What, if anything, is a *Paratrochamminoides*? A key to the morphology of the Cretaceous to Cenozoic species of *Conglophragmium* and *Paratrochamminoides* (Foraminifera)

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ABSTRACT

We present a review of the current taxonomical status of the genus *Paratrochamminoides* Soliman, 1972. We recognise five main subgroups of this genus based upon the following modes of coiling: trochospiral, streptospiral, glomospiral, triloculine or milioline, and thalmannamminiform. Species that display streptospiral coiling and an interiomarginal aperture are placed in the genus *Conglophragmium* Bermúdez & Rivero, 1963, whereas the genus *Paratrochamminoides* is here understood to encompass all other coiling modes. The morphological characters of 23 named and unnamed species that we recognise as belonging to *Paratrochamminoides* and *Conglophragmium* are presented in tabular form. Of these, 22 are considered here to be valid species. Emended descriptions are provided for both genera, and diagnoses are given for each of the species.

INTRODUCTION

The genus *Paratrochamminoides* and related forms constitute a morphologically diverse group of foraminifera that are commonly found in flysch-type and abyssal deep sea assemblages. The group has been found in deep-sea sediments of all the major oceans, ranging in age from Early Cretaceous to Recent. Although the genus *Paratrochamminoides* is often cited in the literature, its taxonomical status is in fact tenuous at best, and very often specimens are not determined to the species level.

In this study, we review the character traits that can be used to determine the known species belonging to this morphologically diverse group. We also address the problem of the validity of the generic names applied to the Cretaceous to Cenozoic members of the Lituotubidae, and we speculate on the possible polyphyletic origins of the group.

Previous Studies

Species that are now regarded as belonging to the family Lituotubidae were first described from deep-sea samples recovered during the HMS CHALLENGER Expedition. In his monograph of the CHALLENGER foraminifera, Brady (1884) illustrated the species *Lituotuba lituiformis* Brady, 1879, *Trochammina coronata* Brady, 1879, and *Trochammina conglobata* Brady, 1884. The illustrations presented in the Challenger Report served as the basis for the descriptive work of fossil material from the Carpathian flysch.

Until the 1970's, all but one of the original descriptions of fossil species that we regard as belonging to the *Paratrochamminoides* group were based on specimens collected from the Carpathian flysch sediments in Poland and the Ukraine. In his monographs of foraminifera from the Polish part of the Carpathians, Grzybowski (1896, 1898, 1901) described several new species that he placed in the genus *Trochammina*. Another species (*Trochammina multiloba*) was subsequently described by Grzybowski's student Maria Dylà˝anka in 1923. Later Carpathian micropaleontologists (e.g., Jurkiewicz, 1967, Jednorowska, 1968, 1975; Neagu, 1962; Hanzlíková, 1972; Sandulescu, 1973) have all attempted to use the species nomenclature established by Grzybowski.

In his study of the *Globotruncana*-bearing Carpathian flysch from (the former) eastern Hungary, Majzon (1943) described two species within the genus *Trochamminoides* Cushman, 1910 (*T. koeroesmezooensis,* and *T. transitus).* Soliman (1972) established the new genus *Paratrochamminoides* based on his studies of specimens from the Ukrainian Carpathians.

North American micropaleontologists have traditionally placed all varieties of *Paratrochamminoides* into a single species, and this trend has continued until the present. White (1928) described the species *Trochamminoides irregularis* from the Paleocene Velasco Shale of Mexico. It has been subsequently reported by many authors, but the species quickly became a "garbage can" designation, and many subsequent citations of the species are erroneous. Later reports of this species by Cushman & Jarvis (1932) from the Lizard Springs Formation of Trinidad and by Cushman (1946) from the Gulf Coast are misleading because Cushman included all fossil species now regarded as *Paratrochamminoides* under the designation "*Haplophragmoides coronata*".

Studies of the Lituotubidae took a rapid turn with

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the discovery of Cretaceous abyssal agglutinated foraminiferal assemblages by Krashenninikov (1973). Krashenninikov described four new species that he provisionally placed in Soliman's new genus *Paratrochamminoides*. Since the early studies of Krashenninikov (1973, 1974), the genus *Paratrochamminoides* has been used to denote a loosely-defined group of "bizarre" deep-sea forms that display a remarkable array of coiling and chamber shape. The continuing studies of deep-sea material by our group (e.g., Kuhnt, 1987, 1990; Kuhnt & Kaminski, 1990; Kaminski *et al.* 1988, 1989, 1996) have revealed additional representatives of the group that have thus far defied assignment to any known species. Up to now we have used open nomenclature for certain well-defined species.

In their monograph of Paleogene foraminifera from the North Sea, Charnock & Jones (1990) revived the use of the genus *Conglophragmium* Bermúdez & Rivero, 1963. Because of their attempts to synonymize all modern and fossil species of the group known to them, Charnock & Jones only recognised a single species, *Conglophragmium coronatum* (Brady), which in their opinion ranges from Santonian to Recent.

1. VALIDITY OF THE GENUS *PARATROCHAMMINOIDES* SOLIMAN, 1972

Current Definitions

The definition (and validity) of the genus *Paratrochamminoides* and related forms is presently buried under the weight of problems with semantics, synonymy, and subsequent interpretations. We begin our discussion with a review of the problems that have led to the current confused state of affairs.

Soliman (1972) originally erected the new genus *Paratrochamminoides* for "all forms which have changing in the axis of coiling and which are at the early stages undivided and streptospirally coiled, but at the later stages are planispirally coiled". He gave the following diagnosis for the genus:

> "Shell free, irregular in form. Proloculus globular or ellipsoidal. Second chamber semitubular. At the early stages it is undivided but at the later stages is divided into chambers. The axis of coiling varies at approximately right angle. Aperture septal. Wall agglutinated, monolayered, comprised of quartz grains with siliceous cement
> "

Soliman originally considered the genus to encompass the species *P. koeroesmezooensis* (Majzon, 1943), *P. irregularis* (White, 1928), *P. folius* (Grzybowski, 1898) and "*P. elewski* (Grzybowski)" [= *P. olszewskii* (Grzybowskii, 1898)].

In their classification of foraminiferal genera, Loeblich & Tappan (1987) had basically followed the original description of the genus *Paratrochamminoides* by Soliman, with only a few additions and corrections. They defined the genus as follows:

> Test enrolled, proloculus followed by a **streptospirally** coiled and undivided tubular second chamber, later with numerous ovate to globular chambers per whorl and an abrupt change in coiling, to a planispiral final whorl; wall agglutinated, of firmly cemented quartz grains; aperture rounded.

Loeblich & Tappan placed the genus in the family Lituotubidae, which was defined as encompassing forms with a proloculus followed by an enrolled non-septate portion and later elongate and irregularly septate chambers, that may uncoil, and possess a simple interiomarginal to terminal aperture.

However, it is worth mentioning that Loeblich & Tappan (1987) had a very broad interpretation of the meaning of the word "streptospiral". They included under this term at least three distinctly different modes of coiling. These coiling modes have been recently reviewed by Platon (1997). We understand the term "streptospiral" in the strict sense, meaning a coiling mode that changes gradually and regularly as in the planktonic species *Pulleniatina obliquiloculata*. However, it is clear that Loeblich & Tappan also included "recurvoidiform" and "thalmannamminiform" coiling (in the sense of Platon, 1997) under the heading of streptospiral, and therefore their definition of the genus could be interpreted in a much broader sense.

