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Ammonites and Stratigraphy of the Terminal Part of the Middle Volgian Substage (Upper Jurassic; Epivirgatites nikitini Zone and Its Equivalents) of the Panboreal Realm: 2. *Titanites* and *Glaucolithites*

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Abstract—The genera *Titanites* and *Glaucolithites*, which were previously known only from the Portlandian of Northwestern Europe are now established in Epivirgatites nikitini Zone of European Russia. The Volgian species of *Titanites* are represented by both the endemic taxa *Titanites (Paratitanites) manipulocostatus* subgen. et sp. nov. and *T. (Pseudogalbanites) triceps* subgen. et sp. nov. and *Titanites (Titanites)* ex gr. *titan* Buckman of the Portland type. A new species *Glaucolithites gardarikensis* is described. It is likely that these ammonites migrated to the Central Russian Sea from northwestern Europe via the Norway-Greenland seaway and further to the Mezen-Pechora system of straits, which is supported by occurrences of *Titanites* in the north of Central Russia and *Glaucolithites* in East Greenland and on Spitsbergen. The direct and indirect correlations show that the middle part of the Nikitini Zone (Lahuseni Subzone) should at least partly be correlated with the Portlandian Kerbeus Zone.

Keywords: Volgian Stage, Portlandian, correlation, ammonites, morphogenesis, systematics
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INTRODUCTION

The main problems of the intraboreal correlations of the Middle Volgian Substage with the Portlandian are primarily connected with the essential biogeographic differentiation of Boreal ammonites and with the poorly resolved taxonomy of the ammonite family Dorsoplanitidae. The zonal and infrazonal scales of the Portlandian and Middle Volgian Substage of European Russia are mainly based on the stratigraphic distribution of species and genera of dorsoplanitids. Therefore, all difficulties arising in correlation of the Volgian and Portlandian scales directly depend on the degree of the systematic study of that family, and the subfamily Dorsoplanitinae in particular. The existing problems in the dorsoplanitin taxonomy were discussed in detail in the first paper in this cycle (Kiselev, 2017) and earlier publications (Kiselev, 2015a, 2015b), and therefore they will not be discussed in detail here.

Previously, shell diameter, a very important character, which is measured on the terminal body chamber (TBCh) near the terminal peristome, was not sufficiently taken into account in dorsoplanitins studies. On the basis of study of numerous characters using the analysis of statistical distributions, it was shown that dorsoplanitins, like many other Jurassic ammonites, have size polymorphism, and therefore the terminal shell diameter has taxonomic significance. However, the manifestation of this dimorphism complicates the recognition of various size groups. In contrast to examples of classical dimorphism, which includes microconchs and macroconchs (Callomon, 1963), dorsoplanitins with small terminal size, or minimorphs (according to Kiselev, 2015a, 2017), are represented by the morphogroup of macroconchs, whereas large shells, or macromorphs, are represented by megaconchs. Minimorph and macromorphic dorsoplanitins are usually assigned to different genera: *Epivirgatites* Spath, 1924, *Lomonossovella* Ilovaisky, 1937, *Crendonites* Buckman, 1923, *Kerberites* Buckman, 1924, *Paracraspedites* Swinnerton, 1925, *Taimyrosphinctes* (*Udschasphinctes*) Mesezhnikov, 1972 are minimorphs, whereas *Titanites* Buckman, 1921, *Galbanites* Buckman, 1921, *Glaucolithites* Buckman, 1922, and *Taimyrosphinctes* (*Taimyrosphinctes*) Mesezhnikov, 1972 (partly) belong to macromorphs. *Praechetaites* can possibly be represented by micro- and macroconchs (Rogov, 2010); recently, megaconchs of *Prae-*

chetaites, which like macroconchs, possess smoothened ornamentation on the TBCh were discovered in the sections of the Kheta River.

Confusion in the taxonomy of dorsoplanitins often resulted from the fact that the adult shells of minimorph taxa were often considered as young and immature shells of macromorphs. Macromorph specimens represented by megaconchs were frequently identified as minimorph taxa, and vice versa. This is particularly noticeable in the Russian-language literature on ammonites and biostratigraphy of the Middle Volgian Substage. In particular, the Middle Volgian megaconchs from the Epivirgatites nikitini Zone were identified in various studies as

(1) *Titanites*: Pavlow and Lamplugh, 1892; Pavlow, 1901 (as "Grande *Ammonites* rapprochés de *Perisph. giganteus*"); Arkell, 1946 and others; Gerasimov et al., 1962; Sasonova and Sasonov, 1979; Kiselev, 2015a, 2015b, 2017;

(2) *Paracraspedites*: Ivanov et al., 1987; Muravin, 2013;

(3) *Epivirgatites*: Spath, 1936; Ivanov et al., 1987; Muravin, 2013; Mitta, 1993, 1994; Kiselev et al., 2003, 2012;

(4) *Lomonossovella*: Muravin, 1979, 1989, 2013; Ivanov et al., 1987; Mitta, 1993, 1994.

This example demonstrates that the generic taxonomy of this group is clearly instable, confusing, and poorly understood. Minimorphic dorsoplanitins from the Middle Volgian Substage of the genera *Lomonossovella* and *Epivirgatites* are better studied. The macromorph group was not a subject of special study; hence, the macromorph taxa were not recognized or established (except the poorly studied genus *Taimyrosphinctes*). On the other hand, zonal biostratigraphy of the Portlandian is mainly based on the distribution of the macromorph taxa *Titanites*, *Galbanites*, and *Glaucolithites*.

Thus, it becomes evident that the main difficulty in the correlation of the Portlandian and Middle Volgian Substage is related to the uncertainty of the systematic position of the Middle Volgian megaconchs from the Nikitini Zone. Despite the fact that the Volgian and Portlandian megaconchs have the same morphogenetic style (Kiselev, 2017), it is still unclear to what extent the Volgian megaconchs are similar to the genus *Titanites* and other macromorph Portlandian genera. This uncertainty is rooted in the absence of studies with a thorough comparative morphological investigation of both groups. Similarly, it is difficult to compare the Middle Volgian megaconchs with the genus *Taimyrosphinctes* known mainly from Siberia, because the papers by Mesezhnikov (1972, 1984), where this genus is described and discussed, do not show any specimen at a megaconch stage, and at the same time, some species established there are obvious minimorphs.

The purpose of this paper is to determine the systematic position of the Middle Volgian megaconchs from the Nikitini Zone, which will allow the elaboration of an adequate correlation of the upper part of the Middle Volgian Substage with the Portlandian. Although megaconchs of well-preserved dorsoplanitins are frequently found in the Middle Volgian sections of European Russia, comparison of these ammonites with the insufficiently studied Portlandian taxa is extremely difficult. The taxonomy of Portlandian macromorph taxa is contradictory for a number of subjective reasons. None of the known, extremely rare, publications dealing with this group of Portlandian ammonites contains systematic comparative morphological studies. For most Portlandian megaconchs, the morphology of the shell inner whorls is unknown, and for some species, primarily for those described by S. Buckman from other collectors' material, the stratigraphic position of the types is not precisely known.

Therefore, before studying the Volgian taxa and comparing them with Portlandian ammonites, it is necessary to reconsider the diversity of the latter on the basis of a new method.

PORTLANDIAN MACROMORPH DORSOPLANITINS

The first taxonomy of the Portlandian ammonites was proposed by Buckman (1909–1930), who recognized 21 genera mainly on the basis of nomenclatural types, i.e., on a single specimen. All these taxa, according to Buckman, were autochthonous, mainly of English origin. Among these, the following genera definitely finish their morphogenesis up to the megaconch stage: *Titanites* Buckman, 1921; *Galbanites* Buckman, 1921; *Briareites* Buckman, 1921; *Gigantites* Buckman, 1921; *Trophonites* Buckman, 1922; *Behemoth* Buckman, 1922; *Glaucolithites* Buckman, 1922; *Glottoptychinites* Buckman, 1923; *Pleuromegalites* Buckman, 1924; *Hippostratites* Buckman, 1924; *Aquistratites* Buckman, 1924; *Vaumegalites* Buckman, 1924; *Polymegalites* Buckman, 1925; *Gyromegalites* Buckman, 1925; *Hydrostratites* Buckman, 1926. As in the case with most of Buckman's ammonite taxa, their author did not give any diagnoses or comparative morphological descriptions of the Portlandian genera (except *Kerberites* and *Shotoverites*). The descriptions of most taxa included only an illustration of the nomenclatural type citing the size and stratigraphic occurrence. Thus, the stratigraphic age has in fact become the main principle of recognition of taxa. The true morphology of these genera is not possible to identify from the illustrations of type specimens of the type genera for most megaconch taxa. On one hand, Buckman figured "giants" mainly on the basis of adult specimens that reached the terminal stage without figuring the inner whorl. At that stage, Portlandian macromorphic dorsoplanitins are quite similar; hence, many of Buckman's genera are interpreted as formal taxa. This problem is exacerbated by Buckman often choosing poorly preserved specimens for holotypes of the type species, usually with a completely covered umbilicus or even with an incomplete last whorl (*Titanites*, *Trophonites*, *Pleuromegalites*, *Polymegalites*, *Hydrostratites*, *Vaumegalites*, *Aquistratites*, and *Glaucolithites*). This approach to type designation was a source of complicated diagnostic problems, which will probably never be completely resolved by any subsequent revision of this group. The situation is somewhat humorous at same time as being serious, especially if one considers that, in the holotype of the type species of the most important stratigraphic marker of the Portlandian, the genus *Titanites* (Buckman, 1909–1930, pl. 231), of all parts of the shell, only the fragment of the terminal whorl is preserved.

Spath (1931, 1936) was the first to revise Buckman's system and propose his own taxonomy for the Portlandian genera (Spath, 1936, pp. 33–37), which he himself referred to as a "treatment" of the previous taxonomy. He synonymized most of Buckman's "giant" genera in the three genera: *Behemoth*, *Titanites*, and *Kerberites*. These genera he placed in the new subfamily Pavloviinae Spath, 1931.

Spath also justifiably criticized the choice of Buckman's types, calling some of them unsuitable or even "despicable." To revise the taxonomy of these genera, Spath studied the inner whorls of megaconchs that he collected in "*Titanites* beds" of the type sections and proposed the first diagnoses of genera on the basis of the morphological characters of both adult and young whorls. He showed that the inner whorls of most "giants" belong to the same morphotype, which is characterized by triplicate or *Kerberites*-like ornamentation. Accordingly, he assigned several of Buckman's macromorph genera (*Gigantites*, *Briareites*, *Pleuromegalites*, *Hippostratites*, *Polymegalites*, and *Titanites*) to *Titanites*. The name of the valid genus was chosen on the basis of seniority, although Spath himself noted that Buckman's figured type of *Titanites* was a "form of unknown affinities" (Spath, 1936, p. 36).

Other "giants", with inner whorls possessing coarser ornamentation and low cross section (which Spath referred to as cadiconic), were placed in the genus *Kerberites*, which included *Trophonites*, *Glottoptychinites*, *Vaumegalites*, and some (according to the context) *Hippostratites* and *Galbanites* and junior synonyms.

The subdivision of "giants" into two groups Spath considered a relatively conventional solution because of little difference between them. There are intermediate forms between the thinly ribbed and coarsely ribbed varieties of "giants," which create so much diversity that, according Spath, the subdivision of these ammonites into two groups provides very little possibility for a practical solution (Spath, 1936, p. 33).

Spath laid a foundation of principles of the macrosystematics of titanoid ammonites, which give only a general understanding of the diversity of this group. Unfortunately, apart from a four-page essay, he did not provide a detailed description of these ammonites, except for a single specimen of *Glaucolithites* from Greenland.

The last revision of Portlandian ammonites was made about 40 years ago by W. Wimbledon. The results of this revision were in the most complete way represented in his unpublished dissertation (Wimbledon, 1974). The stratigraphic conclusions of this study were published in two papers (Wimbledon and Cope, 1978; Wimbledon, 1984), whereas the paleontological results remained unpublished (except for a description of a new species). The subdivision of zones into subzones proposed in the more recent of these two papers (Wimbledon, 1984) cannot be considered appropriate because no index species were proposed for any of the units, whereas subzones in the Kerberus and Okusensis zones were designated by letters "a" and "b." Moreover, the characterization of the zones and subzones published in various papers was contradictory.

Wimbledon, like Spath, assigned the Portlandian ammonites to the subfamily Pavloviinae. His system includes five macromorph genera: *Titanites* with subgenera *Titanites* s. str. (four species), *T. (Briareites)* (two species), *T. (Glottoptychinites)* (one species), *T. (Polymegalites)* (two species), and new taxa *T. (Portlandia)* (one species) and *T. (Ophiolithites)* (four species); *Glaucolithites* (seven species); *Galbanites* including three subgenera *Galbanites* s. str. (three species), *G. (Kerberites)* (three species), and a new subgenus *G. (Crassicostites)* (five species); *Hydrostratites* (one species); *Vaumegalites* (one species); and one minimorph genus *Crendonites* with subgenera *Crendonites* s. str. (two species) and a new subgenus *C. (Fittonia)* (one species). Descriptions of the subgenera *Portlandia*, *Ophiolithites*, *Crassicostites*, and *Fittonia* remained unpublished; they are only present in the unpublished thesis (Wimbledon, 1974).

Wimbledon's system of Portlandian ammonites was based on the study of an assemblage of characters, which includes the density of ornamentation and its change in the morphogenesis, style and ribbing coefficient in the inner and outer whorls, proportions and shape of the shell cross section, the relative umbilicus diameter, angular length of body chamber, and the terminal shell diameter. He measured 169 specimens, and for 100 specimens, he gave parameters of the ribbing density for more than one whorl. Unfortunately, he did not use these measurements for comparative-morphological studies using ribbing density curves, with the result that not all the morphogenesis is adequately described, and the range of variability of the described genera and species not always reliably estimated.

Wimbledon's work marked considerable progress compared to the previous studies, primarily because of the flawless nomenclatural and stratigraphic descriptions. However, its results do not allow a substantiated demarcation between different taxa, in particular, between the morphologically similar taxa. For the same reason, it does not provide a tool for the recognition of parallelisms.

To solve the problem of recognition of fine morphological differences between closely similar taxa of macromorphic dorsoplanitins from the Portlandian and Middle Volgian Substage, it is necessary to study an assembly of taxonomically significant shell characters, with compulsory use of methods of comparative-morphometric analysis. Below, we discuss the results of such a study and accordingly an amended model of the systematics of the ammonite group under consideration.

MATERIALS AND METHODS

In order to establish the most objective morphological boundaries between taxa, we used the principle of morphometric modeling of the available selection on the basis of the leading characters with compulsory study of referent specimens. The nomenclatural types are chosen as reference points, and the most stable characters, allowing the reliable recognition of taxonomic boundaries, are chosen as leading characters.

In Portlandian macromorphs, different parameters of ornamentation density were used as leading characters, as this is one of a few characteristics that can be readily traced at different morphogenetic stages of one megaconch shell without it being uncoiled. The density of ornamentation correlates with whorl shape and reflects the comprehensive shell morphotype. Using this character, it is possible to consider a large sample of the ammonoid group discussed alongside the reference specimens.

In studying the morphogenesis of dorsoplanitins, we used two parameters of ornamentation density:

(1) number of ribs per a whorl—character widely used in persphinctid studies; changes in this parameter in the morphogenesis is shown in the form of ribbing curves;

(2) length of the interval of five or ten primary ribs, measured near the umbilical shoulder—parameter of the absolute density of ornamentation (in mm); use of this parameter was described in detail previously (Kiselev, 2017), where it was designated as POD (parameter of ornamentation density).

The umbilicus diameter is used as a parameter of the morphogenetic age of the shell, and it is coordinated with each measurement of the parameter of ornamentation density.

The measurements were made from photographs of specimens imported into graphics software. Altogether, 34 specimens of Portlandian dorsoplanitins, of which 20 were holotypes, were so measured. We mainly selected well-preserved specimens with a completely prepared umbilicus, but in some rare cases for reference taxa, we used poorly preserved specimens allowing only one (last) whorl to be measured. Specimens at the TBCh stage were preferred, but in some cases, immature species were used. We measured figured megaconchs in Buckman (1909–1930) and Wimbledon (1974) and photographs of cited and figured specimens or topotypes from the collections of the Natural History Museum (London) and the National Museum of Wales (Cardiff). Additionally, we used measurements of 56 specimens mentioned in Wimbledon's monograph.

COMPARATIVE MORPHOGENESIS OF PORTLANDIAN MACROMORPHS

In describing the diversity of Portlandian ammonites, we in general use Wimbledon's scheme proposed in his dissertation (Wimbledon, 1974); hence, we retained his original nomenclature. The morphometric studies mainly included ammonites from the upper zones of the Portlandian (Okusensis, Kerberus, and Anguiformis) (after Wimbledon, 1984) and to a lesser extent from the Glaucolithes Zone (genus *Glaucolithites*).

All Portlandian macromorphic dorsoplanitins are characterized by a single shell morphotype, which at the intermediate and adult stages is represented mainly by semievolute or evolute whorls possessing equicostate ornamentation. Young whorls are usually semi-involute. The generic diversity is defined by the ultimate shell sizes: ammonites of the mean terminal size (250–350 mm) belong to the genus *Galbanites*, and larger ones (over 500 mm) belong to the genus *Titanites*. Subgenera and species are determined by different combinations of the following characters: proportions and shape of the whorl cross section; density of primary ribs; ribbing style and ribbing coefficient in the young and adult whorls; height and prominence of the ribs. In general, the morphotype of these ammonites is relatively uniform, which complicates their identification.

The uniform growth type of the shell determines the uniform pattern of the ribbing development throughout morphogenesis: ornamentation density in a whorl gradually increases from young whorls to the ultimate whorl (Fig. 1). This developmental pattern in characteristic of all ammonites with equicostate ribbing.

Differences between the equicostate and variocostate patterns are manifested by different pace of morphogenetic changes: in the equicostate pattern, the interrib space changes more slowly than the expansion of the umbilical spiral, and with approximately the same rate. The larger the shell of the equicostate type, the more ribs will be present on the last whorl. Thus, there is a distinct correlation between

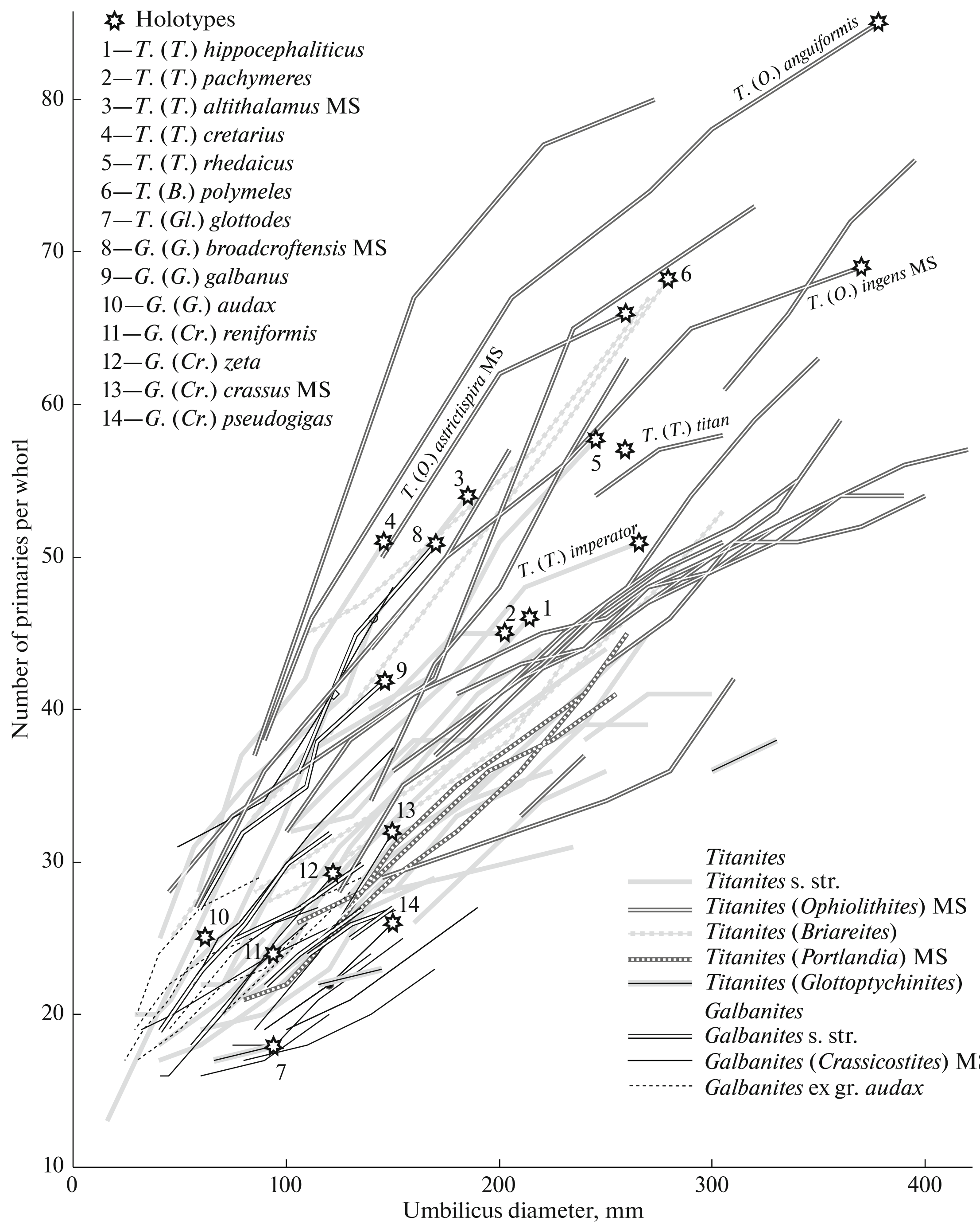


Fig. 1. Change in the ornamentation density in morphogenesis of Portlandian macromorphic dorsoplanitins. The number of curves describing the ribbing density corresponds to the number of measured specimens. Reference specimens (holotypes) are indicated by asterisks. The umbilicus diameter is used as the parameter of the morphogenetic age.

the relative umbilicus diameter and ribbing density in the equicostate mode of development. This correlation will increase if there are fewer changes in the differences in the interrib spaces during morphogenesis. In an ideal case, the ornamentation density will be determined only by the umbilicus diameter if the interrib space remains constant at all growth stages. Such growth should be referred to as “completely uncompensated.” An increase in the interrib space in linear size causes the effect of compensation of interrib space and umbilical growth. This type of growth is to a certain extent “compensated.” Finally, if the number of primary ribs remains unchanged in all whorls, this type of growth is “completely compensated.” In that

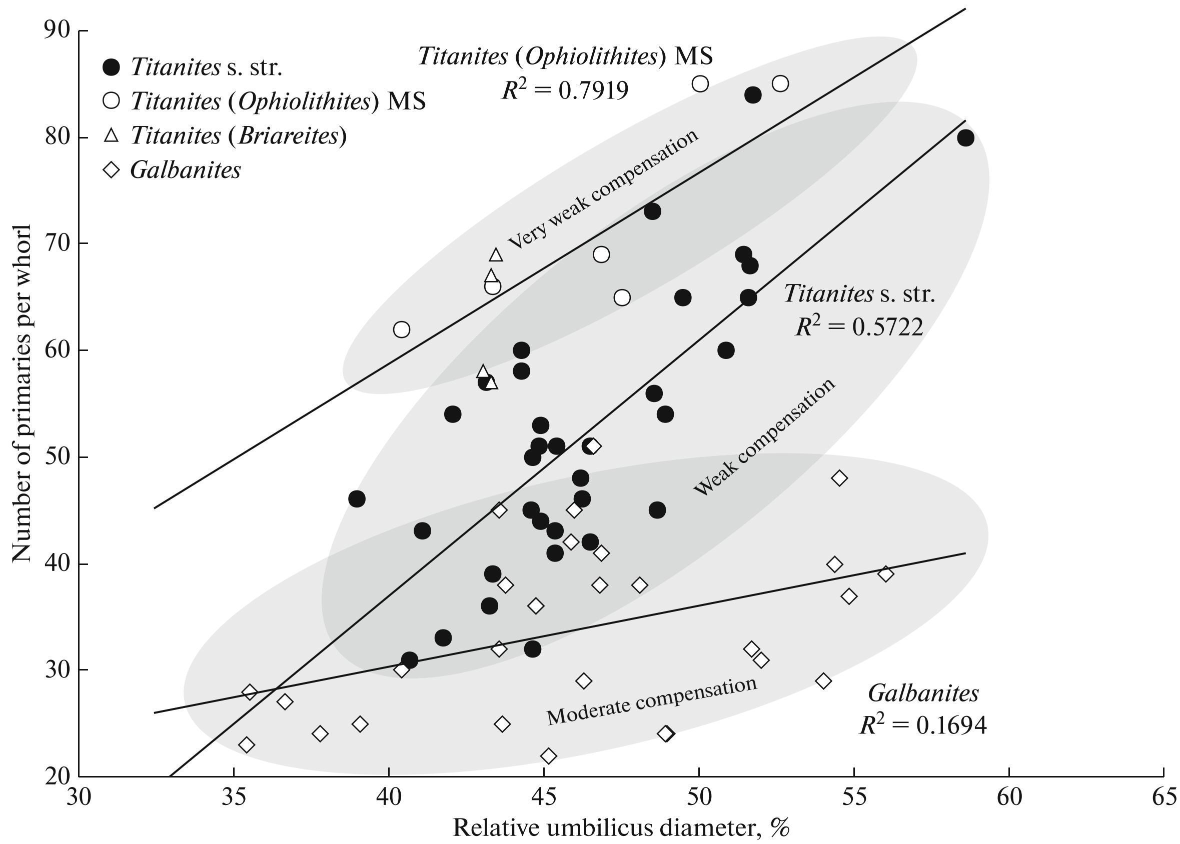


Fig. 2. Type of correlation the ornamentation density and relative umbilicus diameter at the terminal stage of morphogenesis in various groups of Portlandian dorsoplanitins. Each group corresponds to its own type of compensation growth of the ribbing density (explanation see in the text). Only adult specimens were measured. Two measurements in the terminal whorl were made in each specimen: at the minimum and maximum diameters.

case, the ribbing curve will flatten and become horizontal. In the case of uncompensated growth of the umbilicus, the ribbing curve is at an angle and follows the formula $y = ax + b$. The angle of the curve is expressed by the coefficient a, which we term the index of the angle of the ribbing curve. In the case of the horizontal ribbing curve, $a = 0$, and the formula is $y = b$. In the case of a completely compensated growth, the curve will follow the equation $y = ax$.

