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Suevisphinctes – a new perisphinctid ammonite genus from the Lower Tithonian (Hybonotum Zone) of Southern Germany

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Key words: Jurassic, Tithonian, Submediterranean Province, ammonites, biostratigraphy.

Abstract. A new Upper Jurassic perisphinctid ammonite genus, *Suevisphinctes* (type species: *Suevisphinctes josefkelleri* nov. gen., nov. sp.), is established. At present, it is recorded from the *laisackerensis* biohorizon (Early Tithonian, Hybonotum Zone, Rueppellianus Subzone) of SW Germany. A historical ammonite specimen of supposed Tithonian age from the Polish Klippen of Iskrzyczyn may be assigned to *Suevisphinctes* as well and thus indicates a possible Tethyan origin of this enigmatic genus.

INTRODUCTION

After more than thirty years of study of the ammonite faunas and stratigraphy of the Upper Jurassic in southern Germany, a significant collection of ammonites has accumulated. One of the most relevant outcrops for the sampling of Tithonian ammonites – not only in SW Germany but also in the entire Submediterranean Province – is a large, still active limestone quarry east of the village Liptingen, about 8 kilometres south of the Danube Valley (Figs. 1, 2). The geological architecture and parts of the ammonite fauna of this quarry were previously studied by Zeiss (1994), Schweigert, Scherzinger (1995), Schweigert (1996), Zeiss *et al.* (1996), Dimke (1997), Dimke, Zeiss (1997), Scherzinger *et al.* (2006, 2015, 2018), and Schweigert *et al.* (2020). The ammonites are excellently preserved and are common in the bedded limestones of the Hangende-Bankkalke Formation surrounding a large sponge-microbial buildup assigned to the Oberjura-Massenkalke Formation. The latter is the main target of exploiting high quality limestone used for various technical, chemical and food technologies. Within the bedded limestone (Fig. 2) there occur several large reefal olistoliths originating from the adjacent autochthonous buildup (Schweigert, 1996).

Among over 1.300 ammonite specimens collected from the Liptingen Quarry and from a few other localities of the same area (Fig. 1), we noticed some large-sized macroconchiate biplicate perisphinctid ammonites, which apparently differ from all previously described genera of the Upper Kimmeridigan and Lower Tithonian. The aim of this study is to describe this new material and to discuss its phyletic and biogeographical relationships. In this context, it became necessary to review several superficially similar evolute ammonites with a predominantly biplicate ribbing style from the Late Kimmeridgian and Early Tithonian.

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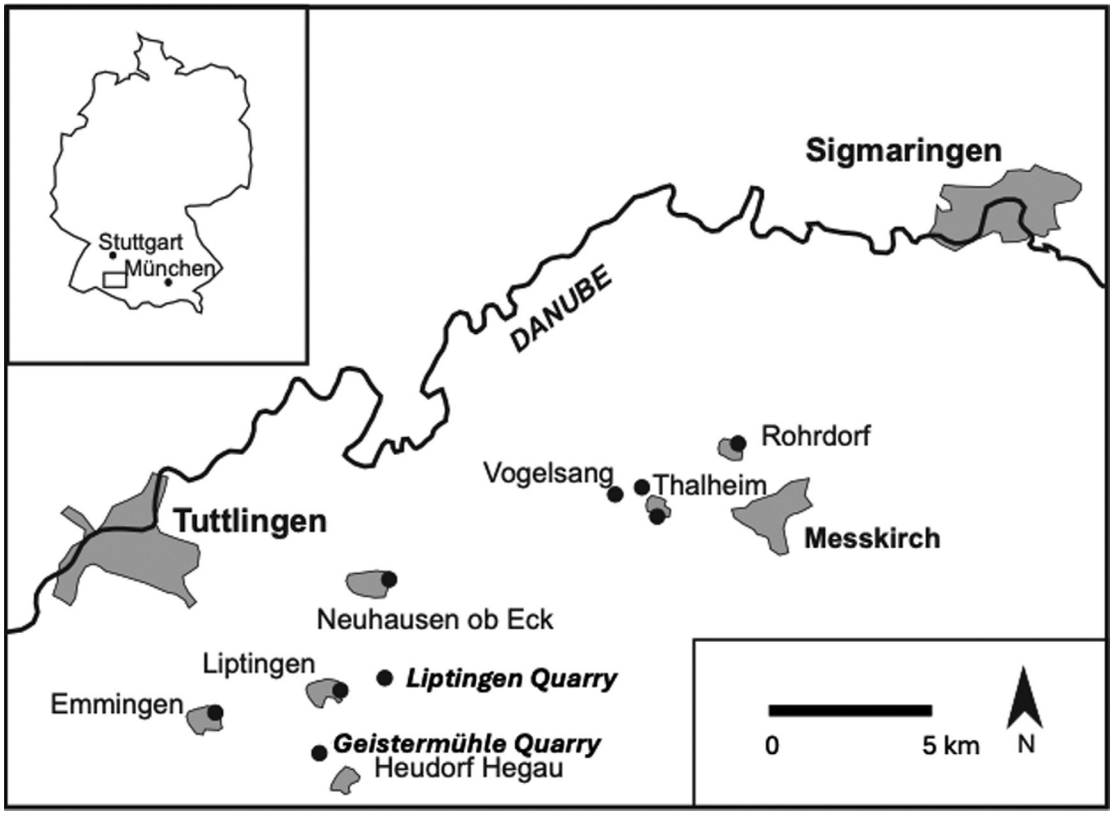

