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Coleoids from the Lower Devonian Black Slate („Hunsrück-Schiefer") of the Hunsrück (West Germany)

Coleoidea aus dem unterdevonischen Schwarzschiefer („Hunsrück-Schiefer") des Hunsrück (Westdeutschland)

By

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With 39 figures in the text

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Abstract: Three new genera of endocochleate cephalopods from the Lower Devonian cast new light on the evolution of modern and fossil coleoids. *Protoaulacoceras* n. g. represents the rostrum-bearing line of aulacocerid-belemnitid type, while the ontogeny shows still features of the michelinoceratid ancestors. In contrast, *Boletzkya* n. g. and *Naefiteuthis* n. g., in which the chambered part of the shell looses its function during ontogeny, show a trend towards Mesozoic Loligosepiidae and recent teuthids.

Key words: New taxon, Coleoidea, Siegenian, Hunsrück-Shale, shell, test, ontogeny, phylogeny, classification; Rhenish Massif (Hunsrück, Gmünden), Rhineland Palatinate.

Zusammenfassung: Die neuen Formen endocochleater Cephalopoden aus dem Unterdevon werden die Vorstellungen über die Evolution der fossilen wie auch der modernen Cephalopoden verändern. Im Falle von *Protoaulacoceras* n. g. handelt es sich um eine rostrumtragende Form, wie die späteren Aulacocerida und Belemnitida, deren Gehäusejugendstadien noch den michelinoceratiden Vorfahren gleicht. Die Gattungen *Boletzkya* n. g. und *Naefiteuthis* n. g. zeigen dagegen eine Entwicklung in Richtung auf die mesozoischen Loligosepiidae und Verwandte und die rezenten Teuthiden, indem der gekammerte Teil der Schale während der Ontogenese immer stärker reduziert wird.

Introduction

Since hundreds of years the Lower Devonian of the Hunsrück has been the source of unusually well preserved fossils. They are embedded in a black slate and more or less converted into pyrite. This pyrite gives a good contrast in radiographs and in some cases reveals even remains of soft parts,

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so that a lot of unknown details of animals of the Devonian sea could be found (STÜRMER & BERGSTRÖM 1973). Data regarding the radiographic technique and informations about the properties of the ancient Hunsrück-Sea can be gathered from STÜRMER (1969). The coleoids described here come from the famous "Kaisergrube" near Gmünden, an old slate mine that had been in use for over 100 years. At the site of the now closed mine, an outcrop has been excavated for scientific purpose. It is from here and from the old waste of the mine that the material has been collected. The slate slabs are split into 5 to 10 mm thin plates in the field and are screened with X-rays right in the quarry.

Diagenesis

During deposition of the "Hunsrück-Schiefer" (Lower Devonian) pelitic sediments were dominant. Rock forming processes have transformed these muds into slates. The original lamination is preserved because in this locality the plane of schistosity is parallel to original bedding planes. The bulk of the rocks studied is from totally undisturbed sediments. Only a few specimens show burrowing by trace fossils, mainly *Chondrites*.

The fossilisation of the cephalopods generally corresponds to the following preservational history:

After death and decay of the soft parts, the shell dropped to the seafloor and was subsequently mud-covered. Many of the shells, particularly the smaller ones, were enclosed in fecal pellets when they reached the seafloor. Evidence for this can be seen in the living chambers of the juvenile shells of cephalopods that were only partly sediment-filled. Since they were partly clogged by fecal material, fine grained bottom sediment could not enter. This portion of the living chamber may have been filled later with pyrite (Figs. 7, 9, 24) and was often misinterpretated as remains of the soft parts. As soon as the shell was covered with sediment, may be even earlier, it definitely came under anaerobic conditions. Then pyrite formation started. Water-filled lumina totally or partly became filled with pyrite. Also organic shell became partly transformed into pyrite. More or less at this time, the aragonitic shell portions totally dissolved, so that only the organic components of the shell were left behind. At this stage, the fossil had not yet been deformed.

During further compaction of the sediments the fossils became flattened with different parts of the fossil reacting differently. Pyrite-filled portions, like chamber lumina, behaved like rigid blocks, while demineralized conchs could be stretched (Figs. 12, 20, 24) and more solid and thicker organic conchs became irregularly fragmented (Figs. 17, 19, 22, 31). Rigid blocks could be rotated during compaction to some degree, while the plastic organic material surrounding them became deformed, stretched and flattened. Much later, during the tectonic formation of schistosity, the whole fossil became further deformed. Rigid elements could break up by distension cracks (Figs. 1, 2) and could be deformed in this general shape. This rather complicated course of diagenesis has to be taken into consideration when the fossils are reconstructed.

Systematic description

Subclass Coleoidea BATHER 1888
Superorder Belemnomorpha REITNER & ENGESER 1982
Order Aulacocerida STOLLEY 1919
Family Protoaulacoceratidae n. fam.
Type genus *Protoaulacoceras* n. g.

Family diagnosis: First chamber egg-shaped, phragmocone longiconic with circular cross-section, septal distance wide. Guard formation late during ontogenesis. Guard constructed of superimposed concentric shell material. Living chamber long; aperture circular.

Included genera: only *Protoaulacoceras* n. g.

Genus *Protoaulacoceras* n. g.

Type species: *Protoaulacoceras longirostris* n. g. n. sp.
Diagnosis: see family diagnosis.
Differential diagnosis: see species differential diagnosis.

Protoaulacoceras longirostris n. g. n. sp.

Derivatio nominis: According to the latin words "longus" = long, "rostrum" = spur of a roman war-ship.

Holotype: Fig. 1, 2, Bayrische Staatssammlung für Paläontologie und historische Geologie München (BSSPHGM) no. 6016.

Paratypoids: Figs. 3, 4, 9 BSSPHGM no. 6017, negative no. 126, 214, 186.

