A NEW SPECIES OF THE AMMONITE GENUS *NEOCHETOCERAS* SPATH (OPPELIIDAE) FROM THE HYBONOTUM ZONE (LOWER TITHONIAN) OF SOUTHERN GERMANY, WITH COMMENTS ON THE PHYLOGENY OF THE GENUS

Armin SCHERZINGER, Horacio PARENT & Günter SCHWEIGERT

Boletín del Instituto de Fisiografía y Geología

Scherzinger A., Parent H. & Schweigert G., 2015. A new species of the ammonite genus *Neochetoceras* Spath (Oppeliidae) from the Hybonotum Zone (Lower Tithonian) of Southern Germany, with comments on the phylogeny of the genus. *Boletín del Instituto de Fisiografía y Geología* 85: 1-12. Rosario, 15-09-2015. ISSN 1666-115X.

Received: 27/07/2015
Accepted: 05/09/2015
Online first: 15/09/2015

Editor: E. P. Peralta

Abstract: We here introduce a new species of the Submediterranean oppeliid genus *Neochetoceras*, *N. mohri* n.sp., represented by both macro- and microconchs. *N. mohri* n. sp. is better recorded than any other nominal species of this genus and links the early representatives of the lineage with the type species, *N. steraspis* (Oppel). Possible phyletic ancestors and the biogeographic distribution are briefly discussed. The *Neochetoceras* succession in the uppermost Kimmeridgian (Beckeri Zone) to Lower Tithonian (Hybonotum and Mucronatum zones) is summarized.

Keywords: Jurassic, Tithonian, Submediterranean Province, stratigraphy, sexual dimorphism.

Zusammenfassung: ***Eine neue Art der Ammonitengattung*** **Neochetoceras** ***Spath (Oppeliidae: Taramelliceratinae) aus der Hybonotum-Zone (Unter-Tithonium) von Süddeutschland, mit Bemerkungen zur Phylogenie dieser Gattung.*** Wir beschreiben hier eine neue Art der submediterranen Oppeliiden-Gattung *Neochetoceras*, *N. mohri* n.sp., von der sowohl Makrocoche als auch Mikroconche vorliegen. *N. mohri* n. sp. ist besser dokumentiert als jede andere nominale Art dieser Gattung. Sie verbindet die frühen Vertreter dieser Entwicklungslinie mit der Typusart *N. steraspis* (Oppel). Mögliche phylogenetische Vorläufer der Gattung und deren biogeographische Verbreitung werden kurz diskutiert. Die Abfolge von *Neochetoceras* vom obersten Kimmeridgium (Beckeri-Zone) und im Unter-Tithonium (Hybonotum- und Mucronatum-Zone) wird dargestellt.

Schlüsselwörter: Jura, Tithonium, Submediterrane Provinz, Sratigraphie, Geschlechtsdimorphismus.

Resumen.- ***Una nueva especie del género*** **Neochetoceras** ***Spath (Ammonoidea: Oppeliidae) de la Zona Hybonotum (Tithoniano Inferior) del Sur de Alemania, con discusión sobre la filogenia del género***.- Se introduce una nueva especie del género de oppélidos submediterráneos *Neochetoceras*, *N. mohri* n. sp., representada por macro y microconchas. *N. mohri* n. sp. presenta el mejor registro de todas las especies nominales del género, y relaciona a los representantes mas tempranos del linaje con la especie tipo *N. steraspis* (Oppel). Se discuten brevemente posibles ancestros filogenéticos y la distribución biogeográfica del linaje.

Palabras clave: Jurásico, Tithoniano, Provincia Submediterránea, estratigrafía, dimorfismo sexual.

Adresses of the authors:

A. Scherzinger [Armin.Scherzinger@t-online.de]: *Lämmerhalde 3, 71735 Eberdingen, Germany.*

H. Parent [parent@fceia.unr.edu.ar]: *Laboratorio de Paleontología, IFG-FCEIA, Universidad Nacional de Rosario, Pellegrini 250, 2000 Rosario, Argentina.*

G. Schweigert [guenter.schweigert@smns-bw.de]: *Staatliches Museum für Naturkunde, Rosenstein 1, 70191 Stuttgart, Germany.*

INTRODUCTION

After more than twenty-five years of our study of the ammonite faunas and stratigraphy of the Upper Jurassic in southern Germany, a significant collection of well-preserved ammonites accumulated. One of the most relevant outcrops for the sampling of Tithonian ammonites in the entire Submediterranean Province of Europe is a large limestone quarry east of the village Liptingen, several kilometers south of the Danube Valley (Fig. 1). Some parts of the ammonite fauna from this quarry were previously studied by Schweigert & Scherzinger (1995), Schweigert (1996), Zeiss et al. (1996), Dimke (1997, unpublished thesis), Dimke & Zeiss (1997), and Scherzinger et al. (2006). The ammonite material is excellently preserved and fairly common in the beds in the close surroundings of a large sponge-microbial buildup, which is the main target of exploiting for high quality limestones. Within the section there are remarkably large olistholiths, which stem from the nearby autochthonous reef.

A group of ammonites collected in this Liptingen Quarry in SW Swabia as well as in several other localities of the same area (Fig. 1) was recognized to be somewhat similar to the Franconian *Neochetoceras steraspis* (Oppel) but showing significant differences pointing to a still undescribed species (Fözy & Scherzinger 2013). These differences have been commonly overlooked by previous authors (e.g. Barthel & Schairer 1977), who had lumped them in a single taxon. Our study shows that the macroconchs of these ammonites can be differentiated from *N. steraspis* by their sculptural features, which are noted from complete, well-preserved specimens. The new material from the Liptingen Quarry comes from the *laisackerensis* Hz., whereas *N. steraspis* occurs in the still younger *rueppellianus* Hz. (type horizon) and continues up to the *moernsheimensis* Hz. of the Hybonotum Zone (Fig. 2).

The main purpose of this report is to describe these ammonites as a new species of the *laisackerensis* Hz. of the Hybonotum Z., Lower Tithonian. Additionally, in the light of new information, it became necessary to review

