Stuttgarter Beiträge zur Naturkunde
Serie B (Geologie und Paläontologie)

Herausgeber:

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart

Stuttgarter Beitr. Naturk.	Ser. B	Nr. 356	15 S., 3 Abb., 1 Taf.	Stuttgart, 5. 12. 2005

The occurrence of the Tethyan ammonite genus *Meneghiniceras* (Phylloceratina: Juraphyllitidae) in the Upper Pliensbachian of SW Germany

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Abstract

The Tethyan ammonite genus *Meneghiniceras* Hyatt is recognized for the first time in the Amaltheenton Formation (Upper Pliensbachian, *Margaritatus* Zone) of the Swabian Lower Jurassic. Hitherto pyritic inner whorls of this genus described from this area as '*Ammonites tortisulcoides* Quenstedt' were misidentified as belonging to the genus *Sowerbyceras*. The juraphyllitid genera *Meneghiniceras* Hyatt, 1900 und *Harpophylloceras* Spath, 1927 are treated as synonyms, because their type-species are linked by intraspecific variation. In Swabia *Meneghiniceras* is restricted to the basal part of the *Gibbosus* Subzone, where it is accompanied by several other Tethyan immigrants. A preliminary overview is given on Tethyan immigration events in the Upper Pliensbachian of southwestern Germany.
Keywords: Ammonites, Phylloceratoidea, taxonomy, Lower Jurassic, Tethyan immigrants.

Kurzfassung

Aus der Amaltheenton-Formation (Ober-Pliensbachium, *Margaritatus*-Zone) des Schwäbischen Unter-Jura wird die tethyale Ammonitengattung *Meneghiniceras* Hyatt, 1900 erstmals erkannt. Pyritisierte Innenwindungen dieser Gattung waren aus dieser Region ursprünglich als *Ammonites tortisulcoides* Quenstedt beschrieben und später fälschlicherweise der Gattung *Sowerbyceras* zugerechnet worden. Die juraphyllitiden Gattungen *Meneghiniceras* Hyatt, 1900 und *Harpophylloceras* Spath, 1927 werden als synonym angesehen, da ihre Typusarten durch innerartliche Variation miteinander verknüpft sind. Das Vorkommen von *Meneghiniceras* beschränkt sich auf die basale *Gibbosus*-Subzone, in der auch einige andere tethyale Einwanderer auftreten. Zu den Einwanderungsereignissen aus der Tethys im Ober-Pliensbachium Südwestdeutschlands wird eine vorläufige Übersicht gegeben.

Contents

1. Introduction

The Liassic Amaltheenton Formation (Upper Pliensbachian) of Swabia crops out in the northern foreland of the Swabian Alb (Fig. 1; URLICHS 1977). In contrast to the underlying Numismalismergel Formation, it contains a relatively low diverse ammonite fauna, which is, however, often rich in specimens. The Amaltheenton s. str., which is sandwiched between the Zwischenkalke Member in the top of the Numismalismergel Formation and the Costatenkalk Member (Fig. 2), is characterized by the occurrence of the ammonite genus *Amaltheus*. This genus is classically considered typical of the Subboreal realm (e. g., MACCHIONI & CECCA 2002). Its migration towards the South was forced by cool currents, which are indicated by the scarceness of carbonates in the predominant clay facies of the Amaltheenton s. str. contrasting the more marly lithologies below and above, in which ammonites of Tethyan origin are widespread. Although the amaltheids strongly predominate in the ammonite faunas of SW Germany, for short periods some other ammonite groups spread from the Tethys. The same as for amaltheids may be said for pleuroceratids which are typical of the marly Costatenkalk Member. Tethyan faunal elements, however, are crucial for correlation and palaeobiogeographic aspects. Hence, in the past much attention was paid to these rare finds of 'exotic' ammonites from the Amaltheenton Formation, but some of them have got out of mind (e. g., OPPEL 1853, 1854; QUENSTEDT 1856–1858, 1885–1888; POMPECKJ 1893; ENGEL 1887, 1890, 1908; ZWIESELE 1898, 1899; BEURLEN 1924; FRENTZEN 1934; LÖRCHER 1953; SCHMIDT-EFFING 1972; FISCHER 1975; URLICHS 1977; SCHLATTER 1982, 1985). Several attempts of collecting ammonites bed-by-bed in the Amaltheenton Formation have been made in the past, but the results are insufficient because that material often lacks illustrations and therefore the original determinations cannot be verified

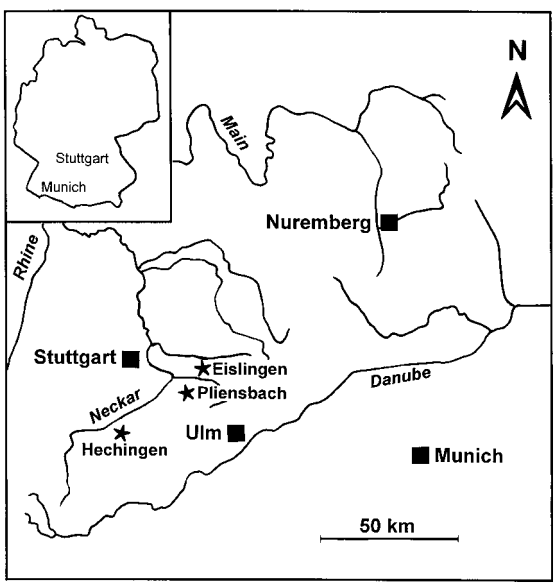

Fig. 1. Collecting localities of *Meneghiniceras* in the Upper Pliensbachian of SW Germany.

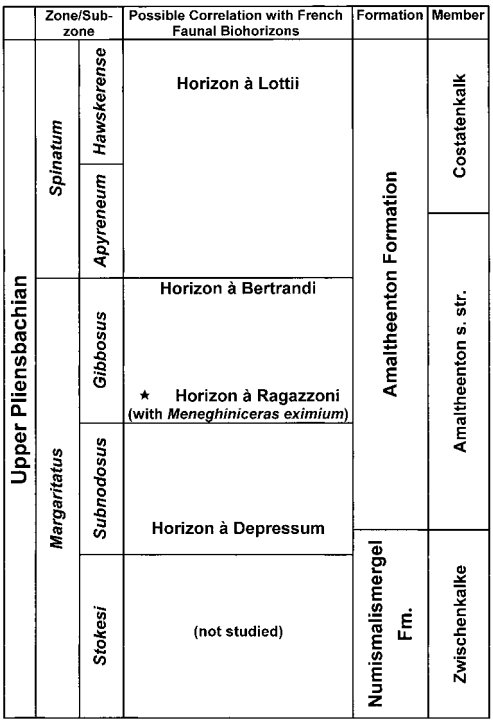

Fig. 2. Litho- and biostratigraphic subdivision of the Upper Pliensbachian of SW Germany, tentatively correlated with France.

without the original specimens. Today they are mostly lost due to pyrite dissolution or other unfavourable circumstances.

