Remarks on the possible function of the apophyses of the Middle Jurassic microconch ammonite *Ebrayiceras sulcatum* (Zieten, 1830), with a discussion on the palaeobiology of Aptychophora in general

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With 8 figures and 1 table

Abstract: A newly found adult specimen of the aptychophoran ammonite microconch *Ebrayiceras* from the Lower Bathonian of Sengenthal, Oberpfalz (Germany, Bavaria) exhibits completely preserved prominent peristomal apophyses. The specimen is described and figured in some detail in order to demonstrate the extreme constriction of the aperture by the apophyses. These peristomal lappets are interpreted to represent a kind of protection shield, particularly against intersexual cannibalism during mating when the ammonite had to expose soft parts. It can be assumed that the adult *Ebrayiceras* was able to protrude only small brachia and hyponome through the minute apertural openings which raises the question how the animal could gather sufficient food. We suggest the possibility of mucous web feeding in *Ebrayiceras* as is e.g. the case in modern holoplanktic and planktotrophic thecosome gastropods. Such a feeding strategy would allow the ammonite to capture fair amounts of small planktic prey using relatively short brachia and without the necessity of protruding its head. It must be concluded that only because of such or a similar feeding strategy the extreme peristomal constriction of *Ebrayiceras* was possible. It is speculated that other aptychophoran ammonites also used a mucous web to capture planktic prey.

Key words: microconch ammonites, Aptychophora, behaviour, palaeobiology, Thecosomata.

1. Introduction

Peristomes which are constricted in relation to the body chamber are quite common in ammonoids. Such shell features exist since the Palaeozoic, e.g. in Arcestidae and Scaphitidae, and show particular characteristics in the Mesozoic Aptychophora sensu Engeser & Keupp (2002). Especially since the Middle Jurassic corresponding peristomes were modified by the formation of lateral lappets (= apophyses) in various taxa such as Haploceratoidea, Stephanoceratoidea and Perisphinctoidea. The evo-lution of certain peristome features may be related to sexual dimorphism which could be demonstrated with the aid of shared pre-adult ontogenetic shell characters in the context of common stratigraphical and geographical occurrences of male and female morpho-types, with the males usually significantly smaller (microconchs) than the females (macroconchs). Examples of such dimorphic couples (male/female) are *Normannites/Stephanoceras, Otoites/ Emilieia, Ebrayiceras/Morphoceras, Oecoptychius/ Phlycticeras, Sutneria/Physodoceras* and *Parata-xioceras/Ataxioceras* (cf. Westermann 1964;

Fig. 1. *Ebrayiceras sulcatum* (ZIETEN), 27 mm in diameter, from the Lower Bathonian of the Winnberg-quarry near Sengenthal/Oberpfalz showing the hammer-like lateral and the small ventral apophyses (MAn-3031).

SCHWEIGERT 1997; SCHWEIGERT & DIETZE 1998 1999; KEUPP 2000). On the other hand dimorphic couples have been postulated which have to be re-evaluated, e.g. *Taramelliceras/Glochiceras*, because minute differences in pre-adult shell ontogeny coincide with differences in stratigraphical distributional patterns (see ZIEGLER 1974; DAVIS et al. 1996). In this case, the true dimorphic relationships are *Taramelliceras/Lingulaticeras* and *Ochetoceras/Glochiceras* (pers. comm. G. SCHWEIGERT).

The formation of apophyses projecting laterally or more seldom additionally ventrally from the peristome seems to be confined to microconchs of Aptychophora except for single lappet bearing specimens of Early Jurassic *Juraphyllites* MÜLLER, 1939 (e.g. COPE 1992) belonging to the phylloceratid stem group of all other Jurassic and Cretaceous ammonites (ARKELL 1950). The terminal formation of apophyses may lead to an apertural constriction which can be extreme in the case of distally converging shell projections. Such extreme constrictions have been reported from the microconch morphoceratid *Ebrayiceras* (DOUVILLÉ 1881; BERRY 1928; HAHN 1970; MANGOLD 1970). The functional morphology of such shell features has been discussed in different respects. E.g. BERRY (1928) and BAYER (1970) considered such ammonites microphagous, however, did not use this conclusion to

re-evaluate the feeding strategies of ammonoids in general. Considering that macroconchs do not exhibit the extreme apertural constrictions of certain microconch counterparts, the question arises whether intersexual niche divergence existed. Taking into account that there are no intraspecific differences known neither between juveniles and adults nor between microconchs and macroconchs, regarding the spectrum of predators (personal observation H.K.), it could be assumed that intraspecific and particularly intersexual niche divergence is unlikely. We here seize the opportunity of having an excellently preserved *Ebrayiceras sulcatum* (ZIETEN 1830) at our hands, in which peristomal apophyses can be studied in detail. The functional morphology of these shell features is re-evaluated and the possible consequences for the palaeobiology of aptychophoran ammonoids in general are discussed.

2. *Ebrayiceras sulcatum* (ZIETEN, 1830) from the Middle Jurassic of Sengenthal, Oberpfalz, southern Germany

The microconch *Ebrayiceras sulcatum* (Fig. 1) has been found in 2007 in complete preservation by WALTER ESBERGER, Rosstal, who collected the spe-

Fig. 2. *Morphoceras macrescens* (Buckman), the macroconch counterpart of *Ebrayiceras*, Lower Bathonian of St. Benin d'Azy, France (MAn-3001), 52 mm in diameter.

cimen from the Winnberg quarry in Sengenthal south of the village of Neumarkt and subsequently used airbrasive to expose the details of the shell. The conch rests with its left side on the matrix. It has a maximum diameter of 25 mm (excluding apophyses) and 27 mm (including apophyses) respectively. The measurements (relative whorl height: 33.5 %; relative whorl width: 30 %; relative width of umbilicus: 39.5 %) are within the known range for the species (cf. Hahn 1970).

The ammonite originates from "bed 11" termed in the description of the outcrop by Callomon et al. (1987). Within the highly condensed upper Middle Jurassic, bed 11 represents the Early Bathonian subzone of *Morphoceras macrescens*. Beside bed 11 the Bathonian of Sengenthal is represented by three more carbonatic Fe-oolithic beds: bed 10 represents the *Parkinsonia convergens* subzone; bed 12 represent the Middle Bathonian; bed 13 probably represents the Upper Bathonian and Lower Callovian exhibiting exclusively re-deposited ammonites from the Lower and Middle Bathonian. The exclusive joint occurrence of *Ebrayiceras sulcatum* and *Morphoceras macre-*

scens (Buckmann) in bed 11 (cf. Fischer 2008) supports the statement by Hahn (1970) that this dimorphic couple is confined to the *Morphoceras macrescens* Subzone in southern Germany.

