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 semifforme Zone at least. The panderi Zone is correlative with the interval from the middle Tithonian fallausti 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 at least. The panderi Zone is correlative with the interval from the middle Tithonian fallausti 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.

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 Anaspido
ceras neoburgense (Oppel). The representative of the same species was likely described by Sokolov [5], p. 23 as Aspidoceras sp. a few years later. 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-

1In 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 *lillowaiskya klimovi* (Ilov.), Tithonian, Volgian, and Portlandian (sensu gallico), species that is characteristic of the lower Tithonian, Volgian, and Portlandian (sensu gallico), preserved. Therefore, despite a wide distribution of *Aulacostephanus*... The belonging of these beds to the *Oppelia (Ochetoceras) sio 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 Nizhni Novgorod oblast from the uppermost Kimmeridgian (Isady locality) and Volgian (Muzrits locality). At the same time, in the Chuvash Republic they are of the early Volgian age and contain either *Paralingulaticeras efimovi* (Rogov) and *llowitzkya 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 Ulyanovsk oblast of the Volga region [16]. In addition, Sazonov [17] showed the occurrence of *Gravestia* in the lower Volgian Substage. This species previously established in England [18] grounded definition of the *gravesiana Zone* in the Russian plate [19]. The species from the Russian plate has not been figured, however, and is recorded only in the Gorodische section (the upper part of the *klimovi Zone*), where ammonites are poorly preserved. Therefore, despite a wide distribution of *Gravestia* species that is characteristic of the lower Tithonian, Volgian, and Portlandian (sensu gallico), *llowitzkya klimovi* (Ilov.) is more suitable for being used as index species of the basal Volgian zone. 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 *Sarratapisphinctes fallax* (How.) to *llowitzkya 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 stratigraphic position should be attributed to the lower Tithonian genus *Berchmeria* Schweigert et Zeiss, 1998.

Soon after, Mikhailov [21] demonstrated the occurrence of *Glochiceras* and *Neochetoceras* in the *klimovi Zone* of the Ulyanovsk Volga region. In addition, he described a form from the *sokolovi Zone* and referred it, in the open nomenclature, to the species *Franconites vimines* 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, Spitsbergen, and sub-Polar Urals) and attributed to the Mediterranean genera *Ber-riasella*, *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 *Zarasikites scythicus* [29]. 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].
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 zigas 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 Zarai skimites 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 Gorodische section under guidance of M.S. Mesezhnikov substantially augmented our knowledge on composition and stratigraphic distribution of Mediterranean elements in ammonite faunas from the lower-middle Volgian [39]. Glochiceras (Paralingulaticeras) was reported from klimovii and sokolovi zones, and Neocheiloceras 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, Pseudolisoscerceras 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 Zarai skimites 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 Pseudovirgatitites.6 It should be noted that a similar assemblage from the Kletnice Beds includes mainly specimens collected by Veters [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 simpitsphinctes Zone.

Kutek and Zeiss published several articles dealing with stratigraphy of the Volgian Stage in the Bzrostówka section near Tomaszów Mazowiecki (Poland). They described several new Pseudovirgatitites 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, Zarai skimites forms from the upper Tithonian, on the one hand, and Pseudovirgatitites 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 oppelids and Sutneria. Subsequently, Schweigert [51] revised determinations of Submediterranean ammonites and attributed Usseliceras forms of Malinowskayka to the genus Pseudovirgatitites.

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 microcanthus 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 microcanthus Zone. Simultaneously, Kutek and Zeiss [53] who studied drill cores established distribution range of Neocheiloceras in Poland and concluded that the lower Tithonian should be correlated with the lower Volgian klimovii and sokolovi zones. Soon, Neocheiloceras, 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-

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

6According to Mesezhnikov [50], the ammonite specimen figured by A. Zeiss is indeterminable and cannot be attributed to Pavlovia iatriensis.
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 oppelids Neochetoceras fridengense (Berc. 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 Sarmatispinctes 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 lümbricarius (Schneid.) as a possible ancestor of D. panderi (Orb.) [57] is also poorly substantiated, because these species are separated by a stratigraphic gap and characteristic of different basins.