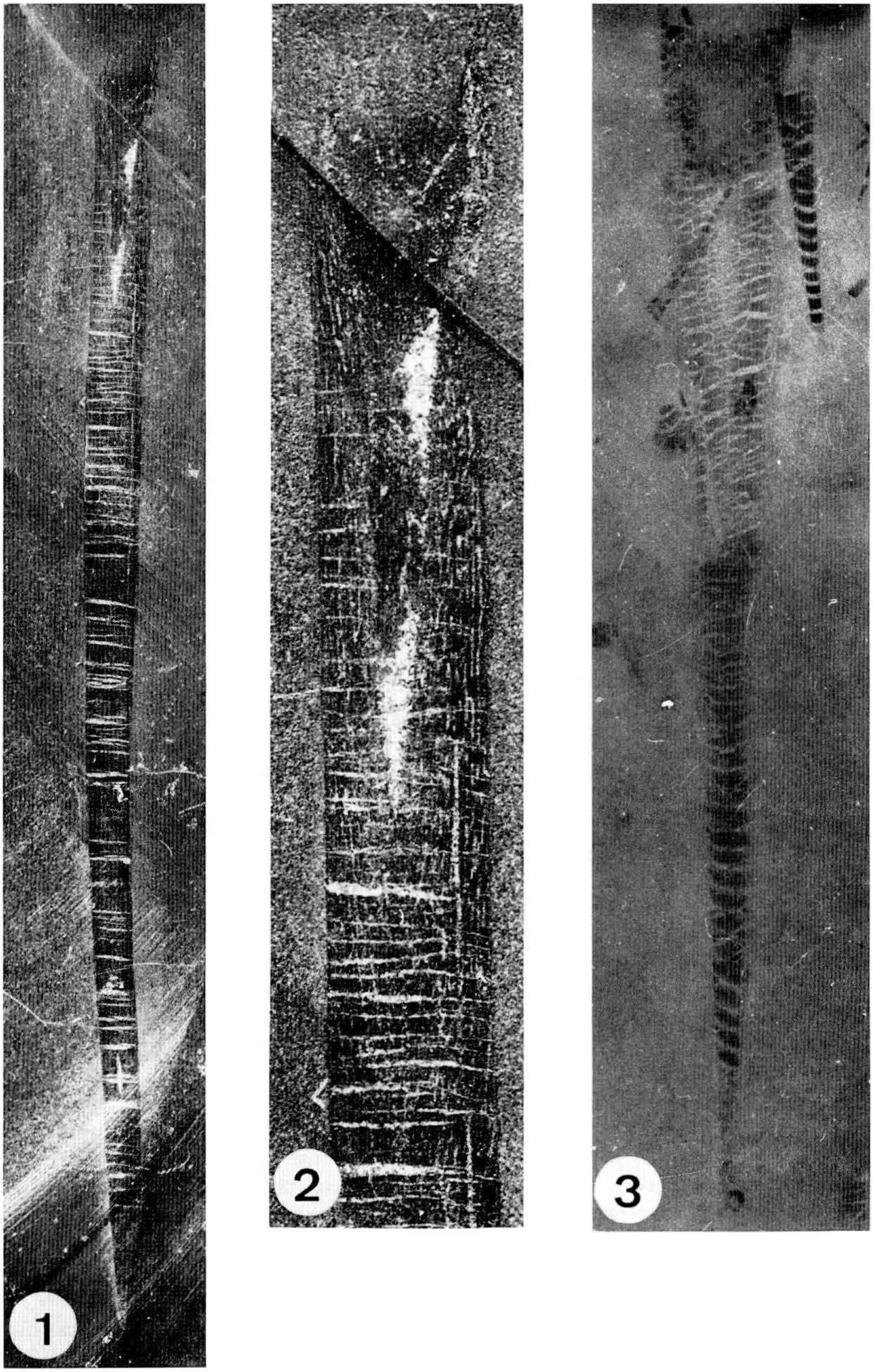
Locus typicus: Kaisergrube, Hunsrück, West Germany.

Stratum typicum: "Hunsrückschiefer", Lower Devonian.

Diagnosis: First chamber (protoconch) 0,3 to 0,4 mm wide and 0,8 to 1,3 mm long. The 18—25 camerae are generally about as long as wide. Apical angle 2—5°. Shell surface smooth. Sutures straight, simple and transverse. Camerae spacing after the 20th more variable than before. Main guard formation postdates formation of the 40th septum and 35 mm conch length. With 6 mm conch length the guard is very thin; at about 15 cm in central position it measures 6 mm. Siphuncle subcentral and cylindrical. Irregularities in septal spacing common.

Description of the holotype (Figs. 1, 2)

The holotype, an adult specimen, consists of a 15,6 cm long guard that has been cut longitudinally to demonstrate the existence of an alveole. The section does not follow the median plane throughout, but cuts the alveole adapically. The guard is composed of black material, now probably mainly



Figs. 1—3. *Protoaulacoceras longirostris* n. g. n. sp.

1: Guard of adult individual cut along long axis. Type species no. 6016, x 1.

2: Portion of guard illustrated in Fig. 1, showing alveole and concentric shell layers, x 1.

3: Whole conch of a young adult with phragmocone and living chamber covered by first mineral deposits of the guard. Paratypoid 1, no. 6017, neg.no. 126, x 2,5.

apatite, definitely not pyrite. Its consists of concentric lamellae, each about 0,1—0,2 mm thick.

Transversal cracks have developed during diagenesis and are now filled with carbonate. The width of a guard at the proximal end is 0,7 cm, its apical angle 6—7° and its alveole angle about 5°.

Description of the paratypoids

Paratypoid 1 (Fig. 3; negative no. 126)

The conch of this late juvenile specimen is 6,5 cm long. Its phragmocone is somewhat longer than the living chamber. The whole conch is covered with thin rostral deposits. The aperture is straight with an inner and outer lip at the same level.

Paratypoid 2 (Fig. 4; negative no. 214)

Juvenile specimen with a conch length of 35 mm. Only the phragmocone with 41 septa is preserved. Adapical width 1 mm, apical 0,4 mm. Apical angle 2—3°. First 21 septa higher than wide, later ones wider than high.

Paratypoid 3 (Fig. 9; negative no. 186)

Early juvenile specimen; conch length 3,5 mm. Composed of a bullet-shaped phragmocone with 2 chambers, 1,1 mm in length, and a living chamber.