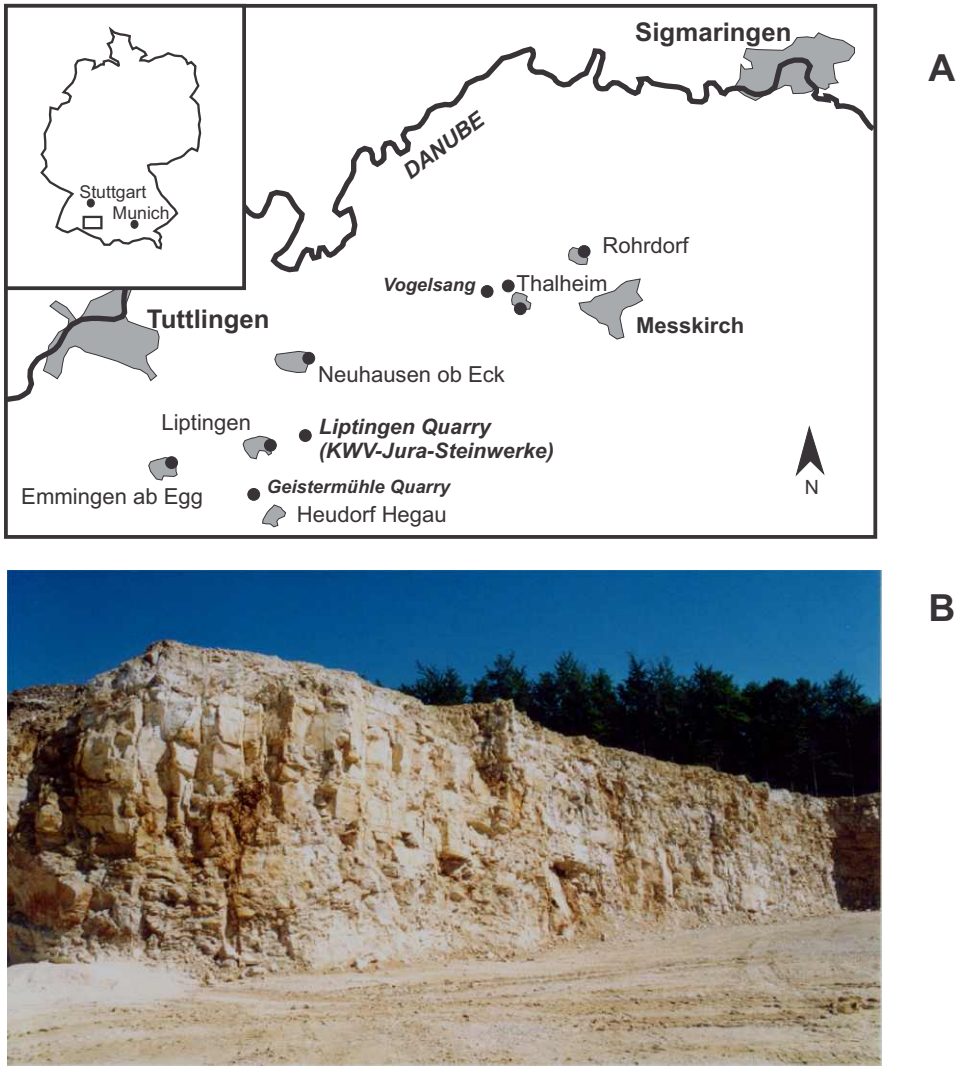


Figure 1. **A**: The most important Tithonian localities under study. Gray areas indicate urbanized areas; black points indicate location of sections or quarries. **B**: Former wall of Liptingen Quarry (exposed to NE direction, date of photograph 2004, A.S.). The wall shows the higher part of the limestone beds of the *laisackerensis* Hz. From this part of the quarry most of the specimens of *N. mohri* n. sp. comes from.

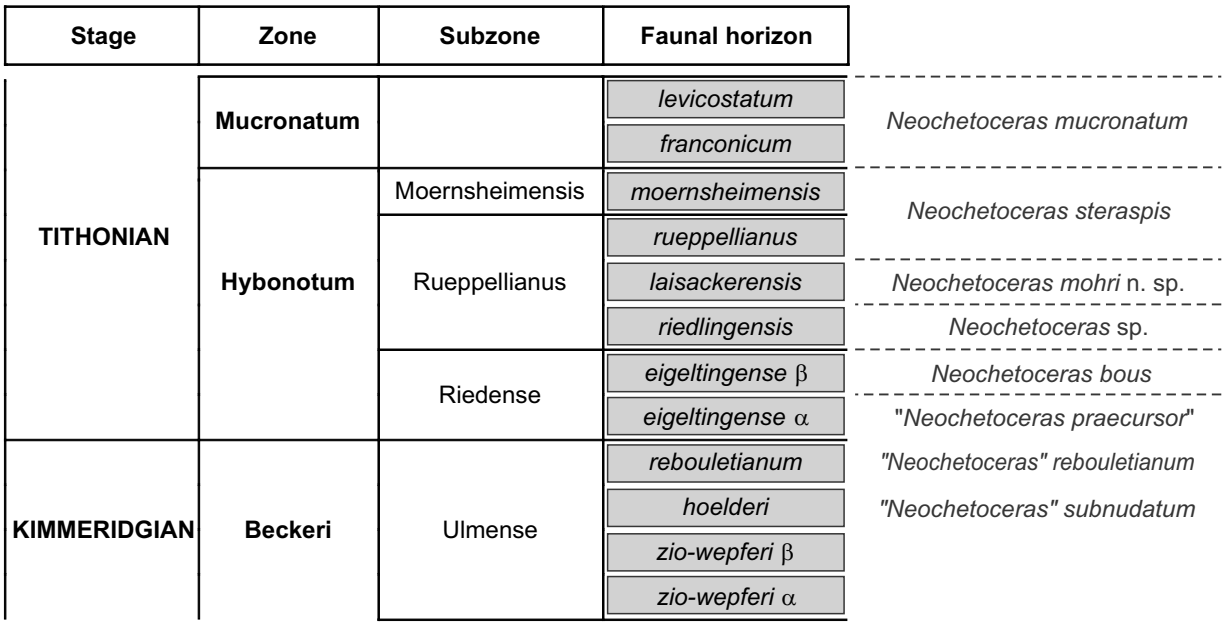


Figure 2. Chronostratigraphy and ammonite horizons of the upper Beckeri to Mucronatum zones in Southern Germany, with indication of the stratigraphic ranges of the species attributed to *Neochetoceras*. Succession of biohorizons according to Schweigert (2015 in print).

the succession of ammonite biohorizons through the Hybonotum Z. Finally, we comment on the species of the genus *Neochetoceras* which, in the context of the revised succession of ammonite horizons, conform a well-delimited lineage through the Hybonotum to Mucronatum zones.

HORIZONS OF THE HYBONOTUM ZONE

The sediments deposited during the Hybonotum Zone in southern Germany show different lithologies such as bedded limestones, lithographic limestones, marly limestones, sponge-microbial limestones, and coraliferous limestones. Both in Swabia and in Franconia a succession of ammonite biohorizons was recognized (e.g., Schweigert 1996, 2000, 2007, 2015 in press, Scherzinger & Schweigert 2003). In the beginning of our studies, however, the correlation between Swabian and Franconian successions was not clear because some of the Franconian biohorizons could not be identified in Swabia and vice versa. In this context, one of the main problems was the exact position of the above-mentioned *laisackerensis* biohorizon, which was recognized both in Swabia and in Franconia, but only in isolated outcrops. The study of phyletic lineages within age-diagnostic ammonite genera, especially *Hybonoticeras*, *Neochetoceras*, and *Gravesia*, helped for testing the stratigraphic concept, which finally led to the herein presented succession of biohorizons (Fig. 2).

SYSTEMATIC PALAEONTOLOGY

The material described is housed in the Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS), in the Jura-Museum Eichstätt, Germany (SOS) and in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany (BSPM). Macroconch (female): [M], microconch (male): [m]. Measurements are indicated as follows: diameter (D), diameter at the last adult septum (D_{ls}), final adult diameter at peristome (D_p), umbilical width (U), whorl width (W), whorl height (H_1), and whorl ventral (or apertural) height (H_2), all given in millimeters [mm]; length of bodychamber (L_{BC}) in degrees [°].

Superfamily Haploceratoidea Zittel, 1884
Family Oppeliidae Douvillé, 1890
Subfamily Taramelliceratinae Spath, 1928
Genus *Neochetoceras* Spath, 1925

Type species: *Ammonites steraspis* Oppel, 1863, by original designation.

Remarks: A diagnosis was presented by Arkell (1957); later Berckhemer & Hölder (1959) provided a more detailed characterization of the genus. Nevertheless, the adult macroconch bodychamber and the corresponding microconchs were not included in these descriptions. These microconchs have been formerly mostly described as species of the morphogenus *Lingulaticeras* Ziegler, 1958 (type species: *Ammonites nudatus* Oppel, 1863). Once recognized as a sexual dimorphic couple, both dimorphs should logically be merged in a single specific name. In this sense the microconch of the newly described species is treated here as part of the species, just noting the "microconch" morphospecies to which it was previously compared in the literature.