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 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 bavariicum 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.
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 haploceratids from the Russian plate are those from the Gorodishche and Polievye Bikshi 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]. 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 bavarium 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 bavarium Zone with the entire middle Tithonian [70]).

The stratigraphic 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 eucinus Zone) in Tunisia [72], as it was noted first by Imlay [73].

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. zitelli included) coexist with Durganites and Buchia mosquensis (!). In Argentine, Pseudolissoceras is known from the lower part of the middle Tithonian [78].

In the Far East, Pseudolissoceras occurs in the zitelli Zone (=primoryense Zone after Khudolei [79]).

7 According to oral communication of A.G. Oifer’ev, data on ammonites in the scheme were summarized by M.S. Meseznikov. Unfortunately, no Pseudolissoceras forms are found so far in the Meseznikov’s collection stored at the VNIGRI.

8 Burckhardt [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 Primortys primoroyense Chud. 1960, as a synonym of Pseudolissoceras zitelli, thus changing the zone index for zitelli.

10 Upper Kimmeridgian ammonites from the Gorodishche section determined as Haploceras most likely belong to Neochetoceras ex gr. subnudatum.

11 Previously, I attributed these forms to Glochiceras aff. contrac-tum [90].
virtually identical to 291, Plate 2, figs. 1, 2, 4, 7-9). These ammonites are from Cuba should probably be referred to the genus mentioned from the middle Tithonian of Iraq [102] belong most likely to a new species. In the opinion of Sei and Kalacheva (pers. comm.), they from the Primor'e. In Antarctica [104], [98] to species described by Sei and Kalacheva [81] and by Collignon beginning from Diener [100] who consider this species as neoteny in their development. Similar populations of European platform and ornamentation characteristic of inner whorls of European ammonites that were characteristic of Boreal ammonites that developed keel. Therefore, the middle Tithonian Lingulaticeras 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 fallax 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 Ilovaïskya sokolovi flow. 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 tubercles. 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 Solnhofener Formation to become abundant in the overlying Münchner Formation. In the Schwabian Alb, rare G. lithographic-
cum occur in the riedlingensis faunal horizon of the hybonotum Zone [115]. According to G. Schweigert (pers. communication), this area is unfortunately lacking 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, [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 Mönsheimer Beds of the Franconian Alb, which yield abundant Paralingulaticeras [36], and to a portion of the laisackensis 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 Metaklapperus 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 Meseznikov'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 microcanthus 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 eigelingense 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 Argentina: 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 eigelingense 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 Kimmeridgian beckerti Zone of southeastern France only [144]. Other Fontannesiella species, such as F. valen-
tina, are sometimes mentioned among ammonites from the higher stratigraphic level of the darwini Zone, where Paralinguatlaceras is unknown [145].

7. Sutneria. This genus is widespread almost everywhere 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 Neoechitoceras 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. 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 Bikhaili 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 Argentina, 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 Eurynoticeras 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 illustrate the septal suture of these ammonites, which most likely belong to the genus Pty-chophyllhoceras. 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 semiforne 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. Pseudovirgattites. In Russia, ammonites similar to Pseudovirgattites 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. Unfortunately, all specimens figured by him are fragmentary, and morphology of their internal whorls (more exactly, positioning of costae branching points) is unknown. Pseudovirgattites specimens are reported from both the Vetyanka and Gorodishche sections (similar forms were described byl Semenov v [4] as Perispinctes capillaceus). In my collection, there are specimens of P. puschi found in the puschi faunal horizon crowning the pseudoscythica Zone in the Gorodishche and Polevye Bikhaili 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 Pseudovirgattites 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 Pseudovirgattites 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 Pseudovirgattites associated with Semiformiceras fallauxi. Pseudovirgattites 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 semiforne and Uhligites lymani [155] characteristic of the middle Tithonian. Relationships between Pseudovirgattites 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 Florensksii [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 Pseudovirgattites and vice versa in Zaraiskites shells. Ornamentation patterns on external whorls of some Zaraiskites quendetti are virtually identical to those of Pseudovirgattites forms.

