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A review of the systematic relationships and classification of Middle Jurassic heteromorph ammonites

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Key words: Spiroceratoidea, Lytoceratoidea, *Spiroceras*, *Parapatoceras*, *Acuariceras*, *Sulcohamites*, taxonomy, phylogeny, systematics, stratigraphical ranges.

Abstract. Middle Jurassic heteromorph ammonites comprise five genera: *Spiroceras*, *Parapatoceras*, *Acuariceras*, *Paracuariceras*, and possibly *Sulcohamites*. The taxonomic status of the genus *Spiroceras* is clarified herein. This genus was not formally introduced by Quenstedt in 1856 as stated before but subsequently by Hyatt in 1900, with *Hamites bifurcati* Quenstedt, 1857 as its type species, not by *Spiroceras bifurcatum* Hyatt, 1900. A neotype is designated herein for *Hamites bifurcati* Quenstedt, 1857. The genera *Spiroceras* Hyatt, 1900 and *Parapatoceras* Spath, 1924 are most likely monophyletic and are grouped in Spiroceratoidea Hyatt, 1900, an offshoot of Stephanoceratoidea Neumayr, 1875. The uncoiled genera *Acuariceras* Spath, 1933 and *Paracuariceras* Schindewolf, 1963 are considered to be synonymous. Their phyletic origin, however, does not lie in Parapatoceratinae Buckman, 1926, as proposed by most previous authors, but in Lytoceratoidea, more precisely in Megalytocertinae Spath, 1927. This is clearly evidenced from a couple of unique lytoceratid characters not shared with any Spiroceratoidea or Stephanoceratoidea, respectively. Consequently, *Acuariceras* is herein assigned to Acuariceratinae Schindewolf, 1963 as a heteromorphic offshoot of Megalytoceratinae. The monotypic *Sulcohamites eimensis* Wetzel, 1937 was a normally coiled evolute ammonite of still unknown systematic affinity.

INTRODUCTION

In the past, heteromorph ammonites were often considered as degenerate and unsuccessful evolutionary mistakes despite of their repeated diversification and wide geographic distribution during long periods of Earth history (Schindewolf, 1950; Wiedmann, 1969). Together with normally coiled ammonites they suffered severe extinctions at critical times, such as at the end of the Devonian, at the end of the Triassic, and finally in the earliest Palaeogene (Hoffmann *et al*., 2021). Another period when heteromorph ammonites flourished was the Middle Jurassic. They abruptly appeared in the Late Bajocian, and again in the Late Bathonian, and continued until the Middle Callovian (or Early Oxfordian, see Bert, Courville, 2016). Apart from a larger gap spanning most of the Early and Middle Bathonian, at least some of these forms showed an almost pandemic distribution, except for the Boreal regions. At a closer look, however, these heteromorphs are not recorded continuously through the sections. Times of mass occurrences alternated with times of complete absence. Frequent short-time immigration events might be coupled with sea-level highstands, currents or favourable ecological factors (*e.g.*, Hölder, 1978; Dietl, 1981; Pandey *et al.*, 1994; Jain, Pandey, 1997; Gulyaev, 2002; Fernández-López *et al.*, 2014; Mitta, 2017, 2025; Jain, 2018). On the other hand, lucky circumstances still enhance our knowledge and even in long-studied European areas new discoveries are possible (*e.g.*, Dietl, Niederhöfer, 1986; Fernández-López, 2001; Galácz, Földvári, 2024).

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Descriptions of heteromorphic Middle Jurassic ammonites go back to the middle of the 19th century, when most of the presently known species were introduced (Deshayes, 1831; d'Orbigny, 1842–1851; Baugier, Sauzé, 1843; Morris, 1845; Quenstedt, 1857). Several attempts and discussions were undertaken to classify the various species and genera, starting with Hyatt (1900), followed by Potonié (1929), Arkell *et al.* (1957), Schindewolf (1963), Dietl (1978), and Callomon (1981). In another approach, some Middle Jurassic heteromorphs were interpreted as the macroconchiate partners of co-occurring normally coiled lappeted microconchs (Besnosov, Kutuzova, 1990). It took a rather long time of research until the first lappeted microconchs were reported among heteromorphs themselves (*e.g.*, Mitta, 2017, 2025; Dietl, 2021). In a *Spiroceras* specimen already illustrated by Potonié (1929, pl. 18, fig. 18; SMNS 62371) a lappeted aperture is present but was overlooked (Fig. 1). The apparent sexual dimorphism in spiroceratids makes the systematic approach by Besnosov and Kutuzova (1990) unreliable. The most recent systematic placement of Middle Jurassic heteromorphs was presented by Howarth (2017). In this study we correct various misinterpretations about Middle Jurassic heteromorphs in previous studies, and we provide the current state of the art.

Fig. 1. *Spiroceras* cf. *annulatum* (Deshayes, 1831) [m], SMNS 62371 (= Orig. Potonié, 1929, pl. 18, fig. 18), with lappeted aperture (arrow)

Specimen coated with ammonium chloride. Upper Bajocian, Garantiana Zone, Bielefeld, NW Germany (ex coll. W. Lange). Scale bar equals 20 mm

Abbreviations: SNSB-BSPG – Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; SMNS – Staatliches Museum für Naturkunde Stuttgart, Germany; [m] – microconch; [M] – macroconch.

WHO WAS THE AUTHOR OF *SPIROCERAS*?

The present definition of *Spiroceras* as a valid ammonite genus (Howarth, 2017) is based on an earlier brief analysis and discussion by Howarth and Melville (1984), who tried to fix a type species and who erected a neotype for that species. According to these authors, it was Friedrich August Quenstedt who had introduced the genus *Spiroceras* in 1856 (*sic*), without defining a type species, and Hyatt (1900) subsequently introduced a new species *Spiroceras bifurcatum* (*sic*) for the missing type species. However, the arguments put forward by these authors in favour of such a taxonomic procedure are based on several erroneous assumptions and linguistic misinterpretations and cannot be followed at all. We therefore have to present here the correct historical facts and conclusions.

The taxonomic problems involved with the genus *Spiroceras* are threefold. The first question concerns the authorship of the genus, the second one concerns its type species, and the third one concerns the syntypes of the type species.

The answer to the first question is quite easy. The term '*Spiroceras*' appears for the first and only time in Quenstedt (1857, p. 407), when he discussed the great morphological variation within his studied sample from the Upper Bajocian Hamitenton Formation ('Braunjura δ') of Eningen unter Achalm in the area of the middle Swabian Alb. From Quenstedt's original wording it is clear that he never intended to introduce a new genus name. The term '*Spiroceras*' was only used ironically for a special morphological variety within his species *Hamites bifurcati* – namely for the twisted specimen illustrated on his pl. 55, fig. 10 that unfortunately has not survived – and he referred to other such, in his view, completely superfluous names used by French authors. Consequently, the name '*Spiroceras*' was neither used in the figure captions nor in his later monograph on Middle Jurassic ammonites (Quenstedt, 1887) nor in any other subsequent papers, and thus Quenstedt should not be quoted as the valid author of a nominal ammonite genus '*Spiroceras*'. In 1900, Hyatt published a first valid systematic attempt, in which he distinguished between spirally coiled heteromorphs and straightened ones. For the latter he introduced a new genus *Apsorroceras*, with *Hamites baculatus* Quenstedt, 1857 as its type species. For the former, he adopted Quenstedt's informal term '*Spiroceras*' as a genus name, contrary to Quenstedt's intention, with *Spiroceras bifurcatum* (*sic*) Quenstedt as its type species. In this way *Spiroceras* became validated as a genus name by Hyatt (1900), who therefore has to be considered its nominal author.

