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Soft Tissue Attachment Structures on Pyritized Internal Moulds of Ammonoids

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6 Text-Figures and 1 Plate

Ammonoidea
Palaeozoic
Mesozoic
Attachment Structures
Soft Body Organization

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Zusammenfassung

Es werden dunkle Fleckenmuster auf Pyrit-Steinkernen von Ammonoideen aus dem Ober-Devon, der Trias, aus Jura und Unterkreide beschrieben und interpretiert. Paarige Muster sind entlang des Nabels und auf den Flanken, unpaarige auf der Mitte der Dorsal- und der Ventralseite zu sehen. Sie zeigen sich in Form von Flecken, Bändern, Linien und Schleppstreifen. Ein ventraler Muskel hinterlässt kleine, rundliche Flecken auf der Ventralseite, ein kleiner Dorsalmuskel verursacht raue Stellen vor den Dorsalloben. Kräftige Lateralmuskeln hinterlassen paarige Doppellinien auf den Flanken der Steinkerne. Von paarig am hinteren Ende des Weichkörpers sitzenden dorsolateralen Muskeln zeugen Flecken entlang des Nabels; sie verschmelzen häufig zu einem Band. Linien, Bänder und Schleppstreifen hinter den Lobenspitzen belegen punktuelle Anheftungsstellen des hinteren Mantelbereiches und ihre Verlagerung vor der nächsten Septenbildung. Während Goniatiten ein laterales und ein ventrolaterales paariges Muskelsystem besaßen, zeigen Neoammoniten paarige Lateral- und Dorsolateralsysteme und je ein unpaariges auf der Ventral- und Dorsalseite. Mesoammoniten besaßen lediglich ein paariges laterales und ein unpaariges dorsales Muskelsystem.

Abstract

Dark coloured lines, bands, small rounded or crescent shaped areas and tracking bands, observable on pyritized internal moulds of Upper Devonian, Triassic, Jurassic and Lower Cretaceous ammonoids are described and interpreted. Paired structures are developed along the umbilicus and on the flanks of the moulds, unpaired ones appear on the middle of their dorsal and ventral sides. Strong lateral muscles cause paired double lines on the flanks of the phragmocone and of the body chamber. A ventral muscle is deduced from small rounded areas on the ventral side, and a middorsal muscle is documented by small roughened areas in front of each dorsal lobe. Small dark areas along the umbilicus, often connected with a band-like structure, are remains of a pair of small dorsolateral muscles at the posterior end of the soft body. Dark bands, lines and rows of small crescent shaped structures behind the tips of sutural lobes are due to spotlike attachment sites of the posterior part of the mantle and their translocation before subsequent septal secretion. Goniatites had a paired system of lateral and ventrolateral muscles, whilst Mesoammonoids show only a paired lateral and an unpaired dorsal one. Neoammonoids have a paired lateral and dorsolateral system, and, additionally, an unpaired system on the ventral and on the dorsal side.

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1. Introduction

One of the main problems in ammonoid palaeobiology is to get an idea about the soft body organisation of the animal. The muscular system mainly results from ecological adaptation of organisms and thus muscular attachment structures can give a better understanding of the locomotion and, ultimately, of the mode of life of extinct animals.

JORDAN (1968) first described specific dark coloured areas and bands on pyritized internal moulds of ammonites and interpreted them as documents of muscle and ligament attachment.

Through new studies of 1.603 pyritized internal moulds of *Amaltheus* and *Fuciniceras* (RICHTER, 1992) the observations of JORDAN have been confirmed and many new observations of structures added. Previous studies by CRICK (1898), VOGEL (1959), JONES (1961), RAKUS (1978), SARIKADZE et al. (1990), DOGUZHAEVA & MUTVEI (1991, 1996) support the fact that attachment structures preserved as dark areas on pyritized moulds can be interpreted as documents of muscle and ligament attachment.

This study based on a large amount of well preserved pyritized moulds of Mesozoic and Palaeozoic specimens permits statements about attachment structures and their relation to the systematic position and about probable changes in the course of phylogeny of the Ammonoidea.

For the first time attachment structures for Devonian cheiloceratids and tornoceratids are confirmed. The attachment structures of both families are different in detail. Marked differences in the attachment structures exist between Palaeozoic and Mesozoic specimens indicating a different organization of the muscular system.

The problems associated with detachment, translocation and reattachment of the soft body during the chamber formation process had required the development of a special translocation mechanism for ammonoids. Characteristic structures behind the sutural lobes and saddles on the phragmocone can be interpreted as temporary attachment sites of the rear septal mantle during the movement of the body inside the chamber. In previous studies by HÖLDER (1954), ZABORSKI (1986), HEWITT et al. (1991), LOMINADZE et al. (1993) and TANABE et al. (1997) distinctive structures such as pseudosutures, drag bands and telescoped pseudolobules were described that were recognized on internal moulds of Palaeozoic and Mesozoic specimens.

Characteristic markings of soft body translocation are confirmed on pyritized moulds of ammonites and goniatites. It turns out that traces of soft body translocation are relatively common structures on pyritized moulds of ammonoids.

Compared with goniatites with simplier sutures, in ammonites the septal formation process is more complicated. The more complex the sutures are the more structures of temporary attachment of the mantle margin, such as lines of longitudinal contacts and pseudosutures, occur (LOMINADZE et al., 1993).

A short overview of the observed structures and their functional interpretation is given here. Coherences between attachment structures and changes in the course of ontogeny and phylogeny, their relation to the shell and septum morphology and between attachment structures and the systematic position will be presented in a later publication.

2. Material

The main part of the studied material was kindly contributed by private collectors (see below).