An ammonite finding (Pl. 1, Fig. 1) from the Amaltheenton Formation of Eislingen near Göppingen during the works of a road cutting in April 2004 stimulated this study. After the identification of the specimen as a phylloceratid belonging to the Tethyan genus *Meneghiniceras* HYATT, it was thought to be the first record of this genus from the Jurassic of SW Germany. Until now a single but excellently preserved adult specimen from the Lower Toarcian of England (Fig. 3) was regarded as the unique record outside the Tethyan realm (HOWARTH 1976). However, many specimens from the museums' collections including material collected bed-by-bed indicate that this genus is fairly common in Swabia, although the very small, mostly pyritic specimens have never been compared with this Mediterranean genus. QUENSTEDT (1885) was the first to describe these juvenile, minute specimens, which he termed *Ammonites tortisulcoides*. Although the shape of the constrictions and the sculpture strongly differs from *Sowerbyceras*, and in some little larger grown specimens also a keel is developed (POMPECKJ 1893), they were often erroneously attributed to this genus (WIEDMANN [in: DEUTSCHE SUBKOMMISSION FÜR JURA-STRATIGRAPHIE] 1973; SCHLEGELMILCH 1976; URLICHS 1977), which is hitherto only known from the Bathonian onward (JOLY 2000: 11). Most recently, MORARD (2004) interpreted *Ammonites tortisulcoides* QUENSTEDT as an early representative of *Holcophylloceras*, disregarding the presence of a keel.

Fig. 3. *Meneghiniceras eximium* (v. HAUER, 1854), var. *lariense* (MENEGHINI, 1875), adult specimen figured by HOWARTH (1976, text-figs. 1–2), Hawsker Bottoms, Whitby, Yorkshire, Jet Rock Series, Grey Shales, *Tenuicostatum* Zone, *Semicelatum* Subzone; BNHM no. BM C. 79625 (coll. U. LEHMANN). – Natural size.

Abbreviations

BNHM	British Natural History Museum, London
IFGT	Institut für Geowissenschaften der Universität Tübingen, Germany
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany

D	Diameter
H	Whorl height [in mm]
U	Umbilicus width [in mm]
W	Whorl width [in mm]

Acknowledgements

MARTIN KAPITZKE (SMNS) provided an important ammonite find from his collection. Drs. CHRISTIAN MEISTER (Geneva, Switzerland), GERD DIETL (SMNS), and MAX URLICHS (SMNS) supported valuable comments and information on Swabian sections. Many thanks should go to the referees MAX URLICHS (SMNS) and an anonymous one who helped substantially improving an earlier draft. Literature was kindly provided by Prof. FRANCESCO VENTURI (Perugia, Italy), Dr. FRANCESCO MACCHIONI (Vancouver, Canada), and Prof. Dr. REINHARD SCHMIDT-EFFING (Marburg, Germany). Dr. HARTMUT SCHULTZ (Tübingen, Germany) kindly loaned additional specimens. STEVE BAKER (BNHM) prepared excellent pho-

tographs of the specimen from Yorkshire. Dr. BARBARA KARWATZKI (Reutlingen, Germany) is thanked for some information about the missing collection of HEINRICH ZWIESELE.

2. Relationship between *Meneghiniceras* HYATT, 1900 and *Harpophylloceras* SPATH, 1927

A revision of the Late Pliensbachian juraphyllitids is beyond the scope of this study. However, some previous statements exist which elucidate the close relationship between the two genera *Meneghiniceras* and *Harpophylloceras*.

When introducing *Meneghiniceras* with its type species *Ammonites lariensis*, HYATT (1900: 568) did not give any diagnosis or comment. In the same way SPATH (1927: 38) erected *Harpophylloceras* (type species *Ammonites eximius* v. HAUER, 1854). BONARELLI (1895) distinguished two varieties of *'Rhacophyllites' lariensis*, var. *bicicolae* and var. *dorsinodosus* (BONARELLI 1895: 335). The variety *bicicolae* is based on a specimen published by MENEGHINI (1875, pl. 17, fig. 3), and the variety *dorsinodosum* is based on another specimen originally included in *Ammonites (Phylloceras) lariensis* by MENEGHINI (1875, pl. 17, fig. 1). Other varieties of *lariense* were described by FUCINI (1899, pl. 20, fig. 3, var. *costicillatum*) and by VENZO (1952, var. *mavigliai*, without illustration). Interestingly, FUCINI (1920) later assigned the taxon *eximius* to *Meneghiniceras*.

The type species of *Meneghiniceras* and that of *Harpophylloceras* are treated here as synonyms. For the first time FANTINI SESTINI (1974) focussed on a close relationship between these taxa. She was the first who supposed that they could even represent the same species, and she included the three above mentioned varieties introduced by BONARELLI (1895) and FUCINI (1899) in *M. lariense*. However, like most other authors, she strictly separated two nominal taxa according to the presence or absence of ventral clavi. PINNA (1969) and VENTURI & FERRI (2001) maintained two species of *Meneghiniceras*, the type species *M. lariense* (MENEGHINI) and the smaller *M. dorsinodosum* (BONARELLI). WIEDENMAYER (1977) did not use *Meneghiniceras*. When discussing *Harpophylloceras eximium* he placed the *costicillatum* variety in *Harpophylloceras* instead in *Meneghiniceras*, and he considered *H. costicillatum* (FUCINI, 1899) as a transitional form between *Harpophylloceras* and *Meneghiniceras*. At least MACCHIONI (2001, 2002) placed *Harpophylloceras* as a subgenus of *Meneghiniceras*, giving *Meneghiniceras* nomenclatorial priority.

The undulating keel said to be diagnostic of *Meneghiniceras*, with tooth-shaped clavi in large adults, is not developed in the juvenile stage. It was observed in specimens from a diameter of about 25 mm onwards. Constrictions occur in both taxa, but they vary both in strength and number. It strongly depends on the preservational state if the constrictions are well discernible or not (e. g., FANTINI SESTINI 1974; WIEDENMAYER 1977). Also a ribbed sculpture of medium ontogenetic stages is only discernible in specimens with preserved test, whereas in the internal moulds the ribbing appears at a larger diameter. Within the supposed variability between the taxa *eximium* and *lariense* the strength of ribbing directly correlates with the development of ventral clavi. The stronger the ribbing the more distinct are the observed clavi. The reason for this correlation is of course that the clavi are formed by bundled ribs projecting into the venter. This is excellently visible in the large specimen described by HOWARTH (1976) (Fig. 3), but also in the pre-adult specimen from

Swabia (Pl. 1, Fig. 1), which stimulated this study. In weakly ornamented specimens the clavi are either absent or occur only at the end of the body chamber where the ribbing becomes strongest (e. g., FARAONI et al. 1994, pl. 1, fig. 5; WIEDENMAYER 1977, pl. 9, figs. 9–10).

