

Morphogenesis Rate Variability and Modularity of Development in Jurassic Ammonites of the Genus *Arcticoceras* Spath, 1924

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Abstract—The high variability of ammonites is largely due to the diversity of combinations of individual heterochronies (bradimorphy, tachymorphy, bradygeronty, and tachygeronty) and the modularity of development. Using the genus *Arcticoceras* as an example, it was shown that heterochronies of various directions can be combined in any number of characters, and individual heterochronies differ from phylogenetic ones by their smaller range, and a larger number of combinations. The study of such combinations allowed intraspecific morphs to be recognized, and available *Arcticoceras* species to be revised. During the Early and Middle Bathonian, the family Cardioceratidae evolved through a series of pedomorphosis, and after the appearance of Cadoceratinae, through accelerations.

Keywords: heterochronies, mosaic development, taxonomy, ammonites, Cardioceratidae, Bathonian

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INTRODUCTION

There has been a recent resurgence of interest in the analysis of heterochronies in modern and fossil organisms. This is largely due to the concept of modularity, relatively independent (mosaic or dissociated) development in the ontogeny of organs, characters and their combinations, which are considered as modules that determine the structural complexity of the body (Isaeva, 2014). With modular development, heterochronies in the development of different characters operate at different rates, thereby significantly complicating periodization of morphogenesis (ontogeny) and taxonomic identifications (at least at the species level). For this reason, the study of the variability of the rate of development by a set of characters has not only theoretical, but also practical significance. Generally, it facilitates revision of taxonomic diversity, allows a more objective determination of taxon boundaries, and the number of available species if they represent different kinds of morphs or variations of valid species.

Different rates of change of various characters of the same organism in ontogeny or phylogeny is a fundamental principle of the concept of heterochrony, which was postulated in most theoretical papers on this subject (Cope, 1868; Severtsov, 1921, 1939; Schmalhausen, 1938; 1939; De Beer, 1940; Gould, 1977; McNamara, 1986 and others). Based on this principle, it was proposed to distinguish between general (or global) heterochrony, which occurs on the scale of the whole organism, and dissociated (local, mosaic) heterochrony, which manifests itself only in

individual characters (McKinney, 1984; McKinney and McNamara, 1991). The same principle applies to the analysis of other varieties of heterochrony. In particular, the possibility of dissociated development of characters is expected to a greater extent for neoteny, postdisplacement, acceleration, predisplacement and, to a lesser extent, for progenesis and hypermorphosis (McNamara, 1986). In extreme terms, such a mosaic pattern can lead to a situation where, in the ontogenesis of the same organism, development is delayed on one basis and accelerated on another (Leonova, 2012; McNamara, 2012).

Ammonites have been used as an object for studying heterochrony, considered in the categories of peramorphosis or pedomorphosis or their conceptual analogues, for more than a hundred years (Pavlov, 1901; Schindewolf, 1925; Spath, 1932; Ivanov, 1945a, 1945b, 1976; Landman, 1988; Korn, 1992, 1995; Landman and Geysant, 1993; Leonova, 2012, 2015, 2016; etc.).

The main subject of study in such studies is heterochrony, leading to phylogenetic changes and the emergence of new taxa. The results of studying intraspecific variability of retardation or accelerations in the development of individual characters or whole set of characters, observed in the ontogeny of individuals, are much less frequently published. Such variability was studied both in Paleozoic (Schmidt, 1924; Korn and Vöhringer, 2004) and in Mesozoic ammonites (Michalski, 1890; Ivanov, 1945a, 1945b, 1976; Dommergues et al., 1986; Landman, 1988; Mitta, 1990;

Courville and Crônier, 2003; Kiselev and Rogov, 2018). The phenomenon of modularity is better manifested in the intraspecific variability of ontogenetic processes than in phylogeny, where the final results of such changes are already visible. Dissociation of the development of ammonite shell characters can be observed in the case when morphogenesis is studied simultaneously for several characters, provided that the measurements of the parameters of the characters are clearly fixed to the shell diameter. Ivanov (1945a, 1976), using the genus *Keplerites* as an example, showed that the main characters used to periodize morphogenesis (shell diameter, in which: (a) lateral nodes disappear, (b) apertural ratio is equal to 1, and (c) lateral nodes are covered by the next whorl) develop at different rates, as a result of which, in different individuals, the boundary between the morphogenetic stages can be recognized by one character or by a combination of two or three characters. Nevertheless, the differentiation of the stages of morphogenesis in *Keplerites* (*sub-Kosmoceras* and *Keplerites* stages) by Ivanov is carried out by a combination of all the characteristics that on average change almost synchronously. If a different rate of development of individual characters becomes a phylogenetic trend, then the evolution of taxa occurs by retardation or acceleration of the development of one or more modules. For processes of phylogenetic deceleration of development, Ivanov (1969) referred to this type of heterochrony as partial bradygenesis. Subsequently, similar varieties observed in other heterochronies were referred to as local heterochronies (McKinney and McNamara, 1991).

One of the consequences of the modularity of shell development in ammonites may be the appearance of a high diversity of morphotypes within the same species. This produces certain difficulties for taxonomy, since forms with a different combination of the development of characters at different stages of morphogenesis may be recognized as separate species. It is proposed to consider this problem using the Jurassic ammonite genus *Arcticoceras* Spath, 1924, the most important stratigraphic marker for the Boreal Lower and Middle Bathonian, as an example

ON SPECIES DIVERSITY IN THE GENUS *ARCTICOCERAS*

The genus *Arcticoceras* Spath, 1924 (type species of the genus is *A. ishmae* (Keyserling, 1846)) is the most important stratigraphic marker for the Boreal Lower and Middle Bathonian; therefore, the issues of its systematics and assessment of species diversity are of practical significance. Currently, it includes 10 available species and subspecies, as well as four unavailable species and two subgenera, described only in manuscript. In stratigraphic practice, these species are commonly used as stratigraphic indices for various zones or infrazonal units. However, there is good reason to

believe that most of the selected species belong to morphs of intraspecific variability and are accordingly invalid.

This problem requires a revision of the taxonomy of the genus based on the analysis of all specific characters. The revision of this group of ammonites was discussed in detail in my previous paper (Kiselev, 2020), where it was shown that most available species and subspecies, including *A. ishmae tenuicostatum* Repin, *A. kochi* Spath, *A. pseudolamberti* Spath, *A. stepankovi* Tuchkov, *A. excentricum* Voronez, *A. harlandi* Rawson, and *A. pseudishmae* (Spath) are junior synonyms of *A. ishmae* (Keyserling). The intraspecific variability of *A. ishmae* is so high that individuals with a contrasting morphotype can be mistakenly considered as separate species. We have treated such varieties as morphs, characterized by a different combination of characters, primarily the whorl shape and rib density. Presumably, the main mechanism of this variability is associated with heterochronies, which will be considered in this paper.

