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A microconchiate *Hypowaagenia* Schweigert and Schlampp, 2020 (Aspidoceratidae, Hybonoticeratinae) from the Upper Jurassic of Southern Germany

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Key words: ammonites, Aspidoceratidae, dimorphism, palaeobiogeography, Germany.

Abstract. The previously unknown microconch which corresponds to the recently introduced Late Jurassic aspidoceratoid ammonite genus *Hypowaagenia* Schweigert and Schlampp, 2020, is reported from beds of the topmost Platynota Zone or basal Hypselocyclum Zone of Franconia. This record indicates that these exotic ammonite findings are not of long-drifting necroplanktonic shells, but stem from animals that have spread over this area after immigration from the Tethys.

INTRODUCTION

Ammonites are among the most common fossils of marine deposits in the Jurassic and Cretaceous. Scientifically described from the 19th Century onwards, they have often been successfully used for biostratigraphy and dating of the beds from which they come. In contrast, autecology of ammonites is still poorly understood and to some degree speculative. Since the 1960s, numerous Jurassic ammonite genera have been demonstrated to show a remarkable dimorphism in size, with the supposed males often being smaller compared to the related females (*e.g.*, Makowski, 1962; Callomon, 1963; Davis *et al.*, 1996; Klug *et al.*, 2015), *vice versa* as in Recent nautilids (Saunders, Landman, 1987). Since sexuality is hard to prove without the preservation of soft part anatomy, the dimorphic partners are often classified as 'macroconchs' and 'microconchs' instead of terming them females and males. In some ammonite families it is rather easy to recognize the corresponding partners, whereas in others the antidimorphs look so different that only the presence of well-preserved material or fortunate circumstances may help identifying the correct partners. In some cases, however, the corresponding partners have not been identified yet for various reasons. In genera which are extremely rare the partner can be missing due to collecting bias. Small or poorly sculptured specimens are easily overlooked or they may be hidden within the body chambers of macroconchs. Taphonomic filters also often favoured large-sized specimens. A good example is the ammonitico rosso lithology, which is widespread on the submerged Jurassic carbonate platforms of western Tethys. In this lithology, the macroconchs are often strongly corroded and the microconchs as well as the macroconchs of smaller-sized taxa and juveniles are completely dissolved. However, the "missing" microconchs had been originally present there as well, as demonstrated by the content of contemporaneous submarine dykes and/or ammonite coquinas showing a very early lithification (*e.g.*: Sicily: Wendt, 1971, 2017; Trento Platform:

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Sturani, 1971; Benetti *et al.*, 1987; Polish Carpathians: Wierzbowski *et al.*, 2004).

Recently, we introduced a new macroconchiate genus of aspidoceratoids, *Hypowaagenia* Schweigert and Schlampp, 2020, based on only a small sample of six specimens, some of which, however, are of giant size. Of these six specimens, one came from the *geniculatum* Biohorizon (Platynota Zone, Lower Kimmeridgian), another one possibly from a slightly younger bed belonging to the early Hypselocyclum Zone, and one cf.-specimen from a significantly older level (*planula* Biohorizon, Lower Kimmeridgian). Meanwhile, we have identified a further macroconchiate specimen of *Hypowaagenia endressi* in the private collection of Erich Schneider (Heiningen). His specimen derives from a limestone bed belonging to the *geniculatum* Biohorizon of Geisingen quarry in the southwestern part of the Swabian Alb (see Fig. 1). In Geisingen quarry, the bed with *Hypowaagenia* is known for its abundance of *Oxydiscites laffoni* (Moesch, 1867), another exotic immigrant in the Jurassic of southwestern Germany (see Schweigert, Kapitzke, 2018: fig. 3G). In the course of describing the new genus we were unable to identify the corresponding microconch and we speculated from ancestral forms about what this possibly had looked like. Meanwhile the missing microconch has appeared and the aim of this report is its description.

Material. The studied microconchiate specimen is housed in the collection of the Stuttgart Natural History Museum (no. SMNS 70609). The compared macroconchiate specimen is housed in the Palaeontological Collection of Tübingen University (no. GPIT/CP/10343).