The general angle of the curve for the genera *Titanites* and *Galbanites* is approximately the same in distribution and mean values (arithmetic mean), but in *Galbanites* is generally somewhat smaller: 0.1241 instead of 0.1299.

The compensation of the umbilicus growth can change throughout morphogenesis. Near the terminal stage (mainly on the last whorl), the Portlandian taxa show more difference than is revealed by the analysis of the total angle of the ribbing density curves. The extent of this compensation can be determined by the correlation of the rib density and the umbilicus size expressed in percent. In Portlandian macromorphic dorsoplanitins, the developmental compensation is considerably different beginning from the subgeneric level (Fig. 2). The following groups can be recognized for the terminal stage of the morphogenesis, at which the taxon distinguishing characters are the most pronounced:

1. Group with *very weak compensation*. Ammonites that fall into this group are characterized by the largest terminal shells, strongly evolute whorls, and the largest number of ribs on the last whorls among all *Titanites*. These are mainly late *Titanites*, which include *T. anguiformis* (Wimbledon) and two similar species, which Wimbledon assigned to the unpublished subgenus *Ophiolithites*. The genus *Titanites (Briareites)* has the same type of compensation.

2. The group with a *weak compensation* includes the subgenus *Titanites* s. str. As in the first group, the compensation is manifested by the noticeable difference in the rib density in involute and evolute adult shells. However, the rib density is in general less than in the first group.

3. Group with *moderate compensation*. Shells of this type characteristically show no correlation between the relative umbilicus diameter and rib frequency. This suggests that the increase in the interrib space follows the increase in the umbilicus diameter; hence, the rib

density in the involute and evolute whorls approximates a constant. Species of the genus *Galbanites* belong to this group.

The extent of compensation is observed in the angle of the ribbing curve: the higher the compensation, the more flattened the curve approximates the horizontal orientation (Fig. 1).

In the case of the equicostate development, the terminal rib frequency is determined not only by the rate of the increase in the interrib space but also by the *initial conditions*—the number of ribs which initially appear in early whorls. The more ribs appear on a young shell, the more ribs will be present on the adult shell. The distribution of macromorphs in Fig. 1 clearly shows that the rib curves run parallel or subparallel to each other and hardly intersect. The taxonomic significance of the rib number at early stages and at the end of the morphogenesis can be understood only by evaluating the degree of variability of this character.

As shown in Fig. 1, the rib frequency varies greatly within genera or subgenera and on the whole does not have a great taxonomic significance. To understand the species affinity of this character, we will consider its distribution by example of two species of the same geochronological age (Kerberus Zone) with a relatively good sample size—*Titanites (Titanites) titan* (Buckman) and *T. (T.) bononiensis* (de Loriol) (Fig. 3).

Both species significantly differ in the rib density: in the former species it is high, with a broad range of almost not intersecting curves of ribbing density; in the latter species, the variability is very low—the curves intersect at several points. How can such a considerable difference be explained? On one hand, variability in different species can indeed differ for objective reasons. However, if the species is interpreted too broadly, a false impression of high variability can also be given. The distribution of species in Figs. 1 and 3 is shown according to their interpretation by Wimbledon, including specimens from the synonymy lists and material from morphometric tables (Wimbledon, 1974). For instance, Wimbledon placed the holotypes of five of Buckman's species, four of which were measured, in the synonymy list of *T. (T.) titan* (Fig. 3). These specimens for a group near the reference measurement of the holotype of the species *T. titan* hence can indeed be considered to be related or to be synonyms of one species. Another group of specimens is outlined separately, forming a cluster on the right. A gap is observed between the left and right clusters. The same situation is true for the samples of other species of *Titanites*, such as *T. (T.) giganteus* (Buckman), *T. (Briareites) polymeles* (Buckman) (Fig. 1), and *T. (Ophiolithites) ingens* Wimbledon MS. In all these cases, there are two clusters of specimens separated by a gap.

A high degree of variability of species leads to a considerable overlap of their morphospaces. The most populated area of the entire morphospace lies in the axial part of the field describing the entire macromorph group, with the maximum multiple overlaps (Fig. 4). Almost all morsphospaces of ammonites of the lower part of the Kerberus Zone (Kerberus Subzone) to some extent overlap one another. How does this affect the diagnostic value of characters? Primarily this can be addressed to the most closely related synchronous species (in this case belonging to one subgenus). Of ten species recorded in the Kerberus Subzone, three species of *Titanites* s. str., *T. (T.) titan* Buckman, *T. (T.) altithalamus* Wimbledon MS, and *T. (T.) giganteus* (Sowerby), and three species of *Galbanites (Crassicostites)* Wimbledon MS, *G. (Cr.) pseudogigas* (Salfeld), *G. (Cr.) zeta* (Buckman), and *G. (Cr.) crassus* Wimbledon MS, belong to such groups. The upper part of the Kerberus Zone contains only two such species—*T. (T.) titan* and *T. (T.) altithalamus*. In the Anguiformis Zone, all three species recorded there belong to this group.

These cases of multiple overlap of the morphospace of characters can be attributed to subjective reasons, i.e., to the presence of presumably erroneous, invalid species in the assemblage. In particular, *T. (T.) altithalamus* remains undescribed; therefore, all specimens of its type series, noted in the dissertation, can be identified as *T. (T.) titan* or *T. (T.) giganteus*. These two species also strongly overlap each other morphologically and can also be synonymous. The same applies to the species from the Anguiformis Zone: of three species recognized in Wimbledon's dissertation, only one species, *T. ("O.") anguiformis*, is valid because it was described validly under the ICZN Code. Two specimens from the type series of *T. (O.) ingens*, including the holotype, were later placed in the synonymy of *T. (O.) anguiformis* (Wimbledon and Cope, 1978). It is possible that a broad range of variability is typical of these species, whereas low variability in some of the species is simply due to the lack of material. However, in any event, this question cannot be answered without additional research. Therefore, in this paper we accept Wimbledon's interpretation of these taxa, as the most reliable basis for future studies.

The use of the morphometric analysis on the whole supports the validity of the macrosystematics of the Portlandian dorsoplanitids proposed by Wimbledon. For example, he correctly united Buckman's species and genera in two genera, *Titanites* and *Galbanites*. He also correctly separated representatives of *Titanites* of the Anguiformis Zone into a separate subgenus *Ophiolithites*, which unfortunately remained undescribed. The distribution of the subgenus *T. (Briareites)* is distinguishable. It is interesting that the rank of this subgenus was elevated to genus in Wimbledon (1984).

Individual curves of the relative ornamentation density have taxonomic significance only for species, whereas for the subgenera and genera the type of compensatory development of ornamentation is diagnostic. The use of this character allows the evaluation of similarity and disparity of the Portlandian and Middle

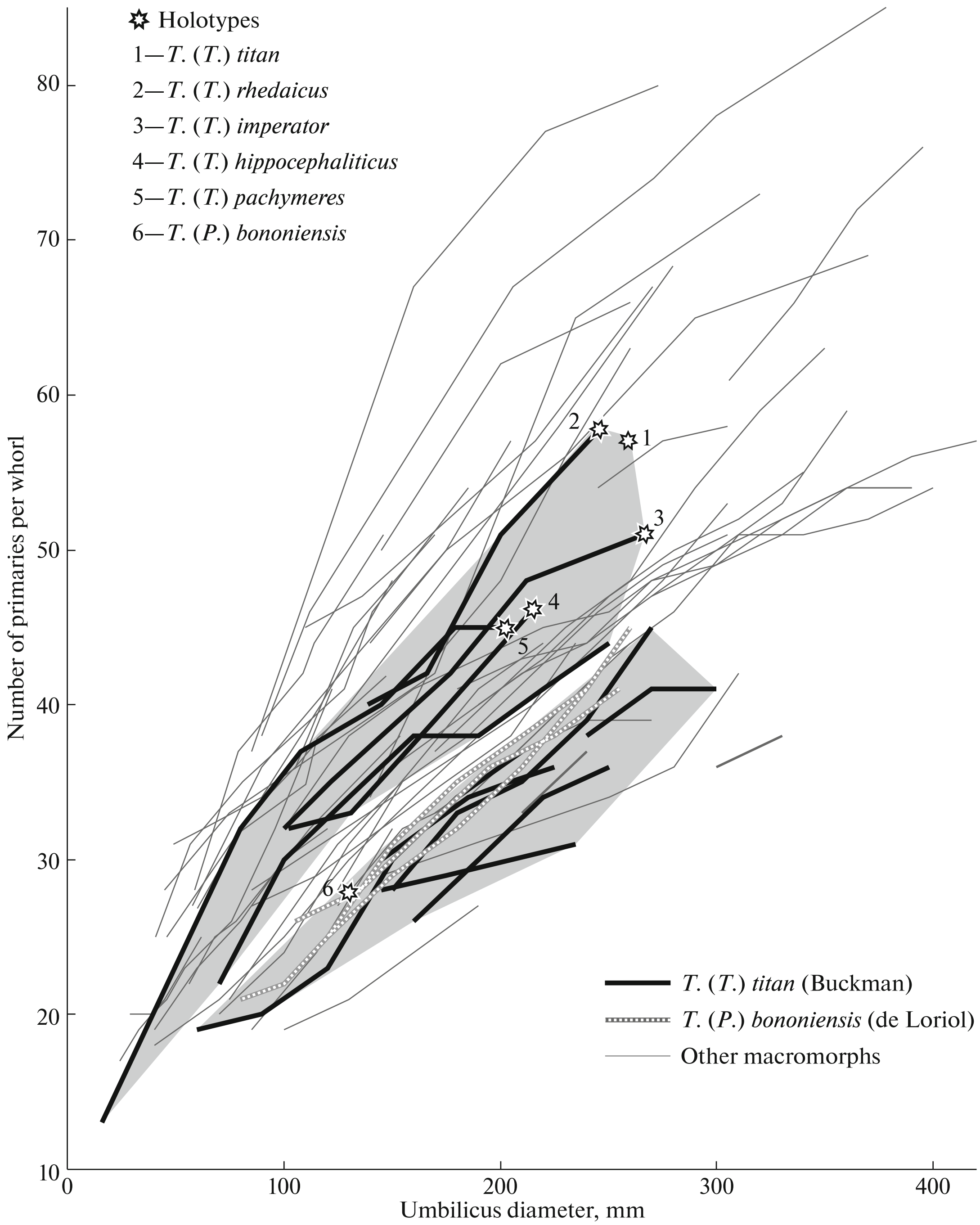


Fig. 3. The ribbing density variations in two species of Portlandian *Titanites—T. (Titanites) titan* (Buckman) and *T. bononiensis* (de Loriol). The taxonomy of the species follows Wimbledon (1974).

Volgian "giants" and objective delineation of these two groups.

MIDDLE VOLGIAN MACROMORPH DORSOPLANITINS

Volgian macromorphs reach over 900 mm in diameter (Sasonova, 1977, pp. 26–27), although the modally dominant size of the terminal shell is 450 mm. By these characters, they occupy an intermediate position between the Portlandian *Titanites* and *Galbanites*, in which the mean terminal diameter is 350 and 540 mm, respectively (Kiselev, 2017). It was previously shown that the morphogenesis of Volgian macromorphs is not fundamentally different from that of Portlandian macromorphs, and it sometimes coincides to the

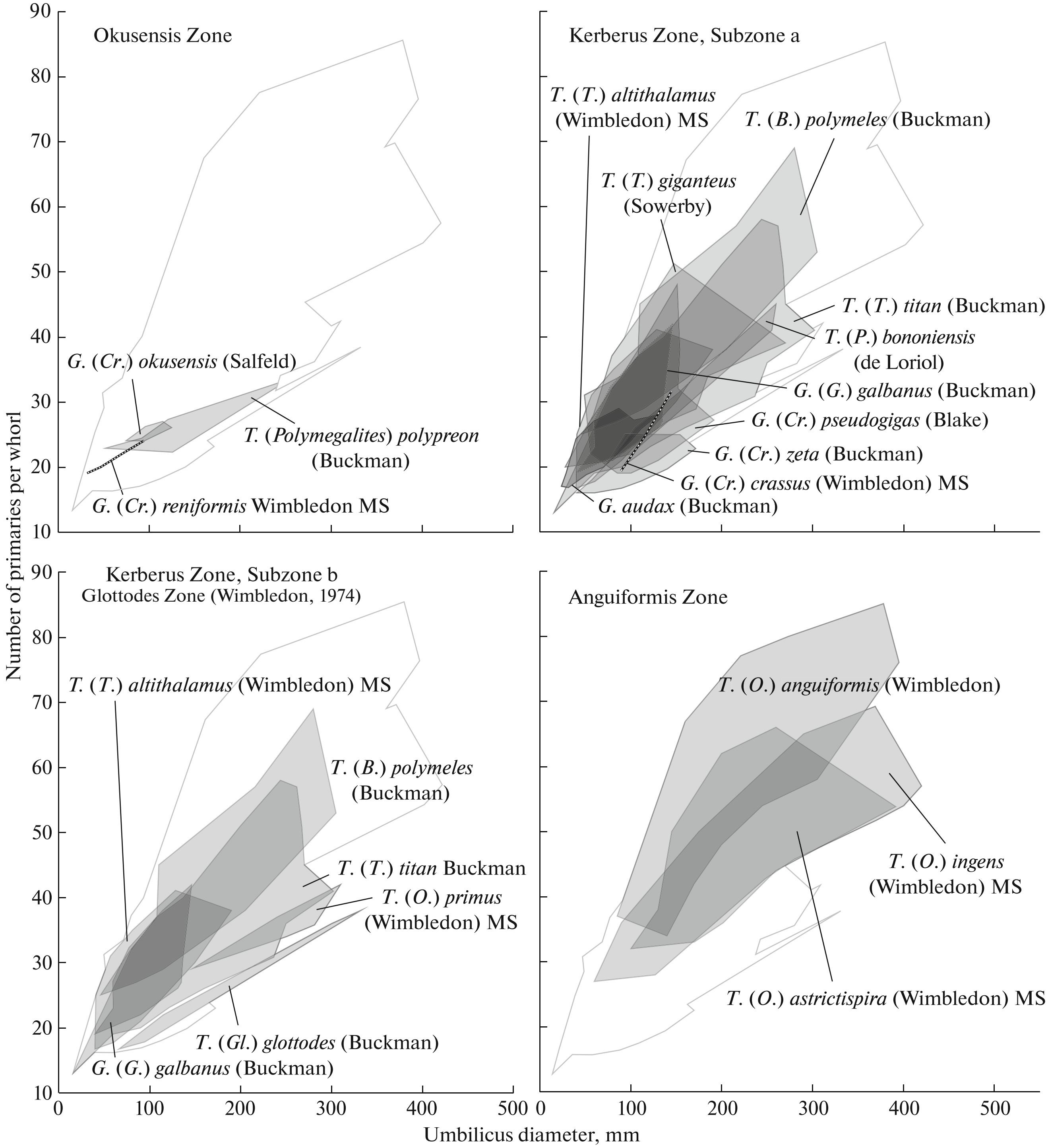


Fig. 4. The overlapping of species morphogenetic ranges in ornamentation density in macromorphic dorsoplanitins for four Portlandian zones. Based on the diagram of Fig. 1. Species composition for each zone was listed using Wimbledon (1974, 1984). The total range of all species is outlined.

smallest details, even the structure of periodization (Kiselev, 2017). This indicates their certain close relationships and taxonomic closeness. The distinction between these groups is so small that the provincial differences can only be visualized statistically. Further on, we will discuss the study of the diversity of the Volgian macromorphs using the same method that was used for the Portlandian taxa.

Traditionally, megaconchs of the Epivirgatites nikitini Zone were considered as the adult stage of the genus *Epivirgatites* and also assigned to other genera, which were shown to be minimorph taxa. Additional evidence supporting the closeness of the Volgian megaconchs and Portlandian *Titanites* were discovered after their inner whorls, which are very rarely preserved in the shells of "giants," were studied. Poor preservation of initial whorls is observed in both the Volgian and Portlandian megaconchs, which for a long time precluded adequate comparison of these groups.

It is now apparent that the inner whorls of the Volgian specimens are involute or semi-involute and are covered by fasciculate or *Kerberites*-like ornamentation, i.e., with a triplicate branching of secondary ribs at one point. Along with the fasciculate ribs, there are triplicate ribs with bimonotomous branching from two points. This type of inner whorls is found in several subgenera of *Titanites* and *Galbanites* in the Portlandian and is completely absent in the Volgian minimorphs genera, such as *Epivirgatites* and *Lomonossovella*. Of the Middle Volgian genera, it is only found in *Taimyrosphinctes*.

We used specimens of titanoid "giants" from the Epivirgatites nikitini Zone of the Middle Volgian Substage in the sections in the Yaroslavl and Ulyanovsk Povolzhye of European Russia. The bulk of material comes from the stratotype sections of the Volgian Stage near the village of Glebovo (hypostratotype) and the village of Gorodishchi (lectostratotype). For morphometric studies, we selected megaconch specimens of which nine specimens come from the Ulyanovsk sections and 31 come from the section near the village of Glebovo.

The general trend of morphogenesis of the Volgian megaconchs belongs to the same type as in the Portlandian specimens (Fig. 5): ornamentation density increases from the early whorls to the later ones owing to the continuous uncoiling of the umbilical spiral and increase in the umbilicus diameter. Both groups have similar equicostate morphotypes. In spite of this, there as number of statistical differences between them, which are certainly not random. These include the following:

(1) The early whorls at the umbilicus diameter of 20–30 mm for Volgian megaconchs have much denser ornamentation: 23–36 ribs per a whorl instead of 13–20 in the Portlandian taxa. This means that the initial conditions of morphogenesis in both groups were different. The relative density ornamentation, which is observed in the Volgian specimens at the umbilicus diameter of 30 mm, appears in Portlandian megaconchs on average at the umbilicus diameter of 100–120 mm. In the Portlandian form, the early whorls are mainly infrequently and coarsely ribbed, and only with age does this character disappear. Interestingly, this difference was first noticed by Mikhailov (1957) when he compared his new species *Kerberites mosquensis* with the Portlandian equivalents. The observation was made on the basis of one specimen, and only the author's intuition made him notice in this difference a statistically important meaning.

(2) The equicostate development of the ribbing in Volgian ammonites was less pronounced than in the Portlandian ammonites, which is observed in the smaller angles of the curves describing the ribbing density (Fig. 6a). An increase in number of ribs in Volgian ammonites with age slows down noticeably and is occasionally altogether absent, in which case the ribbing curves are subhorizonal or even horizontal. This means that, in the Volgian megaconchs, the ribbing development was *more strongly compensated* than in the Portlandian ones and sometimes was *completely compensated*. This is mainly characteristic of the Glebovo specimens and to a lesser extent of the Ulyanovsk specimens. The latter are much closer to the *Titanites* specimens of the English kind than to the Glebovo ones. This allows their assignment to one subgenus, whereas the Glebovo *Titanites* should be assigned to other subgenera.

3. At the terminal stage of morphogenesis, the Glebovo megaconchs, like the Portlandian genus *Galbanites*, belong to the group of ammonites with a *high degree of compensation* (Figs. 2, 6b), because they show a low correlation between the relative umbilicus diameter and density of ornamentation. As in Galbanites, ornamentation density in these species is on average lower than in other groups of "giants." Therefore, the adult whorls of the Glebovo megaconchs are often homeomorphically similar to *Galbanites*. Some specimens of the Glebovo megaconchs have a very high degree of compensation of ornamentation, which is manifested by the same number of ribs in several whorls. This means that, in this ammonite group, the high rates of increase of the interrib space coincide with the rates of the umbilicus growth.

This is rarely observed in the Portlandian specimens of *Titanites*. The smallest degree of increase in the interrib space in observed in the largest and latest *Titanites* of the *T. ("Ophiolithites")* and *T. (Briareites)* groups (Figs. 7, 8), and this happens during the entire individual development. Representatives of *Titanites* s. str. have a similar pattern of equicostate development, but have a somewhat higher degree of compensation. Morphogenesis of the Glebovo megaconchs includes two stages: the first stage, occupying 2/3 of morphogenesis, beginning with early whorls, is marked by a pronounced compensated development, which is observed in a steep rise of the curve describing the interrib spaces (Fig. 7), after which growth slows down, followed by an increased density of the ribbing at the second, terminal, stage of development. In megaconchs with completely preserved terminal body chamber, the final decrease in the growth rate is constantly observed (Kiselev, 2017; this paper, Fig. 8). The Portlandian *Galbanites* has the same growth patterns.

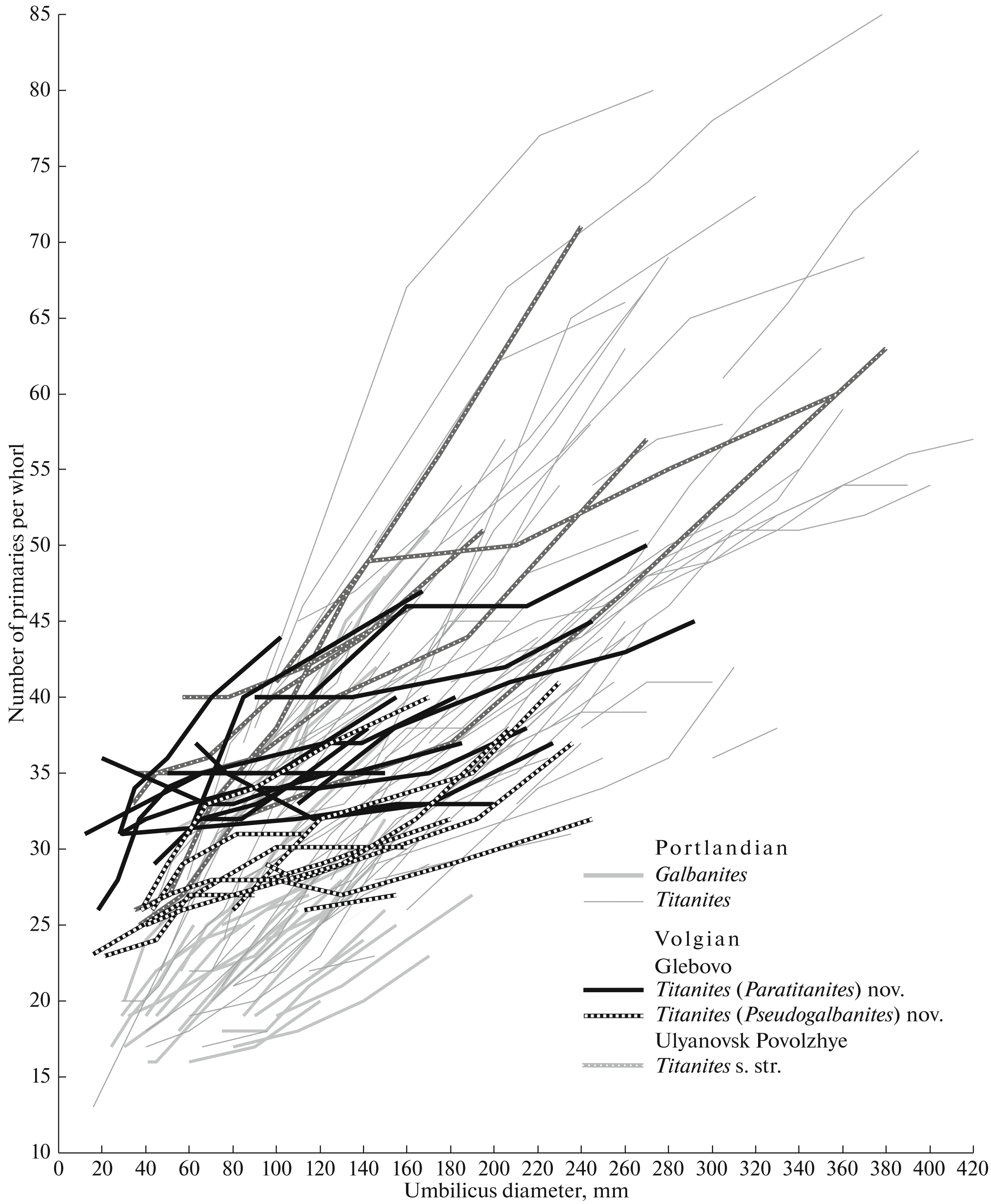


Fig. 5. Comparative morphogenesis of the ornamentation density in macromorphic dorsoplanitins from the Portlandian and Middle Volgian Substage (Nikitini Zone). The number of curves of the ribbing density corresponds to the number of measured specimens. The umbilicus diameter is used as the parameter of the morphogenetic age.