Fig. 1. Some Tithonian localities in SW Germany under study

MATERIAL AND METHODS

The ammonites described herein were collected by the first author (A.S.) during numerous visits of the Liptingen Quarry and two other localities. The specimens were prepared mechanically with various fine pneumatic chisels, needles and a mortising machine. All the studied material from SW Germany is housed in the collection of the Staatliches Museum für Naturkunde Stuttgart, Germany (acronym: SMNS). Studied material for comparison is housed in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany (acronym: SNSB-BSPG).

AMMONITE FAUNA OF THE *LAISACKERENSIS* HZ.

The *laisackerensis* Hz. of the Lower Tithonian Hybonotum Zone was introduced by Schweigert, Scherzinger (1995), and named after the surprising record of a heteromorph ammonite in Rohrdorf (Fig. 1). It was basically founded on the ammonite assemblage of the Franconian site Laisacker near Neuburg a.d. Donau and that of the coeval Liptingen Quarry in Swabia. Ammonites from these localities were reported by Barthel (1959), Barthel, Schairer (1977, 1978), Schairer, Barthel (1979, 1981), Ohmert, Zeiss (1980), Zeiss (1994), Schweigert, Scherzinger (1995), Zeiss *et al.* (1996), Dimke (1997), Dimke, Zeiss (1997), Scherzinger *et al.* (2006, 2015, 2018), Scherzinger, Schweigert (2016), and Schweigert *et al.* (2020). In contrast to ammonite faunas occurring below and above, the ammonite assemblage of the *laisackerensis* Hz. is highly diverse and comprises a mixture of taxa of Mediterranean, Submediterranean and Subboreal origin. This seems to be the result of a high sea-level during the middle part of the Hybonotum Zone leading to an easy faunal exchange between neighboring areas.

Ammonite taxa of the *laisackerensis* Hz.: *Neochetoceras mohri* Scherzinger *et al.*, 2015 [M], *Lingulaticeras* cf. *solenoides* (Quenstedt, 1888) [m], *Haploceras* sp. [M], *Haploceras carachtheis* (Zeuschner, 1846) [m], *Physodoceras widerai* Scherzinger *et al.*, 2018 [M], *Sutneria eugyra* Barthel, 1959 [m], *Gravesia gigas intermedia* Hantzpergue, 1989 [M + m], *Suevisphinctes josefkelleri* nov. gen, nov. sp. [M], *Euvirgalithacoceras copei* (Ohmert, Zeiss, 1980) [M], *Subplanites rueppellianus* sensu Schairer, Barthel (1981) non Quenstedt, 1888 [m], *Euvirgalithacoceras liptingense*

Fig. 2. Former wall of Liptingen quarry (exposed to NE direction, now exploited; photograph A.S., 2004)

The wall exposed the upper part of the limestone beds containing the *laisackerensis* Hz, where the holotype of *Suevisphinctes josefkelleri* n. sp. comes from

(Dimke, Zeiss, 1997) [M], *Subplanites laisackerensis* Schairer, Barthel, 1981 [m], *Hegovisphinctes roettgeri* Zeiss *et al.*, 1996 [M + m], *Lithacoceras* nov. sp. [M], *Silicisphinctes* nov. sp. [m], *Hybonoticeras hybonotum* (Oppel, 1863) [M + m], *Pseudogravesia gravesiforme* Hantzpergue, 1989 [M], *Protancyloceras guembeli* (Oppel, 1865) [m].

Records of the *laisackerensis* Hz.: Heudorf im Hegau, Liptingen, Emmingen ab Egg (Hegau area, Baden-Württemberg, Germany), Neuhausen ob Eck, Worndorf, Vogelsang, Thalheim, Rohrdorf (western Swabian Alb, Baden-Württemberg, Germany) and Laisacker near Neuburg an der Donau (southern Franconian Alb, Bavaria, Germany). In the vicinity of Bad Urach (middle Swabian Alb, Baden-Württemberg, Germany) beds of the *laisackerensis* Hz. are completely eroded and only represented by silicified relics of rocks and fossils (Schweigert *et al.*, 2020).

The study of phyletic lineages within age-diagnostic ammonite genera in Swabia and Franconia, especially those of *Hybonoticeras*, *Neochetoceras*, *Physodoceras*/*Sutneria*, *Gravesia* and *Pseudogravesia*, has helped to test and refine the stratigraphic concept, which finally led to the recognition of a detailed succession of biohorizons (Fig. 3).

