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Stages of the Early Triassic Ammonoid Evolution in the Eastern Boreal Province

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Abstract—The history of the evolution of the Early Triassic ammonoid communities in the eastern Boreal province is discussed with due regard for the peculiarities of their biogeographic differentiation and phylogenetic relations. The evolution is shown to include two rhythms of fauna development in the Induan and Olenekian stages, four stages, and 11 phases corresponding to 22 zones and subzones of the biostratigraphic zonation of the Lower Triassic in southeastern Asia.

Key words: *Early Triassic, ammonoids, rhythm, stage, substage, phase, zone.*

The Early Triassic ammonoid communities of the eastern Boreal province included immigrants and species representing several endemic phylogenetic lines. Some immigrants were ancestral for these endemic lines. Not all phylogenetically related species were truly endemic. Some of them were emigrants, which migrated into other Boreal basins and the Tethys from a speciation center located in the eastern part of the Boreal province. Since the composition of ammonoid communities in the eastern Boreal basin was mixed, the history of their development is considered with due allowance for the peculiatities of geographic differentiation and for the phylogenesis of all ammonoids of the basin. The history of the development of ammonoids is accepted as a basis for biostratigraphic zonation of the Lower Triassic in northeastern Asia (Dagys and Ermakova, 1993; Dagys, 1994).

In biogeographic terms of Enay (1980), the Early Triassic of the eastern Boreal province reveals two classical rhythms of ammonoid fanna development, which correspond to two Lower Triassic stages, i.e., the Induan and Olenekian. Each rhythm consisted of two periods spanning the substages. As a rule, the first period was a time of the appearance and flourishing of cosmopolitan ammonoids, whereas the second was characteristic of an endemic community. The substages are divided into several phases of development of one or several genera and spanning one or several zones of the Lower Triassic biostratigraphic zonation. The phases may include smaller subdivisions corresponding to the evolution time of one or several species.

The evolution of the Induan ammonoids had two substages (Fig. 1). In the early Induan time of a global transgression, the ammonoids were diversified little, and the common genera dominated in basins of different paleolatitudes (Dagys and Ermakova, 1996). In the eastern part of the Boreal province, two invasions of genetically incoherent groups of ammonoids probably appeared at the first substage of the first rhythm. The first invasion was that of the *Otoceras* genus, if arctic Canada is assumed to be a center of its dispersal. However, neither arctic Canada, nor eastern Verkhoyansk regions provide data for tracing a connection of *Otoceras concavum* with its ancestral forms. Therefore, the problem of the *Otoceras* dispersal center cannot be definitely solved. If this center was in the eastern Verkhoyansk region, then the migration of ammonoids to the eastern part of the Boreal province could be triggered at the beginning of the period, as also the invasion that followed and caused the appearance of representatives of the *Tompophiceras* genus and all ophiceratids genetically associated with it. The radiation center of *Tompophiceras* was in the western part of the Boreal province. Other Boreal regions do not show such a distinct differentiation between the *Otoceras* and the *Ophiceras* faunas. In eastern Greenland (Spath, 1930; 1935), arctic Canada (Tozer, 1994) and Spitsbergen (Korchinskaya, 1986), the *Otoceras*, *Tompophiceras*, and ophiceratids coexisted within the *boreale* Zone.

The majority of the early Induan genera from northeastern Asia are immigrants, which is probably the cause of a limited applicability of phylogenetic methods to this period. Only short phyletic lines of species from the *Otoceras*, *Tompophiceras* and *Wordieoceras* genera can be detected. Nonetheless, two early Induan phases are identified in the ammonoid evolution, and the subdivision of this substage is based on the phylogenetic lines of the *Otoceras*, *Tompophiceras*, and *Wordieoceras* genera. The first phase of the early substage in development of the Early Triassic ammonoids correlates with the *concavum* and *boreale* zones and is characterized by the appearance of *O. concavum* and