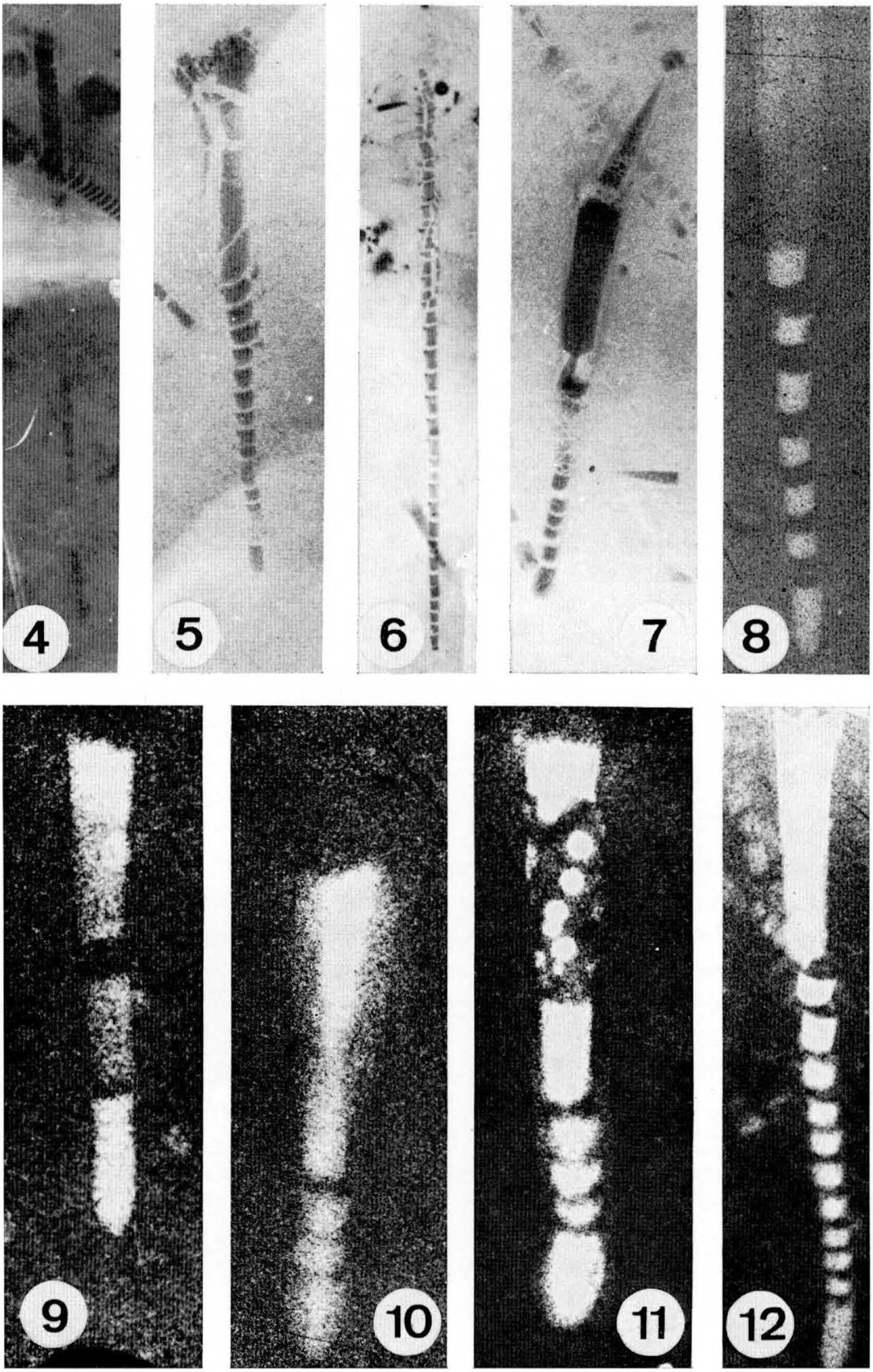
Differential diagnosis

The juvenile shell and the position of the siphuncle (without rostrum) very closely resemble orthoceratids such as *Michelinoceras grande* (see SERPAGLI & GNOLI 1977). In this Upper Silurian Michelinoceratid the first chamber is somewhat shorter and septal spacing is more regular, but the main different is the absence of a guard in *Michelinoceras grande* in contrast in its presence in *Protoaulacoceras longirostris.*

The adult shell of the Carboniferous genus *Hematites* (FLOWER & GORDON 1959), the earliest Aulacocerid known so far, shows a short and solid rostrum and a marginal (ventral) siphuncle. While the guard of *Protoaulacoceras* consists of organic material, it was probably aragonitic in *Hematites,* as it is in most Aulacocerid cephalopods (JELETZKY & ZAPFE 1967). The *Hematites* phragmocone shows an apical angle of about 10—15° in contrast to 2—5° in *P. longirostris.*

Paleobiology

The abundance of juvenile shells at some levels of the "Hunsrück-Schiefer" enabled us to establish to ontogeny of *Protoaulacoceras*: The animal hatched with a shell 3 mm long from an egg that must have been



Figs. 4—12 (Legend see p. 403)

longer than wide, measuring at least 5 mm in greatest length. At this stage the shell phragmocone had only one phragmocone chamber and living chamber almost twice as long. The newly hatched animal was most likely a miniature adult, like in most endocochleates, with the muscle mantle covering the whole shell. Subsequent growth stages with two and more (up to 10) camerae are also common (hundreds of specimens). In a conch with 5 chambers the living chamber measured 6 mm in length, with 10 chambers 10—12 mm, with 12 camerae 13 mm, with 15 camerae about 15 mm. Septal spacing is commonly irregular. A guard begins to form after the conch has reached 5,5—6,5 cm in length. It is possible that in earlier stages the animal used only the liquid in the phragmocone to balance its body, while additional weight was added with further growth by secretion of a rostrum onto the endocochleate shell.

Superorder Palaeoteuthomorpha n. superordo

Diagnosis: Coleoidea with primitive phragmocone dominant early and a teuthid living chamber later in ontogeny in contrast to the Teuthida which have a reduced living chamber (gladius) throughout.

Order Boletzkyida n. ordo

Including families: Boletzkyidae, Naefiteuthidae.
Diagnosis: s. a.

Figs. 4—13. *Protoaulacoceras longirostris* n. g. n. sp.

4: Phragmocone of a late juvenile with 41 septa but still without a guard. Paratypoid 2, neg.no. 214, x 2.

5: Juvenile conch with phragmocone and living chamber preserved. 15 chambers are present; the living chamber has been fractured during compaction. Paratypoid 3, neg.nos. 186 and 95, x 4.

6: Late juvenile shell with only phragmocone preserved. Of the 29 chambers only the last 4 are wider than high, neg.no. 214, x 2,2.

7: Juvenile with "living chamber" and a phragmocone with 11 chambers of variable hight. At this stage the living chamber is relatively large compared to the phragmocone, no. 6014, x 4,3.