METHODS

Variability of the rate of development in *Arcticoceras*, as well as in other ammonites, is expressed by the asynchronous appearance of marker characters in different individuals, according to which it is possible to interpret periodization of morphogenesis (ontogeny). These characters primarily include the final shell diameter, smoothing of the ribbing on the last body chamber (LBC), changes in the rate of ribs branching in morphogenesis, and density of primary ribs. These characters are sometimes considered diagnostic for some species of *Arcticoceras* (Meledina, 1973, 1987; Poulton, 1987; Callomon, 1993). The terminal shell (last body chamber) in *Arcticoceras* is readily distinguished by the presence of a number of specific features, which include the following: terminal aperture with a ventral projection; deep pre-apertural constriction, noticeable mainly on the molds; a slow opening of the umbilicus and gradual or sharp smoothing of the ornamentation until its complete disappearance. To study variability, the diameter of the shell is used as a universal development chronometer (according to: Ivanov, 1945b, 1976), relative to which the appearance or disappearance other characters is recorded. A delayed development of characters leads to a morphotype typical of earlier whorls being observed in some individuals with a larger shell diameter ("Bradymorphie"; Schmidt, 1924). In some cases, developmental delay can lead to an increase in terminal size or bradygeronty (Teisseyre, 1889, emend. Mitta, 1990). Accelerated development leads to characters appearing at a smaller diameter ("tachymorphie" (Schmidt, 1924)) or a decrease in the diameter of the terminal shell (tachygeronty (Teisseyre, 1889, emend. Mitta, 1990)). Accordingly, in the sample one can distinguish, on the one hand, bradygerontic, normogerontic, and tachy-

gerontic specimens, and, on the other hand, brady-morphic, normomorphic, and tachymorphic specimens. The development rate is determined by average indicators. The remaining characters of the shell (proportions of the cross-section, relative diameter of the umbilicus and rib density) can also be used to periodize morphogenesis. Nevertheless, using them to analyze heterochronies is difficult, since the available material is not suitable to study these characters at all whorls of each specimen in a qualitative sample. Usually, measurements of these characters can be done on one or two adjacent whorls.

To assess the effect of deceleration or acceleration of development, the concept of heterochronie range is used. For intraspecific heterochronies, it is calculated as the temporal or dimensional duration of the morphogenesis (ontogeny) of the individual, corresponding to the value of the heterochronous shift relative to that stage or moment in morphogenesis, which is characterized by average values of the character for the entire sample. The initial value of the range of heterochrony is calculated on dimensional quantities (shell diameter), after which it is translated into the number of whorls. For phylogenetic heterochronies, range is calculated as the interval between those moments in the morphogenesis of the ancestor and descendant, where the average statistical values of the trait are recorded.

The material used for the study of *Arcticoceras* at the terminal stage of development was 23 last body chambers, of which 12 were from sections of the Pechora River basin. The sample for measuring characters in internal whorls included 102 individuals, of which about half come from the Timan-Pechora region, and the rest from various regions of the Arctic (Northern and Eastern Siberia, Novaya Zemlya, Svalbard, Eastern Greenland, and Arctic Canada). Measurements were obtained both from specimens and from photographs of the published specimens.

MORPHOGENESIS RATE VARIABILITY IN *ARCTICOCERAS*

The terminal shell diameter (TD), measured near the final aperture, characterizes the moment of natural completion of ontogenesis (senile stage). In *Arcticoceras*, it varies over a wide range, from 110 to 161 mm. The average value that fixes the norm is 128 mm. All specimens having a smaller terminal diameter should be considered as rapidly aging, or tachygerontic (Pl. 3, fig. 4). Accordingly, specimens with a large finite diameter are bradygerontic (Pl. 4, figs. 1, 5). The area of normogeronty (mainly normal values near the average) is determined statistically and for this sample corresponds to an interval of values from 123.7 to 149.5 mm. In this area there are 13 specimens, of which nine come from sections of the Pechora River basin (Pl. 3, figs. 2, 3), 2 specimens from Northern Siberia, 2 specimens from East Greenland and one

from the Yukon (Fig. 1). The tachygerontic range of values (TD less than 123.7 mm) mainly includes specimens from the same regions, with the exception of Siberia. In the bradygerontic area (TD greater than 149.5 mm), Pechora specimens are absent, but specimens appear from the vicinity of Saratov, as well as from Northern Siberia and East Greenland. In this picture, no significant pattern is observed, particularly if the insufficient sampling in most regions except Timan-Pechora is taken into account. The variability of the Pechora *Arcticoceras* can be considered moderate (coefficient of variation 8.2%). It is difficult to assess the variability of populations of other regions on the available material. However, if the scale of variability seen in the Pechora population is accepted as normal for *Arcticoceras*, then the range of variability of the Arctic populations should be much wider.

Rib smoothing on the last body chamber. In *Arcticoceras*, as in most Arctocephalitinae, the sculpture is reduced at the terminal whorl and the last body chamber until it disappears completely, resulting in a stage with a smooth shell. While, the field of the terminal whorl covered with ornamentation (Lr) may differ in size in different species, so the angular length of this area may have diagnostic value. In particular, Melidina (1987) suggested that *A. harlandi* differs from *A. ishmae*, in addition to a set of other distinctive features, by the more later smoothing of the ribs. This can probably be a species level character, provided that its manifestation in morphogenesis is stable, due to low variability.

To test this hypothesis, we studied a sample of *Arcticoceras* specimens at the terminal stage, in which the length of the smooth and ornamented part in angular quantities was measured. The sample is dominated by specimens from the Pechora River basin, based on which the extent and range of variability of this character can be assessed.

Among the *Arcticoceras* of the Pechora sample, there are perfectly smooth specimens ($Lr = 0^\circ$, Pl. 3, figs. 4, 5) and partially ribbed ($360^\circ > Lr > 0^\circ$, Pl. 3, figs. 1–3, 6), but no specimens, completely covered with ornamentation ($Lr = 360^\circ$). The length of the ribbed part of the terminal whorl varies from 0° to 169° degrees; the mean is about 77.7° . The variability of this character is very high (coefficient of variation 64%).

