demerara Rise).

***Lunatriella fayose* (Petters, 1983) - emended**

Fig. 2: 1-16

Heterohelix pulchra (Brotzen 1936). Eicher and Worstell, 1970a, pl. 1, figs 1-2.

Heterohelix pulchra (Brotzen 1936). Eicher and Worstell, 1970b: 296, pl. 8, fig. 9.

Heterohelix fayose sp. nov. Petters, 1983, p. 43, pl. 1, figs 8-10.

Heterohelix pulchra (Brotzen 1936). Friedrich et al., 2008, pl. 1, fig. 17.

Emended diagnosis. *Lunatriella* with globular or reniform chambers in the adult stage.

Emended description. Test consists of 8-11 chambers. Proloculus is followed by chambers that are alternately added with respect to the test growth axis resulting in a biserial arrangement; earlier chambers are subglobular, those in the adult stage reniform. Sutures are distinct and depressed, straight to curved, and oblique to the test growth axis; subtriangular depressed areas occasionally occur along the central zigzag suture due to the chamber reniform shape. Test compressed and symmetrical in edge view, with rounded and simple periphery. Aperture is a high arch at the base of the last-formed chamber; symmetrically developed orthoflanges border the aperture on each side. Chamber surface is smooth. Test is calcitic, hyaline and perforate; pores are simple, circular in shape, and have a diameter of 0.9-1.0 μ m.

Remarks. *Lunatriella fayose* differs from *Planoheterohelix moremani* (Cushman, 1938) by (i) reniform chambers in the adult stage, (ii) less evident chamber overlapping, and (iii) larger pores (0.9-1.0 μ m rather than 0.5-0.7 μ m).

Age. Late Cenomanian-Early Turonian.

Geographic distribution. USA (Colorado, South Dakota) and western Africa (Nigeria).

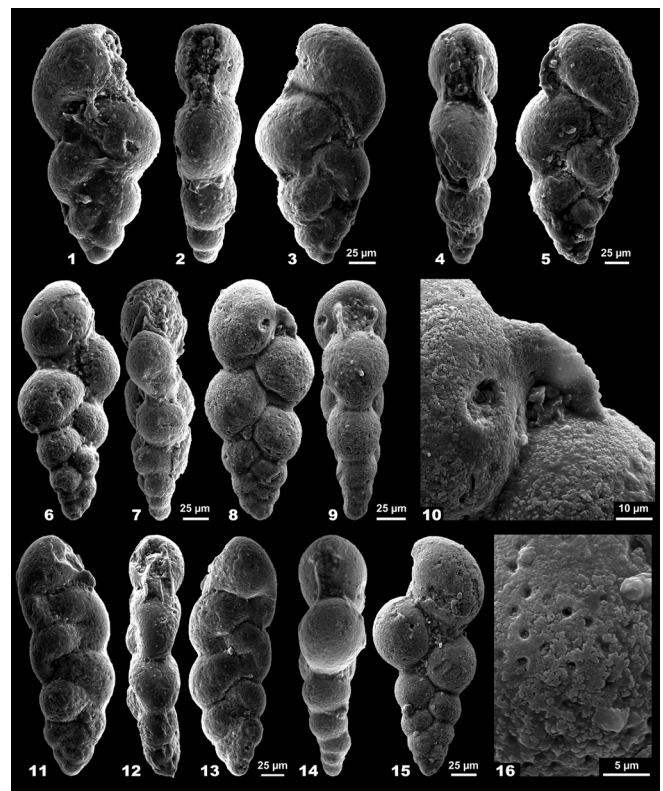


Fig. 2. Hypotypes of *Lunatriella fayose* (Petters, 1983) from the Fairport Shale Member (early Turonian) of Kansas and South Dakota, USA. **1-3)** Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62 (UCM 27866), previously figured by Eicher and Worstell (1970a, pl. 1, fig. 1 and 1970b, pl. 8, fig. 9); Hamilton County, Kansas; **4-5)** Specimen from Locality 2 of Eicher and Worstell, 1970a, Sample 46; Fall River County, South Dakota; **6-7)** Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62; Hamilton County, Kansas; **8-10)** Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62; Hamilton County, Kansas; **11-13)** Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62; Hamilton County, Kansas; **14-16)** Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62; Hamilton County, Kansas.

Lunatriella digitata* (Masella, 1959)*Fig. 3: 1-13**

Heterohelix digitata sp. nov. Masella, 1959, p. 15, pl. 1, figs 1-10.

Heterohelix pulchra (Brotzen, 1936). Eicher and Worstell, 1970a, pl. 1, fig. 4.

Lunatriella spinifera Eicher and Worstell 1970a. Eicher and Worstell, 1970a, pl. 1, fig. 5.