The minute specimens from southwestern Germany originally described as *Ammonites tortisulcoides* QUENSTEDT are interpreted representing juveniles of *M. eximium*. Despite of this supposed synonymy, the taxon name *lariense* may be used intrasubspecifically as a variety, released from specific status of the ICZN, to express the morphology of a concrete specimen within the morphological variation of the palaeobiospecies. This procedure is exhaustively explained by DIETZE et al. (2005) for the case of sonniniid ammonites from the Middle Jurassic.

3. Systematic palaeontology

Suborder Phylloceratina ARKELL, 1950
Superfamily Phylloceratoidea ZITTEL, 1884
Family Juraphyllitidae ARKELL, 1950

Genus *Meneghiniceras* HYATT, 1900
(Syn.: *Harpophylloceras* SPATH, 1927)

Type species: *Ammonites (Phylloceras) lariensis* MENEGHINI, 1875 (subjective synonym: *Ammonites eximius* v. HAUER, 1854, type species of *Harpophylloceras* SPATH, 1927). For discussion see above and below.

Meneghiniceras eximium (v. HAUER, 1854)
Fig. 3, Pl. 1

* 1854 *Ammonites eximius*. – HAUER, p. 863, pl. 2, figs. 1–4.
1856 *Ammonites heterophyllus*. – QUENSTEDT, p. 172 pars, pl. 21, fig. 4. [in QUENSTEDT 1856–1858]
1875 *Ammonites (Phylloceras) lariensis*. – MENEGHINI, p. 80, pl. 17, figs. 1–2. [in MENEGHINI 1867–1881]
1885 *Ammonites tortisulcoides*. – QUENSTEDT, pp. 338f., pl. 43, figs. 15–16 [in QUENSTEDT 1885–1888]
1893 *Phylloceras tortisulcoides* QUENST. sp. – POMPECKJ, p. 195, text-fig. 9, pl. 2, figs. 10–11.
1898 *Phylloceras tortisulcoides* QU. sp. – ZWIESELE, pp. 18f., 23, 28.
1898 *Harpoceras parvicarinatum* n. sp. – ZWIESELE, p. 32, pl. 1, fig. 3.
1908 *Phylloceras tortisulcoides* QU. sp. – ENGEL, p. 253.
1934 *Rhacophyllites eximius* (HAUER). – MONESTIER, p. 18, pl. 6, figs. 20, 25–31, pl. 7, figs. 5–6.
1934 *Rhacophyllites Balmelli*. – MONESTIER, p. 19, pl. 6, figs. 7–8, 12.
1974 *Meneghiniceras lariense* (MENEGHINI, 1875). – FANTINI SESTINI, p. 217, pl. 19, figs. 1–2. [with large list of synonyms]
1974 *Harpophylloceras eximium* (HAUER, 1854). – FANTINI SESTINI, p. 217. [with large lists of synonyms]
1976 *Meneghiniceras lariense* (MENEGHINI). – HOWARTH, p. 773, figs. 1–2.
1976 *Sowerbyceras tortisulcoides* (QU.). – SCHLEGELMILCH, p. 26, pl. 1, figs. 5–6.
1977 *Sowerbyceras tortisulcoides* (QUENSTEDT). – URLICHS, p. 3, pl. 2, fig. 8.
1977 *Harpophylloceras eximium* (HAUER, 1854). – WIEDENMEYER, p. 41, pl. 9, figs. 6–13. [with large list of synonyms]

1989 *Juraphyllites (Harpophylloceras) eximius* (HAUER, 1854). – MEISTER, p. 31, pl. 3, figs. 1–3.
1991 *Juraphyllites (Harpophylloceras) eximius* (HAUER 1854). – BLAU & MEISTER, p. 178, pl. 1, figs. 4–5.
1993 *Juraphyllites (Harpophylloceras) eximius*. – MEISTER, p. 131, figs. 1, 5c.
1993 *Juraphyllites (Meneghiniceras) lariensis*. – MEISTER, p. 131, figs. 1, 5e.
1994 *Meneghiniceras lariense* (MENEGHINI). – FARAONI et al., p. 249, pl. 1, fig. 5.
1994 *Juraphyllites* gr. *eximius*. – MEISTER et al., p. 144, text-fig. 5.
1994 *J. (Harpophylloceras) eximius*. – MEISTER et al., p. 145, text-fig. 6.
1996 *Harpophylloceras eximium* (HAUER). – EL HARIRI et al., p. 154, pl. 2, fig. 3.
1998 *Juraphyllites (Harpophylloceras) eximius* (HAUER 1854). – GÉCZY & MEISTER, p. 96, pl. 4, figs. 4, 7.
1998 *Juraphyllites (Meneghiniceras) lariensis* (MENEGHINI 1875). – GÉCZY & MEISTER, p. 97.
1998 *Meneghiniceras lariense*. – VENTURI, fig. 10A.
2000 *Harpophylloceras eximium* (HAUER, 1854). – JOLY, p. 17, text-fig. 1, pl. 1, fig. 1.
2001 *Juraphyllites* (*Meneghiniceras) lariense* (MENEGHINI). – MACCHIONI, pl. 1, figs. 15, 18.
2001 *Harpophylloceras* sp. indet. – VENTURI & FERRI, p. 74, figs. g–j.
2001 *Meneghiniceras dorsinodosum*. – VENTURI & FERRI, p. 74, figs. d–f.
2002 *Meneghiniceras (M.) lariense* (MENEGHINI, 1867). – MACCHIONI in PAVIA & CRESTA, p. 77, fig. 37.
2002 *Meneghiniceras* sp. indet. – MACCHIONI in PAVIA & CRESTA, p. 78, fig. 38.
2002 *M. (Harpophylloceras) eximium* (HAUER, 1854). – MACCHIONI in PAVIA & CRESTA, p. 79, fig. 39.
2003 *Meneghiniceras (Meneghiniceras) lariense* (MENEGHINI, 1875). – MACCHIONI & MEISTER, p. 378, pl. 1, figs. 15–16.
2003 *Meneghiniceras (Harpophylloceras) eximium* (HAUER, 1854). – MACCHIONI & MEISTER, p. 379, pl. 1, figs. 9–10.
2004 *Harpophylloceras eximium* (VON HAUER, 1854b). – MORARD, p. 6, pl. 1, fig. 1.
2004 *Meneghinicers lariense* (MENEGHINI, 1875). – MORARD, p. 6, pl. 1, fig. 2.
non 2004 *Holcophylloceras tortisulcoides* (QUENSTEDT, 1885c). – MORARD, p. 15, fig. B.1.9.

