The ammonoid recovery after the end-Permian mass extinction: Evidence from the Iran-Transcaucasia area, Siberia, Primorye, and Kazakhstan

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Investigations of the Upper Permian strata in the Iran-Transcaucasia resulted in identification of 32 ammonoid genera. The majority of ammonoids in this collection belong to the order Ceratitida (75%). Among Dzhulfian ceratitid ammonoids representatives of the family Araxoceratidae (Otoceratoidea) are most abundant. The assemblage structure changed radically during latest Permian (Dorashamian) time, bringing a domination of the family Dzhulfitidae. The Induan (Lower Triassic) succession in the Verkhoyansk area provided a few groups of ammonoids which are Palaeozoic in type: families Episageceratidae (*Episageceras*), Xenodiscidae (*Aldanoceras* and *Metophiceras*), and Dzhulfitidae (*Tompophiceras*) and superfamily Otoceratoidea (*Otoceras* and *Vavilovites*). It demonstrates the survival of ammonoids belonging to these groups the Permian–Triassic (P–T) boundary extinction event and their quick migration to the vast areas of higher latitudes (together with some representatives of the Mesozoic-type families). Induan–Olenekian ammonoid successions in South Primorye, Mangyshlak, and Arctic Siberia illustrate the high rate of Early Triassic ammonoid recovery in both the Tethys and the Boreal realm. New ammonoid taxa are described: Proptychitina subordo nov., Ussuritina subordo nov., *Subbalhaeceras shigetai* gen. and sp. nov. (Flemingitidae), *Mesohedenstroemia olgae* sp. nov. (Hedenstrormiidae), and *Inyoites sedini* sp. nov. (Inyoitidae).

Key words: Ammonoidea, recovery, Permian, Triassic, Russia, Azerbaijan, Kazakhstan, Iran.

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Introduction

The P–T boundary is associated with the most widespread biotic crisis, largest extinction event in Phanerozoic times (e.g., Baud et al. 1989; Campbell et al. 1992; Wignall and Hallam 1993; Erwin 1994; Retallack et al. 1996; Shen and Shi 1996; Visscher et al. 1996; Yin and Zhang 1996; Wignall and Twitchett 1996; Kozur 1998; Bowring et al. 1999; Broecker and Peacock 1999; Chen et al. 2005). Significant biotic turnover at the phylum level took place at the P–T transition: among invertebrates, for instance, the brachiopod domination was replaced by the mollusc (including ammonoid) domination. It seems to be linked to possible short-term cooling (Zakharov et al. 1999, 2008; Kozur 2007) and/or the oceanic superanoxia (Wignall and Hallam 1992; Hallam 1994; Isozaki 1997; Erwin et al. 2002; Wignall and Twitchett 2002) at the P–T boundary transition. Well oxygenated conditions took place apparently only in the late Griesbachian (Hautmann et al. 2011; Hermann et al. 2011).

In spite of significant progress in investigation of Late Permian and Early Triassic ammonoids in the past decades (e.g., Zhao et al. 1978; Bando 1979; Zakharov 1992; Dagys and Ermakova 1990; Shevyrev 1990, 1995; 1999, 2000, 2002; Tozer 1994; Krystyn et al. 2007; Brayard et al. 2006, 2007, 2009; McGowan and Smith 2007; Brayard and Bucher 2008; Brühwiler et al. 2008, 2010a, b, 2012; Shigeta et al. 2009; Zakharov and Ehiro 2010), our knowledge this very important group of invertebrates during this crucial for their evolution time remains incomplete.

The main aim of this presentation is the analysis of stratigraphical distribution and diversity patterns of Late Permian and Early–Middle Triassic ammonoids from Russia, Azerbaijan, Kazakhstan, and Iran (based on original and published data) for some recovery and phylogenetic reconstructions and description of new ammonoid taxa.

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Institutional abbreviations.—DVGI, Dal'nevostočnyj geologičeskij institut [Far Eastern Geological Institute].

Other abbreviations.—D, diameter of the shell; H, height of the whorl; I, inner lateral lobe; L, lateral lobe; V, ventral lobe; W, width of the whorl; U, umbilicus (diameter).

Material

Original material on Late Permian and Early–Middle Triassic ammonoids used for our investigation was obtained from sections of the Wuchiapingian–Changhsingian (Dzhulfian–Dorashamian) of the Iran-Transcaucasia and South Primorye areas, the Induan of Transcaucasia, Verkhoyansk, and South Primorye, the Olenekian of Siberia, South Primorye, and Mangyshlak (Kazakhstan) and the lowest Anisian of Arctic Siberia and South Primorye (Fig. 1). Material from South Primorye was collected by YDZ during the last five years. Other material used for our analyses was collected by the same worker in the Olenek, Setorym, Burgagandzha, and Kenyelichi rivers in Siberia and northern Russian Far East (1967–1971), Transcaucasia (Azerbaijan), and Mangyshlak (Kazakhstan) before the split of the USSR (1977–1984). NMA and Mehdi Yazdi's collections of Late Permian ammonoids from the Hambast Formation of Central Iran, recently found, were also used for our analysis.

Late Permian to Early Triassic ammonoid succession in the Iran-Transcaucasia area, Siberia, Far East, and Kazakhstan

The ammonoid-bearing Lower Triassic is rather well developed throughout Himalaya (e.g., Waagen 1895; Kummel and Teichert 1970; Guex 1978; Waterhouse 1994, 1996a, b; Krystyn et al. 2007; Brühwiler et al. 2012), where the base of the Triassic System was adopted at the base of the *Otoceras woodwardi* and *Hindeodus parvus* zones, as well as in Arctic Canada (e.g., Tozer 1994) and Idaho-Nevada-California area (e.g., Kummel and Steele 1962; Kummel 1969). The P–T ammonoid successions are known in South China (Chao 1959, 1965; Zhao et al. 1978; Mu et al. 2007; Brayard and Bucher 2008; Brayard et al. 2009). However, information on ammonoids from the Meishan section, in the Global Boundary Stratotype Section and Point (GSSP) for the base of the Triassic (Yin and Zhang 1996) is restricted.

Among other areas, perspective for the detailed investigation of P–T cephalopod successions and investigated by us are the following: Transcaucasia, Iran, Siberia, Russian Far East, and Kazakhstan (Fig. 1).

In the Iran-Transcaucasia area the main sections of cephalopod-bearing Wuchiapingian, Changhsingian, and Early Induan sequenses are located mainly in the Nakhichevan area, Armenia and Hambast, Central Iran (e.g., Abich 1878; Stoyanov 1910; Ruzhencev and Shevyrev 1965; Shevyrev 1965; Bando 1979; Teichert et al. 1973; Kotlyar et al. 1983; Zakharov 1983b, c, 1986, 1992; Zhou et al. 1989; Zakharov and Kozur 2010; Zakharov et al. 2010a) (Fig. 2).

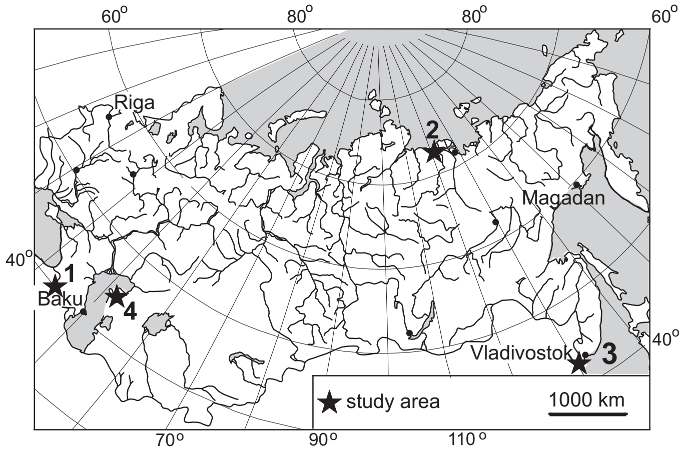

Fig. 1. Study areas: 1, Iran-Transcaucasia area; 2, Siberia and northern Russian Far East; 3, southern Russian Far East (South Primorye and Amur River); 4, Mangyshlak, Kazakhstan.

Dzhulfian.—The Dhulfian in Transcaucasia is represented by the upper part of the Khachik Formation, corresponding to the *Clarkina niuzhyangensis* and *Pseudodunbarula arpaensis–Araxilevis intermedius* zones, and the lower part of the Akhura Formation, corresponded to the *Araxoceras latissimum* and *Vedioceras ventrosulcatum* zones (Zakharov et al. 2005a, Zakharov and Kozur 2010), in Central Iran by Member 5 of the Abadeh Formation and members 6 and 7 (lower part) of the Hambast Formation (Taraz et al. 1981; Korte et al. 2004). The Dzhulfian of these regions, corresponded to the Wuchiapingian and the lowest portion of the Changhsingian (Zakharov et al. 2005a), is composed mainly of limestone and calcareous clayey sediments with chert nodules at the base, about 20–45 m thick.

Representatives of four ammonoid orders have been discovered in the Dzulfian of the Iran-Transcaucasia area: Prolecanitida, Tornoceratida, Goniatitida, and Ceratitida, with domination of ceratitid ammonoids (Fig. 3). However, in contrast to the Dzhulfian portion of the Khachik Formation in Transcaucasia, no ammonoids were discovered in the Abadeh Formation in Central Iran.

Araxoceratid ammonoids (Otoceratina), very specific elements for the Dzulfian cephalopod fauna, are represented by *Eoaraxoceras*, *Kingoceras*, *Vescotoceras*, *Araxoceras*, *Rotaraxoceras*, *Prototoceras*, *Pseudotoceras*, *Abadehceras*, *Dzhulfoceras*, *Vedioceras*, *Avushoceras*, and *Urartoceras* (Fig. 3). Goniatitid ammonoids, playing a secondary role in the Dzhulfian assemblages, are represented by *Strigoniatites*, *Pseudogastioceras*, *Timorites*, *Changhsingoceras*, *Epadrianites*, and *Stacheoceras.* Tornoceratid (*Neoaganides*) and medlicottiid (*Eumedlicottia*) ammonoids are particularly rare in this area.

Dorashamian.—The main sections of ammonoid-bearing Dorashamian sediments, represented by the upper part of the Akhura Formation (*Phisonites triangularis*, *Iranites transcaucasius*, *Dzhulfites spinosus*, *Shevyrevites shevyrevi*, and

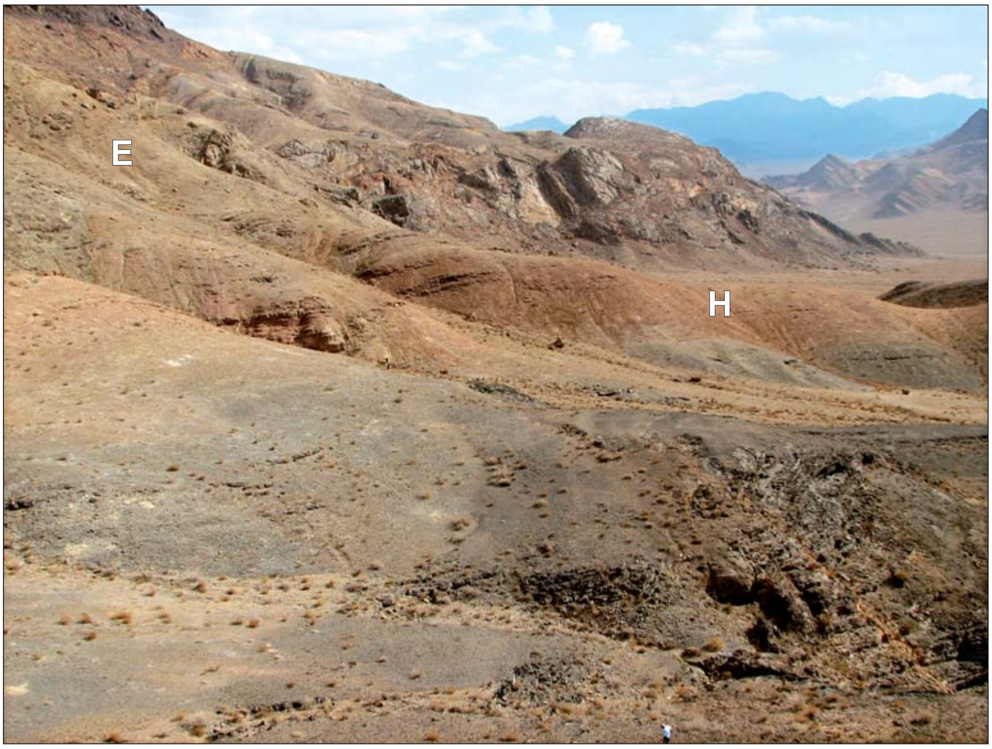

Fig. 2. View of the Permian–Triassic sequences of the section from the Wuchiapingian–Changhsingian Hambast (H) Formation to latest Changhsigian–Induan Elikah (E) Formation at the Hambast region, 28 km to south-western of the village of Abaraku, Abadeh, Central Iran.

