



Cephalopod jaws from the Middle Jurassic of central Russia

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With 26 figures and 2 tables

Abstract: Three-dimensionally preserved ammonoid and coleoid jaw elements are described from the Lower Callovian of the Unzha-river region. Isolated praestriptychi are attributed to the kosmoceratid ammonites *Kepplerites/Sigaloceras* based on correlation between their shape with the outlines of aperture of ammonite conchs found in the same strata. The width/length-ratios of the aptychi cluster into four morphotypes representing macro- and microconchs of two species. Only one incomplete praestriptychus valve may represent a perisphinctid. The praestriptychi of *Kepplerites/Sigaloceras* exhibit a thin lamellar calcite coating composed of rosette-like calcification centres. Two complete jaw apparatuses of the aptychophoran kosmoceratid *Kepplerites* show reduced rostra of their upper jaws of the same length as the lower jaws. The reduced or complete absence of a rostrum suggests that the aptychus bearing ammonites did not eat large prey, because they could not hold and cup up it. Therefore, we suggest that the Middle Jurassic aptychophoran ammonoids fed on plankton or other minute organisms. We find the function of aptychi as an operculum more important than as a specialized feeding apparatus. In contrast to the simplified morphology of upper ammonoid jaws, the associated upper jaws of coleoids, probably belonging to belemnites, are characterized by prominent rostra. A small isolated shovel-like jaw element may represent the lower jaw of a vampyromorph coleoid.

Key words: Middle Jurassic, Central Russia, cephalopd jaws, ammonoids, coleoids.

1. Introduction

One of the apomorphies of the cephalopods which distinguish this group from other conchiferan molluscs is a powerful chitinous biting apparatus similar to the parrot's beak, consisting of a usually larger upper and a more gracile lower jaw (GUPTA et al. 2008). The ammonites differ from other cephalopods by inverted proportion of both elements, the lower jaw being generally larger than the upper one (KEUPP 2000). Whereas the upper jaw is homologues with jaws of other molluscs like monoplacophorans, scaphopods, and gastropods (HASZPRUNAR & SCHÄFER 1997; SHIMEK & STEINER 1997; LEUCHTEL et al. 1997; v. BOLETZKY 1999, 2007), the lower jaw represents a new development of the cephalopods. The outer lamella of the upper jaw

forms mostly a more-or-less prominent rostrum (= hood). While biting, it moves downwards along the inner side of the biting edge of the lower jaw. Functional morphological aspect in modern coleoid cephalopods of the buccal musculature system, which guarantees a muscular articulation of the beaks, is described in detail by UYENO & KIER (2005). In Recent cephalopods, jaws are of taxonomic value on genus level (CLARKE 1962, 1986; SAUNDERS et al. 1978; CLARKE & MADDOCK 1988; NEIGE & DOMERGUES 2002; XAVIER & CHEREL 2009).

Calcified jaws of nautilids (rhyncholites = upper jaw) and conchorhynchus = lower jaw) have been reported from many Mesozoic and Cenozoic localities (e.g., KNORR 1768; v. SCHLOTHEIM 1820; OWEN 1832; QUENSTEDT 1849; RUTTE 1962; MÜLLER 1963a, b, 1968,

1969; HUCKRIEDE 1971; MUNDLOS 1971, 1973; GEYSANT & GEYER 1972; TUUK 1980; RIEGRAF & SCHMITT-RIEGRAF 1987, 1998; RIEGRAF & LUTERBACHER 1989; REIN 1998; KLUG 2001, 2009; DIETL & SCHWEIGERT 2004; NEMOTO & TANABE 2008; PACAUD 2010).

By contrast, only few descriptions of fossil jaws of coleoid cephalopods exist due to the absence of calcification. Well preserved coleoid jaws are therefore very rare in the fossil record (DZIK 1986) and their occurrence is often restricted to conditions of Konservat-Lagerstätten (BRONN 1859; PINNA 1985; NAEF 1922; KEAR et al. 1995; HARZHAUSER 1999; HAAS 2002; KLUG et al. 2005, 2010; SCHWEIGERT et al. 2009). The oldest known are those from the Carboniferous Mazon Creek biota (JOHNSON & RICHARDSON 1968; KLUESSENDORF & DOYLE 2000). TANABE et al. (2006, 2008) and TANABE & HIKIDA (2010) described isolated jaw elements from Cretaceous calcareous nodules. A questionable coleoid jaw element was described from the Permian by ZAKHAROV & LOMINADZE (1983).

Numerous publications describe jaw elements of ammonoids from the Devonian to the earliest Paleocene (MATERN 1931; FRYE & FELDMANN 1991; SURLYK & NIELSEN 1999). Since Lehmann (1972) demonstrated that the bivalved, mostly externally calcified aptychi of Jurassic and Cretaceous ammonoids are homologous with the lower jaw-elements, a highly controversial discussion of its possible function has started (cf. MORTON 1981; KEUPP 2000; 2003, SCHWEIGERT 2009). Closely similar aptychi characterize some Silurian orthoconic nautiloids (TUREK 1978; DZIK 1981; STRIDSBERG 1984) and probably Carboniferous (LANDMAN & DAVIS 1988). It was proposed that they are homologous to the operculum of other conchiferan mollusks that extended their function and displaced it close to the mouth (DZIK 1981). They functioned both as a biting apparatus and as an operculum, according to DZIK (1981) and LEHMANN & KULICKI (1990). In contrast, SEILACHER (1993) neglected the double function of aptychi and postulated a transformation of the jaw apparatus into an operculum. Complete jaw apparatuses consisting of lower and upper jaws are known from many ammonoids (see Table 1). Their wide morphological variation indicates specialized feeding functions (KRUTA et al. 2011).

All Palaeozoic and Triassic ammonoids bore single unit lower jaws (= anaptychi), while true paired aptychi first appeared within the Hildoceratidae in the Early Toarcien (RIEGRAF et al. 1984; ENGESER & KEUPP 2002) with only weakly calcified cornaptychi (LOMAX & HYDE 2012). The identification of Paleozoic (Devo-

nian, Carboniferous and Permian) aptychi, described by D'ARCHIAC & DE VERNEUIL (1842), FOORD & CRICK (1897), TRAUTH (1935), YOCHELSON (1983), THOMPSON et al. (1980) and CLOSS et al. (1964), is highly questionable (KEUPP 2000). Aptychophoran ammonites dominated from the Middle Jurassic to the Late Cretaceous, nevertheless anaptychophoran ammonites, like the phylloceratids and lytoceratids, which are characterized by rhynchaptychi (TANABE et al. 2012, 2013), as well as some heteromorphic taxa persisted up to the end of the Cretaceous.

The anaptychophoran jaw apparatuses are generally characterized by large, shovel-formed lower jaws. Only some durophagous taxa, known from the Middle Triassic (DAGYS & DAGYS 1975; KEUPP 2000) up to the Cretaceous (= "Neanaptychus": NAGAO 1931a; "Rhynchaptychus": LEHMANN et al. 1980, LEHMANN 1990, TANABE & LANDMAN 2002), show calcified anaptychi. Probably, the calcified upper jaws, described as *Rhynchoteuthis* by D'ORBIGNY (1845) (= *Hadrocheilus* TILL, 1907), which were widely distributed in the Cretaceous, but also in the Jurassic Tethyan environment, represent the antagonistic elements of the rhynchaptychi (RIEGRAF & SCHMITT-RIEGRAF 1995; RIEGRAF & MOOSLEITNER 2010; TANABE et al. 2013). Complete jaw apparatuses of the rhynchaptychus-type were recently found by TANABE et al. (2013) in situ of Late Cretaceous *Hypophylloceras* and *Phyllopachyceras*. Normally both jaw elements of anaptychophorans are chitinous and therefore easily undergoing diagenetic compaction. The shape of the lower jaws correlates sometimes with the shell-morphology as it is the case in Triassic and Jurassic ammonoids. KEUPP (2000: 108) demonstrated that the anaptychi of the Early Triassic *Rudolftruempyceras lenaense* (DAGYS & KONSTANTINOV), characterized by a low whorl expansion rate and a subquadratic whorl section, are short, whereas *Nordophyceras karpinskii* (MOJSISOVICS), with a higher whorl expansion rate and a larger whorl-height, has elongated anaptychi. Also the anaptychi of the middle Liassic genus *Amaltheus*, characterized by oxyconic whorl-sections, are elongated, whereas the anaptychi of planulate *Pleuroceras*, with subquadratic whorl-sections, are isometric (cf. ARKELL et al. 1957; DAGYS & DAGYS 1975; KEUPP 2000). A particular anaptychus with strong radial folds was found by ENGESER & KEUPP (2002) and FRERICHS (2003) inside the bodychamber of *Aegocrioceras* (Early Cretaceous, Hauterivian). Referring to observations on Liassic hildoceratids, LEHMANN (1972) pointed out that the outlines of the aptychi change in ontogeny together with the whorl-section

Table 1. Published records on complete jaw apparatuses of ammonoids. ^a = aptychi.

Taxon	Stratigraphy	Author
<i>Girtyoceras</i>	Early Carboniferous	DOGUZHAEVA et al. 1997
<i>Rhadinites</i> , <i>Anthracoceras</i>	Early Carboniferous	LANDMAN et al. 2010
<i>Eoasianites</i>	Late Carboniferous	CLOSS 1967
<i>Aristoceras</i> , <i>Prothalassoceras</i>	Late Carboniferous	DOGUZHAEVA 1999
not designed	Upper Pennsylvanian	TANABE et al. 2001
<i>Ceratites</i> , <i>Keyserlingites</i>	Anisian, Late Scythian	LEHMANN 1988
<i>Keyserlingites</i> , <i>Svalbardiceras</i> , <i>Anagymnotoceras</i> , <i>Parapopanoceras</i> , <i>Aristoptychites</i>	Spathian Spathian Middle Anisian Middle Anisian Upper Ladinian	DAGYS & WEITSCHAT 1988
<i>Ceratites</i>	Anisian	REIN 1994, KLUG & JERJEN 2012
<i>Eleganticeras</i> ^a	Lower Jurassic	LEHMANN 1967
<i>Psiloceras</i> , <i>Arnioceras</i> , <i>Pleuroceras</i>	Lower Jurassic	LEHMANN 1970
<i>Arnioceras</i>	Lower Jurassic	LEHMANN 1971
<i>Asteroceras</i>	Lower Jurassic	KEUPP 2000
<i>Pleuroceras</i> , <i>Asteroceras</i>	Lower Jurassic	KEUPP 2012
<i>Parkinsonia</i> ^a	Middle Jurassic	LEHMANN 1978
<i>Costacadocheras</i> ^a	Middle Jurassic	MITTA & KEUPP 2004
Perisphinctidae indet. ^a	Upper Jurassic	KULICKI & WIERZBOWSKI 1983
<i>Physodoceras</i> ^a	Upper Jurassic	SCHWEIGERT & DIETL 1999, 2001
<i>Physodoceras</i> ^a , <i>Fontanesiella</i> ^a	Upper Jurassic	KEUPP 2003, 2007
<i>Fontanesiella</i> ^a	Upper Jurassic	SCHWEIGERT 2007
<i>Metahaploceras</i> ^a	Upper Jurassic	DIETL et al. 2007
<i>Lingulaticeras</i> ^a	Upper Jurassic	SCHWEIGERT 2009
<i>Aconeceras</i> ^a	Early Cretaceous	DOGUZHAEVA & MUTVEI 1992
<i>Australiceras</i> ^a	Early Cretaceous	DOGUZHAEVA & MIKHAILOVA 2002
<i>Gaudryceras</i>	Late Cretaceous	TANABE et al. 1980a
<i>Scalarites</i> ^a	Late Cretaceous	TANABE et al. 1980b
<i>Gaudryceras</i> , <i>Tetragonites</i>	Late Cretaceous	LEHMANN et al. 1980, KANIE 1982
<i>Anagaudryceras</i> , <i>Pachydiscus</i>	Late Cretaceous	TANABE et al. 2012
<i>Phyllophylloceras</i>	Late Cretaceous	TANABE & LANDMAN 2002, TANABE et al. 2013
<i>Hypophylloceras</i>	Late Cretaceous	TANABE et al. 2013
Scaphitidae ^a	Late Cretaceous	LANDMAN & WAAGE 1993
Placenticeratide ^a	Late Cretaceous	SUMMESBERGER et al. 1999
<i>Rhaeboceras</i> ^a	Late Cretaceous	KENNEDY et al. 2002
<i>Menuites</i> , <i>Damesites</i> ^a , <i>Reesidites</i> ^a , <i>Scalarites</i> ^a , <i>Subptychoceras</i> ^a <i>Jeletzkytes</i> ^a	Late Cretaceous	TANABE & LANDMAN 2002
<i>Placenticeras</i> ^a , <i>Neogastrolites</i> ^a	Late Cretaceous	LANDMAN et al. 2006
<i>Didymoceras</i> ^a	Late Cretaceous	KRUTA et al. 2010
<i>Polyptychoceras</i> ^a	Late Cretaceous	TANABE 2011
<i>Baculites</i> ^a	Late Cretaceous	KRUTA et al. 2011

