

# Internal ventral keels in Triassic ceratid ammonoids: description and functional interpretation as muscle scars

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Dedicated to Prof. Dr. VOLKER JACOBSHAGEN, Berlin

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**Abstract:** The Middle Triassic (Anisian) ammonoid species *Czekanowskites tumaefactus* and *Arctohungarites involutus* (both Ceratitida, Czekanowskitidae) were collected from several localities in the vicinity of the Laptev Sea (Arctic Siberia). The internal shell of the two species exhibits two parallel ventral ridges, running at short distance along both sides of the ventral, external, median keel. The internal ridges can be traced back into the phragmocone and terminate in the posterior third of the body chamber of adult specimens. Position and structure of the ridges suggest that they represent attachment scars reflecting part of the retractor muscle system. In other ammonoideans, e.g. of the Middle Jurassic *Hecticoceras*, usually a single ventral scar or ridge had been formed. Some taxonomic confusions result from the paired construction of internal ridges in adult *C. tumaefactus* and *A. involutus* due to the tricarinate ventral side of steinkerns.

**Kurzfassung:** Zwei interne, durch die innere Prismenschicht gebildete, ventrale Schalenleisten beidseitig des Mediankiesels auf Phragmokon und hinterem Wohnkammerabschnitt der Ammonoideen-Arten *Czekanowskites tumaefactus* und *Arctohungarites in-*

*volutus* (Ceratitida, Czekanowskitidae) aus der Mitteltrias (Anisium) verschiedener Fundorte Arktisch Sibiriens (Umgebung der Laptev See) werden als Ansatzstellen des Trichtermuskelsystems gedeutet. Die durch die internen Leisten scheinbar tricarinate Ausbildung der Externseite von Steinkernen vergleichbarer Arten führte zu taxonomischen Fehlbeurteilungen. So wird *Lenotropites ? tricarinatus* TOZER 1994 als Synonym zu *Groenlandites kummeli* TOZER 1994 erkannt.

**Keywords:** Ceratitida (Czekanowskitidae), shells, internal ridges, paleobiology, functional morphology, systematics, Anisian.

North Siberian Plain, Olenek Bay, Russia.

## Introduction

Modern *Nautilus* LINNAEUS, 1758 has certainly been abused as a functional model for ammonoids in general and in particular. In respect of closer systematic relations of ammonoids and coleoids, the palaeobiology of the former has been increasingly correlated with the latter i.e. in the course of the last years (see e.g. ENGESER 1990; JACOBS & LANDMAN 1993). This is a fruitful avenue of research, however, despite of overemphasis on the model *Nautilus* in the past, the trivial fact remains that we have no other living ectocochleate cephalopod and certain behaviours as e.g. retraction of the animal cannot be understood using the coleoid model.

The body of modern *Nautilus* is attached to the shell by two large, dorsolateral retractor muscles and by anterior and posterior myoadhesive bands (MUTVEI et al. 1993, pers. observ.). The areas where the muscles attach are covered by organic membranes (= "horny mat-

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Fig. 1: The pyritic steinkern of a Middle Jurassic (Late Callovian) *Hecticoceras* (*Lunuloceras*) sp. from the Calvados Coast (Villers-sur-Mer, Northern France) exhibit remains of the retractor system by both, a ventral groove originated by a single internal ridge and a light colored ventrolateral sinus (= „Einbuchtung“ sensu JORDAN 1968). Specimen MAN-1132, diameter: 15 mm, legit: August Ilg, Düsseldorf.

Abb. 1: Der Pyrit-Steinkern eines *Hecticoceras* (*Lunuloceras*) sp. aus dem Ober-Callovium von Villers-sur-Mer (Normandie, Frankreich) läßt Ansätze des Retraktor-Muskelsystems in zweifacher Weise erkennen: eine mediane Furche, welche durch eine interne Schalenleiste hervorgerufen wird, und eine heller gefärbte, ventrolaterale Einbuchtung (sensu JORDAN 1968). MAN-1132, Durchmesser 15 mm; legit: August Ilg, Düsseldorf.

ter” OWEN 1832; “membranous disc” GRÉGOIRE 1962), secreted by the overlying mantle. The attachment conditions modifications of the inner prismatic shell layers (GRÉGOIRE 1962, 1987) and thus can be recognized in fossils. The retractor muscle systems in Ammonoidea are obviously different (e.g. DOGUZHAeva & KABANOV 1988; DOGUZHAeva & MUTVEI 1991), however, the attachment scars are pronounced in a very similar way as in *Nautilus*.

