VOLUMINA JURASSICA, 2017, XV: 1–16
DOI: 10.5604/01.3001.0010.3920

Comments on the identification of *Ammonites planula* Hehl in Zieten, 1830 (Upper Jurassic, SW Germany)

Günter SCHWEIGERT[1], Horst KUSCHEL[2]

Key words: Ammonoidea, Late Jurassic, Oxfordian, Kimmeridgian, Ataxioceratinae, Idoceratinae, taxonomy.

Abstract. *Ammonites planula* Hehl in Zieten, 1830 is the type species of the Late Jurassic ammonite genus *Subnebrodites* Spath, 1925 and the index species of the well-established Planula Zone of the Submediterranean Province. Recently, Enay and Howarth (2017) classified this stratigraphically important ammonite species as a 'nomen dubium' and considered it to be the possible macroconch counterpart of *Idoceras balderum* (Oppel, 1863). These authors claimed "*Subnebrodites planula* Spath, 1925" instead of *Ammonites planula* (Hehl in Zieten, 1830) to be the type species of *Subnebrodites*. However, their nomenclatorial acts are based on erroneous assumptions. For future taxonomic stability we here propose a neotype for *Ammonites planula* (Hehl in Zieten, 1830) and a lectotype for *Ammonites planula gigas* Quenstedt, 1888. In addition, dimorphism within the stratigraphically much younger *Idoceras balderum* (Oppel) is demonstrated showing that there is no morphological resemblance and no closer relationship with *Ammonites planula* (Hehl in Zieten, 1830).

INTRODUCTION

Recently, Enay and Howarth (2017) classified the commonly used Late Jurassic ammonite *Ammonites planula* Hehl in Zieten, 1830 as a 'nomen dubium' and considered it as the possible macroconch counterpart of *Idoceras balderum* (Oppel, 1863). Subsequently, the genus *Subnebrodites* Spath, 1925 was newly based on "*Subnebrodites planula* Spath, 1925" taking for its lectotype a specimen illustrated by Quenstedt (1888) which was explicitly quoted by Spath when he introduced the genus. However, based on the original illustration by Zieten (1830), the well-known type locality and horizon as well as from Spath's intention and interpretation, we have to reject that procedure. In the following we shed light on the true type species of *Subnebrodites* Spath, 1925, its provenance, synonymy and relationships with *Idoceras* Burckhardt, 1906.

Abbreviations: HT = holotype; [m] = microconch; [M] = macroconch; GPIT = Institut für Geowissenschaften, University of Tübingen, Germany; SMNS = Staatliches Museum für Naturkunde Stuttgart, Germany.

WHICH IS THE TYPE SPECIES OF *SUBNEBRODITES* SPATH, 1925?

Based on ammonite material from the Upper Jurassic of Central Europe and from Mexico, Burckhardt (1906) introduced a new genus *Idoceras* without designation of a type species. Spath (1925) separated some species including *Ammonites balderus* Oppel, 1863 from the group of *Ammonites planula* Hehl in Zieten, 1830 and introduced a new genus *Subnebrodites* for the latter. Prior to this decision he inter-

[1] Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70194 Stuttgart, Germany; guenter.schweigert@smns-bw.de.
[2] Liutbrandstr. 8, 73035 Faurndau, Germany; hoku64@aol.de.

preted two specimens to be conspecific with Hehl's species despite their having morphological differences with the drawing by Zieten (1830). One of them was a rather poorly preserved ammonite from the Upper Jurassic of Swabia lacking a precise locality which Spath had found in the collection of the late T. White. The other compared one is a specimen illustrated by Quenstedt (1888, pl. 108, fig. 2). Enay and Howarth (2017) re-illustrated the latter (Fig. 1A), a lappeted microconch, as the lectotype of *Subnebrodites planula* Spath, 1925 and the specimen from the White collection as the paralectotype. The latter shows evolute coiling and a diameter almost identical with that of the lectotype. This nomenclatural procedure was claimed to be covered by Article 67.13.1 of the ICZN (1999). Spath, however, never intended to introduce a new species under his own authorship. Enay and Howarth (2017) erroneously stated that Spath (1925) had deliberately designated an erroneous type species for *Subnebrodites*, *Ammonites planula gigas* Quenstedt, 1888, instead of *Ammonites planula* Hehl in Zieten, 1830. However, the specimen of Quenstedt's pl. 108, fig. 2 (Fig. 1A), which Spath interpreted as being conspecific with Hehl's taxon, is definitely not *Ammonites planula gigas*.

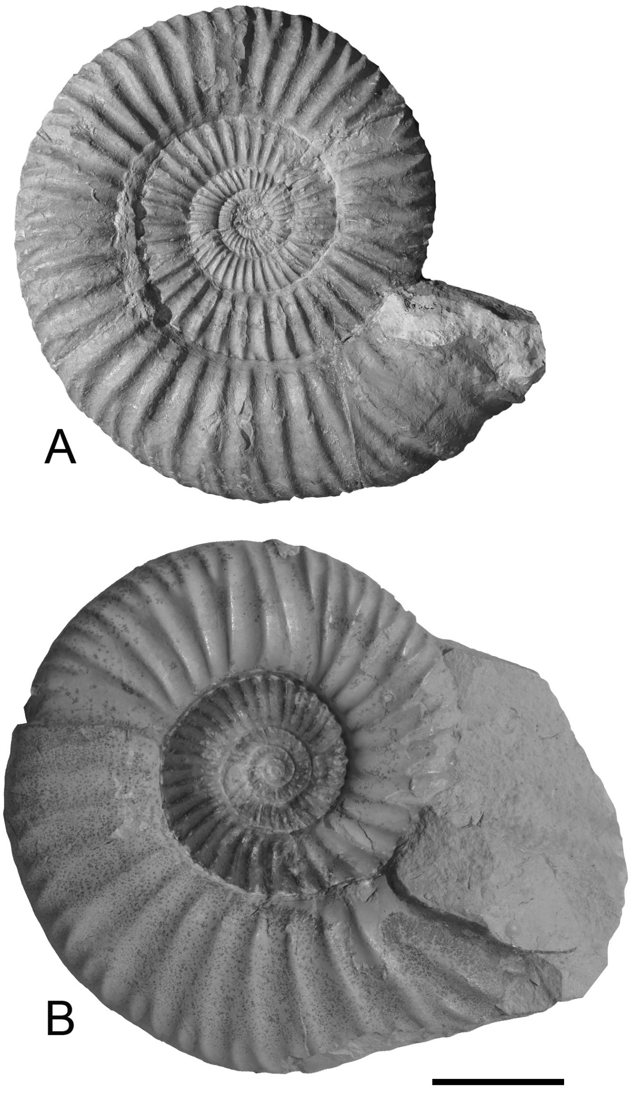

Fig. 1. *Subnebrodites planula* (Hehl in Zieten, 1830)

A. GPIT/CP/10069, microconch (= *Ammonites planula* Hehl in Quenstedt 1888, pl. 108, fig. 2), Wohlgeschichtete-Kalke Formation, Planula Zone, Aalen-Wasseralfingen, eastern Swabian Alb, SW Germany. **B.** SMNS 70397/1, macroconch, an involute variety with preadult aperture, Wohlgeschichtete-Kalke Formation, Planula Zone, Reichenbach am Heuberg, Swabian Alb, SW Germany (leg. E. Hak). Scale bar = 2 cm

When compiling the plate captions of Quenstedt's monograph, an assistant of the publishers (not the author himself!) quoted the specimen of pl. 108, fig. 1 as "*Ammonites planula gigas*" and the following specimens including that of pl. 108, fig. 2 as "*ditto*" [identical], but this was incorrect. From the text (Quenstedt, 1888: 974) it is evident that Quenstedt assigned the relatively small specimen of pl. 108, fig. 2 to "*Ammonites planula*" – not to the much bigger "*Ammonites planula gigas*". The third, subspecific name "*gigas*" was often used by Quenstedt to characterize big-sized specimens. Hence, both Quenstedt himself and Spath concurred that this specimen (pl. 108, fig. 2) belongs to *Ammonites planula* Hehl in Zieten, and Spath based *Subnebrodites* clearly on Hehl's and not on Quenstedt's species. In consequence, the nomenclatorial acts by Enay and Howarth (2017) are redundant.

STATUS OF *AMMONITES PLANULA GIGAS* QUENSTEDT, 1888

Quenstedt (1888) used the name *Ammonites planula gigas* twice, first for the big specimen illustrated on his pl. 128, fig. 1 and then for another big specimen illustrated on pl. 109, fig. 8. Furthermore, he mentioned another big specimen from Dürnau near Bad Boll (Quenstedt 1888: 974), which is still in the collection. A lectotype for *Ammonites planula gigas* Quenstedt, 1888 was not designated by Ziegler (1959), contrary to the statement of Geyer (1961). We here consider the specimen illustrated on pl. 128, fig. 1 as the lectotype of *Ammonites planula gigas*, because Quenstedt (1888: 985) himself tentatively proposed the praeoccupied name "*Ammonites planula plicatilis*" for the second specimen illustrated on his pl. 109, fig. 8 ("*Nebrodites gigas* [Quenstedt]" in Ziegler 1959). The lectotype of *Ammonites planula gigas* (Fig. 2) was said to come from the "Mittlerer Weissjura" of Melchingen. According to the lithology of the rock matrix this specimen can be assigned to spongiolithic

Fig. 2. ***Nebrodites cafisii*** **(Gemmellaro, 1872)**

Lectotype of *Ammonites planula gigas* Quenstedt, 1888, GPIT/CP/10070. From spongiolithic beds overlying the Lacunosamergel Formation, Acanthicum Zone, Melchingen, Swabian Alb, SW Germany. Scale bar = 5 cm

limestones occurring at the base of the Acanthicum Zone in that area. Ziegler (1959) assigned this specimen to *Idoceras* ("*Idoceras gigas* [Quenstedt]"), but he did not illustrate it. The serpenticonic coiling and very dense ribbing style shows that this macroconchiate specimen represents a species of *Nebrodites* Burckhardt, 1910. We identify this perfectly preserved specimen as an adult *Nebrodites cafisii* (Gemmellaro, 1872). The unfigured specimen from Dürnau mentioned by Quenstedt (1888) is another *Nebrodites cafisii* coming from the same stratigraphic horizon as the lectotype. In contrast, the very coarsely ribbed specimen illustrated on Quenstedt's pl. 109, fig. 8, from the Planula Zone of Neidlingen (not from the "Weißer Jura δ" as suggested by Schlegelmilch 1994: 182), could be a transient linking the genera *Passendorferia* Brochwicz-Lewiński, 1973 and *Nebrodites*.