3. Description of the peristome

Only the right flank of the conch is completely preserved in respect of the peristome which exhibits lateral as well as ventral apophyses (Fig. 1). The right lateral apophysis is 11.5 mm long and shows a hammer-like outline, the "hammer handle" being 3.6 mm wide, the "hammerhead" having a width of 10 mm. The distal parts of the lateral apophyses converge frontally (cf. Mangold 1970). Dorsally the lateral projections leave a slit-like recess of 2.2-2.5 mm width. The ventral part of the peristome shows two additional small shell projections having a length of 4.2 mm and distally converging with the "hammer-heads" of the lateral apophyses. By these two ventro-lateral oval openings are formed having a maximum length of 5 mm and a maximum width of 3.5 mm. The

Fig. 3. *Lingulaticeras solenoides* (QUENSTEDT) from the Solnhofen plattenkalks of Schönau near Eichstätt (Lower Tithonian) showing the hammer-like apophysis and the lamellaptychus in situ. MAa-44, diameter 32 mm.

enclosure between the ventral apophyses is slit-like, 5 mm long and 1.5 mm wide, terminally tapering between the "hammerheads".

The macroconch counterpart of *Ebrayiceras sulcatum, Morphoceras macrescens* (Fig. 2), exhibits a maximum diameter in a range of 5-10 cm. The peristome of *M. macrescens* shows no external projections, the aperture, however, is also lessened in extent by an internal thickening of the shell. The diameter of the body-chamber is larger in early ontogeny than in late ontogeny. On the other hand the length of the body-chamber is enlarged from three quarters of a whorl to one whorl during late ontogeny. This means that the volume remains more or less constant despite the decrease in whorl diameter.

4. Comparable peristomal projections in other molluscan taxa

4.1. Examples from the Aptychophora sensu ENGESER & KEUPP (2002)

Lappet-like peristomal shell projections in microconch taxa appear in the fossil record since Late Toarcian und Early Aalenium, respectively, initially within the superfamily Hildoceratoidea (families Phymatoceratidae HYATT, 1867, Hildoceratidae Hyatt, 1867 and Graphoceratidae BUCKMAN, 1905), the stem-group of the Aptychophora and later in the Jurassic in increasing numbers within the Haploceratoidea, Stephanoceratoidea and Persphinctoidea (Figs. 3-4). Within the Cretaceous aptychophoran taxa Desmoceratoidea and Acanthoceratoidea the number of microconch taxa with peristomal projections is much lower. Lateral peristomal lappets can elsewhere be found in Ancyloceratina sensu WIEDMANN 1969, particularly in the Otoscaphitinae, a basal group of scaphitids. Moreover, Scaphitidae represent the only group of "Ancyloceratina" with aptychi. It is thus suggested that their phylogenetic origin lies within the Perisphinctoidea and "Ancyloceratina" therefore have to be considered polyphyletic (ENGESER & KEUPP 2002). Table 1 compiles some but not all representatives of aptychophoran (and "ancyloceratinan") microconch taxa bearing lateral apophyses and, if known, their lappet-free macroconch antidimorphs.

4.2. Examples from gastropods

There are no modern cephalopods exhibiting peristomal shell projections which could be investigated
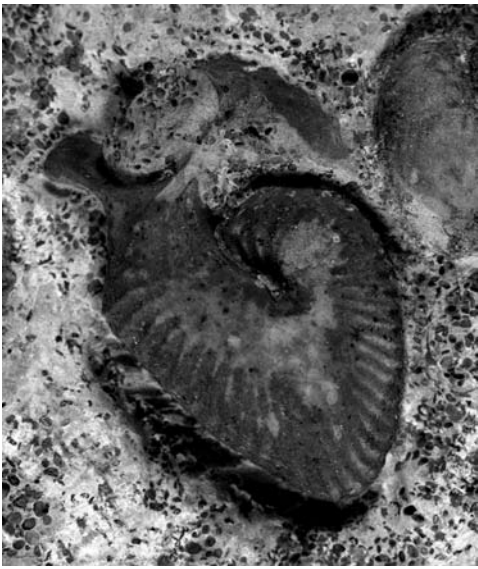
Fig. 4. Dimorphic pair of *Oecoptycius* (left, diameter: 22 mm) and *Phlycticeras* (right, diameter: 55 mm), Middle Callovian from Pas de Jeu near Poitou, France (from KEUPP 2000).

in order to understand the functional morphology of their ammonoidean counterparts. The best modern analogue has to be searched for within the gastropods. These are considered to represent the sister-group of cephalopods because both groups share the apomorphic character of having cephalic eyes. The search for analogous shell characters is restricted to planktonic gastropods. There are some groups of shelled gastropods which are holoplanktonic such as Heteropoda (Caenogastropoda) and Thecosomata (Heterobranchia) (cf. LALLI & GILMER 1989). Moreover, the early ontogenies of many gastropod taxa are characterised by shelled planktotrophic veliger larvae which feed and develop in the pelagic environment from a few weeks to more than a year (see RIEDEL 2000 and references therein).

Teleoconchs of Heteropoda do not exhibit pronounced peristomal projections (personal observations F.R.). Thecosomata comprise species with lappet-like, beak-like or spine-like apertural apophyses (e.g. see VAN DER SPOEL 1967, personal observations F.R.). Such features, however, are confined to certain Euthecosomata of the Thecosomata and are not developed at all in the Pseudothecosomata, the second group of thecosomes. Thecosomata are characterised by a pair of wing-like foot extensions which are mainly used for swimming, particularly for escape movements and diurnal vertical migrations (e.g. see RICHTER 1977; personal observations F.R.). In contrast to the euthecosomes, the two wings are fused in pseudothecosomes. Thus, a peristomal shell projection can be pronounced between the two separate wings of Euthecosomata while it cannot be formed in Pseudothecosomata. To our knowledge the function of peristomal projections which occur in certain Euthecosomata such as *Cavolina longirostris* (LESUEUR in BLAINVILLE, 1821) has not been discussed yet. At least in some euthecosomes which do not exhibit apertural apophyses such as *Creseis* spp. the soft parts are comparatively more exposed from the shell while the animals swim (personal observation F.R. on specimens from the western Mediterranean and the Bahamas). This exposure goes beyond the separated winged part of the foot and thus apertural processes would hamper the gastropod in its swimming movements. The primary function of apertural apophyses in euthecosomes has to be considered passive defence. Apertural projections are often matched by 2-3 lateral and terminal spines respectively (e.g. LALLI & GILMER 1989). The formation of peristomal lappets and beaks leads to a shield-like protection of the aperture which becomes more or less crescent-shaped, e.g. in *Cavolina longirostris* (Fig. 5). In contrast to simple spines these broader structures may be used by

Table 1. Compilation of some post-Lower Jurassic apophyses-bearing Aptychophora concerning following authors: Callomon 1963; Dietze et al. 2002, 2005; Donavan et al. 1980; Engeser & Keupp 2002; Keupp 2000; Maeda 1993; Palframan 1966; Schairer & Dietze 1998; Schairer & Schlampp 1991; Schweigert 1997, 1998; Schweigert & Callomon 1997, Schweigert & Dietl 2001, 2008; Schweigert & Scherzinger 2004, Schweigert & Zeiss 1999, Schweigert et al. 2000, 2003, 2007; Westermann 1964; Wright et al. 1996; Ziegler 1974.