Note that, among the Volgian "giants," the highly compensated development is observed only in specimens from the section near the village of Glebovo. Macromorphs of the Ulyanovsk Povolzhye are considerably different from the Glebovo specimens in the patterns of morphogenesis and a number of other features, which allows their assignment to a separate group. Ornamentation in these specimens occurs in

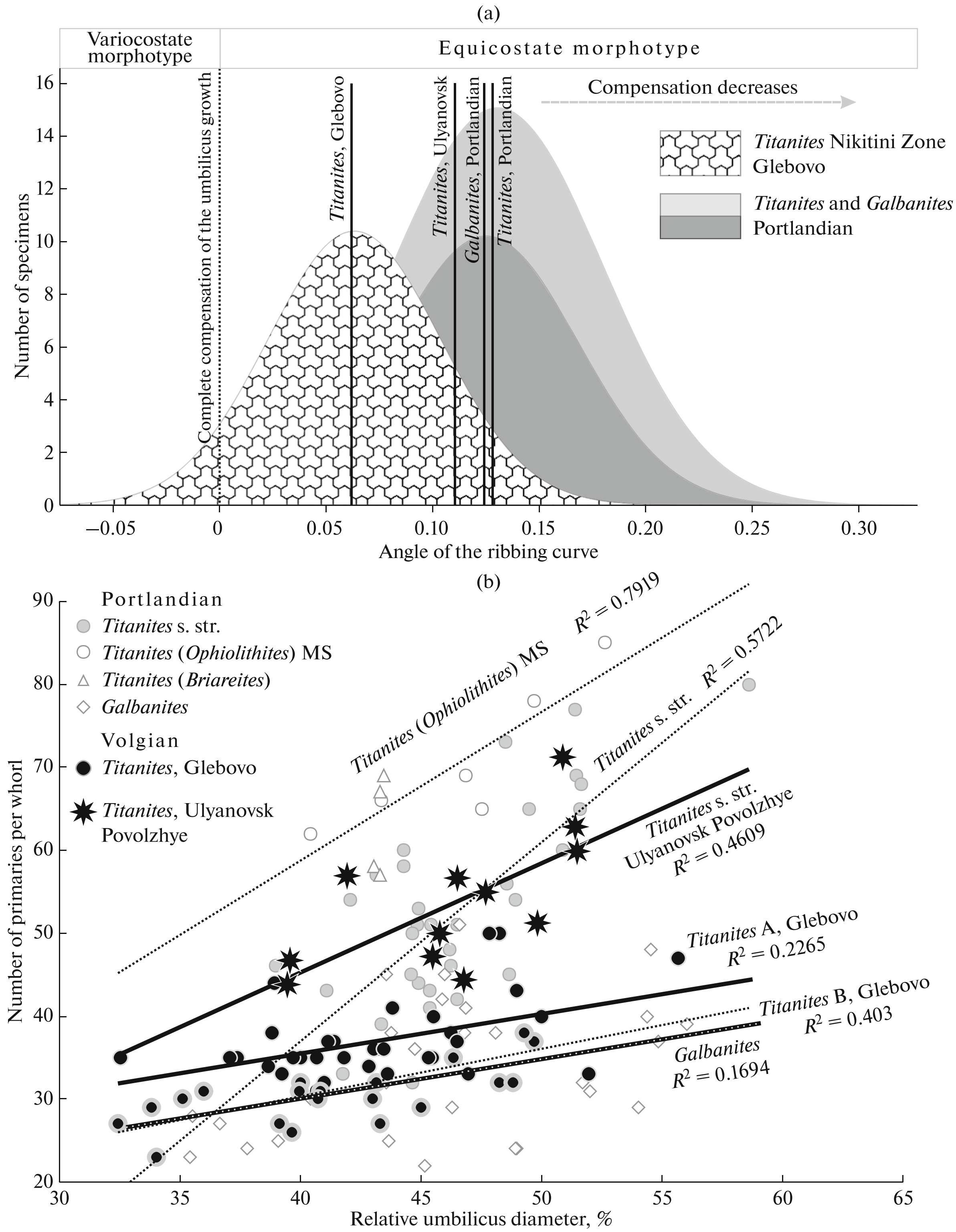


Fig. 6. Correlation of type of ornamentation density and relative umbilicus diameter for macromorphic dorsoplanitins of the Portlandian and Middle Volgian (Nikitini Zone). (a) For the entire morphogenesis by the angle of the ribbing curve (ARC), which characterizes the degree of compensation growth of the interrib space. ARC is the coefficient "a" from the formula of linear regression $y = ax + b$, which corresponds to any ribbing curve with equicostate development. With $a = 0$, the ribbing curve is completely horizontal ($y = b$) and the number of ribs is the same in all whorls. With $a = 0.5$, the number of ribs increases to the same extent as the umbilicus diameter, which corresponds to zero growth of the interrib space and lack of the compensation of growth. The theoretical curves of the normal distribution are made for Portlandian *Titanites* and *Galbanites* and *Titanites* from Glebovo. For the Ulyanovsk *Titanites*, a curve is not constructed because of the paucity of the sample. The vertical black lines show mean arithmetical values of ARC for four groups of ammonites; (b) at the terminal stage of morphogenesis. Explanations are in the text.

much the same way as in the Portlandian *Titanites* s. str. (Figs. 6a, 6b), which is characteristic of groups with a low degree of compensation, whereas in the shape of their curves of the interrib spaces they sometimes approximate (Figs. 7b, 8) *T. ("Ophiolithites")* and *T. (Briareites)*, i.e., a group with a very low degree of compensation. In other characters—shape of the whorls, low ribbing coefficient, and branching style—these specimens are little different from the English *Titanites titan* or *Titanites giganteus*, which allows their assignment to the subgenus *Titanites* s. str. Specimens with widely spaced rib, most similar to the genotype of *Titanites* s. str., are assigned here to *Titanites (T.)* cf. *titan* (Fig. 7b; Plate VI, fig. 6; Plate VIII, fig. 2; Plate IX, figs. 1, 2), whereas specimens with dense ribbing, similar to *T. (Ophiolithites)*, are designated as *Titanites (T.)* aff. *titan* (Fig. 7b; Plate VI, fig. 5; Plate VIII, fig. 3).

The Nikitini Zone near the village of Glebovo contained megaconchs of morphotypes different from those from Ulyanovsk. They were clearly subdivided into groups: macromorphs with widely spaced ribs at all stages of morphogenesis and specimens with dense ribbing. Statistically, these groups are distinctly separated by both the relative (Figs. 5, 6b) and absolute (Figs. 7, 8) ornamentation density. Adult shells of both groups have very similar morphotypes, and ribbing curves can overlap and coincide. The study of specimens with preserved inner whorls showed that both groups at the shell diameter up to 100 mm are fundamentally different in a whole assembly of characters. Therefore, there is no overlap in the ribbing frequency in the early whorls between these groups. These groups are described below as two new subgenera of *Titanites—T. (Paratitanites)* (densely ribbed group) and *T. (Pseudogalbanites)* (with widely spaced ribs).

The comparison of the Middle Volgian and Portlandian megaconchs by various characters of the suture gives additional evidence of their phylogenetic and taxonomic affinity. The comparison of the sutures of the same morphogenesis stage in specimens of approximately the same size shows complete coincidence of elements (lobes and saddles) of the first level and almost complete coincidence of the second level of complexity (Fig. 9a). The position of the whorl contact is similar in both cases—at the distal half of the saddle (from lobe V) within the lobe formed owing to the division of I_2. The proportions of the sutures are generally very similar (Fig. 9b). It is difficult to say to what extent other, smaller, differences in the suture are random or represent provincial differences. They can be found after their distributions are studied statistically.

Thus, macromorphic dorsoplanitins of the Nikitini Zone represent a single group with Portlandian representatives of *Titanites*. They included both *Titanites* s. str., which can be assigned to new species, and the provincial subgenera *T. (Paratitanites)* subgen. nov. and *T. (Pseudogalbanites)* subgen. nov., only found so far in European Russia. Both subgenera are products of an initial divergence within this group of dorsoplanitins. The Ulyanovsk *Titanites* (in the sample studied) are so similar to those of the Portlandian that they can be interpreted as migrants. This allows these finds to be used for direct comparison of the zonal succession of England and European Russia. Biogeographically, provincial subgenera are considered as vicariants of some Portlandian representatives of *Titanites* s. str. and *Galbanites*, which allows an indirect correlation of the zones of the English Portlandian with the zones of the Middle Volgian Substage.

The results of the comparative-morphological studies of the Volgian and Portlandian taxa allow their taxonomic position to be emended at the subfamilial level. The recognition of a separate subfamily Pavloviinae Spath, 1936 for the Portlandian taxa seems unnecessary. A considerable similarity of the Volgian and Portlandian ammonites, except for the subfamily Laugeitinae Lominadze et Kvantaliani, 1985 (which has intermediate characters between the families Dorsoplanitidae and Craspeditidae and can be assigned to the latter), allows them to be considered as one subfamily Dorsoplanitinae Arkell, 1950. Morphologically and biogeographically, the Middle Volgian–Ryazanian *Praechetaites*, *Chetaites*, and *Externiceras* constitute a separate group of dorsoplanitins. It is possible that this group should be assigned to a separate subfamily.

CORRELATION OF THE EPIVIRGATITES NIKITINI ZONE AND PORTLANDIAN BASED ON *Titanites*

The third, conclusive, part of this trilogy will be dealing with the detailed study of the biostratigraphy of the Middle Volgian Substage. Below, we consider only those possibilities of correlation that derived from the study of the genus *Titanites*.

The idea of the correlation of the upper part of the Middle Volgian Substage and Portlandian on the basis of ammonites of this group is not new. Without going too deep into the general history of this problem that was discussed in the first paper, we note that the direct correlation of the Epivirgatites nikitini Zone (in various interpretations) with Portlandian zones on the basis of the common taxa (species or genera) was accepted by Pavlow (1890, 1896, 1901; Pavlow and Lamplugh, 1892), Arkell (1946), Mikhailov (1957), Casey (1968, 1973; Casey and Mesezhnikov, 1986), Ivanov (Ivanov and Muravin, 1986; Ivanov et al., 1987), and the authors of this paper (Kiselev and Rogov, 2005; Rogov and Zakharov, 2009; etc.). For example, Pavlow recorded frequent occurrences of ammonites of the "giganteus" type in the Syzran, Simbirsk, and Moscow Jurassic; therefore, Pavlow showed the Perisphinctes giganteus Zone and Portlandian Stage in the scale of Russian Jurassic that he

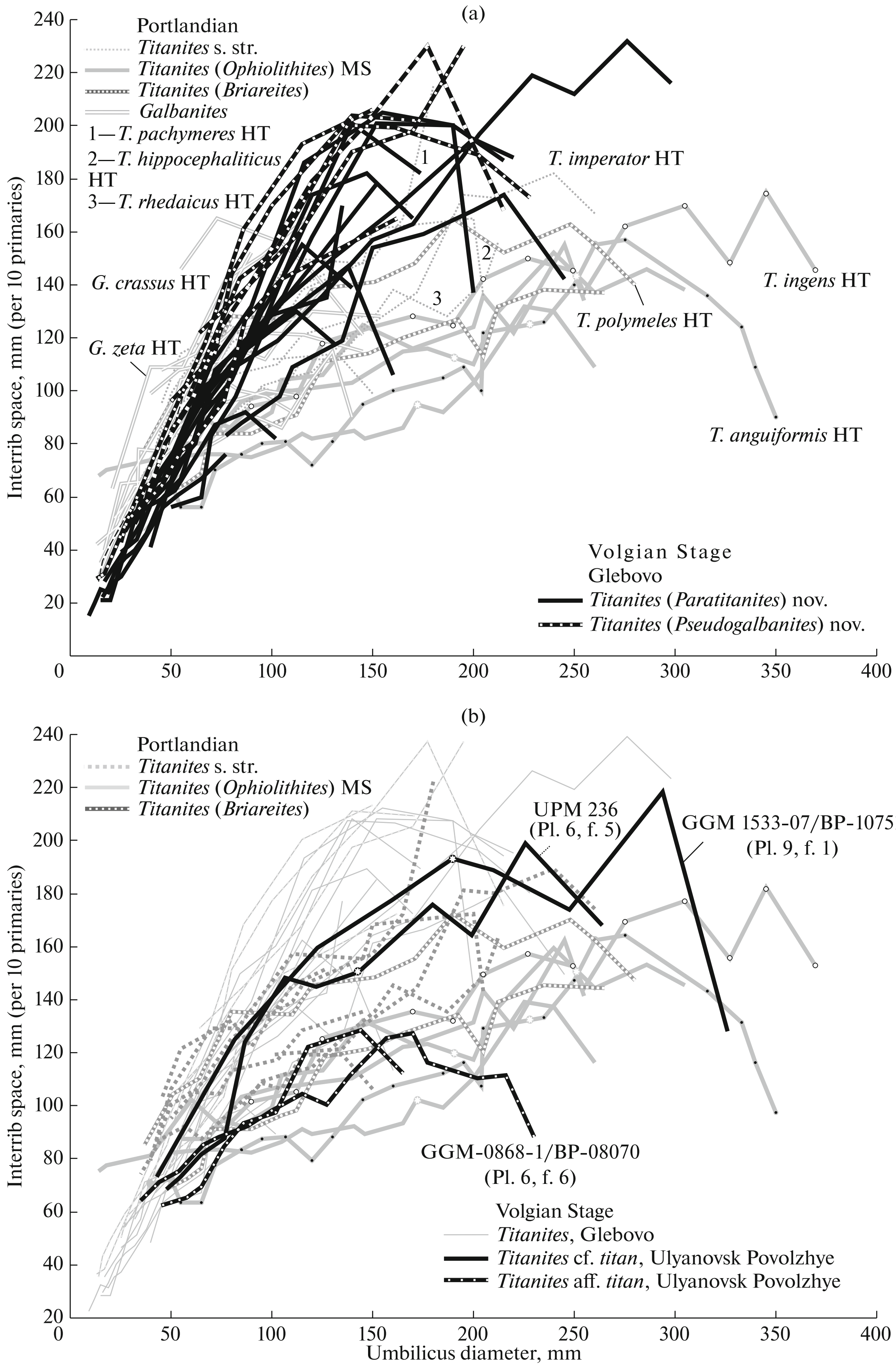

(a)
Portlandian
Titanites s. str.
Titanites (Ophiolithites) MS
Titanites (Briareites)
Galbanites
1—T. pachymeres HT
2—T. hippocephaliticus HT
3—T. rhedaicus HT
G. crassus HT
G. zeta HT
T. imperator HT
T. ingens HT
T. polymeles HT
T. anguiformis HT
Volgian Stage
Glebovo
Titanites (Paratitanites) nov.
Titanites (Pseudogalbanites) nov.
Interrib space, mm (per 10 primaries)
(b)
Portlandian
Titanites s. str.
Titanites (Ophiolithites) MS
Titanites (Briareites)
UPM 236
(Pl. 6, f. 5)
GGM 1533-07/BP-10751
(Pl. 9, f. 1)
GGM-0868-1/BP-08070
(Pl. 6, f. 6)
Volgian Stage
Titanites, Glebovo
Titanites cf. titan, Ulyanovsk Povolzhye
Titanites aff. titan, Ulyanovsk Povolzhye
Interrib space, mm (per 10 primaries)
Umbilicus diameter, mm

Fig. 7. Changes in the growth rate of interrib spaces in morphogenesis of species of macromorphic dorsoplanitins of the Portlandian and Middle Volgian Substage by the curves constructed for individual specimens. (a) Volgian (Glebovo) and Portlandian species of *Titanites* and *Galbanites*; (b) diversity of *Titanites* s. str. from the sections of Ulyanovsk Povolzhye (compared to other taxa). Reference specimens—holotypes (HT) and collection nos. for individual specimens. MS designates an unpublished species. For the specimen numbers from the village of Glebovo, see Fig. 14. GGM—Vernadsky State Geological Museum; UPM—Undory Paleontological Museum. The asterisks on specimens indicate the beginning of the body chamber.

developed (Pavlow and Lamplugh, 1892; Pavlow, 1901). Later, Arkell used the name *Titanites* to designate one of the zones of the Volgian Stage. According to Arkell (1946), the Titanites blakei Zone, approximately corresponding to the Nikitini Zone in the modern understanding, corresponded to the entire English-Bulogne Portlandian including the Gorei, Okusensis, and Giganteus zones.

Mikhailov (1957) proposed the correlation scheme of the Middle Volgian Substage and Portlandian zones and accepted the "Epivirgatites nikitini and Lomonossovella lomonossovi" zones as an equivalent only the uppermost Giganteus Zone (Fig. 10).

The subsequent changes in the stratigraphic schemes of various authors were related not only to the new ammonite occurrences, but more so to the interpretation of the Epivirgatites nikitini Zone and the index species, which led to contradictory and confusing correlation schemes.

Spath (1936) determined ammonoids similar to *Epipallasiceras ammonites* found at the base of the Portland Sand Formation as *Epivirgatites* (Rogov and Zakharov, 2009), and later, Casey (1967) on the basis of similar occurrences correlated the Nikitini Zone with the Albani Zone. This idea was widely accepted by other English authors (Cope, 1978; Wimbledon and Cope, 1978; Wimbledon, 1984; Callomon and Cope, 1995), although Casey himself after careful study of the USSR collections of Boreal ammonites rejected this point of view (Casey et al., 1977, 1988). As a result, a gap for several Portlandian zones appeared in the correlation schemes between the Nikitini Zone and Upper Volgian Substage. Some authors, e.g., Wimbledon, still maintain this view (Wimbledon, 2008).

A similarly contradictory correlation was proposed by Callomon and Birkelund (1982). In the upper part of the Middle Volgian Substage they showed two zones—Nikitini and Blakei. The former corresponds, as in Casey's scheme, to the base of the Portlandian, and the latter is placed in the middle part of the interval with the mentioned gap (Fig. 10). This model contradicts the firmly established facts of more or less synchronous occurrences of *Lomonossovella* and *Epivirgatites*, while *Lomonossovella* appears earlier, at the base of the Virgatus Zone, and disappears before the end of the Nikitini Zone; hence, the placement in the same scale of the Epivirgatites and Lomonossovella zones appears to be a clear anachronism.

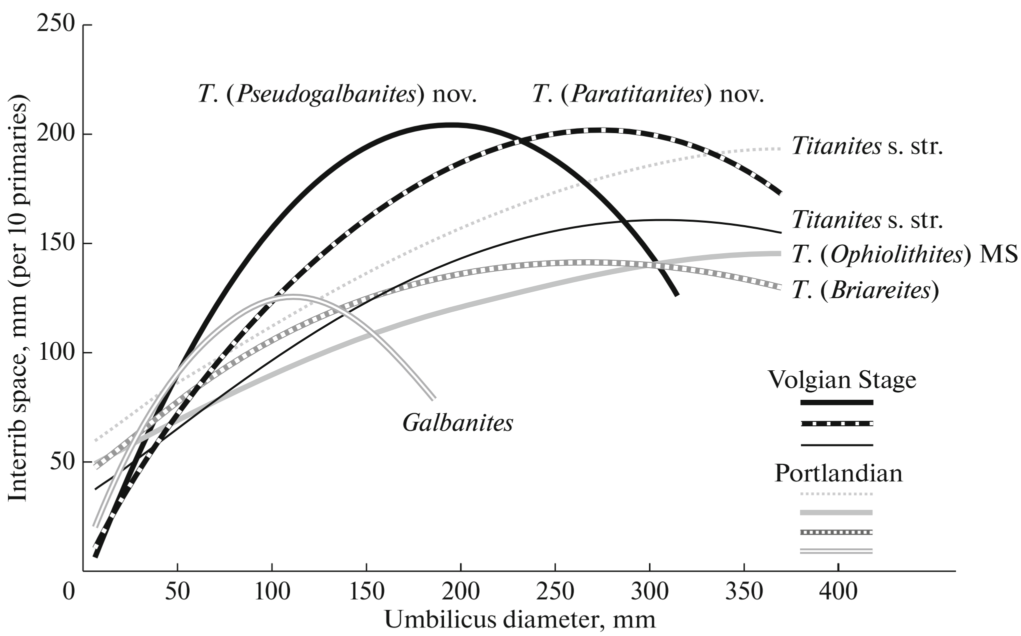


Fig. 8. Change in the growth rates of the interrib spaces in morphogenesis of various species of macromorphic dorsoplanitins from the Portlandian and Middle Volgian Substage along the trend lines. In all cases, quadratic polynomials are constructed on the basis of the data from the individual curves.

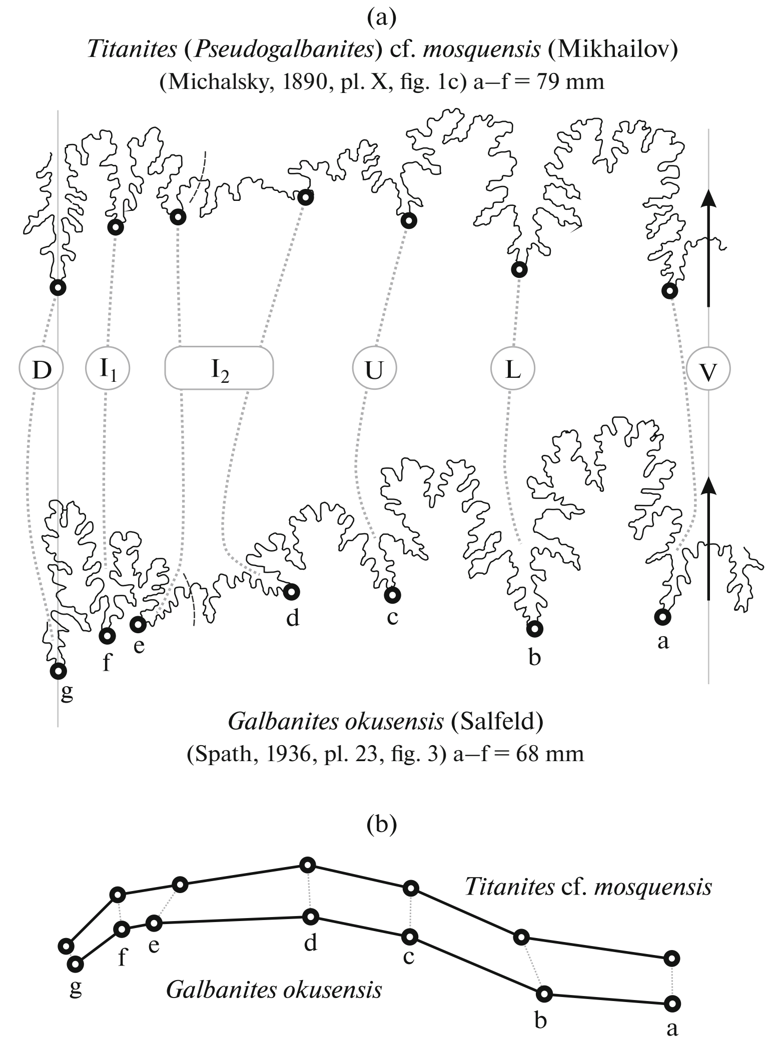


Fig. 9. Sutures of the macromorphic dorsoplanitins of the Portlandian *Galbanites okusensis* (Salfeld) and Middle Volgian Substage *Titanites (Pseudogalbanites)* cf. *mosquensis* (Mikhailov), drawn from the adult whorls of a similar size. (a) Elements of the suture; (b) comparison of proportions of the saddle widths at the critical points a–d (lower points of the main lobes).

