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Ammonite-Based Correlation of the Lower and Middle (*Panderi* Zone) Volgian Substages with the Tithonian Stage

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Abstract — Based on stratigraphic distribution of ammonite genera in common for the Volgian and Tithonian stages, a new correlation scheme of the lower-middle Volgian with the Tithonian is proposed. The lower Volgian Substage corresponds to the lower Tithonian Substage coupled with the middle Tithonian *semiforme* Zone at least. The *panderi* Zone is correlative with the interval from the middle Tithonian *fallauxi* Zone to the upper part of the upper Tithonian *microcanthum* Zone. The absence of ammonite genera in common hinders the direct correlation between higher levels of the Volgian and Tithonian stages. Peculiarities in Boreal-Tethyan migrations of ammonites during the early-middle Volgian are discussed. *Lingulaticeras blaschkei,* a species very important for correlation of the *panderi* Zone with the Mediterranean zonation is described and figures of some other ammonite species, such as *Sutneria asema* and *S.* cf. *eugyra,* are given for the first time.

Key words: ammonites, Boreal-Tethyan correlation, Volgian, Tithonian.

Since the 1960s, some specialists in stratigraphy of the Jurassic-Cretaceous boundary beds (e.g., R. Casey, A. Zeiss) called in question the equality of ranges of the Volgian and Tithonian stages. During last decades, new schemes based on mixed ammonite assemblages with Boreal and Mediterranean elements were proposed for correlation of these stratigraphic units. According to the Interdepartmental Stratigraphic Committee resolution, the Tithonian Stage is now considered as representing a stratigraphic equivalent of the lower-middle Volgian substages with the lower Volgian Substage corresponding to the lower-middle Tithonian [1]. Stratigraphic distribution of perisphinctids occurring both in the Boreal and Submediterranean realms is consistent with such a correlation.

Nevertheless, new data obtained during the last three decades on distribution of Submediterranean aspidoceratids, oppeliids, and haploceratids in the lower and middle Volgian substages of the Russian plate, which were virtually not taken into account until recently, allowed a new variant of the Volgian-Tithonian correlation to be proposed [2]. The availability of several different correlation schemes based on ammonoid succession implies the necessity to analyze all the data on co-occurrence of Subboreal and Submediterranean ammonite genera.

AMMONITE GENERA IN COMMON FOR THE VOLGIAN AND TITHONIAN STAGES: A REVIEW

In 1881, S.N. Nikitin [3] proposed the name *Volgian Formation* (Stage subsequently) for the post-Kimmeridgian sediments of the Russian plate because of a high provincialism of their ammonite faunas and impossibility of tracing in Russia the zonal units previously proposed for the Tithonian and Portlandian stages. Slightly later on, some ammonite species known from the Tithonian were found, however, in sediments, which are now referred to the lower Volgian Substage. For instance, Semenov [4] described *Aspidoceras* sp. from the Orenburg oblast. The examination of the Semenov's collection stored at the Chair of Historical Geology of the St. Petersburg University (no. 95) revealed that this form belongs to the lower Volgian species *Anaspidoceras neoburgense* (Oppel). The representative of the same species was likely described by Sokolov ([5], p. 23) as *Aspidoceras* sp. a few years later.[1] Soon after, Rozanov, ([6], p. 29) mentioned a fragment of ammonite “characterized by the Tithonian habitus and close probably to *Hoplites callisto*” in sediments referred recently to the *virgatus* Zone and Subzone of the middle Volgian Substage. Unfortunately, this ammonite was not figured and no similar forms were ever recorded in the *virgatus* Zone.

Approximately at that time, first data on the occurrence of Boreal and Subboreal ammonites in areas adjacent to the Russian plate appeared. Par example, Abel [7] mentioned *Ammonites virgatus* from Lower Austria and Vetters ([8], Plate 22, fig. 5) figured *Perisphinctes* cf. *nikitini.* The last form was subsequently revised and described as a new species *Isterites austriacus* [9]. *Dor-*

[1] In his description, Sokolov paid attention to the absence of any tubercles in this form, which feature characterizes A. *neoburgense.*

soplanites panden from the North Caucasus was also described and figured ([10], Figs. 1,2). Simultaneously, Renz [11] reported on the occurrence of *Dorsoplanites dorsoplanus* and *Lomonossovella lomonossovi* in the North Caucasus, although he did not reproduce their figures.

In the 1930s, ammonites characteristic of the West European Jurassic were mentioned from Volgian sections in several works dedicated to geology of the Volga region. N.T. Zonov was the first to pay attention (without mentioning of particular sections) to the occurrence of a peculiar horizon with oppeliids within the Kimmeridgian-Volgian boundary beds of the Volga region. He emphasized ([12], p. 39) that "...of significant interest is the presence of poorly preserved forms similar to both some lower Tithonian *Ochetoceras* and upper Kimmeridgian *Haploceras,* for instance, to *H. (Glochiceras)* ex *gr.fialar,* in the uppermost layers with *Aulacostephanus.* Higher, these beds with *Glochiceras(?)-Ochetoceras* are defined as an autonomous marly unit lacking any signs of *Aulacostephanus...* The belonging of these beds to the *Oppelia (Ochetoceras) zio* Subzone, i.e., to the basal part of the *O. steraspis* Zone is highly probable". In the Gor'kii oblast and Chuvash Republic, Gerasimov and Kazakov [13] noted the occurrence of a peculiar horizon enclosing large bun-shaped concretions with *Oppelia* sp. and *Perisphinctes* sp. above the last finds *of Aulacostephanus.* Similar concretions are known in the Nizhnii Novgorod oblast from the uppermost Kimmeridgian (Isady locality) and Volgian (Murzitsy locality). At the same time, in the Chuvash Republic they are of the early Volgian age and contain either *Paralingulaticeras efimovi* (Rogov) and *llowaiskya* cf. *klimovi* (Ilov.) (Poretskoe Village, Sura River), or an older assemblage with *Neochetoceras steraspis* and *Lingulaticeras solenoides* (Polevye Bikshiki Village). A similar horizon with "rare slightly deformed ammonites referred to the *Ochetoceras-Haploceras (Glochiceras)* group" above the last finds *of Aulacostephanus* was also registered in the Tatar Republic [14].

Slightly later on, first figures of lower Volgian *Anaspidoceras neoburgense* (Oppel), which previously were only described or mentioned in the faunal lists, were reproduced by Ilovaiskii and Florenskii ([15], Plate XXIII, figs. 42, 42a). Soon after, this species was found in the Moscow outskirts and in the Ul'yanovsk oblast of the Volga region [16]. In addition, Sazonov [17] showed the occurrence of *Gravesia* in the lower Volgian Substage. This species previously established in England [18] grounded definition of the *gravesiana* Zone in the RuЯsian plate [19]. The species from the Russian plate has not been figured, however, and is recorded only in the Gorodishche section (the upper part of the *klimovi* Zone), where ammonites are poorly preserved. Therefore, despite a wide distribution of *gravesiana* species that is characteristic of the lower Tithonian, Volgian, and Portlandian (sensu gallico), *llowaiskya klimovi* (Ilov.) is more suitable for being used as index species of the basal Volgian zone[2]. The species is common in sediments of the Russian plate, where it occurs beginning from the base of the Volgian Stage. Simultaneously, the transition from *Sarmatisphinctes fallax* (How.) to *llowaiskya klimovi* (Ilov.) is very gradual and, if ammonites are poorly preserved, the boundary between Kimmeridgian and Volgian stages can be established more confidently based on the last occurrence *of Aulacostephanus.*

In their work dedicated to stratigraphy of the upper Upper Jurassic succession and relevant ammonites of southern Germany, Berckhemer and Hölder ([20], p. 58, Plate 14, fig. 68) described a species among ammonites from the upper Kimmeridgian-lower Tithonian referred it to the Boreal genus *Pavlovia (?Acuticostites).* This form differing from typical *Acuticostites* in ornamentation patterns at early ontogenetic stages and in stratigraphie position should be attributed to the lower Tithonian genus *Berkhemeria* Schweigert et Zeiss, 1998.

Soon after, Mikhailov [21] demonstrated the occurrence of *Glochiceras* and *Neochetoceras* in the *klimovi Zone* of the Ul'yanovsk Volga region. In addition, he described a form from the *sokolovi* Zone and referred it, in the open nomenclature, to the species *Franconites vimineus* known from southern Germany ([22], p. 56, Plate 11, fig. 1).

I should mention also ammonites found mainly in the upper Volgian Substage of North Siberia (and later on in eastern Greenland, Spitzbergen, and sub-Polar Urals) and attributed to the Mediterranean genera *Berriasella, Virgatosphinctes,* and *Lemencia* [23]. Prevailing among *Virgatosphinctes* forms, there were species similar to Indian and Argentinean taxa [24]. In neighboring areas, similar forms were unknown, and their occurrence among Boreal ammonites called in question the correctness of species identification. I tend to accept the standpoint of some researchers [25] who consider these forms as descendants of some Boreal ammonites, which have nothing to do with true *Virgatosphinctes.*

Approximately at the time, when first data on *Neochetoceras* and *Glochiceras* from Volgian sediments of the Volga region appeared, first Haplocerataceae or "indeterminable oppeliids" were found in the Volgian Stage of Poland. Their range was assumed to extend up to the middle Volgian Beds with *Zaraiskites scythicus*[3] [29].[4] These "indeterminable oppeliids" were figured by Kutek ([30], Plate XX, figs. 2-3), and shortly after they were preliminary determined as *Glochiceras)* [31] and *Neochetoceras* [32]. Later on,

[2]Hantzpergue [27] defines the synonymous faunal horizon and subzone in the upper part of the *gigas* Zone of the Portlandian in France.

[3]Subsequently, the data on stratigraphie position of these oppeliids *(Neochetoceras)* changed, and according to recent viewpoint they disappear within the *sokolovi* Zone [28].

[4]K. Pawłowska mentioned *Aspidoceras* sp. from the lower Volgian beds, although subsequently she did not publish anything about these ammonites.

Rotkite [33] mentioned indeterminable haploceratins from the Volgian sediments of the Baltic region.

At the beginning of the 1960s, Geyer [34] described and figured *Pavlovia (Sphinctoceras) crassa (=Subdichotomoceras* cf. *subcrassum* after Schweigert, 1993) from the *gigas* Zone of southern Germany (Baden-Württemberg). Soon after that, Zeiss [36] mentioned several *Ilowaiskya* species among other lower Tithonian ammonites from the Franconian Alb. Unfortunately, he did not figured them except for *Ilowaiskya* aff. *pavida juvenilis* ([37], Plate 22, fig. 4), the form that is very close to *I. pavida* (Ilov.). Simultaneously, he figured ammonite from the Neuburg Formation and determined it as *Zaraiskites* cf. *zarajskensis* (Mich.) ([37], Plate 26, fig. 7). Soon afterward both forms were reinterpreted and attributed to the other genus [38].

Works of the 1970s brought new information on joint occurrence of Tithonian and Volgian ammonites. A group of specialists who studied in detail the Gorodishche section under guidance of M.S. Mesezhnikov substantially augmented our knowledge on composition and stratigraphie distribution of Mediterranean elements in ammonite faunas from the lower-middle Volgian [39]. *Glochiceras (Paralingulaticeras)* was reported from *klimovi* and *sokolovi* zones, and *Neochetoceras* from the entire lower Volgian Substage, while *Sutneria* and *Haploceras* were found to occur up to the middle part of the lower Volgian *panden* Subzone. Later on, *Pseudolissoceras* forms were found in the *panderi* Zone [40] and the range of *Haploceras* was extended in the North Caspian region up to the upper boundary of this zone [41]. Naturally, such a diverse assemblage of Tithonian ammonites found in the Volgian Stage attracted the researchers' attention and brought to idea that "*Glochiceras* and *Haploceras* found in the lower part of the *panderi* Zone enable a more confident correlation of the Gorodishche and Neuburg sections" ([42], p. 101). Later on, Mesezhnikov [41] proposed the first variant of that correlation. Unfortunately, the correlation was based on haploceratids only, and this resulted in assumption that upper boundaries of *bavaricum* and *panderi* zones coincide because Tethyan ammonites disappear at this level.[5]

Abundant data on Boreal ammonites from the Tithonian of West and East Europe and on some Submediterranean forms from the Volgian sediments of Poland appeared at the beginning of the 1970s. The Subboreal *Ilowaiskya* forms were found in Hungary [43], and *Zaraiskites* was detected in the upper Tithonian of the Polish Carpathians [44] and Bulgaria [45]. Figured ammonites identified as *Pavlovia iatriensis* Ilov. [46] have been reported from the upper Tithonian of Austria, where they occur together with *Pseudovirgatites*.[6] It should be noted that a similar assemblage from the Kletnice Beds includes mainly specimens collected by Vetters [8], positions of which in the section have not been indicated. Later on, it was established that they occur in the interval from the middle Tithonian *ponti* Zone to the upper Tithonian *simptisphinctes* Zone.