Paratirolites kittli zones), and basal beds of the Karabaglyar Formation (*Pleuronodoceras occidentale–Xenodiscus jubilaearis* Zone) in Transcaucasia, the upper part of the Hambast and the lower part of the Elikah formations in Central Iran, locate in the Dhulfian Canyon, Akhura, Sovetashen, Vedi and Hambast areas (Ruzhencev and Shevyrev 1965; Taraz et al. 1981; Kotlyar et al. 1983; Korte et al. 2004; Zakharov et al. 2005a, Zakharov and Kozur 2010). The Dorashamian, corresponded, apparently, to the main part of the Changhsingian (Zakharov et al. 2005a), consists of limestone and marl, 7–8 m thick.

Dorashamian ammonoids composed of only two orders: Goniatitida (Goniatitina) and Ceratitida (Paraceltitina and Otoceratina). Among Dorashamian ceratitid ammonoids, representatives of the Xenodiscidae (*Xenodiscus*, *Phisonites*, and *Shevyrevites*), Tapashanitidae (*Sinoceltites*), Pleuronodoceratidae (*Pleuronodoceras*), Dhulfitidae (*Dzhulfites*, *Abichites*, and *Paratirolites*), and Araxoceratidae (*Dzhulfotoceras*) are known (Fig. 3). However, only a single goniatite genus (*Pseudogastrioceras*) has been discovered in the Dorashamian.

Induan.—Induan sediments of both the lower part of the Karabaglar Formation (interval "a" without ammonoids (*Hindeodus parvus* Conodont Zone), *Lytophiceras medium* and *Kymatites* beds and also interval "b" without ammonoids (*Clarkina planata* and *Neospathodus dieneri* conodont zones) in Transcaucasia and the lower part of the Elikah Formation (*Hindeodus parvus*, *Isarcicella isarcica*, *Hindeodus postparvus*, and *Neospathodus dieneri* zones) consist of clay rocks and stromatolite limestone at the base and mainly limestone above, 28–66 m thick (Zakharov et al. 2005a).

No Palaeozoic-type ammonoids at generic or family levels have been determined in the Induan of the Iran-Transcaucasia area, but only a few representatives of ceratitid ammonoids: *Lytophiceras* (Ophiceratidae), *Gyronites*, *Koninckites*, and *Kymatites*, corresponding to the Mesozoic-type families Ophiceratidae and Meekoceratidae (Meekoceratina) (Fig. 3). However, it has to be taken into account that no ammonoids have been discovered in the basal beds of the Induan, 1.4–3.4 m thick, characterised by presence of conodont *Hindeodus parvus* (Zakharov et al. 2005a; Zakharov and Kozur 2010).

Eastern Russia

Permian ammonoids in this area were investigated by us only in the South Primorye region and Amur River basin. Besides the mentioned regions, Early–Middle Triassic ammonoids were collected by us in the upper Kolyma River, Verkhoyansk area, Olenek River basin, and Olenek Bay area (Laptev Sea). Evidences on Early and Middle Triassic ammonoids from Taimyr and Buur River have been reported by Dagys and Sobolev (1995) and Dagys and Ermakova (1990), respectively.

Siberia and northern Russian Far East

In the Lower–Middle Triassic ammonoid succession of Siberia and northern Russian Far East representatives of the two

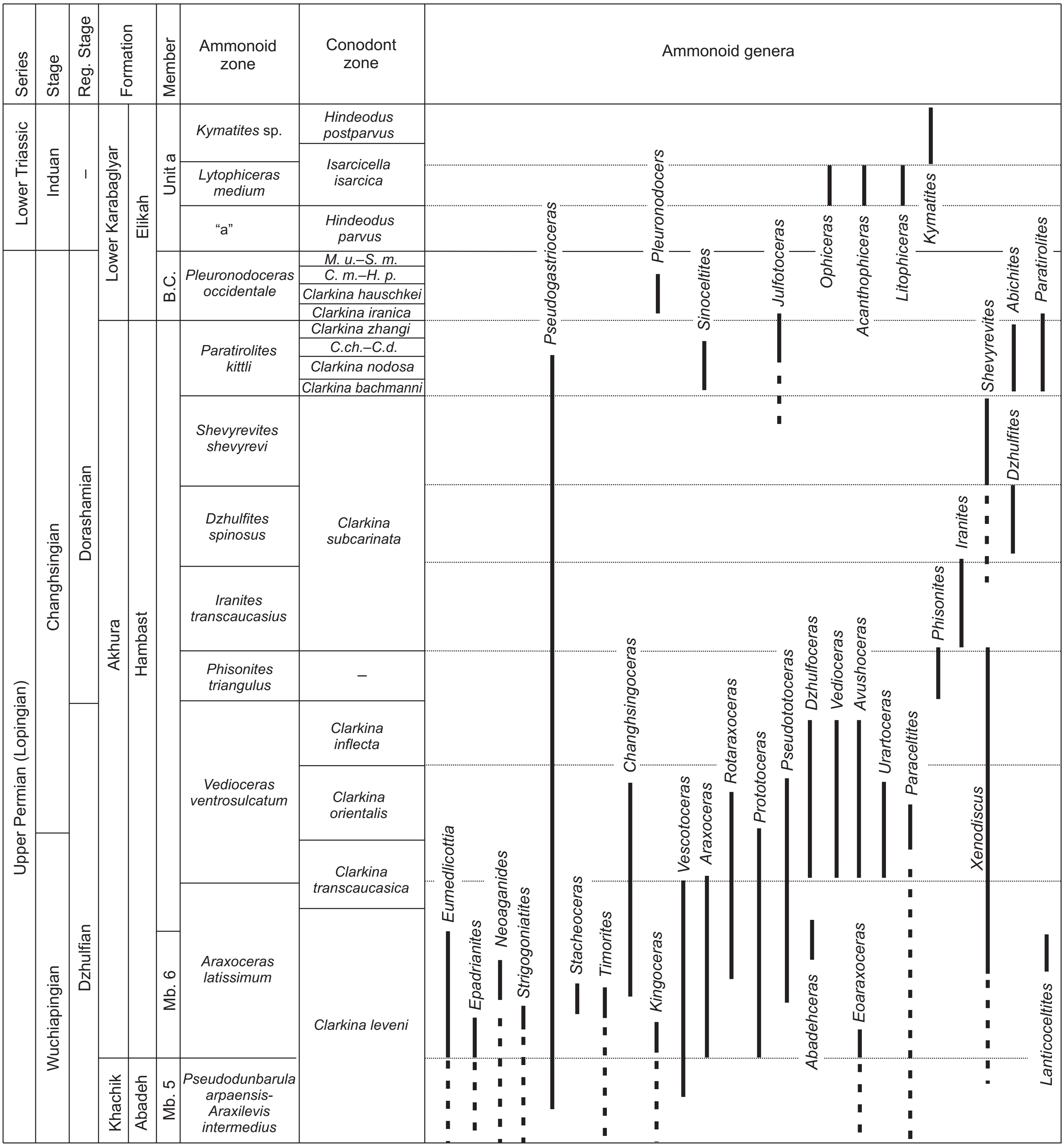

Fig. 3. Iran-Transcaucasia area: temporal ranges of ammonoid genera of the Wuchiapingian–Induan interval. Orders: Prolecanitida (*Eumedlicottia*), Tornoceratida (*Neoaganides*), Goniatitida (*Epadrianites*, *Strigogoniatites*, *Pseudogastrioceras*, *Stacheoceras*, *Timorites*, and *Changhsingoceras*), Ceratitida (Paraceltitina: *Paraceltites*, *Xenodiscus*, *Lanticoceltites*, *Phisonites*, *Iranites*, *Dzhulfites*, *Shevyrevites*, *Paratirolites*, *Abichites, Sinoceltites*, and *Pleuronodoceras*; Meekoceratina: *Ophiceras*, *Acanthophiceras*, *Lytophiceras*, and *Kymatites*; Otoceratina – other genera). Abbreviations: *C. m.–H .p.*, *Clarkina meishanensis–Hindeodus praeparvus*; *M. u.–S. m.*, *Merrillina ultima–Stephanites mostleri*; *C. ch.–C. d.*, *Clarkina changxingensis–Clarkina deflecta*; B.C., boundary clay rocks; Mb., member.

orders can be recognized: Ceratitida and Prolecanitida. The former was very diversed, but latter was represented only a few taxa.

Lower Induan (Griesbachian).—Griesbachian ammonoid-bearing sediments in Siberia have been particularly well investigated in the Setorym River basin, Verkhoyansk area,

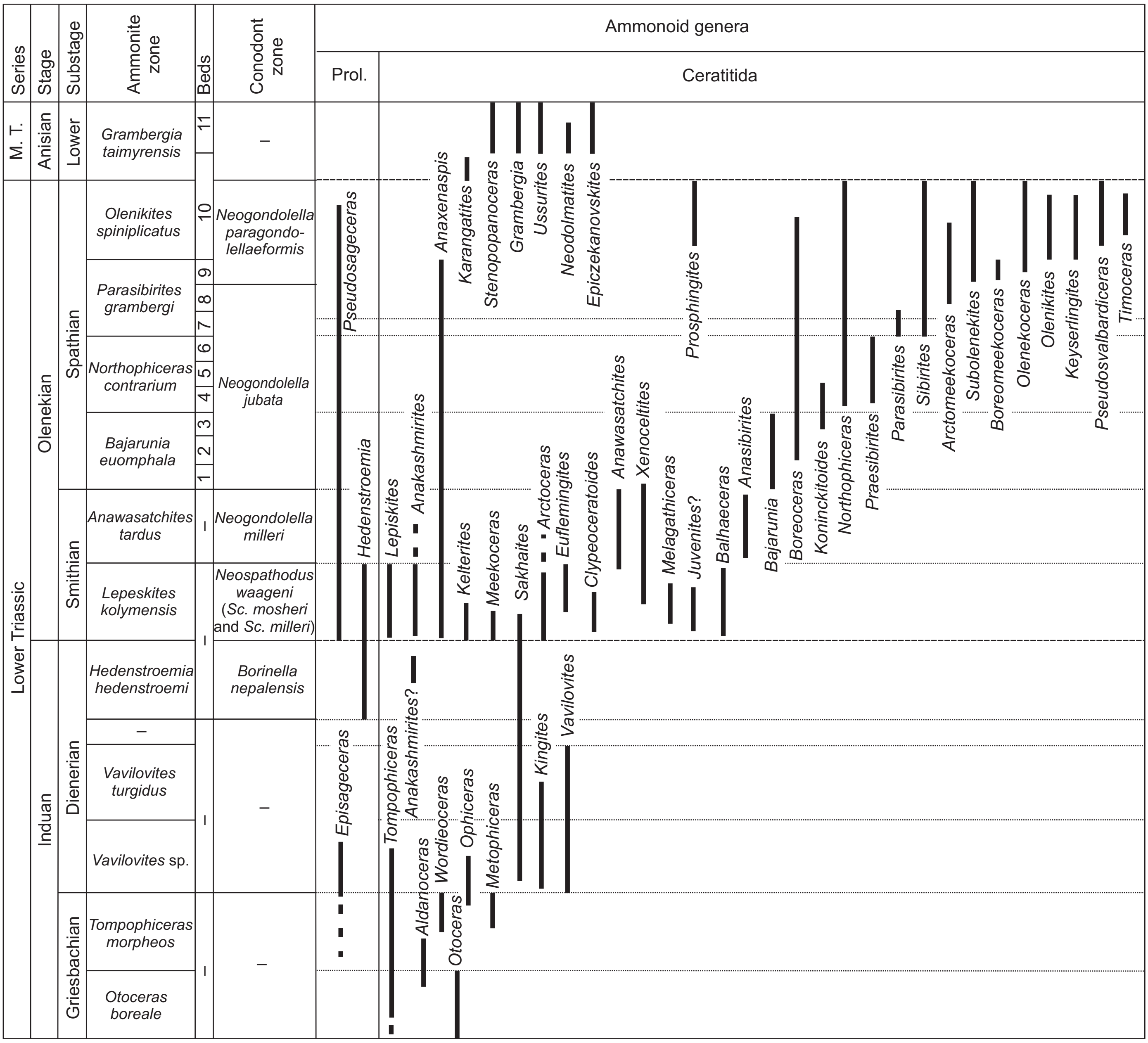

Fig. 4. Siberia: temporal ranges of ammonoid genera of the Induan–lower Anisian interval. Abbreviations: 1, *Bajarunia eiekitensis*; 2, *Boreoceras planorbis*; 3, *Boreoceras apostolicum*; 4, *Boreoceras lenaense*; 5, *Praesibirites tuberculatus*; 6, *Praesibirites egorovi*; 7, *Parasibirites kolymensis*; 8, *Parasibirites mixtus*; 9, *Parasibirites efimovae*;10, *Karangatites evolutus*; 11, *Grambergia olenekensis*; M.T., Middle Triassic, Prol., Prolecanitida.

where they are represented by dark grey siltstone and mudstone with calcareous-clayey nodules and rare intercalations of fine-grained sandstone of the lower Nekuchan Formation, 42 m thick (*Otoceras boreale* and *Tompophiceras morpheos* zones) (Popov 1961; Zakharov 1971, 2002; Archipov 1974; Dagys and Ermakova 1996; Zakharov et al. 2008; this study).

