

# *Hypowaagenia* nov. gen., a rare genus of giant aspidoceratid ammonite from the Upper Jurassic of Southern Germany

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**Key words:** ammonites, Aspidoceratidae, taxonomy, biostratigraphy, Germany.

**Abstract.** A new genus, *Hypowaagenia* (type species: *H. endressi* nov. sp.), is introduced for previously unknown large-sized macroconchiate aspidoceratid ammonites with an umbilical and a ventrolateral row of spines. In the medium and adult stages irregular ribs interconnect these spines. The oldest unequivocal record of this genus comes from the Early Kimmeridgian Planula Zone, whereas the type material of *H. endressi* nov. sp. comes from the upper Platynota Zone/? lowermost Hypselocyclum Zone. Corresponding microconchs have not yet been identified. Although all unequivocal records come from Southern Germany, a Tethyan origin is most likely for these aspidoceratids. Another, stratigraphically younger species tentatively included in *Hypowaagenia* is *Aspidoceras acanthomphalum* (Zittel, 1870), which is, however, only recorded yet by mesoconchiate specimens. The ammonite fauna of the type horizon of *H. endressi* nov. sp. is briefly characterized and termed as the *geniculatum* Biohorizon of the late Platynota Zone.

## INTRODUCTION

Jurassic ammonites are among the best-known and longest-studied invertebrate fossils. They are successfully used for biostratigraphy since their evolution was faster than in all other groups of animals. In consequence, the time scale of the marine Jurassic is divided into ammonite zones, sub-zones and biohorizons (e.g., Oppel, 1862–1863; Callomon, 1994, 1995; Cariou, Hantzpergue, 1997; Ogg, Hinnov, 2012; Schweigert, 2015; Page, 2017, and references therein). Despite the enormous knowledge accumulated on ammonites over centuries, we have to be aware that there are several severe biases hampering our understanding of their evolution. Rare taxa can only be detected in large samples. This needs large and easily accessible outcrops of fossiliferous beds. Sampling often focuses on bigger-sized and completely preserved specimens, whereas small or incompletely pre-

served ones as well as smooth-shelled forms are easily overlooked or discarded by amateur collectors. Moreover, there are primary taphonomic filters such as poor preservation in strongly corroded *ammonitico rosso* lithologies or even complete dissolution of ammonite shells in deep-sea deposits, among others. Finally, large areas of marine Jurassic deposits suffered metamorphism or subduction along active continental margins, so that information from these regions is completely lost.

In the late Middle Jurassic and Late Jurassic, ammonites of the family Aspidoceratidae Zittel, 1895 were diverse and wide-spread, and some of them have an almost cosmopolitan distribution, except for the Polar Regions. This makes some of them potentially good tools for long-distance correlations, but, on the other hand, their identification is often very difficult due to common homoeomorphism. Their correct systematic placement strictly considering phyletic relation-

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ships is complicated not only due to sexual dimorphism (e.g., Makowski, 1962; Callomon, 1963; Énay, 1979; Davis *et al.*, 1996; Klug *et al.*, 2015), but there are additional phenomena related to autecological responses of ammonite populations, which are not yet fully understood. Recently, sexual change during individual life as well as accelerated sexual maturity resulting in small-sized females, so-called “mesoconchs” (Chandler, 2019), has been demonstrated for some Late Jurassic aspidoceratids (Parent *et al.*, 2008; Scherzinger *et al.*, 2018). There exist several attempts at a classification of aspidoceratids, ranging from a conservative morphological view (Hyatt, 1900; Schindewolf, 1925; Spath, 1931; Arkell *et al.*, 1957; Donovan *et al.*, 1981 *partim*; Checa, 1985) to a more progressive one considering at least sexual dimorphism in this family (Donovan *et al.*, 1981 *partim*; Énay, Howarth, 2019). However, further studies are needed for a convincing biological classification. Here we add a new aspidoceratid genus from the Upper Jurassic of Southern Germany which has led us to thinking about its relationship to other aspidoceratid taxa.

## GEOLOGICAL SETTING

There are a few very big limestone quarries in the area of the Franconian Alb, east of Nürnberg, where lower parts of the Franconian Upper Jurassic are exposed (Fig. 1). Two big quarries close to the village of Gräfenberg expose Oxfordian

and Lower Kimmeridgian beds, respectively, partly rich in ammonites. This is especially the case for the base of the Late Oxfordian Hypselum Zone in Deuerlein quarry, where a very rich and diverse fauna has been described as representing the *semimammatum* Biohorizon (Schairer, Schlamp, 2003). Higher up in the section, the Arzberg Formation (formerly “Malm Gamma”, see Niebuhr, Pürner, 2014) of Early Kimmeridgian age has been sampled intensively by numerous amateur collectors and a few scientists. A numbering system helps collectors to identify and characterize the exact limestone bed within the section from which specimens have been collected, but only a limited amount of material from this interval has been described (e.g., Keupp, 1977; Schlamp, 2009a, b). The characteristic lithologies of the rock matrix and the typical states of preservation of ammonites often allows the allocation of loosely collected ammonite material to the correct horizon, whereas most historical ammonite material from Franconia lacks such detailed information (e.g., Wegele, 1929; Schneid, 1939; Geyer, 1961). In this study we focus on the marly limestones of the upper Platynota Zone in the Endress quarry at Gräfenberg which are rich in ammonites and from which most specimens of the herein described new taxon come (Fig. 2). For the biostratigraphic frame of the Early Kimmeridgian biohorizons, from which our studied material comes, see Table 1.

**Material.** The studied material is housed in the collection of the Stuttgart Natural History Museum (acronym: SMNS) except specimen GPIT/CP/10343, which is housed



Fig. 1. Map showing records of *Hypowaagenia* in Southern Germany

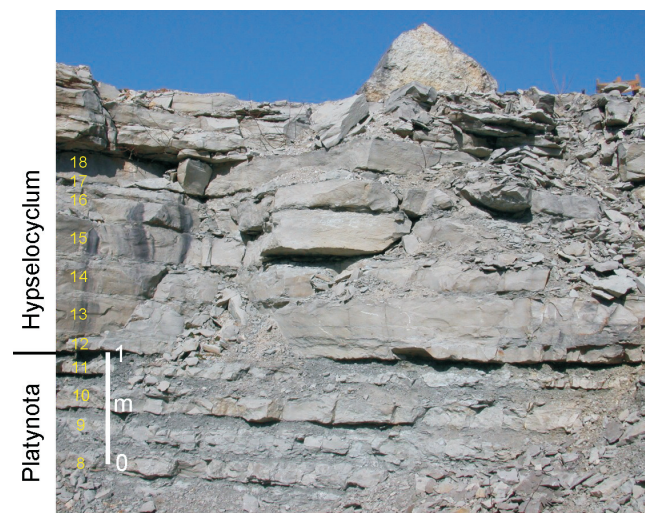


Fig. 2. Section of the Arzberg Formation exposed in the Endress quarry at Gräfenberg showing the transition from the marly interval of the upper Platynota Zone (beds 7 to 11) up to the more calcareous lower Hypselocyclum Zone (beds 12 and above)

Most specimens of *Hypowaagenia endressi* nov. gen. nov. sp. come from bed 9. Photograph: Victor Schlamp

**Table 1**  
**Early Kimmeridgian biozonation in the Submediterranean Upper Jurassic of Southern Germany**

	Zones	Subzones	Biohorizons
Early Kimmeridgian	Divisum	Divisum	<i>atavum</i>
			<i>balderum</i>
			<i>crusoliense</i>
	Hypselocyclum	Lothari	<i>perayensis</i>
			(not studied)
			<i>planulatum</i>
		Hippolytense	(not studied)
			<i>guembeli</i>
	Platynota	Guilherandense	<b><i>geniculatum</i></b>
			<i>thieuloyi</i>
		Desmoides	(not studied)
			<i>polygratus</i>
			<i>subtilicaelatum</i>
	Planula	Galar	<i>falcula</i>
			<i>wenzeli</i>
		Planula	<i>schroederi</i>
<b><i>planula</i></b>			
<i>tonnerrense</i>			
Bimammatum	Hauffianum	<i>bauhini</i>	
		<i>tizianiformis</i>	
	Bimammatum	<i>bimammatum</i>	

Biohorizons from which *Hypowaagenia* specimens have been recorded are bolded.

Lower boundary of the Kimmeridgian after Wierzbowski *et al.*, 2016. Biohorizons modified after Atrops, 1982; Cariou, Hantzpergue, 1997; Schweigert, Callomon, 1997; Schick, 2004; and own unpublished observations

in the Palaeontological Collection of Tübingen University (acronym: GPIT). The latter was found by the late Ernst Dieterich during the fieldwork for his doctoral thesis (Dieterich, 1940), but it was not illustrated therein.

