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

Neue Aufsammlungen der dimorphen Ammoniten *Physodoceras hermanni* (Berckhemer) [M] und *Sutneria subeumela* Schneid [m] aus dem Oberjura (Beckeri-Zone, Subeumela-Subzone, *subsidens*-Horizont) der Schwäbischen Alb erbringen den Erstnachweis von innerartlichem Polyphenismus der Aspidoceratidae. Bei den Makroconchen lassen sich zwei Größenklassen unterscheiden, die unterschiedlichen Beginn der Geschlechtsreife anzeigen. Dies führt zu kleinen Individuen und großen Individuen. Bei den Mikroconchen ist eine kontinuierliche Variationsbreite festzustellen. Daneben wurde ein möglicher Fall von Geschlechtsumwandlung im subadulten Stadium gefunden, was auf das Vorkommen von Zwittrigkeit bei Ammoniten deuten könnte.

Resúmen

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 contínua 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 amonites.

Contents

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 (Zeiss 1979; Olóriz & Rodríguez-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-

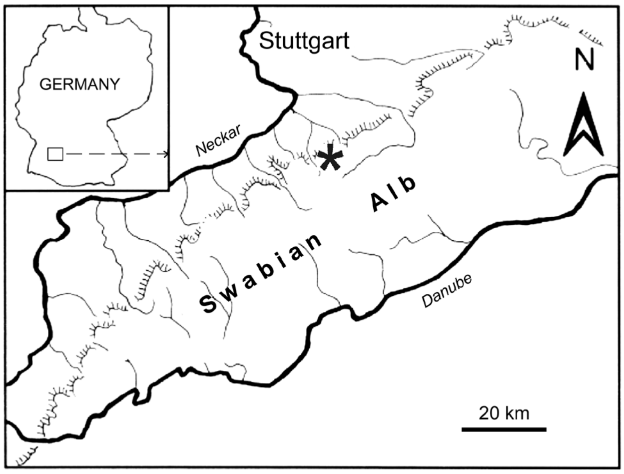

Fig. 1. Map showing the locality (asterisk) of provenance of the studied ammonites.

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 & HÖLDER 1959). Both taxa have been also recorded outside their type areas, from Le Pouzin in SE France (HÖLDER & 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 & HÖLDER (1959: 61–62) and HÖLDER & ZIEGLER (1959: 194). The ventral furrow in *S. subeumela* led to a generic separation of *Enosphinctes* SCHINDEWOLF,

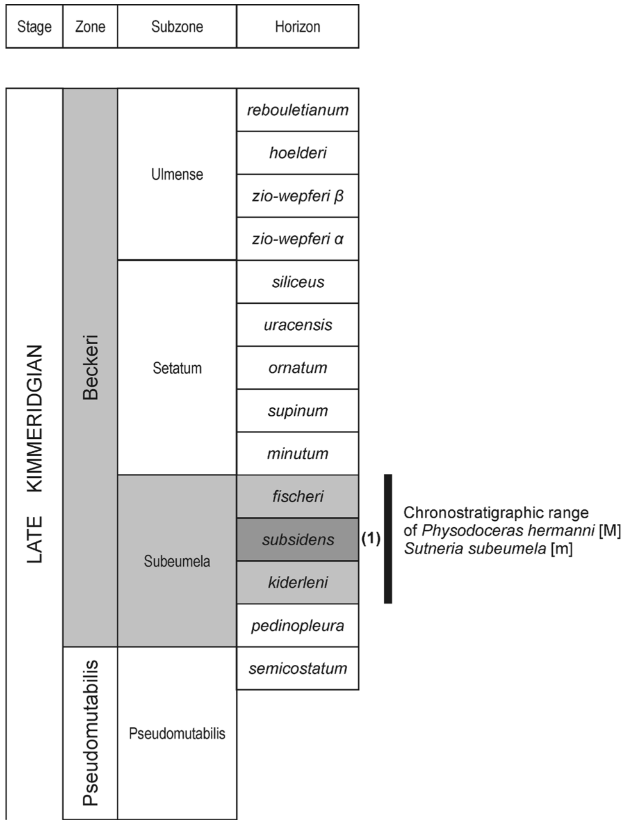

Fig. 2. Chronostratigraphic age and range of *Physodoceras hermanni* (BERCKHEMER) and *Sutneria subeumela* SCHNEID. Chronostratigraphy after SCHWEIGERT (2007). (1): Type horizon of *P. hermanni* and most probably of *S. subeumela*. The Pseudomutabilis Zone is not yet studied in detail.