Synonymy of the designated type species with *P. heteromorphus*

Soliman cited the species *Trochamminoides koeroesmezooensis* Majzon, 1943 as the type species of the genus. Majzon's type figure of *T. koeroesmezooensis* depicts a specimen with trochospiral initial coiling with round chambers and an uncoiled terminal part. Majzon described the specimen as having "three irregular coils". This specimen is in our opinion, conspecific with *Trochammina heteromorphus* Grzybowski, 1898 and therefore the latter species would automatically become the type species of the genus in accordance with the rules of the ICZN. One of the problems with the current definition of *Paratrochamminoides* is that the type species designated by Soliman neither displays streptospiral coiling, nor "an abrupt change in coiling", nor "a planispiral final whorl". Moreover, it typically uncoils as in the genus *Lituotuba*.

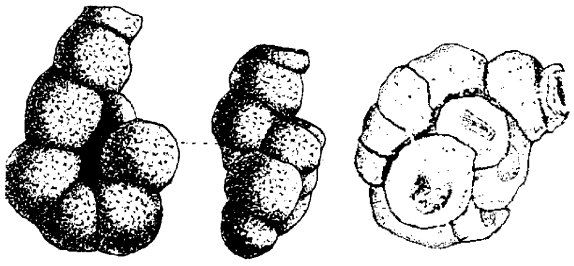


Figure 1. Left: drawing of T. heteromorphus from Grzybowski (1901), right: type specimen of Trochamminoides koeroesmezooensis from Majzon (1943).

Misidentification of the type species

Soliman (1972, pl. 1, figs. 18, 19, 24) illustrated a specimen that has little in common with Majzon's *Tro-*

chamminoides koeroesmezooensis and in our opinion, Soliman's specimen has been incorrectly identified. The clear differences between the coiling of *T. koeroesmezooensis* [=*T heteromorphus*] and the species illustrated by Soliman has implications for the definition of the genus *Paratrochamminoides*. The specimen determined as "*P. koeroesmezooensis*" by Soliman and reproduced by Loeblich & Tappan conform's with Soliman's description of the genus. The coiling appears to be glomospiral to "recurvoidiform" (*sensu* Platon, 1997), not strictly streptospiral. The chambers are irregular, with some rounded to reniform and others more elongated. The thin section illustrated by Soliman shows that the initial portion of the test is unchambered. The coiling appears to change abruptly and at right angles, and the final whorl consists of eight chambers. Soliman's specimen was collected from the Turonian of the Jalovetskai Formation of the Ukrainian Carpathians. In our previous studies, we have generally lumped such early Senonian forms under the designation "primitive *Paratrochamminoides* spp." (see taxonomic section below). These forms typically have irregular or mixed coiling modes that can be best compared to that observed in the species *Glomospira irregularis* (Grzybowski). More detailed work is required to resolve the variability of these Turonian forms.

Because Soliman's figure is a misidentification of a previously established species, *P. koeroesmezooensis* [or *T heteromorphus*] has no formal status as type species for *Paratrochamminoides* under the rules of the ICZN. In such a case, the matter of designating a type species for a genus is to be refered to the International Commisson on Zoological Nomenclature under Article 70 of the ICZN. Under this article, the Commission may designate whichever species that "will in its judgement best serve stability and uniformity of nomenclature."

In our opinion, the species *Paratrochamminoides olszewskii* (Grzybowski) best serves this purpose. Of the named species originally listed by Soliman as belonging to *Paratrochamminoides*, it best conforms to the original definition. The species has a globular proloculus followed by a glomospirally coiled latter part that is initially unchambered. The other species by Soliman listed belong in different genera.

Figure 2. Specimen of *Paratrochamminoides* from Soliman (1972).

Krashenninikov's definition of *Paratrochamminoides*

In his descriptions of the abyssal foraminifera from the North Pacific Krashenninikov (1973) adopted the use of Soliman's genus for "peculiar, irregularly coiled forms" that that form "an irregular trochospiral coil, sometimes coiling approximately planispiral [or] disordered and whimsical". For these forms, Krashenninikov used the name *Paratrochamminoides*(?). In his next paper, Krashenninikov (1974), dropped the use of the question mark, and described the genus *Paratrochamminoides* as "variable, irregularly trochospiral, irregularly planispiral [=glomospiral in our usage] and of bizarre shape".

Subsequent workers including ourselves (Kuhnt, 1990, Kaminski *et al*. 1996) have used the term *Paratrochamminoides* in the broad sense following the usage of Krashenninikov. In our concept of the genus up to now, we have even included species that can be placed in *Conglophragmium* Bermúdez & Rivero, 1963.

Relationship to *Conglophragmium*

Bermúdez & Rivero (1963) defined the genus *Conglophragmium* based on the specimens of "*Trochammina conglobata* Brady" illustrated in the HMS CHALLENGER report (Brady, 1884, pl. 40, figs. 8-9). This modern species possesses streptospiral coiling, large irregular chambers, and basal aperture. Bermúdez & Rivero described the genus as follows:

> Concha comparativamente grande, subglobular, formada por una serie de cámaras globosas y no completamente tabicadas, las que aumentan de tamaño gradualmente sugún se forman; y crecen envolviéndose y dando unas vueltas que cambian de eje (estreptospiral) para formar una concha glomerosa, pared gruesa, imperforada, microgranular, consistendo de material fibroso fino y firmemente compactado; abertura simple, en la base de la última cámera. Dimensión, 2,0 - 1,25 mm.

In their remarks, Bermúdez & Rivero stated the coiling resembles that of a juvenile *Trochamminoides*, but they emphasized that the genus differs in lacking both an initial unchambered early portion and a terminal planispiral part.

In our opinion the genus *Conglophragmium* is not a junior synonym of *Thalmannammina* as suggested by Loeblich & Tappan (1987). It is quite similar to the specimens of *Paratrochamminoides* illustrated by Soliman (1972), and instead belongs in the *Paratrochamminoides* group because of its irregular chambers and smooth, thin wall. The name *Conglophragmium* is available according to the rules of the ICZN, is senior to the genus *Paratrochamminoides*, and may be applied with certainty to the streptospirally-coiled forms with basal apertures.

However, as currently defined by Loeblich & Tappan (1987) the genus *Paratrochamminoides* includes only forms that are initially **streptospirally coiled** with a final planispiral whorl. If the definition of *Paratrochamminoides* by Loeblich & Tappan (1987) is accepted at face value, the name would need to be supressed in favour of *Conglophragmium*.

Charnock & Jones (1990) and Jones (1994) recognised *Conglophragmium* as a valid genus, and included species that are not only streptospiral, but also forms that "tend to become planispiral in later stages".

Table 1. Character states in the *Conglophragmium – Paratrochamminoides* group. Position of a question mark indicates the probable (or suspected) state of the character. The type species of a genus are indicated in **bold** type.

species	Trochospiral	Streptospiral	Glomospiral	Triloculine	Thalmannammina	irreg. or multi-ple	last plani-spiral whorl?	Uncoiling?	rounded	sausage	tubular	Nr.in Final whorl	basal	areal
acervulatus	X								X			8+	X	
challengeri			X				X				X			X
conglobatus		X							X			6+	X	
corpulentus		X									X	5	X	
deformis		X					X			X		5+		?
draco			X					X			X	5		?
gorayskii				X							X	3		?
intricatus	X					X			X			9+	X	
irregularis		X							X			5	X	
heteromorphus	X							X	X			7		X
korozmezoensis	X							X	X			<7		?
mitratus				X					X			10+		X
multilobus		X			X > > X				X			15+		?
olszewskii			X								X	3 - 4		X
pseudointermedius	X								X > > X			4	X	
semipellucidus			X							X		6		X
transitus				?					X			8		
uviformis	X					X			X			7		
valvulinariaformis	X >	>X							X			6.5	?	?
vitreus				X					X			6		X
sp. 3	X									X		4+		?
sp. 4			X					X	X			6+		X
sp. 5					X				X			12+		?