Among Griesbachian ammonoids from the Setorym River basin ceratitid ammonoids are abundant, prolecanitid ammonoids in contrast are represented by rare individuals. However, most of known ceratitids are representatives of Palaeozoic-type taxa at the family and superfamily levels: Dzhulfitidae (Paraceltitina), represented by *Tompophiceras*, Xenodiscidae (Paraceltitina), represented by *Aldanoceras* and *Metophiceras*, and Otoceratoidea (Otoceratina), represented by *Otoceras* (Fig. 4). The Ophiceratidae (Meekoceratina), consisting of *Wordieoceras* and *Ophiceras*, seems to be a single Mesozoic-type family, discovered in the upper Griesbachian (*Tompophiceras morpheos* Zone).

A single Permian-type prolecanitid ammonoid genus *Episageceras* (Medlicottiina) has been discovered by us only in the *Tompophiceras morpheos* Zone of the Burgagandzha River basin, Verkhoyansk area (Zakharov 1978).

Upper Induan (Dienerian).—Dienerian ammonoid-bearing sediments, exposed in the Verkhoyansk area (e.g., Popov

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1961; Vavilov 1967; Dagys et al. 1979; Zakharov 1978; Ermakova 1981), upper Kolyma River basin (Kulu, Kenyelichi) (Popov 1939; Bytchkov 1972; Zakharov 1978), and Buur River basin in Arctic Siberia (Dagys and Ermakova 1990) consist mainly of dark grey siltstone and mudstone with calcareous nodules and sandstone (*Vavilovites* sp. and *Vavilovites turgidus* zones, and the lower part of the *Hedenstroemia* Beds, corresponding to the *Hedenstroemia hedenstroemi* Zone), 320–400 m thick. The *H. hedenstroemi* Zone seems to be latest Induan because early Olenekian conodont index *Neospathodus waageni* seems to be discovered only in overlying sediments (Dagis 1984; Zakharov et al. 2009a), although it needs verification. The thickness of the *H. hedenstroemi* Zone in the Buur River basin is about 15 m (Dagys and Ermakova 1990).

The upper Induan, as well as the lower Induan, of the Verkhoyansk area is characterised by presence of the two ammonoids orders: (i) Prolecanitida (latest representatives of the Episageceratidae and ealiest representatives of the Hedenstroemiidae) and (ii) Ceratitida, consisting of Xenodiscidae (Paraceltitina), Vavilovitidae (Otoceratina), Clypeoceratidae (Proptychitina), and Ophiceratidae, (Meekoceratina) (Fig. 4). This evidences that some Palaeozoic-type taxa at the generic (*Episageceras*), family (Episageceratidae and Xenodiscidae) and superfamily? (Otoceratoidea) levels occur in the upper Induan.

Lower Olenekian (Smithian).—Smithian ammonoid-bearing sequenses in Siberia and northern Russian Far East, investigated in detail in Arctic Siberia (e.g., Dagys and Ermakova 1996), the Verhoyansk area (e.g., Vavilov 1967; Ermakova 1981) and upper Kolyma River basin (Kulu, Kenyelichi) (Bytchkov 1972; Zakharov 1978) consist mainly of dark grey siltstone and mudstone with clayish calcareous nodules and lenses of limestone (*Lepiskites kolymensis* and *Wasatchites tardus* zones), about 320–420 m. Representatives of three orders (Prolecanitida, Ceratitida, and Phylloceratida), have been found in this level in Siberia and northern Russian Far East.

The early Smithian *Lepiskites kolymensis* Zone of Kolyma and Verkhoyansk shows up against other Early Triassic zones in Siberia by its highest ammonoid diversity at the generic level. However, only Mesozoic-type ammonoid families are known from this zone except for the latest representatives of the xenodiscid *Sakhaites* (Xenodiscidae), found in its loweast part. The ammonoids from this area are as follows: Arctoceratidae (suborder Proptychitina), Xenoceltidae, Meekoceratidae and Prionitidae (Meekoceratina), Melagathiceratidae (Ptychitina), Flemingitidae and Palaeophyllitidae (Ussuritina) (Fig. 4). Among Mesozoic-type prolecanitid ammonoids Sageceratidae and Hedenstroemiidae (Sageceratina) were encountered, but no Palaeozoic-type prolecanitid ammonoids were discovered.

Middle Olenekian (lower Spathian).—Lower Spathian outcrops, known in the Eastern Taimyr area, Lena River basin, Verkhoyansk area, and upper Kolyma River basin (Kenyelichi) (Bytchkov 1972; Zakharov 1978; Ermakova 1981; Dagys and Sobolev 1995), are represented by dark grey and greenish-grey siltstone and mudstone with clayish calcareous nodules alternating with light-grey and dark-red sandstone, 220–680 m thick. The three zones have been recognized in the Lower Spathian in Eastern Taimyr (Dagys and Sobolev 1995): (i) *Bajarunia euomphala* (it includes, from below, the beds of *Bajarunia eiekitensis*, *Boreoceras planorbis*, and *B. apostolicum*); (ii) *Northophiceras contrarium* (*Boreoceras lenaense*, *Praesibirites tuberculatus*, and *P. egorovi* beds); and (iii) *Parasibirites grambergi* (*Parasibirites kolymensis*, *P. mixtus*, and *P. efimovae* beds).

Only Mesozoic-type ammonoid families are known from the lower Spathian of Siberia (Fig. 4): Proptychitidae (Proptychitina), Dieneroceratidae, Meekoceratidae, Olenekitidae and Keyserlingitidae (Meekoceratina), Melagathiceratidae, Paranannitidae (Ptychitina), Procarnitidae (Megaphyllitina), Palaeophyllitidae (Ussuritina), and Sageceratidae (Sageceratina).

Uppermost Olenekian (upper Spathian).—The upper Spathian in Siberia has been most detail investigated in the Mengilyakh Creek section (e.g., Mojsisovics 1886; Lazurkin and Korchinskaya 1963; Zakharov 2007; Zakharov et al. 2008; this study), represented by the Pastanakhskaya and Ystannakhskaya formations. Ammonoid-bearing sequences consist mainly of mudstone with calcareous nodules, 220 m thick, yielding numerous aragonite preserved cephalopods of the *Olenikites spiniplicatus* Zone.

In Mengilyakh, we recognize 13 ceratitid ammonoid genera there, belonging to the six Mesozoic-type families of the orders Ceratitida and Phylloceratida: Meekoceratidae, Olenikitidae, Keyserlingitidae, Sibiritidae (Meekoceratina), Paranannitidae (Ptychitina), and Palaeophyllitidae (Ussuritina) (Fig. 4). Representatives of prolecanitid Sageceratidae (Sageceratina) are very rare there.

Lowest Anisian.—The basal beds of the Anisian in Arctic Siberia (Olenek River basin) consists of dark grey mudstone with numerous calcareous nodules and calcareous sandstone layers, about 23 m thick (Popov 1968; Zakharov 2007).

Bed correlative to the lower part of the *Grambergia taimyrensis* Zone (*Karangatites evolutus* and *Grambergia olenekensis* beds) are probably present as indicated by presence of the next ammonoid assemblage: *Karangatites*, *Stenopopanoceras*, *Grambergia*, *Ussurites*, *Neodolmatites*, and *Epiczekanovskites* (Fig. 4). Only Mesozoic-type families of the Ceratitida and Phylloceratida orders were discovered among earliest Anisian ammonoids of the Olenek River basin (Longobarditidae, Paranannitidae Parapopanoceratidae, Danubitidae, and Ussuritidae) (Fig. 4).

Southern Russian Far East (South Primorye)

Early and Middle Triassic ammonoids in South Primorye were firstly collected by Vasilij P. Margaritov and Dmitry L. Ivanov, who made reconnaissance geologic work for the

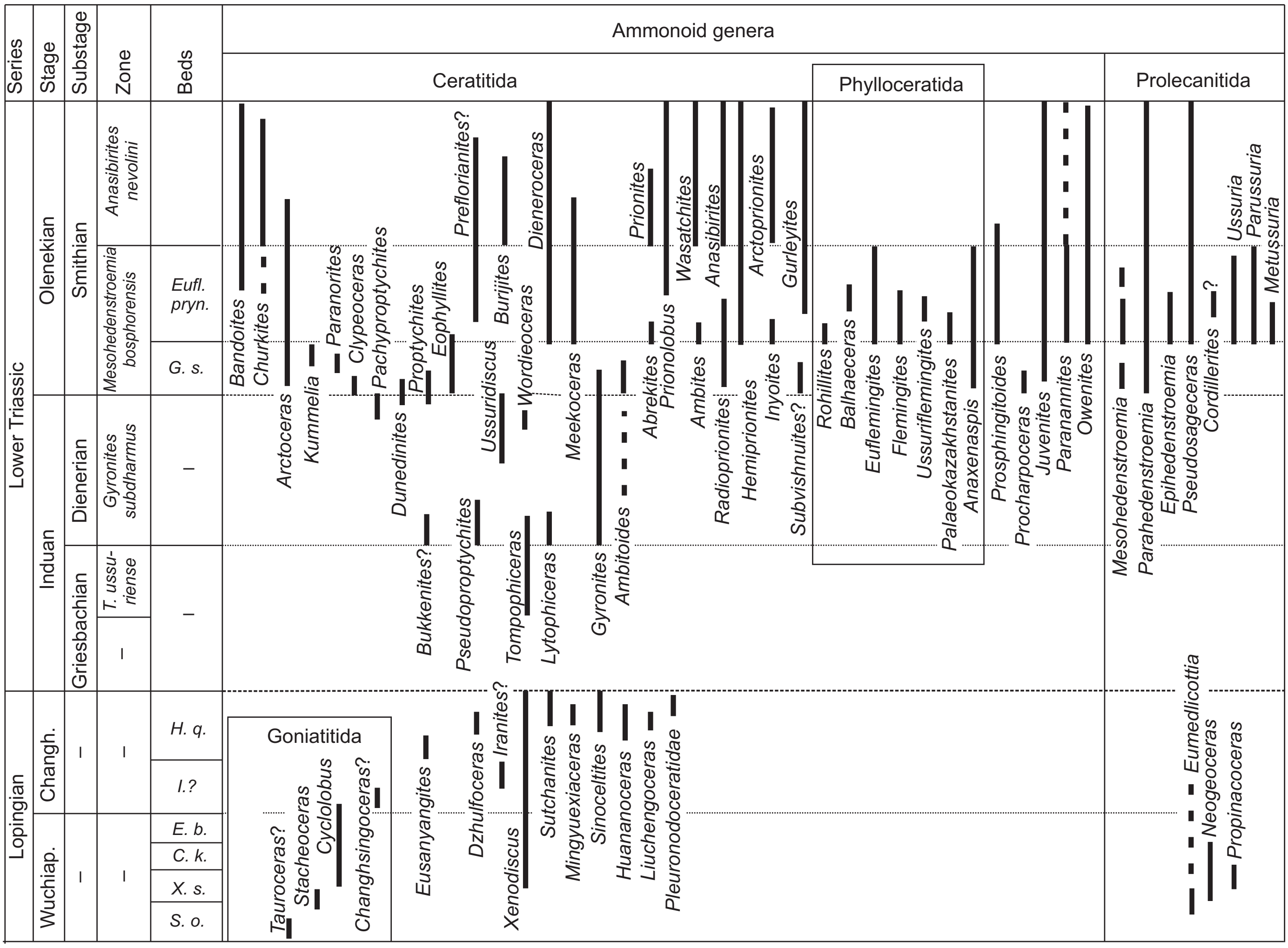

Fig. 5. South Primorye: temporal ranges of ammonoid genera of the Wuchiapingian–Lower Olenekian interval. Abbreviations: *T. ussuriense*, *Tompophiceras ussuriens*; *S. o.*, *Stacgeoceras orientale*; *X. s.*, *Xenodiscus subcarbonarius*; *C. k.*, *Cyclolobus kiselevae*; *E. b.*, *Eusanyangites bandoi*; *I.?*, *Iranites*? sp.; *H. q.*, *Huananoceras qianjiangense*; *G. s.*, "*Gyronites separatus*"; *Eufl. pryn.*, *Euflemingites prynnadai*.

construction of the military outpost Vladivostok and Trans-Siberian railroad in 1880s. On the initiative of Alexander P. Karpinsky, President of the Russian Academy of Sciences, the collected Triassic ammonoids were forwarded to Karl Diener (Vienna), who described them in 1895 (Diener 1895). Later some other monographs (e.g., Kiparisova 1961; Zakharov 1968, 1978) were published on this topic. Permian ammonoids of South Primorye and the adjacent Amur-Trans-Baikal area have been investigated much later (e.g., Popov 1963; Ruzhencev 1976; Zakharov and Oleinikov 1994; Kotlyar et al. 2006; Zakharov and Ehiro 2010).

