Sexual phenomena in Late Jurassic Aspidoceratidae (Ammonoidea). Dimorphic correspondence between *Physodoceras hermanni* (BERCKHEMER) and *Sutneria subeumela* SCHNEID, and first record of possible hermaphroditism

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**Abstract**

New collections of the dimorphic ammonite species *Physodoceras hermanni* (BERCKHEMER) [M] and *Sutneria subeumela* SCHNEID [m] from the Upper Jurassic (Beckeri Zone, Subeumela Subzone, *subsidens* horizon) of Swabia demonstrates first time evidence of intra-sexual polyphenism in Aspidoceratidae. In the macroconchs two size classes demonstrate different times of maturity, leading to small and large adults. In the microconchs, besides a continuous size range of adults, a unique case of possible sexual change in a subadult stage is observed that could point to the occurrence of hermaphroditism in ammonites.

**Keywords:** Ammonitina, Physodoceratinae, ontogeny, sexual dimorphism, polyphenism, Late Jurassic.

**Zusammenfassung**


**Resumen**

Colecciones recientes del par dimórfico conformado por *Physodoceras hermanni* (BERCKHEMER) [M] y *Sutneria subeumela* SCHNEID [m] del horizonte *subsidens*, Subzona Subeumela, Zona Beckeri (Jurásico Superior) obtenidas en Swabia demuestran por primera vez evidencia de polifenismo intra-sexual en la familia Aspidoceratidae. En las macroconchas la existencia de dos clases de talla adulta demuestra diferentes momentos de maduración sexual. Esta estrategia reproductiva origina adultos pequeños por maduración sexual precoz y adultos de mayor talla. En las microconchas, con variación continua de talla adulta, un caso notable de posible cambio de sexo en un estado subadulto es observado, lo cual podría interpretarse como un caso de hermafroditismo en ammonites.

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**1. Introduction**

The strongest argument for sexual dimorphism in ammonoids is the identity of juvenile ontogenies between pairs of contemporaneous ammonites which attain differential adult sizes and characteristic morphologies (e.g., MAKOWSKI 1962; CALLOMON 1963; recent review in DAVIES et al. 1996); the larger dimorph or macroconch should be the female and the smaller or microconch the male. Dimorphic correspondence between the macroconch species of *Physodoceras hyatt*, 1900 (type species: *Ammonites circumspinosus* OPPEL, 1863 = *Ammonites circumspinosus* QUENSTEDT, 1849) and the microconch species of *Sutneria zittel*, 1884 (type species: *Nautilus platynotus* REINECKE, 1818) has been suggested (ENAY 1977: 109; SCHWEIGERT 1997). The systematic position of *Sutneria* was long a case of controversial debate, and for a long time it was tentatively included in Aulacostephaninae (ZIESS 1979; OLORIZ & RODRIGUEZ-TOVAR 1996). Recently, SCHWEIGERT (1998) has demonstrated that *Sutneria* belongs to the family Aspidoceratidae by the possession of a laevaptychus. Nevertheless, it seems that there are no published studies on correspondence between species in particular. *Sutneria* and *Physodoceras* are geographically wide-spread, espe-
cially in peri-Tethyan basins and shelves, the western Tethyan Realm itself, and migrated even into the Subboreal, Andean and Indo-Madagascan provinces (e. g. Steuer 1897; Geyer 1969; Zeiss 1979).

Physodoceras hermanni [M] (Berckhemer, 1922) and Sutneria subeumela [m] Schneid, 1915 frequently occur associated to each other (often even in the same piece of rock) in the Subeumela Subzone (Beckeri Zone, Late Kimmeridgian) of Southern Germany (Schneid 1915; Berckhemer 1922; Roll 1931; Berckhemer & Holder 1959). Both taxa have been also recorded outside their type areas, from Le Pouzin in SE France (Holder & Ziegler 1959), and from Bulgaria (Sapunov 1977). Sutneria subeumela was also recorded in the Volgian Gorodishche section of Central Russia (Geyer 1969; Scherzinger & Mitta 2006), and a very close specimen was described from Ethiopia (Zeiss 1979). Therefore, the microconch Sutneria subeumela is considered as a very good example of a geographically widespread guide-fossil. The macroconchs are much less significant and often show homoeomorphism, perhaps following a pattern of slower or less conspicuous morphologic evolution.