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

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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$_3$–A$_4$). 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. 3A$_1$–A$_2$). The type horizon of *P. hermanni* is the *subsidens* horizon of the Subeumela Subzone (Fig. 2). Checa (1985) included *Aspidoceras hermanni* Berckhemer in *Pseudowaagenia* Spath, 1931 (type species: *Ammonites haynaldi* Herbich, 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., Schweigert 1998), but not developed or irregularly arranged in the innermost whorls, in contrast to the strongly bituberculate ornamentation of inner whorls in *Aspidoceras* s. str. We consider the genus *Pseudowaagenia* Spath, 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*.

Schneid (1915) based the definition of *Sutneria subeumela* 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 Schneid (1915, pl. 6, fig. 7) was refigured photographically by Schlegelmilch (1994, pl. 59, fig. 12) erroneously as the "holotype", following Barthel (1959) and Zeiss (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 topotype, was mentioned as the "paratype" by Barthel (1959) who illustrated the suture line of this specimen (see Fig. 3C). The lectotype and topotype of *S. subeumela* were collected from an unspecified horizon, but according to co-occurring oppeliids illustrated by Schneid (1915) it is very likely that it comes from the *subsidens* horizon (see Fig. 2).

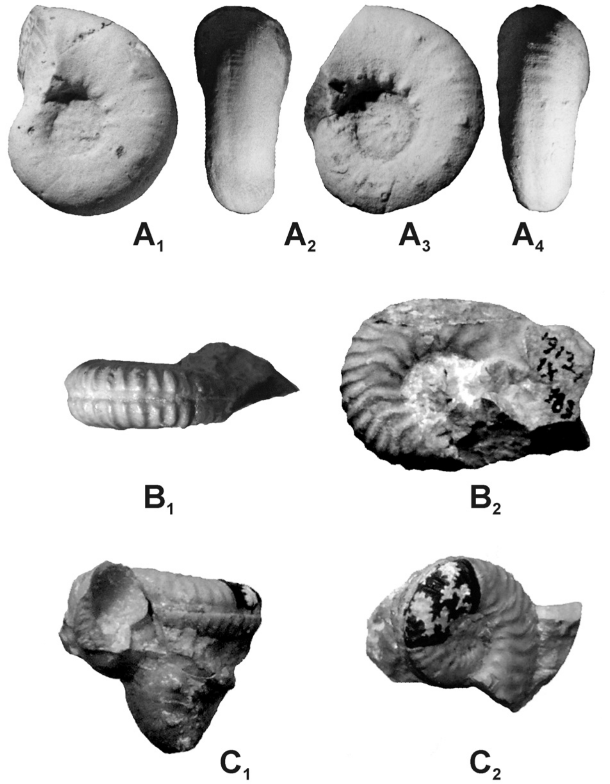

Fig. 3. **A**. *Physodoceras hermanni* (Berckhemer) [M], lectotype; *subsidens* horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian; Kaltental near Grabenstetten, near Bad Urach, SW Germany. – **A$_1$–A$_2$**. Plastercast (SMNS 60042/2) of the damaged original specimen (**A$_3$–A$_4$**: SMNS 60042/1). **A$_1$**, **A$_3$**. Lateral views. **A$_2$**, **A$_4$**. Ventral views.
B–C. *Sutneria subeumela* Schneid [m]; *subsidens* horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian; Galgenberg near Wellheim, S Germany. – **B**. Lectotype (BSPM 1913 IX 183). **B$_1$**. Ventral view. **B$_2$**. Lateral view. **C**. Syntype (BSPM 1913 IX 183a). **C$_1$**. Ventral view. **C$_2$**. Semilateral view. – All natural size.