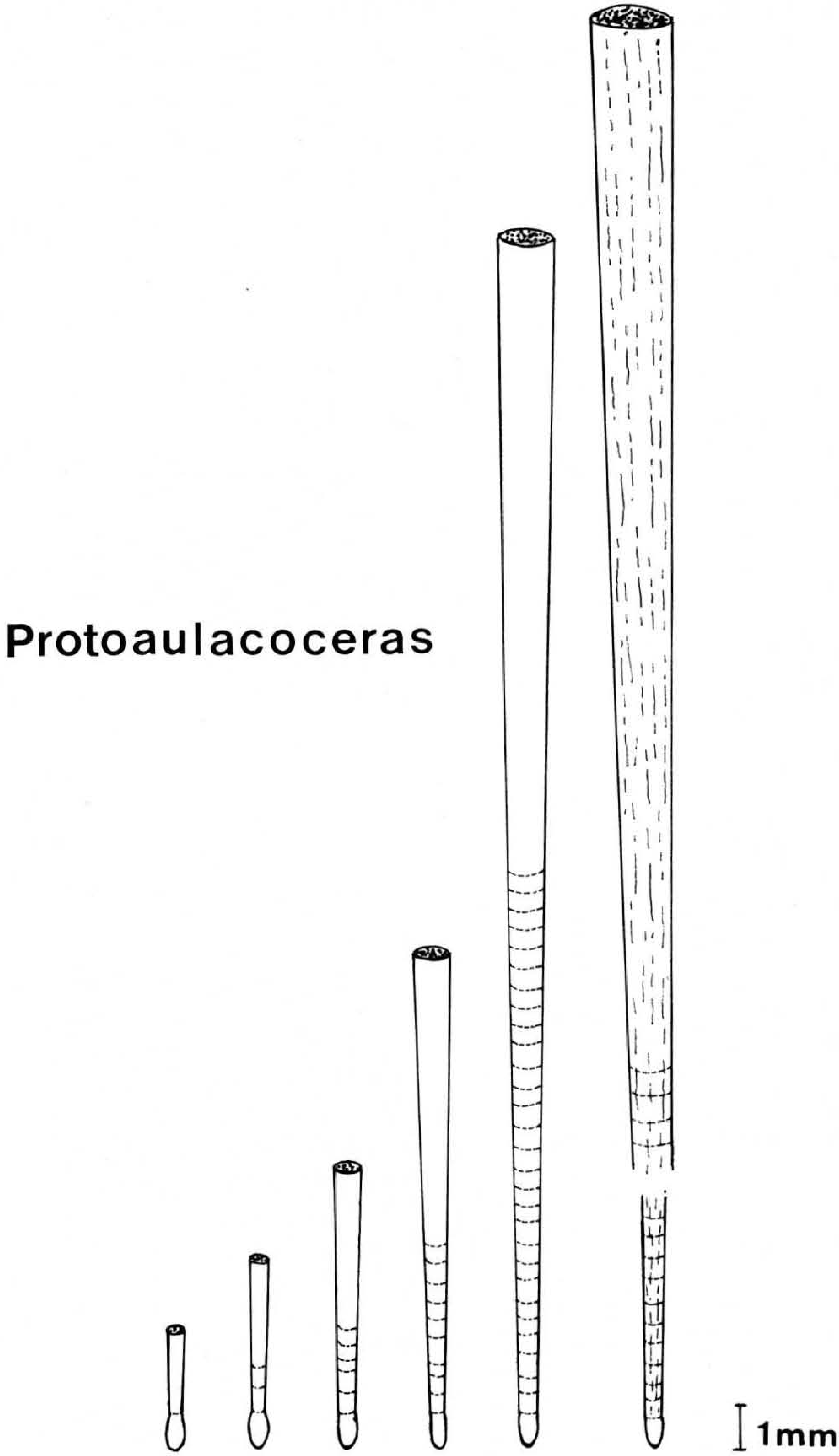
8: Juvenile with 6 or 7 chambers and the bullet shaped initial chamber. During diagenesis the "living chamber" has become demineralized and folded along a median line which should not be mistaken for a siphuncular tube, neg.no. 85, x 12.

9: Paratypoid 3. Early juvenile specimen composed of the bullet shaped first chamber and one additional one. Upon hatching the conch was little smaller and had only the first chamber completed, neg.no. 186, x 15.

10: Early juvenile with 3 chambers completed.

11: Early juvenile with 4 chambers completed. The living chamber is partly filled by fecal material and apically with pyrite, x 13.

12: Complete conch of juvenile with 11 chambers which after pyrite-filling and demineralization became deformed.



13: Sketch demonstrating the ontogenetic development of *Protoaulacoceras longirostris* n. g. n. sp. Shell at hatching stage; intermediate stages are of *Michelinoceras*-type; eventually (right) a guard forms.

Family Boletzkyidae n. fam.

Type genus: *Boletzkya* n. g.

Diagnosis: First chamber spherical. Early juvenile conch longicone, septal chambers wider than long, cross-section circular. Septa simple and transversal. Living chamber with simple, rounded aperture. In later juvenile stages the septa become crowded and inclined. At the same time the living chamber is enlarged relative to the phragmocone and developes a dorsal median keel and two lateral keels, corresponding to a central and two lateral projection of the aperture. Inner (ventral) lip shorter than outer (dorsal) one.

Genus *Boletzkya* n. g.

Type species: *Boletzkya longa* n. g. n. sp.

Diagnosis: Boletzkyidae with small apical angle. Juvenile phragmocone with at least 5 transversal septa.

Derivatio nominis: In honour of the distinguished cephalopod specialist SIGURD VON BOLETZKY.

Paratypoids: Figs. 19, 16, 21, 24 BSSPHGM no. 6009, negative no. 195,

Boletzkya longa n. g. n. sp.

Derivatio nominis: According to the latin word "longus" = long.

Holotype: Fig. 14 BSSPHGM no. 11059.

Paratypids: Figs. 19, 16, 21, 24 BSSPHGM no. 6009, negative no. 195, 85, 94.

Locus typicus: Kaisergrube, Hunsrück, West Germany.

Stratum typicum: "Hunsrück-Schiefer", Lower Devonian.

Diagnosis: First chamber subspherical, 0,5—0,9 mm wide and a little less in hight. Septa more or less regularly spaced, chambers usually wider than long. In stages with less than 5 camerae, phragmocone and living chamber are about equal in length (4 mm each) and the aperture is round and simple. In later stages (8 mm conch length) a dorsal keel develops and two lateral keels are added. At stages with 6th to 10th chambers the septa become inclined and crowded, while the living chamber increases in size relative to the phragmocone.

Description of the holotype (Fig. 14)

Adult specimen 16,5 cm in length with an apical angle of 9° and maximum width of 1,7 cm.

Description of the paratypoids

Paratypoid 1 (Fig. 19)

The nearly adult specimen is 31 mm long with a phragmocone 7 mm in length and 8 chambers; apical angle 5°.

Paratypoid 2 (Fig. 16; negative no. 195)

The late juvenile specimen is 19 mm long. It has a phragmocone with 7 straight and 5 inclined chambers and a living chamber 2x phragmocone length. A median keel begins to form at the base of the living chamber.

Figs. 14—17 (Legend see p. 407)

P a r a t y p o i d 3 (Fig. 24; negative no. 85)
The juvenile specimen is 17 mm long with rounded aperture; 7 septa are present, all transversal. The first chamber is spherical.

P a r a t y p o i d 4 (Fig. 24; negative no. 94)
The early juvenile specimen is 5 mm long and has only 2 septa.

Differential diagnosis

Juveniles of *Boletzkya* have a more spherical and wider first chamber (protoconch) than *Protoaulacoceras*. Also the septal distances are smaller. Juveniles of *B. longa* are very similar to those of *B. hunsrueckensis* n. sp. The apical angle is between 5—10° in juvenile and adult conchs, always less than in *Naefiteuthis*. Juvenile shells of *Boletzkya* and *Naefiteuthis* resemble the early ontogenetic stages of *Sphaerorthoceras* and related genera (RISTEDT 1969, SERPAGLI & GNOLI 1977).

Paleobiology

On the basis of our material the ontogenetic history of the species can be reconstructed. The animal must have hatched from the egg with only one septum completed and a conch about 3—4 mm long. It resembled the adult, but was comparatively shorter. With 2 septa completed the living chamber was up to 5 mm long. Septa tend to be regularly spaced, but septal crowding as well as very high camerae may also occur. During later juvenile life, the phragmocone increased in size relative to the living chamber until, at about 8 mm conch length, it reached equal length. Afterwards the median keel made its appearance and the inner (ventral) lip was retarded in growth while the outer (dorsal) lip grew into a gladius-like proostracum. Together with the formation of the keel, the 6th—10th septa became inclined and distances between them decreased simultaneously. The "gladius" became enlarged so rapidly that specimens with phragmocone lengths slightly above 4 mm had already grown to a length to 15 mm; i.e. the

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Figs. 14—17. *Boletzkya longa* n. g. n. sp.