Kutek and Zeiss published several articles dealing with stratigraphy of the Volgian Stage in the Brzostówka section near Tomaszów Mazowiecki (Poland). They described several new *Pseudovirgatites* species from this section and a presumable *Lemencia* from the uppermost part of the lower Volgian Substage. In addition, they mentioned several *Isterites* species from the uppermost lower Volgian Substage of this section and new species *Isterites mazoviensis* from the *scythicus* Zone. Precisely these finds, *Zaraiskites* forms from the upper Tithonian, on the one hand, and *Pseudovirgatites* and *Isterites* forms from the lower-middle Volgian, on the other, served as a basis for correlation of the lower Volgian Substage with the lower and middle Tithonian [48]. Soon after that, Malinowska [49] described the early Tithonian ammonites and paleobiogeography of the extra-Carpathian part of Poland. The described mixed assemblage of Subboreal *Ilowaiskya* and Submediterranean *Usseliceras* and *Subplanites* from the lower Volgian sediments also includes oppeliids and *Sutneria.* Subsequently, Schweigert [51] revised determinations of Submediterranean ammonites and attributed *Usseliceras* forms of Malinowskaya to the genus *Pseudovirgatites.*

After the detailed subdivision of the *scythicus* Zone in Poland, where two subzones and four faunal horizons were defined, Kutek [52] specified correlation between the Volgian and Tithonian stages. For instance, ammonites found in Bulgaria together with calpionellids [45] and appearing in the upper part of the *microcanthum* Zone were revised and determined as *Zaraiskites regularis* Kutek. This species characterizes a synonymous faunal horizon within the *Zaraiskites* Subzone of the Volgian Stage in Poland, and Kutek correlated this horizon with an upper part of the *microcanthum* Zone. Simultaneously, Kutek and Zeiss [53] who studied drill cores established distribution range of *Neochetoceras* in Poland and concluded that the lower Tithonian should be correlated with the lower Volgian *klimovi* and *sokolovi* zones. Soon, *Neochetoceras, Haploceratina,* and *Sutneria* from the lower Volgian Stage of Poland were figured [28]. It should be noted that revision of earlier data led to conclusion that *Sutneria* and *Haploceratina* are missing from sediments younger than the *sokolovi* Zone.

Schweigert [35] described some Boreal and Subboreal ammonites from the upper Kimmeridgian sediments (the *beckeri* Zone) of southern Germany, among them *Eosphinctoceras magnum* Mesezhn., the index species of the basal zone of the Volgian Stage in the sub-Polar Urals. With due regard to this species, he correlated the *magnum* Zone with the upper part of *autis-*

[5] These were haploceratids proper, as I think, because Submediterranean *Isterites* exist above the *bavaricum* Zone in the Neuburg section.

[6] According to Mesezhnikov [50], the ammonite specimen figured by A. Zeiss is indeterminable and cannot be attributed to *Pavlovia iatriensis.*

siodorensis Zone. However, *Aulacostephanus autissiodorensis* (Cotteau) is unknown in the sub-Polar Urals, and the synonymous zone is established there based on indirect evidence. The *magnum* Zone, at least partly, is probably of the Kimmeridgian age, because *Gravesia lafauriana* of Hantzpergue [54] *(=Gravesia polypleura,* Zakaharov and Meseahnikov [55], Plate 1, fig. 1) was found at this level in the sub-Polar Urals. However, a distinctly Tithonian *Gravesia* form *(?Gravesia gravesiana* [54] = *Gravesia* sp.[55], 1974, Plate 1, fig. 2) is reported to occur in the same zone, and both finds of *Gravesia* are confined to the lower part of the zone. Therefore, the Kimmeridgian-Volgian boundary in the sub-Polar Urals can be placed preliminarily within the *magnum* Zone. On the other hand, the oppeliid succession suggests that the base of the Volgian Stage in central Russia corresponds to the base of the Tithonian Stage in Germany. The terminal faunal horizon of the upper Kimmeridgian Substage in Germany and the upper part of the *fallax* Zone in the Russian plate contain one and the same form *?Neocheloceras fridingense* (Berck. et Hölder) that replaces in both areas *N. rebouletianum* and *N. zlatarskii* with coarse ornamentation ([56], Plate 1, fig. 5).

Recently, two middle Tithonian species described from the Neuburg section [57] were attributed to *Sarmatisphinctes* and *Dorsoplanites* [58]. Unfortunately, their attribution to Boreal genera is substantiated insufficiently, because both forms are represented by holotypes only and their ornamentation in ontogenesis is unknown. The idea to regard *Dorsoplanites lumbricarius* (Schneid) as a possible ancestor of *D. panderi* (Orb.) [57] is also poorly substantiated, because these species are separated by a stratigraphie gap and characteristic of different basins.

AMMONITE-BASED VARIANTS OF CORRELATION BETWEEN VOLGIAN AND TITHONIAN STAGES

Relationships between the Volgian and Tithonian stages are mainly interpreted based on ammonites in common for both stratigraphic units. Joint finds of Tethyan ammonites and buchiids play a significant role in correlation of upper Volgian and younger sediments.

Inferences of researchers used to be based on different ammonite groups. For instance, Kutek and Zeiss [59] take into consideration mainly the distribution of perisphinctids, such as *Zaraiskites, Pseudovirgatites, Pavlovia,* and *Isterites.* Only recently, they used data on distribution of oppeliids *Neochetoceras steraspis* (Oppel) and *N. mucronatum* (Berck. et Hölder) to substantiate correlation of the lower Tithonian with the Volgian *klimovi* and *sokolovi* zones [60]. It should be noted that the group of variable perisphinctids consists of several parallel phylogenetic lineages, interpretation of which considerably affects correlation. Par example, if ammonites from the Neuburg section originally identified as *Zaraiskites* cf. *zarajskensis* (Mich.) [37] are taken for true *Zaraiskites zaraiskensis* [61], or for homeomorphs only [38], the resultant biostratigraphic schemes turn out to be different by a substage. On the other hand, if we take into consideration a poor preservation of late Tithonian *Zaraiskites* and admit, following Kutek and Zeiss, that descendant *Isterites* with *Virgatites-like* ribs existed in the Submediterranean Province, we should question whether they are true *Zaraiskites* or not? Anyway, neither ornamentation patterns nor peculiarities of their septal suture are known.

It should be noted that correlation of the lower Volgian Substage with the lower-middle Tithonian does not contradict in principle to assumable equivalency of the Volgian and Tithonian stages. Mikhailov [62] accepted precisely that variant of correlation, which allowed him to admit correspondence of the Volgian and Tithonian stages. In their early correlation scheme, Kutek and Zeiss ([9], p. 513, Table 1) also admitted equality of these stages, despite the fact that they correlated the upper Tithonian with the lower (partly), middle, and upper Volgian substages.

On the other hand, Mesezhnikov [63] substantiated his interpretations based on Tethyan elements occurring in the Volgian Stage of the Russian plate. He proposed to correlate upper boundaries of the *bavaricum* and *panderi* zones, assuming that haploceratins disappear synchronously in the Neuburg section and Russian plate. In my opinion, the disappearance of that ammonite group in two separate basins, while it continued to exist southerly, does not necessarily indicate synchronism of the events. In addition, the impoverished taxonomic composition of ammonites in the upper part of the Neuburg Formation is likely connected with desalination, whereas signs of similar event cannot be observed across the boundary between *panden* and *virgatus* zones.

In 2001, I undertook a preliminary attempt to compile all the available data on ammonites occurring in both the Volgian and Tithonian stages [64], but the detailed analysis of their distribution was out of the scope of that work.

STRATIGRAPHIC AND GEOGRAPHIC RANGES OF AMMONITE GENERA FROM VOLGIAN AND TITHONIAN STAGES

A correct correlation of the Tithonian and Volgian stages should be based on firmly established stratigraphic ranges of ammonites occurring in both units. Unfortunately, many ammonite taxa important for solution of the problem have not been figured or described, being mentioned only among others. In discussion below, I consider therefore the probable erroneous identifications of the forms in question. Nevertheless, it seems reasonable to assume that ammonite taxa listed in publications are correct at the generic level at least. We may also assume that stratigraphic ranges of Tethyan ammonites in the Russian plate and adjacent areas of West Europe are comparable, although they can be different in remote areas. At present, we know over ten ammonite genera occurring in both the Volgian and Tithonian stages and considered below (in all cases, unless it is indicated otherwise, the Volgian haplocer-atins from the Russian plate are those from the Gorod-ishche and Polevye Bikshiki sections, the Batyrevskii area of the Chuvash Republic).

1. *Pseudolissoceras.* In European Russia, representatives of this genus are known only from the *panderi* Zone [40].[7] I found disputable specimens of the genus in the middle part of the *pseudoscythica* Zone *(neoburgense* faunal horizon) ([65], Plate, fig. 10). In Hungary and the Polish Carpathians, the genus occurs up to the middle Tithonian *fallauxi* Zone [66]. In Romania [67] and Hungary [43], its representatives disappear in the *fallauxi* Zone. They occur up to the top of *the fallauxi* Zone also in Spain [68] and to the middle part of this zone in Italy [69]. Thus, it is reasonable to conclude that the *bavaricum* Zone of the Neuburg section (and the lower part of the *panden* Zone at least) is not older than the *fallauxi* Zone [61], being incompletely correlative to the middle Tithonian, as is frequently accepted (I mean correlation of the *bavaricum* Zone with the entire middle Tithonian [70]).

The stratigraphie range of the genus in southerly areas is substantially wider. It occurs in the lower part of the upper Tithonian in Algeria and Iraq [71] and up to the lower part of the Berriasian (analogues of the *euxinus* Zone) in Tunisia [72], as it was noted first by Imlay [73].[8] This distribution peculiarity was used by Jeletzky [61] for age determination of the Neuburg Formation.

In Central and South America, *Pseudolissoceras* likely occurs in the middle Tithonian only (the middle Tithonian was originally established based on the taxon occurrence precisely in this region). Burckhardt [75] described several *Pseudolissoceras* species (the type species inclusive) from Mexico and later on, discussing the taxon occurrence in the Mexican middle Tithonian, Verma and Westermann [76] correlated partly the *zarajskensis* Zone with this level also (I am of the same opinion). Imlay [77] reported, however, on the *Pseudolissoceras* occurrence in the lower upper Tithonian of Mexico, where its species *(P. zitteli* included) coexist with *Durganites* and *Buchia mosquensis* (!!).[9] In Argentine, *Pseudolissoceras* is known from the lower part of the middle Tithonian [78].

In the Far East, *Pseudolissoceras* occurs in the *zitteli* Zone *(=primoryense* Zone after Khudolei [79]). Sei and Kalacheva [80] correlate this zone with the synonymous unit of Argentine, which corresponds approximately to the *semiforme* Zone [82]. In opinion of Khudolei [79], it corresponds to the *bavaricum* Zone of the Franconian Alb. Based on finds of *Buchia mosquensis* and *B. rugosa* in the same layers, Sei and Kalacheva [83] assumed that these zones are correlative with the lower to middle (partly) Volgian sudstages. It should be noted that the mentioned *Buchia* species continue to occur also in the *fanden* Zone of the Russian plate [84] and *Buchia mosquensis* is abundant in the *Epivirgatites nikitini* Zone of East Siberia [85]. In opinion of Parent [86] who revised the genus in question, none of figured *Pseudolissoceras* forms is known even from the upper part *of the fallauxi* Zone. Thus, *Pseudolissoceras* forms do not occur in Europe above the *fallauxi* Zone, and their prйsense in the middle Volgian *panden* Zone indicates that the last unit corresponds, at least partly, to the *fallauxi* Zone.

