

A new belemnite species from the Aalenian of the Swabian Alb (SW Germany) and its position in the phylogeny of Megateuthididae (Belemnitida)

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With 5 figures

Abstract: A new belemnite species from the Aalenian of the Swabian Alb is introduced herein. *Acrocoelites ippolitae* WEIS n. sp. is hitherto the youngest representative of the genus *Acrocoelites* in NW Europe (lower to upper Aalenian). Specimens tentatively assigned to the new species (*A. cf. ippolitae*) are known also from lower Bajocian strata of Luxembourg. The unique morphology of the apical grooves distinguishes it chiefly from other coeval megateuthid taxa. Considering the peculiar position of the ventral groove, *A. ippolitae* is suggested to be part of an ancestral lineage leading to the megateuthid genus *Eocylindroteuthis*, from the lower Bajocian.

Key words: Belemnite, Megateuthididae, systematics, phylogeny, Aalenian, Achdorf Fm, Southern Germany.

1. Introduction

The Jurassic belemnites of the Swabian Alb have been treated extensively in the classic works of QUENSTEDT (1845–1849; 1856–1857; 1885), ZIETEN (1830–1833), OPPEL (1856–1858), WERNER (1912), and SCHWEGLER (1961–1971). They have been revised using more recent taxonomic standards by RIEGRAF (1980, 1981), RIEGRAF et al. (1984), SCHLEGELMILCH (1998), and WEIS & MARIOTTI (2008). Nonetheless, at a closer look, our knowledge of the Aalenian and early Bajocian belemnites is still incomplete. This is partially due to the relative rareness of belemnites in parts of the Achdorf and Wedelsandstein formations (DIETZE et al. 2019), but also to the lack of outcrops. It is thus not surprising that these apparently intensively studied strata may still yield new fossil taxa. During the 1980's, one of the authors (W.R.†) collected the herein reported rostra in the Wilflingen-Bank of the Wochenberg hill (western Swabian Alb). These rostra repre-

sent a new belemnite species, which opens up some questions concerning the phylogenetic relationships of early Middle Jurassic belemnites.

2. Material and methods

The material described herein originates from the eastern slope of the Wochenberg hill near Schömberg-Schörzingen, in the western Swabian Alb, South Germany (Fig. 1). Already QUENSTEDT (1886–1887) described upper Aalenian ammonites from the Wochenberg hill. Nearly one century later, RIEBER (1963, fig. 2c) described a detailed section of the Aalenian beds at this site. The Wilflingen-Bank (formerly referred to as Comptumbank; DIETZE et al. 2021) corresponds to the lowermost part of the Achdorf Formation (FRANZ & NITSCH 2009). At the Wochenberg hill, its thickness is about 1.4 m (Fig. 2). It consists of grey to brown calcareous marl, with sandy and chamosite oolitic parts. Ammonites of the genus *Leioceras* are very abundant in the Wilflingen-Bank, whereas belemnites are rare (RIEBER 1963). Biostratigraphically, the Wilflingen-Bank corre-