In Southern Germany (Fig. 1) both taxa occur in the kiderleni, subsidens and fischeri horizons of the Subeumela Subzone (Fig. 2). Enay (1977: 109) was the first who suggested they conform a sexual dimorphic pair based in the fact that they are the only species of Physodoceras and the only Sutneria with a well-defined ventral furrow. Arkell (1957: L327) proposed the ventral furrow could be due to the lost of the sipho, according to an idea of Schneid (1915: 124), but this was later definitely dismissed by Berckhemer & Holder (1959: 61–62) and Holder & Ziegler (1959: 194). The ventral furrow in S. subeumela led to a generic separation of Enosphinctes Schindewolf, 1925. Schindewolf (1925), on the one hand, did not recognize the relationship between Enosphinctes and Sutneria, but interestingly included Sutneria in the same family as Physodoceras. After consideration of the close relationship between Sutneria eumela and Sutneria subeumela several authors assigned both species to Sutneria (e. g. Berckhemer & Hölder 1959; Hölder & Ziegler 1959; Enay 1977; this paper). Also Barthel (1959) argued that Enosphinctes and Sutneria are synonymous, whereas Geyer (1969) considered Enosphinctes as a subgenus of Sutneria s. str. and pointed out that only the type species of Enosphinctes, Sutneria subeumela, is characterized by a ventral furrow.

Acronyms of institutions

BSPM Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
SMNS Staatliches Museum für Naturkunde Stuttgart, Germany
LPB Laboratorio de Paleontología, Universidad Nacional de Rosario, Argentina
Acknowledgements

Prof. Dr. John H. Calammon (London) is cordially thanked for numerous fruitful discussions and comments on ammonites and dimorphism. Dr. Martin Nose (Munich) kindly loaned the type specimens of Sutneria subeumela for study. Dr. Martin Roper (Solnhofen) communicated data on the locality of Brunn in Eastern Bavaria. Dr. Maria E. Re (Puerto Madryn) kindly provided recent specific literature. Prof. Dr. Pierre Hantzper-gue (Lyon) and an anonymous reviewer gave valuable suggestions as reviewers of the journal.

2. Antecedents and new material

Berckhemer (1922) based the definition of Physodoceras hermanni on ten specimens (currently stored in the SMNS, but only partly identifiable as being part of the syntypes series) coming from various localities in the Upper Jurassic of Swabia (Fig. 1) but he did not designate any of these specimens as the type. The specimen from Grabenstetten illustrated by Berckhemer (1922, pl. 1, fig. 12), erroneously said to be the “holotype” (Checa 1985: 130), is here designated as the lectotype and refigured photographically (Fig. 3A–A4). This specimen was slightly damaged by fire during Second World War; an older plaster cast of the specimen in original dimensions is still available (Fig. 3A1–A2). The type horizon of P. hermanni is the subsidens horizon of the Subeumela Subzone (Fig. 2).

Checa (1985) included Aspidoceras hermanni Berckhe-mer in Pseudowaagenia Spatth, 1931 (type species: Ammonites haynaldi Herich, 1868), because of the presence of an outer row of spines. This outer row of spines, however, is also present in other species of Physodoceras (e.g., Schweger 1998), but not developed or irregularly arranged in the innermost whorls, in contrast to the strongly bituberculate ornamentation of inner whorls in Aspisdoceras s. str. We consider the genus Pseudowaagenia Spatth, 1931 to represent a junior synonym of Physodoceras Hyatt, 1900, although several taxa with a remarkably evolute whorl expansion included by Checa (1985) in that genus (e.g. Aspidoceras acanthomphalus Zittel) may represent another lineage giving rise to Hybonoticeras.

