Swiss J Palaeontol (2015) 134:281–287
DOI 10.1007/s13358-015-0082-1

Soft-tissue preservation in the Middle Jurassic ammonite *Cadoceras* from Central Russia

Aleksandr A. Mironenko[1]

Received: 19 February 2015 / Accepted: 19 May 2015 / Published online: 21 July 2015

Abstract The findings of fossilized ammonite soft tissues are extremely rare, so each specimen may be important for understanding the anatomy of these cephalopods. This paper deals with soft tissue fragments and imprints preserved in the rear part of the body chamber of the Middle Jurassic ammonite *Cadoceras stupachenkoi* from Central Russia. At the base of the body chamber of this ammonite in front of the last septum, a mantle fragment with clearly visible longitudinal fibers and imprints of the palliovisceral ligament are preserved. In front and slightly to the side of the mantle fragment, a small area with branched structures is located; probably, these structures are fragments of gills. In general, the structure of the soft tissues in the rear part of the ammonite body looks very similar to that of modern nautilids, with one exception: mantle fibers are not directed forward as observed in *Nautilus*, but to the mid-ventral line, probably to the ventral muscle.

Keywords Ammonoids · Middle Jurassic · Soft tissues · *Cadoceras* · Russia

Introduction

The study of fossilized soft tissue allows better understanding of the anatomy and biology of ancient animals. Findings of soft tissues are particularly important for the study of completely extinct groups, such as ammonoids, which have left no descendants. Unfortunately, fossilized ammonoid tissues are extremely scarce and many parts of the ammonoid body (e.g., arms, hyponome) have never been found. Nevertheless, several non-mineralized organs of ammonoids such as gills, oesophagus, digestive tract, cephalic cartilage with questionable eye capsules, mantle tissues, and siphuncular blood vessels were found and described (Lehmann 1967, 1979, 1985; Lehmann and Weitschat 1973; Riegraf et al. 1984; Tanabe et al. 2000; Doguzhaeva et al. 2004, 2007; Wippich and Lehmann 2004; Klug and Jerjen 2012; Klug et al. 2012). Mantle tissues can be considered as one of the rarest known types of ammonite soft tissues: fragments of the mantle with preserved muscle structure have been described only twice, both times in the Late Triassic ammonoid *Austrotrachyceras* (Doguzhaeva et al. 2004, 2007). The structures which are located at the rear part of the ammonoid body chamber, such as ventral and dorsolateral muscle scars are well studied (Doguzhaeva and Mutvei 1996; Klug et al. 2007), but usually, only hard parts of the shell or occasionally unstructured phosphatized remnants (Klug et al. 2007) rather than the soft tissues itself are preserved.

This article describes the preserved fragment of mantle tissue, imprints of the palliovisceral ligament and putative remnants of gills, found in the rear part of the body chamber of the Middle Jurassic (Lower Callovian) ammonite *Cadoceras stupachenkoi* from Central Russia. The findings of soft tissues and their imprints allow better understanding of the structure of the rear part of the ammonoid soft body.

Materials and methods

The specimen studied herein is a Middle Jurassic ammonite *Cadoceras stupachenkoi* (Fig. 1). It is a cadiconic macroconch, which was found in Middle Jurassic deposits