Two types of presumed muscle scar preservation have been described in ammonoids: imprints or dark coloured areas on pyritic steinkerns (CRICK 1898; JONES 1961; JORDAN 1968; RICHTER & FISCHER 1992; ZIMMERMANN 1985), and structural modifications of inner layers of aragonitic and phosphatic shells (BANDEL 1982; DOGUZHAeva & MUTVEI 1986; LANDMAN & BANDEL 1985; WEITSCHAT 1986). We add here the description and interpretation of a differently pronounced retractor muscle system.

In contrast to *Nautilus* (cf. BLIND 1976), at least four structurally conspicuous areas – two of which are paired – have been supposed to re-

flect attachment of retractor muscles in ammonoids:

1. The dorsal muscle scar found in Middle Jurassic *Quenstedtoceras*, presumably representing the attachment area of the main retractor muscle, changed in the course of the early ontogeny from a paired to a single scar (BANDEL 1982), which then is similarly pronounced as e.g. in Devonian bacitritids (RISTEDT 1971). A similar example with a single dorsal presumed muscle scar from the Triassic was presented by LEHMANN (1990) who figured *Amphipopanoceras*.

2. Shapes and structures of a single ventral muscle scar and paired ventrolateral and dorsolateral scars (near the umbilical edge) (e.g. DOGUZHAeva & MUTVEI 1991; JORDAN 1968) may differ significantly, interspecifically as well as intraspecifically.

Reconstruction of muscle attachment usually means correlation of structures from different taxa, some of which showing ventrolateral others only dorsolateral scars. In some cases, however, the complete retractor muscle system is exhibited in a single specimen, found

e.g. in Triassic *Stolleites* (oral comm. W. WEITSCHAT, Hamburg). This accounts also for pyritic steinkerns of *Aconeceras*, *Amaltheus* or *Quenstedtoceras* on which dark coloured spots presumably represent the attachment areas (DOGUZHAeva & MUTVEI 1991; JORDAN 1968; RICHTER & FISCHER 1992; ZIMMERMANN 1985). In some species e.g. of *Hecticoceras* the unpaired ventral muscle attached to a more or less prominent ridge (Fig. 1), while the other attachment areas can be recognized as dark coloured spots which is usual in pyritic steinkerns. In ammonoids with shell preservation, the attachment of the dorsolateral muscle pair may be reflected by ridges along the umbilical edge, which has been described from Jurassic longidome ammonites, in particular from Liasic dactyloceratids and some Late Jurassic perisphinctids (cf. reconstructions in HENGSBACH 1978; MUTVEI 1964).

Functional morphologies based upon presumed retractor muscle systems in ammonoids are still under controversé discussion. Most of the so-called "Sipho-Strukturen", which have been described by JORDAN (1968) from phragmocones of different ammonite taxa and been interpreted as part of the retractor system, actually show a similar position as the ventral muscle scar in the posterior body chamber of e.g. *Aconeceras* (DOGUZHAeva & MUTVEI 1991). BAYER (1974), however, argued in favour of a suspension function of the siphuncle (compare HÖLDER 1957). Similar "Haftbänder" were figured by WEITSCHAT (1986: Taf. 5) who studied Triassic ammonoids. MUTVEI & REYMENT (1973) considered ventral muscle scars of Mesozoic ammonites, which are pronounced in the posterior parts of body chambers, to represent remains of the ctenidia retractor, homologous with modern dibranchiate cephalopods. A single, small, ventral muscle scar can be found in many Jurassic and Cretaceous ammonoids, such as *Aconeceras*, *Hecticoceras* or *Amaltheus*. The lateral and dorsolateral scars are paired in these taxa. The functional interpretation of the ventral scar given by DOGUZHAEVA & MUTVEI (1991) included the correlation with a hypothetical ligament, which may have had maintained shape and position of the circum-siphonal invagination in the posterior part of the ammonoid animal.