The material from the collection Krause (Wenningsen, Germany) is of Jurassic (Liassic, Domerium) age and was collected at Empelde (Hannover, Germany). It is housed in the collection of the "Institut für Geologie und Paläontologie der Universität Hannover" (IGPH). The material from the collection Ebbighausen (Odenthal, Germany) is of Upper Devonian age (Famennian), was collected at Bergisch-Gladbach, Germany (Knoppenbießener Schichten) and is housed in the Humboldt-Museum of Berlin. The material from the collection Ilg (Düsseldorf, Germany) was collected in the Normandy, France (Houlgate, Villers-Sur-Mer) and is of Middle Jurassic age (Callovium). It is housed in the collection of the IGPH. The material from the collection Tilsley (Sheffield, Great Britain) is of Jurassic (Liassic, Carixium) age and was collected at Saltburn/Cleveland. It is also housed in the collection of the IGPH. The material contributed by Dr. W. Weitschat (Hamburg, Germany) is of Triassic age. It derives from Spitzbergen and is housed in the collection of the IGPH. Weitschat additionally provided two specimens from the Upper Cretaceous of South Dakota, USA (Pierre Shale Formation). They are housed in the collection of the "Staatliches Geologisch-Paläontologisches Institut und Museum Hamburg" (SGPIMH). Additional material of Jurassic and Lower Cretaceous ammonites was studied in the collection of the "Bundesanstalt für Geowissenschaften und Rohstoffe" in Hannover (BGR).

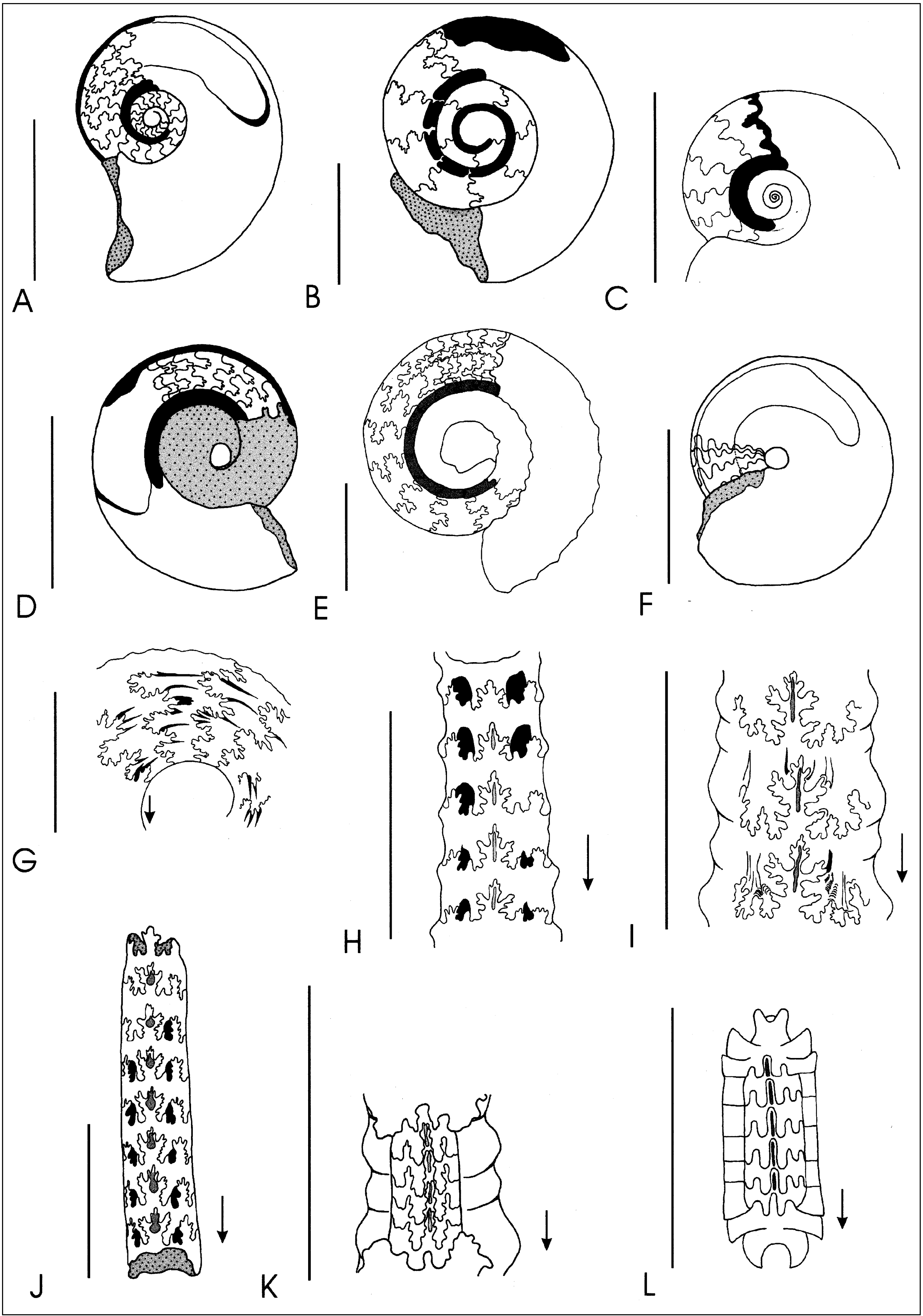
3. Preservation and Morphology of Attachment Areas on Pyritized Moulds

The attachment sites can frequently be distinguished by a black colour caused by a thin layer of fine crystalline pyrite. In some cases the sites are bordered by incised lines on the mould. SPILLE (1998) found that the dark colour is caused by fine grained pyrite which creates a tuberculate surface within the attachment areas. There the light is not reflected as normally done by pyrite, but absorbed more or less completely so that the attachment sites appear dark or black on the mould.

The formation of these thin dark layers started early at the beginning of diagenesis with a substitution of the myostracal shell layer by pyrite. The presence of remains of organic material at/in this shell layer encouraged fast formation of small pyrite crystals (SPILLE, 1998).

The incised line bordering the dark attachment sites corresponds to a slender ridge bordering the myostracal shell layer which was formed by addition to the inner shell wall (see CRICK, 1898).