Wuchiapingian.—Lower Upper Permian (Wuchiapingian) sediments of the lower part of the Lyudyansa Formation (*Stacheoceras orientale*, *Xenodiscus subcarbonarius*, *Cyclolobus kiselevae*, and *Eusanyangites bandoi* beds) in South Primorye, exposed in the Nakhodka area, Neizvestnaya Bay and Artyomovka River basin, are represented by limestone, shales with calcareous nodules and lenses and sandstone, 470–480 m thick (e.g., Zakharov 1983b, 1992; Zakharov and Ehiro 2010; this study).

Representatives of the three ammonoid orders are recognized in the Wuchiapingian of South Primorye: (i) Goniatitida (Neostacheoceratidae and Cyclolobidae), (ii) Prolecanitida (Medlicottiidae and Propinacoceratidae), and (iii) Ceratitida (Araxoceratidae and Xenodiscidae) ammonoids. In this level the prolecanitids are the most abundant group (Fig. 5).

Changhsingian.—Upper Upper Permian (Changhsingian) ammonoid-bearing sequences of the upper part of the Lyudyanza Formation and Kapreevka siltstone member, exposed in the Partizanskaya, Artyomovka, and Ussuri (Krylovka) river basins and Neizvestnaya Bay area in South Primorye (e.g., Zakharov and Oleinikov 1994; Zakharov et al. 1997; this study), are represented by dark grey mudstone and siltstone, yellowish green tuffite intercalated with sandstone and acidic tuff and lenses of marl, about 170 m thick. These sediments are characterised mainly by presence of ceratitid ammonoids (Araxoceratidae, Xenodiscidae, Pleuronodoceratidae, and Huananoceratidae) (Fig. 5). From the order Goniatitida only a single bad preserved cyclolobid ammonoid *Changhsingoceras*? sp. was discovered.

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Induan.—Induan sequences are exposed in many regions of southern Russian Far East, but they are better investigated in the western Ussuri and Abrek bays in South Primorye (e.g., Zakharov 1968, 1996; Zakharov et al. 2009a; Shigeta et al. 2009; this study). These sequenses (Lazurnaya Bay Formation) everywhere in southern Russian Far East consist mainly of conglomerate, sandstone with lenses of calcareous sandstone-coquina and mudstone with calcareous nodules, 60–145 m thick. The lower part of the Induan is represented by the *Tompophiceras ussuriense* Zone, its upper part by *Gyronites subdharmus* Zone (Zakharov 1968, 1978; Markevich and Zakharov 2004; Markevich et al. 2005). Only representatives of the order Ceratitida were discovered among Induan ammonoids of southern Russian Far East. The Induan ammonoid succession in South Primorye includes a single ceratitid ammonoid genus (*Tompophiceras*), belonging to a Permian-type family Dhulfitidae (Paraceltitina). Other ammonoids are representatives of Mesozoic-type taxa at the family level: Proptychitidae, Clypeoceratidae (Proptychitina), Ophiceratidae, Meekoceratidae (Meekoceratina) and possibly Paranannitidae (Ptychitina) (Fig. 4).

Lower Olenekian (Smithian).—The best sections of the Lower Olenekian in Far East are located in South Primorye (e.g., Kiparisova 1961; Zakharov 1996, 1997a; Zakharov et al. 2009b, 2010b; Shigeta et al. 2009). There are two Lower Olenekian lithological facies in this region: shallow-water sandy facies in the western part of South Primorye, 110 m thick (e.g., Tobizin Cape Formation on Russian Island), and deeper silty-clayey facies in its eastern part, about 120 m thick (e.g., the lower part of the Zhitkov Cape Formation in the eastern coast of Ussuri Gulf, Artyom and Smolyaninovo areas, Artyomovka River and Abrek Bay). Intermediate type facies was discovered at the Lower Olenekian of western Ussuri Gulf (Tri Kamnya Cape section), composed of intercalation of sandstone and siltstone with calcareous nodules and lenses, about 120 m thick.

The following ammonoid zones and beds are recognized within the Lower Olenekian in South Primorye: *Mesohedenstroemia bosphorensis* Zone (it includes, from below, the beds of *Ussuriflemingites abrekensis* [= "*Gyronites separatus*"] and *Euflemingites prynadai*) and *Anasibirites nevolini* Zone (Zakharov 1997b; Zakharov et al. 2010b; this study).

Early Olenekian ammonoids of southern Russian Far East are represented by three orders: Ceratitida, Prolecanitida, and Phylloceratida. The former consists of Meekoceratina (Dieneroceratidae, Meekoceratidae, Inyonitidae, Prionitidae, and Xenoceltitidae), Proptychitina (Clypeoceratidae, Proptychitidae, and Arctoceratidae), and Ptychitina (Melagaticeratidae, Paranannitidae, and Columbitidae). Among prolecanitids and phylloceratids that are characteristic of the Far Eastern lower Olenekian some representatives of the suborders Sageceratina (Sageceratidae, Khvalynitidae, Ussuriidae, Aspenitidae, and Hedenstroemiidae) and Ussuritina (Femingitidae and Palaeophyllitidae) have been recorded respectively (Fig. 5).

All these characteristics suggest that the mentioned ammonoid succession is dominated by ceratitid ammonoids. No Palaeozoic-type families have been detected.

Upper Olenekian (Spathian).—Most representative sections for the Upper Olenekian in southern Russian Far East, yielding abundant ammonoids, are the sequences located in South Primorye (e.g., Kiparisova 1961; Zakharov 1997a; Burij and Zharnikova 1981; Markevich and Zakharov 2004).

There are two lower Spathian *Tirolites*-bearing lithological facies in this region: shallow-water calcareous-sandy facies in the western part of South Primorye, 40 m thick (Zhitkov Cape Formation on Russian Island) and deeper silty-shaly facies in its eastern part, about 40–50 m thick (the middle part of the Zhitkov Formation at the eastern Ussuri Gulf).

The upper Spathian *Columbites*-bearing facies almost everywhere in South Primorye, including Russian Island, are represented by deeper silty-shaly facies (the upper part of the Zhitkov Formation), 82–113 m thick. Only in the western Amur Gulf (western South Primorye) the Zhitkov Formation is largely replaced by the more sandy upper Spathian Atlasov Formation, 64 m thick (Zakharov et al. 2005b).

The following ammonoid zones and beds are recognized within the Upper Olenekian in South Primorye: *Tirolites–Amphistephanites* (*Bajarunia dagysi* and *Tirolites ussuriensis* beds), *Neocolumbites insignis*, and *Subfengshanites multiformis* zones.

The Upper Olenekian in southern Russian Far East is characterised by presence of numerous Mesozoic-type ceratite ammonoid families: Tirolitidae, Stephanitidae, Meekoceratidae, Xenoceltitidae, Keyserlingitidae, Olenikitidae, Proptychitidae, Columbitidae, and Megaphyllitidae (Fig. 6). First six taxa are the representatives of the suborder Meekoceratina, but others belong to Proptychitina (Proptychitidae), Ptychitina (Columbitidae), and Megaphyllitina (Megaphyllitidae). Among prolecanitids and phylloceratids the Sageceratina (Sageceratidae, Khvalynitidae, Ussuriidae, and Aspenitidae) and Ussuritina (Palaeophyllitidae and ?Danubitidae) were recognized respectively. No Palaeozoic-type families were discovered.

Lowest Anisian.—Anisian sediments in South Primorye and the Amur area are represented by the Karazin Cape Formation, composed mainly of fucoid sandstone with large calcareous septarian nodules, more than 129 m thick. From the base of the Anisian in South Primorye, the *Ussuriphyllites amurenses* Zone was reported (Zakharov et al. 2005b).

This zone exposed at the western Amur Gulf and Tchernyschew Bay consists of spotted sandy siltstone with calcareous sandy siltstone nodules, yielding in particular Mesozoic-type ceratitid ammonoid families: Prionitidae, Olenikitidae, Keyserlingitidae, Acrochordiceratidae, Megaphyllitidae (Fig. 6). First four taxa listed above are the representatives of the suborder Meekoceratina, last one (Megaphyllitidae) belongs to Megaphyllitina.

Among prolecanitids and phylloceratids representatives of the Sageceratina (Sageceratidae—rare *Parasageceras*) and Ussuritina (Palaeophyllitidae, Ussuritidae, and ?Danubitidae) have been recorded respectively.

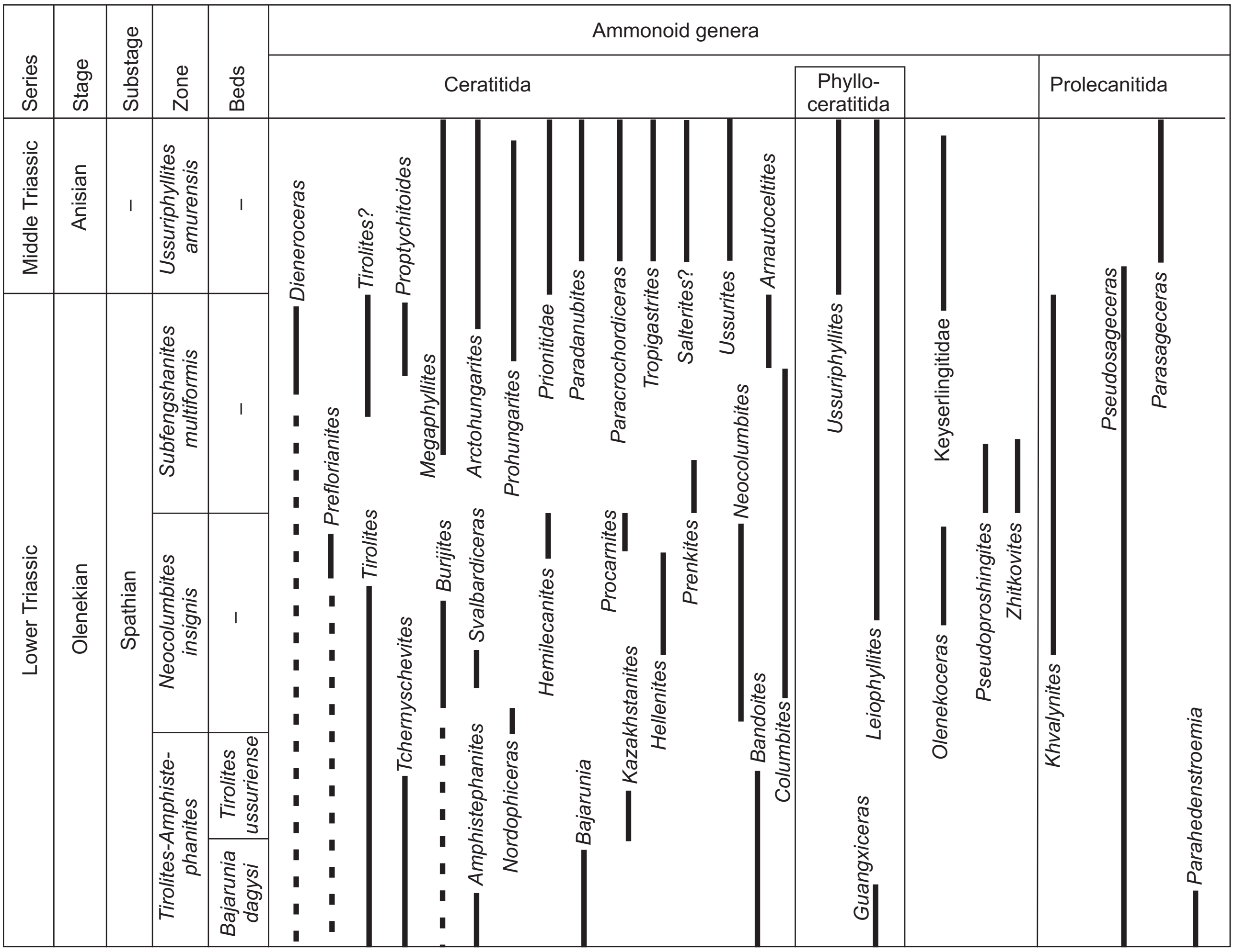

Fig. 6. South Primorye: temporal ranges of ammonoid genera of the upper Olenekian–lowest Anisian interval.

