

SYSTEMATICS OF THE MIDDLE JURASSIC HETEROMORPHIC AMMONITES

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ABSTRACT: The stratigraphic distribution, phylogenetic relationships, and systematics of the Middle Jurassic heteromorph ammonites and their relationship to the monomorph ammonites are considered. *Sulcohamitoides* gen. nov. and *Garantiana asarjani* sp. nov. are described.

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The vast majority of Middle Jurassic heteromorph ammonites are shells with a spiral developing early in one plane, all the way to the formation of a straight tube in the outer part of the phragmocone and in the living chamber. They are also characterized by reduction of the U and I lobes in ontogenesis, manifested to a greater or lesser degree, and by only slight dissection of their lobes and saddles.

The following generic names of the Jurassic heteromorphs are given in the literature.

Arcuceras Potonié, 1929, for which the family Arcuceratidae Arkell, 1950 has been proposed. This genus is based on a single species, *A. marthae* Potonié, from the Pliensbachian of Germany, the only specimen of which has been lost. Repeated searches at the type locality have been unsuccessful. It has been suggested that the dating is erroneous, or that the species and genus are based not on a heteromorph ammonite, but on acrinoid stem.

Apsorroceras Hyatt, 1900, occurs in the lower half of the *subfurcatum* zone of the Upper Bajocian and has usually been combined with *Spiroceras* Quenstedt, 1858, from which it differs in its less reduced U and I lobes and its finer sculpture.

Spiroceras Quenstedt, 1858, from the upper half of the *subfurcatum* zone, is the most common and most often described Middle Jurassic heteromorph.

Sulcohamites Wetzell, 1937, is based on a single fragment of a phragmocone from the Lower Bathonian of Germany.

Parapatoceras Spath, 1924, combines species homeomorphic with *Spiroceras*, which occur from the Late Bathonian to the Middle Callovian inclusive. The holotype has been described from the Callovian. The genus *Metapatoceras* Schindewolf, 1964, has been proposed for the Middle Callovian forms resembling *Parapatoceras* but differing from it in the lesser dissection of their suture line.

Acuariceras Spath, 1933 (Lower Callovian, *macrocephalus* zone--Middle Callovian, *jason* zone), and *Paracuariceras* Schindewolf, 1963 (Middle Callovian, *jason* zone), differ from the synchronous *Parapatoceras* and *Metapatoceras* in their very slightly dissected lobes and in indistinct or absent costation.

The genera proposed by S. Buckman: *Rhabdoites* Buckman, 1923 and *Plagiamites* Buckman, 1925 from the *subfurcatum* zone are, like *Patoceras* Meek, 1876, considered to be synonyms of *Spiroceras*. *Criocconites* Buckman, 1925, is included among the synonyms of *Parapatoceras*.

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The presence of heteromorphic ammonites in the Toarcian, Aalenian and Upper Oxfordian has not been confirmed [10]--that is, the Jurassic heteromorphic ammonites occur discretely in time and do not form unbroken successions of taxa.

The grouping of the above genera and families and their relation to the ammonites with normally coiled shells are subjects of dispute. Arkell [5, 6] accepts the superfamily Spirocerataceae with the families Arcuceratidae Arkell, 1950 and Spiroceratidae Hyatt 1900 (the genera *Apsorroceras*, *Spiroceras* and *Parapatoceras*). He includes *Sulcohamites* with a question mark in the Morphoceratidae Hyatt, 1900. Arkell assigns the Spirocerataceae (and all other Cretaceous heteromorphic ammonites) to the Lyatoceratida.

Schindewolf [19-21] accepts the families Spiroceratidae (*Apsorroceras*, *Spiroceras*, *Sulcohamites*, *Parapatoceras*, *Metapatoceras*) and the family Acuariceratidae Schindewolf, 1961 (*Acuariceras*, *Paracuariceras*), that was derived from it. He derives the Spiroceratidae from the normally coiled Parkinsoniidae Buckman, 1920, and *Strenoceras* Hyatt, 1900.