SYSTEMATIC PALAEONTOLOGY

Order Ammonitida Haeckel, 1866

Suborder Ammonitina Fischer, 1882

Superfamily Perisphinctoidea Steinmann, in Steinmann, Döderlein, 1890

Family Perisphinctidae Steinmann, in Steinmann, Döderlein, 1890

Subfamily Torquatisphinctinae Tavera, 1985

Genus *Suevisphinctes* nov.

Type species. *Suevisphinctes josefkelleri* nov. gen., nov. sp., by monotypy.

Etymology. After Swabia, Swabian Alb, a region in SW Germany famous for its Jurassic deposits and fossils, and -sphinctes, a common ending of generic names of perisphinctids related to the constrictions.

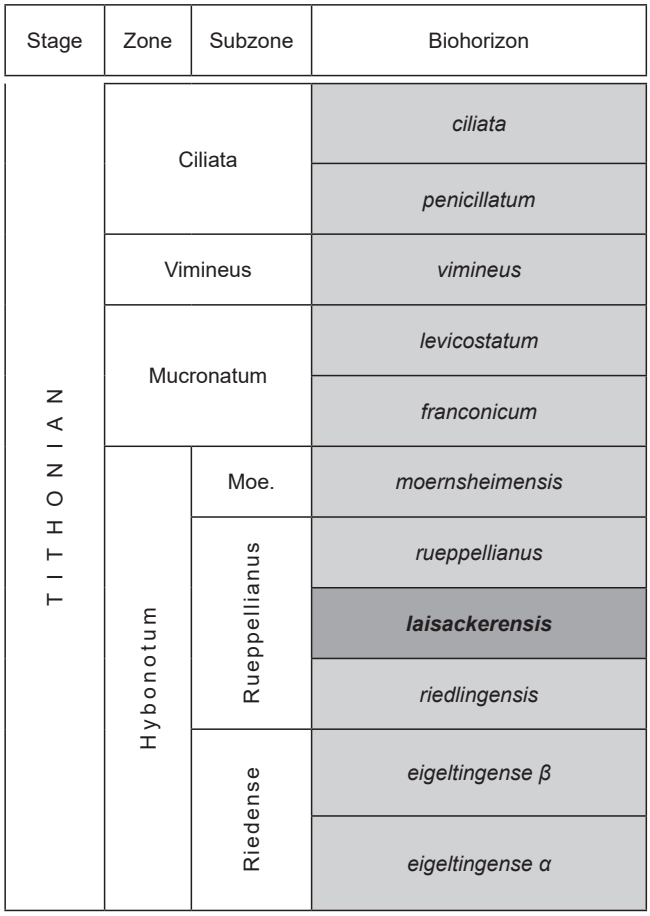

Fig. 3. Chronostratigraphy and ammonite biohorizons of the Hybonotum to Ciliata zones in Southern Germany, with indication of the stratigraphic position of the new species

Succession of biohorizons modified after Schweigert (2015), Scherzinger *et al.* (2015, 2018), Scherzinger, Schweigert (2016, 2017)

Diagnosis. See diagnosis of type species.

***Suevisphinctes josefkelleri* nov. gen., nov. sp.**
Figs. 4, 5

1995. *Indodichotomoceras* cf. *biplicatus* (Uhlig) – Schweigert, Scherzinger: 314.

1997. *Indodichotomoceras* cf. *biplicatus* (Uhlig) – Dimke: 37

2006. "*Subdichotomoceras*" sp. – Scherzinger *et al.*: 245

Holotype. SMNS 70694/1, illustrated in Fig. 4A, B.

Paratypes. Paratype 1, SMNS 70694/2 (Fig. 5A, B), [Liptingen]; paratype 2 SMNS 70694/3 (Fig. 5C), [Rohrdorf]; paratype 3 (unfigured); SMNS 70694/4 [Thalheim].

Etymology. In honour of the first author's late teacher and friend Josef Keller (1910–2000) at Ippingen, SW Germany, who was a renowned expert in the geology, palaeontology, botany and history of his home country.

Type locality and section. Liptingen Quarry, N Hegau area, Baden-Württemberg, SW Germany (Figs. 1, 2).

Type horizon. Weißjura Group, Hangende-Bankkalke Formation (*laisackerensis* Hz., Rueppellianus Subz., Hybonotum Z., Lower Tithonian; Fig. 3).

Diagnosis. Large-sized macroconchiate perisphinctid. Subdactilicone coiling with weakly compressed whorl section. Predominantly rigid biplicate ribbing, with point of bifurcation located high on the flank. Direction of ribbing variable, but predominantly rectiradiate to rursiradiate. Pseudo-polygyrate ribs rarely occur, mainly before constrictions, which are often immediately followed by a single solitary rib. Rib distances rising constantly, except in the adult stage.

Microconchs are smaller-sized, with identical ribbing style, but more evolute coiling; aptychi unknown.

Dimensions: See Table 1.

Table 1
Dimensions of *Suevisphinctes josefkelleri* nov. gen., nov. sp.

