

Are the Upper Jurassic ammonite genera *Progeronia* Arkell, 1953 and *Hugueninsphinctes* Atrops, 1982 a dimorphic pair? A fresh look upon their type species

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Abstract. The type species of the Upper Jurassic ammonite genera *Progeronia* Arkell, 1953 and of its supposed dimorphic partner *Hugueninsphinctes* Atrops, 1982 are analyzed. *Perisphinctes progeron* v. Ammon, 1875, type species of *Progeronia*, is based on an incomplete phragmocone that originated from beds of the Platynota or Hypselocyclum zones, or even from older beds of the Galar Subzone. Its phyletic relationship with ammonites of the Acanthicum Zone commonly assigned to *Progeronia* is still unresolved and a matter of further discussion. At present, we consider the genus *Progeronia* a *nomen dubium* and restrict it to its type species. *Ammonites polyplocus breviceps* Quenstedt, 1887, the type species of *Hugueninsphinctes*, is confirmed to originate from much younger beds of the Acanthicum Zone. We suggest including also the corresponding macroconchiates of the Divisum and Acanthicum zones into this better-defined genus.

INTRODUCTION

Although ammonites from the Jurassic belong to the most common and most iconic marine invertebrate fossils and have been studied over centuries, their systematic treatment suffers from common homoeomorphism, a low number of involved experts and numerous historical biases. Historical taxa are often based on ‘potatoes’, specimens lacking reliable information about type locality, type horizon and intraspecific variation. In the 1960s, soon after the publication of the respective volume of the ‘Treatise on Invertebrate Paleontology’ by Arkell *et al.* (1957), the co-occurring of small lappeted forms (microconchs) and much larger unlappeted forms (macroconchs) was convincingly interpreted as

sexual dimorphism (Makowski, 1962; Callomon, 1963), and the microconchs were considered as the males, whereas the macroconchs were believed to be the corresponding females. More recently, these results became slightly modified by the adding of ‘mesoconchs’, which probably represent females which became mature at an earlier stage than usual (Chandler, 2019). Also gender reversals could be demonstrated (Parent *et al.*, 2008; Frau, Boursicot, 2021). For *Perisphinctoidea*, the revised version of the Ammonite Treatise (Énay, Howarth, 2019) may be regarded as a compilation of taxa, but their systematic interrelationships are debatable. As an example, we comment here on the Upper Jurassic perisphinctid genus *Progeronia* Arkell, 1953, which is an often cited genus in the Submediterranean and Mediterranean provinces.

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A BRIEF HISTORY OF THE GENUS *PROGERONIA* ARKELL, 1953

The ammonite genus *Progeronia* was established by Arkell (1953) as a replacement name for the genus *Ammonia* Ilovaisky, Florensky, 1941. Ilovaisky and Florensky had overlooked that this genus name was preoccupied even multiple times, primarily by *Ammonia* Brönnich, 1771, a genus established for foraminifera (not for ammonites as stated by Énay, Howarth, 2019). The Russian authors had introduced the name *Ammonia* in honour of the Bavarian geologist Ludwig von Ammon (1850–1922), who had studied Jurassic relics in Lower Bavaria, located along the southern margin of the Bavarian Forest. They assigned four ammonite taxa to their new genus, *Ammonia kurmani* from the Jurassic of Russia and three other taxa previously established by v. Ammon in his monograph: *Perisphinctes eggeri* v. Ammon, 1875, *Perisphinctes progeron* v. Ammon, 1875 and *Perisphinctes suberinus* v. Ammon, 1875. Arkell (1953) replaced the preoccupied name *Ammonia* by *Progeronia* and selected *Perisphinctes progeron* as its type species, referring to the illustration provided by v. Ammon. Arkell further included *P. eggeri* v. Ammon and *P. ernesti* (Quenstedt) as figured by Schneid (1915, pl. 1, fig. 5) in *Progeronia*. Any comments on the further status of *P. suberinus* and *Ammonia kurmani* are missing in Arkell's article.

Subsequently, Geyer (1961a) used *Progeronia* as a subgenus of *Lithacoceras* Hyatt, 1900. He illustrated a plaster cast of the specimen from the Munich collection which he thought to be the holotype of *Perisphinctes progeron*. At the time of his studies, the original specimen could not be traced in the collection of the Geologische Bundesanstalt in Vienna, Austria. The same cast was re-figured by Schlegelmilch (1994). Also in two later publications dealing with the specimen illustrated by v. Ammon (1875, pl. 1, fig. 2), it was erroneously considered to be the monotypic holotype (Gröschke, 1985; Schlögl, Zorn, 2012). It was overlooked by these authors that originally v. Ammon (1875) had reported a second specimen of *P. progeron* coming from the 'untere Tenuilobatus-Schichten' of Theuern near Amberg in Upper Palatinate. In modern stratigraphic terms, this information refers to the Platynota Zone of the basal Arzberg Formation (Niebuhr, Pürner, 2014). However, the whereabouts of this syntype are unknown, and therefore we take previous statements of the illustrated specimen being the type, going back to de Loriol (1877), as a formal lectotype designation.