## SYSTEMATIC PALAEOLOGY

Superfamily Perisphinctoidea Steinmann, 1890

Family Aspidoceratidae Zittel, 1895

Subfamily Hybonoticeratinae Olóriz, 1978

**Remarks.** In its original definition, members of Hybonoticeratinae share a ventral sulcus (Olóriz, 1978). Since there is no doubt that these forms originate in “*Pseudowaagenia*”-like forms (see Donovan *et al.*, 1981; Énay, Howarth, 2019, and discussion below), we here include ancestral forms lacking a ventral sulcus in this subfamily as well. Like in many Euaspidoceratinae, their sculpture com-

prises two rows of spines occasionally connected by ribs; however, this special branch differs by its periumbilical spines pointing strictly towards the umbilicus. The dense, irregular ribbing style persisting until the adult stage is unique among Hybonoticeratinae.

### Genus *Hypowaagenia* nov.

**Type species.** *Hypowaagenia endressi* nov. sp.

**Etymology.** After Greek *hypos* = lower, guest, because of the early occurrence in the Upper Jurassic, and *-waagenia*, the original name used for ammonites of the genus *Hybonoticerat*, later replaced by Breistroffer (1947) due to preoccupation.

**Included species.** *Hypowaagenia endressi* n. sp.; (? *Aspidoceras acanthomphalum* Zittel, 1870).

**Diagnosis.** See diagnosis of type species.

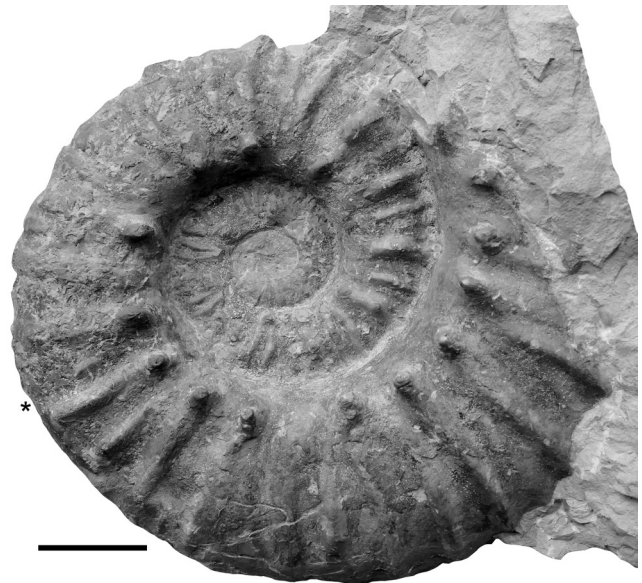
**Distribution.** Kimmeridgian of Southern Germany, ? Pakistan.

### *Hypowaagenia endressi* nov. sp.

Figs. 3–7

**Holotype.** Specimen illustrated in Fig. 3, SMNS 70524/1, from Gräfenberg (ex coll. Anton Hostalka, Ebermannstadt).

**Paratypes.** PT 1, SMNS 70524/2, (ex coll. Jürgen SMNS 70524/4, Fig. 6, both from Gräfenberg (coll. V. Schlampp). PT 4, SMNS 70524/5, Fig. 7, from Bischberg (ex coll. Franz Janin, Nürnberg). For measurements see Table 2.



**Fig. 3.** *Hypowaagenia endressi* nov. gen. nov. sp., holotype, late Platynota Zone (?or basal Hypselocyclum Zone), Gräfenberg, Franconia. SMNS 70524/1 (ex coll. Anton Hostalka, Ebermannstadt). Asterisk indicates beginning of bodychamber. Scale bar equals 5 cm

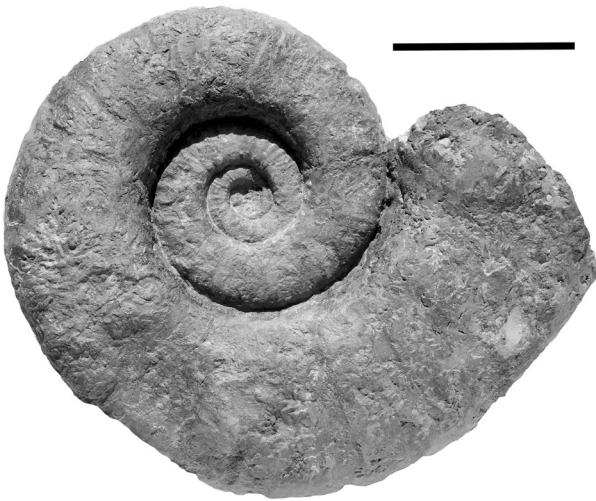


Fig. 4. *Hypowaagenia endressi* nov. gen. nov. sp., paratype 1; Arzberg Formation, bed 9 of Schlampp (2009b); Platynota Zone, *geniculatum* Biohorizon, Gräfenberg, Franconia. SMNS 70524/1 (ex coll. Jürgen Schwarz, Igensdorf). Scale bar equals 5 cm



Fig. 5. *Hypowaagenia endressi* nov. gen. nov. sp., paratype 2; Arzberg Formation, bed 9 of Schlampp (2009b); Platynota Zone, *geniculatum* Biohorizon, Gräfenberg, Franconia. SMNS 70524/3. Asterisk indicates beginning of bodychamber. Scale bar equals 5 cm

**Etymology.** Named after Wolfgang Endreß (Gräfenberg), who provided access to the quarry in his property and allowed us sampling fossils for scientific purpose.

**Type locality.** Gräfenberg, Franconia (Fig. 1).

**Type horizon.** Arzberg Formation; Early Kimmeridgian, Platynota Zone, Guilhaendense Subzone, *geniculatum* Biohorizon (= bed 9 in Schlampp, 2009b).

**Occurrences.** Upper Jurassic, Lower Kimmeridgian, uppermost Platynota Zone – ? basal *Hypselocyclum* Zone of Franconia, cf.-specimen (Fig. 8) from the Planula Zone of Swabia.

**Diagnosis.** Macroconchiate, large- to giant-sized aspidoceratids with steep umbilical wall and evolute coiling. Inner whorls mainly sculptured by growth lines bundled to irregular ribs, with a periumbilical row of densely spaced spines directed towards the umbilicus and a less pronounced ventromarginal row of spatulate spines. In the medium and adult stages both rows are connected by coarse, irregularly spaced ribs. Ribs and umbilical spines continue to the end of the adult bodychamber whereas ventrolateral row of spines disappears earlier. On the connecting ribs, additional swellings may occur at mid-flank. Whorl section high-subtrapezoidal, ribs crossing the rounded venter un-interrupted.

**Descriptions.** The holotype (Fig. 3) is the most complete specimen of this taxon. It is a moderately compressed steinkern showing all growth stages except of the initial stage, which is not preserved. Proximal part of bodychamber ventrally broken off prior to burial. Bodychamber length is approximately half a whorl. Sculpture very irregular; a periumbilical row of prominent spines is developed in the last whorl; giving rise to one or two retroradiate, concave ribs crossing the venter uninterrupted. In the final stage the ribbing is strongly retroradiate. A few secondaries occur as well on the bodychamber. In the beginning of the last whorl some of ribs clearly bear ventrolateral nodes, which disappear later on the bodychamber. At mid-distance between the periumbilical and ventrolateral nodes some of the ribs show swellings.