Charnock & Jones separated *Conglophragmium* from *Trochamminoides* and *Paratrochamminoides* based on the fact that the latter genera are "initially aseptate". Charnock & Jones synonymised *Trochammina conglobata* Brady with *Trochammina coronata* Brady, 1879, thereby assigning the latter the status of type species of *Conglophragmium*. In this manner they combined wholly streptospiral and streptospiral – planispiral forms into a single category (and regarded the genus *Budashevaella* Loeblich & Tappan, 1964 as synonymous), a view that we reject here.

If we uphold a distinction between *Trochamminoides* and *Paratrochamminoides* based on the presence or absence of planispiral coiling, we would need to apply identical criteria to the species of the *Conglophragmium* group. Also, we prefer to maintain the separation between *Conglophragmium* and *Budashevaella* based on fundamental differences in wall structure. The latter genus encompasses species with regular chambers and a thick, coarsely agglutinated wall.

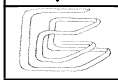
2. THE VALID SPECIES OF *PARATROCHAMMINOIDES*

In our studies of Cretaceous to Paleogene flysch-type and abyssal agglutinated foraminiferal assemblages, we recognise 21 species belonging to the *Conglophragmium–Paratrochamminoides* group. We have adopted the following first-order characters to distinguish the various named and unnamed species of *Paratrochamminoides:*

1. Mode of coiling (trochospiral, streptospiral, glomospiral, triloculine, thalmannaminiform, mixed or irregular).
2. Shape of chambers (rounded or beadlike, reniform or sausagelike, tubular).

Additionally, we recognise subordinate characters that are useful for recognising individual species of *Paratrochamminoides*. These are:

Table 2. A classification of the species of *Paratrochamminoides* according to coiling mode and chamber shape. Species that are uncoiled are indicated in **bold** type.

Coiling \ Chambers	Rounded or beadlike	Elongate or sausagelike
 Trochospiral	*P. acervulatus* *P. uviformis*	*P.* sp. 3 (Kuhnt, 1990)
 Streptospiral	*C. conglobatus, C. irregularis,* *C. pseudointermedius*	*C. corpulentus,* *C. deformis*
 Irregular trochospiral to streptospiral or **uncoiled**	*C. intricatus* ***P. heteromorphus*** ***[=P. koeroesmezooensis]***	*P. contortus*
 Glomospiral	*P.* sp. 4 (Kaminski *et al.*, 1996)	*P. semipellucidus* *P. olszewskii* ***P. draco*** *P.challengeri*
 Triloculine or milioline	*P. mitratus, P. vitreus*	*P. gorayskii*
 Thalmann-amminiform	*P.* sp.5 (Kaminski *et al.* 1996) *P. multilobus*	not observed

1. the position of aperture
2. shape and length of chambers
3. presence of an unchambered early portion
4. the number of whorls
5. the number of chambers in the final whorl.
6. the tendency to uncoil or to have a planispiral last whorl.

The accompanying matrix (Table 1) presents the differential diagnoses of the various species. The full name, and synonymy, and remarks to each species are given in the Systematics section (below).

3. GROUPS OF SPECIES BASED ON MODE OF COILING

Within the *Paratrochamminoides* group we recognise five basic modes of coiling (Table 2). A sixth category incudes species that change their coiling modes during ontogeny. We use here the subdivision of coiling modes previously included under the heading "streptospiral" as explained by Platon (1997). The restricted definition of the term streptospiral is used for species in which the direction of coiling changes gradually and regularly. We now place these forms in the genus *Conglophragmium*. Another mode of coiling that would have been previously lumped under the heading "streptospiral" is the thalmannamminiform coiling, in which the whorl is coiled about two orthogonal axes as in the genus *Thalmannammina*. This type of coiling results in a quadrate, "box-shaped" test. It is best visible in our *Paratrochamminoides* sp. 5.

In other groups of foraminifera, the mode of coiling is normally a fundamental aspect of test construction that is used to differentiate genera or even families. While the known species of *Paratrochamminoides* can also be split into groups based on coiling modes, we have resisted the temptation to split the *Paratrochamminoides* group into different new genera. One reason for this is the fact that all species in the genus display coiling that is somewhat irregular. Secondly, the stability of taxonomic concepts at the species level is still at an early stage, with many forms remaining in open nomenclature. At this point, we believe it is prudent to concentrate efforts on resolving the morphology of the various species within the group, before questions of the higher classification of the group can be resolved.

4. THE STRATIGRAPHICAL RECORD OF *PARATROCHAMMINOIDES*

Streptospiral forms with rounded chambers that can be placed in genus *Conglophragmium* are first encountered in Lower Cretaceous abyssal claystones at Site 765 on the Argo Abyssal Plain (Kaminski *et al.*, 1992). Other streptospirally coiled forms are known from "mid-Cretaceous" sediments, for example the report of "*Trochamminoides valvulineriaformis*" by Tairov (1961) from the lower Cenomanian of Astrakhan. It would then appear that the genus *Conglophragmium* constitutes a distinct and more ancient group of species, ranging from at least the lowermost Cretaceous to the Recent.

Species with different modes of coiling placed in the genus *Paratrochamminoides* are found consistently from the Turonian in abyssal red claystones. Up to now, we have included these diverse forms in a group we called "primitive *Paratrochamminoides*" (e.g., Kuhnt *et al.*, 1989). We speculate that this group of *Paratrochamminoides* evolved from unchambered forms such as *Glomospira irregularis* during the Turonian radiation of abyssal agglutinated foraminifera.

The diversity of coiling modes increased with time during the Late Cretaceous as the number of species within each group also increased. By the Campanian, the Carpathian flysch-type faunas contained a wide variety of species, including glomospiral, trochospiral, and uncoiled forms. In the Paleocene to early Eocene, the diversity of the group reached a maximum, with

triloculine and thalmannamminiform species. Eocene green clays from the Carpathians and from ODP Hole 647 yield several species, including *P. acervulatus, P. mitratus, P. irregularis*, *P. gorayskii*, and *Paratrochamminoides* sp. 4. The diversity of the group apparently declined in the Oligocene, and by the Miocene the group was extremely rare. Only the species *Paratrochamminoides challengeri* and *Conglophragmium conglobatus* are recognised in the modern ocean.

5. AFFINITY TO *GLOMOSPIRA* AND OTHER GENERA – A POSSIBLE POLYPHYLETIC ORIGIN?

Already in 1901, Grzybowski recognised the possible connection between his "*Trochammina*" species and those of "*Ammodiscus*". In the introduction to his paper Grzybowski wrote "especially among species of *Trochammina* and *Ammodiscus*, we observe an extreme diversity in the type of building plan, as well as in the presence of intermediate and transitional forms." Grzybowski must have recognised that certain species that we now place in *Paratrochamminoides* and *Glomospira* are homeomorphic. For example, *P. gorayskii* has identical coiling to that of *Glomospira serpens*, and *P. olszewskii* is analagous to *Glomospira gordialis.*

The diversity of building plans and presence of stratigraphically older homeomorphic species suggests multiple origins of the *Paratrochamminoides* group. It is possible that the oldest lineage, *Conglophragmium*, derived from a streptospirally coiled ancestor some time during the late Jurassic or earliest Cretaceous. The genus *Annectina*, an ammodiscid that is initially coiled in a triloculine manner, is known from the Early Cretaceous. It is likely that *Paratrochamminoides gorayskii* (or its ancestor) evolved through the progressive acquisition of a chambered test (rather than an undivided tubular second chamber as in *Glomospira serpens*). The fact that some species of *Paratrochamminoides* have an unchambered initial portion provides additional weight to Grzybowski's suggestion that the group evolved from the ammodiscids. If the evolution of *Paratrochamminoides* from unchambered ancestors can be documented and the group is indeed comprised of separate lineages that are polyphyletic, then (as in the planktonic foraminifera or Steven J. Gould's zebras) a case may be argued for splitting the group into different genera based upon evolutionary descent. While we realise that *Paratrochamminoides* is probably a mixed group of unrelated species, in our opinion it would still be premature to attempt to split the group further until more detailed evolutionary studies can be carried out.