A dorsolateral pair of muscle scars, pronounced near the umbilical edges of several ammonoidean taxa (BANDEL 1982; CRICK 1898; DOGUZHAEVA & MUTVEI 1986, 1991; JORDAN 1968; LANDMAN & BANDEL 1985; SHARIKADZE et al. 1988; ZIMMERMANN 1985) was often considered to represent the main retractor attachment (HENGSBACH 1978; JORDAN 1968; MUTVEI & REYMENT 1973). JORDAN (1968) figured and described single pairs of more or less dorsolateral muscle scars from *Pleurolytoceras*, *Pleuroceras*, *Pseudamaltheus* and *Dorsetensia*. JORDAN (1968) coined the term "Schleppstreifung" (= tracking bands) for the formation of two continuous, dark coloured bands, which run parallel to the umbilical edges of pyritic steinkerns, e.g. of *Asteroceras*, *Ludwigia*, *Paroecotraustes*, *Arietoceras* or *Tragophylloceras*. Similar, but light-coloured bands found at the umbilical edges of *Staufenia* and *Leioceras* have been shown to represent myoadhesive formations of the inner prismatic shell layers (DOGUZHAeva & KABANOV 1988; DOGUZHAEVA & MUTVEI 1991). DOGUZHAEVA & MUTVEI (1991) rejected the idea that the dorsolateral scars represent remains of the hypnomete retractor, but of the cephalic retractor system.

Large ventrolateral muscle scars (JORDAN 1968: "Einbuchtung") are usually only poorly preserved. Size and shape varies between different ammonoidean taxa (cf. figures in CRICK 1898; JORDAN 1968; RICHTER & FISCHER 1992). JORDAN (1968) mentioned the similarity of such scars in ammonoids to those of the retractor muscles in modern *Nautilus* and discussed an analogous function. The bilobate outline of the ventrolateral muscle scars of *Aconeceras* was discussed by DOGUZHAEVA & MUTVEI (1991) to represent the probable attachment areas of hypnomete as well as of cephalic retractors. Consequently DOGUZHAEVA & MUTVEI (1991) reconstructed *Aconeceras* as an effective jet-powered swimmer, a functional morphology, which can possibly be applied also to other genera showing corresponding muscle scars, such as *Quenstedtoceras*, *Amaltheus*, *Hecticoceras*, *Lytoceras* or *Pseudogrammoceras* (see JORDAN 1968).