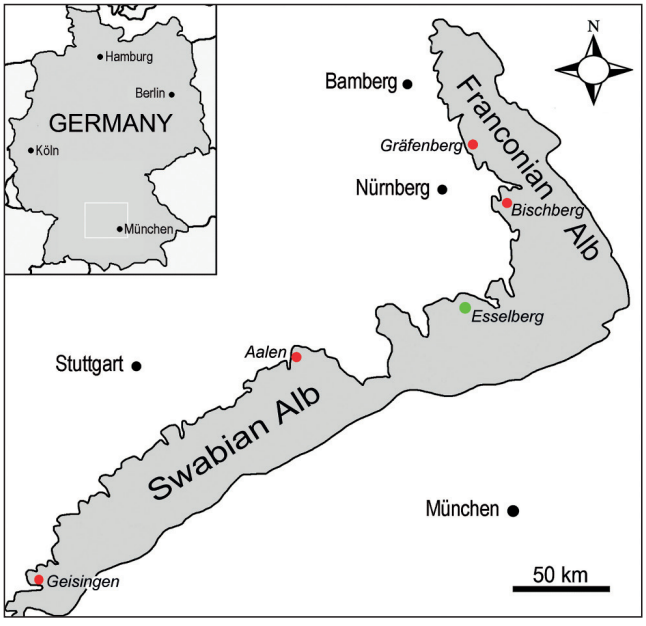

Fig. 1. Geographic map showing all hitherto known records of *Hypowaagenia* in Southern Germany

Red: macroconch occurrences; green: microconch occurrence. Modified from Schweigert, Schlampp (2020)

GEOLOGICAL SETTING

In 1991, Schairer and Schlampp described a large sample of small-sized oppeliids of the exotic genus *Cymaceras* Quenstedt, 1888 from *ex-situ* collected material near Esselberg in Franconia (Fig. 1) comprising both macroconchs and the corresponding microconchs. However, the entire sample was said to come from only a few successive limestone beds. For the microconchs of *Cymaceras*, Schairer and Schlampp (1991) introduced *Trochiskioceras*, as a subgenus of *Cymaceras*. This is a taxonomic procedure, which has long been adopted to name dimorphic couples of ammonites, especially if the antidimorphs are morphologically rather distinct from each other (see Westermann, 1969). After an evaluation of the accompanying ammonite taxa the sample with *Cymaceras* spp. was dated into the basal Hypselocyclum Zone (Schairer, Schlampp, 1991) of the "Malm Gamma 2" (now assigned to the Arzberg Formation, see Niebuhr, Pürner, 2014). Subsequently, the biostratigraphic level characterized by the mass-occurrence of *Cymaceras guembeli* (Oppel, 1863) – then termed the *guembeli* Biohorizon – has been recorded from numerous other localities in the Upper Jurassic of Swabia and Franconia (Schick, 2004; Schlampp, 2009). Within the ammonites from Esselberg, however, there was a morphologically distinct species of *Cymaceras*, *C. franziskae* Schairer and Schlampp, 1991, originally represented only by the holotype. Later finds of bed-by-bed collected *Cymaceras* spp. from various sections in Franconia, Swabia and adjacent Switzerland indicated that *C. franziskae* was a phyletic forerunner of *C. guembeli* and characterizes the uppermost Platynota Zone (Gradl, Schairer, 1997; Schick, 2004; Moor, 2009). In consequence, we conclude that the ammonite fauna described by Schairer, Schlampp (1991) is not completely of the same age, but ranges down to the topmost Platynota Zone.

Within unpublished material of the same sample still kept in the private collection of the finder (V.S.), there was a piece of rock (Fig. 2A) containing a small, incomplete, spinose ammonite, which was long regarded as exotic, but not determinable. Now, we interpret this specimen (Fig. 2B) as the missing microconch that corresponds to *Hypowaagenia endressi* Schweigert and Schlampp, 2020. In the same piece of rock, there is a fragment of an ataxioceratid ammonite. Unfortunately, the fragment is too small to be identified at the species level. Hence, it is impossible to decide whether the microconchiate *Hypowaagenia* derives from the uppermost Platynota Zone (*geniculatum* Biohorizon) or from the

lowermost Hypselocyclum Zone (*guembeli* Biohorizon). However, despite this uncertainty, this short stratigraphic interval of two succeeding biohorizons corresponds exactly to the known stratigraphical range of *Hypowaagenia endressi* in the area, and thus we can be sure that these macro- and microconch ammonites occurred at the same time.