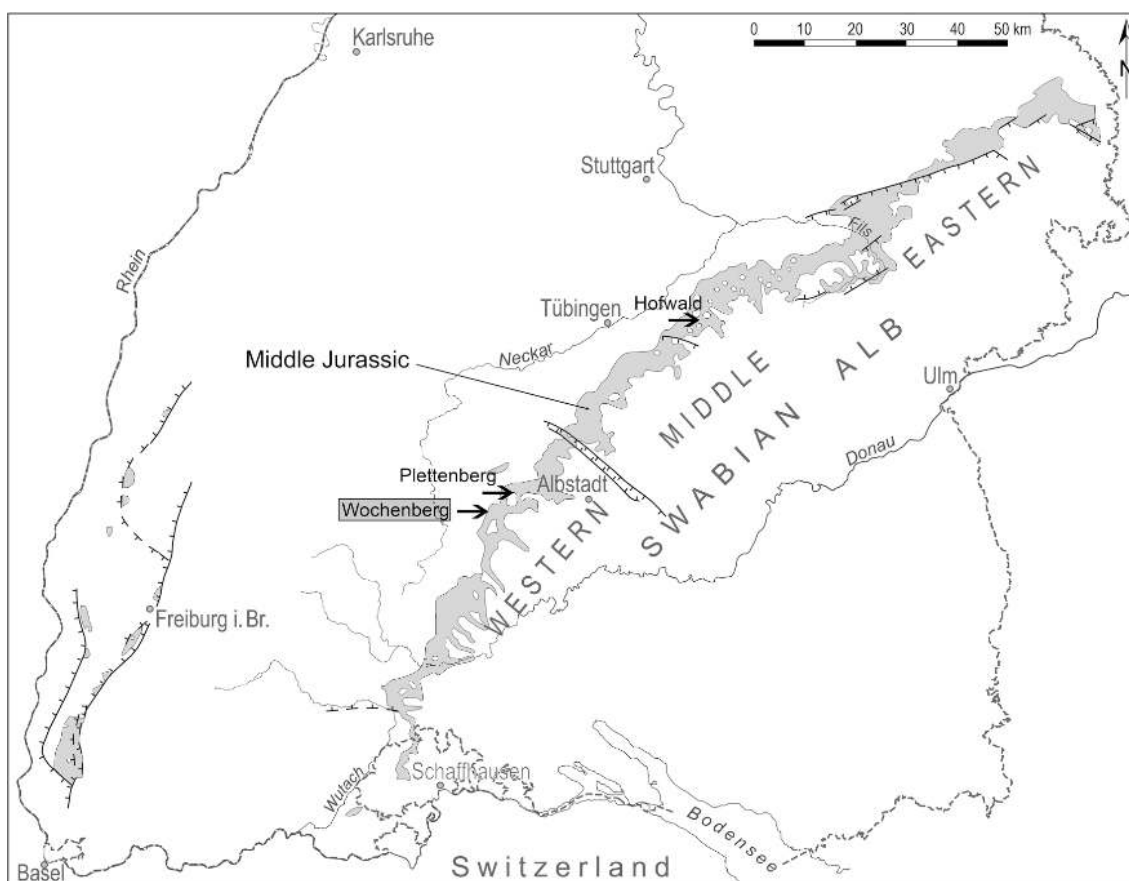


Fig. 1. Location of the outcrops in SW Germany. Modified from [DIETZE et al. \(2019\)](#).

sponds to the *crassicostatum* horizon (Bifidatum Subzone) (former Comptum Subzone), Opalinum Zone, lower Aalenian; [DIETZE et al. 2021](#)).

All specimens from the Wilflingen Bank were extracted mechanically from the embedding matrix. The illustrated specimens were coated with magnesium oxide to obtain a better contrast. The specimens are stored in the following repositories: SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany; MNHNL: Musée national d'histoire naturelle, Luxembourg.

3. Systematic palaeontology

Order Belemnitida ZITTEL, 1895
 Suborder Belemnitina ZITTEL, 1895
 Family Megateuthididae SACHS & NALNJAIEVA, 1967
 Genus *Acrocoelites* LISSAJOUS, 1915

Type species: *Belemnites oxyconus* HEHL in ZIETEN, 1831; by original designation.

Acrocoelites ippolita WEIS n. sp.

Figs. 3A–C, 4A, B, D, E

? 1980 “Fragment of a belemnite apex” – RIEGRAF, p. 154, text-fig. 14,.

Etymology: In honour of Ms. IPPOLITA BUTTIGLIONE (Luxembourg and Monopoli, Italy), for her continuous support over the past years.

Type material: The holotype hereby designated is specimen SMNS 70177 (Fig. 3A). Eleven paratypes are also designated (SMNS 70021, 70178–70184 and 70187a–c; MNHNL BEL544, BEL545). The type material, except specimen SMNS 70021 and BEL544–545, has been collected by W. RIEGRAF† in 1984 (old collection numbers: WR.702/5784/5785/5786) and has been donated to the palaeontological collections of the Staatliches Museum für Naturkunde, Stuttgart (SMNS) in February 2014. Specimen SMNS 70021 has been collected and donated by private collector F. BEMMERER in 1988. Specimens MNHNL BEL544 and BEL545 have been collected and donated by private collector NORBERT WANNENMACHER in 2017.