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-

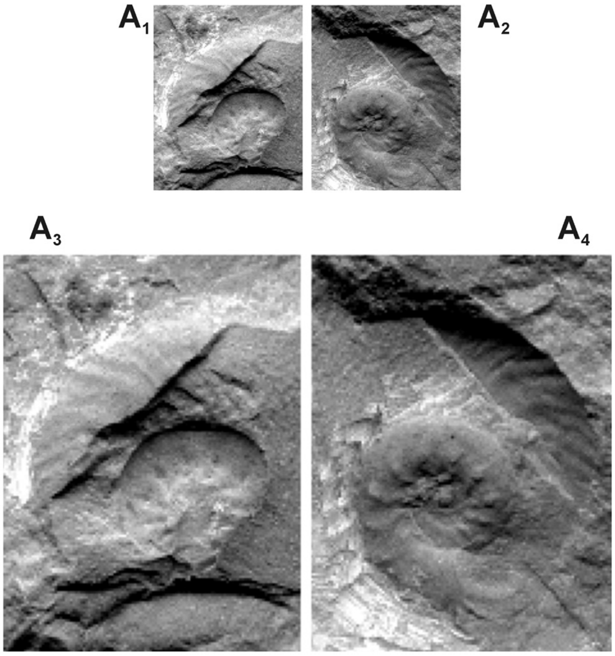

Fig. 4. *Sutneria subeumela* SCHNEID [m]; *subsidens* horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian; Grabenstetten near Bad Urach, SW Germany. Adult specimen (SMNS 67288/1; leg. A. SCHERZINGER) showing the phragmocone with the exact morphology of the macroconch, passing in the body-chamber to the typical morphology of the microconch. – **A_1–A_2**: Natural size; **A_3–A_4**: Double size.