THE TYPE LOCALITY AND HORIZON OF *AMMONITES PLANULA* HEHL IN ZIETEN, 1830

The holotype of *Ammonites planula* Hehl in Zieten, 1830 (Fig. 3A) was said to come from Jurassic limestones in the vicinity of Donzdorf, a small town in the eastern part of Swabia. More precisely, Quenstedt (1888) mentioned that Hehl's type specimen had a diameter of 130 mm – Zieten's drawing therefore seems to be slightly enlarged – and that it was collected from the "Weisse Kalke [white limestones] of Donzdorf". This corresponds to the Wohlgeschichtete-Kalke Formation in present usage (= Weißjura β), a term going back to Quenstedt (1843). Biostratigraphically the white sublithographic limestones of this formation represent the Planula Zone of the "late Oxfordian" in the Submediterranean biozonation. However, the Planula Zone corresponds to an Early Kimmeridgian age when taking the presently accepted Oxfordian/Kimmeridgian boundary in the Subboreal Realm as the international standard (for an exhaustive discussion see Wierzbowski *et al.*, 2016). In the East and Southeast of Donzdorf, the Wohlgeschichtete-Kalke Formation outcrops along the hillside of the Swabian Alb. In former times these limestones have been exploited in numerous small quarries for road metal. Engel (1883) mentioned a quarry at the southwestern slope of the "Wäldenbühl" [today: Waldenbühl] East of Donzdorf. He reported that in that quarry only the limestones of the "Weißjura β" had been exposed and that *Ammonites planula* Hehl was common there. Another abandoned quarry, which is still accessible, is located along the road (Messelsteige) connecting Donzdorf with the village Schnittlingen. Several further outcrops of the Wohlgeschichtete-Kalke Formation still exist in the vicinity of Donzdorf, *e.g.* along the footpath connecting the hamlets Unterweckerstell and Oberweckerstell.

Although Quenstedt knew well the rock formation from which Hehl's type specimen of *Ammonites planula* was collected (Quenstedt, 1888: 973), he discussed this taxon in his chapter dealing with ammonites from the "Weißjura γ" (today: Lacunosamergel Formation) and he lumped some ammonites from different stratigraphical levels in the same taxon. Later, these misplacements as well as the illustrations of homoeomorphic forms caused confusion about the stratigraphic horizons of some relevant taxa of "*Idoceras*" (*e.g.*, Loriol, 1878; Siemiradzki, 1899; Dacqué, 1903, 1914), but finally field studies in Franconia and Swabia resulted in the recognition of a "Planula Zone", an interval, which was originally placed within Oppel's Tenuilobatus Zone (Salfeld, 1914; Wegele, 1929). When Spath (1925) introduced his new genus *Subnebrodites*, he reported the previous stratigraphic misinterpretations by various authors and provided absolutely correct information about the type horizons

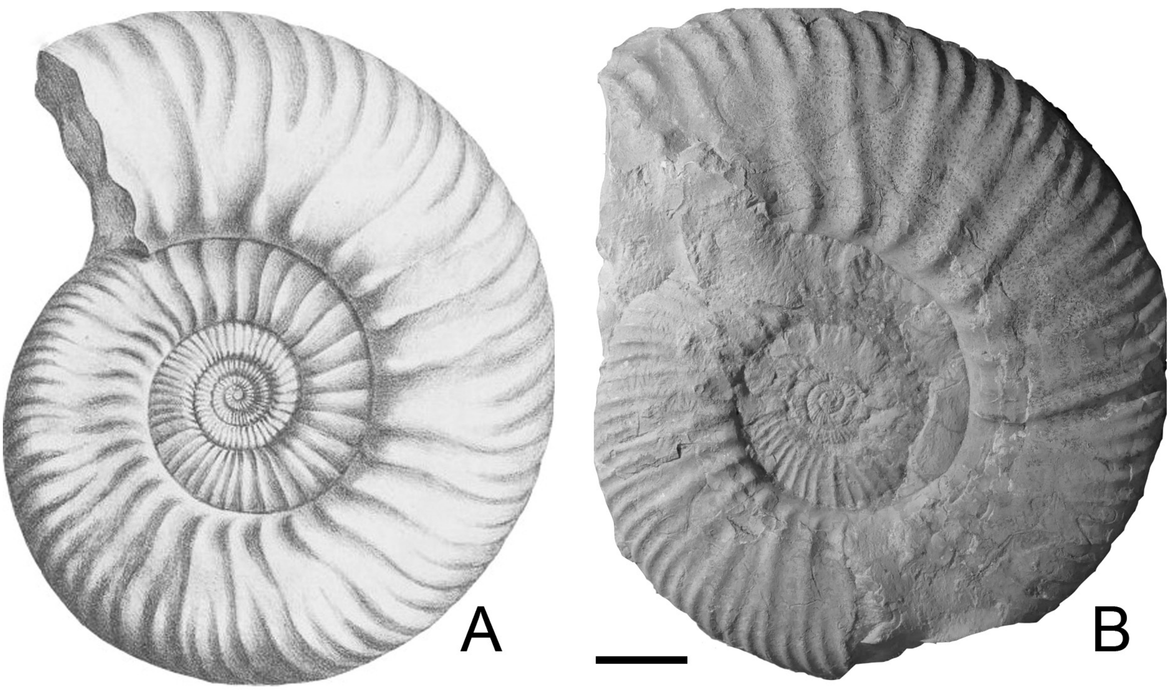

Fig. 3. ***Subnebrodites planula*** **(Hehl in Zieten, 1830)**

A. Illustration of the lost holotype. **B.** GPIT/CP/10071, involute variety, which fits almost perfectly with Hehl's specimen. Wohlgeschichtete-Kalke Formation, Planula Zone, Gosheim, western Swabian Alb, SW Germany. Scale bar = 2 cm of *Subnebrodites planula* (from "Weißjura β" = Wohlgeschichtete-Kalke Formation in modern usage) and *Idoceras balderum* (from "Weißjura γ" = Lacunosamergel Formation in modern usage), respectively. Later, Dieterich (1940) sampled extensively material from the "Weißjura β" of Swabia, but he illustrated only a few new taxa from these beds. Dieterich confirmed the occurrence of "*Idoceras*" *planula* and several closely related forms in that formation. Following Arkell's compilation (1956, table 10) and the biostratigraphic studies by Karvé-Corvinus (1966) in SE France the Planula Zone became well-established (Cariou *et al.* 1997) and is widely used in the Submediterranean latest Oxfordian ("Lusitanian") of France, N Switzerland, Spain, Portugal, the Balkans, and extra-Carpathian Poland. More recently, this Submediterranean Planula Zone was recognized as being Early Kimmeridgian in age when taking the Subboreal zonal succession as international standard (*e.g.*, Matyja and Wierzbowski, 1988, 1994, 1995, 1997; Wierzbowski, 1991; Atrops *et al.*, 1993; Schweigert, 1995; Schweigert and Callomon, 1997; Wierzbowski *et al.*, 2010; Wierzbowski and Matyja, 2014; Wierzbowski *et al.*, 2016).

The type horizon of *Subnebrodites planula* (Hehl in Zieten) ranges in the middle part of the Wohlgeschichtete-Kalke Formation of Swabia (Dieterich, 1940) and time-equivalent formations in adjacent Franconia (Schmidt-Kaler, 1962; Nitzopoulos, 1974; Zeiss, 1977), where it characterizes the *planula* biohorizon (Schweigert and Callomon, 1997; Schweigert, 2000). Citations of this taxon from near the base of this formation (Koerner, 1963) refer to the ancestral *Subnebrodites tonnerrensis* (Loriol, 1893) or come from sections with a hiatus at the base of the formation. Within the micritic, sublithographic limestones of the Wohlgeschichtete-Kalke Formation there are only a few beds relatively rich in fossils, whereas the rocks in-between are poorly fossiliferous and mostly yield only scattered shell fragments of ammonites due to predation activities. A *planula* biohorizon (or subzone) within the Planula Zone has been distinguished also in the Keltiberian Chains of Spain (*e.g.*, Meléndez, 1989; Pérez-Urresti *et al.*, 1996) and in the Prebetic (Olóriz *et al.*, 1999), although the latter one is based on a misidentification of the index species.