Specimen	d [mm]	wh [mm]	uw [mm]	ww [mm]	uw/d	ww/d
SMNS 70694/1, holotype, Fig. 3	235.5	59.0	122.5	(58.3)	0.52	(0.25)
idem	212.3	55.8	109.5	73.0	0.52	0.34
idem	189.8	50.0	93.3	70.7	0.49	0.37

Hz. = biohorizon; [M] = Macroconch (female); [m] = microconch (male); d = diameter; wh = whorl height; ww = whorl width; uw = umbilical width. Measurements in brackets are distorted due to diagenetic compaction of the specimen

Description. The holotype, SMNS 70694/1 (Fig. 4), is a complete adult macroconch partly three-dimensionally preserved as a mould with superimposed shell, with parts of the smooth peristome. Last third of body-chamber and entire phragmocone diagenetically depressed. The body-chamber comprises *ca.* 330 degrees of the outer whorl. In the center and on the outer whorl some oysters (*Argutostrea roemeri* [Quenstedt, 1843]) with xenomorphic sculptures were attached; one big valve of an oyster has been removed during preparation to display the median whorls of the ammonite. Inner whorls are only preserved on one flank. The big evolute (subdactilicone *sensu* Kutygin, 1998) conch exhibits a weakly compressed well-rounded whorl section. Bipartite ribbing is coarse and relatively regular from the very beginning of ontogeny, although innermost stages are incompletely preserved. Rib distances show a strikingly constant increase until the beginning of the body-chamber, were the primaries become more distantly arranged for half a whorl; but rib density increase again in the last third of the

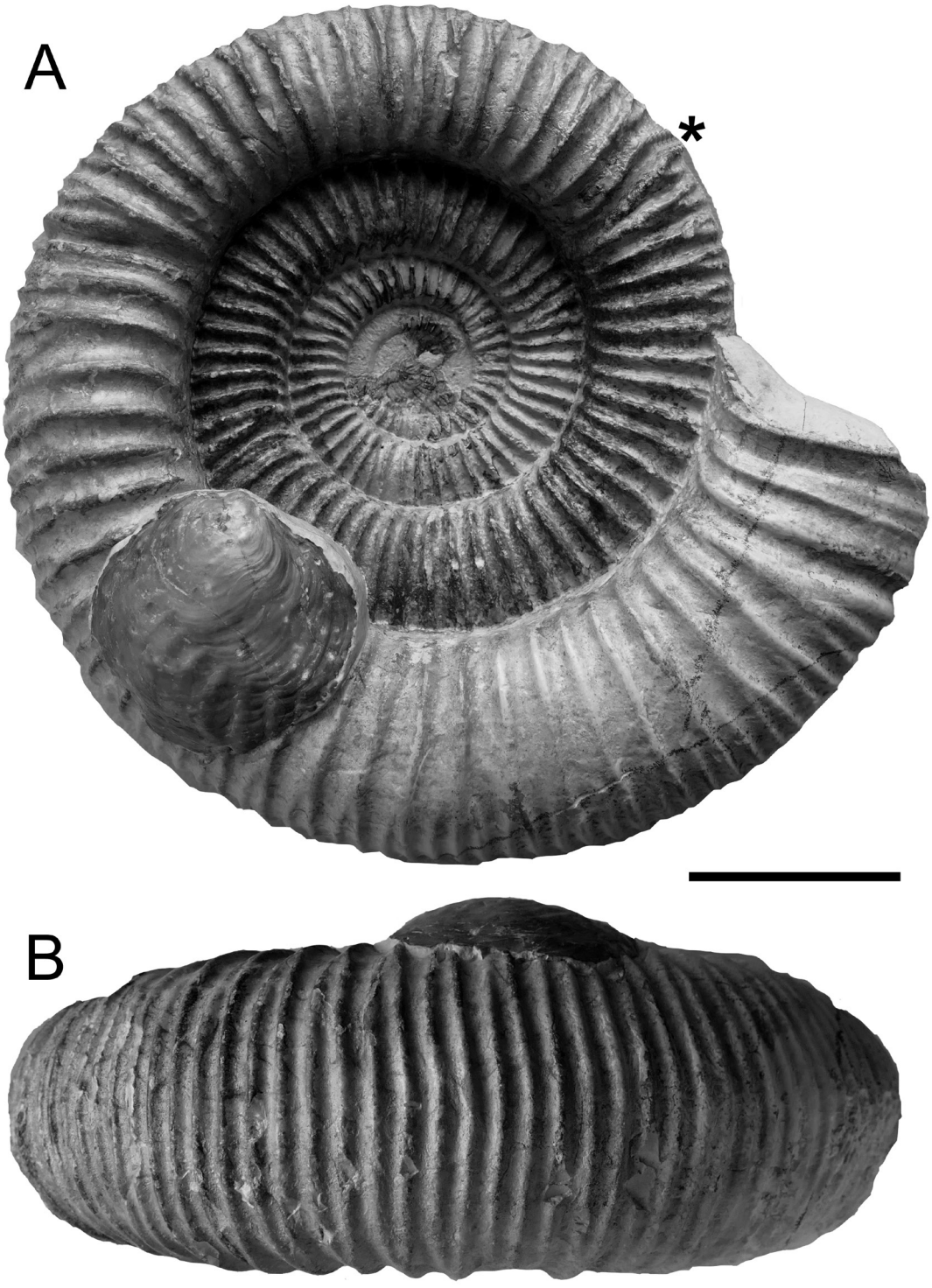

Fig. 4. *Suevisphinctes josefkelleri* nov. gen., nov. sp., holotype, SMNS 70694/1, Liptingen Quarry, *laisackerensis* Hz., Hybonotum Z.