Text-Fig. 1. ►▷►
Lateral and dorsal structures in ammonites and ceratites.
A: *Amaltheus* sp. (1999 IV 1), lateral view.
B: *Arieticeras* aff. *falciplicatum* (L249, originally figured in JORDAN [1968, Tab. 5, Fig. 2]), lateral view.
C: *Oedania delicata* (Ma 13442), lateral view.
D: *Hecticoceras* sp. (1999 IV 2), lateral view.
E: *Polymorphites (Uptonia) bronni* (L2552a), lateral view.
F: *Stolleyites tenuis* (1999 IV 3), lateral view.
G: *Amaltheus* sp. (1999 IV 4), lateral view of the phragmocone.
H: *Ancyloceras trispinosum* (Ma 13443), dorsal view of phragmocone.
I: *Crioceratites* cf. *tuba* (Ma 13444), dorsal view of the phragmocone.
J: *Bochianites undulatus* (Ma 13445), dorsal view of the phragmocone.
K: *Amaltheus gibbosus* (1999 IV 5), dorsal view of the phragmocone.
L: *Stolleyites tenuis* (1999 IV 6), dorsal view of the phragmocone.
Scale bar = 1 cm.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4. Description of Attachment Structures

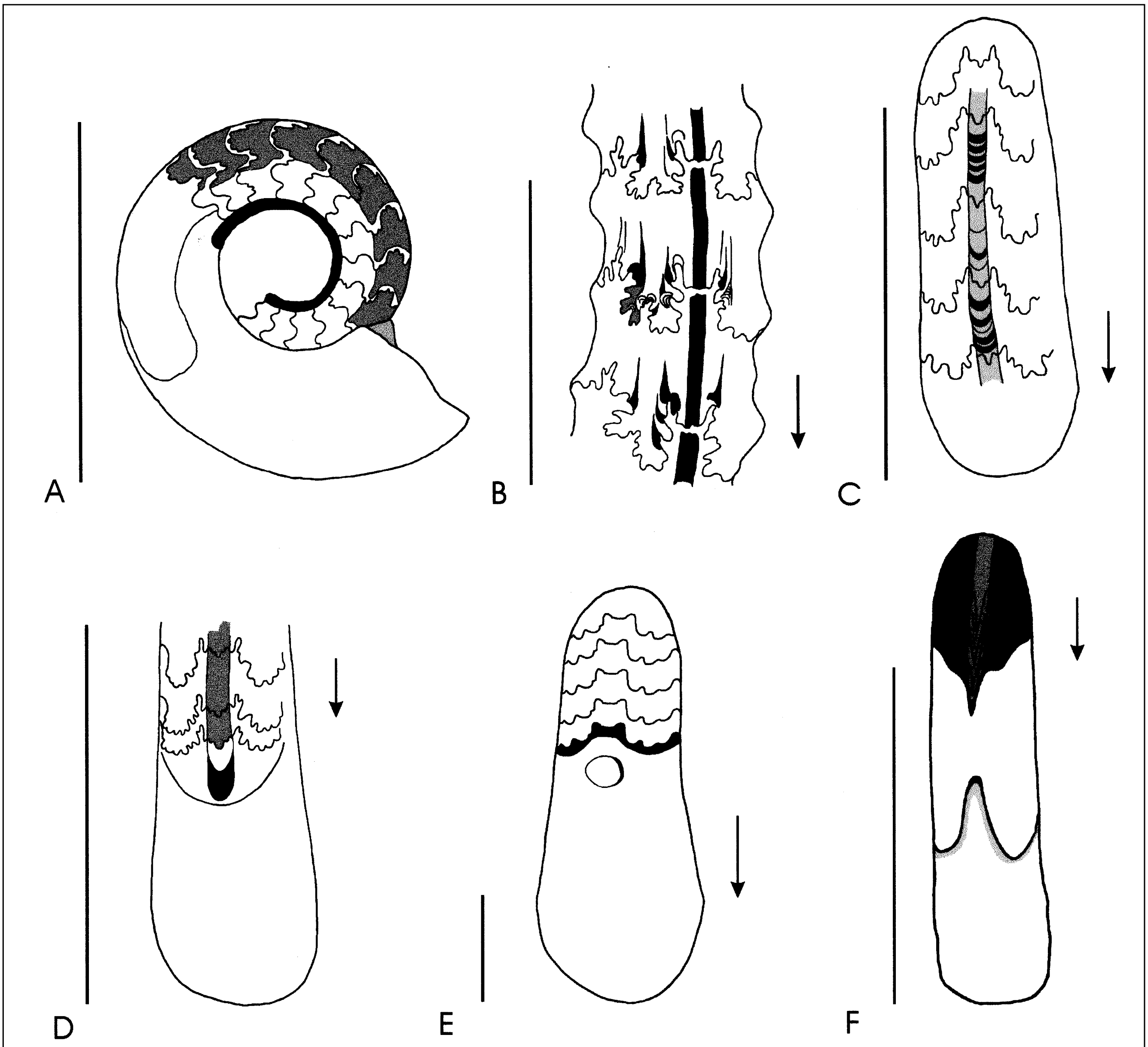
4.1. Lateral and Dorsal Structures in Ammonites and Ceratites

The characteristic attachment sites in ammonites, with exception of heteromorphic ones, are a lateral black double line in the body chamber closed at its anterior end and a continuous umbilical tracking band on the phragmocone and in the posterior part of the body chamber (Text-Fig. 1A, D). In some cases short double lines are situated ventrolaterally and the area between the lines is preserved in dark pyrite. Small individual areas situated dorsolaterally beside each septum are connected by a dark umbilical tracking band. In earlier growth stages the band is developed continuously (Text-Fig. 1B).

In ceratites the paired double lines can also appear as fine black spiral lines running parallel to the venter and the umbilicus and can also be observed on the phragmocone (Text-Fig. 1F).

