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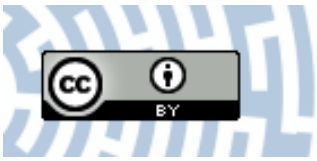
Citation style: Parent Horacio, Zatoń Michał. (2016). Sexual dimorphism in the Bathonian morphoceratid ammonite Polysphinctites tenuiplicatus. "Acta Palaeontologica Polonica" (Vol. 61, iss. 4 (2016), s. 875-884), doi 10.4202/app.00261.2016.



Sexual dimorphism in the Bathonian morphoceratid ammonite *Polysphinctites tenuiplicatus*

HORACIO PARENT and MICHAŁ ZATOŃ

Parent, H. and Zatoń, M. 2016. Sexual dimorphism in the Bathonian morphoceratid ammonite *Polysphinctites tenuiplicatus*. *Acta Palaeontologica Polonica* 61 (4): 875–884.

Asphinctites tenuiplicatus [M] and *Polysphinctites secundus* [m] from the *Asphinctites tenuiplicatus* Zone (Early Bathonian), are usually considered as a sexual dimorphic pair, although authors describe them as separate species. We used statistical methods to test the sexual dimorphic correspondence between those morphospecies, based on a rather large sample of well-preserved macro- and microconchs derived from a single horizon of calcareous concretions in the Polish Jura. Our results indicate that both dimorphs or sexes have identical ontogeny up to a critical diameter, from which they diverge towards the characteristic morphology and sculpture of each dimorph. Thus, both dimorphs are described as a single species: *Polysphinctites tenuiplicatus* [M and m]. After review of the several nominal species usually assigned to the genera *Asphinctites* and *Polysphinctites* throughout their stratigraphic and biogeographic range in the Early Bathonian of the Tethys, it is concluded that they actually correspond to only two species of a single lineage. The corresponding name for the lineage should be *Polysphinctites* (= *Asphinctites* as a junior synonym).

Key words: Ammonoidea, Morphoceratidae, dimorphism, macroconch, microconch, Jurassic, Poland.

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Received 9 March 2016, accepted 24 June 2016, available online 11 July 2016.

Introduction

Sexual dimorphism is virtually universal in living and fossil cephalopds. In ammonites, it has been considered in modern terms from the papers by Makowski (1962), Callomon (1963), and Westermann (1964), reviewed by Callomon (1981), Davis et al. (1996), and Klug et al. (2015). From a developmental point of view, sexual dimorphism in ammonites can be described as two classes of individuals with juvenile ontogeny identical up to a size (shell diameter) from which two different morphotypes develop: a macroconch (female) and a microconch (male). The morphological differentiation occurs from a more or less variable diameter in each species, which usually coincides with the diameter at the last adult septum of the microconch and can be considered the point at onset of its sexual maturation.

In many cases it is possible to recognize the sexual dimorphic correspondence between two morphs by direct, visual inspection of adults dissected and/or from growth series (specimens of different diameters). Nevertheless, homoeomorphies or similarities between phylogenetically close forms, especially in their inner whorls, can in some cases hamper a reliable recognition of the dimorphic correspondences. In these cases statistical comparisons usually provide strong support to the standard morphologic analysis. However, considering the wide geographical and phylogenetical intraspecific variability of most ammonites, statistical analysis must be applied to stratigraphically controlled samples for meaningful results. Most conveniently, the comparison should be made among samples coming from a single ammonite horizon. It is generally assumed that macroconch ammonites were the females and the microconchs the males (e.g., Palframan 1966; Guex 1970; Verma and Westermann 1973; Lehmann 1981; Schweigert 1997; Westermann et al. 2002; Landman et al. 2010; among many others). Nevertheless, it remains useful to add the former terms mainly because of some complex cases reported which seem to involve some form of hermaphroditism or sex change (e.g., Parent et al. 2008).

The macroconch ammonite *Asphinctites tenuiplicatus* (Brauns, 1865) and the microconch *Polysphinctites secundus* (Wetzel, 1950) from the Early Bathonian *P. tenuiplicatus* Zone, are commonly assumed or suggested to conform