14: Holotype preserved as compressed fossil on the bedding plane, no. 11059, x 1.

15: Large "living chamber" of a young animal with prominent median and lateral keels ending in three apertural projections. Only the last phragmocone chambers are preserved, no. 6030, neg. no. 224, x 2.

16: Paratypoid 2 of late juvenile individual with "living chamber" grown to almost double the size of the phragmocone, neg.no. 195, x 3,5.

17: Conch of young animal with three keels projecting on the aperture and phragmocone broken in two pieces with about 10 septa visible of the 19 present, neg.no. 83, x 4,3.

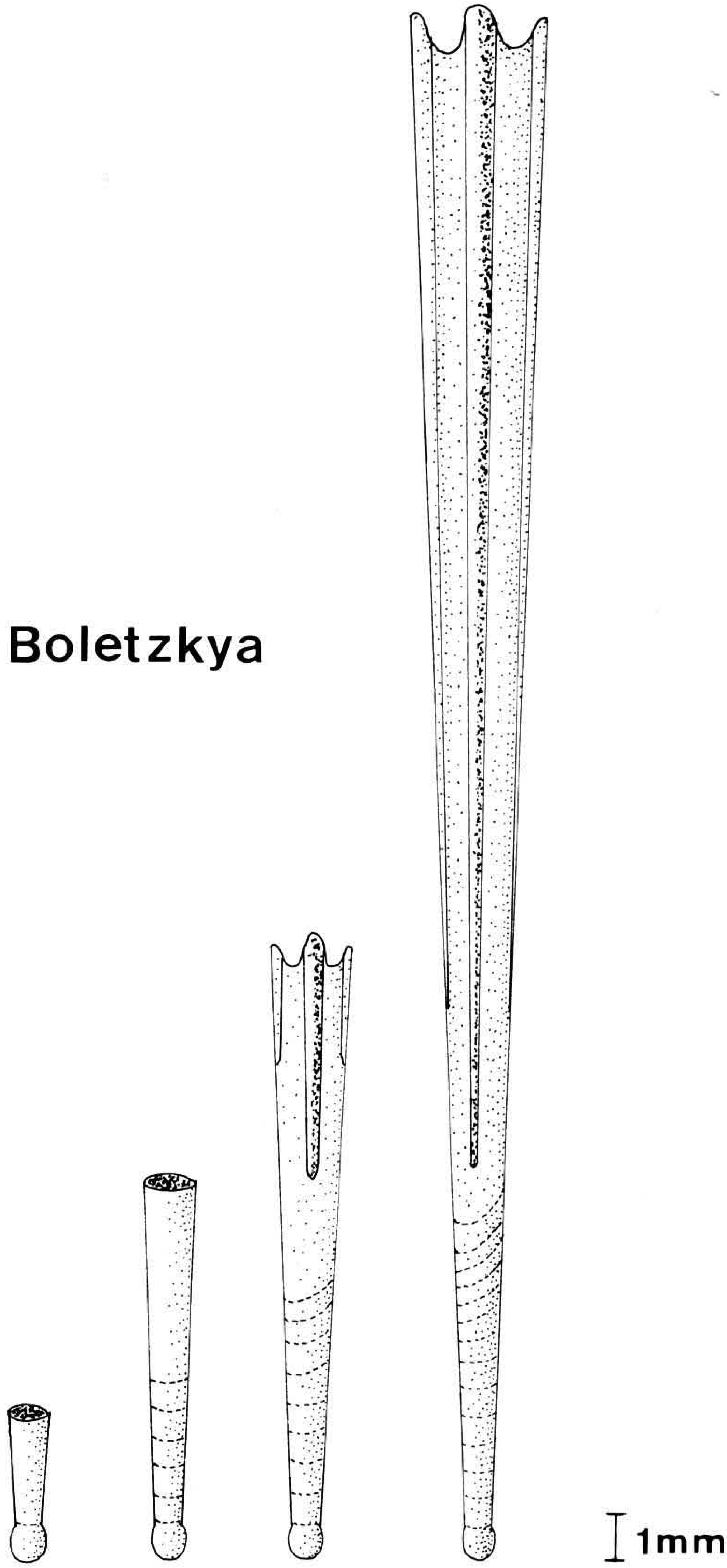


Fig. 18. Sketch demonstrating the ontogenetic development of *Boletzkya longa* n. g. n. sp. Left: hatching stage. Next stage is *Michelinoceras*-like while in the following one a keel makes its appearance and the typical gladius-like shape of the "living chamber" dominates more and more over the phragmocone size (right).

living chamber section had reached almost three times the length of the phragmocone and with 9—13 chambers the "gladius" increased to three to five times the length of the chambered conch. A 70 mm long "gladius" thus corresponds to a phragmocone of about 13 mm with 20 septa, a 100 mm gladius to a chambered shell of only about 15 mm. The adult animal was slender and streamlined and could move by jet propulsion of the funnel, stabilized by the fins of the muscle mantle.

Boletzkya hunsrueckensis n. sp.

Derivatio nominis: According to the German landscape Hunsrück.
Holotype: Figs. 25, 26; BSSPHGM no. 6025.
Paratypoid: Fig. 27; BSSPHGM no. 1862.
Locus typicus: Kaisergrube, Hunsrück, West Germany.
Stratum typicum: "Hunsrück-Schiefer", Lower Devonian.
Diagnosis: Apical angle 10—14° in juvenile and 10—18° adult shells. Dorsal median keel appears at conch length of 15 mm. Up to 11 septa are straight and transversal, subsequent septa increasingly inclined.

Description of the holotype (Figs. 25, 26)

Conch fragment of an early adult specimen 35 mm in length with 25—27 septa of increasing inclination, preserved as body fossil and studied by X-ray. Apical angle 11°.

Description of the paratypoid (Fig. 27)

Nearly adult phragmocone 37 mm in length with an apical angle of 16° and 17 inclined septa; juvenile septa are poorly preserved.