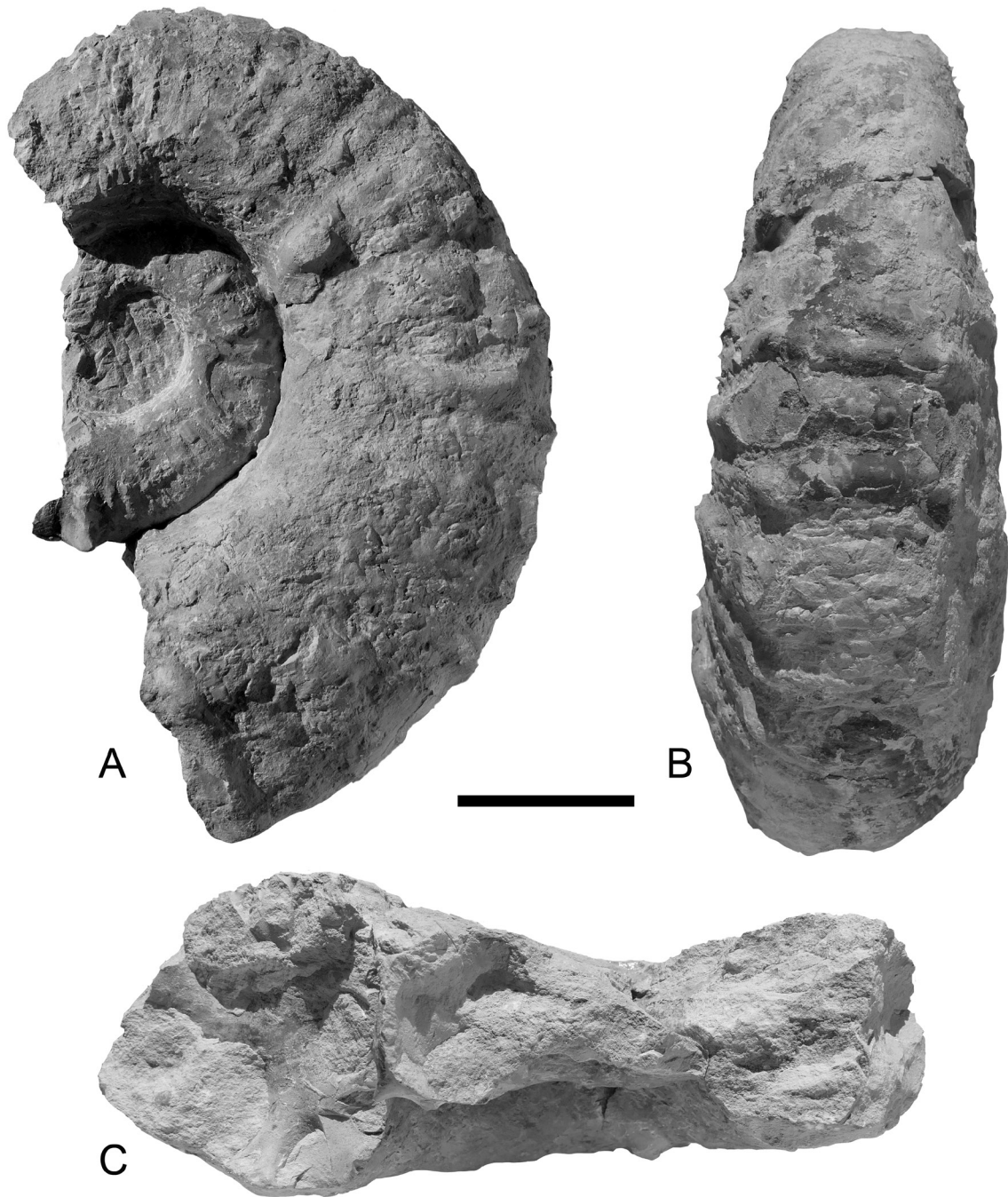
Paratype 1 (Fig. 4) is preserved as a moderately compressed phragmocone. The unfigured flank of the specimen is strongly flattened. Due to its preservation as a steinkern

Table 2

Dimensions [mm]

Specimen	D	U	H	W
HT, 70524/1	280	110	105	–
PT 1, 70524/2	164	60	60	–
PT 2, 70524/3	335	130	125	–
PT 3, 70524/4	230	81	92	92
PT 4, 70524/5	570	225	205	–

HT – holotype; PT – paratype; D – diameter; U – umbilical width; H – whorl height; W – whorl width

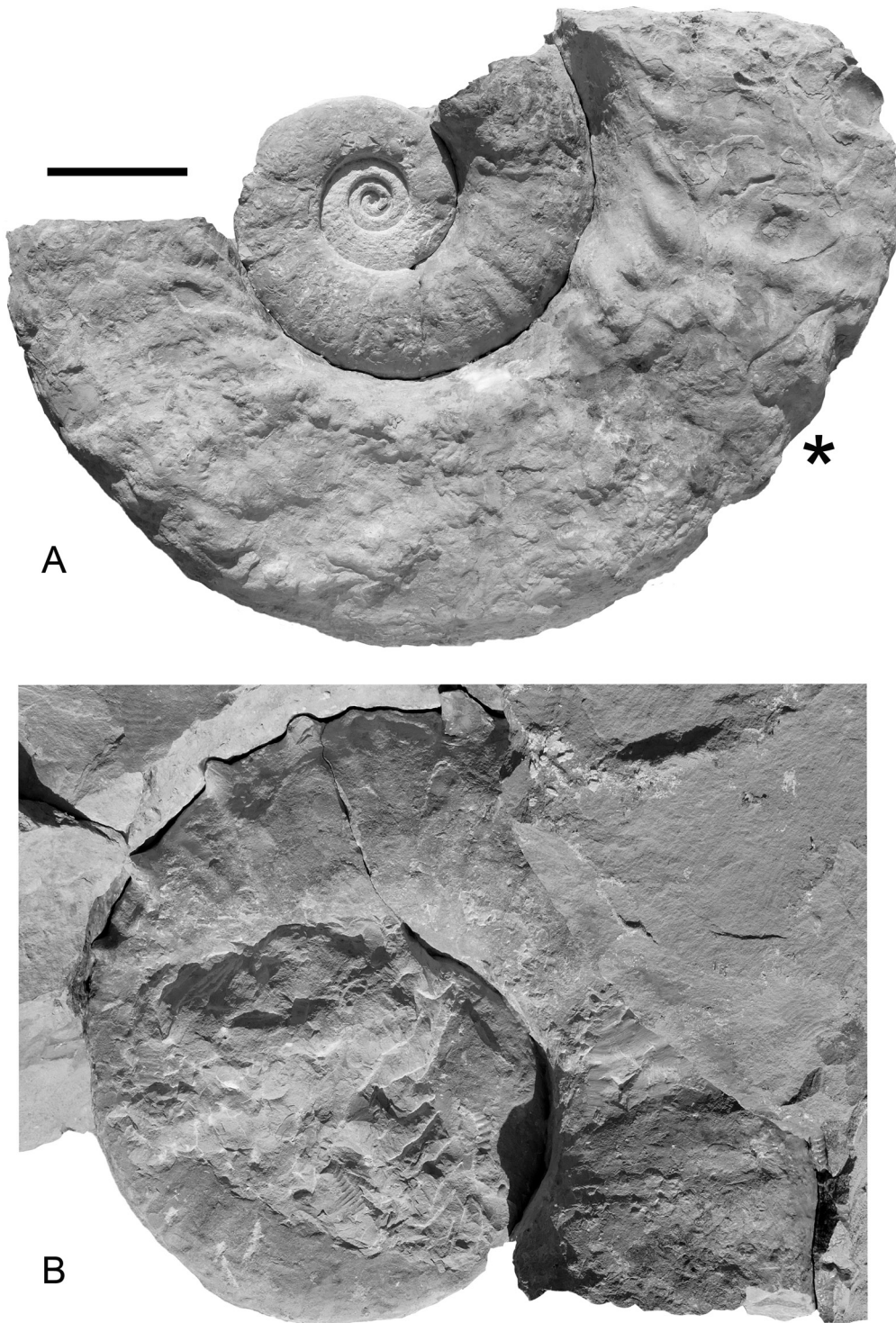


**Fig. 6.** *Hypowaagenia endressi* nov. gen. nov. sp. Paratype 3; Arzberg Formation, bed 9 of Schlampp (2009b); Platynota Zone, *geniculatum* Biohorizon, Gräfenberg, Franconia; SMNS 70524/4

A. Lateral view; B. Ventral view; C. View of whorl sections. Scale bar equals 5 cm

the originally floored hollow spines are not preserved. Juvenile whorls, however, are best discernible in this specimen except for the innermost nucleus. They show a very dense

and fine, slightly convex ribbing with tubercles along the umbilical edge. During ontogeny these ribs become gradually coarser and more distant. Occasionally two ribs may



**Fig. 7.** *Hypowaagenia endressi* nov. gen. nov. sp.

**A.** Paratype 4, Platynota Zone, *guilherandense* Biohorizon, Berg bei Neumarkt in der Oberpfalz-Bischberg, Franconia. Note that inner whorls are not preserved (incorrect reconstruction by the finder); SMNS 70524/5 (ex coll. Franz Janin, Nürnberg). Asterisk indicates beginning of bodychamber. Scale bar equals 10 cm; **B.** Close-up view of opposite flank of SMNS 70524/5 showing some ventrolateral spines preserved (not to scale)