2. *Haploceras.* This genus is of little use for reliable correlation, because its shells are poorly preserved in the Russian plate, being undeterminable at the species level (the *Haploceras* sp. in lists),[11] and the genus proper occurs almost worldwide from the lower Kimmeridgian to the uppermost Berriasian. In addition, most of European species of the genus represent probably a single form characterized by polymorphism [87]. In the Gorodishche section, *Haploceras* sp. occurs at least from the upper part of the *klimovi* Zone ([65], Plate, fig. 11) to the *panden* Zone of the middle Volgian Substage [88]. In addition to the Gorodishche section, *Haploceras* form are known from the upper part of the *pnaderi* Zone of the North Caspian region [41].

3. *Lingulaticeras.* In the Russian plate, *Lingulaticeras* s. l. are recorded in the interval from the upper Kimmeridgian *autissidorensis* Zone to the middle Volgian *panderi* Zone [89]. In addition, Gerasimov's collection (PIN no. 4861) includes one undoubted specimen of *Lingulaticeras blaschkei* (Cecea et Enay) from the *panderi* Zone found in the Kimry outskirts, the Tver oblast, and V.V. Mitta donated me several specimens of this species from the *panderi* Zone of the Chuvash Republic.[12] When defining the *Glochiceras* subgenera (individual genera in this work), Ziegler [91] demonstrated importance of the aperture structure (presence or absence of hood, incline of the apertural margin, and other features). The aperture is rarely preserved in middle Tithonian *Glochiceras* forms, only one of which was figured by Blaschke ([92], Plate 1, fig. 7). Judging from its structure, the *blaschkei* form can confidently be attributed to the genus *Lingulaticeras,* like the problematic ammonite forms, which were recently found in the *neoburgense* faunal horizon of the Gorodishche

[7] According to oral communication of A.G. Olfer'ev, data on ammonites in the scheme were summarized by M.S. Mesezhnikov. Unfortunately, no *Pseudolissoceras* forms are found so far in the Mesezhnikov's collection stored at the VNIGRI.

[8] Howarth [74] had cast doubts on the occurrence of post-middle Tithonian *Pseudolissoceras* forms both in Tunisia and Iraq because they were never figured. The forms have not been figured.

[9] Sei and Kalacheva [81] consider *Primorytes primoryense* Chud. 1960, as a synonym of *Pseudolissoceras zitteli,* thus changing the zone index for *zitteli.*

[11] Upper Kimmeridgian ammonites from the Gorodishche section determined as *Haploceras* most likely belong to *Neochetoceras* ex gr. *subnudatum.*

[12] Previously, I attributed these forms to *Glochiceras* aff. *contractum* [90].

section. In Germany, *Glochiceras* s. l. are undoubtedly known from sediments, which are younger than the lower part of the *bavaricum* Zone, and in the Neuburg section, they occur in Bed 22 [93]. The same bed yields *Virgatosimoceras* cf. *albertinum,* the index species of the *darwini/albertinum* Zone, the upper one of the lower Tithonian [93, 94]. In Poland, probable *Glochiceras* s. l. are mentioned form the *klimovi* and *sokolovi* zones [28], although they are not figured, like in Russia. In France and Italy, *Glochiceras* s. l. is characteristic of the middle Tithonian *fallauxi* Zone [95]. Moreover, *Lingulaticeras blaschkei* is described from the Ardèche section in France. Unfortunately, the exact stratigraphie positions of *L. blaschkei* in Czechia, (Stramberg) and the North Caucasus are not indicated. *"Oppelia strambergensis"* mentioned (but not figured) from the middle Tithonian of the Crimea [96] probably belongs to the genus *Lingulaticeras.* Poorly preserved *Glochiceras* s. l. are known from the middle Tithonian of Romania [97]. In Madagascar, *Lingulaticeras* is found in the middle Tithonian *kobelli* Zone [98]. In addition, it cannot be ruled out that some ammonites of Madagascar, which are referred to the genus *Hildoglochiceras,* belong in fact to *Lingulaticeras* forms (e.g., *"Hildoglochiceras" nudum* Collignon, 1960). Specimens of *Lingulaticeras umbilicocrenatum* Collignon described from Madagascar are also known from the upper part of the middle Tithonian in the Far East [81]. Until recently, ammonites of the last region were classed with ?*Glochiceras jollyi* Oppel. However, shells 'of *Ammonites jollyanus* ([99], p. 271, Plate 75, fig. 4) are up to 10 cm across (i.e., twice larger than the largest known *Glochiceras* specimens) and have no lateral furrow. Moreover, their septal suture is of peculiar shape different from that of *Glochiceras,* and the aperture structure is unknown. In opinion of H. Schairer (oral communication), the original specimen from the Oppel's collection (SMNS, Inv. No. 1872 XV 4) should probably be referred to Triassic Gymnitidae such as *Ammonites lamarcki* Oppel, 1863, a type species of the genus *Anagymnites* Hyatt, 1900. This is consistent with the viewpoint of specialists on Triassic ammonites, beginning from Diener [100] who consider this species as the Triassic one. Therefore, I attribute the forms described by Sei and Kalacheva [81] and by Collignon [98] to species *L. umbilicocrenatum* [101]. Simultaneously, *Glochiceras* forms from the Primor'e bear some peculiar features untypical of *L. umbilicocrenatum* and, in the opinion of Sei and Kalacheva (pers. comm.), they belong most likely to a new species. *Glochiceras* forms mentioned from the middle Tithonian of Iraq [102] should probably be referred to the genus *Hildoglochiceras. Glochiceras* specimens are also known from Cuba *(Glochiceras (?Lingulaticeras)* sp. in [103], p. 291, Plate 2, figs. 1, 2, 4, 7-9). These ammonites are virtually identical to *L. umbilicocrenatum* (Collignon) from the Primor'e. In Antarctica [104], *Glochiceras* similar to *Lingulaticeras* (=Oppelid gen. nov., Plate III, fig. g) is found in the lower Tithonian. Morphologically similar ammonites of the genus *Hildoglochiceras* are known from the middle Tithonian only. Enay [105] considered these forms as confined to the upper Tithonian, but new data suggest their middle Tithonian age [106]. At the same time, the late Tithonian *"Rapidoceras"* and *Hildoglochiceras (Salinites)* from Mexico and Cuba have the distinctive ornamentation in the upper part of the whorl. In addition, *Hildoglochiceras (Salinites)* forms, which occur in Mexico up to the lower part of the upper Berriasian Substage, have the well-developed keel. Therefore, the middle Tithonian *Lingulaticeras* from Cuba and the Primor'e can hardly be referred to the subgenus *Salinites,* as it was done by Myczynski [109]. In Ardèche section (France), *Lingulaticeras blaschkei* (Cecea et Enay) characterizes a relatively narrow interval within the middle part of the *fallauxi* Zone (Beds 8a, 10) reflecting the second and third episodes of the strengthened Mediterranean influence during this period [110].

4. *Paralingulaticeras.* Representatives of this genus were found in the *klimovi* and *sokolovi* zones of central Russia [111]. In addition, the Mesezhnikov's collection (VNIGRI) includes *Paralingulaticeras* with labels indicating the "sokolovi" Zone. Unfortunately, it is unknown, whether these ammonites characterize the entire zone or a part of it. Judging from the light coloration of the host rock, they are from the lowermost part of the zone in question, which encloses also *Ilowaiskya sokolovi* Ilow.

All the *Paralingulaticeras* specimens from the Russian platform can probably be attributed to one very variable species *Paralingulaticeras efimovi* (Plate, fig. 7). This species differs from European *Paralingulaticeras* forms in smaller dimensions and absence of developed ventrolateral tubercules. Small dimensions of *Paralingulaticeras* representatives from the Russian platform and ornamentation characteristic of inner whorls of European *L. lithographicum* suggest neoteny in their development. Similar populations were characteristic of Boreal ammonites that penetrated into the Submediterranean Province [112].

First finds of subgenus *Paralingulaticeras* are reported from the *eudoxus* Zone [113], although these early forms are of peculiar appearance. In the Franconian Alb [36], rare *Paralingulaticeras* specimens appear beginning from the base of the *lithographicum* Subzone in the upper part of the Solnhofer Formation to become abundant in the overlying Мцrnsheimer Formation. In the Schwabian Alb, rare *G. lithographi-*

[13] The former genus was described without diagnosis and indication of the type species [107] among Cuban ammonites previously referred to the genus *Haploceras* [108].

[14] The *lithographicum* Subzone is defined in the Franconian Alb by Barthel and Schairer ([114], p. 12): "Das untere Untertithon umfät die Zone des *Hybonoticeras hybonotum;* ihren oberen Abschnitt kann man als Subzone des *Glochiceras lithographicum* (Obere Solnhofer Plattenkalke und Mörnsheimer Schichten) ausschieden". Its base is placed at the appearance level of *G. lithographicum.*

cum occur in the *riedlingensis* faunal horizon of the *hybonotum* Zone [115]. According to G. Schweigert (pers. communication), this area is unfortunately lacking the level with abundant *P.* ex gr. *lithographicum* and, thus, the *efimovi* faunal horizon can be correlated with Swabian biohorizons only arbitrarily. These ammonites occur in the lower Tithonian *hybonotum* Zone and its analogues in Spain [116], Italy [117], Poland [66], Bulgaria [118], Czechia [119], Romania [120], France [121], and Albania [122]. Noteworthy is that in Poland they are unknown from the *klimovi* Zone, while the *sokolovi* Zone encloses forms very similar to coarsely costate *P. lithographicum (=Ochetoceras* or *Tammelliceras,* [28], Plate 31, fig. 7). *Paralingulaticeras* is characteristic almost exclusively of Europe, where it never occurs above the *hybonotum* Zone. Beyond Europe, one locality of this subgenus is known in Madagascar [123], and one specimen (not figured) is I reported from Antarctica [124].

Although *Paralingulaticeras efimovi* is unknown outside the Volga region, it can be used for correlation, because its appearance was concurrent to wide distribution of other *Paralingulaticeras* forms in West Europe. If events of *Paralingulaticeras* disappearance were synchronous in different basins, then the lower part of the *sokolovi* Zone in the Russian plate should be correlated with the upper part of the *hybonotum* Zone. The *efimovi* faunal horizon of Central Russia corresponds to a greater part of Mörnsheimer Beds of the Franconian Alb, which yield abundant *Paralingulaticeras* [36], and to a portion of the *laisackerensis* faunal horizon (and, probably, to cf. *eystettense* faunal horizon) of the Schwabian Alb [65]. It cannot be also ruled out that the base of the *efimovi* faunal horizon corresponds to the *riedlingensis* horizon of Swabia, where first, although not numerous *Paralingulaticeras* specimens appear.

5. *Neochetoceras.* In the Gorodishche section, *N.* cf. *steraspis* are persistently occurring in the *klimovi* Zone [125]. Nevertheless, it seems quite probable that some *Metahaploceras* could be taken for *Neochetoceras.* According to my observations, *N. steraspis* replaces species *N. fridingense* and *N.* ex gr. *subnudatum* occurring in the uppermost Kimmeridgian Stage of the Volga region. In the Gorodishche section, this species is common in the lower part of the *klimovi* Zone (Beds with *Lingulaticeras solenoides* and *Neochetoceras steraspis)* but rare in the overlying *efimovi* faunal horizon [65]. Recent data indicate the *Neochetoceras* occurrence in the higher *pseudoscythica* Zone [40]; the Mesezhnikov's collection (VNIGRI) includes ammonites from the *sokolovi* Zone close to *Neochetoceras.* Because of poor preservation and gradual morphological changes of ammonites in majority of the examined sections, it is difficult to trace the transition from Kimmeridgian to Volgian *Neochetoceras* species. For instance, the Kimmeridgian-Tithonian boundary layers in the Gorodishche section include an interval approximately 0.3 m thick, where *Neochetoceras* specimens are indeterminable at the species level and other stratigraphically important ammonites are missing. *Neochetoceras* forms occur beginning from the second half of the Kimmeridgian to the beginning of the middle Tithonian in Germany [126] and also in younger sediments (up to the middle Tithonian *fallauxi* Zone) in Spain [127], France [128], and Italy [129]. A similar distribution of the genus is probably characteristic of Mexico [130]. The youngest *Neochetoceras* forms are known from the *microcanthum* Zone of Hungary [131]. In Poland, *N. steraspis* occurs in the *klimovi* Zone and close *N. mucronatum* in the upper part of the *klimovi* and in the *sokolovi* zones [28]. In the North Caucasus, *N. praecursor* is known from the basal part of the lower Tithonian [132]. This species characterizes as well the *eigeltingense* faunal horizon, the lowermost Tithonian unit of southern Germany [133]. In the Russian plate, analogues of this level are not established so far. In the Gorodishche section, *N.* cf. *steraspis* appears abruptly at the base of the *klimovi* Zone. Recently, *Neochetoceras* sp. of poor preservation was reported from the *hybonotum* Zone of Antarctica ([124], fig. 7A). Representatives of the genus migrated to this region most likely from East Africa, where they are known for a long time [134]. In addition, *Neochetoceras* sp. was recently found in the Andes of Argentine: in the lower Tithonian *mendozanus* Zone [135] and in the middle Tithonian *proximus* Zone, an approximate analogue of the *fallauxi* Zone [136].