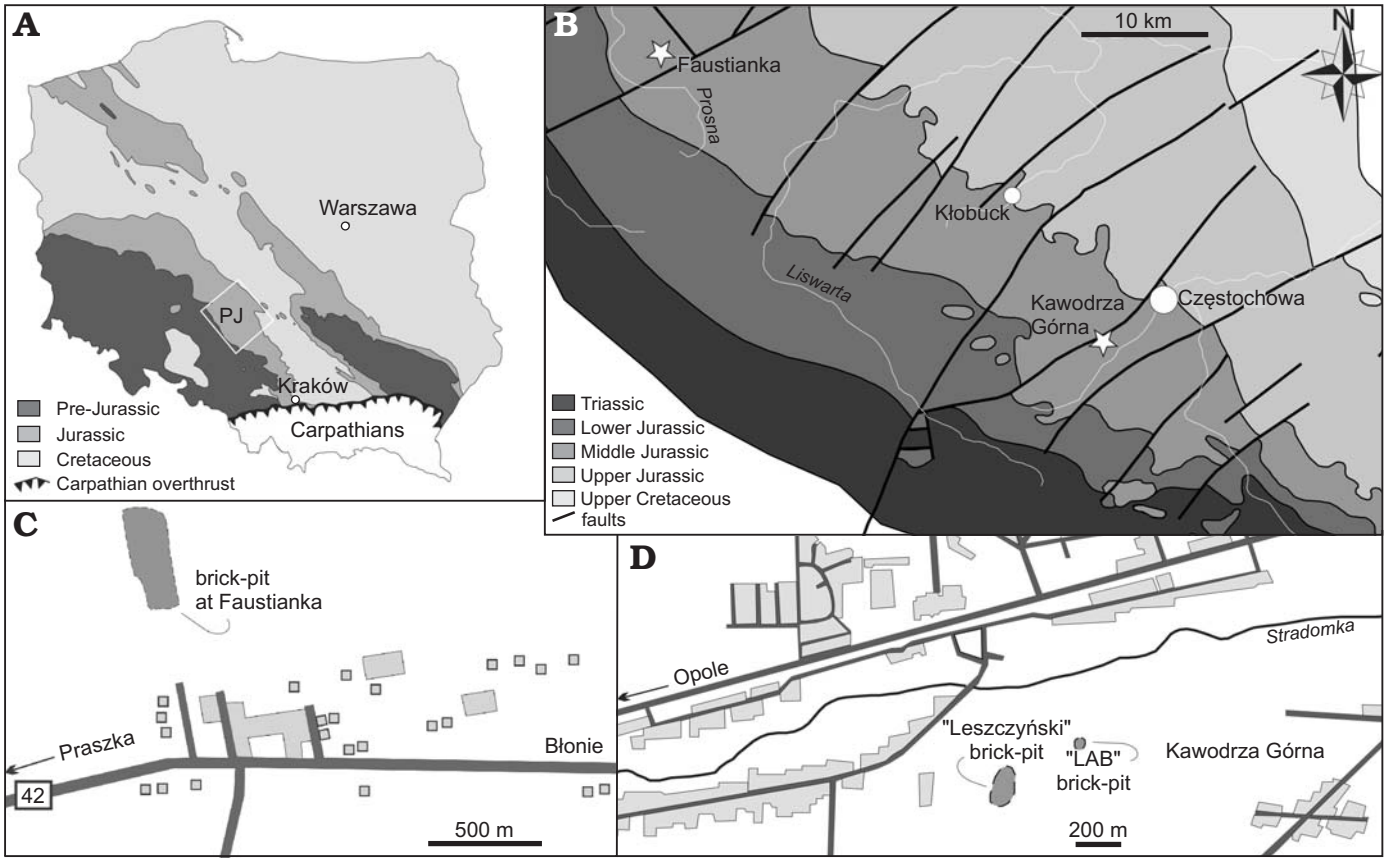

Fig. 1. **A**. Geological sketch-map of Poland with the investigated part of the Polish Jura area (PJ). **B**. Part of the Polish Jura area showing the sampled localities at Kawodrza Górna and Faustianka. Sketch-maps showing the localities of the sampled Lower Bathonian deposits at Faustianka (**C**) and Kawodrza Górna (**D**), modified after Zatoń (2010a, b).

a sexual dimorphic pair (e.g., Dietze et al. 1997; Matyja and Wierzbowski 2001; Zatoń 2010b). The smaller morphotype bears lateral lappets in the aperture, whereas the larger one has simple aperture. Nevertheless, the two ammonites are traditionally described as separate morphospecies assigned to different genera. Recently, Zatoń (2010b) described both morphospecies under a single specific name: *Asphinctites tenuiplicatus* [M and m].

The objectives of this paper are: (i) to report the results of a detailed study of the sexual dimorphic correspondence between *A. tenuiplicatus* and *P. secundus* from well preserved adults coming from a single stratigraphic horizon studied previously by Zatoń (2010b). The comparison of their ontogenies is based on the standard morphologic analysis supported by a simple statistical methodology of sequential comparisons (Parent 1997). (ii) To discuss the systematics and taxonomy of the species and the lineage to which it belongs to.

Institutional abbreviations.—GIUS, Faculty of Earth Sciences, University of Silesia at Sosnowiec, Poland; IGPUW, Faculty of Geology, University of Warsaw, Poland.

Other abbreviations.—Bc, body chamber; CV = 100 s/m, percentual variation coefficient; D, diameter; D_p, diameter at adult peristome; D_{ls}, diameter at last adult septum; H_1/D, whorl height ratio; H_2/D, ventral (or apertural) whorl height ratio; L_{Bc}, length of the body chamber (given in angular degrees); [M], female macroconch; [m], male microconch; m, arithmetic mean; n, sample size; P, number of primary ribs per half-whorl; Ph, phragmocone; s, standard deviation; U/D, umbilical width ratio; W/D, whorl width ratio.

Geological setting, material and methods

The studied material consists of a sample with macro- and microconchs, coming from two localities of the Polish Jura: Kawodrza Górna near Częstochowa (most of the material) and Faustianka (Fig. 1A, B). In both localities the Middle Jurassic (Upper Bajocian–Upper Bathonian) clay deposits hosting carbonate concretions and massive siderite beds occur. This complex is referred to as the "Ore-Bearing Częstochowa Clay Formation" (e.g., Kopik 1998; Majewski 2000; Matyja and Wierzbowski 2000; Zatoń 2010a, b; Gedl and Kaim 2012). In Kawodrza Górna, two brick-pits have been sampled: "Leszczyński" and "LAB" (Fig. 1D). In the "Leszczyński" brick-pit, the section exposed consists of 12 m of dark-grey clay intercalated with two main concretionary horizons and one horizon of small carbonate concretions

in its uppermost part (see Fig. 2). In the "LAB" brick-pit, the topmost 5 m of clay with concretions which are exposed at the "Leszczyński" brick-pit occur. The upper part of the section at the "Leszczyński" brick-pit and the correlative succession at the "LAB" brick-pit represent the Early Bathonian *A. tenuiplicatus* Zone on the basis of the presence of the index species *Asphinctites tenuiplicatus* (Brauns, 1865) and *Polysphinctcites secundus* (Wetzel, 1950) (Matyja and Wierzbowski 2000, 2001; Zatoń 2010a, b). In Faustianka, located in the northern part of the Polish Jura (Fig. 1B, C), ca. 6 m of clay intercalated with six horizons of carbonate concretions used to be exposed (Matyja and Wierzbowski 2000, 2001; Zatoń 2010a, b; Fig. 2). The presence of ammonites of the species *A. tenuiplicatus* and *P. secundus* in the lowermost concretionary horizon points to the Early Bathonian *A. tenuiplicatus* Zone of that part of the section (Matyja and Wierzbowski 2000, 2001; Zatoń 2010a, b).

The specimens have been collected from a single concretionary horizon in all three outcrops (Fig. 2). The following reasons support the near-contemporaneous (in geological sense) condition of the horizon exposed in these outcrops: (i) the presence of abundant *A. tenuiplicatus* and *P. secundus* (see also Matyja and Wierzbowski 2000, 2001; Zatoń 2010a, b), and (ii) the presence of the same associated ammonites of the species *Oxycerites limosus* (Buckman, 1925) and *Oxycerites nivernensis* (De Grossouvre, 1919), both treated as dimorphs of the species *Oxycerites yeovilensis* Rollier, 1911 by Zatoń (2010a), and *Oxycerites seebachi* (Wetzel, 1950) (see Matyja and Wierzbowski 2000; Zatoń 2010a).

The material includes 37 macroconchs and 80 microconchs, plus several juvenile specimens which were not considered in the statistical analysis.

Thanks to the good quality of the samples coming from a single horizon, we were able to investigate the composition of the total range of variation within the sample, assuming that the variation within the samples of a single species corresponds to individual (intraspecific) variation (including sex) and not to taphonomic or sampling biases. Our sample should not be affected by significant amounts of variation produced by geographic distribution through different environments (ecophenotypic variation) and/or from phyletic evolution.

Dimensions considered for description of the ammonite morphology and calculation of shell-shape parameters or indices are shown on Fig. 3A. Levels of significance adopted: non-significant (°) if probability > 0.05, and significant (*) if probability < 0.05.