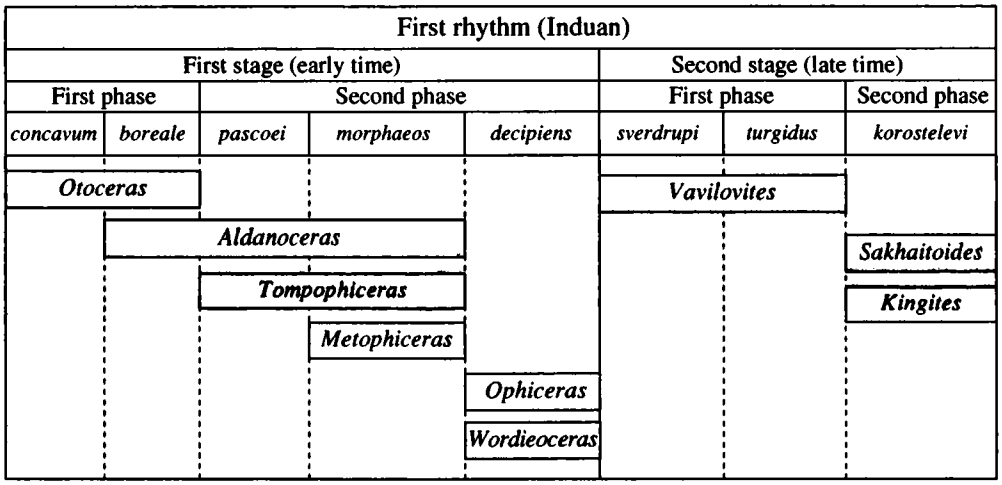

Fig. 1. The evolutionary stages of the Induan ammonoids.

O. boreale, the latter representing a result of evolutionary transformations of the former. Moreover, at the end of that substage, the *Aldanoceras* genus appears as the only taxon of the Triassic xenodiscids. In the western part of the Boreal province, *Tompophiceras*, *Ophiceras*, and *Vishnuites* forms coexisted with *O. boreale* during the middle of the first phase.

The second phase of the early substage spans the *pascoei, morphaeos,* and *decipiens* zones. Its beginning in the eastern part of the Boreal province coincides with the origin of two western Boreal species of the *Tompophiceras* genus: *T. pascoei* and *T. gracile*. Their evolution gave rise to the endemic species *T. morphaeos* and *T. bychkovi*. In the middle and at the end of this phase, there appeared two immigrant genera associated genetically with the genus *Tompophiceras*. In the eastern Boreal area, each of them is represented by one species only, namely by *Metophiceros subdemissum* and *Ophiceras transitorium*. The former species initiated the philogenetic series that developed in the late Induan and early Olenekian. The second phase terminated with the appearance of yet another western Boreal *Wordieoceras* genus represented by species *W. decipiens*, the evolutionary transformations of which resulted in the appearance of *W. tompoense*.

In the second substage of the first rhythm, apparently in connection with the decrease of the eustatic level of the World Ocean, the geographic differentiation of marine invertebrate faunas, ammonoids included, suddenly increased. At that time, basins located at different latitudes were in fact populated by various types of faunas. There is a certain indication of isolation of the eastern and western parts of the Boreal province. In in the east of the Boreal area, two late Induan phases become evident in the ammonoid evolution. The first of them corresponded to the time of the *Vavilovites* genus development. The biozonation of the lower part of the upper Induan Substage is based on the evolution of this genus demonstrating a gradual change of taxa from the relatively thin forms with the narrow ventral side to the swelled species (particularly, near the umbilical part) with the wide ventral side. The first phase corresponds to the *sverdrupi* and *turgidus* zones (*subtriangularis* and *umbonatus* subzones of the latter) and is characterized by the absolute predominance of the *Vavilovites* genus. In the western part of the Boreal province, the *Proptychites* genus was prolific along with the early *V. sverdrupi* species, and the immigrant genus *Prionolobus* arrived from Tethys. The *Vavilovites*, forms of a later period which are widespred in northeastern Asia, are unknown in western Boreal regions.

The second phase of the late Induan substage corresponds to the *korostelevi* Zone and is characterized by the appearance of the endemic *Sakhaitoides* genus apparently associated in genesis with *Metophiceras* forms and represented by two species; the *korostelevi* species that appeared simultaneously are tentatively referred to the *Kingites* genus. The origin center of the *Kingites* genus is unknown so far. In the western part of the Boreal province, its representatives coexisted with the *Vavilovites* and newly appearing forms of the *Koninckites* and *Flemingites* genera. Moreover, Tozer (1994) reported from Arctic Canada about the coeval *Xenodiscoides calnanani* and *Wyomingites scapulatus* species, whose systematic position is debatable.