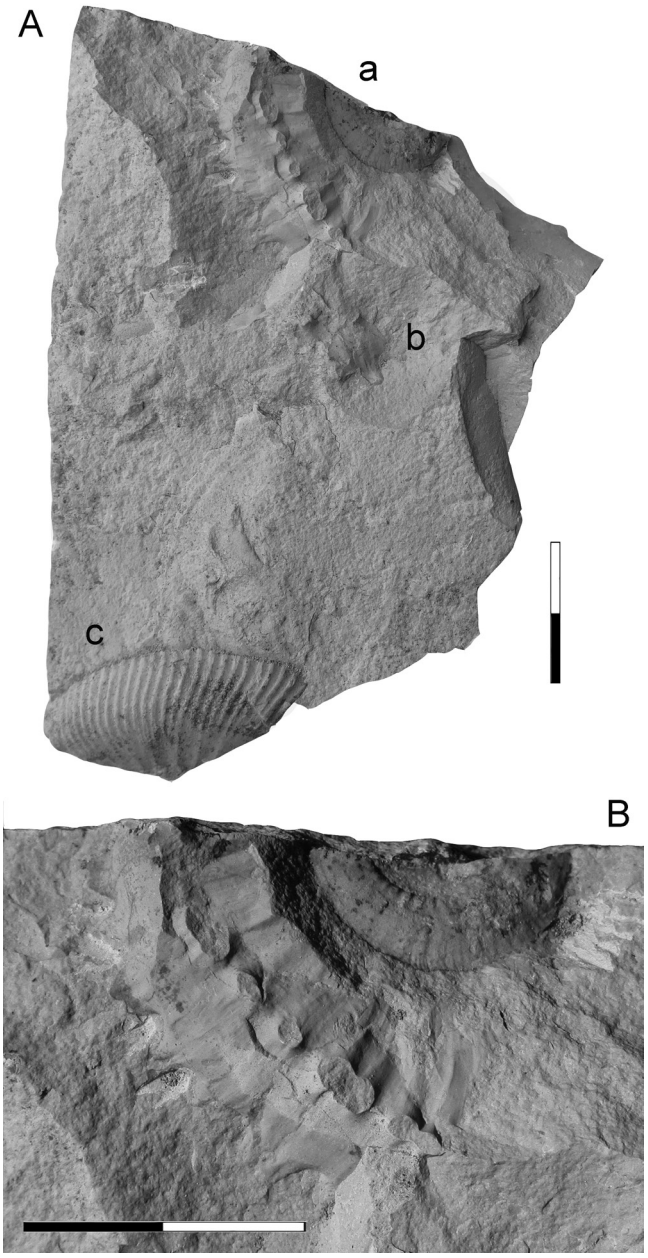

Fig. 2. *Hypowaagenia endressi* Schweigert and Schlampp, 2020, microconch

A. Piece of rock containing the microconchiate specimen (a), an isolated shell fragment of its body chamber (b), and the fragment of an ataxioceratid (c); **B.** Close-up view of the microconch. Arzberg Formation, uppermost Platynota or basal Hypselocyclum Zone, *geniculatum* or *guembeli* Biohorizon, Esselberg, Franconia, Germany. SMNS 70609 (leg. Victor Schlampp, Rednitzhembach). Scale bars equal 20 mm

SYSTEMATIC PALAEONTOLOGY

Superfamily Aspidoceratoidea Zittel, 1895
sensu Parent, Schweigert and Scherzinger, 2020

Family Aspidoceratidae Zittel, 1895

Subfamily Hybonoticeratinae Olóriz, 1978

Genus *Hypowaagenia* Schweigert and Schlampp, 2020

Type species. *Hypowaagenia endressi* Schweigert and Schlampp, 2020.

Remark. Although in the past many microconchiate aspidoceratoids have been described completely independent from their macroconchiate counterparts in their own microconchiate genera and species (*e.g.*, *Mirosphinctes*, *Sutneria*, *Simosphinctes*), we refrain from erecting a separate genus for the males of *Hypowaagenia*.