In his exhaustive monograph on the ataxioceratid ammonite faunas of southern and southeastern France, Atrops (1982) suggested restricting the use of the genus *Progeronia* for macroconchiate forms of the Divisum and Acanthicum zones and he introduced a new genus, *Hugueninsphinctes*,

for their corresponding microconchs. Subsequent authors did not accept or at least strongly questioned the validity of the genus *Hugueninsphinctes* Atrops, 1982 since it was said to be just the microconchiate partner of *Progeronia*, and consequently the former has to be considered a junior synonym of the latter (*e.g.*, Schlamp, 1991; Schlegelmilch, 1994; Moliner, 2009; Énay, Howarth, 2019).

Since its introduction in 1953, the species content of *Progeronia* has greatly varied (Fig. 1; Table 1). The diagnoses or descriptions given by various authors are not really diagnostic, although they have been repeatedly emended (Arkell, 1953; Arkell *et al.*, 1957; Geyer, 1961a; Malinowska, 1972; Schairer, 1974; Olóriz, 1978; Wierzbowski, 1978; Sarti, 2002; Moliner, 2009; Énay, Howarth, 2019). Reports of *Progeronia* (in rather different interpretations) focus on the Submediterranean Province, namely from southern Germany (Geyer, 1961a, b; Bantz, 1970; Schairer, 1974; Gröschke, 1985; Schlamp, 1991, 2003, 2004, 2009; Schlegelmilch, 1994), southern Poland (Wierzbowski, 1978, 2024), northern Switzerland (Gygi, 2003; Comment *et al.*, 2015; Hêche, 2016), south-eastern France (Karvé-Corvinus, 1966; Atrops, 1982), eastern France (Courville, Lorin, 2002), eastern Spain (Fezer, Geyer, 1988; Finkel, 1992; Moliner, Olóriz, 1999; Moliner, 2009), Romania (Dobrogea: Neagu *et al.*, 2014), the western Balkans (Anđelković, 1966; Sapunov, 1979; Rabrenović *et al.*, 2000), and Iran (Fantini Sestini, Assereto, 1970). Other authors reported species of *Progeronia* even from Mediterranean areas: Southern Alps (Pavia *et al.*, 1987; Sarti, 1993; Petti *et al.*, 2011), Sicily (Christ, 1960; Sarti, 2002), southern Spain (Olóriz, 1978), Hungary (Fözy, Scherzinger, 2013; Bujtor *et al.*, 2021; Fözy *et al.*, 2022), Carpathians (Romania: Grigore, 2011; Ukraine: Réhaková *et al.*, 2011), Caucasus (South Ossetia, Georgia: Paichadze, 1973), Morocco (Benzaggagh, Atrops, 1997), and Ethiopia (Zeiss, 1984). Various ammonites from the Abadia Marls of the Lusitanian Basin described by Choffat (1893) were very often assigned to *Progeronia* as well (see Table 1). Énay, Howarth (2019), when listing Russia, probably referred to the material of *Ammonia kurmani* Ilovaisky, Florensky, 1941 from the Orenburg Oblast in the southeastern foreland of the Ural Mountains.

Their exist controversial opinions or hypotheses on the ancestry and phylogeny of the genus *Progeronia* (Moliner, 2009; Wierzbowski, 2024), and it is still unclear what "typical" *Progeronia* is. It has been suspected that the genus *Progeronia* is highly polyphyletic in its present usage and in need of a thorough revision (Fözy, Scherzinger, 2013; Fözy *et al.*, 2022). Such a revision is hampered by the incompleteness of the fossil record, the rarity of complete adult specimens and uncertainties about the described type specimens. However, we have analysed herein this genus by going back to its roots.