An adult macroconch with complete body-chamber in lateral (**A**) and ventral (**B**) views. Scale bar: 50 mm; asterisk indicates the last septum

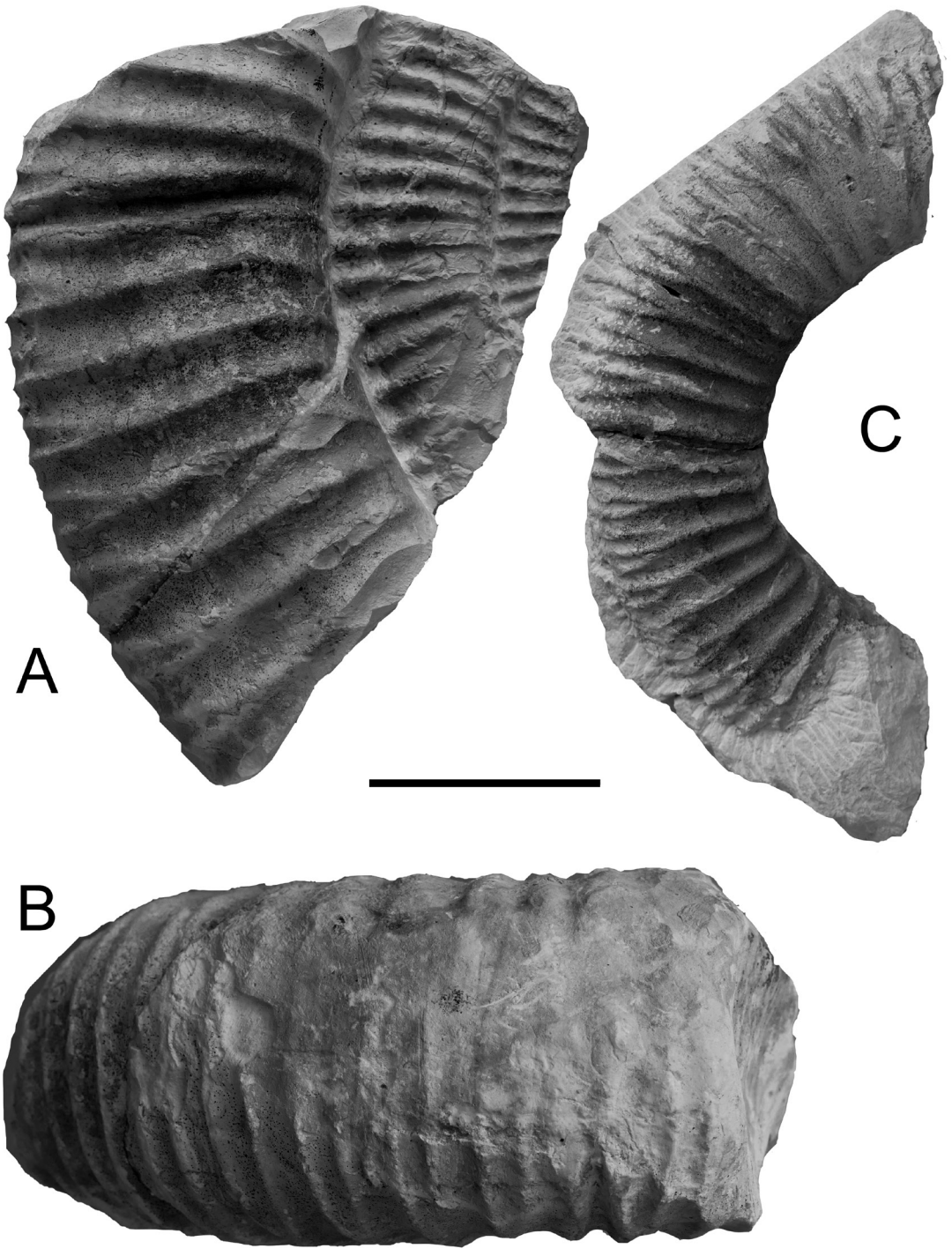

Fig. 5. *Suevisphinctes josefkelleri* nov. gen., nov. sp. A, B – Paratype 1, SMNS 70694/2, Liptingen Quarry, *laisackerensis* Hz., Hybonotum Z.