According to data on *Neochetoceras* distribution, the *pseudoscythica* Zone is, at least partially, not younger than the middle Tithonian *fallauxi* Zone. Beds with *Neochetoceras steraspis* and *Lingulaticeras solenoides* of central Russia approximately correspond to *rueppelianum* and *riedlingensis* faunal horizons and to unnamed unit between the *rueppelianum* and *eigeltingense* horizons of the Swabian Alb. *Neochetoceras* ex gr. *steraspis* and *Lingulaticeras solenoides* occur at all these levels, while *Paralingulaticeras* forms are missing or scarce (G. Schweigert, pers. communication).

6. *Fontannesiella.* I found several *Fontannesiella* aff. *prolithographicum* specimens among ammonites from the *efimovi* faunal horizon of the Gorodishche section ([65], plate, fig. 5). Unlike typical *Fontannesiella,* these ammonites, as well as coexisting *Paralingulaticeras,* are lacking developed tubercles. *F. prolithographicum* associate usually with *Paralingulaticeras lithographicum* and probably represent macroconchs of the latter [137]. Finds of *F. prolithographicum* are known from the *hybonotum* Zone of the North Caucasus [138], Spain [127], Portugal [139], Ethiopia [140], southern Germany [141], southeastern France [142], and Sicily ([143], fig. 144), while forms determined in the open nomenclature are reported from Antarctica ([124], fig. 6C). The species never occurs above the *hybonotum* Zone, being reported from the upper Kimmerdgian *beckeri* Zone of southeastern France only [144]. Other *Fontannesiella* species, such as *F. valen-*

tina, are sometimes mentioned among ammonites from the higher stratigraphie level of the *darwini* Zone, where *Paralingulaticeras* is unknown [145].

7. *Sutneria.* This genus is widespread almost every where in the Kimmeridgian of the Northern Hemisphere and in the Tithonian of Europe. In the Russian plate, representatives of the genus span the interval from the upper Kimmeridgian to the *panderi* Zone [39], where Volgian forms are very scarce. The Beds with *Neochetoceras steraspis-Lingulaticeras solenoides* of the *klimovi* Zone contain *S.* cf. *eugyra* (Plate, fig. 4) in several sections. Similar *Sutneria* forms are also known from the *klimovi* Zone of Poland ([28], *Sutneria* cf. or aff. *bracheri,* Plate 31, figs. 1-4). *S. eugyra* is a species of the *hybonotum* Zone *(laisackerense* faunal horizon) of southern Germany [115] and of the lower Tithonian in Romania [146].

In the Gorodishche and Polevye Bikshiki sections, relatively abundant *Sutneria asema* occur only in the *neoburgense* faunal horizon. This species is recorded up to the *fallauxi* Zone in the Polish Carpathians [66] and Romania [147]. In Germany, *S. asema* is known from two lower faunal horizons of the Neuburg Formation [58], where they associate with *Pseudolissoceras bavaricum* and *Anaspidoceras neoburgense* [93]. *S. asema* was also found in the upper part of the lower Tithonian: in the *darwini* [148] and (in Germany) *vimineus* zones (A. Scherzinger, personal communication). Representatives of the genus *Sutneria* are also reported from Argentine, but their stratigraphic position remains unclear so far (H. Parent, pers. communication). Slavin ([149], Plate II, figs.-11-14) attributed ammonites from the lower Valanginian (=Berriasian) sequences of the Ukrainian Carpathians to *Euryno-ticeras* aff. *asema* (= *Sutneria).* These forms are lacking costae at their sides, however, and have instead small constrictions in the lower part of the whorl. Such morphological peculiarities are untypical of *Sutneria* (e.g., [150], Plate III, figs. 8,9; lectotype of *S. asema).* Unfortunately, Slavin did not illustrated the septal suture of these ammonites, which most likely belong to the genus *Pty-chophylloceras.* Khalilov and Abdulkasumzade [151] meant probably these very forms, when they argued that *S. asema* ranges from the Kimmeridgian to Berriasian. The last *Sutneria* specimens are characteristic of the *semiforme* Zone or of the level that is not higher, at least, than the *fallauxi* Zone of the middle Tithonian. Consequently, the lower part of the *panderi* Zone is not younger than the *fallauxi* Zone.

8. *Pseudovirgatites.* In Russia, ammonites similar to *Pseudovirgatites* described from the upper part of the *pseudoscythica* Zone of platform areas in Poland [48] were figured by Mikhailov [22] under the name *Pectinates (Wheatleyites) arkelli.* Unfortunatelly, all specimens figured by him are fragmentary, and morphology of their internal whorls (more exactly, positioning of costae branching points) is unknown. *Pseudovirgatites* specimens are reported from both the Vetlyanka and Gorodishche sections (similar forms were described byl Semeno v [4] as *Perisphinctes capillaceus).* In my collection, there are specimens of *P. puschi* found in the *puschi* faunal horizon crowning the *pseudoscythka* Zone in the Gorodishche and Polevye Bikshiki sections ([65], Plate, fig. 13). One ammonite fragment with the high branching coefficient of costae from the *puschi* faunal horizon of the Gorodishche section can be identified as *P.* aff. *seorsus* (Plate, fig. 8). Well known in| West Europe are *Pseudovirgatites* specimens (the species unknown from Poland and central Russia) occurring mainly in the upper Tithonian. They are described from France [121], Spain [152], the Polish Carpathians [66], and Hungary [43], where they occur up to the upper Tithonian. The less frequently mentioned are the middle Tithonian or stratigraphically uncertain *Pseudovirgatites* forms. They are reported from the middle Tithonian of Hungary ([153]; new species) and uppermost middle Tithonian of Czechia (Stramberg) [61] together with "ancient ammonites" of the *fallauxi* or *ponti* zones. Nowak [154] reported on *Pseudovirgatites* associated with *Semiformiceras fallauxi. Pseudovirgatites* is also known from the middle Tithonian of Romania [67]. In Austria, representatives of this genus are found together with *"Pavlovia iatrensis"* [46] (my comments to this species see above), although formerly they were described from the same localities together with *Semiformiceras semiforme* and *Uhligites lymani* [155] characteristic of the middle Tithonian. Relationships between *Pseudovirgatites* and *Zaraiskites* remain unclear so far. Some researchers [156] consider the former taxon as ancestor of the latter (I share this viewpoint) and see, following Ilovaiskii and Florenskii [15], the main difference between genera in different position of the costae branching points, which is low on internal and higher on external whorls of *Pseudovirgatites* and vice versa in *Zaraiskites* shells. Ornamentation patterns on external whorls of some *Zaraiskites quenstedti* are virtually identical to those of *Pseudovirgatites* forms.

Kutek and Zeiss considered *"Ilowaiskya" tenuicostata* (Mich.) as ancestral taxon of *Pseudovirgatites.* This species appears earlier than *Pseudovirgatites puschi.* In the Gorodishche section, its first representatives (Plate, fig. 9) are known from the upper part of the *neuburgense* faunal horizon. Consequently, *the puschi* and *neoburgense* faunal horizons can be considered as subdivisions of the *tenuicostata* Subzone. *"Ilowiaskya" tenuicostata* shows morphological features of both *Ilowaiskya* (absence of costae characteristic of *Virgatites)* and *Pseudovirgatites* (low position of costae branching point on internal whorls). This species begins most likely the *Pseudovirgatites* phylogenetic lineage and consequently belongs to this genus. Thus, *Pseudovirgatites* from the Volgian Stage definitely suggest only that the *tenuicostata* Subzone (at least) of the *pseudoscythica* Zone can be correlated with a part of the middle Tithonian. Discrimination of the *tenuicostata* Zone in the Russian plate is inconsistent with the fact that corresponding beds yield true *Ilowaiskya* I forms (*I. pseudoscythica* of the *neoburgense* faunal horizon) and can be ranked as a subzone only.

9.*Danubisphinctes.* In the European part of Russia, undoubted finds of these ammonites are unknown. Only the Polevye Bikshiki section yields rare and small coarsely ornamented ammonites, which can be attributed to this genus. In addition, *Perisphinctes (?llowaiskya)* sp. indet. (not figured) is suggested to resemble ([15], p. 107) *Pseudovirgatites (Danubisphinctes) palmates,subpalmatus.* Species of the genus *Danubisphinctes (=Isterites* after Kutek and Zeiss) occur in the *tenicostata* Subzone of the lower Volgian and in the *scythicus* Zone of the middle Volgian in Poland [157]. *Danubisphinctes* is widespread in the lower-middle Tithonian sediments, and its late coarsely ornamented forms *(=Isterites* auct.) are of interest for this work. In the Neuburg Formation, young representatives of the genus appear in the middle part of the Unterhausen Beds (Bed 60) and disappear in the lower part of the Oberhausen Beds [158]. *The palmatus* faunal horizon, the highest ammonite-containing level of the formation, yields *Danubisphinctes* species known from the *puschi* Zone of Poland. In Hungary, *?Isterites* sp. is reported from the *"Burckhardticeras"* Zone, which used to be correlated with the terminal *ponti* Zone of the middle Tithonian [43].[15] The same age is characteristic of *"Isterites"* from Spain [159]. *D. spurious* present in the upper part of the *tenuicostata* Zone of Poland and in the upper faunal horizon of the Neuburg Formation indicates a partial overlapping of these stratigraphie units.

10. *Ilowaiskya.* In the Russian plate, representatives of this genus occur only in the lower Volgian Substage as index species of all zones. A similar stratigraphic range is characteristic of them also in Poland, where *Ilowaiskya* s. 1. is missing only from the *tenuicostata* Subzone. In southern Germany, the genus appears in the upper part of the Rennertshofener Formation (the *palatinum* Zone) [160]. *Ilowaiskya* cf. *pseudoscythica* (not figured) from the Neuburg Formation [161] occurs in the lower part of the Unterhausen Beds and disappears before the first occurrence level of *Isterites.* In Bed 22, the species associates with *Virgatosphinctes* cf. *albertinum,* the index species of synonymous zone correlated with the *darwini* Zone [94].[16] In Hungary, *Ilowaiskya* ex gr. *klimovi* (not figured) is found in the basal *hybonotum* Zone of the lower Tithonian [43]. Unfortunately, none of Tithonian *Ilowaiskya* forms is figured, except for *"Ilowaiskya* aff. *pavida juvenilis "* ([37], Plate 22, fig. 4; *=Sublithacoceras penicillatum* (Schneid) after Scherzinger and Schweigert [58]), and it is probable that researchers considered the morphologically close representatives of Mediterranean perisphinctids. For instance, Scherzinger and Schweigert [58] revised *Ilowaiskya* cf. *pseudoscythica* ([37], p. 117) and identified it as *Danubisphinctes. Ilowaiskya* forms are quite suitable for correlation of lower Volgian sections in different regions. Their distribution in the Tithonian Stage (provided that identifications are correct) suggests that the *pseudoscythica* Zone is correlative, at least partly, with the *darwini* Zone of the lower Tithonian.