Differential diagnosis

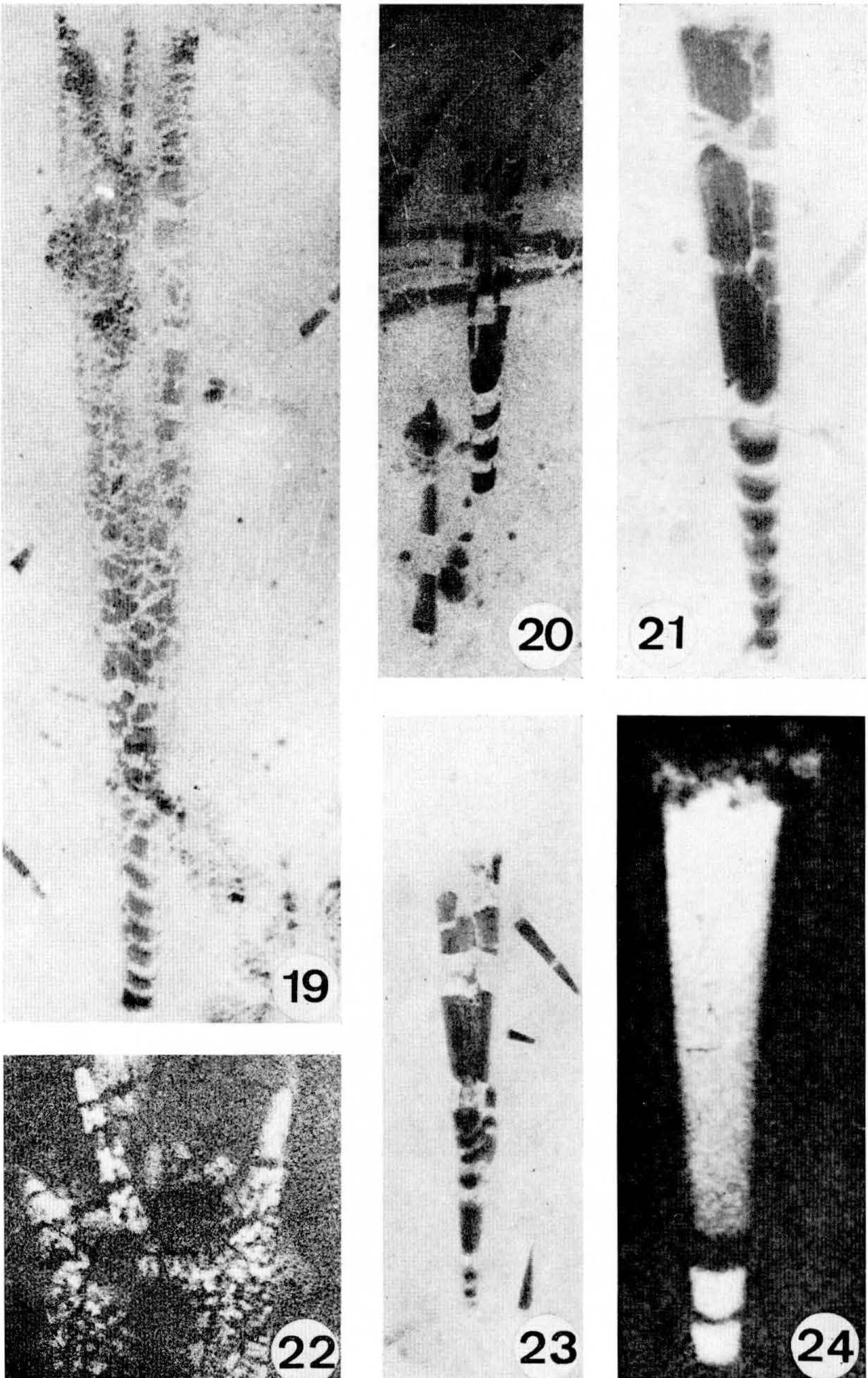
The difference to *B. longa* lies in the wider apical angle of the early and late stages and in continued increase of the phragmocone.

Family Naefiteuthididae n. fam.

Type genus: *Naefiteuthis* n. g.
Diagnosis: Apical angle large, juvenile shell with less than 5 septa. Phragmocone does not develop well.

Genus *Naefiteuthis* n. g.

Type species: *Naefiteuthis breviphragmoconus* n. g. n. sp.
Derivatio nominis: In honour of the cephalopod worker ADOLF NAEF.
Diagnosis: see family diagnosis.
Differential diagnosis: see differential diagnosis of type species.



Figs. 19—24 (Legend see p. 411)

Naefiteuthis breviphragmoconus n. g. n. sp.

Derivatio nominis: Latin "brevis" = short and greek "phragmos" = perforated and "konos" = cone.

Holotype: Fig. 31; BSSPHGM no. 6015.

Paratypoids: Figs. 33, 36; negative nos. 83, 109.

Locus typicus: Kaisergrube, Hunsrück, West Germany.

Stratum typicum: "Hunsrück-Schiefer", Lower Devonian.

Diagnosis: First chamber 0,5—0,6 mm wide and spherical, following chambers equal height, but rapidly increasing in width. Beyond the 3rd—4th chamber, septa are less distinct and appear, if at all, as a transversal striation of very slow increase in width. At a length of 2 mm the conch develops a dorsal median keel and two lateral keels. Apical angle between 18—30°.

Description of the holotype (Fig. 31)

Conch length 20 mm. First septa indistinct (about 5), initial chamber not preserved. Median keel well developed, reaching onto the phragmocone. Lateral keel strong. Right ventral side of living chamber side folded outwards, as in Jurassic Loligosepiidae. Apical angle 18°.

Description of the paratypoids

Paratypoid 1 (Fig. 33; negative no. 83)

13 mm long; first septa indistinct, initial chamber not preserved. Median keel strong, lateral keels occur later. Aperture with well developed projections of the three keels. Apical angle 20°.

Paratypoid 2 (Fig. 37; negative no. 109)

6 mm long; first chamber spherical, 3—4 indistinct septa. Median keel indistinct. Apical angle 19°.

Figs. 19—24. *Boletzkya longa* n. g. n. sp.
(Figs. 21, 22, 24 could also belong to *B. hunsrueckensis*)

19: Paratypoid 1: young adult specimen with well preserved "living chamber" and incomplete phragmocone. No. 6009, neg.no. 95, x 4.

20: Late juvenile individual with three well developed keels on "living chamber" which is only slightly larger than the (fractured) phragmocone, neg.no. 269, x 4.

21: Paratypoid 3: juvenile with conical "living chamber", simple aperture and 7 straight septa, neg.no. 85, x 4.

22: Apical end of the "living chamber" with three thorns representing the projections of the three keels, ne.no. 109, x 7,5.

23: Late juvenile stage with phragmocone bearing 9 septa of which the last two are inclined. Keels present at the aperture, neg.no. 200, x 4.

24: Paratypoid 4 of early juvenile specimen with long "living chamber" and two chambers only. neg.no. 94, x 14.

Figs. 25—30 (Legend see p. 413)

Differential diagnosis

In contrast to *Boletzkya*, *Naefiteuthis* does not develop a clear phragmocone. Also the median keel appears very early in ontogeny.

Paleobiology

The animals probably hatched with the first 2—3 septa completed and a conch length of about 2 mm. Immediately afterwards the three keels appeared. The phragmocone was perhaps only weakly calcified. The hatching stage closely resembled adult animals in shape. An adult specimen may be represented by an individual that is embedded in ventral position. It measures 16,1 cm in length, 3,5 cm in maximum width and an apical angle of 20—25°. The shape of the living chamber resembles that of a Triassic *Aulacoceras* (JELETZKY 1966, pl. 5 + 6). The median keel is seen as a ridge on the dorsal side while one of the lateral keels is seen in dorsoventral position.

Discussion

The early ontogenetic conchs of *Protoaulacoceras* n. g. and *Boletzkya* n. g. resemble that of Upper Silurian michelinoceratid cephalopods (RISTEDT 1969, SERPAGLI & GNOLI 1977), while later ontogenetic stages resemble more modern coleoids.