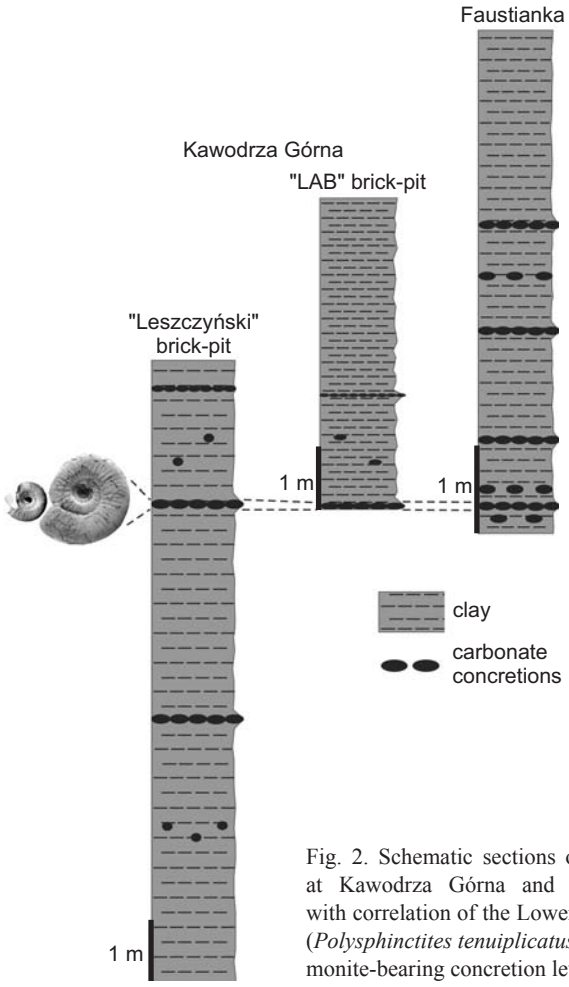

Fig. 2. Schematic sections outcropping at Kawodrza Górna and Faustianka, with correlation of the Lower Bathonian (*Polysphinctites tenuiplicatus* Zone) ammonite-bearing concretion level.

The statistical methodology adopted herein for contrasting the morphologic analysis of sexual dimorphic correspondence was proposed previously by Parent (1997). It is based on the comparison of the ontogenies of the proposed sexual dimorphs by stages, following the developmental concept of sexual dimorphism given above. The core of the method consists of the statistical evaluation of morphologic similarity of the inner whorls up to a fixed diameter of sexual differentiation (critical diameter), followed by differentiation of the

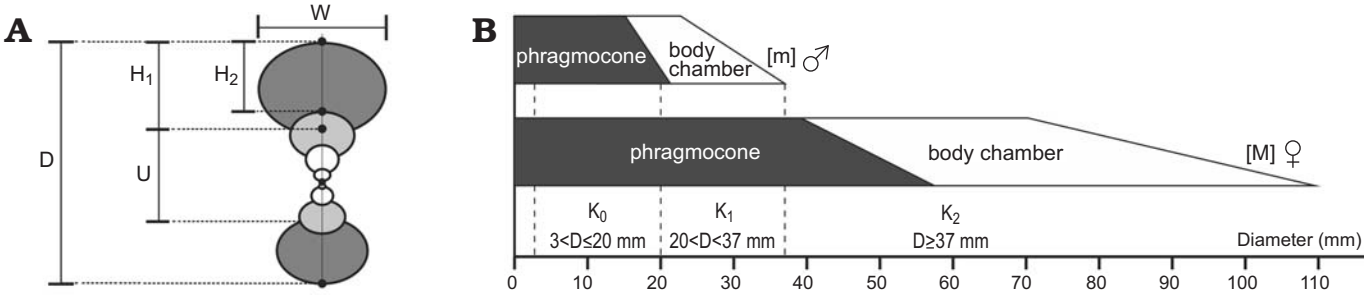

Fig. 3. **A**. Dimensions considered for description of the ammonite morphology. D, diameter; H_1, whorl height; H_2, ventral (or apertural) whorl height; U, umbilical width; W, whorl width. **B**. Comparative representation of the ontogenies of the sexual dimorphs with indication of the developmental stages (K_0, K_1, and K_2) considered for statistical comparison of the ontogenies (definitions in the text). All values representing the studied material.

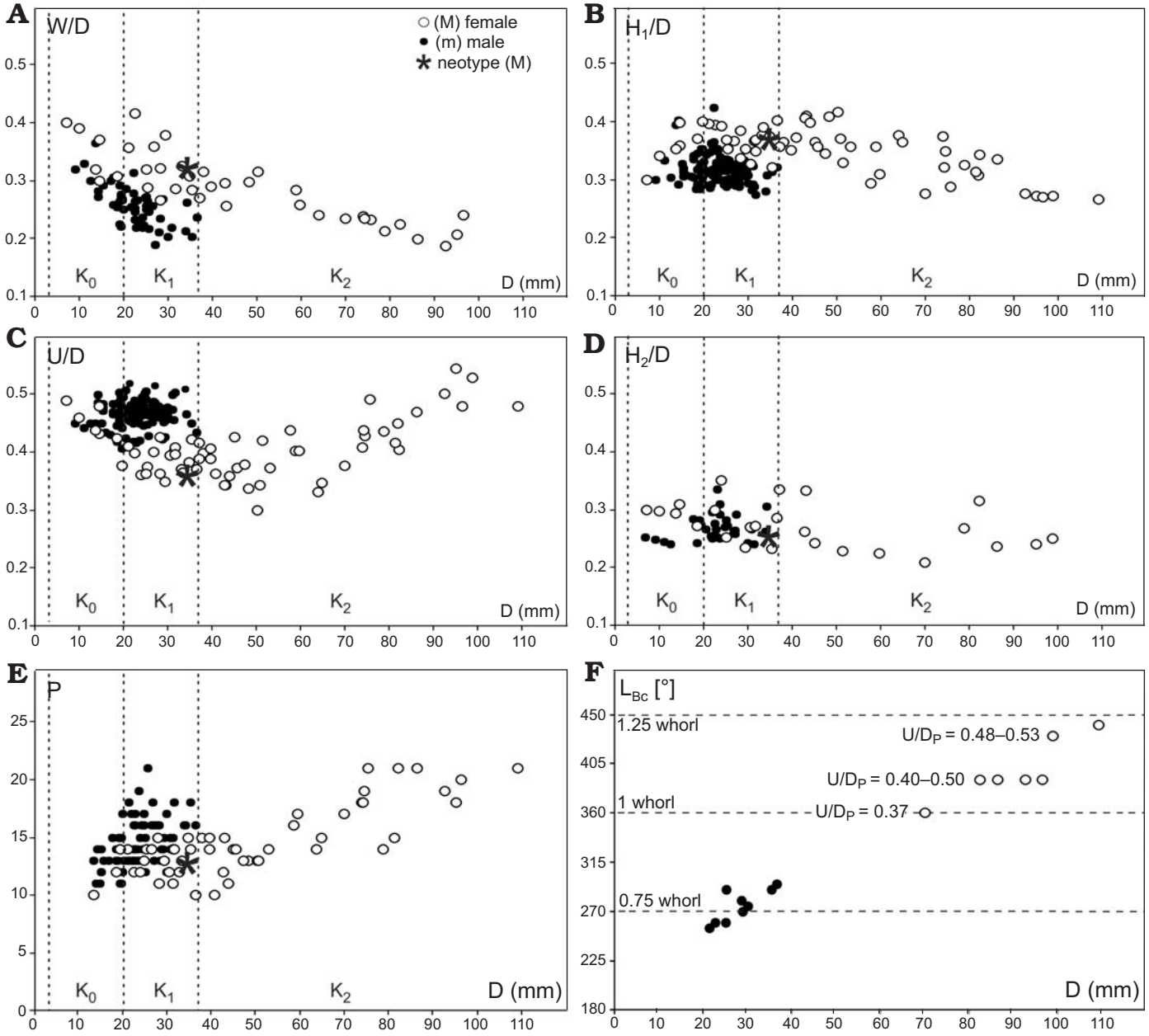

Fig. 4. Morphoceratid ammonite *Polysphinctites tenuiplicatus* (Brauns, 1865) [M and m], Lower Bathonian, *Polysphinctites tenuiplicatus* Zone, Polish Jura. Scatter plots of relative morphology of the studied sample: whorl width ratio (**A**), whorl height ratio (**B**), umbilical width ratio (**C**), ventral (or apertural) whorl height ratio (**D**), rib density (**E**), body chamber length of adults (**F**) versus diameter. The values of relative umbilical width at peristome indicated for macroconchs (U/D_p), covariating positively with L_{Bc} and D_p; K_0, K_1, and K_2, developmental stages (see Fig. 3B). Abbreviations: D, diameter; D_p, diameter at adult peristome; H_1/D, whorl height ratio; H_2/D, ventral (or apertural) whorl height ratio; L_{Bc}, length of the body chamber; P, number of primary ribs per half-whorl; U/D, umbilical width ratio; W/D, whorl width ratio.