Kutek and Zeiss considered "Ilovaiskaya" tenuicostata (Mich.) as ancestral taxon of Pseudovirgattites. This species appears earlier than Pseudovirgattites puschi. In the Gorodishche section, its first representatives (Plate, fig. 9) are known from the upper part of the neoburgense faunal horizon. Consequently, the puschi and neoburgense faunal horizons can be considered as subdivisions of the tenuicostata Subzone. "Ilovaiskaya" tenuicostata shows morphological features of both Ilovaiskaya (absence of costae characteristic of Virgattites) and Pseudovirgattites (low position of costae branching point on internal whorls). This species begins most likely the Pseudovirgattites phylogenetic lineage and consequently belongs to this genus. Thus, Pseudovirgattites 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, undisputed 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* (?*Ilowaiskya*) 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 *teniocostrata* Subzone of the lower Volgian and in the *scythiscus* 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 *puschii* Zone of Poland. In Hungary, *Istarites* sp. is reported from the "Burckhardticeras" Zone, which used to be correlated with the terminal *ponti* Zone of the middle Tithonian [43]. The same age is characteristic of *Istarites"* from Spain [159]. *D. spuriosus* present in the upper part of the *teniocostrata* Zone of Poland and in the upper faunal horizon of the Neuburg Formation indicates a partial overlapping of these stratigraphic 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 *teniocostrata* Subzone. In southern Germany, the genus appears in the upper part of the Rennertshöfer 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 *Virgatoshpinctes* cf. *albertinum*, the index species of synonymous zone correlated with the *darwini* Zone [94]. 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; =*Subthiacoceras* *penicillatum* (Schneider) 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 correlativ, 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. zaraisensis* [37] were subsequently attributed to other genera [38]. Single *Zaraiskites* specimens are known from the upper Tithonian (the age confirmed by C. Corssicola) 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 *Zaraiskites*, 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 *zaraisensis* Subzone of Poland (the middle Volgian *scythiscus* 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 *micranthum* 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. *Anaspideroceras*. Ammonites from the neoburgense faunal horizon of the Gorodishesche 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 *Anaspideroceras* genus and is a single species lacking tubercles like specimens from the Gorodishesche section. In distinction from ammonites of the last section, the form figured by Ilovaikii 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.
In the Polish Carpathians, the species in question occurs mainly in the darwini and semiuniforme zones [66] and appears again, after a significant stratigraphic gap, in the lower Berriasian exuina 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 jacobigrandis (=exuina) Zone. Abundant specimens of this species are characteristic of the semiuniforme 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 "Burchhardticeras" Zone, it appears again only in the Berriasian. Because of Anaspisoceras abundance in the semiuniforme 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. latreilli 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. Doroplanites. 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 Doroplanites sp. has been figured by Khimishashvili ([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 Doroplanites lumbriticus is correctly identified by Scherzinger and Schweigert [58], this species cannot be used for correlation. It is undoubtedly older than other known Doroplanites species, because it appears below first Danubispinctes ex gr. spurius in the Neuburg section.

15. Subdichotomoceras (Spinocercopites). Representatives of this subgenus are characteristic of the sub-

\[ \text{crassum} \] Zone in the sub-Polar Urals and the Boreal realm in general. They are known from England (the \[ \text{wheatleyensis} \] 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 \[ \text{kimovizi} \] Zone and are occasionally registered in the sokolovi Zone. The ammonites in question are mentioned also as present in the \[ \text{hybonotum (=gigas after Geyer} [34]) \] 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 Paralingulaticeps and with correlation between the lower part of the sokolovi Zone and the uppermost part of the \[ \text{hybonotum} \] Zone.

16. Francoites. Mikhailov ([22], p. 56, Plate 11, fig. 1) described ammonites from the sokolovi Zone of central Russia under the name Francoites 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 Francoites 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]. Francoites from the sokolovi Zone of the Russian plate, together with doubtful \[ \text{llovaiskya pavida} \] and \[ \text{I. cf. pseudoscythica} \] from the vimineus Zone of the Franco-

\[ \text{rian Alb}, \text{suggest that boundary between the sokolovi} \] and \[ \text{pseudoscythica} \] 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 \[ \text{palmatus} \] and ponti/"Burchhardticeras" zones of the Tethyan areas [145]. It is clear, however, the last idea is inconsistent with data on distribution of Lingulaticeps, Sutneria, and Pseudolissoceras. The joint occurrence of these genera in the \[ \text{panderi} \] Zone indicates that its lower part at least is correlatable with the level not lower than the \[ \text{fallauxi} \] Zone (Fig. 1).