Hypowaagenia endressi Schweigert and Schlampp, 2020 [m]
Fig. 2

Locality. Esselberg, Franconia (Fig. 1).

Horizon. Arzberg Formation; Early Kimmeridgian, transitional beds of the Platynota/Hypselocyclum zones, *geniculatum* or *guembeli* Biohorizon.

Emended diagnosis. For macroconchs see diagnosis of the type species (Schweigert, Schlampp, 2020). Microconchs very small; aperture lappeted. Whorl section subquadrate. Juvenile stage with dense periumbilical row of nodes giving rise to irregularly bundled growth lines. Adult stage with long hollow ventromarginal spines that emerge from looped bundles of growth lines, occasionally ending in double- or triple-tips.

Description. The microconch corresponding to *Hypowaagenia* is a laterally slightly compressed steinkern with superimposed shell. It consists of the distal part of a subquadrate whorl section of body chamber ending in a short lappet and one half of the penultimate whorl. Close to the specimen, there is a small shell fragment showing a venter with one pair of spines most likely belonging to the posterior part of the body chamber. The sculpture of the body chamber consists of broadly bundled striae ventromarginally emerging to hollow spines. Some of these ventromarginal spines of the body chamber have double-tips; in one case, even a triple-tip is developed. The spines are not orientated perpendicular

to the shell coiling plane, but curve upwards in a low angle. The venter is slightly convex. The umbilical edge of the body chamber is broken away and hence, there is no information about its shape and ornamentation. The penultimate whorl shows a periumbilical row of small nodes, from which irregularly spaced bundles of growth lines arise. Poorly preserved remains of the previous whorl show the same ornamentation. Along the umbilical seam, there is no indication of any ventromarginal spines at this stage. Due to the incompleteness of the specimen it is not clear at which size the venter started to become ornamented with spines. Most likely, the umbilical row of nodes persisted until the end of the body chamber.

Comparison. The ornamentation of the herein described microconch is unique and previously not described from anywhere else. The only somewhat similar specimen possibly assignable to *Hypowaagenia* sp. as well is a still unpublished microconchiate ammonite from the Kimmeridgian fissure filling of Rocca Drago near Corleone in Sicily (Cecca, Pochettino, 2000; Martire *et al.*, 2002), after photographs kindly shown by courtesy of Carlo Sarti (Bologna).

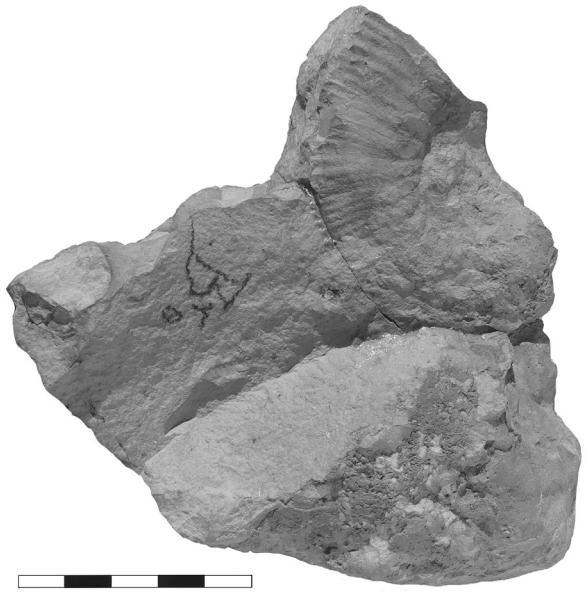

Fig. 3. *Hypowaagenia* cf. *endressi* Schweigert and Schlampp, 2020, showing a very similar ornamentation of its juvenile stage as in the preadult stage of the microconchiate *Hypowaagenia endressi* illustrated in Fig. 2. Braunenberg quarry area near Aalen-Wasseralfingen, Swabia, Germany (Early Kimmeridgian, Planula Zone, *planula* Biohorizon); GPIT/CP/10343 (leg. Ernst Dieterich), refigured from Schweigert, Schlampp (2020: fig. 8). Scale bar equals 50 mm