Material: ca. 60 specimens in the collections of the SMNS and IFGT.

Records in SW Germany: Eislingen, Zell unter Aichelberg-Pliensbach, Hechingen, see Fig. 1; according to literature data also from Kirchheim unter Teck, Betzgenried near Göppingen, and Reutlingen in the same area (Middle Swabia).

Geographic distribution: Western Tethys (Eastern and Southern Alps, Apennines, Hungary, Morocco); SW Germany, England, France.

Stratigraphic occurrence in SW Germany: Lower Jurassic, middle part of the Amaltheenton Formation (Late Pliensbachian, *Margaritatus* Zone, basal *Gibbosus* Subzone).

Stratigraphic range: Middle Carixian (Ibex Zone, Valdani Subzone) – Early Toarcian (Tenuicostatum Zone, Semicelatum Subzone).

For description and types: See FANTINI SESTINI (1974).

4. Description of a newly collected specimen from SW Germany

In the newly collected specimen from Eislingen (Pl. 1, Fig. 1) the inner whorls and even the protoconch are preserved as a pyritic internal mould, with the calcified test. Three weak prorsiradiate constrictions are discernible in the inner whorls. They are only visible in oblique illumination due to the covering test. The outer whorl is partly septate. The suture line is visible where the test is broken away. It matches exactly with the figures of the suture line of *Ammonites tortisulcoides* QUENSTEDT given by POMPECKJ (1893) and SCHLEGELMILCH (1976). This suture line is identical also in larger specimens included in the taxon *lariense* (FUCINI 1899, text-fig. 3). Most like-

ly the anterior half of the outer whorl is already part of the body chamber, like in many other much smaller specimens from the Upper Pliensbachian of SW Germany. The venter exhibits a weak keel that becomes stronger and very slightly undulating during growth. The inner whorls of the internal mould are smooth. The sculpture of the flanks consists of falcoid ribs which occur only on the covering test. In the outer third of the flank bundles of very fine secondary ribs are developed. In the final part of the outer whorl, these secondary ribs become coarser but decrease in number. The slight undulation of the keel is caused by the bundled arrangement of the secondary ribs joining in the venter. This is typical of *Meneghiniceras* as described above. Between these bundled units the keel remains lower and smooth.

The studied specimen is little larger than another one from the Amaltheenton Formation of Reutlingen described in 1898 by ZWIESELE, therein termed as *'Harpoceras parvicarinatum'*. The palaeontological collection of ZWIESELE could not be traced and seems to be lost. Most other specimens from SW Germany are much smaller than the studied one from Eislingen. Several other representative specimens illustrated here (Pl. 1, Figs. 2–9), among them the lectotype of *Ammonites tortisulcoides* QUENSTEDT (Pl. 1, Fig. 2), show some variation in the strength of their constrictions, but are otherwise very similar in respect of their coiling, a falcoid ribbing and the presence of a keeled stage. In none of these specimens an undulation of the keel is developed due to their very small size.

The morphology of the innermost whorls of the British specimen of *Meneghiniceras lariense* from the Early Toarcian (Fig. 3, see also HOWARTH 1976, text-fig. 1) matches very well with the Swabian specimens of *Ammonites tortisulcoides* QUENSTEDT.

Measurements:

	D	H	U	W	H/D	U/D	W/D
SMNS 65517	28.7	12.5	7.3	7.0	0.44	0.28	0.24
SMNS 28172/1	13.7	5.8	3.7	3.0	0.42	0.27	0.22
IFGT 1902/1	17.3	7.5	5.5	4.6	0.43	0.32	0.27

5. Palaeobiogeographic occurrence of *Meneghiniceras*

Outside the Tethyan realm the Early Jurassic genus *Meneghiniceras* is only accessory. An overview on the genus was given by MEISTER (1989), who distinguished *Meneghiniceras* from *Harpophylloceras*. At that time, there was only a single recognized record of *Meneghiniceras* outside the Tethys, from the Lower Toarcian of England (HOWARTH 1976). JOLY (2000) therefore did not mention *Meneghiniceras* from France, but like in southwestern Germany it is also well present there by juvenile specimens, always determined as *Harpophylloceras*. These specimens recorded from France clearly exhibit a keeled venter, like in *Ammonites tortisulcoides* QUENSTEDT from southern Germany, but they do not reach the undulating or clavate *'lariense'* stage of the keel because of their small size.

In NW Germany *Meneghiniceras* (and also *Harpophylloceras* in a morphogeneric sense) is unknown, but other Tethyan ammonites sporadically occur, e. g., *Arieticeras*, *Protogrammoceras*, *Canavaria* (FISCHER 1975), or the recently described *Lioceratoides* sp. from the *Apyreneum* Subzone of the Late Pliensbachian (SCHUBERT & FISCHER 2003).

The records of *Meneghiniceras* from SW Germany indicate that these ammonites never reached their adult size in this area. Although many of the small specimens exhibit their body chambers, none of them shows any hints that they are adult, and the last suture lines are never approximated as in adults. The juvenile specimens immigrated into the Late Pliensbachian sea of SW Germany but they did not find appropriate life conditions there and therefore did not propagate.

6. Tethyan immigrants in the Amaltheenton Formation of Swabia

After the experience of numerous fossil collectors in Swabia since the middle of the 19th century, Tethyan immigrants are not randomly scattered through the Amaltheenton Formation, but restricted to discrete levels (ENGEL 1887, 1890; ZWIESELE 1898, 1899; FRENTZEN 1934; URLICHS 1977). Already in 1885, QUENSTEDT reported the co-occurrence of large specimens of *'Ammonites heterophyllus'* (= *Zetoceras zetes* (D'ORBIGNY)) besides *'Ammonites striatus'* (= *Becheiceras gallicum* (SPATH)) in the embankment of the Breitenbach stream near Reutlingen. QUENSTEDT remarked that most records of *'Ammonites heterophyllus'* in Swabia come from this special locality. The finding horizon with *Zetoceras zetes* (D'ORBIGNY) and *Becheiceras gallicum* (SPATH) was said to be located near the top of the clay facies at this place (ZWIESELE 1898; ENGEL 1908). It is no longer accessible since a long time.