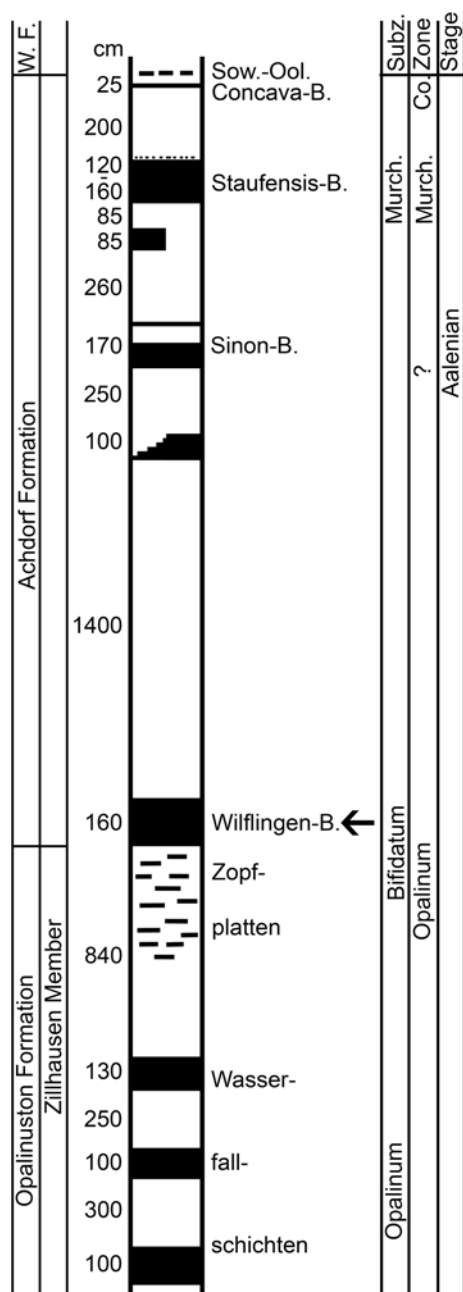


Fig. 2. Section of the type locality of *A. ippolitae* WEIS n. sp. at the Wochenberg hill (modified from RIEBER 1963). A biostratigraphical subdivision of the interval between Staufensis-Bank and Wilflingen-Bank is currently not possible due to the lack of ammonite findings.

Type locality: Wochenberg hill near Schömburg-Schörzingen (western Swabian Alb, SW Germany).

Type horizon: Wilflingen-Bank (former “Comptumbank”), Achdorf Fm. (lower Aalenian, Opalinum Zone, Bifidatum

Subzone (former “Comptum” Subzone), *crassicoelatus* horizon).

Additional material studied: (hereby excluded from the paratype series) 1 apical fragment from the ‘Opalinoidea-Bank’ (= Sinon-Bank sensu RIEBER 1963, fig. 2, section d), Achdorf Formation (middle Aalenian, Murchisonae Zone, Haugi Subzone) from the northern flank of the Plettenberg hill near Balingen, western Swabian Alb, SW Germany (SMNS 70185); 1 complete rostrum from the ‘Concava-Bank’, Achdorf Formation (upper Aalenian, Concavum Zone, Concavum Subzone), Hofwald near Metzingen (middle Swabian Alb, SW Germany) (SMNS 70186).

Diagnosis: Large-sized, elongate *Acrocoelites*. Outline symmetrical, cylindrical-cylindriconeal. Profile asymmetrical, cylindriconeal-conical. Transverse sections elliptical, compressed. Apex sharp, elongate, bearing two well-developed dorsolateral apical grooves and a shallow medio-ventral groove, accompanied by a ventral flattening. Broad, shallow lateral lines. Alveolus ventrally eccentric, occupying one third to one quarter of the rostrum.