WHAT IS THE TYPE SPECIES OF *SPIROCERAS*?

When validating *Spiroceras* as a genus, Hyatt (1900) did not intend to introduce a new species '*bifurcatum*' as erroneously stated by Howarth and Melville (1984). Instead, Hyatt clearly referred to Quenstedt as being the author of that species both in the text and figure caption. It is true that Quenstedt never used the spelling *Hamites bifurcatus*. The original spelling *Hamites bifurcati* was used in all of Quenstedt's publications (1846 [in 1845–1849], 1852, 1857, 1867, 1885, 1887). Howarth and Melville (1984) asserted that *bifurcati* means a plural and thus was invalid as a species name. This is definitely wrong, because Quenstedt named this taxon not because of the occurrence of bifurcating ribs – which are completely absent – but because of a supposed relationship with the informal ammonite group of the Bifurcati, the present stephanoceratoid genus *Strenoceras* Hyatt, 1900. It was not unlikely that any material studied by Hyatt (1900) had been erroneously labelled as "*Hamites bifurcatus*". This spelling appears even on some old labels from the Tübingen and Munich university collections, but others from the same collections bear the correct spelling *bifurcati*. Hence, *bifurcatum* as it was used by Hyatt (1900) is not a newly introduced species name but was nothing but a misspelling of Quenstedt's species *bifurcati*, and consequently, the correct name of the type species of *Spiroceras* Hyatt, 1900 is *Hamites bifurcati*. Most strangely, Potonié (1929) continued using the incorrect spelling '*bifurcatum*' although he quoted a letter to him from the Swiss palaeontologist Louis Rollier, who had explicitly pointed out that this spelling (by Zittel) was erroneous. Indeed, not Hyatt (1900) but Zittel (1895) was the first to use *Spiroceras* informally as a genus name, with this incorrect spelling in the figure caption of a *Spiroceras* from the classical locality Eningen (see below).

After clarifying the authorship and type species of *Spiroceras*, we have to analyse the complex taxonomical history of the type species. The binomen '*Hamites bifurcati*' was used by Quenstedt for the first time in 1846. Both Arkell (in Arkell *et al*., 1957) and Dietl (1978) did not question the publication date for *Hamites bifurcati* and accepted Quenstedt, 1846 as being valid. However, at that time, Quenstedt did not intend to introduce a nominal species since he was fully convinced that his material represents pathological specimens of co-occurring normally coiled *Ammonites bifurcatus* Zieten, 1830. It is obvious that Quenstedt (1846 [in 1845–1849]) had only a few very incomplete specimens of which he illustrated two examples in the corresponding atlas volume that appeared delayed in 1849. His view of a pathology was maintained for some time (see also Quenstedt, 1852) until he received more and more material. In 1857, Quenstedt had changed his opinion that the uncoiled specimens represent pathological specimens of a normally coiled ammonite species completely, and from then onwards he continued using the informal term *Hamites bifurcati* as a valid species name. Also in the 2nd and 3rd edition of his 'Handbuch der Petrefaktenkunde' (Quenstedt, 1867, 1885) he changed the wording of his text accordingly.

WHAT IS THE TYPE SPECIMEN OF *SPIROCERAS BIFURCATI*?

In the text-book of his 'Jura', Quenstedt (1857, p. 404) provided an exact statement about the syntypes belonging to his new species *Hamites bifurcati*. Contrary to Howarth and Melville, 1984, who cited 1856 as the year when Quenstedt's monograph was published, the correct publication date for the respective part is 1857 (see Lambrecht *et al*., 1938). Interestingly, of the two fragments illustrated in 1849, Quenstedt (1857) excluded the larger one on pl. 11, fig. 15 from the species *H. bifurcati*, which is then fully restricted to specimens from the Swabian locality Eningen unter Achalm which he interpreted as belonging to a morphologically extremely variable palaeobiospecies. In consequence, the original syntype series of *H. bifurcati* Quenstedt, 1857 includes the fragmentary specimen of Quenstedt (1849, pl. 11, fig. 14) and twelve additional syntypes (Quenstedt, 1857, pl. 55, figs. 1–12). Subsequently, two different lectotypes for *H. bifurcati* were selected, the first one by Arkell (see Arkell *et al*., 1957) and the second one – indirectly – by Dietl (1978), who was not aware about Arkell's (1957) previous designation and included only the specimen of Quenstedt's pl. 11, fig. 15 in *Spiroceras orbignyi* (Baugier, Sauzé, 1843), which he considered as a senior subjective synonym of *Hamites bifurcati*. Indeed, the two specimens illustrated by Quenstedt in 1849 most likely belong to two different taxa. The specimen of Quenstedt's pl. 11, fig. 14 – Arkell's lectotype of *Hamites bifurcati* – was assigned to *Spiroceras annulatum* (Deshayes, 1831) (Dietl, 1978, p. 40). Dietl's (1978) indirect lectotype designation is invalid because it was preceded by Arkell's (1957) designation. The lectotype designated by Arkell is meanwhile lost due to pyrite decay and thus cannot be re-studied. And the second specimen illustrated in Quenstedt (1849, pl. 11, fig. 15) had not been part of the type series when the species *Hamites bifurcati* became validated in 1857.

In strong contrast to this evaluation, Howarth and Melville (1984) took a specimen illustrated by Hyatt (1900) as the 'holotype' of *Spiroceras bifurcatum* Hyatt, 1900. However, that specimen was just illustrated for the reader as a typical example of Quenstedt's species but never as the type of a taxon. Since Howarth and Melville (1984) were unable to locate the illustrated specimen in the palaeontological collection of Harvard University, they declared the pyritized specimen illustrated by Quenstedt 1887, pl. 70, fig. 36 as a neotype for their fictional '*Spiroceras bifurcatum* Hyatt, 1900'. However, Hyatt (1900) definitely did not illustrate a specimen from the Harvard collection. This is evident since the same illustration as used by Hyatt (1900) was already figured by Zittel (1895, p. 430, fig. 1184), with the same incorrect spelling '*Spiroceras bifurcatum* Quenst. sp.' in its caption! And the same illustration appears even earlier, in Zittel's famous encyclopedic text-book 'Handbuch der Palaeontologie' (1881–1885, p. 482, fig. 672), therein captioned with '*Crioceras bifurcatus* Quenst. sp.'. Hence, the original of the repeatedly illustrated specimen was most likely stored in the collection at Munich, where Zittel was employed as a university professor, and Hyatt (1900) just copied Zittel's original drawing. In the present collection at Munich (SNSB-BSPG) only two small historical specimens of *Spiroceras bifurcati* from the 19th century have survived. None of these two specimens can be identified with Zittel's (and Hyatt's) illustration. Hence, we must assume that the original specimen was either destroyed during World War II or by pyrite decay.