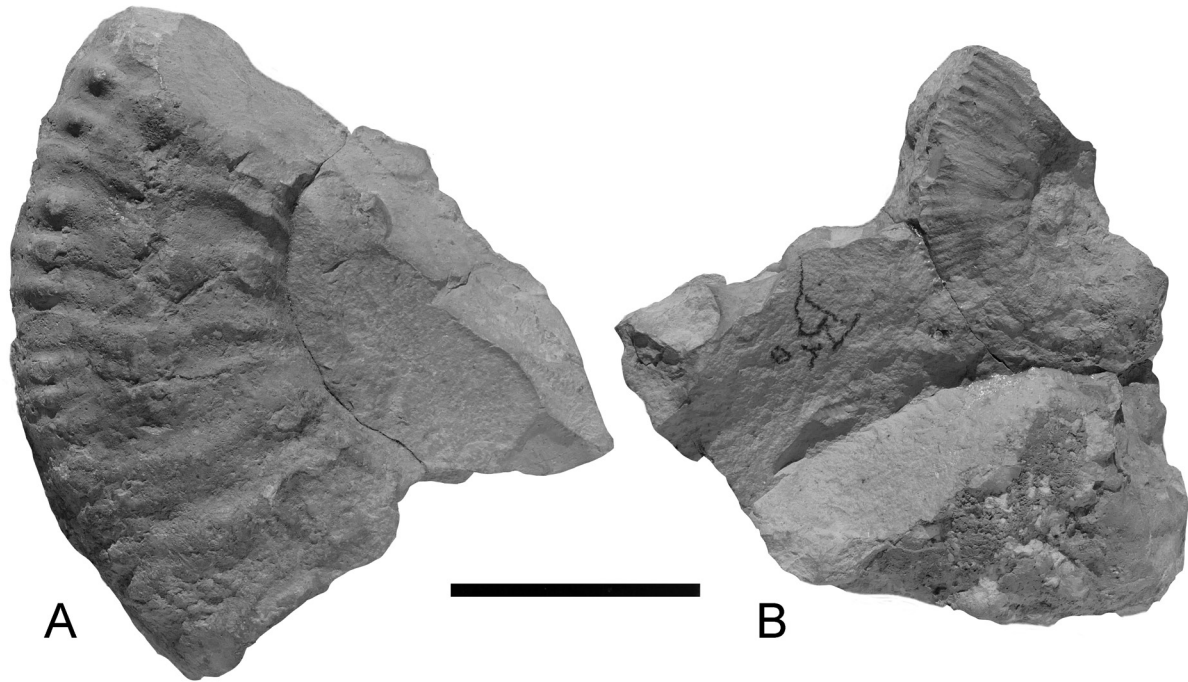


Fig. 8. *Hypowaagenia cf. endressi* nov. gen. nov. sp., Braunenber quarry near Aalen-Wasseralfingen, Swabia (Early Kimmeridgian, Planula Zone, *planula* Biohorizon); GPIT/CP/10343 (leg. Ernst Dieterich)

A, B. Lateral views. Scale bar equals 5 cm

originate from one umbilical spine. Outer whorl shows very irregularly spaced, retroradiate ribs crossing the rounded venter without interruption. Extremely evolute coiling strongly resembling lycoceratids.

Paratype 2 (Fig. 5) is a very large, moderately compressed almost complete steinkern with its bodychamber and about one whorl of the phragmocone. Inner parts of the phragmocone are missing. In the phragmocone and on one flank also on the bodychamber periumbilical spines pointing towards the umbilicus are developed. Ventrolateral spines are not developed in the bodychamber and most likely not preserved in the previous stage because of their floored sockets, which hampered their filling. Irregularly arranged rectiradiate, slightly concave ribbing on the phragmocone changes to rectiradiate ribbing on the bodychamber. Periumbilical spines give rise to one or two ribs; a few additional secondaries occur. Ribs cross the rounded venter without interruption.

Paratype 3 (Fig. 6) is a large, uncompressed phragmocone fragment with parts of two whorls. It is preserved as a steinkern. Indistinct strongly rectiradiate ribs on the steep umbilical wall, occasionally forming umbilical nodes, from which they either continue or diverge into two coarser rectiradiate ribs. One well-preserved spatulate spine is preserved

on the ventral margin of the inner whorl. Venter rounded in the outer whorl, but almost flat in the inner whorl. Whorl section subquadratic in the inner whorl, changing into subtrapezoidal in the latest preserved stage. There is hardly any overlap between the two succeeding whorls resulting in a *Lycoceras*-like appearance of the coiling.

Paratype 4 (Fig. 7) is a giant example of the species with a preserved diameter of *ca.* 570 mm. Despite this enormous size it is still incomplete, since only one quarter of the outer whorl belongs to the bodychamber. The final adult diameter is estimated at *ca.* 750 mm, with an assumed bodychamber length of half a whorl. The specimen is almost uncompressed, but worn on one flank. Innermost whorls are not preserved. On the reverse flank spatulate ventrolateral spines occur like the sole one in paratype 3. Adult ribbing persists without weakening until the end of the conch.

A fragmentary specimen from the Early Kimmeridgian (*sensu* Wierzbowski *et al.*, 2016) Planula Zone of eastern Swabia (Fig. 8) shows an inner whorl with a periumbilical row of spines pointing towards the umbilicus. Each spine gives rise to an irregular bundle of fine rectiradiate to retroradiate ribs. The preserved part of the outer whorl exhibits an additional ventrolateral row of nodes connected with the

periumbilical ones by coarse ribs. A few ribs lack the ventrolateral node. On mid-flank some of the ribs show swellings. This sculpture is identical to that of the stratigraphically younger specimens of *H. endressi*. More complete specimens are necessary to decide whether this species is morphologically conservative and has a long stratigraphical range or if it represents a different species of this genus. We here tentatively assign this specimen to *H. cf. endressi*.

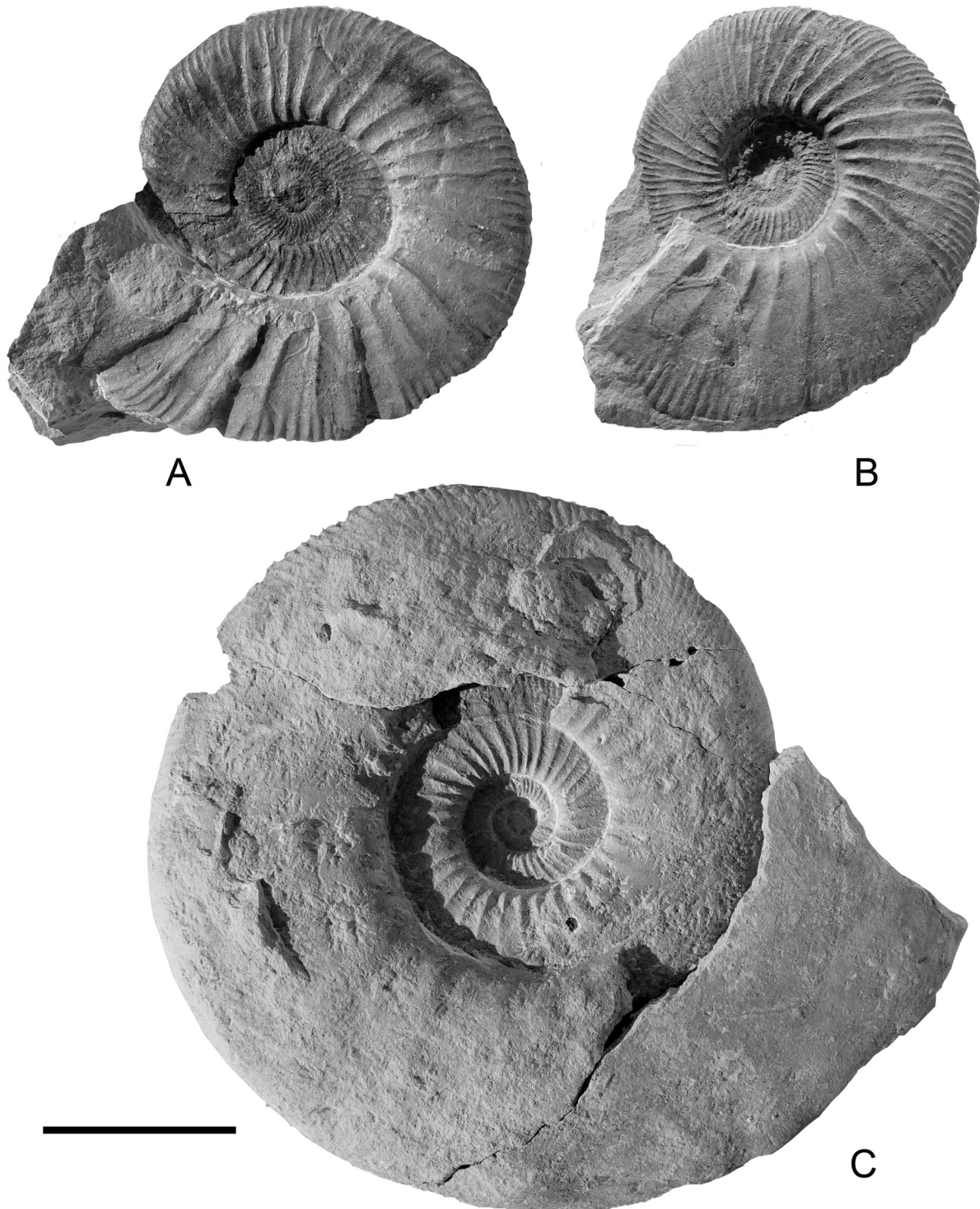
**Discussion.** *Hypowaagenia* nov. gen. differs from all other aspidoceratid genera by its very irregular coarse ribbing connecting a periumbilical row of spines with a ventrolateral one. The dense row of periumbilical spines pointing towards the umbilicus of the ammonite is rather significant and also seen in a few other aspidoceratids, especially in the Late Kimmeridgian – Early Tithonian genus *Hybonoticer* Breistroffer, 1947. If the specimens had developed a ventral sulcus we would not have hesitated to include *H. endressi* in the latter. To our knowledge, the only Kimmeridgian ammonite somewhat resembling the adult state of *Hypowaagenia endressi* in its ribbing style is a very large bodychamber fragment illustrated by Fatmi and Zeiss (1999, pl. 18, fig. 1a, b) from Pakistan as “*Metagravesia cf. M. decipiens* Spath”. However, no umbilical spines have been reported from that specimen and the whorl-section is said to be trapezoidal; hence its allocation to *Hypowaagenia* remains doubtful.