SYSTEMATIC PALAEONTOLOGY

Superfamily **Perisphinctoidea** Steinmann in Steinmann and Döderlein, 1890

Family **Ataxioceratidae** Buckman, 1921

Subfamily **Ataxioceratinae** Buckman, 1921

Genus ***Subnebrodites*** Spath, 1925

Type species. – *Ammonites planula* Hehl in Zieten, 1830, by original designation.

Subnebrodites planula (Hehl in Zieten, 1830) [M + m] Figs. 3–5

*1830. *Ammonites planula* Hehl in Zieten, p. 9, pl. 7, fig. 5 [M; Fig. 3A].

non 1846. *Ammonites planula* Hehl. – Orbigny, p. 416, pl. 144 [= *Wagnericeras wagneri* (Oppel)].

pars 1849. *Ammonites planula*. – Quenstedt, p. 164, non pl. 12, fig. 8 [= *Subnebrodites tonnerrensis* (Loriol)].

1864. *Ammonites Roemeri* Mayer, p. 377 [M].

1865. *Ammonites Roemeri* Mayer, pl. 7, fig. 2 [M].

non 1878. *Ammonites* (*Perisphinctes*) *planula*, Hehl. – Loriol, p. 98, pl. 16, fig. 1 [= *Subnebrodites schroederi* (Wegele)].

1878. *Ammonites* (*Perisphinctes*) *Roemeri* C. Mayer. – Loriol, p. 96, pl. 15, fig. 6 [M].

1879. *Perisphinctes planula* Hehl var. *laxevoluta*. – Fontannes, p. 72, pl. 11, fig. 2 [m].

pars 1888. *Ammonites planula*. – Quenstedt, p. 973 ff., pl. 108, fig. 2 [m; Fig. 1A], 4 [?M], non figs. 3, 5.

non 1888. *Ammonites planula gigas*. – Quenstedt, pp. 974, 984, pl. 108, fig. 1; pl. 109, fig. 8.

1888. *Ammonites planula cornutus*. – Quenstedt, p. 978, pl. 108, fig. 13 [M; Fig. 5].

1893. *Perisphinctes planula* var. *laxevoluta*, Font. – Choffat, p. 52, pl. 11, fig. 2 [m].

1893. *Perisphinctes planula*, Hehl. – Choffat, p. 52, pl. 11, fig. 3 [m].

non 1903. *Perisphinctes planula* Hehl var. *laxevoluta* Font. – Dacqué, p. 147, pl. 14, fig. 15.

1908. *Ammonites planula* Hehl. – Engel, fig. on p. 388 [?m].

pars 1914. *Idoceras montejuntense* nov. sp. – Dacqué, p. 5, non pl. 1, fig. 1.

1925. *Subnebrodites*, *Ammonites planula* Hehl, Zieten. – Spath, p. 129.

1929. *Idoceras planula* Hehl. – Wegele, p. 76, pl. 9, fig. 3 [M].

1929. *Idoceras Roemeri* Mayer. – Wegele, p. 77, pl. 9, fig. 4 [M].

pars 1929. *Idoceras schroederi* n. sp. – Wegele, p. 77, pl. 9, fig. 5 only [M].

1938. *Idoceras planula* (Hehl). – Roman, p. 242, pl. 22, fig. 228 [M; re-figuration of HT].

1957. *Idoceras planula* (Hehl). – Arkell, p. L323, fig. 413.3 [?m].

1959. *Idoceras planula* (Hehl). – Ziegler, p. 27, pl. 1, fig. 9 [M].

1959. *Idoceras laxevolutum* (Fontannes). – Ziegler, p. 28, pl. 1, fig. 6 [m].

1964. *Idoceras planula*. – Geyer and Gwinner, pl. 9, fig. 6 [M].

pars 1974. *Idoceras planula* (Hehl). – Nitzopoulos, p. 72, pl. 8, figs. 1, 2, 4, 6; pl. 9, figs. 1–3 [M], 4, 5 [m]; non pl. 8, figs. 3, 5.

1976. *Idoceras laxevolutum* (Hehl). – Brochwicz-Lewiński and Różak, pl. 37, fig. 2.

1977. *Idoceras (Subnebrodites) laxevolutum* (Fontannes). – Ziegler, pl. 2, fig. 2 [m].

1978. *Idoceras planula* (Hehl). – Olóriz, p. 137, pl. 12, fig. 3 [?m].

1978. *Idoceras laxevolutum* (Fontannes). – Olóriz, p. 140, pl. 11, fig. 5, pl. 12, fig. 4 [?m].

1978. *Idoceras planula* (Hehl). – Wierzbowski, p. 186, pl. 8, fig. 1 [M].

1979. *Idoceras planula* (Hehl). – Geyer and Gwinner, pl. 8, fig. 3 [M].

non 1979. *Idoceras* cf. *planula* (Hehl in Zieten). – Sapunov, pl. 29, figs. 1, 2.

1987. *Idoceras (Subnebrodites) laxevolutum* (Fontannes). – Ziegler, pl. 1, fig. 7 [m].

1989. *Idoceras (Subnebrodites) planula* (Hehl in Zieten). – Schairer, p. 99ff., pl. 1, figs. 1–3 [M], 4 [?m], pl. 3, figs. 1, 2, pl. 4, fig. 1 [M].

1989. *Idoceras (Subnebrodites) laxevolutum* (Fontannes) sensu Ziegler. – Schairer, p. 101ff, pl. 4, figs. 2 [?M], 3–7, pl. 5, figs. 1–4 [m].

1989. *Idoceras (?) laxevolutum* (Fontannes). – Schairer, p. 103, pl. 5, fig. 3 [m].

1989. *Idoceras (Subnebrodites)* aff. *laxevolutum* (Fontannes). – Schairer, p. 101ff, pl. 5, figs. 6, 7; pl. 6, figs. 1, 2 [M], 3 [?m].

1991. *Idoceras (Subnebrodites) planula* (Hehl). – Schlampp, p. 130, pl. 16, fig. 1 [M].

1991. *Idoceras (Subnebrodites)* cf. *laxevolutum* (Fontannes). – Schlampp, p. 130, pl. 16, fig. 3 [?m].

1994. *Idoceras planula* (Hehl in Zieten). – Schlegelmilch, p. 71, pl. 25, fig. 7 [M].

1997. *Idoceras (Subnebrodites) planula* (Hehl). – Matyja and Wierzbowski, pl. 9, figs. 1, 6 [M].

1997. *Subnebrodites planula* (Quenstedt). – Cariou *et al.*, pl. 22, fig. 4 [M].

non 1999. *Subnebrodites planula* (Hehl). – Olóriz *et al.*, figs. 3–4.

2000. *Subnebrodites planula* (Quenstedt). – Gygi, p. 93, pl. 11, fig. 5 [m].

2000. *Subnebrodites schroederi* (Wegele). – Gygi, p. 63, pl. 13, fig. 4 [M].

non 2000. *Subnebrodites laxevolutus* (Fontannes). – Gygi, p. 93, pl. 11, fig. 4 [= *Subnebrodites tonnerrensis* (Loriol)].

2003. *Subnebrodites planula* (Quenstedt). – Gygi, p. 62, fig. 60 [M].

2003. *Subnebrodites* cf. *schroederi* (Wegele). – Gygi, p. 63, fig. 61 [M].

2007. *Idoceras (Subnebrodites) planula* (Hehl in Zieten). – Głowniak and Wierzbowski, p. 117, fig. 72 [M].

2017. *Subnebrodites planula* Spath. – Enay and Howarth, figs. 1A–D [m], 2 [M; re-figuration of HT].

Types. – Holotype, by monotypy, is the specimen illustrated in Zieten, 1830, pl. 7, fig. 5, which is untraceable. For nomenclatorial stability of this long-known and well-established taxon we here designate SMNS 70398, illustrated in Fig. 4, a topotypic macroconch, as the neotype.

Type locality and horizon. – Donzdorf, Swabian Alb, Southwestern Germany; outcrop along a footpath connecting the hamlets Unterweckerstell and Oberweckerstell, in an altitude of *c.* 580 m above sea-level; Wohlgeschichtete-Kalke Formation (= “Weißjura β” in older literature), *ca.* 10 metres above the base of the formation; Planula Zone, *planula* biohorizon (Early Kimmeridgian).

Diagnosis. – Medium-sized ataxioceratid ammonite with subevolute coiling; predominant radiate to prorsiradiate biplicate ribs becoming coarse and more distant spaced on body chamber; ribs ventrolaterally forward curved, forming a chevron on the venter. Pre-adult peristomes common. Microconchs with less coarse adult ribbing and lappeted mouth border. Remarkable plasticity in adult size, involution and ribbing density both in macroconchs and microconchs.

Description. – The neotype is a slightly compressed macroconchiate specimen with a maximum diameter of 150 mm, an umbilical width of 73 mm (49%), and a whorl height of 40 mm (26.7%). Peristome is simple with a short ventral horn. Whorl cross section of the body chamber is high-oval; maximum width of cross section behind aperture is ca. 25 mm, but this value is not the original state due to compaction. One third of the body chamber behind the adult peristome there is a strong proverse constriction developed marking the position of a pre-adult peristome. Beginning of the body chamber and suture lines of the phragmocone are not detectable because the shell is overprinted on the inner mould. Sculpture predominantly consists of radiate to proverse biplicate ribs, with a few simple ribs, and occasionally intercalated secondaries with tripartite appearance on the outer whorl. In front of the pre-adult peristomal constriction the ribbing is irregular for a short distance. Inner whorls show a very evolute coiling and sharp ribbing with only few constrictions; on the last chamber the ribbing style changes to a coarser and more distant spaced adult style. On the body chamber the secondaries project slightly forward. They meet on the venter at a blunt angle and become weaker but do not fade out.