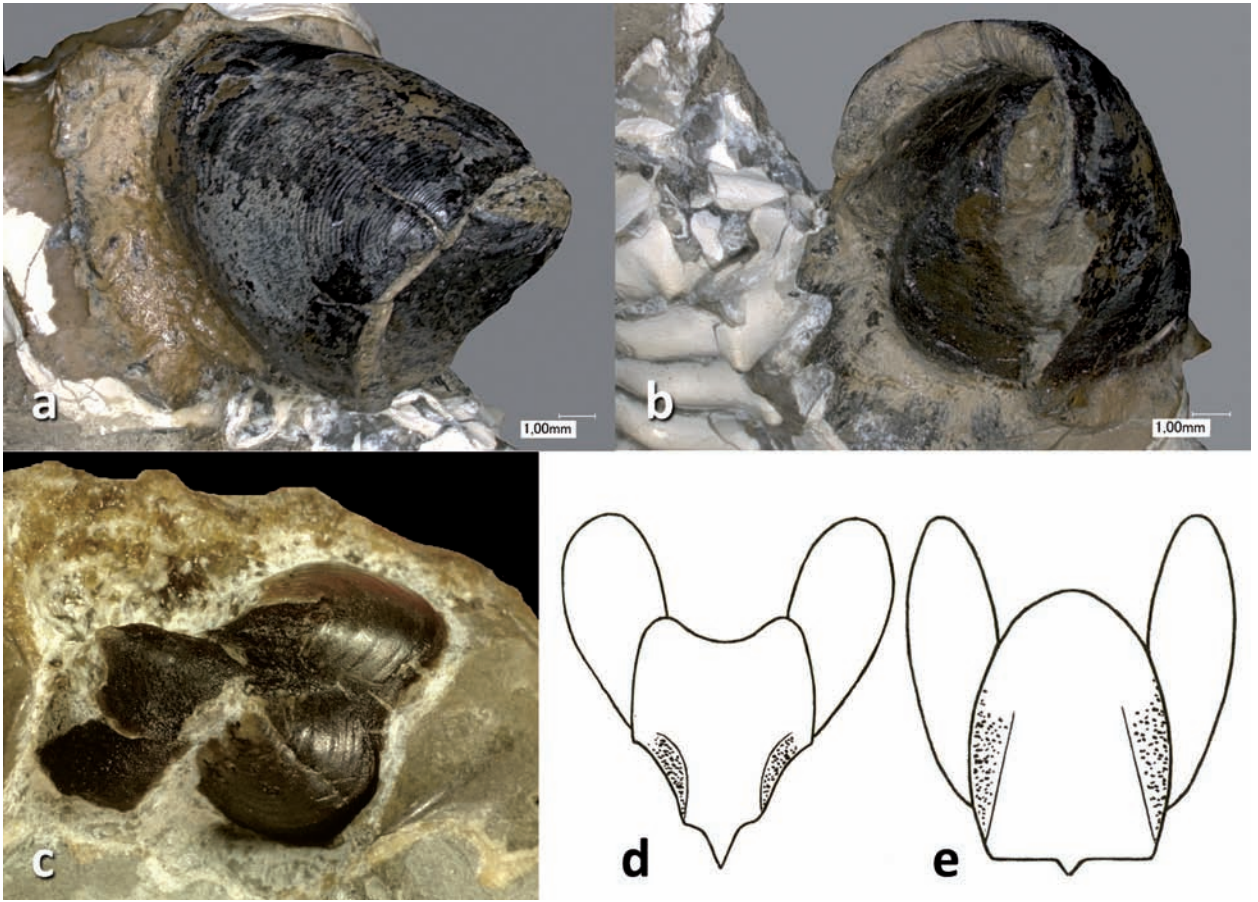


Fig. 1. Two anaptychophoran jaw apparatuses of Early Jurassic ammonites: *Pleuroceras spinatum* (BRUGIÈRE), Late Pliensbachian of Unterstürmig, southern Germany (a, b, e) and *Asteroceras obtusum* (Sowerby), Sinemurian of Lyme Regis, England (c, d). **a** – Ventral view on the lower jaw (anaptychus). **b** – Dorsolateral view on the upper jaw. **c** – The larger lower jaw (on the right side of the photograph) is taphonomically deformed (flattened). **d** – Schematic drawing of the upper jaw of *Asteroceras* in dorsal view. **e** – Schematic drawing of the upper jaw of *Pleuroceras*.

of the conch. Also the different anaptychophoran upper jaws indicate different functions. Some probably performed biting function, as they had a more-or-less prominent hood (rostrum) at the anterior edge (e.g., *Goniatites* sp.: DOGUZHAeva et al. 1997; *Dactylioceras*: LEHMANN 1979; *Lytocera*toidea, *Menuites*: TANABE & LANDMAN 2002); others had reduced rostrum (e.g.: *Eoasianites*: CLOSS 1967). The jaw apparatuses of Early Jurassic *Asteroceras* and *Pleuroceras* (Fig. 1) show the variation of the upper jaw morphology presumably connected with different feeding adaptations.

Most of the upper jaws of aptychus-bearing ammonites have reduced lateral wings of the inner lamella, which are connected by a small anterior bridge, and lack any prominent rostrum, as figured for *Parkinsonia*

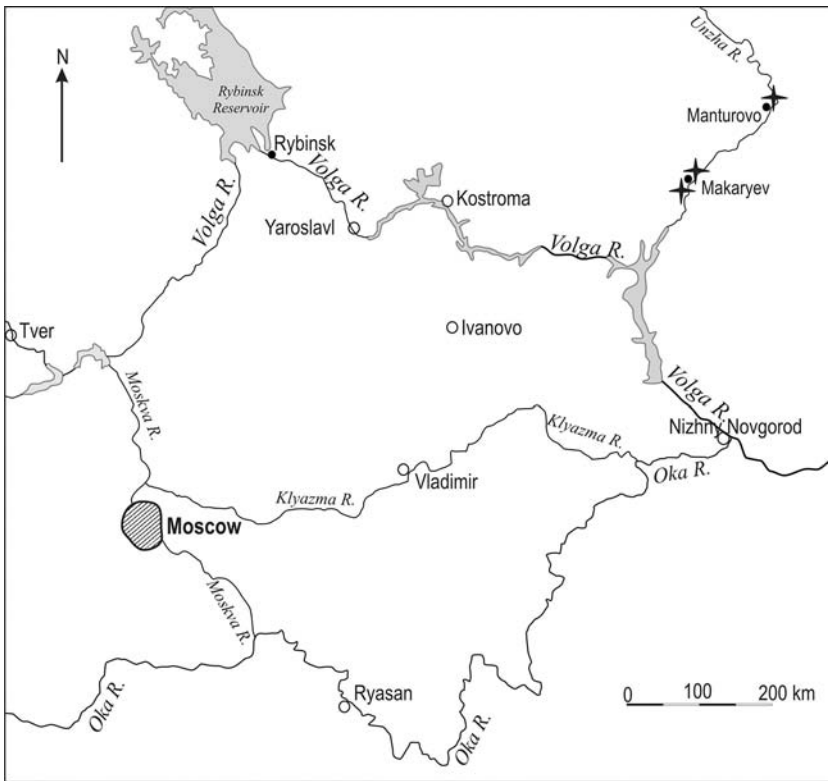
by LEHMANN (1978), *Australiceras* by DOGUZHAeva & MIKHAILOVA (2002), *Costacadoceras* by MITTA & KEUPP (2004), and *Placenticeras* by SUMMESBERGER et al. (1999) and LANDMAN et al. (2006).

Descriptions of cephalopod jaw elements from the Callovian are restricted to ammonoid aptychi belonging to the kosmoceratids, cadoceratids, perisphinctids, and opelids (e.g., QUENSTEDT 1856, 1887; LAHUSEN 1883; NIKITIN 1884; TRAUTH 1938; LEHMANN 1972; DZIK 1986; SCHWEIGERT 2000; KEUPP 2003; ROGOV & GULYAEV 2003; ROGOV 2004; MITTA & KEUPP 2004; Table 2).

The first reports on upper jaws of the Callovian ammonites, associated with praestriptychi, was by MITTA & KEUPP (2004). They were found in calcareous

Table 2. Described types of lower ammonoid jaws from the Callovian and its attribution to ammonoid taxa.

Type of Aptychus	Genus	References
<i>Granulaptychus</i> TRAUTH, 1930 (= <i>Kosmogranulaptychus</i> ROGOV, 2004)	Kosmocerotids: <i>Sigaloceras</i> <i>Kosmoceras</i> Kosmocerotid	TRAUTH 1930 NIKITIN 1884,1885 SCHWEIGERT 2000, ROGOV 2004 MITTA & KEUPP 2004
<i>Granulaptychus</i> TRAUTH, 1930	<i>Quenstedtoceras</i> rather attributed to kosmocerotids	LEHMANN 1972, DZIK 1986, SCHWEIGERT 2000
<i>Praestriaptychus</i> TRAUTH, 1927	<i>Costacadoceras</i>	MITTA & KEUPP 2004
<i>Praestriaptychus</i> TRAUTH, 1927	<i>Proplanulites</i>	ROGOV & GULYAEV 2003
<i>Lamellaptychus</i> TRAUTH, 1927	<i>Lissoceras</i>	KEUPP 2003

**Fig. 2.** Schematic map showing three localities of cephalopod jaws in the Lower Callovian of the Kostroma Region along the Unzha River (asterisks) from south to north: Makaryev South, Makaryev North and Znamenka.

nodules from Poretckoe at the Sura river, central Russia. These isolated jaw apparatuses have been attributed to the microconch of *Costacadoceras*, the most abundant ammonite within the same horizon.

We describe here more associations of cephalopod beaks from the Callovian calcareous nodules of the

Unzha region in Russia (Fig. 2). Isolated coleoid jaw elements are present there. Jaw apparatuses of ammonites are sometimes completely preserved. The new material provides an opportunity to infer trophic preferences of these cephalopods.

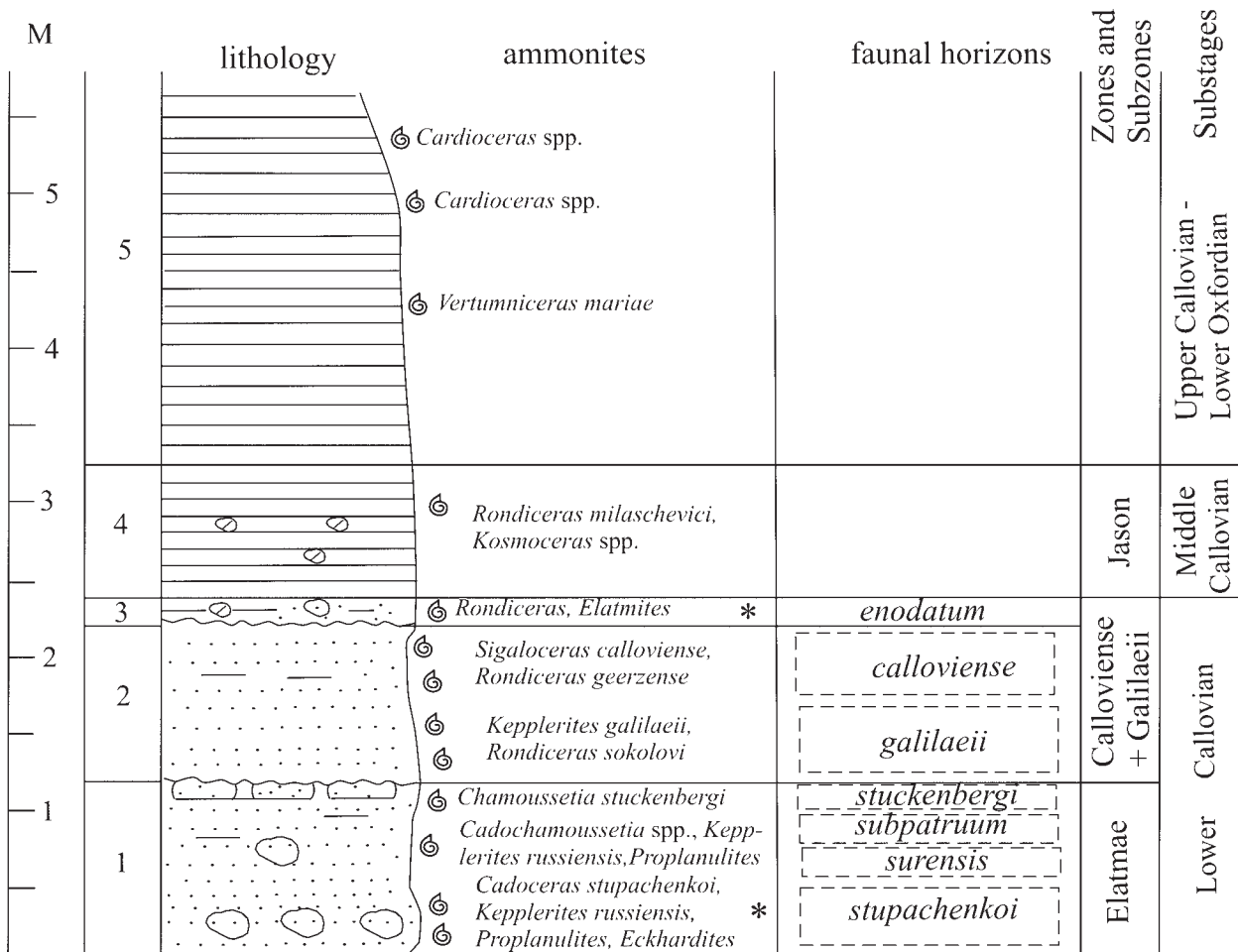


Fig. 3. Compiled section of the Callovian near the town of Makaryev, Kostroma Region (Makaryev South and North localities, generalized). * marks horizons with cephalopod jaw elements.

2. Material

More than 100 jaw elements described in this paper come from three outcrops of the Lower Callovian on the right bank of the Unzha River in the Kostroma Region (Fig. 2). The figured jaw elements are hosted at the Freie Universität Berlin (Department of Earth Sciences, collection H. KEUPP, under the abbreviations SHK MAa-xxx); the illustrated ammonites (Figs. 8-11) are in the collection of the Paleontological Institute of the Russian Academy of Science, Moscow. Only the specimen of Fig. 12 is part of the private collection of A. STUPACHENKO (Moscow).