***Neochetoceras mohri* n. sp.**
Figs. 3-6, Table 1

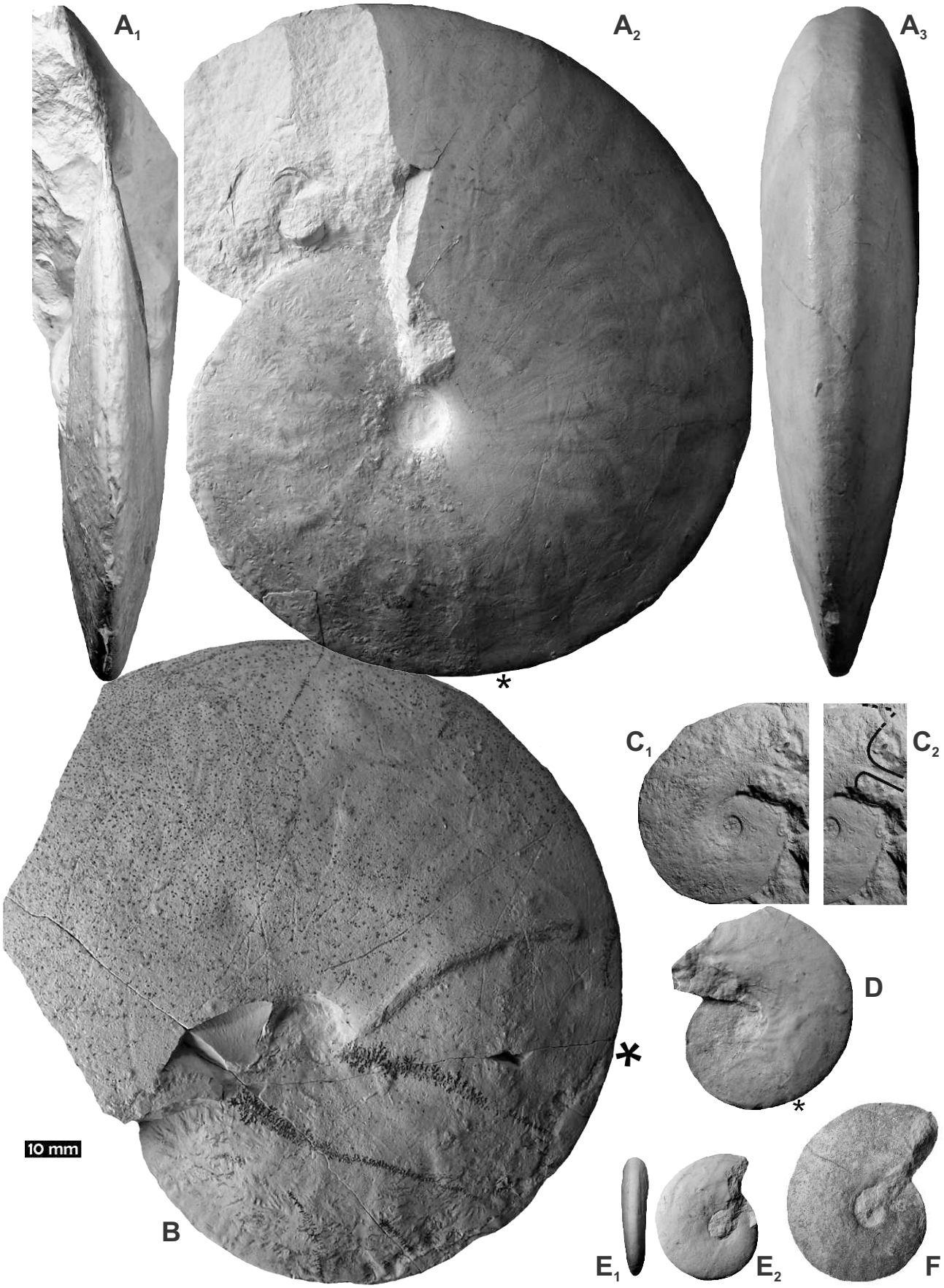


Figure 3. *Neochetoceras mohri* n. sp., Liptingen Quarry, *laisackerensis* Hz., Hybonotum Z. **A**: Holotype, adult macroconch with incomplete bodychamber (SMNS 70283/1. **B**: adult macroconch with bodychamber (SMNS 70283/2), Paratype I. **C**: complete adult microconch (SMNS 70283/7). **D**: complete adult microconch (SMNS 70283/8). **E**: incomplete adult microconch (SMNS 70283/9). **F**: incomplete adult microconch (SMNS 70283/10). - All natural size (x1); the asterisk indicates the last septum.

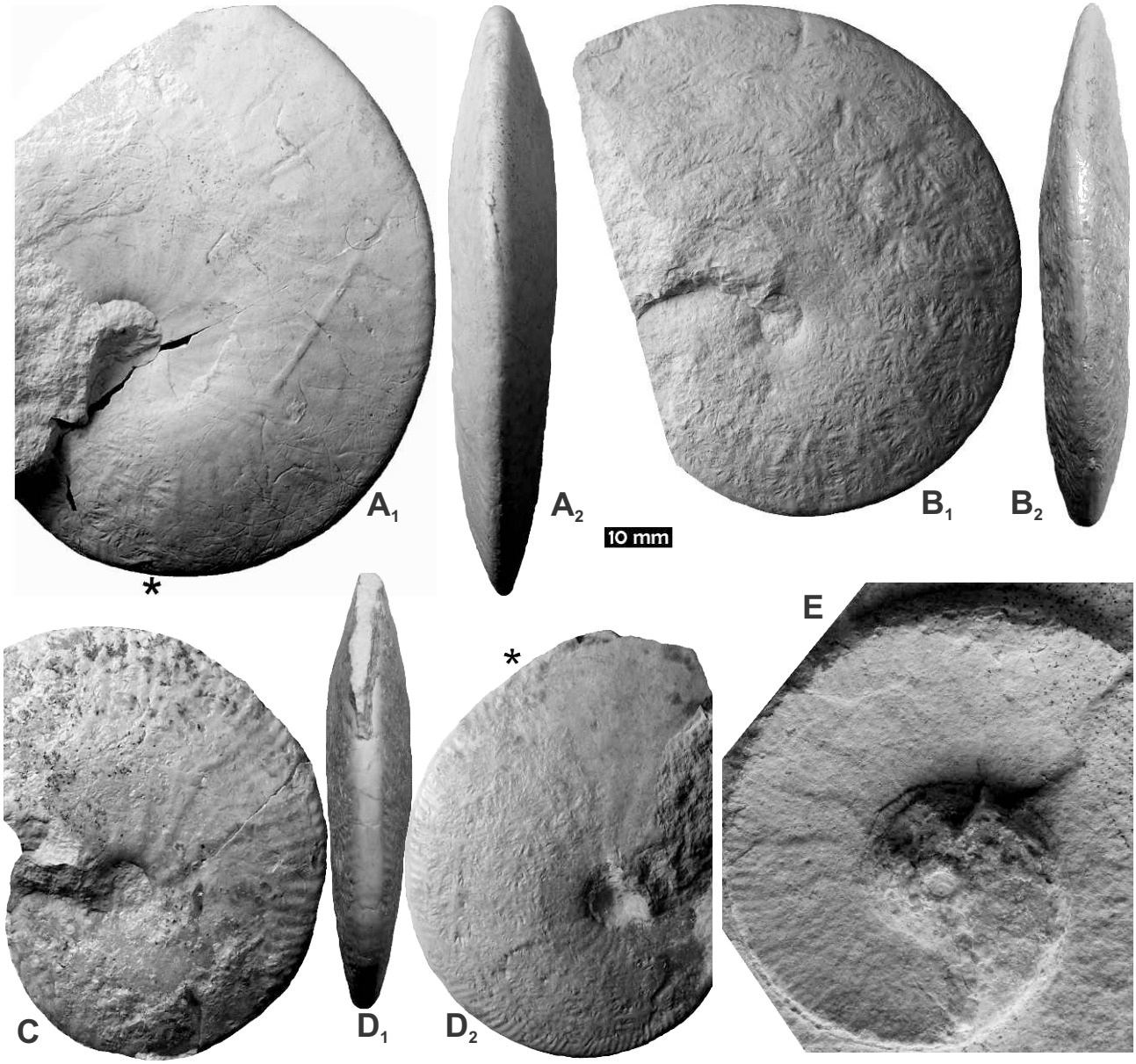


Figure 4. *Neochetoceras mohri* n. sp., *laisackerensis* Hz., Hybonotum Z. **A**: adult? macroconch with bodychamber (SMNS 70283/3), Paratype II, Liptingen Quarry. **B**: adult? macroconch phragmocone (SMNS 70283/4), Paratype III, Liptingen Quarry. **C**: macroconch phragmocone (SMNS 70283/5), Paratype IV, Liptingen Quarry. **D**: macroconch phragmocone with beginning of bodychamber (SMNS 70290/1), Emmingen ab Egg. **E**: macroconch with bodychamber from the Solnhofen area, Gemeindesteinbruch Solnhofen (Jura-Museum Eichstätt, SOS 5155). - All in natural size; asterisk indicates the last septum.