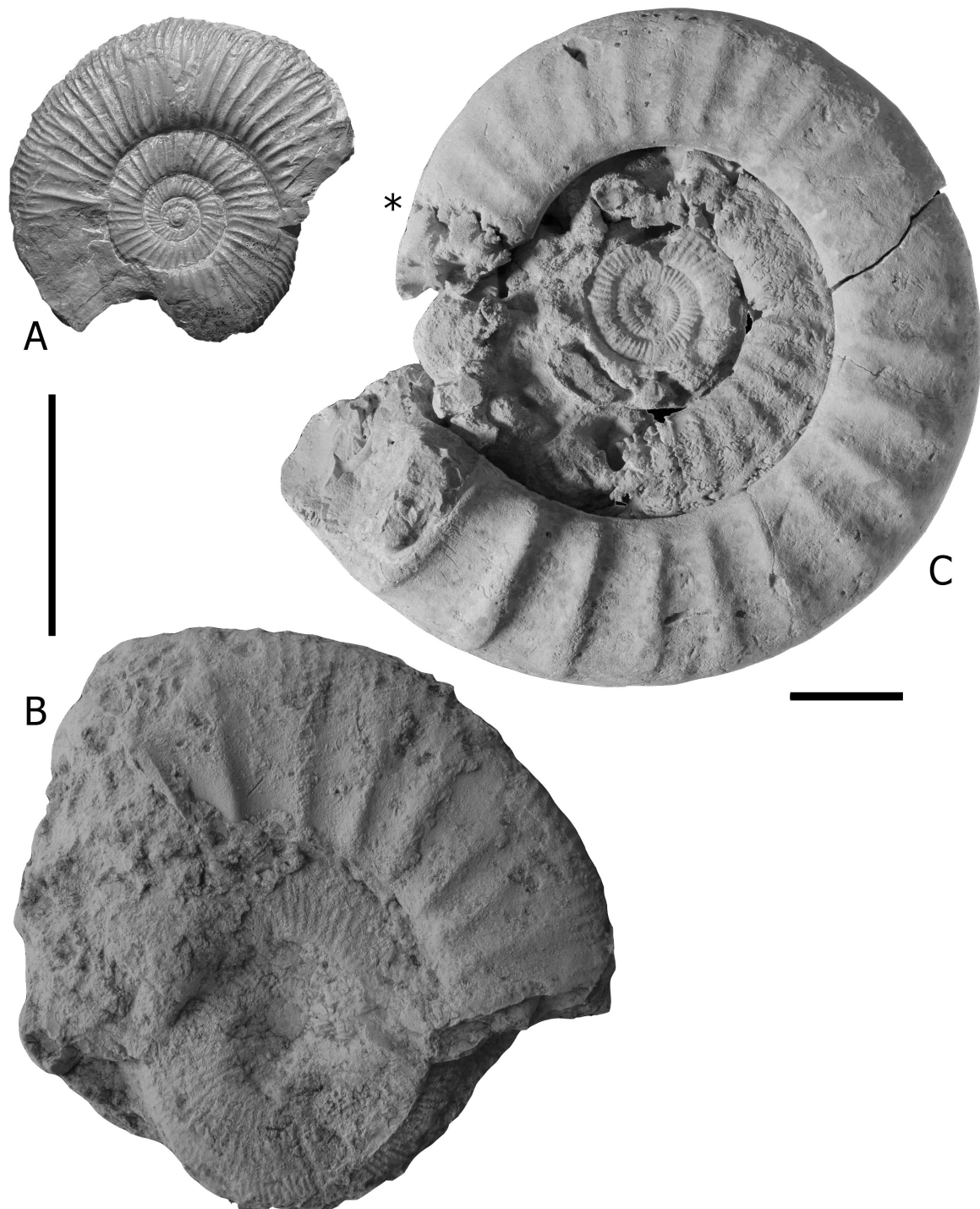


Fig. 1. Examples of several unrelated taxa previously included in *Progeronia* Arkell, 1953

A. *Ammonites triplex* Zieten, 1830, neotype, designated by Quenstedt (1887, p. 925), GPIT-PV-61980. Lower Kimmeridgian, Lacunosamergel Formation, Hausen Member, Bad Ditzgenbach-Auendorf, Germany. **B.** *Perisphinctes metamorphus* Neumayr, 1873, lectotype (Neumayr, 1873, pl. 34, fig. 1), Geological and Geophysical Collection of the Supervisory Authority for Regulatory Affairs, Budapest, no. J. 998, upper Kimmeridgian, ? Acanthicum Zone, Ghilcoş, Carpathians of Romania. **C.** *Progeronia bruntrutense* Hantzpergue in Comment *et al.*, 2015, holotype, upper Kimmeridgian, TCH007-93, collection PAL A16, Reuchenette Formation, Courtedoux Member, Mutabilis Zone, Courtedoux, Switzerland. Asterisk indicates beginning of body-chamber. Photo: © OCC-SAP. Scales equal 50 mm

Table 1

List of taxa formerly, tentatively or temporarily included in *Progeronia* and/or *Hugueninsphinctes*