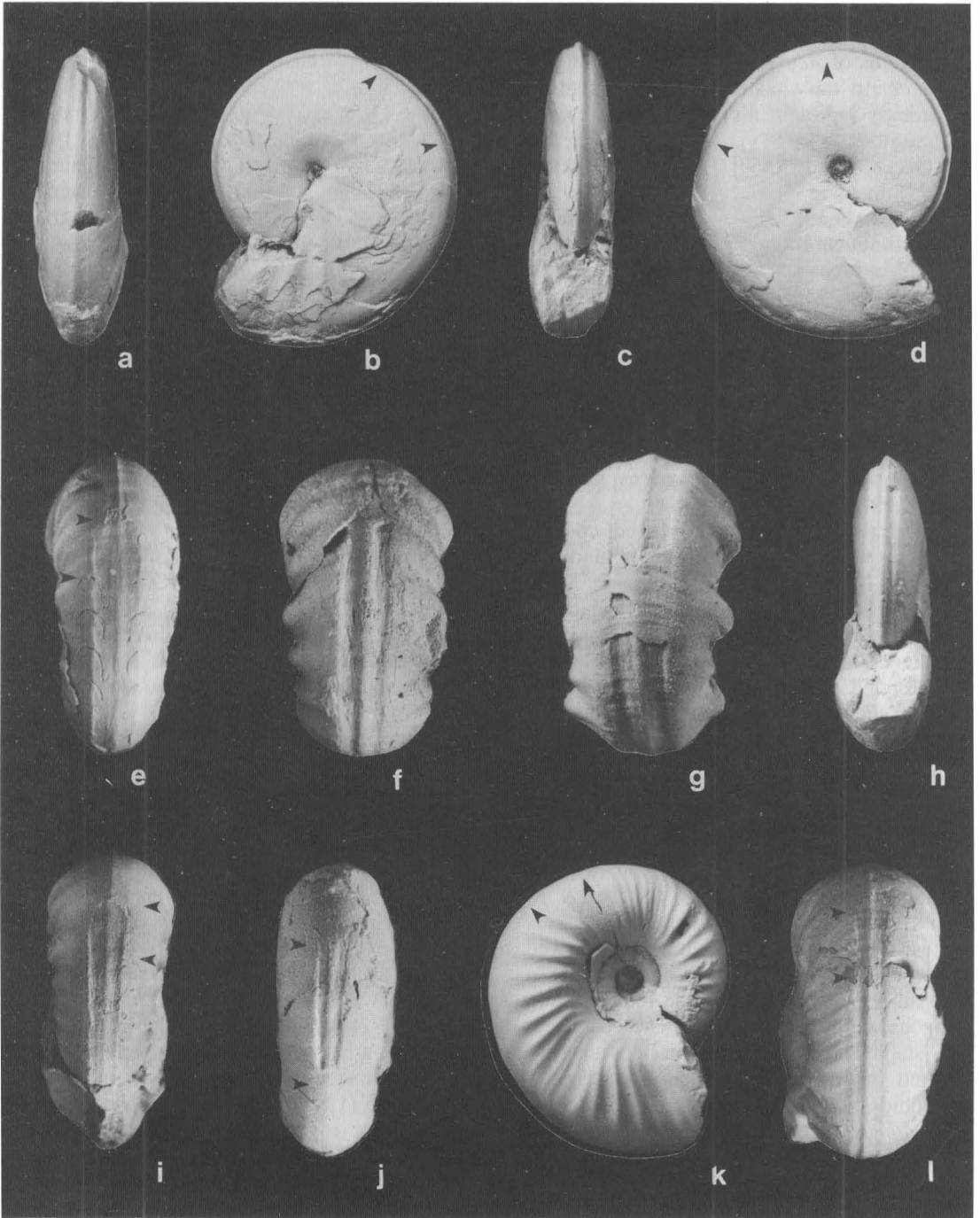


Plate I: *Arctohungarites involutus* (KIPARISOVA) (figs. a–d, h) and *Czekanowskites tumaefactus* VAVILOV (figs. e–g, i–l) from Lower Anisian (T<sub>2</sub>) of the Olenek Bay, Arctic Siberia with exhibit two parallel ventral grooves on steinkerns. Position and structure of the internal ridges suggest that they represent attachment cars reflecting  
(continued next page)

## Material

The here studied ammonoids were collected in different regions of the eastern Taimyr Peninsula and the Kharaulakh Range (both Arctic Siberia, Russia), but mainly originate from Ulak-

han-Krest Creek and Stan-Khaya-Yurege Creek (Olenek Bay, Laptev Sea) and Cape Tsvetkov (also Laptev Sea). The shell structures, which are considered here to represent muscle scars could be recognized in the two Lower Anisian species, *Czekanowskites tumaefactus* VAVILOV

Legend plate I continued:

the retractor muscle system of the hyponome (the first arrow marks the position of last septum, the second arrow the posterior end of supposed muscle scars) :

Figs. a–c: Complete specimen (MAM-461) of 32 mm diameter. The muscle scars can be traced back from the posterior quarter of body chamber on the phragmocone at least to the beginning of the last whorl.

Figs. d, h: The ventral grooves of this steinkern (MAM-462), 26 mm in diameter, are quite distinct and occupy about 80° of the posterior body chamber. The ventral view (fig. h) demonstrates that the lack of the left groove is due to the partly preservation of shell relicts.

