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INTRASPECIFIC VARIABILITY IN THE VOLGIAN AMMONITES*

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ABSTRACT: The ammonites from the middle substage of the Upper Jurassic Volgian stage on the Russian craton have long attracted investigators because of their wide intraspecific variability, which has at times hindered the drawing of boundaries between species. Therefore, quite often, especially in small collections, "atypical" specimens have been described as separate species, and the variation within a species has not been taken into account. In this paper, I have revised the families Virgatitidae and Dorsoplanititidae on the basis of the polytypic concept of the species, and in so doing I have attempted to analyze the variation in the Volgian ammonites.

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The intraspecific variation in the Volgian ammonites, in sample populations of well-preserved specimens, can be broken down into three main types: brady- and tachymorphy (the result of variation in rate of morphogenesis of the shell), brady- and tachygeronticity (the presence of "pathologic giants" and "dwarves"), and sexual dimorphism. All three variations can be seen in the Virgatitidae, the Dorsoplanitidae, and also the Craspedititae.

The different rates of shell morphogenesis in individuals of the same species were first noted, in the Volgian ammonites, by Michalskiy [5] and later came to be known as tachymorphy and bradymorphy [13, 14]. In the tachymorphic species, the shell or separate elements of it (the sculpture, cross-sectional shape, width of the umbilicus, angle of inclination of the umbilical wall) even at small diameters have already taken on an appearance usually typical of a later stage of development. In the bradymorphic individuals the shell for a long time retains features typical of a younger individual. Brady- and tachymorphy are most clearly manifested in the duration of one or another stage of development of the sculpture, the extreme representatives of the variation series (typical bradymorphs and typical tachymorphs) often differing so strongly that, if the collections do not contain "normal" (or normomorphic) forms, they may be described as different species, although they occur at the same stratigraphic level. Figure 1a-c shows specimens of *Virgatites pusillus* (Mich.) from the same stratigraphic level (the upper part of the *Virgatites virgatus s. str.* subzone) and from the same locality (open pit No. 9 of the Lopatinskiy phosphorite mine in the Moscow region). They have phragmocones of similar size and, judging by the decrease in involutedness of the last whorl from the beginning of the living chamber, also similar final diameters. The individuals shown in figure 1a, c are the extreme or end members of the variation series (the sample population consists of 24 specimens), and the specimen represented in figure 1b is an average member of this series. In this last (normomorphic) specimen, the change from the virgatotome stage of development to the bifurcate stage occurs at the diameter of about 75 mm. In the bradymorphic specimen (fig. 1a) the virgatotome stage is "drawn out" in

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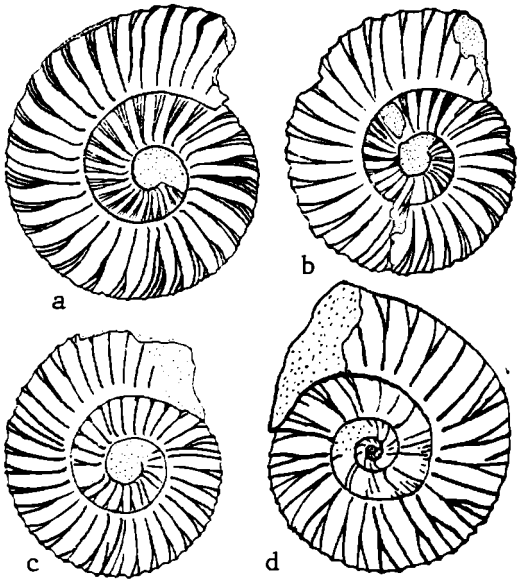

Fig. 1. Variation in Volgian ammonoid *Virgatites pusillus* (Michalskiy) from open pits of Lopatinskiy phosphorite mine (Moscow region; *Virgatites virgatus* subzone): *a* - Spec. PIN 3990/121, bradymorphic individual; *b* - Spec. PIN 3990/120, normomorphic individual; *c* - Spec. PIN 3990/152, tachymorphic individual; open pit No. 9 (*a-c* ×0.35); *d* - Spec. PIN 3990/104, tachygerontic individual; open pit No. 9-bis (×0.7).

time and the first bifurcate costae appear only at the diameter of more than 100 mm. In the tachymorphic specimen (fig. 1c) the virgatotome stage of costation is strongly curtailed, and bifurcate ribs already appear at a diameter of about 45 mm; in the latter, the virgatotome costae are associated exclusively with constrictions.