Donovan et al. [10] retain in the superfamily Spirocerataceae, the one family Spiroceratidae, subdivided into two subfamilies: the Spiroceratinae (genus *Spiroceras*) and the Parapatoceratinae Buckman, 1926 (*Parapatoceras*, *Paracuariceras*, *Acuariceras* and also presumably *Epistrenoceras* Bentz, 1928, and *Sulcohamites*).

Roman [17] includes the genera *Apsorroceras*, *Spiroceras*, and *Parapatoceras* (together with *Garantiana* and *Strenoceras*) in the composition of the Kosmoceratidae Douvillé, 1890 [sic]. A similar position is adopted in the Principles of Paleontology [3]. Hyatt [12] and Spath [22] associated the Spiroceratidae with the Reinckiiidae Hyatt, 1900, and with the Kosmoceratidae.

Sturani [23] proposed that *Spiroceras*, which has an aperture with simple margins and accordingly combines macroconchs, forms a dimorphic pair with *Strenoceras*, all of which are microconchs. We have supported this hypothesis [2]. But in a later publication [24] Sturani rejected this hypothesis, adopting the previous view that *Strenoceras* forms a dimorphic pair with *Garantiana* Mascke, 1907 [9]. This view has also been supported by Parsons [14] and by Donovan et al. [10].

The closeness of *Spiroceras* and *Strenoceras* has been noted by many investigators [20-22]. This similarity is manifested in the sculpture, consisting predominantly of simple, more rarely bifurcating costae, pairs of lateral and of ventral rows of comparatively large spines (pl. I, figs. 4, 5) (see below), in the development of the suture line in the early stages of ontogenesis, and in the overall pattern of its elements in the later stages (disregarding the reduction of U and I in *Spiroceras*). The main differences between them, apart from the uncoiling of the shell in *Spiroceras*, lie in the structure of the aperture: with straight lateral margins in *Spiroceras*, and with lateral auricles in *Strenoceras*--that is, in a feature that is now regarded as a criterion of sexual dimorphism. *Strenoceras* and *Spiroceras* existed synchronously and are usually found together.

Before answering the question of the relationships of *Spiroceras* and *Strenoceras*, however, we must determine the systematic position of the latter among Jurassic ammonites. *Strenoceras* Hyatt, 1900, which is often erroneously regarded as cryptogenic, is closely associated by descendent-ancestor links with *Pseudogarantiana* Bentz, 1928. The morphological similarity between these two genera is so great that some *Pseudogarantiana* have been described as *Strenoceras* [8, table 11, fig. 1; 11, table 7, fig. 6; 18, table 6, figs. 1-6, 12-17]. *Pseudogarantiana* in turn is morphologically close to the microconchs of *Caumontisphinctes* (*Infraparkinsonia*) Buckman, which originated from *Praebigotites* Wetzel. *Praebigotites* -- *Infraparkinsonia* -- *Pseudogarantiana* -- *Strenoceras* during *subfurcatum* time formed a rapidly evolving series, characterized by a gradual increase in shell size and a progressive development of the ventral and lateral spines, and by coarsening and rarification of the costation (pl. I, figs. 1-4). Since *Caumontisphinctes* is ancestral to the parkinsoniids [2], the relationship of *Strenoceras* is undoubted.

The Parkinsoniidae also includes *Orthogarantiana* Bentz, 1928, *Garantiana* Mascke, 1907 and *Hlawiceras* Buckman, 1921. These three genera share macroconchs with a simple apertural margin and strongly branching (always into more than two branches) costae, which bear a tubercle at the point of branching (pl. I, figs. 6, 7). The differences between these genera appear in the outer whorls of the phragmocone and in the living chamber. *Orthogarantiana* occurs in the *subfurcatum* zone, *Garantiana* in the upper part of the *subfurcatum* zone and in the *garantiana* zone, and *Hlawiceras* in the *garantiana* zone.