3. Geological setting

Two of the localities are near the town of Makaryev: one (Makaryev South) in the southern vicinity of the town and the other (Makaryev North) 5 km upstream

of the previous one, in the northern vicinity of the town. The third outcrop is 80 km northwest of the other two, near the village of Manturovo (Znamenka section); it yielded previously described aptychi (NIKITIN 1884; MITTA & KEUPP 2004, 2007, 2008; MITTA 2009). Remains of jaws have been found in all three localities, restricted to different horizons within the Lower Callovian: the Elatmae Zone, Subpatrum Subzone (Makaryev South), Galilaeii and Calloviense subzones of the Gowerianus and Calloviense zones (Znamenka), and the Enodatium Subzone of the Calloviense Zone (Makaryev North) (Fig. 3).

The Jurassic sections near the town of Makaryev have been known since the famous MURCHISON expedition (MURCHISON et al. 1845). However, researchers primarily focused on the Upper Jurassic clayey de-

posits (Oxfordian and Kimmeridgian), well exposed there (MESEZHNIKOV et al. 1989; HANTZPERGUE et al. 1998a, b). The Middle Jurassic beds and their fossils were studied in much less detail. Ammonites from the upper part of the Lower Callovian and partly from the Middle Callovian were described by MELEDINA (1987). MITTA (2000) was the first to give a detailed description of the Middle Jurassic, predominantly sandy beds. The stratigraphical succession from bottom to top:

3.1. Lower Callovian, Elatmae Zone

Light-grey and yellowish-grey sand, quartz sand, brownish at the top, medium-grained, and in places clayey. In the lower part, the bed contains a layer of calcareous sandstone nodules, often phosphatized, with inclusions of pyrite. These nodules contain numerous shells of well-preserved ammonites – *Cadoceras stupachenkoi* MITTA [M, m], less common *Keplerites* (*Gowericeras*) *russiensis* MITTA [M, m], *Proplanulites* sp. [m], even less common – *Eckhardites dietli* MITTA [M, m]. These nodules also yielded rostra of *Pachyteuthis* sp. and frequent remains of cephalopod jaws. Apparently the underlying beds contained infrequent, washed out shells of *Cadoceras tchernyschewi* SOKOLOV [M]. Clayey layers in the upper part of the series contain nodules of grey phosphatized marl with *Cadochamousetia surensis* (NIKITIN) [M], *C. subpatruum* (NIKITIN) [M], and less frequent *Keplerites* (*Gowericeras*) *russiensis* MITTA [M, m] and *Proplanulites* sp. [m]. Layers of dark-coloured, medium-grained phosphatized sandstone in the upper part of the series, (3-8 cm thick) contain shells of *Chamousetia stuckenbergi* (LAHUSEN) [M, m], less common *Keplerites* (*Gowericeras*) aff. *toricellii* (OPPEL) [M, m], and *Rondiceras* sp. nov. [M, m], frequent and poorly preserved rostra of *Pachyteuthis* sp., carbonaceous remains of wood and fragments of reptile bones. At the top of the bed, a discontinued bed (up to 7 cm) of coquina formed by fragile shells of *Astarte* sp., *Gresslya* sp., and infrequent *Chamousetia* sp. [M, m]. The visible thickness is up to 1.2 m. This bed is only accessible when the water level is low (Makaryev South).

3.2. Lower Callovian, Calloviense Zone, Calloviense Subzone

Yellowish-grey sand, quartz, with nodules of a yellowish-brown ferruginous sandstone; in places becoming yellowish-brown compact sandy-clayey rock. The lower part contains rare shells of *Keplerites* aff.

curtilobus BUCKMAN [M], *Rondiceras* sp. [M, m], in the upper section – more frequent *Keplerites galilaei* (OPPEL) [M], *Rondiceras sokolovi* (KISELEV) [M], in the upper part – *Sigaloceras calloviense* (Sowerby) [M, m], less common *Rondiceras* sp. [M, m]. This bed also contains rostra of *Pachyteuthis* cf. *cuneata* GUSTOMESOV. A few loosely collected *Oxycerites czapskii* MITTA also derive from this bed. The visible thickness of the bed is up to 1 m. It is accessible for study in the low stand season (Makaryev North).

3.3. Lower Callovian, Calloviense Zone, Enodatum Subzone

Sandy bluish-grey weakly micaceous clay, horizontally becoming grey clayey sand, with phosphoritic sandy-clayey nodules, with rare shells of *Elatmites* sp. [m], *Sigaloceras enodatum* (NIKITIN) [M], *Rondiceras tscheffkini* (D'ORBIGNY) [M, m], *Indosphinctes* cf. *mutatus* (TRAUTSCHOLD) [M], and also rare remains of cephalopod jaws. Thickness up to 0.1 m (Makaryev North).

3.4. Middle Callovian, Jason Zone

Dark-grey and grey, silty, weakly micaceous clay. In the low and middle portions, the bed contains frequent nodules of calcareous sideritic phosphorite with *Rondiceras milashevici* (NIKITIN) [M, m], *Kosmoceras* ex gr. *jason* auct. [M, m], *Indosphinctes* spp. [M], *Elatmites* spp. [m], *Choffatia* sp. [M, m], various bivalves and the brachiopod *Ivanoviella alemanica* (ROLLIER). The bed contains small, often crushed shells and imprints of *Rondiceras* sp. [M, m] and *Kosmoceras* sp. [M, m]. Thickness up to 0.9 m.

3.5 Upper Callovian – Lower Oxfordian

Dark-grey and grey, compact clay; at the base with light-grey marl with a dark-grey freshly broken surface, in places pyritized, up to 10-20 cm in diameter. The bed contains nodules of the similar type marl, 3-5 cm in diameter. The lower third of the bed yielded *Vertumniceras mariae* (D'ORBIGNY) and in the middle-upper portion frequent *Cardioceras* spp. Thickness 3.8 m. Upward in the section, the succession continues into a thick unit of dark Middle-Upper Oxfordian clay (with a smaller bed of bituminous fissile clay in the lower part) and Kimmeridgian clay (with a marl bed in the upper part) (for a detailed description see HANTZPERGUE et al. 1998a, b).

koi, *galilaei* and *calloviense* horizons, these are large, isometric, sandy, phosphatic-calcareous, well-cemented nodules, with abundant shell detritus and well-preserved shells of ammonites, bivalves, gastropods, and belemnite rostra. The size of the shells varies from small (0.2 mm) to large (150 mm). In addition, the nodules contained carbonized remains of fossil wood and cephalopod jaws clearly discernible on the generally light-coloured background of the rock matrix. Organic remains are distributed randomly and constitute up to 50% of the rock matrix of nodules. Ammonite phragmocone septa and sometimes interior cavities of shells of other molluscs are encrusted with pyrite. The *enodatum* horizon, which is represented by a thin bed, contained small nodules, with higher clay content.

Cephalopod jaw remains are associated with infrequent belemnite rostra *Pachyteuthis*. No skeletal remains of other coleoid taxa have been found. Ammonites mainly belong to the families Cardioceratidae, Kosmoceratidae, and Perisphinctidae (Figs. 8-11). The synchronous Lower Callovian horizons of the basin of the Unzha River also contain some species of oxyconic Oppeliidae – *Oxycerites czapskii* MITTA (MITTA 2004) and heteromorphic Spiroceratidae – *Parapatoceras tuberculatum* (BAUGIER & SAUZE) (GULYAEV 2002; MITTA & SELTZER 2006). Because of the infrequency of their occurrence, it is assumed that jaw remains of members of the two latter families are probably not present in our collection. Below we give a brief characterization of ammonite taxa that are found together with the remains of jaw material.

The cardioceratids belonging to the subfamily Cadoceratinae are the most numerous. These are species of *Cadoceras* (*C. stupachenkoi* MITTA) and its direct descendants that are traditionally assigned by Russian palaeontologists to *Rondiceras* (*R. sokolovi* (KISELEV), *R. geerzense* (BEHRENDSEN in WERMBTER), and *R. tscheffkini* (D'ORBIGNY)). All these ammonites have inflated and strongly inflated, cadiconic cross-sections of adult whorls. Microconchs of *Cadoceras* and *Rondiceras* are classified under *Costacadoceras* and *Novocadoceras*, and have very similar highly oval whorls with an annulate venter. This character readily distinguishes them from the whorls of macroconchs of similar size. *Eckhardites* (*E. dietli* MITTA) has a very different suboxyconic whorl cross-section. However, microconchs of *Eckhardites* have a shell morphology similar to that of *Costacadoceras* and *Novocadoceras*, but with a higher whorl cross-section.

Members of the Kosmoceratidae, which are still infrequent in the *stupachenkoi* faunal horizon, be-

came as abundant as the Cardioceratidae by the end of the Early Callovian. Macro- and microconchs of early kosmoceratids are classified in different subgenera and genera. Macroconchs of *Keplerites* (*Gowericeras*) *russiensis* MITTA correspond to microconchs of *K. (Toricellites) unschensis* MITTA, macroconchs of *K. (Gowericeras) galilaei* (Oppel) to microconchs of *K. (T.) curticornutus* BUCKMAN. Macroconchs of *Sigaloceras* (*Sigaloceras*) *calloviense* (SOWERBY) and *S. (S.) micans* (BUCKMAN) correspond to microconchs of *S. (Gulielmina) quinqueplicata* (BUCKMAN), whereas macroconchs of *S. (Catasigaloceras) enodatum* (NIKITIN) are part of a dimorphic pair with *Kosmoceras anterior* BRINKMANN. The shells of these kosmoceratids, especially the macroconchs, vary in cross-section of the adult whorls. In *Sigaloceras* it varies from oval to rounded-triangular or trapezoid. Extremely inflated morphs with coarse ornamentation are found along with the typical *Keplerites galilaei* (closely related to the type specimen) slightly lower in the section. These may represent a separate species. In early *Gowericeras* (= *Keplerites russiensis*) the cross-section also varies from rounded to suboval.

The Early Callovian perisphinctids of the Russian Platform are rather poorly known. This primarily results from their homeomorphy with those of the Late Bajocian and other ages, and their limited significance for the Middle Jurassic biostratigraphy. The *stupachenkoi* Horizon (Makaryev South Section) shows the first appearance of the family in the Callovian of the Russian Platform. Their fossils are either juvenile whorls with a rounded cross-section or fragments of body-chambers with high-oval sections, which suggests they belong to *Proplanulites*. In the *galilaei* and *calloviense* horizons (Znamenka), specimens are much better preserved, especially microconchs found in nodules (*Proplanulites*), whereas large macroconchs (*Crassiplanulites*) are difficult to extract intact from the rock matrix. The *enodatum* horizon (Makaryev North) contains frequent *Homoeoplanulites* or *Elatmites* microconchs, and fragments of macroconchs of *Homoeoplanulites* (or *Indosphinctes*). All these peresphinctids have rounded young whorls, and an elongated, almost oval whorl cross-section in adults.

5. The jaw elements

5.1. Description of isolated aptychi

Most of the isolated aptychi are black due to diagenetic alteration of the original chitinous material and show more or less concentric growth lines. Often only single

valves are preserved. The very thin calcareous coating of their outer surfaces is often exfoliated, sometimes diagenetically dissolved, sometimes during specimen preparation, and they mostly remain on the counterpart. According to the typological terminology used by TRAUTH (1927) and MOORE & SYLVESTER-BRADLEY (1967) all isolated aptychi found in the Unzha Region belong to the *Praestriptychus* type that developed within the Stephanoceratidae in the Middle Jurassic and characterizes also underived descendents of this ammonite family, particularly perisphinctids and related taxa (e.g., olcostephanids, scaphitids) (see ENGESER & KEUPP 2002). Correlation of isolated aptychi with the ammonoid species found in the three outcrops studied (see Fig. 2) remains problematic. But if the outline of the open aptychus is compared with the shape of the conch aperture (SCHINDEWOLF 1958; LEHMANN & KULICKI 1990; KEUPP 2003), identification seems possible. The width/length-index (cf. Fig. 5) demonstrates an ontogenetic change from low to higher whorls in the kosmoceratids, while the perisphinctids exhibit significantly higher whorls during their growth. We have not found any aptychi that fit into the extremely broad apertures of the cadicone cadoceratids.

Thirty-five complete valves fit with their width/length ratio into five morphometric groups of planulate ammonoids. Besides the single large specimen (length of the symphysis 5 cm) four clusters correlate with micro- and macroconchs of two species characterized by smaller and broader conch whorl sections (Fig. 7).

Most specimens found at the Makaryev South and Znamenka localities show outlines corresponding with the subtrapezoid whorl-sections of the kosmoceratids *Kepplerites* and *Sigaloceras*, which have convex flanks. The symphysis lengths of microconchs range between 5 and 15 mm, those of the macroconchs between 18 and 25 mm (up to 50 mm). The praestriptychi of taxa with broad whorl sections show width/length indices mostly between 60 and 80 %, in contrast to 45–60 % of the taxa with smaller apertures. The morphological clusters of praestriptychi correspond with *Kepplerites russiensis/galilaeii* and *Sigaloceras calloviense*, respectively. The whorl sections of *Sigaloceras enodatum* are intermediate and not clearly attributable to any group. This is confirmed by the find of the broad praestriptychi within the conch of *Kepplerites galilaeii* (Fig. 12). The bivalved aptychus (width/length index 75 %) is preserved in the posterior part of the body chamber. The length of the symphysis (2.45 cm) corresponds exactly with the height of the shell aperture along the median line.