SYSTEMATICS

Genus ***Conglophragmium*** Bermúdez & Rivero, 1963

Conglophragmium Bermúdez & Rivero, 1963, p. 177; type species: *Trochammina conglobata* Brady, 1884, p. 341; OD.

Conglobatoides Saidova, 1981, p. 18 (name not available, ICZN Art. 13 (a) (i). no description); type species: *Trochammina conglobata* Brady, 1884; OD (isotypic synonym).

Test free, compact, coiled streptospirally with axis of coiling changing regularly and gradually, involute, with embracing chambers that are sometimes irregularly shaped. The test is chambered at all stages of ontogeny. Chambers may be rounded or elongated in the direction of growth and are separated by depressed sutures. Wall finely agglutinated with a smooth surface, imperforate, with organic cement. Aperture an elongated interiomarginal slit. Early Cretaceous to Holocene; abyssal DSDP/ODP sites, Carpathians, Caucasus, Cosmopolitan.

Remarks. Loeblich & Tappan (1987) regarded *Conglophragmium* as a junior synonym of *Thalmannammina* Pokorny, 1951. Neagu & Platon (1994) redefined *Thalmannammina* based on the original description of Pokorny (1951) and observations of type specimens of the type species (*Haplophragmium subturbinatum* Grzybowski, 1898): *Thalmannammina* differs in possessing U-shaped coiling about two more or less orthogonal axes (thalmannamminiform coiling). The chamber interiors are subspherical, and the wall is thick and coarsely agglutinated. The aperture is areal, an oval to elliptical slit. We separate the two genera based on differences in the coiling mode, wall structure, chamber shape, and apertural position.

As pointed out by Bermúdez & Rivero (1963) the genus differs from *Trochamminoides* [and *Paratrochamminoides*] in lacking an initial aseptate portion. The genus was initially described as belonging to the family Lituolidae.

Conglophragmium conglobatus (Brady, 1884)

Trochammina conglobata Brady, 1884 , p. 341, pl. 40, figs. 8-9.
Conglophragmium conglobatum (Brady). –Bermúdez & Rivero, 1963, p. 177, pl. 18, figs. 11, 12.
pars *Conglophragmium coronatum* (Brady). –Jones, 1994, p. 45, pl. 40, figs. 8-9 (not figs. 10-12).

Remarks. This is the only Recent species of the genus. It is distinguished by its large dimensions (>1 mm), and numerous low chambers that may display irregular growth, or be slightly elongated in the direction of coiling. The aperture is a very broad interiomarginal slit.

In his revision of Brady's Challenger Report, Jones (1994) regarded *Trochammina conglobata* Brady, 1884 as a junior synonym of *Trochammina coronata* Brady, 1879, and listed the latter as the type species of *Conglophragmium* by virtue of this subjective synonymy. We do not uphold this synonymy, since this would mean significantly altering the definition of *Conglophragmium* as originally defined by Bermúdez & Rivero (1963). *Trochammina coronata* Brady differs in possessing a small streptospirally coiled early stage followed by a distinctly planispiral latter stage. Adult specimens may have as many as three planispiral whorls. Chambers are much narrower and are less embracing. Instead, we regard

T. coronata as belonging in the genus *Trochamminoides* Cushman, 1910.

Conglophragmium corpulentus (Krasheninnikov, 1973)

Paratrochamminoides (?) corpulentus Krasheninnikov, 1973, p. 121, pl. 3, figs. 3a-c.
Paratrochamminoides conglobatus (Brady). –Hemleben & Tröster, 1984, p. 520, pl. 3, fig. 9.
Paratrochamminoides semipellucidus Krasheninnikov. –Hemleben & Tröster, 1984, p. 520, pl. 3, fig. 9.
Paratrochamminoides sp. 2. –Hemleben & Tröster, 1984, p. 521, pl. 3, fig. 18.
Paratrochamminoides corpulentus Krasheninnikov. –Moullade et al, 1988, p. 365, pl. 3, figs. 8,9. –Wightman & Kuhnt, 1992, p. 257, pl. 3, fig. 15; pl. 4, fig. 1. –Kuhnt & Collins, 1996, p. 213, pl. 1, fig. 11.

Remarks. Distinguished by its elliptical outline and elongated chambers. The aperture is variable, from a high interiomarginal opening in the holotype, to a basal slit. Typically found in the Upper Cretaceous abyssal assemblages.

Conglophragmium deformis (Grzybowski, 1898)

Trochammina deformis Grzybowski, 1898, p. 288, pl. 11, figs. 20-22.
Paratrochamminoides deformis (Grzybowski). –Kaminski & Geroch, 1993, p. 262, pl. 9, fig. 7a-c (lectotype). –Rögl, 1995, p. 256, pl. 2, figs. 15-19.

Test oval in outline. The coiling is initially streptospiral, later becoming planispiral and more evolute, with five to six chambers in the final whorl. Chambers initially globular, few in the early whorl, later becoming elongate, rectangular. Aperture interiomarginal.

Remarks. The designation "*Trochammina deformis* Grzybowski" has not been used correctly since Grzybowski's time. Some authors have listed it as a synonym of other species of *Trochamminoides s.l.*, for example Pflaumann (1964) synonymized it under *T. proteus*; Grün *et al* (1964), Grün (1969) listed it with *T. variolarius*; and Jurkiewicz (1967) regarded it as a synonym of *T. coronatus*. Rögl (1995) reported it as common in the upper Kahlenberg beds in the Vienna flysch.

Conglophragmium irregularis (White, 1928)

Trochammina acervulata Friedberg (non Grzybowski). –Friedberg, 1901, p. 284, pl. 1, fig. 9a-b. (by OD of White).
Trochamminoides irregularis White, 1928, p. 307, pl. 42, fig. 1.
Trochamminoides irregularis (White). –Kaminski *et al.* 1988, p. 191, pl. 4, fig. 18.
Paratrochamminoides irregularis Kuhnt, 1987, pl. 2, fig. 8. –Kuhnt, 1990, p. 320, pl. 5, fig. 10. –Beckmann, 1994, pl. 20, fig. 24. –Bubík, 1995, p. 84, pl. 10, figs. 7-9. –Kaminski *et al.* 1996, p. 16, pl. 4, fig. 8.

Test large, comprised of a small number of large rounded chambers, often compressed. Coiling involute, with the last chambers covering much of the early part of the test. Sutures distinct, depressed. Wall thin, medium to finely agglutinated, occasionally with a roughened surface. Aperture a low wide interiomarginal arch.

Remarks. Deep sea specimens have low, rounded chambers that are usually collapsed. The test shape is flattened spheroidal, and is suboval or subround in outline. The aperture is observed to be a low, wide arch at the base of the last chamber.

The species is widely distributed in both flysch-type and abyssal sediments. However, the species name has been used for many years as a "rubbish bin" for many different species of the *Conglophragmium* and *Paratrochamminoides* group. Therefore, the published reports of this species require verification.

Conglophragmium multilobus (Dylà˝anka, 1923)

Trochammina uviformis Grzybowski var. *multiloba* Dylà˝anka, 1923, p. 74, pl.1, fig. 10.
Trochamminoides irregularis (White). –Glaessner, 1937, p. 360, pl. 1, fig. 9a,b.
Trochamminoides irregularis White. –Neagu, 1962, p. 59, pl. 4, fig. 61.
Paratrochamminoides multilobus (Dylà˝anka). –Kaminski & Geroch, 1993, p. 282, pl. 17, fig. 10a,b.