1977 *Glochiceras solenoides* (Quenstedt). – Barthel & Schairer: 104, fig 1, pl. 9: 1-2.
1977 *Taramelliceras subnudatum* (Fontannes). – Barthel & Schairer: 106, fig. 1, pl. 9: 3.
1977 *Taramelliceras* sp. – Barthel & Schairer: 107, pl. 9, fig. 4.
1977 *Neochetoceras steraspis* (Oppel). – Barthel & Schairer: 107, fig. 2, pl. 9: 5-7, pl. 10: 7.
1995 *Neochetoceras steraspis* (Oppel). – Schweigert & Scherzinger: 314.
1995 *Glochiceras solenoides* (Quenstedt). – Schweigert & Scherzinger: 314.
1996 *Neochetoceras steraspis* (Oppel). – Zeiss et al.: 134.
1996 *Glochiceras solenoides* (Quenstedt). – Zeiss et al.: 134.
1996 *Neochetoceras steraspis* (Oppel) [M]. – Schweigert: 298, non pl. 3, fig. 5.
1996 *Glochiceras solenoides* (Quenstedt) [m]. – Schweigert: 298.
1997 *Neochetoceras steraspis* (Oppel). – Dimke: tab. 3 .
1997 *Glochiceras solenoides* (Quenstedt). – Dimke: tab. 3.
1997 *Neochetoceras steraspis* (Oppel). – Dimke & Zeiss: 77-79
1997 *Glochiceras solenoides* (Quenstedt). – Dimke & Zeiss: 77, 79

Type locality and section: Liptingen Quarry, Baden-Württemberg, SW Germany (Fig. 1).

Table 1. *Neochetoceras mohri* n.sp. – Measurements of the holotype, paratypes and other specimens studied. Ph-Bc indicates observations at the last adult septum, transition from phragmocone (Ph) to bodychamber (Bc).

	D [mm]	*U/D*	*W/D*	H_1/D	Ph/Bc	
Holotype – SMNS 70283/1 – adult macroconch	121	0.07	0.21	0.57	Bc	
	85	–	–	–	Ph-Bc	Fig. 3A
	75	–	0.13	0.48	Ph	
Paratype I – SMNS 70283/2 – adult macroconch	116	0.08	–	0.59	Bc	Fig. 3B
	92	0.07	–	0.54	Ph-Bc	
Paratype II – SMNS 70283/3 - adult? macroconch	85	0.09	0.18	0.59	Bc	Fig. 4A
Paratype III – SMNS 70283/4 – adult? macroconch	80	0.08	0.16	0.55	Ph	Fig. 4B
Paratype IV – SMNS 70283/5 – macroconch	67	0.10	–	0.54	Ph	Fig. 4C
SMNS 70283/7 – adutl? macroconch	59	0.10	0.20	0.56	Ph-Bc	Fig. 4D
Paratype V – SMNS 70283/6 – adult macroconch	87	–	–	0.53	Bc	Fig. 5
SMNS 70283/7 – adult microconch	36	0.19	–	0.47	Bc	Fig. 3C
SMNS 70283/10 – adult microconch	32	0.22	–	0.47	Bc	Fig. 3F
SMNS 70283/9 – adult microconch	23	0.17	0.17	0.43	Bc	Fig. 3E

Type horizon: Hangende Bankkalke Formation, *laisackerensis* Hz., Hybonotum Z., Lower Tithonian.

Type material: Holotype (SMNS 70283/1), Paratype I (SMNS 70283/2), Paratype II (SMNS 70283/3), Paratype III (SMNS 70283/4), Paratype IV (SMNS 70283/5), and Paratype V (SMNS 70283/6).

Additional material: Macroconchs: SMNS 70290/1 [Emmingen ab Egg], SOS 5155 [Eichstätt], BSPM 1957 II 396 [Laisacker]. Microconchs: SMNS 70283/7 to 70283/10 [Liptingen], BSPM 1957 II 393 to 395 [Laisacker].

Etymology: After Rolf Mohr, the present quarry owner, who allowed and supported the field works in the Liptingen Quarry.

Diagnosis: Macroconchs large, diameter at peristome usually 110 to 150 mm, bodychamber ventrally tabulated. Phragmocone feeble to strongly ribbed by falcate primaries, with secondary and intercalatory ribs commonly ending in a small node. Microconchs one third to one fifth of the size of the macroconch; lower flank of bodychamber smooth, upper flank smooth or with weak retrocostate ribs; lappets straight and narrow.

Description: The holotype is an almost complete adult macroconch. The phragmocone is oxyconic, very involute, with compressed subtriangular whorl section. The umbilical wall is low and vertical with rounded shoulder passing to the flanks which are high and converge into a narrow, rounded venter. Ribbing on the last whorl of phragmocone consists of well marked falcate primaries, which divide somewhat higher than on mid-flank, into two to four secondaries, together with few intercalatories forming a densely ribbed upper third of flank. All ribs end on the inconspicuous, rounded ventro-lateral shoulder. The bodychamber begins at *D* = 85 mm and extends along about 230º, becoming inflated with slightly lower flanks and the venter smooth and widely flattened. The primary ribs remain falcate but undivided, becoming weaker and crowded, and fading out towards the peristome.

Macroconch paratypes and additional specimens are very similar in their whorl section and involution, and more or less strongly ribbed. The phragmocone is very feebly ribbed in some of the specimens, but most of them are more strongly ribbed, with secondary and intercalatory ribs, occasionally sometimes ending in a small tubercle or node on the ventro-lateral shoulder. The largest complete adult macroconch in our material has *D* = 150 mm at its peristome.

Microconch: Adults range in diameter at the peristome from 25 mm to 35 mm. The whorl section of the bodychamber is compressed suboval, with flat flanks passing to a narrow and rounded venter. The umbilicus is relatively wide. The peristome bears long and straight lateral lappets.

Remarks and comparison: The species is very variable in the strength of ribbing of the phragmocone; there is a continuous spectrum of morphologies from weakly ribbed specimens (Fig. 4A-B) passing to more strongly ribbed ones (Fig. 3A-B, 4C). The latter morph shows characteristic small tubercles or bullae on the end of the secondary and intercalatory ribs on the phragmocone (Figs. 4D, 5). The tabulation of the venter is developed along the adult macroconch bodychamber.

N. mohri n. sp. should have evolved from *Neochetoceras bous* (Oppel), whose macroconchs are completely smooth and which is known from the

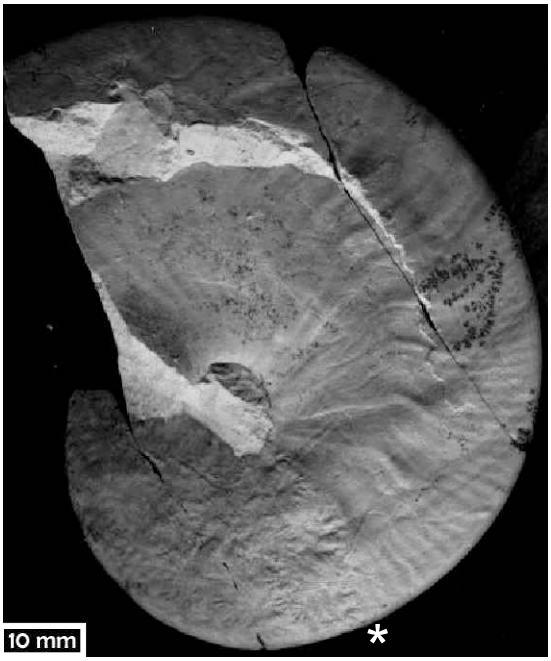
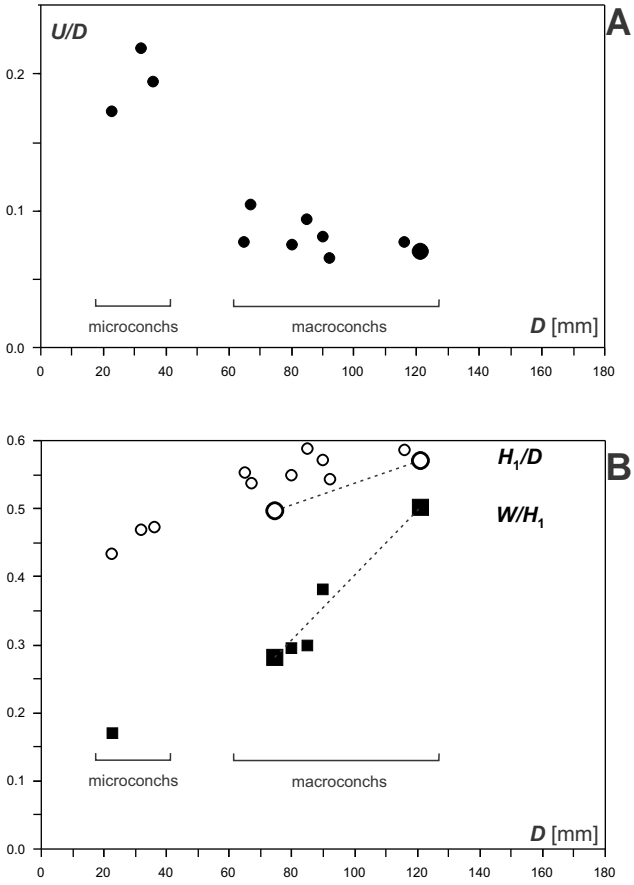