Description: The large-sized rostra are moderately robust and typically elongate (maximum length ca. 180 mm, maximum diameter ca. 25 mm). The outline is symmetrical and cylindrical to cylindriconeal. The profile is asymmetrical and cylindriconeal to moderately conical. The alveolar end is slightly enlarged, “trumpet”-like. Transverse sections of the rostrum are elliptical, compressed along the whole rostrum. The apical region is sharp, markedly elongate and has a sword-like aspect in adult specimens; it is short-conical in earlier ontogenetic stages. The striated apex shows a weak epirostral growth, visible in sections. The apex bears two deeply incised dorsolateral grooves, which may reach up to 40 mm of length. A shallow ventral groove is more or less developed in the apical region; it may start at the tip of the apex, but typically starts 5–10 mm from the tip, occupying a medio-ventral position. This ventral groove is accompanied by a weak flattening of the venter. Lateral lines are developed as broad, shallow depressions on both flanks. The distinctly eccentric alveolus is inclined towards the venter; it occupies approximately one third to one quarter of the total rostrum length. The apical line is goniolineate, the alveolar angle is 28°.

Ontogeny: The ontogeny shows an almost regular growth. Earliest juvenile stages are strongly conical and remain such until the latest growth stages, presumably corresponding to the adult stage; at this stage, the rostrum grows only in length, and the typical elongate, sword-like apical region develops. At this late stage, a weak epirostral growth is present, close to the apex.

Remarks: *A. ippolitae* WEIS n. sp. shows a close similarity to *Megateuthis beneckeii* SCHWEGLER, 1938 from the upper Aalenian of the Swabian Alb (SCHWEGLER 1938; SCHLEGELMILCH 1998); however, the ventral groove chiefly distinguishes it from the latter. *Homaloteuthis spinata* QUENSTEDT, 1848 and *H. murielae* WEIS & MARIOTTI, 2008 from the upper Aalenian differ by their stronger compression and the grooveless apex. Some specimens of *Acrocoelites quenstedtii* show an abnormally long ventral groove



Fig. 3. *Acrocoelites ippolita* WEIS n. sp., Bifidatum Subzone, Opalinum Zone, lower Aalenian, Wochenberg hill near Schörzingen, SW Germany. **A** – Holotype, SMNS 70177 (former coll. RIEGRAF n° WR5785); A₁, lateral view, venter left; A₂, ventral view. **B** – Paratype, SMNS 70178; B₁, lateral view, venter right; B₂, ventral view. **C** – Paratype, longitudinal section, venter left, SMNS 70180. All specimens in natural size. Scale bar equals 20 mm.

(Fig. 4F) and may resemble juvenile or subadult *A. ippolita* WEIS n. sp.; however, they can be distinguished by their cylindrical profile. The genus *Eocylindroteuthis* RIEGRAF, 1980 from the lower Bajocian, and especially *E. corneliaschmit-*

tae RIEGRAF, 1980 show also a great resemblance in rostrum morphology; however, their lack of dorsolateral apical grooves allows to safely distinguish them from *A. ippolita*. By the more or less cylindrical shape of the rostrum, one

can see some similarities between *Acrocoelites ippolitae* WEIS n. sp. and representatives of the cylindroteuthiid genus *Cylindroteuthis*, although the presence of dorsal-lateral grooves and short-conical earlier ontogenetic stages in the former permit to distinguish these genera and families.

Stratigraphic and geographic distribution: Aalenian (Opalinum–Concavum zones) of SW Germany.

Acrocoelites cf. *ippolitae* WEIS n. sp.
Fig. 4C

Material: One complete rostrum from the “Couches à Sonninia” (lower Bajocian, Laeviuscula Zone) from the Hutberg section, near Rumelange (southern Luxembourg), reported as *A. cf. ippolitae* (MNHN BU300).

Description: The *Acrocoelites*-like rostrum shows an elongate-conical profile and a cylindric outline. The flanks are laterally compressed, the cross section is elliptical. The elongate, acute apex bears two well-incised and long dorsolateral grooves. A circa 50 mm long flattened area is present on the ventral apical part and fades out on the stem part.

Remarks: This single rostrum from the Bajocian of southern Luxembourg bears great resemblance with coeval *Eocylindroteuthis*, which is found in the same beds (WEIS & MARIOTTI 2008; SADKI et al. 2015); however, it is distinguished by its well-developed dorsolateral grooves, and thus approaches *Acrocoelites ippolitae*. We interpret this rostrum as a transitional form linking the genera *Acrocoelites* and *Eocylindroteuthis*.