Superfamily	Family	examples of microconch genera with lateral lappets	corresponding macroconch genera
Hildoceratoidea Hyatt, 1867 (stem group of the Aptychophora)	Phymatoceratidae Hyatt, 1867	microconchs of *Haugia* Buckman, 1888	*Haugia* Buckman, 1888
	Hildoceratidae Hyatt, 1867	*Tmetoites* Westermann, 1964 *Leioceras* Hyatt, 1867 pars	*Tmetoceras* Buckman, 1892 *Leioceras* Hyatt, 1867 pars
	Graphoceratidae Buckman, 1905	*Pseudographoceras* Buckman, 1899 *Graphoceras* (*Ludwigella* Buckman, 1901)	*Ludwigia* Bayle, 1878 *Graphoceras* (*Graphoceras* Buckman, 1898)
	Sonniniidae Buckman, 1892	*Pelekodites* Buckman, 1923 *Nannoceras* Buckman, 1923	*Witchellia* Buckman, 1889 *Fontannesia* Buckman, 1902
Haploceratoidea Zittel, 1884 (excl. Aconeticeratinae)	Strigoceratidae Buckman, 1924	*Cadomoceras* Munier-Calmas, 1892 *Oecoptychius* Neumayr, 1878	*Strigoceras* Quenstedt, 1886 *Phlycticeras* Hyatt, 1900
	Haploceratidae Zittel, 1884 (incl. Glochiceratidae Hyatt, 1900)	*Glochiceras* Hyatt, 1900 *Lingulaticeras* Ziegler, 1958 *Lingulaticeras* Ziegler, 1958 *Lingulaticeras* Ziegler, 1958	*Ochetoceras* Haug, 1885 *Taramelliceras* Del Campana, 1904 *Metahaploceras* Spath, 1925 *Neochetoceras* Spath, 1925
	Oppeliidae Douvillé, 1890	*Creniceras* Munier-Chalmas, 1892 *Trimarginites* Rollier, 1909 pars *Cymaceras* (*Trochiskioceras* Schairer & Schlampp, 1991) *Cyrtosiceras* Hyatt, 1900	*Streblites* Hyatt, 1900 *Trimarginites* Rollier, 1909 pars *Cymaceras* (*Cymaceras* Quenstedt, 1887) *Semiformiceras* Spath, 1925
?	Aconeceratinae Spath, 1923	*Sanmartinoceras* Bonarelli, 1921	*Aconeceras* Hyatt, 1903
Stephanoceratoidea Neumayr, 1875 (excl. Kosmoceratidae Haug, 1887)	Otoitidae Mascke, 1907	*Otoites* Mascke, 1907 *Trilobiticeras* Buckman, 1919	*Emileia* Buckman, 1898 *Docidoceras* Buckman, 1919
	Stephanoceratidae Neumayr, 1875	*Normannites* Munier-Chalmas, 1892 *Polyplectites* Mascke, 1907 *Pseudogarantiana* Bentz, 1928	*Stephanoceras* Waagen, 1869 *Cadomites* Munier-Chalmas, 1892 *Orthogarantiana* Bentz, 1928
	Sphaeroceratidae Buckman, 1920	none	
	Tulitidae Buckman, 1921	*Morrisiceras* (*Holzbergia* Torrens, 1971)	*M.* (*Morrisiceras* Buckman, 1920)

Table 1 cont.

	Macrocephalitidae BUCKMAN, 1922 Pachyceratidae BUCKMAN, 1918 Mayaitidae SPATH, 1928, Cardioceratidae SIEMIRADZKI, 1891	none	
Perisphinctoidea BUCKMAN, 1920	Kosmoceratidae HAUG, 1887	*Spinikosmoceras* BUCKMAN, 1924	*Kosmoceras* WAAGEN, 1869
(incl. Kosmoceratidae HAUG, 1887)	Parkinsoniidae BUCKMANN, 1920	*Strenoceras* HYATT, 1900	
	Morphoceratidae HYATT, 1900	*Ebrayiceras* BUCKMAN, 1920	*Morphoceras* DOUVILLÉ, 1880
	Reineckeiidae HYATT, 1900	*Reineckeites* BUCKMAN, 1924	
	"Perisphinctidae" STEINMANN, 1890	*Cleistosphinctes* ARKELL, *1953* *Prorsisphinctes* BUCKMAN, 1920 *Zigzagiceras* BUCKMAN, 1920 *Homoeoplanulites* BUCKMAN, 1922 *Siemieradzkia* HYATT, 1900 *Grossouvria* SIEMIRADZKI, 1898 *Elatmites* SHEVYREV, 1960 *Dichotomosphinctes* BUCKMAN,1926 *Microbiplices* ARKELL, 1936 *Orthosphinctes* SCHINDEWOLF, 1925 *Parataxioceras* SCHINDEWOLF, 1925 *Prorasenia* SCHINDEWOLF, 1925 *Parapallasiceras* SPATH, 1925	*Leptosphinctes* BUCKMAN, 1920 *Vermisphinctes* BUCKMAN, 1920 *Procerozigzag* ARKELL, 1953 *Parachoffatia* MANGOLD, 1970 *Procerites* SIEMIRADZKI, 1898 *Choffatia* SIEMIRADZKI, 1898 *Indosphinctes* SPATH, 1930 *Kranaosphinctes* BUCKMAN, 1921 and other *Ringsteadia* SALFELD, 1913 *Pseudorthosphinctes* ENAY, 1966 *Ataxioceras* FONTANNES, 1879 *Eurasenia* GEYER, 1961 *Danubisphinctes* ZEISS, 1968
	Aspidoceratidae ZITTEL, 1895	*Epipeltoceras* SPATH, 1924 *Mirosphinctes* SCHINDEWOLF, 1926 *Sutneria* ZITTEL, 1884 *Hybonotella* BERCKHEMER & HÖLDER, 1959 *Simocosmoceras* SPATH, 1925	*Clambites* ROLLIER, 1922 *Euaspidoceras* SPATH, 1931 pars *Physodoceras* HYATT, 1900 *Hybonoticeras* BREISTROFFER, 1947 *Pseudhimalayites* SPATH, 1925
	Polyptychidae WEDEKIND, 1918	none	
	Olcostephanidae HAUG, 1910	*Olcostephanus* NEUMAYR, 1875 *Spiticeras* UHLIG, 1903	
	Neocomitidae SALFELD, 1921	*Berriasella* UHLIG, 1905 *Thurmanniceras* COSSMANN, 1901	
„Desmoceratoidea ZITTEL, 1895"	Desmoceratidae ZITTEL, 1895	*Hauericeras* DE GROSSOUVRE, 1894	
(polyphyletic because of different types	Kossmaticeratidae SPATH, 1922	*Yokoyamaoceras* WRIGHT & MATSUMOTO, 1954 pars	*Yokoyamaoceras* WRIGHT MATSUMOTO, 1954 pars
of jaws)	Cleoniceratidae WHITEHOUSE 1926, Pachydiscidae SPATH 1922	none	

Table 1 cont.