Test consists of a mass of small, rounded chambers coiled in an irregular evolute streptospire. The chambers are nearly spherical. Aperture is indistinct.

Remarks. This holotype of Dylà˝anka (1923) is a distinctive species characterised by its numerous small, globular chambers that increase in size extremely slowly or not at all. It appears to be mostly coiled streptospirally without a distinct plan of coiling, but a one point the coil turns 180° suggesting thalmannamminiform coiling. It differs from the species *C. irregularis* (White) in having much smaller, more numerous chambers. We have only encountered it in Upper Cretaceous samples from the Magura Unit in Poland. The specimen illustrated as "*T. irregularis*" by Glaessner (1937) from Ilskaya (Caucasus) and the specimen figured by Neagu (1962) from the Upper Cretaceous of the Romanian Carpathians have far too many chambers to be placed in that species. Both specimens conform well to our concept of *C. multilobus.*

Conglophragmium valvulineriaformis (Tairov, 1959)

Trochamminoides valvulineriaformis Tairov, 1959, p. 243, pl. 5, fig. 1a-c. –Tairov, 1961, pl. 22, fig. 1a-c.

The specimen illustrated by Tairov (1959, 1961) was described as follows: "Test small, trochoid, with a circular outline. Only the six chambers of the final whorl are clearly visible. Chambers have irregular growth, and various dimensions. Sutures are distinct. Aperture not completely visible, located at the base of the last chamber. Wall agglutinated, fine grained." Tairov added in the remarks that the species "differs from *Trochamminoides irregularis* in the smaller size and different arrangement of the chambers". The holotype (Figure 3) is apparently irregularly trochospiral to streptospiral, with globular chambers, and consisting of two whorls.

Remarks. Tairov's drawing depicts a specimen with well-formed chambers coiled in about two whorls. The aperture was unfortunately described as poorly defined, and we must accept Tairov's opinion that is is interiomarginal. If this indeed the case, this makes C. *valvulineriaformis* the stratigraphically oldest validly described species of *Conglophragmuim* known to us. Tairov (1959) reported the holotype from the lower Cenomanian of Astrakhanka, northern Kobistan. In the same paper, Tairov also described two additional new species of "*Trochamminoides*", *T. elliptica* and *T. placopsilinoides*. However, neither the drawings nor the descriptions are detailed enough to allow assignment to a particular genus. These specimens need to be re-studied.

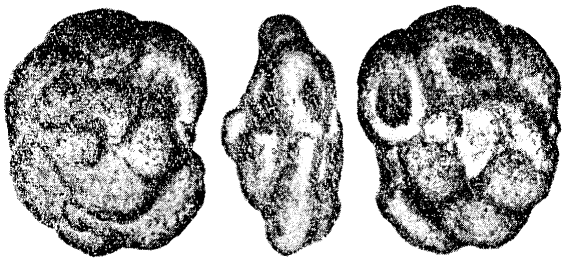


Figure. 3. Specimen of *Trochamminoides valvulineriaformis*, from Tairov (1969).

Conglophragmium spp.

Paratrochamminoides spp. –Holbourn & Kaminski, 1997, p. 42, pl. 11, figs. 2-4.

Remarks. These early forms of *Conglophragmium* from the Indian Ocean DSDP/ODP sites are characterised by their spherical chambers and variable agglutination. They differ from the Late Cretaceous forms in possessing few chambers. The oldest recorded occurrence is from the Tithonian to Valanginian at ODP Site 765, Argo Abyssal Plain. These specimens are finely agglutinated and appear to have a basal aperture. Specimens from the Lower Cretaceous of Hole 263 resemble the genus *Recurvoides*, which brings into question the relationship between the two genera.

Genus *Paratrochamminoides* Soliman, emend. Krasheninnikov, 1974.

Type species: *Trochamminoides koeroesmezooensis* Majzon, 1943 (nom. corr. pro. *T. körösmezŒensis*, = subjective junior synonym of *Trochammina heteromorphus* Grzybowski, 1898). OD.

Test free, coiling may be irregularly glomospiral, trochospiral, triloculine, or thalmannamminiform, and may have either a single planispiral outer whorl, become irregularly coiled, and/or have a tendency to uncoil. Chambers may be rounded, reniform, sausage-shaped, or elongated tubular. The early part of the test, and/or the terminal (uncoiled) stage in some species may be unchambered. Wall finely agglutinated with a smooth surface, imperforate, with organic cement. Aperture generally a round areal opening, but may be near the base of the last chamber, a basal arch, or in the case of uncoiled forms, simply the open end of the tube. Late Cretaceous (Turonian) to Holocene; Carpathians, DSDP/ODP Sites, Cosmopolitan.

Remarks. The low irregularly trochospiral coiled forms of *Paratrochamminoides* exhibit a gradual overlap with the irregularly planispirally coiled genus *Trochamminoides*. Many species belonging to the genus *Trochamminoides* are not planispirally coiled in the early part of the test. The differences in coiling between *Trochamminoides* and *Paratrochamminoides* are comparable to those between *Glomospirella* and *Glomospira*. We regard all species with two or more irregularly planispiral whorls as belonging in *Trochamminoides*.

Paratrochamminoides acervulatus (Grzybowski, 1896)

Trochammina acervulata Grzybowski, 1896, p. 274, pl. 9, fig. 4. -Liszka & Liszkowa, 1981, p. 176, pl. 3, fig. 1a-c.
Paratrochamminoides acervulatus (Grzybowski). –Kuhnt *et al.* 1998, pl. 1, fig. 13.

Specimens are generally oval in outline, coiled in an irregular conical trochospire of as many as four whorls. The ventral side generally has an umbilical depression. The wall is thick, finely agglutinated.

Remarks. This species characterises the trochospiral group of *Paratrochamminoides*. Specimens from ODP Site 647 have a round interiomarginal aperture with overhanging lip. Liszka & Liszkowa (1981) re-illustrated Grzybowski's type specimen.

Paratrochamminoides challengeri (Rögl, 1995)

Trochammina proteus Karrer. –Brady, 1884, p. 341, pl. 40, figs. 1-2 (not fig. 3).
Trochamminoides proteus (Karrer). –Cushman, 1910, p. 98, figs. 142-144.
Paratrochamminoides olszewskii (Grzybowski). –Jones, 1994. pl. 40, figs. 1-2.
Trochamminoides challengeri Rögl, 1995. p. 256.

Remarks. Rögl (1995) separated this modern species from the Upper Cretaceous to Paleogene species *P. olszewskii*, based on its much larger dimensions, thicker wall, and planispiral outer whorl. It is not clear whether this species belongs in *Paratrochamminoides* or in *Trochamminoides*. We place it here in *Paratrochamminoides* because we consider it to be the modern descendent of *P. olszewskii.*

Paratrochamminoides contortus (Grzybowski, 1898)

Trochammina contorta Grzybowski, 1898, p. 287, pl. 11, figs. 12-14.
Paratrochamminoides contortus (Grzybowski). –Kaminski & Geroch, 1993, p. 260, pl. 8, figs. 1-5. [lectotype is pl. 8, fig. 1a,b]

The lectotype has an elliptical test, displays an irregularly coiled initial portion and a planispiral last whorl with five tubular chambers. The chambers in the initial portion are more rounded or bean-shaped than the later chambers.

Because of its planispiral last whorl, the morphology of the species is close to that of the genus *Trochamminoides*. It differs from *Paratrochamminoides olszewskii* in having a distinctly chambered initial portion, and from *P. deformis* in having more elongated chambers in the last whorl.