Together with phylloceratids also lytoceratids sporadically occur in the Amaltheenton Formation, e. g. *Derolytoceras tortum* (QUENSTEDT) and *Lytoceras furcicrenatum* BUCKMAN. These two species are restricted to the lowermost part of this Formation (URLICHS 1977: fig. 1). Other Tethyan or NW European immigrants in the Amaltheenton Formation of Baden-Württemberg are represented by the genera *Fuciniceras*, *Arieticeras*, and *Protogrammoceras* (FISCHER 1975; URLICHS 1977). Liparoceratids are widespread in the NW European Jurassic, but also inhabited the Tethyan realm, especially the genus *Becheiceras* (FERRETTI & MEISTER 1994; MEISTER & STAMPFLI 2000). In the Amaltheenton Formation *Becheiceras gallicum* (SPATH) and its corresponding microconch partner *Metacymbites centriglobus* (OPPEL) occurs in some levels. A modern high-resolution biostratigraphy using ammonite faunal horizons is not yet established in the Upper Pliensbachian Amaltheenton Formation, contrary to the French Jurassic which was studied in detail by MEISTER (1989). Hence a precise dating and correlation of the immigration events in SW Germany with the faunal horizons established in France is only tentative.

In the vicinity of the town of Göppingen (Eislingen, Pliensbach) *Meneghiniceras* occurs in the basal *Gibbosus* Subzone together with *Amaltheus* ex gr. *gibbosus* (SCHLOTHEIM), *Amauroceras ferrugineum* (SIMPSON), the Tethyan species *Fuciniceras compressum* (MONESTIER) and *Protogrammoceras depressum* (QUENSTEDT), and *Becheiceras gallicum* (SPATH), the latter considered as a 'Euroboreal' faunal element (FERRETTI & MEISTER 1994; MEISTER & STAMPFLI 2000), together with *Metacymbites centriglobus* (OPPEL). The exact stratigraphic position of other ammonites of undoubted Tethyan origin in Swabia, like *Protogrammoceras kurrianum* (OPPEL), or of the genera *Arieticeras* and *Fuciniceras*, is mostly unknown. In the uppermost part of the Amaltheenton Formation, the Costatenkalk Member, again some Tethyan immigrants appear (SCHLATTER 1982, 1985). A reinvestigation of the

ammonite described by SCHLATTER (1985, pl. 3, fig. 3) as *Leptalaeoceras* cf. *sublaeve* (MONESTIER) indicated that it most likely represents *Emaciaticeras emendatum* (GEMMELLARO), which thus allows a correlation of the finding layer with the Emaciatum Zone of the Tethyan Late Pliensbachian timescale (cf. MACCHIONI in PAVIA & CRESTA 2002: 140).

Dactylioceratids have been said to occur very rarely in the Amaltheenton Formation of Swabia (ZWIESELE 1899; BEURLEN 1924), but most of these ammonites were not figured. Unfortunately the specimens from private collections are all lost. Only the more recently published finds of *'Eodactylites'* cf. *simplex* (FUCINI) and *Dactylioceras pseudocommune* (FUCINI) from the Costatenkalk Member of western Swabia and adjacent Switzerland (SCHMIDT-EFFING 1972; SCHLATTER 1982, 1985) have a solid identification.

As a preliminary result at least four immigration events are distinguishable in the Amaltheenton Formation (Fig. 2):

1.) Basal part of *Subnodosus* Subzone, with *Derolytoceras torosum*, *Lytoceras furcicrenatum*, *Arieticeras amalthei*, *Metacymbites centriglobus*, and *Becheiceras gallicum*; possibly an equivalent of the Horizon à Depressum in France (MEISTER 1989, table 3).

2.) Basal part of *Gibbosus* Subzone, with *Becheiceras gallicum*, *Metacymbites centriglobus*, *Meneghiniceras eximium*, *Fuciniceras compressum*, *Protogrammoceras depressum*; possibly an equivalent of the Horizon à Ragazzoni in France, although the occurrence of *P. depressum* could at first sight also point to the Horizon à Depressum (MEISTER 1989, table 3).

3.) ? Top of *Gibbosus* Subzone, with *Zetoceras zetes*, *Calliphylloceras bicicolae*, *Becheiceras gallicum*, *Metacymbites centriglobus*, and *Arieticeras retrorsicostum*. According to the last occurrence of *B. gallicum* this horizon is interpreted as an equivalent of the Horizon à Bertrandi in France (MEISTER 1989, table 3). In France, there are two additional younger biohorizons in the *Gibbosus* Subzone, pointing to a stratigraphic gap at the top of the *Gibbosus* Zone of Swabia.

4.) Marly limestone bed within upper part of *Spinatum* Zone, *Hawskerense* Subzone, containing *'Eodactylites'* cf. *simplex*, *Dactylioceras pseudocommune*, *Protogrammoceras* sp., *Emaciaticeras emendatum*, *Canavaria* cf. *occidentale*. According to the occurrence of *Emaciaticeras* this level may be interpreted as an equivalent of the Horizon à Lottii in France (MEISTER 1989, table 3), but further studies are necessary to clear up, if the material from different sections represents only one or even more immigration events. The co-occurrence of *Emaciaticeras* and *'Eodactylites'* cf. *simplex* which is unknown from Tethyan sections points to some condensation or slightly different ages. In Tethyan sections *'Eodactylites' simplex* (FUCINI) and *Dactylioceras pseudocommune* (FUCINI) mark the beginning of the Toarcian. Obviously there is an overlap between Tethyan and Boreal zonations around the Pliensbachian/Toarcian boundary (see MACCHIONI 2002; CECCA & MACCHIONI 2004, and references therein), because these dactylioceratids have been found in the same bed as pleuroceratids, and a reworking can be excluded from their state of preservation.

Outside of these discrete horizons Tethyan immigrants are almost absent, and the ammonite fauna consists exclusively of amaltheids or pleuroceratids. At first sight it

becomes obvious from literature data that there are more biohorizons distinguishable in France than in Swabia – but only the section of Pliensbach itself has been yet studied in detail. The longer immigration route from the West with climatically less favourable conditions results both in a smaller faunal diversity and in an overall lower percentage of Tethyan elements of the total ammonite fauna. Moreover, the studied sections in Swabia seem to be less complete than those of France, especially in the higher part of the *Gibbosus* Subzone, due to stratigraphical gaps.