✉ Aleksandr A. Mironenko
paleometro@gmail.com

1 Kirovogradskaya st. 28, 117519 Moscow, Russia

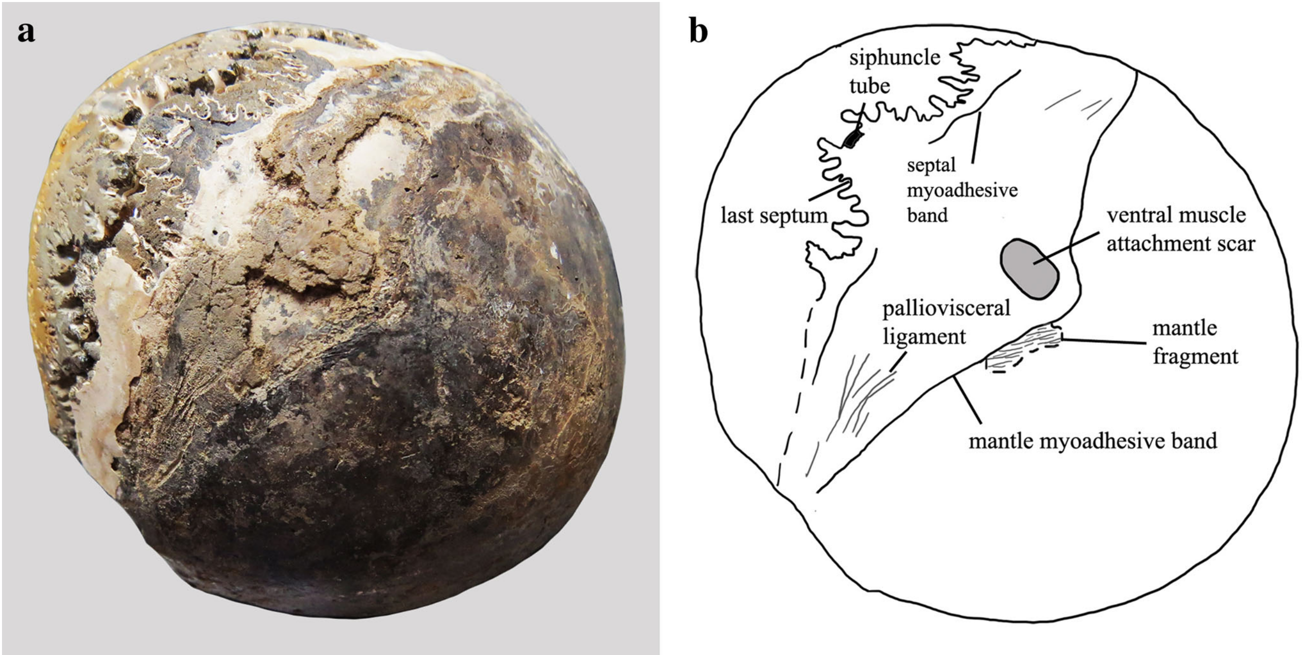

Fig. 1 *Cadoceras stupachenkoi* with fossilized fragments of the soft tissues. **a** Overview over the studied specimen MSU 119/1. **b** Scheme of the specimen MSU 119/1

(Lower Callovian, Elatmae Zone, Stupachenkoi Subzone) in the Unzha-river region, not far from the town of Makaryev in Russia (Keupp and Mitta 2013: Fig. 2). The specimen comes from a layer of calcareous sandstone nodules, often phosphatized, with inclusions of pyrite (see Keupp and Mitta 2013 for taphonomy and geological setting). The diameter of the specimen is about 10 cm. Only the posterior part of the body chamber with a small fragment of the phragmocone is preserved. The aragonitic shell layers were partially preserved, but removed for examination of the internal mould of the body chamber. The specimen is housed at Moscow State University Museum, Russia, with the collection number MSU 119.

The ammonite was studied using a binocular microscope and a scanning electron microscope SEM TESCAN// VEGA with a BSE detector at the Paleontological Institute of the Russian Academy of Science in Moscow. It was examined in an uncoated state in low vacuum conditions at 30 kV.

Results

A poorly preserved ventral attachment scar and the anterior border of the annular elevation are located at a distance of 14 and 30 mm from the last siphuncle tube, respectively (Fig. 1). Along the front edge of the annular elevation near the ventral muscle attachment scar, a small, presumably carbonized, piece of mantle tissue is located. It is 3–7 mm wide, dark grey, and visible to the naked eye. The binocular observation allows to recognize long branched longitudinal fibers (Fig. 2). This mantle tissue is very thin with only one layer of muscle fibers. All these fibers are directed to the mid-ventral line of the body chamber. On the SEM images, the remnants of dark carbonized tissues and small fibers branching off from the large muscles are visible (Fig. 3).

Behind the anterior border of the annular elevation (mantle myoadhesive band) and the mantle fragment, imprints of the palliovisceral ligament are located (Fig. 4). This area shows a double-layered structure: there are small transverse stripes on the top layer and beneath them rough and sharp transverse folds (Fig. 4b). There are no fossilized soft tissues in these rough folds, but imprints of these tissues composed of middle-grained sandstone, which fills the body chamber.

The third type of preserved soft tissues is small branched feather-like structures located in front of the annular elevation. They are very tiny and mostly grouped in small cluster, the size of the entire cluster is not more than 1 cm^2 (Fig. 5a, b). Nearby, separate branched structures are located outside of this cluster at the rear part of the body chamber. However, in the cluster, the structures are better preserved and concentrated. The branched structures are arranged in several layers. In SEM images, small transverse ridges are visible in these objects (Fig. 5c, d). These structures resemble small parts of gills.