Remarks. Grzybowski's collection contains an assortment of laterally compressed specimens of *Paratrochamminoides* and *Trochamminoides*, mostly with few, large chambers. The most common form in the collection seems to be identical with *Paratrochamminoides irregularis* (White). Other specimens in the collection may be laterally compressed forms of *Trochamminoides subcoronatus* (Grzybowski). This species is often reported from the Upper Cretaceous and Paleogene of the Alpine-Carpathian region (e.g., Geroch, 1960; Grün *et al.*, 1964; Jurkiewicz, 1967, Grün, 1969; Sandulescu, 1973). Other authors have included it as a synonym of *Trochamminoides coronatus* (Brady) (e.g., Pflaumann, 1964; Jednorowska, 1968). However, because the name has been used indiscriminately for many years (as is the case with *C. irregularis* in North America), reports of this species in the literature require verification.

Paratrochamminoides draco (Grzybowski, 1901)

Trochammina draco Grzybowski, 1901, p. 280, pl. 8, fig. 10.
Paratrochamminoides draco (Grzybowski). –Kaminski & Geroch, 1993, p. 277, pl. 16, fig. 5a-c. –Kaminski *et al.* 1996, p. 16, pl. 3, fig. 8. –Bubík, 1995, p. 84, pl. 3, fig. 2a,b.

Test large, oval in outline. Coiling initially glomospiral, consisting of 2-3 whorls, with the axis of coiling reversing 180°, doubling back, and finally uncoiling. Chambers are well-separated, elongate, with 4-5 in the last whorl. Sutures depressed. Aperture at the open end of the tube. Wall thick, finely agglutinated.

Paratrochamminoides gorayskii (Grzybowski, 1898)

Ammodiscus gorayskii Grzybowski, 1898, p. 283, pl. 11, fig. 5.
Glomospira gorayskii (Grzybowski). –Jednorowska, 1968, p. 40, pl. 3, fig. 3.
Paratrochamminoides gorayskii (Grzybowski). –Kaminski & Geroch, 1993, p. 255, pl. 5, fig. 8a-d. –Kaminski *et al.* 1996, p. 16, pl. 4, figs. 6-7.

Test small, oval in outline. Coiling triloculine, coiled in three planes, with the long axis of the test in the line defined by the intersection of the planes. Chambers poorly defined but with rudimentary septae, long, two or three per whorl. Wall thick, medium to finely agglutinated.

Remarks. The coiling mode is identical to that of *Glomospira serpens* (Grzybowski). Jurkiewicz (1967) and Jednorowska (1968) recorded it as *Glomospira gorayskii* from the Paleogene of the Carpathian flysch. Jednorowska noted that her specimen possessed a "very faint constriction that imitates a suture". The illustration of Grzybowski's specimen by Kaminski & Geroch (1993) in immersion reveals that this species is chambered. Though externally resembling *G. serpens* in outline, its wall is typically more coarsely agglutinated. We also observed *P. gorayskii* in the Eocene at Site 647 in the Labrador Sea and in the Numidian flysch of northern Morocco.

Paratrochamminoides intricatus Krasheninnikov, 1973

Paratrochamminoides (?) intricatus Krasheninnikov, 1973, p. 212, pl. 3, fig. 2a-c.
Paratrochamminoides intricatus Krasheninnikov, 1974, p. 638, pl. 4, fig. 2a-c.

Test initially coiled in a low trochospiral, later becoming streptospiral, with a 90° change in coiling direction between stages. Chambers round, aperture interiomarginal.

Remarks. The coiling of this species has characters of both *P. acervulatus* and *P. mitratus*, but *P. intricatus* is significantly smaller in size, has a thinner wall, and a smaller number of chambers and whorls.

Paratrochamminoides heteromorphus (Grzybowski, 1898)

Trochammina heteromorpha Grzybowski, 1898, p. 286, pl. 11, fig. 16.
Trochamminoides koeroesmezooensis Majzon, 1943, p. 156, pl. 2, fig. 16a-c.
Trochamminoides heteromorphus (Grzybowski). –Jednorowska, 1968, p. 51 pl. 6, figs. 1-4.
Trochamminoides irregularis heteromorpha (Grzybowski). –Neagu, 1970, p. 38, pl. 2, fig. 18.
pars Tolypammina prava Mjatliuk, 1970, p. 74, pl. 17, fig. 1a-b (not fig. 2).
Lituotuba lituiformis (Brady). –Beckmann, 1994, pl. 20, fig. 22.
Paratrochamminoides heteromorphus (Grzybowski). –Kuhnt, 1990, p. 320, pl. 5, fig. 18. –Kaminski & Geroch, 1993, p. 258, pl. 7, figs. 3a-5b. –Bubík, 1995, p. 84, pl. 11, figs. 4, 10. –Kaminski *et al.* 1996, p. 16, pl. 4, figs. 3-5.

Test initially irregularly trochospiral, or becoming streptospiral, later uncoiling. Initial portion comprised of several round, globular chambers. Chambers are larger in the uncoiled portion, may increase in length, and become tubular with constrictions. Aperture terminal, round, on the open end of the tube.

Remarks. *Paratrochamminoides heteromorphus* is distinguished from other species of *Paratrochamminoides* by its large size, irregularly trochospiral part with rounded chambers and in the presence of an uncoiled part.

Majzon's specimen of "*Trochamminoides köröz-mezŒensis*" is in our opinion conspecific with *P. heteromorphus*, and therefore *T. heteromorphus* would then become the type species of the genus under Article 67(e) of the ICZN. Majzon's type figure depicts a specimen with trochospiral initial coiling with round chambers and an uncoiled terminal part. Majzon described the specimen as follows:

> Test finely agglutinated, clearly forming three irregularly superimposed coils. The part above the last segment is broken away, but it is possible to observe that it is extending from the periphery of the test. This trend is already visible at the penultimate segment. The depressions between the segments are not equally deep, and the separated parts of the tests show a rounded or somewhat oval shape, with a slightly depressed center. Diameter 1.1 mm, thickness 0.55 mm.

Majzon uses the term segments instead of chambers (as he does in other species descriptions). This may indicate that he regarded at least the later part of the test to be not clearly chambered, but as a tube separated by sutural depressions.

One of the paratype specimens of *Tolypammina prava* Mjatliuk, 1970 conforms well with our concept of *P. heteromorphus*. This specimen (Mjatliuk Collection nr. 433-80) differs from the holotype (Mjatliuk Collection nr. 433-79) in being distinctly chambered with large irregular chambers. It is in our view identical to *P. heteromorphus*.

Paratrochamminoides mitratus (Grzybowski, 1901)

Trochammina mitrata Grzybowski, 1901, p. 280, pl. 8, fig. 3. –Dylà˝anka, 1923, p. 72.
? *Trochamminoides transitus*, Majzon, 1943, p. 155, pl. 2, fig. 12 (see remarks below)
Trochamminoides mitratus (Grzybowski). –Jednorowska, 1968, p. 54, pl. 7, fig. 1a,b.
Paratrochamminoides mitratus (Grzybowski). –Kaminski & Geroch, 1993, p. 277, pl. 16, fig. 4a,b; 6a,b (fig. 4 is the lectotype). –Bubík, 1995, p. 84, pl. 3, fig. 3a,b. –Kaminski *et al.* 1996, p. 16, pl. 4, fig. 9. –Nagy *et al.* 2000, pl. 5, fig. 7.

Test large, coiling is evolute, triloculine, with the direction of coiling changing abruptly. Successive whorls cross previous whorls at a high angle. About three whorls are generally visible from the exterior. Chambers increase in size very slowly, and are globular, with depressed sutures. Specimens typically have 10 or more chambers in the final whorl. Aperture a round areal opening, or the open end of the tube.