Another characteristic lateral structure in ammonites is a narrow black preseptal area situated immediately in front of the last septum, bordered by a black line following the outline of the last suture. The preseptal area is often connected with the paired dorsolateral areas in front of the last septum (Text-Fig. 1C). In some cases only a single preseptal line is present. This line often connects the small paired dorsolateral and ventral attachment sites in the same specimen (Text-Fig. 1E).

Common structures on the lateral side of the phragmocone are black tracking lines and broader tracking bands behind the sutural lobes and sometimes behind the saddles (Text-Fig. 1G). These sutural tracking structures can frequently be observed in many of the studied Mesozoic specimens, as well as the umbilical tracking bands.



Text-Fig. 2.
Ventral structures in ammonites.
A: *Amauroceras ferrugineum* (1999 IV 7), lateral view.
B: *Ancyloceras trispinosum* (Ma 13443), ventral view of phramocone.
C: *Polymorphites interruptus* (1999 IV 8), ventral view of phragmocone.
D: *Amaltheus wertheri* (1999 IV 9), ventral view of phragmocone and body chamber.
E: *Oedania delicata* (Ma 13442), ventral view of phragmocone and body chamber.
F: *Hecticoceras* sp. (1999 IV 2), ventral view of the body chamber.

Scale bar = 1 cm.

Characteristic unpaired dorsal structures of ammonites and ceratites appear as rows of individual slender or rounded areas between the dorsal lobes. The surface of these sites is often slightly roughened or preserved in faint dark pyrite (Text-Fig. 1I, J, L). In some cases these small areas are in contact with the preceeding septum (Text-Fig. 1J, K).

In many cases of heteromorphic specimens the small unpaired areas occur together with larger paired dorsal attachment sites in the same specimen (Text-Fig. 1H, J).

Behind the dorsal lobes and saddles black tracking lines, fine incised lines, and small crescent shaped tracking structures can also be discerned on the dorsal side of the whorl (Text-Fig. 1I).

4.2. Ventral Structures in Ammonites

A common structure preserved on the ventral side of the phragmocone is a narrow continuous black siphonal band, which sometimes can be interrupted by the sutures (Text-Fig. 2B). Another frequently preserved structure is a broad external band, which can also be interrupted by the sutures. This band often appears together with an umbilical tracking band and a fine black double line in the body chamber (Text-Fig. 2A). The narrow siphonal band and the broader external band can often be observed together in the same specimen. The siphonal band and individual crescent shaped small areas between the sutures can also occur together in the same specimen (Text-Fig. 2C). Sutural tracking structures described above for the lateral and dorsal sides of the phragmocone are also developed on the ventral side (Text-Fig. 2B).

On the ventral side of the body chamber a small crescent shaped attachment site often occurs at the end of the black continuous siphonal band. In addition, in front of the crescent shaped area the preseptal line is preserved (Text-Fig. 2D).

In some cases the small oval shaped ventral area is preserved as a peripheral ridge on the mould. Behind this oval attachment site the dark preseptal area is preserved in front of the last septum (Text-Fig. 2E).

In some cases a large black area can be observed immediately in front of the last septum. In the middle of this area the end of the siphonal band is preserved with tracking structures at its anterior end. The siphonal band and the black broad area are connected with paired double lines, which are situated close together ventrolaterally (Text-Fig. 2F). These characteristic structures are observed only on the moulds of *Hecticoceras*.

4.3. Lateral Structures in Goniatites

On the lateral sites of the body chamber and the phragmocone the characteristic structures of cheiloceratids are distinct black paired spiral lines closed at the anterior end. They extend from the phragmocone approximately to the middle of the body chamber. The lines run parallel to the venter and the edge of the umbilicus. Between the lines distinct black crescent shaped tracking lines are developed or the area is completely filled with dark pyrite (Text-Fig. 3A, C). In some cases several pseudosuture lines can be observed. They are connected with the spiral lines and the tracking structures between the lines (Text-Fig. 3B).

On the lateral sides of the body chamber of tornoceratids one can also observe paired double lines being closed at the anterior end. These faint lines are not preserved as distinct black lines but always as fine incised lines, developed only in the body chamber and not on the phragmocone (Text-Fig. 3D, E, F). The double lines are either preserved together with broad black preseptal zones placed in front of the last suture (Text-Fig. 3F) or together with a dark external band which ends at the posterior part of the body chamber (Text-Fig. 3D). The ventral part of the double line sometimes borders the external band or parts of the preseptal area (Text-Fig. 3D, E).

On the lateral sides of the phragmocone in goniatites distinct tracking structures can be observed in the spaces between the sutures. The structures are preserved as fine black pseudosuture lines running parallel with the following septum. The space between two sutures is divided by these pseudosutures in several narrow zones which are preserved in faint dark or black pyrite (Text-Fig. 3G).