Taxon	Sources/comments	Present status/our opinion
<i>Ammonites triplex</i> Zieten, 1830	Neotype, designated by Quenstedt 1887, p. 925, pl. 110, fig. 9; Fig. 1A	nomen dubium
<i>Perisphinctes fasciferus</i> Neumayr, 1873	Fözy, Scherzinger, 2013	<i>Lithacoceras fasciferum</i>
<i>Perisphinctes metamorphus</i> Neumayr, 1873	Fözy, Scherzinger, 2013; Fig. 1B	?new genus
<i>Perisphinctes plebejus</i> Neumayr, 1873	Zeiss, 1994; Grigore, 2011	?
<i>Perisphinctes progeron</i> v. Ammon, 1875	This study; Figs. 2, 3	<i>Progeronia progeron</i> , nomen dubium, herein
<i>Perisphinctes eggeri</i> v. Ammon, 1875	Illustrated by Gröschke, 1985, pl. 5, fig. 2	<i>Lithacosphinctes eggeri</i>
<i>Perisphinctes suberinus</i> v. Ammon, 1875	Illustrated by Schlögl, Zorn, 2012, pls. 2, 3	<i>Ataxioceras suberinum</i>
<i>Perisphinctes lictor</i> Fontannes, 1876 in Dumortier, Fontannes, 1876	Atrops, 1982	<i>Hugueninsphinctes lictor</i>
<i>Perisphinctes unicomptus</i> Fontannes, 1876 in Dumortier, Fontannes, 1876	Sarti, 1993; not revised	? <i>Discosphinctoides unicomptus</i>
<i>Perisphinctes ernesti</i> de Loriol, 1877	Zeiss, 1994, p. 513	? <i>Discosphinctoides</i>
<i>Ammonites lictor evolutus</i> Quenstedt, 1887	Type species of <i>Lithacosphinctes</i> Olóriz, 1978	<i>Lithacosphinctes evolutus</i>
<i>Ammonites polyplocus breviceps</i> Quenstedt, 1887	This study; Fig. 5A	<i>Hugueninsphinctes breviceps</i>
<i>Perisphinctes abadiensis</i> Choffat, 1893	Zeiss, 1994, p. 513	? <i>Discosphinctoides</i>
<i>Perisphinctes castroi</i> Choffat, 1893	Atrops, 1982	? <i>Lithacosphinctes</i>
<i>Perisphinctes pseudolictor</i> Choffat, 1893	Hantzpergue, 1989	<i>Ardescia pseudolictor</i>
<i>Perisphinctes ribeiroi</i> Choffat, 1893	Schlegelmilch, 1994; not revised	? <i>Ardescia</i>
<i>Perisphinctes vandellii</i> , Choffat, 1893	Fözy <i>et al.</i> , 2022; not revised	?
<i>Perisphinctes choffati</i> de Riaz, 1898	Malinowska, 1972; Énay, 1966	<i>Arisphinctes choffati</i>
<i>Perisphinctes gerontoides</i> Siemiradzki, 1898	Neagu <i>et al.</i> , 2014; not revised	? <i>Subdiscosphinctes</i>
<i>Perisphinctes familiaris</i> Toulou, 1907	Zeiss, 1984	? nomen dubium
<i>Perisphinctes valens</i> Toulou, 1907	Zeiss, 1984	? nomen dubium
<i>Perisphinctes mombassanus</i> Dacqué, 1910	Zeiss, 1984	?
<i>Perisphinctes anabreviceps</i> Dacqué, 1914	Zeiss, 1984	?
<i>Perisphinctes digitatus</i> Schneid, 1915	Fözy <i>et al.</i> , 2022	? new genus
<i>Perisphinctes heidenheimense</i> Wegele, 1929	Atrops, 1982	<i>Lithacosphinctes heidenheimense</i>
<i>Perisphinctes subachilles</i> Wegele, 1929	Atrops, 1982	<i>Lithacosphinctes subachilles</i>
<i>Perisphinctes uresheimense</i> Wegele, 1929	Geyer, 1961a; not revised	<i>Orthosphinctes polygyratus</i> sensu Atrops, 1982
<i>Ammonia kurmani</i> Ilovaisky, Florensky, 1941	Not revised	?
<i>Lithacoceras dogouense</i> Scott, 1943	Zeiss, 1984	?
<i>Perisphinctes spathi</i> Scott, 1943	Zeiss, 1984	?
<i>Lithacoceras (Progeronia) freybergi</i> Geyer, 1961a	Atrops, 1982	<i>Orthosphinctes freybergi</i>
<i>Lithacoceras (Progeronia) pseudopolyplocoides</i> Geyer, 1961a	Atrops, 1982	<i>Orthosphinctes polygyratus</i> sensu Atrops, 1982
<i>Lithacoceras (Progeronia) rotiforme</i> Geyer, 1961a	Atrops, 1982	<i>Lithacosphinctes evolutus</i>
<i>Lithacoceras unicomptum moravicum</i> Andelkovic, 1966	Not revised	? <i>Discosphinctoides</i>
<i>Progeronia unicompta simplex</i> Sarti, 1993	Not revised	? <i>Discosphinctoides</i>
<i>Progeronia bruntrutense</i> Hantzpergue in Comment <i>et al.</i> , 2015	Fig. 1C	<i>Lithacosphinctes bruntrutensis</i>

THE TYPE SPECIES OF *PROGERONIA*

Linnean taxonomy is based on the principle that each genus is defined by its type species. To get an opinion about the nature of *Progeronia*, we thus have to study its type species. As mentioned above, Arkell (1953) based *Progeronia* on *Perisphinctes progeron* v. Ammon, 1875. The supposed holotype (=lectotype) was illustrated as a lithograph (Fig. 2). Most likely, Arkell did not study the original specimen but

only the illustration. The specimen had not been collected by v. Ammon himself, but by the famous Austrian palaeontologist Franz v. Hauer. This is the reason why the specimen has survived in the collection of the Geologische Bundesanstalt (now GeoSphere Austria) in Vienna. When the relict Jurassic deposits in Lower Bavaria and their ammonites were re-studied, the specimen was illustrated photographically for the first time after some preparation (Gröschke, 1985). Subsequently, Schlögl, Zorn (2012) provided perfect