Remarks. The most distinctive feature of *P. mitratus* is the abrupt and regular changes in the coiling direction. The coiling in this species is not strictly streptospiral, but could more correctly be described as "triloculine" since individual coils are in three different planes. A given whorl encircles the test completely with 8-10 chambers before changing direction. Therefore the test is actually comprised of a series of planispiral whorls that are offset from one another by 60-90°.

Paratrochamminoides olszewskii (Grzybowski, 1898)

Trochammina olszewskii Grzybowski, 1898, p. 286, pl. 11, fig. 6.
Trochamminoides olszewskii (Grzybowski). –Neagu, 1962, p. 60, pl. 4, figs. 55-60.
Paratrochamminoides (?) *semipellucidus* Krasheninnikov, 1973, p. 212, pl. 3, figs. 4a-c.
Paratrochamminoides olszewskii (Grzybowski). –Wightman & Kuhnt, 1992, p. 257, pl. 4, fig. 4. –Kaminski & Geroch, 1993, p. 257, pl. 7, figs. 1a-2b (fig. 1 is the lectotype). –Bubík, 1995, p. 84, pl. 11, fig. 3. –Kaminski *et al.* 1996, p. 16, pl. 4, fig. 10.-Rögl, 1995, p. 257, pl. 2, figs. 20-25. –Kuhnt & Collins, 1996, p. 213, pl. 1, fig. 10. –Nagy *et al.* 2000, pl. 5, fig. 6.

Test rounded to oval in outline, coiling is predominantly glomospiral, with two or three whorls visible from the exterior. Chambering in the initial portion is rudimentary and indistinct, later the tube is subdivided into long tubular chambers of varying length. The tube has slight constrictions at the location of the sutures. The final whorl may be planispiral, inclined at a high angle to the previous whorls, or somewhat irregular, but does not uncoil. Wall is thick, finely agglutinated, with a smooth to slightly roughened finish. Aperture at the open end of the tube.

Remarks. *Paratrochamminoides olszewskii* (Grzybowski) characterises the group of *Paratrochamminoides* with glomospiral coiling (as in *Glomospira gordialis*). It differs from *Paratrochamminoides* sp. 4 in possessing long, tubular chambers in its outer whorls. Chambering develops with ontogeny, and the larger of the two specimens preserved in the Grzybowski collection has four chambers in its last whorl. Large specimens may also display a tendency toward planispirality in the outer whorls.

We first resolved the morphology of this species while carrying out observations of the Grzybowski Collection in the company of Prof. S. Geroch in 1990. To our knowledge, Neagu (1962) gave the only correct citation of *T. olszewskii* in the literature before 1992. The abyssal species *Paratrochamminoides semipellucidus* Krasheninnikov, 1973 may be a junior synonym (Wightman & Kuhnt, 1992). The species is cosmopolitan in distribution – it is one of the few species of *Paratrochamminoides* that is routinely found at high latitudes (Nagy *et al.*, 2000).

Paratrochamminoides pseudointermedius (Sandulescu, 1972)

Trochamminoides pseudointermedius Sandulescu, 1972, p. 35, pl. 14, figs. 5-13.

Taxonomic status: *Nomen dubium*

Sandulescu (1972) described this species as follows: "Test agglutinated of fine material, nearly circular in outline, lobate, compressed. On one side of the test two central chambers are visible, with a rectangular outline, surrounded by four ovoid chambers. On the other side, not more than four oval or circular chambers are visible and an umbilical depression is rather evident. The chambers are generally globular, with a deflated central part in most cases. The interiomarginal aperture is in the shape of an elongated slit, at the base of the last chamber." The stratigraphic range of the species was given as Turonian to Paleocene

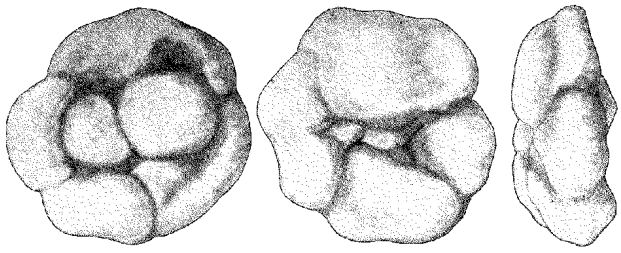


Figure 4. Paratype of "*Trochamminoides pseudointermedius,* from Sandulescu (1972).

The holotype (illustrated by Sandulescu in her pl. 14, fig. 5) was reported to be from the Paleocene, and the description of the species corresponds very well with the illustration. Paratypes of the species display coiling that appears to be irregularly trochospiral. As the species was reported from the Turonian, it may be an early representative of the *Paratrochamminoides* group. However, we cannot exclude the possibility that the holotype is simply a juvenile specimen of another species such as *P. acervulatus* or *P. heteromorphus*. We were unable to find any subsequent citations of this species.

Paratrochamminoides semipellucidus Krasheninnikov, 1973

Paratrochamminoides (?) *semipellucidus* Krasheninnikov, 1973, p. 212, pl. 3, figs. 4a-c.

Taxonomic status: *Nomen dubium*

Remarks. According to Wightman & Kuhnt (1992), this species is a junior synonym of *P. olszewskii*. The coiling is identical in both forms, and *P. semipellucidus* differs only in possessing shorter chambers. However, it is possible that chambering may be an ecological factor. Because of the extremely food-limited environment of the abyssal Pacific, the shorter chambers simply may be a reflection of slower growth stages. The name *semipellucidus* may be useful to distinguish between these two end-members.

Paratrochamminoides transitus (Majzon, 1943)

Trochamminoides transitus Majzon, 1943, p. 155, pl. 2, fig. 12.

Taxonomic status: *Nomen dubium*

The original description of *Trochamminoides transitus* by Majzon (1943), translated from the German summary of the paper is as follows:

> "Test coiled in one plane, agglutinated, made up of almost spherical chambers. The test is thicker in its central part, similar to the figure of *T. conglobata* (Brady) in Grzybowski (1898), but it differs from this species in having two symmetrical sides. The last whorl consists of seven chambers, giving the periphery a bent appearance. The central thickening originates from an abnormal enlargement of the last two chambers, moving out of the coiling plane and diverting from the original growth plane by 90°, thus becoming attached to the surface of the test.
>
> My species *T. transitus* is closest to *T. coronata* Brady, but differs from this species in the above-mentioned cross section. One specimen, from the red marl in the basin of the Kvasni Creek at Sztrojna, 1.0 mm in diameter."

Remarks. From the description, this specimen appears to have been coiled in a manner similar to that of *P. mitratus* or *P. vitreus*. However, the type illustration does not entirely agree with the description – the specimen has eight chambers in the final whorl, and the change in coiling of the last two chambers has not been clearly drawn. In our opinion, *Trochamminoides transitus* is a likely junior synonym of *P. mitratus*. One interpretation of the coiling mode of the type specimen would support the idea that it was coiled in a triloculine manner [compare with Krasheninnikov's (1974, pl. 4, fig. 1a) illustration of *P. vitreus*], but Majon's figure allows other interpretations as well. Unfortunately, Majzon provided only one view of the specimen, and there is no mention of an aperture. Without examining the type specimen it is impossible to verify the mode of coiling. The species is best regarded as *nomen dubium* until a proper revision can be carried out.

Paratrochamminoides uviformis (Grzybowski, 1901)

Trochammina uviformis Grzybowski, 1901, p. 281, pl. 8, figs. 1-2.
Paratrochamminoides uviformis (Grzybowski). –Kaminski & Geroch, 1993, p. 278, pl. 16, fig. 7a,b [lectotype]. –Bubík, 1995, p. 84, pl. 3, fig. 5a,b. –Kaminski *et al.* 1996, p. 16, pl. 3, fig. 6.