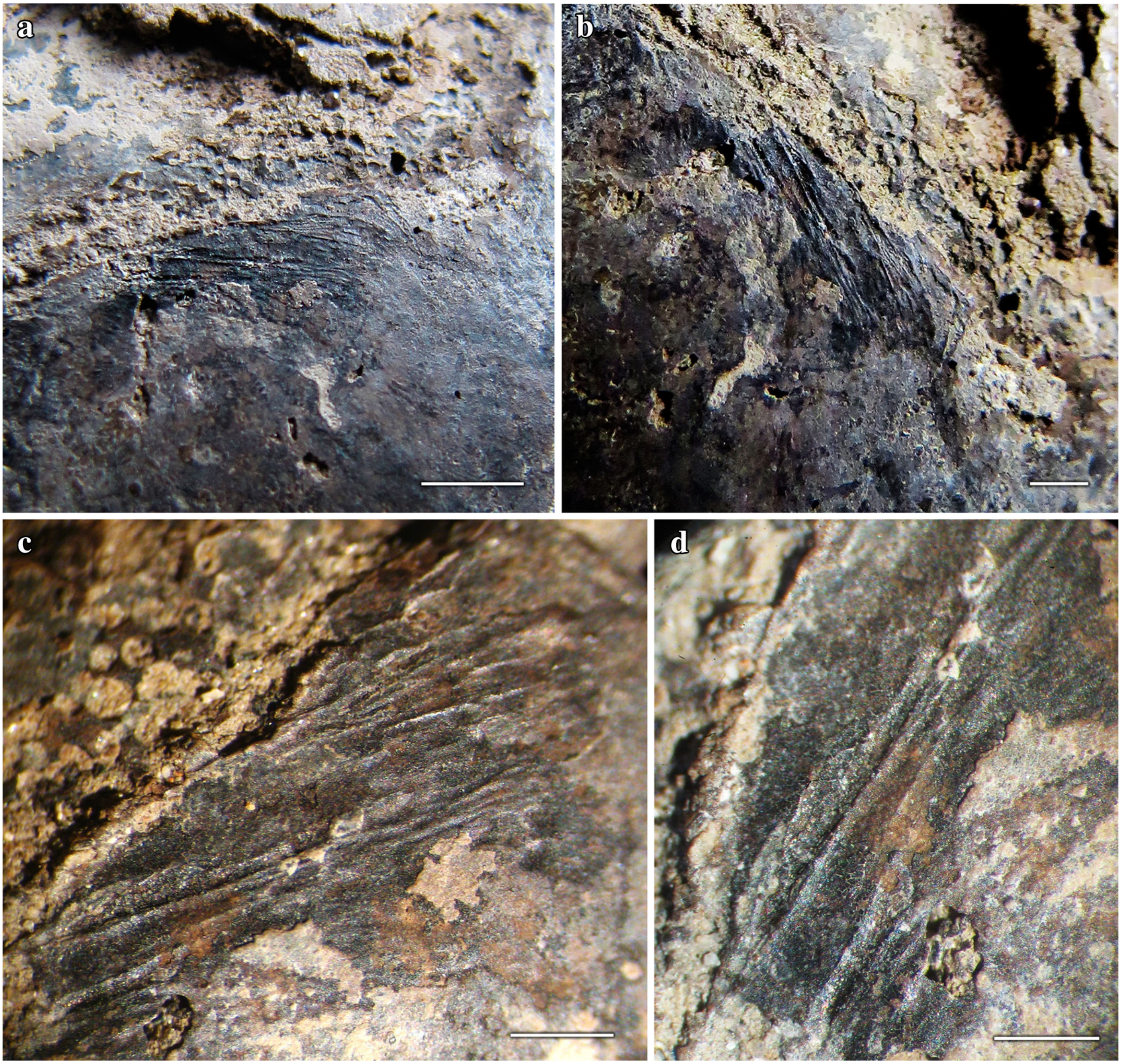

Fig. 2 Fragment of the mantle tissue of the *Cadoceras stupachenkoi.* **a** Overview of the mantle fragment. *Scale bar* 2.5 mm. **b**, **c**, Longitudinal muscle fibers in the mantle fragment. *Scale bars* 1 mm. **d** Two muscle fibers. *Scale bar* 0.5 mm

Discussion

Mantle tissue and imprints of the palliovisceral ligament

Inside the ammonite body chambers, not only ammonite body remnants can be found, but also the fragments or intact shells of other animals, which lived inside empty ammonite shell on the sea bottom, or were transported into the empty shell by sea currents (Fraaye and Jäger 1995a, b; Klompmaker and Fraaije 2012; Vullo et al. 2009). In several cases, the clusters of small invertebrate fragments were interpreted as ammonite crop content (Keupp 2000; Ritterbush et al. 2014). In addition, different epicoles can be attached to the inner walls of the empty ammonite body chamber (Klug and Korn 2001). The scavengers which ate ammonite bodies or animals which lived inside empty shells left their traces, e.g., burrows, fecal pellets, etc., (Fraaye and Jäger 1995a). All of these findings can be confused with the remains of the ammonite soft body. However, there is no doubt that the fossilized fragment in the *Cadoceras* body chamber is in fact part of the