Thus tachy- and bradymorphy mean, respectively, acceleration or retardation in the development of features reflecting variation within a population. They can be clearly discerned in collections from the same stratigraphic level and the same locality. The phenomena of analogous character, differentiated in space or time, are called tachygenesis (author of term, Smith [15]) and bradygenesis (author of term, Grabau [9]). Beginning with Schmidt [13], a number of investigators [3, etc.] have used these terms in somewhat altered form — tachygeny and bradygeny. The processes of tachy- and bradygenesis, however, go beyond the limits of infrasubspecific variation and obviously lead to the formation of new species (or subspecies).

Within a species one occasionally encounters individuals that are two or three times larger or, on the contrary, smaller, than the ordinary representatives of that particular species. In view of the fact that the tachymorphic and bradymorphic specimens are of similar size, it must be supposed that the presence of "giants" and "dwarves" is due to different causes than tachy- and bradymorphy. To designate such forms, I shall use Teisseyre's terms [16] "bradygerontic" (aging slowly) and "tachygerontic" (aging rapidly), which were initially proposed for forms that later came to be called macro- and microconchs [8]. One could probably also use the terminology of Holder [10], who proposed the term "microgerontic" to designate the individuals within a species that have features of senescence at small diameters.

Tachygerontic and bradygerontic individuals occur rarely and are represented by only a few specimens in collections; but since there are cases of their description as separate independent species, this phenomenon must also be taken into account.

Tachygerontic individuals are specimens that reached maturity early and then evidently ceased to grow. They differ from the usual representatives of a species

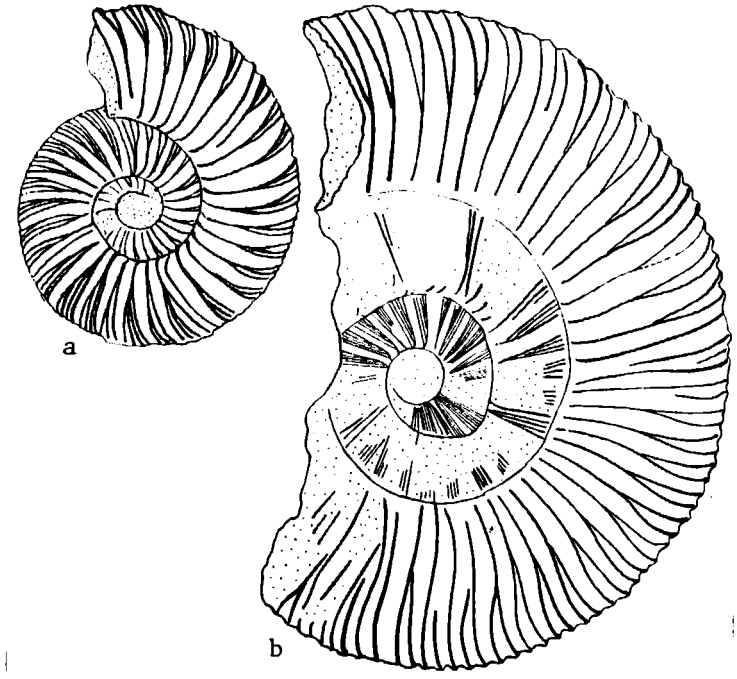

Fig. 2. Normo- and bradygerontic representatives of *Virgatites virgatus* (Buch) from Volgian (*V. virgatus* subzone) in Moscow region: *a* - Spec. PIN 3990/107, normogerontic individual; Yegor'yevskiy phosphorite mine, open pit No. 11 (×0.4); *b* - Spec. PIN 3990/112, bradygerontic individual; Lopatinskiy phosphorite mine, open pit No. 9 (×0.35).

in having adult features of their shell (a slightly involute last whorl and very wide umbilicus) combined with a size two or three times smaller. Figure 1d shows the phragmocone of *Virgatites pusillus* (Michalskiy) with a well-marked uncoiling of the last whorl and a very wide umbilicus, and a mature bifurcate stage of costation. With the living chamber, which occupies three-fourths of a whorl, this specimen will be twice smaller than the usual (normogerontic) representatives of the same species (fig. 1a-c).