Remarks. – The above synonymy lists microconchs (supposed to be males) and macroconchs (supposed to be females) in the same taxon. Formerly, both dimorphic partners have been separately described and the microconchs

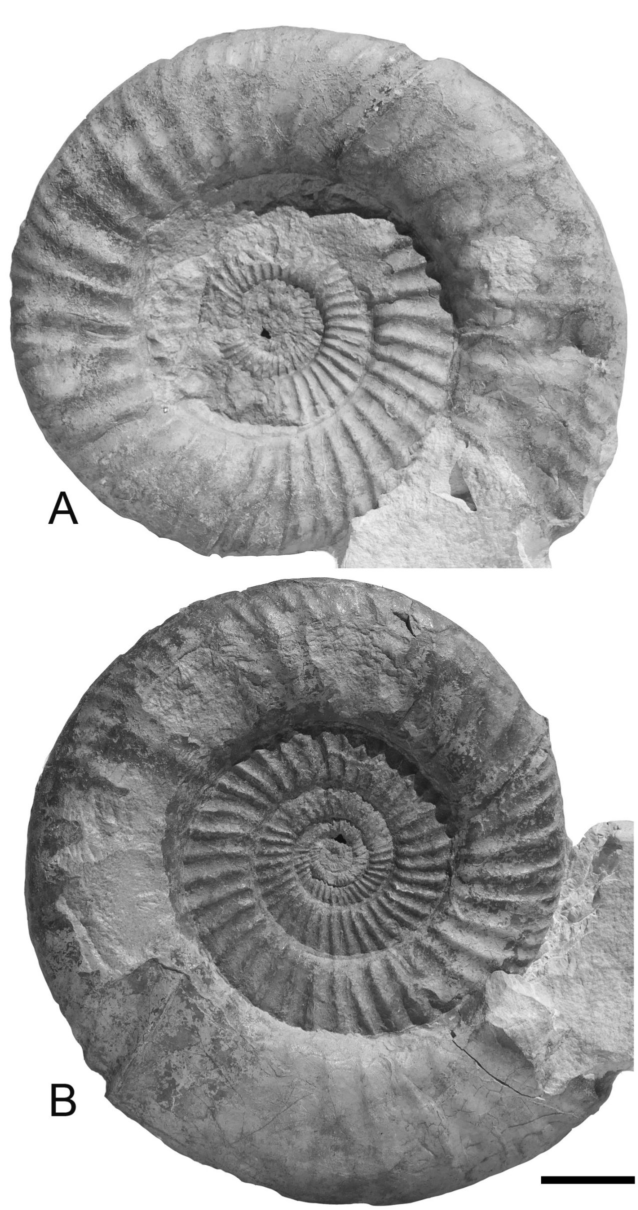

Fig. 4. *Subnebrodites planula* (Hehl in Zieten, 1830)

A, B. Neotype, SMNS 70398, macroconch, lateral views, Wohlgeschichtete-Kalke Formation, Planula Zone, Unterweckerstell near Donzdorf, eastern Swabian Alb, SW Germany (leg. H. Kuschel). Scale bar = 2 cm

corresponding to "*Idoceras*" *planula* (Hehl in Zieten) were identified as "*Idoceras*" *laxevolutum* (Fontannes) without recognizing them as sexual dimorphs at that time (Ziegler 1959) – dimorphism in Jurassic ammonites was demonstrated later by Makowski (1962) and Callomon (1963). However, there exist numerous specimens which are not clearly identifiable as microconchs or macroconchs, because they exhibit a very evolute coiling resembling the microconchs but there then follows a coarse, wide-spaced ribbing stage and a simple aperture strongly recalling the macroconchs. On the other hand we noticed involute specimens with macroconchiate appearance and smooth aperture which are equal-sized or even smaller than some lappeted coeval microconchs. At present these phenomena are not well understood (hermaphroditism?) and more material is needed for a statistical analysis. Dieterich (1940), Nitzopoulos (1974) and Schairer (1989) reported an extreme variability within *Subnebrodites planula* enclosing rather evolute and more involute specimens and coarse-ribbed examples as well as densely ribbed morphs.

In any case we have to keep in mind that if microconchs have diameters of more than 100 mm, the corresponding macroconchs must be expected to reach significantly bigger sizes, however, adult big-sized macroconchs are quite rare. According to Zieten's drawing (Fig. 3A), the lost holotype of *Ammonites planula* Hehl in Zieten had a more involute coiling and a higher whorl section than the lappeted microconch illustrated on Quenstedt's pl. 108, fig. 2. With a diameter of 130 mm Hehl's specimen was not complete since its aperture was broken. In this aspect, the big specimen illustrated by Ziegler (1959, pl. 1, fig. 9 = *Ammonites planula cornutus* Quenstedt, 1888; Fig. 5) was a good example of an adult macroconch of *Subnebrodites planula* (Hehl in Zieten), however, its evolute coiling is almost identical to that of the supposed microconch. *Ammonites planula cornutus* comes from the Wohlgeschichtete-Kalke Formation as well; Quenstedt's indication that it came from the "Mittlerer Weissjura" is somewhat misleading, but he included the sublithographic limestones of his "Weissjura β" in this lithostratigraphic unit. Even Quenstedt (1888) himself was aware that the ventral horn of the specimen is not a specific but only an individual character. This horn corresponds to a pre-adult peristome. Pre-adult peristomes are common in *Subnebrodites planula* (Figs. 1B, 4, 5). Spath (1925) did not mention this specimen when he discussed *Subnebrodites*, as he did not study the original specimens illustrated by Quenstedt (1888) but only their illustrations, and the drawing of *Ammonites planula cornutus* is too incomplete to get an idea how the entire specimen (Fig. 5) looks like. Schairer (1989) stated that – after the drawing by Zieten – the lost holotype of *Subnebrodites planula* was a quite extreme variant within this species. We concur and illustrate a macroconch collected from the Wohlgeschichtete-Kalke Formation (Planula Zone) of Gosheim which matches perfectly with the lost holotype (Fig. 3B). The specimen from Gosheim also resembles the incomplete lectotype of *Subnebrodites schroederi* (Wegele, 1929) both in ribbing density and involution and thus may be a transient to that poorly defined species.

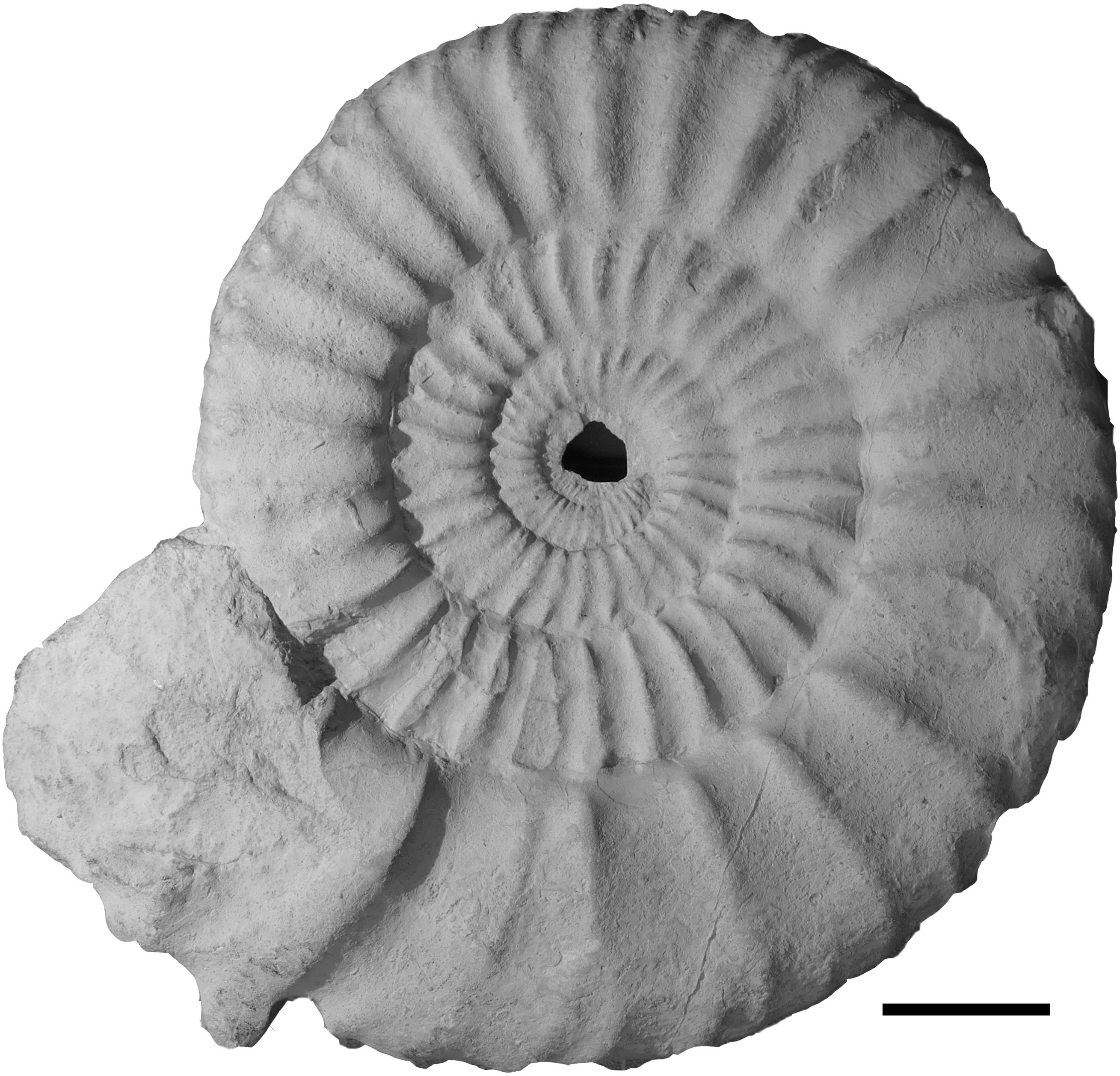

Fig. 5. *Subnebrodites planula* (Hehl in Zieten, 1830)