For the macroconchs of *Orthogarantiana*, Sturani [24] established a dimorphic pair--the microconchs of *Torrensia* Sturani, 1971. At the same time he demonstrated the similarity of *Orthogarantiana* to the stephanoceratids, a similarity so strong that this genus can, in his opinion, with equal justification be included either in

in the Stephanoceratidae Neumayr, 1875 or in the Parkinsoniidae Buckman, 1920. He followed tradition, however, in retaining *Orthogarantiana* in the latter family. Pavia then took the next logical step--he included *Orthogarantiana* and the subfamily Garantianinae Wetzel, 1937 in the family Stephanoceratidae Neumayr, 1875.

Thus *Strenoceras* cannot be the microconchs of *Garantiana*, because of the time of its existence (*Strenoceras* is confined to *subfurcatum* time, *Garantiana* to the end of *subfurcatum* time and to *garantiana* time) and its systematic position (*Strenoceras* is unambiguously derived from the early Parkinsoniidae, whereas *Garantiana* belongs to the Stephanoceratidae), to say nothing of the morphological differences between the shells of *Strenoceras* and *Garantiana*. The only possible pairs for the microconchs of *Pseudogarantiana* and *Strenoceras* in time of existence and shell structure remain *Apsorroceras* and *Spiroceras*.

Another argument in favor of this combination is the morphofunctional analysis of the shells. The development of the sharp spines in *Pseudogarantiana* and *Strenoceras* can presumably be regarded as an adaptation to a planktonic life. The uncoiling of the shell has been considered an analogous adaptation [16, 21].

Having adopted the combination of the microconchs of *Pseudogarantiana* and *Strenoceras* and the macroconchs of *Apsorroceras* and *Spiroceras* as dimorphic pairs, we must also combine them taxonomically in a single family. In spite of the close relation of *Pseudogarantiana* and *Strenoceras* to the Parkinsoniidae, these two microconch genera together with the heteromorphic macroconchs form an independent branch, which is most appropriately retained in the family Spiroceratidae.

To ascertain the full extent of the family Spiroceratidae, we must consider the relation of these four genera to the normally coiled *Parastrenoceras*, *Epistrenoceras* and the Bathonian and Callovian heteromorphic "Spiroceraacea."

Parastrenoceras Ochoterena, 1963, was initially dated as Late Bajocian. Sturani [24] has shown that the greater part of its Mexican and European species belong to the *humphriesianum* zone of the Lower Bajocian. He also associated this genus with *Bajocia* Brasil, 1895, and, following Arkell, assigned both genera to the Sonniniidae Buckman, 1892. Although the systematic position of *Bajocia* and *Parastrenoceras* remains unclear, they cannot be ancestral to *Pseudogarantiana* and *Strenoceras*, whose relation to the Parkinsoniidae is obvious, and they cannot be their descendants because of their stratigraphic distribution. For the same reason *Parastrenoceras* cannot be regarded as ancestral of all the Jurassic heteromorphs, as Wiedmann has suggested. The ammonite described by Krystyn [13] and Rostovtsev [4] as *Parastrenoceras schlageri*, from the *parkinsoni* zone of Austria and the Nakhichevan ASSR, does not belong to this genus and is most likely an aberrant form close to *Zigzagiceras* Buckman, 1902.

Epistrenoceras Bentz, 1928, as its author interpreted the genus, includes two phylogenetically unrelated groups of forms of different ages. The first group combines the Late Bajocian *Strenoceras* in which a lateral chevron was formed by the merging of the bases of the lateral spines: *S. praecontrarium* (Douville), *S. bigoti* (Brasil), *S. semicostatum* Bentz, and *S. apleurum* Buckman. This feature is also developed on part of the shell of the lectotype of the type species of *Strenoceras*, as illustrated by Arkell [6, fig. 381]. The other group includes *Epistrenoceras contrarium* (d'Orbigny) and *E. histicoides* (Rollier) from the Upper Bathonian-Lower Callovian, in which there are no lateral tubercles and the chevron is formed as a result of a sharp break in the costae and their inflation in the middle of the lateral sides. Since the type species of *Epistrenoceras* belongs to this group, this name should be retained for it. Between *Strenoceras* and *Epistrenoceras* there is a long time gap, excluding any direct relationship between them. In view of this, and also of the absence of any original features connecting these two genera, *Epistrenoceras* cannot be combined with *Strenoceras* in the same family. The systematic position of *Epistrenoceras* remains unclear.