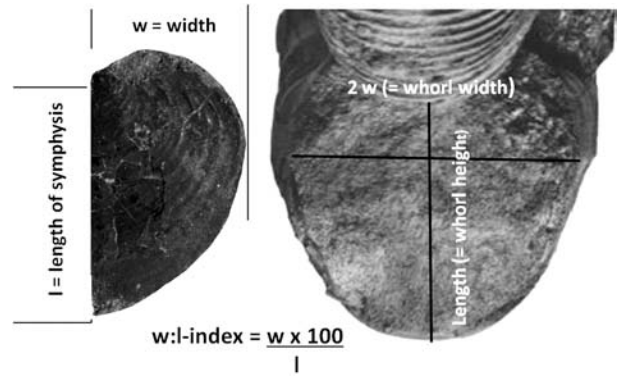


Fig. 5. Measured dimensions of aptychi and the conch-whorl cross-sections.

Taxon	diameter	figured	width:length index
<i>Kepplerites russiensis</i>	9.1 cm	8/1	68 %
<i>Kepplerites russiensis</i>	3.4 cm	9/2	73 %
<i>Kepplerites galilaeii</i>	12.3 cm	8/2	68 %
<i>Kepplerites galilaeii</i>	4.6 cm	9/1	75 %
<i>Sigaloceras enodatum</i>	12.8 cm	9/5	71 %
<i>Sigaloceras enodatum</i>	5.6 cm	10/4	61 %
<i>Sigaloceras calloviense</i>	6.9 cm	10/1	52 %
<i>Sigaloceras micans</i>	6.7 cm	10/2	48 %
<i>Proplanulites</i> sp.	10.7 cm	10/5	41 %
<i>Homoeoplanulites</i> sp.	5.7 cm	11/1	42 %
<i>Homoeoplanulites</i> sp.	13.5 cm	11/3	45 %



Fig. 6. *Lissoceras* sp. from the Upper Callovian of Aichelberg near Göppingen, SW Germany (SHK MAa-401), with opened lamellaptychus perfectly fit into the aperture of the conch. Ø of the ammonite 34 mm (from KEUPP 2003).

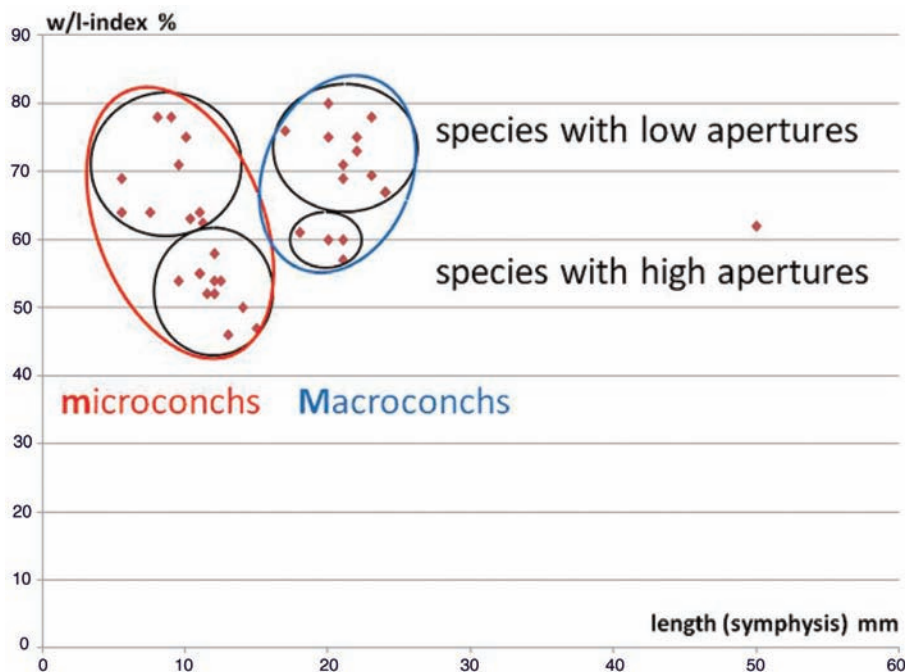


Fig. 7. The length (symphysis): width ratio (%) of 35 praestriptychi from the Lower Callovian of the Unzha region clusters into four clouds corresponding with microconchs and macroconchs of *Keplerites* or *Sigaloceras* species with smaller whorls (= high apertures) and thicker whorls (= low apertures), respectively.

5.2. Descriptions of complete ammonoid jaw apparatuses of *Keplerites*

There are two complete jaw apparatuses, each consisting of lower and upper jaw elements; one is located within the body chamber of a *Keplerites galileii* (MAa-544), one is isolated (MAa-545). The first ap-

paratus (MAa-544, Fig. 15) is preserved within an isolated body chamber of *Keplerites galileii* (M). It consists of the right valve of the praestriptychus and the upper jaw element, which is only visible on the reverse side. But the size of the apptychus (length of symphysis 23 mm, width 18 mm → width/length-index 78 %) is too small to correspond with the whorl section of

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Fig. 8. Lower Callovian Kosmocerotidae from the Elatmae and Gowerianus zones, Central Russia, Kostroma Region, Unzha River; all natural size. **1** – *Keplerites russiensis* MITTA, 1998, macroconch, PIN RAS 5029/116, Subpatruus Subzone, locality Makaryev South a: lateral view; b: apertural view; c: ventral view; **2** – *Keplerites galilaeii* (OPPEL, 1862), macroconch, PIN RAS 5029/117, Galilaeii Subzone, locality Znamenka, a: lateral view; b: apertural view.

Fig. 9. Lower Callovian Kosmocerotidae from the Elatmae, Gowerianus and Calloviense zones, Central Russia, Kostroma Region, Unzha River; all natural sizes. **1** – *Keplerites galilaeii* (OPPEL, 1862), macroconch, PIN RAS 5029/118, Galilaeii Subzone, Ileshevo; a: lateral view; b: apertural view. **2** – *Keplerites russiensis* MITTA, 1998, microconch [= *Keplerites unzhsensis* MITTA, 1998], PIN RAS 5029/119, Subpatruus Subzone, Makaryev South; a: lateral view; b: apertural view. **3** – *Keplerites galilaeii* (OPPEL, 1862), microconch [= *Keplerites curticornutus* (BUCKMAN, 1925)], PIN RAS 5029/120, Galilaeii Subzone, Ileshevo; a: lateral view; b: ventral view. **4** – *Keplerites galilaeii* (OPPEL, 1862), microconch [= *Keplerites curticornutus* (BUCKMAN, 1925)], PIN RAS 5029/121, Galilaeii Subzone, Znamenka; a: lateral view; b: ventral view. **5** – *Sigaloceras calloviense* (J. SOWERBY, 1815), macroconch, PIN RAS 5029/122, Calloviense Subzone, Znamenka; a: lateral view; b: apertural view.

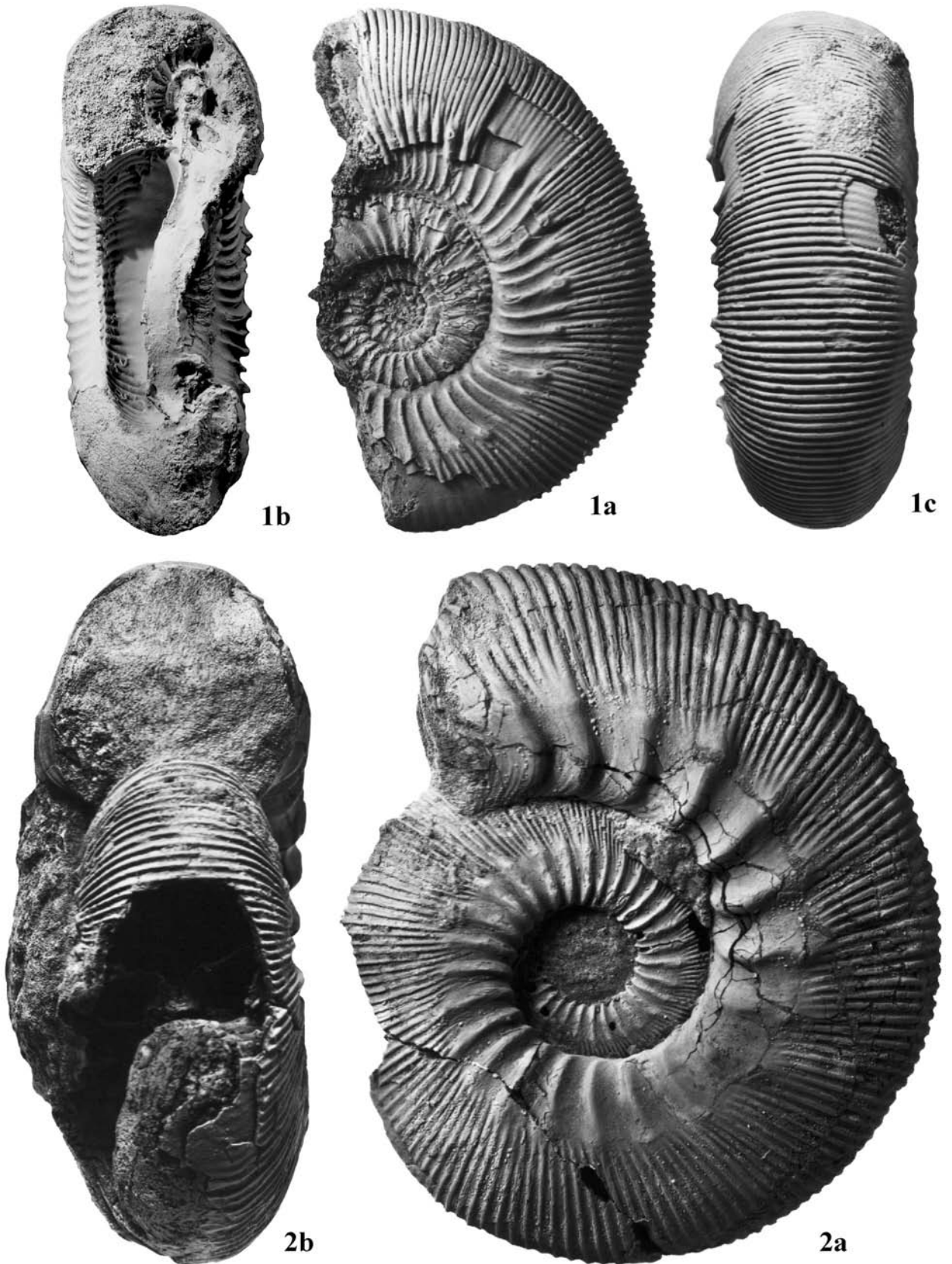


Fig. 8.

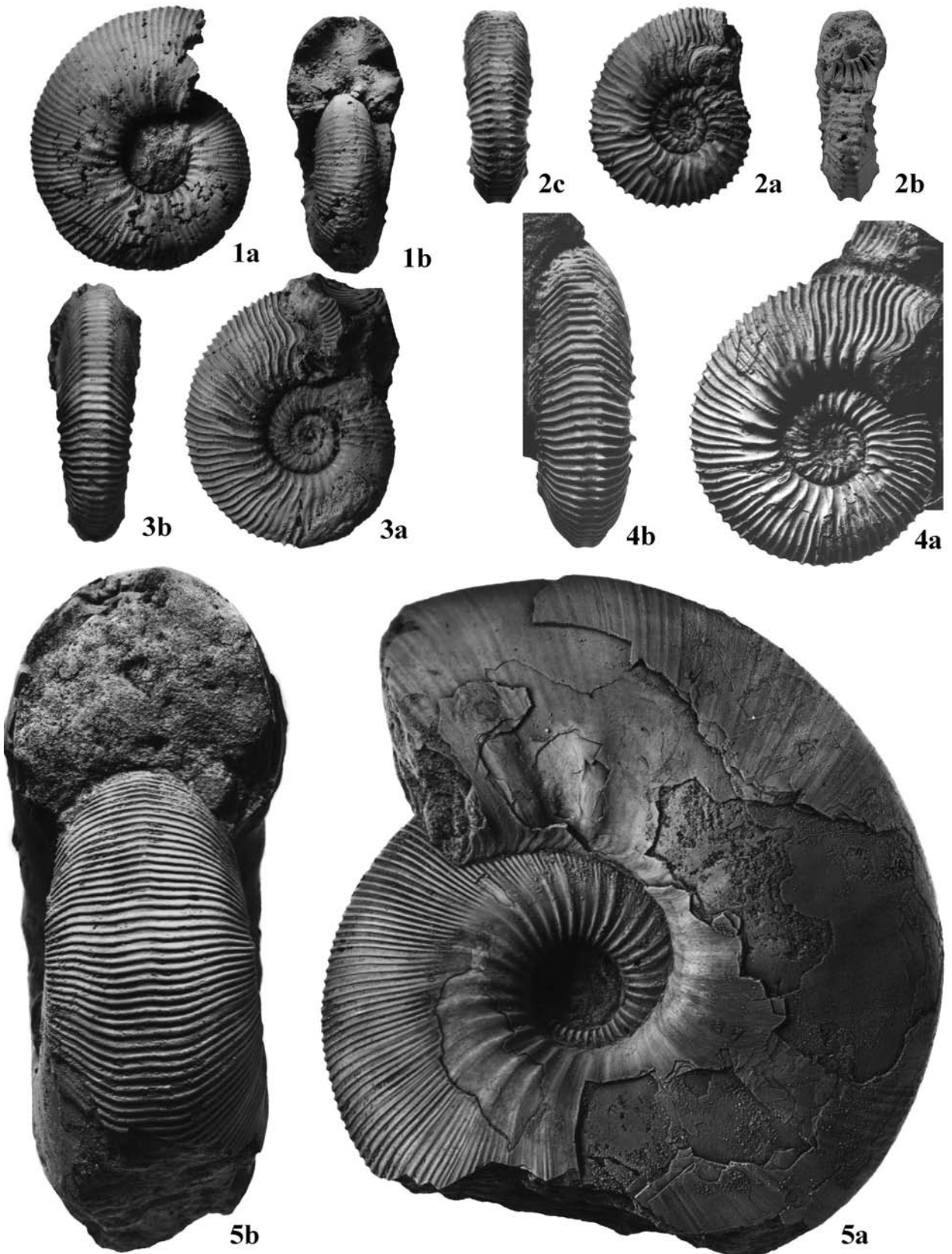


Fig. 9.