Mangyshlak Peninsula

Main information on Early Triassic ammonoids from the Mangyshlak area in Kazakhstan (Kara-Tau Mountains) was reported by Bajarunas (1911, 1936), Astachova (1960), Shevyrev (1968, 2002), Gavrilova (1980, 1989, 2007), Balini et al. (2000) and Zakharov (in Zakharov et al. 2008). The basic upper Olenekian (Spathian) section in Mangyshlak is located at the Dolnapa Well area. Late Olenekian sediments of the Tartalinskaya and Karadzhatykskaya formations in Kara-Tau are represented chiefly by black mudstone with calcareous nodules and lenses of limestone, intercalated in the lower part of the section with black siltstone and grey, fine-grained sandstone, about 1300 m thick.

Late Olenekian ammonoids of Mangyshlak are represented by three orders: Ceratitida (dominant), Phylloceratida, and Prolecanitida. Eight Mesozoic-type ceratite families (Doricranitidae, Tirolitidae, Prionitidae, Dinaritidae, Xenoceltitidae, Olenekitidae [Meekoceratina], Columbitidae [Ptychitina], Procarnitidae [Megaphyllitina]) have been reported (Fig. 7). First four taxa listed above are the representatives of the suborder Meekoceratina, other taxa belong to Ptychitina (Columbitidae) and Megaphyllitina (Procarnitidae). However, only two prolecanitid families (Sageceratina) are known: Sageceratidae and Khvalynitidae. No Palaeozoic-type ammonoid families are present in the late Olenekian Dolnapa ammonoid succession.

Systematic palaeontology

In this paper we adapted the concepts in ammonoid systematics based on ontogenetic development of suture, which were developed by Ruzhencev (1960) in his cornerstone monograph on Palaeozoic ammonoids. Following to a number of workers, e.g., Schindewolf (1961), Ruzhencev (1962), Wiedmann (1966), Lehmann (1981), Michailova (1983), Starobogatov (1983), Shevyrev (1986), Tozer (1994), Waterhouse (1994), Becker and Kullmann (1996), Wiedmann and Kullmann (1996), Bogoslovskaya et al. (1999); Zhou et al. (1999), Leonova 2009; Brühwiler et al. (2010a), and Ware et al. (2011) we treat the Ammonoidea as a rank higher than order, although some specialists on Jurassic and Cretaceous ammonoids (e.g., Wright et al. 1996),

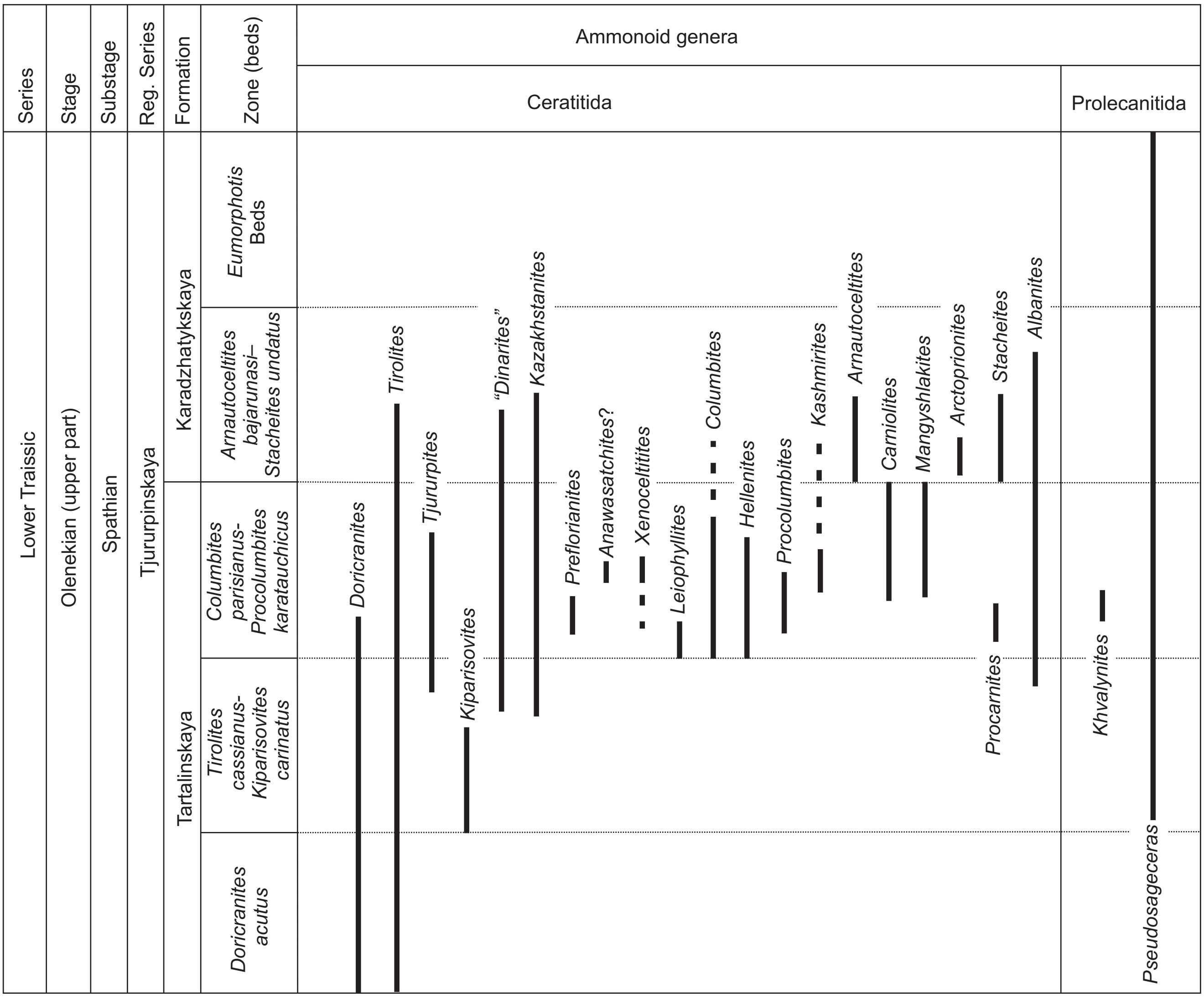

Fig. 7. Mangyshlak, Kazakhstan: temporal ranges of ammonoid genera of the upper Olenekian. Abbreviation: Reg. Series, Regional Series.

following original cocept of Zittel (1884), consider it to be in order rank.

Zakharov's data on ontogenetic development of suture in Permian–Triassic medlicottiid and sageceratid ammonoids first outlined in the Kaliningrad Meeting on Recent and fossil cephalopods in October 1982 (Zakharov 1983a) and then detailed in a series of other publications (Zakharov 1984, 1988) have shown that the following ammonoid stocks can be recognized: (i) Medlicottiida–Sageceratida, characterised by “VLU-VU type” of early lobe development, trilobate to quadrilobate primary suture and multi-lobed suture in late ontogenetic stages (Zakharov 1983a), and (ii) Goniatitida –Ceratitida, characterised by “VLU type” of lobe development and trilobate (for goniatitids and paraceltitids) to quadrilobate (for ceratitids) primary suture (Shevyrev 1986; Zakharov 1988). Jurassic–Cretaceous ammonoids (Lytoceratida and Ammonitida), in contrast, are characterised by quinquilobate to hexalobate primary suture (Michailova 1983). Following Shevyrev (1983) and Bogoslovskaya et al. (1999), we are inclined now to accord a suborder rank to the mentioned medlicottiid and sageceratid taxa.

Untill recently, Late Permian–Anisian ammonoids were assigned to five orders and 12 suborders: (i) order Prolecanitida Miller and Furnish, 1954 (suborders: Prolecanitina Miller and Furnish, 1954; Medlicottiina Zakharov, 1983a; Sageceratina Zakharov, 1983a); (ii) order Goniatitida Hyatt, 1884 (suborder Goniatitina Hyatt, 1884); (iii) order Tornoceratida Wedekind, 1918 (suborder Tornoceratina Wedekind, 1918) (Bogoslovskaya et al. 1999; Leonova 2009); (iv) order Ceratitida Hyatt, 1884 (suborders: Paraceltitina Shevyrev, 1968; Otoceratina Shevyrev and Ermakova, 1979; Meekoceratina Druschits and Doguzhaeva, 1976 [in Druschits et al. 1976]; Ptychitina Hyatt and Smith, 1905; Ceratitina Hyatt, 1884; Pinacoceratina Waagen, 1895; Megaphyllitina Shevyrev, 1983); and (v) order Phylloceratida Arkell, 1950. The present paper provides description of two additional new suborders: Proptychitina suborder nov. (in Ceratitida) and Ussuritina suborder nov. (in Phylloceratida).

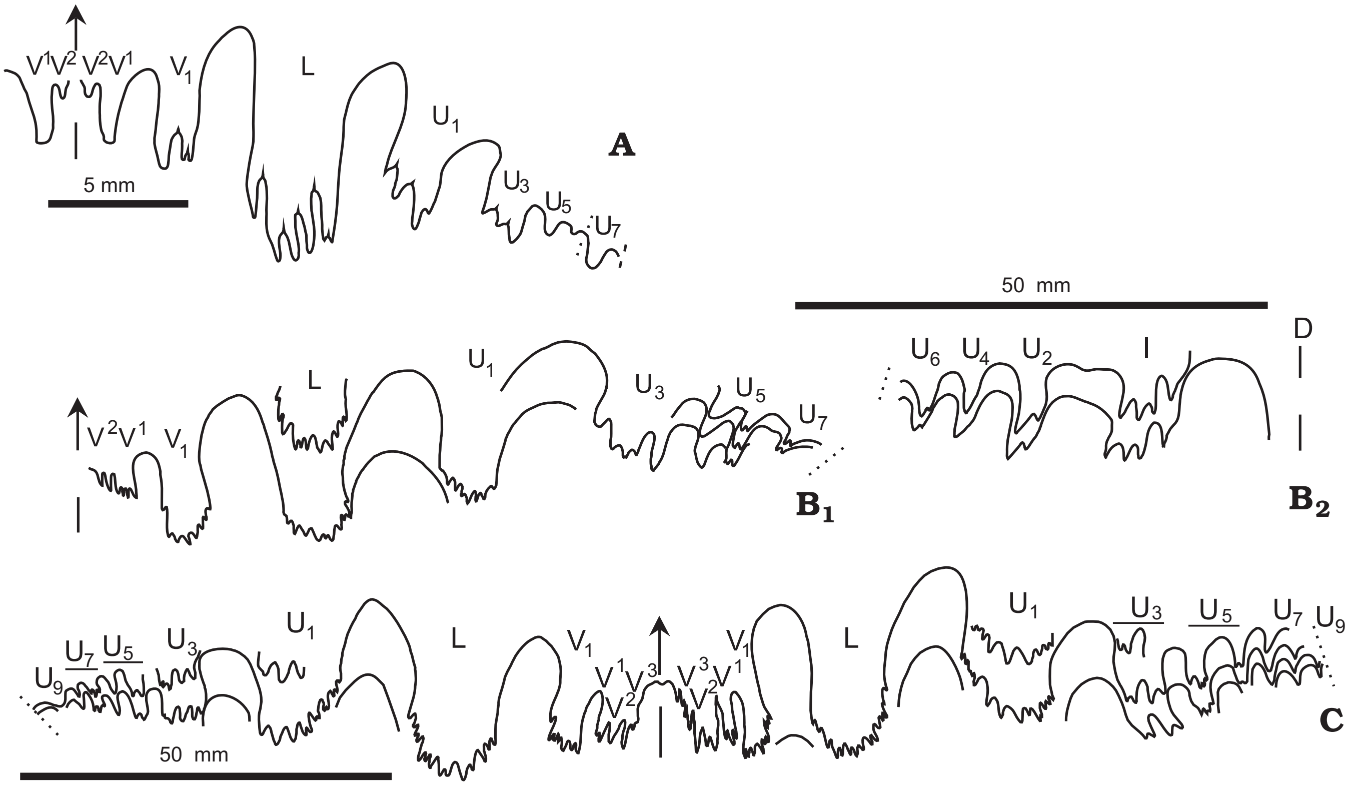

Fig. 8. Suture lines of some Prolecanitida. **A**. *Mesohedenstroemia olgae* sp. nov., DVGI 2/851 (holotype), height 18.4 mm; Lower Olenekian, *Mesohedenstroemia bosphorensis* Zone; SMID quarry at the Artyom environs, south Primorye. **B**, **C**. *Hedenstroemia tscherskii* (Popov, 1961). Lower Olenekian, *Lepiskites kolymensis* Zone; Kenyelichi River, Kolyma River basin. **B**. DVGI 256-3b, height 60.0 mm (B_1) and 73.0 mm (B_2). **C**. DVGI 255-19c, height 73.0 mm. Abbreviations: D, dorsal lobe; I, inner lateral lobe; L, lateral lobe; U, umbilical lobe; V, ventral lobe.