11. *Zaraiskites.* In European Russia and Poland, *Zaraiskites* occurs in the lower part of the middle Volgian Substage. Ammonites from the Neuburg Formation first described as *Z.* cf. *zaraiskensis* [37] were subsequently attributed to other genera [38]. Single *Zaraiskites* specimens are known from the upper Tithonian (the age confirmed by *Crassicolaria)* of Bulgaria [45] and the Polish Carpathians [44], although preservation of these ammonites is not perfect. One more specimen is reported from upper Tithonian sediments of Austria [46]. Recently, Zeiss ([162], p. 62, Plate 14, fig. 2) figured a small ammonite fragment from Ernstbrunne determined as *Zarajskites,* but its poor preservation hinders identification even at the generic level. Kutek [52] attributed the specimen figured by Nowak [45] to *Z. regularis* Kutek, 1994, and correlated the synonymous faunal horizon of the *zaraiskensis* Subzone of Poland (the middle Volgian *scythicus* Zone) with the upper Tithonian *transitorius* Zone. As Kutek noted himself, *Zaraiskites* forms are rather highly variable. This peculiarity and a poor preservation of ammonites from Bulgaria are the obstacles for their confident identification at the species level. In any case, virgatotome ribbing is also characteristic of many Mediterranean middle-upper Tithonian ammonites, e.g., it is typical of internal whorls of *Danubisphinctes mutabilis* ([163], fig. 9). Nevertheless, if the genus identification is correct, it is highly probable that the upper part of the *panderi* Zone is correlative partially with the upper Tithonian *microcanthum* Zone. The *Zaraiskites* successions in Poland and the Volga River basin are likely similar. Anyway, combustible shales of the *panderi* Zone of the Volga region enclose *Z. regularis.*

12. *Anaspidoceras.* Ammonites from the *neoburgense* faunal horizon of the Gorodishche section, which are identified as *A. neoburgense* [164], have never been figured, but my collection includes determinable specimens ([65], plate, fig. 12). According to Cecca [165], *A. neoburgense* crowns the evolutionary lineage of the *Anaspidiceras* genus and is a single species lacking tubercles like specimens from the Gorodishche section. In distinction from ammonites of the last section, the form figured by Ilovaiskii and Florenskii [15] is intact and confidently identified. It seems that Sokolov ([5], p. 23) and Semenov ([4], p. 182) described A. *neoburgense* from the lower Volgian sediments of the Vetlyanka locality as *Aspidoceras* sp. (in any case, ornamentation patterns of the latter are identical to those of A.

[15]The Upper Jurassic genus *Burckhardticeras* Olyriz, 1978, is a homonym of the Lower Jurassic genus *Burckhardticeras* Flores Lopez, 1967 [51], and its name is given in quotes.

[16]In the recent work dedicated to the Neuburg section [58], this species is not mentioned, although the close level is indicated as yielding *V. broilii* [57] characteristic of the same zone.

neoburgense).[17] In the Polish Carpathians, the species in question occurs mainly in the *darwini* and *semiforme* zones [66] and appears again, after a significant stratigraphie gap, in the lower Berriasian *euxina* Zone ([166], Plate 2, fig. 7). In Germany, the species is characteristic of the *ciliata* Zone [58]. In Spain, *A. neoburgense* was also found in the basal Berriasian *jacobi/grandis (=euxinus)* Zone. Abundant specimens of this species are characteristic of the *semiforme* Zone in Hungary [167], although they are common also at lower levels [168]. The species is known as well from the middle Tithonian Substage of Cuba [169], Mexico ([75], Plate XXXII, figs. 3-11, Plate XXXIII), and Argentine [170]. According to Checa *et al.,* [171], distribution of A. *neoburgense* is discrete: after residence in the middle Tithonian *"Burckhardticeras"* Zone, it appears again only in the Berriasian. Because of *Anaspidoceras* abundance in the *semiforme* Zone of West Europe, the *neoburgense* faunal horizon of the Russian plate corresponds, at least partly, to this stratigraphic unit.

13. *Pavlovia.* This Boreal species occurring from England and Greenland to the eastern slope of the sub-Polar Urals is common in the Volgian Stage of European Russia, but in Poland it is recorded only in some areas [172]. Therefore, *P. iatrensis* described by Zeiss from the upper Tithonian Substage of Austria ([46], p. 376, Plate 2, fig. 1) seems to be of a doubtful identification. As was mentioned, Mesezhnikov [50] discredited the original identification by Zeiss. Depending on its understanding, the *Pavlovia* genus proper can be characteristic of either the entire middle Volgian Substage, or its basal zone only. Therefore, if the generic classification by Zeiss is correct, one can conclude that the middle Volgian Substage corresponds partly to the upper Tithonian.

14. *Dorsoplanites.* Until recently, this genus was unknown from West Europe, being considered as characteristic mainly of the middle Volgian in Siberia, Greenland, and, to a lesser extent, in European Russia. One poorly preserved ammonite attributed to *Dorsoplanites* sp. has been figured by Khimshiashvili ([173], Plate 14, fig. 4) from the middle Tithonian Substage of Georgia. In addition, one of the species previously described by Schneid [57] from the middle Tithonian of the Neuburg locality was recently revised and attributed to this genus. Nevertheless, even if *Dorsoplanites lumbricatus* is correctly identified by Scherzinger and Schweigert [58], this species cannot be used for correlation. It is undoubtedly older than other known *Dorsoplanites* species, because it appears below first *Danubisphinctes* ex gr. *spurius* in the Neuburg section.

15. *Subdichotomoceras (Sphinctoceras).* Representatives of this subgenus are characteristic of the *subcrassum* Zone in the sub-Polar Urals and the Boreal realm in general. They are known from England (the *wheatleyensis* Zone), Greenland, and the Pechora River basin, being rare in southerly areas. In the Volga region, first *Subdichotomoceras* appear in the uppermost part of the *klimovi* Zone and are occasionally registered in the *sokolovi* Zone. The ammonites in question are mentioned also as present in the *hybonotum (= gigas* after Geyer [34]) Zone of southern Germany. In England, they appear in younger sediments implying their migration to Germany most likely from the Central Russian basin (via the Pripyat strait). This event happened at the very beginning of the *sokolovi* Chron. The *Subdichotomoceras* occurrence in the basal Tithonian zone of Germany is consistent with data on distribution of *Paralingulaticeras* and with correlation between the lower part of the *sokolovi* Zone and the uppermost part of the *hybonotum* Zone.

16. *Franconites.* Mikhailov ([22], p. 56, Plate 11, fig. 1) described ammonites from the *sokolovi* Zone of central Russia under the name *Franconites* cf. *vimineus.* The ribbing of this species and changes in this character during ontogenesis are similar to those of typical *F. vimineus* described from the lower Tithonian *vimineus* Zone of southern Germany ([37], Plate 14). In this region, the genus *Franconites* proper characterizes the uppermost lower-basal middle Tithonian [174]. Recently, it was also found in the uppermost lower Tithonian Substage (the *darwini* Zone) of Spain [152], Hungary [43], Italy [175], and Mexico [176]. *Franconites* from the *sokolovi* Zone of the Russian plate, together with doubtful *llowaiskya pavida* and *?I.* cf. *pseudoscythica* from the *vimineus* Zone of the Franconian Alb, suggest that boundary between the *sokolovi* and *pseudoscythica* zones may be within the upper part of the lower Tithonian.

DISCUSSION AND PROPOSED CORRELATION SCHEME

At present, the following variant of correlation between the Volgian and Tithonian stages is widely usable: the lower Volgian Substage is correlated with the lower and middle Tithonian and the middle Volgian Substage with the upper Tithonian Substage [177]. Some researchers also correlate the *palmatus* and *ponti/"Burckhardticeras"* zones of the Tethyan areas [145]. It is clear, however, the last idea is inconsistent with data on distribution of *Lingulaticeras, Sutneria,* and *Pseudolissoceras.* The joint occurrence of these genera in the *panderi* Zone indicates that its lower part at least is correlative with the level not lower than the *fallauxi* Zone (Fig. 1).

Relationships between zones in different Tethyan areas are also controversial. None of the sections exhibits here the continuous *Danubisphinctes-Pseudovirgatites-Microcanthoceras* succession. The *Danubisphinctes-Pseudovirgatites* succession is known in Poland (Brzostówka section), and the

[17] I studied the original specimen from Semenov's collection stored at the Chair of Historical Geology of the St. Petersburg University.

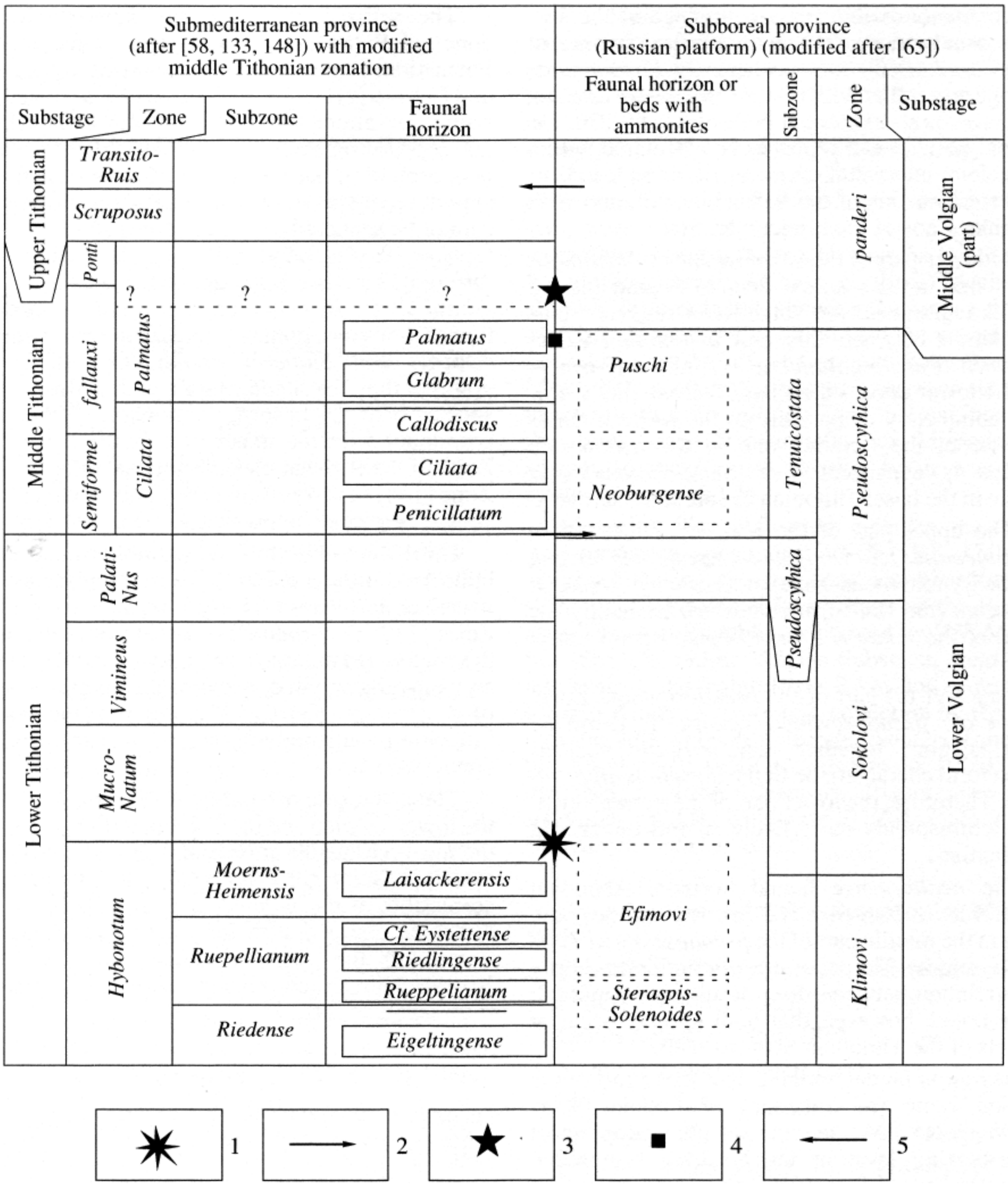

Fig. 1. Correlation of Volgian and Tithionian Stages based on ammonites with indicated changes in their assemblages most important for stratigraphie correlation: (1) disappearance of *Paralingulaticeras, (2)* appearance of *Anaspidoceras neoburgense* and *Sutneria asema* in the Russian plate, (3) disappearance of *Glochiceras* s. 1., *Pseudolissoceras,* and *Sutneria, (4)* appearance of *Danubisphinctes* in Poland and Volga River sections, (5) appearance of *Zaraiskites regularis* in the Submediterranean Province.

Pseudovirgatites-Micmcanthoceras succession is established in Spain, France, and the Carpathians. Moreover, the precise stratigraphie ranges are unknown for *Danubisphinctes* and *Pseudovirgatites* genera. Correlation of the *bavaricum* Zone with the entire middle Tithonian Substage [178] is also unjustified because of aforementioned data on distribution of *Pseudolissoceras* and *Sutneria.*

As it follows from the considered data on ammonite distribution, at least six levels directly correlative with the Tithonian zonation can be distinguished in the Volgian strata of European Russia (Fig. 1).