Figure 5. *Neochetoceras mohri* n. sp. Paratype V (SMNS 70283/6), Liptingen Quarry, *laisackerensis* Hz. Adult macroconch phragmocone with part of bodychamber showing the typical sculpture with ventral ribs endings as small bullae. Note the last septal suture line parallel to the primay rib throughout all the flank. - Natural size (x1); asterisk indicates the last septum.



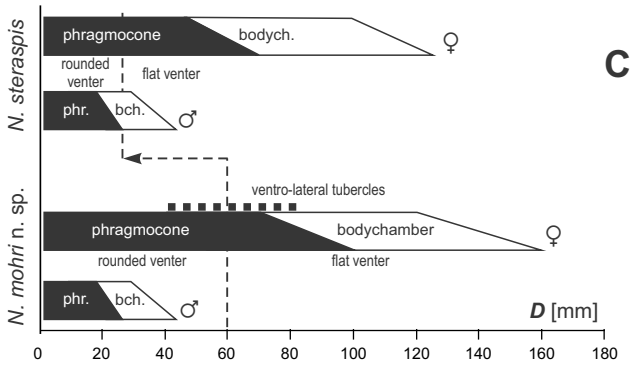


Figure 6. Biometric characterization of the holotype and paratype specimens of *Neochetoceras mohri* n. sp. (**A-B**), and comparison of macro- and microconch ontogenetic features respect to *Neochetoceras steraspis* (**C**); small circles and squares for paratypes and additional material, larger for the holotype. **A**: Relative umbilical width (*U/D*) versus diameter (*D*). **B**: Relative whorl height (H_1/D) and whorl section proportions (W/H_1) versus diameter. **C**: Comparison of approximate ranges of adult size, maximum size of adult phragmocone, and size at onset of ventral tabulation in macro- and microconchs. The diameter-range of occurrence of the ventro-lateral tuberculation in *Neochetoceras mohri* n. sp. is indicated. Data from Barthel & Schairer (1977), Parent et al. (2010), and the material studied herein.

eigeltingense β Hz. (Fig. 2). From the *riedlingensis* Hz. we have collected only some few specimens assignable to the genus *Neochetoceras*, but they are poorly preserved or fragmentary, preventing a specific assignation. In this latter horizon also occurs "*Neochetoceras*" *steraspisoides* (discussed below; see Fig. 7B). Adult macroconchs of *N. steraspis* have a similar ribbing style, but secondary ribbing of the phragmocone do not develop nodes on the ventro-lateral shoulder (see Parent et al. 2010: fig. 6A-C) and the ventral tabulation usually develops from the phragmocone at much smaller diameters, from about 25 mm onwards. The adult macroconchs of *N. steraspis* are usually smaller than those of *N. mohri* n. sp. (Fig. 6). Dimke & Zeiss (1997: 78) noted that the "variant of *N. steraspis*" from Liptingen (= *N. mohri* n. sp.) was of the same age as the material from Laisacker, Franconia. The microconchs of *N. mohri* n. sp. (Fig. 3C-F) and *N. steraspis* (Fig. 8F) are very similar, differing from each other by the tabulate venter of the latter.

The microconchs of *N. mohri* n. sp. would be classified, in morphologic terms, as *Lingulaticeras* ex. gr. *solenoides*. In this case, where the microconchs have not received a formal species name there are no nomenclatural problems associated with the micro- and macroconchs classified in different genera or subgenera.

Occurrences and distribution: The described material comes from the Liptingen Quarry and from temporary outcrops at Emmingen ab Egg, Baden-Württemberg, SW Germany (Fig. 1); these occurrences represent the *laisackerensis* Hz., Rueppellianus Subz., Hybonotum Z., Lower Tithonian (Fig. 2). Additional material from the same ammonite faunal horizon, not illustrated herein, but anyway part of our studied material, comes from Heudorf im Hegau (abandoned Geistermühle Quarry), Rohrdorf, Vogelsang and Thalheim near Meßkirch (all Swabia), and from Laisacker near Neuburg an der Donau (Bavaria).

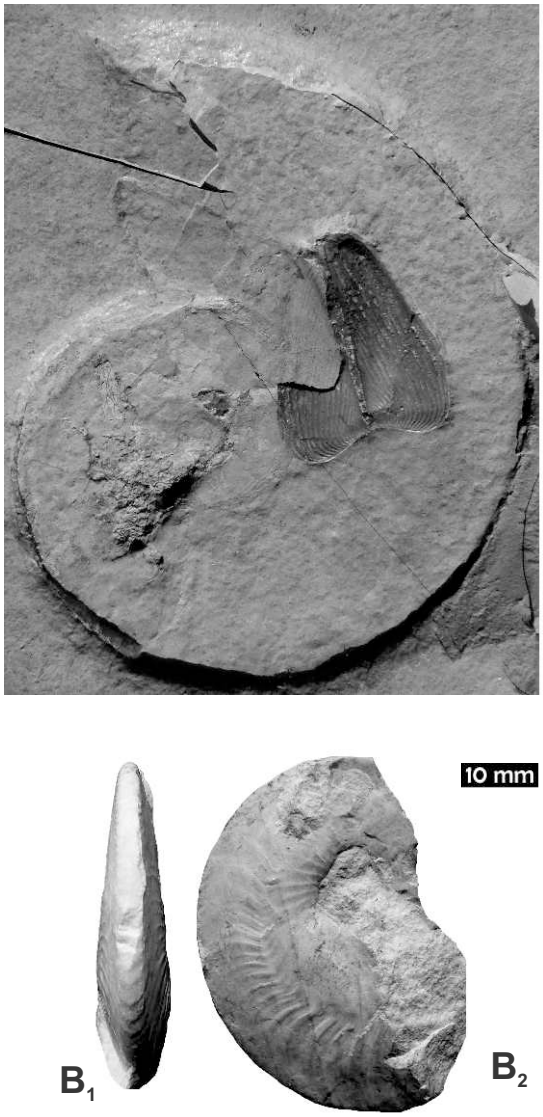


Figure 7. **A**: *Neochetoceras bous* (Oppel, 1863), lectotype (BSPM AS unnumbered), *eigeltingense* β Hz., lithographic limestones in the vicinity of Eichstätt [not from Solnhoifen, as erroneously indicated in the plate caption of Oppel (1863)]. Macroconch with the corresponding lamellaptychus. **B**: „*Oppelia*“ *steraspidoides* Fontannes, 1879 (SMNS 70294), Hangende Bankkalke Formation, Lower Tithonian, *riedlingensis* Hz., Heudorf im Hegau, basal beds of Geistermühle Quarry (Hahn collection). - All natural size (x1).