The bradygerontic specimens are those that two or three times exceed the diameter of the normogerontic representatives. For example, *Virgatites virgatus* (Buch) on the average reaches a diameter of 120 mm (with the living chamber) (fig. 2a). Figure 2b shows a specimen of the same species (phragmocone) reaching a diameter of 230 mm.

Bradygerontic specimens have also been found in other groups of Volgian ammonites. *Kachpurites fulgens* (Trautsch.), the index species of the lower zone of the Upper Volgian substage, on the average reaches 60 mm in diameter, but in a few individual cases 250 mm in diameter. *Garniericeras catenulatum* (Fischer), which also occurs in the Upper Volgian, usually reaches a diameter of 60-80 mm, but individuals reaching 220 mm in diameter have been found [2].

The bradygerontic individuals, because of their anomalously large size, can be readily distinguished against the background of the individuals of normal size and have quite often been described as separate species. For example, large specimens of various species of *Virgatites* have been described [6] as the separate species *Virgatites giganteus*. The holotype of *Pavlovia menneri* Michailov differs from the previously described *Pavlovia pavlovi* (Michalskiy) only in size (which is twice larger), but has middle whorls practically indistinguishable from those of corresponding diameter of the holotype of *P. pavlovi* (the holotype of *P. menneri* is the only known specimen of *Pavlovia* of such size, and the usual representatives of this species have a diameter only half as large).

Bradygeronticity, like tachygeronticity, may be due to various causes, including disturbances in the action of sex glands [7] and gene mutations. In the latter case it is of definite interest to examine the possible connection between bradygeronticity and the frequently observed increase in size of the representatives of a taxon during its period of flourishing just before it becomes extinct. A general increase in size can also be seen both within a species (for example, *Virgatites pusillus*, which occurs in the *virgatus s. str.* subzone, on the whole is larger than the representatives of the same species from the *gerassimovi* subzone) and within a genus (the species of *Dorsoplanites* from the *panderi* zone are far smaller in size than their descendants, which are assigned to the same genus, from the *virgatus* zone). Nevertheless, one must differentiate the bradygeronts from species with a generally large shell, and also from geographic populations with large shells.

The third group of intraspecific differences is represented by sexual dimorphism. At the present time, the existence of micro- and macroconchs is commonly regarded as a manifestation of sexual dimorphism. But in the case of the Volgian ammonites, no very important features of micro- and macroconchs are manifested--the differences are in the structure of the peristome and the length of the living chamber. The peristome (as far as can be judged by the somewhat rare specimens with mouth aperture preserved) in the Volgian ammonites was plain, without ventral and lateral outgrowths, with a more-or-less well manifested funnel and a more-or-less deep constriction. The length of the living chamber in any single genus and, evidently, also family, is also constant. Thus it would not seem possible to distinguish micro- and macroconchs by size among the Volgian ammonites.

Some investigators [2, 11] have considered the variations in shell form and its section and the distinctive features of its sculpture to be expressions of sexual dimorphism. And, indeed, in representative populations the vast majority of species of Volgian ammonites can be broken down into two intraspecific morphological groups (here and below, I shall use this, in my opinion, neutral term that does not imply sexual dimorphism as its cause). These groups are characterized by common differences within a particular higher taxon. In the case of the Dorsoplanitidae one can easily differentiate individuals with a lower cross section and inflated periumbilical costae (dorsoplanoidy) from those with a higher section and costae of equal height throughout their length. For example, Vischniakoff [4, 17] understood the species *Dorsoplanites panderi* (d'Orb.) to include two "varieties"--*typica* [17, pl. 2, fig. 1] and *orbignyana* [17, pl. 1bis, fig. 1], corresponding to my morphological groups within this species. The features enabling a specimen to be assigned to one morphogroup or the other can be discerned beginning with the sixth and in the seventh whorl--that is, in the mature adult whorls. In the case of juvenile individuals it does not seem possible to distinguish between the representatives of the morphogroups (sexes).