In the scheme by Mesezhnikov (1982), the Nikitini Zone is subdivided into two subzones (Fig. 10), of which the upper Blakei Subzone correlates with the Oppressus Zone, whereas the lower Nikitini Zone correlates with the Anguiformis and Kerberus zones. The subzonal subdivision of the Nikitini Zone resembles Callomon's and Birkelund's zonal subdivision, although the zones follow each other with no hiatus, and hence no gap is accepted in the scheme between the Middle Volgian and Upper Volgian Substages.

In the study by Casey and Mesezhnikov (1986), the Nikitini Subzone and Blakei Subzone are reversed compared to the previous scheme (Fig. 10), and the lower Blakei Subzone is correlated with the Okusensis Zone and the lower half of the Kerberus Zone, whereas the Nikitini Subzone correlates with upper part of the Kerberus Zone and the Anguiformis Zone. On the whole, the range of the Nikitini Zone, in comparison with the currently recognized Portlandian zones, coincides with the range of Arkell's Titanites blakei Zone, so the Volgian Stage no longer has a large hiatus, as was supposed by some British authors.

A similar scheme of stratigraphic subdivision and correlation of this interval was published somewhat later by Mesezhnikov (1988). In that scheme, the Blakei and Nikitini subzones were correlated with the Kerberus and Anguiformis zones. Finally, Casey et al. (1988) correlated the Nikitini and Opressus zones of Povolzhye only with the Portlandian Opressus Zone.

After ammonites of the genus *Subcraspedites* were found in the sections of Middle Povolzhye in the Nikitini Zone (Kiselev and Rogov, 2005), a possible correlation of the Nikitini Zone with the Portlandian was proposed, in which the Nikitini Zone was correlated with the interval from the base of the Kerberus Zone to the lower part of the Preplicomphalus Zone. The Anguiformis and Kerberus zones were correlated with the Volgian succession to a large extent tentatively (Rogov and Zakharov, 2009), on the basis of correlation of the ammonite scales of European Russia, Subpolar Urals, and East Greenland and occurrences in these regions of the genus *Crendonites*, which in the Portlandian occurs in the interval from the Okusensis Zone to the lower part of the Kerberus Zone.

The above brief review of the correlation schemes shows that the correlations on the basis of little known or doubtful taxa when these are used as stratigraphic markers are unstable (Fig. 11). The total interval of the positions of the Nikitini Zone in the zonal scale of the Portlandian considerably exceeds the total range of the neighboring zones. Certainly, their species assemblage is much easier to recognize, and the index species are better distinguishable. It appears that the correlation of the Nikitini Zone with the Portlandian scale is based not on ammonites, but rather on ideas and presumptions. Accordingly, different intervals of the Portlandian scale are trustworthy to different extents.

The most popular among researchers, the interval for the correlation of the Nikitini Zone in the Portlandian scale embraces the upper part of the Kerberus Zone and the Anguiformis Zone. This is related, on one hand, to the frequent use of the idea by Arkell (1946, 1957) of the nearness of the Portlandian *Kerberites* and Volgian *Lomonossovella* (the appearance of *Lomonossovella* as early as the base of the Virgatus Zone was not taken into consideration, and the sutures of these genera were not compared). On the other hand, since the study by Casey (1968), it has become "fashionable" to correlate the Nikitini and Oppressus zones by the genus *Paracraspedites* Swinnerton. Interestingly, these three genera belong to minimorphs. Therefore, it is important to understand how the distribution of macromorphic dorsoplanitins corresponds to different stratigraphic schemes.

Stratigraphic Distribution of the Portlandian Macromorph Ammonites

Buckman (1909–1930) developed the most detailed biochronology of the Portlandian by ammonites. In 1927, he recognized 15 hemeras united into two ages. The index species, apart from the others, include 13 macromorph species, of which 10 belong to the titanoid group (*Titanites* and *Galbanites* in their current understanding) (Table 1). Specialists who later studied the Portlandian (Arkell, 1933; Wimbledon, 1974), considered Buckman's succession of hemeras

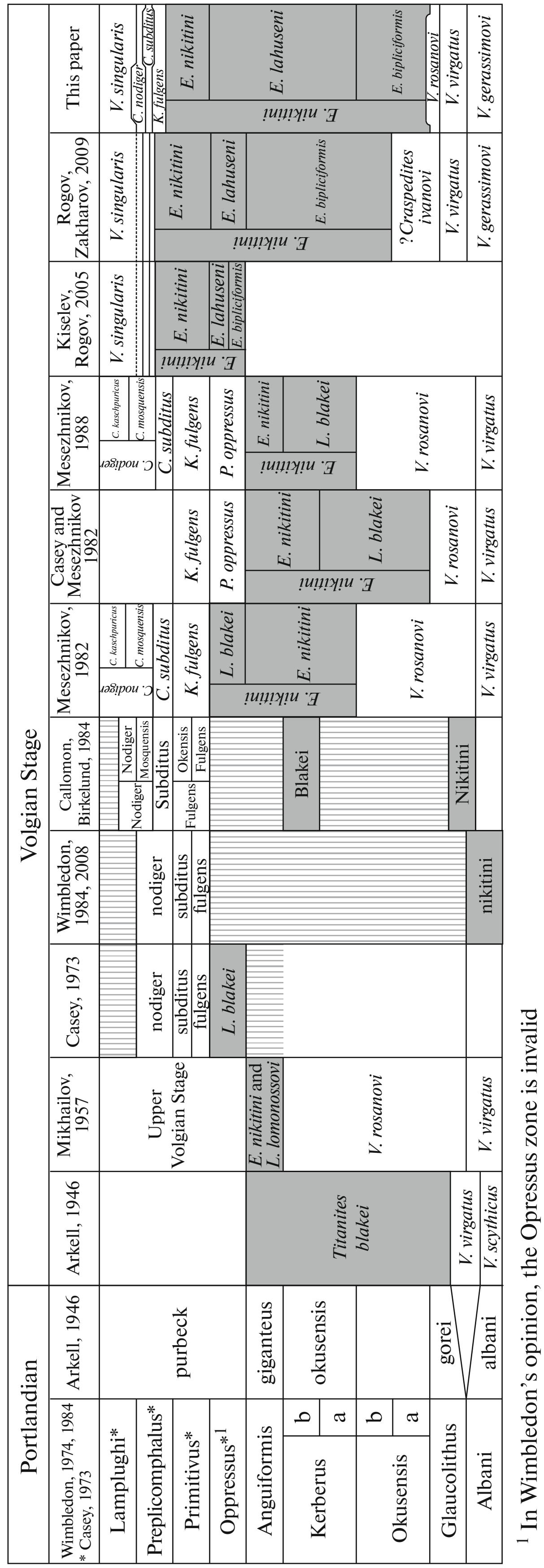


Fig. 10. Position of Epivirgatites nikitini Zone and equivalent Blakei zones in the correlation schemes by different authors (shaded gray). The correlation of the zonal scale by Arkell and Wimbledon follows Wimbledon (1974).

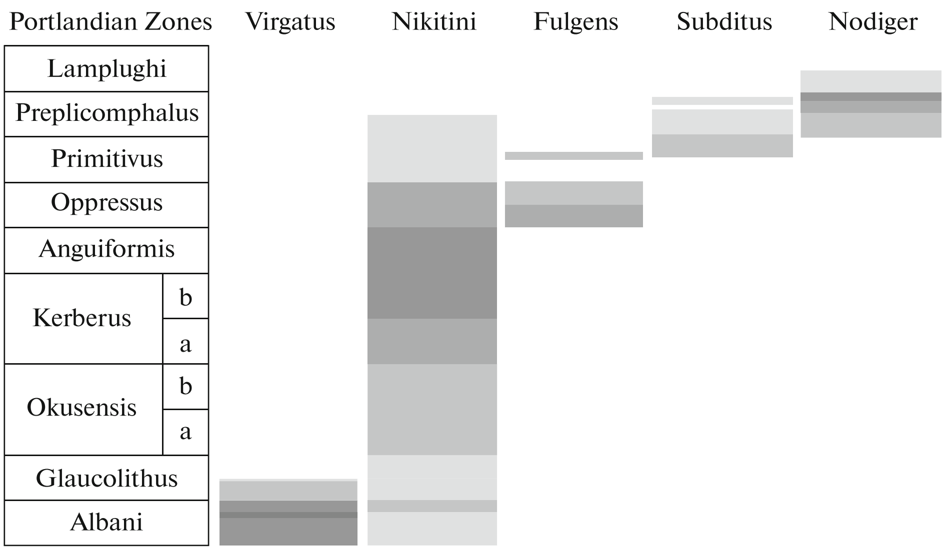


Fig. 11. Combinative stratigraphic interval of the Nikitini Zone and adjacent Middle Volgian zones and the ranges of the Portlandian zones. The scheme is based on Fig. 9 constructed by the superimposition of all correlation schemes. Shading of various intensity shows correlation frequencies for different stratigraphic levels.

as a fantasy. Despite the fact that there is no such succession of ammonites which is supposed by Buckman's hemeras in real sections, in separate intervals his, proposed chronology has a real stratigraphic context. In particular, beds corresponding to the Gigantitan age completely correspond to the currently accepted Kerberus Zone; the upper half of the hemeras (e–h) of the Behemothan age corresponds to the Okusensis Zone and the lowermost part (a–d, except for one hemera) corresponds to the currently accepted Glaucolithus Zone. The study of the succession of ammonites (nomenclatural types) collected by Buckman in the type section near Long Crendon (Buckinghamshire) (Fig. 12d) shows that the successions of individual hemerae and ammonite assemblages to some extent coincide (Fig. 13). This means that Buckman's types can serve as stratigraphic references for zonal scales, and Buckman's hemerae can represent temporal equivalents of the really existing biohorizons.

According to Wimbledon, *Titanites* and *Galbanites* are found only in three zones—Okusensis, Kerberus, and Anguiformis (Plate II, fig. 4). Their highest diversity is characteristic of the Kerberus Zone, especially its lower part (Kerberus Subzone). It is possible that the episode of gigantism and the highest diversity of titanoid dorsoplanitins was isochronous and was manifested geographically over a relatively large region, at least in the Boreal-Atlantic bioherm. This possibly was related not just to the general trend in the evolution of dorsoplanitins of this age, but also had ecological reasons. For example, Buckman tried to explain the explosive gigantism of ammonites during the Behemothan and Gigantitan ages by warming and deepening of the sea (Buckman, 1909–1930, part XXXIV, p. 20).

CORRELATION OF THE NIKITINI ZONE BY *Titanites*

Megaconchs of dorsoplanitins assigned to *Titanites* in this paper come from the Rybinsk and Ylyanovsk sections of the Epivirgatites nikitini Zone. In the section near the village of Glebovo (Fig. 12b), the Nikitini Zone is represented by 5–6 m of sand and sandstone (Kiselev et al., 2012), containing a rich assemblage of dorsoplanitids represented by both dorsoplanitins and laugeiteins. They form a succession which was a basis for recognition in the Nikitini Zone of the Epivirgatites biohorizons and subzones: Bipliciformis (lower 0.8 m), Lahuseni (about 3 m in the middle part of the zone), and Nikitini (upper 1.5 m only in the southern part of the section, near the village of Glebovo). The megaconchs of dorsoplanitins are only found in the Lahuseni Subzone in different intervals, but mainly in the upper part. Two new species are described among these taxa: *Titanites (Paratitanites) manipulocostatus* sp. nov. and *T. (Pseudogalbanites) triceps* sp. nov. Apart from these, the sample of the Glebovo megaconchs contained several forms (including those similar to *Taimyrosphinctes*), the taxonomic affinity of which remains unclear.

Both species are assigned to new subgenera; therefore, they can be used for correlation indirectly through vicariating taxa. The Volgian *Titanites* are very close equivalents of the Portlandian *Titanites*. They show the entire spectrum of characters observed in the shells of the Portlandian taxa, but with a different

Table 1. Nomenclature and stratigraphic distribution of Buckman's species of the macromorph group of Portlandian ammonites (except Glaucolithites), in the authors' interpretation and treated by Wimbledon

Buckman, 1909–1930				Wimbledon, 1974*, Wimbledon, Cope, 1978		Wimbledon, 1984	
Species holotype—HT, chorotype—ChT	Age	Hemera		Wimblendon, 1974	Zones	Genus	Subzones
Glottoptichinites glottodes HT	Gigantitan	g	Glottodes	*Titanites* (*Glottoptichinites*) *glottodes*	Glottodes* U. Kerberus	*Titanites*	Kerberus b
Glottoptichinites audax HT				*Galbanites* (*Kerberites*) *audax*	L. Kerberus	*Galbanites*	L. Kerberus b
Hippostratites hippocephaliticus HT		f	Hippocephaliticus	*Titanites* (*Titanites*) *titan*	(Kerberus)*		
Hippostratites rhedaicus HT				*Titanites* (*Titanites*) *titan*	(Kerberus)*		
Briareites polymeles HT		e	Briareites (Titanites pars.)	*Titanites* (*Briareites*) *polymeles*	Kerberus	*Briareites*	Okusensis b Kerberus a, b
Titanites titan HT		d	Titanites	*Titanites* (*Titanites*) *titan*	Kerberus	*Titanites*	Kerberus a L. Kerberus b
Gigantites giganteus ChT		c	Gigantites	*Titanites* (*Titanites*) *giganteus*	Kerberus	*Titanites*	Kerberus a L. Kerberus b
Galbanites cretarius HT				*Titanites* (*Titanites*) *giganteus*	(Kerberus)*	*Titanites*	Kerberus a L. Kerberus b
Gigantites pachymeres HT				*Titanites* (*Titanites*) *pachymeres*	(Kerberus)*		
Gigantites zeta HT				*Galbanites* (*Crassicostites*) *zeta*	L. Kerberus	*Galbanites*	Kerberus a
Galbanites galbanus HT				*Galbanites* (*Galbanites*) *galbanus*	L. Kerberus	*Galbanites*	Kerberus a, b
Trophonites trophon HT		b	Trophonites	*Titanites* (*Titanites*) *trophon*	(Kerberus)*	*Titanites*	L. Kerberus b
Galbanites mikrolobus HT				*Crendonites mikrolobus*	L. Kerberus	*Crendonites*	Okusensis b
Galbanites fasciger HT		a	Fasciger	*Titanites* (*Briareites*) *polymeles*	(Kerberus)*		
Pleuromegalites forticosta HT				*Galbanites* (*Galbanites*) *forticosta*	L. Kerberus	*Galbanites*	Kerberus a, b
Vaumegalites vau HT	Behemothan	h	Vau	*Vaumegalites vau*	Okusensis*		
Polymegalites polypreon HT		e	Polypreon	*Titanites* (*Polymegalites*) *polypreon*	Okusensis	*Titanites*	Okusensis b
Behemoth megasthenes HT		b	Megasthenes	*Titanites* (*Titanites*) *titan*	(Kerberus)*		

The Kerberus Zone in Wimbledon (1974) was designated as the Triplicatus Zone, the name Wimbledon later rejected in favor of Kerberus. Therefore, the name of the zone is in parentheses. The gray shading shows Buckman's species considered invalid by Wimbledon.

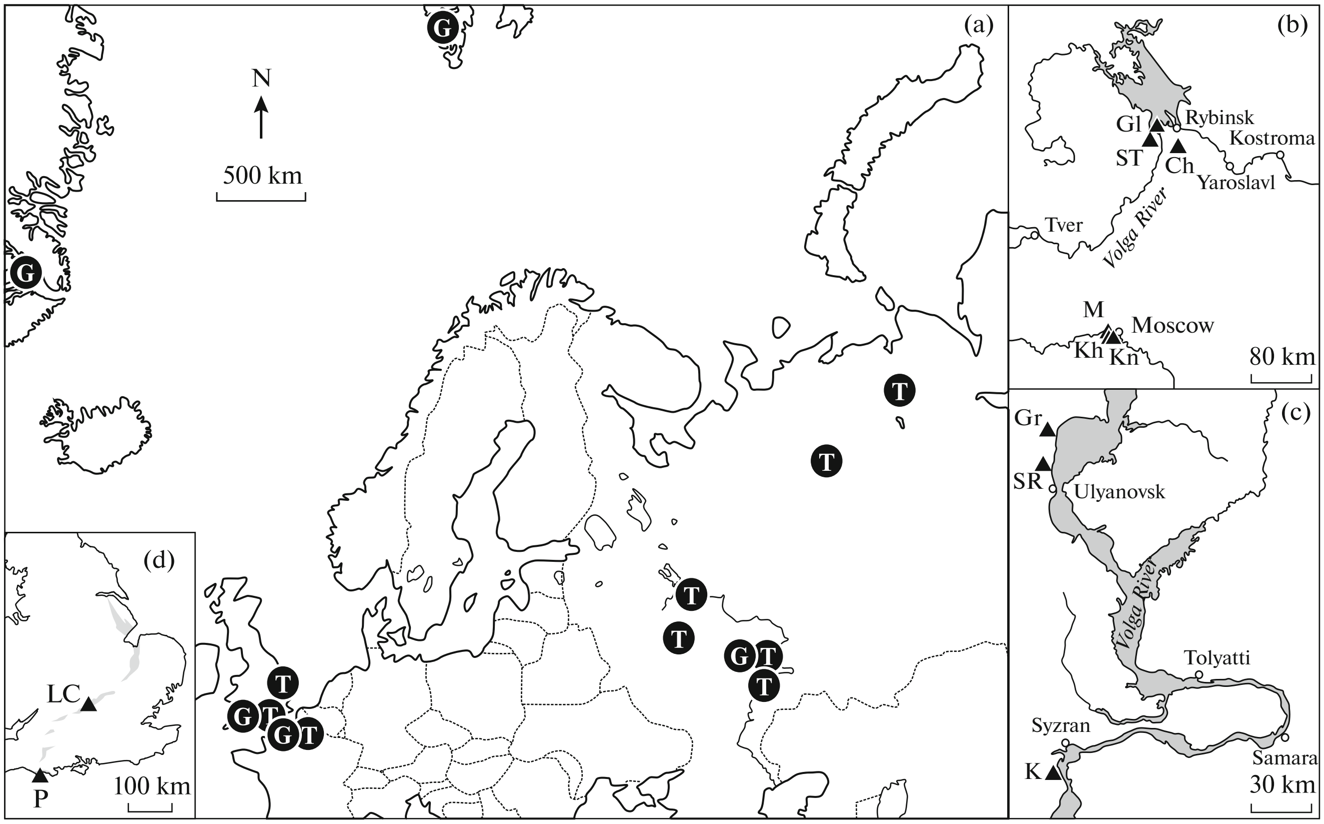


Fig. 12. Sections of the Middle Volgian Substage and Portlandian with the ammonite genera *Titanites* and *Glaucolithites*. (a) Ammonite localities (T—*Titanites*, G—*Glaucolithites*); (b–d) sections: (b) Yaroslavl and Moscow regions; (c) Middle Povolzhye; (d) England (the area of the Portlandian beds is shaded gray, after Cope et al., 1980). Gl, Glebovo; Gr, Gorodishchi; K, Kashpir; Kn, Kuntsevo; M, Mnevniki; SR, Slantsevyi Rudnik; ST, Sutka; Kh, Khoroshevo; Ch, Cheremukha; LC, Long Crendon; P, Portland.

combination at different stages of morphogenesis (see below). It is likely that the evolutionary "melting pot," in which the general phylogenetic trends were formed, was in the same geographic range of the Volgian and Portlandian dorsoplanitins. This facilitated the mixture of faunas and appearance of fine parallelisms, which considerably complicate the taxonomy of these ammonites. Supposedly this "pot" also included Arctic dorsoplanitins, in particular, the genus *Taimyrosphinctes*, in which the inner whorls are similar to those in *Titanites (Briareites)*. However, the delineation of *Taimyrosphinctes* from other macromorph genera is still difficult.

The choice of the vicariating taxa is more convenient on the basis of homeomorph twins—specimens of species which at certain growth stages are very similar to specimens of another species (see the systematic descriptions). For *T. (P.) manipulocostatus*, homeomorph twins are found in *T. (Briareites) polymeles* (Buckman) (for early stages), *T. (T.) bononiensis* (de Loriol) (for intermediate stages), and *Titanites titan* Buckman (for adult stages). All these species are restricted to the Kerberus Zone (Fig. 4, Plate III).

Homeomorphic twins *T. (Pseudogalbanites) triceps* are found in *Galbanites* of the Kerberus Zone, especially in its lower part, primarily in *G. audax* (Buckman) (see below). Thus, it is most likely that the Kerberus Zone and Lahuseni Subzone are stratigraphically equivalent.

In the section near the village of Gorodishchi (Fig. 12c), the Nikitini Zone is represented by three subzones: Bipliciformis, Lahuseni, and Nikitini (Kiselev and Rogov, 2005; Rogov and Zakharov, 2009; Rogov et al., 2015). Megaconchs of dorsoplanitins, as we observed, mainly come from the Lahuseni Subzone. However, all known reasonably well-preserved specimens included in this study were collected by other specialists without precise assignment to beds in the Nikitini Zone. All specimens are housed in the Undory Paleontological museum.

Megaconchs found in this section are quite diverse. They include medium-sized specimens (Dm = 300–400 mm), similar to *Galbanites*, and there are very large specimens (600–700 mm), with a fine ribbing (Plate VI, fig. 6; Plate VIII, fig. 3). In their morphogenesis patterns (see above) and rib morphology, large fine-ribbed specimens are most similar to *Titanites* of the Portlandian type, for example, to the holotype of *Titanites imperator* (Buckman, 1909–1930, pl. 343a, 343b), and are different from the *Titanites* from Glebovo. These taxa are similar not only in morphogenesis but also in the characters of the terminal body chamber: density and branching of the ribs, presence of random triplicate ribs (one in a whorl) amongst the paired and simple ribs. According to Wimbledon's system, *Titanites imperator* is a junior synonym of *Titanites (Titanites) titan* Buckman. Therefore, we identify these taxa as *T. titan*, but in open nomenclature.

Specimens with more widely spaced ribs (Plate VIII, fig. 2; Fig. 7) in their ornamentation density, style of ribbing, and ribbing coefficient are very similar to the types of *Titanites giganteus* (Sowerby) (Buckman, 1909–1930, pl. 256a, 256b) and *T. cretarius* (Buckman) (Buckman, 1909–1930, pl. 621), which Wimbledon considers as junior synonyms (Wimbledon and Cope, 1978).

Several specimens of the same kind are found in the collections of the Vernadsky State Geological Museum (Plate VI, fig. 5; Plate IX, fig. 1). They come from sections near Ulyanovsk, but their precise position is not recorded. Presumably, they originated from the section near the village of Slantsevyi Rudnik (Fig. 12c), also containing *Titanites* of the same state of preservation as the above museum specimens.

According to Wimbledon (1974), *Titanites titan* and *T. giganteus* are characteristic of the entire interval of the Portlandian Kerberus Zone (Table 2). This suggests that the Nikitini Zone in the Ulyanovsk sections should contain an interval corresponding to the Kerberus Zone, but it is not certain which one. It is possible that it will be different than in the Glebovo Section, because no similar taxa have been found in that section.

Thus, taking into account the new and previous data, the Epivirgatites nikitini Zone correlates at least with the middle and upper parts of the Portlandian. Previously, using the method of direct correlation, it was established (Kiselev and Rogov, 2005; Rogov and Zakharov, 2009) that the upper subzone of the Nikitini Zone is equivalent to the Primitivus Zone and possibly the lower part of the Preplicomphalus Zone of the English Scale. It is now clear that the middle subzone of the Nikitini Zone corresponds to the Kerberus (primarily) and Anguiformis zones.

The lower Bipliciformis Subzone in its position and some biostratigraphic markers should approximately correspond to the Okusensis Zone. This is supported by the occurrences in this interval of macromorphic dorsoplanitins, among which the genus *Glaucolithites* Buckman, 1922, represented by *G. gardarikensis* sp. nov. (Plate VII, fig. 1), was identified. This genus was previously known only from the Portlandian sections in the Glaucolithus Zone and lower part of the Okusensis Zone (Wimbledon, 1984), which corresponds to the basal part of the Portlandian (Table 2). The correlation of the Bipliciformis Subzone will be discussed in greater detail in the third paper of this series.