An immigration route of Tethyan ammonites into the SW German basin directly from the South is not very realistic because according to the present data the transgression of the Jurassic sea onto the Vindelician-Alemannian Massif did not take place before the Early Toarcian. Alternatively, the immigration from the West via the French Jurassic seems more likely (see ARIAS & WHATLEY 2004). Immigration events into the French Jurassic should also have reached SW Germany, possibly showing a slight impoverishment of the ammonite fauna. Based on these ideas a correlation of the SW German Upper Pliensbachian with the already established French biohorizons is suggested here (Fig. 2).

7. Conclusions

The ammonite genus *Meneghiniceras* HYATT, 1900 is regarded as a senior synonym of *Harpophylloceras* SPATH, 1927. The morphologies of both type species (*Ammonites eximius* v. HAUER, *Ammonites lariensis* MENEGHINI) are often linked by intermediate forms, like in the largest but still pre-mature specimen from Swabia described herein. The stratigraphical ranges of *Meneghiniceras lariense* and *Harpophylloceras eximium* given in literature (MEISTER 1993; MORARD 2004) are not fully identical because of the strict morphospecific concept of most authors. All juvenile and most pre-adult specimens fall automatically into the *eximium* taxon. According to these data the *'eximium'* morphology lacking ventral clavi sets in somewhere in the Middle Carixian, whereas the first undoubted appearance of the *'lariense'* morphology is somewhat later in the Upper Carixian (MEISTER 1993), or even at the base of the Domerian (MORARD 2004). The *'lariense'* morphology becomes predominant just before the extinction of *Meneghiniceras* that took place within the Tenuicostatum Zone of the Toarcian (MEISTER 1993; CECCA & MACCHIONI 2004; MORARD 2004). Both taxa are interpreted here to represent varieties of a single long-ranging palaeobiospecies. In Swabia only immature specimens of this taxon occur, originally described as '*Ammonites tortisulcoides* QUENSTEDT', and never before recognized as juvenile *Meneghiniceras*.

Thus, the palaeobiogeographic occurrence of *Meneghiniceras* expands from the western Tethyan realm to extra-alpine France and SW Germany, however, only during short immigration events.

8. References

ARIAS, C. & WHATLEY, R. (2004): Distribution patterns of Early Jurassic Ostracoda and possible communication routes through the European epicontinental sea: evidence of changes in ocean circulation patterns and its consequence to climate change. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **232**: 1–55.

BEURLEN, K. (1924): Über einige neue und seltene Ammoniten aus dem Lias δ des Schwäbischen Jura. – Centralblatt für Mineralogie, Geologie und Paläontologie, **1924**: 147–160.
BLAU, J. & MEISTER, C. (1991): Liassic (Pliensbachian) Ammonites from the Lienz Dolomites (Eastern Tyrol, Austria). – Jahrbuch der Geologischen Bundesanstalt, **134**: 171–204.
BONARELLI, G. (1895): Fossili domeriani della Brianza, I. – Rendiconti del Reale Istituto Lombardo di Scienze e Lettere, serie 2, **28**: 326–341.
CECCA, F. & MACCHIONI, F. (2004): The two Early Toarcian extinction events in ammonoids. – Lethaia, **37**: 35–56.
DEUTSCHE SUBKOMMISSION FÜR JURA-STRATIGRAPHIE (1973): F. A. QUENSTEDT. Die Ammoniten des Schwäbischen Jura. Revision der Gattungsnamen und Untergattungsnamen. 50 pp.; Stuttgart (Schweizerbart).
DIETZE, V., CALLOMON, J. H., SCHWEIGERT, G. & CHANDLER, R. B. (2005): The ammonite fauna and biostratigraphy of the Lower Bajocian (Ovale and Laeviuscula zones) of E Swabia (S Germany). – Stuttgarter Beiträge zur Naturkunde, Serie B, **353**: 82 pp.
EL HARIRI, K., DOMMERGUES, J. L., MEISTER, C., SOUHEL A. & CHAFIKI, D. (1996): Les ammonites du Lias inférieur et moyen du Haut-Atlas de Béni-Mellal (Maroc). Taxinomie et biostratigraphie de haute résolution. – Géobios, **29**: 537–576.
ENGEL, T. (1887): Der mittlere Lias im Filsbett bei Eislingen. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **43**: 48–66.
ENGEL, T. (1890): Paläontologische Funde aus dem Lias δ des Filsbettes bei Eislingen. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **46**: 34–49.
ENGEL, T. (1908): Geognostischer Wegweiser durch Württemberg, 3rd edition. XXXI+645 pp.; Stuttgart (Schweizerbart).
FANTINI SESTINI, N. (1974): Phylloceratina (Ammonoidea) del Pliensbachiano Italiana. – Rivista Italiana di Paleontologia e Stratigrafia, **80**: 193–250.
FARAONI, P., MARINI, A., PALLINI, G. & VENTURI, F. (1994): Nuove faune ad ammoniti delle zone ad *E. mirabilis* ed *H. serpentinus* nella valle del F. Bosso (PS) e loro riflessi sulla biostratigrafia del limite Domeriano-Toarciano in Appennino. – Studi Geologici Camerti, volume speciale, "Biostratigrafia dell'Italia Centrale": 247–297.
FERRETTI, A. & MEISTER, C. (1994): Composition des faunes d'ammonites dans l'Apennin des Marches et comparison avec les principales régions téthysiennes et euroboréales. – Palaeopelagos, special publication, **1**: 143–153.
FISCHER, R. (1975): Die deutschen Mittellias-Falciferen (Ammonoidea, *Protogrammoceras*, *Fuciniceras*, *Arieticeras*). – Palaeontographica, Abteilung A, **151**: 47–101.
FRENTZEN, K. (1934): Der Lias Delta (Amaltheen-Schichten) im Gebiete zwischen Aselfingen und Aalen. – Sitzungsberichte der Heidelberger Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, **1934** (2): 1–73.
FUCINI, A. (1899): Ammoniti del Lias medio dell'Appennino centrale esistenti nel Museo di Pisa. – Palaeontographia Italica, **5**: 145–185.
FUCINI, A. (1920): Fossili domeriani dei dintorni di Taormina. – Palaeontographia Italica, **26**: 75–116.
GÉCZY, B. & MEISTER, C. (1998): Les ammonites du Domérien de la montagne du Bakony (Hongrie). – Revue de Paléobiologie, **17**: 69–161.
HAUER, F. v. (1854): Beiträge zur Kenntniss der Heterophyllen der österreichischen Alpen. – Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe, **12**: 861–910.
HOWARTH, M. (1976): An occurrence of the Tethyan ammonite *Meneghiniceras* in the Upper Lias of the Yorkshire coast. – Palaeontology, **19**: 773–777.
HYATT, A. (1900): Cephalopodes. – In: ZITTEL, K. A. & EASTMAN, C. R. (eds.): Textbook of Paleontology: 502–604; London (Macmillan & Co.).
JOLY, B. (2000): Les Juraphyllitidae, Phylloceratidae, Neophylloceratidae (Phylloceratacеae, Phylloceratina, Ammonoidea) de France au Jurassique et au Crétacé. – Géobios, Mémoire spéciale, **23**: 1–204.
LÖRCHER, E. (1953): Ein unerwarteter Ammonitenfund in der Spinatus-Zone (Domérien). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **97**: 51–56.
MACCHIONI, F. (2001): Ammonites of the Domerian-Early Toarcian in the Subbetic Zone and in the Umbria-Marche Apennines. Taxonomy, taphonomy, biostratigraphy and paleobiogeography. – PhD Thesis, Università di Perugia: 183 pp.