Pulchelloidea DOUVILLÉ, 1890		none
Hoplitoidea DOUVILLÉ, 1890		none
Acanthoceratoidea DE GROSSOUVRE, 1894	Acanthoceratidae GROSSOUVRE, 1894 and its derivates	none
	Flickiidae ADKINS, 1928	*Salaziceras* BREISTROFFER, 1936
Suborder „Ancyloceratina WIEDMANN, 1969" (polyphyletic because anaptychid and aptychid jaws occur)		
Ancyloceratoidea GILL, 1871		none
Turrilitoidea GILL 1871		none
Douvilleiceratoidea PARONA & BONARELLI, 1897		
Deshayesitoidea STOYANOW, 1949		none
Scaphitoidea GILL, 1871	Scaphitidae GILL, 1871	*Worthoceras* ADKINS, 1928 *Yezoides* Yabe, 1910

the animal for supporting the bases of the wings and to stabilize the head while swimming.

Peristomal shell projections can also be found in planktotrophic veliger larvae of many caenogastropod taxa such as *Litiopa* RANG, 1829 (Cerithioidea), *Atlanta* LESUEUR, 1817 (Carinarioidea), *Cypraea* LINNÉ, 1758 (Cypraeoidea), *Nassarius* DUMÉRIL, 1806 (Buccinoidea), *Microdaphne* MCLEAN, 1971 (Conoidea), *Coralliophila* ADAMS & ADAMS, 1853 (Muricoidea) or *Drupa* RÖDING, 1798 (Muricoidea) (e.g. BANDEL et al. 1997; RIEDEL 2000; Fig. 6). The typical sinusigera shape of the larval aperture is used by the veliger to stabilize the head while swimming and to support the stalks of the velar lobes (personal observation F.R.). In the case that veligers are attacked and retreat into their conch apertural projections may also act as defence structures.

5. Discussion

The function of peristomal apophyses in Ammonoidea has been interpreted in different ways. In respect of

the large apophyses of *Otoites* spp. WESTERMANN (1954) concluded that the strength of the jet propulsion was increased by this funnel-like feature having allowed these animals to compete in velocity with ammonoidean counterparts with better hydrodynamics. BAYER (1970) regarded *Otoites* spp. and *Normannites* spp. as pelagic floating suspension feeders, the shell projections supporting some kind of particle filtering apparatus. BAYER (1970) suggested a niche divergence between *Otoites* and its macroconch counterpart *Emileia*, assuming that the latter lived in the benthic environment and might have crawled on the substrate. KEUPP & DIETZE (1987) assumed that apertural appendages were used by sexual partners to better attach to each other during copulation (cf. WESTERMANN 1971). LEHMANN (1990) considered pronounced lappet-like peristomal appendages of ammonoids being related to display behaviour. SCHWEIGERT & DIETZE (1998, 1999) analysed the relation between the microconch *Oecoptychius* and its macroconch counterpart *Phlycticeras* and concluded that the apophyses represented a protection for the male against the female. SEILACHER (1999) doubted
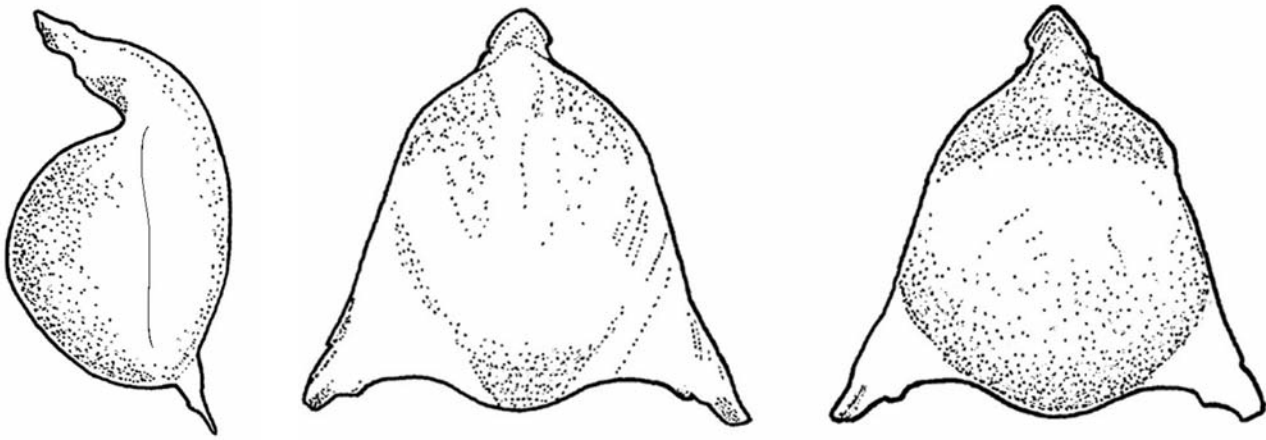
Fig. 5. Shell of the holoplanktic thecosomate gastropod *Cavolina longirostris* from the Andaman Sea (leg. RAJANI PANCHANG, Goa). This species feeds with the aid of a balloon-like mucous web. Left: lateral view with slit and apertural lappet. Middle: ventral view with aperture, Right: dorsal view. Maximum shell length: 4.8 mm.

that protection against predators was the primary function of peristomal lappets and suggested that such a protection would be even more important for the female macroconchs particularly in respect of reproduction success. SEILACHER (1999) interpreted the helmet-like structure below the lateral lappets of *Oecoptychius* as a possible receptacle, e.g. for carrying spermatophores. Additionally the helmet-like structure could have played a role in sexual display.

Moreover, SEILACHER (1999) suggested considering mimesis as a possible function of apertural shell projections.

We believe that the extreme apertural modification in *Ebrayiceras* is exceptionally suitable for discussing the function of peristomal shell projections in microconch ammonoids and that the corresponding conclusions add to the understanding of the palaeobiology of Aptychophora in general.
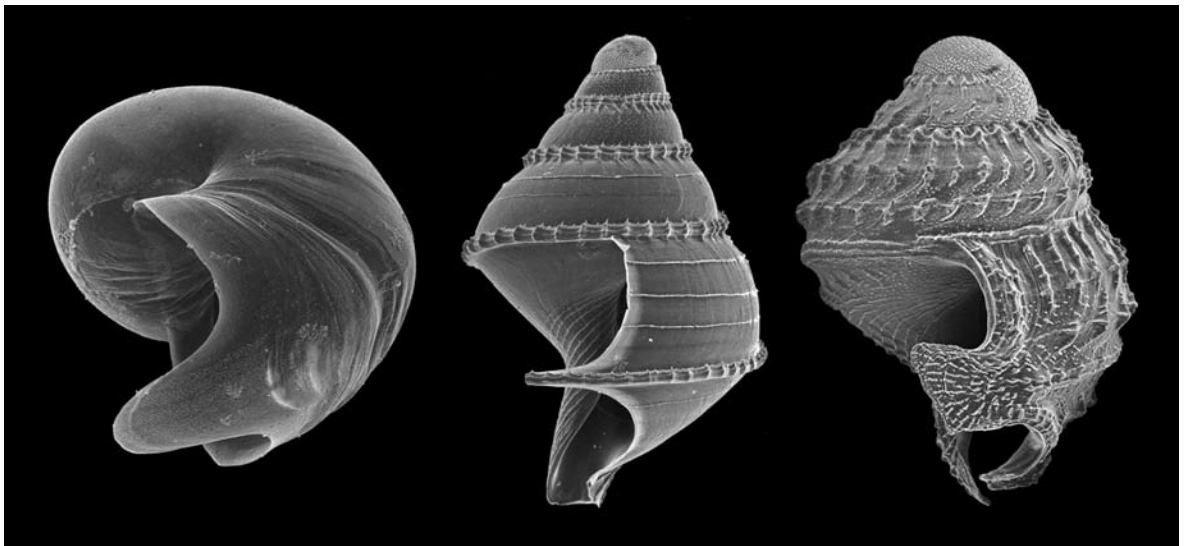