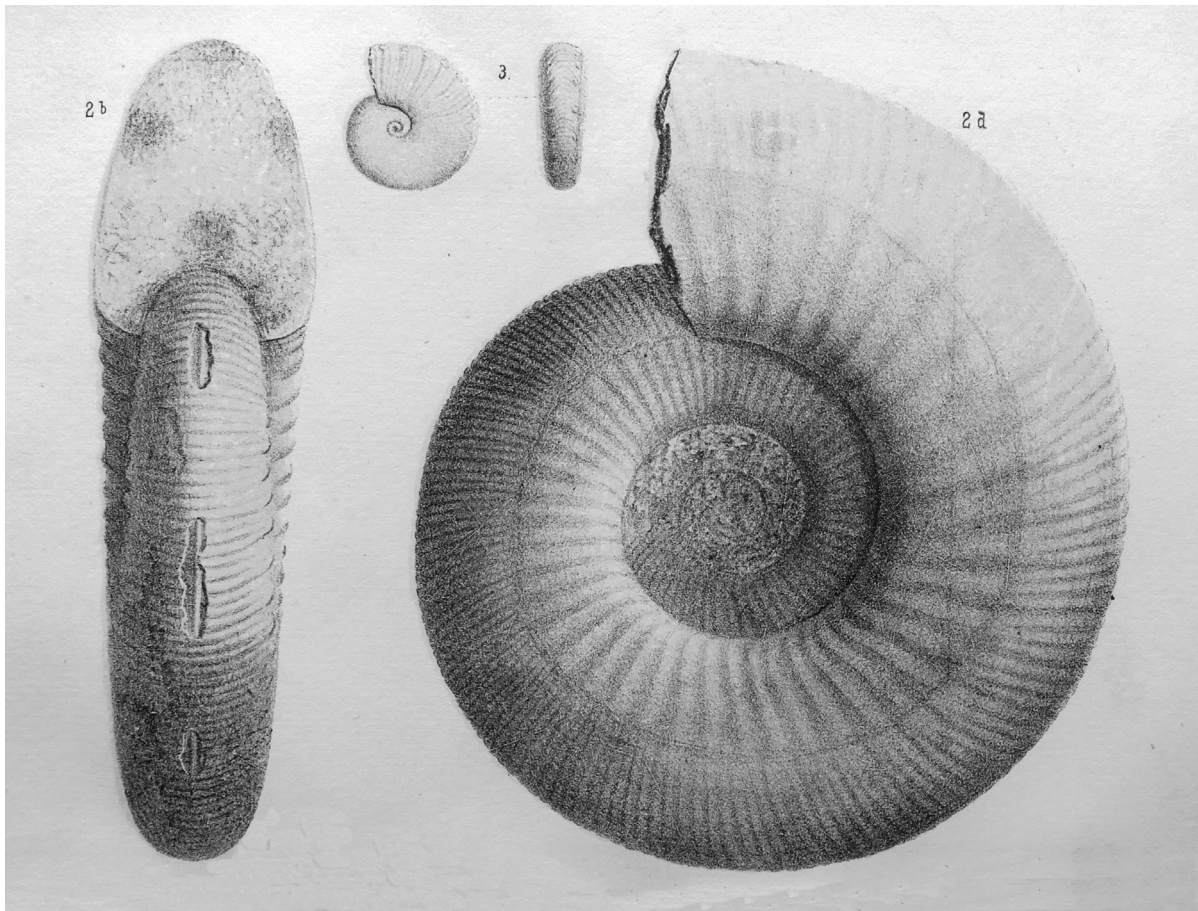


Fig. 2. Idealized drawing of *Perisphinctes progeron* v. Ammon, 1875, lectotype (v. Ammon, 1875, pl. 1, fig. 2a, b)

P. progeron is the type species of the genus *Progeronia* Arkell, 1953.

Not to scale

illustrations of the specimen by coating the specimen with ammonium chloride prior to photography. Here we re-illustrate it without whitening to show the original colour of the rock matrix (Fig. 3). The specimen is heavily worn and incomplete. It represents the fully septate inner whorls of a much larger ammonite, as indicated by the spur line of the missing outer whorl. The original specimen gives a strikingly different image compared with the idealized lithograph. In the drawing, the spur line is placed too deep on the flank so that the shell looks more involute than it really is. Also the ribbing on the mid-flank is hardly discernible. The diverging points of the prorsiradiate ribs are located relatively high on the flank and are fully covered by the following whorls. Because of the loss of the outer whorl it must remain unknown how the sculpture looked in the preadult and adult stages. Before we discuss the type horizon of the specimen we should be aware that the former limestone quarries in the vicinity of Söldenau are no longer accessible

so that it is impossible to look for topotypes. Without knowing about its identity as the lectotype of *Progeronia progeron*, the specimen can be compared with various superficially similar taxa from the Platynota or early Hypselocyclum zones, such as *Ardescia subachilles* (Wegele, 1929), '*Lithacosphinctes gidoni* Atrops, 1982' in Schlegelmilch (1994, pl. 27, fig. 6), *Ataxioceras striatellum* Schneid, 1944 or *Subdiscosphinctes orbignyi* Hantzpergue, 1989. But what is the exact type horizon of *P. progeron*? V. Ammon (1875) did not get primary information about the horizon from where the specimen was collected. Most likely v. Hauer had collected it loose from the scree, and at that time a lithostratigraphic frame was not established and no earlier section published. Hence, v. Ammon tried to reconstruct the horizon from the lithology and colour of the rock matrix. He assigned the specimen to a scarcely fossiliferous rock unit of white colour, and *P. progeron* was the only ammonite assigned to this level. Therefore, the age of this rock interval cannot be



Fig. 3A, B. Original specimen of *Perisphinctes progeron* v. Ammon, 1875, lectotype, GeoSphere Austria, No. 1875/004/0002 from beds now assigned to the lower Kimmeridgian Söldenau Formation (for a discussion on the exact type horizon, see text). Söldenau near Ortenburg, Lower Bavaria, Germany