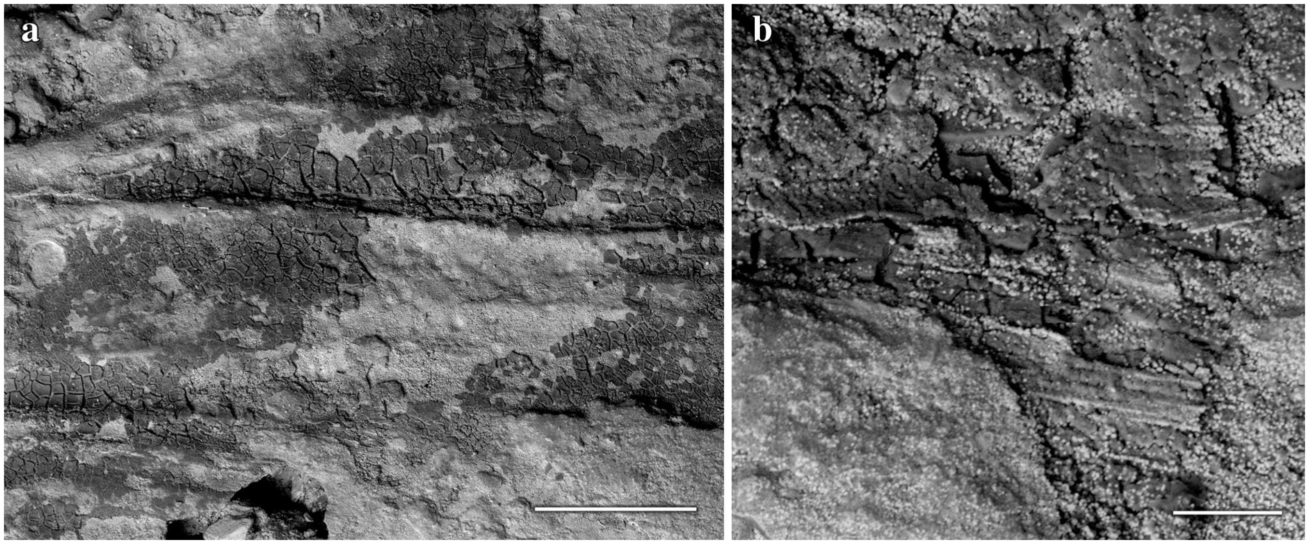

Fig. 3 SEM images of the mantle tissue fragment of the *Cadoceras stupachenkoi*. **a** Large longitudinal fibers and carbonized tissue among them. *Scale bar* 500 µm. **b** Sets of small fibers. *Scale bar* 50 µm

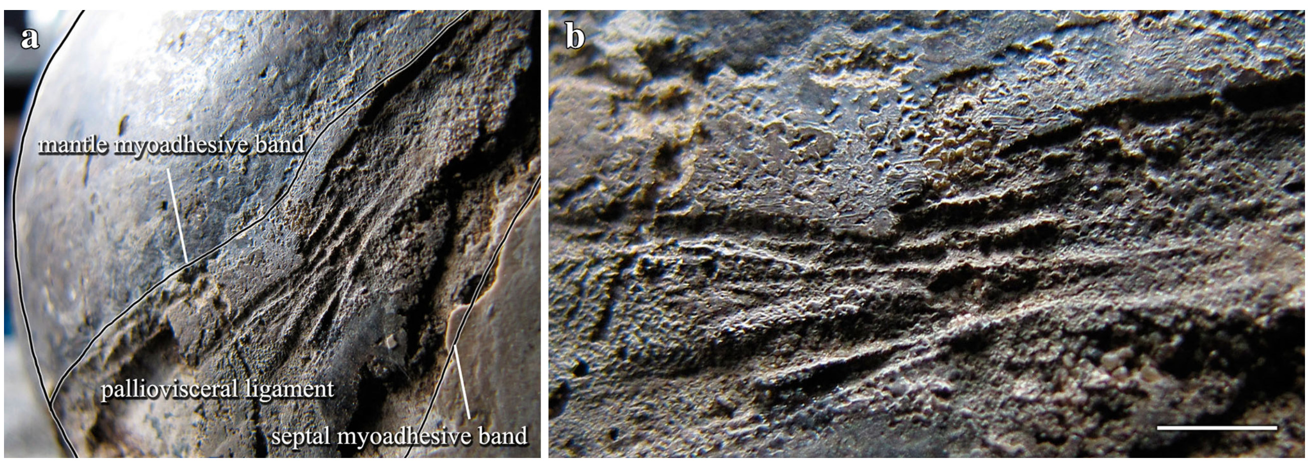

Fig. 4 Area of the palliovisceral ligament. **a** Overview over the area of the palliovisceral ligament. **b** Detail of the sharp transverse folds and small stripes in this area. *Scale bar* 2.5 mm

ammonite mantle (see Allison 1988 for possible mechanisms of soft-tissue fossilization). Its structure (Figs. 2, 3) is very similar to the structure of the longitudinal muscles of fossil coleoids (Allison 1988: Fig. 5B) and mantle muscles of living nautilids (Mutvei et al. 1993: Fig. 9B), but it does not resemble any traces of epicoles or scavengers. Its position on the anterior part of the annular elevation fully corresponds to the attachment area of mantle muscles (Mutvei 1957; Mutvei et al. 1993).