Thus, the position of the smoothing point of the ornamentation in *A. ishmae* from Pechora varies within such wide limits that this feature is unlikely to be taxonomically valuable. The most likely explanation for such significant fluctuations of the character is associated with change in the rate of morphogenesis. Since ribbing is characteristic of earlier stages of development (middle whorls), and a smooth shell is characteristic of the terminal stage, the fluctuation of the smoothing point of the ribs reflects retardation or acceleration of development. An increase in the size of the ribbed part of the final whorl indicates retardation

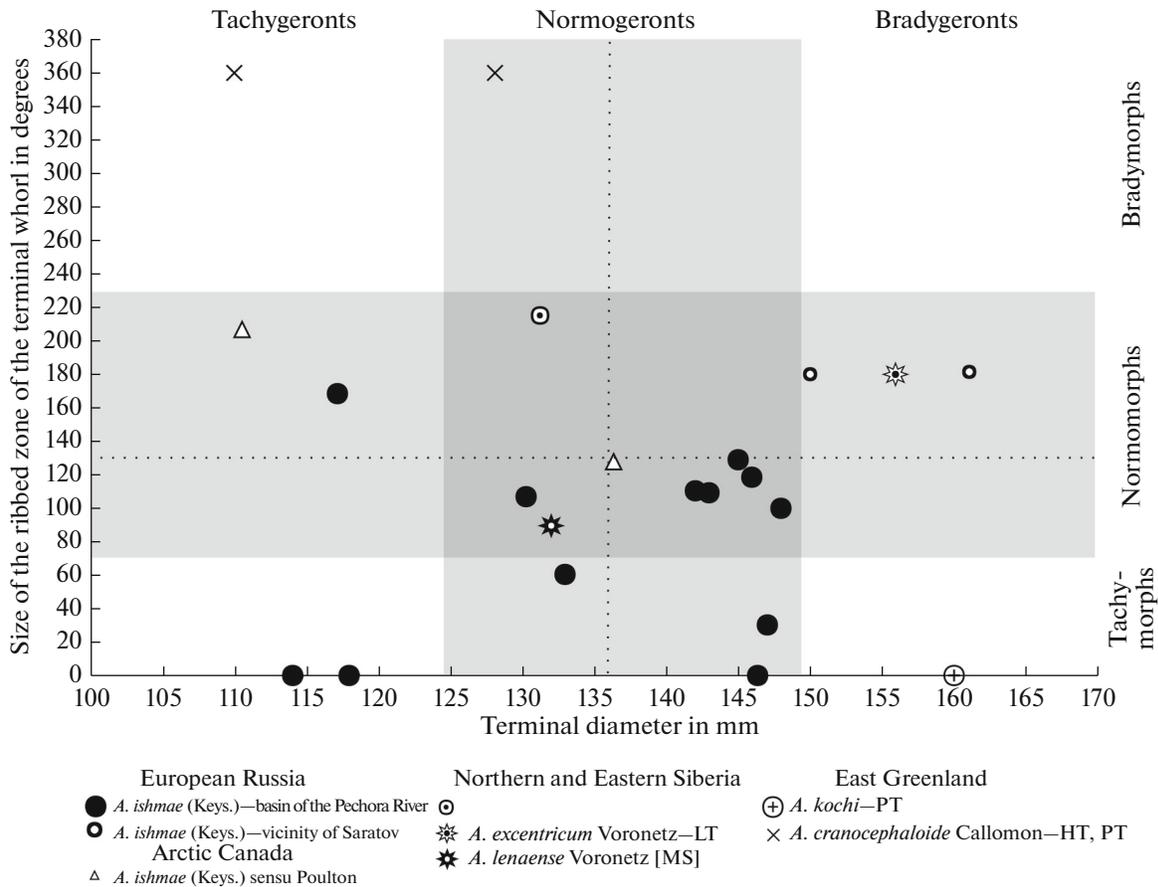


Fig. 1. Distribution of Lower and Middle Bathonian *Arcticoceras* specimens by size of rib area in terminal whorl, and final diameter of the shell. The solid fill shows the normal areas for the final diameter and preservation of the ribs.

in development, or bradymorphy, and vice versa, an increase in the smooth shell sector is a sign of accelerated development, tachymorphy.

The range of variability of all early Bathonian *Arcticoceras*, also including specimens of *A. ishmae* from the vicinity of Saratov and various regions of the Arctic, slightly exceeds that of the Pechora population: $Lr = 0^\circ - 215^\circ$, while the coefficient of variation for the entire sample is slightly less (53.5%). This suggests that a change in the rate of morphogenesis in all early Bathonian *Arcticoceras* occurs within approximately the same boundaries.

In contrast to *A. ishmae*, the middle Bathonian *Arcticoceras* (*A. cranocephaloide*) is distinguished by the absence of a smooth shell stage ($Lr = 360^\circ$). If we include both early and middle Bathonian specimens in the *Arcticoceras* sample, the picture of variability changes somewhat: the average value of the position of the ribbing smoothing point (129°) and the standard deviation (58%) increase. The area of normomorphic specimens is in the range $Lr = 70^\circ - 231.7^\circ$. Lower values, up to $Lr = 0^\circ$, characterize the area of tachymorphic individuals, higher values characterize the area of bradymorphic specimens. Early Bathonian populations

do not pass into the bradymorphic area and are prevalent in the normomorphic area (63% of specimens).

Rib branching. In *Arcticoceras*, branching of the primary ribs leads to the appearance of bipartite or tripartite secondary ribs, with one of the secondary ribs being loosely attached to the branching point, can be considered as intercalating. In the middle whorls ($D = 30 - 60$ mm) double ribs prevail, sometimes alternating with simple ones, which is expressed by a low branching coefficient (from 1 to 2). In adult whorls (with $D > 50 - 60$ mm), at the last whorls before the LBC, simple ribs are usually replaced by double ones, triple ribs appear, which sometimes increases the branching coefficient to 3. Thus, a low branching rate characterizes younger stages of development, and with age, it increases. Accordingly, variability in the rate of development on the basis of branching of the ribs can be manifested either in a decrease in the branching coefficient in adult whorls (bradymorphy), or in an increase in the branching coefficient in middle and early whorls (tachymorphy).

To analyze the development of the branching style of ribs in morphogenesis, a special indicator, the cumulative branching coefficient $R_{(i)}^f$, is used. It is cal-

culated for each rib as the arithmetic mean of the branching coefficients $R_{(i)}^f$ of all previous ribs: $R_{(i)}^f = 1/n(R_{(1)}^f + \dots + R_{(n)}^f)$. Each specimen is represented by a morphogenetic curve, the length of which corresponds to the number of ribs observed. Specimens of different morphogenetic age can be compared with each other according to the diameter of the shell by the method of proportions with a possible error of about 4–5 ribs. A sample of any population is a collection of individuals with different levels of tachymorphy or bradymorphy (Fig. 2).