A fragmentary adult macroconch with partial body-chamber in lateral (**A**) and ventral (**B**) views. **C.** Paratype 2, SMNS 70694/3, Rohrdorf, *laisackerensis* Hz., Hybonotum Z., probably the partial body-chamber of a microconch. Scale bar: 50 mm

body-chamber. A few shallow constrictions occur – in average two per whorl – each of them usually accompanied by a pseudo-polygyrate and a solitary rib without forming prominent collars. The primaries on the innermost whorls jointed at the umbilical shoulder (Fig. 6). In addition, there are a few secondaries not joined to the primaries on the body-chamber. The last half of the body-chamber comprises 27 primaries and 57 secondaries. The point of bifurcation of the ribs is located high on the flank and thus barely discernible on whorls of the phragmocone. Direction of ribbing changes several times from rectiradiate to prorsiradiate or rursiradiate. Only just behind the aperture the ribbing becomes slightly irregular by forming solitary ribs and incomplete secondaries indicating end of growth. The smooth peristome shows fine growth lines.

SMNS 70694/2, paratype 1, from Liptingen Quarry (Fig. 5A, B). This is the fragment of a very big macroconchiate specimen with a regular bipartite ribbing. A single solitary rib is noticed in the centre of a constriction in the outer whorl. The whorl section is broad and well-rounded, and the ribs cross the venter without weakening or interruption.

SMNS 70694/3, paratype 2, from Rohrdorf near Meßkirch (Fig. 5C). This relatively small specimen consists of less the half of an outer whorl of a diagenetically strongly depressed body-chamber; the inner whorls of the phragmocone had been completely flattened, but are lost. Bipartite ribs are regularly spaced, with few intercalated pseudo-polygyrate ribs. Due to the much smaller size and still more evolute coiling at the equal diameter of the holotype, this specimen most likely represents a microconch. The aperture, however, is not preserved.

SMNS 70694/4, paratype 3, from Thalheim near Meßkirch. This is a slightly abraded three-dimensionally preserved fragment of a medium-sized macroconchiate specimen that comprises about one third of an outer whorl. The bipartite ribs are regularly spaced; one solitary rib occurs in the centre of a shallow constriction. The whorl section is weakly compressed and well-rounded; the ribs cross the venter. This specimen is not illustrated because of its poor preservation.

All three paratypes are very similar to the holotype in their ribbing style. The complete holotype has a maximum

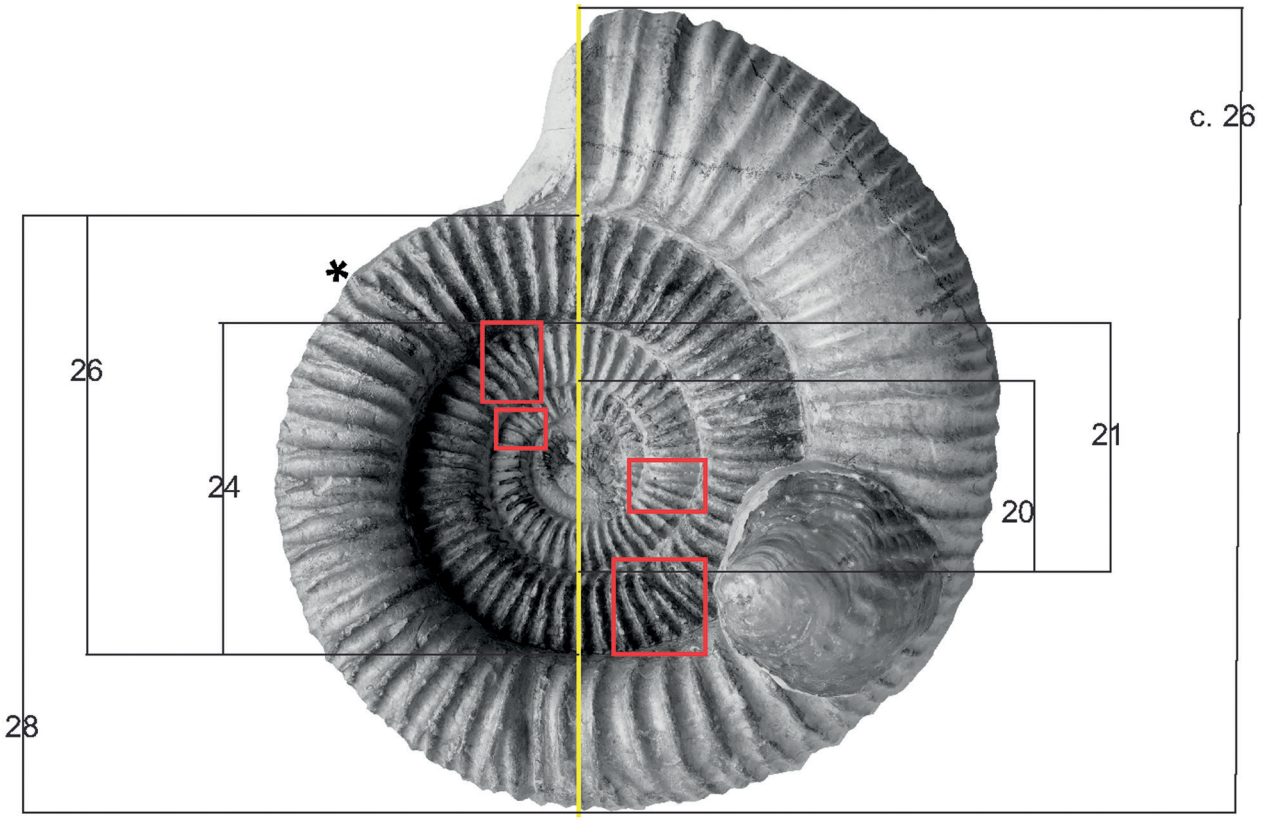

Fig. 6. Red boxes mark pairs of primary ribs joined at the umbilical shoulder

Progressive sequence of number of primary ribs per half-whorl counted from flanks as seen from the umbilicus: 20 – 21 – 24 – 26 – 28 – c. 26

diameter of 235 mm, but the fragmentary paratype 1 clearly indicates that this species must have reached adult diameters of over 350 mm.