subsequent whorls into macro- and microconchs. For this purpose the first step consists of staging, i.e., the subdivision of the ontogenies of both dimorphs in a set of developmental stages, which allows to compare the specimens at equivalent parts of the ontogeny. We have considered two ways for obtaining a meaningful staging: (i) the first is based on the detection of the diameter at which can be approximated more or less coordinated changes in the ontogenetic trajectories U/D, H_1/D, H_2/D, W/D (relative morphology) and P versus diameter (cf. Currie 1944; Kant and Kullmann 1973; Bucher et al. 1996). This way of segmentation could be evaluated by multivariate linear, piece-wise-linear regressions for estimation of breakpoints in the rates of growth of U, H_1, H_2, and W versus D (see Shea and Vecchione 2002 for details on the statistical procedure). (ii) The second way is sharper, and consists of tracing boundaries at (1) the mean diameter of last adult septum of the microconchs, which corresponds to some part of the juvenile phragmocone of the macroconch, and (2) maximum diameter of adult microconchs, which corresponds to much of the adult phragmocone of macroconchs (Fig. 3B).

Both ways of staging have produced similar results, thus three developmental stages (K_0, K_1, and K_2) for the post-nepionic shell are considered (see Figs. 3B, 4A–E): K_0: $3 < D \leq 20$ mm, most adult microconchs have their last septum at about D = 20 mm; K_1: $20 < D < 37$ mm, the largest microconch has D = 36.7 mm; K_2: $D \geq 37$ mm, this developmental stage is only attained by macroconchs.

Comparison of mean relative morphology and rib density between the dimorphs at each developmental stage is worked out by comparison of the mean values of U/D, W/D, H_1/D, H_2/D and P by means of the Welch (1937) modification of the t-Student test. The t-Student test is valid for small samples and produces acceptable results from samples showing a bell-shaped distribution, not necessarily normally distributed. For comparison of mean values it is used the modification named Welch U-test for situations of heteroscedasticity (unequal variances) following Hammer and Harper (2006), see discussion in Fagerland and Sandvik (2009). A parametrical comparison of the growth curves of shell dimensions (U, H_1, H_2, and W) versus D, stage by stage, is the final step of the method in Parent (1997). Nevertheless, the results of these comparisons are not reported herein because the samples do not fulfill the minimum statistical conditions for regressions by least squares or reduced axis. This last step of the method is similar to the approach of Palframan (1966) based on the comparison of growth curves.

In this paper, the binominal italicized names of chronozones result from the policy of the journal that any names derivative of biological species should be written in this way.

Results and discussion

Morphologic analysis.—All the macro- and microconchs dissected show their innermost whorls identical in all respects, being stout serpenticonic, evolute with subrectangular to suboval whorl section and smooth up to 8 mm in diameter (Figs. 4E, 5A). Differences between macro- and microconchs can be established from 15–20 mm in diameter (cf. Fig. 5B–C, I). The microconchs remain serpenticonic but becoming more compressed during ontogeny (Figs. 4A, 5A–H). The ribbing remains almost unchanged with a trend to become denser towards the adult body chamber (Figs. 4E, 5G, H). Distinctly, most macroconchs remain rather stout (Fig. 5I, K, L), and from 30–35 mm in diameter the trend reverts towards a narrowly umbilicate platyconic shell-shape (Figs. 4C, 5J, M, N). The mature body chamber has a wide umbilicus and is densely ribbed (Figs. 4C, E, 5O). A detailed systematic description of both dimorphs/sexes is given below.

Statistical evaluation of variation and differences.—The results of the statistical comparisons are given in Table 1. The inner whorls (K_0) of both dimorphs are statistically identical, although there could be a statistically significant difference in W/D. Nevertheless, this difference in the proportions of the whorl section does not seem to be biologically significant, for they are originated by some few atypical microconchs which mature at a notably smaller size (D ~ 11–12 mm), changing their whorl section earlier than typical specimens. After removing these specimens, the difference is not significant with respect to the macroconchs.

Differentiation between sexes through K_1 is significant for U/D, H_1/D and W/D but not clearly for H_2/D. This non-significant difference is not surprising for H_2/D (the rate of diameter increase) is very constant throughout the ontogeny of both sexes (Fig. 4D). Ribbing, as measured by P, tends to be somewhat denser in microconchs than in macroconchs with significant differences. Both dimorphs show an increase of rib density towards the adult body chamber, but in microconchs from smaller size (Fig. 4E). L_{Bc} is significantly longer in females than in males (see Table 1, Fig. 4F).

Discussion.—The working hypothesis for testing sexual dimorphic correspondence between two groups (dimorphs) of ammonites is that they must have identical inner whorls, followed by differentiation after a critical diameter. From the critical diameter the microconch differentiates from the macroconch because of its earlier sexual maturation, and each sex develops its typical morphology (Makowski 1962; Callomon 1963; Parent et al. 2008; Klug et al. 2015). The studied sample fulfills these conditions. The standard morphologic comparisons are in accord with the hypothesis, as shown in Figs. 4 and 5. The results of the statistical evaluation of sexual dimorphic correspondence, considering the differences due to intraspecific variation, confirm the results of the morphologic comparison. Indeed, there are no significant differences between the inner whorls of macro- and microconchs, and the adult whorls show significant differences (Table 1, Fig. 4).

Therefore, both forms can be considered the two sexual dimorphs of a single species, which is described below as *Polysphinctites tenuiplicatus* (Brauns, 1865).

Systematic palaeontology

Order Ammonoidea Fischer, 1882

Suborder Ammonitina Fischer, 1882

Superfamily Perisphinctoidea Steinmann, 1890

Family Morphoceratidae Hyatt, 1900

Genus *Polysphinctites* Buckman, 1922

Type species: *Polysphinctites polysphinctus* Buckman, 1922, Dorset (England), Lower Bathonian.

Polysphinctites tenuiplicatus (Brauns, 1865) [M and m]

Figs. 4–6.

1865 *Ammonites tenuiplicatus* sp. nov.; Brauns 1865: 135, pl. 25: 8–11.

1865 *Ammonites tenuiplicatus* Brauns; Schloenbach 1865: 186, pl. 29: 3 (holotype, lost), 4.

1950 *Grossouvria secunda* sp. nov.; Wetzel 1950: 79.