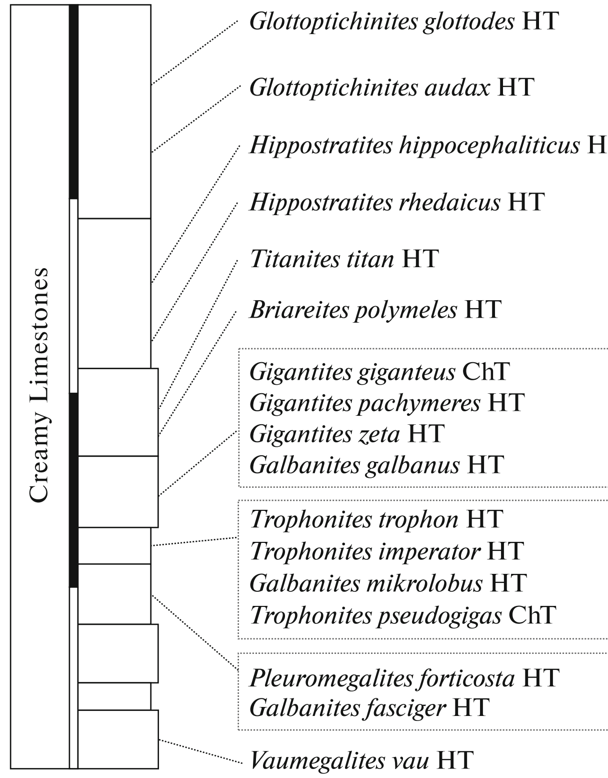


Fig. 13. Succession of nomenclatural types of ammonites recognized by Buckman in the Long Crendon Section, Buckinghamshire (after Wimbledon, 1974, fig. 16, pars). HT—holotype, ChT—chorotype.

The new data in general support the correlation of the Middle Volgian Substage and Portlandian used by Arkell (1946, etc.), Casey and Mesezhnikov (1986), and Rogov and Zakharov (2009) (Fig. 10) and diverge from the view of some British authors who up to now draw a large gap at the base of the Upper Volgian Substage in their schemes.

POSSIBLE MIGRATION PATHWAYS OF *Titanites* AND RELATED GENERA OF DORSOPLANITINS

It is likely that, at the beginning of the *Virgatus* phase, the strait connecting the Central Russian Sea with the Polish Sea ceased to exist, so only nonmarine facies are found above the Gerassimovi Subzone in the non-Carpathian part of Poland. Therefore, the only pathway of *Titanites* distribution could have been the sea via the Norwegian-Greenland Strait and after that through the shelves of the Norwegian and Barents seas, across the Mezen-Pechora system of straits to the Central Russian Sea. Unfortunately, there are not

Table 2. Distribution of dorsoplanitins in the zones of the Lower and Middle Portlandian after (1) Wimbledon, 1974; (2) Wimbledon and Cope, 1978; (3) Wimbledon, 1984

Taxa	Portlandian zones (after Wimbledon, 1974; Wimbledon, 1984, with additions)						
	Glaucolithus	Okusensis		Kerberus		Anguiformis	Oppressus
		Okusensis a	Okusensis b	Kerberus	Glottodes		
MACROMORPHS							
Glaucolithites (*Glaucolithites*) *glaucolithus* Buckman	1, 2, 3						
Glaucolithites (*Glaucolithites*) *polygyralis* (Buckman)	1, 2	?	3				
Glaucolithites (*Glaucolithites*) cf. *polygyralis* (Buckman)		3					
Glaucolithites (*Glaucolithites*) *chicksgrovensis* Wimbledon, MS	1						
Glaucolithites (*Glaucolithites*) *caementarius* (Buckman)	1, 2, 3						
Glaucolithites (*Glaucolithites*) *aguator* (Buckman)	1, 2, 3						
Glaucolithites (*Glaucolithites*) cf. *aguator* (Buckman)		3					
Glaucolithites (*Behemoth*) *lapideus* (Buckman)	1	3	3				
Glaucolithites spp.		1					
Hydrostratites bifurcus Buckman	1						
Lydistratites lyditicus (Buckman)	1	3					
Lydistratites biformis Buckman		3					
Lydistratites cf. *biformis* Buckman	3						
Galbanites (*Crassicostites*)* *okusensis* (Salfeld)		1, 2	1, 2, 3				
Galbanites (*Crassicostites*)* *reniformis* Wimbledon, MS		1	1				
Galbanites (*Crassicostites*)* *pseudogigas* (Blake)				1, 2, 3			
Galbanites (*Crassicostites*)* *zeta* (Buckman)				1, 2, 3			
Galbanites (*Crassicostites*)* *crassus* Wimbledon, MS				1			
Galbanites (*Galbanites*) *galbanus* Buckman				1, 2, 3	1, 3		
Galbanites (*Galbanites*) *forticosta* (Buckman)			2	1, 2, 3	3		
Galbanites (*Galbanites*) *broadcroftensis* Wimbledon, MS				1			
Galbanites audax (Buckman)				1, 2, 3	3		
Galbanites vernensis Wimbledon, MS				1			
Titanites (*Polymegalites*) *polypreon* (Buckman)		1	1, 2, 3	2			
Titanites (*Polymegalites*) *pinguis* Wimbledon, MS		1	1				
Titanites (*Briareites*) *transitorius* (Spath)		1	1				
Titanites (*Briareites*) *polymeles* (Buckman)			2, 3	1, 2, 3	1, 2, 3		
Titanites (*Titanites*) *titan* Buckman				1, 2, 3	1, 2, 3		
Titanites (*Titanites*) *giganteus* (Buckman)				1, 2, 3	2, 3		
Titanites (*Titanites*) *altithalamus* Wimbledon, MS				1	1		
Titanites (*Titanites*) *trophon* (Buckman)				1			
Titanites (*Titanites*) cf. *trophon* (Buckman)					3		

Table 2. (Contd.)

Taxa	Portlandian zones (after Wimbledon, 1974; Wimbledon, 1984, with additions)						
		Okusensis		Kerberus			
	Glaucolithus	Okusensis a	Okusensis b	Kerberus	Glottodes	Anguiformis	Oppressus
Titanites (*Portlandia*)* *bononiensis* (de Loriol)				1, 2, 3	2		
Titanites (*Glottoptychinites*) *glottodes* (Buckman)					1, 2, 3		
Titanites (*Ophiolithites*)* *primus* Wimbledon, MS					1		
Titanites (*Ophiolithites*)* *anguiformis* Wimbledon						1, 2, 3	2
Titanites (*Ophiolithites*)* *astrictispira* Wimbledon, MS						1	
Titanites (*Ophiolithites*)* *ingens* Wimbledon, MS						1	
Titanites spp. A						2	2
Titanites spp. B			1				
Vaumegalites vau Buckman		1, 3	1, 2				
MINIMORPHS							
Paracraspedites opressus Casey						1	3
Crendonites (*Crendonites*) cf. *pregorei* Spath		3					
Crendonites (*Crendonites*) *gorei* (Salfeld)		1	1, 3	3			
Crendonites (*Crendonites*) *leptolobatus* Buckman			1, 2	1, 2			
Crendonites (*Fittonia*)* *mikroloba* (Buckman)			3	1, 2, 3			
Kerberites kerberus Buckman			3	1, 2, 3			
Kerberites spp.		1					
Total: Species (in the manuscript and in publications)	9	16	15	19	11	5	3
Species (in publications)	5	9	11	14	9	2	3
Macromorphs (in the manuscript and in publications)	9	13	11	15	11	4	2
Macromorphs (in publications)	5	8	7	10	9	2	2

The taxonomy of species of genera follows Wimbledon (1974) with small additions. Gray shading shows the citation in the manuscript; black shading indicates citations in publications. MS—unpublished taxon, described in the manuscript. Asterisks indicate subgeneric names proposed only in the manuscript (Wimbledon, 1974).

much available data on the presence of *Titanites* in this way. The occasional occurrences of *Glaucolithites* are found in East Greenland (Spath, 1936) and on Spitsbergen (Rogov, 2010) (Fig. 12a), but geochronologically younger ammonites of the Portlandian type are not found in these regions. Only few Volgian ammonites are found in the borehole cores in the shelf of the Norwegian and Barents seas, and all specimens currently known are represented by small-sized taxa mostly assigned to the microconchs of *Dorsoplanites*. In this context, very interesting is the discovery of a fragment of a *Titanites* megaconch (Plate IX, fig. 3) by A.V. Zhuravsky in a bolder from the Bolzhaya Zemlya tundra in 1903, soon after assigned by Karakash (1904) to the genus *Perisphinctes*. Occurrences of "*Epivirgatites* cf. *lahuseni*" in an outcrop near the village of Porozhsk (Izhma River) are mentioned, but the only ammonite illustrated from this locality (Saks et al., 1976, pl. 25, fig. 4) does not belong to the genus *Epivirgatites*, and it also represents a megaconch similar to some of the ammonites from the Glebovo specimens from the Lahuseni Zone. These occurrences (Fig. 12a) provide additional evidence of migration of

Table 3. Diversity of macromorph dorsoplanitins of the Kerberus and Nikitini zones

Taxa	Zone Kerberus	Zone Nikitini, Subzone Lahuseni
Titanites s. str. Buckman, 1921 (=*Gigantites* Buckman, 1921; *Trophonites* Buckman, 1922; *Hippostratites* Buckman, 1924)	4 (2)	2
T. (*Glottoptychinites*) (Buckman, 1925)	1	–
T. (*Briareites*) (Buckman, 1921)	1	–
T. (*Portlandia*) Wimbledon, 1974 MS	1	–
T. (*Paratitanites*) subgen. nov.	–	1
T. (*Pseudogalbanites*) subgen. nov.	–	2
Galbanites Buckman, 1921	9 (4)	–
Total	15 (9)	5

Figures show the number of species. For the Portlandian, the number of species is determined after Wimbledon (1974) and Wimbledon (1984) (in parentheses). Black shading indicates a taxon used for direct correlations; gray shading indicates a taxon used for indirect correlations by taxa with homeomorphic twins (light gray for *T. (Paratitanites)* and dark gray for *T. (Pseudogalbanites)*).

Portlandian ammonites to the Central Russian Sea through the Norway-Greenland Strait.

SYSTEMATIC PALEONTOLOGY

FAMILY DORSOPLANITIDAE ARKELL, 1950

SUBFAMILY DORSOPLANITINAE ARKELL, 1950

Genus *Titanites* Buckman, 1921

T y p e s p e c i e s. *Titanites titan* Buckman, 1921.

D i a g n o s i s. Macromorphs with a terminal diameter of 450–900 mm. Inner whorls involute or semiinvolute; adult whorls evolute or semievolute, with wide, isometric or high cross section rounded or oval-rounded shape. Terminal uncoiling of spiral gradual, beginning on penultimate whorl or at beginning of the last whorl.

Ornamentation equicostate. In early whorls ribs in different subgenera different (Table 4): triplicate fasciculate (*Kerberites*-like); triplicate, alternating with intercalated ribs; triplicate, becoming bimonotomous; biplicate, alternating with intercalated ribs; biplicate. Adult whorls and terminal body chamber possessing biplicate and simple ribs, often alternating with intercalated, less commonly triplicate ribs. Near terminal peristome ribs usually becoming more densely spaced. At this stage, the number of simple ribs compared to biplicate ribs gradually increases and can become dominant. Phase of final increased rib density from ½ to ¼ of whorl.

Constrictions absent or very rarely present.

S u b g e n e r i c c o m p o s i t i o n: *Titanites* s. str. (3–4 species); *Briareites* Buckman, 1921 (2 species); *Glottoptychinites* Buckman, 1923 (1 species); *Polymegalites* Buckman, 1925 (1 species); *Titanites* subgen A (= *T. (Portlandia)* Wimbledon, 1974 MS) (1 species); *Titanites* subgen B (= *T. (Ophiolithites*) Wimbledon, 1974 MS) (1–2 species); *Paratitanites* subgen. nov. (1 species); *Pseudogalbanites* subgen. nov. (2 species).

C o m p a r i s o n. *Titanites* differs from the macromorph, morphologically and stratigraphically similar genus *Galbanites* Buckman, 1922 in the large terminal diameter of the shell, both statistically mean and maximum, and also in denser and finer ribbing. These differences are difficult to consider as essential because the marginal morphologies in both genera can often be very similar to one another. As a consequence, the genera are separated mainly statistically. It is possible that the genus *Galbanites* should be considered as a subgenus of *Titanites*.

The stratigraphically preceding macromorph genus *Glaucolithites* Buckman, 1922 is distinguished from the genus under description by the presence of clear and relatively frequent constrictions at all stages of morphogenesis, uniform ribbing composed mainly of the biplicate ribs, the smaller shell, and noticeably more evolute early and adult whorls.

R e m a r k s. The generic and subgeneric classifications of the Portlandian and Middle Volgian macromorphic dorsoplanitins are based on the analysis of the assembly of major taxonomic characters (Table 4), allowing morphological delineation of the taxa. The boundaries between the taxa by isolated, most variable characters are indistinct, which reduces the stability of the system used. The relationships between the subgenus *Titanites* and genera *Galbanites* and *Glaucolithites* are to a large extent unresolved. For example, it is usually considered that Portlandian taxa are more related to one another than to the Volgian taxa and vice versa. The complex analysis of the similarity and disparity

Table 4. Complex combinations of the taxonomically significant characters and their modes in the genera of Portlandian and Volgian (Nikitini Zone) macromorphic dorsoplanitins

Shell characters / Morphogenetic stages / Taxa			*Titanites*																		*Galbanites*			*Glaucolithites*		
			Titanites s. str			*Briareites*			"*Ophiolithites*"			"*Portlandia*"			*Paratitanites*			*Pseudogalbanites*								
			I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
Ribbing and branching types		Striated ("growth lines")						●			●															
		Simple	●	●	●●			●	●	●●	●●			●			●						●	●	●	●●
		Intercalated	●	●	●	●	●	●	●	●	●	●	●	●			●	●	●	●●	●	●	●●		●	●
		Biplicate (bipartite)	●●	●●	●●		●●	●●	●●	●●	●●	●●	●●	●●	●	●	●●	●	●●	●●	●●	●●	●●	●●	●●	●●
	Triplicate (tripartite)	Fasciculate (Kerberites-like)	●			●●	●					●	●●	●	●●	●●	●	●●	●●	●	●●	●	●			
		Bimonotomous				●	●						●		●	●●		●●	●		●	●	●			●
		Bidichotomous																							●	
Ornamentation compensation		Very weak						●			●															
		Weak		●	●		●			●			●	●								●			●	●
		Strong														●	●		●	●			●			
Density of sculpture		Low: (10–20 ribs per whorl)	●			●			●			●									●	●		●		
		High: (25–50 ribs per whorl)		●	●		●	●		●			●	●	●	●	●	●	●	●			●	●	●	●
		Very high: 50 ribs per whorl						●			●															
Terminal shell diameter		Small: <350 mm															●			●			●●			●
		Medium: 350–550 mm			●			●						●●			●●			●●			●			●●
		Large: >550 mm			●●			●●			●●			●			●			●						
Whorl cross section		Low, WH/WW < 1		●●	●●		●	●●		●●	●●		●●	●●	●	●		●●	●●	●●		●●	●●		●●	●●
		Isometric WH/WW = 1		●	●	●	●●	●		●	●		●	●	●●	●●	●			●			●		●	●
		High WH/WW > 1				●●	●								●	●	●●									
Coiling type		With moderately expanding spiral		●									●			●			●			●				
		With slowly expanding spiral		●			●			●															●	
Constrictions		Weak or absent		●			●			●			●			●			●			●				
		Well developed in all whorls																							●	

Morphogenetic (ontogenetic) stages (after Kiselev, 2017): I—minimal ornamentation density (juvenile); II—subterminal (mature); III—terminal (late mature). For some characters, the number of circles in cells describes the frequency of occurrence: one circle—rarely or moderately; two circles—frequently.

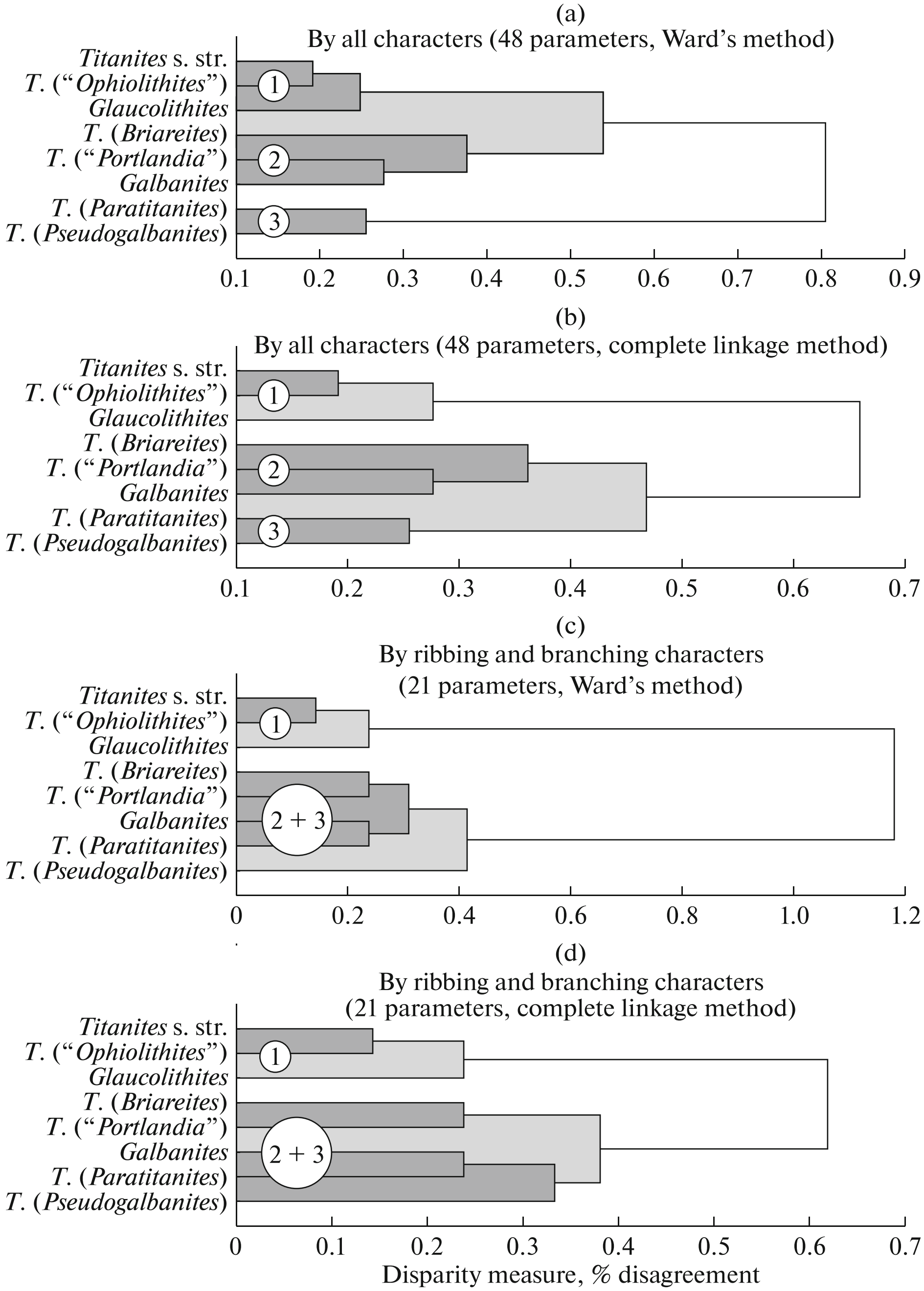
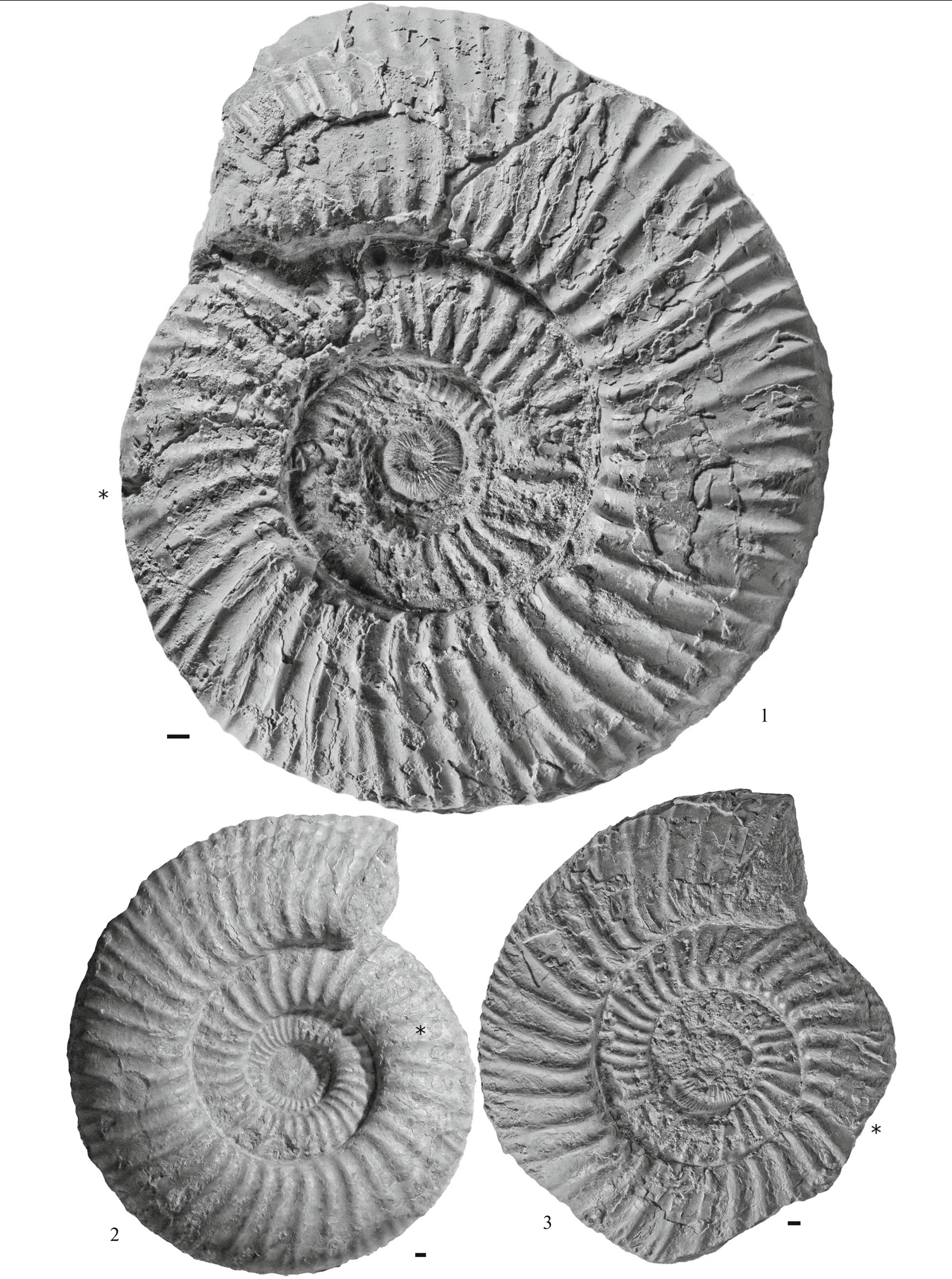


Fig. 14. Cluster analysis of macromorphic dorsoplanitin taxa. (a, b) By all taxonomic characters; (c, d) by types of ribbing and rib branching type. The measure of similarity/disparity matrix is based on Plate IV. The disparity measure in all cases is based on percent disagreement. The clustering was based on various methods: Figs. 14a, 14c—Ward's method; Figs. 14b, 14d—complete linkage method. Shading and numbers show groups of taxa. Explanations are in the text.

Plate I. (1–3) *Titanites (Paratitanites) manipulocostatus* Kiselev sp. nov., Rybinsk District, village of Glebovo, middle substage of the Volgian Stage, Epivirgatites nikitini Zone, Epivirgatites lahuseni Biohorizon: (1) megaconch-tachygeront of tachymorph type, holotype, specimen YarGPU no. GL-1, Dm = 360 mm; (2) megaconch-bradygerontic of normomorph type, paratype, specimen YarGPU no. GL-4, Dm = 348 mm; (3) megaconch-tachygeront of bradymorphic type, specimen no. DB-3, Dm = 488 mm. Here and in Plates II–IX, the scale bar is 1 cm. Abbreviations: GGM—Vernadsky State Geological Museum (Moscow); UPM—Undory Paleontological Museum; YarGPU—Geological Museum of the Yarosavl State Pedagogical University; DB—D. Buev's private collection (Moscow); B.M.—Natural History Museum (London); NMW—National Museum of Wales; GSM—British Geological Survey Museum.