DISCUSSION AND CONCLUSIONS

When describing *Hypowaagenia*, we expected that the corresponding microconch would look similar to its supposed ancestors in a Euaspidoceratinae stock, similar to *Mirosphinctes* Schindewolf, 1926 (Schweigert, Schlampp, 2020). However, the present specimen shows that there are no closer similarities with *Mirosphinctes*. The sculpture of its penultimate whorl is strikingly similar to the early ontogenetic stages of *Hypowaagenia*, especially when compared with the cf.-specimen of *Hypowaagenia endressi* from the Planula Zone of Swabia (Fig. 3). The body chamber exhibits ventrolateral hollow spines, some of them merged and then forming spines with double- or even triple-tips. This peculiar style of ornamentation – recalling the spinose later ontogenetic stages of the macroconchs – is an evolutionary ontogenetic acceleration rarely seen in aspidoceratoid microconchs. Interestingly, very similar spines occur in microconchiate specimens of some *Hybonoticeras* (='*Hybonotella*' in Berckhemer, Hölder, 1959; Olóriz, Villaseñor, 1999), but their orientation is slightly different, emerging at a larger angle, and the venter is not smooth as in *Hypowaagenia*, but double-keeled, at least in the early and medium ontogenetic stages. The similarity between both microconch morphologies provides another argument for the systematic placement of *Hypowaagenia* in Hybonoticeratinae Olóriz, 1978. However, more material is needed to fill the long gap of information between the Early Kimmeridgian Hypselocyclum Zone and the Late Kimmeridgian Beckeri Zone.

The record of a very small microconch in beds of the same age as the giant macroconchs obviously lethally bitten by a predator in the posterior part of its body chamber (cf. Klompmaker *et al.*, 2009) indicates that a living population of *Hypowaagenia endressi* has settled in the Submediterranean sea of southwestern Germany. The remarkably highly diverse ammonite fauna of this time interval with numerous other exotic ammonite taxa (*e.g.*, *Cymaceras*, *Oxydiscites*, *Lessiniceras*) points to a sea-level highstand allowing migrations over extremely long distances. The origination of *Hypowaagenia* from the southern Tethys margin appears likely, analogous to a coeval case in paracenoceratid nautiloids (Schweigert, 2020).

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REFERENCES

BENETTI A., PEZZONI N., ZEISS A., 1987 – A small, but interesting new ammonite fauna from the Western Lessinian Alps (preliminary note). *Atti II Convegno Internazionale, Fossili, Evoluzione, Ambiente*: 33–37.

BERCKHEMER F., HÖLDER H., 1959 – Ammoniten aus dem Oberen Weißen Jura Süddeutschlands. *Beihefte zum Geologischen Jahrbuch*, **35**: 1–135.

CALLOMON J.H., 1963 – Sexual dimorphism in Jurassic ammonites. *Transactions of the Leicester Literary and Philosophical Society*, **57**: 21–56.

CECCA F., POCHETTINO M., 2000 – The Early Kimmeridgian genus *Metastreblites* Olóriz, 1978 (Ammonoidea, Oppeliidae) from Rocca Drago (Western Sicily, Italy). Homeomorphy and iterative evolution within the subfamily Streblitinae. *Geobios*, **33**: 97–104.

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.*). *Topics in Geobiology*, **13**: 464–539. Plenum, New York.

GRADL H., SCHAIRER G., 1997 – Ammoniten von Kälberberg (Nördliche Frankenalb) (Oberoxford bis Unterkimmeridge). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, **37**: 9–26.

KLOMPMAKER A.A., WALJAARD N.A., FRAAIJE R.H.B., 2009 – Ventral bite marks in Mesozoic ammonoids. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **280**: 245–257.

KLUG C., ZATOŃ 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.

MAKOWSKI H., 1962 – Problem of sexual dimorphism in ammonites. *Palaeontologia Polonica*, **12**: 1–92.

MARTIRE L., BERTOK C., PAVIA G., SARTI C., 2002 – Stop 11 Rocca Drago: Mesozoic pelagic sedimentation over the faulted margin of a pelagic platform. *In*: 6th International Symposium on the Jurassic System. General Field Trip Guidebook, Palermo (Ed. M. Santantonio): 91–96

MOESCH C., 1867 – Geologische Beschreibung des Aargauer Jura und der nördlichen Gebiete des Kanton Zürich. *Beiträge zur Geologischen Karte der Schweiz*, **4**: 1–297.