Photos: D. Di Franco. Scale equals 50 mm

dated directly, but only by help of ammonites from below and above. From a deeper level in the limestone quarries at Söldenau, v. Ammon (1875) reported, among several other taxa, *Perisphinctes platynotus*, today *Sutneria platynota* (Reinecke, 1818), the index of the lower Kimmeridgian Platynota Zone. Above the reconstructed horizon that the specimen was thought to have come from, he reported *Perisphinctes involutus* (= *Involuticeras involutum* [Quenstedt, 1849 in 1845–1849]), *Oppelia tenuilobata* (= *Streblites te-*

nuilobatus [Oppel, 1857]) and the bivalve '*Avicula similis*' (= *Aulacomyella similis* [Münster, 1831]). The latter is very characteristic of the Hypselocyclum Zone (Veit, 1936; Jantschke *et al.*, 2021). Still higher up in the section he reported '*Perisphinctes rolandi*', probably a species of the coarse-ribbed aulacostephanid genus *Eurasenia* Geyer, 1961a. In the 1980s, when the youngest beds were still accessible, the horizon with *Idoceras balderum* (Oppel, 1863) was thought to be present (Barthel, Schairer, 1980), but fur-

ther sampling was without success. The ammonite taxa reported by Gröschke (1985) from the uppermost beds of the Söldenau Formation indicate a basal level of the Divisum Zone. In summary, if v. Ammon's lithological identification of the type horizon of *Perisphinctes progeron* was correct, it must lie either in the Platynota Zone or in the Hypselocyclum Zone – but definitely not in the Divisum or Acanthicum zones, where *Progeronia* has been said to be a characteristic element. However, there is still another possibility to be considered. We cannot exclude that v. Ammon was wrong and the correct horizon of *P. progeron* was not in the middle part but in the deepest part of the Söldenau Formation. This view is supported by the grey to yellowish colour of the rock matrix, which does not fit with the white colour of the higher beds. The basal beds of the Söldenau Formation were assigned to the Platynota Zone based only on v. Ammon's description of the section and Gröschke's re-study of the surviving material (Gröschke, 1985; Niebuhr, 2014). In fact, it remains unclear whether the lithological base of the Sölde-

nau Formation coincides exactly with the base of the Platynota Zone, or if this formation still includes biostratigraphically older beds of the Planula Zone, namely of the Galar Subzone. Indeed, some ammonites collected from the Galar Subzone of southwestern Franconia by Nitzopoulos (1974) compare almost perfectly with the lectotype of *P. progeron*. These ammonites were then determined as '*Lithacoceras subachilles* (Wegele, 1929)' but they clearly differ from Wegele's species in their more evolute coiling and the denser ribbing of the initial whorls. Specimens collected by Nitzopoulos (1974) from the Galar Subzone (e.g., Fig. 4) match *Orthosphinctes* (*Lithacosphinctes*) *gidoni* (cf. Atrops 1982, pl. 30, fig. 2; pl. 31, fig. 2). Hence, it is likely that there is specific identity of *P. progeron* with material now referred to '*Lithacosphinctes*' *gidoni* from the Galar Subzone but this cannot be proven with confidence because of the incompleteness of the *P. progeron* type on the one hand and the actual and futural inaccessibility of the beds of the Söldenau Formation on the other.



Fig. 4. This subadult macroconchiate ammonite determined by Nitzopoulos (1974) as '*Lithacoceras subachilles* (Wegele, 1929)' (= *Lithacosphinctes gidoni* Atrops, 1982) from the Dietfurt Formation, lower Kimmeridgian, Planula Zone, Galar Subzone, of Spielberg, Franconia, Germany, is strikingly similar to the lectotype of *Perisphinctes progeron* v. Ammon, 1875 and could be conspecific

Asterisk indicates beginning of body-chamber. Scale equals 50 mm

THE CASE OF *HUGUENINSPHINCTES* ATROPS, 1982

Atrops (1982) correctly stated that the type of *Progeronia*, *Perisphinctes progeron* v. Ammon, 1875 is an incomplete macroconchiate specimen. Several previous authors (e.g., Malinowska, 1972; Wierzbowski, 1978) had used *Progeronia* – as a genus or subgenus – for macroconchiate and microconchiate *Lithacosphinctes*- or *Subdiscosphinctes*-like ammonites of the Oxfordian and lower Kimmeridgian. Conversely, Geyer, (1961a) and Schairer (1974) were of the opinion that *Progeronia* was typically characterized by lapped forms. Then Atrops (1982) suggested restricting the genus *Progeronia* to macroconchiate ammonites of the Acanthicum Zone and he introduced a new genus, *Hugueninsphinctes*, for their corresponding microconchs. As type species he selected *Ammonites polyplocus breviceps* Quenstedt, 1887 in 1887–1888. Despite its resemblance with large-sized lapped ammonites of the middle Platynota Zone, namely with *Orthosphinctes (Ardesia) enayi* Atrops, 1982, he regarded Quenstedt's taxon as originating from the Acanthicum Zone. If this was true, the genus *Hugueninsphinctes* Atrops, 1982 could be expanded from microconchs to macroconchs and replace the dubious genus *Progeronia* Arkell, 1953. Again, we should have a closer look upon the respective type species. *Ammonites polyplocus breviceps* Quenstedt, 1887 is monotypic. The holotype (Fig. 5A) was said to come from the 'Weisser Jura γ ' (now Lacunosamergel Formation, see Bloos *et al.*, 2005) at Auendorf, a village in the district of Bad Ditzgenbach in the area of the middle Swabian Alb. In the vicinity of Auendorf and at numerous places elsewhere, well-bedded limestones of the 'Weisser Jura β ' were quarried for building stones and road gravel. Today this limestone formation is officially termed Wohlgeschichtete-Kalke Formation (Bloos *et al.*, 2005). Biostratigraphically it comprises the lower Kimmeridgian Planula Zone including the Galar Subzone. The boundary between both formations is not very sharp, because the lower part of the overlying Lacunosamergel Formation comprising the Platynota Zone still contains a succession of limestone beds and thin marly interbeds, which were often exposed in the top of the quarries. Upsection there follows a thicker interval of marly strata of the Hypselocyclum Zone which were not quarried. Both Geyer (1961a, b) and Schairer (1974) supposed the type horizon of *Ammonites polyplocus breviceps* to be within the Platynota Zone, contrary to Atrops (1982). Under the name '*Perisphinctes (Progeronia) breviceps* (Quenstedt)' Schairer illustrated three specimens, only one of which (Schairer, 1974, pl. 7, fig. 7) looks superficially close to the holotype. Who of them was right and who was wrong?