4.4. Ventral Structures in Goniatites

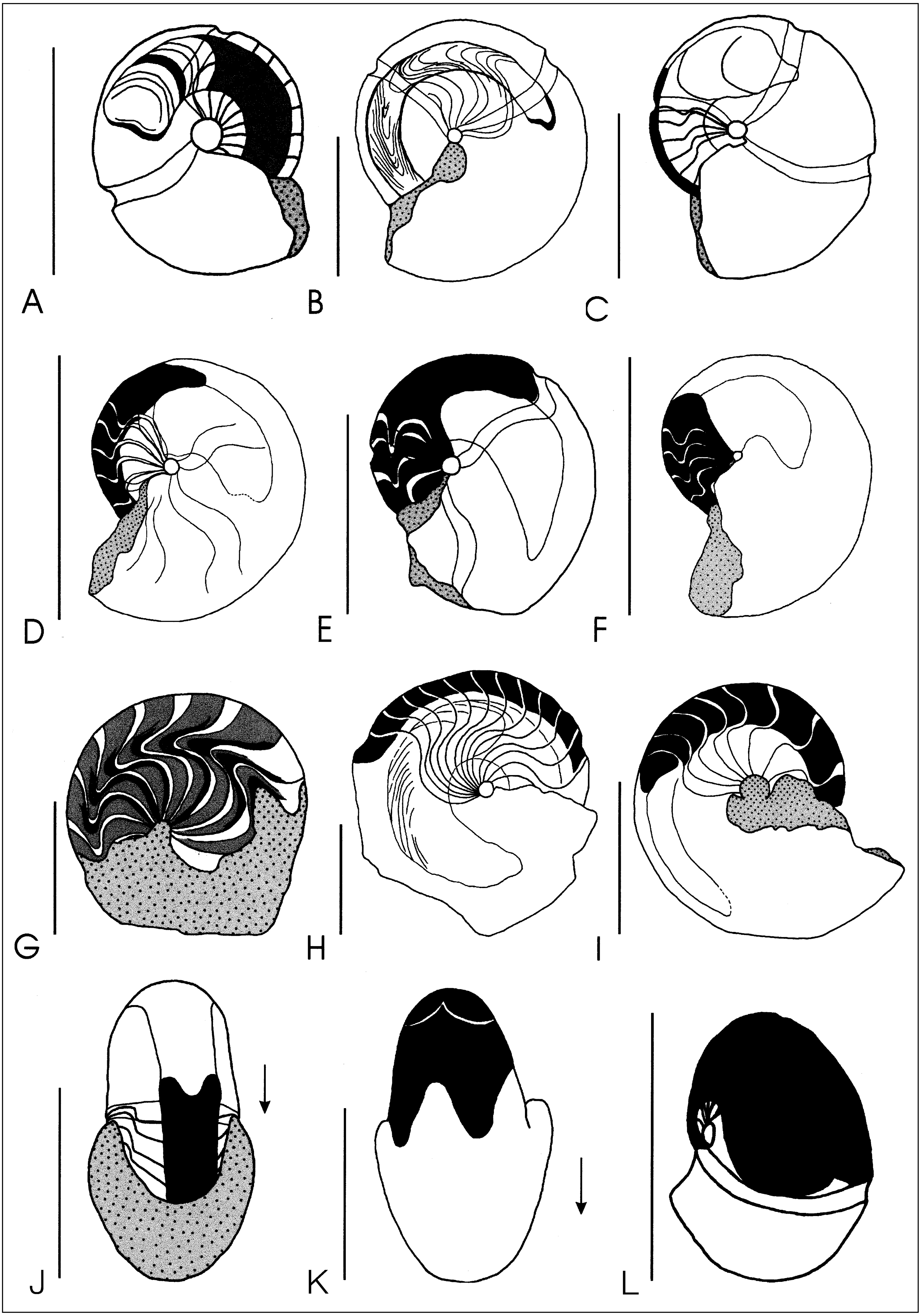
The lateral structures described above frequently occur together with an external band which reaches to the posterior part of the body chamber (Text-Fig. 3C, H, I). The end of the band is rounded or sometimes slightly indented (Text-Fig. 3J, L). In some cases only a broad external band slightly indented at its end is preserved (Text-Fig. 3L). The broad dark preseptal area often can also appear deeply indented ventrally (Text-Fig. 3K).

5. Functional Interpretation of Attachment Structures

5.1. Recent *Nautilus*

In *Nautilus* a pair of powerful cephalic retractor muscles that originate from the lateral sides of the body are attached in large crescent shaped attachment areas to the wall of the body chamber (cr, Text-Fig. 4A, B). These areas occur on the lateral and dorsolateral sides of the body chamber (MUTVEI, 1957; MUTVEI et al., 1993). A second pair of small hyponome retractor muscles is developed on the ventral side of the cephalic retractor muscles (hr, Text-Fig. 4A). The attachment sites of these muscles cannot be distinguished from those of the large cephalic retractors. The powerful cephalic retractor muscles are necessary for swimming by jet propulsion (MUTVEI, 1964). These muscles form a roof above the mantle cavity. Their contraction pulls the head into the body chamber, presses the roof of the mantle cavity down rapidly, expelling the water from the mantle cavity out through the funnel.

Longitudinal mantle muscles originate from the anterior mantle myoadhesive band which is attached along an annular zone in front of the attachment sites of the cephalic retractor muscles (mb, Text-Fig. 4B). A narrow septal myoadhesive band of the body epithelium is attached in front of the last septum (sb, Text-Fig. 4B). The attachment sites of these bands are difficult to distinguish from each other on the inner surface of the shell wall. This area ("annular elevation" of MUTVEI [1957]), is broad on the lateral sides but narrow on the dorsal portion of the body chamber. The annular elevation consists of a thin inner prismatic layer of the shell wall. The mantle epithelium, which is attached to this layer, is composed of "palisade-like cells" (BANDEL & SPAETH, 1983). In adult growth stages, this shell layer forms a narrow ridge on the anterior border of the annular elevation. CRICK (1898) pointed out, that this ridge can usually be observed in fossil ammonoids.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Text-Fig. 3. ◄◁◄
Lateral and ventral structures in goniatites.
A: *Cheiloceras amblylobum* (MB. C2902), lateral view.
B: *Cheiloceras subpartitum* (MB. C2903), lateral view of body chamber.
C: *Cheiloceras verneuili* (MB. C2904), lateral view.
D: *Aulatornoceras auriforme* (MB. C2905), lateral view.
E: *Linguatornoceras guestphalicum* (MB. C2906), lateral view.
F: *Tornoceras typum* (MB. C2907), lateral view.
G: *Cheiloceras longilobum* (MB. C2908), lateral view of phragmocone.
H: *Cheiloceras praelentiforme* (MB. C2909), lateral view.
I: *Armatites aff. planidorsatus* (MB. C2910), lateral view.
J: *Cheiloceras verneuili* (MB. C2904), ventral view of phragmocone and body chamber.
K: *Linguatornoceras haugi* (MB. C2911), ventral view of body chamber.
L: *Cheiloceras pompeckji* (MB. C2912), ventral view of body chamber and phragmocone.
Scale bar = 1 cm.