Microconchs of *Hypowaagenia* have not been recorded yet. Microconchiate aspidoceratids are represented by genera such as *Sutneria*, *Mirosphinctes*, *Hybonotella*, *Simosphinctes*, *Simocosmoceras*, and *Epipeltoceras* (e.g., Énay, 1962, 1979; Bonnot *et al.*, 1994, 2009; Schweigert, 1997, 1998, 2013; Bonnot, Gygi, 2001; Énay, Howarth, 2019). Considering the origin of *Hypowaagenia* within an Oxfordian Euaspidoceratinae stock (see below), these still unknown microconchs are expected to have had a *Mirosphinctes*-like appearance. A small, probably microconchiate ammonite assigned to “*Waagenia*” (former name of *Hybonoticer*) was described by Fischer (1913) from Early Kimmeridgian beds of Swabia. This “*Waagenia suevica*” was based on a single loosely collected specimen, which is unfortunately lost. Subsequently, this specimen has been considered to be a representative of *Amoebopeltoceras* (Schweigert, 1995). Meanwhile, however, more material of the latter genus appeared in various Oxfordian and Kimmeridgian strata and none of it shows any closer resemblance to Fischer’s drawing. From the illustration and description, this enigmatic specimen showing very sharp rectiradiate ribs looks very different from the inner whorls of *Hypowaagenia* but strikingly resembles species of the cardioceratid *Amoebites* Buckman, 1925. “*Waagenia suevica*” is therefore not considered a potential candidate for a corresponding microconch.

## ARE THERE FURTHER SPECIES TO BE INCLUDED IN *HYPOWAAGENIA*?

The sudden and unexpected appearance of *Hypowaagenia* in the Planula and Platynota zones of Southern Germany can be explained either by active immigration or by passive transport from neighbouring areas. Since aspidoceratids in general are diverse and widely distributed in the Tethyan Realm (e.g., Arkell *et al.*, 1957; Collignon, 1959; Geyer, 1969; Zeiss, 1979; Checa, 1985; Énay, Howarth, 2019), a Tethyan origin of this genus is very likely and further species must be expected. Indeed, there is one candidate showing some resemblance in its evolute coiling, a dense periumbilical row of spines and ventrolateral spines: *Aspidoceras acanthomphalum* Zittel, 1870. The latter was originally said to come from beds of Tithonian age, but this appears unlikely since it was later mostly recorded from Late Kimmeridgian beds, namely of the Cavouri and Beckeri zones (Checa, 1985). *Aspidoceras acanthomphalum*, however, is only small- to medium-sized and lacks a final stage with spines interconnected by ribs; hence, in first view it does not match the diagnosis of *Hypowaagenia*. On the other hand, the much smaller size of *Aspidoceras acanthomphalum* could be explained by the presence of mesoconchiate specimens only. Mesoconchs are females which became adult in an early growth stage, probably as an individual response to palaeoenvironmental conditions (Chandler, 2019). In our view, the small-sized aspidoceratid genus *Pseudowaagenia* Spath, 1931, to which *Aspidoceras acanthomphalum* has been assigned (Checa, 1985), is not a monophyletic genus, but a basket of various mesoconchiate aspidoceratids. The long-overlooked phenomenon of mesoconchs is widespread in Middle to Late Jurassic ammonites (Chandler, 2019) and has been previously demonstrated in Aspidoceratidae for some Kimmeridgian and Tithonian species of *Physdoceras* Hyatt, 1900 (Parent *et al.*, 2008; Scherzinger *et al.*, 2018). Therefore, mesoconchs should be expected to occur in other aspidoceratid genera as well. *Aspidoceras acanthomphalum* is very close to *Hybonoticer pressulum* (Neumayr, 1873) lacking only the typical ventral aspect of the latter. *Aspidoceras acanthomphalum* is especially common in the Late Kimmeridgian Cavouri Zone (Checa, 1985) and thus could well be a phyletic ancestor of *Hybonoticer*. Since younger species of *Hybonoticer* show a strong ribbing like in *Hypowaagenia* and become large-sized (although such big specimens are extremely rare), we hypothesize that *Hybonoticer* and *Hypowaagenia* are phyletically linked by intermediate forms such as *Aspidoceras acanthomphalum*, of which neither corresponding microconchs nor large-sized macro-





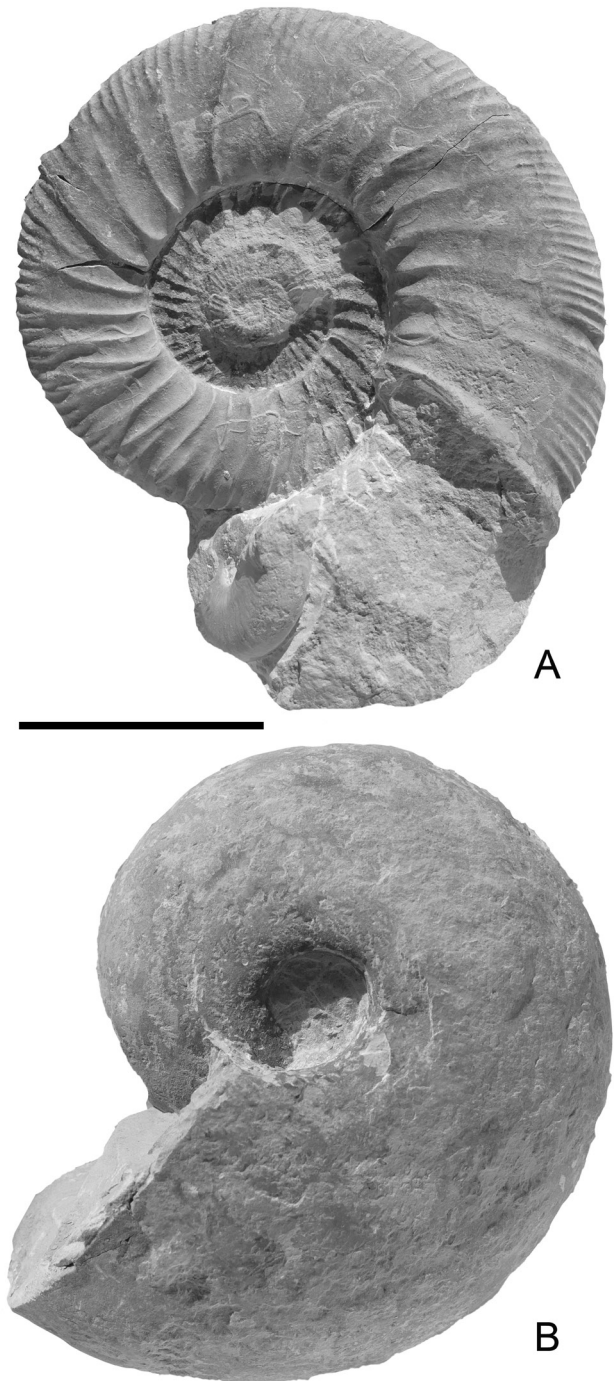
**Fig. 9. Ammonite fauna of the *geniculatum* Biohorizon (Early Kimmeridgian, upper Platynota Zone), Gräfenberg, Franconia, Endress quarry, bed 9**  
**A.** *Ataxioceras geniculatum* (Wegele, 1929), microconch; SMNS 70525/1; **B.** *Ataxioceras geniculatum* (Wegele, 1929), juvenile macroconch; SMNS 70525/2;  
**C.** *Ataxioceras geniculatum* (Wegele, 1929), incomplete macroconch; SMNS 70525/3. Scale bar equals 5 cm

conchs have yet been recorded. We are aware that these ideas and observations challenge both former and current concepts and classifications of aspidoceratids (e.g., Spath, 1931; Roman, 1938; Jeannet, 1951; Arkell *et al.*, 1957; Énay, Howarth, 2019), but when including microconchs and macroconchs in the same biological taxon, mesoconchs have to be considered as well.