The second rhythm of ammonoid evolution, as the first one, included two evolutionary phases of both the Boreal and the low-latitude ammonoids (Zakharov, 1975). Each of these phases spans the time interval corresponding to a substage (Fig. 2). In the early Olenekian, an extensive invasion of the Tethyan taxa into the Boreal basins was recorded, and cosmopolitan genera dominated in the ammonoid communities, which is in good agreement with data on the global transgression that occurred at that time. In this case, as in the first

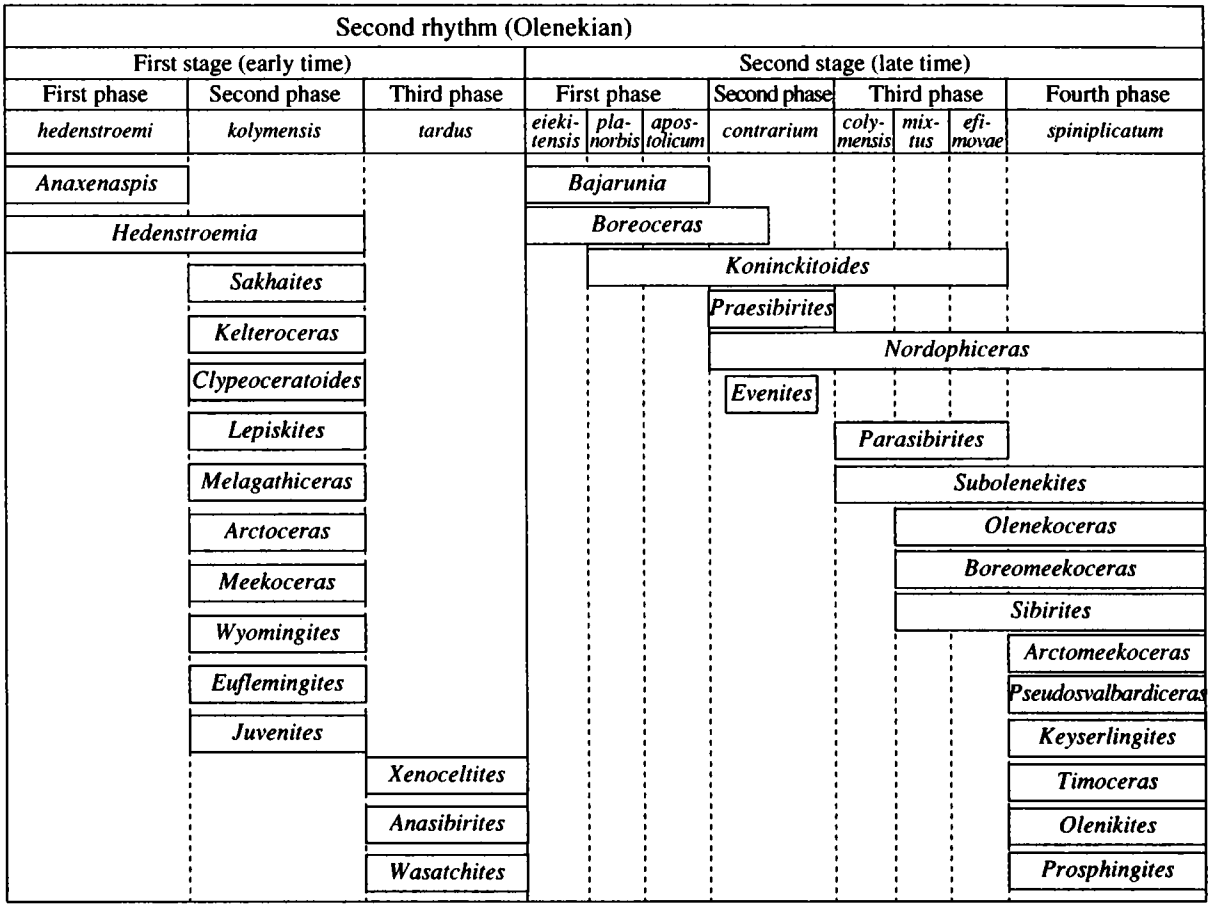

Fig. 2. The evolutionary stages of the Olenekian ammonoids.

rhythm, there could have been the emigration of ammonoids at the beginning of the period, if we assume the eastern Boreal province as a center of the hedenstroemiid dispersal. But even if the Himalayas were that center, the appearance of hedenstroemiids in the western Boreal area was associated with their migration from the eastern part. Concurrently with the cosmopolitan genera, individual endemic phylogenetic lines likewise developed in the eastern part of the Boreal province. Using the historical development of the eastern Boreal ammonoid communities as a basis, the first stage of the second rhythm can be divided into three phases.