An intermediate stratigraphic position between *Strenoceras* and *Epistrenoceras* is occupied by *Sulcohamitoides* gen. nov. from the upper part of the Lower and lower part of the Middle Bathonian in the Greater Balkhan region. *Sulcohamitoides* is homeomorphic with *Strenoceras*, but is separated from it by the *garantiana* and *parkinsoni* time intervals of the Late Bajocian and a large part of the Early Bathonian. The heteromorphic *Sulcohamites* is known from the same stratigraphic level and also from just a single specimen. In spite of the poor preservation and scarcity of the material, the two genera can be considered a dimorphic pair, like *Spiroceras*--*Strenoceras*, because of the similar sculpture of their shells. Wetzel [25] assigned *Sulcohamites* to the Morphoceratidae, on the basis of its stratigraphic position and the general features of its shell. This is probably the best solution for the two genera, whose chronologic and morphological relation to the Morphoceratidae (genus *Ebrayiceras* Buckman, 1920) is more solidly founded than to *Spiroceras* and *Strenoceras*.

Stage	Zone	Heteromorphic ammonites and their dimorphs with normally coiled shells	Ancestral group
Callovian	<i>athleta</i>	Parapatoceratidae	Unknown
	<i>coronatum</i>	Parapatoceratinae Acuariceratinae	
	<i>jason</i>	<i>Parapatoceras</i> <i>Metapatoceras</i> <i>Acuariceras</i> <i>Paracuariceras</i>	
	<i>calloviense</i>		
	<i>macrocephalus</i>		
Bathonian	<i>discus</i>		
	<i>retrocostatum</i>		
	<i>subcontractus</i>	Morphoceratidae	
	<i>progracilis</i>	macroconchs? microconchs? <i>Sulcohamites</i> <i>Sulcohamitoides</i>	
	<i>zigzag</i>		
Bajocian	<i>parkinsoni</i>		
	<i>garantiana</i>	Spiroceratidae	
	<i>subfurcatum</i>	macroconchs microconchs <i>Spiroceras</i> <i>Strenoceras</i> <i>Apsorroceras</i> <i>Pseudogarantiana</i>	
	<i>humphriesianum</i>		<i>Caumontisphinctes</i>

Fig. 1. Systematics and stratigraphic distribution of Middle Jurassic heteromorphic ammonites.

The Upper Bathonian to Middle Callovian heteromorphic ammonites form two groups that differ sharply in the distinctive features of their suture line [20, 21] and sculpture. The first group includes *Parapatoceras* and *Metapatoceras*, with small shells covered with costae having ventral tubercles and with an incompletely reduced inner lateral lobe. The second group combines the indistinctly sculptured *Acuariceras* and *Paracuariceras*, in which the inner lateral lobe may be fully reduced in the early stages of ontogenesis, with a subsequent formation of its analog in the U¹/D saddle. For these two groups it is appropriate to retain the rank of the subfamilies Parapatoceratinae and Acuariceratinae within the family Parapatoceratidae.

The relation of the Parapatoceratidae to other ammonites remains unclear. They can hardly be considered sexual dimorphs, since from the Late Bathonian to Middle Callovian there is not one group of ammonites synchronous with the Parapatoceratidae that has a normally coiled shell and might be their dimorphic partners. Spath [22] and Roman [17] associated the Parapatoceratidae with the Kosmocerotidae. There is justification for this connection, since some of the latter show an unwinding of their shells along the umbilical margin, along with the development of spines and a ventral groove. But both micro- and macroconchs are known among the Kosmocerotidae, and they appeared later than the Parapatoceratidae. In addition, it should be noted that most Parapatoceratidae had very small shells.

It follows from the above that the Jurassic heteromorphic ammonites do not form a single phyletic group but, like the Cretaceous heteromorphs, arose repeatedly as inadaptable branches of various families of the suborder Perisphinctina (fig. 1).