1951 *Siemiradzkia bajociformis* sp. nov.; Arkell 1951: 13, pl. 3: 1.
1958 *Asphinctites tenuiplicatus* (Brauns); Westermann 1958: 86, pl. 45: 3 (neotype), pl. 46: 1, 2.
1958 *Asphinctites gaertneri* sp. nov.; Westermann 1958: 87, pl. 46: 3.
1958 *Asphinctites bathonicus* sp. nov.; Westermann 1958: 88, pl. 46: 4.
1970 *Asphinctites tenuiplicatus* (Brauns); Hahn 1970: 50, pl. 7: 1–5, pl. 8: 14, text-fig. 8.
1970 *Polysphinctites secundus* (Wetzel); Hahn 1970: 57, pl. 8: 11–13.
?1987 *Asphinctites* aff. *tenuiplicatus* (Brauns); Torrens 1987: pl. 2: 7.
1987 *Polysphinctes secundus* Wetzel; Torrens 1987: pl. 2: 8.
1997 *Asphinctites tenuiplicatus* (Brauns); Dietze et al. 1997: 12, pl. 2: 1–8, pl. 3: 1–3 (with synonymy).
1997 *Asphinctites secundus* (Wetzel); Dietze et al. 1997: 14, pl. 1: 5–11, pl. 3: 1.
1997 *Asphinctites* (*Asphinctites*) *tenuiplicatus* (Brauns); Mangold and Rioult 1997: pl. 16: 7.
1998 *Asphinctites tenuiplicatus* (Brauns); Kopik 1998: pl. 6: 5.
2000 *Asphinctites tenuiplicatus* (Brauns); Matyja and Wierzbowski 2000: 207, pl. 7: 4, 5.
2000 *Polysphinctites secundus* (Wetzel); Matyja and Wierzbowski 2000: 207, pl. 7: 3.
2001 *Asphinctites tenuiplicatus* (Brauns); Matyja and Wierzbowski 2001: pl. 1: 1–8, pl. 2: 4, 5, 9, 10.
2001 *Polysphinctites secundus* (Wetzel); Matyja and Wierzbowski 2001: pl. 2: 1–3, 6–8.
2010 *Asphinctites tenuiplicatus* (Brauns) [M and m]; Zatoń 2010b: 163, pl. 13E–I, text-figs. 11B, C, 15, 16A–E.

Material.—37 macroconchs (GIUS 8-2608–2609, 2679, 2687–2691, 2694–2695, 2698–2699, 2702, 2706, 2713–2714, 2716–2719, 2728–2734, 2736–2737; IGPUW/J/133, 139, 183, 200, W5–W8), 80 microconchs and seven juveniles (GIUS 8-2583–2586, 2590–2595, 2597–2607, 2611–2616, 2620–2627, 2629–2631, 2635–2639, 2641–2657, 2664–2666, 2670–2673a-b; IGPUW/J/127, 138, 180, 186, 188–189, 192, 194, 197, 199, 201, 203, 207, 209–210, W1-W4) from the Lower Bathonian (*Polysphinctites tenuiplicatus* Zone) of Kawodrza Górna and Faustianka, Poland.

Description.—*Macroconch/female*: Inner whorls moderately evolute with oval, slightly higher than wide whorl section ($W/H_1 = 0.9$). Fine, prorsi- to rectiradiate ribs are visible from D ~8 mm. Middle whorls, from D ~25–30 mm, more involute with the narrowest relative umbilicus at about D = 50 mm where in most specimens begin the adult body chamber. The whorl section is high-oval with rounded flanks and venter, gradually becoming more compressed towards the adult stage. The primary ribs are recti- to prorsiradiate, sharper on the inner and middle whorls, and more rounded on the outer ones. Rib division is rather irregular, with primaries typically divided from about the mid-flank in 3–4 finer secondaries. Polyschizotomic divisions (furcation of secondaries) are frequent through the adult phragmocone and body chamber; some primaries bifurcate on the lowermost flank and each one divide again slightly above the mid-flank. Ventral ribs cross the venter unchanged. Some specimens show about three weak, prorsiradiate constrictions per whorl. Rib density increases gradually towards the adult peristome, passing from P = 12 (phragmocone) to P = 16–21 (body chamber).

Table 1. Statistical parameters and comparison of relative morphology: length of body chamber (in angular degrees), diameter (in mm), and rib density between dimorphs. Means difference, the statistical significance of the difference between the mean values: (°), non-significant, if probability > 0.05; (*) significant, if probability < 0.05. The comparison of mean values of diameter is given only for indicating the homogenety of the positions of the subsamples of macro- and microconchs within the corresponding developmental stages. Abbreviations: CV = 100 s/m, percentual variation coefficient; m, arithmetic mean; n, sample size; s, standard deviation; D, diameter; H_1/D, whorl height ratio; H_2/D, ventral (or apertural) whorl height ratio; L_{Bc}, length of body chamber; P, rib density, number of primary ribs per half-whorl; U/D, umbilical width ratio; W/D, whorl width ratio.

		Macroconchs (females)						Microconchs (males)						Means difference
		n	m	min	max	s	CV	n	m	min	max	s	CV	
	L_{Bc}	9	397	360	440	24	6%	11	278	255	310	17	6%	
K_0: 3 mm< D ≤ 20 mm	D	7	14.0	7.0	19.7	4.44		33	16.9	6.8	20.0	3.32		(°)
	U/D	7	0.44	0.38	0.49	0.04	9%	33	0.46	0.41	0.50	0.02	4%	(°)
	H_1/D	7	0.36	0.30	0.40	0.03	8%	32	0.32	0.28	0.40	0.03	9%	(°)
	H_2/D	5	0.29	0.27	0.31	0.01	3%	8	0.26	0.24	0.28	0.02	8%	(°)
	W/D	6	0.35	0.30	0.40	0.04	11%	21	0.28	0.22	0.36	0.03	11%	(*)
	P	3	12	10	14	2.00	17%	25	13	11	15	1.38	11%	
K_1: 20 mm < D < 37 mm	D	18	29.4	21.2	36.5	4.52		74	25.7	20.1	36.7	3.82		(°)
	U/D	18	0.39	0.35	0.43	0.02	5%	74	0.47	0.42	0.52	0.02	4%	(*)
	H_1/D	18	0.37	0.32	0.40	0.02	5%	73	0.32	0.27	0.42	0.02	6%	(*)
	H_2/D	8	0.27	0.23	0.35	0.04	15%	24	0.27	0.24	0.33	0.02	7%	(°)
	W/D	12	0.33	0.27	0.42	0.04	12%	33	0.24	0.19	0.31	0.03	13%	(*)
	P	18	13	10	15	1.43	11%	67	15	12	21	1.78	12%	(*)
K_2: D ≥ 37 mm	D	37	63.0	37.1	109.2	20.63								
	U/D	37	0.41	0.30	0.54	0.06	15%							
	H_1/D	35	0.34	0.27	0.44	0.05	15%							
	H_2/D	12	0.26	0.21	0.34	0.04	15%							
	W/D	20	0.25	0.19	0.32	0.04	16%							
	P	31	16	10	21	3.10	19%							