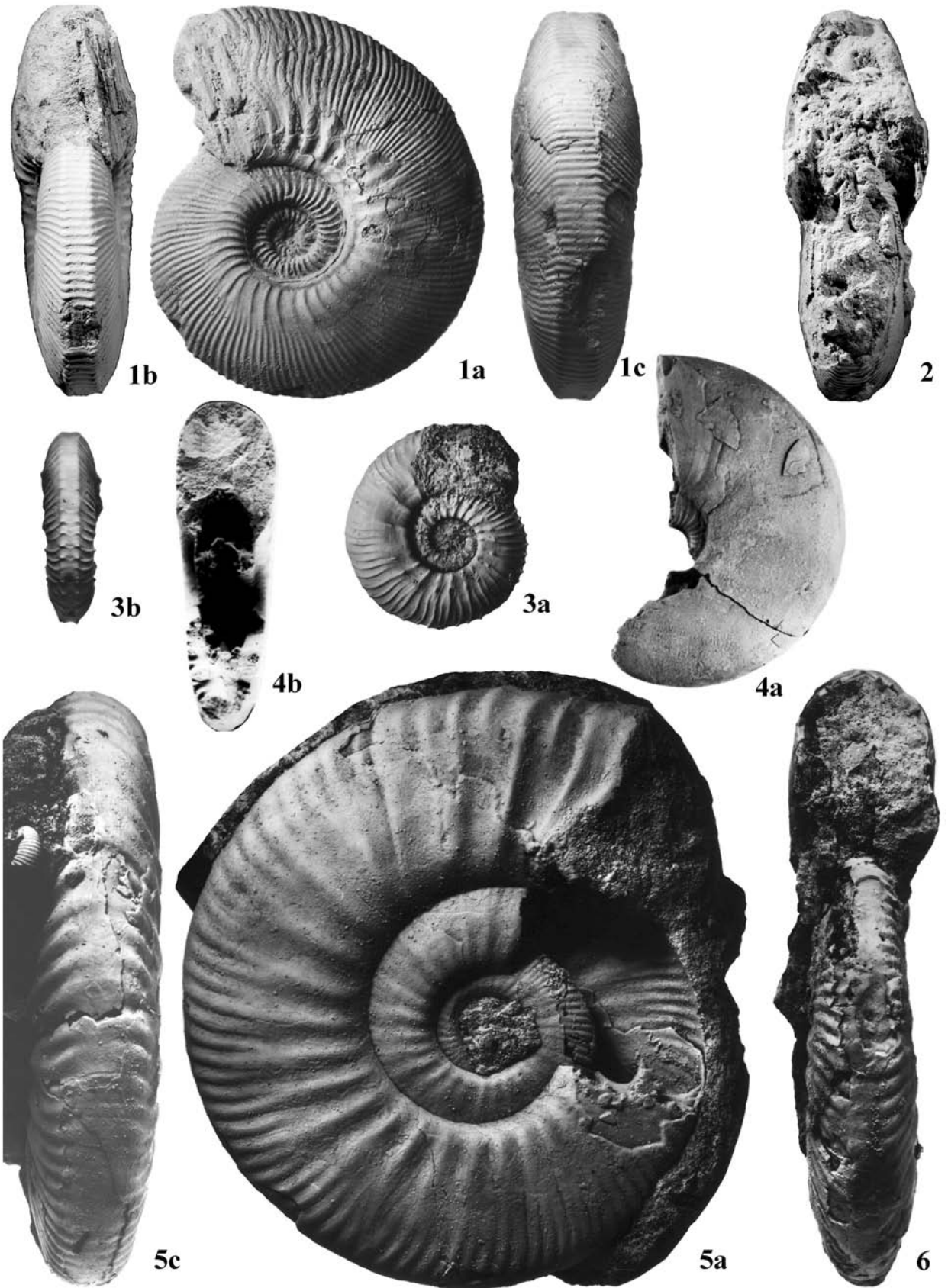


Fig. 10.



Fig. 11.

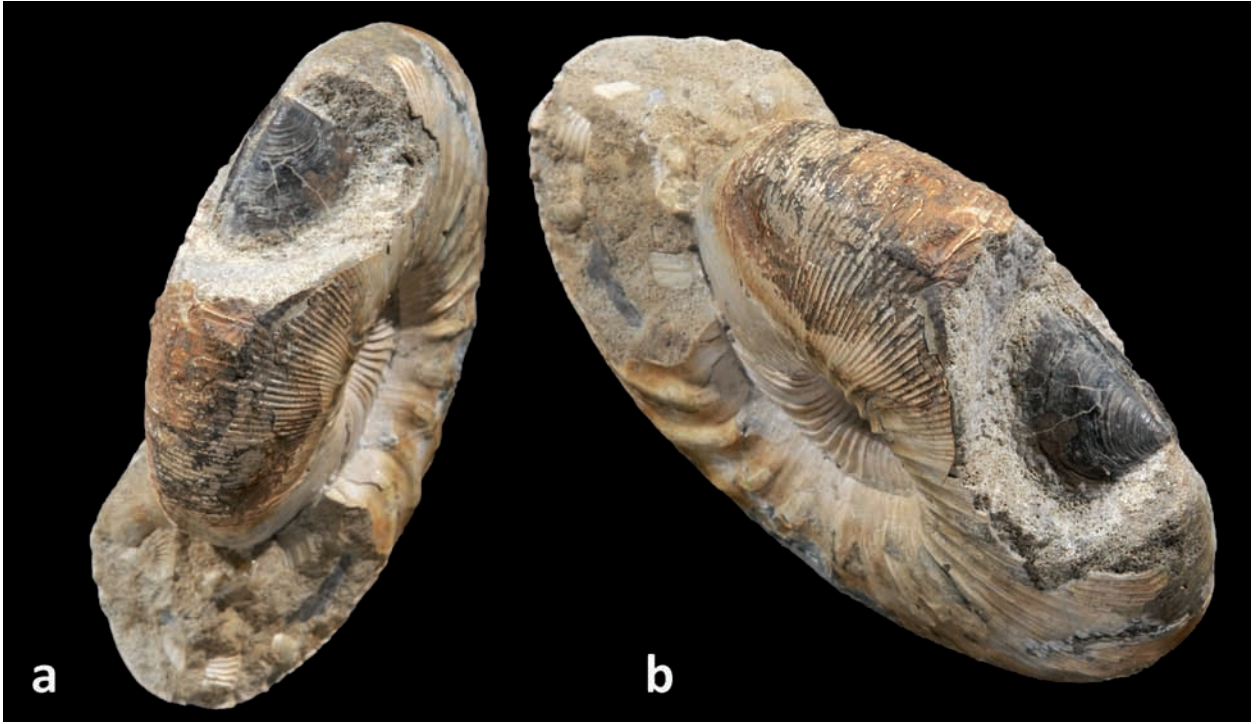


Fig. 12. *Kepplerites galilaei* from the Galilaei Subzone of Znamenka, Ø 11.3 cm. The praestriptychus is dislocated to the posterior part of the body chamber; it fits very well the shell aperture. Length of the aptychus 2, 45 cm (collection of A. STUPACHENKO).

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Fig. 10. Lower Callovian Kosmocerotidae and Perisphinctidae from the Calloviense Zone, Central Russia; all natural sizes. **1** – *Kepplerites calloviense* (J. SOWERBY, 1815), microconch [= *Sigaloceras quinqueplicata* (BUCKMAN, 1926)], PIN RAS 5029/123, Calloviense Subzone, Znamenka; a: lateral view; b: apertural view; c: ventral view. **2** – *Sigaloceras micans* (BUCKMAN, 1921), macroconch, PIN RAS 5029/124, Calloviense Subzone, Znamenka; apertural view (see Fig. 11/2). **3**. *Sigaloceras enodatum* (NIKITIN, 1881), microconch [= *Sigaloceras anterior* (BRINKMANN, 1922)], PIN RAS 5029/125, Enodatum Subzone, Ryasan Region, Oka River, Nikitino; a: lateral view; b: ventral view. **4** – *Sigaloceras enodatum* (NIKITIN, 1881), macroconch, VNIGNI CR-1479, Enodatum Subzone, Bryansk Region, locality Fokino; a: lateral view; b: apertural view (from MITTA 2000, pl. 70, fig. 1). **5** – *Proplanulites* sp., microconch, PIN RAS 5029/126, Calloviense Subzone, Znamenka; a: lateral view; b: ventral view. **6** – *Proplanulites* sp., microconch, PIN RAS 5029/127, Calloviense subzone, Znamenka apertural view.

Fig. 11. Lower Callovian Perisphinctidae and Kosmocerotidae from the Calloviense Zone, Central Russia; all natural sizes. **1** – *Homoeoplanulites* sp., microconch, PIN RAS 5029/128, Enodatum Subzone, Makaryev North; a: lateral view; b: apertural view; c: ventral view. **2** – *Sigaloceras micans* (BUCKMAN, 1921), macroconch, PIN RAS 5029/124, Calloviense Subzone, Znamenka; a: lateral view; b: ventral view; (see Fig. 7.2). **3** – *Homoeoplanulites* sp., macroconch, PIN RAS 5029/129, Enodatum Subzone, Ryasan region, Oka River, Nikitino locality; a: lateral view; b: apertural view.

right side

Fig. 13. Praestriptychi probably of *Kepplerites* cf. *galilaei* (a), and of *Sigaloceras* sp. b, c, d) from the Lower Callovian of Znamenka. **a** – Isolated left valve of a macroconch (Galilaei Zone), MAa-581, length of symphysis 25 mm. **b** – Double-valved aptychus of a microconch (Calloviense subzone), MAa-593, Length of symphysis 10 mm. **c** – Juvenile bivalved aptychus with complete calcareous covering (Gowerianus-/Calloviense zones), MAa-608, length of symphysis 5 mm. **d** – Left valve, secondarily demineralized and therefore crumbled during fossilization (Calloviense Subzone), MAa-648, length of symphysis 10.5 mm. **e** – Largest found double-valved *Praestriptychus* from the Galilaei Subzone, MAa-613, length of symphysis 5 cm, width 6.2. Its width/length-index of 62 % fits with macroconch species of *Kepplerites* and *Sigaloceras*, respectively.

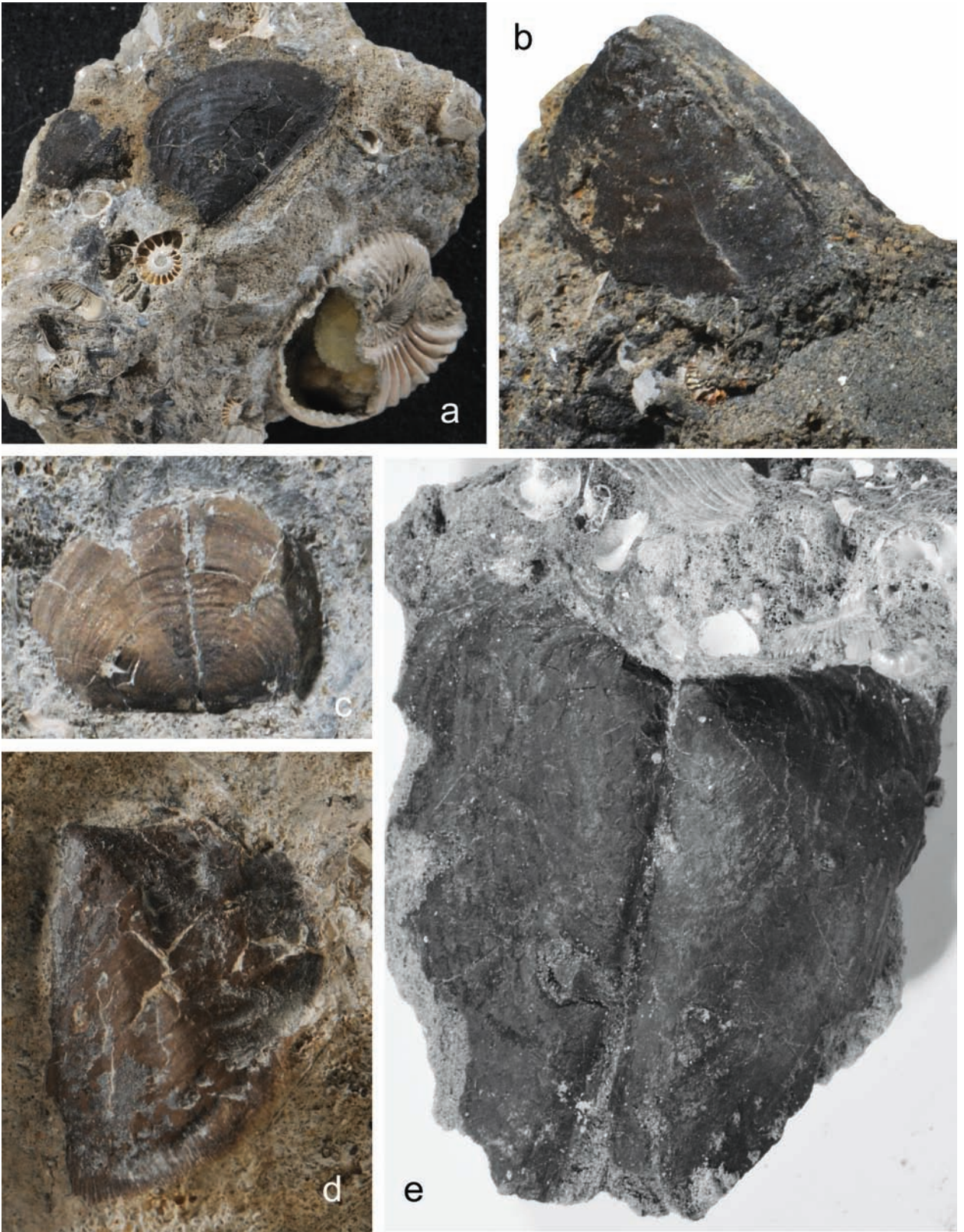


Fig. 13.