FAMILY MORPHOCERATIDAE HYATT, 1900

Genus *Sulcohamitoides* Besnosov, gen. nov.

Type species. *S. karaimanensis* sp. nov.

Diagnosis. Shells small, semi-involute, with whorls overlapping preceding whorls by one-half their height. Section through whorls hexagonal and laterally compressed. Sides flat, bending in middle and converging toward depressed ventral side and toward umbilicus. Sculpture consisting of radial costae, pairs of ventral and pairs of lateral rows of pointed tubercles (spines). Costae on phragmocone sharp, predominantly bifurcate, splitting in middle of lateral sides. Lateral tubercles lying at points of branching of costae, ventral tubercles on ends of costae, along margin of deep ventral groove.

Specific composition. Type species.

Comparison. Differs from *Sulcohamites* in planispiral, fully coiled shell; from homeomorphic *Strenoceras* in predominance of bifurcate costae and large lateral tubercles, and in weakening of costation in anterior part of living chamber; and from *Epistrenoceras* in absence of lateral chevron and in development of lateral tubercles.

Sulcohamitoides karaimanensis Besnosov, sp. nov.

Pl. I, fig. 8

Specific name. From Karaiman wells.

Holotype. VNIGNI 115/7481, limonitized deformed cast of phragmocone and part of living chamber; Greater Balkhan, Karaiman wells; boundary beds of Lower and Middle Bathonian, lower part of Seutlinskaya Formation.

Description. See diagnosis of genus.

Material. Holotype.