Fig. e: The supposed muscle scars in *C. tumaefactus*, which is quite variable in its shell morphology, penetrate the posterior portion of the body chamber only for a short distance (20–40°). Diameter of specimen MAM-463: 19 mm.

Fig. f: The supposed muscle scar traced back often far to the inner whorls (only phragmocone, specimen MAM-464, diameter 20 mm).

Fig. g: Inner part of phragmocone (specimen MAM-465, diameter 10 mm): the fastigate ventral sculpture can be observed where the shell is preserved, while the steinkern exhibits clearly the ventral grooves.

Fig. i: The 21 mm large specimen (MAM-466) exhibits clearly the lingulate anterior end of the supposed muscle scars.

Fig. j: The supposed muscle scars are restricted to the posterior part of the body chamber in few specimens only and can not be traced back into the phragmocone. Specimen MAM-467, diameter 26 mm.

Figs. k, l: Normally, the short muscle scars of the posterior part of the body chamber traced back to the phragmocone more or less significantly. Specimen MAM-468, diameter 25 mm.

Tafel I: *Arctohungarites involutus* (KIPARISOVA) (Fig. a–d, h) und *Czekanowskites tumaefactus* VAVILOV (Fig. e–g, i–l) aus dem Unter-Anis (T<sub>2</sub>) von der Olenek Bucht, Arktisches Sibirien, mit jeweils zwei parallelen Furchen auf der Ventralseite der Steinkerne. Position und Struktur der internen Schalenleisten lassen ihre Funktion als Anheftung des Trichter-Muskelsystems vermuten. (der erste Pfeil markiert jeweils die Lage des letzten Septums, der zweite Pfeil das Ausklingen der mutmaßlichen Muskelansatzleisten) :

Fig. a–c: Vollständig erhaltenes, 32 mm großes Individuum (MAM-461). Die Muskelansatzleisten können vom hinteren Viertel der Wohnkammer auf dem Phragmokon bis mindestens zum Beginn der äußeren Gehäusewindung verfolgt werden.

Fig. d, h: Die deutlichen ventralen Furchen des 26 mm messenden Steinkerns MAM-462 reichen 80° in den hinteren Abschnitt der Wohnkammer hinein. In der Ventralansicht (Fig. h) ist die linke Ventralrinne infolge der partiellen Schalenhaltung nicht erkennbar.

Fig. e: *C. tumaefactus* ist in seiner Gehäusemorphologie sehr variabel. Die mutmaßlichen Muskelansatzleisten reichen bei diesem Exemplar (MAM-463, Durchmesser 19 mm) nur 20 bis 40° in die hintere Wohnkammer hinein.

Fig. f: Der 20 mm messende, isolierte Phragmokon (MAM-464) läßt erkennen, daß sich die ventralen Leisten oft bis in die frühen Innenwindungen zurückverfolgen lassen.

Fig. g: Isolierte Innenwindung eines Phragmokons (MAM-465, Durchmesser 10 mm): Im Bereich der Schalenhaltung ist die fastigate Ventralplastik erkennbar, während der Steinkern deutlich die beiden Ventral-Furchen zeigt.

Fig. i: Das Vorderende der Muskelleisten im hinteren Wohnkammerabschnitt erscheint zungenförmig (MAM-466, Durchmesser 21 mm).

Fig. j: Bei wenigen Exemplaren (z.B. MAM-467, Durchmesser 26 mm) bleibt die Anlage der Muskelansatzleisten auf die Adultphase – und somit die Position im hinteren Wohnkammer-Abschnitt beschränkt – und fehlt im juvenilen Stadium (Phragmokon).

Fig. k, l: In der Regel reichen aber die ventralen Muskelansatzstellen vom hinteren Wohnkammerbereich weit in den Phragmokon zurück. MAM-468, Durchmesser 25 mm.

Tab. 1: Frequency of shells exhibiting ridge-like presumed muscle scars.

Tab. 1: Häufigkeit von Gehäusen mit ventralen mutmaßlichen Muskelansatz-Leisten.