Superorder Ammonoidea Zittel, 1884

Order Prolecanitida Miller and Furnish, 1954

Suborder Sageceratina Zakharov, 1983c

Superfamily Sageceratoidea Hyatt, 1884

Family Hedenstroemiidae Waagen, 1895

Genus *Mesohedenstroemia* Chao, 1959

Type species: *Mesohedenstoemia kwansiana* Chao, 1959; *Flemingites* beds, Lower Olenekian, Lower Triassic, South China.

Species included: Five species from South China and South Primorye: *Mesohedenstroemia kwansiana* Chao, 1959, *M. inflata* Chao, 1959, *M. planata* Chao 1959, *M. bosphorensis* (Zakharov, 1968), and *M. olgae* sp. nov.

Brayard and Bucher (2008) have described two forms from northwestern Guangxi, determined as *Mesohedenstroemia kwansiana* Chao, 1959 and *M. planata* Chao, 1959. Based on these fossils they believe that *Mesohedenstroemia* additionally differs from *Hedenstroemia* by a simple suture line without adventious elements. However, the forms reported by Brayard and Bucher (2008) are rather reminiscent of some representatives of *Ussuridiscus* Shigeta and Zakharov in Shigeta et al. 2009.

Emended diagnosis.—Laterally compressed Hedenstroemiidae with involute coiling and broad, distinctive tabulate venter. Suture like in *Hedenstroemia* but with significantly simpler auxiliary series.

Remarks.—From *Hedenstroemia* Waagen, 1895 (e.g., Waagen 1895; Popov 1961; Zakharov 1988; Dagys and Ermakova 1990) and *Pseudohedenstroemia* Kummel, 1957 (e.g., Arkell et al. 1957) it differs by a distinctively wider tabulate venter with angular ventral shoulders and simpler auxiliary series (Fig. 8).

Geographic and stratrigraphic range.—South China, Primorye; lower Olenekian (lower Smithian).

Mesohedenstroemia olgae sp. nov.

Figs. 8A, 9A.

Etymology: Named after Olga P. Smyshyaeva (Far Eastern Geological Institute, Vladivostok).

Holotype: DVGI 3/851, fully preserved adolescent phragmocone.

Type locality: SMID quarry at Artyom environs, South Primorye.

Type horizon: *Mesohedenstroemia bosphorensis* Zone, Zhitkov Formation, Olenekian, Lower Triassic (see Zakharov 1978) (found from float block).

Diagnosis.—Laterally compressed *Mesohedenstroemia*, with broad tabulate venter. Suture with a pair of well developed adventitious lobes.

Description.—The shell is thinly discoidal, extremely involute, with a broad, distinctively tabulate venter, angular ventral shoulders and gently convex flanks with maximum whorl width at about two thirds of whorl height. Umbilicus very narrow and deep with rounded shoulders. Ornamentation consists

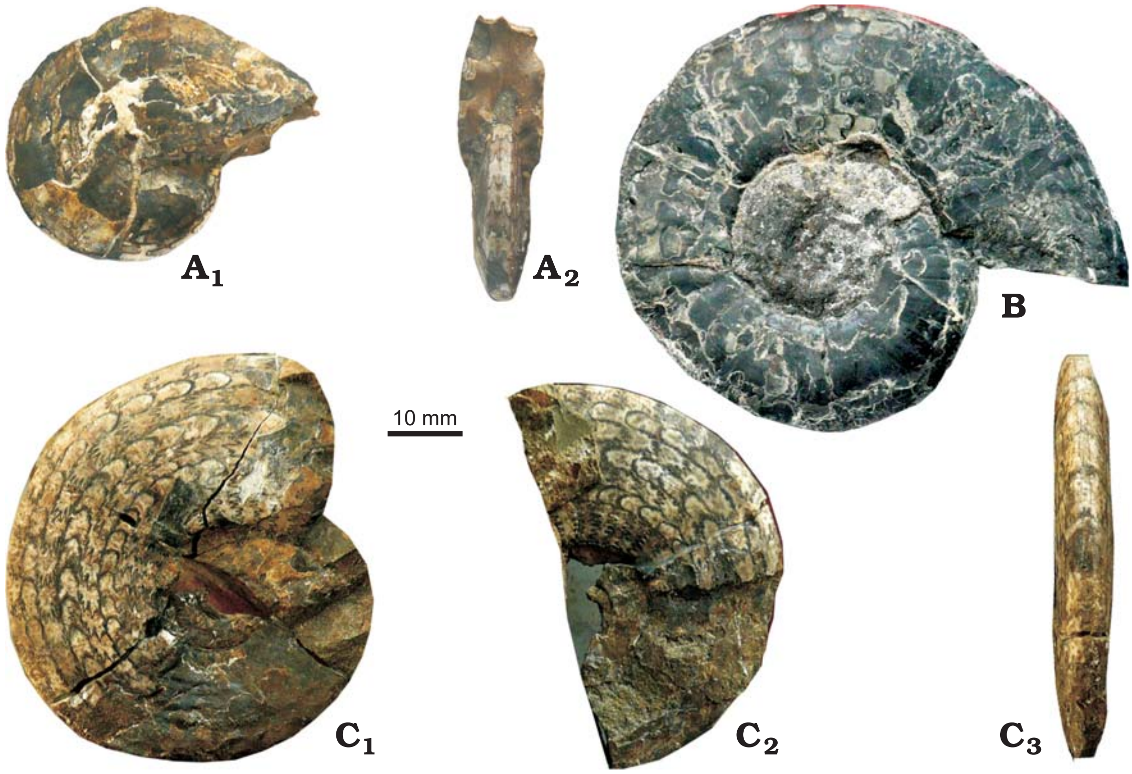

Fig. 9. Some Early Olenekian Prolecanitida, Ceratitida, and Phylloceratida from Lower Olenekian, *Mesohedenstroemia bosphorensis* Zone; SMID quarry at the Artyom environs, South Primorye. **A**. Prolecantid *Mesohedenstroemia olgae* sp. nov., DVGI 2/851 (holotype), right lateral (A_1) and ventral (A_2) views. **B**. Ceratitid *Inyoites sedini* sp. nov., DVGI 1/851 (holotype). **C**. Phylloceratid *Subbalhaeceras shigetai* gen. and sp. nov., DVGI 2/851 (holotype), right lateral (C1), left lateral (C_2), ventral (C_3) views.

of fine, sinuous growth lines as well as low and narrow radial folds, curving lightly forward on the lateral sides.

Suture ceratitic with slender lateral saddles. The ventral lobe (V) is very wide and shallow, divided by a medial saddle, in which a pair of adventitious lobes (V^1 and V^2) are well developed on its each side. The outer branch (V_1) of the ventral lobe terminates with two denticulations at its base, one of which is accompanied by two smaller denticulations. The lateral lobe (L) is the largest, and is equipped with five denticulations, one of which is also accompanied by two smaller denticulations; the lobe U_1 is shorter with four denticulations. The shallow lobe U_3 is trident at its base, other auxiliary elements (e.g., U_5 and U_7) remain simple.

Dimensions in mm and ratios:

Specimen no.	D	H	W	U	H/D	W/D	U/D
Holotype DVGI 3/851	47?	29?	12.2	2.0	0.62?	0.26?	0.04?
DVGI 3/851	29.5	17.4	9.2	0.8	0.59	0.31	0.03

Remarks.—The new species is distinguished from *Mesohedenstroemia bosphorenses* (Zakharov, 1968) from South Primorye by presence of two adventitious lobes, the narrower outer branch of the ventral lobe, deeper lateral lobe and simpler auxiliary series. More complicated adventitious elements, high first lateral lobe and more complicated auxiliary series differentiate it from *M. kwangsiana* Chao, 1959, *M. planata* Chao, 1949, and *M. inflata* Chao, 1959 from South China (Chao 1959).

Stratigraphic and geographic range.—Type locality and type horizon only.

Order Ceratitida Hyatt, 1884

Suborder Proptychitina nov.

Diagnosis.—Large involute to semi-evolute discocones, with rounded venter and deep umbilicus, without any tendency of having prominent umbilical shoulders. Surface, marked by radial folds and growth lines, rather with fine spiral lirae mainly in venter. Suture line ceratitic like in ancestral Otoceratina, but more advanced, with denticulated branches of the ventral lobe. The type of early lobe ontogeny like in Otoceratina: VL : ID – (V_1V_1) LU^1 : ID – (V_1V_1) LU^1U^2 : I(D_1D_1).

Remarks.—Differs from the Otoceratina Shevyrev and Ermakova, 1979 by lack of prominent umbilical shoulders and more advanced septal necks (amphichoanitic to prochoanitic within whorls 3 and 4, but not retrochoanitic). A single superfamily Proptychitoidea Waagen, 1895 (families: Proptychitidae Waagen, 1895, Arctoceratidae Arthaber, 1911, and Clypeoceratidae Waterhouse, 1996a). Lower Triassic (Induan–Olenekian).

Suborder Meekoceratina Druschits and Doguzhaeva in Druschits et al., 1976

Superfamily Meekoceratoidea Waagen, 1895

Family Inyoitidae Spath, 1934

Genus *Inyoites* Hyatt and Smith, 1905

Type species: *Inyoites oweni* Hyatt and Smith, 2005; Inyo County, California; *Meekoceras* Beds, Olenekian, Lower Triassic.

Inyoites sedini sp. nov.

Figs. 9B, 10A.

Etymology: Named after Alexander Sedin (Institute of Pacific Oceanology, Vladivostok, Russia).

Holotype: DVGI 1/850, fully preserved adolescent phragmocone.

Type locality: SMID quarry at Artyom environs, South Primorye.

Type horizon: Zhitkov Formation, *Mesohedenstroemia bosphorensis* Zone of Zakharov (1978) (found in a floated nodule in suitable ammonoid association).

Diagnosis.—Thinly discoidal, evolute *Inyoites*, with a weak ventral keel and small auxiliary lobe, serrated at the base.

Description.—The shell is thinly discoidal, evolute, with lanceolate venter and a week keel, rounded ventral shoulders and slightly convex flanks. Umbilicus wide, with low, oblique wall and rounded shoulders.

The surface is ornamentated with dense, radial ribs that run from the umbilicus sinuously up the sides and disappear below the base of the keel.

The ventral lobe (V) is subdivided by a high and wide median saddle into two branches, serrated at the base and within the median saddle wall. The first and second lateral saddles are large, the third one is significantly smaller. The lateral lobe (L) is deep and wide, the first umbilical lobe (U^1) is somewhat shorter, both are serrated at the base. The auxiliary lobe (U^3) is significantly smaller, but still serrated.

Dimensions in mm and ratios:

Specimen no.	D	H	W	U	H/D	W/D	U/D
Holotype DVGI 1/851	66.7	23.8	12.6	27.3	0.36	0.19	0.41

Remarks.—The new species is distinguished from *Inyoites spicini* Zakharov, 1968 from South Primorye by considerably more evolute shell and weeker keel, from *I. oweni* Hyatt and Smith, 1905 from California by somewhat considerably more evolute shell, weeker keel and more denticulated ventral lobe, from *I. krystyni* Brayard and Bucher, 2008 from South China by more complex outline of the the umbilical portion of the suture and weeker keel, from *I. striatus* Chao, 1959 and *I. oblicatus* Chao, 1959 from South China by more strongly evolute shell.

Stratigraphic and geographic range.—Type locality and type horizon only.

Order Phylloceratida Arkell, 1950

Suborder Ussuritina nov.

Diagnosis.—Semiinvolute to evolute derivates of Meekoceratina with more or less simple monophyllic suture. The type of early lobe ontogeny like in Meekoceratina and Otoceratina: VL : ID – (V_1V_1) LU^1 : ID – (V_1V_1) LU^1U^2 : I(D_1D_1).