A change in the rate of development of the trait is well manifested on the last two whorls before the smooth shell stage. In the adult stage (the last whorl before the smooth shell stage), the bradymorphic specimens are characterized by a branching index of less than 2.1, normomorphic specimens are in the range 2.1–2.6, and tachymorphic ones are above 2.6. At the middle stages of development, these boundaries are determined by lower values of the branching coefficient: bradymorphic individuals are in the range of values less than 1.2–1.6, normomorphic ones are 1.8–2.1, and tachymorphic ones are higher. The distribution of morphogenetic curves shows the following:

(A) Most of the specimens are characterized by an individual trend of branching, which, in general, is determined either by high values along the entire morphogenetic curve (for individuals with tachymorphic development) or low values (for bradymorphic individuals). This indicates that the acceleration or deceleration of development on this basis is inherent in most of the studied sector of morphogenesis, and not for some of its individual stages. Each individual is characterized by its own initial conditions of morphogenesis, which determine further development; therefore, the relative position of individual morphogenetic curves is not of use at the species level.

(B) Samples from the Pechora River basin are very variable. Nevertheless, most of the studied specimens (78%) are normomorphs. The lectotype of *A. ishmae* belongs to the same group (Fig. 2). The remaining groups, bradymorphic and tachymorphic are subordinate (5 and 17%). Different populations of this region

differ somewhat in the range of variability: the sample from Adzva sections only includes specimens from the tachymorphic and normomorphic groups, in contrast to the sample from the Izhma River. The same applies to a sample of *Arcticoceras* from the vicinity of Saratov. Probably, these differences do not reflect real provincial differences and are random in nature, due to the small sample size.

(C) Most of the specimens from the type series of *A. harlandi* are in the lower area of the normomorphic group and almost repeat the morphogenesis of the lectotype of *A. ishmae*. Only the smallest specimen (Rawson, 1982, pl. 2, fig. 5) partially relates to the bradymorphic group. Specimens of *Arcticoceras* from Yukon are mainly characterized by the values of the tachymorphic group. In this group they occupy a high position, which is not very characteristic of *A. ishmae*. Possibly, these differences can already be interpreted as taxonomic.

Combinations of intraspecific heterochronies. Comparison of the pattern of variability of three characters (terminal diameter, size of the ribbed area on the terminal whorl and the branching parameter of the ribs) shows that the change in the rate of development proceeds unequally for different reasons. According to two characteristics, several types of such combinations can be distinguished in various specimens (Table 1). The largest number of specimens are in the normal range ($N = 9$), however, the total sample from marginal areas is numerically predominant ($N = 13$). This means that the population has a lot of evasive forms, which can, depending on subjective preferences, be taken for species in their own right.

The combination of different developmental rates in three ways has a more complex picture. One can distinguish 27 types of such combinations, from the state of complete tachymorphy to complete bradymorphy (Table 2).

It is difficult to determine the frequency ratio of these combinations, since the type of combination cannot be fully determined for each shell, but only on a specimen suitable for uncoiling with a last body chamber or, in some cases, without LBC, but with the penultimate whorl that retains the final septa. Unfor-

Fig. 2. Changes in the cumulative branching coefficient $R_{(i)}^f$ in the morphogenesis of *Arcticoceras ishmae* (Keys.) specimens from different regions of the Panboreal Superrealm. The horizontal axis shows N_r —the ordinal number of the ribs, while the minimum value ($N_r = 0$) corresponds to the last rib before the smooth shell stage. (HT) holotype, (LT) lectotype, (PT) paratype. Vertical dashed lines indicate the averaged position of the boundaries of whorls. (TW) terminal whorl. An asterisk indicates the beginning of the last body chamber. (1) Mitta and Seltzer (2002, pl. 3); (2) specimen YarGPU, no. Dr/2-2; (3) specimen YarGPU, no. Dr/2-1; (4) Mitta et al., 2015, figs. 6-2; (5) Mitta et al., 2015, figs. 6-3; (6) specimen YarGPU, no. Dr/2-4; (7) Mitta et al., 2015, fig. 5-1; (8) Repin et al., 2006, pl. 8, fig. 5 (= *A. ishmae tenuicostatum* Repin, HT); (9) Repin et al., 2006, pl. 13, figs. 1a–1d (= *A. ishmae ishmae* (Keyserling), HT); (10) Mitta et al., 2015, fig. 5-2; (11) specimen YarGPU, no. Dr/2-5; (12) specimen YarGPU, no. ADZ-7; (13) specimen YarGPU, no. ADZ-2; (14) specimen YarGPU no. ADZ-10; (15) specimen YarGPU no. ADZ-13; (16) specimen YarGPU, no. ADZ-11; (17) specimen YarGPU, no. ADZ-12; (18) Poulton, 1987, pl. 20, fig. 1; (19) Poulton, 1987, pl. 20, figs. 5–8; (20) Poulton, 1987, pl. 19, fig. 5; (21) Poulton, 1987, pl. 19, fig. 2; (22) Poulton, 1987, pl. 20, fig. 3, 4; (23) Poulton, 1987, pl. 21, fig. 5; (24) Rawson, 1982, pl. 2, fig. 2; (25) Rawson, 1982, pl. 2, fig. 4 (= *A. harlandi* Rawson, HT); (26) Rawson, 1982, pl. 2, fig. 7; (27) Rawson, 1982, pl. 2, fig. 5.