The beginning of this period was associated with the appearance of two cosmopolitan *Hedenstroemia* and *Anaxenaspis* genera. In all probability, the eastern part of the Boreal province was actually the center of origin and dispersal of these genera, if my supposition about their origin is correct. The most likely ancestor of hedenstroemiids is the late Induan *Kingites* genus, whereas the roots of the *Anaxenaspis* genus must be among the evolute forms that departed from the *Vavilovites* genus at the beginning of the late Induan. The first phase of the first stage of the second rhythm corresponds to the *hedendstroemi* Zone and is characterized by the domination of *Hedenstroemia hedenstroemi* and genetically associated *H. tscherskii*. The evolution of hedenstroemiids progressed toward the complication of their lobe line. The appearance of *Anaxenaspis olenekensis* was concurrent with that of the hedenstroemiids. The phase may also mark the first occurrence level of *Sakhaites* taxa known only as fragments recovered at a single site at the Vendyavkiri Brook, the left-hand tributary of the Buur River. This supposition, however, is premature without supporting data from other sections (Dagys and Ermakova, 1990). In the eastern part of the Boreal province, hedenstroemiids were recovered from two sites in arctic Canada (Dagys and Tozer, 1989; Tozer, 1994); in all other regions, a paleontological hiatus is recorded as corresponding to the evolution time of ammonoids at the phase in question.

The second phase of the early Olenekian substage corresponds to the *kolymensis* Zone and has been distinguished by an extensive invasion of cosmopolitan genera such as *Arctoceras, Meekoceras, Wyomingites, Euflemingites, Melagathiceras*, and *Juvenites*. The phylogenetic lines of concurrent endemic genera *Lepiskites* and *Clypeoceratoides*, which were genetically

related to the genus *Anaxenaspis*, likewise appeared; their evolution was characterized by the complication of the lobe line and by a greater degree of the shell convolution. The *Sakhaites* and *Kelteroceras* genera were genetically related to the late Induan *Sakhaitoides* and evolved toward the simplification of their morphology, mainly in the lobe line structure. The *Hedenstroemia* genus terminated its evolution and was represented in the phase under consideration only by a single species described in the open nomenclature. It should be noted that the endemic phylogenetic lines of the eastern Boreal ammonoids, the origin of which goes as far back as the Induan, completed their evolution in this phase. The phase is distinguished by the greatest taxonomic diversity of the Early Triassic ammonoids in the eastern part of the Boreal province. In the western part of the Boreal basin, the second phase corresponds to the *romunderi* Zone as diverse in the taxonomic aspect as that in the eastern Boreal province. Apart from genera in common (*Meekoceras, Arctoceras, Euflemingites, Juvenites, Melagathiceras*), the western basin was populated by *Kashmirites, Oxyussuria*, and *Paranannites* forms, which were probably immigrants from the Tethys.

The third phase of the early Olenekian Substage corresponds to the *tardus* Zone characterized exclusively by cosmopolitan *Wasatchites*, *Anasibirites*, and *Xenoceltites* genera. In other words, the invasion of ammonoids from the Tethys and western Boreal province continued at this phase. The *Wasatchites* and *Anasibirites* forms were not abundant in the eastern part of the Boreal area. The *Xenoceltites* genus of two taxa (*X. subevolutus* and *X. matheri*) was obviously dominant, and its evolution toward a more complicated lobe line and changes in ornamentation produced two endemic branches that extensively developed in the second substage of the rhythm. Ammonoids of the considered third phase were not considerably diverse. In the western Boreal basin, the third phase corresponds to the *tardus* zone characterized by a similar ammonoid community, though of a larger taxonomic diversity.