Remarks.—Differs from the Meekoceratina Druschits and Doguzhaeva in Druschits et al. 1976 and Phylloceratina Arkell, 1950 by monophyllic suture and more advanced or more primitive septal necks, respectively (amphichoanitic type for *Monophyllites* was fixed at the end of the second whorl; see Zakharov 1978). From Phylloceratina new suborder seems to be distinguished additionally by simpler (four-lobes) primasuture. Possibly two superfamilies: (i) Ussuritoidea Hyatt, 1900 (families: Flemingitidae Hyatt, 1900, Palaeophyllitidae Popov, 1958 (in Kiparisova and Popov 1958), Ussuritidae Hyatt, 1900), and (ii) ?Danubitoidea Spath, 1951 (at least family Danubitidae Spath, 1951). Lower (Olenekian)–Upper (Carnian) Triassic.

Superfamily Ussuritoidea Hyatt, 1900

Family Flemingitidae Hyatt, 1900

Genus *Subbalhaeceras* nov.

Etymology: From *Balhaeceras* and Latin *sub*, nearly.

Type species: *Subbalhaeceras shigetai* sp. nov.; lower Olenekian, *Mesohedenstroemia bosphorensis* Zone, South Primorye.

Diagnosis.—Laterally compressed Flemingitidae with semiinvolute coiling, tabulate to concave venter and ceratitic suture line with the very wide ventral lobe, significantly denticulated L and U_1 lobes, subphylloid saddles and some auxiliary elements (lobes U_3, U_5, U_7, and U_9) in its umbilical part.

Species included.—Type species only.

Remarks.—The subphylloid saddles of the suture line of the new genus justify its assignment to the Flemingitidae. The new genus can not be distinguished from *Balhaeceras* (Shigeta et al. 2009) on the basis of the external features. The main difference is in the suture-line, broader and complicated ventral lobe and more denticulated other lobes, including longer auxiliary series.

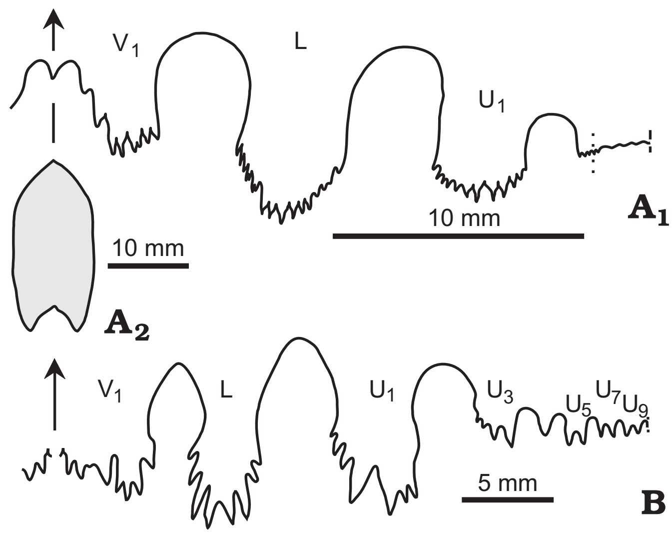

Fig. 10. Ammonoids suture lines from lower Olenekian, *Mesohedenstroemia bosphorensis* Zone; SMID quarry at the Artyom environs, south Primorye. **A**. Ceratitid *Inyoites sedini* sp. nov., DVGI 1/851 (holotype). Suture line, height 21.2 mm (A_1); whorl cross-section, height 21.1 mm (A_2). **B**. Suture line of phylloceratid *Subbalhaeceras shigetai* gen. and sp. nov., DVGI 2/851 (holotype). Abbreviations: L, lateral lobe; U, umbilical lobe; V, ventral lobe.

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Subbalhaeceras shigetai sp. nov.

Figs. 9C, 10B.

Etymology: Named after Dr. Yasunari Shigeta (National Museum of Nature and Science, Tsukuba, Japan).

Holotype: DVGI 2/851, fully preserved adolescent phragmocone.

Type locality: SMID quarry at Artyom environs, South Primorye.

Type horizon: *Mesohedenstroemia bosphorensis* Zone, Zhitkov Formation, Olenekian, Lower Triassic (see Zakharov 1978) (found in a float block).

Description.—The shell is thinly discoidal, semiinvolute, with tabulate to concave venter, subangular ventral shoulders and slightly convex flanks with maximum whorl width at about one thirds of whorl height. Umbilicus fairly broad with low, oblique wall and rounded shoulders. The surface is ornamentated with rare radial folds in inner whorls.

Suture ceratitic (Fig. 10B) with subphylloid saddles and very wide ventral lobe (V) subdivided by a low median saddle into two broad branches serrated in a complicated manner at their base and within the significant part of the median saddle. The second lateral saddle is larger, than the first and third ones. The lateral lobe (L) is deep, denticulated at the base and lower parts of its walls. The first umbilical lobe (U^1) is also deep, but wider then the L-lobe, denticulated at the base and lower parts of the one of its walls. The auxiliary series at external part of suture consists of some short lobes (U_3, U_5, U_7, and U_9), mainly bicaspid ones. A short radial rib was found at H = 14 mm.

Dimensions in mm and ratios:

Specimen no.	D	H	W	U	H/D	W/D	U/D
Holotype DVGI 2/851	54.2	21.9	8.0	16.3	0.40	0.15	0.30

Stratigraphic and geographic range.—Type locality and type horizon only.

Discussion

Late Permian ammonoid suborders and their phylogenetic relationships.—Main evidences on Late Permian ammonoids were reported from five regions of the world: (i) Transcaucasia (e.g., Ruzhencev and Shevyrev 1965; Kotlyar et al.1983; Zakharov et al. 2005a), (ii) Iran (Bando 1979;

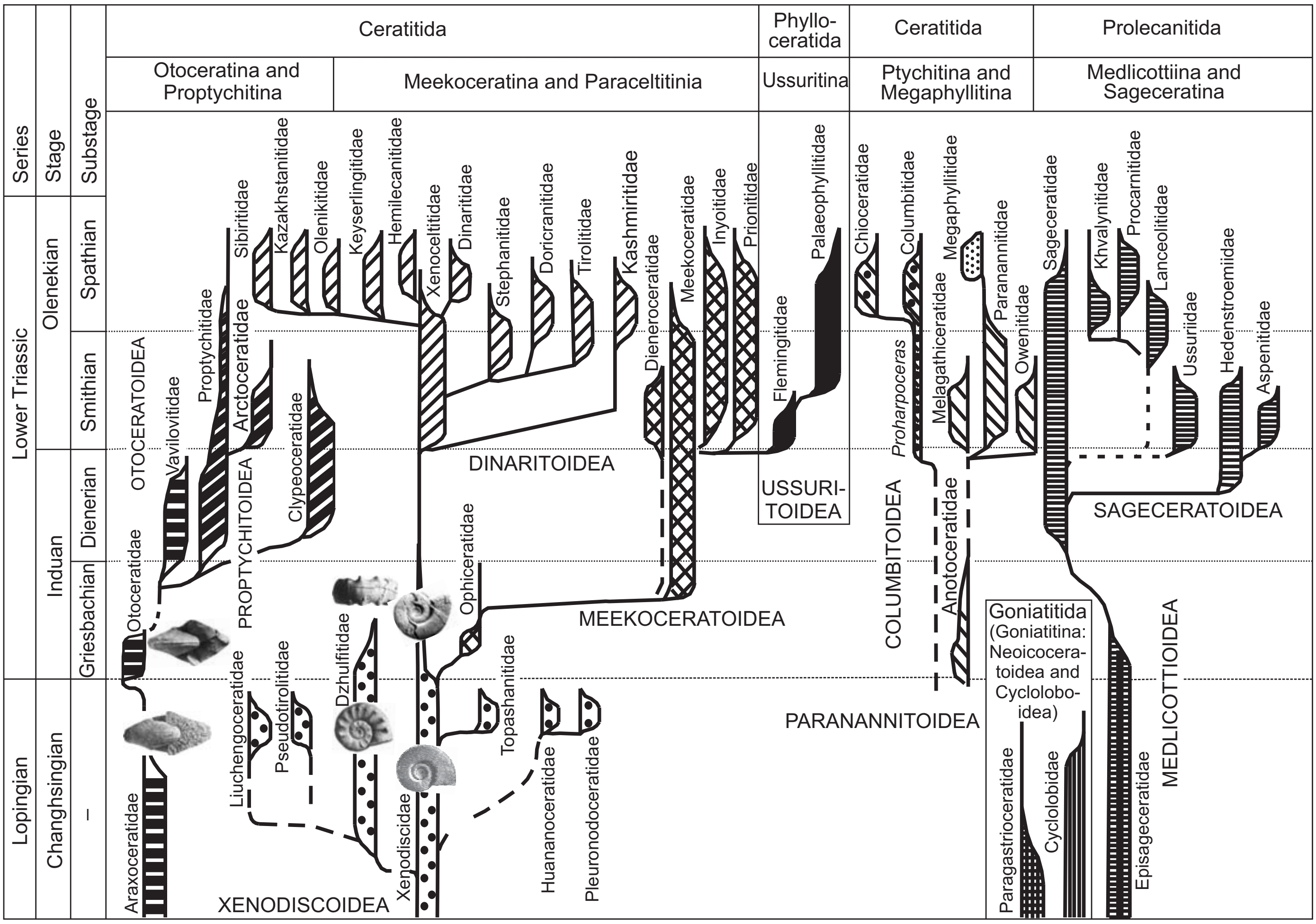

Fig. 11. Suggested phylogenetic relationships in the Changhsingian–Olenekian goniatitid, prolecanitid, ceratitid, and phylloceratid ammonoid superfamilies and families.

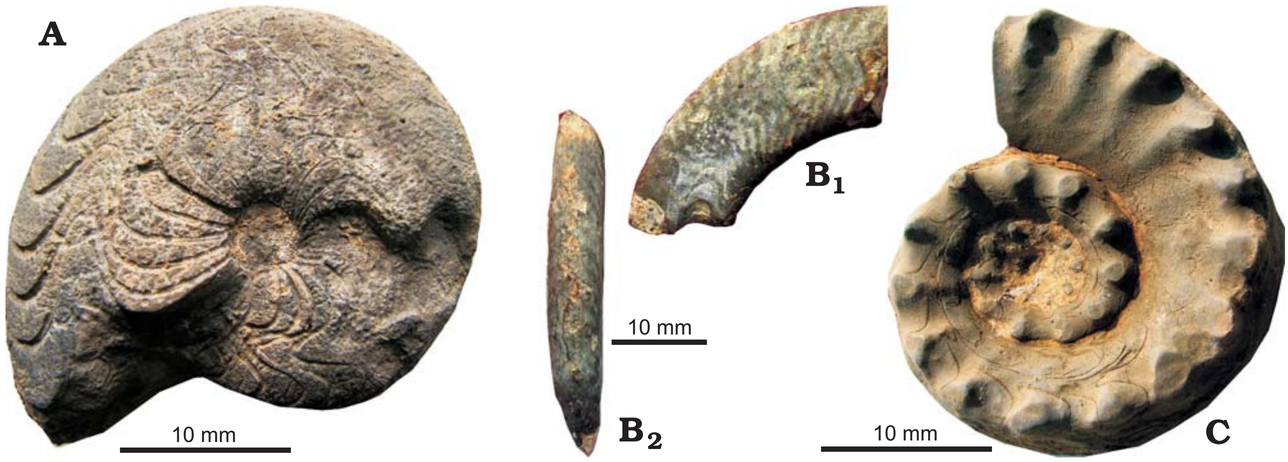

Fig. 12. Representatives of Wuchiapingian ammonoids from the Hambast Formation of Abadeh, Central Iran. **A**. *Pseudogastrioceras abichianum* (Möller, 1879), DVGI, no. 10/850 (most likely *Clarkina leveni* Zone). **B**. *Paraceltitites* sp., DVGI, no. 1/850 (most likely *Clarkina transcaucasica* Zone): right lateral (B_1) and ventral (B_2) views. **C**. *Paratirolites waageni* (Stoyanov, 1910), DVGI no. 11/850 (Hambast Formation, upper Member 7), late Dorashamian *Paratirolites kittli* Zone.

Taraz et al. 1981; Zhou et al. 1989; Zakharov et al. 2010a), (iii) South China (e.g., Chao 1965; Zhao et al. 1978), (iv) Japan (Ehiro 2010), and (v) South Primorye (Zakharov and Ehiro 2010). All these data and new evidences show that the Late Permian ammonoids are represented by the four orders, listed below: (i) Prolecanitida (Medlicottiina), (ii) Goniatitida (Goniatitina), (iii) Tornoceratida (Tornoceratina), and (iv) Ceratitida (Otoceratina and Paraceltitina). A main body of Late Permian cephalopod fossils is formed by ceratitid ammonoids (Figs. 3, 5, and 11).