(1) The base of the *klimovi* Zone. Based on the appearance level of *Neochetocems* cf. *steraspis* and on the disappearance level of *N. fridigense* (Berckh. et Hölder), the base of the *klimovi* Zone can be correlated with the base of the Tithonian *hybonotum* Zone.

(2) The base of the *efimovi* faunal horizon. The mass appearance of *Paralingulaticeras* forms replacing the

Neochetoceras-Lingulaticeras assemblage in the section corresponds most likely with similar changes in sections of southern Germany, where rare *Paralingulaticeras* appear together with first *Neochetoceras steraspis* in the *riedlingensis* faunal horizon [115]. The *efimovi* faunal horizon can probably be correlated with a part of the joint interval of cf. *eystettense* and *laisackerensis* faunal horizons of the Swabian Alb and with Mörnsheimer Beds of the Franconian Alb.

(3) The lower part of the *sokolovi* Zone. *Paralingulaticeras* found in the *sokolovi* Zone of Poland and the Ul'yanovsk region near the Volga River suggest a partial correlation between this and *hybonotum* Zone, above which *Paralingulaticeras* is missing every where. The lower part of the *sokolovi* Zone likely corresponds completely or partially to the *laisackerensis* faunal horizon, the terminal one in the *hybonotum* Zone. This is consistent with *Subdichotomoceras* occurrence in the basal Tithonian of southern Germany.

(4) ?The upper part of the *sokolovi* Zone, which yields *Franconites* cf. *vimineus,* corresponds to that part of the synonymous zone in Germany, where *I. pavida* occurs (the last form characterizes mainly the upper part of the *sokolovi* Zone in Poland and Central Russia).

(5) The lower (?) part of the *pseudoscythica* Zone. *Ilowaiskya* cf. *pseudoscythica* occurs in Germany (Neuburg section) together with *Virgatosimoceras broilii,* the form characteristic of the *darwinni/albertinium* Zone. Therefore, the lower part of *the pseudoscythica* Zone corresponds most likely to the uppermost lower Tithonian.

(6) The *neoburgense* faunal horizon. Abundant *Anaspidoceras neoburgense* and *Sutneria asema,* both occurring in the middle part *of the pseudoscythica* Zone and in the middle Tithonian *semiforme* Zone, imply partial correlation between these stratigraphie units. It should be noted, however, that both species occur at lower levels of the Tithonian Stage as well.

(7) The *puschi* faunal horizon.The upper part of the *tenuicostata* Zone (or Subzone) of Poland yields *Danubisphinctes* characteristic of the uppermost ammonite-bearing level of the Neuburg Formation. Therefore, the *puschi* faunal horizon of the lower Volgian can be correlated, to a certain extent, with the *palmatus* faunal horizon of the Tithonian.

(8) The lower part of the *panderi* Zone. Basal layers of the *panderi* Zone contain *Lingulaticeras blaschkei, Pseudolissoceras,* and *Sutneria.* Inasmuch as all these forms never occur in Europe above *thefallauxi* Zone of the middle Tithonian, at least the lower part *of the panderi* Zone is not younger than the *fallauxi* Zone.

(9) The upper part of the *panderi* Zone. *Zaraiskites* ex gr. *regularis* from the upper Tithonian Substage of Poland and Bulgaria offers a possibility to correlate the upper part of the *panderi* Zone with a part of the *transitorius* Subzone of the upper Tithonian *microcanthus* Zone.

The scheme of correlation between the Volgian zones of Poland and the Tithonian zones of Neuburg Formation, which has been proposed by Scherzinger and Schweigert ([58], Fig. 1), can be accepted, though with reservations. In this scheme, the *tenuicostata* Zone corresponds approximately to the *palmatus* Zone (this is acceptable), but the *ciliata* Zone is shown to correspond to a hiatus in sections of Russia and Poland (this cannot be accepted). Views of these and French stratigraphers ([148], Table XIII) on relationships between different Tithonian zones are unacceptable. At least, the *ciliata* Zone, in which basal *penicillatum* and *ciliata* faunal horizons contain *Anaspidoceras neoburgense* (Oppel) and *Sutneria asema* (Oppel), cannot be younger than the *semiforme* Zone that also yields these species (Fig. 1). In turn, the *palmatus* Zone, which is correlated with the upper part of the *pseudoscythica* Zone of the Russian plate, is not equivalent to the *ponti* Zone [148]or to a part of it[58], and its upper boundary should be placed below that of *thefallauxi* Zone.

Until the correction by additional data, the upper boundary of the *panderi* Zone can be placed within the *transitorius* Subzone. In any case, the idea of Kutek and Zeiss [179] to correlate the last stratigraphic unit with the *regularis* faunal horizon only cannot be considered as well-substantiated, because the single (!) specimen of Z. *regularis* Kutek, 1994, found in the *transitorius* Subzone means nothing with respect to correlation of zonal boundaries.

Thus, the proposed variant of correlation between the lower Volgian and the Tithonian (Fig. 1) seems to be the most reasonable at present. I should note in addition that the reliable correlation with the Tithonian Stage is admissible at the moment only for the lower Volgian Substage coupled with the lower part of the *panderi* Zone. For the *virgatus-nodiger* interval, the direct Boreal-Tethyan correlation based on ammonites is impossible so far.

APPENDIX 1

DESCRIPTION OF *LINGULATICERAS BLASCHKEI* (CECCA ET ENAY, 1991) AND *SUTNERIA ASEMA* (OPPEL, 1865)

Many Mediterranean ammonites from the Volgian Stage of the Russian plate are poorly preserved and, unfortunately, they have never been described and figured. That is why I give below description of species *Lingulaticeras blaschkei* and *Sutneria asema,* which are important for the Boreal-Tethyan correlation. The described specimens are stored at the Paleontological Institute (PIN) RAS (collection no. 4861), the Vernadsky State Geological Museum (VSGM) (collection BX 17), and the Geological Institute (GIN) RAS (collections MIV and MK).

Suborder Haploceratina Besnosov et Michailova, 1983

Suprafamily Haplcerataceae Zittel, 1884

Family Haploceratidae Zittel, 1884

Subfamiliy Glochiceratinae Hyatt, 1900

Genus *Lingulaticeras* Ziegler, 1958

Lingulaticeras blaschkei (Cecca et Enay, 1991)

Plate, figs. 1-3

Oppelia strambergensis: Blaschke, 1911, [91] p. 154, Plate 1, fig. 7 (non fig. *6=Neochetoceras strambergensis* Blaschke); Khudyaev, 1932, [181] p. 838, Plate 1, figs. 2, 3 (cf.); Khimshiashvili, 1957, [173] p. 55, Plate VII, fig. 3.

Streblitinae sp: Cecca *et al,* 1990, [180] Plate 6, fig. 5.

"Glochiceras" blaschkei: Cecca and Enay, 1991, [128] p. 48, Plate 2, figs. 6-10, fig. 18 in text.

Glochiceras (?Lingulaticeras) blaschkei: Rogov and Egorov, 2002, [101] figs. 1, 2a, 2b.

non *Oppelia strambergensis:* Khudyaev, 1932, [181] p. 838, Plate IV, fig. 5 (=Streblitinae gen. ind.).

Holotype. Specimen FSL 162 510; figured in [128], Plate 2, fig. 7; France, Ardиche, La Pusin; middle Tithonian, *fallauxi* Zone, *richteri* Subzone.

Shape. Shell is discoid with a high oval cross section, narrow ventral side, and maximum thickness of the whorl in the lower third of the lateral side. The side furrow is noticeable only on the living chamber. Umbilicus is moderately narrow, step-wise.

No.	Wb	Wh	D	Uw	Wb/Wh	Wb/D	Wh/D	Uw/D
VSGM BX17/1	4.8	10.3	20.4	4.5	46	23	50	22

Ornamentation is mainly represented by growth lines. Only in the upper part of the lateral side near the living chamber, there are rare, poorly distinguishable ribs. Some specimens have ribs slightly inclined forward, which appear already on phragmocone, in the lower part of its lateral side. Septal suture is slightly differentiated, though composed of relatively numerous elements (six lobes are distinguishable on the lateral side by the whorl height of 10 mm).

Comparison. In comparison with *?L. steueri* ([78], p. 20, Plate 1, figs. 3a, 3b), the species has larger dimensions and less distinct ornamentation. In distinction from *?L. umbilicocrenatum* ([98], Plate CXLIII, fig. 543), it is lacking developed costae in the lower part of the lateral side and has tapered ventral side. Some specimens of *L. blaschkei* ([128], Plate 2, fig. 6; this work, Plate, fig. 1) bear also well-developed internal robs, but they differ from *?L. umbilicocrenatum* by the arrow-shaped cross section of the test.

Distribution: the middle Tithonian *(fallauxi* Zone, *richteri* Subzone) of France, Italy, the North Caucasus, ?Crimea, Czechia (Stramberg) and the middle Volgian *panderi* Zone of the Russian plate (Chuvash Republic and Tver' oblast).

Notes. Ammonites from the Caucasus described as *Oppelia strambergensis* [182] are conventionally included into synonymy, since their ornamentation and lateral furrows cannot be observed because of a poor preservation. After examination of Khudyaev's original material stored at the TsNIGR Museum (collection no. 2925), I established that only one of figured specimens ([181], Plate 1, fig. 3; this article, fig. Id) can be attributed, with sufficient confidence, to *L. blaschkei.* In distinction from it, other specimens, not figured inclusive, have rounded transverse section and relatively large dimensions of the test lacking the living chamber. In addition, septal sutures of these specimens are strongly differentiated, showing the large L lobe characteristic of the family Streblitinae. As was mentioned, *Lingulaticeras blaschkei* Cecca et Enay from France (Ardèche) is characteristic of a narrow stratigraphic interval within the *fallauxi* Zone that exhibits signs of the strengthened Tethyan influence. Migration of this species to the Central Russian basin was probably related to this episode.

Material. The collection includes the following well-preserved specimens: VSGM BX 17/1, middle Volgian Substage, *panderi* Zone, Yanyshar Ravine, outskirts of the Pervomaiskoe Village of the Batyrevskii area, Chuvash Republic, collection by V.V. Mitta; PIN no. 4861/25, middle Volgian Substage, *panderi* Zone, left bank of the Volga River 3 km downstream of the town of Kimry, Tver' oblast, collection by PA. Gerasimov; middle Volgian Substage, *panderi* Zone (probably, lower part); TsNIGR Museum no. 40/2925, Tithonian Stage, North Caucasus, Tuapse area (original specimen by I.E. Khudyaev ([176], Plate 1. Fig. 3: *Oppelia strambergensis).*

Suborder Perisphinctina Besnosov et Michailova, 1983

Suprafamily Perisphinctaceae Steinmann, 1890

Family Aspidoceratidae Zittel, 1895

Genus *Sutneria* Zittel, 1884

Sutneria asema (Oppel, 1865)

Plate, figs. 5, 6

Ammonites asemus: Oppel, 1865, [183] p. 252.

Oppelia asema: Zittel, 1870, [184] p. 66, Plate 3, fig. 12.

Sutneria asema: Barthel, 1962, [150] p. 21, Plate 3, figs. 8-18; Holder, 1964, fig. 73.10; Kutek and Wierzbowski, 1986, [66] p. 303, Plate 3, figs. 2, 3.

Sutneria (Sutneria) asema: Schlegelmilch, [185] 1994, p. 114, Plate 59, fig. 10.

Non *Eurynoticeras* aff. *asema:* Slavin, 1953, [149] p. 52, Plate 2, figs. 11-14 *(=Ptychophylloceras)* sp.

Holotype. Specimen AS III 54, figured in Zittel, 1870, [184] Plate 3, fig. 12; reproduced in Barthel, 1962, [150] Plate 3, figs. 8, 9; Schlegelmilch, 1994, [185] Plate 59, fig. 10; Poland, Rogoznik; Tithonian.