Fig. 14. Smaller praestriptychi (length of symphysis 12 mm each) presumably of a microconch *Sigaloceras calloviense* from the Lower Callovian (Calloviense Subzone) of Znamenka. **a** – MAa-596. **b** – MAa-622b with preserved remnants of a white calcareous coating.

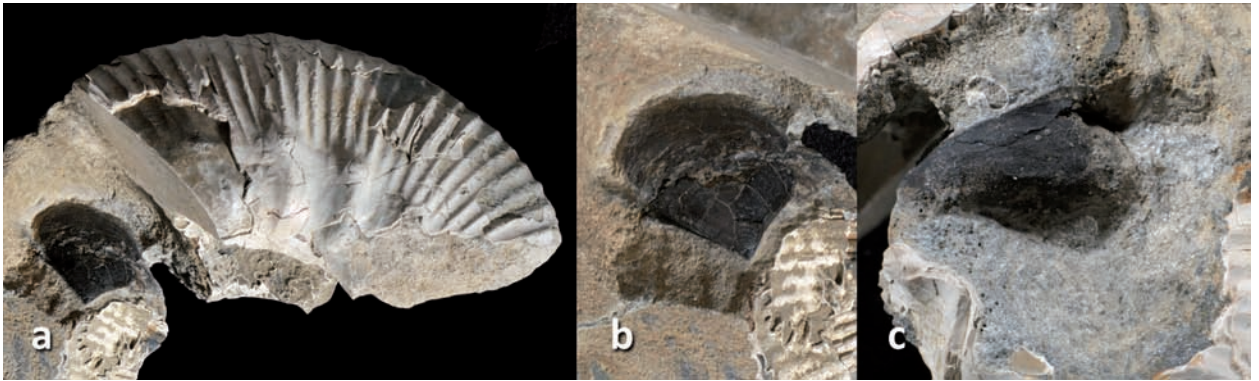


Fig. 15. Complete jaw apparatus of a *Kepplerites*, washed into the body chamber of a larger specimen of *Kepplerites galilaei* from the Galilaei Subzone of Znamenka. **a** – Fragment of the body chamber, length: 12.5 cm. **b** – Right valve of the praestriptychus (length of symphysis 23 mm. **c** – upper jaw element on the reverse side of the aptychus (length 19 mm).

Fig. 17. Isolated upper jaw elements possibly belonging to the kosmoceratids *Kepplerites* and *Sigaloceras* from the Lower Callovian. **a** – From Makaryev North in dorsal view, MAa-551, length 7 mm. **b** – From Makaryev North associated with a perisphinctid ammonite in latero-frontal view MAa-577, length 18 mm. **c-d** – From Znamenka in dorsal and latero-frontal view, length 18 mm, symphysis 5 cm, width 6.2. Its width/length-index of 62 % fits with macroconch species of *Kepplerites* and *Sigaloceras*, respectively.



Fig. 16. Complete, 22 mm long jaw apparatus MAa-545 of a macroconch *Keplerites* from the Calloviense Subzone of Znamenka. **a** – Left valve of the praestriptychus and its symphysis. **b** – Two valves of the aptychus (foreground of the photograph) enclose the wings of the upper jaw, lateral view. **c** – Wings of the upper jaw in the dorsal view.

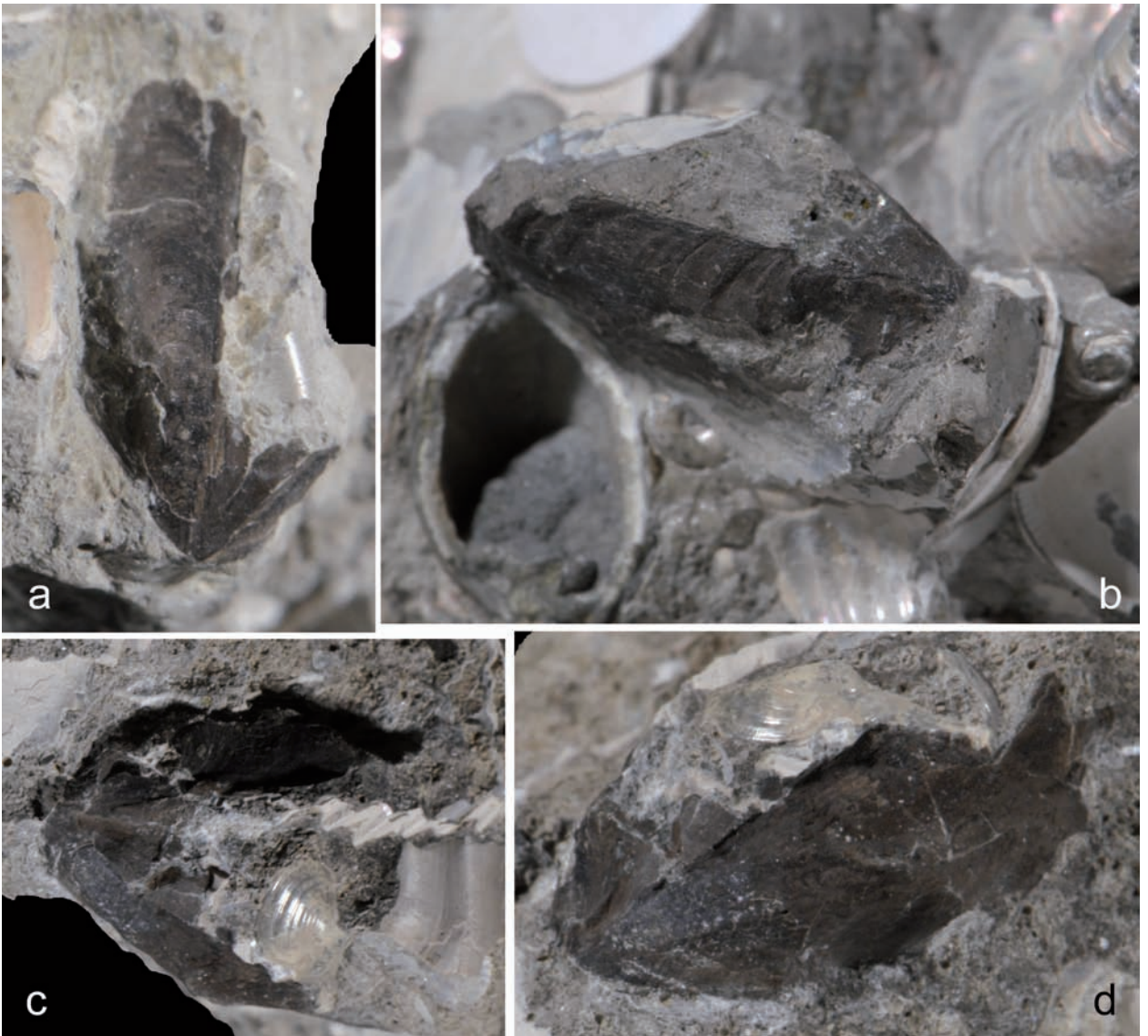


Fig. 17.

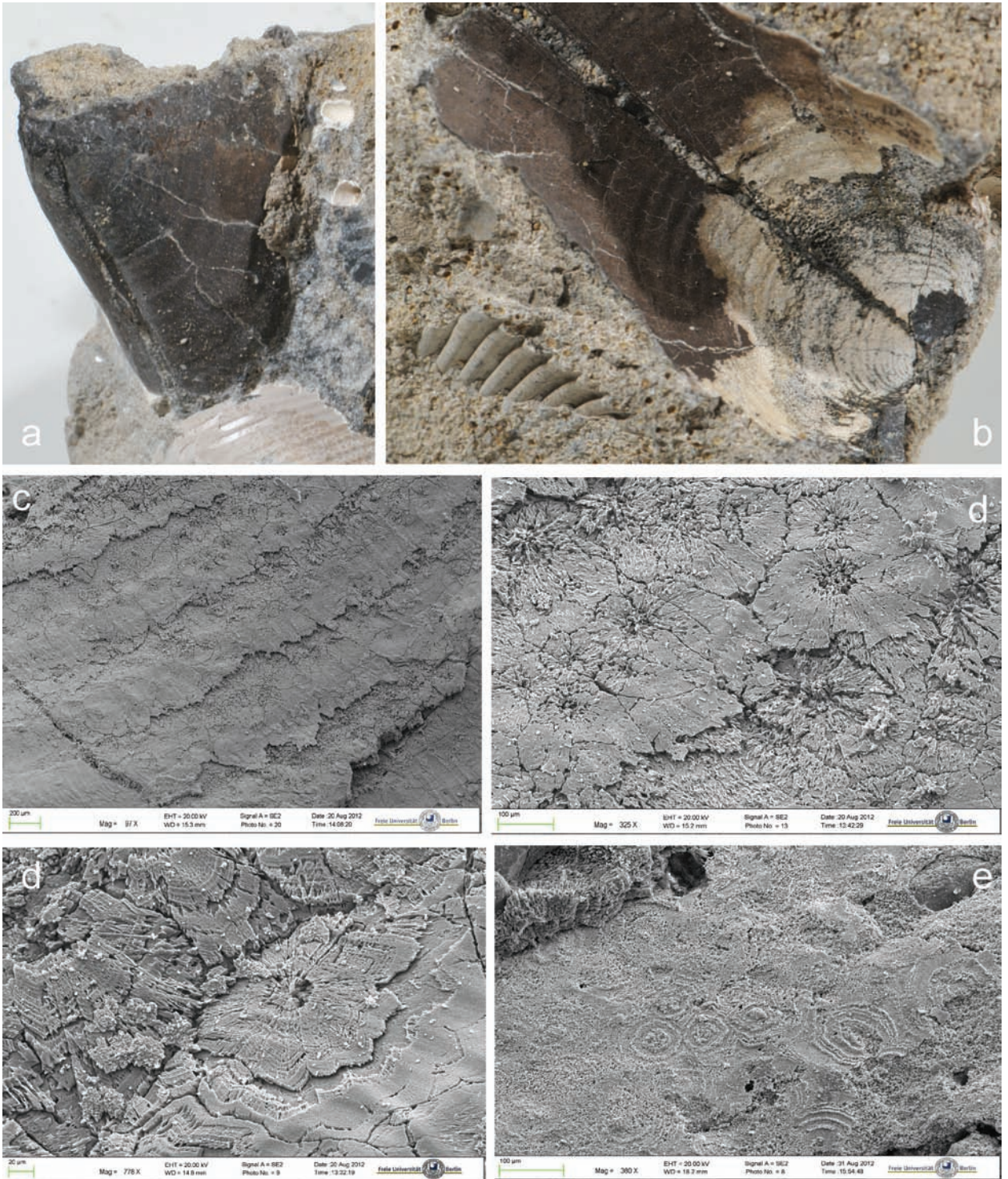


Fig. 18. Bivalved praestriptychus (MAa-614) from the Lower Callovian of Znamenka, length of symphysis 23 mm. **a** – The organic layer preserved on the part. **b** – The thin calcareous coating remains at the counterpart. **c–e** – SEM-pictures of the lamellar structure of the calcareous coating; each layer is built of flattened calcitic spherulites. **f** – Growth pattern of each spherulite of the calcareous coating imprinted on the surface of the organic outer lamella of aptychus MAa-645.

the ammonite, which shows the height of 33 mm near the aperture. In spite of its correct orientation with the anterior part facing forwards, we presume that the jaw apparatus did not belong to this conch of *Keplerites*, but was displaced into the empty body chamber during deposition. No relicts of the calcareous coating are visible on the outside of the black aptychus valve. The corresponding upper jaw element consists of two long lateral wings (19 mm long and up to 11 mm wide in the anterior part). The anterior parts of both wings are connected by a 3 mm long bridge with a small median longitudinal furrow. No rostrum or hood is recognizable.

The second jaw apparatus is 22 mm long and was found isolated in a nodule of the Calloviense Subzone from Znamenka (MAa-545, Fig. 16). The bivalved aptychus overlaps the upper jaw element. The left valve of the praestriptychus is preserved completely (length of symphysis about 20 mm, width 15 mm → width/length-ratio 75 %), while the right valve is partly removed in order to exhibit the upper jaw. No relicts of the calcareous coating are present on the outer surface. The upper jaw element is 22 mm long and consists of two wings. The small connecting bridge at the anterior part is damaged and therefore not recognizable. Like the previous specimen, this jaw apparatus has no rostrum. Isolated upper jaw elements of this type were also been found (Fig. 17).