In the mantle tissue fragment of the *Cadoceras*, muscle fibers are directed to the mid-ventral line of the body chamber. In the rear part of the mantle of recent *Nautilus pompilius,* mantle fibers are pointing towards the aperture (Mutvei et al. 1993: Fig. 9B). It appears unlikely that the direction of the fibers in the ammonite is a result of postmortem shifting. Although the shell orientation of the ammonite carcass on the sea floor during the decomposition of its soft tissues is unknown, all preserved soft tissue remnants are located on the right side of the body chamber. Therefore, this side was most likely lower during the burial of the shell. In this case, if the muscles shifted downward under the influence of gravity, they must have shifted to the right side, not to the mid-ventral line of the body chamber as it actually is preserved. Therefore, the preserved orientation of the muscle fibers might represent the syn vivo position. Nevertheless, more material with this kind of preservation is needed to support this hypothesis. Possibly, these muscles were connected to the ventral muscle which was directed forward from the ventral attachment scar, as was earlier suggested by other authors (Jordan 1968; Dagys

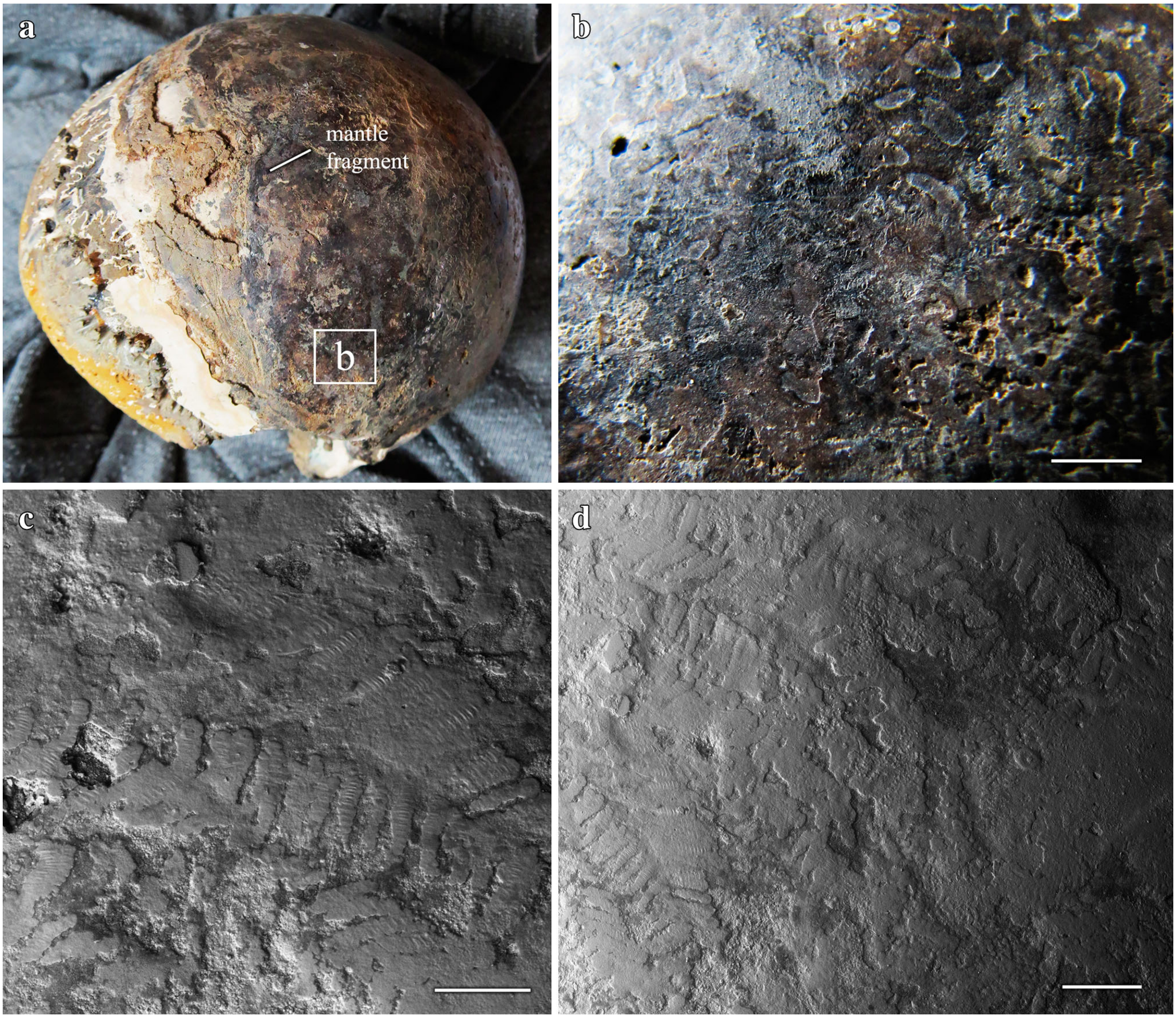

Fig. 5 Gill fragments of *Cadoceras stupachenkoi.* **a** Overview of the specimen with marked location of gill imprints. **b** Detail of the gill imprints. *Scale bar* 2 mm. **c, d** SEM images of the gill imprints. *Scale bars* 250 and 500 µm, respectively

and Keupp 1998). If this orientation of the mantle muscles represents the syn vivo-orientation, it would resemble the connection of the inner mantle layers of coleoids with the ventral mantle adductor muscle (Bizikov 2004). While the coleoid mantle is thick, the ammonite mantle appears to be very thin, containing possibly, only one layer of muscle tissue similar to nautilids. Unfortunately, the direction of the fibers, located far from the central part of the myoadhesive band, remains unknown.