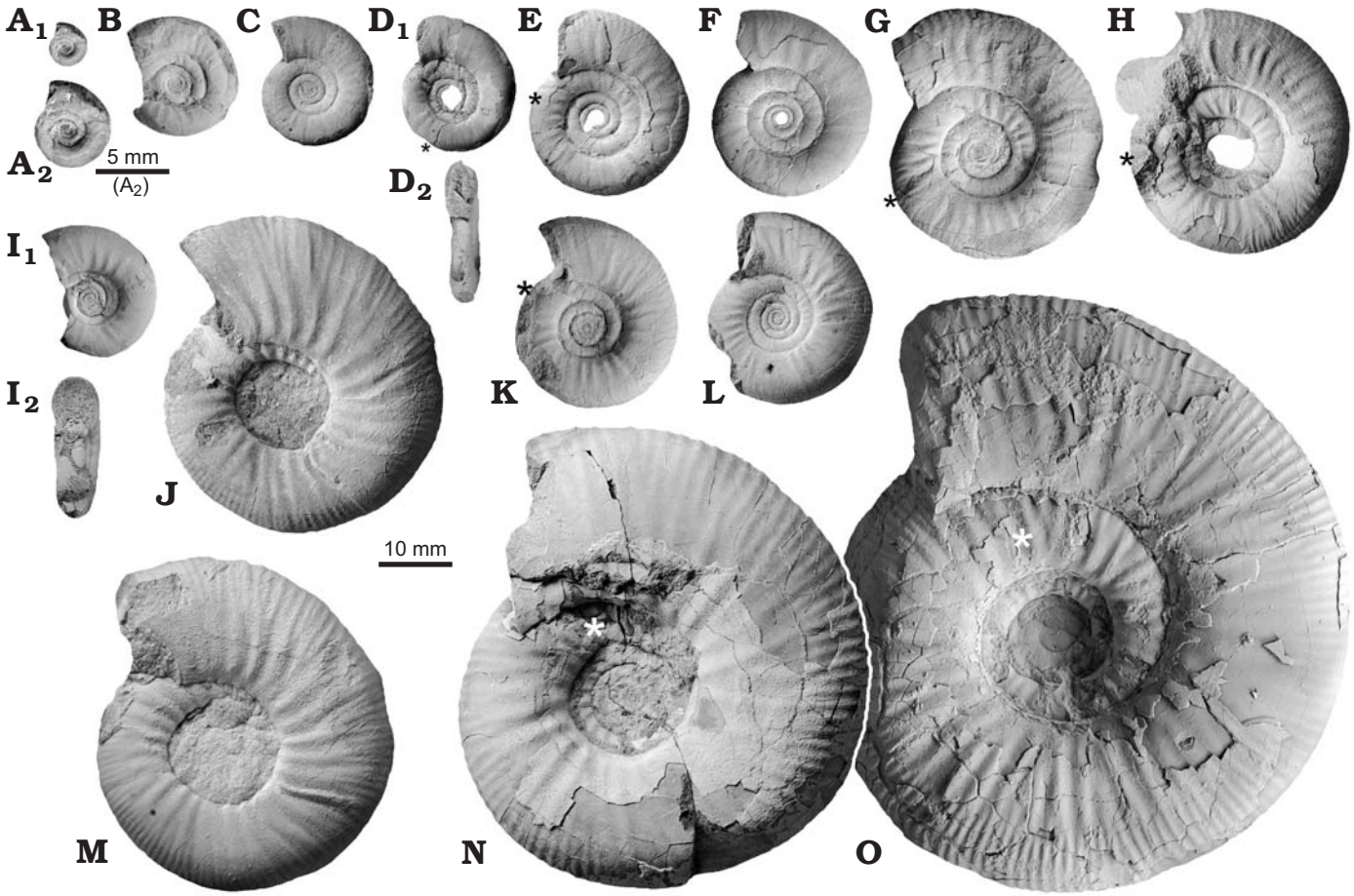

Fig. 5. Morphoceratid ammonite *Polysphinctites tenuiplicatus* (Brauns, 1865) [M] and [m] showing successive growth stages, Lower Bathonian, *Polysphinctites tenuiplicatus* Zone, Polish Jura, Kawodrza Górna (A–N) and Faustianka (O). **A**. GIUS 8-2592, juvenile with beginning of body chamber; natural size (A_1), enlargement (A_2). **B**–**H**. Microconchs, males. **B**. GIUS 8-2590. **C**. GIUS 8-2594. **D**. GIUS 8-2611, lateral (D_1) and apertural (D_2) views. **E**. GIUS 8-2646. **F**. GIUS 8-2593. **G**. GIUS 8-2640. **H**. GIUS 8-2622. **I**–**O**. Macroconchs, females. **I**. GIUS 8-2608, lateral (I_1) and apertural (I_2) views. **J**. GIUS 8-2703. **K**. GIUS 8-2687. **L**. GIUS 8-2717. **M**. GIUS 8-2710. **N**. GIUS 8-2733. **O**. GIUS 8-2715. H, O, examples of complete adult specimens with peristome. The asterisks indicate the last septum. All natural size, except A_2.

The body chamber is longidomic, ranging 360–440° in length. The aperture is simple and may be preceded by a shallow constriction. Adult size is very variable, ranging D_p = 70.0–109.2 mm. The septal suture line has the typical perisphinctoid design, in the adult phragmocone is finely frilled.

Microconch/male: Identical to the inner whorls of the macroconch up to D = 15–20 mm, although some few specimens can be differentiated from D ~11–12 mm by the whorl section being more compressed with lower flanks respect to the macroconchs at similar size. The whorl-section is subrectangular, higher than wide up to about D = 13 mm, then passing to high-oval with a narrowly rounded venter. Primary ribs are thin, recti- or slightly prorsiradiate, divided into 3–4 finer secondaries from the middle of the flank or slightly above. Primary ribs become thicker and convex adaperturally in the last half of the adult body chamber. At the peristome, large, well rounded spatulate lateral peristomatic lappets emerge. The length of the body chamber is significantly shorter than that in the macroconch, ranging 255–295°. Adult size ranges D_p = 21.4–36.7 mm. The septal suture line has the same structure and design of the macroconch, but less frilled.

Remarks.—The variability of shell-shape and sculpture in macro- and microconchs is low (Table 1: CV), especially in the phragmocone, with respect to what is commonly observed in ammonites (e.g., Sturani 1971; Callomon 1985; Parent 1998; Kennedy 2013; De Baets et al. 2015). The variation in adult size is rather broad in both dimorphs (Fig. 3B). It is, however, virtually identical in the Polish material studied by Matyja and Wierzbowski (2001), slightly larger than the representatives in other areas of the Tethys.

The neotype, designated by Westermann (1958: pl. 45: 3), corresponds to a macroconch phragmocone which perfectly matches our specimens, at comparable size, in shell-shape and ribbing (cf. Figs. 4A–E, 5I, K, L).