Fig. 6. Shells of three different neogastropod veliger larvae exhibiting apertural processes. Left: lateral view of newly hatched *Nassarius reticulatus* (LINNÉ, 1758) from off Roscoff, France (leg. F. RIEDEL, Berlin). Middle: shell of muricid veliger larva from the Red Sea (leg. K. BANDEL, Hamburg). Right: shell of coralliophilid veliger from the Red Sea (leg. K. BANDEL, Hamburg). Not to scale.
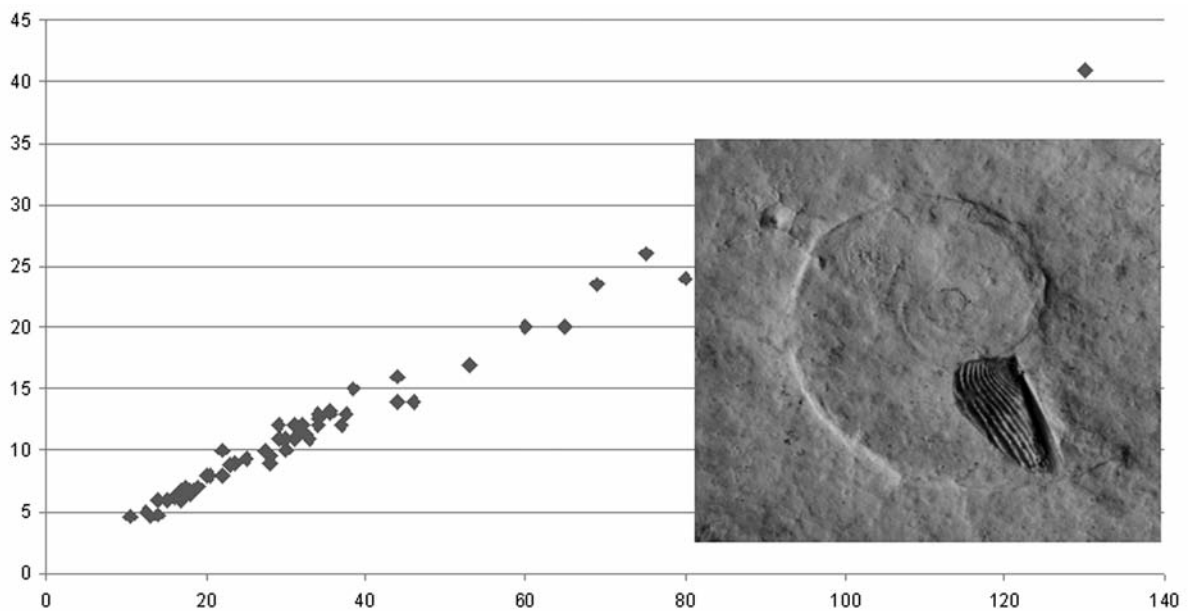
Fig. 7. The length (x-axis in mm) of *in situ* preserved lamellaptychi of oppeliid ammonites (*Neochetoceras*) from the Solnhofen plattenkalks (Lower Tithonian) increase linearly with the shell diameter (y-axis in mm). Therefore, a calculation of maximum prey size of captured juvenile ammonites is possible owing to the aptychi remains inside of the crop content.

We follow SCHWEIGERT & DIETZE (1999) who suggested that the primary function of the peristomal apophyses is protection against intersexual cannibalism. Only during mating *Ebrayiceras* had to expose soft parts being in direct contact with another cephalopod while it could seal the aperture with the aptychus under different circumstances. Cannibalism is commonly known from modern and fossil cephalopods (e.g. HANLON & MESSENGER 1996; KEUPP & VEIT 1996). Sexual cannibalism was suspected to exist but could be observed only recently, in the field in *Octopus cyanea* GRAY, 1849 (HANLON & FORSYTHE 2008) and in an aquarium tank in *Octopus joubini* ROBSON, 1929 (written communication JENNIFER MATHER 2008). In both cases the much larger female had successfully attacked and eaten the male, either after copulation or after the refusal of mating (in *Octopus joubini*).

The peristomal lappets of microconch ammonoideans define the safe distance between the sexual partners during mating. The protective function can be also seen in a more general way. Aquatic predators are strongly size-selective (NEILL 1992) which means that it is advantageous to increase the conch diameter by appendages. This is even true for minute gastropod veliger larvae (see RIEDEL 2000 and references therein). Moreover, a predator which is not able to consume a microconch ammonoidean as a whole usually attacks the aperture to get access to the soft parts of the prey (e.g. see BAYER 1970; LANDMANN & WAAGE 1986; KEUPP 1984/1985, 1997, 2000, 2006; KRÖGER 2000). Therefore, shell projections in front of the actual aperture make it more complicated for the predator to reach the retracted animal. In respect of cannibalism in modern cephalopods, such as *Martialia hyadesi* (ROCHEBRUNE & MABILLE, 1889), it appears that juveniles (and thus smaller prey) are clearly preferred for food consumption (see IVANOVIC et al. 1998). This coincides with fossil stomach contents of Late Jurassic ammonites which exhibited remains (aptychi) of juvenile counterparts (MICHAEL 1894; LEHMANN & WEITSCHAT 1973; KEUPP & VEIT 1996). E.g. the crop content of two macroconch oppelids (*Neochetoceras* with conch diameters of 7.5 cm and 13 cm) from the Upper Jurassic Solnhofen plattenkalks, exhibited comparatively small, up to 3.5 mm long lamellaptychi (KEUPP & VEIT 1996) With the aid of the size of the lamellaptychi it can be calculated that the captured juveniles had conch diameters of up to 10 mm (Fig. 7).
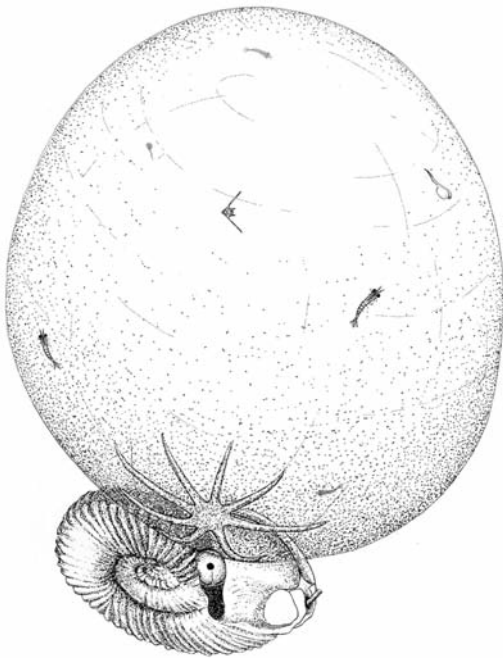
Fig. 8. Reconstruction of living *Ebrayiceras* with a balloon-like mucous web for trapping plankton (drawing by M. BULANG-LÖRCHER).