THE SUCCESSION OF SPECIES OF *NEOCHETOCERAS* IN SOUTHERN GERMANY

A brief account of the stratigraphic distribution of the genus *Neochetoceras* was given by Főzy & Scherzinger (2013). The new material and additional stratigraphical information allow us to offer an expanded revision of the successive species of this genus through the Hybonotum to the Mucronatum zones, referred to the scale in Fig. 2. The following discussion is based on the studied material, new records, type specimens in the Munich collection and most relevant papers dealing with species of the genus (e.g. Ziegler 1958, Hölder & Ziegler 1959, Berckhemer & Hölder 1959, Zeiss 1968, Barthel & Schairer 1977, Schweigert 1996, 1998, 2000, Kutek & Zeiss 1997, Scherzinger & Schweigert 2003, Scherzinger & Mitta 2006, and references therein).

Mucronatum Zone

***Neochetoceras mucronatum* Berckhemer & Hölder, 1959, *franconicum* and *levicostatum* horizons**. The lectotype, designated by Zeiss (1968: 123), is the specimen figured by Berckhemer & Hölder (1959: pl. 27: fig. 145), probably a juvenile macroconch. An indisputable microconch with long lappets which could be assigned to *N. mucronatum* is the specimen figured by Zeiss (1968: pl. 26: 4). The species has been further illustrated in Schlegelmilch (1994: pl. 13: 4), and by Scherzinger & Schweigert (2003: pl. 1: 6) with material from the *levicostatum* Hz. of Ammerfeld, Franconia. The ventral area of *N. mucronatum* is similar to that of the nearly coeval *Semiformiceras darwini* (Neumayr, 1873), but the corresponding microconch of the latter is quite different (i.e. a morphospecies of *Cyrtosiceras*, see Schweigert et al. 2002: 9, Főzy & Scherzinger 2013: 221).

"*Neochetoceras usselense* Zeiss, 1968", from the Usseltal Formation just above the Mörnsheim Formation, is based on very poorly preserved fragments of a single specimen, hence we consider it as a *nomen dubium*.

Hybonotum Zone

***Neochetoceras steraspis* (Oppel, 1863), *moernsheimensis* Hz. and *rueppellianus* Hz.** The lectotype (Oppel 1863: pl. 69: 1; refigured by Barthel & Schairer 1977: pl. 10: 1) comes from the *rueppellianus* Hz. of Solnhofen (Altmühltal Formation, Solnhofen Member). There are four paralectotypes, which are shown in Fig. 8A-D. These specimens are all very similar to the lectotype, densely ribbed and involute. The specimen in Fig. 8D shows the dense ribbing well preserved from the penultimate whorl of the phragmocone. Only the specimen in Fig. 8B has the ribs more stronger and widely spaced. The microconch (illustrated by a complete and well-preserved specimen in Fig 8F) is very similar to that of *N. mohri*, previously mentioned in the literature as *L.* cf. *solenoides*. Its aptychus is a typical lamellaptychus, preserved in the bodychamber of the specimens illustrated in Fig. 8A-B, a quarter whorl behind the aperture. The septal suture line is typical of the Taramelliceratinae, well exposed in the specimen of Fig. 8C (cf. Barthel & Schairer 1977: fig. 2: BSPM 1957 II 155).

Macro- and microconchs of *N. steraspis* show the tabulated venter from about $D = 25$ mm onwards (Fig. 8E-F). Thus, this feature is developed much earlier in ontogeny than in *N. mohri* n. sp., whose macroconchs become ventrally tabulated from about $D = 60$ mm (Fig. 3A). The microconchs of *N. mohri* n. sp. reach maximum sizes of $D = 35$-40 mm and do not develop any ventral tabulation.

***Neochetoceras mohri* n. sp., *laisackerensis* Hz.** See above.

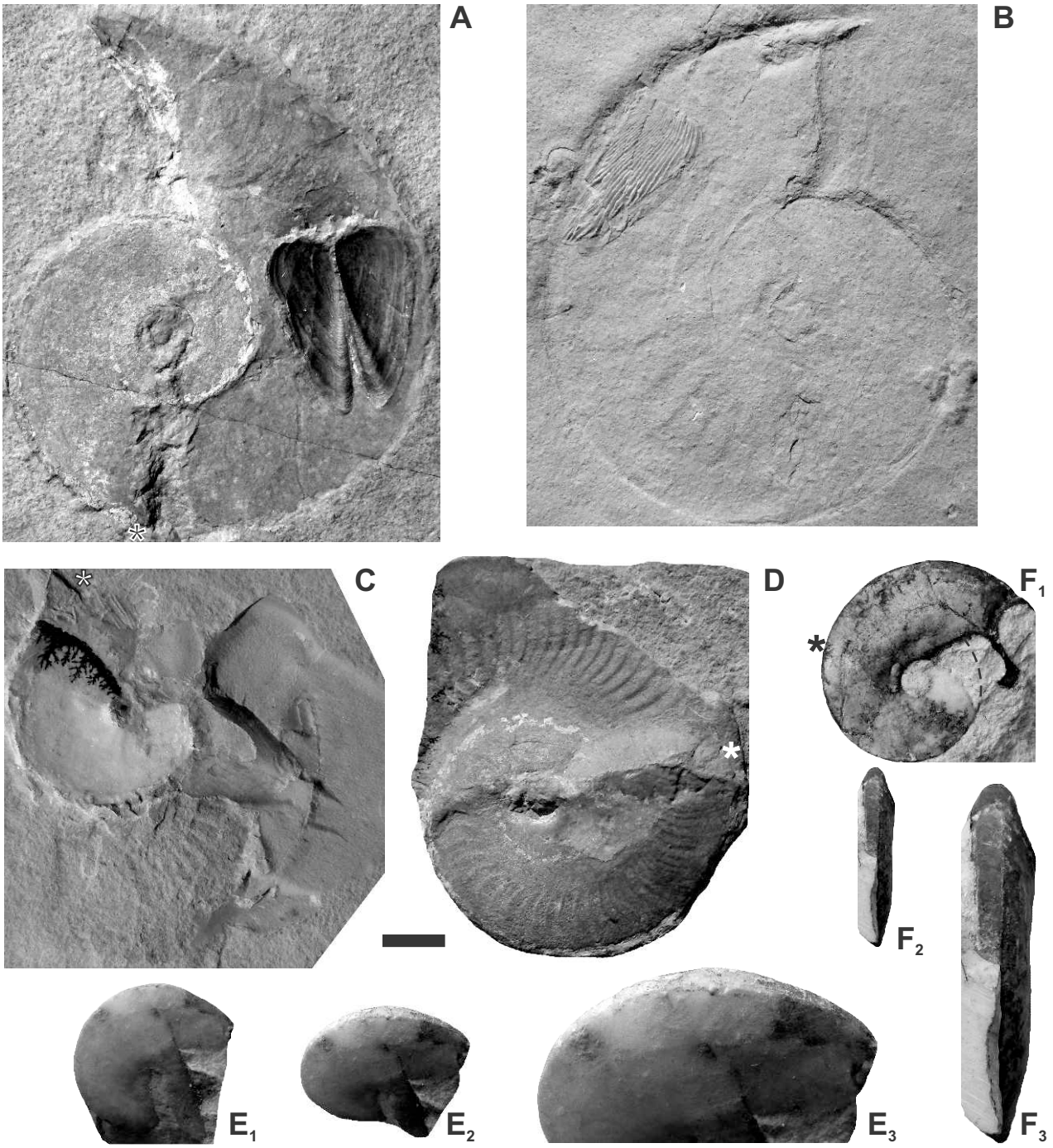


Figure 8. *Neochetoceras steraspis* (Oppel, 1863). **A**: Paralectotype I (BSPM, AS unnumbered), macroconch with lamellaptychus in its bodychamber. **B**: Paralectotype II (BPSM, AS VI 6), macroconch with lamellaptychus in its bodychamber. **C**: Paralectotype III (BPSM, AS VI 8), macroconch with phragmocone preserved, showing the septal suture line and the crushed bodychamber. **D**: Paralectotype IV (BPSM, AS VI 7), macroconch with crushed bodychamber. **E**: Juvenile macroconch (SMNS 70291/1, Solnhofen, Hummelberg Quarry, *moernsheimensis* horizon), venter tabulated from about $D = 25$ mm; $\mathbf{E}_3$: enlarged (x2) view of the flattened venter. **F**: Complete adult microconch (SMNS 70291/2, Solnhofen, Hummelberg Quarry, *moernsheimensis* horizon), venter tabulated from about $D = 25$ mm; $\mathbf{F}_3$: enlarged (x2) view of the flattened venter. Asterisk indicates the last septum. - All natural size (x1) except E_3 and F_3. Scale bar equals 10 mm except for E_3 and F_3 (5 mm).