Plate I



allows the recognition of justified groups and criteria of their congregation (Fig. 14).

Three groups of macromorph taxa can be recognized using cluster analysis for the entire assembly of characters (Figs. 14a, 14b):

Group 1 (Portlandian) including the subgenera *Titanites* s. str. and *T. ("Ophiolithites")* and the genus *Glaucolithites*;

Group 2 (Portlandian) uniting the subgenera *Titanites (Briareites)* and *T. ("Portlandia")* and the genus *Galbanites*;

Group 3 (Middle Volgian) composed of the subgenera *Titanites (Paratitanites)* and *T. (Pseudogalbanites)*.

To what extent are these groups discrete and what are their relationships? The first group is very clearly separated from the other with any combinations of the cluster analysis parameters (distance measure and method of clustering), both by the entire assemblage of characters (Figs. 14a, 14b) and separately by the ribbing characters (Figs. 14c, 14d). The taxa assigned to this group do not overlap stratigraphically and they chronologically replace one another in the succession *Glaucolithites*–*Titanites* s. str.–*T. ("Ophiolithites")* (Table 2). The origin of *T. ("Ophiolithites")* from *Titanites* s. str. is certain, while the problem of the origin of *Titanites* s. str. from *Glaucolithites* needs a separate study.

The second and third groups are recognized as separate units only by the entire assembly of characters, while by the ribbing characters they represent a relatively uniform group. These ammonites are only slightly different in the rib furcation style. Therefore, different clustering methods show that both groups are considerably more different in the rib furcation style from the first group than from each other (Figs. 14c, 14d). Of seven clustering methods used in this study, in six cases, i.e., in 86% of cases, the second and third groups are joined together by the ribbing characters (only) in one cluster. This similarity can be equally explained by close phylogenetic similarity and parallelism.

In more complex analysis (Figs. 14a, 14b), the disparity between the second and third groups can be strikingly different: the second group is joined either with the first group (Fig. 14a) or with the third one (Fig. 14b). The first result was obtained in five clustering methods, i.e., in 71% of cases. This result clearly delineates the Volgian taxa (from Glebovo) from the Portlandian taxa, which is primarily supported by the different style of the ornamentation compensation and different proportions of the ribbing density at different stages of morphogenesis (see above). The second result was obtained in only one case (14%). The second result is supported by the considerable similarity of the Portlandian (group 2) and Volgian (group 3) taxa in other characters.

The percentage of clustering cases in using different methods can be to some extent considered as the probability of nonrandomness of various groups. In this case, the situation in Fig. 14a, repeated in 71% cases, should to a large extent reflect the phylogenetic relationships between the considered taxa. Thus, the instability of the group of the Portlandian and Volgian taxa using the entire assembly of characters suggests a considerably genetic and taxonomic communality of these groups. Their phylogenetic relationships at a more detailed level can be emended by studying the morphogenesis of their sutures. Unfortunately, no such studies have been performed, as they are difficult because of poor preservation of both Volgian and Portlandian specimens.

O c c u r r e n c e. Middle part of the Portlandian of England and France (Boulogne), Okusensis, Kerberus, and Anguiformis zones; middle substage of the Volgian Stage, Epivirgatites nikitini Zone of European Russia, Epivirgatites lahuseni Subzone.

Subgenus *Paratitanites* Kiselev subgen. nov.

Epivirgatites (pars): Ivanov and Muravin in Ivanov et al., 1987, pp. 50–51; Muravin, 1989, p. 14; Mitta, 1993, p. 104; Mitta, 1994, p. 30.

Titanites subgen nov. A: Kiselev, 2017, p. 111.

T y p e s p e c i e s. *Titanites manipulocostatus* Kiselev sp. nov., Epivirgatites nikitini Zone of the middle substage of the Volgian Stage, village of Glebovo.

D i a g n o s i s. Macromorphs reaching stage of megaconch with terminal diameter up to 600 mm. Inner whorls semievolute, with high (WH > WW) or isometric (WH = WW) proportions. Whorl cross section subtrapezoid. Adult whorls evolute or semievolute, with wide (WW > WH) or isometric (WH = WW) proportions of rounded cross section.

Ornamentation of highly compensated type. Early whorls possess ribs with triplicate fascinated branching and biplicate and intercalated ribs; adult whorls and terminal body chamber are characterized biplicate and simple ribs (Plate IV). Constrictions absent.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. In some characters, this subgenus is similar to several subgenera of Portlandian *Titanites*: with *T. (Briareites)* in the shell proportions and branching types of ribs on the inner whorls (only);

Plate II. (1–3) *Titanites (Paratitanites) manipulocostatus* Kiselev sp. nov., Rybinsk district, village of Glebovo, middle substage of the Volgian Stage, Epivirgatites nikitini Zone, Epivirgatites lahuseni Biohorizon: (1) megaconch-bradygeront of bradymorphic type, specimen no. DB-1, Dm = 547 mm; (2, 3) paratype, specimen YarGPU no. GL-78, inner whorls megaconch (Dm ~ 450 mm); (4) *Titanites bononiensis* (de Loriol), specimen NMW77.30G.96, England, Portland Island, Basal Shell Bed, Broadcroft, Portlandian, Kerberus Zone, Dm = 340 mm.

Plate II

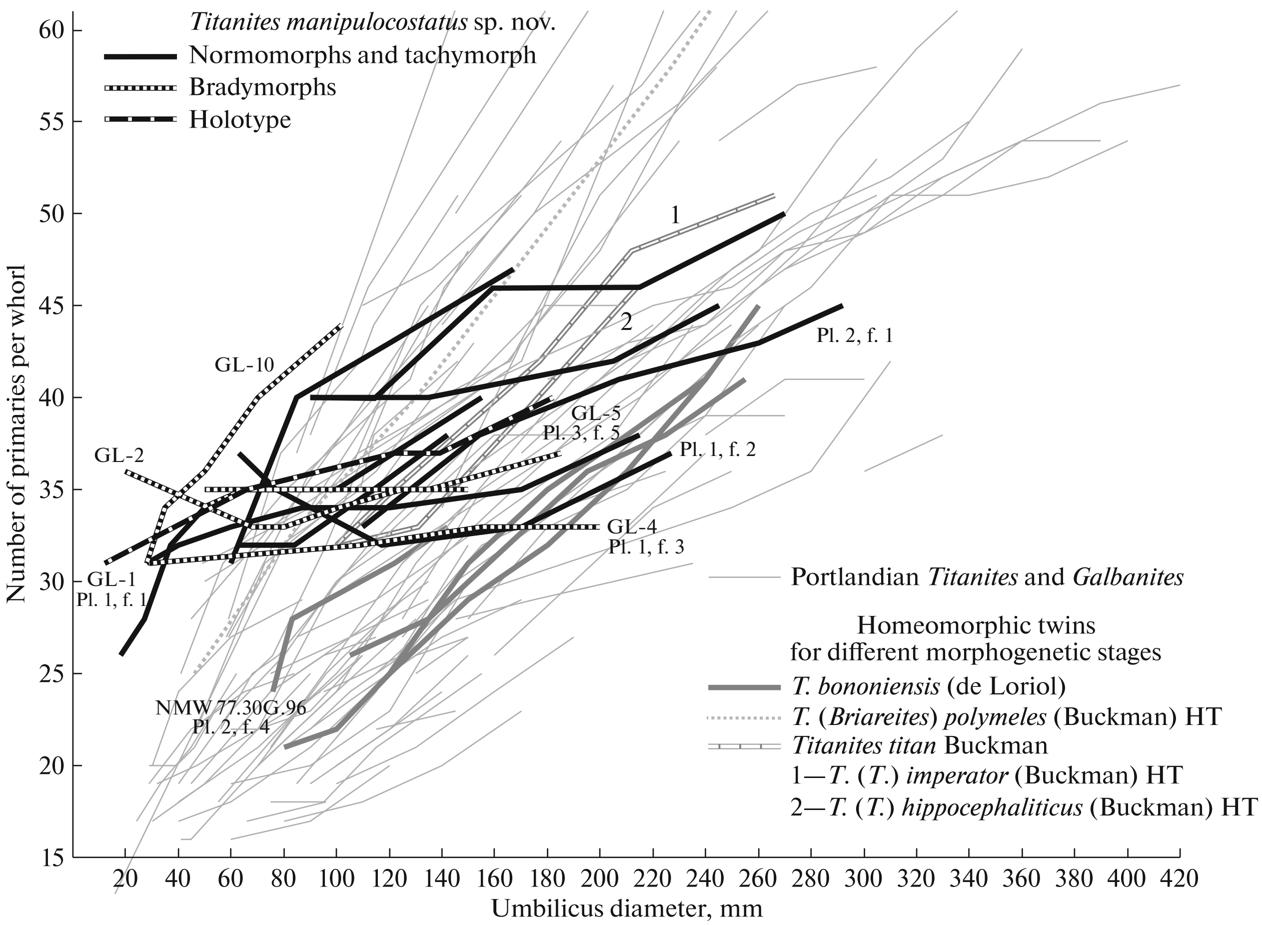


Fig. 15. Changes in morphogenesis ribbing density in *Titanites manipulocostatus* sp. nov. The gray shading shows morphogenetic groups of homeomorphic twins of Portlandian taxa. Samples are indicated by collection nos.: GL—YarGPU, Yaroslavl; NMW—National Museum of Wales, England.

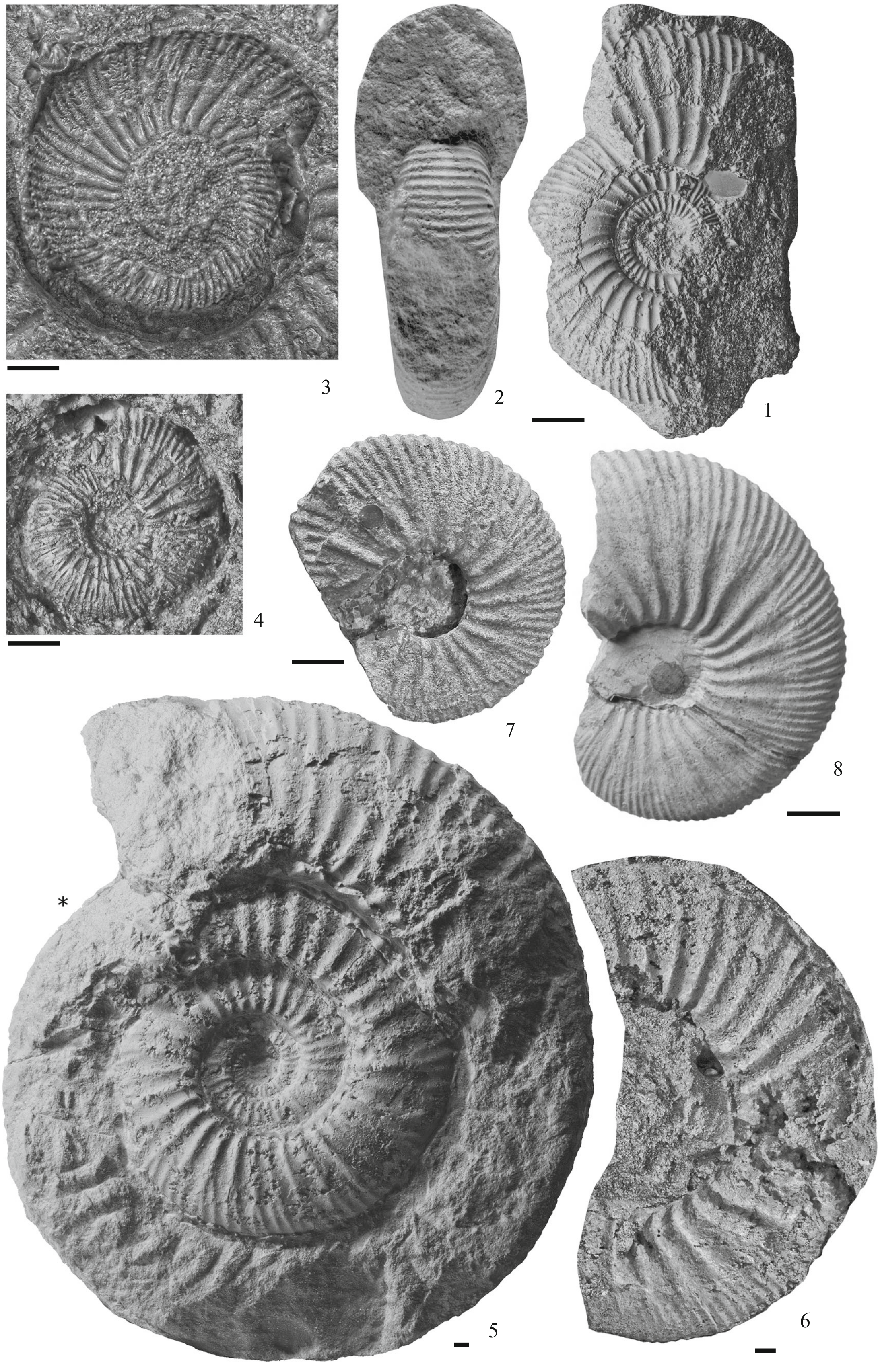
with the *T. bononiensis* group (subgenus *T. (Portlandia)* unpublished by Wimbledon) in the high ribbing coefficient in adult whorls, and sometimes also on the terminal body chamber; with *Titanites* s. str. in the shell proportions and in some cases by the rib density on adult whorls; with *Galbanites* s. str. in the statistically average terminal sizes and for some specimens in the relatively coarse ornamentation. However, no Portlandian taxon shows a complex combination of these characters.

In general, the new subgenus is most similar to *Galbanites* and *T. (Portlandia)* and to a lesser extent to *T. (Briareites)* in the type of ribbing (Fig. 14).

The inner whorls of the *T. (Paratitanites)* representatives morphologically, especially in the furcation type, are similar to those of some members of the Siberian genus *Taimyrosphinctes* Mesezh., with the semi-involute coiling, e.g., *T. trikraniformoides* Mes. (Mesezhnikov, 1972, pl. 12, fig. 2), *T. elegans* Mes. (Mesezhnikov, 1972, pl. 11, figs. 2, 3), and *T. excentri-*

Plate III. (1–6) *Titanites (Paratitanites) manipulocostatus* Kiselev sp. nov., Rybinsk District, village of Glebovo, middle substage of the Volgian Stage, Epivirgatites nikitini Zone, Epivirgatites lahuseni Biohorizon: (1, 2) paratype, specimen YarGPU no. GL-78, inner whorls megaconch with Dm = 450 mm; (3) paratype, specimen YarGPU no. GL-2, inner whorls megaconch with Dm = 345 mm; (4) holotype, specimen YarGPU no. GL-1, inner whorls megaconch with Dm = 360 mm; (5) megaconch-bradygeront of tachymorph type, paratype, specimen YarGPU no. GL-5, Dm = 484 mm; (6) paratype, specimen YarGPU no. GL-4, fragment –2 whorls of megaconch with Dm = 348 mm; view from the opposite side see in Plate I, fig. 2; (7, 8) *Titanites (Briareites) polymeles* (Buckman): (7) specimen B.M.C.26697, England, Portlandian, holotype of *Kerberites subswindonensis* Spath, 1936, pl. 20, figs. 4a, 4b.; (8) GSM 37302, England, Barrel Hill, Buckinghamshire, Barrel Hill, Long Crendon, Creamy Limestones, Haddenham Member, Portlandian, holotype of *Galbanites fasciger* Buckman, 1923, pl. 451, from the GB3D Type Fossil site.

Plate III



cus Mes. (Mesezhnikov, 1984; pl. 57, fig. 1). However, these genera are difficult to compare because adult whorls at the megaconch stage are not illustrated for *Taimyrosphinctes*; unfortunately, we could not find such specimens in M.S. Mesezhnikov's collection. Mesezhnikov (1972, pp. 122–123) established the replacement of the mainly biplicate ribs in the inner whorls (up to 60–70 mm in diameter) by the alternating biplicate and triplicate ribs at later ontogenetic stages in *Taimyrosphinctes (T.) excentricus*. In one of the specimens he measured at the shell diameter of 460 mm, the ribbing coefficient reached 2.41. Later, Mesezhnikov (1984) also noted biplicate ribs in the inner whorls in descriptions of other macroconchs of *Taimyrosphinctes*. *Titanites*, in contrast, show a decrease in the ribbing coefficient with shell growth. A confirmed megaconch of *Taimyrosphinctes* was found by M.A. Rogov in the Middle Volgian Substage on the Kheta River (Khatanga Depression, northern Central Siberia, Plate VIII, fig. 1). Like other megaconchs described in this paper, that ammonite retains a well-developed ornamentation to the end of the TBCh, but is distinguished from the typical "Portlandian" megaconchs by the less pronounced ribs at all ontogenetic stages.

Titanites (Paratitanites) manipulocostatus **Kiselev sp. nov.**

Plate I, figs. 1–3; Plate II, figs. 1–3; Plate III, figs. 1–4, 5, 6; Plate VIII, fig. 4

Epivirgatites nikitini: Ivanov and Muravin in Ivanov et al., 1987, pl. 1, fig. 2; pl. 3, fig. 2; Muravin, 1989, pl. 4, fig. 4; pl. 5, fig. 2.

Epivirgatites cf. *variabilis*: Kiselev et al., 2003, pl. 33, fig. 1.

Epivirgatites sp.: Kiselev and Rogov in Kiselev et al., 2012, pl. 55, fig. 1.

E t y m o l o g y. From the Latin *manipulus* (fascies) and costa (rib).

H o l o t y p e. Specimen YarGPU, no. GL-1, Ivanov Geological Museum, Rybinsk district, village of Glebovo, middle substage of the Volgian Stage, *Epivirgatites nikitini* Zone, E. lahuseni biohorizon.

D e s c r i p t i o n. The morphotype of this species is studied mainly from the last five whorls, counting this from the terminal peristome or depending on the state of preservation pre-peristome part of the TBCh. Earlier whorls are usually not preserved. They can be observed as fragments in a few specimens.

At the diameter of about 20 mm, at approximately the sixth whorl, the shell has mainly biplicate ribs. In the fifth whorl at the diameter of about 40–50 mm, the shell is at the morphogenetic *stage of minimal ornamentation density* (according to Kiselev, 2017). The whorls are moderately involute, covered by fine bi- and triplicate ribs. They alternate in various proportions over 0.5–1 whorls, after which the biplicate ribs disappear and are completely replaced by triplicate ribs (Plate III, figs. 1–4). The complete replacement by triplicate ribs occurs on the fourth or third whorl, at the subterminal stage of ontogeny (Kiselev, 2017). The whorls at this stage are covered by triplicate ribs (Plate II, fig. 2), sometimes in combination with intercalated ribs (Plate III, fig. 8), which is characteristic of fasciculate ornamentation with high ribbing coefficient. The branching style of the triplicate ribs can be fasciculate and with characters of bimonotomous branching. The whorl cross-section shape at the subterminal stage is rounded-trapezoid. At that stage, the shell is in the megaconch size category.

At the *terminal stage* of ontogeny represented by the terminal body chamber, the shell becomes moderately evolute (Plate I, figs. 1–3) or evolute (Plate II, fig. 1) with rounded cross section. The ornamentation is represented by biplicate and triplicate ribs, and the number of the biplicate ribs increases nearer to the terminal peristome. At that moment, the branching can become more irregular; the interrib space becomes the maximum in the morphogenesis (Plate I, figs. 1, 2). At the phase of the final increased ribbing density, triplicate ribs disappear, and simple ribs appear along with the biplicate ribs (Plate I, fig. 1).

V a r i a b i l i t y. The variability is manifested by terminal sizes, shell proportions, and morphogenesis rate.

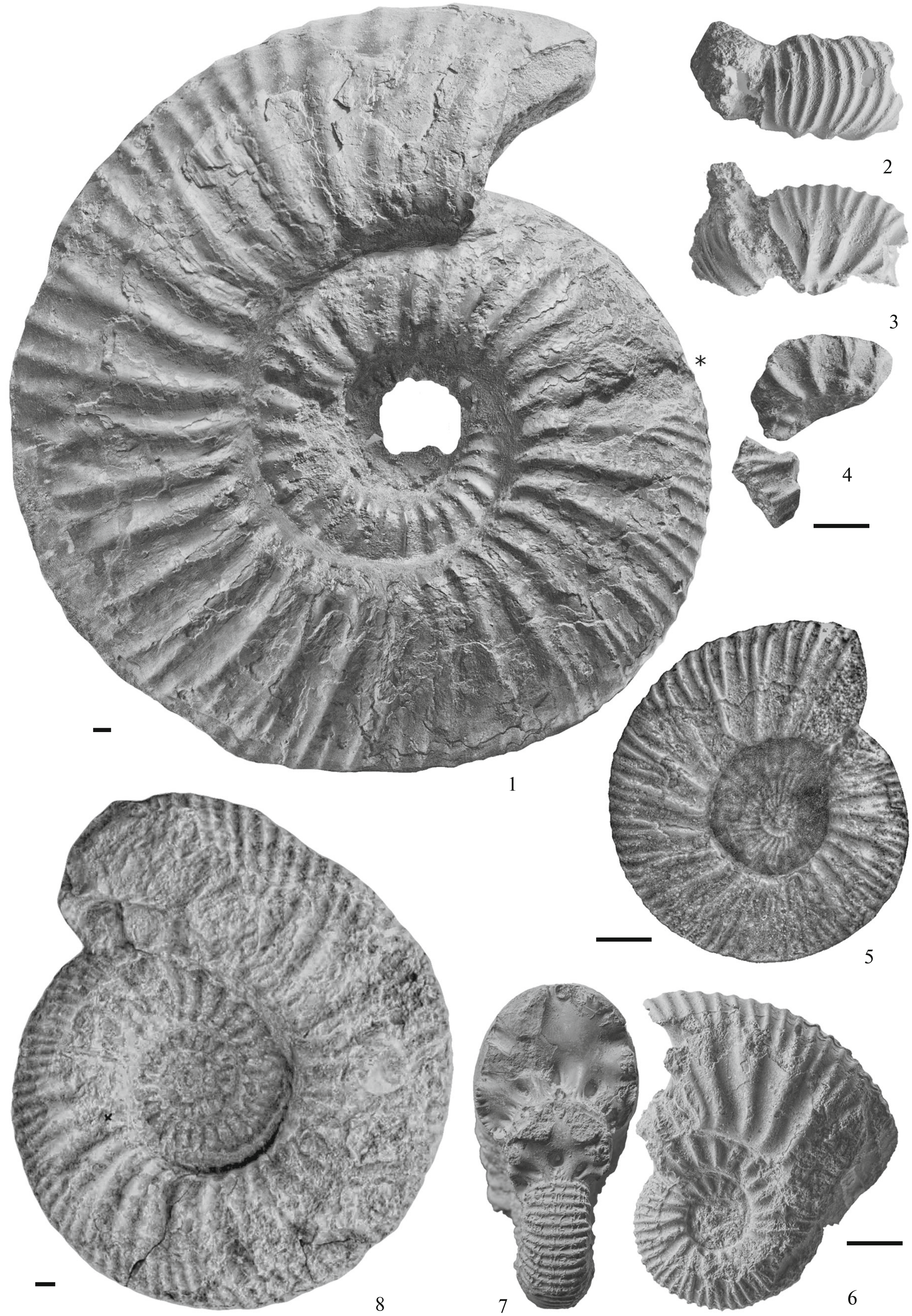
The sample contains small (tachygerontic) forms with the terminal diameter of about 370–400 mm, large (normogerontic) forms with Dm = 450–500 mm, and giant (bradygerontic) forms with Dm > 500 mm. The mean terminal diameter is 450 mm, although the maximum known size is 570 mm. One of the largest bradygerontic specimens (Dm = 547 mm) is depicted in Plate II, fig. 1.

Semievolute specimens at the terminal stage prevail and constitute the species norm. Their ratio to the evolute shells, such as in Plate II, fig. 1, is approximately 3 : 1.

The morphogenesis rate is highly variable. In tachymorph (with accelerated ontogeny at the terminal stage) specimens, biplicate and simple ribs are dominant (Plate I, fig. 1; Plate II, fig. 5), which is characteristic of most adult *Titanites*. Bradymorphous specimens retain the ornamentation of the subterminal stage (triplicate fasciculate ribs) up to the end of the TBCh (Plate I, figs. 2, 3). In this case, a phase of

Plate IV. (1–7) *Titanites (Pseudogalbanites) triceps* Kiselev sp. nov., Rybinsk District, village of Glebovo, middle substage of the Volgian Stage, Epivirgatites nikitini Zone, Epivirgatites lahuseni biohorizon: (1–4) megaconch-normogerontic of bradymorphic type; holotype, specimen YarGPU no. GL-18, Dm = 423 mm; (5) specimen YarGPU no. 31/12, depiction from Muravin, 1989, pl. 17, fig. 4; (6, 7) specimen YarGPU no. 19/12; (8) *Galbanites audax* (Buckman), specimen N.10, Dm = 240 mm, England, Portland Island, Basal Shell Bed (Verne Member), Nicodemus Knob, Portlandian, Kerberus Zone, after Wimbledon, 1974, pl. 21 (by his kind permission).