Two out of four Late Permian ammonoid orders (Tornoceratida and Goniatitida) have not survived P–T boundary event. Latest representative of the Tornoceratida (*Neoaganides*) was discovered in the Dzhulfian in Transcaucasia (Zakharov et al. 2010a), but there is an evidence that this genus existed during the Late Carboniferous–Permian, including Changhsingian (Bogoslovskaya et al. 1999; Zhou et al. 1999; Leonova 2009). However, the position of a latest representatives of the *Pseudogastrioceras* (Goniatitida), which was most abundant during the early Wuchiapingian (Fig. 12), was documented by us with some degree of certainty in the late Dorashamian (Changhsingian) *Paratirolites kittli* Zone, at 3–4 m below the Permian–Triassic boundary, according to data on the sections Dorasham II-2, Akhura, and Karabaglyar-2. One of suborders of prolecanitid ammonoids (Medlicottiina) and both suborders of the Ceratitida (Otoceratina and Paraceltitina), known in the upper Permian, in contrast, crossed the P–T boundary.

We agree with Spinosa et al. (1975) and Shevyrev (1986) that the family Paraceltitidae (Paraceltitina) seems to be an initial group of ceratitid ammonoids, appearing in the Middle Permian. A single representative of this ceratitid family, *Paraceltites* sp. (Fig. 12) was recently discovered by us in the Dzhulfian *Clarkina transcaucasica* Conodont Zone, about 21–22 m above the base of the member 6 of the Hambast Formation in Central Iran (Zakharov et al. 2010a). The exact interval of a stratigraphical distribution of *Paraceltites* is still under discussion (Bogoslovskaya et al. 1999; Spinosa et al. 1975; Zhou et al. 1999). However, our finding of *Paraceltitites* sp. in the Dhulfian of Abadeh seem to be in accordance with a point of view (Spinosa et al. 1975) that representatives of *Paraceltitites* existed in both the Middle and the Late Permian. Paraceltitidae appears to be directly ancestral to the suborders Meekoceratina and Otoceratina.

Early Triassic ammonoid suborders and their phylogenetic relationships.—According to published (e.g., Zhao et al. 1978; Shevyrev 1990; Brayard et al. 2006a, b, 2007, 2009; Brayard and Bucher, 2008; Brühwiler et al. 2008) and our own data, Early Triassic ammonoids are represented by three orders, listed below: (i) Prolecanitida (Medlicottiina and Sageceratina), (ii) Ceratitida (Paraceltitina, Otoceratina, Proptychitina, Meekoceratina, Ptychitina, and Megaphyllitina), and (iii) Phylloceratida (Ussuritina).

Medlicottiina, Paraceltitina, and Otoceratina are known from both the Late Permian and the Early Triassic, but other suborders (Proptychitina, Meekoceratina, Ussuritina, Megaphyllitina and possibly Ptychitina) apparently firstly appeared in the Early Triassic. Ceratitid ammonoids continued to be a dominant group among Early Triassic ammonoids. However, there is no information concerning the phylogenetic connections of the suborder Ptychitina, specifically Paranannitoidea (Anotoceratidae, Paranannitidae, Melagathiceratidae) and Columbitoidea (Columbitidae and Chioceratidae) (Fig. 11). The suborder Proptychitina (Proptychitidae and Arctoceratidae) originated apparently from the Otoceratina (Vavilovitidae). Triassic Ussuritina (Flemingitidae, Palaeophyllitidae, ?Danubitidae) seems to be an ancestral group for Phylloceratina, widely developed during the Jurassic and Cretaceous.

Proceeding from the assumption that the P–T boundary in the Boreal realm locates at the base of the *Otoceras* beds, as it

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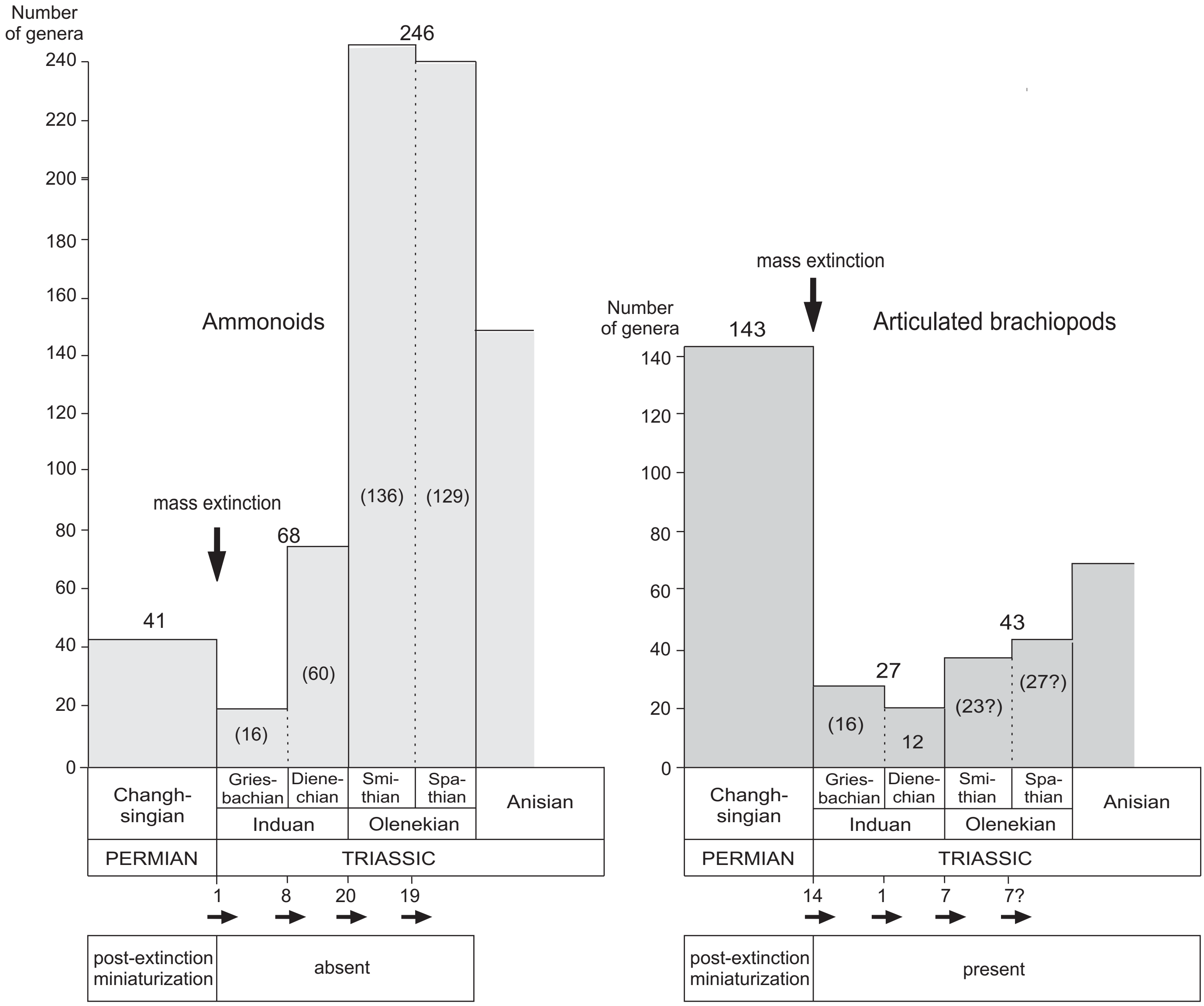

Fig. 13. Early Triassic generic richness recovery of the ammonoid fauna. Number in parenthesis means number of genera in substages; number above the horizontal arrows indicate quantity of genera crossed the corresponding boundary interval (e.g., Bogoslovskaya et al. 1999; Tozer 1994; Ermakova 2002; Brayard et al. 2006a, b; Mu et al. 2007; Shigeta et al. 2009; Brühwiler et al 2010a, b, 2012; Guex et al. 2010; Ware et al. 2011; this study). Data on the brachiopod fauna (Zakharov and Popov in press) is given for comparison.

is in the Himalayas (this version, however, needs in stronger basis now, taking into account the new carbon-isotope data from the P-T boundary transition of the Boreal realm [Horachek et al. 2012]), Permian-type medlicottiid ammonoid *Episageceras* seems to be a single ammonoid genus crossing through the end-Permian crisis. The genus is reported in the Triassic sediments in several regions of the world, incuding the Boreal realm, where it was found in the Induan of the following localities: (i) in the early Griesbachian *Otoceras boreale* Zone of the Kobyuma River basin, Verkhoyans area, Siberia (Popov, 1961), (ii) in the late Griesbachian *Tompophiceras morpheos* Zone of the Burgagandzha River, Verkhoyansk area, Siberia (Zakharov 1978), and (iii) in the early Dienerian *Vavilovites turgidus* Zone of the Okhotsk area, Far East Russia (Dagys and Ermakova 1996). Other Induan ammonoid genera (15 Griesbachian and 59 Dienerian) are Mesozoic in type (Fig. 13). However, all Olenekian ammonoid genera (136 Smithian and 129 Spathian ones, respectively), are all entirely Mesozoic-type.

Besides Episageceratidae only two other lineages at the family level (Xenodiscidae and Dzhulfitidae) and also a single lineage at superfamily? level (Otoceratoidea) survived the end-Permian mass extinction.

Going through the end-Permian mass extinction, ammonoids lost many taxa, including the order Goniatitida (Fig. 11), but have quickly exceeded their former taxonomic diversity and abundance by the end of the Induan (Dienerian) (Fig. 13). As it was calculated by Brayard et al. (2010), Triassic ammonoids reach levels of diversity higher than in the Permian less than 2 million years just after the end-Permian mass-extinction. By the end of the Smithian, their level of diversity seems to be about 270% of the one in Changhsingian (Fig. 13), mainly because of the rapid diversification of the suborders Meekoceratina, Proptychitina, and Sageceratina (Fig. 11).

Migration to higher latitudes.—Most diversed Permian and Triassic ammonoid faunas inhabited subequatorial areas, including the Tethys (e.g., Zakharov 1974, 1977, 1980; Brayard et al. 2007; Zakharov et al. 2008). However, taxonomic diversity of Late Permian ammonoid assemblages at higher latitudes seems to be extremely restricted. At least one Late Permian ammonoid genus *Paramexicoceras* known from the Boreal realm was found in the Imtachan Formation of the Verkhoyansk area (Popov 1970; Andrianov 1985; Zakharov and Ehiro 2010) and in the Foldvik Creek Formation of Greenland (Nassichuk 1995; Zakharov and Ehiro 2010). It may be partly connected with a change in the reduced salinity of sea-waters in some basins of the Boreal realm during Late Permian time (Zakharov 1980), though, this problem is still under discussion.

Earlier we hypothesized that otoceratid and some other ceratitid ammonoids, which were inhabitant of the tropical-subtropical climatic zone (e.g., such as that in the Iran-Transcaucasia area) migrated into higher latitudes, including the Boreal realm, following phytoplankton, crustaceans, and other organisms, probably to restore its food supply that had been disrupted in many low-latitude areas by end-Permian conditions (Zakharov et al. 2008). Under the influence of the end-Permian event they possibly got capability for living under reduced salinity conditions of Early Triassic marine basins, documented based on the oxygen isotopic data from Arctic Siberia (Zakharov et al. 1999). However, during the Early Triassic, numerous Mesozoic-type ammonoid taxa occupied several high latitude regions (Zakharov et al. 2008; Zakharov and Popov in press).

Conclusions

- Among four known ammonoid orders from the Late Permian, only two (Prolecanitida and Ceratitida) survived P–T boundary. Among the 11 ammonoid suborders (Medlicottiina, Tornoceratina, Goniatitina, Paraceltitina, Otoceratina, Sageceratina, Proptychitina, Meekoceratina, Ussuritina, Ptychitina, and Megaphyllitina) known from the Upper Permian–Lower Triassic interval, only last six have apparently evolved after the end-Permian mass extinction.
- In spite of the fact that only a few ammonoid lineages survived the Late Permian mass extinction (at least one lineage [*Episageceras*] at the generic level, three lineages [Episageceratidae, Xenodiscidae, and Dhulfitidae] at the family level, and one lineage [Otoceratoidea] at the superfamily? level), ammonoids have exceeded their former taxonomic diversity at the generic level during a short time-interval of Griesbachian–Dienerian.
- Immediately after the end-Permian extinction event, Tethyan ammonoids occupied several higher latitude regions (e.g., Boreal realm, where taxonomic diversity of Late Permian ammonoids was very restricted), subsequently inhabiting these areas also during all Triassic time.

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