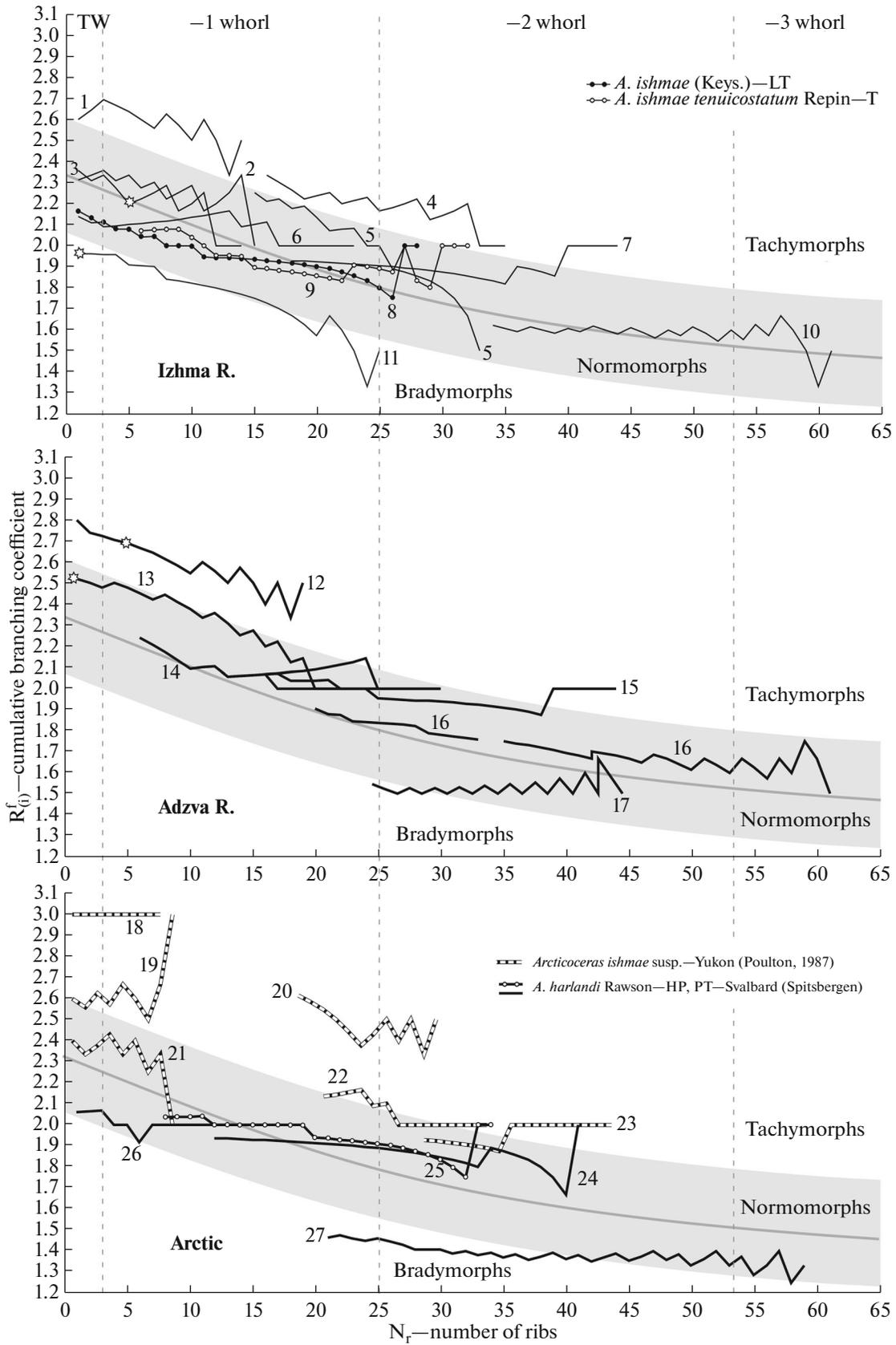


Table 1. Combinations of different modes of changing the rate of development in *Arcticoceras* by two characters, the size of the rib smoothing zone in the final whorl (SRS) and the terminal shell diameter (row above). The sample contains only specimens with a complete last body chamber. The numbers indicate the number of specimens per each combination

	Tachygeronty	Normogeronty	Bradygeronty	Total
Tachymorphy by SRZ	2	3	0	5
Normomorphy by SRZ	2	9	3	14
Bradymorphy by SRZ	1	1	1	3
Total	5	13	4	22

Table 2. Combinations of different modes of change in the developmental rate of *Arcticoceras* by three characters, including the size of the ribbed zone in the terminal whorl (SRZ), the terminal shell diameter (TD), and the branching coefficient (BC). In the combination formula, the first letter indicates the mode according to SRZ, the second letter according to BC, and the third letter according to TD

	Tachygeronty (TD)			Normogeronty (TD)			Bradygeronty (TD)		
	Tachymorphy for BC	Normomorphy for BC	Bradymorphy for BC	Tachymorphy for BC	Normomorphy for BC	Bradymorphy for BC	Tachymorphy for BC	Normomorphy for BC	Bradymorphy for BC
Tachymorphy for SRZ	TTT	TNT	TBT	TTN	TNN	TBN	TTB	TNB	TBB
Normomorphy for SRZ	NTT	NNT	NBT	NTN	NNN	NBN	NTB	NNB	NBB
Bradymorphy for SRZ	BTT	BNT	BBT	BTN	BNN	BBN	BTB	BNB	BBB

unately, this is not possible to determine from most of the available specimens, so we consider only some examples of combinations.

NNB-morph: specimen ADZ-2 from a section on the Adzva River (pl. IV, fig. 4, text-fig. 2 (13)), studied from the last two whorls, including the terminal whorl. The whorls are moderately high, closer to isometric, with prominent ornamentation.

BTN-morph: specimen ADZ-7 from the section to the Adzva River (pl. 3, fig. 3; pl. 4, fig. 1; fig. 2 (12)). It is characterized by an elegant morphotype, high whorls covered with a weakly prominent ornamentation. According to $R_{(i)}^f$, this specimen is located on the border of the normomorphic and tachymorphic area,

and according to TD, it is the tachygerontic and normogerontic area.

BNB-morph: specimen Dr / 2-1 from the section on the river. Dreshchanka (pl. 3, fig. 6; fig. 2 (3)), found at the bottom of the *Arcticoceras* sandstone layer. High whorls, ornamentation moderately prominent.

BBB-morph: specimens are completely bradymorphic, sometimes considered typical of *A. ishmae*. Presumably, the specimen from the Pechora River basin described by Spath (1932, pl. 15, fig. 7) can be assigned to this morph. From my sample, a specimen from the Dreshchanka River section Dr/2-5 (pl. 4, fig. 3, fig. 2 (11)), represented by a complete phragmone with the last septum, also belongs to this morph. The lectotype of *A. ishmae* is very similar to this spec-

Explanation of Plate 3

Fig. 1–6. *Arcticoceras ishmae* (Keys.): (1) bradygerontic normomorph; specimen TsNIGR Museum, no. 6/1370 (specimen illustrated from the opposite side by Sokolov (1912, pl. 1, fig. 1) as *Macrocephalites ishmae* Milach.); (2) normogerontic normomorph; specimen YarGPU, no. ADZ-8; (3) normogerontic bradymorph (BTN-morph); specimen YarGPU, no. ADZ-7; (4) tachygerontic tachymorph; specimen YarGPU, no. ADZ-3; (5) bradygerontic tachymorph; specimen YarGPU, no. ADZ-1; (6) bradygerontic bradymorph (BNB-morph); specimen YarGPU no. Dr/2-1.

All specimens are represented by last body chamber with terminal apertures; (1–5) Adzva River, Nikiforov Shcheliya; (6) Dreshchanka River, section no. 5. All specimens illustrated come from the Lower Bathonian, *Arcticoceras ishmae* Zone.