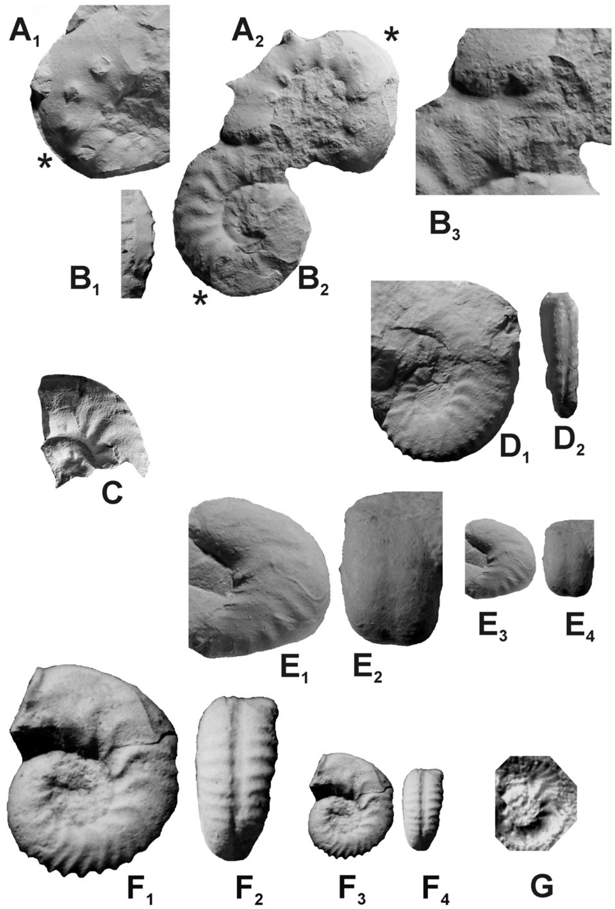

Fig. 5. *Physodoceras hermanni* (BERCKHEMER) [M] / *Sutneria subeumela* SCHNEID [m], *subsidens* horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian. – **A–E**: Möck quarry at Grabenstetten near Bad Urach, SW Germany (leg. H. PARENT). **A**. Small adult macroconch (LPB 1071/1). **A_1**. Left lateral view. **A_2**. Right lateral view. **B**. Complete adult microconch (LPB 1071/2). **B_1**. Ventral view. **B_2**. Lateral view. **B_3**. Detail of lappet, double size. **C**. Adult microconch (LPB 1077), lateral view. **D**. Complete adult microconch (LPB 1075). **D_1**. Lateral view. **D_2**. Ventral view. **E**. Inner whorls of an inflated microconch (LPB 1076). **E_1**. Lateral view. **E_2**. Ventral view. Double size. **F**. Complete adult microconch (SMNS 67289; leg. G. SCHWEIGERT); vicinity of Lenningen-Schopfloch, SW Germany. **F_1**, **F_3**. Lateral views. **F_2**, **F_4**. Ventral views. **F_1**, **F_2**: Double size. **G**. Complete adult microconch (SMNS 67288/2; leg. A. SCHERZINGER); Grabenstetten near Bad Urach, SW Germany. – Asterisk at last septum. All natural size, otherwise indicated.

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 falcoid 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$_2$, 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 & HÖLDER 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

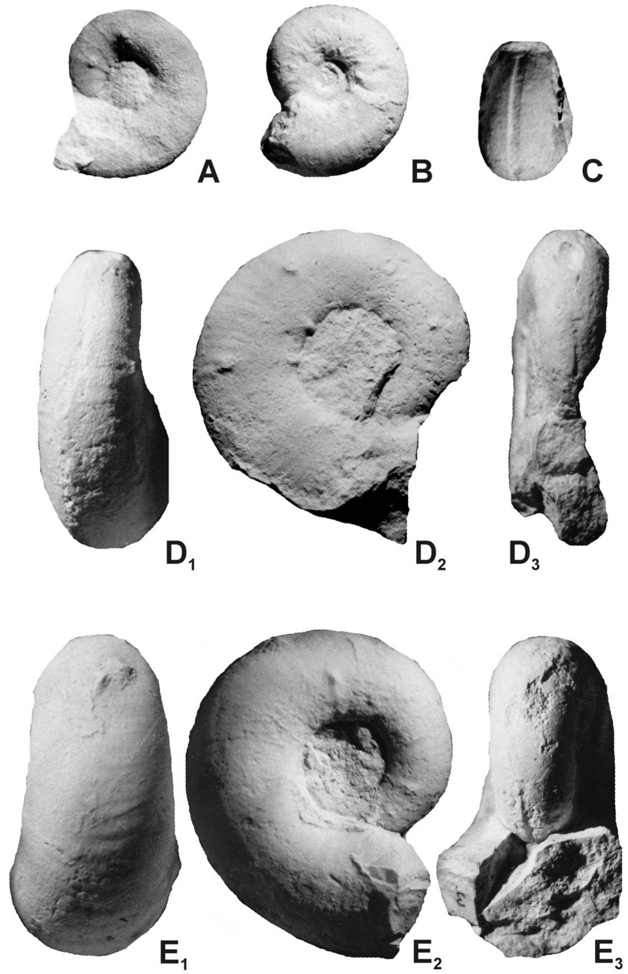

Fig. 6. *Physodoceras hermanni* (BERCKHEMER) [M]. – **A**. Syntype (SMNS 60042/3; HERMANN collection); *subsidens* horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian; Kaltental near Grabenstetten, near Bad Urach, SW Germany. **B–D**. Three specimens (SMNS 67291/1–3; BRACHER collection) from *subsidens* horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian; Herrlingen-Lautern near Ulm, SW Germany. **C**. Ventral view of inner whorls of a large macroconch showing the ventral furrow. **E**. Specimen (SMNS 67293; leg. G. SCHWEIGERT) from *kiderleni* horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian; vicinity of Lenningen-Schopfloch, SW Germany. – Asterisk at last septum. All natural size.