Schick (2004) studied the lithostratigraphy of the Lacunosamergel Formation of Swabia and introduced the term 'Progeronienbänke' (= beds with *Progeronia*) for the uppermost part of this formation. Biostratigraphically, this unit belongs to the upper Kimmeridgian Acanthicum Zone. Occasionally, Quenstedt (1887–1888) had assigned these beds to his 'Weisser Jura δ ' (now Untere-Felsenkalke Formation, Bloos *et al.*, 2005) and he described various ammonites from these beds under this chapter. The rock matrix of the virtually uncompressed holotype of *Ammonites polyplocus breviceps* is a grey mudstone, but it is biotrititic, containing small fragments of lithified microbial crusts (tuberoids). This lithology is indeed characteristic for the 'Progeronienbänke' and does not occur in the Platynota Zone at Auendorf because of the absence of spongiolithic limestones at this level. In consequence, Atrops (1982) was absolutely right when he assigned the type species of *Hugueninsphinctes* to the Acanthicum Zone. Beds of the Acanthicum Zone have never been quarried at Auendorf and are mostly covered by scree from rock-forming spongiolithic limestones. There must have been a temporary exposure from which also the fragmentary *Ammonites polyplocus nulliceps* illustrated by Quenstedt (1887, pl. 103, fig. 3) might stem, because it exhibits the same lithology and preservation. The latter also shows the same terminal ribbing stage as the holotype of *breviceps* but it formed an unlapped aperture.

From another locality, the Boßler hill (misspelled 'Bosler' by Quenstedt) near Gruibingen – not far away from Auendorf – Quenstedt illustrated two other lapped microconchiate specimens showing the same biotrititic lithology as *Hugueninsphinctes breviceps* under the name *Ammonites Ernesti* Lorient (Quenstedt, 1888, pl. 123, figs. 1, 2). These specimens are considered as being conspecific with *H. breviceps* and demonstrate some variation in final size. A third specimen illustrated under this name (Quenstedt 1888, pl. 123, fig. 3) differs by its bigger size, a more evolute coiling, and the furcation point of the ribs located in the outer third of the flank. This combination of characters clearly excludes it from the genus *Hugueninsphinctes*. Its bright beige rock matrix shows a non-biotrititic mudstone lithology typical of the Galar Subzone or Platynota Zone; this interval is also exposed in the landslide area at Boßler hill.

As already pointed out by Atrops (1982), microconchiate *Hugueninsphinctes* can be distinguished from otherwise strikingly homoeomorphic species of *Ardesia* by their having a deeper point of rib furcation, located at mid-flank or even below. The same deep rib furcation occurs in the corresponding macroconchs (*Ammonites lictor* in Quenstedt 1888, pl. 105, fig. 3; re-illustrated on Figure 5B), one of the forms erroneously included in '*Progeronia*' prior to this study. In these macroconchiate *Hugueninsphinctes*, the sub-