Howarth and Melville's illegitimate 'neotype' is a juvenile macroconch which is now stored – like all other surviving pyritized specimens from Quenstedt's collection – in the collection of the Stuttgart Natural History Museum under the inventory number SMNS 28238. Since this specimen has not been part of the syntype series of Quenstedt (1857) it cannot be accepted as the type for *Hamites bifurcati* Quenstedt, 1857. For nomenclatorial stability, we here designate a neotype for *H. bifurcati* from Quenstedt's surviving syntype series. We herein select the specimen illustrated by Quenstedt (1857, pl. 55, fig. 2; SMNS 28245), re-illustrated on Figure 2. Concurrently, this microconchiate neotype can be considered as an allotype for *Spiroceras orbignyi* (Baugier, Sauzé, 1843), the type of which is based on a macroconchiate specimen of the same geological age.

In summary, the misunderstood genus *Spiroceras* is redefined as follows: *Spiroceras* Hyatt, 1900, with *Hamites bifurcati* Quenstedt, 1857 as its type species, and SMNS 28245 as the neotype. *Spiroceras bifurcati* (Quenstedt, 1857) is a junior subjective synonym and the microconchiate partner of *Toxoceras orbignyi* Baugier and Sauzé, 1843 (see Dietl, 1978). At Mougon near Niort, the type locality of *T. orbignyi*, both dimorphic partners frequently occur in the

Fig. 2. *Spiroceras orbignyi* (Baugier, Sauzé, 1843) [m], SMNS 28245 (= Orig. Quenstedt, 1857, pl. 55, fig. 2; Quenstedt, 1887, pl. 70, fig. 42), neotype of *Hamites bifurcati* Quenstedt, 1857, designated herein, and a hand-written label, not by Quenstedt himself, with the correct spelling of the species

Hamitenton Formation, Upper Bajocian, Niortense Zone, Eningen unter Achalm, middle Swabian Alb, SW Germany. Asterisk marks beginning of body-chamber. Scale bar equals 20 mm

same limestone bed, and the microconchiate ones are occasionally preserved even with their lappets (Fig. 3). The position of the type horizon is the Upper Bajocian Strenoceras niortense Zone, Orthogarantiana baculata Subzone.

PHYLETIC RELATIONSHIPS BETWEEN *SPIROCERAS* AND *PARAPATOCERAS*

The cryptic origin of the genus *Spiroceras* is still a matter of debate (see Dietl, 1978; Callomon, 1981; Schweigert, Dietl, 2026) and not further discussed here. Howarth (2017)

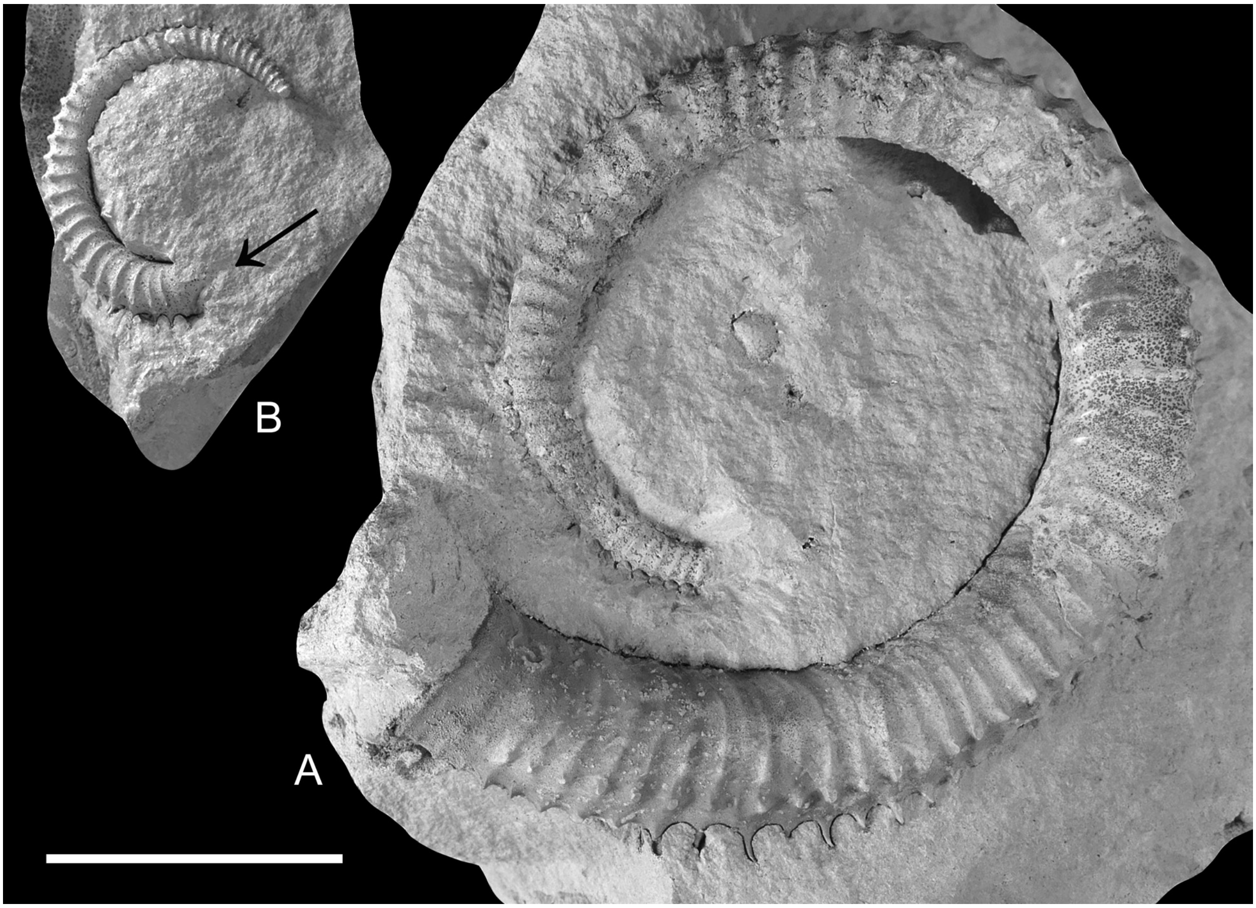

Fig. 3A. *Spiroceras orbignyi* (Baugier and Sauzé, 1843) [M], SMNS 70661/1, a topotype. **B.** *S. orbignyi* (Baugier and Sauzé, 1843) [m], SMNS 70661/2, specimen with preserved lappeted aperture (arrow)

Upper Bajocian, Niortense Zone, Mougon near Niort, Département Deux-Sèvres, western France (ex coll. R. Bopp). Scale bar equals 50 mm