GPIT/CP/10068, macroconch, evolute variety with coarse ribbing in the adult stage (= *Ammonites planula cornutus* Quenstedt 1888, pl. 108, fig. 13), Wohlgeschichtete-Kalke Formation, Planula Zone, Spaichingen, western Swabian Alb, SW Germany. Scale bar = 2 cm

DIMORPHISM IN *IDOCERAS BALDERUM* (OPPEL, 1863) AS A KEY FOR ITS SYSTEMATIC PLACEMENT

When erecting his new genus *Subnebrodites*, Spath (1925) restricted the older genus *Idoceras* Burckhardt, 1906 to the group of *Ammonites balderus* Oppel ["the true *Idoceras*"]. This procedure is widely accepted as a subsequent genotype designation and we concur. Arkell (1956), however, erroneously followed Roman (1936), who was not aware of Spath's earlier designation and took *Ammonites planula* Hehl as the type species of *Idoceras*, so that in the "Treatise" *Subnebrodites* erroneously became an objective junior synonym of *Idoceras*, and Arkell (1956) illustrated another specimen of *Ammonites planula* from Quenstedt (1888, pl.

108, fig. 4) as a typical *Idoceras* a specimen, which is most likely a subadult macroconch of *Subnebrodites planula* (Hehl in Zieten). In their recent effort for stabilizing the type species of *Subnebrodites*, Enay and Howarth (2017) surmised a possible specific identity of *Ammonites planula* Hehl in Zieten, 1830 and *Ammonites balderus* Oppel, 1863 – this assumption goes back to Enay (1966); hence we will discuss the latter taxon here as well.

Originally described from a condensed interval in the Upper Jurassic Baden Formation of northern Switzerland, *Idoceras balderum* (Oppel, 1863) has been recognised much later as an easily identifiable ammonite species in the Upper Jurassic of Southwestern Germany (*e.g.*, Engel, 1883, 1891, 1897; Haizmann, 1902; Geyer, 1961; Barthel, 1963; Barthel and Schairer, 1980). In Swabia this species is quite common, but restricted to a short interval in the higher part of the Lacunosamergel Formation (Geyer, 1961; Schick, 2004). *Idoceras balderum* (Figs. 6–8) characterizes the 'Balderumbänke' Member, the age of which lies within the Divisum Zone of the late Early Kimmeridgian. In southeastern France an equal horizon à *Idoceras balderum* is developed (Atrops 1982). Since there are no common ancestral forms recorded from the underlying beds, we suppose that the short range of *Idoceras balderum* results from a strong immigration pulse from the Tethys. For this reason the use of a 'Balderum Zone' for this short-range event seems not to be appropriate.

Gygi (2003) illustrated a unique, rather evolute specimen of *Idoceras*, which he determined as *I. hararinum* Venzo, from a stratigraphically somewhat older bed of the Baden Formation of Switzerland. Very similar or identical forms occur in the Early Kimmeridgian of the Tethyan Realm (*e.g.*, Olóriz, 1978, 2002a, 2002b; Sarti, 1993). The question remains whether or not the morphologically striking similar taxa included in *Idoceras* by Burckhardt (1906, 1912) from Mexico or those from East Africa, adjacent Yemen and Iran (Dacqué, 1903, 1914; Venzo, 1959; Howarth 1998; Schairer *et al.*, 2003) belong to the same genus as the Submediterranean type species of *Idoceras*, *Ammonites balderus* Oppel (Enay and Howarth, 2017).

The type series of *Ammonites balderus* originally consisted of three specimens, of which one was illustrated (Oppel, 1863). The latter, a nucleus, is therefore not the holotype as indicated in the figure caption by Enay and Howarth (2017), but it was designated as lectotype by Gygi (2003: 89). This lectotype shows moderately evolute coiling. Prominent, proversely curved constrictions mostly run more strongly proverse than the preceding ribs. In this character *Idoceras balderum* (Oppel) differs already in its early ontogenetic stages from *Subnebrodites* spp. Ziegler (1959) illustrated two examples of *Idoceras balderum*; he distinguished involute and evolute forms within the same taxon. The phenomenon observed by Ziegler (1959) is, however, not fully covered by intraspecific variation as supposed by him, but again reflects sexual dimorphism, with the evolute forms usually representing the microconchs (Figs. 6C, 8) and the involute ones the corresponding macroconchs (Figs. 6A, B, 7). In addition there is a remarkable variation in the degree of involution both in microconchs and macroconchs. This variation in coiling somewhat recalls the enormous morphological plasticity demonstrated for *Subnebrodites planula* (Schairer 1989) – again a case of hermaphroditism (see Parent *et al.*, 2008), with individual, possibly ecologically induced differences in the time when the sex of a specimen became determined, or a case of environmental polymorphism *sensu* Matyja (1986)? In this respect, it seems impossible to decide whether the lectotype of *Idoceras balderum* is the nucleus of a microconch or that of a macroconch. Adult macroconchs of *Idoceras balderum* (Fig. 7) are extremely rare, mostly fragmentary, and have never been illustrated before. The apparent rarity of macroconchs can be explained by environmental conditions favouring microconchs. When invading the Submediterranean Province the *Idoceras balderum* population possibly attained maturity quicker than in its Tethyan home. In consequence, this opportunistic lifestyle lead to a predominance of microconchs. The involute specimen illustrated by Ziegler (1959, pl. 1, fig. 3) still shows a subadult stage. Fragmentary specimens show that the adult macroconchs can reach more than twice the diameter of the microconchs. In microconchiate specimens of *Subnebrodites* spp. lappets are developed (*e.g.*, Quenstedt, 1849; 1888; Ziegler, 1959; Nitzopoulos, 1974; Schairer, 1989; Enay and Howarth, 2017), whereas not a single microconch of *Idoceras balderum* (Oppel) with lappets has been recorded yet. Either such lappets were not developed in the microconchs of true *Idoceras*, or the shell at the mouth border was very thin and the lappets broke away prior to burial. We favour the first possibility, because several completely preserved microconchs within our studied sample (*e.g.*, Fig. 8) exhibit a terminal peristome with a short ventral horn but lack any indications of lappets. Hence, it seems sure that lappets were absent in *Idoceras*. Only in the lectotype of *Idoceras hodiernae* (Gemmellaro) Olóriz (2002b) suspected the existence of "small, wide lappets", but the aperture of that specimen is incompletely preserved. In microconchiate specimens from Mexico assigned to *Idoceras* lappets have not been recorded either (pers. comm. A.B. Villaseñor March 27th, 2017). Together with the striking similarities in ornamentation and dimorphism (see below) and the same mode of how constrictions formed (own observ.), this unusual character strongly supports the traditional assignment of the Mexican species to *Idoceras*. The apparent lack of lappets in *Idoceras* is a good argument: 1) to follow Spath (1925) in separating *Subnebrodites* and *Ido-*