Stratigraphic and geographic distribution: Lower Bajocian (Laeviuscula Zone) of Luxembourg.

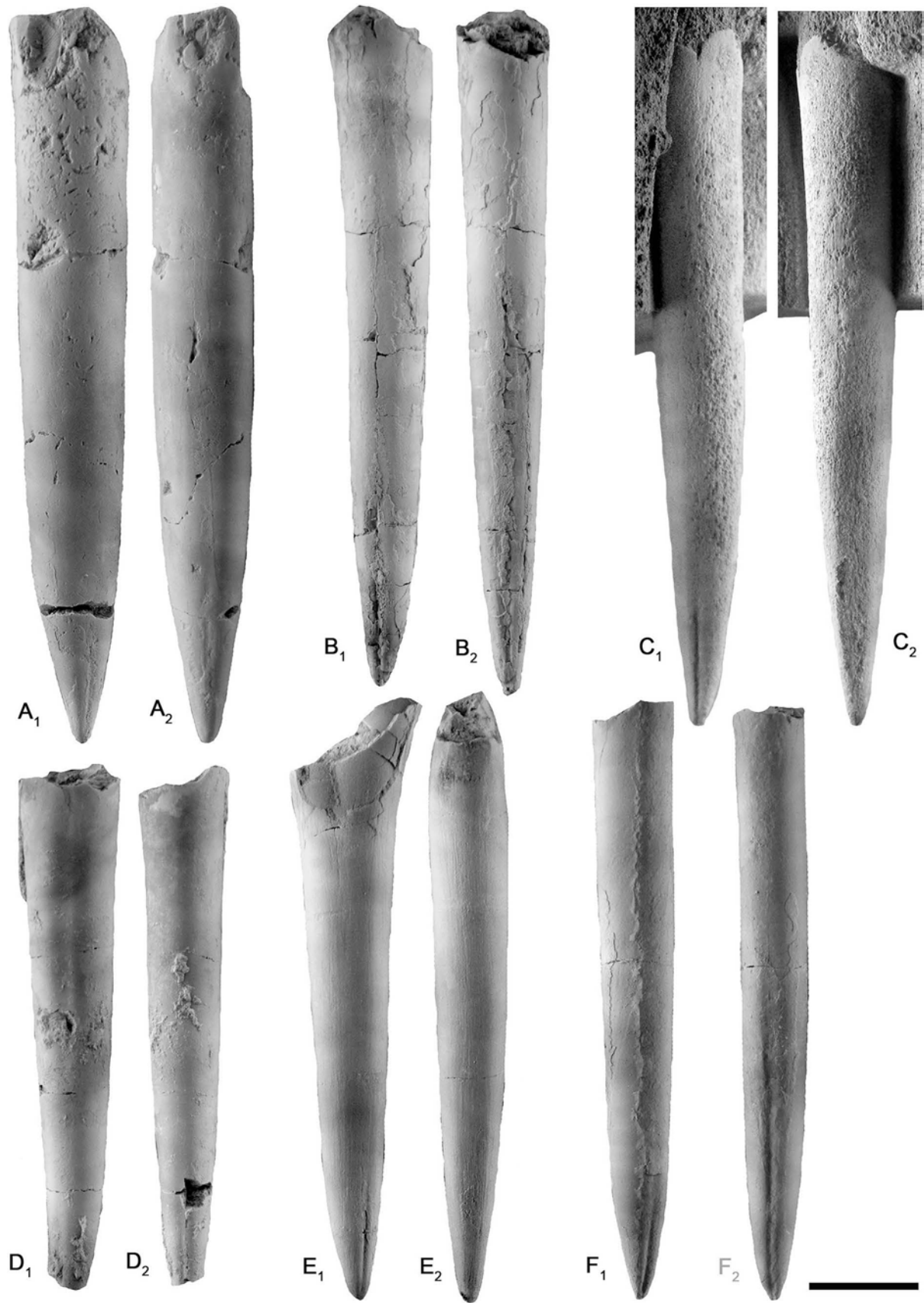
4. Systematic position of *A. ippolitae* and its relationships with coeval Megateuthididae