In the Craspeditidae, which some investigators consider to be descendants of the Dorsoplanitidae [1], the morphological groups are similarly manifested. In *Craspedites okensis* (d'Orb.) there are individuals with and without distinct periumbilical tubercles [2]; in *Kachpurites fulgens* (Trautsch.), the forms *adulta* and *junior* have been distinguished respectively by the analogous criterion [12, pl. K, figs. 85, 86].

The morphological groups are somewhat differently distinguished in these Virgatitidae. Here the differences lie in the points of branching of the costae and also, as in the preceding cases, in the height and shape of the cross section (fig. 3) (the specimens of *Virgatites pusillus* used for the illustration of bradymorphy and tachymorphy (fig. 1a-c) belong to the same morphological group).

Although the morphological groups show a general similarity of the differences within a family, they differ in details at the generic level, and in more particular details between species within a genus. The numerical ratios of the representatives of both morphological groups within each species found at the same stratigraphic level are approximately equal.

The mutual intercombination of the three main types of variability described here in the Volgian ammonites hinders detection of the boundaries of a species, but can be quite easily recognized, if sufficiently representative collections are available. Curiously enough, the tachgerontic and bradygerontic individuals cannot be assigned to one morphogroup or the other; however, this may be due to the uniqueness of the finds of such specimens.

Thus, it follows that:

1. The variation in rate of morphogenesis of the shell or its individual elements is a characteristic feature of the Volgian ammonites, not clearly manifested in the duration of one or another stage of development of the sculpture. Specimens are tachymorphic if at an early age they show features usually characteristic of

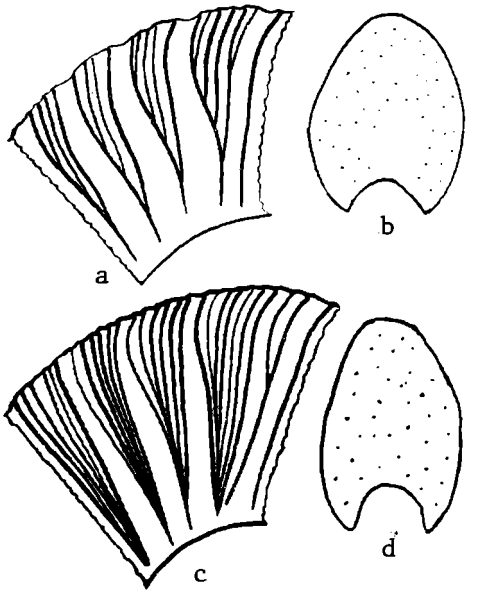

Fig. 3. Morphological groups of *Virgatites gerassimovi* Mitta in Volgian (*V. gerassimovi* subzone) of Lopatinskiy phosphorite mine (×2/3): *a*, *b* - Spec. PIN 3990/80, open pit No. 14; *c*, *d* - Spec. PIN 3990/83, open pit No. 7-2-bis.

more mature individuals, and are bradymorphic in the opposite case. Brady- and tachymorphy have the character of intraspecific variability if the specimens are confined to one stratigraphic level of a concrete exposure. The analogous phenomenon is called brady- and tachygenesis (brady- and tachygeny) if the bradymorphic and tachymorphic specimens are differentiated in space or time. Brady- and tachygenesis lead to the rise of new species (subspecies) and go beyond the limits of infrasubspecific variation.

2. Within a species, one finds bradygerontic (macrogerontic) and tachygerontic (microgerontic) individuals, which are represented by a few solitary specimens and have a final diameter correspondingly somewhat larger or smaller than the normally developed individuals. Brady- and tachygerontic specimens should not be distinguished as independent species; bradygerontic must be differentiated from species and also from populations with large shells.

3. The absence, in the ammonites of the Volgian age, of differences on the basis of which micro- and macroconchs can be distinguished--in shape of the peristome or in length of the living chamber--compels us to infer a greater variety of manifestations of sexual dimorphism than only the presence of macro- and microconch forms. The existence of two morphological groups characterized by variations in cross-sectional form and sculpture in all thoroughly studied Dorsoplanitinae, Virgatitinae, and some Craspeditinae enables these groups to be presumably regarded as particular cases of sexual dimorphism.

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