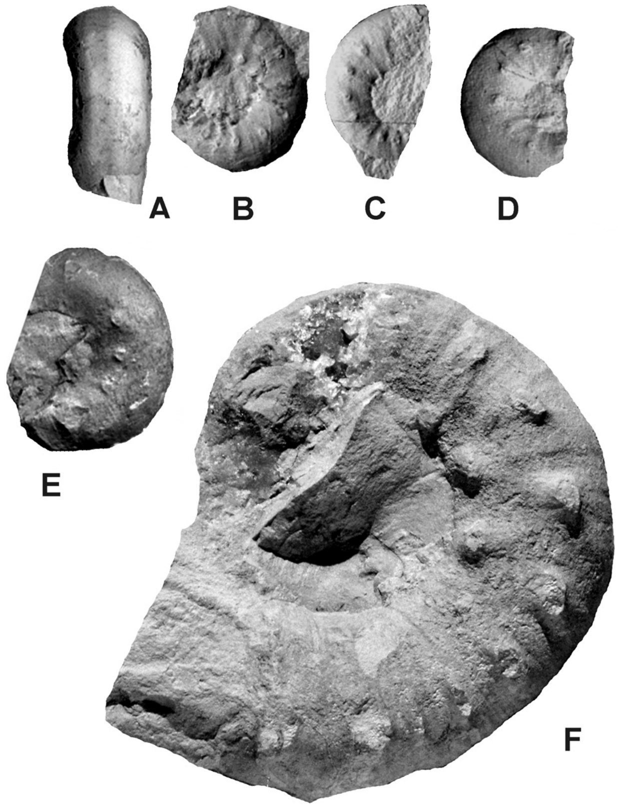

Fig. 7. *Physodoceras hermanni* (BERCKHERMER) [M]; *subsidens* horizon, Subeumela Subzone, Beckeri Zone, Late Kimmeridgian; Grabenstetten near Bad Urach, SW Germany. – **A–E**. Macroconchs of the small morphotype with nearly complete body-chamber (SMNS 67292, five specimens; leg. A. SCHERZINGER). **A**. Ventral view showing the ventral furrow. **F**. Adult macroconch of the large morph, almost complete (SMNS 67293; leg. G. SCHWEIGERT); Lenningen-Schopfloch, near Grabenstetten. – **A–E**: Natural size, **F**: × 0.6.

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 (SCHWEIGERT 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 of *Sutneria* – *Physodoceras*, e. g. *S. platynota* (REINECKE, 1818) and *P. circumspinosum* (QUENSTEDT, 1849) the macroconchs are approximately 5 to 6 times larger than the corresponding microconchs. In contrast, the small *P. hermanni* morph is only one and a half to two times larger than the microconch *S. subeumela*. [A quite similar observation can be made in *Sutneria casimiriana* (FONTANNES, 1879) and the co-occurring physodoceratids from the *ornatum* horizon of the Setatum Subzone of Swabia, but this is not outlined here]. We therefore suggest that, in the studied case, sexual maturation was accelerated as a special environmental response or reproductive strategy. It is less probable that the variations within sexes were originated in individuals maturing at different sizes after faster or slower growth, as discussed by MATYJA (1986), because of the identity of the inner whorls. Strong variation in size-at-age and timing of maturation is a well-known, dominant feature in living coleoid cephalopods (e. g. BOYLE & BOLETZKY 1996; ROCHA et al. 2001).

Considering the herein described morphological identity of inner whorls of *P. hermanni* [M] and *S. subeumela* [m] 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 biospecies. 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 & RÉ 2006), and sex change or intersexuality (HOVING et al. 2006). HOVING et al. (2006) found within samples of *Ancistrocheirus lesueurii* (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 & CALLOMON (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 & SCHLAMPP 2003). From the Oxfordian of Scotland, a specimen of *Ringsteadia caledonica* SYKES & CALLOMON, 1979 showing the subadult sculpture of a macroconch unexpectedly developed a lappet and thus obviously changed into a microconch (SYKES & CALLOMON 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.

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