MOOR E., 2009 – *Oxydiscites* und *Cymaceras* vom Schaffhauser Randen. *Mitteilungen der naturforschenden Gesellschaft Schaffhausen*, **49**: 1–38.

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.

OLÓRIZ F., 1978 – Kimmeridgiense–Tithonico inferior en el sector central de las Cordilleras Béticas (Zona Subbética). Paleontologia. Bioestratigrafia. *Tesis Doctorales, Universidad Granada*, **184**: 1–729.

OLÓRIZ F., VILLASEÑOR A.B., 1999 – New microconchiate *Hybonoticeras* from Mexico. *Geobios*, **32**, 4: 561–573.

OPPEL A., 1862–1863 – Ueber jurassische Cephalopoden. *Palaeontologische Mittheilungen aus dem Museum des koeniglich Bayerischen Staates*, **1**: 127–266.

PARENT H., SCHWEIGERT G., SCHERZINGER A., 2020 – A review of the classification of Jurassic aspidoceratid ammonites – the Superfamily Aspidoceratoidea. *Volumina Jurassica*, **18**, 1: 47–52.

QUENSTEDT F.A., 1887–1888 – Die Ammoniten des Schwäbischen Jura. 3. Der Weiße Jura: 817–994 (1887), 945–1140 (1888); Schweizerbart, Stuttgart.

SAUNDERS W.B., LANDMAN N.H., 1987 – *Nautilus*: The biology and paleobiology of a living fossil. Plenum Press, New York.

SCHAIRER G., SCHLAMPP V., 1991 – *Cymaceras* (Ammonitina, Ochetoceratinae) von Esselberg. *Münchner geowissenschaftliche Abhandlungen, Reihe A*, **19**: 101–128.

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., 1926 – Zur Systematik der Perisphincten. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Bände*, **B55**: 497–517.

SCHLAMPP V., 2009 – *Oxydiscites* und *Cymaceras* (Ammonoidea, Phlycticeratinae Spath) aus dem Malm Gamma 1 und 2 von Gräfenberg. *Der Aufschluss*, **60**: 203–210.

SCHWEIGERT G., 2020 – First records of *Somalinautilus* (Cephalopoda: Nautiloidea) in the Jurassic of Southern Germany – inferences for transprovincial faunal migrations. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **298**, 2: 137–146.

SCHWEIGERT G., KAPITZKE M., 2018 – *Neopetitclercia*, a new ammonite genus (Strigoceratidae: Phlycticeratinae) from the lower Kimmeridgian (Upper Jurassic) of SW Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **288**, 2: 121–127.

SCHWEIGERT G., SCHLAMPP V., 2020 – *Hypowaagenia* nov. gen., a rare genus of giant aspidoceratid ammonite from the Upper Jurassic of Southern Germany. *Volumina Jurassica*, **18**, 1: 23–36.

STURANI C., 1971 – Ammonites and stratigraphy of the "*Posidonia alpina*" beds of the Venetian Alps (Middle Jurassic, mainly Bajocian). *Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova*, **28**: 1–190.

WENDT J., 1971 – Genese und Fauna submariner sedimentärer Spaltenfüllungen im mediterranen Jura. *Palaeontographica*, **A136**: 121–192.

WENDT J., 2017 – A unique fossil record from neptunian sills: the world's most extreme example of stratigraphic condensation (Jurassic, western Sicily). *Acta Geologica Polonica*, **67**, 2: 163–199.

WESTERMANN G.E.G., 1969 – Sexual dimorphism in fossil metazoa and taxonomic implications. Schweizerbart, Stuttgart. IV + 250 p.

WIERZBOWSKI A., AUBRECHT R., KROBICKI M., MATYJA B.A., SCHLÖGL J., 2004 – Stratigraphy and palaeogeographic position of the Jurassic Czertezik Succession, Pieniny Klippen Belt (Western Carpathians) of Poland and Eastern Slovakia. *Annales Societatis Geologorum Poloniae*, **74**: 237–256.

ZITTEL K.A., 1895 – Grundzüge der Paläontologie. R. Oldenburg. Munich and Leipzig. VIII + 971 p.