Heterohelix digitata Masella, 1959. Masters, 1977, p. 341.

Heterohelix americana (Ehrenberg, 1843). De Klasz et al., 1995, p. 361, pl. 5, figs 5-7, pl. 2, figs 1-2.

Lunatriella spinifera (Eicher and Worstell, 1970a). Friedrich et al., 2008, pl. 1, figs 18-19.

Heterohelix americana (Ehrenberg, 1843). Georgescu and Huber, 2009, p. 348, pl. 6, figs 1-6.

Diagnosis. *Lunatriella* with the last-formed chambers with an incipient peripheral backward extension.

Description. Test consists of 8-11 chambers. Proloculus is followed by chambers that are alternately added with respect to the test growth axis resulting in biserial chamber arrangement. Earlier chambers are subglobular then reniform; last-formed one or two chambers with one more or less developed peripheral backward extension. Test is compressed and asymmetrical in

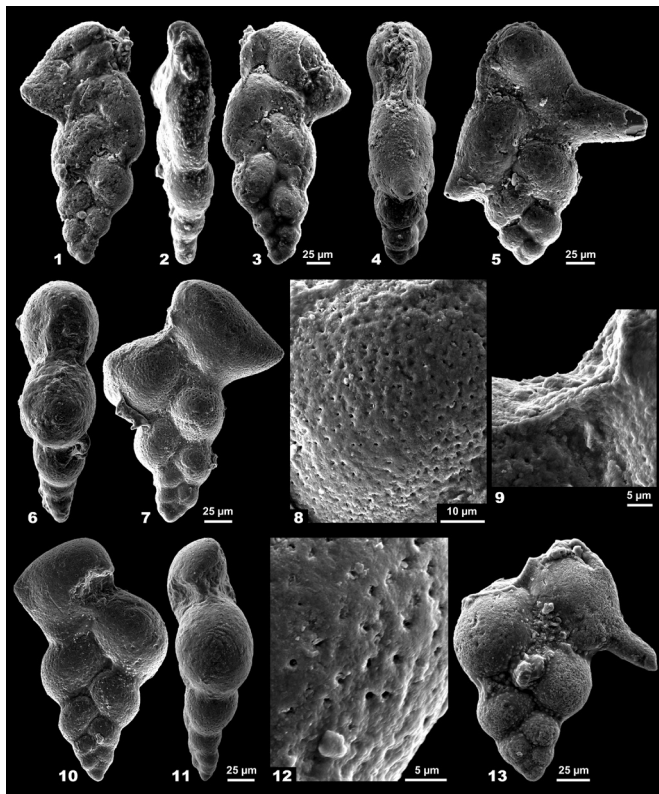


Fig. 3. Hypotypes of *Lunatriella digitata* (Masella, 1959) from the Fairport Shale Member (early Turonian) of Kansas, USA (1-5, 13) and uppermost Cenomanian-lowermost Turonian sediments of Senegal, well R2d. 1-3) Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62 (UCM 27869), previously figured by Eicher and Worstell (1970a, pl. 1, fig. 4); Hamilton County, Kansas; 4-5) Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62; Hamilton County, Kansas; 6-9) Specimen from well R2d of Senegal, Sample 1651-1660 m (USNM 473378), previously figured by Georgescu and Huber (2009, pl. 6, figs 1-3); 10-12) Specimen from well R2d of Senegal, Sample 1651-1660 m (USNM 473378), previously figured by Georgescu and Huber (2009, pl. 6, figs 4-6); 13) Specimen from Locality 2 of Eicher and Worstell, 1970a, Sample 46; Fall River County, South Dakota.

edge view, and with rounded and simple periphery. Aperture is a high arch at the base of the last-formed chamber, and is bordered by orthoflanges symmetrically developed on each side. Chamber surface is smooth. Test calcitic, hyaline and perforate; pores are simple, circular and with a diameter of 0.4-0.9 µm.

Remarks. The emendation is made to include the test ultrastructure features and periapertural structure redescription. *Lunatriella digitata* differs from *L. fayose* by having the last-formed one or two chambers with one peripheral backward extension and a tendency to become loosely biserial (sensu Kaminski et al., 2011).

Age. Latest Cenomanian-Early Turonian.

Geographic distribution. Europe (Italy), USA (Colorado, South Dakota), western Africa (Senegal) and western Central Atlantic Ocean (Demerara Rise).

Lunatriella spinifera* Eicher and Worstell, 1970a*Fig. 4: 1-12**

Lunatriella spinifera sp. nov. Eicher and Worstell, 1970a, p. 118, pl. 1, figs 6-17.