Plate IV



the final increased ribbing density can be absent at the terminal stage.

The variability of species is complicated by the fact that the bradymorph specimens can be both bradygerontic (Plate II, fig. 1) and tachygerontic (Plate I, fig. 3) or normogerontic. The same is observed in tachymorph specimens, which can be bradygerontic (Plate III, fig. 5), normogerontic (Plate I, fig. 2), and tachygerontic (Plate I, fig. 1). All this causes known diagnostic difficulties in cases where complex combination of the variability of ontogeny and morphogenesis is not taken into account.

C o m p a r i s o n. Differences between *T. (P.) manipulocostatus* and Portlandian species, even in the case of local similarity, have a fundamental character at the level of subgenera and provincial taxa and are related to ontogenetic changes in the ribbing density. The most similarity between the separate specimens of different species appears at the points of coincidence of morphometric parameters at the same shell sizes (Fig. 15). Using this principle, any specimen of the species under comparison can be paired with a homeomorph twin of another species. These are specimens that have similarity only at a certain morphogenetic stage, whereas during the remaining morphogenetic stages they are considerably different.

At the stage of minimal ornamentation density, the shell morphotype is most similar to that of *Titanites (Briareites)* Buckman, 1921 (Plate III, figs. 7, 8). The similarity is in the presence of the fasciculate branching of the triplicate ribs in combination with the involute morphotype. However, in *T. (Briareites)*, an intercalating rib is frequently present between the triplicate ribs, thereby increasing the ribbing coefficient. In the new species, the intercalated ribs appear less commonly and at the later whorls (from –4 to –2).

A similar morphotype is observed in the early whorls in *Taimyrosphinctes* from the *T. (T.) excentricus* Mesezhn. group. However, as noted above, in *Taimyrosphinctes*, the biplicate ribs are usually present before the diameter of 60–70 mm, and later the ribbing coefficient increases.

The bradymorph specimens have a noticeable similarity to *Titanites (T.) bononiensis* (de Loriol) because of the high ribbing coefficient at the penultimate and terminal whorls, which is related to the frequent presence of the triplicate ribs. Apparently because of this, megaconchs from the village of Glebovo were once assigned to this species (Gerasimov et al., 1962). The most similarity between these two species is observed at intermediate whorls (Plate II, fig. 4; Fig. 14).

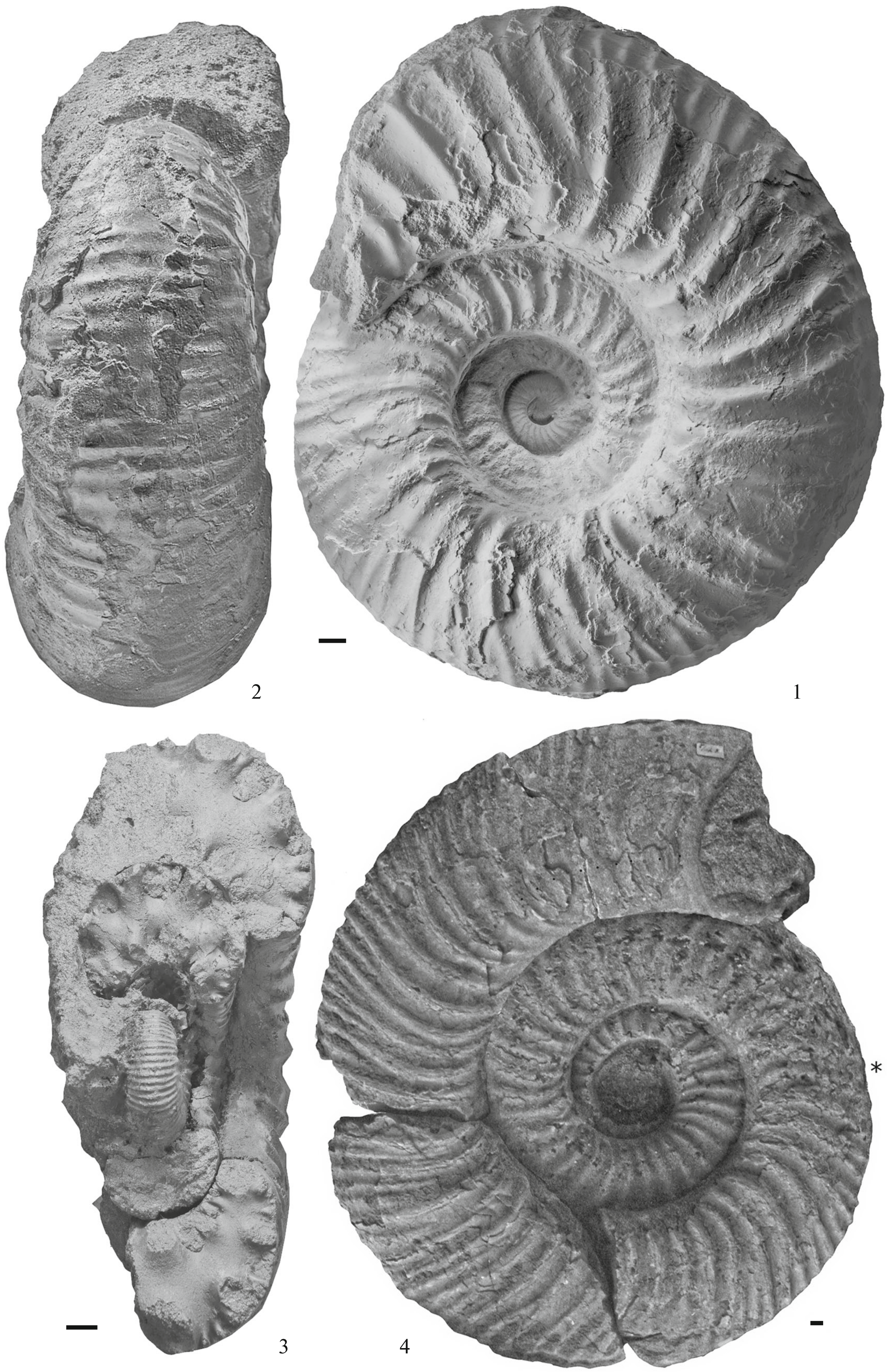
The normomorph and tachymorph specimens of this species at the terminal stage are morphologically similar to the Portlandian *Titanites* s. str. In particular, the holotypes of *T. (T.) imperator* (Buckman) and *T. (T.) hippocephaliticus* (Buckman), which Wimbledon (1974) considered to be a junior synonym of *Titanites titan* Buckman, could be homeomorph twins of such specimens at the same or similar sizes (Kiselev, 2015b, pl. 1, figs. 1 and 2a).

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen no.	Dm	WH	WW	UW	sR	RC	WH/WW	UW%
GL-1 holotype	360	120	116	182	40	2.1	1.034	50.55
		75	75	139	37	2.3	1	
	40	16		12	31			30
GL-2 paratype	345	109	–	150	35	2.7	–	43.47
				125	35	2.5		
GL-4 paratype	390	109	80	182	33	2.8	1.3625	46.66
				155	33	2.8		
GL-5 paratype	484	130	115	215	38	2.2	1.13	44.42
				170	35	2.2		
				120	34	2.4		
				87	34	2.4		
GL-78 paratype	225	70	74	90	30	2.91	0.94	40
	195	67	72	66			0.93	
	79	28	31	25.5			0.9	32.27

Plate V. (1–4) *Titanites (Pseudogalbanites) triceps* Kiselev sp. nov., Rybinsk district, village of Glebovo, middle substage of the Volgian Stage, Epivirgatites nikitini Zone, Epivirgatites lahuseni Biohorizon: (1, 2) megaconch-tachygeront of tachymorph type, paratype, specimen YarGPU no. GL-15, Dm = 369 mm; (3) phragmocone, cross section (lateral view see in Plate VII, fig. 2), specimen YarGPU GL-14, Dm = 233 mm; (4) megaconch-bradygeront of normomorph type, specimen YarGPU no. 56/2, Dm = 525 mm.

Plate V



M a t e r i a l. 23 specimens from the section near the village of Glebovo.

O c c u r r e n c e. Middle substage of the Volgian Stage, Epivirgatites nikitini Zone, Epivirgatites lahuseni Subzone and Biohorizon of Yaroslavl Povolzhye (Rybinsk and Nekouz districts and Ulyanovsk Povolzhye (section near the village of Slantsevyi Rudnik).

Subgenus *Pseudogalbanites* Kiselev subgen. nov.

Ol. lomonossovi Group (pars): Mikhalski, 1890, pp. 175–198.

Lomonossovella (pars): Krymgholz, 1949, p. 243; Muravin, 1979, p. 18; Muravin in Ivanov et al., 1987, pp. 63–64; Muravin, 1989, p. 46; Mitta, 1993, p. 93; Mitta, 1994, p. 29.

Epivirgatites (pars): Ivanov in Ivanov et al., 1987, p. 60; Muravin, 1989, pp. 145–20.

Paracraspedites (pars): Ivanov and Muravin in Ivanov et al., 1987, pp. 505–51; Muravin, 1989, p. 38.

Titanites subgen nov. B: Kiselev, 2017, p. 111.

T y p e s p e c i e s. *Titanites triceps* sp. nov., Epivirgatites nikitini Zone, *E. lahuseni* Biohorizon of the middle substage of the Volgian Stage, village of Glebovo.

D i a g n o s i s. Macromorphs up to 550 mm in diameter. Inner whorls semi-involute, with isometric (WH = WW) or low (WH < WW) proportions. Cross section broadly oval. Inner whorls mainly semievolute, less commonly evolute, with wide (WW > WH), less commonly isometric (WH = WW) proportions of cross section. Venter rounded and gradually fused with flanks.

Ornamentation of high compensation type. Early whorls covered by coarse widely spaced ribs with triplicate fasciculated branching (Table 4). In adult whorls, triplicate ribs prevailing; at terminal body chamber, biplicate and simple ribs (in normomorph specimens). Constriction absent.

S p e c i e s c o m p o s i t i o n: Two species—type species and *T. (Ps.) mosquensis* (Mikhailov) (Mikhailov, 1957, pl. 1, fig. 4).

C o m p a r i s o n a n d r e m a r k s. In the practice of identification of the Middle Volgian ammonites, the representatives of this subgenus are most frequently assigned to the genus *Lomonossovella* Ilovaisky, 1937. This is explained by the similarity of *Lomonossovella* and *Titanites (Pseudogalbanites)* in the inner whorls. Both taxa are characterized by the coarsely ribbed morphotype and wide cross section of whorls. The incorrectness of this approach was to some extent predetermined by the study of K.O. Mikhalski, who in one of the plates figured a phragmocone of a macromorph specimen of a relatively large size and assigned it to *Ol. lomonossovi* (Mikhalski, 1890, pl. 10, fig. 1). The paralectotype of the species housed in Vishnyakoff's collection (GGM VI-64/11, Vischniakoff, pl. 2, fig. 5, refigured by Mitta et al., 1999, pl. 9 (2), fig. 1), is a minimorph shell; hence, the macromorphs specimen from Mikhalski's paper should be assigned to a different taxon. In our view, it should be assigned to the subgenus *T. (Pseudogalbanites)*.

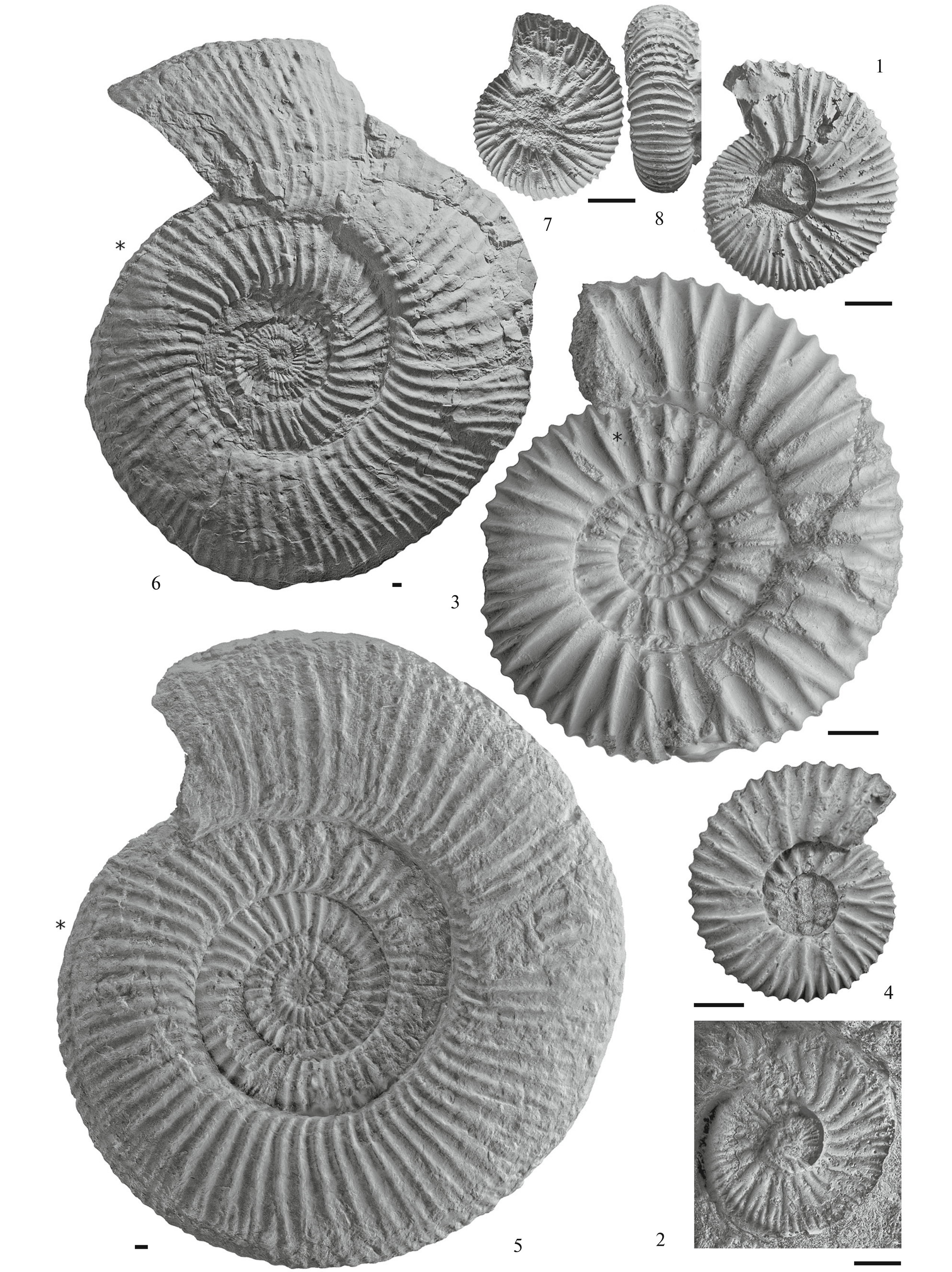
The minimorph genus *Lomonossovella* forms a terminal body chamber at a small diameter, not more than 150 mm (on average about 100 mm), and is characterized by an extremely evolute morphotype and very sharp, relief ribs with a lower ribbing coefficient in the TBCh (Plate VI, figs. 3, 4).

The genus *Lomonossovella* also traditionally includes an involute coarsely ribbed specimen from A.P. Pavlow's collection (Pavlow, 1890, pl. 2, figs. 1, 2), which was most often considered to be a junior synonym of *Lomonossovella lomonossovi* (Vischn., 1882). Pavlow identified this specimen as the Portlandian species *Olcostephanus triplicatus* (Blake). Later, this specimen was chosen by N.P. Mikhailov as the holotype of the new species *Kerberites mosquensis* Mikhailov. The morphology of this specimen completely corresponds to the inner whorls of *Titanites* (Plate VI, fig. 1); hence, it is incorrect to assign it to *Lomonossovella*. The sample of specimens of the type species *T. (Pseudogalbanites)* contains specimens (Plate VI, fig. 2) which are quite similar to Mikhailov's type, so we assign *T. (Ps.) mosquensis* to *T. (Pseudogalbanites)*.

The new subgenus is the most similar to the genus *Galbanites*, which is reflected in its name. This similarity is especially characteristic of the tachygerontic specimens of *T. (Pseudogalbanites)* with a small terminal diameter. The inner whorls of both taxa have a wide or inflated cross section with coarse and widely spaced ribs, which are mostly triplicate. This morphotype is often present at all stages of morphogenesis. Also, both genera are similar in the compensation type of ontogeny (Fig. 6b) and the ribbing style (Figs. 14c, 14d). Among *Galbanites*, the most similarity with this subgenus is observed in the *Galbanites audax* (Buckman) group, and to a lesser extent in *Galbanites* s. str. It is logical to

Plate VI. (1) *Titanites (Pseudogalbanites) mosquensis* (Mikhailov), holotype, specimen GGM no. VI-6/1, vicinity of Moscow near the village of Mnevniki (now within Moscow), "from glauconitic sands with *Lomonossovella lomonossovi*" (Mikhailov, 1957, pl. 1, fig. 4); (2) *Titanites (Pseudogalbanites) triceps* Kiselev sp. nov., paratype, specimen YarGPU no. GL-15, inner whorls of the specimen depicted in Plate V, figs. 1, 2, Glebovo, Epivirgatites nikitini Zone, Epivirgatites lahuseni Biohorizon; (3, 4) *Lomonossovella blakei* (Pavlow): (3) specimen at the TBCh stage, specimen YarGPU no. GL-67, Glebovo, Epivirgatites nikitini Zone; (4) lectotype, specimen GGM. VI-6/4, vicinity of Moscow, near the village of Mnevniki (now within Moscow; (5) *Titanites (Titanites)* cf. *titan* Buckman, specimen GGM-0868-1/BP-08070, Dm = 488 mm, Ulyanovsk oblast, Epivirgatites nikitini Zone; (6) *Titanites (Titanites)* aff. *titan* Buckman, specimen UPM no. 236, Dm = 660 mm, Ulyanovsk oblast, village of Gorodishchi, Epivirgatites nikitini Zone; (7, 8) *Titanites (Pseudogalbanites) triceps* Kiselev sp. nov., paratype, specimen YarGPU no. 19/13, Glebovo, Epivirgatites nikitini Zone, Epivirgatites lahuseni Biohorizon.

Plate VI



consider the subgenus *T. (Pseudogalbanites)* as an isochronous vicariant of *Galbanites* for European Russia.

In contrast to *Galbanites*, the new subgenus reaches larger terminal sizes, in general characteristic of the genus *Titanites*, and it is distinguished by the narrower cross section of the adult whorls, less coarse and prominent ornamentation, and noticeably denser ribbing at all stages, especially at the early and middle stages of morphogenesis (Fig. 5).

This subgenus is distinguished from other *Titanites*, including the co-occurring *Titanites (Paratitanites)* subgen nov., by the inflated whorls at all stages of morphogenesis and coarse ornamentation. A similar morphology is observed in the insufficiently studied subgenus *T. (Glottoptychinites)* Buckman, 1923, in which the coarsely ribbed "*Galbanites*-like" morphotype is described only from the middle whorls.

Titanites (Pseudogalbanites) triceps Kiselev sp. nov.

Plate IV, figs. 1–7; Plat V, figs. 1–4; Plate VI, figs. 2, 7, 8; Plate VII, fig. 2

Lomonossovella lomonossovi: Muravin, 1979, pl. 4, fig. 1.

Lomonossovella michalskii: Muravin, 1989, pl. 17, figs. 3, 4.

Epivirgatites lahuseni: Ivanov and Muravin in Ivanov et al., 1987, pl. 3, fig. 1; text-fig. 12.1; Muravin, 1989, pl. 7, fig. 3; pl. 8, fig. 2.

Epivirgatites sp.: Kiselev and Rogov in Kiselev et al., 2012, pl. 55, fig. 2.

E t y m o l o g y. From the Latin *triceps* (tripleheaded).

H o l o t y p e. Specimen YarGPU no. GL-18, Ivanov Geological Museum, Rybinsk district, village of Glebovo, middle substage of the Volgian Stage, Epivirgatites nikitini Zone.

D e s c r i p t i o n. The stage of the minimum ornamentation density (from –6 to –5 whorls): the shell is moderately involute. The whorls are wide, inflated (WH/WW < 1). The initial ornamentation density is 23–26 ribs per whorl, after which it gradually increases. The ribs are coarse and short, triplicate at the diameter of 50 mm. The triplicate ribs alternate with biplicate ribs and intercalated ribs. There is one biplicate rib per two–three triplicate ribs.

The subterminal stage begins from –4 whorl at the diameter of 70–100 mm and terminates at the beginning of the terminal whorl (–1 whorl) at the shell diameter of 300–400 mm, occasionally at 500 mm. The shell remains moderately involute and inflated. The ribbing is of reasonably compensated type: the number of ribs per whorl increases slowly, from 27 to 32 (Fig. 5), approximately 1.2 times, whereas the interrib space increases by 2–3 times in three whorls. The rib branching varies: bradymorph specimens mainly have triplicate ribs with fasciculated branching, whereas in tachymorph specimens biplicate ribs prevail.

The *terminal stage* is marked by the development of a terminal body chamber sometimes possessing a slight uncoiling of the spiral. The cross section is inflated, widely oval or rounded. The rib density becomes the largest in morphogenesis—from 30 to 37 per whorl. In the middle part of the TBCh, the interrib space becomes the largest, after which it begins gradually and slightly decreasing (*final increased ribbing density* stage). In the normomorph specimens, the TBCh possesses biplicate ribs, alternating with triplicate ribs at the ratio of 3/1 or 4/1 (Plate V, fig. 4). In the tachymorph specimens, the biplicate ribs prevail from the –2 whorl, and on the TBCh, they alternate with simple and very rarely with triplicate ribs (Plate V, figs. 1, 2). In bradymorph specimens, triplicate ribbing prevails (Plate IV, fig. 1).

V a r i a b i l i t y is manifested by primarily the terminal size and rates of morphogenesis and hence by the rib density and ribbing coefficient.

The tachygerontic specimens are characterized by the shell diameter from 283 to 350 mm, while the maximum diameter of bradygerontic specimens is 530 mm. The average terminal diameter is 420 mm. The beginning of the terminal stage, fixed by the appearance of TBCh, also varies (Fig. 16).

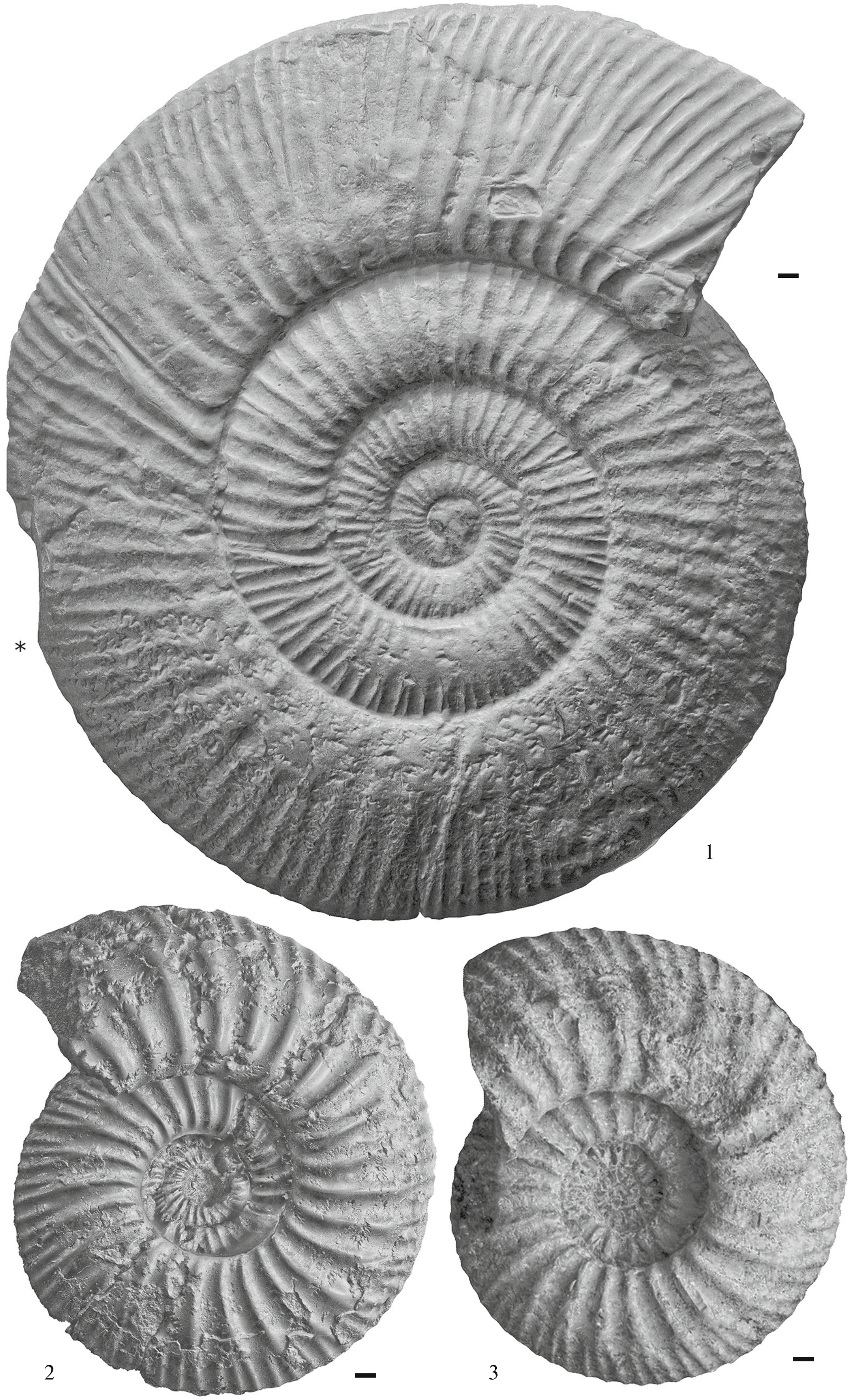
The rate of morphogenesis varies considerably, which allows the recognition of the tachymorph, normomorph, and bradymorph specimens at the terminal stage of ontogeny (see the description). In our material, the ratio of the specimens of tachy-, normo-, and bradymorph types is 1 : 4 : 2, respectively.