The late Olenekian substage of the second rhythm of ammonid evolution corresponded to the time of their excessive endemism and greater geographic differentiation; this time probably marked an essential lowering of the World Ocean level. Sea basins in the lower and higher latitudes were populated by different types of faunas, and there were only certain short periods when individual boreal genera penetrated into the boundary Tethyan basins and, vice versa, when the Tethyan forms appeared in the boreal ammonoid communities. There were four phases of the ammonoid evolution in the eastern part of the Boreal province during the second Olenekian Substage. The first phase corresponds to the *eikitensis, planorbis* and *apostolicum* zones. The beginning of the phase is marked by the simultaneous appearance of two endemic genera *Bajarunia* and *Boreoceras* phylogenetically associated with the different species of the *Xenoceltites* genus. The evolution of the *Bajarunia* genus, represented by six species (*B. eiekitensis, B. taimyrensis, B. alexandri, B. eumphala, B. alexeevae*, and *B.* sp.), is confined exclusively to the first phase. The evolutionary transformations of the genus are recorded in insignificant complications of the lobe line. Three *Boreoceros* species (*B. planorbis, B. apostolicum,* and *B. demokidovi*) do not occur beyond the three aforementioned zones. In the middle of the first phase, another endemic genus *Koninckitoides* appeared as the terminal one in the phylogenetic line *Anaxenaspis–Lepiskites–Clypeoceratoides*. The appearance of this genus was associated with the simplification of the taxa organization. In the western Boreal regions, ammonoids of the first phase are unknown, and a paleontological hiatus spanning three zones is inferred for this province.

The second phase of the substage corresponds to the *contrarium* Zone divided into the *lenaense, tuberculatus*, and *egorovi* subzones. Its beginning coincides with the appearance of the *Nordophiceras* genus departed from the *Bajarunia* line because of evolutionary transformations that resulted in the disappearance of peculiar sculptural elements of the latter. In the first half of the second phase, the *Boreoceras* genus (*B. lenaense* and *B. mirabile*) terminated its evolution; the evolutionary changes of the genus toward the enhancement of sculptural elements resulted in the appearance of another endemic genus *Praesibirites*. The evolution of this genus, represented by two species (*P. tuberculatus* and *P. egorovi*), was confined entirely to the second phase, when it coexisted with the *Koninckitoides* genus. In the middle of this phase, there appeared the *Evenites* genus, an immigrant taxon from the Tethys, whose existence time is limited by the zonal *tuberculatus* event. In the western part of the Boreal province, the ammonoides of the second phase, like those of the first, are unknown.

The appearance of *Subolenekites pilaticus*, an immigrant species from western regions of the Boreal province, and the advent of the *Parasiberites* genus, as a result of evolutionary transformations of *Praesibirites*, marked the beginning of the third phase of the late Olenekian. It corresponds to the *kolymensis, mixtus*, and *efimovae* zones. At that phase, four species of the *Subolenekites* genus originated. Two of them (*S. pilaticus* and *S.? shevyrevi*) were ancestral for the *Olenekoceras* and *Boreomeekoceras* genera. The evolution of the *Parasibirites* genus (*P. grambergi, P. kolymensis, P. subpretiosus, P. mixtus, P. efimovae*) is confined exclusively to the third phase. All the changes in the genus shells concern only different sculptural elements; the duration of the sculptural transformations; and, insignificantly, the shell shape. In the middle of this phase, the *Sibirites* genus departed from the *Parasibirites* line and evolved separately, displaying a simplification of sculptural elements and the lobe line. Two species (*S. elegans* and *S. pretiosus*) appeared at different moments of the third phase, when *Nordophiceras* forms continued their evolution. At the beginning of the

phase, two new-comers (*Nordophiceras menense* and *N. kasakovi*) appeared amid the latter and existed until the end of the phase. The *Koninckitoides* genus is terminal in the phylogenetic branch, whose origin goes back to the late Induan and is completed within the phase. This phase of the ammonoid evolution is also traceable in the western part of the Boreal province (arctic Canada), where only one species *Subolenekites pilaticus* is reliably established and initially assigned by Tozer (1967) to the *Olenikites* genus. Later, Tozer (1994) described the new species *Olenikites subtilis* that belongs in all probability again to the *Subolenekites* genus together with *Neomeekoceras scalariforme* practically identical to *Nordophiceras menense* and, apparently, occupying the same position in the ammonoid systematics.