5.3. Calcification of aptychi

A very thin calcitic coating, only about 100 µm thick, covers the outer surface of the black, presumably originally chitinous, outer lamella of the praestriptychi of *Keplerites*/*Sigaloceras*. This coating is often lost (Fig. 18a) probably before embedding into the sediment rather than by diagenetic dissolving, because of the excellent preservation of the associated original aragonitic shells. The organic lamella alone is easily deformed and sometimes crumbled (Fig. 13.5). SEM exhibits the lamellar structure of the calcareous coatings. Each layer (about 10-30 µm thick) is built of flattened, laterally intergrown spherulites of diameters of 100 to 400 µm (Fig. 18). The radially arranged crystals show an episodic growth. These concentric crystallites of the calcareous coating leave imprints on the surface of the organic outer lamella (Fig. 18.6). This microstructure differs from those hitherto known (SCHINDEWOLF 1958; MICHALIK 1996), but shows similarities with the aragonitic coatings of the lower jaws of the Cretaceous desmoceratoid *Damesites*, figured by TANABE et al. (2012).

5.4. Perisphinctid praestriptychus

We found only one elongated praestriptychus that nearly fits the apertures of the perisphinctids *Proplanulites* and *Homoeoplanulites* (width/length-indices between 40 and 50 %). The first in situ finding of an aptychus within the bodychamber of *Proplanulites* was described by ROGOV & GULYAEV (2003), who showed correspondence between aptychus and the whorl-section (width/length-index 52%). Examination of this specimen (holotype of *Praestriptychus koenigi* ROGOV & GULYAEV, hosted at the Paleontological Institute of the Russian Academy of Sciences Nr.GGM 571-2), revealed remains of the upper jaw (Fig. 20). Unfortunately, its morphology is not recognizable.

A large valve of praestriptychus (about 3.5 cm long) found in the body chamber of a small *Elatmites* sp. in the Enodatum Subzone of the Makaryev North locality and exhibits strong subconcentric growth lines (Fig. 21). This horizon yielded only small kosmoceratid specimens (*Sigaloceras enodatum*) besides perisphinctids. Therefore, it is attributed rather to a peri-

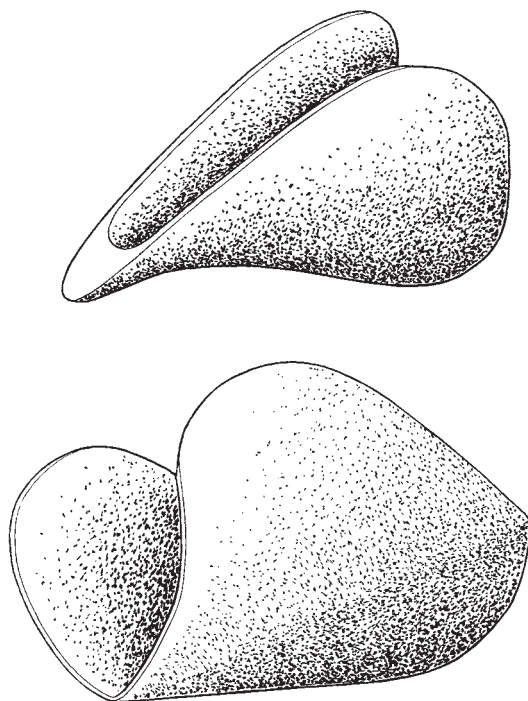


Fig. 19. Reconstruction of the primitive jaw apparatus of the kosmoceratids *Keplerites* and *Sigaloceras* with a praestriptychus and upper jaws, which consist only of the inner lamella forming long lateral wings. Left lateral view (drawing by M. BULANG-LÖRCHER).

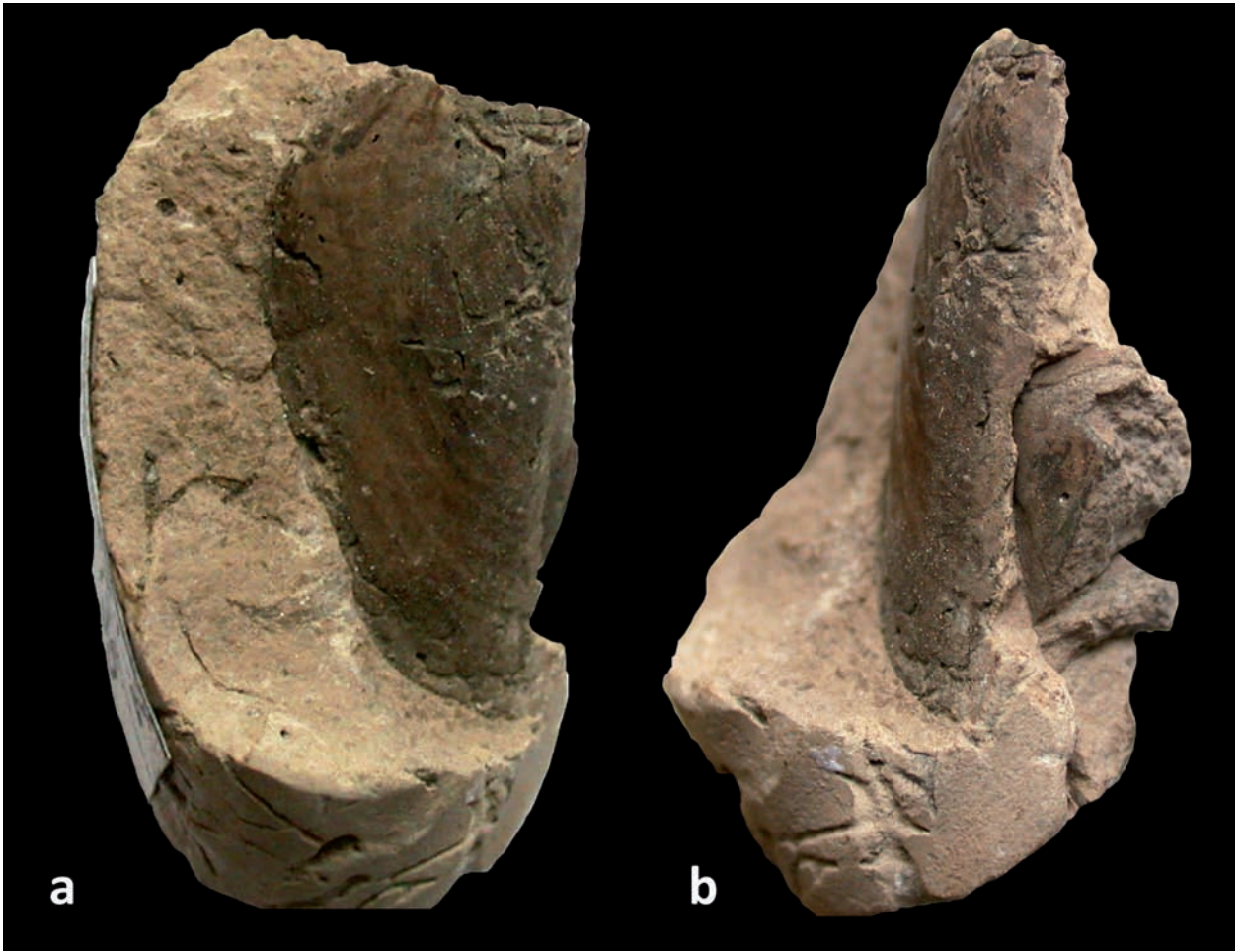


Fig. 20. The *Praestriptychus koenigi* figured by ROGOV & GULYAEV (2003) within the bodychamber of *Proplanulites koenigi* (SOWERBY) from the Lower Callovian of the Kursk Region. The width/length-index of the aptychus is 52 %. **a** – lateral view of the right valve. **b** – dorsal view with remnants of the upper jaw overlapped by the 2.3 cm long aptychus valve (photograph by D. FUCHS).

sphinctid macroconch ammonite. The relatively small width/length-ratio of about 52 % corresponds with the praestriptychus of *Proplanulites* found *in situ* by ROGOV & GULYAEV (2003).

6. Descriptions of coleoid jaw elements

The first report of isolated three-dimensionally preserved Callovian coleoid jaw elements was given by DZIK (1986), who described two types of upper jaw elements in calcareous concretions from Łuków, Poland, and interpreted as belonging to belemnites. Our material contains different jaw elements, particularly from the Makaryev North and Znamenka localities.

The upper jaws exhibit a more or less prominent hood with a pointed rostrum which projects over the inner lamellae. The upper jaw terminology used here follows CLARKE (1986). We also describe lower coleoid jaw elements of uncertain systematic position (Figs. 24–26).

- An incomplete upper beak hood was found by A. STUPACHENKO in the Enodatium Subzone of Makaryev North (Fig. 22). It is 15 mm long, slightly curved and pointed, showing a small median ridge. The rostral tip is pointed. An inner lamella consisting of crest and lateral wall is not preserved in the two coleoid upper jaws; it was presumably



Fig. 21. Incomplete praestriptychus valve MAa-549 (length 3.5 cm) probably by chance deposited in the bodychamber of a small *Elatmites* sp. from the Enodatium Subzone of Makaryev North.

lost during the taphonomy. The angle of the jaw in dorsal view is 51° . In lateral view, the configuration of the sinus between the rostrum and the protruding lateral wings is not recognizable because of its incomplete preservation, but the rounded jaw angle seems to be more than 100° . The long and acute rostrum resembles many modern decabrachiate and octobrachiata coleoids (XAVIER & CHEREL 2009) and also fossil jaws of *Hibolithes* figured and described by KLUG et al. (2010) from the Kimmeridgian Nusplingen Plattenkalk as well as the presumed belemnite jaws of types A and B (*Aulacoteuthis* or *Cylindroteuthis*) described by DZIK (1986).

- A second type of upper jaw, found at the Enodatium Subzone of Makaryev North (MAa-578, Fig. 23) and of the Calloviense Subzone from Znamenka (MAa-650), differs from the previous specimen by a shorter rostrum, exhibiting an open angle of 70° . In lateral view, the rounded jaw angle is less than 90° , forming a deep sinus between rostrum and protruding lateral wing. The posterior part of the prominent hood rises far above the crest of the

inner lamella. Thus, the hood remains in the rock matrix while it is crushed. Only the inner lamella is preserved (Fig. 23, right). A similar morphology is shown by the giant upper jaws of uncertain affinity from the Early Cretaceous described as *Yezoteuthis* by TANABE et al. (2006).

- One isolated coleoid lower jaw element MAa-611, 7 mm broad and 5 mm long, has been found in Makaryev North, associated with the perisphinctid ammonite *Homoeoplanulites* sp. (Fig. 24). The characteristic protruding lateral wings are narrow; the subquadratic hood is broad and short. The rostral tip is tiny. The overall morphology corresponds with the lower jaws of modern octo- and decabrachiata coleoids and a similar morphology may have characterized the presumed common ancestors of both groups, as well as the Belemnitida (FUCHS 2006). Therefore, an affinity with belemnites (possibly *Pachyteuthis*), which are also represented by upper jaws within the same sediments and the same locality seems likely. The lower jaw resembles that attributed to the Late Jurassic vampyromorph *Trachyteuthis* by KLUG et al. (2005), phyleti-

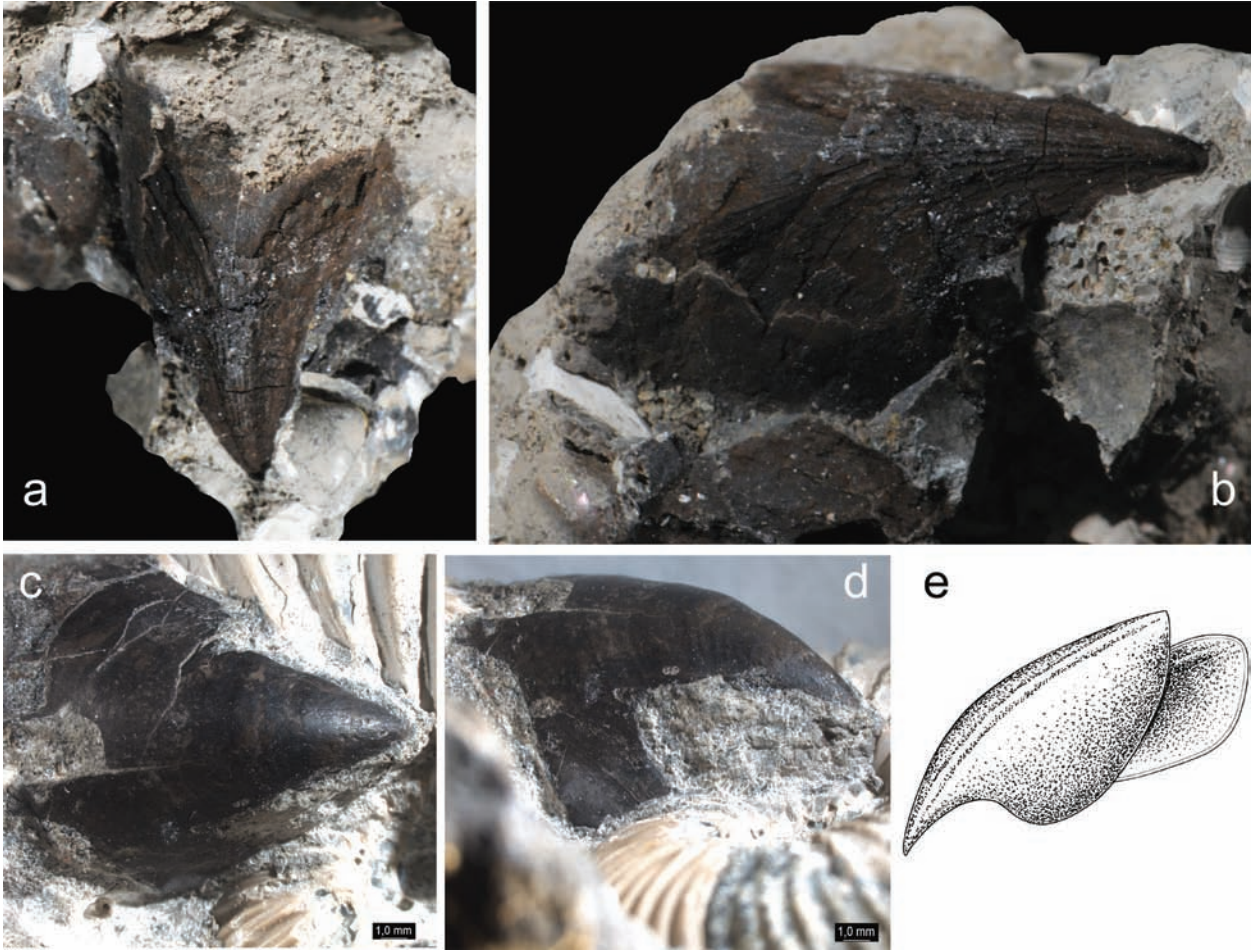


Fig. 22. Two upper jaws presumably of a belemnite, with small pointed rostrum in dorsal and lateral views. **a, b** – MAa-579, length 15 mm, Enodatium Subzone from the Makaryev North locality. **c, d** – Specimen MAa-653, length 16 mm, Calloviense Subzone of Znamenka. **e** – Reconstruction of the jaw (drawing by M. BULANG-LÖRCHER).

cally positioned as a separate lineage near the root of the modern cirroctopods (FUCHS 2009). The lower jaw of the modern cirroctopods differs from more derived jaws of the Octopodida by widely open outer lamella, paired wings prominently expanded posteriorly, and a broad hood (NAEF 1922; CLARKE 1962, 1986; CLARKE & MADDOCK 1988; KUBODERA 2000; NEIGE & DOMMERGUES 2002). By contrast, in *Vampyroteuthis infernalis*, the extant representative of the most basic group of octobrachiata Vampyromorphida, the lower jaw is large and shovel-like, similar to the lower jaw of the nautilids (KAISER & LEHMANN 1971; KLUG et al. 2005).