Test is made up of numerous chambers coiled in a high trochospire consisting of about three whorls. Chambers rounded. Aperture interiomarginal. Grzybowski's drawing of the type specimen, which could not be found in the collection, shows a clear basal apertural arch.

Remarks. Grzybowski reported that the coiling in "*T. uviformis*" does not follow any distinct plan. However, the specimens preserved in the collection appear to be coiled in an irregular, high trochospire, or even about a vertical axis, which begs comparison with *Glomospira charoides*. (Jones & Parker). *Paratrochamminoides uviformis* can be readily distinguished from *Paratrochamminoides acervulatus* (Grzybowski) by its more compact test and high trochospiral coiling with a change of coiling direction in the last whorl (*G.charoides*-like coiling) whereas the latter is consistently trochospiral with a somewhat lower coil.

Paratrochamminoides vitreus Krasheninnikov, 1973

Paratrochamminoides vitreus Krasheninnikov, 1973, p. 212, pl. 3, fig. 1a-c.

Test small, oval in outline, with lobate periphery. Chambers oval or spherical, increasing in size very slowly or of nearly equal size. Coiling appears to be triliculine, with three whorls visible from the exterior. Aperture a round areal opening in the center of the apertural face.

Remarks. Differs from *Paratrochamminoides mitratus* mainly in its small size, very finely agglutinated wall, and more oval outline. This species has been reported from Upper Cretaceous abyssal assemblages, while the latter is typical of flysch assemblages. However, there is little doubt that the two forms are related because they share a common mode of coiling. It is not outside the realm of speculation that the two forms may constitute a morphological cline in the same way that *P. semipellucidus* may be related to *P. olszewskii*.

Paratrochamminoides sp. 3

Paratrochamminoides sp. 3, Kuhnt, 1990, p. 233, pl. 5, fig. 17.

Test oval, coiled in an irregular low trochospire of two to three whorls. Chambers elongated, four to five in the last whorl. Wall finely agglutinated.

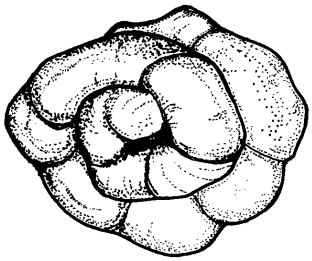


Figure 5. A specimen of *Paratrochamminoides* sp. 3, redrawn from Kuhnt (1990).

Remarks. Differs from *Paratrochamminoides acervulatus* in possessing elongated rather than globular chambers.

Paratrochamminoides sp. 4

? Trochammina deflexiformis Noth, 1912, p. 14, pl. 1, fig. 10 (nomen dubium).
Trochamminoides heteromorphus (Grzybowski). –Jednorowska, 1975. p. 47, pl. 4, fig. 1.
pars. *Trochamminoides mitratus* (Grzybowski). –Jednorowska, 1975. p. 47, pl. 4, fig. 2.
Paratrochamminoides sp. 4. Kaminski *et al.* 1996. p. 16, pl. 3, figs. 10-11.

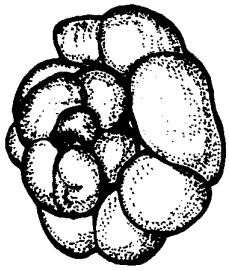


Figure 6. A specimen of *Paratrochamminoides* sp. 4, redrawn from Kaminski *et al.* (1996).

Test large, oval in outline. Coiling is glomospiral (as in *Glomospira gordialis*), with as many as three whorls, and an open umbilicus. The chambers are numerous, subspherical, increasing in size very slowly, with 8-10 in the final whorl. Wall is thick, finely agglutinated, with a smooth surface. Aperture is probably areal. There is an occasional tendency to uncoil.
Remarks. *Paratrochamminoides* sp. 4 is characterised by glomospiral coiling, as in the species *Paratrochamminoides olszewskii*. It differs from the latter in its rounded subglobular chambers and larger size. It differs from *Paratrochamminoides mitratus* in its larger dimensions, oval outline, and in possessing an open umbilical area.

It is possible that the specimen illustrated by Noth (1912) as *Trochammina deflexiformis* from the red clays of Barwinek (Poland) actually belongs in this species. The locality described by Noth consists of lower Eocene claystones of the Magura Unit that contain abundant and diverse specimens of *Trochamminoides* and *Paratrochamminoides*. However, the Noth Collection no longer exists (F. Rögl, personal communication to MAK), making it impossible to verify its morphology. For now, regard *Trochammina deflexiformis* to be nomen dubium pending a complete revision of the fauna from Noth's type locality.

We have illustrated it as *Paratrochamminoides* sp. 4 from the Paleocene and lower Eocene of the Tangier Unit of northern Morocco. We have also observed it in samples from the Maastrichtian of the Inoceramian Beds of the Magura Unit in Poland, and in samples from the Paleocene of the Lizard Springs Formation of Trinidad.

Paratrochamminoides sp. 5

Paratrochamminoides sp. –Rögl, 1995, pl. 2, figs. 26, 27.
Paratrochamminoides sp. 5. –Kaminski *et al.* 1996, p. 16, pl. 5, fig. 1a-2

Specimens small, compact, quadrate in outline, possessing rounded chambers. Coiling changes abruptly at 180° angles, and is arranged around two orthogonal axes as in the genus *Thalmannammina*. Five or six chambers in one 180° volution. Wall smooth, finely finished. Aperture at the open end of the tube.
Remarks. The thalmannamminiform mode of coiling sets it apart from other species of *Paratrochamminoides*. This species has now been recorded from the Maastrichtian and Paleocene in Austria and Morocco.

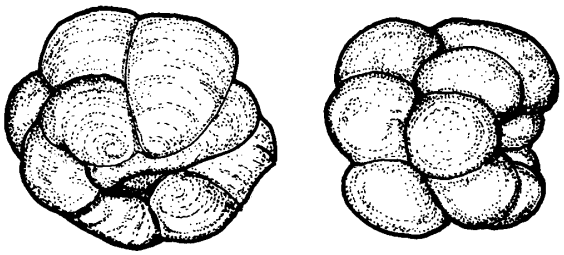


Figure 7. A specimen of *Paratrochamminoides* sp. 5, redrawn from Kaminski *et al.* (1996).

"primitive" *Paratrochamminoides* spp.

Paratrochamminoides korosmezoensis (Majzon). –Soliman, 1972, pl. 1, figs. 18, 19, 24; pl. 2, fig. 7
Paratrochamminoides sp. –Kuhnt, 1987, pl. 4, fig. 15-16
Paratrochamminoides spp. –Kuhnt *et al.*, 1989, pl. C-4, figs. 3-6

Spherical or ovoid proloculus, followed by a variable glomospirally, streptospirally or thalmannamminiform coiled later stage, composed of a tubuluar second chamber and more and more globular adult chambers. First individuals of this group are observed after the global anoxic event straddling the Cenomanian/Turonian boundary, and this group is the only representative of *Paratrochamminoides* in most red sub-CCD claystone of the Turonian - Santonian in the Tethys. We speculate, that this group of *Paratrochamminoides* evolved from species such as *Glomospira irregularis* during the Turonian radiation of abyssal agglutinated foraminifera. Figured individuals include specimens from the Turonian-Santonian Argille scagliose of the Parma Apennines (Rubbiano quarry) and the Massylian flysch of the Moroccan Rif. We do not intend to formalize the taxonomy of the group at this stage, mainly because it includes a variety of coiling modes.

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