Lunatriella spinifera Eicher and Worstell, 1970a. Eicher and Worstell, 1970b, p. 296, pl. 8, figs 7-8, 12.

Lunatriella spinifera Eicher and Worstell, 1970a. Masters, 1977, p. 358, pl. 3, figs 5-6.

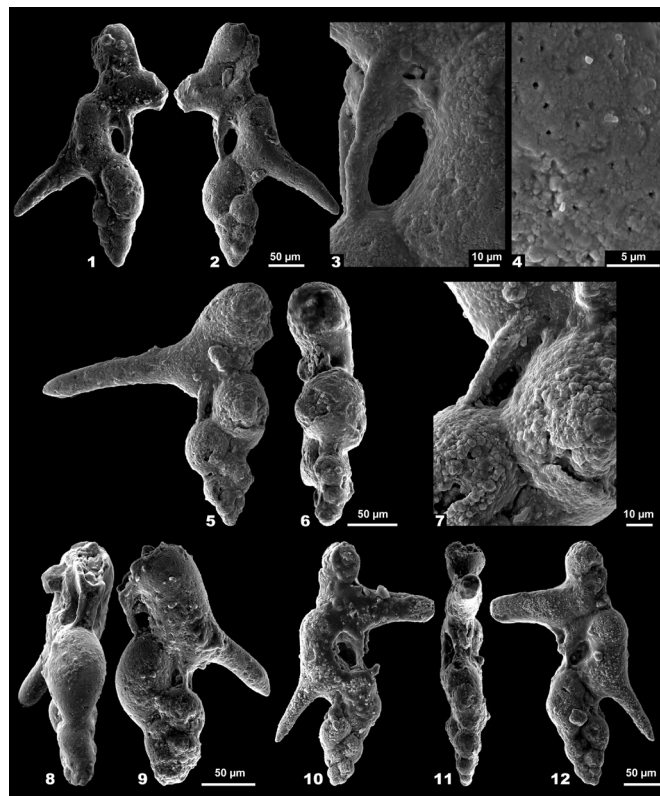


Fig. 4. Holotype and paratypes of *Lunatriella spinifera* Eicher and Worstell, 1970a from the Fairport Shale Member (early Turonian) of Kansas, USA. 1-4) Holotype from Locality 5 of Eicher and Worstell, 1970a, Sample 62 (UCM 27375), previously figured by Eicher and Worstell (1970a, pl. 1, fig. 6); 5-7) Paratype from Locality 5 of Eicher and Worstell, 1970a, Sample 62 (UCM 27879), previously figured by Eicher and Worstell (1970a, pl. 1, fig. 12); 8-9) Paratype from Locality 5 of Eicher and Worstell, 1970a, Sample 62 (UCM 27878); 10-12) Paratype from Locality 5 of Eicher and Worstell, 1970a, Sample 62 (UCM 27871), previously figured by Eicher and Worstell (1970a, pl. 1, fig. 7 and 1970b, pl. 6, fig. 12).

Lunatriella spinifera Eicher and Worstell, 1970a. Petters, 1983, p. 45, pl. 1, figs 6-7.

Diagnosis. *Lunatriella* with the last-formed one or two chambers with well-developed peripheral backward extension.

Description. Test consists of 8-10 chambers. Proloculus is followed by chambers that are alternately added with respect to the test growth axis resulting in biserial arrangement; later chambers become loosely biserial and finally lax-uniserial. Earlier chambers are subglobular, then elongate, with the elongation axis almost parallel to the test growth axis; the last-formed one or two chambers with one well-developed peripheral backward extension, which is oblique to perpendicular to the test growth axis. Sutures are distinct and depressed, straight to curved and oblique to the test growth axis. Test is compressed and symmetrical in edge view; periphery rounded in the test early portion and pinched in the chambers with backward extension. Aperture is a high arch at the base of the last-formed chamber; symmetrically developed leptoflanges, which in the adult stage are attached to the anterior portion of the previous chamber, border the aperture on each side. Chamber surface is smooth. Test wall is calcitic, hyaline and perforate; pores are circular, simple and with diameter of 0.5-1.2 μm .

Remarks. *Lunatriella spinifera* is the end member of the *Lunatriella* directional lineage. It differs from *L. fayose* and *L. digitata* mainly by (i) its tendency for chambers to become loosely biserial and finally lax-uniserial in later chambers, (ii) the well-developed peripheral backward extensions of the last-formed one or two chambers, and (iii) aperture bordered by leptoflanges. It is the first species to develop leptoflanges in the heterohelical group; similar structures occur through iterative evolution in a species of the late Campanian-Maastrichtian, namely *Braunella brauni* Georgescu, 2007b.