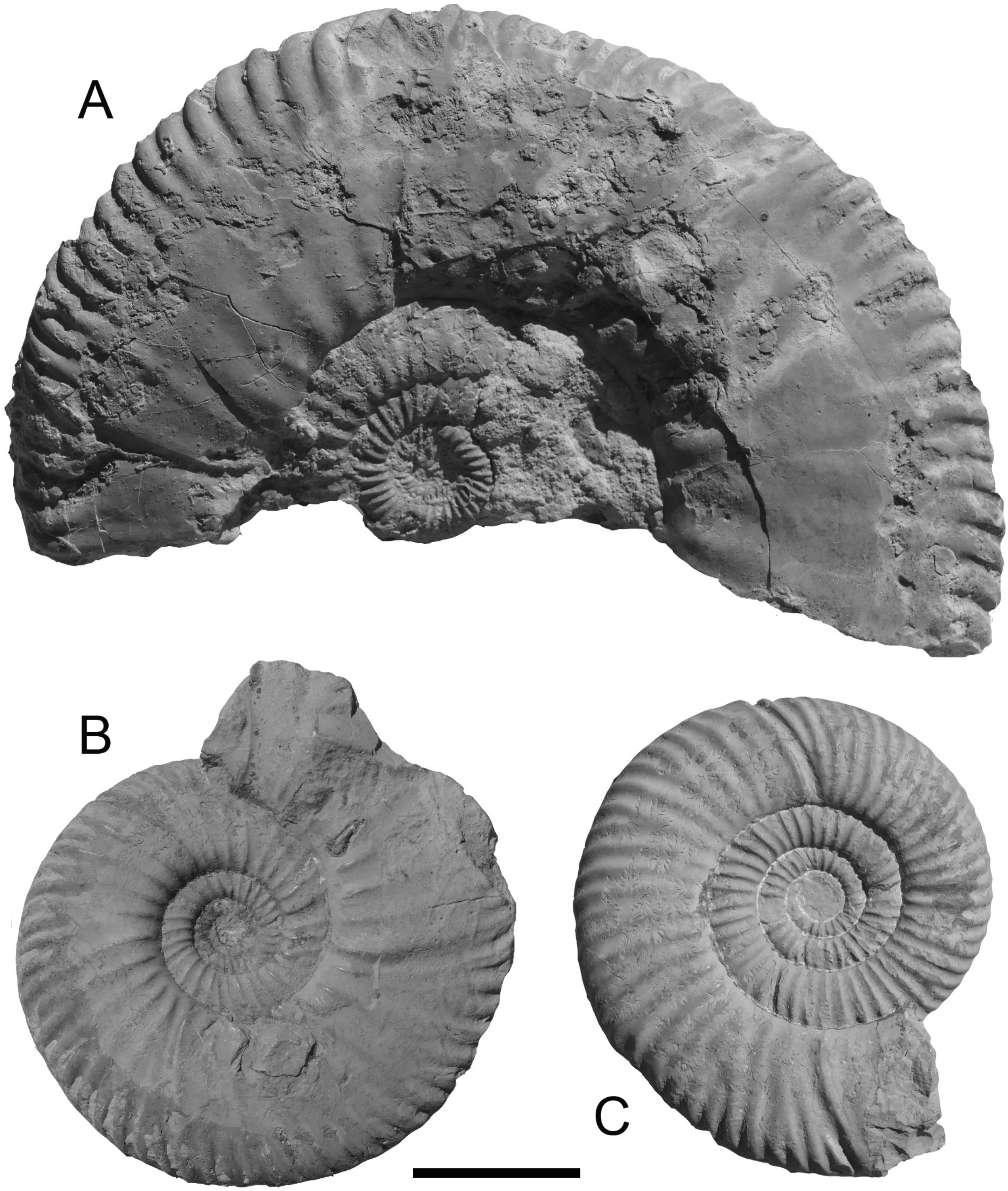

Fig. 6. ***Idoceras balderum*** **(Oppel, 1863)**

Lacunosamergel Formation, Divisum Zone, *balderum* horizon, Swabian Alb, SW Germany. **A.** SMNS 70397/6, macroconch, Bärenthal (leg. A. Hagenlocher). **B.** SMNS 70397/3, nucleus of macroconch, Weilheim (leg. W. Bechter). **C.** SMNS 70397/2, nucleus of microconch, Oberdigisheim (leg. A. Hagenlocher). Scale bar = 2 cm

Fig. 7. *Idoceras balderum* (Oppel, 1863)

SMNS 70397/7, adult macroconch, Lacunosamergel Formation, Divisum Zone, *balderum* horizon, Böttingen near Spaichingen, western Swabian Alb, SW Germany (leg. E. Hak). Scale bar = 5 cm

ceras as individual genera, 2) to exclude *Subnebrodites* from the subfamily Idoceratinae Spath, 1924, emend. Olóriz 2002a, b, and 3) to maintain the subfamily Idoceratinae Spath, 1924 at least for the genus *Idoceras* Burckhardt, 1906 itself.

Due to the sculpture and dimorphism of *Subnebrodites* and considering their early representatives from the base of the Planula Zone (Nitzopoulos 1974) this genus is assigned to Ataxioceratinae Buckman, 1921 (see also *e.g.*, Pérez-Urresti *et al.*, 1996; Meléndez *et al.*, 1997, 2006). Villaseñor and Olóriz (2006) suggested an inclusion of *Idoceras* in Ataxioceratinae as well. If *Idoceras* roots in *Subnebrodites*, the loss of lappets in the microconchs must have happened sometimes during the Early Kimmeridgian. A similar case of loss of lappets is reported from the Subboreal ammonite genus *Pectinatites* (see Dzik, 1994).

RELATIONSHIP BETWEEN *IDOCERAS BALDERUM* AND HEHL'S *AMMONITES PLANULA*

In the microconchs of *Idoceras balderum* deep wide-spaced, proverse constrictions are developed. In the nuclei of macroconchs these constrictions are much less prominent. In the medium and adult ontogenetic stages, both dimorphic

Fig. 8. *Idoceras balderum* (Oppel, 1863)

SMNS 70397/5, microconch with preserved aperture, Lacunosamergel Formation, Divisum Zone, *balderum* horizon. Hausen near Bad Überkingen, eastern Swabian Alb, SW Germany (leg. H. Schick). Scale bar = 2 cm

partners show a characteristic ribbing style with radiate primaries and densely arranged, strongly thickened secondaries meeting ventrally in a chevron with a smooth ventral band, which is often hidden due to compaction. In the adult stage, the primaries become weaker and finally disappear on the flanks whereas the densely spaced ventral branches of the secondaries persist – a feature that is shared with a macroconch *Idoceras* ex gr. *durangense* (Burckhardt, 1906) from Mexico (see Villaseñor and Olóriz, 2006, fig. 1). In ventral view, *Idoceras balderum* and the illustration of *Ammonites planula* Hehl in Zieten as well as other *Subnebrodites* spp. are rather close, because the secondaries are forwardly projecting in all of these taxa. The very thin whorl section provided in Zieten's drawing does not show the original uncompressed condition; it clearly results from diagenetic compaction and thus cannot be taken as a diagnostic character of this species. However, in lateral view, there is no resemblance of the illustration of *Ammonites planula* Hehl in Zieten, 1830 (Fig. 3A) with *Idoceras balderum* (Oppel, 1863) (Figs. 6–8) at all, the former showing coarse, widespaced biplicate ribs and occasional intercalatories in the outer whorl probably already belonging to the body chamber. Constrictions are not discernible in Zieten's drawing but the changes in the direction of ribbing and several irregularly spaced ribbing units indicate their presence. Rectiradiate ribs such as on the body chamber of Hehl's specimen are not very common but may occur in *Subnebrodites planula* (*e.g.*, Fig. 1B). Hence, both from morphological and stratigraphical points of view we can put aside the speculative suggestion by Enay (1966) recently revived by Enay and Howarth (2017) that Hehl's taxon *Ammonites planula* was the macroconch of *Idoceras balderum*. There is no other ammonite species in the Upper Jurassic of Southern Germany better fitting with Zieten's drawing than *Subnebrodites planula* (Hehl in Zieten) in the traditional interpretation of Engel, 1891, 1897, Wegele, 1929, Ziegler, 1959, Nitzopoulos, 1974, Schairer, 1989, *etc.*). Nevertheless, without the neotype designated herein this opinion would remain a subjective view.

CONCLUSIONS

The introduction of a neotype for the lost holotype of *Ammonites planula* Hehl in Zieten, 1830, which is the true type species of *Subnebrodites* Spath, 1925, provides an unambiguous basis for this stratigraphically important taxon. The neotype of *Subnebrodites planula* is a macroconch, whereas the corresponding microconchs are usually smaller, slightly more evolute and bear lappets.

Idoceras balderum (Oppel, 1863), the type species of *Idoceras* Burckhardt, 1906, shows a remarkable dimorphism as well. The genus *Idoceras* Burckhardt, 1906, which was often considered as synonymous with *Subnebrodites* Spath, 1925, differs from the latter in the apparent lack of lappets in the microconchs. For this important difference we assign *Subnebrodites* to Ataxioceratinae Buckman, 1921 and *Idoceras* to Idoceratinae Spath, 1924. *Subnebrodites planula* (Hehl in Zieten) is part of a phyletic lineage in the Submediterranean Province and characterizes the *planula* biohorizon within the Planula Zone. In contrast, *Idoceras balderum*

(Oppel) marks a short immigration event (*balderum* biohorizon) from the Tethys within the Divisum Zone of the Early Kimmeridgian. Fortunately, the well-intentioned publication by Enay and Howarth (2017) has no severe consequences since their illegitimately proposed lectotype for "*Subnebrodites planula* Spath, 1925" corresponds to the microconch partner of *Subnebrodites planula* (Hehl in Zieten, 1830) which is a subjective junior synonym of *Subnebrodites laxevolutus* (Fontannes, 1879). The herein designated lectotype of *Ammonites planula gigas* Quenstedt, 1888 is illustrated photographically for the first time and identified as a *Nebrodites cafisii* (Gemmellaro, 1872) from the basal Acanthicum Zone.

Acknowledgements. Dr. Ingmar Werneburg (Tübingen, Germany) and Dr. Alexander Nützel (Munich, Germany) gave access to the collections under their care. Dr. Ana Bertha Villaseñor (Mexico City) kindly provided useful information on *Idoceras* from Mexico. The manuscript benefitted from careful reviews by Dr. Carlo Sarti (Bologna, Italy) and Prof. Dr. Andrzej Wierzbowski (Warsaw, Poland).

REFERENCES

ARKELL W.J., 1956 – Jurassic Geology of the World. – 1–804 pp.; Edinburgh and London (Oliver and Boyd).

ARKELL W.J., 1957 – Cephalopoda, Ammonoidea. *In*: Treatise on Invertebrate Palaeontology, Part L, Mollusca 4: L80–L490 (ed. R.C. Moore); Lawrence (Kansas University 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 de Lyon*, **83**: 1–463.

ATROPS F., GYGI R., MATYJA B.A., WIERZBOWSKI A., 1993 – The *Amoeboceras* faunas in the Middle Oxfordian–lowermost Kimmeridgian, Submediterranean succession, and their correlation value. *Acta Geologica Polonica*, **43**, 3/4: 213–227.

BARTHEL K.W., 1963 – Einige Idoceratinae (Ammonoidea) aus dem südlichen Fränkischen Jura. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, **3**: 27–33.