Comparisons. The closest resemblance to *Suevisphinctes josefkelleri* nov. gen., nov. sp. within all compared material is seen in a medium-sized macroconchiate perisphinctid ammonite from Iskritschin in Moravia (today Iskrzyczyn, Poland, Cieszyn Silesia) in the SNSB-BSPG collection labeled as "*Perisphinctes* aff. *biplex* Sowerby" (Fig. 7). With *Suevisphinctes josefkelleri* nov. gen., nov. sp. it shares not only the biplicate ribbing, compressed section and evolute coiling, but also the sculpture at the constrictions shows an identical succession. The Polish specimen differs from *S. kelleri* mainly in a generally wider-spaced ribbing of the early and medium ontogenetic stages and a stronger prorsiradiate ribbing in the medium stage. Zittel (1868: 7, 86) cited *Haploceras carachtheis* (Zeuschner, 1846) from the same locality. Not far away from that locality is the village of Wilamowice (formerly Willamowitz), the type locality of *Richterella richteri* (Oppel, 1865). From there, some other significant Tethyan ammonite taxa of Lower Tithonian age are reported, *e.g.*, *Semiformiceras fallauxi* (Oppel, 1865) and *Volanoceras volanense* (Oppel, 1865) (see Blaschke, 1911). Thus, we conclude that the specimen from Iskrzyczyn is most likely also of Tithonian age, as indicated on its historical label. The limestones of Wilamowice and Iskrzyczyn represent exotic Štramberk-type limestone mega-boulders embedded in younger flysch deposits (Kołodziej, 2015; Hoffmann *et al.*, 2021) and contain typical Tethyan ammonite assemblages (Vašíček, Skupien, 2014, 2016). Due to the uncertainty about the exact age and the presence of only a single specimen we refrain to establish a new taxon for the Polish perisphinctid, but its affiliation to *Suevisphinctes* appears to be highly reliable.

Occurrences. Lower Tithonian of SW Germany, ? Tithonian of S Poland.

COMPARISONS WITH SIMILAR BUT APPARENTLY UNRELATED PERISPHINCTIDS

In first view, the herein introduced *Suevisphinctes josefkelleri* nov gen., nov. sp. somewhat resembles the very poorly known ammonite genus *Hoelderia* Ohmert, Zeiss, 1980 (type species: *Hoelderia schreineri* Ohmert, Zeiss, 1980) due to its bipartite ribbing. In *Hoelderia*, however, the points of bifurcation are located markedly deeper on the flank and the flanks are more rounded in *Suevisphinctes*. Moreover, *Hoelderia* has a much higher whorl section and a narrower section than in *Suevisphinctes*. However, it should be noted that *Hoelderia schreineri* was initially based on two specimens of different relationship; in fact, only the holotype (Ohmert, Zeiss, 1980: pl. 11, fig. 1) is a true representative of the genus *Hoelderia*, whereas the paratype (Ohmert, Zeiss, 1980: pl. 11, fig. 2) belongs to *Pseudogravesia gravesiforme* Hantzpergue (see Scherzinger, Schweigert, 2016: 290, 294).

Another co-occurring biplicate ammonite genus is *Hegovisphinctes* Zeiss *et al.*, 1996 (type species: *Hegovisphinctes roettgeri* Zeiss *et al.*, 1996). In *Hegovispinctes*, the ribs are much wider-spaced than in *Suevisphinctes* nov. gen. and have a deeper point of bifurcation. In the adult stage, they become very thick and simple. The whorl section is higher than broad in all ontogenetic stages. Constrictions are markedly wider and less deeply incised.

The contemporaneous genus *Gravesia* Salfeld, 1913 differs from *Suevisphinctes* nov. gen. in its having a more involute coiling and a very coarse, wide-spaced ribbing, with a markedly deeper point of furcation of the ribs that may split into three or more secondaries in the adult stage and a smooth body-chamber at the very end near the peristome.

Also *Pseudogravesia* Hantzpergue, 1989, which is closely related to *Gravesia*, has a more involute coiling, a broader whorl section and a more distant ribbing, again with deep points of furcation, like in *Hoelderia* or *Subdichotomoceras* as noted by Énay, Howarth (2019: 120, „*Subdichotomoceras*-like").