The ontogenetic development of the phragmocone suggests that in *Protoaulacoceras* it played an important role throughout life while in *Boletzkya* it seems to have lost its importance in the adult and in *Naefiteuthis* it was functional at most during very early ontogenetic stages.

Figs. 25—27. *Boletzkya hunsrueckensis* n. g. n. sp.

25: Surface photograph of holotype representing uncomplete phragmocone of an adult individual, no. 6025, x 2.

26: X-ray radiograph of holotype showing the numerous, closely spaced and strongly inclined septa; x 2.

27: Paratypoid 1: note the wide apical angle characteristic for this species as well as some of the narrowly spaced septa of the adult, no. 1862, x 2.

Figs. 28—30. Adult ? *Naefiteuthis breviphragmoconus* n. g. n. sp.

28: Negative impression of individual figured in Fig. 29 showing laterally compressed "living chamber" with median keel, lateral keels and longitudinal striation, no. 11124, x 1.

29: Positive to Fig. 28. In X-ray radiograph these fossils can not be traced. They may represent adult individuals of the species *Naefiteuthis breviphragmoconus* n. g. n. sp. which is based on juvenile individuals, x 1.

30: Crushed impression of living chamber possibly representing an adult *Naefiteuthis* without preserved phragmocone (without traces also on X-ray radiograph), x 1.

Figs. 31—37 (Legend see p. 415)

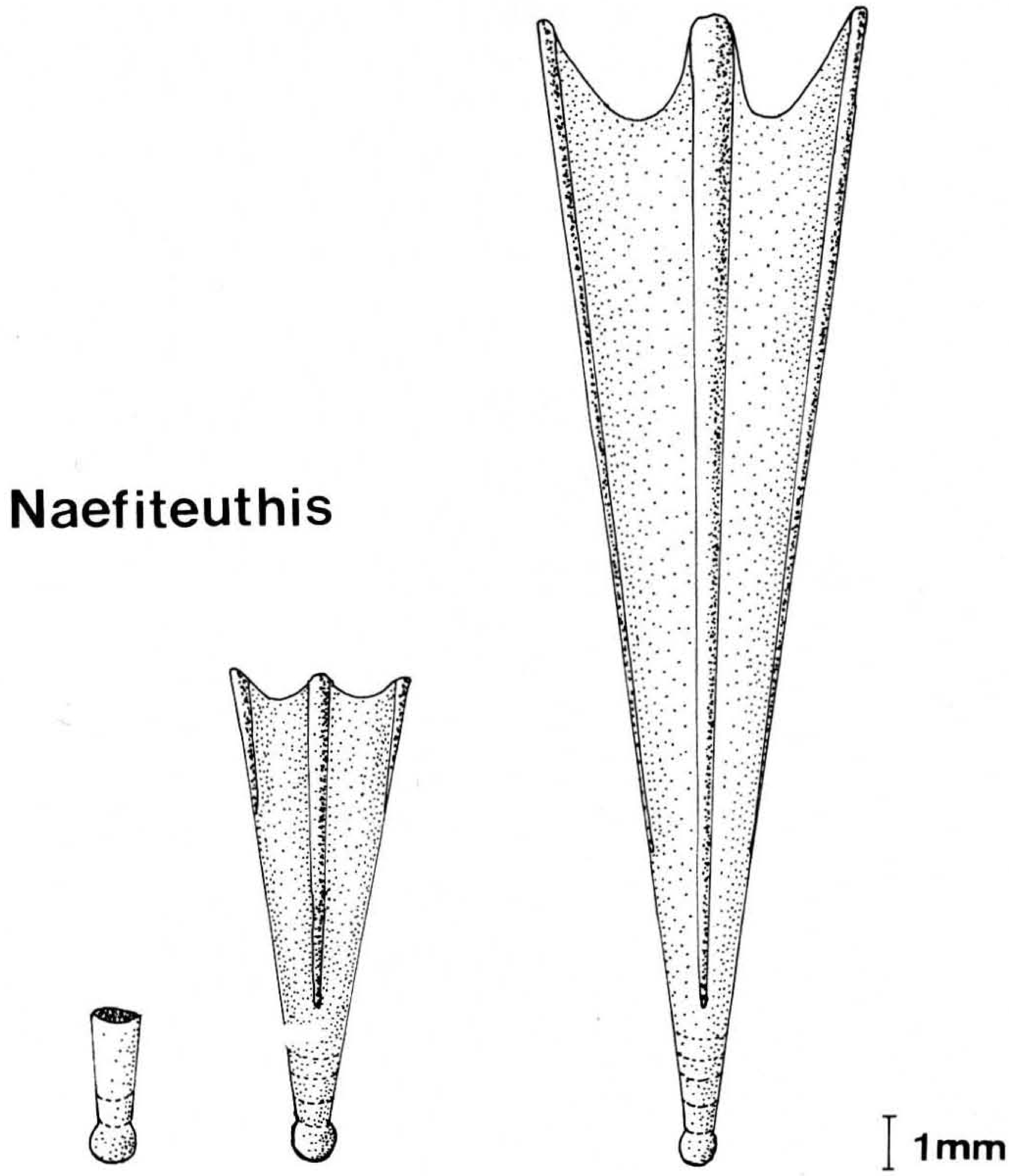


Fig. 38. Sketch demonstrating the ontogenetic development of *Naefiteuthis breviphragmoconus* n. g. n. sp. Left: hatching stage. Right: later stages with a keel forming and the *Loligosepia*-like appearance present throughout further life.

Figs. 31—37. *Naefiteuthis breviphragmoconus* n. g. n. sp.

31: Holotype with indistinct short phragmocone and distinct three keels. The aperture is eroded and the right ventral side of the conch is folded off laterally, no. 6015, x 6.

32: Conch with spherical first chamber and 3 following septa visible. "Living chamber" poorly preserved, neg.no. 101, x 4.

33: Paratypoid 1. The characteristic three keels appear very early and continue into well developed aperture hooks, neg.no. 83, x 4.

34: Juvenile conch with keels and 3—4 indistinct chambers in the short phragmocone, neg.no. 269, x 4.

35: Short conch with 3 indistinct chambers in short phragmocone and very prominent median keel, neg.no. 116, x 4.

36: Fragment of the apertural edge of the living chamber with very prominent median keel, neg.no. 186, x 8.

37: Paratypoid 2. Conch of early juvenile with keel formation starting on phragmocone with 5 chambers including spherical initial chamber, neg.no. 109, x 12.

Two adaptional strategies are represented by the small Lower Devonian coleoid fauna. One *(Protoaulococeras)* represents a trend, in which the combination of phragmocone and rostrum resembles the large group of the Triassic Aulacocerida and the Jurassic and Cretaceous belemnites.

The other trend *(Boletzkya, Naefiteuthis)* leads to gladius-bearing forms with reduced or missing phragmocone and thus to modern squids.