The structure of the palliovisceral ligament of *Cadoceras* resembles that described from nautilids (Mutvei et al. 1993). In general, the entire rear part of the *Cadoceras* soft body is very similar to the corresponding part of the living and ancient Nautilida (see Mutvei 1957, 1964; Mutvei et al. 1993; Klug and Lehmkuhl 2004) with the exception of the ventral muscle attachment structure. As in *Nautilus*, the ammonite mantle, which was attached to the myoadhesive band, is thin, with clearly separate and distinguishable long fibers. However, this similarity does not mean that the front end of the ammonite mantle was identical to the mantle of nautilids. Several ammonite shells have parabolic nodes (Bucher et al. 1996; Doguzhaeva 2012) and adult apertural modifications (e.g., lappets; see Makowski 1962), which have never been observed in modern or ancient nautilids. The presence of such structures in ammonite shells may indicate that the ammonite mantle edge was different from the mantle edge of nautilids and probably was more muscular and complex. However, findings of preserved anterior parts of the mantle are needed to clarify these assumptions; in the specimen studied herein, there are no traces of this part of the mantle.

Presumable ammonite gills

The author considered several versions of the origin of small branched structures located in front of the annular elevation (Fig. 5): imprints of scavenger jaw apparatus, which was used to eat the ammonite mantle; fragments of the mantle tissue; fragments of the gills. The first version, which interprets these structures as bite or radula marks of scavengers, seems to be unlikely due to the shape and layered structure of these objects. The idea that these structures are remnants of decomposed mantle tissue cannot be completely ruled out, but it seems unlikely, since all these objects are about the same size and shape. It is more likely that these fragments are remnants of the ammonite gills. Probably, these gill fragments came to rest on the shell wall after the local decomposition of the mantle.

Structures interpreted as ammonite gills were described several times (Lehmann and Weitschat 1973; Lehmann 1979, 1985). The findings of fossilized gills of coleoid cephalopods are also known (e.g., Reitner 2009). However, the microstructure of fossilized gills has never been depicted and described. In the case of *Cadoceras*, if the objects described herein are actually the remains of gills, they are only small fragments, because the length of each object is about 1–1.2 mm.

Recent Nautilida (*Nautilus* and *Allonautilus*) have two pairs of gills, whereas all coleoids have only one pair. The number of ammonoid gills is still unknown. Shigeno et al. (2008) showed that the two pairs of *Nautilus* gills do not form simultaneously, but successively. This adds additional weight to the hypothesis that earliest cephalopods had one pair of gills (Engeser 1996; Sasaki et al. 2010), whereas, a second pair appeared later during evolution, likely as an adaptation to low concentrations of oxygen in nautilid habitats (Wells et al. 1992). Due to this assumption and closer phylogenetic relationship of ammonoids and coleoids (Engeser 1996; Jacobs and Landman 1993; Kröger et al. 2011; Ritterbush et al. 2014), it is now widely accepted that ammonoids likely have only one pair of gills. Currently, it is impossible to clarify this question by the examination of the herein described *Cadoceras* specimen, as just a few parts of its gills are preserved. However, these fragments can help to clarify the position of the ammonoid gills: they were located (at least their posterior parts) very deep inside the body chamber, not far from the last septum (unless they were translocated post mortem). It may reflect the great length of the mantle cavity of *Cadoceras*. This fact should be taken into account for reconstructions of ammonoid anatomy and calculations of the lifetime orientation of ammonite shells (for recent calculations of *Cadoceras* hatchling see Lemanis et al. 2015).

Conclusions

The fragments of the mantle, gills, and soft tissue imprints preserved in the rear part of the *Cadoceras stupachenkoi* body chamber indicate a similarity of the apical parts of the soft body of ammonoids and nautilids. However, some differences are observed: muscle fibers of the ammonite mantle are not directed forward to the aperture as in *Nautilus*, but to the center of the ventral side, likely to the ventral muscle. The number of ammonite gills remains unknown, but findings not far from the rear part of the mantle of their fragments, indicate a large ammonoid mantle cavity size.