The pseudo-polygyrate ribs occasionally present in *Suevisphinctes* nov. gen. resemble the polygyrate ribs in the median ontogenetic stages of some Tithonian ammonite genera such as *Euvirgalithacoceras* Zeiss *et al.*, 1996, *Hegovisphinctes* Zeiss *et al.*, 1996, *Danubisphinctes* Zeiss 1968, or *Dorsoplanitoides* Zeiss, 1968. All these taxa have a more involute coiling and another less rounded whorl section than *Suevisphinctes* nov. gen.

The still undescribed microconch of *Euvirgalithacoceras copei* (Ohmert, Zeiss, 1980) with its predominantly bipartite ribbing mainly differs by a deeper bifurcation and a high-oval whorl section; true polygyrate ribs are more common.

Geyer (1962: 339–342) described and determined a very evolute, coarse-ribbed perisphinctid from the Lower Tithonian Hangende-Bankalke Formation of Thalheim near Meßkirch under the name *Pavlovia* (*Sphinctoceras*) *crassa* (Neaverson, 1925). Subsequently, Schweigert (1993: 145–146) reassigned this specimen to the Subboreal ammonite species *Subdichotomoceras* (*Sphinctoceras*) *subcrassum* Mesezhnikov, in Zakharov, Mesezhnikov, 1974) originally described from the Volgian of Iatra River. The holotype of the latter (Zakharov, Mesezhnikov, 1974: 83, pl. 7, figs. 1a, b) has a more compressed whorl section compared with *Suevisphinctes josefkelleri* nov. gen., nov. sp. This leads to a more involute appearance. Additionally, the bifurcation points are

Fig. 7. *Suevisphinctes* nov. sp., SNSB-BSPG AS III 887, Iskrzyczyn, S Poland; ? Tithonian

Scale bar: 50 mm; asterisk indicates the last septum

located deeper on the flank in the Russian specimens and simple ribs are more abundant, not only occurring along constrictions. Hence, the Russian *Subdichotomoceras* (*Sphinctoceras*) are easily distinguishable from all biplicate perisphinctid ammonites of S Germany. The type species of *Subdichotomoceras* Spath, 1925, *Subdichotomoceras lamplughi* Spath, 1931, from the Upper Kimmeridge Clay of Yorkshire, is much younger than the beds with *Suevisphinctes* (cf. Cope, 1967).

Remarkably similar to Geyer's specimen is the much younger holotype and still solely known specimen of "*Perisphinctes*" *constrictor* Schneid, 1915 from the Lower Tithonian

of Unterhausen near Neuburg a.d. Donau. Subsequently, Scherzinger, Schweigert (1999) had assigned this enigmatic taxon to *Sarmatisphinctes* Kutek, Zeiss, 1997. However, the type species of *Sarmatisphinctes*, *Divisosphinctes fallax* Ilowaisky, in Ilovaisky, Florensky, 1941, differs from "*P.*" *constrictor* by its having a significantly denser ribbing already in the nucleus and a less evolute (or more involute) coiling. The sculpture of "*P.*" *constrictor* is characterized by an irregular ribbing style with numerous simple and bipartite ribs and very deep, prominent constrictions bordered by collars. In consequence, "*Perisphinctes*" *constrictor* Schneid, 1915 must belong to another still unnamed and poorly known perisphinctid lineage, to which we also assign Geyer's (1962) specimen as an ancestral form.

Sphinctoceras Neaverson, 1925 (type species: *Sphinctoceras crassum* Neaverson, 1925) was reported from the Upper Kimmeridge Clay, Wheatleyensis Zone, Nodule Bed, of Wheatley (Oxon), England (Neaverson, 1925: 23). This bed is much younger than the latest occurrences of *Gravesia* in England (Cope, 1967) und hence also much younger than *Suevisphinctes josefkelleri* nov. gen., nov. sp. In comparison with *Suevisphinctes*, there is a longer persisting stage of dense ribbing and a coarser ribbed sculpture on the outer whorls as well as a thicker whorl section. Énay, Howarth (2019) considered *Sphinctoceras* Neaverson, 1925 as a synonym of *Subdichotomoceras* Spath, 1925.

Indodichotomoceras Krishna, Pathak, 1993, from the Upper Kimmeridgian of India (Kachchh), is strikingly homoeomorphic to *Subdichotomoceras*, as already reported by Énay, Howarth (2019: 132). The bipartite ribbing of *Indodichotomoceras* shows a similar density as in *Suevisphinctes josefkelleri* nov. gen., nov. sp. and the rounded whorl section is shared in both taxa, but simple ribs are much more common in *Indodichotomoceras* and in the latter, the furcation point of the biplicate ribs lies significantly deeper on the flank. In the type species of *Indodichotomoceras*, *Subdichotomoceras inversum* Spath, 1931, any constrictions are hardly detectable.

DISCUSSION

At present, there are no records of ammonites assignable to *Suevisphinctes* nov. gen. from any Upper Jurassic beds of southern Germany that are older or younger than the *laisackerensis* Hz. of the Hybonotum Zone. This points to an immigration from neighboring areas. Since an ammonite assignable to this genus is also reported here from Štramberk-type limestone of the Polish Outer Carpathians we strongly suspect a Tethyan origin of this enigmatic genus.

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