Shape. The shell is discoid, with oval cross section and rounded ventral side. The maximum thickness of

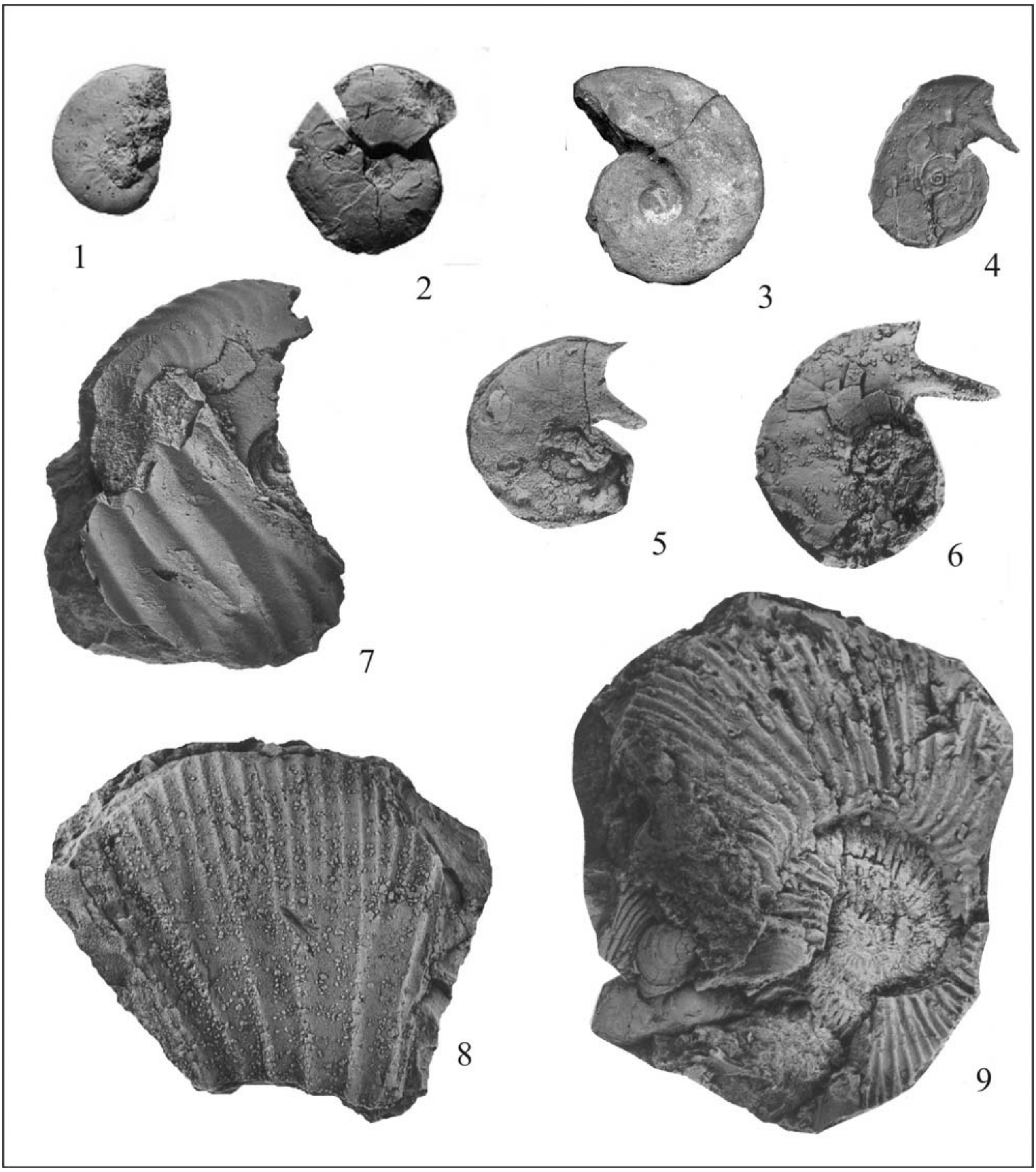

Plate. Some lower-middle Volgian ammonites important for stratigraphic correlation (real size, except for figs. 4-7 magnified x2; specimens, if not specified otherwise, are from author's collection).
(1-3) *Lingulaticeras blaschkei* (Cecca et Enay, 1991): (1) Specimen PIN 4861/25; town of Kimry, Tver' oblast collection of P.A. Gerasimov, (2) Specimen VSGM BX 17/1, Pervomaiskoe Village outskirts, Batyrevskii area of the Chuvash Republic collection by V.V. Mitta, *panderi* Zone of the Middle Volgian Substage, (3) Specimen TsNIGR 40/2925, original specimen, figured in [181] (Plate 1, fig. 3: *Oppelia strambergensis),* North Caucasus, Tuapse area, Tithonian; (4) *Sutneria* cf. *eugyra* Barthel, 1959, Specimen MIV667/1, right bank of the Volga River near the Gorodishche Village, Ul'yanovsk area, lower Volgian Substage, *klimovi* Zone, Beds with *N straspis-L. solenoides,* 0.7 m below the base of the *efimovi* faunal horizon; (5, 6) *Sutneria asema* (Oppel 1865) right ank of the Volga River near the Gorodishche Village, Ul'yanovsk area, lower Volgian Substage, *pseudoscythica* Zone, *tenuicostata* Subzone, *neoburgense* faunal horizon: (5) specimen MIV 644, 0.48 m below the base of the *puschi* faunal horizon; (6) Specimen MK576, 0.45 m below the base of the *puschi* faunal horizon; (7) *Paralingulaticeras efimovi* (Rogov 2002) quarry near the Murzitsy Village, Sechenovskii area of the Nizhni Novgorod oblast, lower Volgian Substage *klimovi* Zone, *efimovi* faunal horizon; (8) *Pseudovigratites* aff. *seorsus* (Oppel, 1865), Specimen MK594, right bank of the Volga River near the Gorodishche Village; Ul'yanovsk oblast, lower Volgian Substage, *pseudoscythica* Zone, *tenuicostata* Subzone, *puschi* faunal horizon, 0.6 m above the base of the *puschi* faunal horizon; (9) *Pseudovirgatites tenuicostatum* (Mikhailov, 1964), Specimen MK540, right bank of the Volga River near the Gorodishche Village, Ulianovsk oblast, lower Volgian Substage, *pseudoscythica* Zone, *tenuicostata* Subzone *neoburgense* faunal horizon, 0.6 m below the base of the *puschi* faunal horizon.

whorls is in the lower third of the lateral side. Umbilicus is moderately wide, and umbilical wall is gently sloping. Aperture has well-developed elongated lappets and small near-umbilical constriction.

Ornamentation is differently developed in various specimens. Usually present are slightly developed retrocostate ribs in the upper part of the lateral side, which become more distinct on the ventral side and form a well-developed bench extending away from the aperture.

Comparison. In distinction from *S.* cf. *eugyra* (Plate, fig. 4), the described species has well-developed ribs only on the ventral side and is lacking ornamentation in the lower part of the whorl. Ornamentation patterns differ this species from older *Sutneria* forms.

Distribution: the lower *(darwini* and *vimineus* zones) and middle *(semiforme* and *ciliata* zones) Tithonian substages of France, southern Germany, Romania, Azerbaijan, and the Polish Carpathians; the Tithonian of Argentine; the lower Volgian (the *pseudoscythica* Zone, *tenuicostata* Subzone, *neoburgense* faunal horizon) of the Volga River basin. *Sutneria* forms from the lower part of the *panderi* Zone of the Gorodishche section probably belong to this species.

Notes. As is mentioned by consideration of *Sutneria* stratigraphic and geographic distribution, data on these ammonites from the Lower Cretaceous sediments [149] are doubtful. *Anaspidoceras neoburgense* used to be considered as antidimorph of *S. asema* is known however from the lower Berriasian. Therefore, it is probable that the stratigraphie range of *Sutneria* can be extended in future up to the Berriasian.

Material. Five well-preserved specimens (MK 560, 573,576,577, MIV 644) are from the Gorodishche section (Ul'yanovsk district of the Ul'yanovsk oblast; all samples are slightly deformed); specimen MK 609 is from a ravine located eastward of the Polevye Bikshiki Village (Batyrevskii area of the Chuvash Republic); lower Volgian Substage, *pseudoscythica* Zone, *tenuicostata* Subzone, *neoburgense* faunal horizon.

APPENDIX 2

BOREAL-TETHYAN AMMONOID MIGRATIONS IN THE NORTHERN HEMISPHERE DURING THE EARLY-MIDDLE VOLGIAN TIME

Many researchers who studied the lower-middle Volgian ammonites and stratigraphy discussed various aspects of paleobiogeography and possible migration paths of these organisms. The data generalized above specify distribution of ammonite taxa in the key areas of Volgian and Tithonian sediments and are important in this aspect.

During the early and initial middle Volgian time, the Central Russian sea basin was open, as repeatedly before, for ammonite migration from the Arctic, North Caucasian, and Polish basins [186]. Its unique position between the Panboreal and Tethys-Panthalassa super-

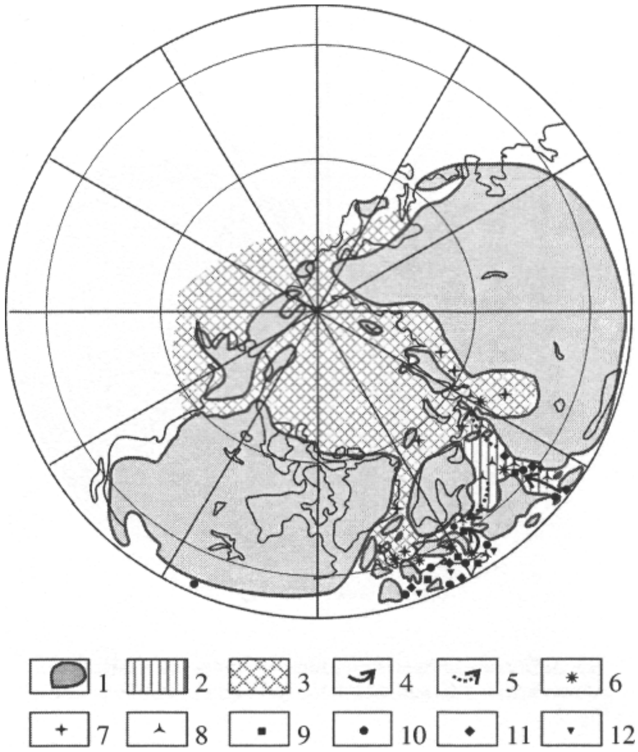

Fig. 2. Boreal-Tethyan migrations of ammonites during the *klimovi-sokolovi* chrons of the early Volgian (paleogeography after [198] modified): (1) land; (2) distribution area of Subboreal ammonites; (3) distribution area of Boreal ammonites; (4) northward and eastward migrations of Submediterranean ammonites; (5) migrations of Subboreal *llowaiskya* and *Gravesia (klimovi* Chron); (6) finds of *Gravesia (klimovi* Chron) and *Danubisphinctes (pseudoscythica-panderi* chrons); (7) finds of *Pectinatites, Subdichotomoceras* (early Volgian time), *Pavlovia,* and *Dorsoplanites* (middle Volgian time); (8) finds of *llowaiskya* (early Volgian time) and *Zaraiskites* (middle Volgian time); (9) finds of *Sutneria* and *Anaspidoceras (pseudoscythica* Chron); (10) finds of *Neochetoceras;* (11) finds of *Lingulaticeras;* (12) finds of *Haploceras* and *Pseudolissoceras.*

realms is reflected in the peculiar composition of ammonites, which populated the Central Russian basin and have a high potential for the Volgian-Tithonian correlation. The detailed paleobiogeographic zoning of the basin is out of the scope of this work dedicated to mixed Boreal-Tethyan ammonite assemblages of the Northern hemisphere and to ammonite migration regardless of past biochoremas.

Based on distribution of ammonites, one can confidently suggest that the Central Russian and Polish sea basins communicated during the entire period under consideration, from the initial early to the middle Volgian time (at least to the *virgatus* Chron), although some researchers think differently [49].

Ammonite taxa whose migrations are discussed below have been either figured, or comprehensively considered above, as it was done, for instance, for *Pseudolissoceras* from the *panderi* Zone of the Volga

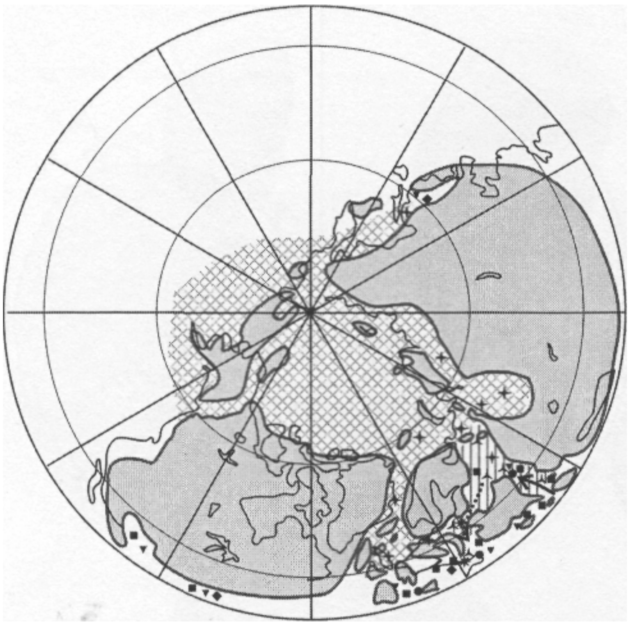

Fig. 3. Boreal-Tethyan migrations of ammonites diring the *pseudoscythica* Chron of the early Volgian (symbols as in Fig. 2).