The fourth phase of the late Olenekian corresponds to the *spiniplicatus* Zone. In the degree of taxonomic diversity of ammonoids, it differs only slightly from the second phase of the early Olenekian substage. The beginning of the phase coincides with the appearance of as many as five new endemic genera: *Olenikites, Timoceras, Pseudosvalbardiceras, Keyserlingites*, and *Arctomeekoceras*. At this time, the *Nordophiceras* genus continued its evolution by producing three new species (*N. karpinskii, N. popovi, N. schmidti*). The *N. ordophiceras* genus evolution, which resulted in the flattening of ventral shell sides, produced a new endemic genus *Pseudosvalbardiceras*, the taxon important for further development of ammonoids in the Middle Triassic. The fourth phase of the late Olenekian was a time of an extreme diversification in the *Olenekoceras* line, when *O. middendorffi* became extinct and two new species of the genus (*O. shrenki, O. nikitini*) appeared. The evolution of the genus increased the shell size and resulted in the origin of more prominent sculptural elements and a more intricate lobe line. As a consequence of further development of lobe lines and new sculptural elements in this direction, the monotype *Keyserlingites* genus departed from the *Olenekoceras* line and spread throughout the entire Boreal area. Two other monotype genera (*Timoceras* and *Olenikites*) appeared as a result of evolutionary transformations of *Subolenekites altus* that terminated its evolution at this stage. The *Arctomeekoceras* genus appeared at the beginning of the stage. The *Sibirites* and *Boreomeekoceras* genera terminated their evolution at this stratigraphic level, and the *Proshingites* genus, an immigrant from the Tethys, appeared. In the western part of the Boreal province, the fourth phase coincides with an extensive invasion of Tethyan ammonoids. Of a large ammonoid assemblage of *Preflorianites, Proshingites, Isculitoides, Popovites, Zenoites, Monacanthites, Metadagnoceras, Svalbardiceras, Keyserlingites, Procarnites*, and *Leiophyllites* taxa, only two species (*Keyserlingites subrobustus* and *Proshingites czekanowskii*) are known to be inherent to both parts of the Borael province together with a few species attributed by Tozer (1994) to the *Olenikites* genus.

The analysis given above shows that the biostratigraphic zonation of ammonoids from northeastern Asia corresponds, in general features, to the rhythms, stages and phases of their evolution in the eastern part of the Boreal province. The established rhythms correspond to stratigraphic stages; the lesser periods, to substages; and phases, to one or several zones. A similar stage sequence in the ammonoid evolution is also established for the western part of the Boreal province. Consequently, an assumption that the rhythms and lesser evolutionary periods detectable in the Boreal province may correspond to the global phases of the ammonoid evolution cannot be ruled out.

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REFERENCES

Dagis, A.S. and Ermakova, S.P., *Ranneolenekskie ammonoidei Sibiri* (Early Olenekian Ammonoids from Siberia), Moscow: Nauka, 1990.

Dagis, A.S. and Ermakova, S.P., A Detailed Biostratigraphic Scheme of the Boreal Lower Triassic, *Stratigr. Geol. Korrelyatsiya*, 1993, vol. 1, no. 2, pp. 26–36.

Dagys, A. and Ermakova, S., Induan (Triassic) Ammonoids from Northeastern Asia, *Rev. Paleobiol.*, 1996, vol. 15, no. 2, pp. 401–447.

Dagis, A.S. and Tozer, E.T., Triassic Correlations between Northern Canada and Siberia, *Geol. Geofiz.*, 1989, no. 6, pp. 11–17.

Enay, R., Paleobiogeographie et ammonites jurassiques: "rhythmes fauniques" et variations du niveau marin; voies d'echanges, migrations et domaines biogeographiques, *Mem. Soc. Geol. France*, 1980, no. 10, pp. 261–281.

Korchinskaya, M.V., Induan Biostratigraphy of Spitsbergen, in *Geologiya osadochnogo chekhla arkhipelaga Shpitsbergen* (Geology of the Sedimentary Cover of the Spitsbergen Archipelago), Leningrad: Sevmorgeologiya, 1986, pp. 77–93.

Spath, L.F., The Eotriassic Invertebrate Fauna of East Greenland, *Medd. Greenland*, 1930, vol. 83, no. 1, pp. 1–90.

Spath, L.F., Additions to the Eotriassic Invertebrate Fauna of East Greenland, *Medd. Greenland*, 1935, vol. 98, no. 2, pp. 1–115.

Tozer, E.T., A Standard of Triassic Time, *Bull. Geol. Surv. Can.*, 1967, no. 156, pp. 1–103.

Tozer, E.T., Canadian Triassic Ammonoid Faunas, *Bull. Geol. Surv. Can.*, 1994, no. 467, pp. 1–663.

Zakharov, Yu.D., *Rannetriasovye ammonoidei Vostoka SSSR* (Early Triassic Ammonoids of the Eastern USSR), Moscow: Nauka, 1975.