MACCHIONI, F. (2002): Myths and legends in the correlation between the Boreal and Tethys Realms. Implications on the dating of the Early Toarcian mass extinctions and the Oceanic Anoxic Event. – Géobios, **35**: 150–164.

MACCHIONI, F. & CECCA, F. (2002): Biodiversity and biogeography of middle-late liassic ammonoids: implications for the early Toarcian mass extinction. – Géobios, Mémoire spéciale, **24**: 165–175.

MACCHIONI, F. & MEISTER, C. (2003): Ammonite biostratigraphy of some Mediterranean sections. 2: The succession of the Gola de F. Burano (Umbria-Machigiano Basin, Apennine), a reference section for Tethyan Domain. – Revue de Paléobiologie, **22**: 363–420.

MEISTER, C. (1989): Les ammonites du Domérien des Causses (France). – Cahiers de Paléontologie, 80 pp.

MEISTER, C. (1993): L'évolution parallèle des Juraphyllitidae euroboréaux et téthysien au Pliensbachien: le rôle des contraintes internes et externes. – Lethaia, **26**: 123–132.

MEISTER, C., BLAU, J. & BÖHM, F. (1994): Ammonite biostratigraphy of the Pliensbachian stage in the Upper Austroalpine Jurassic. – Eclogae Geologicae Helvetiae, **87**: 139–155.

MEISTER, C. & STAMPFLI, G. (2000): Les ammonites du Lias moyen (Pliensbachien) de la Neotéthys et de ses confins; compositions fauniques, affinités paléogéographiques et biodiversité. – Revue de Paléobiologie, **19**: 227–292.

MENEGHINI, G. (1867–1881): Monographie des fossiles du Calcaire rouge ammonitique (Lias supérieur) du Lombardie et de l'Apennin Central. – In: STOPPANI, A. (ed.): Paléontologie Lombarde, **4**: 242 pp.; Milano.

MONESTIER, J. (1934): Ammonites du Domérien de la région du sud-est de l'Aveyron et de quelques régions de la Lozère à l'exclusion des Amalthéidés. – Mémoires de la Societé géologique de France, nouvelle série, **23**: 1–102.

MORARD, A. (2004): Les événements du passage Domérien-Toarcien entre Téthys occidentale et Europe du Nord-Ouest. – Thèse de doctorat Université de Lausanne, vol. 2/2: paléontologie. 146 pp.; Lausanne. – [unpublished]

OPPEL, A. (1853): Der Mittlere Lias Schwabens. 92 pp.; Stuttgart (Ebner & Seubert).

OPPEL, A. (1854): Der Mittlere Lias Schwabens. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **10**: 39–136.

PAVIA, G. & CRESTA, S. (2002): Revision of Jurassic ammonites of the GEMMELLARO collections. – Quaderno Museo Geologico "G. G. Gemmellaro", **6**: 406 pp.

PINNA, G. (1969): Revisione delle ammoniti figurate da GIUSEPPE MENEGHINI nelle tav. 1–22 della "Monografie des Fossiles du Calcaire Rouge Ammonitique" (1867–1881). – Memorie della Società Italiana di Scienze Naturale, **18**: 7–21.

POMPECKJ, J. F. v. (1893): Beiträge zu einer Revision der Ammoniten des Schwäbischen Jura. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **49**: 151–248.

QUENSTEDT, F. A. (1856–1858): Der Jura. 842 pp.; Tübingen (Laupp).

QUENSTEDT, F. A. (1885–1888): Die Ammoniten des Schwäbischen Jura. **1–3**: 1140 pp.; Stuttgart (Schweizerbart).

SCHLATTER, R. (1982): Zur Grenze Pliensbachian – Toarcian im Klettgau (Kanton Schaffhausen, Schweiz). – Eclogae Geologicae Helvetiae, **75**: 759–771.

SCHLATTER, R. (1985): Eine bemerkenswerte Ammonitenfauna aus dem Grenzbereich Pliensbachium/Toarcium der Baar (Baden-Württemberg). – Stuttgarter Beiträge zur Naturkunde, Serie B, **112**: 27 pp.

SCHLEGELMILCH, R. (1976): Die Ammoniten des süddeutschen Lias. 212 pp.; Stuttgart & New York (Fischer). – [2nd edition published 1992]

SCHMIDT-EFFING, R. (1972): Die Dactylioceratidae, eine Ammoniten-Familie des unteren Jura. – Münstersche Forschungen zur Geologie und Paläontologie, **25/26**: 1–255.

SCHUBERT, S. & FISCHER, R. (2003): *Lioceratoides* sp. indet., ein mediterranes Faunenelement aus der *Pleuroceras apyreneum*-Subzone (Ober-Pliensbachium) von Ennigloh bei Bünde. – Geologie und Paläontologie in Westfalen, **60**: 5–11.

SPATH, L. F. (1927–1933): Revision of the Jurassic Cephalopod fauna of Kachh (Cutch). – Memoirs of the Geological Survey of India, Palaeontologica Indica, new series, **9**: VII+945 pp.

URLICHS, M. (1977): Stratigraphy, Ammonite fauna and some Ostracods of the Upper Pliensbachian at the Type Locality (Lias, SW-Germany). – Stuttgarter Beiträge zur Naturkunde, Serie B, **28**: 13 pp.