Age. Early Turonian.

Geographic distribution. USA (Colorado, Kansas, South Dakota, Utah, Wyoming), western Africa (Nigeria) and western Central Atlantic Ocean (Demerara Rise).

Directional Lineage *Steineckia*, Georgescu 2009a

Steineckia gen. nov. Georgescu, 2009a, p. 325.

Species included. IS: *Steineckia* sp. and FDS: *S. steinecki* Georgescu, 2009a.

Diagnosis. Late Cenomanian-Turonian lineage of planktic foraminifera with chambers alternately added with respect to the test growth axis resulting in a biserial arrangement and ornamentation consisting of large pore mounds (3.1-6.4 μm).

Description. The test consists of chambers alternately added with respect to the test growth axis resulting in biserial arrangement. Earlier chambers are subglobular, those in the adult stage reniform, and with a subtriangular-rounded depression in the posterior part in the initiating species. Sutures are distinct and depressed, straight to curved and oblique to the test growth axis. Test compressed and symmetrical in edge view; periphery is rounded, simple. Aperture a medium high arch at the base of the last formed chamber; symmetrically developed orthoflanges border the aperture on each side. Chamber surface is ornamented with pore mounds that increase in size from 3.1-5.0 μm in the initiating species to 4.0-6.4 μm in the first descendant species. Test wall is calcitic, hyaline and perforate; pore mounds are simple, circular, and with a diameter of 0.4-0.8 μm .

Remarks. *Steineckia* is the earliest lineage of Cretaceous planktic foraminifera that developed ornamentation consisting of pore mounds; it became extinct near the Turonian/Coniacian

boundary. The second and last known lineage of serial planktics that developed ornamentation consisting of pore mounds is *Laeviheterohelix* Nederbragt, 1991, which was emended and redefined as a directional lineage in the evolutionary classification by Georgescu (2009a). Its reviewed stratigraphic range is upper Santonian-Campanian. No tests with pore mounds are known from the Coniacian-lower Santonian stratigraphic interval. *Steineckia* differs from the *Laeviheterohelix* lineage by lacking the pustulose periapertural area and having the chamber surface ornamented with larger pore mounds (3.1-6.4 μm rather than 1.7-2.8 μm) (Georgescu, 2009a).

Age. Turonian.

Geographic distribution. Falkland Plateau (South Atlantic Ocean) and USA (Colorado, South Dakota, Wyoming).

Steineckia sp.

Fig. 5: 1-12

Heterohelix pulchra (Brotzen, 1936). Eicher and Worstell, 1970a, pl. 1, fig. 3.

Heterohelix pulchra (Brotzen, 1936). Friedrich et al., 2008, pl. 1, fig. 17.

Diagnosis. *Steineckia* with elongate test.

Description. Test consists of 11-13 chambers. Proloculus is small, and followed by chambers that are added alternately with respect to the test growth axis; early chambers subglobular, those in the adult stage reniform, with a subtriangular-rounded depression in the posterior part. Sutures are distinct and depressed, straight to curved function of the development of reniform chambers, and oblique to the test growth axis. Test is compressed and symmetrical in edge view; periphery rounded and simple. Aperture is a medium high at the base of the last-formed chamber; symmetrically developed orthoflanges border the aperture on each side. Chamber surface is ornamented with circular pore mounds, with a diameter of 3.1-5.0 μm . Test wall is calcitic, hyaline and perforate; pores simple and circular (0.5-0.8 μm in diameter), and are situated at the center of or, more rarely between the pore mounds.

Remarks. *Steineckia* sp. differs from *S. steinecki* by (i) the test consisting of more chambers (11-13 rather than 10-11), (ii) smaller W/L ratio that results in a narrower test and with elongate aspect, and (iii) smaller pore mounds (3.1-5.0 μm rather than 4.0-6.4 μm). It differs from *L. fayose* by (i) the test consisting of more chambers (11-13 rather than 8-11), and (ii) chamber surface ornamented with pore mounds rather than smooth. It differs from *Laeviheterohelix pulchra* (Brotzen, 1936) by (i) the test with fewer chambers (11-13 rather than 15-18), (ii) ornamentation consisting of larger pore mounds (3.1-5.0 μm rather than 1.7-2.8 μm) and (iii) by lacking the pustulose periapertural area.

Age. Early Turonian.

Geographic distribution. USA (Colorado, South Dakota, Wyoming).

Directional lineage *Pseudoplanoglobulina* Aliyulla, 1977 – emended

Tesserella gen. nov. Aliyulla, 1977, p. 204.

Pseudoplanoglobulina gen. nov. Aliyulla, 1977, p. 204.