Scheide (1915) based the definition of Sutneria subeu-mela on three specimens: the one figured in the pl. 6, fig. 7 of his paper coming from the vicinity of the village Wellheim in Franconia, a second one from the same locality and bed, and a further specimen from Nusplingen in Swabia, published as Ammonites n. sp. by Haizmann (1902, pl. 14, fig. 5). The specimen originally figured by Scheide (1915, pl. 6, fig. 7) was refigured photographically by Schlegalmilch (1994, pl. 59, fig. 12) erroneously as the “holotype”, following Barthel (1959) and Zees (1979). This specimen (Fig. 3B) is herein formally designated as the lectotype. The other specimen from Wellheim, now representing not only a syntype but also a toptype, was mentioned as the “paratype” by Barthel (1959) who illustrated the suture line of this specimen (see Fig. 3C). The lectotype and toptype of S. subeumela were collected from an unspecified horizon, but according to co-occurring oppelids illustrated by Scheide (1915) it is very likely that it comes from the subsidens horizon (see Fig. 2).

Present authors have collected abundant ammonites from the type horizon of both species (subsidens horizon, Subeumela Subzone) at Grabenstetten near Bad Urach, Swabia and other localities nearby, including several specimens of P. hermanni and S. subeumela.

Surprisingly, one of these newly collected specimens of S. subeumela is exceptionally well-preserved, showing, after dissection, its inner whorls identical, at comparable diameter, with those of P. hermanni collected in the same horizon (Fig. 4). The last whorl of the phragmocone of this well preserved microconch specimen is moderately evo-
lute with compressed subelliptical whorl section, slightly higher than wide. The flanks are gently convex and the venter rounded. There are two rows of tubercles, one of them on the umbilical shoulder and the remaining on mid-flank. There is a single primary rib connecting an umbilical tubercle with a lateral tubercle. The rib is confined between the tubercles; the upper flank and venter are completely smooth. The whorl section of the body-chamber is higher than wide, covered by densely spaced, strong fal-coid ribs; most of them bifurcate on mid flank given rise to a weak tubercle.

*S. subeumela* usually shows a wide range of morphological variation in adult size. However, within the studied material the evolute specimen with bituberculated inner whorls described above is unique. Other specimens exhibit a typical morphology of the inner whorls, smooth with a row of periumbilical lamelliform tubercules (much like in the innermost whorls of *Physodoceras* in general at about 5 < D < 10 mm), but never bituberculate (cf. Figs. 3C, 5B–5F).

*P. hermanni* is represented by a wide variety of morphotypes in two classes of adult size and ornamentation. The smaller specimens (Figs. 3A lectotype, 6A–B, 6D–E, 7A–7E) with a diameter ranging within 25–55 mm (see BERCKHEMER 1922: 76) and the much larger specimens (Fig. 7F) with adult diameters at the body-chamber which may be of 120 mm or more (previously determined as ‘Aspidoceras longispinum’, e.g. BERCKHEMER & HOLDER 1959). Inner whorls of all the macroconchs show the ventral furrow which is characteristic of the species (inner whorls of a large macroconch are shown in Fig. 6C). Like in *S. subeumela* the ventral furrow is only well visible in

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**Fig. 4.** *Sutneria subeumela* SCHNEID [m]; subsidens horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian; Grabenstetten near Bad Urach, SW Germany. Adult specimen (SMNS 67288/1; leg. A. SCHERZINGER) showing the phragmcone with the exact morphology of the macroconch, passing in the body-chamber to the typical morphology of the microconch. – *A*–*A*: Natural size; *A*–*A*: Double size.

**Fig. 5.** *Physodoceras hermanni* (BERCKHEMER) [M] / *Sutneria subeumela* SCHNEID [m], subsidens horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian; vicinity of Lenningen-Schopfloch, SW Germany. – *A*: Complete adult microconch (SMNS 67288/2; leg. A. SCHERZINGER); vicinity of Lenningen-Schopfloch, SW Germany. – Asterisk at last septum. All natural size, otherwise indicated.
few cases because when the steinkerns were laterally compressed during early diagenesis, the ventral furrow disappeared. Even in the lectotype the furrow is very weak. Preservation of the furrow, however, is much better if the specimens are vertically embedded. Then, if there is no lateral compression, the furrow shows its original dimension (Figs. 6C, 7A). The smaller adults have a rather weak ornamentation which fades out on the body-chamber, but in the larger specimens the ornamentation continues almost to the end of the body-chamber. Representative specimens are shown in Figs. 3A, 5A, 6A–B, 6D–E and 7A–7E. When comparing the macroconchs, the smaller ones seem to have the ontogenetic development precociously halted by early sexual maturation (progenesis) in respect to the larger ones.