Another question is the possible phyletic origin of *Hypowaagenia*. Having in mind the inner whorls of its oldest unequivocal representative from the Planula Zone of Swabia (Fig. 6) and the dense periumbilical row of spines in combination with spatulate ventrolateral spines, Dorn (1931) illustrated small- to medium-sized aspidoceratids sharing this feature, but lacking an irregular ribbing stage, as “*Aspidoceras tietzei* Neumayr” (especially Dorn, 1931, pl. 17, figs. 4, 8). These specimens have been reported from the Hypselum Zone, as well as *Euaspidoceras radisense* (d’Orbigny, 1850), to which these specimens probably belong, and should not be confused with co-occurring species of *Clambites* Rollier, 1922. Possibly, these enigmatic forms could be mesoconchiate ancestors of *Hypowaagenia*; however, this hypothesis can hardly be tested since the Dorn collection is missing and complete large macroconchs are needed for comparison. In the much more involute *Cubaspidoceras* Myczyński, 1976, two rows of spines occur of which the periumbilical one looks similar to *Hypowaagenia* as well. However, *Cubaspidoceras* is very poorly known, only recorded from Cuba and based on juveniles (Myczyński, 1976), hence no reliable comparisons are possible.

### AMMONITE FAUNA OF THE TYPE HORIZON OF *HYPOWAAGENIA ENDRESSI*

The marly limestones containing the rare records of *Hypowaagenia endressi* are very rich in more or less compacted ammonites often showing a thin green-coloured coating. The bulk of the ammonite fauna comes from bed 9 in the numbering of the sequence of the Gräfenberg quarry by Schlampp (2009b). The underlying bed 8 yields abundant smaller-sized specimens of the same taxa and most likely corresponds to the ‘horizon à Thieuloyi’ of Atrops (1982), whereas the following beds 10 and 11 are generally poor in ammonites. The ammonite fauna is by far dominated by the Submediterranean perisphinctid *Ataxioceras geniculatum* (Wegele, 1929) (Figs. 9, 10A). This extremely variable ammonite taxon, which we interpret as a senior subjective synonym of *Ataxioceras guilherandense* (Atrops, 1982), comprises more than 95% of the fauna. Aspidoceratids are rare and comprise the zonal index *Sutneria platynota* (Reinecke,



**Fig. 10. Ammonite fauna of the *geniculatum* Biohorizon (Early Kimmeridgian, upper Platynota Zone), Gräfenberg, Franconia, Endress quarry, bed 9**

- A. *Ataxioceras geniculatum* (Wegele, 1929), juvenile macroconch with long-persisting microconchiate ribbing style (? gender reversal); SMNS 70525/4;  
 B. *Physodoceras circumspinosum* (Quenstedt, 1849); SMNS 70525/5

1818) and its macroconch counterpart *Physodoceras circumspinosum* (Quenstedt, 1849) (Fig. 10B) besides the above described *H. endressi*. OPELLIIDS are extremely rare and represented by *Metahaploceras* sp. only. Subboreal perisphinctids are represented by occasional *Eurasenia gothica* (Schneid, 1939) (Fig. 11A), Mediterranean perisphinctids by very rare *Lessinicerias raschii* (Canavari, 1897) (Fig. 11B). Boreal elements such as cardioceratids have not been recorded in this biohorizon. Phylloceratids and lytoceratids are missing as well. The composition of this Submediterranean ammonite assemblage fits well with the Guilhaerandense Subzone of the Platynota Zone (Atrops, 1982; Schick, 2004). Within the Guilhaerandense Subzone Atrops (1982) distinguished two biohorizons, a ‘Horizon à Thieuloyi’ at the base and a ‘Horizon à Guilhaerandense’ above. In this respect, the larger-sized ammonite fauna of bed 9 in the Gräfenberg section corresponds to the latter biohorizon, here termed as *geniculatum* Biohorizon. The same biohorizon occurs in the Lacunosamergel Formation of Swabia (e.g., Salmendingen, SMNS collection) in a limestone bed just below the Hypselocyclum Zone. In Spain, larger-sized but typical microconchs of *Ataxioceras geniculatum* (Schneid) from the Guilhaerandense Subzone have been assigned to a supposedly endemic genus *Olorizia* (Moliner in: Moliner, Olóriz, 2009). The occurrence of *Lessinicerias raschii* (Canavari, 1897) links the *geniculatum* Biohorizon of the late Platynota Zone with the basal Strombecki Zone of the Southern Alps (Pavia *et al.*, 1987; Sarti, 1993).

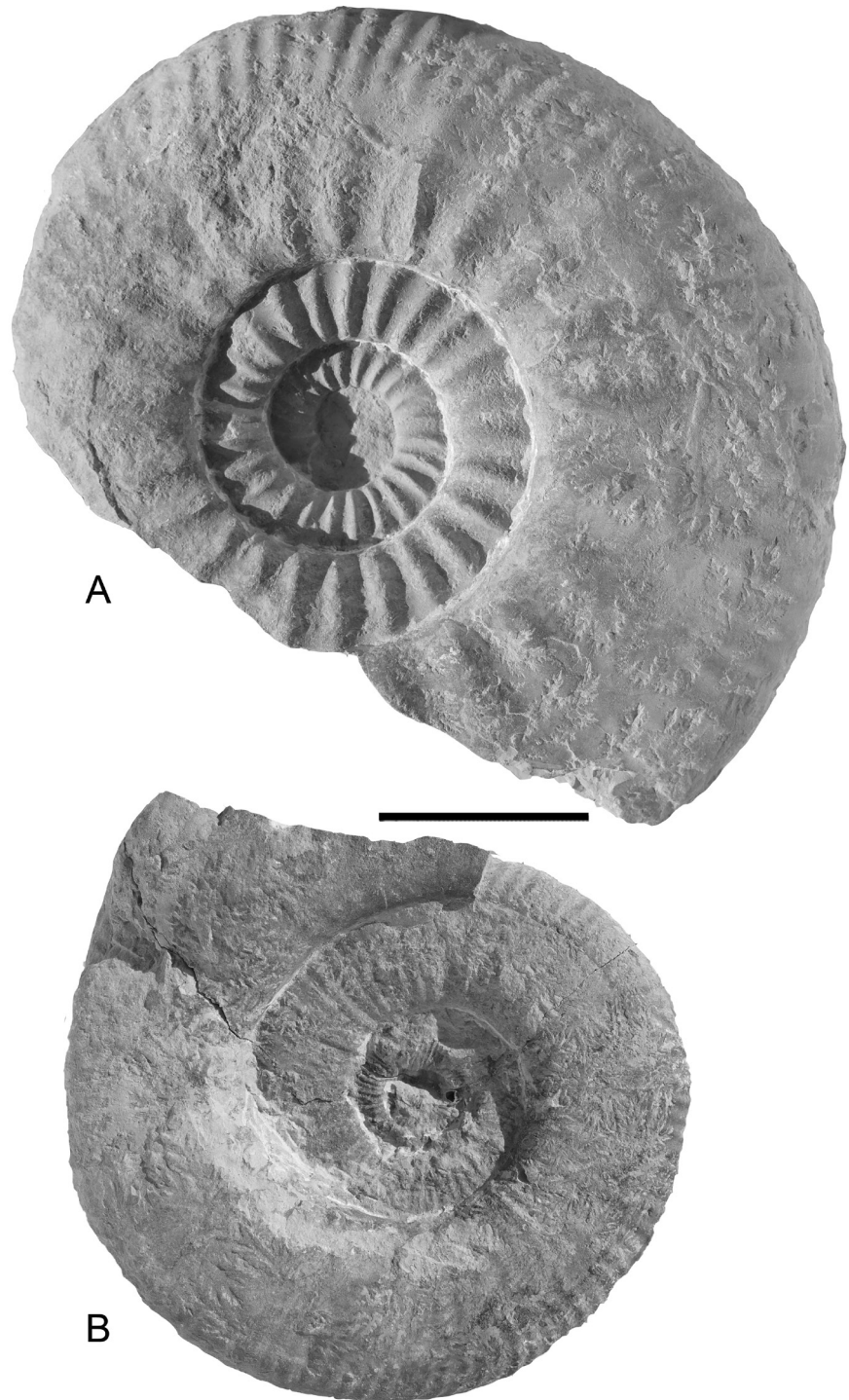


Fig. 11. Ammonite fauna of the *geniculatum* Biohorizon (Early Kimmeridgian, upper Platynota Zone), Gräfenberg, Franconia, Endress quarry, bed 9