BARTHEL K.W., SCHAIRER G., 1980 – Zur Verbreitung von *Idoceras balderum* (Oppel) (Ammonoidea, oberstes Unterkimmeridge) im südlichen Fränkischen Jura. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, **20**: 11–15.

BROCHWICZ-LEWIŃSKI W., 1973 – Some remarks on the origin of the subfamily Idoceratinae Spath, 1924 (Perisphinctidae, Ammonoidea). *Acta Palaeontologica Polonica*, **18**: 299–318.

BROCHWICZ-LEWIŃSKI W., RÓŻAK, Z., 1976 – Oxfordian Idoceratids (Ammonoidea) and their relation to *Perisphinctes* proper. *Acta Palaeontologica Polonica*, **21**, 4: 373–390.

BUCKMAN, S.S., 1919–1921 – Yorkshire type ammonites, **3**: 5–64; London (Wesley and Son).

BURCKHARDT C., 1906 – La faune Jurassique de Mazapil, avec un appendice sur les fossiles du Crétacique inférieur. *Boletín del Instituto Geológico de México*, **23**: 216 pp.

BURCKHARDT C., 1910 – Neue Untersuchungen über Jura und Kreide in Mexiko. *Centralblatt für Mineralogie, Geologie und Paläontologie*, **1910**: 622–631.

BURCKHARDT C., 1912 – Faunes Jurassiques et Crétaciques de San Pedro del Gallo, Durango. *Boletín del Instituto Geológico de Mexico*, **29**: 264 pp.

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

CARIOU É., ENAY R., ATROPS F., HANTZPERGUE P., MARCHAND D., RIOULT M., 1997 – Oxfordien. *In*: Biostratigraphie du Jurassique ouest-européen et méditerranéen (eds. É. Cariou, P. Hantzpergue). *Bulletin du Centre des Recherches Elf Explorations Productions, Mémoires*, **17**: 79–86.

CHOFFAT P., 1893 – Description de la faune jurassique du Portugal. Classe des céphalopodes. 82 pp.; Lisbonne (Imprimerie de l'Académie Royale des Sciences).

DACQUÉ E., 1903 – Beiträge zur Geologie des Somalilandes. *Beiträge zur Geologie und Paläontologie Österreich-Ungarns und des Orients*, **17**: 119–160.

DACQUÉ E., 1914 – Neue Beiträge zur Kenntnis des Jura in Abessynien. *Beiträge zur Geologie und Paläontologie Österreich-Ungarns und des Orients*, **27**: 1–17.

DIETERICH E., 1940 – Stratigraphie und Ammonitenfauna des Weißen Jura β in Württemberg. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **96**: 1–40.

DZIK J., 1994 – Sexual dimorphism in the virgatitid ammonites. *Palaeopelagos, special publications*, **1**: 129–141.

ENAY R., 1966 – L'Oxfordien dans la moitié sud du Jura français; Étude stratigraphique. Deuxiéme partie; contribution à la connaisance des Périsphinctidés. *Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon*, **2**, 8: 331–625.

ENAY R., HOWARTH M., 2017 – The Upper Oxfordian and Lower Kimmeridgian ammonite genera *Idoceras* Burckhardt, 1906, and *Subnebrodites* Spath, 1925. *Paleontological Contributions, Kansas University*, **17**: 1–3.

ENGEL T., 1883 – Geognostischer Wegweiser durch Württemberg, 1st edition. – 326 pp.; Stuttgart (Schweizerbart).

ENGEL T., 1891 – Bemerkungen zu etlichen Typen aus Quenstedt's Ammoniten des schwäbischen Jura. *Jahreshefte des Vereines für vaterländische Naturkunde in Württemberg*, **47**: 29–34.

ENGEL T., 1897 – Zwei Grenzbänke im schwäbischen Weißen Jura mit ihren Leitammoniten (Weiß β/γ und γ/δ). *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **53**: 56–67.

ENGEL T., 1908 – Geognostischer Wegweiser durch Württemberg, 3rd edition. – 645 pp.; Stuttgart (Schweizerbart).

FONTANNES F., 1879 – Descriptions des Ammonites des Calcaires du Château de Crussol – Ardèche (Zones à *Oppelia tenuilobata* et *Waagenia Beckeri*). XI+122 pp.; Lyon and Paris (Savy).

GEMMELLARO G.G., 1872 – Sopra i cefalopodi della zona con *Aspidoceras acanthicum* Opp. di Burgilamuni presso Favara, provincia di Girgenti. *Giornale di Scienze Naturale ed Economiche di Palermo*, **8**: 30–52.

GEYER O.F., 1961 – Monographie der Perisphinctidae des unteren Unterkimeridgium (Weißer Jura γ, Badenerschichten). *Palaeontographica*, **A117**: 1–157.

GEYER O.F., GWINNER M.P., 1964 – Einführung in die Geologie von Baden-Württemberg (1st edition). Stuttgart (Schweizerbart).

GEYER O.F., GWINNER M.P., 1979 – Die Schwäbische Alb und ihr Vorland. *Sammlung geologischer Führer*, **67**: 271 pp.; Stuttgart and Berlin (Borntraeger).

GŁOWNIAK E., WIERZBOWSKI A., 2007 – Taxonomical revision of the perisphinctid ammonites of the Upper Jurassic (Plicatilis to Planula zones) described by Józef Siemiradzki (1891) from the Kraków Upland. *Volumina Jurassica*, **5**: 31–137.

GYGI R.A., 2000 – Integrated stratigraphy of the Oxfordian and Kimmeridgian (Late Jurassic) in northern Switzerland and adjacent southern Germany. *Denkschriften der Schweizerischen Akademie der Naturwissenschaften*, **104**: 1–149.

GYGI R.A., 2003 – Perisphinctacean ammonites of the Late Jurassic in northern Switzerland. *Schweizerische Paläontologische Abhandlungen*, **123**: 1–232.

HAIZMANN W., 1902 – Der Weiße Jura gamma und delta in Schwaben. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Bände*, **B15**: 473–561.

HOWARTH M.K., 1998 – Ammonites and nautiloids from the Jurassic and Lower Cretaceous of Wadi Hajar, southern Yemen. *Bulletins of the Natural History Museum of London (Geology)*, **54**: 33–107.

ICZN, 1999 – International Code of Zoological Nomenclature, 4th edition. – 306 pp.; London (The International Trust for Zoological Nomenclature).

KARVÉ-CORVINUS G., 1966 – Biostratigraphie des Oxfordium und untersten Kimmeridgium am Mont Crussol, Ardèche, im Vergleich mit Süddeutschland. *Neues Jahrbuch Geologie und Paläontologie Abhandlungen*, **126**, 2: 101–141.

KOERNER U., 1963 – Beiträge zur Stratigraphie und Ammonitenfauna der Weißjura α/β-Grenze (Oberoxford) auf der westlichen Schwäbischen Alb. *Jahreshefte des Geologischen Landesamtes Baden-Württemberg*, **6**: 337–394.

LORIOL P. de, 1878 – Monographie paléontologique des Couches de la zone à *Ammonites tenuilobatus* (Badener Schichten) de Baden (Argovie). *Mémoires de la Société Paléontologique Suisse*, **5**: 77–200.

LORIOL P. de, 1893 – Description des mollusques et brachiopodes des couches séquaniennes de Tonnerre (Yonne), par P. de Loriol, accompagnée d'une étude stratigraphique, par J. Lambert. – 212 pp.; Genève (Aubert-Schuchardt).

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

MAYER M.C., 1864–1865 – Descriptions des coquilles des terrains jurassiques. *Journal de Conchyliologie*, **12** (1864): 368–378; **13** (1865): pls. 7, 8.

MATYJA B.A., 1986 – Developmental polymorphism in Oxfordian ammonites. *Acta Geologica Polonica*, **36**, 1–3: 37–68.

MATYJA B.A., WIERZBOWSKI A., 1988 – The two *Amoeboceras* invasions in Submediterranean Late Oxfordian of Central Poland. *In*: 2nd International Symposium on Jurassic Stratigraphy (eds. R.B. Rocha, A.F. Soares), **1**: 421–432; Lisboa.

MATYJA B.A., WIERZBOWSKI A., 1994 – On correlation of Submediterranean and Boreal ammonite zonations of the Middle and Upper Oxfordian: new data from Central Poland. *Geobios, Mémoire spécial*, **17**: 351–358.

MATYJA B.A., WIERZBOWSKI A., 1995 – Biogeographic differentiation of the Oxfordian and Early Kimmeridgian ammonite faunas of Europe, and its stratigraphic consequences. *Acta Geologica Polonica*, **45**: 1–8.

MATYJA B.A., WIERZBOWSKI A., 1997 – The quest for a uniform Oxfordian/Kimmeridgian boundary: implications of the ammonite succession at the turn of the Bimammatum and Planula zones in the Wieluń Upland, central Poland. *Acta Geologica Polonica*, **47**, 1/2: 77–105.

MELÉNDEZ G., 1989 – El Oxfordiense en el sector central de la Cordillera Ibérica (Provincias de Zaragoza y Teruel). – 418 pp.; Zaragoza and Teruel (Institución Fernando Católico, Instituto de Estudios Turolenses).

MELÉNDEZ G., ATROPS F., RAMAJO J., PÉREZ-URRESTI I., DELVENE G., 2006 – Upper Oxfordian to Lower Kimmerigian successions in the NE Iberian Range (E Spain): some new stratigraphical and palaeontological data. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **241**, 2: 203–224.