Pseudoplanoglobulina Aliyulla, 1977. Loeblich and Tappan, 1987, p. 455.

Species included. IS: *P. directa* (Aliyulla, 1965) and FDS: *P. nakhitschevanica* Aliyulla, 1977.

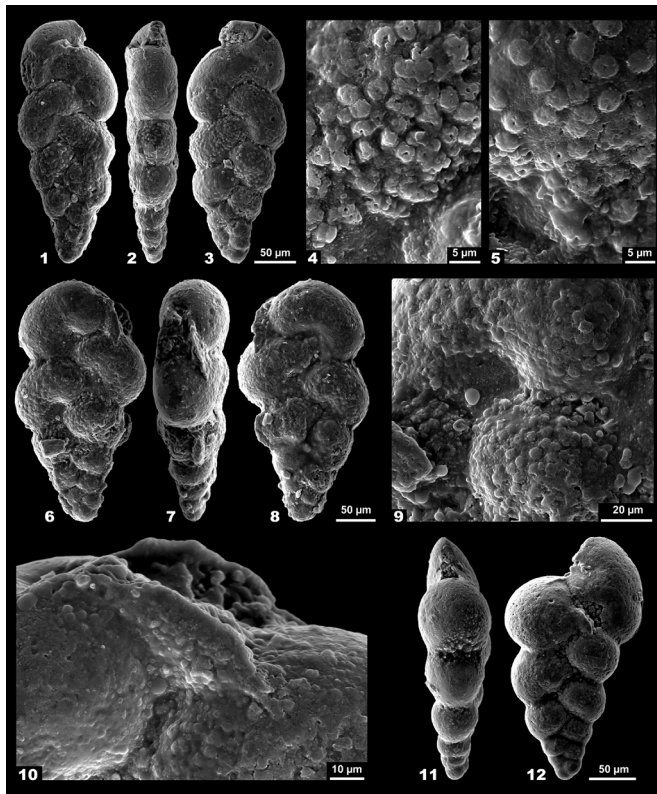


Fig. 5. Hypotypes of *Steineckia* sp. from the Fairport Shale Member (early Turonian) of Kansas, USA. **1-5)** Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62; Hamilton County, Kansas; **6-10)** Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62 (UCM 27868), previously figured by Eicher and Worstell (1970a, pl. 1, fig. 3 and 1970b, pl. 8, fig. 10), Hamilton County, Kansas; **11-12)** Specimen from Locality 5 of Eicher and Worstell, 1970a, Sample 62; Hamilton County, Kansas.

Emended diagnosis. Turonian-Santonian lineage of serial planktics with smooth chamber surface and orthofoflanges bordering the aperture, which develop multichamber growth in the adult stage.

Emended description. Test in the initiating species consists of chambers alternately added with respect to the test growth axis resulting in a biserial arrangement; first descendant species is characterized by multichamber growth in the adult stage. Early chambers are subglobular, and subrectangular or reniform in the last growth stage. Sutures are distinct and depressed, straight and oblique to the test growth axis. Test compressed and symmetrical in edge view, with rounded and simple periphery. Aperture is a low to medium high arch at the base of the last-formed chamber; aperture singular in the biserial tests and multiple in those with multichamber growth in the adult stage. Symmetrical orthofoflanges border the aperture on each side. Chamber surface is smooth, excepting for the periapertural pustulose area. Test wall is calcitic, hyaline and perforate. Pores are simple and circular, with a diameter of 0.4-1.0 µm.

Remarks. *Pseudoplanoglobulina* is reviewed in evolutionary classification to accommodate a lineage of heterohelicids with periapertural structures consisting of orthofoflanges, smooth chamber surface, and simple and small pores (0.4-1.0 µm in diameter). Multichamber growth occurs in the first descendant species (*P. nakhtschevanica*) of the early Turonian, which evolved from the initiating species (*P. directa*), a completely biserial species of the Turonian-Santonian. Aliyulla (1977) described two genera based on the two species: *Tesserella* and *Pseudoplanoglobulina* respectively. *Tesserella* was described as having smooth or pustulose ornamentation; Aliyulla (1977) made

this genus unusable by choosing the costate *T. pseudotessera* (Cushman 1938) of the Campanian-Maastrichtian its type species. *Pseudoplanoglobulina* is thereby preferred, although its description follows that of *Tesserella* in the original work (Aliyulla 1977).

Age. Turonian-Santonian.

Geographic distribution. Cosmopolitan.

Pseudoplanoglobulina directa (Aliyulla, 1965) - emended

Fig. 6: 1-16

Gümbelina tessera (Ehrenberg, 1854). Cushman, 1932, p. 338, pl. 51, figs 4-5.