A. *Eurasenia gothica* (Schneid, 1939); SMNS 70525/6; B. *Lessinicerias raschii* (Canavari, 1897); SMNS 70525/7. Scale bar equals 5 cm

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## REFERENCES

- ARKELL W., KUMMEL B., WRIGHT C.W., 1957 – Mesozoic Ammonoidea. In: *Treatise on Invertebrate Paleontology*, Part L, Mollusca 4, Cephalopoda, Ammonoidea (Ed. R.C. Moore): 80–490. Lawrence, University of Kansas Press.
- ATROPS F., 1982 – La sous-famille des Ataxioceratinae (Ammonitina) dans le Kimméridgien inférieur du Sud-Est de la France. Systématique, évolution, chronostratigraphie des genres *Orthosphinctes* et *Ataxioceras*. *Documents des Laboratoires de Géologie Lyon*, **83**: 1–463.
- BONNOT A., GYGI R., 2001 – Les Euaspidoceratinae (Ammonitina, Aspidoceratidae) de la zone à Transversarium (Oxfordien moyen) de Suisse septentrionale (cantons d’Argovie et de Schaffhouse). *Eclogae geologicae Helveticae*, **94**, 3: 427–445.
- BONNOT A., NEIGE P., TARKOWSKI R., MARCHAND D., 1994 – *Miroosphinctes* Schindewolf et *Euaspidoceras* Spath du niveau vert de Zalas (Pologne) (Oxfordien inférieur, Zone à Cordatum): Dimorphes sexuels? *Bulletin of the Polish Academy of Sciences, Earth Sciences*, **42**: 181–208.
- BONNOT A., MARCHAND D., COURVILLE P., FERCHAUD P., QUEREILHAC P., BOURSICOT P.-Y., 2009 – Le genre *Epipeltoeras* (Ammonitina, Perisphinctaceae, Aspidoceratidae) sur le versant parisien du seuil du Poitou (France): faunes ammonitiques, biostratigraphie et biozonation de la zone à Bimammatum pars (Oxfordien supérieur). *Revue de Paléobiologie*, **28**, 2: 371–411.
- BREISTROFFER M., 1947 – Notes de Nomenclature paléozoologique. I. Ammonites jurassiques et crétaées. *Procès-verbal Mensuel de la Société Scientifique du Dauphiné*, **195**: 99–103.
- BUCKMAN S.S., 1925 – Type Ammonites, vol. 5, parts 50–52A: 1–4, 49–88, pl. 154, 179, 259, 307, 440, 486, 511, 513, 531, 537–576. Wheldon & Wesley, London.
- CALLOMON J.H., 1963 – Sexual dimorphism in Jurassic ammonites. *Transactions of the Leicester Literary and Philosophical Society*, **57**: 21–56.
- CALLOMON J.H., 1994 – Palaeontological methods of stratigraphy and biochronology: some introductory remarks. *Geobios, Mémoire Spécial*, **17**: 16–30.
- CALLOMON J.H., 1995 – Time from fossils: S.S. Buckman and Jurassic high-resolution geochronology. In: *Milestones in Geology* (Ed. M.J. Le Bas). *Geological Society Memoirs*, **16**: 127–150.
- CANAVARI M., 1897 – La fauna degli strati con *Aspidoceras acanthicum* di M. Serra presso Camerino. *Palaeontographia Italica*, **3**: 201–234.
- CARIOU É., HANTZPERGUE P., 1997 – Biostratigraphie du Jurassique ouest-européen et méditerranéen. *Bulletin du Centre de Recherches Elf Exploration et Production, Mémoires*, **17**: XIV + 422 pp.
- CHANDLER R.B., 2019 – Two new stephanoceratid ammonites from the Aalenian–lower Bajocian (Middle Jurassic, Dorset, UK) and their phylogenetic significance. *Proceedings of the Geologists’ Association*, **130**: 307–325.
- CHECA A., 1985 – Los Aspidoceratiformes en Europa (Ammonitina, Fam. Aspidoceratidae, Subfamilias Aspidoceratinae y Physodoceratinae). Facultad de Ciencias, Departamento de Paleontología y Geología general, Thesis doctoral, Universidad de Granada. 1–27, 413 p.
- COLLIGNON M., 1959 – Atlas des fossiles caractéristiques de Madagascar, Fasc. IV: Argovien – Rauracien. Service Géologique de Madagascar, Tananarive.
- DAVIS R.A., LANDMAN N.H., DOMMERGUES J.-L., MARCHAND D., BUCHER H., 1996 – Mature modifications and dimorphism in ammonoid cephalopods. In: *Ammonoid Paleobiology* (Eds. N.H. Landman *et al.*). Plenum, New York.
- DIETERICH E., 1940 – Stratigraphie und Ammonitenfauna des Weißen Jura β in Württemberg. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **96**: 1–40.
- DONOVAN D.T., CALLOMON J.H., HOWARTH M.K., 1981 – Classification of the Jurassic Ammonitina. In: *The Ammonoidea* (Eds. M.R. House, J.R. Senior). *The Systematics Association, Special Volume*, **18**: 101–155. Academic Press, London.
- DORN P., 1931 – Die Ammoniten des untersten Malm der Frankenalb. *Palaeontographica, Abteilung A*, **74**: 1–92.
- ÉNAY R., 1962 – Contribution à l’étude paléontologique de l’Oxfordien supérieur de Trept (Isère): I. Stratigraphie et Ammonites. *Travaux du Laboratoire de Géologie Lyon, nouvelle série*, **8**: 7–81.
- ÉNAY R., 1979 – À propos du dimorphisme chez les ammonites jurassiques. Quelques réflexions. *Haliotis*, **6**: 97–118.
- ÉNAY R., HOWARTH M.K., 2019 – Part L, revised, volume 3B, chapter 7. Systematic descriptions of the Perisphinctoidea. *Treatise Online*, **120**: 1–184.
- FATMI A.N., ZEISS A., 1999 – First Upper Jurassic and Lower Cretaceous (Berriasian) ammonites from the Sembar Formation (Belemnite shales), Windar Nai, Lasbela – Balochistan, Pakistan. *Memoirs of the Geological Survey of Pakistan*, **19**: 1–114.
- FISCHER E., 1913 – Über einige neue oder in Schwaben bisher unbekannte Versteinerungen des Braunen und Weißen Jura. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **69**: 31–59.
- GEYER O.F., 1961 – Monographie der Perisphinctidae des unteren Unterkimmeridgium (Weißjura gamma, Badener Schichten) im süddeutschen Jura. *Palaeontographica, Abteilung A*, **117**: 1–157.
- GEYER O.F., 1969 – The ammonite genus *Sutneria* in the Upper Jurassic of Europe. *Lethaia*, **2**: 63–72.