The family Megateuthididae has recently been revised by DZYUBA et al. (2015). In Northwest and Central Europe, belemnite diversity during the Aalenian is particularly low (RIEGRAF 1980; WEIS 1999; WEIS & MARIOTTI 2008; DERA et al. 2016). From these areas (Germany, Luxembourg, Belgium, central and eastern France, northern Switzerland), only the megateuthiid genera *Megateuthis*, *Acrocoelites*, *Homaloteuthis*, *Brevibelus*, and the holcobelid genus *Holcobelus* are known (WEIS & MARIOTTI 2008; MARIOTTI et al. 2010, 2012; WEIS et al. 2017), with a total number of six species (Fig. 5). This is in striking opposition with northern Siberia (MELEDINA et al. 2005), where 16 genera and a total of 48–50 species establish the

Aalenian as the stage with the highest belemnite diversity. The reasons of this shift in diversity are yet largely unexplored; a conspicuous divergence remains even taking into consideration that the Siberian belemnite faunas from the Toarcian–Aalenian have not been revised since the early 1970’s and that a revision at species level would probably result in synonymizing some species. Perhaps this can be partly explained as a consequence of the early Toarcian Oceanic Anoxic Event (T-OAE), which dramatically affected the fauna of European seas during the *Dactylioceras tenuicostatum* – *Harpoceras falciferum* zone transition (DERA et al. 2016; NEIGE et al. 2021). This event was associated with the almost complete disappearance of Passaloteuthididae in the seas of Northwest and Central Europe (ULLMANN et al. 2014; DZYUBA et al. 2015), and, subsequently the development of endemic Boreal-Arctic belemnite faunas (DOYLE 1987; MELEDINA et al. 2005; DZYUBA et al. 2015).

The phylogenetic relationships of genera within the family Megateuthididae are still not entirely clarified, despite the long history of studying the representatives of this family and its global distribution in the Toarcian–Bajocian. At the early stage of belemnite evolution (Early–Middle Jurassic), the predominant development of taxa with unstable morphological characters, such as varying apical grooves, is quite expected, which complicates phylogenetic reconstructions within families.

The new belemnite species described herein is especially interesting for the peculiarities of the development of the ventral groove, which is shallow medio-ventral. This feature brings *Acrocoelites ippolitae* WEIS n. sp. closer to typical representatives of the megateuthiid genus *Eocylindroteuthis*. Earlier, it was established that in some specimens of *Eocylindroteuthis corneliaschmittae* RIEGRAF, 1980 and *E. riegrafi* DZYUBA & C.D. SCHRAER in DZYUBA et al., 2019 the ventral groove may reach the apex like in typical *Acrocoelites* (SADKI et al. 2015; DZYUBA et al. 2019). This can be interpreted as an atavistic character, hinting at the derivation of the genus *Eocylindroteuthis* from the genus *Acrocoelites*, by loss of the dorsolateral grooves and evolution of the ventral apical groove to median ventral. *Eocylindroteuthis* has first been described by RIEGRAF (1980) from the Swabian Jurassic (lowermost Bajocian), and later also from Luxembourg (WEIS 2006; WEIS & MARIOTTI 2008; SADKI et al. 2015). More recently, the genus has been reported from the Russian Volga Basin (IPPOLITOV 2018) and southcentral Alaska (DZYUBA et al. 2019). RIEGRAF