***Neochetoceras* sp., *riedlingensis* Hz.** Rare and poorly preserved material was collected from the Hangende Bankkalke Formation of W Swabia (Neuhausen ob Eck, Thalheim near Meßkirch; coll. A.S.). Specimens assignable to "*N.*" *steraspisoides* (Fontannes, 1879) occur in this horizon as well (e.g. Fig. 7B; see also the specimen figured by Schweigert 1996: pl. 3: 5). Nevertheless, these specimens are small adults, which need to be studied in detail later, since they could either represent a late form of *Metahaploceras* Spath, 1925, or a dwarfish offshoot of *Neochetoceras* itself.

***Neochetoceras bous* (Oppel), *eigeltingense* β Hz.** The lectotype (Fig. 7A) comes from the lithographic limestones in the vicinity of Eichstätt (Altmühltal Formation, Eichstätt Member). Barthel & Schairer (1977: 111) supposed *N. bous* could be a synonym of *N. steraspis*. Our studies demonstrate that both species have their type horizon in two different levels containing different ammonite faunas. Zeiss (1968: 121, 123) considered *N. steraspis* as a microconch form with lappets and so that *N. bous* should be the corresponding macroconch. Barthel & Schairer (1977: 111) rejected that proposal because the latter form is completely smooth, whereas *N. steraspis* is densely ribbed even in the flatted preservation of lithographic limestones.

"*Neochetoceras praecursor* Zeiss, 1968", *eigeltingense* α Hz. This form is poorly known but different from *N. bous*, which is completely smooth (as shown by the lectotype and other topotypic material). On the other hand "*N. praecursor*" could well be synonymous with "*Neochetoceras*" *rebouletianum* (top of Beckeri Zone, *rebouletianum* Hz.). In the *eigeltingense* α Hz. in W Swabia (e.g. the Talmuhle section) occur some relatively small specimens (*D* = 40-50 mm) which bear fine periumbilical striae (see Ohmert & Zeiss 1980: pl. 13: 4). Other specimens have a sculpture closely comparable with that of "*N. rebouletianum*" with falcate-flexuous, irregular primary ribs and fine ventral ribs.

Evolutionary changes in the lineage of *Neochetoceras* through the Hybonotum to Mucronatum zones can be interpreted in the framework of developmental heterochronies, changes in relative timing of appearance or rate of development of ancestral characters. The most notable change in the phyletic sequence *N. mohri* n. sp.–*N. steraspis*–*N. mucronatum*, is the size at which the ventral tabulation is developed. In *N. mohri* n. sp. the venter is tabulated through the adult macroconch bodychamber (Figs. 3A, 6). This feature is developed gradually earlier in the ontogenies of *N. steraspis* (Figs. 6, 8E) and *N. mucronatum*, showing a peramorphic trend, by which the juvenile descendants still resemble the adult ancestors. This peramorphic pattern must have been generated by higher rates of morphologic development (acceleration, see McNamara 1986) during the ontogeny of *N. steraspis* with respect to its ancestor *N. mohri* n. sp. In *N. mucronatum* the venter is flatten even earlier, below 20 mm in diameter and soon becomes bisulcate (see Berckhermer & Hölder 1959: figs. 84, 86, and 145-146 in pl. 27). This trend of morphologic evolution within the entire lineage suggests a relative stability of environmental conditions through time.

The microconchs of *Neochetoceras* are, as in most ammonites, paedomorphic by progenesis. They mature at an earlier developmental stage, and at smaller sizes in respect to the macroconchs (see Neige et al. 1997, Parent 1997). The morphologic consequence of this early maturation makes that the microconch of *N. mohri* n. sp. does not develop the ventral tabulation, because its growth stopped at a smaller size than the onset of tabulation in the macroconchs at about *D* = 60 mm (Fig. 6). On the other hand, in the descendant *N. steraspis* the macroconchs develop the ventral tabulation from *D* = 25 mm onwards, and the microconchs (Fig. 8F), which grow up to about *D* = 30-40 mm, are tabulated from the beginning of the bodychamber (at *D* = 20-25 mm).

Searching for the phyletic roots of the the genus *Neochetoceras*, there are some candidates from the uppermost Beckeri Zone which could be closely related, such as "*Neochetoceras*" *rebouletianum* (Fontannes, 1879), *rebouletianum* Hz., and "*Neochetoceras*" *subnudatum* (Fontannes, 1879), *hoelderi* Hz. The type specimens of these taxa figured by Fontannes (1879) are incomplete phragmocones, which show close similarities with the phragmocone of some variants of *N. mohri* n. sp. (e.g. Fig. 4D). However, considering the morphological similarities, the temporal continuity and the palaeobiogeographical compatibility with the distribution of the early representatives of *Neochetoceras*, it seems possible that "*N.*" *rebouletianum* and "*N.*" *subnudatum* are part of the lineage as well. Thus, *Neochetoceras* could have been originated from slender forms of *Taramelliceras*, such as *Oppelia franciscana* Fontannes, 1879, by the loss of the ventral tubercles. In this sense the sculpture with small ventral tubercles of *O. franciscana* is very similar to *N. mohri* n. sp.

The palaeogeographic distribution of *Neochetoceras* seems to be mainly confined to the Submediterranean Province of SE France, N Switzerland and especially Southern Germany. However, there are brief excursions during the *moernsheimensis* Hz., as reported from Hungary (Főzy & Scherzinger 2011, 2013). Kutek & Zeiss (1997: pls. 29-30) have presented a series of ammonites from the Tithonian of Central Poland which they assigned to *N. steraspis* (Klimovi Zone) and *N. mucronatum* (Sokolovi Zone), respectively. Nevertheless, that material is poorly preserved and fragmentary, and therefore these identifications are dubious (cf. Scherzinger & Mitta 2006).

The succession of species described above (see Fig. 2), showing a tractable sequence of gradual changes in shell-shape and sculpture, has been completely recorded only in the Lower Tithonian of the Swabo-Franconian Basin (western Swabian Alb and southern Franconian Alb), but not elsewhere yet. This unique continuous record of adult and juvenile macro- and microconchs strongly suggests the species have been eudemic (sensu Callomon 1985) in this area, since they have surely bred and evolved therein. In other words, this area was the evolutionary centre of the lineage, from which, during times with favourable conditions, brief temporary and spatial excursions occurred.

Acknowledgements: We thank Dr. István Főzy (Budapest) for discussions and the opportunity to compare material from Hungary, Dipl.-Geol. Martin Ebert (Eichstätt) for providing access to the ammonite collection of the Jura-Museum, and Dr. Alexander Nützel (Munich) for access to the collection of the Bayerische Staatssammlung in Munich. Dr. Johannes Baier (Tübingen) and Denys Petrenko (Eberdingen) shared some fieldwork with one of the authors (AS). Special thanks to our friends, the workers in the Liptingen Quarry and Dr. Rolf Mohr (Immenstaad) for his support and the oppurtunity to study the section. Valuable suggestions and comments by I. Főzy (Budapest) and A. Wierzbowski (Warszawa) as reviewers of the journal, considerably improved the paper.

REFERENCES

Arkell W.J., 1957. Jurassic ammonites. *In* W.J. Arkell, B. Kummel & C.W. Wright: Treatise on Invertebrate Paleontology, (L) Mollusca 4, R.C. Moore (*ed.*). University of Kansas Press and Geological Society of America, Kansas and New York, 22+490 pp.