MELÉNDEZ G., BELLO J., DELVENE G., PÉREZ-URRESTI I., 1997 – El Jurásico Medio y Superior (Calloviense-Kimmeridgiense) en el sector de la llanura de Arcos (Ariño-Oliete, Teruel): Análisis tafonómico y bioestratigrafía. *Cuadernos de Geología Ibérica*, **23**: 269–300.

NITZOPOULOS G., 1974 – Faunistisch-ökologische, stratigraphische und sedimentologische Untersuchungen am Schwammstotzenkomplex bei Spielberg am Hahnenkamm. *Stuttgarter Beiträge zur Naturkunde*, **B16**: 1–121.

OLÓRIZ F., 1978 – Kimmeridgiano-Tithonico inferior en el sector central de las Cordilleras Beticas (Zona Subbetica). Paleontologia, Bioestratigrafia. *Tesis doctorales Universidad de Granada*, **184**: 758 pp.; Granada.

OLÓRIZ F., 2002a – *Idoceras daedalum* (Gemmellaro, 1878). *In*: Revision of Jurassic ammonites of the Gemmellaro collections (eds. G. Pavia, S. Cresta). *Quaderni del Museo Geologico G.G. Gemmellaro*, **6**: 289–292.

OLÓRIZ F., 2002b – *Idoceras hodiernae* (Gemmellaro, 1878). *In*: Revision of Jurassic ammonites of the Gemmellaro collections. (eds. G. Pavia, S. Cresta). *Quaderni del Museo Geologico G.G. Gemmellaro*, **6**: 292–293.

OLÓRIZ F., REOLID M., RODRÍGUEZ-TOVAR F.J., 1999 – Fine-resolution ammonite biostratigraphy at the Rio Gazas-Chorro II section in Sierra de Cazorla (Prebetic Zone, Jaen Province, Southern Spain). *Profil*, **16**: 83–94.

OPPEL A., 1863 – Ueber jurassische Cephalopoden. *Palaeontologische Mittheilungen aus dem Museum des koeniglich Bayerischen Staates*, **3**: 163–266.

ORBIGNY A. de, 1842–1851 – Paléontologie Française. Description zoologique et géologique de tous les Animaux mollusques et rayonnés fossiles de France, comprenant leur application à la reconnaissance des couches. Terrains oolithiques ou jurassiques, 1, Céphalopodes. – 624 pp.; Paris (Masson).

PARENT H., SCHERZINGER A., SCHWEIGERT G., 2008 – Sexual phenomena in Late Jurassic Aspidoceratidae. Dimorphic correspondence between *Physodoceras hermanni* (Berckhemer) and *Sutneria subeumela* Schneid, and first record of possible hermaphroditism. *Palaeodiversity*, **1**: 181–187.

PÉREZ-URRESTI I., BELLO VILLALBA J., MELÉNDEZ G., 1996 – La subfamilia Ataxioceratinae (Ammonoidea) en el Oxfordiense Supérior de la Provincia Submediterránea: origen y evolucion. *Geogazeta*, **20**, 1: 246–249.

QUENSTEDT F.A., 1843 – Das Flözgebirge Würtembergs. Mit besonderer Rücksicht auf den Jura. 558 pp.; Tübingen (Laupp).

QUENSTEDT F.A., 1845–1849 – Petrefaktenkunde Deutschlands. 1/1. Cephalopoden. IV+580 pp.; Tübingen (Fues).

QUENSTEDT F.A., 1887–1888 – Die Ammoniten des Schwäbischen Jura. 3. Der Weisse Jura: 817–944; Stuttgart (Schweizerbart).

ROMAN F., 1938 – Les ammonites jurassiques et crétacées. Essai de génera. – 554 pp.; Paris (Masson).

SALFELD H., 1914 – Die Gliederung des oberen Jura in Nordwestdeutschland von den Schichten mit *Perisphinctes martelli* Oppel an aufwärts auf Grund von Ammoniten. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Bände*, **37**: 125–246.

SAPUNOV I.G., 1979 – Les Fossiles de Bulgarie III **3**. Jurassique supérieur, Ammonoidea. – 263 pp.; Sofia (Académie Bulgare des Sciences). [in Bulgarian]

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**: 144 pp.

SCHAIRER G., 1989 – Die Cephalopodenfauna der Schwammkalke von Biburg (Oberoxford, Südliche Frankenalb): Idoceratinae (Ammonitina). *Münchner geowissenschaftliche Abhandlungen*, **A15**: 97–138.

SCHAIRER G., FÜRSICH F.T., WILMSEN M., SEYED-EMAMI K., MAJIDIFARD M., 2003 – Stratigraphy and ammonite fauna of Upper Jurassic basinal sediments at the eastern margin of the Tabas Block (east-central Iran). *Geobios*, **36**: 195–222.

SCHICK H., 2004 – Gliederung und Typusprofil der Lacunosamergel-Formation (Ober-Jura, Schwäbische Alb). *Stuttgarter Beiträge zur Naturkunde*, **B346**: 1–25.

SCHLAMPP V., 1991 – Malm-Ammoniten. – 184 pp.; Korb (Goldschneck).

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

SCHMIDT-KALER H., 1962 – Ammonitenfauna und Stratigraphie des Malm Alpha und Beta in der südlichen und mittleren Frankenalb. *Erlanger geologische Abhandlungen*, **44**: 1–48.

SCHWEIGERT G., 1995 – Zum Auftreten der Ammonitenarten *Amoeboceras bauhini* (Oppel) und *Amoeboceras schulginae* Mesezhnikov im Oberjura der Schwäbischen Alb. *Jahreshefte der Gesellschaft für Naturkunde in Württemberg*, **151**: 171–184.

SCHWEIGERT G., 2000 – Immigration of Amoeboceratids into the Submediterranean Upper Jurassic of SW Germany. *In*: Advances in Jurassic Research 2000 (eds. R.L. Hall, P. Smith). *GeoResearch Forum*, **6**: 203–210.

SCHWEIGERT G., CALLOMON J.H., 1997 – Der *bauhini*-Faunenhorizont und seine Bedeutung für die Korrelation zwischen tethyalem und subborealem Oberjura. *Stuttgarter Beiträge zur Naturkunde*, **B247**: 1–69.

SIEMIRADZKI J., 1899 – Monographische Beschreibung der Ammonitengattung *Perisphinctes*. *Palaeontographica*, **45**: 161–352.

SPATH L.F., 1924 – On the Blake collection of ammonites from Kachh, India. *Palaeontologica Indica, new series*, **9**, 1: 1–29.

SPATH L.F., 1925 – Part VII. Ammonites and aptychi. *Monographs of the Hunterian Museum, University of Glasgow*, **1**: 111–164.

STEINMANN G., DÖDERLEIN L., 1890 – Elemente der Paläontologie. – 848 pp.; Leipzig (Engelmann).

VENZO S., 1959 – Cefalopodi neogiurassici degli Altipiani Hararini. *Studi sulla missione geologiche dell'AGIP (1937–1938)*, **4**: 1–59; Roma (Academia Nazionale dei Lincei).

VILLASEÑOR A., OLÓRIZ F., 2006 – Ontogeny in a macroconchiate *Idoceras* from Mexico: a key for interpreting suprageneric classification of genus *Idoceras* based on phenotype expression. *Volumina Jurassica*, **4**: 245–247.

WEGELE L., 1928–1929 – Stratigraphische und faunistische Untersuchungen im Oberoxford und Unterkimmeridge Mittelfrankens. *Palaeontographica*, **71**: 117–210 (1928); **72**: 1–94 (1929).

WIERZBOWSKI A., 1978 – Ammonites and stratigraphy of the Upper Oxfordian of the Wieluń Upland, Central Poland. *Acta Geologica Polonica*, **28**, 3: 299–333.

WIERZBOWSKI A., 1991 – Biostratigraphical correlations around the Oxfordian/Kimmeridgian boundary. *Acta Geologica Polonica*, **41**: 149–155.

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. *Volumina Jurassica*, **14**, 1: 14–49.

WIERZBOWSKI A., GŁOWNIAK E., PIETRAS K., 2010 – Ammonites and ammonite stratigraphy of the Bimammatum Zone and lowermost Planula Zone (Submediterranean Upper Oxfordian) at Bobrowniki and Raciszyn in the Wieluń Upland, central Poland. *Volumina Jurassica*, **8**: 49–102.

WIERZBOWSKI A., MATYJA B.A., 2014 – Ammonite biostratigraphy in the Polish Jura sections (central Poland) as a clue for recognition of the uniform base of the Kimmeridgian Stage. *Volumina Jurassica*, **12**, 1: 45–98.

ZEISS A., 1977 – Jurassic stratigraphy of Franconia. *Stuttgarter Beiträge zur Naturkunde*, **B31**: 1–32.

ZIEGLER B., 1959 – *Idoceras* und verwandte Ammoniten-Gattungen im Oberjura Schwabens. *Eclogae geologicae Helvetiae*, **52**: 19–56.

ZIEGLER B., 1977 – The "White" (Upper) Jurassic in Southern Germany. *Stuttgarter Beiträge zur Naturkunde*, **B26**: 1–79.

ZIEGLER B., 1987 – Der Weiße Jura der Schwäbischen Alb. *Stuttgarter Beiträge zur Naturkunde*, **C23**: 1–71.

ZIETEN, C.H., von, 1830–1833 – Die Versteinerungen Württembergs, p. 1–16, pls. 1–12 (1830); p. 17–32, pls. 13–24 (1831); p. 33–64, pls. 25–48 (1832); p. 65–102, pls. 49–72 (1833); Stuttgart (Schweizerbart).