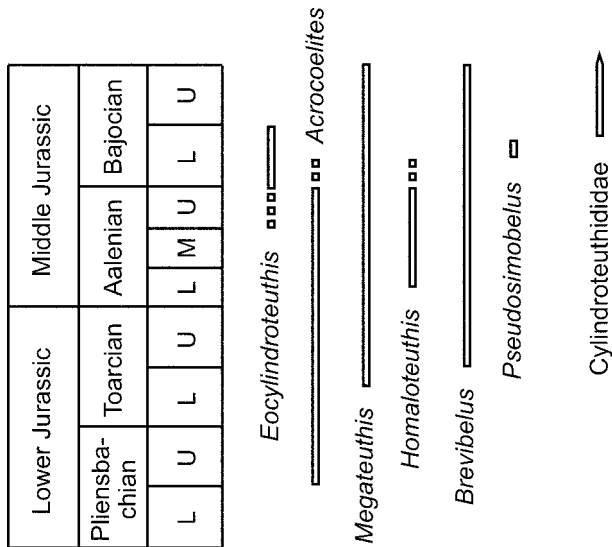


Fig. 5. Stratigraphic chart showing the distribution of the discussed genera belonging to Megateuthididae and Cylindroteuthididae. The cylindroteuthidid lineage continues into younger strata.

(1980: 154), RIEGRAF *et al.* (1998), and SCHLEGEL-MILCH (1998) considered *Eocylindroteuthis* as the ancestor of *Cylindroteuthis* and as the oldest member of Cylindroteuthididae. Due to its conical early ontogeny and the evident morphological affinities with coeval Megateuthididae, DZYUBA (2011) included *Eocylindroteuthis* into the family Megateuthididae, followed by DZYUBA *et al.* (2015) and IPPOLITOV (2018). The newly introduced megateuthidid genus *Pseudosimobelus* from the lower Bajocian of southcentral Alaska has recently been considered as a putative ancestor to Cylindroteuthididae (DZYUBA *et al.* 2019); this hypothesis is currently favoured by the authors.

5. Conclusions

The well-studied Swabian Jurassic occasionally reveals still new fossil taxa: rare belemnite findings from the Wilflingen-Bank (Opalinum Zone, lower Aalenian) of the Wochenberg hill are identified here as *A. ippolitae* WEIS n. sp. Further findings attributed to the same taxon are reported from the Murchisonae and Concavum zones of the Swabian Alb. Yet, the new species is the youngest *Acrocoelites* in the European Middle Jurassic and thus extends the stratigraphic range of the genus up to the upper Aalenian. As far as known, the taxon is endemic to the Swabian Jurassic, though a related form (*A. cf. ippolitae*) has been identified from the lower Bajocian of Luxembourg. The new species can be distinguished by its peculiar apical groove morphology from coeval Megateuthididae. The medio-ventral position of the ventral groove indicates a strong phylogenetical relationship with the lower Bajocian megateuthidid genus *Eocylindroteuthis* that is widespread in the Peri-Tethyan domains of Western Europe and the Russian Platform as well as in the East Pacific domain of Alaska.

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Fig. 4. A, B – *Acrocoelites ippolitae* WEIS n. sp., Bifidatum Subzone, Opalinum Zone, lower Aalenian, Wochenberg hill near Schörzingen, SW Germany. A, Paratype, SMNS 70179; A₁, lateral view, venter left; A₁, ventral view, ventral groove obliterated during preparation. B, Paratype, SMNS 70181; B₁, lateral view, venter right; B₂, ventral view. **C** – *Acrocoelites cf. ippolitae* WEIS n. sp., Laeviuscula Zone, lower Bajocian, Hutberg hill near Rumelange, Luxembourg, MNHNL BU300; C₁, lateral view, venter right; C₂, ventral view, showing the flattened area. **D, E** – *Acrocoelites ippolitae* WEIS n. sp., Bifidatum Subzone, Opalinum Zone, lower Aalenian, Wochenberg hill near Schörzingen, SW Germany. D, Paratype, juvenile or subadult growth stage, apex missing, SMNS 70182; D₁, lateral view, venter right; D₂, ventral view. E Paratype, juvenile or subadult growth stage, SMNS 70021; E₁, lateral view, venter left; E₂, ventral view, ventral groove obliterated during preparation. **F** – *Acrocoelites cf. quenstedti* (OPPEL, 1856), with abnormally long ventral groove, lowermost part of Opalinum Subzone, Opalinum Zone, lower Aalenian, Heiningen (clay pit), SW Germany, SMNS 70018 (former coll. G. SCHWEIGERT); F₁, lateral view, venter left; F₂, ventral view. All specimens in natural size. Scale bar equals 20 mm.

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