accepted a paraphyletic origin of the two heteromorph genera *Spiroceras* and *Parapatoceras* within a common superfamily Spiroceratoidea Hyatt, 1900, following the study by Dietl (1978). The latter author noted a stratigraphical gap or non-record between the last occurrence of *Spiroceras* in the (lower) Parkinsonia parkinsoni Zone and the abrupt appearance of *Parapatoceras* in the Upper Bathonian. He suspected that the Late Bathonian genus *Epistrenoceras* Bentz, 1928 was the direct ancestor of *Parapatoceras*. Later, the stratigraphical gap comprising at least the entire Lower and Middle Bathonian became a little shortened by the record of an uncoiled ammonite from the Lower Bathonian Zigzagiceras zigzag Zone of Hungary. This fragmentary specimen was determined as '*Parapatoceras* sp.' (Galácz, 1980). More recently, Jain (2018) pointed out that in India, *Epistrenoceras* occurs somewhat earlier than *Parapatoceras* and concluded that *Epistrenoceras* could be a secondarily re-coiled descendant of a continuous *Spiroceras–Parapatoceras* lineage. Galácz (2019) replied that his sole heteromorphic specimen from the Zigzag Zone of Hungary was more likely a late representative of *Spiroceras annulatum* (Deshayes, 1831) than an early *Parapatoceras*. This leads to the question if and how both genera can be distinguished from each other. Dietl (1978) noted that *Parapatoceras* has a simpler suture line than *Spiroceras*, and the ribbing on the dorsal side is weakened and anteriorly projecting in the latter. It was the absence of a dorsal anterior-projecting of the ribs that has led to Galácz's original determination of the specimen from the Zigzag Zone as a *Parapatoceras*. Indeed, in *Spiroceras annulatum* but also in *S. obliquecostatum* (Quenstedt, 1887) and in *S. cylindricum* (Baugier and Sauzé, 1843) a dorsal anterior-projecting of the ribs or growth lines is weakly developed or even absent, and the ribs may cross the dorsal side without interruption (Figs. 4, 5). Moreover, the suture lines in the former two taxa are rather simple and indistinguishable from those of stratigraphically younger species of *Parapatoceras*. It must be emphasized that the suture lines of *Parapatoceras* must be relatively simple because of the much smaller conch diameters even of adult macroconchs. Only in *S. cylindricum* is the suture line still unknown since all available specimens are either body-chamber fragments or phragmocones preserved with their calcitic replacement shell. Therefore, *S. annulatum*, *S. obliquecostatum* and *S. cylindricum* cannot be distinguished morphologically from *Parapatoceras* spp. and therefore these three Upper Bajocian taxa could alternatively be assigned also to the latter genus.

Dietl (2021) discussed the presence of sexual dimorphism in *Parapatoceras* and illustrated an example of both of the dimorphic partners. In the purported macroconchiate fragment he reported a crowding of the suture lines; however, the anterior part of the body-chamber is not preserved. Crowding of suture lines alone is not enough evidence for adulthood and may also occur under stress conditions. Indeed, lappeted specimens have not yet been reported from any Late Bathonian or Callovian *Parapatoceras*, but having in mind the extreme rareness of lappeted specimens in *Spiroceras*, this virtual absence may reflect collection biases

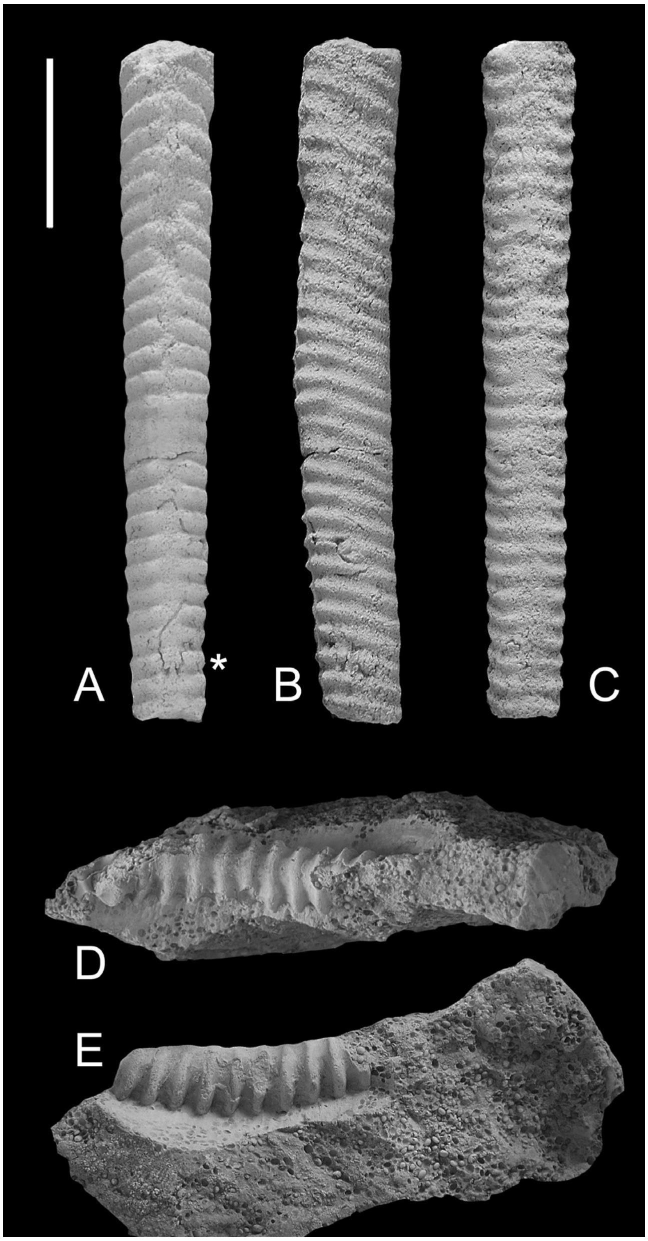

Fig. 4A–C. *Spiroceras* cf. *annulatum* (Deshayes, 1831) [m], SMNS 70661/19, in ventral (**A**), lateral (**B**) and dorsal (**C**) views to show the near absence of anteriorly projecting ribs or growth lines. Upper Bajocian, Celles-sur-Belle near Niort, Deux-Sèvres, W France (ex coll. R. Bopp). **D–E.** *Spiroceras annulatum* (Deshayes, 1831) [m], SMNS 70661/20, in dorsal (**D**) and lateral (**E**) views. Oolite ferrugineuse de Bayeux, Upper Bajocian, Parkinsoni Zone, Évrecy, Normandy, France (ex coll. Slg. R. Bopp). Specimens coated with ammonium chloride. Asterisk marks beginning of body-chamber. Scale bar equals 20 mm

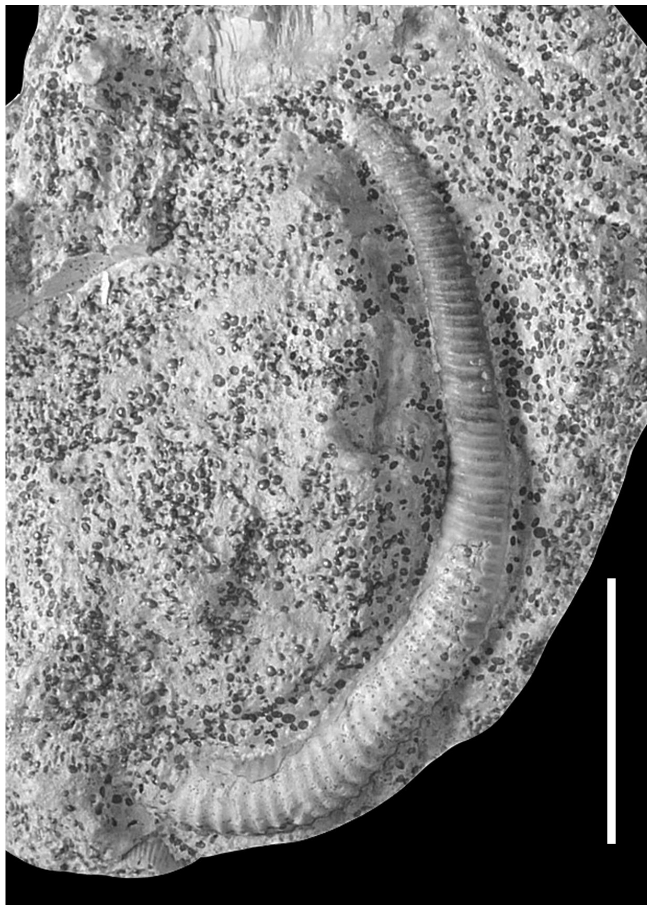

Fig. 5. ***Spiroceras obliquecostatum* (Quenstedt, 1886) [M], SMNS 70661/6**

Oolite ferrugineuse de Bayeux, Upper Bajocian, Parkinsoni Zone, St. Vigor near Bayeux, Normandy, France (ex coll. R. Bopp). Scale bar equals 20 mm and was most likely caused by the fragile nature of the aperture and of the entire shell.