In the sampled horizons, due to the very hard and pure limestone and the frequent presence of fragmented shells, it is impossible to collect their ammonite content in quantity. This situation precludes accessory statistical analysis of the described patterns of structure of the species. However, after several years of sampling it became obvious that the abundance of microconchs, small and large macroconchs markedly differs in various outcrops. In the central part of the Swabian Alb (e.g. vicinity of Grabenstetten, Lenningen-Schopfloch), the small specimens of *P. hermanni* and the corresponding microconch *S. subeu­mela* are almost equally frequent, whereas the large macroconchs are rare, always less than 5% of the samples.
Another rather large sample comes from scientific excavations in the laminated limestones of Brunn in Eastern Bavaria (Röper et al. 1996). There, *S. subeumela* and the large morph of *P. hermanni* are both extremely rare, whereas the small *P. hermanni* – interpreted by Röper et al. (1996) as juveniles – is the most common ammonite of this locality, and the ratio between microconchs and small macroconchs is ca. 1 : 100. The small specimens of *P. hermanni* (‘Aspidoceras’ in Keupp et al. 1999) are often settled with barnacles during life. The locality of Brunn is dated in the *kiderleni* horizon of the Subeumela Subzone (Schwegert 2007).

3. Discussion and conclusion

In summary *P. hermanni* and *S. subeumela* are characterized by a wide variety of morphotypes in a continuous series of intraspecific variation, and additionally by a co-occurring larger morphotype of *Physodoceras*. Therefore, besides a sexual dimorphism between microconchs and macroconchs, a second macroconch morph occurs. This observation points to different times of sexual maturation of macroconchs within the populations. It is the question which of the two size classes of macroconchs is the normal for the genus. Considering other dimorphic pairs in species, it can be concluded they belonged to a single biozone horizon of the Setatum Subzone of Swabia, and the co-occurrence of both taxa in exactly the same horizons in different, geographically widely separated localities, it can be concluded they belonged to a single bi-species. The strong variation observed in both dimorphs is assumed intra-sexual polyphenism, that is the occurrence of two or more morphotypes (phenotypes) originated in environmental variation, rather than genetic variation.

The unique microconchiate *S. subeumela* showing a bituberculate sculpture stage, undoubtedly typical for females, suggests either a weak sex determination (hermaphroditism?) or a sex change in the subadult stage. This phenomenon is not unusual in gastropods (e.g., *Calyptraea Lamarck*, 1799) and other mollusks, but there are only two recently described, rather inconclusive cases in cephalopods: pseudohermaphroditism (Ortiz & Re 2006), and sex change or intersexuality (Hoving et al. 2006). Hoving et al. (2006) found within samples of Ancistrocerus leseuerii (d’Orbigny, 1842) some intersexual males (intermediate in size between normal males and females) with nidamental glands, but they attributed the phenomenon to some external environmental factors not related with the natural environment of the species. In the fossil case it may be questioned if such phenomenon is unique or widespread but overlooked. Indeed at least one other hot candidate for an intersexual microconch has been illustrated by Sykes & Calmon (1979) in another family of Jurassic ammonites, in the genus Ringsteadia Salfeld, 1913. Usually the genus Ringsteadia is coupled with the microconch genus Microbiplices Arkell, 1936 (see, e.g., Schairer & Schlamp 2003). From the Oxfordian of Scotland, a specimen of Ringsteadia caledonica Sykes & Calmon, 1979 showing the subadult sculpture of a macroconch unexpectedly developed a lappet and thus obviously changed into a microconch (Sykes & Calmon 1979, pl. 121, fig. 9). Moreover, some specimens described as Ataxioceras (Schneidia) by Atrops (1982) exhibit an unusually narrow umbilicus strongly resembling female, macroconch, individuals, but they develop lappets at their mouth borders.

4. References


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Manuscript received: 22.4.2008, accepted: 15.10.2008.