On the dorsal side a small unpaired scar occurs in front of the last septum. This scar represents the principal attachment site of the palliovisceral ligament (pvl, mda, Text-Fig. 4B).

5.2. Ammonites

The paired lateral double lines preserved on the flanks of the body chamber can be interpreted as outlines of preceeding attachment sites of paired strong cephalic retractor muscles and a pair of small hyponome retractor muscles (Text-Fig. 5: dl, cr, hr).

The small paired dorsolateral areas preserved along the umbilical edge can be interpreted as attachment sites of a second pair of cephalic retractor muscles. These muscles could have been used to draw the head into the body chamber and to attach the posterior part of the soft body close to shell wall. The probable function of the small unpaired ventral muscle was to attach the ventral part of the body close to shell wall and also to support the withdrawal of the head into the body chamber (Text-Fig. 5: dp, v).

The preseptal area and the preseptal line preserved in front of the last septum in the posterior part of the body chamber correspond to the attachment area of the septal and mantle myoadhesive band in Recent *Nautilus* (Text-Fig. 5: mb).

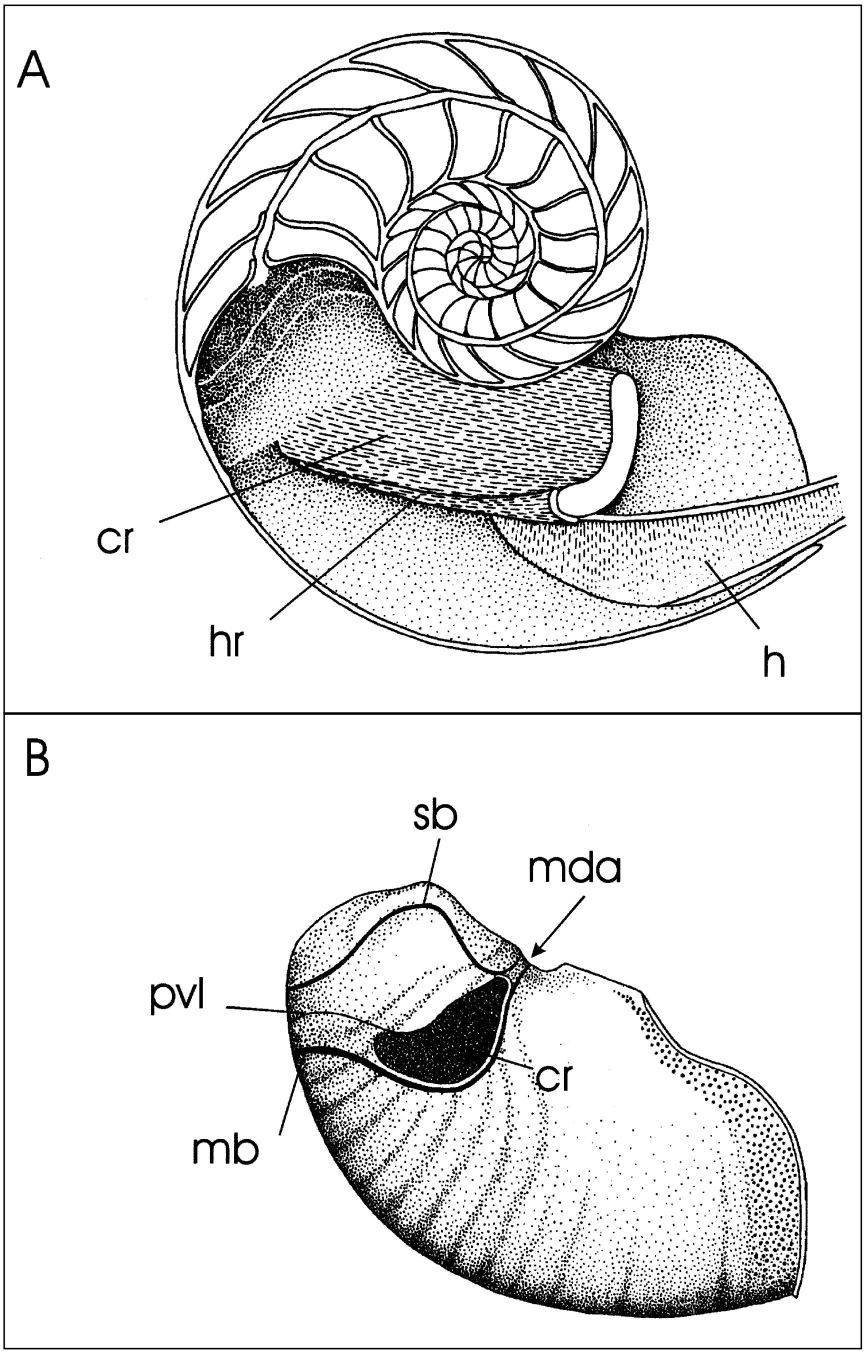
The sutural tracking structures associated with the lobes and saddles of the suture lines can be interpreted as attachment points of parts of the mantle margin corresponding to the incisions of the sutures during soft body translocation and subsequent septal secretion.

The small middorsal attachment areas preserved between the dorsal lobes of the successive septa probably represent the principal attachment sites of the palliovisceral ligament, similar to that arrangement in Recent *Nautilus*.

The function of the ventral structure such as the broad external band is still obscure.