The non-record of Spiroceratoidea in parts of the Lower Bathonian and in the Middle Bathonian can be explained by a crisis which was survived by some populations in unknown refuge areas. Especially the early Middle Bathonian was a critical time not only for many ammonite taxa (Arkell, 1956, p. 609) but also for nautilids, for which a similar gap has been reported (Branger, 2004). If this view is correct, *Spiroceras* and *Parapatoceras* are linked by intermediate forms occurring already in the Late Bajocian and most likely represent a monophyletic lineage thus making the distinction of a stratigraphically younger subfamily Parapatoceratinae redundant.

CONSIDERATIONS ON THE ANCESTRY OF ACUARICERATINAE

In the recent classification suggested by Howarth (2017), the genera *Acuariceras* Spath, 1933 and *Paracuariceras* Schindewolf, 1963 were included in Parapatoceratinae Buckman, 1926, a view that followed Dietl's (1978) opinion about their phyletic relationships. Dietl (1978) supposed a direct ancestry of *Paracuariceras* from *Parapatoceras*, which was coupled not only with a general simplification of the suture line but also a reduction of the lobes from a quinquelobate to a quadrilobate condition. Furthermore, *Acuariceras*/*Paracuariceras* gave up the initial spiral coiling which is still well-present in *Parapatoceras* (Dietl, 1981). The hitherto oldest known record of *Paracuariceras* is remarkable. Fernández-López (2001) reported a specimen of this genus from the Upper Bathonian of Spain which came from the same bed as a *Parapatoceras*. Previously, the oldest records of *Paracuariceras* were described from the Lower Callovian, also partly co-occurring with *Parapatoceras* (Dietl, 1978, 1981; Munk, 1979; Dietl, Niederhöfer, 1986). In the Apuseni Mountains of Romania, both genera were reported from a strongly condensed bed of Late Bathonian to Early Callovian age (Patrulius, 1996).

If we consider the very different morphological characters of *Parapatoceras vs. Acuariceras*/*Paracuariceras*, these unexpected stratigraphically early co-occurrences make a common ancestry unlikely. Inspired by the morphological differences, Schindewolf (1963) included the latter two genera in their own subfamily Acuariceratinae. Interestingly, he briefly discussed a possible ancestry of this subfamily from lytoceratids mainly based on characters of Cretaceous heteromorphs; however, finally he followed the traditional view and included Acuariceratinae again in Parapatoceratidae. Later, Schindewolf's interesting view of a possible independent origination of Acuariceratinae from lytoceratids was no longer discussed and became forgotten.

A very large sample of specimens from the Lower Callovian of a single locality in SW Germany comprised two co-occurring 'species' of *Paracuariceras* described as *P. giganteum* Dietl, 1981 and *P. acuforme* Dietl, 1981 (Fig. 6). The holotypes of both taxa differ only in their whorl sections. Recently, Dietl (2021) explained this co-occurrence as an expression of sexual dimorphism, with *P. giganteum* with its oval section as being the macroconch and *P. acuforme* with its rounded section as the corresponding microconch. If this is true, the two taxa must be considered synonymous. In the Middle Callovian, another such dimorphic pair occurs, *Acuariceras acuarius* (Quenstedt, 1848) [m] and

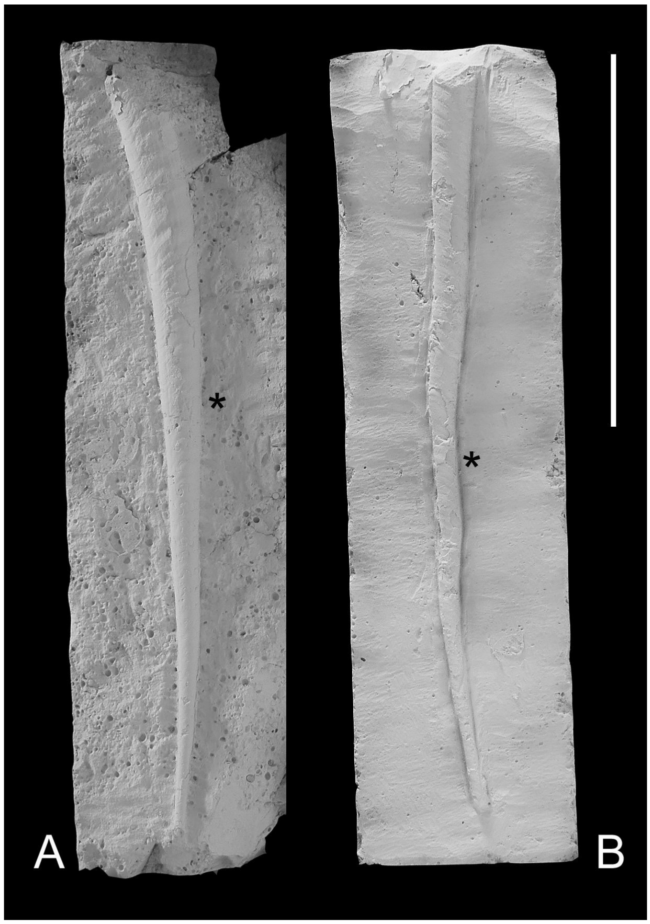

Fig. 6A. *Acuariceras giganteum* (Dietl, 1981) [M], SMNS 26309, holotype. **B.** *Acuariceras giganteum* (Dietl, 1981) [m], SMNS 26321, allotype (= holotype of *A. acuforme* (Dietl, 1981))

Ornatenton Formation (Macrocephalenoolith Member), Lower Callovian, Macrocephalites herveyi Zone, *quenstedtiforme* Biohorizon, Klingenbach creek near Bisingen-Thanheim, SW Swabian Alb, SW Germany. Specimens coated with ammonium chloride. Asterisks mark beginning of body-chamber. Scale bar equals 50 mm

Paracuariceras incisum Schindewolf, 1963 [M]. The two taxa differ again in their whorl section but also in adult size thus confirming sexual dimorphism. This interpretation makes the distinction between *Acuariceras* and *Paracuariceras* purely artificial, then giving nomenclatorial priority to *Acuariceras* Spath, 1933. The same view was followed by Bert, Courville (2016).