VENTURI, F. (1998): Ammoniti Phylloceratina nel "Rosso Ammonitico" umbro-marchigiano. – Il Monteluco, **10** (10): 30–35.
VENTURI, F. & FERRI, R. (2001): Ammoniti Liassici del'Appenino Centrale. 268 pp.; Perugia (Tiberograph).
VENZO, S. (1952): Nuove faune ad ammoniti del domeriano-aaleniano dell'Alpe Turati e dintorni (alta Brianza); la successione stratigrafica. – Atti della Società italiana Science naturali e Museo civico Storia naturale in Milano, **91**: 95–123.
WIEDENMAYER, F. (1977): Die Ammoniten des Besazio-Kalkes (Pliensbachian, Südtessin). – Schweizerische paläontologische Abhandlungen, **98**: 1–169.
ZWIESELE, H. (1898): Der Amaltheenthon bei Reutlingen. – Inaugural-Dissertation zur Erlangung der philosophischen Doktorwürde der hohen philosophischen Fakultät der Universität Bern. 39 pp.; Bern (Lack, Aeschlimann & Jost).
ZWIESELE, H. (1899): Ein neuer Lias-Delta-Aufschluss. – Mitteilungen des naturwissenschaftlichen Vereins Reutlingen, **1899**: 1–12.

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Manuscript received: 8.2.2005, accepted: 5.10.2005

Plate 1

Figs. 1–9. *Meneghiniceras eximium* (v. HAUER, 1854), Amaltheenton Formation, Upper Pliensbachian, *Margaritatus* Zone, *Gibbosus* Subzone. – All specimens coated with ammonium chloride, enlargement x2.

Fig. 1a–c. *M. eximium* (v. HAUER, 1854), var. *lariense* (MENEGHINI, 1875), pre-adult specimen, Eislingen, road cutting of Bundesstraße 10; SMNS 65517 (coll. M. KAPITZKE).

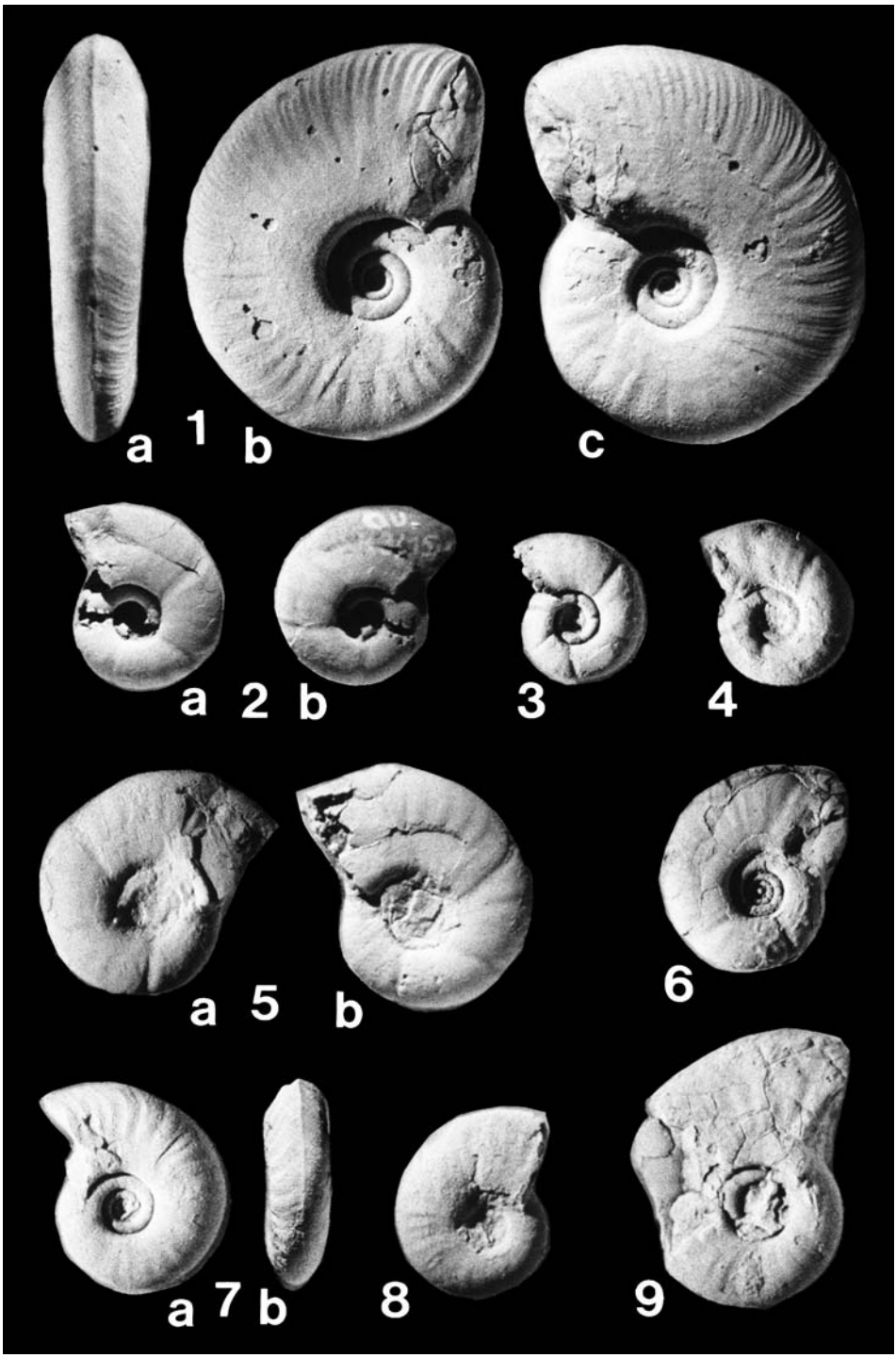
Fig. 2a, b. Juvenile specimen, figured as *Ammonites tortisulcoides* by QUENSTEDT (1885, pl. 43, fig. 15, lectotype, designated by SCHLEGELMILCH 1976: 26), Eislingen; SMNS 28172/1.

Figs. 3–4. Juvenile specimens, described as *Ammonites (Phylloceras) tortisulcoides* by POMPECKJ (1893: 45), Kirchheim unter Teck; SMNS 29580/1–2.

Fig. 5a, b. Juvenile specimen, Hechingen; IFGT 1902/1.

Fig. 6. Juvenile specimen, Fils river near Eislingen; SMNS 65518 (coll. WAIDELICH).

Figs. 7–9. Juvenile specimens, reported as *Sowerbyceras tortisulcoides* by URLICHS (1977), Pliensbach brook near Zell-Pliensbach; SMNS 65519/1–3 (leg. M. URLICHS).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ISSN 0341-0153

Autoren-Richtlinien: http://www.naturkundemuseum-bw.de/stuttgart/schriften
Schriftleitung: Dr. Ronald Böttcher, Rosenstein 1, 70191 Stuttgart
Gesamtherstellung: Gulde-Druck, 72072 Tübingen