1. <i>Arctohungarites involutus</i> from Olenek Bay			
carbonate concretion	total number of specimens	specimens with ventral ridges	percentage
1	45	8	18
2	145	3	2
3	51	1	2
4	13	2	16
5	36	3	8
6	38	2	5
7	46	7	15
8	56	11	20
9	80	12	15
10	57	11	19
11	304	33	11
12	36	2	5
13	49	3	6
1-13	957	98	10.2

2. <i>Arctohungarites involutus</i> from Cape Tsevtkov			
carbonate concretion	total number of specimens	specimens with ventral ridges	percentage
1	26	1	4
2	11	0	0
3	27	3	11
4	39	3	8
5	18	2	11
6	17	1	6
7	20	2	10
1-7	158	12	7.6

3. <i>Czekanowskites tumaefactus</i> from Olenek Bay and Olenek River			
carbonate concretion	total number of specimens	specimens with ventral ridges	percentage
1	186	41	22
2	146	11	8
3	52	4	8
4	65	6	7
5	44	8	18
1-5	493	70	14.2

1978, which was collected in the upper part of the *taimyrensis*-zone, and *Arctohungarites involutus* (KIPARISOVA 1937) originating from the *caurus*-zone (cf. DAGYS & KAZAKOV 1984).

The specimens were usually preserved with secondary calcitic shell. The internal ridges described and discussed below, however, were first recognized as grooves on some steinkerns.

The lithology of the two ammonoid zones comprised clayey siltstones and mudstones with carbonate concretions, which usually exhibited monospecific ammonoid assemblages. In few cases concretions contained *Arctohungarites involutus* (KIPARISOVA) in association with *Lenotropites caurus* (MCLEARN) or *Czekanowskites tumaefactus* jointly with *Grambergia taimyrensis* POPOV.

Monospecific concretions, which contained *Arctohungarites involutus*, presumably exhibited only adult shells and did not show biostratonomical differentiations, i.e. in respect to shell size and shape. Body chambers are preserved in a fair amount of specimens. In contrast, populations of *Czekanowskites tumaefactus* included shells of various sizes, reflecting different ontogenetic stages. Body chambers are rarely preserved.

The total number of specimens within single carbonate concretions is given in Table 1. Voucher material is deposited at the Institut für Paläontologie, Freie Universität Berlin (coll. Keupp: MAm-461 to -468, and MAN-1132)

## Description

Steinkerns of *Czekanowskites tumaefactus* and *Arctohungarites involutus* exhibit most clearly the ventral structures along both sides of the median keel (Plate 1). Calcitic shells show the elevated, ridge-like character of the conspicuous structures, which resemble two oblong-ovate platforms tracking backwards as parallel bands. The internal ridges usually have a homogenous appearance. The total length, with a range from less than a quarter whorl (cf. pt. 1, fig. j: only on body chamber) to more than three whorls (pt. 1, fig. g) is variable as well as is the terminal position, which ranges at distances between 20–80° to the last septum. In most cases the ridges can be traced from the posterior ventral portion of the body chamber back to about three-quarter of the last phragmocone whorl. Some specimens of *Arctohungarites involutus* exhibit the ridges only in the phragmocone and not in the body chamber, which,

however, may represent an artefact of preservation. In *Czekanowskites tumaefactus* the internal ridges may be traced back for almost four whorls. The position of the ridges appears to be correlated with the corresponding shell shape. In the subcadiconic, subevolute shell of *C. tumaefactus*, the ridge-like structures terminate at a distance of 20–40° (pt. 1, figs. e,i,j,k,l) to the last septum, while in the suboxyconic to platyconic shells of the involute species *A. involutus* the two ridges reach further into the body chamber, terminating at a distance of 50–80° to the last septum (pt. 1, figs. d,h).