According to the synonymy considered above many of the nominal species of *Asphinctites* do not differ significantly from *Polysphinctites tenuiplicatus* [M]. Especially it concerns the species *Asphinctites recinctus* (Buckman, 1924), which is the index-species of the Lower Bathonian *Asphinctites recinctus* Zone, corresponding to the *Oxycerites yeovilensis* Zone of the North-West European Province (Subboreal Province; see Mangold and Rioult

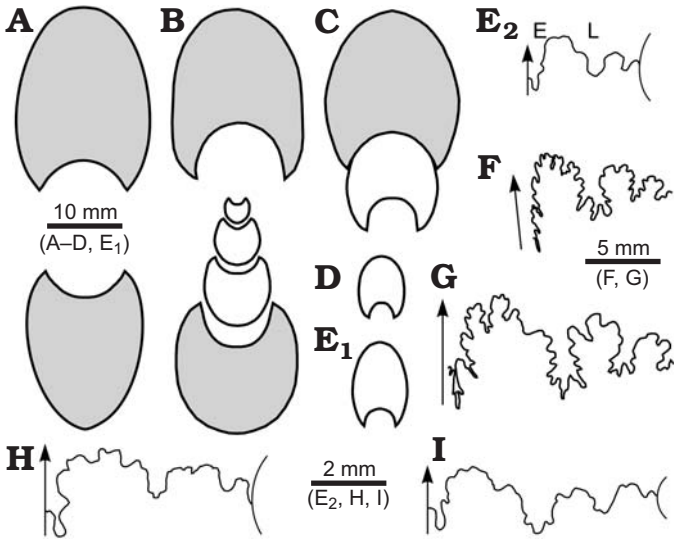

Fig. 6. Morphoceratid ammonite *Polysphinctites tenuiplicatus* (Brauns, 1865) [M and m], Lower Bathonian, *Polysphinctites tenuiplicatus* Zone, Polish Jura, Kawodrza Górna and Faustianka. Representative whorl sections (A–D, E_1), body chamber gray; and septal suture lines (E, E_2, G–I). **A–D**, **G**. Macroconchs, females. **A**. GIUS 8-2736. **B**.GIUS 8-2715. **C**. GIUS 8-2713. **D**. GIUS 8-2735. **G**. GIUS 8-2595. **E**, **F**, **H**, **I**. Microconchs, males. **E**. GIUS 8-2590. **F**. GIUS 8-2616. **H**. GIUS 8-2702. **I**. IGPUW/J/129. Nomenclature: E, external lobe; L, lateral lobe.

1997). Dietze et al. (1997) considered it as a synonym of *Polysphinctites tenuiplicatus*, as earlier suggested by Torrens (1987: 98). Indeed, although the holotype is very similar (see Buckman 1924; Arkell 1955), its stratigraphic position is not known accurately. Moreover, *Asphinctites recinctus* in Mangold and Rioult (1997: pl. 16: 9) does not resemble the holotype and may represent a different, probably undescribed species (Volker Dietze, written communication 2005).

According to Hahn (1970), the older macroconchiate form *Asphinctites patrulii* Hahn, 1970, occurring in the *Oxycerites yeovilensis* to *Polysphinctites tenuiplicatus* zones (Hahn 1970; Dietze et al. 1997), differs by its delicate and denser ribbing, as well as by the more involute inner whorls bearing deep constrictions. *A. replictum* (Buckman, 1922) is more involute not only in the inner whorls, but also in the outer ones. Unfortunately, its stratigraphic position („Zigzag Bed" according to Arkell 1955: 137) has not been established accurately. *A. pinguis* (De Grossouvre, 1919) is characterized by its inflate whorl-section and involute inner whorls that rapidly become evolute. Its stratigraphic position, on the other hand, is confined to the *Parkinsonia convergens–Oxycerites yeovilensis* zones (see Torrens 1987; Mangold and Rioult 1997).

The microconch *Polysphinctites polysphinctus* Buckman, 1922, on the other hand, differs from microconchs of *P. tenuiplicatus* by its distinct, deep and prorsiradiate constrictions (3 per whorl) starting from the inner whorls, as well as denser ribbing. Its stratigraphic position is limited to the *P. convergens–O. yeovilensis* zones (see Schairer 1994; Schlögl et al. 2005). At least a part of the specimens presented by Hahn (1970: pl. 8: 8–10) as *P. polysphinctus* and coming from the *Polysphinctites tenuiplicatus* Zone, because of the lack of morphological differences, should in fact belong to *P. tenuiplicatus*.

Dimorphism.—Soon after the papers by Makowski (1962) and Callomon (1963), many authors (e.g., Callomon 1969; Westermann 1969; Guex 1973) made efforts trying to find a general rule or protocol for taxonomic arrangement of sexual dimorphs which, in many cases have been, or remain assigned to different taxa (even family and superfamily in the worst cases, see e.g., Maeda 1993). Nevertheless, it has become clear that these taxonomic problems must be treated almost case by case after sexual dimorphic correspondences are demonstrated. The present material is virtually indistinguishable in significant features from the other material figured in the literature of both dimorphs. Thus, the indistinguishable morphology of the inner whorls as well as their co-occurrence in large numbers in the Polish Jura (Matyja and Wierzbowski 2001; Zatoń 2010b) and southern Germany (Hahn 1970; Dietze et al. 1997) leave no doubts that all specimens belong to a sexual dimorphic pair.

After the studies of Hahn (1970), Dietze et al. (1997), Matyja and Wierzbowski (2001), and the discussion above, it seems clear that the *Polysphinctites–Asphinctites* complex is composed by two species in direct phyletic succession: *Asphinctites pinguis* (De Grossouvre, 1919) [M] / *Polysphinctites polysphinctus* Buckman, 1922 [m] (*Parkinsonia convergens–Oxycerites yeovilensis* zones) followed by *P. tenuiplicatus* [M and m] (*Polysphinctites tenuiplicatus* Zone). *A. pinguis/P. polysphinctus* (including the many synonyms indicated in Matyja and Wierzbowski 2001) differs from *P. tenuiplicatus* by the consistent occurrence of strong constrictions, the more involute middle whorls of the macroconchs and the finer sculpture of the microconchs. These differences are not very strong and, in this sense, Westermann and Callomon (1988: 15) have even considered these forms as the end-members in the range of variability of *Morphoceras*.

According to the proposed composition of the lineage, including the several nominal species currently assigned to *Asphinctites* and/or *Polysphinctites*, the corresponding genus name should be *Polysphinctites* (= *Asphinctites* as a junior synonym).

Stratigraphic and geographic range.—*Polysphinctites tenuiplicatus* is the index species of the highest zone of the Early Bathonian and its stratigraphic range seems to be confined to its nominal chronostratigraphic zone (see e.g., Dietze et al. 1997). The geographic distribution of the species is relatively wide, a non-exhaustive list includes: Poland (Kopik 1979; Matyja and Wierzbowski 2000, 2001), Germany (Hahn 1970; Dietze et al. 1997), France (e.g., Mangold and Rioult 1997), England (Buckman 1924; Arkell 1951; see also Dietze et al. 1997).

Conclusions

Sexual dimorphic correspondence between *Asphinctites tenuiplicatus* (Brauns, 1865) [M] and *Polysphinctites secundus* (Wetzel, 1950) [m], already suggested by several authors, is confidently confirmed from our samples from a single stratigraphic horizon analyzed with statistical support. The juvenile ontogeny is identical in both sexes up to about 15–20 mm in diameter, then differentiation leads to the typical dimorphic morphologies.