The variability of the morphogenesis rate is associated with variability of the terminal diameter, but to a lesser extent than in *T. manipulocostatus*. The bradygerontic morphotype is observed only in normomorph specimens (Plate V, fig. 4), and the tachygerontic morphotype, in tachymorph specimens (Plate V, figs. 1, 2). The shells of bradymorph specimens are usually normogerontic (Plate VI, fig. 1). However, this trend is insufficiently supported statistically.

At early whorls, at the diameter of 40–50 mm, the variability is observed in the whorl width and height and correlatively the relative umbilicus diameter. The varieties with higher whorls are at the same time more strongly involute (Plate VI, fig. 2), similar to the morphotype of *T. (Ps.) mosquensis* (Mikhailov) (Plate VI, fig. 1).

Plate VII. (1) *Glaucolithites gardarikensis* Kiselev sp. nov., holotype, UPM, specimen no.186, Dm = 460 mm, Ulyanovsk oblast, village of Gorodishchi, Epivirgatites nikitini Zone; (2) *Titanites (Pseudogalbanites) triceps* Kiselev sp. nov., phragmocone, lateral view (cross section see in Plate V, fig. 3), specimen YarGPU GL-14, Dm = 233 mm, Glebovo, Epivirgatites nikitini Zone, Epivirgatites lahuseni Biohorizon; (3) *Galbanites audax* (Buckman), phragmocone, specimen N.2, Dm = 215 mm, England, Portland Island, Basal Shell Bed (Verne Member), Nicodemus Knob, Portlandian, Kerberus Zone, after Wimbledon, 1974, pl. 22 (by his kind permission).

Plate VII



A more strongly evolute variety at the same time has wider (and even inflated) whorls (Plate IV, figs. 2–4, 5–7).

Comparison and remarks. This species is distinguished at the early stages from the more closely similar species *T. (Ps.) mosquensis* by the more strongly evolute shell, whorl width, and the nature of ribbing: for *T. (Ps.) mosquensis*, the "*Kerberites*-like" branching style is less pronounced. Triplicate ribs are formed by the bimonotomous branching or by intercalating ribs. The absence of adult whorls and the lack of data on the species variability complicate further comparisons. Supposedly, a large phragmocone, illustrated by Mikhalski (1890, pl. 10, fig. 1), in fact belongs to *T. (Ps.) mosquensis*. It differs from the whorls of a similar size of the new species in the coarse and prominent ornamentation.

Representatives of *Galbanites* often include homeomorphic twins of different stages of *Titanites triceps* (Fig. 16). At the middle and late stages, *Galbanites audax* is the most similar (Buckman, 1909–1930, pls. 717a, 717b) (Plate IV, fig. 8; Plate VII, fig. 3). The terminal body chamber of the normomorphic specimens (Plate V, fig. 4) is morphologically similar to that of the holotype of *Galbanites forticosta* (Buckman, 1909–1930, pl. 513).

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	sR	RC	WH/WW	UW%
GL-18 holotype	423	140	169	180	32	2.56	0.83	42.5
				120	29	2.91		
		16.4	17.8				0.92	
GL-15 paratype	369	120	147.6	160	30	2.4	0.81	43.3
	41	14		13	23	2.8		31.7
GL-3 paratype	478	149	185	236	37	2.1	0.8	49.3
	465			192	32	2.1		41.29
GL-19 paratype	424	115	119	170	40	2.3	0.96	40.09
				125	37			
	233	75	99	87	28	2.64	0.75	37.33
GL-14 paratype	203	65	94	70			0.69	34.48
	117	45	57	41			0.79	35.04
52/6 paratype	525	158.5	163.4	230	41	2	0.97	43.80
				190	35			
GM 66 paratype	38.4	14.3	15.8	12.2	23	2.57	0.9	31.77
GM 107 paratype	135	37.5	49	48.7			0.76	36.07
	46	14.2	19.3	18	18	3.1	0.74	39.13

Material. 23 specimens from the section near the village of Glebovo.

Occurrence. Middle substage of the Volgian Stage, Epivirgatites nikitini Zone and Epivirgatites lahuseni Subzone and Biohorizon of the Yaroslavl Povolzhye.

Genus *Glaucolithites* Buckman, 1922

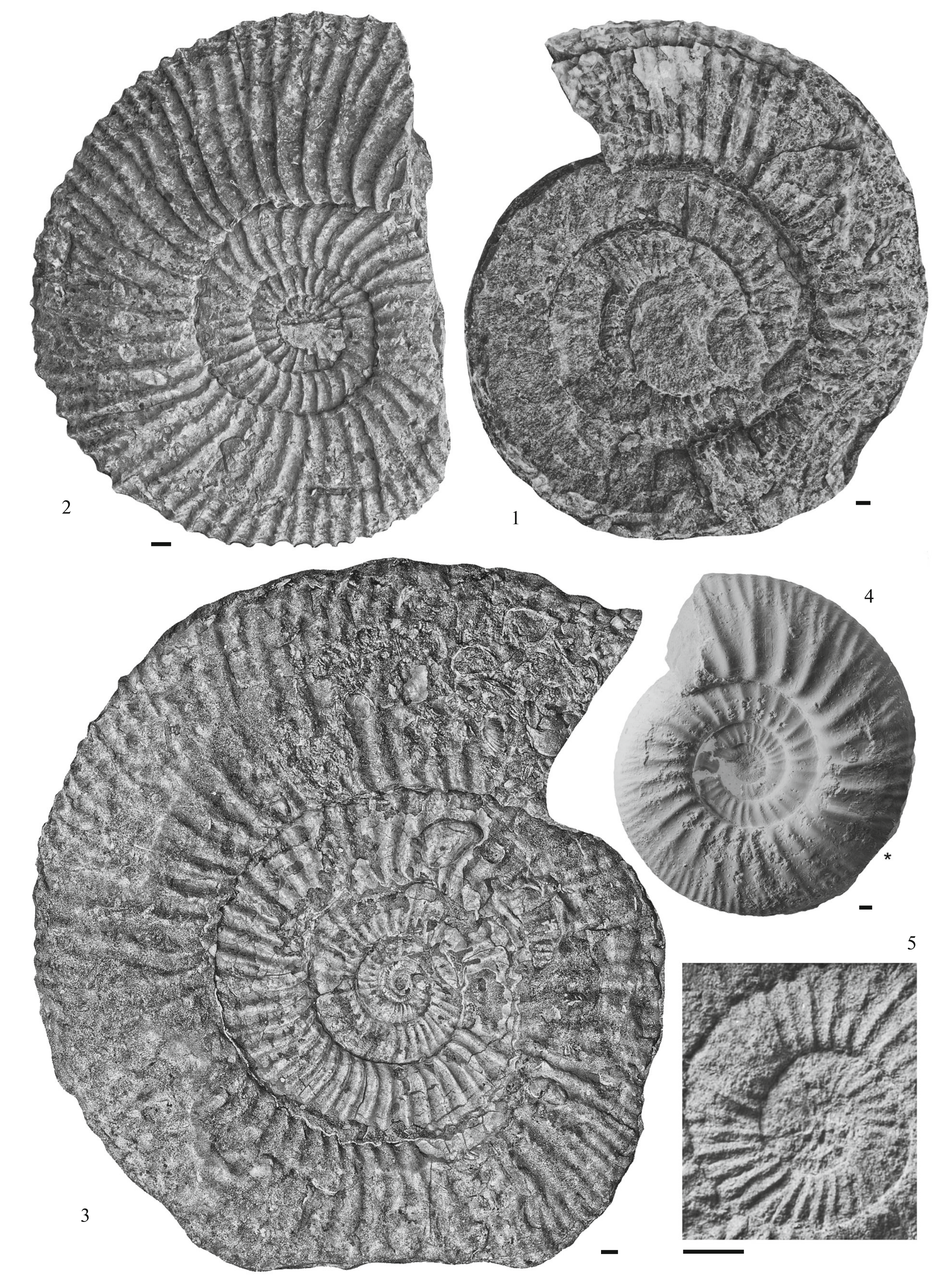
Glaucolithites gardarikensis Kiselev sp. nov.

Plate VII, fig. 1

Etymology. From the Old Norse *Gårdarike* (garð = Gorodishchi = land of the farms), term used

Plate VIII. (1) *Taimyrosphinctes* sp., megaconch with Dm = 415 mm, Kheta River, Outcrop 22 (after Saks et al., 1969), talus of the Middle Volgian Substage (Maximus–Exoticus zones); (2) *Titanites (Titanites)* cf. *titan* Buckman, specimen with an intermediate body chamber, UPM, specimen no. Gr-1, Dm = 265 mm, Ulyanovsk oblast, village of Gorodishchi, Epivirgatites nikitini Zone; (3) *Titanites (Titanites)* aff. *titan* Buckman, specimen with an incomplete body chamber, UPM, specimen no. Gr-2, Dm = 400 mm, Ulyanovsk oblast, village of Gorodishchi, Epivirgatites nikitini Zone; (4) *Titanites (Paratitanites) manipulocostatus* Kiselev sp. nov., paratype, specimen, not having reached the terminal stage, specimen YarGPU no. GL-83, Dm = 280 mm, Glebovo, Epivirgatites nikitini Zone, Epivirgatites lahuseni Biohorizon; (5) *Glaucolithites polygyralis* (Buckman), fragment of an inner whorl with a bidichotomous rib, specimen GSM 47824, England, Wiltshire, Swindon, Okus Quarry, sandstone beds below the Cockly bed, Portlandian, holotype of *Gyromegalites polygyralis* Buckman, 1925, pl. 620a, from the GB3D Type Fossil site.

Plate VIII



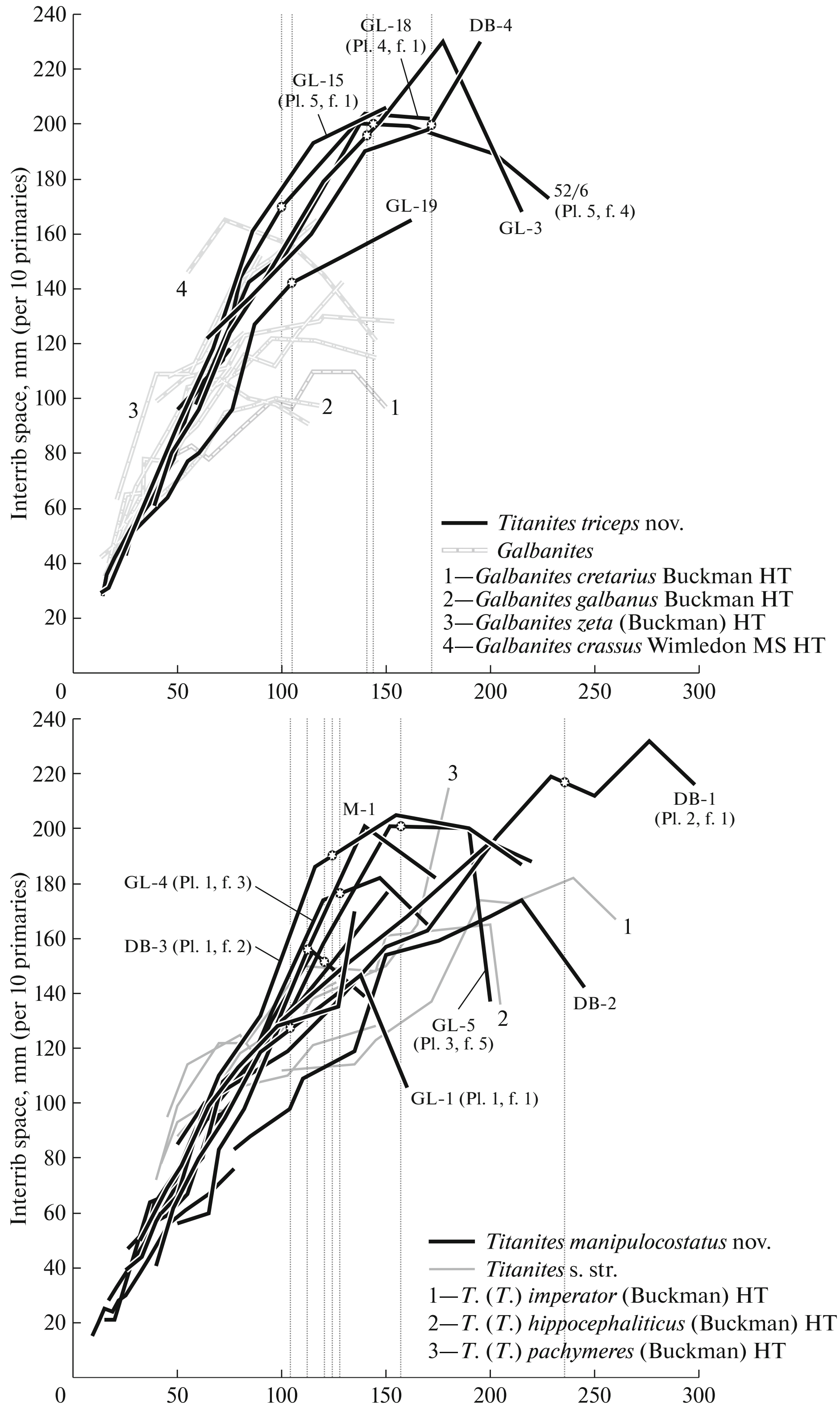


Fig. 16. Changes in the growth rate of the interrib spaces in morphogenesis of two species of the Middle Volgian *Titanites*: *Titanites triceps* sp. nov and *Titanites manipulocostatus* sp. nov. All measured specimens come from the Nikitini Zone in the section near the village of Glebovo. The beginning of the body chamber is shown by asterisks; the vertical lines show projections on the horizontal axis. The gray shading shown the morphogenetic curve for homeomorphic twins of the Portlandian taxa. Each specimen is numbered: GL—YarGPU; M—M. Shikhanov's private collection (Yaroslavl); DB—D. Buev's private collection (Moscow).

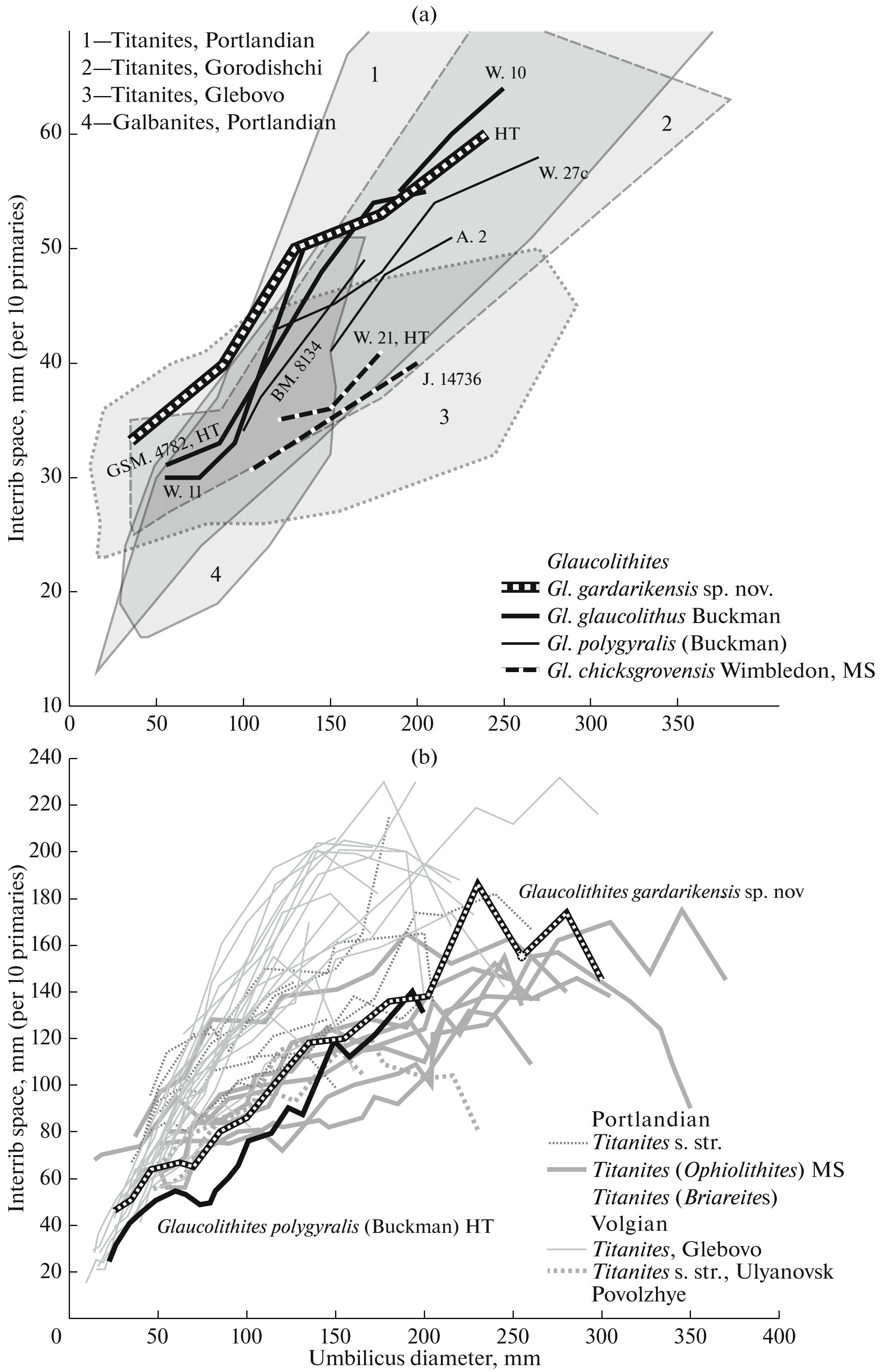


Fig. 17. Comparative morphogenesis of the ornamentation density of four species of the genus *Glaucolithites*. (a) Curves showing the number of ribs per whorl; (b) curves of the interrib space. The number of the ribbing density curves corresponds to the number of measured specimens. The umbilicus diameter is used as a parameter of the morphogenetic growth. Gray shading shows the morphological fields of *Titanites* and *Galbanites* (based on Figs. 1 and 5). The measurements of the Portlandian species and numbers designations are taken from Wimbledon (1974). HT—holotype, MS—unpublished species.

Plate IX

1

2

3

Plate IX. (1, 2) *Titanites (Titanites)* cf. *titan* Buckman: (1) specimen with a terminal body chamber, specimen GGM-1533-07/BP-10751, Dm = 730 mm; (2) specimen with a partly preserved terminal body chamber, specimen GGM-488-25/BP-05863, Dm = 580 mm, Ulyanovsk oblast, presumably right bank of the Volga River near the village of Slantsevyi Rudnik, Epivirgatites nikitini Zone; (3) *?Titanites* sp., a fragment of an adult whorl, unnumbered specimen, Bolshaya Zemlya tundra, bolders, A.V. Zhuravsky's collection (Paleontological-Stratigraphic Museum of the Department of Dynamic and Historical Geology of St. Petersburg State University).

in medieval times for the states of Kievan Rus (Russia); the name of the type locality.

Holotype. Undory Paleontological Museum, no. 186; Ulyanovsk oblast, village of Gorodishchi, Epivirgatites nikitini Zone.

Description. The holotype is a slightly laterally compressed mold 460 mm in diameter. The shell is moderately evolute, with pronounced constrictions up to the last whorl. Three last whorls have eight constrictions. The ornamentation is equicostate, with uncompensated development in morphogenesis. The rib number gradually increases to 35 ribs at the intermediate whorls, and at the umbilicus diameter of 55–60 mm, up to 60 ribs in the terminal whorl (Fig. 17). The middle whorls possess biplicate, simple, and, less commonly, intercalated ribs. In the biplicate ribs, the bifurcation point is at 1/3 or 1/2 of the whorl height; hence, the secondaries are observed below the umbilical seam of the overlapping whorls. In ribs lying before the constrictions, the bifurcation point lowers down to the umbilical shoulder, and in one case (in the penultimate whorl), there is a rib with a biditochomous branching. The ribbing coefficient in the intermediate whorls is 1.64, and in the last whorl, 2.17. The ornamentation of the last whorl is composed of biplicate, triplicate bimonotomous, simple, and intercalating ribs, which increases the ribbing coefficient.

In the phragmocone, the last septum is observed at the diameter of 370 mm. Before that, the interseptal distances gradually become smaller. This determines the beginning of the terminal shell. The terminal body chamber is incompletely preserved, approximately half of it. It has two constrictions. The number of the triplicate bimonotomous ribs, compared to the preceding whorls increases; hence, the ribbing coefficient of the TBCh is 2.22.

Comparison and remarks. This species is characterized by a morphotype which is not observed in other macromorphs of the Nikitini Zone. Its assignment to the genus *Glaucolithites* is supported by a number of characters: presence of frequent constrictions, uniform ribbing density, biplicate ribbing in most whorls, irregular rib branching in the late whorls and TBCh. A similar ornamentation is clearly observed in the Greenland specimen of *Glaucolithites*, identified by Spath as *Behemoth groenlandicus* Spath (Spath, 1936, pl. 23, fig. 1). The English types are rarely depicted at this growth stage; hence, the comparison of the terminal whorls is difficult.

The new species also shows a low position of the rib bifurcation point—character often observed in the more finely ribbed *Glaucolithites* species from the English Portlandian, e.g., in *Gl. polygyralis* (Buckman) (Buckman, 1909–1930, pl. 620a, 620b). In that species, as in the new one, the rib bifurcation point is lower before the constrictions, and simple ribs are also present. At the same time, both species are similar in the density of ornamentation, especially at the late stages of ontogeny (Fig. 17). The new species is distinguished from other species of *Glaucolithites* by the noticeably stronger ribbing density.

The size of the last whorl of the holotype is within the variability range of the ultimate diameter of this genus: from 330 to 515 mm, on average 404 mm (from 11 specimens in Wimbledon, 1974).

The new species is distinguished from the Portlandian specimens by more irregular branching in the last whorl with alternation of biplicate, triplicate bimonotomous, simple, and intercalating ribs. This type of branching is sometimes observed in English specimens, for example, in the holotype of *Gl. chicksgrovensis* Wimbledon, MS (Wimbledon, 1974, pl. 17), but on the whole is not very common in *Glaucolithites*. Also, the new species ornamentation is more strongly transformed before the constrictions, sometimes leading to the appearance of bidichotomous branching. However, this type is also known in the Portlandian species. For instance, for the holotype of *Gl. polygyralis* at the umbilicus diameter of about 40 mm, there is a rib with a bidichotomous branching, occurring immediately before the constriction (Plate VIII, fig. 5).

Dimensions in mm and ratios:

Specimen no.	Dm	WH	WW	UW	sR	RC
Holotype	460	131	–	240	60	2.17
	–	93	–	180	53	1.64

Material. Holotype.

Occurrence. Middle substage of the Volgian Stage, Epivirgatites nikitini Zone. Holotype apparently comes from the lower part of the zone, i.e., the Bipliciformis Subzone.

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