The extreme constriction of the aperture in the (male) *Ebrayiceras* might hint at a particular aggressive (female) *Morphoceras*. If this is true, intersexual niche divergence must have existed. Sexual dimorphism and niche divergence was described e.g. by VOIGHT (1995) for the octopod *Eledonella pygmaea* VERRILL, 1884 (for a general discussion see e.g. FAIRBAIRN 1997; BOLNICK & DOEBELI 2003). Our primary argument for intersexual niche divergence is that it can be ruled out that *Ebrayiceras* was preying on animals of considerable size, while *Morphoceras* was able to do so (e.g. to attack its mate) because of its non-constricted peristome. The dorsal narrow apertural opening of *Ebrayiceras* did not allow the protrusion of the head and its brachial crown in order to capture larger prey. Even if it was not necessary to protrude the head for capturing prey, captured animals of larger size could not have passed the narrow slit-like aperture to be ingested.

It thus must be concluded that *Ebrayiceras* was feeding exclusively on small prey. Capture of smaller prey at the size of micro-plankton was described for modern cirrate octopods such as *Stauroteuthis*

VERILL, 1879, *Cirroteuthis* ESCHRICHT, 1836 and *Cirrothauma* CHUN, 1911 which exhibit a web between the arms usually formed to a bell-shape (e.g. see VECHIONE & YOUNG 1997; COLLINS & HENRIQUES 2000). In order to capture sufficient food the cirrated brachial bell of these octopods has to be quite voluminous. In a species with non-cirrated brachia (and we assume that *Ebrayiceras* and probably all other aptychophoran ammonoids had non-cirrated brachia) such a filter apparatus must be even larger for supplying enough food. Consequently such a hypothetical ectocochleate cephalopod would not have been able to retract all its soft parts into the living chamber because of the huge size of the brachial apparatus. Although we cannot completely exclude that certain ammonoids developed defence mechanisms (e.g. acidic mantle secretions which are known from gastropods such as *Lamellaria* MONTAGU, 1815 (see RIEDEL 2000 and references therein)) having allowed them to keep soft parts permanently protruded, we suggest that ammonoids generally could retract completely into their living chamber. The latter is particularly true for aptychophoran ammonoids of which we assume that they have used their lower jaw to seal the aperture when having been under attack (e.g. see KEUPP et al. 1999; KEUPP 2000). Even if the operculum-like function of jaws in aptychophoran ammonoids is queried, the peristomal constrictions in *Ebrayiceras* make only sense in respect of a complete retraction being possible. From the phylogenetic context (Perisphinctoidea) it must be concluded that morphoceratids represent true Aptychophora although aptychi have not yet been found in these ammonoideans. This can possibly be explained by a reduced mineralization of the aptychi in morphoceratids. Strongly mineralized aptychi, e.g., have been found within the body chambers of the microconch genera *Lingulaticeras* and *Sutneria* which are both characterized by large lateral lappets (Fig. 3) similar to those of morphoceratids.

How did *Ebrayiceras* feed? We suggest that *Ebrayiceras* used a mucous web to trap planktonic organisms. Such a web is known otherwise from thecosome gastropods, e.g. from species of the genera *Cavolina* ABILDGAARD, 1791 (= *Cavolinia* ABILDGAARD, 1791), *Clio* LINNÉ 1767, *Limacina* BOSC, 1817 and *Peracle* FORBES, 1844 (= *Peraclis* PELSENEER, 1888) (see GILMER & HARBISON 1986). The webs are balloon-like, being 3-10 times larger in diameter than the corresponding gastropod shells. In *Cavolina tridentata* (NIEBUHR, 1775), e.g., a spe-

cimen of 15 mm shell length produced a mucous web of about one litre volume (GILMER & HARBISON 1986). In respect of cephalopods it has been speculated that hatchlings of ommastrephids are suspension feeders using cilia and mucous to trap microplankton (O'DOR et al. 1985). Due to its specific weight being lower than that of water a mucous web has to be set up on top of the animal which produces it. In respect of *Ebrayiceras* it means that the aperture would have pointed to the water surface. This assumption coincides with corresponding calculations on the orientation of *Oecoptychius* and other lappet bearing ammonites in the water column by TRUEMAN (1941). The slit-like opening for the hyponome in *Ebrayiceras* and the two ovate openings for mantle cavity water to be exchanged would be directed laterally then. Excrements disposed from the mantle cavity would not have interfered with the mucous web. The mucous web of *Ebrayiceras* would have been secreted most likely by the brachia which then represented the basal "platform" of the web (see Fig. 8). The narrow slit-like dorsal apertural opening was advantageous for supporting the brachia (analogous to corresponding appendages in certain modern Thecosomata and gastropod veliger larvae), which had to keep a certain position at the basis of the web. Apart from handling the mucous web one of the brachia was probably used for transferring spermatophores. *Ebrayiceras* followed the diurnal vertical plankton migration with the aid of its phragmocon. The hyponome was probably solely used for keeping or reaching a horizontal position. We do not consider that *Ebrayiceras* had the capability of escaping from a predator. It had to survive an attack within its sealed conch. Assuming that *Ebrayicras* migrated with the zooplankton to greater depth during the day and to lower depth during the night, it can be concluded that such behaviour would have reduced the chance of being detected by visual predators (e. g. DE MEESTER et al. 1995).

What can be generalized for other aptychophoran ammonoids? We do not believe that *Ebrayiceras* changed its feeding behaviour with the development of its peristomal apophyses. The feeding strategy must have existed already in its ancestors and thus it is very likely that other aptychophoran ammonoids, if not all, also fed on plankton, possibly using a mucous web. Certainly differences existed in respect of size-selection, and feeding via a mucous web does not exclude direct encountering of prey as we assume was the case in the presumed cannibalistic *Morphoceras*.

References

ARKELL, W. J. (1950): A classification of the Jurassic ammonites. – Journal of Paleontology, **24**: 354-364.

BANDEL, K., RIEDEL, F. & WEIKERT, K. (1997): Planktonic gastropod larvae from the Red Sea: A synopsis. – Ophelia, **47**: 151-202.

BAYER, U. (1970): Anomalien bei Ammoniten des Aaleniums und Bajociums und ihre Beziehung zur Lebensweise. – Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **135**: 19-41.

BERRY, E. W. (1928): Cephalopod adaptations – the record and its interpretations. – Quarterly Review of Biology, **3**: 92-108.

BOLNICK, D. I. & DOEBELI, M. (2003): Sexual dimorphism and adaptive speciation: Two sides of the same ecological coin. – Evolution, **57**: 2433-2449.

CALLOMON, J. H. (1963): Sexual dimorphism in Jurassic ammonites. – Transactions of the Leicester Literature and Philosophical Society, **57**: 21-56.