Acuariceras material from the Middle Callovian of Swabia was extensively described and discussed by Schindewolf (1963). Dietl (1978) expanded the research on *Paracuariceras* and reported additional specimens from the Lower Callovian of southeastern France. All the material studied consisted of small pyritized fragments of inner moulds. In contrast, the newly described specimens from the Lower Callovian of southern Germany were preserved with their calcified replacement shells. Dietl (1981) incidentally reported a longitudinal striation on the shell of the body-chambers (Fig. 7). Since his contribution is written in the German language and the illustrations do not show any details of the shell surface, this important character was

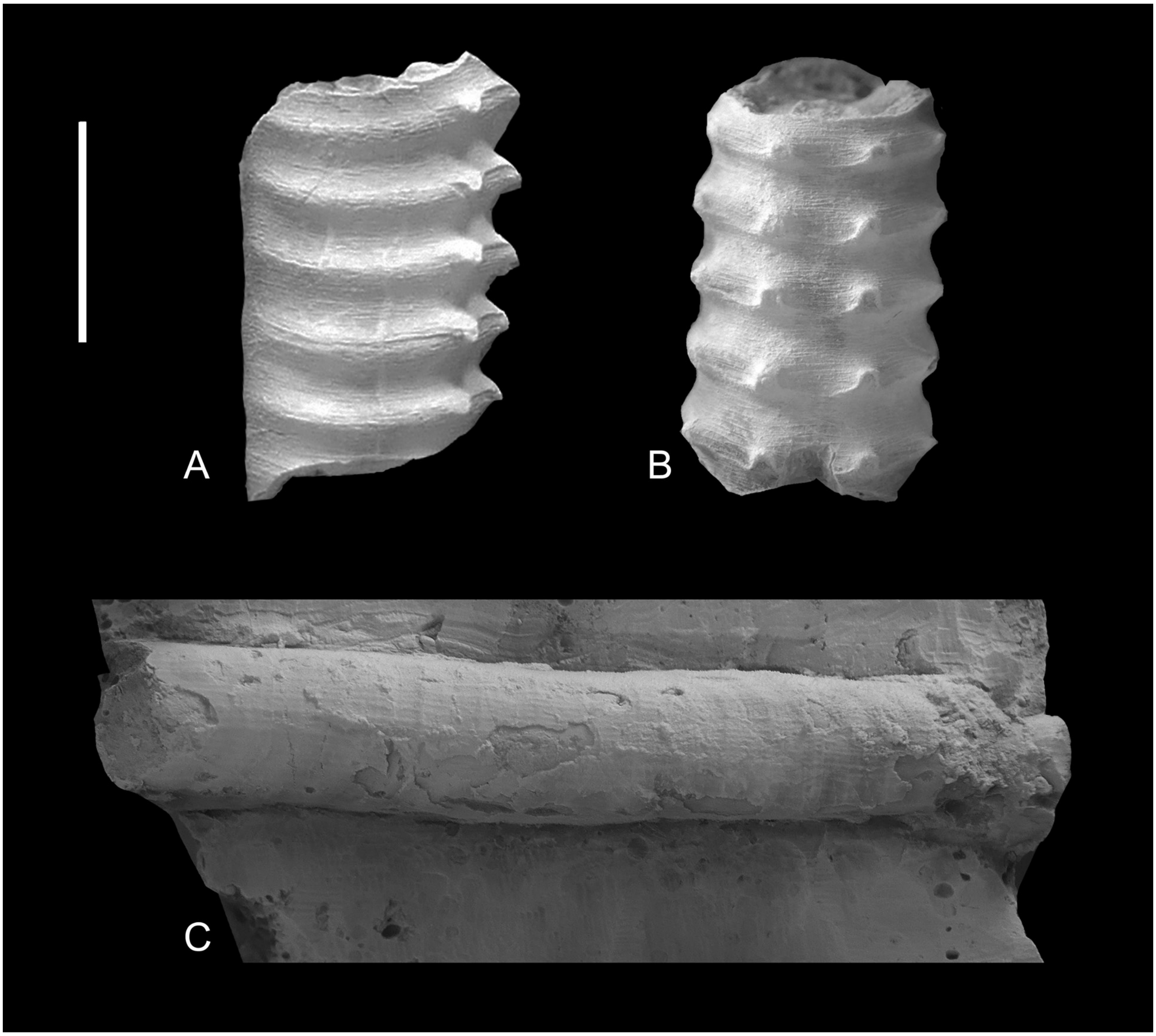

Fig. 7. Comparison of shell ornamentation between *Spiroceras* and *Acuariceras*

A, B. Fragment of *Spiroceras sauzeanum* (d'Orbigny, 1850), SMNS 61814/1, with calcitic replacement shell perfectly showing the growth lines. Hamitenton Formation, Upper Bajocian, Niortense Zone, former motorway construction site at 'Franzosenschlucht' gorge between Aichelberg and Gruibingen, middle Swabian Alb, SW Germany. **C.** *Acuariceras giganteum* (Dietl, 1981), SMNS 70769/1, topotype, showing longitudinal striation. Ornatenton Formation (Macrocephalenoolith Member), Lower Callovian, Herveyi Zone, *quenstedtiforme* Biohorizon, Klingenbach creek near Bisingen-Thanheim, SW Swabian Alb, SW Germany. Specimen coated with ammonium chloride. Scale bar equals 10 mm overlooked. In larger specimens the longitudinal striation is discernible also on parts of the phragmocone and even on inner moulds of their body-chambers. The same striation occurs on the pyritic body-chamber of *Acuariceras acuarius* illustrated by Schindewolf (1963, pl. 6, fig. 2), but this is only discernible on very close inspection.

Additional specimens of *Acuariceras* spp. from the Upper Bathonian or Lower Callovian of Romania (Patrulius, 1996) were described as *Parapatoceras elmii* and *P. perconstrictum*. The first one is probably conspecific with *A. giganteum* (Dietl, 1981). The latter species, *P. perconstrictum*, is based on two small fragmentary specimens showing remarkably deep and well-developed constrictions. Patrulius (1996) introduced a monotypic subgenus *Lytospiroceras* for this species. Similar constrictions are present in *A. acuarius* and *A. incisum* (see Schindewolf, 1963, pls. 6, 7) but have never been observed in any true *Spiroceras* or *Parapatoceras*. The illustration of the paratype of *P. perconstrictum* seems to show a lappeted aperture, although this feature was not reported in the original description.

Another specimen representing a Late Bathonian representative of *Acuariceras* is the holotype of *Toxoceras tenuis* Baugier and Sauzé, 1843. It is a body-chamber with a rather dense, oblique ribbing and equally oblique constrictions, one of which is followed by a noticeable kinking similar to those observed in stratigraphically younger species of *Acuariceras*. As an explanation for this change of growth direction, which would be very strange for *Parapatoceras*, Dietl (1978) suggested that different fragmentary specimens were artificially glued together. Later, it became evident that the fragments indeed must have belonged to a single individual and the kinking was then explained as a traumatic pathology since in addition the sculpture abruptly weakens immediately after the kinking (Dietl, Gauthier in Fischer, 1994). At that time, however, *Toxoceras tenuis* was still assigned to *Parapatoceras*, disregarding its aberrant characters. Occasionally, it is also the case that fragments of body-chambers of true *Parapatoceras tuberculatum* Baugier and Sauzé, 1843) have been misidentified as "*P.*" *tenue* because of their rather dense, oblique ribbing style, despite their clearly showing remnants of spines and lacking constrictions (compare Dietl, 2020, pl. 1: h, pl. 2: f).