Explanation: (LBC) last body chamber, (YarGPU) A.N. Ivanov Geological Museum (Yaroslavl State Pedagogical University); (TSNIGR Museum) F.N. Chernyshev Central Research Geological Exploration Museum (St. Petersburg). The asterisk (*) indicates the beginning of the last body chamber. Scale bar 10 mm.



imen, although it is a normomorph according to its $R_{(i)}^f$ value (Fig. 2 (8)).

BTF-morph: specimens are often characterized by very rough ornamentation on adult whorls. They are known from the Izhma River basin and are most often identified as *A. harlandi* (Meledina, 1987, pl. 29, fig. 1; Mitta and Seltzer, 2002, pl. 3, fig. 1) or *A. aff. cranocephaloide* (Meledina, 1987, pl. 28, fig. 1).

BNN-morph: specimen with an almost complete LBC, found in the vicinity of Saratov (Mitta and Seltzer, 2002, pl. 3, fig. 1).

Evidently, the rate of development for all three characters rarely changes in one direction, i.e., in the direction of bradymorphy or tachymorphy. Most commonly, the morphotype develops with a set of characters changing simultaneously.

DISCUSSION

The results show that the variability of the rate of morphogenesis includes not only the variability of the development of individual characters (intraspecific heterochrony, according to Reilly et al., 1997), but also the variability of combinations of intraspecific heterochronies. The latter reflects the phenomenon of modularity of development. In *Arcticoceras*, it was revealed by few characters, but probably all the characters of the shell to one degree or another could develop asynchronously. This is especially true for characters where change occurs according to a distinct trend. Among *Arcticoceras*, among other shell characters, this trend is characterized by the development of the density of primary ribs. It noticeably decreases exponentially towards the last whorls (Kiselev, 2020), therefore, the bradymorphic specimens on adult whorls should be characterized by frequent ribbing, and tachymorphic by widely spaced ribbing. At present, this trend has only been identified statistically (mainly from a sample of the Pechora River basin), therefore, based on this, only preliminary conclusions can be drawn on the variability of the development of *Arcticoceras*. However, it can be assumed that this feature behaves asynchronously in relation to others. This is clearly visible in two specimens from the Pechora River basin (pl. 3, figs. 3, 6). They are both bradymorphic in terms of degree of smoothing of the ribs, but at the same time in terms of density of the ribs one of them is bradymorphic (pl. 3, fig. 6), and the other is tachymorphic (pl. 3, fig. 3). Without taking into

account such combinations of variability, these specimens could be attributed to different species, which often occurs in biostratigraphic practice. Similar results were obtained on other groups of ammonites. In particular, the mosaic development of shell features is observed in two species of the genus *Titanites*, which also show different combinations of bradygeronty and tachygeronty with bradygeronty and tachygeronty according to several characters (Kiselev and Rogov, 2018).

Analysis of the sutural complexity, which has proven itself in the study of Paleozoic ammonoids, offers great prospects in the study of heterochrony in Mesozoic ammonites. It was shown that individual elements of the suture develop asynchronously, i.e., at different rates (Leonova, 2012, etc.). This feature is considered on the basis of an analysis of only phylogenetic heterochronies, but it is probably also inherent in intraspecific heterochronies. Unfortunately, in *Arcticoceras*, poor preservation of specimens prevents the study of the variability of the septum shape on bulk material.

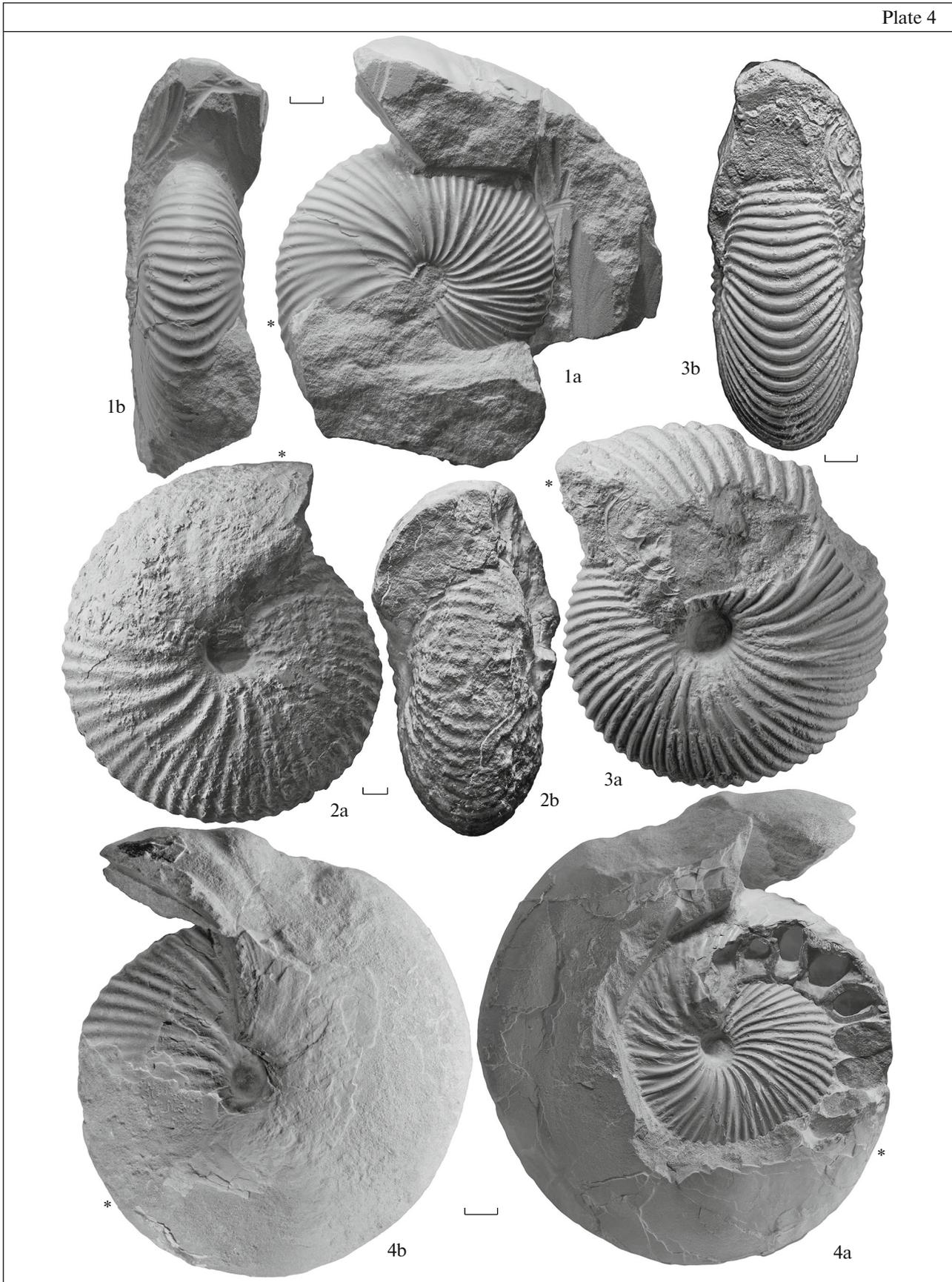
According to the studied characters, only the mainly Early Bathonian *Arcticoceras* can be most reliably distinguished from the mainly Middle Bathonian. Thus, *A. cranocephaloide* (Middle Bathonian) differs dramatically from the stratigraphically preceding *A. ishmae* (Early Bathonian), primarily due to the absence of a smooth shell stage in the final whorl. The last body chamber of this species is covered with pronounced ribs, most commonly with a low branching coefficient.