The ventral ridges appear on the corresponding steinkerns as symmetric, usually narrow grooves. In some specimens where the ridges had been pronounced more prominently, the steinkerns show well developed grooves giving the venter a characteristic tricarinate shape – usually an important feature for the classification of the boreal Anisian ammonoids – which, however, cannot be recognized when the shell is preserved (cf. pt.1, figs. g,h). Thus taxonomic misinterpretation may occur. Such characteristic steinkerns of *C. tumaefactus* and *A. involutus* which are e.g. very similar to contemporaneous species of the Groenlanditinae genus *Lenotropites* POPOV or juveniles of the genus *Intornites* ASSERETO (cf. TOZER 1994) or i.e. corresponding shells of *A. involutus* may be confused with the more or less synchronous taxon "*Hungarites*" *yatesi* (see SMITH 1932; WANG 1978: pt.2/7-9).

The original microstructure of the two ventral ridges had been changed during calcitization. Thin sections, however, show clearly that the ridges had been formed by thickening of the inner prismatic shell layer, which is not developed at the ventral margin of the body chamber.

Table 1 compiles statistical data such as total numbers of ammonoid specimens within carbonate concretions. The great majority of the specimens lack internal ridges, however, except for one concretion, each contained such characteristic shells, in a frequency from about two to twenty-two percent (see Table 1). Differences between collecting sites are generally not significant, but in the outcrops at Olenek Bay, within the *tardus*-zone, a vertical increase of specimens showing internal ridges, can be documented. The *tardus*-zone is here characterized

by a series of mudstone-beds of 2 to 3 m in thickness with 5 to 6 horizons, which contain carbonate concretions with populations of *Archonungarites involutus*. In the lower half of this section the percentage of shells with internal ridges is comparatively low, which in respect to different outcrops, varies between 2 and 6%. In contrast, populations extracted from concretions of the upper *taurus*-zone contained as much as 15 to 20% specimens, which exhibit the conspicuous ridges.

## Conclusions

The described pair of ventral, internal keels is interpreted to represent attachment scars of the retractor muscle system. The position of the ridges, which may be formed as far as 80° in front of the last septum, excludes the possible interpretation as a "Haftband" of the siphuncle (BAYER 1974: pt. 9; HÖLDER 1957; WEITSCHAT 1986: pt. 5). The formation of the presumed myoadhesive ridges by thickening of the inner prismatic layer closely resembles analogous dorsolateral muscle scars in dactylioceratids. Ventral muscle scars have been documented from various Mesozoic ammonoids (cf. MUTVEI & REYMENT 1973), but in contrast to the here described species only a single internal ridge had been formed (Fig.1). BANDEL'S (1982) research on Middle Jurassic *Quenstedtoceras* demonstrated a possible analogous reduction with regard to the dorsal muscle attachment scar which has had developed from a paired anlage.

The ventral pair of ridges are considered to reflect attachment of the hyponome retractor. The occurrence of ventral keels only in part of the populations is somewhat strange. The increase of *A. involutus* specimens, which exhibit the ventral keels, within the *tardus*-zone, may indicate a speciation process. The synchronous occurrence of *C. tumaefactus* showing the same conspicuous structural elements, however, demonstrates that more likely ecological and/or taphonomical factors were responsible for the characteristic phenotypes.

Several thousand specimens of more or less contemporaneous species of the family Czekanowskitidae such as *Czekanowskites rieberi* DAGYS & WEITSCHAT, *C. decipiens* (MOJSISO-

VICSZ), *C. hayesi* (MCLEARN), *C. gastroplanus* POPOV, *Arctohungarites triformis* (MOJSSOVICSZ), *A. kharaulakhensis* POPOV and *A. laevigatus* POPOV, have also been examined in respect of ventral internal ridges, but not a single shell with such muscle scars was found.

Finally the results point at a taxonomic problem. TOZER (1994, locality 68203) described the new species *Lenotropites ? tricarinatus* from Lower Anisian of British Columbia, based upon a single specimen found among the abundant species *Groenlandites kummeli* TOZER 1994. *L. ? tricarinatus* shows a fastigate venter where the shell is preserved, while the steinkern portion exhibits a tricarinate venter (TOZER 1994: pt. 45/9). The tricarinate ventral structure, however, clearly reflects the same presumed muscle attachment system as is here described for *C. tumaefactus* and *A. involutus*. It thus can be concluded that *Lenotropites ? tricarinatus* TOZER 1994 is a junior synonym of *Groenlandites kummeli*.

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