As another unusual character, Schindewolf (1963) noted the presence of a shallow keel in *Paracuariceras incisum*. This keel-like structure is a conchal furrow, an enigmatic shell structure which occurs not only in ammonites but also in other ectoconchiate cephalopods (Chirat, von Boletzky, 2003; Klug *et al.*, 2008). Within other Middle Jurassic heteromorphs, a conchal furrow was only found in a single specimen assigned to *S. sauzeanum* (d'Orbigny, 1850) (Fig. 8), possibly as a pathology.

Altogether, the different suture lines, different shell structure, absence of sharp ribbing and spines and the occurrence of constrictions as well as the first appearance of specimens in the Late Bathonian make an ancestry of *Acuariceras* from *Parapatoceras* impossible and we therefore have to look for alternatives. At this point we should remember Schindewolf's (1963) idea about an origination from lytoceratids. In the Bajocian, Bathonian and still in the Lower Callovian, Megalytoceratinae are present with the relatively small-sized genus *Nannolytoceras* Buckman, 1905, which has an almost pandemic distribution (Pugin, 1964; Galácz, Kassai, 2012; Hoffmann, 2010, 2015; Galácz, 2019). Since the stratigraphic ranges of *Nannolytoceras* and *Acuariceras*

Fig. 8A, B. *Spiroceras sauzeanum* (d'Orbigny, 1850), SMNS 22950, a unique example showing a shallow keel-like structure on its venter (B), a conchal furrow ('Fadenkiel' in older literature) (= Dietl, 1978, pl. 5, fig. 1)

Upper Bajocian, Niortense Zone, Rabanera del Pinar, Spain (ex coll. G. Dietl). Asterisk marks beginning of body-chamber. Specimen coated with ammonium chloride. Scale bar equals 50 mm overlap, the latter might have originated either from the former, or at least from a common ancestor. This idea is fully consistent with all observed morphological characters: a reduced suture line, a quadrilobate instead of a quinquelobate suture, deep constrictions, and the absence of sharp ribbing or spines. Finally, a longitudinal striation of the shell is unknown from any other Stephanoceratoidea or Spiroceratoidea but typical of some lytoceratids (*e.g.*, Besnosov, 1958; Hoffmann, 2010; Fig. 9). This character, however, is very rarely preserved and requires a perfect preservation of the shell, which is why it is rarely reported, and specimens of *Nannolytoceras* spp. are mostly represented by internal moulds lacking their shell. If there is really a lappeted aperture present in *P. perconstrictum*, even this observation does not contradict a lytoceratid origin of the genus, because its supposed phyletic ancestor or close relative *Nannolytoceras* was lappeted as well (Fig. 10; see also Sturani, 1971, pl. 3, fig. 5). Of course, the formation of lappets in this lytoceratid clade is convergent with those in other Jurassic ammonoids. In conclusion, there remain no more doubts about a lytoceratid origin of *Acuariceras*. Systematically, *Acuariceras* has to be excluded from Spiroceratoidea, and the subfamily

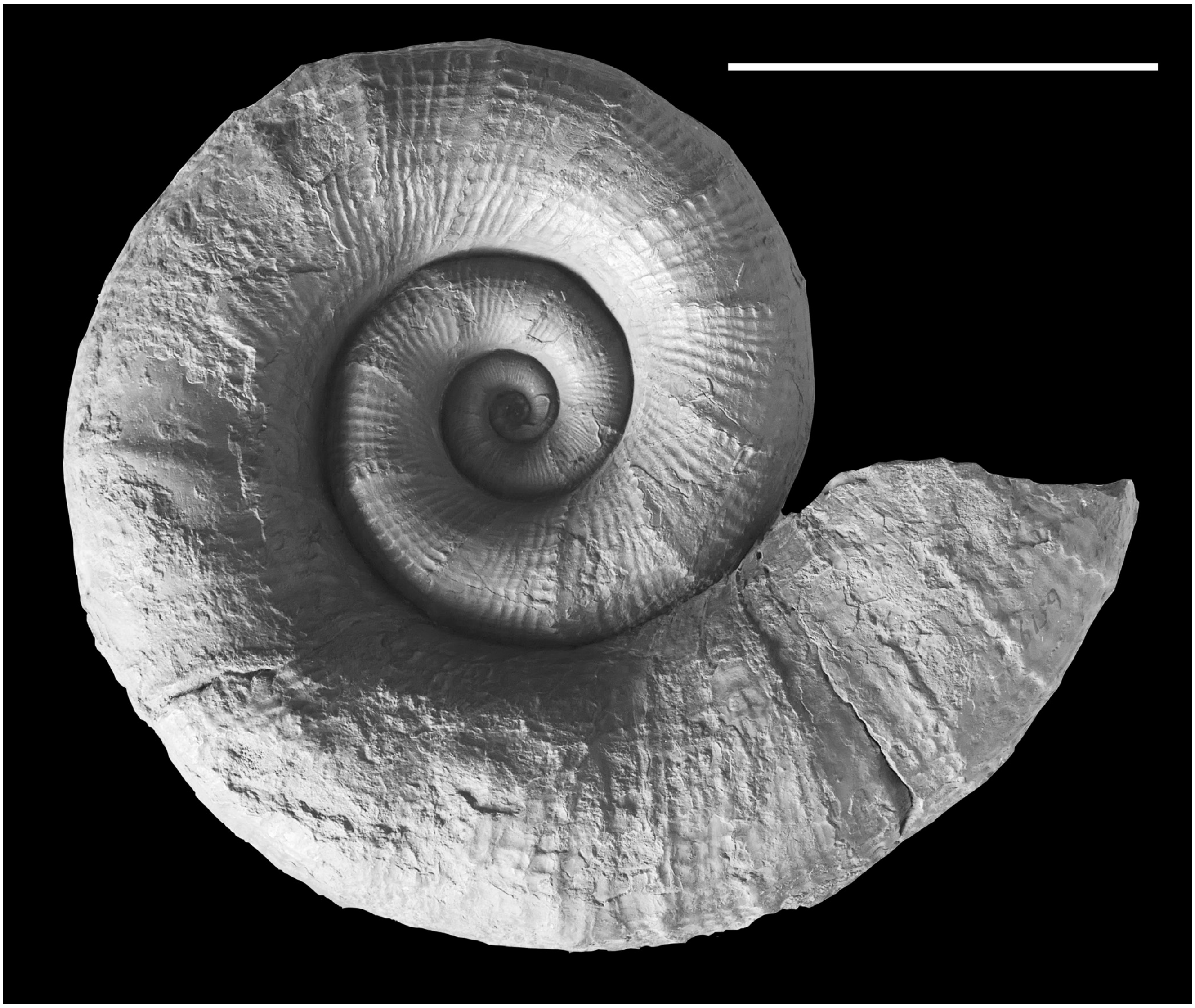

Fig. 9. *Lytoceras cornucopia* (Young and Bird, 1822), SMNS 6519, its shell showing an ornamentation with longitudinal striae well comparable with that in *Acuariceras giganteum* (Dietl, 1981)

Toarcian, La Verpillière near Lyon, SE France. Scale bar equals 100 mm

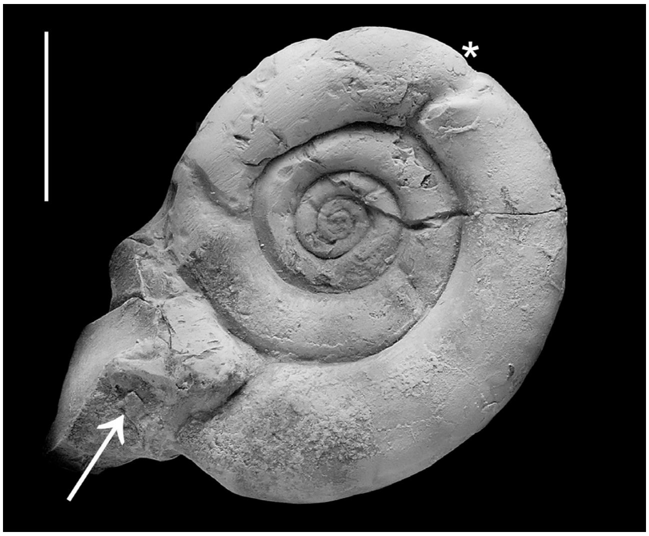

Fig. 10. *Nannolytoceras tripartitum* (Raspail, 1831), SMNS 70770, with preserved lappeted aperture (arrow).