The origin of *A. cranocephaloide* is probably due to retardation (a type of paedomorphosis). This is indicated by the presence at the terminal stage of development of characters observed in the early and middle whorls of the ancestral Early Bathonian *Arcticoceras*, i.e., preservation of ribs with a low branching coefficient along the entire length of the last body chamber and a large relative umbilical diameter. The range of retardation for all the studied characters exceeds the range of intraspecific heterochronies, but for different characters this excess is not the same (Table 3). This is most characteristic of the size of the zone with smoothed ribs, the delay of occurrence of which (0.76 whorl) exceeds the individual fluctuations in the rate of morphogenesis in *A. ishmae* by 5.63 times. However, according to the range of the delay, the

Explanation of Plate 4

Figs. 1–4. *Arcticoceras ishmae* (Keys.): (1) normogerontic bradymorph (BTN-morph); specimen YarGPU, no. ADZ-7 (illustrated from the opposite side in pl. 3, fig. 3); Adzva River, Nikiforova Shcheliya section; (2) bradygerontic bradymorph (BTB-morph); specimen TsNIGR Museum, no. 5/274, coll. A.N. Zamyatin; Izhma River, Razlivnoi Rapids; (3) bradygerontic bradymorph (BBB-morph); specimen YarGPU, no. Dr/2-5; Dreshchanka River, section no. 5; (4) bradygerontic normomorph (NNB-morph); specimen YarGPU, no. ADZ-2; R. Adzva, Nikiforova Shcheliya section. Figures 1 and 4 show the last body chambers with a terminal aperture. All illustrated specimens come from the Lower Bathonian, *Arcticoceras ishmae* Zone.

Explanations are as for Plate 3. Scale bar 10 mm.



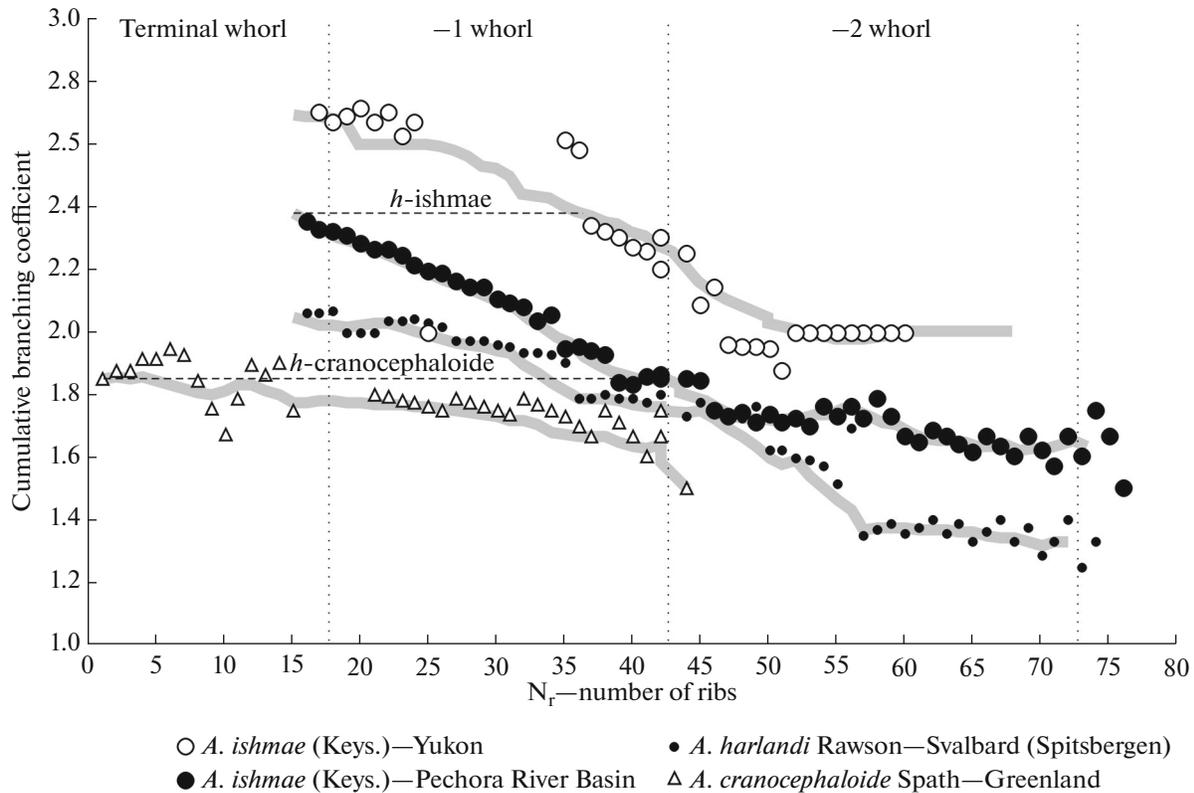


Fig. 3. Change in average cumulative branching coefficient $R_{(i)}^f$ in the morphogenesis of *Arcticoceras ishmae* of the Pechora River basin, Yukon, and Svalbard (Spitsbergen) and *A. cranocephaloide* of East Greenland. Morphogenetic curves are plotted based on average values of $R_{(i)}^f$ of each rib of all specimens (in Fig. 2) of the sample of the corresponding region. Gray line shows the trend line (filter line). Vertical dashed lines show an averaged position of the whorl boundaries, horizontal lines show range of pedomorphosis for *A. ishmae* and *A. cranocephaloide*.

branching coefficient is in first place (1.16 whorls) among the characters (Fig. 3).