Gümbelina tessera (Ehrenberg, 1854). Loetterle, 1937, p. 34, pl. 5, fig. 4.

Heterohelix (*Chilogümbelina*) *pseudotessera* Cushman subsp. *directa* ssp. nov. Aliyulla, 1965, p. 224, pl. 1, fig. 1.

Tesserella pseudotessera (Cushman, 1938). Aliyulla, 1977, pl. 3, figs 1-3.

Heterohelix pulchra (Brotzen, 1936). Frerichs et al., 1975, p. 301, pl. 1, figs 7-8.

Heterohelix pulchra (Brotzen, 1936). Petters, 1980, pl. 1, fig. 17.

Heterohelix pulchra (Brotzen, 1936). Petters, 1983, p. 43, pl. 1, figs 18, 20.

Diagnosis. *Pseudoplanoglobulina* with chambers alternately added with respect to the test growth axis resulting in biserial chamber arrangement.

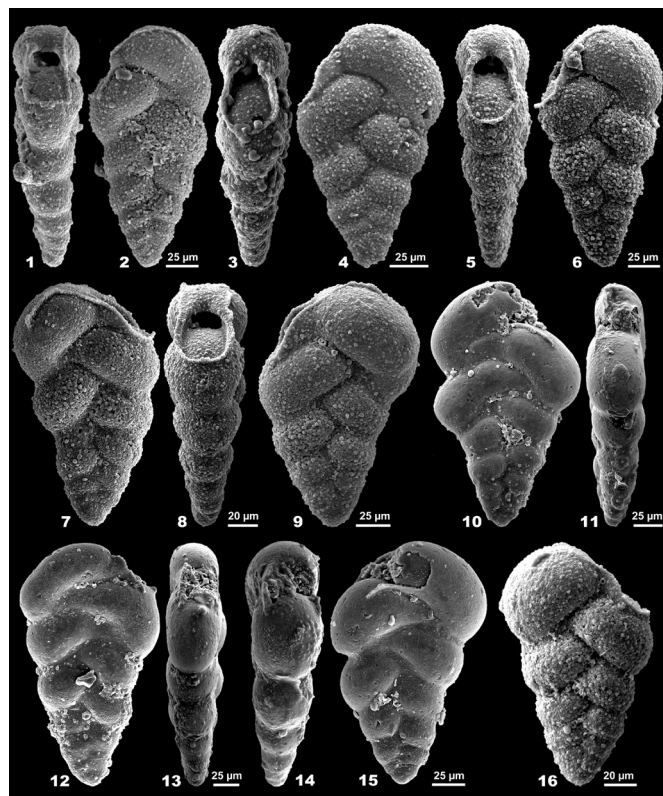


Fig. 6. Hypotypes of *Pseudoplanoglobulina directa* (Aliyulla, 1965) from the Coniacian-lower Santonian sediments of the DSDP Site 463 (Mid-Pacific Mountains, Central Pacific Ocean) (1-9, 16) and upper Santonian Niobrara Formation, Smoky Hill Shale Member of Upper Missouri from the Ehrenberg Collection (10-15). **1-9, 16)** Sample 62-463-26-5, 53-58 cm (Coniacian-lower Santonian); **10-11)** Specimen ECO 053-05; **12-13)** Specimen ECO 053-10; **14-15)** Specimen ECO 053-07.

Description. Test consists of 12-15 chambers. Proloculus is small, followed by alternating chambers with respect to the test growth axis resulting in a biserial arrangement. Early chambers are subglobular, those of the adult stage subrectangular, then reniform. Sutures are distinct, depressed, straight and oblique to the test growth axis. Test is compressed and symmetrical in edge view; periphery is rounded and lacks peripheral structures. Aperture is a low to medium high arch at the base of the last-formed chamber; symmetrical orthoflanges border the aperture on each side. Chamber surface is smooth; periapertural pustulose area occurs in the chamber anterior portion. Test wall is calcitic, hyaline and perforate; pores are simple, circular, and with a diameter of 0.4-1.0 μm .

