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Quantitative and qualitative aspects of changes in shell size through the evolution of Volgian ammonites in the Russian Sea: Cope's rule, Lilliput effect, dimorphism, and polymorphism

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Recent advances in studies of biodiversity changes and evolution of fossil lineages through time rarely considered quantitative changes in fossil populations. Investigations of changes in size through evolution are relatively common, but mainly focus on mass-extinction time-intervals and usually do not include observations on dimorphism and polymorphism. Here I am presenting a few examples of evolution of Volgian ammonite faunas in the Russian Sea, showing quantitative and qualitative aspects of changes in shell size.

(1) Cope's rule in the evolution of Volgian ammonites

The Volgian Stage is well-known as a time when giant ammonites were common, but rate and time of size increase differ significantly within lineages. Members of the Virgatitidae family, endemic to the Subboreal Russian and Polish seas, show a gradual increase in the size of macroconchs during the Early and Middle Volgian, while the size of microconchs remains nearly constant (see also below). Larger virgatitids (megaconchs *Virgatites giganteus* and *V. rosanovi*, attaining more than 0.5 m in diameter) are known from the Virgatus Zone of the Middle Volgian just before the extinction of this family. Nearly the same pattern in shell-size changes characterized the dorsoplanitid lineage, but it started later, because Lower Volgian dorsoplanitids were uncommon on the Russian Platform and only since the beginning of the Middle Volgian these ammonites became abundant. Occasionally, the same gradual increase in shell size was recognized within successive populations of the species (*Lomonossovella lomonossovi*; see MITTA 1993). The maximum diameter of megaconchs of *Epivirgatites* at the beginning of the Nikitini Chron was slightly less than 1 m, well comparable with the size of Portlandian giants of the same age. But the upper subzone of the Nikitini Zone was characterized by a strong reduction in size of dorsoplanitid ammonites across the Arctic and extinction of nearly all genera. First craspeditid ammonites, belonging to three geographically separated subfamilies, all show a very small size at the end of the Middle Volgian and at the very beginning of the Late Volgian (ROGOV 2013). During the Late Volgian these ammonites show different patterns in shell-size evolution, and only their Valanginian and especially Hauterivian descendants show a size of macroconchs comparable with that of the Middle Volgian age.

(2) Miniaturisation in response to stress environments and Lilliput effect as post-extinction phenomenon

Volgian ammonite faunas show few miniaturization events of different nature. In the beginning of the Early Volgian, invasion of ammonites of Submediterranean origin (*Paralingulaticeras*) led to appearance of endemic species, which are characterized by smaller size (~1/2 the size of this genus in Submediterranean faunas) and absence of ventrolateral nodes, which are typical for late growth stages in typical *Paralingulaticeras*. Such a size decrease was accompanied by a high abundance of these ammonites (up to ~60% of all ammonite records; see ROGOV 2010). Other Submediterranean ammonites in the Lower Volgian are also usually relatively small-sized (*Neochetoceras*) or represented mainly by small-sized morphotypes (dwarf macroconchs of *Schaireria*). The miniaturization event in *Paralingulaticeras* and partially in other Submediterranean taxa strongly resembles the response of cardioceratid populations in untypical environments after their southwards immigration (MATYJA & WIERZBOWSKI 2000) and could be considered as stress-related phenomenon. Another type of miniaturization event occurred in the latest Middle Volgian just after extinction of giant megaconchs. At this time the oldest *Kachpurites*, dwarf descendants

of *Laugeites* (with shell diameter of mainly ~3 cm compared with at least 8-10 cm in microconchs of *Laugeites*) are blooming. At all known localities their shells form coquinas, consisting of hundreds of specimens, while other ammonites (the last relatively small-sized *Epivirgatites*) remain uncommon. These *Kachpurites* are also characterized by evolute coiling and relatively simple ribbing (mainly fine biplicate ribs and intercalatories) and do not reveal significant size dimorphism. It should be noted that miniaturization occurred within all Boreal lineages near to the Middle/Late Volgian transition, but it was not simultaneous in the various taxa. Such a remarkable post-extinction event is easily comparable with other simplification and dwarfism in ammonites, described by GUEX (2001) as special response to enormous stress (for review see NEVO 2011), and as "Lilliput effect" (URBANEK 1993), because these small species also show high abundance but very low diversity. Significantly, just after its appearance the genus *Kachpurites* shows very fast evolution accompanied at some levels by a very high variability. During all the time when evolution of this genus (and of the descendant genus *Garniericeras*) was rapid, these ammonites dominated in all studied populations of the Russian Sea, usually accounting for up to 80-90% of all records. Nevertheless members of *Kachpurites* mainly remained small-sized during the early part of the Fulgens Chron and even among full-grown macroconchs commonly attained only 5-6 cm in diameter, while big macroconchs (20-25 cm) were very uncommon. In the latest part of the Late Volgian (Nodiger Chron) a higher evolutionary speed was typical of members of the other craspeditid subfamily (Craspeditinae), also accompanied by size decrease at the beginning. Late Volgian ammonite faunas of all Boreal regions with a rare exception (large-sized *Chetaites* at the end of the Volgian in Northern Siberia) consisted of ammonites which were much smaller than Middle Volgian ones (ROGOV 2013).

(3) Dimorphism and polymorphism in shell size of Volgian ammonites

Recognition of dimorphism and polymorphism as well as their interpretation met some problems in the Volgian ammonites, as they are mainly lacking any mature modifications. Thus micro- and macroconchs are here used as morphological terms only. Lower and Middle Volgian dorsoplanitids and virgatitids usually show two or three separate size groups, while specimens of intermediate size are absent or very uncommon. Virgatitid microconchs have a shell diameter of usually between 8 and 15 cm and are characterized by nearly constant type of ribbing at the body chamber and phragmocone or by changes in the rib ratio. Macroconchs show biplicate ribbing or smoothing of sculpture on the outer whorls; they are usually less numerous than microconchs. Macroconchs are also uncommon within dorsoplanitids from the Panderi Zone, while in the overlying Virgatus Zone macroconchs of the genus *Dorsoplanites* dominate. Dorsoplanitids from the Middle Volgian Nikitin Zone are mainly characterized by three size morpho-groups (microconchs, macroconchs, and big macroconchs (megaconchs)). Three size groups are also very typical of the latest Middle to Late Volgian Garniericeratinae. It should be noted that early garniericeratins (*Kachpurites*) are represented by microconchs (~3-4 cm), small macroconchs (6-7 cm) and relatively rare large macroconchs (up to 20-25 cm); the small-large macroconch ratio changed significantly within different populations. *Garniericeras*, a late member of this subfamily, shows two size groups in nearly all assemblages (microconchs and small or large macroconchs). Interpretation of the discussed polymorphism in shell size includes developmental polymorphism sensu MATYJA (1986) and/or discrete adaptive norms (see NIGMATULLIN 2012 for example of DAN in modern cephalopods) coupled with possible sexual dimorphism.

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