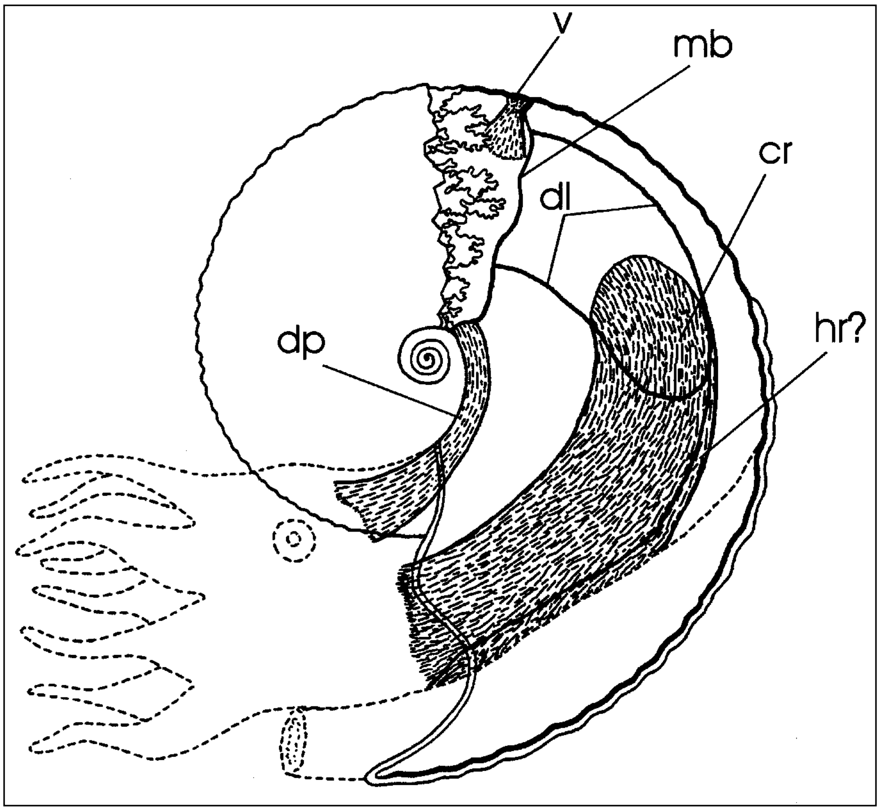
5.3. Goniatites

By contrast to ammonites, in goniatites a pair of lateral muscles and a pair of small ventral muscles can be observed. The paired double or spiral lines can be interpreted as outlines of previous attachment sites of paired strong cephalic retractor muscles, similar to those in ammonites (Text-Fig. 6: dl, cr).



Text-Fig. 4.
Muscles and muscle attachment sites in Recent *Nautilus*.
A: Diagrammatic cross section through a specimen of Recent *Nautilus* (modified from Doguzhaeva & Mutvei, 1996, Fig. 4A).
cr = cephalic retractor muscle; hr = hyponome retractor muscle; h = hyponome.
B: Diagrammatic lateral view of the attachment sites in the body chamber of Recent *Nautilus* (modified from Doguzhaeva & Mutvei, 1996, Fig. 5B).
cr = attachment site of the cephalic retractor muscle; mb = mantle myoadhesive band; sb = septal myoadhesive band; pvl = palliovisceral ligament.

Text-Fig. 5.
Soft body reconstruction of a generalized ammonite (modified from DOGUZHAEVA & MUTVEI, 1996, Fig. 7A).
dl = aperturally closed double line; cr = cephalic retractor muscle; hr = hyponome retractor muscle; dp = paired dorsolateral muscle; mb = myoadhesive band; v = unpaired ventral muscle.

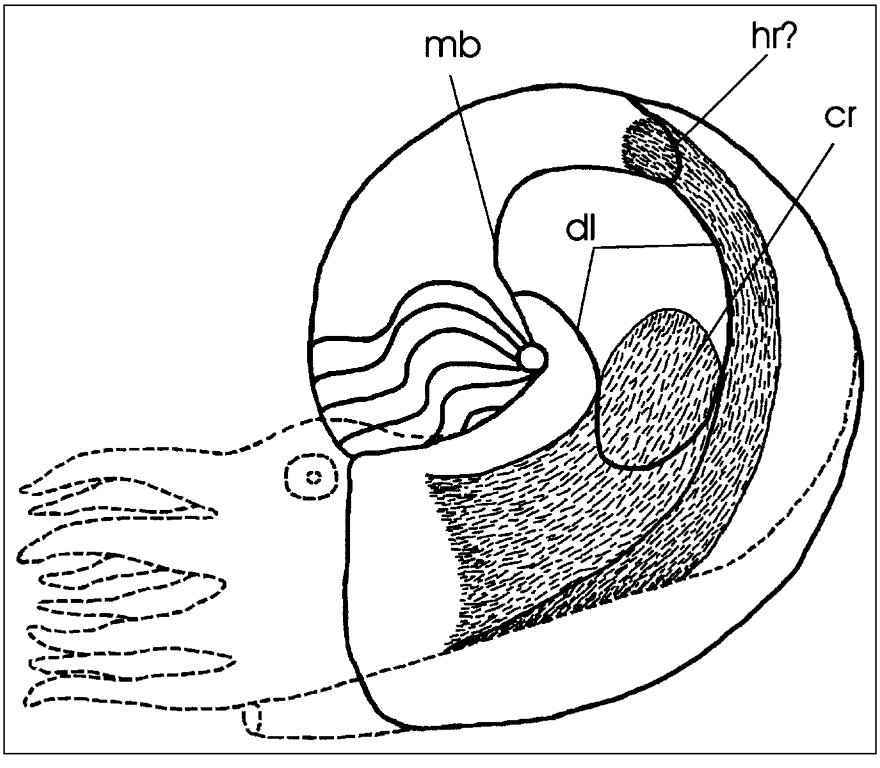


The indented ventral part of the broad preseptal area and the indented end of the external band in the posterior part of the body chamber can be interpreted as attachment sites of small paired hyponome retractor muscles (Text-Fig. 6: hr).

The preseptal area and the preseptal line correspond to the attachment site of a septal and mantle myoadhesive band, similar to that in ammonites and *Nautilus* (Text-Fig. 6: mb).