Barthel K.W. & Schairer G., 1977. Die Cephalopoden des Korallenkalks aus dem Oberen Jura von Laisacker bei Neuburg a.d. Donau. II. *Glochiceras*, *Taramelliceras*, *Neochetoceras* (Ammonoidea). – *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* **17**: 103-113.

Berckhemer F. & Hölder H., 1959. Ammoniten aus dem oberen Weißen Jura Süddeutschlands. – *Beihefte Geologisches Jahrbuch* **35**: 23-135.

Callomon J.H., 1985. The evolution of the Jurassic ammonite family Cardioceratidae. – *Special Papers in Palaeontology* **33**: 49-90.

Dimke M., 1997. Fazies und Diagenese der Tithon-Massenkalke und Hangenden Bankkalke südöstlich von Tuttlingen aus Blatte Neuhausen ob Eck (8019), nebst einigen angewandten Aspekten ihrer Nutzung als Rohstoff (Farbe, Brech- und Mahlverhalten). – Unpubl. PhD thesis, Naturwissenschaftliche Fakultät III, Universität Erlangen-Nürnberg, 181 pp.

Dimke M. & Zeiss A., 1997. Die Hangenden Bankkalke östlich von Liptingen (Unter-Tithon, südwestliche Schwäbische Alb) – Stratigraphie, Faziesübersicht und neue Fossilfunde. – *Geologische Blätter für Nordost-Bayern* **47**: 71-98.

Douvillé H., 1890. Sur la classification des Cératites de la Craie. – *Bulletin de la Societé géologique de France (série 3)* **18**: 275-292.

Fontannes F., 1879: Description des Ammonites des calcaires du Château de Crussol, Ardèche (Zones à Oppelia tenuilobata et Waagenia Beckeri). – XI + 123 pp., Lyon (Georg), Paris (Savy).

Főzy I. & Scherzinger A., 2011. *Simoceras szentei* n. sp., a new ammonite species from the lowermost Tithonian of the Gerecse Mountains (Hungary) - the earliest record of the genus. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **262**: 117-127.

Főzy I. & Scherzinger A., 2013. Systematic descriptions of Tithonian ammonites of the Gerecse Mountains. *In*: I. Főzy (*ed.*): Late Jurassic-Early Cretaceous fauna, biostratigraphy, facies and deformation history of the carbonate formations in the Gerecse and Pilis mountains (Transdanubian Range, Hungary): 207-292. Institute of Geosciences, University of Szeged, Szeged.

Hölder H. & Ziegler B., 1959. Stratigraphische und faunistische Beziehungen im Weißen Jura (Kimeridgien) zwischen Süddeutschland und Ardèche. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **108**: 150-214.

Kutek J. & Zeiss A., 1997. The highest Kimmeridgian and Lower Volgian in Central Poland; their ammonites and biostratigraphy. – *Acta Geologica Polonica* **47**: 107-198.

McNamara K.J., 1986. A guide to the nomenclature of heterochrony. – *Journal of Paleontology* **60**: 4-13.

Neige P., Marchand D. & Laurin B., 1997. Heterochronic differentiation of sexual dimorphs among Jurassic ammonite species. – *Lethaia* **30**: 145-155.

Ohmert W. & Zeiss A., 1980. Ammoniten aus den Hangenden Bankkalken (Unter-Tithon) der Schwäbischen Alb (Südwestdeutschland. – *Abhandlungen des Geologischen Landesamtes Baden-Württemberg* **9**: 5-50.

Oppel A., 1863. Über jurassische Cephalopoden. – *Palaeontologische Mittheilungen aus dem Museum des königlich Bayerischen Staates* **3**: 163-266.

Parent H., 1997. Ontogeny and sexual dimorphism of *Eurycephalites gottschei* (Tornquist) (Ammonoidea) of the Andean Lower Callovian (Argentina – Chile). – *Geobios* **30**: 407-419.

Parent H., Myczynski R., Scherzinger A. & Schweigert G., 2010. *Cieneguiticeras*, a new genus of Tithonian oppeliids (Ammonoidea, Late Jurassic). – *Geobios* **43**: 453-463.

Scherzinger A. & Schweigert G., 2003. Ein Profil in der Usseltal- und Rennertshofen-Formation der südlichen Frankenalb (Unter-Tithonium). – *Zitteliana* **A43**: 3-17.

Scherzinger A. & Mitta V.V., 2006. New data on ammonites and stratigraphy of the Upper Kimmeridgian and Lower Volgian (Upper Jurassic) of the Middle Volga Region (Russia). –*Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **241**: 225-251.

Scherzinger A., Schweigert G. & Parent H., 2006. Considerations on dimorphism and aptychus in *Gravesia* Salfeld (Ammonoidea, Late Jurassic). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **241**: 269-286.

Schlegelmilch R.,1994. Die Ammoniten des süddeutschen Malms. VII+297 pp.; Stuttgart, Jena & New York (G. Fischer).

Schweigert G., 1996. Die Hangende Bankkalk-Formation im schwäbischen Oberjura. – *Jahresberichte und Mitteilungen des oberrheinischen geologischen Vereins, Neue Folge* **78**: 281-308.

Schweigert G., 1998. Die Ammonitenfauna des Nusplinger Plattenkalks (Ober-Kimmeridgium, Beckeri-Zone, Ulmense-Subzone, Württemberg). – *Stuttgarter Beiträge zur Naturkunde* **B267**: 1-61.

Schweigert G., 2000. New Biostratigraphic Data from the Kimmeridgian/Tithonian. *In*: R.L. Hall & P. Smith (*eds.*): Advances in Jurassic Research 2000. – *GeoResearch Forum* **6**: 195-202.

Schweigert G., 2007. Ammonite biostratigraphy as a tool for dating Upper Jurassic lithographic limestones from South Germany – first results and open questions. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **245**: 117-125.

Schweigert G., 2015 (in press). Biostratigraphie der Plattenkalke der Südlichen Frankenalb. – *In*: G. Arratia, H.-P. Schultze, H. Tischlinger & G. Viohl (eds.): Solnhofen – Ein Fenster in die Jurazeit, pp. 57-60; München (Pfeil).

Schweigert G. & Scherzinger A., 1995. Erstnachweis heteromorpher Ammoniten im Schwäbischen Oberjura. – *Jahresberichte und Mitteilungen des oberrheinischen geologischen Vereins, Neue Folge* **77**: 307-319.

Schweigert G., Scherzinger A. & Parent H., 2002. The *Volanoceras* lineage (Ammonoidea, Simoceratidae) – a tool for long-distance correlations in the Lower Tithonian. – *Stuttgarter Beiträge zur Naturkunde* **B326**: 1-43.

Spath L.F., 1925. On the collection of fossils and rocks from Somaliland made by B.K.N. Wyllie and W.R. Smellie. Part 7: Ammonites and aptychi. – *Monographs of Geological Department of the Hunterian Museum* **1**: 111-164.

Spath L.F., 1927-1933. Revision of the Jurassic cephalopod fauna of Kachh (Cutch). – *Palaeontologica Indica (new series 9)* **2(1-6)**: 1-945.

Zeiss A., 1968. Untersuchungen zur Paläontologie der Cephalopoden des Unter-Tithon der Südlichen Frankenalb. – *Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, Neue Folge*, **132**: 1-190.

Zeiss A., Schweigert G. & Scherzinger A., 1996. *Hegovisphinctes* n. gen. eine neue Ammonitengattung aus dem Unter-Tithonium des nördlichen Hegau und einige Bemerkungen zur Taxonomie der Lithacoceratinae. – *Geologische Blätter für Nordost-Bayern* **46**: 127-144.

Ziegler B., 1958. Monographie der Ammonitengattung *Glochiceras* im epikontinentalen Weißjura Mitteleuropas. – *Palaeontographica* **A110**: 93-164.

Zittel K.A., 1884. Cephalopoda. In: K.A. Zittel (*ed.*): Handbuch der Palaeontologie, München & Leipzig (Oldenbourg), vol. 1, Abt. 2 (3), Lief. 3: 329-522.