River localities and for *Ilowaiskya* from the lower Tithonian of Hungary. In terms of paleogeographic interpretation, it is convenient to regard ammonite migrations coordinating them with the Subboreal ammonite scale of the Russian plate. Inasmuch as migrations of early Volgian ammonites were discussed recently in the other work [65], the main attention is focused this time on the middle Volgian migration events.

Since the very beginning of the Volgian Age, the role of Mediterranean and Subboreal ammonites was gradually decreasing in the Subboreal and Submediterranean seas, respectively. The fairly abundant Subboreal *Gravesia* and *Tolvericeras* occur in Germany only in the basal Tithonian *(hybonotum* Zone). Subsequent migrations of Subboreal ammonites to the Submediterranean province are evident only from single finds of their shells, which are frequently in a poor preservation state. *Gravesia* appeared in France, where the most complete *Tolvericeras-Gravesia* succession is known [27], probably in the terminal Kimmeridgian. Representatives of this genus then migrated far to the east and penetrated in sea basins of Central Russia and sub-Polar Urals at the very end of the Kimmeridgian. Thus, these ammonites followed mainly the migration path similar to that of *Neochetoceras.* Although, *Gravesia* is unknown so far from Poland, the alternative migration path, for instance around Scandinavia, seems less probable. During the *klimovi* and *sokolovi* chrons, like in the Kimmerdgian, haploceratins penetrated in the Central Russian sea via the Pripyat strait, although some of them could migrate from the Caucasus (Fig. 2).

In addition to open seaways, one of the main factors responsible for ammonoid migration was probably an insignificant thermal gradient between waters of the Central Russian and Submediterranean seas. The mass migration of haploceratins to the Cantral Russian sea can also be explained by the fact that oppeliids dwelt in relatively deep areas of the basin, where the temperature gradient was lower than near the surface. However, *Paralingulaticeras* forms abundant in the *klimovi* Zone of the Russian plate were most likely shallow-water dwellers, because in southern Germany they occur in lagoonal sediments (Solnhofen and others localities).

Like in the terminal Kimmeridgian, when *Sarmatisphinctes* ([187], Plate 2, fig. 2) migrated from the Central Russian sea via Poland to Germany, Subboreal *Ilowaiskya* continued to migrate westward during the early Volgian. The last genus likely reached the Polish sea only, because its occurrence in Germany has been questioned recently [58]. Simultaneously, the abundance of *Ilowaiskya* decreased in the northeastern direction. In the sub-Polar Urals, only doubtful *Subplanites (Ilowaiskya)* sp. ([55], p. 86, Plate 4, figs. 2,3), which may belong to *Pectinatites,* are known. *Ilowaiskya* from the Lena River lower course [188] have not been figured and are doubtful as well. Intense migrations of Boreal *Subdichotomoceras* southward and of Subboreal *Ilowaiskya* and *Gravesia* northward continued via the Timan-Pechora region at least during the *klimovi-sokolovi* chrons. Therefore, the assumption that the Central Russian sea had no connections with the Arctic basin [189] is inconsistent with the ammonite records.

The path of *Paralingulaticeras* and *Fontannesiella* migration during the early Volgian time in the Central Russian basin is unclear. Their absence in Poland, except for doubtful specimens in the *sokolovi* Zone, evidences against migration from the west. Both genera could probably migrate from the south, from the North Caucasian basin, but their absence in Jurassic sediments of the Orenburg oblast seems strange in this case. The dispersal *of Paralingulaticeras* and *Fontannesiella* in the Central Russian sea could probably be caused by a local warm current. No signs of Subboreal ammonites migration to the Caucasus during the early Volgian time are recorded.

In the greater part of the *sokolovi* Zone in Central Russia, molluscan assemblages are of a low diversity and consist of abundant *Ilowaiskya,* single *Subdichotomoceras* (ammonites), *Buchia,* and rare *Ostrea* forms similar to those from bivalve faunas of the sub-Polar Urals. The *sokolovi* Chron evidently marks the strengthened influence of the Arctic basin on the Central Russian sea. Simultaneously, the occurrence of rare Trigonidae and *Franconites* cf. *vimineus* in Central Russia is indicative of some warming episodes during this period.

Counter migrations of ammonites via the Pripyat' strait continued up to the end of the *sokolovi* Chron, whereas later on, only migrations of Subboreal ammonites to Poland are registered [65]. In the platform part of Poland, southern ammonites *(Neochetoceras)* occur up to the top of the *sokolovi* Zone, replaced higher by prevalent Subboreal taxa. The sole exception is *Danubisphinctes* whose representatives penetrated into the Polish and then into the Central Russian seas at the end of the *pseudoscythica* Chron.

Ammonites abruptly changed their migration paths to the Central Russian sea during the *pseudoscythica* Chron (by the beginning of the *neoburgense* hemera). In addition to westward migration of *Ilowaiskya,* the mass invasion of Tethyan ammonites from the south happened owing to restoration of water exchange with the North Caucasian basin. Anyway, the complete absence of Mediterranean ammonites outside the Carpathian part of Poland suggests only this migration path that is consistent with occurrence of *Sutneria* and *Aspidoceras* s. l. in the Tithonian sediments of the Caucasus [190]. These thermophilic ammonites migrated to the Central Russian sea most probably with some warm currents, like during the *efimovi* hemera, because they are, for instance, more abundant and diverse in the Ul'yanovsk area near the Volga River and in the Chuvash Republic than in Jurassic sections of the Orenburg oblast located far away to the south (Fig. 3). On the other hand, during the *neoburgense* hemera, thermophilic elements from the Caucasian basin advanced farther to the north, up to the Moscow region, as compared with the earlier migration episode. It is noteworthy that substantial changes in the ammonite assemblages were accompanied by changes in other molluscan faunas: diversity of bivalves became almost an order of magnitude higher and belemnites turned out to be represented solely by thermophilic *Hibolithes* (first in the Middle Volga region). Nevertheless, bottom waters remained probably relatively cold because *Buchia* were still abundant. This inference is consistent with data on benthic foraminifers, because their assemblages from the *pseudoscythica* Zone are similar to those from the *sokolovi Zone* [191].

During the *puschi* hemera, the character of ammonite migrations to the Central Russian sea slightly changed again. The influence of the North Caucasian basin became negligible, as it follows from changes in molluscan assemblages. Ammonites are represented only by rare *Pseudovirgatites* spp., which are known from the Polish basin as well, and by scarce *Danubisphinctes (?).* Like at the beginning of the early Volgian, *Cylindroteuthis porrecta* appears among belemnites and *Buchia* forms amid bivalves. The strengthened Boreal influence is also recorded in West Europe, because *Pseudovirgatites tenuicostatum* appeared in Austria precisely at that time [46].

Northwest of the Polish sea, the early Volgian Subboreal population with *Ilowaiskya* and *Pseudovirgatites* was quickly replaced by the Boreal community with *Pectinatites* whose shells were found in ice-rafted

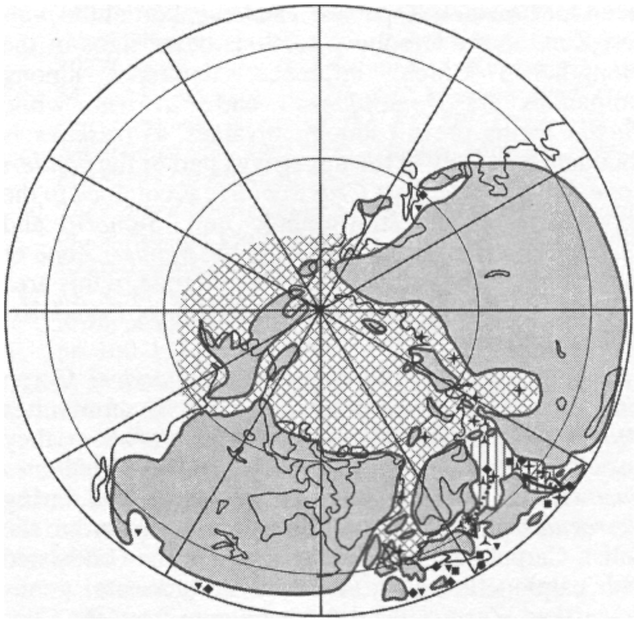

Fig. 4. Boreal-Tethyan migrations of ammonites diring the *panderi* Chron of the middle Volgian (symbols as in Fig. 2).

boulders in Denmark ([192], *Perisphinctes (Zaraiskites)* cf. *scythicus,* p. 154, Plate 5, fig. 2; *P. (Z.) quenstedti,* p. 156, Plate V, fig. 3).

Typical Subboreal ammonites *(Ilowaiskya)* did not penetrate far northward: their single finds are known from the Pechora River basin and sub-Polar Urals region [193]. During the *pseudoscythica* Chron, Submediterranean ammonites were represented outside the Carpathian part of Poland only by *Danubisphinctes* species similar to those recorded in southern Germany. Several specimens of coarsely ornamented ammonites resembling *Danubisphinctes* were recently found in Poland, and this implies their penetration farther eastward.

Beginning from the middle Volgian time *(panderi* Chron), migration paths of ammonites changed again. Rare finds of Boreal *Dorsoplanites* are registered in the Caucasus, and some *Lingulaticeras blaschkei* migrated from this region as far northward as the 57°N (Fig. 4). This is indicative of a lower temperature gradient between the Central Russian and North Caucasian basins that was favorable for counter migration of ammonites. The Boreal-Tethyan migration of ammonites in this region was not significant, although a slightly strengthened influence of warm waters is again registered in the Orenburg oblast. The joint occurrence of *Ilowaiskya* and *Crassicolaria* is noted in the Mt. Khanskaya section [194]. If we assume that calpionellids are identified correctly, then we should admit the erroneous identification of ammonites, because such a high stratigraphic position of *Ilowaiskya* relative of the Tethyan zonal succession is inconsistent with all other available data. It seems that *Zaraiskites* forms were taken for *Ilowaiskya* species. The lower part of the *panderi* Zone in the Orenburg sections bears signs of the strengthened Boreal influence: dominant among ammonites are *Dorsoplanites* and *Pavlovia,* while *Buchia* forms prevail among bivalves. *Zaraiskites* is abundant here only in the uppermost part *of the panderi* Zone. It is probable that *Crassicolaria* is confined to the upper part of this stratigraphic unit. *Sutneria* and *Pseudolissoceras* mentioned from the *panderi* Zone of the Gorodishche section could also migrate to this area from the south and, thus, one should expect *Pseudolissoceras* finds also in the Caucasus.

Like the early Volgian time, the *panderi* Chron marks a wide development of Boreal ammonites beyond the Carpathian areas of Poland, where they associate with endemic species *Danubisphinctes mazowiensis.* Some *Zaraiskites* forms migrated during the *regularis* hemera from this region southward to the Polish Carpathian and Bulgaria, where they coexisted with calpionellids (Fig. 4). Like the ancestral genus *Ilowaiskya, Zaraiskites* did not migrate from the Central Russian basin far northward. Between the Orenburg and Arctic regions, the latter were gradually replaced by Boreal *Dorsoplanites,* and only sporadic *Zaraiskites* finds are known in the Pechora River basin [195]. In this connection, the occurrence of *Dorsoplanites* instead of *Zaraiskites* in the Caucasus seems unexpected. *Haploceras* forms from the upper part of the *panderi* Zone of the North Caspian region, which have not been figured however [41], are the youngest Jurassic ammonites reliably evidencing the Tethyan influence on the Central Russian sea.

The last Jurassic episode of ammonites migration from the Central Russian basin was during the *virgatus* Chron. *Virgatites* is found in Poland [196] and *Lomonossovella lomonossovi* (not figured) is mentioned among ammonites from the Maikop area [197]. Penetration of thermophilic ammonites in Central Russia at that time is not recorded.

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