The earliest ontogenetic stages, found in all 4 species, demonstrate that these up to now most ancient coleoids had no larvae, but hatched with a basically adult design. In this respect Lower Devonian coleoids resemble modern coleoids (Boletzky 1974).

The shape of the first chamber and the size of the hatching individuals indicates that diameter of egg and capsule were similar to those in modern *Spirula* (Bandel & Boletzky 1979). The living chamber of *Boletzkya* and *Naefiteuthis* can be compared with Triassic (Reitner 1978) and Jurassic (Reitner & Engeser 1981) Loligosepiidae in which the inner lip (ventral wings in modern Teuthida) has become successively reduced in size.

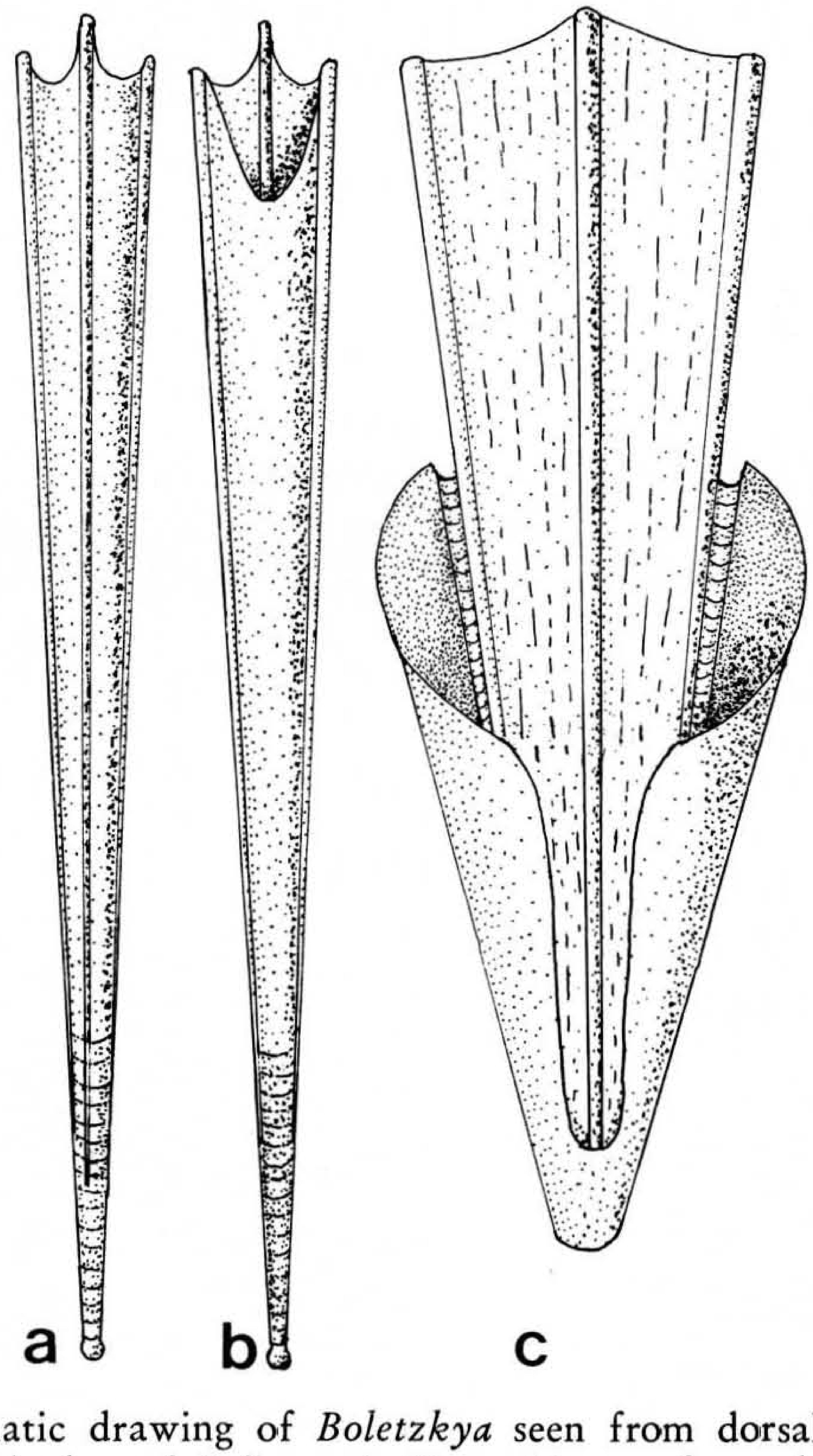


Fig. 39a, b, c. Schematic drawing of *Boletzkya* seen from dorsal (a) and ventral (b) side compared with that of *Loligosepia* (Jurassic) seen from the ventral side (c).

Literature

BANDEL, K. & BOLETZKY, S. v. (1979): A comparative study of the structure, development and morphological relationships of chambered cephalopod shells. — The Veliger, **21**: 313—354; Berkeley.

BOLETZKY, S. v. (1974): The "larvae" of Cephalopoda: A review. — Thalassis Jugosl., **10** (1/2): 45—76; Zagreb.

FLOWER, R. H. & GORDON, M. (1959): More Mississippian belemnites. — J. Paleont., **33**: 809—842; Tulsa.

JELETZKY, J. A. (1966): Comparative morphology, phylogeny, and classification of fossil coleoidea. — Univ. Kansas Paleont. Contr., Mollusca, Art. **7**: 1—162; Lawrence, Kansas.

JELETZKY, J. A. & ZAPFE, H. (1967): Coleoid and Orthocerid Cephalopods of the Rhaetian Zlambach Marl from the Fischerwiese near Aussee, Styria (Austria). — Ann. Naturhist. Mus. Wien, **71**: 68—106; Wien.

REITNER, J. (1978): Ein Teuthiden-Rest aus dem Obernor (Kössener-Schichten) der Lahnwies-Neidernachmulde bei Garmisch-Partenkirchen (Bayern). — Paläont. Z., **52**: 205—212; Stuttgart.

REITNER, J. & ENGESER, T. (1981): Eine neue Teuthiden-Art aus dem unteren Sinemurium (Lias alpha 3, „Ölschiefer") von Dusslingen bei Tübingen (Baden-Württemberg). — N. Jb. Geol. Paläont., Mh., **1981**: 425—430; Stuttgart.

RISTEDT, H. (1969): Zur Revision der Orhoceratidae. — Abh. Akad. Wiss., math. naturwiss. Kl., **1968** (4): 213—287; Mainz.

SERPAGLI, E. & GNOLI, M. (1977): Upper Silurian Cephalopods from Southwestern Sardinia. — Boll. Soc. Paleont. Ital., **16** (2): 153—196; Roma.

STÜRMER, W. (1969): Pyrit-Erhaltung von Weichteilen bei devonischen Cephalopoden. — Paläont. Z., **43**: 10—12; Stuttgart.

STÜRMER, W. & BERGSTRÖM, J. (1973): New discoveries on trilobites by X-rays. — Paläont. Z., **47**: 104—141; Stuttgart.

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