- HYATT A., 1900 – Cephalopods. In: Textbook of Paleontology (Eds. K.A. v. Zittel, C.R. Eastman): 502–604. Macmillan & Co., London.
- JEANNET A., 1951 – Die Eisen- und Manganerze der Schweiz: Stratigraphie und Paläontologie des oolithischen Eisenerzlagerns von Herznach und seiner Umgebung. *Beiträge zur Geologie der Schweiz. Geotechnische Serie, Lieferung*, **13**, 5: 1–240.
- KEUPP H., 1977 – *Simosphinctes tieringensis* (Fischer) – ein seltener Ammonit von Gräfenberg (Mittlere Frankenalb). *Geologische Blätter für NO-Bayern und angrenzende Gebiete*, **27**, 3/4: 169–173.
- KLUG C., ZATON M., PARENT H., HOSTETTLER B., TAJIKA A., 2015 – Mature modifications and sexual dimorphism. In: Ammonoid Paleobiology. From Anatomy to Ecology (Eds. C. Klug et al.). *Topics in Geobiology*, **43**: 253–320. Springer, Dordrecht.
- MAKOWSKI H., 1962 – Problem of sexual dimorphism in ammonites. *Palaeontologia Polonica*, **12**: 1–92.
- MOLINER L., OLÓRIZ F., 2009 – Correlation potential of the Upper Jurassic (lower Kimmeridgian) Platynota Chronozone deposits in northeastern Spain. *GFF*, **131**: 205–213.
- MYCZYŃSKI R., 1976 – A new ammonite fauna from the Oxfordian of the Pinar del Rio province, western Cuba. *Acta Geologica Polonica*, **26**, 2: 261–296.
- NEUMAYR M., 1873 – Die Fauna der Schichten mit *Aspidoceras acanthicum*. *Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt*, **5**: 141–257.
- NIEBUHR B., PÜRNER T., 2014 – Plattenkalk und Frankendolomit – Lithostratigraphie der Weißjura-Gruppe der Frankenalb (außeralpiner Oberjura, Bayern). *Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften*, **83**: 5–71.
- OGG J.G., HINNOV L.A., 2012 – Jurassic. In: The geological time scale (Eds. F.M. Gradstein et al.): 731–791. Elsevier, Amsterdam.
- OLÓRIZ F., 1978 – Kimmeridgiense–Titonico inferior en el sector central de las Cordilleras Béticas (Zona Subbética). *Paleontologia. Bioestratigrafía. Tesis Doctorales, Universidad Granada*, **184**: 1–758.
- OPPEL A., 1862–1863 – Ueber jurassische Cephalopoden. *Palaeontologische Mittheilungen aus dem Museum des königlich Bayerischen Staates*, **1**: 127–266.
- d'ORBIGNY A., 1850 – Paléontologie française – Terrains jurassiques, Tome I, Céphalopodes (livr. 56): 529–536.
- PAGE N.K., 2017 – From Opper to Callomon (and beyond): building a high-resolution ammonite-based biochronology for the Jurassic System. *Lethaia*, **50**: 336–355.
- PARENT H., SCHERZINGER A., SCHWEIGERT G., 2008 – Sexual phenomena in Late Jurassic Aspidoceratidae (Ammonoidea). Dimorphic correspondence between *Physodoceras hermanni* (Berckhemer) and *Sutneria subeumela* Schneid, and first record of possible hermaphroditism. *Palaeodiversity*, **1**: 181–187.
- PAVIA G., BENETTI A., MINETTI C., 1987 – Il Rosso Ammonitico dei Monti Lessini Veronesi (Italia NE). Fauna ad Ammoniti e discontinuità stratigrafiche nel Kimmeridgiano inferiore. *Bolletino della Società Paleontologica Italiana*, **26**: 63–92.
- QUENSTEDT F.A., 1846–1849 – Petrefactenkunde Deutschlands, 1. Abteilung, 1. Band, Cephalopoden. L.F. Fues, Tübingen.
- REINECKE J.C.M., 1818 – Maris protogaei Nautilus et Argonautae vulgo Cornua Ammonis in Agro Coburgico et vicino reperiundos, descripsit et delineavit, simul Observationes de Fossilium Prototypis. Ahl, Coburg.
- ROLLIER L., 1922 – Phylogénie des Ammonoïdes. *Eclogae geologicae Helvetiae*, **17**, 3: 358–360.
- ROMAN F., 1938 – Les Ammonites Jurassiques et Crétacées. Masson, Paris.
- SARTI C., 1993 – Il Kimmeridgiano delle Prealpi Veneto-Trentine: fauna e biostratigrafia. *Memorie del Museo Civico di Storia naturale di Verona, Sezione Scienze della Terra*, **5**: 1–144.
- SCHAIRER G., SCHLAMPP V., 2003 – Ammoniten aus dem Ober-Oxfordium von Gräfenberg/Ofr. (Bimammatum-Zone, Hypselum-Subzone, *semimammatum*-Horizont). *Zitteliana*, **43**: 17–43.
- SCHERZINGER A., PARENT H., SCHWEIGERT G., 2018 – A new species of the ammonite genus *Physodoceras* Hyatt (Aspidoceratidae, Aspidoceratinae) from the Hybonotum Zone (Lower Tithonian) of Southern Germany, with comments on the phylogeny of the genus. *Boletín del Instituto de Fisiografía y Geología*, **88**: 11–24.
- SCHICK H., 2004 – The stratigraphical significance of *Cymaceras guembeli* for the boundary between Platynota Zone and Hypselocyclum Zone, and the correlation between Swabian and Franconian Alb. *Zitteliana*, **A44**: 51–59.
- SCHINDEWOLF O.H., 1925 – Entwurf einer Systematik der Perisphincten. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Bände B*, **52**: 309–343.
- SCHLAMPP V., 2009a – *Oxydiscites* and *Cymaceras* (Ammonoidea, Phylloceratinae Spath) aus dem Malm Gamma 1 und 2 von Gräfenberg. *Der Aufschluss*, **60**: 203–210.
- SCHLAMPP V., 2009b – Neue Banknummerierung für den Malm Gamma 1 im Steinbruch Gräfenberg. *Der Aufschluss*, **60**: 335–344.
- SCHNEID T., 1939 – Über Raseniiden, Ringsteadiiden und Pictoniiden des nördlichen Frankenjura. *Palaeontographica, Abteilung A*, **89**: 117–184, **91**: 79–119.
- SCHWEIGERT G., 1995 – *Amoebopeltoceras* n. g., eine neue Ammonitengattung aus dem Oberjura (Ober-Oxfordium bis Unter-Kimmeridgium) von Südwestdeutschland und Spanien. *Stuttgarter Beiträge zur Naturkunde, Serie B*, **227**: 1–12.
- SCHWEIGERT G., 1997 – Die Ammonitengattungen *Simoceras* Spath und *Pseudhimalayites* Spath (Aspidoceratidae) im süddeutschen Oberjura. *Stuttgarter Beiträge zur Naturkunde, Serie B*, **246**: 1–29.
- SCHWEIGERT G., 1998 – Die Ammonitenfauna des Nusplinger Plattenkalks (Ober-Kimmeridgium, Beckeri-Zone, Ulmense-Subzone, Baden-Württemberg). *Stuttgarter Beiträge zur Naturkunde, Serie B*, **267**: 1–61.
- SCHWEIGERT G., 2013 – *Epaspidoceras* und *Simosphinctes* – ein Dimorphenpaar? *Fossilien*, **30**, 5: 289–293.
- SCHWEIGERT G., 2015 – Ammonoid biostratigraphy in the Jurassic. In: Ammonoid Paleobiology: From macroevolution to paleogeography (Eds. C. Klug et al.). *Topics in Geobiology*, **44**: 389–402. Springer, Dordrecht.
- SCHWEIGERT G., CALLOMON, J.H., 1997 – Der *bauhini*-Faunenhorizont und seine Bedeutung für die Korrelation zwischen

- tethyalem und subborealem Oberjura. *Stuttgarter Beiträge zur Naturkunde, Serie B*, **247**: 1–69.
- SPATH L.F., 1927–1933 – Revision of the Jurassic Cephalopod fauna of Kachh (Cutch). *Memoirs of the Geological Survey of India, Palaeontologia Indica, new Series*, **9**: 7 + 945 pp.
- STEINMANN G., 1890 – Cephalopoda. In: *Elemente der Paläontologie* (Eds. G. Steinmann, L. Döderlein): 344–475. Engelmann, Leipzig.
- WEGELE L., 1929 – Stratigraphische und faunistische Untersuchungen im Oberoxford und Unterkimmeridge Mittelfrankens. II. Palaeontologischer Teil. *Palaeontographica*, **72**: 1–94.
- WIERZBOWSKI A., ATROPS F., GRABOWSKI J., HOUNSLOW M., MATYJA B.A., OLÓRIZ F., PAGE K., PARENT H., ROGOV M.A., SCHWEIGERT G., WIERZBOWSKI H., WRIGHT J.K., 2016 – Towards a consistent Oxfordian-Kimmeridgian global boundary: current state of knowledge. *Volume Jurassica*, **14**, 1: 14–49.
- ZEISS A., 1979 – Neue Sutnerien-Funde aus Ostafrika. Ihre Bedeutung für Taxonomie und Phylogenie der Gattung. *Paläontologische Zeitschrift*, **53**: 259–280.
- ZITTEL K.A., 1870 – Die Fauna der älteren Cephalopoden führenden Tithonbildungen. *Palaeontographica, Supplement-Bände*, **2**, 2: 74–89.
- ZITTEL K.A., 1895 – Grundzüge der Paläontologie. R. Oldenburg. Munich & Leipzig. 8 + 971 p.