Relationships between zones in different Tethyan areas are also controversial. None of the sections exhibit here the continuous \[ \text{Danubispinctes-Pseudovirgatites-Microcanthoceras} \] succession. The \[ \text{Danubispinctes-Pseudovirgatites} \] succession is known in Poland (Brzostówka section), and the
Fig. 1. Correlation of Volgian and Tithonian Stages based on ammonites with indicated changes in their assemblages most important for stratigraphic 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 stratigraphic ranges are unknown for Danubisphinctes and Pseudovirgatites genera. Correlation of the bavari.cum 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 changes in sections of southern Germany, where rare Paralingulaticeras appear together with first Neochetoceras steraspis in the riedlingensis faunal horizon [115]. The efinmovi faunal horizon can probably be correlated with a part of the joint interval of cf. eystettense and laisackerenensis 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 Ufyanovsk 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 laisackerenensis 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. Ilowoiska cf. pseudoscythica occurs in Germany (Neuburg section) together with Virgatosimoceras broili, the form characteristic of the darwinni/albertinum 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 stratigraphic 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 palma tus 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. Zaraikites 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 Vemsky State Geological Museum (VSGM) (collection BX 17), and the Geological Institute (GIN) RAS (collections MIV and MK).

Suborder Haploceratina Besnosov et Michailova, 1983
Oppelia strambergensis: Blaschke, 1911, [91] p. 154, Plate 1, fig. 7 (non fig. 6=Neochetoceras strambergensis Blaschke); Khudyayev, 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" blashkei: Cecca and Enay, 1991, [128] p. 48, Plate 2, figs. 6-10, fig. 18 in text.
non Oppelia strambergensis: Khudyayev, 1932, [181] p. 838, Plate IV, fig. 5 (=Streblitinae gen. ind.).

Holotype. Specimen FSL 162 510; figured in [128], Plate 2, fig. 7; France, Ardèche, 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.

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. umbilicocranatum ([198], Plate CXIIII, fig. 543), it is lacking developed costae in the lower part of the lateral side and has tapered ventral side. Some specimens of L. blashkei ([128], Plate 2, fig. 6; this work, Plate, fig. 1) bear also well-developed internal ribs, but they differ from ?L. umbilicocranatum 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 Khudyayev'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. blashkei. 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 blashkei 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, Yanyshev Ravine, outskirt of the Pervomaiskoe Village of the Batyrevskii area, Chuvash Republic, collection by V.V. Mitra; 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 P.A. 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. Khudyayev ([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
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 (=Psychophylloceras) 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. Mitina; (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 bank 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) Pseudovigratites tenuicostatum (Mikhailov, 1964), Specimen MK540, right bank of the Volga River near the Gorodishche Village, Ul'yanovsk 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 retrococostate 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. eugya* (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 (*semitruncata* and *ciliata* zones) Tithonian substages of France, southern Germany, Romania, Azerbaijan, and the Polish Carpathians; the Tithonian of Argentina; the lower Volgian (the *pseudoscythica* Zone, *tenuiocostata* 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 stratigraphic 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 (Batyrsevskii area of the Chuvash Republic); lower Volgian Substage, *pseudoscythica* Zone, *tenuiocostata* 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-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...
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 [63], 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* chron, like in the Kimmeridgian, 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 Central Russian sea can also be explained by the fact that oppelids 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 Sub-Planites (*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* chron. 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. 1. 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 U'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 molluscans 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 molluscans assemblages. Ammonites are represented only by rare Pseudoovirgatites spp., which is 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 abd bivalves. The strengthened Boreal influence is also recorded in West Europe, because Pseudoovirgatites tenuicostatum appeared in Austria precisely at that time [46].

Northwest of the Polish sea, the early Volgian Subboreal population with Ilowaiskya and Pseudoovirgatites was quickly replaced by the Boreal community with Pectinatites whose shells were found in ice-raftered 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 (puschi Chron), migration paths of ammonites changed again. Rare finds of Boreal Dorisoplantes 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 Crassialorica 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 Crassiscoria 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). As 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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