Remarks. *Pseudoplanoglobulina directa* differs from *P. nakhitschevanica* by lacking the multichamber growth in the adult stage. It differs from *L. fayose* by (i) the less developed chamber overlapping and (ii) straight and simple sutures between the last-formed chambers rather than with subtriangular depressed areas. It differs from *Protoheterohelix obscura* Georgescu and Huber, 2009 of the Late Albian-Early Turonian by having (i) symmetrical tests in edge view and (ii) symmetrically developed periapertural structures. It differs from *L. pulchra* by (i) the test consisting of fewer chambers (12-15 rather than 15-18) and (ii) chamber surface smooth rather than ornamented with pore mounds. The taxonomical revision of *P. directa* was in parallel with that of *L. pulchra* because they can be easily confused for each other in the optical microscope-based studies; the similarities in the test architecture and the fact that the smooth species (*P. directa*) precedes the ornamented one (*L. pulchra*) in the stratigraphic

record may indicate a possible phylogenetic relationship between them. Georgescu (2009a, fig. 8: 3a-c) illustrated longitudinal ornamentation structures coexisting with the pore mounds in *L. pulchra*; such structures were interpreted as vestigial costae and were considered an argument demonstrating that *L. pulchra* evolved from the costate species *P. planata* (Cushman, 1938). With the taxonomic revision of *P. directa* it appears more plausible to consider the origins of *L. pulchra* among this smooth species; in this new interpretation, the short longitudinal structures with the same ultrastructure as the test wall, can only represent temporary structures generated during pore mound development.

Age. Turonian-Santonian.

Geographic distribution. Cosmopolitan.

DISCUSSION AND CONCLUSIONS

New data on three heterohelical lineages that evolved near the Cenomanian/Turonian boundary provide interesting insights on the early evolution of the group. For the first time it can be demonstrated the extensive branching generated by the convergent and iterative evolution patterns in the early evolution of this planktic foraminiferal group (Fig. 7), a perspective that contrasts to those elaborated by Masters (1977) and Nederbragt (1991), in which fewer than five species of late Albian-Turonian age were recognized.

Lunatriella is redefined as a directional lineage in the evolutionary classification; it evolved from *P. moremani* in the latest Cenomanian (Petters, 1983), and continued its evolution in the early Turonian. *Lunatriella fayose* of the late