Acknowledgments I am very grateful to Dmitry Buev (Moscow, Russia) for donating the valuable *Cadoceras* specimen. SEM photos were made with the generous help by Roman Rakitov (PIN RAS, Moscow, Russia). I am also very grateful for the important and very helpful comments from Christian Klug (Paläontologisches Institut und Museum, Universität Zürich, Switzerland), René Hoffmann (Ruhr Universität Bochum, Germany), and an anonymous reviewer, their comments helped to greatly improve the article.

References

Allison, P. A. (1988). Phosphatized soft-bodied squids from the Jurassic Oxford Clay. *Lethaia, 21*, 403–410.

Bizikov, V. A. (2004). The shell in Vampyropoda (Cephalopoda): morphology, functional role and evolution. *Ruthenica, Supplement, 3*, 1–88.

Bucher, H., Landman, N. H., Klofak, S. M., & Guex, J. (1996). Mode and rate of growth in ammonoids. In N. H. Landman, K. Tanabe, & R. A. Davis (Eds.), *Ammonoid paleobiology* (Vol. 13, pp. 408–461)., Topics in Geobiology New York: Plenum Publishing Corporation.

Dagys, A. S., & Keupp, H. (1998). Internal ventral keels in Triassic ceratid ammonoids: description and functional interpretation as muscle scars. *Zeitschrift der Deutschen Geologischen Gesellschaft, 149*, 81–89.

Doguzhaeva, L. A. (2012). Functional significance of parabolae, interpreted on the basis of shell morphology, ultrastructure and chemical analyses of the Callovian ammonite *Indosphinctes* (Ammonoidea: Perisphinctidae), Central Russia. *Revue de Paléobiologie, 11*, 89–101.

Doguzhaeva, L. A., Mapes, R. H., Summesberger, H., & Mutvei, H. (2007). The preservation of body tissues, shell, and mandibles in the ceratitid ammonoid *Austrotrachyceras* (Late Triassic), Austria. In N. H. Landman, R. A. Davis, & R. H. Mapes (Eds.), *CephalopodsPresent and Past: New Insight and Fresh Perspectives* (pp. 221–237). Dordrecht: Springer.

Doguzhaeva, L. A., & Mutvei, H. (1996). Attachment of the body to the shell in ammonoids. In N. H. Landman, K. Tanabe, & R. A. Davis (Eds.), *Ammonoid paleobiology* (Vol. 13, pp. 44–64)., Topics in Geobiology New York: Plenum Press.

Doguzhaeva, L. A., Mutvei, H., Summesberger, H., & Dunca, E. (2004). Bituminous soft body tissues in Late Triassic ceratitid

Austrotrachyceras. *Mitteilungen aus dem Geologisch Paläontologischen Institut der Universität Hamburg, 88*, 37–50.

Engeser, T. (1996). The position of the Ammonoidea within the Cephalopoda. In N. H. Landman, K. Tanabe, & R. A. Davis (Eds.), *Ammonoid Paleobiology* (Vol. 13, pp. 3–23)., Topics in Geobiology New York: Plenum Press.

Fraaye, R. H. B., & Jäger, M. (1995a). Decapods in ammonite shells: examples of inquilinism from the Jurassic of England and Germany. *Palaeontology, 38*, 63–75.

Fraaye, R. H. B., & Jäger, M. (1995b). Ammonite inquilinism by fishes: examples from the lower Jurassic of England and Germany. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte, 9*, 541–552.

Jacobs, D. K., & Landman, N. H. (1993). *Nautilus*—a poor model for the function and behavior of ammonoids? *Lethaia, 26*, 101–111.

Jordan, R. (1968). Zur Anatomie mesozoischer Ammoniten nach den Strukturelementen der Gehäuse-Innenwand. *Beihefte zum Geologischen Jahrbuch, 77*, 1–64.

Keupp, H. (2000). *Ammoniten—paläobiologische Erfolgsspiralen*. Stuttgart: Jan Thorbecke Verlag.

Keupp, H., & Mitta, V. (2013). Cephalopod jaws from the Middle Jurassic of Central Russia. *Neues Jahrbuch für Geologie und Paläontologie, 270*(1), 23–54.

Klompmaker, A. A., & Fraaije, R. H. B. (2012). Animal behavior frozen in time: gregarious behavior of Early Jurassic lobsters within an ammonoid body chamber. *PLoS One, 7*(3), e31893.

Klug, C., & Jerjen, I. (2012). The buccal apparatus with radula of a ceratitic ammonoid from the German Middle Triassic. In P. Neige, I. Rouget (Eds.), *8th International Symposium. Cephalopods—present and past* (Vol. 45, pp. 1–10)., Geobios,

Klug, C., & Korn, D. (2001). Epizoa and post-mortem epicoles on cephalopod shells—examples from the Devonian and Carboniferous of Morocco. *Berliner geowissenschaftliche Abhandlungen, 36*, 145–155.

Klug, C., & Lehmkuhl, A. (2004). Soft-tissue attachment structures and taphonomy of the Middle Triassic nautiloid *Germanonautilus*. *Acta Palaeontologica Polonica, 49*(2), 243–258.