CALLOMON, J. H., DIETL, G., GALÁCZ, A., GRADL, H., NIEDERHÖFER, H.-J. & ZEISS, A. (1987): Zur Stratigraphie des Mittel- und Oberjuras in Sengenthal bei Neumarkt/Opf. (Fränkische Alb). – Stuttgarter Beiträge zur Naturkunde, (B), **132**: 53 pp.

COLLINS, M. A. & HENRIQUES, C. (2000): A revision of the family Stauroteuthidae (Octopoda: Cirrata) with redescriptions of *Stauroteuthis syrtensis* and *S. gilchristi*. – Journal of the Marine Biological Association of the United Kingdom, **80**: 685-697.

COPE, J. C. W. (1992): Dimorphism in a Tethyan early Jurassic *Juraphyllites*. – Lethaia, **25** (4): 439-441.

DAVIS, R. A., LANDMAN, N. H., DOMMERGUES, J.-L., MARCHAND, D. & BUCHER, H. (1996): Mature modifications and dimorphism in ammonoid cephalopods. – In: LANDMAN, N. H., TANABE, K. & DAVIS, R. A. (Eds.): Ammonoid Paleobiology, 464-539, New York & London (Plenum Press).

DE MEESTER, L., WEIDER, L. J. & TOLLRIAN, R. (1995): Alternative antipredator defences and genetic polymorphism in a pelagic predator-prey system. – Nature, **378**: 483-485.

DIETZE, V., CALLOMON, J. H., SCHWEIGERT, G. & CHANDLER, R. B. (2005): The ammonite fauna and biostratigraphy of the Lower Bajocian (Ovale and Laeviscula zones) of E Swabia (S Germany). – Stuttgarter Beiträge zur Naturkunde, (B), **353**: 82 pp.

DIETZE, V., SCHWEIGERT, G., CALLOMON, J. H. & GAUTHIER, H. (2002): Garantiana- und frühe Parkinsoni-Zone (Ober-Bajocium, Mittlerer Jura) am Ipf (östliche Schwäbische Alb, SW-Deutschland) mit Bemerkungen

zur Phylogenie der Ammonitengattung *Garantiana* MASCKE, 1907. – Stuttgarter Beiträge zur Naturkunde, (B), **315**: 89 pp.

DONOVAN, D. T., CALLOMON, J. H. & HOWARTH, M. K. (1980): Classification of the Jurassic Ammonitina. – In: HOUSE, M. R. & SENIOR, J. R. (Eds.): The Ammonoidea. – Systematics Association, Special Volume, **18**: 101-155.

DOUVILLE, H. (1881): Noté l'*Ammonites pseudo-anceps* et sur la forme de son ouverture. – Bulletin de la Société de Géologie de France, **3** (8): 239-246.

ENGESER, T. & KEUPP, H. (2002): Phylogeny of the aptychi-possessing Neoammonoidea (Aptychophora nov., Cephalopoda). – Lethaia, **34**: 79-96.

FAIRBAIRN, D. J. (1997): Allometry for sexual size dimorphism: Pattern and process in the coevolution of body size in males and females. – Annual Reviews in Ecology and Systematics, **28**: 659-687.

FISCHER, W. (2008): Faszination Winnberg 2005-2007. – 252 pp.; Schriesheim (Published by the author).

GILMER, R. W. & HARBISON, G. R. (1986): Morphology and field behaviour of pteropod molluscs: feeding methods in the families Cavoliniidae, Limacinidae and Peraclididae (Gastropoda: Thecosomata). – Marine Biology, **91**: 47-57.

HAHN, W. (1970): Die Parkinsoniidae S. BUCKMAN und Morphoceratidae HYATT (Ammonoidea) des Bathoniums (Brauner Jura ε) im südwestdeutschen Jura. – Jahrbuch des Geologischen Landesamtes Baden-Württemberg, **12**: 7-62.

HANLON, R. T. & FORSYTHE, J. W. (2008): Sexual cannibalism by *Octopus cyanea* on a Pacific coral reef. – Marine and Freshwater Behaviour and Physiology, **41**: 19-28.

HANLON, R. T. & MESSENGER, J. B. (1996): Cephalopod Behaviour. – 232 pp.; Cambridge (Cambridge University Press).

IVANOVIC, M. L., BRUNETTI, N. E., ELENEA, B. & ROSSI, G. R. (1998): A contribution to the biology of the ommastrephid squid *Martialia hyadesi* (ROCHEBRUNE and MABILLE, 1889) from the South-West Atlantic. – South African Journal of Marine Science, **20**: 73-79.

KEUPP, H. (1984-1985): Pathologische Ammoniten: Kuriositäten oder paläobiologische Dokumente? Part 1 & 2. – Fossilien, **1984** (6): 258-262, 267-275, **1985** (1): 23-35.

– (1997): Paläopathologische Analyse einer „Population" von *Dactylioceras athleticum* (SIMPSON) aus dem Unter-Toarcium von Schlaifhausen/Oberfranken. – Berliner Geowissenschaftliche Abhandlungen, (E), **25**: 243-267.

– (2000): Ammoniten, Paläobiologische Erfolgsspiralen. – 164 pp.; Stuttgart (Thorbecke).

– (2006): Sublethal punctures in body chambers of Mesozoic ammonites (forma aegra *fenestra* n. f.), a tool to interpret synecological relationships, particularly predator-prey interactions. – Paläontologische Zeitschrift, **80**: 112-123.

KEUPP, H. & DIETZE, V. (1987): Analyse eines pathologischen Perisphinctiden. – Fossilien, **1987** (6): 274-277.

KEUPP, H. & VEIT, R. (1996): Ein *Phylloceras* mit Anaptychus. – Fossilien, **1996** (6): 343-351.

KEUPP, H., RÖPER, M. & SEILACHER, A. (1999): Paläobiologische Aspekte von *syn vivo*-besiedelten Ammonoideen des Ober-Kimmeridgiums im Plattenkalk von Brunn in Ostbayern. – Berliner Geowissenschaftliche Abhandlungen, (E), **30**: 121-145.

KRÖGER, B. (2000): Schalenverletzungen an jurassischen Ammoniten – ihre paläobiologische und paläoökologische Aussagefähigkeit. – Berliner Geowissenschaftliche Abhandlungen, (E), **33**: 97 pp.

LALLI, C. M. & GILMER, R. W. (1989): Pelagic snails: The biology of holoplanktonic gastropod mollusks. – 259 pp.; Stanton (Stanford University Press).

LANDMAN, N. H. & WAAGE, K. M. (1983): Shell abnormities in scaphitid ammonites. – Lethaia, **19**: 211-224.

LEHMANN, U. (1990): Ammonoideen, Leben zwischen Skylla und Charybdis. – 257 pp.; Stuttgart (Enke)

LEHMANN, U. & WEITSCHAT, W. (1973): Zur Anatomie und Ökologie von Ammoniten. Fund von Kropf und Kiemen. – Paläontologische Zeitschrift, **47**: 69-76.