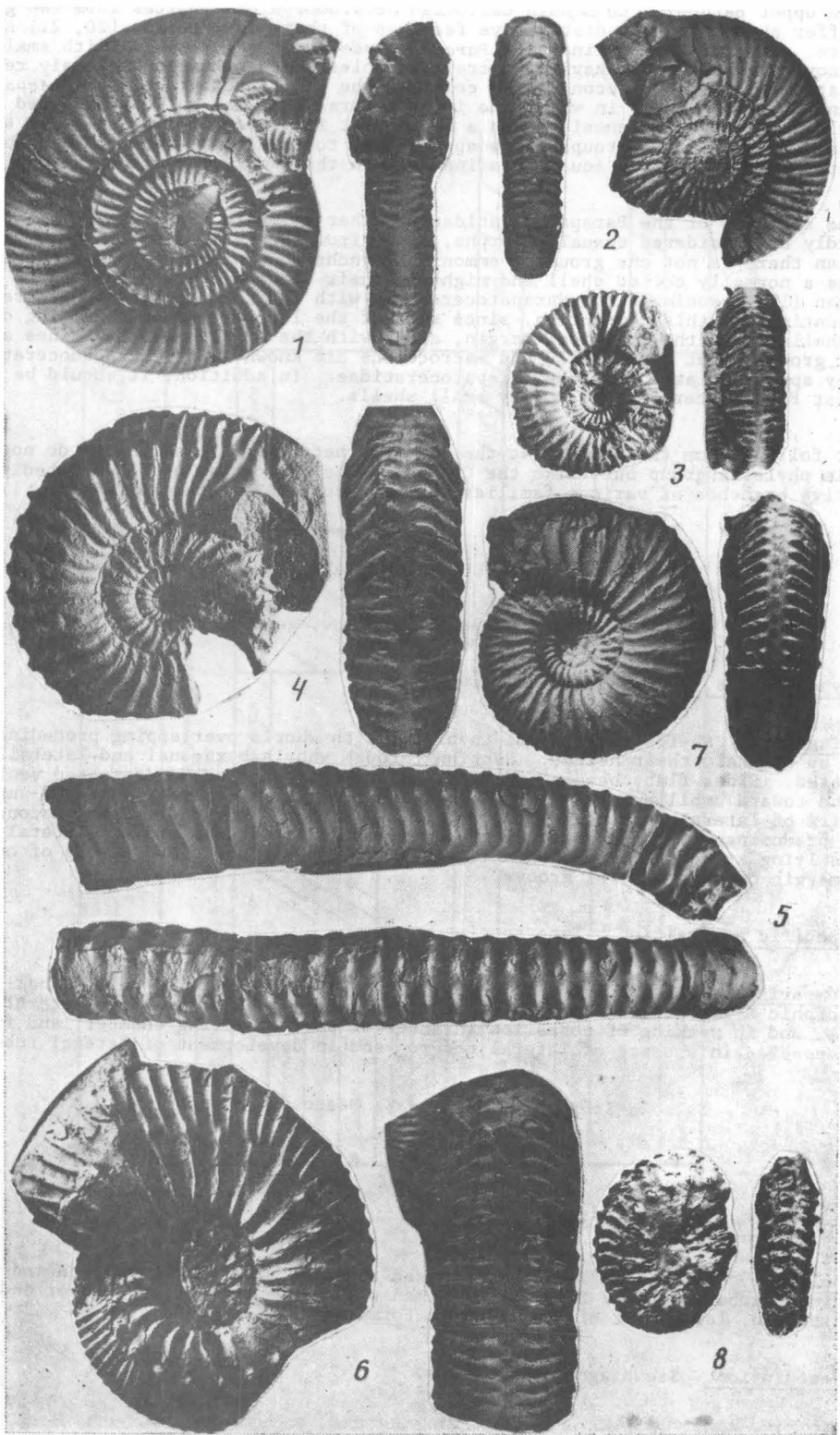


PLATE I

FAMILY STEPHANOCERATIDAE NEUMAYR, 1875

SUBFAMILY GARANTIANINAE WETZEL, 1937

Genus *Garantiana* Mascke, 1907

Garantiana asarjani Besnosov, sp. nov.

Pl. I, fig. 7

Garantiana (Orthogarantiana) bifurcata: Azaryan, 1982, p. 128, pl. 28, figs. 6, 7; pl. 34, fig. 8; Bentz, 1928, p. 186, pl. 17, fig. 2.

Specific name. In memory of palaeontologist N. R. Azaryan.

Holotype. VNIGNI 115/2447; Dagestan, Irganay settlement; Upper Bajocian, *subfurcatum* zone, base of Tsudakhar Formation.

Shell form. Shells small, up to 50 mm in size, with slowly growing whorls that overlap preceding whorls by one third their height. Section through whorls oval-rectangular, and laterally compressed. Lateral sides slightly convex, and bending to approach narrow, depressed ventral side with wide groove. Living chamber occupying half of one whorl.

Dimensions in mm and ratios:

Spec. No.	D	H	W	Du	H/D	W/D	Du/D
Holotype 115/2447	35	13.5	13.5	13	0.39	0.39	0.37
115/2451	30	11	11	11	0.37	0.37	0.37
115/3931	43	15.5	13	16	0.36	0.30	0.37
115/3932	46	18	14	15.5	0.39	0.30	0.34

Sculpture. Costation sharp, varying in density, on the whole becoming sparser in anterior part of living chamber. Costae radial or inclined slightly forward, and dividing into two just beyond middle of lateral sides. On living chamber, connection of one of two branches to axis of costa becoming weaker and lost, and additional intercalary ribs appearing. At points of bifurcation, costae bearing tubercles, and smaller tubercles developed on costae along margins of ventral groove. One-half whorl containing 15-17 lateral costae; coefficient of branching 1.8-2.1.

Comparison. Differs from *G. garantiana* (d'Orbigny) in small size, whorls growing more slowly in height and thickness, smaller coefficient of branching of costae and their forward inclination.

Remarks. The new species is close to the forms described as *Garantiana bifurcata* (Zieten) (see Synonyms, and also [11, pl. 2, fig. 6; pl. 3, figs. 3-5]). Bentz [7, pl. 17, fig. 2] illustrated a specimen from the Münster collection, which had served as the basis for the species *Ammonites bifurcatus* Zieten, 1830. This specimen, which should be considered the lectotype of *Orthogarantiana (Orthogarantiana)*

KEY TO PLATE I

All figures natural size

Fig. 1. *Praebigotites (Otiosphinctes)* sp.: Spec. 115/2472; Dagestan, Irganay settlement; Upper Bajocian, *subfurcatum* zone.