Klug, C., Montenari, M., Schulz, H., & Urlichs, M. (2007). Soft-tissue attachment of Middle Triassic Ceratitida from Germany. In: R. H. Landman, R. A. Davis, R. H. Mapes (Eds.), *Sixth International Symposium Cephalopods Present and Past. New Insights and Fresh Perspectives* (pp. 205–220). New York: Springer.

Klug, C., Riegraf, W., & Lehmann, J. (2012). Soft-part preservation in heteromorph ammonites from the Cenomanian-Turonian Boundary Event (OAE 2) in the Teutoburger Wald (Germany). *Palaeontology, 55*(6), 1307–1331.

Kröger, B., Vinther, J., & Fuchs, D. (2011). Cephalopod origin and evolution: A congruent picture emerging from fossils, development and molecules. *BioEssays, 33*, 602–613.

Lehmann, U. (1967). Ammoniten mit Kieferapparat und Radula aus Lias-Geschieben. *Paläontologische Zeitschrift, 41*, 38–45.

Lehmann, U. (1979). The jaws and radula of the Jurassic ammonite *Dactylioceras*. *Palaeontology, 22*, 265–271.

Lehmann, U. (1985). Zur Anatomie der Ammoniten: Tintenbeutel, Kiemen, Augen. *Paläontologische Zeitschrift, 59*, 99–108.

Lehmann, U., & Weitschat, W. (1973). Zur Anatomie und Ökologie von Ammoniten: Funde von Kropf und Kiemen. *Paläontologische Zeitschrift, 47*, 69–76.

Lemanis, R., Zachow, S., Fusseis, F., & Hoffmann, R. (2015). A new approach using high-resolution computed tomography to test the buoyant properties of chambered cephalopod shells. *Paleobiology, 41*(2), 313–329.

Makowski, H. (1962). Problem of sexual dimorphism in ammonites. *Palaeontologia Polonica, 12*, 1–92.

Mutvei, H. (1957). On the relations of the principal muscles to the shell in *Nautilus* and some fossil nautiloids. *Arkiv för Mineralogi och Geologi, 10*, 219–253.

Mutvei, H. (1964). Remarks on the anatomy of recent and fossil Cephalopoda. *Stockholm Contributions in Geology, 11*(4), 79–112.

Mutvei, H., Arnold, J. M., & Landman, N. H. (1993). Muscles and attachment of the body to the shell in embryos and adults of *Nautilus belauensis* (Cephalopoda). *American Museum Novitates, 3059*, 1–15.

Reitner, J. (2009). Preserved gill remains in *Phragmoteuthis conocauda* (Quenstedt, 1846-49) (Toarcian, Southern Western Germany). *Berliner paläobiologische Abhandlungen, 10*, 289–295.

Riegraf, W., Werner, G., & Lörcher, F. (1984). Der Posidonienschiefer. Biostratigraphie, Fauna und Fazies des südwestdeutschen Untertoarciums (Lias epsilon). Stuttgart: Enke.

Ritterbush, K. A., Hoffmann, R., Lukeneder, A., & De Baets, K. (2014). Pelagic palaeoecology: the importance of recent constraints on ammonoid palaeobiology and life history. *Journal of Zoology, 292*, 229–241.

Sasaki, T., Shigeno, S., & Tanabe, K. (2010). Anatomy of living *Nautilus*: Reevaluation of primitiveness and comparison with Coleoidea. In K. Tanabe, Y. Shigeta, T. Sasaki, & H. Hirano (Eds.), *Cephalopods—Present and Past* (pp. 35–66). Tokyo: Tokai University Press.

Shigeno, S., Sasaki, T., Moritaki, T., Kasugai, T., Vecchione, M., & Agata, K. (2008). Evolution of the cephalopod head complex by assembly of multiple molluscan body parts: evidence from *Nautilus* embryonic development. *Journal of Morphology, 269*, 1–17.

Tanabe, K., Mapes, R. H., Sasaki, T., & Landman, N. H. (2000). Soft-part anatomy of the siphuncle in Permian prolecanitid ammonoids. *Lethaia, 33*, 83–91.

Vullo, R., Cavin, L., & Clochard, V. (2009). An ammonite–fish association from the Kimmeridgian (Upper Jurassic) of La Rochelle, Western France. *Lethaia, 42*, 462–468.

Wells, M. J., Wells, J., & O'Dor, R. K. (1992). Life at low oxygen tensions: the behaviour and physiology of *Nautilus pompilius* and the biology of extinct forms. *Journal of the Marine Biological Association of the United Kingdom, 72*, 313–328.

Wippich, M. G. E., & Lehmann, J. (2004). *Allocrioceras* from the Cenomanian (mid-Cretaceous) of the Lebanon and its bearing on the palaeobiological interpretation of heteromorphic ammonites. *Palaeontology, 47*, 1093–1107.