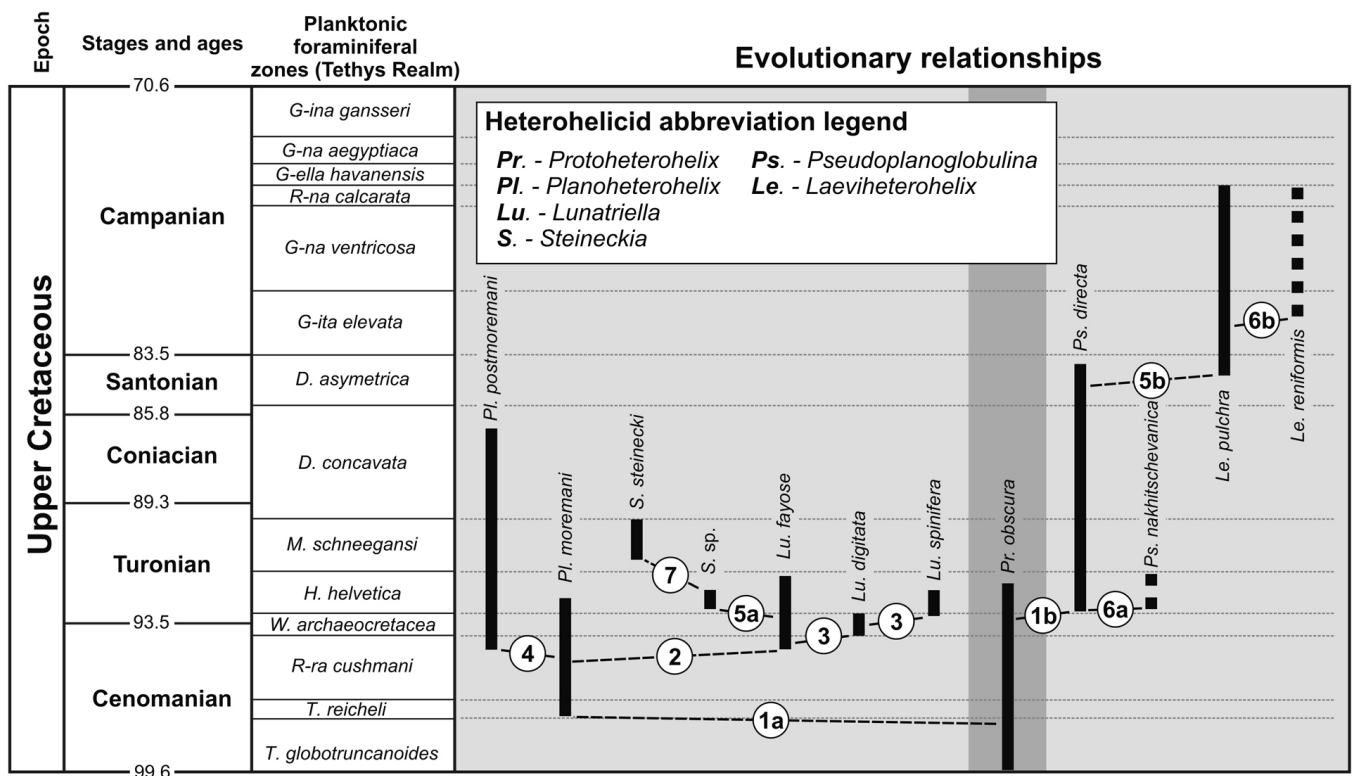


Fig. 7. Evolutionary relationships and major trends among some Cenomanian-Campanian heterohelicalids, showing the lineage *Lunatriella*, *Steineckia* and *Pseudoplanoglobulina* origins. Background legend: dark grey-tests with asymmetrical periapertural structures; light grey-completely symmetrical tests. Trend legend: 1a-b) development of symmetrical tests; 2) development of reniform chambers in the adult stage with a subtriangular depression towards the posterior part; 3) development of peripheral chamber backward extensions; 4) development of costate ornamentation; 5a-b) development of ornamentation consisting of pore mounds; 6a-b) development of multichamber growth in the adult stage; 7-loss of elongate test aspect through the reduction of chamber number. Ages are after Gradstein et al. (2004). Planktic foraminiferal zonation is after Robaszynski and Caron (1995); abbreviated genera in the biozonation framework: D=Dicarinella, G-ella=Globotruncanella, G-na=Gansserina, G-ita=Globotruncanella, H=Helvetoglobotruncana, M=Marginotruncana, R-na=Radotruncana, R-ra=Rotalipora and T=Thalmaninella.

Cenomanian-early Turonian is the initiating species, and it evolved through the development of reniform chambers in the adult stage. The first and second descendant species, *L. digitata* and *L. spinifera* gradually develop peripheral chamber backward extension and a tendency to become lax-uniserial, which is in an incipient stage in the former and well-developed in the latter. Periapertural structures consist of orthoflanges in the initiating and first descendant species and leptoflanges in the second descendant. Tests included in the *Lunatriella* lineage have smooth tests, simple test wall, and simple and circular pores, with a diameter of 0.4–1.0 µm.

Steineckia is emended and redefined as a directional lineage in the evolutionary classification. Specimens of the early Turonian herein assigned to *Steineckia* sp. have ornamentation consisting of pore mounds (3.1–5.0 µm in diameter), demonstrating that the lineage evolved earlier than late Turonian as previously considered by Georgescu (2009a); additional material is necessary to clarify the taxonomic status of *Steineckia* sp. The first descendant species is *S. steinecki* of the upper Turonian sediments of the Falkland Plateau (South Atlantic Ocean). The *Steineckia* directional lineage evolved from *L. fayose* as indicated by the similarities in the test architecture and occurrences in sediments at the same stratigraphical level.

Pseudoplanoglobulina is emended to accommodate a lineage consisting of unornamented heterohelics. The initiating species is *P. directa* of the Turonian-Santonian, which has a biserial chamber arrangement; the first descendant species, *P. nakhitschevanica*, of early Turonian age developed a multichamber growth in the adult stage. *Pseudoplanoglobulina* is the earliest known lineage in the heterohelid evolutionary history that led to the development of multichamber growth in the adult stage.

The taxonomic re-evaluation of the three lineages, as part of the ongoing process of developing an evolutionary classification framework for the Cretaceous planktic foraminifera casts a new perspective on the heterohelid early evolution, and helps in assessing the effects of convergent and iterative patterns in the group evolutionary history. The heterohelid group evolved in the late Albian from the small calcareous benthic foraminifers of the genus *Praeplanctonia* Georgescu 2009b (Georgescu, 2009b). The earliest heterohelids are included in the genus *Protoheterohelix* Georgescu and Huber, 2009, and they form a lineage in which the major evolutionary trend is the gradual achievement of symmetrical tests in edge view; *P. obscura*, which is the latest evolved species of *Protoheterohelix*, has the test asymmetry reduced to that of the periapertural structures (archaeoflanges) (Georgescu, 2010).

The evolution of completely symmetrical tests in edge view was achieved in the middle Cenomanian as demonstrated by the *P. obscura*-*P. moremani* lineage (Georgescu, 2009b; Georgescu and Huber, 2009). It is shown in this study that completely symmetrical tests iteratively evolved in the early Turonian, in the *P. obscura*-*P. directa* lineage (Fig. 7). In addition, the evolutionary relationships inferred between the species of the Cenomanian-Campanian lineages considered in this study show that all the features in the heterohelid test morphology occurred iteratively in different lineages, and each lineage has its own evolutionary trends.

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