- Other small (up to 1 cm) shovel-like jaw elements bear only short posteriorly expanded wings re-

sembling non-mineralized conchorhynchi of nautiloids. Some show a more or less subquadratic outline (type A, Fig. 25); some are elongated (type B, Fig. 26). Specimens of type A are characterized by a broad hood with a prominent rostrum. TANABE et al. (2008) described similar but larger jaws from the Upper Cretaceous of Vancouver Island and Japan under the names *Nanaimoteuthis* and *Paleocirroteuthis*. They were classified in the Cirroctopodida YOUNG, 1989, the lineage probably rooted in the Early Jurassic teudopsids (HAAS 2002; FUCHS 2009) which is characterized by a successive reduction of the median field of the gladius. Therefore, the lower jaws of type A may be attributed to the *Teudopsis*–*Muensterella* lineage.

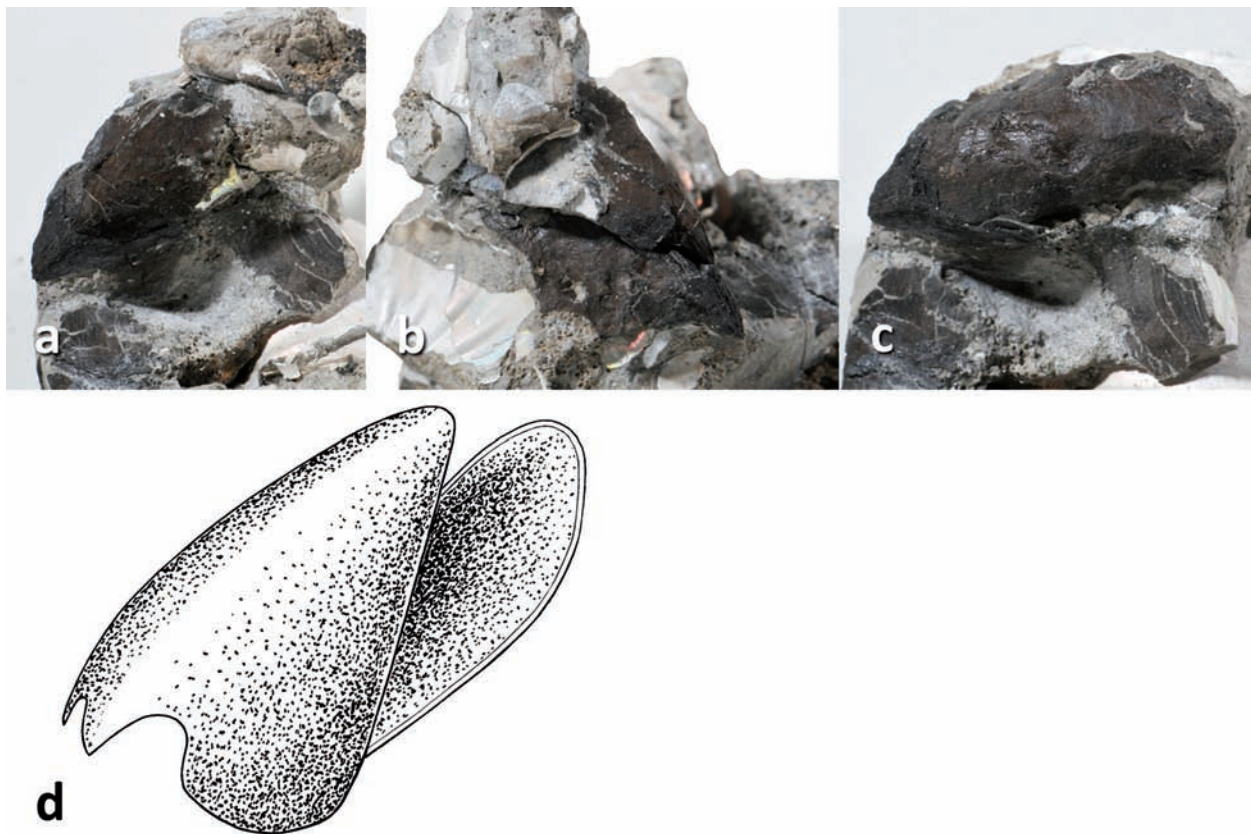


Fig. 23. Upper jaw MAa-578 of a coleoid of unknown affinity from Makaryev North (Enodatum Subzone). **a, b** – Dorso-lateral and dorsal view. **c** – The removed hood expose the inner lamella (length 2 cm). **d.** Reconstruction (drawing by M. BULANG-LÖRCHER).

In the type B of small lower coleoid jaws (Fig. 26) the elongated jaw elements are broader at the posterior than at the anterior end. The outer lamella forms a prominent convex hood with a pointed rostral tip that protrudes only weakly over the anterior biting edge. The flattened lateral wings are weakly expanded. The short inner lamella does not project over the outer lamella. TANABE & HIKIDA (2010) introduced a Late Cretaceous species of *Nanaimoteuthis* showing (except of the size) a similar morphology. Thus, we attribute the lower jaws of type B to the vampyromorph coleoids.

7. Discussion and conclusions

Two different types of aptychi occur within the kosmocerotids, the praestriptychi and the granulptychi (= kosmogranulptychi sensu ROGOV 2004). For the first time, TRAUTH (1930, pl. 5, Fig. 17) attributed the *in situ* finding of an aptychus of *Sigaloceras calloviense*

by NIKITIN (1884) (also from the Kostroma Region, near Manturovo) to praestriptychi and named it *Praestriptychus kostromensis*. Granulptychi with irregular pustulation of their outer surfaces characterize the genus *Kosmoceras* WAAGEN and seem to be a derived morphotype within the kosmocerotid lineage, whereas the praestriptychus represents a primitive state (ENGESER & KEUPP 2002). An analogous development happened within the perisphinctid lineage, in which the basal groups are characterized by praestriptychi, and the derived species of the Late Jurassic (e.g. *Subplanites* SPATH) by similar “granulptychi” with regular rows of granules. On account of the at least diphyletic origin, SCHWEIGERT (2000) splitted the parataxonomic genus *Granulptychus* TRAUTH into the Callovian *Granulptychus* TRAUTH, 1930 s.str. (type species: *G. suevicus* MOORE & SYLVESTER-BRADLEY, 1957) and the Late Jurassic *Strigogranulptychus* SCHWEIGERT, 2000 (type species: *S. planulati* (QUENSTEDT), see TRAUTH



Fig. 24. Coleoid lower jaw element MAa-611 (width 7 mm, length 5 mm) possible of a belemnite. Endodatum Subzone from Makaryev North. **a** – Ventral view. **b** – Ventrolateral view.

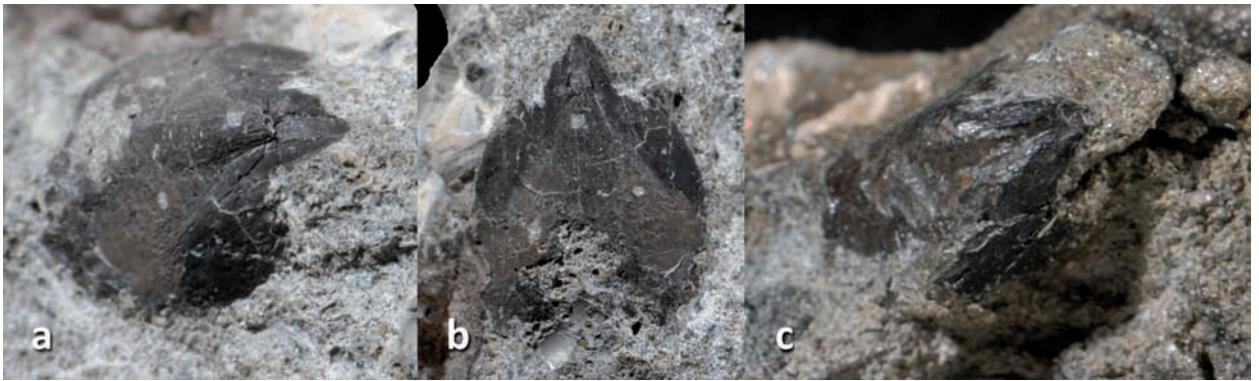


Fig. 25. Shovel-like lower jaws type A (outer lamella) of presumed paleocirroctopod affinity. **a, b** – MAa-595 (10 mm) from the Calloviense Subzone of Znamenka. **c** – MAa-552 (9 mm) from Makaryev South (Elatmae Zone).

1937). Generally, the kosmoceratids were classified within the Stephanoceratoidea (ARKELL et al. 1957; DONOVAN et al. 1980). A systematic classification of the kosmoceratids within the Perisphinctoidea, based only on the presence of similar granulaptychi (ENGESER & KEUPP 2002), can no longer be upheld.

At least with the reduction of hoods (rostra) of the upper jaw elements of aptychophoran ammonites, a functional adaptation of the jaw apparatus was com-

pleted. But the trend to a gradual reduction of the biting function started much earlier in some anaptychophoran taxa. Thus, the rostrum of the flattened hood, still prominent in the Early Liassic *Asteroceras*, has been reduced to a tiny tip in the middle Liassic *Pleuroceras* (Fig. 1). Its complete reduction is associated with the aptychophoran architecture, established in the Late Liassic. Therefore, we propose a microphagous or planktrophic behaviour for most aptychophoran ammonites



Fig. 26. Elongated, shovel-like lower jaws of probable vampyromorphic affinity from the Calloviense subzone of Znamenka. **a** – Outer lamella MAA-585 (length 6 mm). **b, c** – After removal of the hood, the inner lamella is visible, MAA-630a (length 10 mm) and MAA-627 (length 6 mm).

(KEUPP 2000; DOGUZHAeva & MIKHAILOVA 2002; WIPICH & LEHMANN 2004; SCHWEIGERT 2009; KRUTA et al. 2011). In combination with the calcification of aptychi, their enlarged outer lamella became stabilized. In order to withdraw the body into the body chamber, the rigid and enlarged lower beak had to become bivalved and foldable along the median ligament (= symphysis). The function of the aptychophoran jaw apparatus is still under discussion. DZIK (1981, 1986) thought that the lower jaws of ammonoids functioned primarily as opercula and got secondarily and additionally biting function during phylogeny. His idea based on calcareous aptychi in Silurian nautiloids (TUREK 1978; STRIDSBERG 1984; EDGEComb & CHATTERTON 1987), but it contradicts the primitive character state of the jaw apparatus of all cephalopods. Therefore, LEHMANN & KULICKI (1990) inverted the functional succession and postulated also a double function, but with an original biting function and they derived secondarily the additional opercular protection against enemies (SCHINDEWOLF 1958). SEILACHER (1993) proposed a possible way to transform the lower jaw into an operculum, because of a functional change. Recently some authorities proposed a specialized feeding function of the aptychi in connection with the strong radulae bearing long teeth (SCHWEIGERT 2009; KRUTA et al. 2011). The opercular function of aptychi cannot be dismissed for the following reasons:

1. The aptychi outlines covariate with the ontogenetic change of whorl sections (LEHMANN 1972).

2. The often observed growth disturbances of aptychi due to mechanical injuries of their aboral part (KEUPP 2000, 2012) are hardly due to action of parasites (SCHWEIGERT 2009) and they are not comparable with damage by hard parts of the prey (mostly crustaceans) on the modern nautilus jaws.

The diverse spectrum of isolated and three-dimensionally preserved coleoid jaws from the Callovian is consistent with the evidence on diversity of the Middle Jurassic cephalopod faunas based on their fossil conchs and gladii. Some of the specimens from the Russian Callovian are attributed to belemnoids; others seem to belong to vampyromorphs, possibly also to the cirroctopod lineage.

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