MAEDA, H. (1993): Dimorphism of Late Cretaceous false-puzosiine ammonites, *Yokohamaoceras* WRIGHT and MATSUMOTO, 1954 and *Neopuzosia* MATSUMOTO, 1954. – Transactions of the Proceedings of the Palaeontological Society of Japan, N.S., **169**: 97-128.

MANGOLD, C. (1970): Morphoceratidae (Ammonitina – Perisphinctaceae) Bathoniens du Jura méridional, de la Nièvre et du Portugal. – Géobios, **3** (1): 43-130.

MICHAEL, R. (1894): Ammoniten-Brut mit Aptychen in der Wohnkammer von *Oppelia steraspis* OPPEL sp. – Zeitschrift der Deutschen geologischen Gesellschaft, **46**: 697-702.

NEILL, W. E. (1992): Population variation in the ontogeny of predator-induced vertical migrations of copepods. – Nature, **356**: 54-57.

O'DOR, R. K., HELM, P. & BALCH, N. (1985): Can rhynchoteuthions suspension feed? (Mollusca: Cephalopoda). – Vie et Milieu, **35**: 267-271.

PALFRAMAN, D. F. B. (1966): Variation and ontogeny of some Oxfordian ammonites: *Taramelliceras richei* (DE LORIOL) and *Creniceras renggeri* (OPPEL), from Woodham, Buckinghamshire. – Palaeontology, **9**: 290-311.

RICHTER, G. (1977): Jäger, Fallensteller und Sammler. Zur Ernährung planktischer Schnecken. – Natur und Museum, **107**: 221-234.

RIEDEL, F. (2000): Ursprung und Evolution der « höheren » Caenogastropoda. – Berliner Geowissenschaftliche Abhandlungen, (E), **32**: 240 pp.

SCHAIRER, G. & SCHLAMPP, V. (1991): *Cymaceras* (Ammonitina, Ochetoceratinae) von Esselberg. – Münchner Geowissenschaftliche Abhandlungen, (A), **19**: 101-128.

SCHWEIGERT, G. (1997): Die Ammonitengattungen *Simocosmoceras* SPATH und *Pseudhimalayites* SPATH (Aspidoceratidae) im süddeutschen Oberjura. – Stuttgarter Beiträge zur Naturkunde, (B), **146**: 29 pp.

– (1998): Die Ammonitenfauna des Nusplinger Plattenkalks (Ober-Kimmeridgium, Beckeri-Zone, Ulmense-Subzone, Schwäbische Alb). – Stuttgarter Beiträge zur Naturkunde, (B), **267**: 61 pp.

SCHWEIGERT, G. & CALLOMON, J. H. (1997): Der *bauhini*-Faunenhorizont und seine Bedeutung für die Korrelation zwischen tethyalem und subborealem Oberjura. – Stuttgarter Beiträge zur Naturkunde, (B), **247**: 69 pp.

SCHWEIGERT, G. & DIETL, G. (2001): Die Kieferelemente von *Physodoceras* (Ammonitina, Aspidoceratidae) im Nusplinger Plattenkalk (Ober-Jura, Schwäbische Alb). – Berliner Geowissenschaftliche Abhandlungen, (E), **36**: 11-143.

SCHWEIGERT, G. & DIETL, G.(2008): Miscellanea aus dem Nusplinger Plattenkalk (Ober-Kimmeridgium, Schwäbische Alb). 9. Eine neue Aptychen-Formgattung. – Jahresberichte und Mitteilungen des Oberrheinischen geologischen Vereins, Neue Folge, **90**: 45-55.

SCHWEIGERT, G. & DIETZE, V. (1998): Revision der dimorphen Ammonitengattungen *Phlycticeras* HYATT – *Oecoptychius* NEUMAYR (Strigoceratidae, Mitteljura). – Stuttgarter Beiträge zur Naturkunde, (B), **269**: 59 pp.

– (1999): *Oecoptychius* – des Rätsels Lösung. – Fossilien **1999** (1): 51-58.

SCHWEIGERT, G. & SCHERZINGER, A. (2004): New efforts for a revision and correlation of the Neuburg Formation (Tithonian, SW Germany). – Rivista Italiana Paleontologia e Stratigraphia, **110**: 311-320.

SCHWEIGERT, G., DIETZE, V. & BALLE, T. (2000): Dimorphismus und Phylogenie der Ammonitengattung *Csernyeiceras* GÉCZY (Früher Mitteljura, Phlycticeratinae). – Stuttgarter Beiträge zur Naturkunde, (B), **294**: 1-13.

SCHWEIGERT, G., DIETZE, V., CHANDLER, R. B. & MITTA, V. (2007): Revision of the Middle Jurassic dimorphic ammonite genera *Strigoceras/Cadomoceras* (Strigoceratidae) and related forms. – Stuttgarter Beiträge zur Naturkunde, (B), **373**, 74 pp.

SCHWEIGERT, G., DIETZE, V. & DIETL, G. (2003): Neue Nachweise von *Phlycticeras* und *Oecoptychius* (Ammonitina: Strigoceratidae: Phlycticeratinae). – Stuttgarter Beiträge zur Naturkunde, (B), **335**: 21 pp.

SEILACHER, A. (1999): *Oecoptychius*-Rätsel. – Fossilien, **1999** (3): 131.

TRUEMAN, A. E. (1941): The ammonite body-chamber and mode of life of the living ammonite. – Quarternarly Journal of the Geological Society (London), **96**: 339-383.

VAN DER SPOEL, S. (1967): Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda). – Dissertation Amsterdam University. – 375 pp.; Gorinchem (Noorduijn).

VECHIONE, M. & YOUNG, R. E. (1997): Aspects of the functional morphology of cirrate octopods: locomotion and feeding. – Vie et Milieu, **47**: 101-110.

VOIGHT, J. R. (1995): Sexual dimorphism and niche divergence in a mid-water octopod (Cephalopoda: Bolitaenidae). – Biological Bulletin, **189**: 113-119.

WESTERMANN, G. (1954): Monographie der Otoidae (Ammonoidea). – Beihefte zum Geologischen Jahrbuch, **15**: 364 pp.

– (1964): Sexual-Dimorphismus bei Ammonoideen und seine Bedeutung für die Taxionomie der Otoitidae. – Palaeontographica, (A), **124**: 33-73.

– (1971): Form, structure and function of shell and siphuncle in coiled Mesozoic ammonoids. – Life Science Contribution Royal Ontario Museum, **78**: 39 pp.

WIEDMANN, J. (1969): The heteromorphs and ammonoid extinction. – Biological Reviews, **44**: 563-602.

WRIGHT, C. W., CALLOMON, J. H. & HOWARTH, M. K. (1996): Cretaceous Ammomoidea. – Treatise on Invertebrate Paleontology, part L, Mollusca 4 (revised). – 362 pp.; Boulder & Lawrence (Geological Society of America & University of Kansas Press).

ZIEGLER, B. (1974): Über Dimorphismus und Verwandtschaftsbeziehungen bei „Oppeliden" des oberen Juras (Ammonoidea, Haplocerataceae). – Stuttgarter Beiträge zur Naturkunde, (B), **11**: 43 pp.

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