Upper Bajocian, Parkinsoni Zone, Chaudon near Digne, SE France (leg. V. Dietze). Asterisk marks beginning of body-chamber. Specimen coated with ammonium chloride. Scale bar equals 20 mm

Acuariceratinae Schindewolf, 1963 represents nothing but a latest offshoot of Megalytoceratinae characterized by dwarfism and uncoiling.

REMARKS ON THE STRATIGRAPHICAL RANGES OF *PARAPATOCERAS* AND *ACUARICERAS*

Bert and Courville (2016) have expanded the known stratigraphical range of *Parapatoceras* from the Middle Callovian Kosmoceras jason Zone to the Upper Callovian Peltoceras athleta Zone, and that of *Acuariceras* from the Jason Zone even to the Lower Oxfordian Cardioceras cordatum Zone. These stratigraphical expansions were not reported by Howarth (2017), most likely because of cross-publishing. The poor and fragmentary preservation of the sole *Parapatoceras* specimen from the French Athleta Zone leaves the possibility that this specimen has been reworked from older beds. Condensation and/or reworking are not uncommon in Submediterranean deposits of this time interval (*e.g.*, Jantschke *et al*., 2025). Hence, a latest occurrence of *Parapatoceras* in the Athleta Zone cannot be ruled out but must be seen with great caution.

A specimen in even worse condition was described as the holotype of the monotypic *Acuariceras acucostis* Bert and Courville, 2016. The fragment of a body-chamber is too incomplete for a reliable interpretation. The big size of the fragment, the formation of secondary ribs, the subrounded whorl section and the absence of a striation speaks against an assignment to *Acuariceras*. Alternatively, we suspect a perisphinctid affinity of this fragment, possibly belonging to *Otosphinctes paturattensis* (Loriol, 1901) (compare examples illustrated in Jantschke *et al.*, 2025).

REMARKS ON THE GENUS *SULCOHAMITES*

In his comprehensive monograph on Middle Jurassic heteromorph ammonites (Dietl, 1978) the genus *Sulcohamites* Wetzel, 1937 was only briefly cited. This monotypic genus is based on a single fragmentary specimen from the Lower Bathonian of Eimen, Hils Mountains, northwestern Germany. Wetzel (1937) considered *S. eimensis* (misspelled '*eminensis*' by Howarth, 2017) as an uncoiled offshoot of Morphoceratidae. Since its description no further specimens have been reported. Besnosov and Kutuzova (1990) accepted Wetzel's placement in Morphoceratidae and described a new genus *Sulcohamitoides* as its possible microconchiate (!) partner. Subsequently, Howarth (2017) interpreted *Sulcohamitoides* as a junior subjective synonym of *Epistrenoceras* and the holotype of *Sulcohamites eimensis* as the whorl fragment of an *Epistrenoceras*. The almost pandemic genus *Epistrenoceras* is said to occur typically in the Upper Bathonian (*e.g.*, Sandoval *et al.*, 1990; Fernández-López *et al.*, 1994; Fernández-López, 2001; Jain, 2018; Goto, Sakai, 2021), whereas the type horizon of *Sulcohamites* is older, Early Bathonian in age. Moreover, the nuclei of *Epistrenoceras* show ventral ribs and spines, whereas there are no traces of any spines or ribs on the dorsal side of the whorl fragment. Instead, the dorsal side of *S. eimensis* shows narrow parallel lines which indicate that the fragmentary whorl was loosely attached to the next older whorl, and the complete ammonite was rather evolute but not uncoiled. Similar ventral tubercles and smooth, narrow inner whorls occur in the enigmatic microconchiate genus *Kumetaceras* recently described from the Upper Bathonian of Sicily and Hungary (Galácz, 2019). The latter genus exhibits prominent prorsiradiate constrictions on the inner whorls; this character clearly speaks against an assignment to Spiroceratoidea.

CONCLUSIONS

The definition of the ammonite genus *Spiroceras* is reviewed and clarified. It was formally erected by Hyatt (1900), based on *Hamites bifurcati* Quenstedt, 1857 as its type species. A neotype is selected among Quenstedt's syntype series of *Hamites bifurcati* and illustrated herein. This taxon represents the microconchiate partner of the coeval

Toxoceras orbignyi Baugier and Sauzé, 1843 and thus can be considered a junior subjective synonym of the latter.

Spiroceras Hyatt, 1900 and *Parapatoceras* Spath, 1933 are part of a monophyletic lineage that originates in the Late Bajocian. This lineage shows an evolutionary trend to a smaller size which leads to a decreased complexity of the quinquelobate suture line. The subfamily Parapatoceratinae Buckman, 1926 is considered as synonymous with Spiroceratinae Hyatt, 1900 and thus redundant.

The uncoiled genera *Acuariceras* Spath, 1933 and *Paracuariceras* Schindewolf, 1963 are treated as subjective synonyms since their subtle diagnostic differences vary even between microconchs and corresponding macroconchs. These late Middle Jurassic heteromorphs evolved independently from Spiroceratoidea Hyatt, 1900 and originated in Megalytoceratinae Spath, 1927. Their lytoceratid nature is proven by their simple, quadrilobate suture line, presence of oblique constrictions, absence of sharp ribbing, absence of spines, and characteristic striate shell. *Toxoceras tenue* Baugier and Sauzé, 1843, previously interpreted as a rare dense-ribbed species of *Parapatoceras*, is recognized as a Late Bathonian representative of *Acuariceras*. The normally coiled genus *Nannolytoceras* Buckman, 1905 is suspected of being either a phyletic predecessor of *Acuariceras*, or possibly both genera share a common ancestor.

The stratigraphical ranges for *Parapatoceras* and *Acuariceras* are reviewed. *Parapatoceras* has its roots in the Late Bajocian taxa '*Spiroceras*' *annulatum* (Deshayes, 1831) and '*S.*' *obliquecostatum* (Quenstedt, 1886) of the Garantiana and Parkinsoni chrons and ends in the Middle Callovian Jason Chron; a survival until the Late Callovian Athleta Chron is possible. *Acuariceras* ranges from the Late Bathonian up to the mid-Callovian Jason Chron. Its proposed survival until the Early Oxfordian Cordatum Chron is not confirmed by a reliable record.

The still enigmatic genus *Sulcohamites* Wetzel, 1937 is based on the fragment of a normally coiled ammonite, not of a heteromorph.

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