Fig. 2. *Caumontisphinctes (Infraparkinsonia) debilis* (Wetzel, 1937): Spec. 115/1380; Dagestan, Irganay settlement; Upper Bajocian, *subfurcatum* zone.

Fig. 3. *Pseudogarantiana dichotoma* Bentz, 1928: Spec. 115/2; Dagestan, Irganay settlement; Upper Bajocian, *subfurcatum* zone.

Fig. 4. *Strenoceras subfurcatum* (Zieten, 1830): Spec. 115/3766; Greater Balkhan, Shorli wells; Upper Bajocian, *subfurcatum* zone.

Fig. 5. *Spiroceras annulatum* (Deshayes, 1831): Spec. 115/1417; Northern Caucasus, Kuban' River, Mt. Dzhangura; Upper Bajocian, *subfurcatum* zone.

Fig. 6. *Orthogarantiana (Orthogarantiana) baculata* (Quenstedt, 1858): Spec. 115/1431; Northern Caucasus, Kuban' River, Mt. Dzhangura; Upper Bajocian, *subfurcatum* zone.

Fig. 7. *Garantiana asarjani* Besnosov, sp. nov.: Holotype VNIGNI 115/2447; Dagestan, Irganay settlement; Upper Bajocian, *subfurcatum* zone.

Fig. 8. *Sulcohamitoides karaimanensis* Besnosov, sp. nov.: Holotype VNIGNI 115/7481; Greater Balkhan, Karaiman wells; upper part of Lower to lower part of Upper Bathonian.

differs from our new species in its thicker whorls and the absence of a forward inclination of the costae on the ventral side--that is, in the features that differentiate *Orthogarantiana* from *Garantiana*.

Distribution. Upper Bajocian, *subfurcatum* zone; Caucasus.

Material. Northern Caucasus, Kuban' River, Krasnogorskaya Station, 2 specimens from lower part of Upper Dzhangur subformation; Dagestan, Irganay settlement, 6 specimens from base of Tsudakhar Formation.

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NEW MIDDLE DEVONIAN SPIRIFERIDS FROM SOUTHERN TIEN SHAN

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ABSTRACT: New spiriferid species and subspecies, *Kimatothyris sanzarensis* and *Warrenella praekirki aristanensis*, belonging to previously known genera are for the first time described from Central Asia.

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This article describes new spiriferids: *Kimatothyris sanzarensis*, sp. nov. and *Warrenella praekirki aristanensis*, subsp. nov. The first of these were found in the Mal'guzar Mountains (fig. 1a), on the right bank of the Sanzar River, in two localities: 1 km west of the village of Katta-kara-shakshak, and 2 km upstream from the same village. They are from the so-called Suppinskiye beds, which are represented by dark gray bituminous limestones of varying thickness, with thin siltstone stringers along the bedding planes. Their visible thickness exceeds 250 m. The presence in these beds of numerous *Reticulariopsis dereimsi* (Oehlert) and *Rhynchospirifer altus* M. et Breivel, and also the fact that they underlie deposits with abundant Renssellandiinae such as *Bornhardtina*, *Chascothyris* and *Denckmanella*, enables the beds to be dated Eifelian [5].

The subspecies *Warrenella praekirki aristanensis* was found in the Aristantau Mountains (Central Kyzyl-kumy region) (fig. 1) at two stratigraphic levels: in the upper part of the Izas Formation, which is dated Eifelian [3-5], and at the base of the Ayakkuduk Formation, which is assigned to the Givetian [4, 5]. In the first case, the new species comes from thin-bedded black limestones, and is associated with such brachiopod species as *Spinulicosta spinulicosta* (Hall), *Kransia parallelepipedata* (Bronn), *Vagrana (Mimatrypa) flabellata* (Roem), *Plectospira ferita* (Buch), *Chascothyris tshernyshevi* Holzapfel, *Bornhardtina uncitoides* Schulz, etc., and also with conodonts of the *costatus costatus* zone and the tentaculites *Nowakia ex gr. holynensis* and *N. ex gr. Otomaria* [3-5].

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