The origin of the Middle Bathonian *Arcticoceras* is due to retardation, mainly according to two ornamentation traits (SRZ and BC). This indicates an insignificant disparity of this heterochrony. Perhaps the retarda-

tion associated with the appearance of *A. cranocephaloide* is combined with progenetic hypomorphosis (Schmalhausen, 1939, sensu Reilly et al., 1997) or pre-displacement. This is indicated by an average statistical decrease in the final diameter of the shell of this species, corresponding to a range of 0.19 whorls. This

Table 3. Mean range of individual heterochronies (bm, tm, bt, tt) in *Arcticoceras ishmae* (Keys.) and phylogenetic heterochronies (RI, R) in *Arcticoceras*. All range values are given in the number of whorls. The ratio of the range of phylogenetic heterochronies to the individual heterochronies is shown at the bottom of the table. Shading shows areas of impossible combinations

Heterochronies	Primary rib density (PRD)	Terminal diameter (TD)	Size of ribbed zone (SRZ)	Branching coefficient (BC)
Bradymorphy (bm)	0.31		0.1	0.48
Tachymorphy (tm)	0.43		0.17	0.43
Bradygeronty (bt)		0.08		
Tachygeronty (tt)		0.12		
Partial retardation (RI)				0.8
Retardation (R)	0.41	0.19	0.76	1.16
R/(bm, tm, bt, tt)	1.14	1.9	5.63	2.55

Stage, substage		Subfamily, genus, subgenus		Species	Heterochronies	
Bathonian	Early	Arctocéphalitiinae	Arcticoceras	<i>A. ishmae</i> (Keys.) subsp.	Partial retardation	Paedomorphosis
	Middle			<i>A. ishmae ishmae</i> (Keys.)		
	Late			<i>A. cranocephaloide</i> Spath	Partial acceleration	
Callovian	Early	Cadoceratinae	Cadoceras (Catacadoceras)	<i>C. variabile</i> Spath		Acceleration
				<i>C. barnstoni</i> (Meek.)		
			Cadoceras (Paracadoceras)	<i>C. infimum</i> Gul. et Kis.		
				<i>C. breve</i> (Blake)		
Cadochamoussetia	<i>C. frearsi</i> (Orb.)					
	<i>C. elatmae</i> (Nik.)					
Chamoussetia	<i>Cdch. tschernyschewi</i> Sok.					
	<i>Cdch. surensis</i> (Nik.)					
	<i>Cdch. subpatruus</i> (Nik.)					
			<i>Ch. chamousseti</i> (Orb.)			

Fig. 4. The role of heterochrony in the phylogeny of early Cardioceratidae. See text for explanations.

is almost twice as great as the fluctuations of individual decelerations and accelerations for this trait in the ancestral species *A. ishmae*.

The immediate descendants of *Arcticoceras* are cadoceratins, whose appearance dates back to the Late Bathonian. Further evolution of this group is due to a change in the morphotype of the last body chamber and the re-appearance of the smooth shell stage. The first representatives of cadoceratins (*Cadoceras* (*Catacadoceras*) *variabile* Spath) are characterized, like the Middle-Bathonian *Arcticoceras*, by the preservation of ribs on the LBC. However, ornamentation in the final whorl already shows signs of reduction. We see a slight phylogenetic acceleration of development, which does not lead to the emergence of a new morphological stage at the end of ontogeny. This type of heterochrony corresponds to partial acceleration. The further path of evolution, already in the Early Callovian Chron, when the adult whorls of cadoceratins are substantially or completely smoothed out, is due to anaboly, i.e., by complete acceleration (Fig. 4).

For the early Bathonian *Arcticoceras* sample, two characters—the size of the smoothing rib zone in the final whorl and the terminal shell diameter—have no taxonomic significance either for the allocation of species or for finer, subspecific, differentiation. According to these characteristics, differences between available species are random and reflect only the randomness of the sample. Similar results were previously obtained from the study of the variability of other shell traits, i.e., the proportions of the cross section, diameter of the umbilicus, and rib density (Kiselev, 2020).

Therefore, most of these species (*A. stepankovi*, *A. kochi*, *A. pseudishmae*, *A. excentricum*, and *A. harlandi*) should be considered invalid. All of the above species are considered here as synonyms of the species *A. ishmae*. Its variations are morphs of intraspecific variability, the specificity of which is more or less related to intraspecific heterochronies. Bradymorphic species include specimens with a sparsely ornamented adult shell, close to *A. stepankovi* and *A. excentricum* (*A. ishmae* morpho *stepankovi*). Tachymorphic variations in the density of ribs include often-ribbed forms, which are sometimes considered as an independent subspecies of *A. ishmae tenuicostatum* Repin (holotype: Repin et al., 2006, pl. 8, fig. 5). The same morphotype in terms of branching coefficient belongs to a normomorphic group. *Arcticoceras* from Yukon dominated by tachymorphic varieties (Poulton, 1987) are more readily distinguished among the Early Bathonian populations by rib branching (Fig. 3). On average, they are characterized by a higher branching coefficient at all studied stages of morphogenesis (last 2.5 whorls) compared to *A. ishmae* of the Timan-Pechora region.

Considerable differences between the Yukon *Arcticoceras* and the Pechora *Arcticoceras* are also observed in other characters (Kiselev, 2020), therefore, probably, they should differ taxonomically at the subspecies level. It has been shown (Kiselev, 2020) that the Yukon subspecies is older than *A. ishmae ishmae*, therefore the latter should be considered as a phylogenetic descendant. Its origin is associated with a delay in branching coefficient, with a range of 0.8 whorl. Since the terminal stage of morphogenesis (smooth shell) does not occur in this case, such heterochrony should be attributed to partial retardation or bradygenesis. It is possible that large samples from different regions

may reveal mean values with stable statistical differences, but at the moment there is clearly not enough material to obtain such data.

CONCLUSIONS

Modularity in the individual morphogenesis of the ammonite shell manifests itself in a combination of intraspecific heterochronies of different traits, i.e., decelerations and accelerations of the development of a whole complex of characters. The criterion for such delays or accelerations in the morphogenesis of an individual is the deviation of the development of characters relative to the mean values characteristic of the population as a whole, and not the confinement of the character to one or another stage of morphogenesis, as is typical for phylogenetic heterochrony. Also, intraspecific heterochronies differ from phylogenetic ones by a significantly lower disparity and smaller range of individual traits. In *Arcticoceras*, intraspecific heterochronies are noted at the middle and late stages of development, which are characterized by specific characters. The variability of the combinations of intraspecific heterochrony is the reason for the high morphological diversity within the *A. ishmae* species, which allows most of the Early Bathonian species of *Arcticoceras* to be synonymized. The phylogenetic development of *Arcticoceras* during the Early and Middle Bathonian occurs along the path of stepwise paedomorphosis, first partial and then general retardation, which ultimately manifests itself in the loss (reduction) of the smooth shell stage in the terminal whorl in the last representatives of this genus.

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