6. Conclusions

1) Pyritized internal moulds of ammonoids show various soft tissue attachment structures. The structures described in the classical study of JORDAN (1968) were confirmed and new observations of structures added:
   - Lateral double lines, closed at the anterior end.
   - Different sutural tracking structures.
   - A broad external band.
   - Dark preseptal areas in ammonites and goniatites.
2) All of these structures are interpreted as attachment sites of muscles and ligaments, but only some of the observed structures are also present in the Recent *Nautilus*. For this reason the interpretation of the function of attachment scars in ammonoids remains speculative or obscure because of the difficulties of comparing these scars with those in Recent *Nautilus*. In ammonoids the body chamber is longer and more compressed than in *Nautilus* and the shape of the apertural margin differs markedly from that in fossil nautiloids and *Nautilus*.
3) Differences in the form and position of attachment sites between ammonoids and Recent *Nautilus* indicate different soft body organization. Different soft body organization may depend on shell morphology and on a different mode of life.
4) Differences in the form and position of attachment structures between goniatites and ammonites may indicate an increasing differentiation of the muscular system in the phylogeny of this group. Differences in the modes of life and different habitats are proved by the differences in the attachment structures.



Text-Fig. 6.
Soft body reconstruction of a generalized goniatite.
dl = aperturally closed double line; cr = cephalic retractor muscle; hr = hyponome retractor muscle; mb = myoadhesive band.

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Plate 1

Lateral and ventral attachment structures of some Palaeozoic and Mesozoic specimens.

A: *Tornoceras typum* (MB. C2907).
Lateral view.

B: *Cheiloceras verneuili* (MB. C2904).
Lateral view.

C: *Linguatornoceras haugi* (MB. C2911).
Ventral view of the body chamber.

D: *Linguatornoceras guestphalicum* (MB. C2906).
Lateral view.

E: *Cheiloceras subpartitum* (MB. C 2913).
Lateral view.

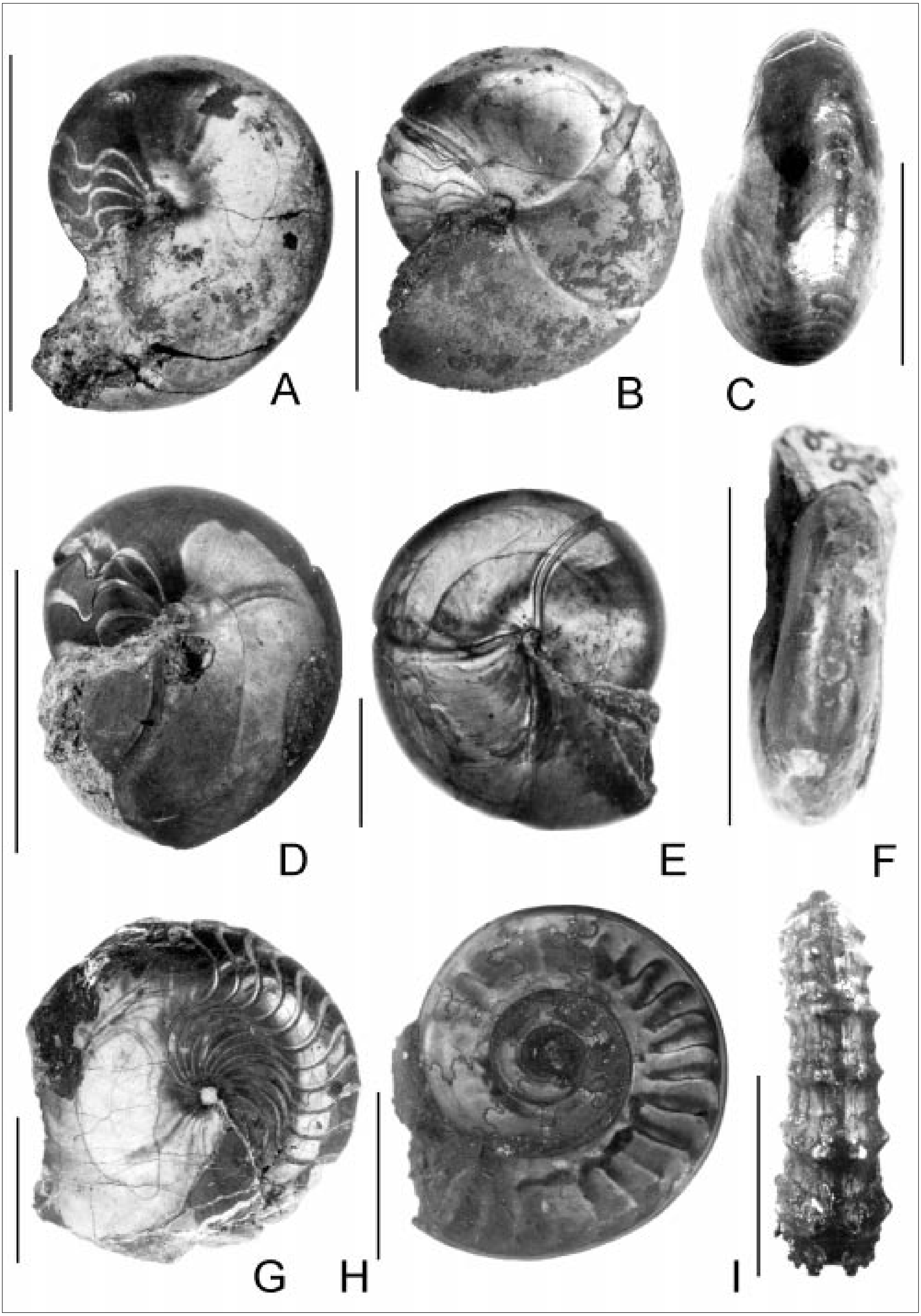
F: *Oedania delicata* (Ma 13442).
Ventral view of the phragmocone and body chamber.

G: *Cheiloceras praelentiforme* (MB. C2909).
Lateral view.

H: *Arieticeras* aff. *falciplicatum* (L249, originally figured in JORDAN 1968, Tab. 5, Fig. 2).
Lateral view.

I: *Ancyloceras trispinosum* (Ma 13443).
Ventral view of the phragmocone.

Scale bar = 1 cm.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