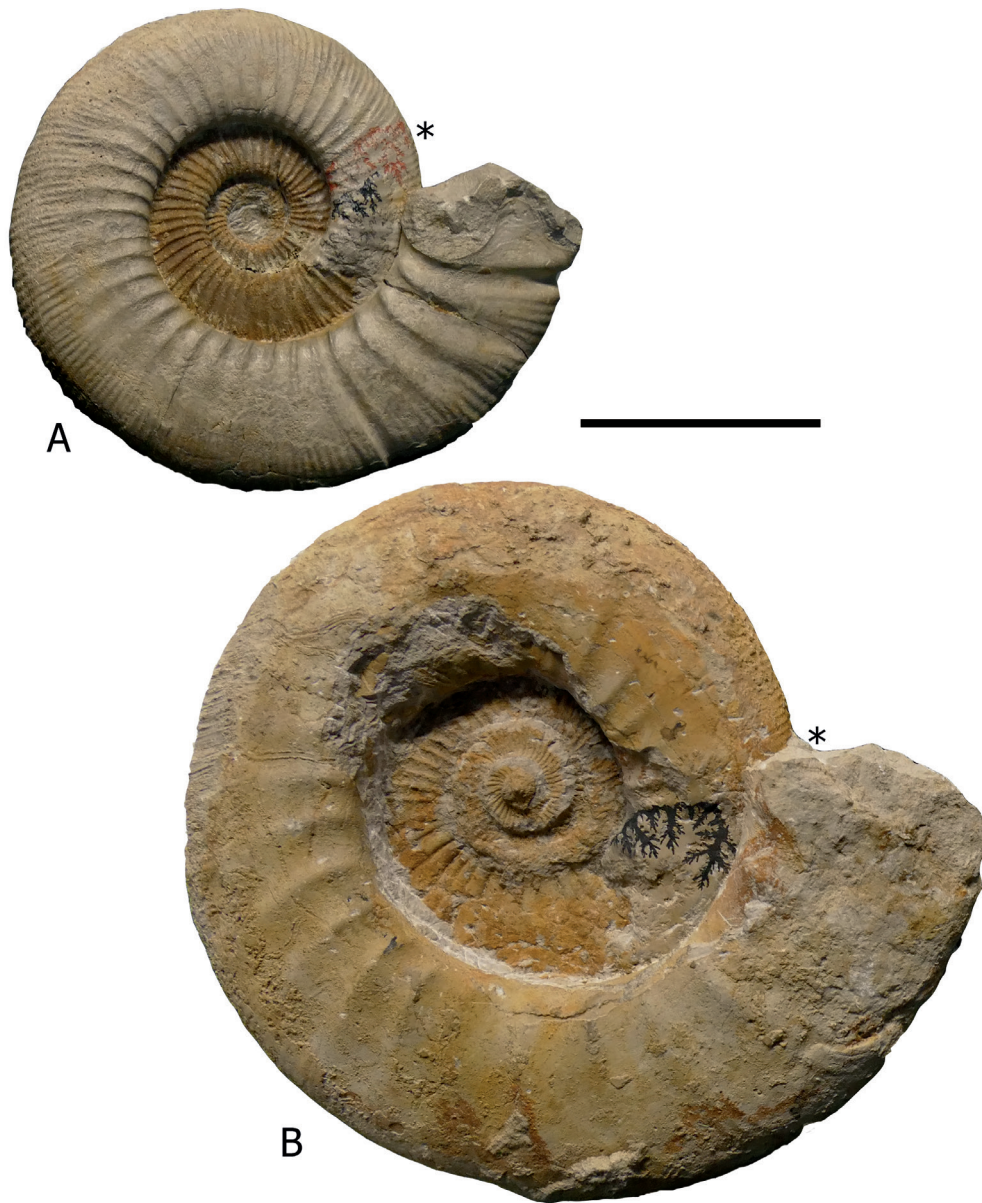


Fig. 5A. *Hugueninsphinctes breviceps* (Quenstedt, 1887 in 1887–1888), holotype, GPIT-PV-62004. Lacunosamergel Formation, Drackenstein Member, ‘Progeronienbänke’, upper Kimmeridgian, Acanthicum Zone, vicinity of Bad Ditztenbach-Auendorf, Swabia, Germany. **B.** Macroconchiate *Hugueninsphinctes* sp. (= ‘*Ammonites lictor* Fontannes’ in Quenstedt, 1888 in 1887–1888, pl. 105, fig. 3), GPIT-PV-62023; note that juvenile whorls are identical to those of *Hugueninsphinctes breviceps* in Figure 5A; Lacunosamergel Formation, ‘Progeronienbänke’, upper Kimmeridgian, Acanthicum Zone, Melchingen, Swabia, Germany

Asterisk indicates beginning of body-chamber; a spur line on the opposite flank indicates that some part of the body-chamber was lost before burial. Photos: G. Schweigert. Scale equals 50 mm

adult ribbing style becomes fascipartite. In the latest ontogenetic stage, if preserved, several coarse and distant ribs may occur, due to gradual further growth. This terminal stage is shown here in the complete specimen previously illustrated by Quenstedt (1888, pl. 105, fig. 1); re-illustrated on

Figure 6. The latter specimen was tentatively included in *Lithacosphinctes pseudoachilles* (Wegele, 1929) by Atrops (1982, p. 135), although he already had suspected its true identity as a ‘*Progeronia*’ of the Acanthicum Zone (Atrops, 1982, p. 139).



Fig. 6. An adult specimen of *Hugueninsphinctes* sp. (= '*Ammonites lictor* Fontannes' in Quenstedt, 1888 in 1887–1888, pl. 105, fig. 1), GPIT-PV-62024; subadult fascipartite ribbing stage continues into a very irregular coarse adult ribbing due to several growth interruptions. Lacunosamergel Formation, 'Progeronienbänke', upper Kimmeridgian, Acanthicum Zone, Geislingen an der Steige, Swabia, Germany

Asterisk indicates beginning of body-chamber.

Photo: G. Schweigert. Scale equals 50 mm

CONCLUSIONS

The poor preservation and incompleteness of the lecto-type of *Progeronia progeron* in combination with unsolvable uncertainties about its type horizon makes this taxon a *nomen dubium*. Having a dubious type species, the genus *Progeronia* Arkell, 1953 becomes taxonomically dubious as well. In contrast, the stratigraphic position of type species of the genus *Hugueninsphinctes* Atrops, 1982, which was introduced for the microconchiate partners of '*Progeronia*' of the Acanthicum Zone, is confirmed to be located within the Acanthicum Zone. Due to the dubious

status of '*Progeronia*', *Hugueninsphinctes* can be expanded to corresponding macroconchs of the Divisum to Acanthicum zones. However, further studies and discussions are needed to clarify the ancestry and relationships of *Hugueninsphinctes*. Also, various ammonites of the late Divisum and Acanthicum zones and many other species from different stratigraphic levels previously lumped in '*Progeronia*' will have to be carefully re-studied considering their stratigraphic position, ontogenetic stages, sexual dimorphism, and biogeographic distribution. This study is only a first step for deciphering the confused phyletic relationships among this ataxioceratine clade.

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