The large number of nominal species of *Asphinctites* and *Polysphinctites* can be arranged in two species conforming a single Early Bathonian lineage, to which the genus name *Polysphinctites* (= *Asphinctites* as a junior synonym) should correspond. Thus, the species is described as *Polysphinctites tenuiplicatus* (Brauns, 1865) [M and m].

The change of the generic name of the index-species, from *Asphinctites tenuiplicatus* to *Polysphinctites tenuiplicatus*, has no any chronostratigraphic implication.

Acknowledgements

Volker Dietze (Nördlingen, Germany) and Günter Schweigert (Staatliches Museum für Naturkunde, Stuttgart, Germany) are thanked for discussion and information. Haruyoshi Maeda (The Kyushu University Museum, Fukuoka, Japan), Jose Sandoval (Universidad de Granada, Spain), and a third anonymous reviewer are acknowledged for their constructive criticism and remarks which helped to improve the present paper.

References

Arkell, W.J. 1951–1959. The English Bathonian ammonites. *A Monograph of the Palaeontolographical Society London* 1951: Part 1, Vol. 104, 1–46; Part 2, Vol. 105, 47–72; 1952: Part 3, 73–104; 1954: Part 4, Vol. 107, 103–127; 1955: Part 5, Vol. 108, 129–140; 1956: Part 6, Vol. 110, 141–162; 1958: Part 7, Vol. 111, 163–208; 1959: Part 8, Vol. 112, 209–264.

Brauns, D. 1865. Die Stratigraphische und Paläontologie des südöstlichen Theiles der Hilsmulde auf Grund neuer, bei den Eisenbahngauten in den Jahren 1861–1864 angestellter Beobachtungen. *Palaeontographica* 13: 75–146.

Bucher, H., Landman, N.H., Klofak, S.M., and Guex, J., 1996. Mode and rate of growth in Ammonoids. *In*: N.H. Landman, K.Tanabe, and R.A. Davis (eds.), Ammonoid Paleobiology. *Topics in Geobiology* 13: 407–461.

Buckman, S.S. 1909–1930. *Yorkshire Type Ammonites (continued as Type Ammonites), 7 Vols*. 790 plates with explanatory text. Published by the author, London.

Callomon, J.H. 1963. Sexual dimorphism in Jurassic ammonites. *Transactions of the Leicester Literary and Philosophical Society* 57: 21–56.

Callomon, J.H. 1969. Dimorphism in Jurassic ammonites: some reflections. *In*: G.E.G. Westermann (ed.), *Sexual Dimorphism in Fossil Metazoa and Taxonomic Implications (IUGS, Series A1)*, 111–125. Schweizerbart, Stuttgart.

Callomon, J.H. 1981. Dimorphism in ammonoids. *In*: M.R. House and J.R. Senior (eds.), The Ammonoidea. *Systematics Association Special Volume* 18: 257–273.

Callomon, J.H. 1985. The evolution of the Jurassic ammonite family Cardioceratidae. *Special Papers in Palaeontology* 33: 49–90.

Currie, E.D. 1944. Growth stages in some Jurassic ammonites. *Transactions of the Royal Society of Edinburgh* 61: 171–198.

Davis, R.A, Landman, N.H., Dommergues, J.-L., Marchand, D., and Bucher, H. 1996. Mature modifications and sexual dimorphism in ammonoids. *In*: N.H. Landman, K.Tanabe, and R.A. Davis (eds.), Ammonoid Paleobiology. *Topics in Geobiology* 13: 463–539.

De Baets, K., Bert, D., Hoffmann, R., Monnet, C., Yacobucci, M.M., and Klug, C. 2015. Ammonoid intraspecific variability. *In*: C. Klug, D. Korn, K. DeBaets, I. Kruta, and R.H. Mapes (eds.), Ammonoid Paleobiology: From Anatomy to Ecology. *Topics in Geobiology* 43: 359–426.

De Grossouvre, A. 1919. Bajocien–Bathonian dans la Nièvre. *Bulletin de la Societé Géologique de France* 18: 337–459.

Dietze, V., Krieger, T., and Schweigert, G. 1997. Über *Oecoptychius subrefractus* (Buckman), *Asphinctites tenuiplicatus* (Brauns) und *Polysphinctites secundus* (Wetzel) (Ammonoidea) aus dem Unter-Bathonium (Mittlerer Jura) der Oberplatz (Nodost-Bayern, Süddeutchland). *Stuttgarter Beiträge zur Naturkunde B* 245: 1–25.

Fagerland, M.W. and Sandvik, L. 2009. Performance of five two-sample location tests for skewed distributions with unequal variances. *Contemporary Clinical Trials* 30: 490–496.

Fischer, P.H. 1882. *Manuel de conchyliologie et de paléontologie conchyliologique*. 1369 pp. Librairie F. Savy. Paris.

Gedl, P. and Kaim, A. 2012. An introduction to the palaeoenvironmental reconstruction of the Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków–Silesia Homocline, Poland. *Acta Geologica Polonica* 62: 267–280.

Guex, J. 1970. Sur le sexe des ammonites. *Bulletin de la Société Vaudoise des Sciences Naturelles* 70: 241–246.

Guex, J. 1973. Dimorphisme des Dactylioceratidae du Toarcien. *Eclogae geologicae Helvetiae* 66: 545–583.

Hahn, W. 1970. Die Parkinsoniidae S. Buckman und Morphoceratidae Hyatt (Ammonoidea) des Bathoniums (Brauner Jura ε) im südwestdeutschen Jura. *Jahrbuch geologische Landesamt Baden-Württemberg* 12: 7–62.

Hammer, O. and Harper, D.A.T. 2006. *Paleontological Data Analysis*. 351 pp. Blackwell Publishing, Oxford.

Hyatt, A. 1900. Cephalopoda. *In*: C.R. Eastman (ed.), *Text-book of Paleontology by Karl A. von Zittel*, 502–604. Macmillan and Co., New York.

Kant, R. and Kullmann, J. 1973. "Knickpunkte" im allometrischen Wachstum von Cephalopoden-Gehäuse. *Neues Jahrbuch fur Geologie und Paläontologie Abhandlungen* 142: 7–114.

Kennedy, W.J. 2013. On variation in *Schloebanchia varians* (J. Sowerby, 1817) from the Lower Cenomanian of western Kazakhstan. *Acta Geologica Polonica* 63: 443–468.

Kopik, J. 1979. Stratygrafia jury środkowej regionu bełchatowskiego. *Kwartalnik Geologiczny* 23: 179–193.

Kopik, J. 1998. Lower and Middle Jurassic of the north-eastern margin of the Upper Silesian Coal Basin. *Biuletyn Państwowego Instytutu Geologicznego* 378: 67–120.

Klug, C., Zatoń, M., Parent, H., Hostettler, B., and Tajika, A. 2015. Mature modifications and sexual dimorphism. *In*: C. Klug, D. Korn, K. DeBaets, I. Kruta, and R.H. Mapes (eds.), Ammonoid Paleobiology: From anatomy to ecology. *Topics in Geobiology* 43: 253–320.

Landman, N.H., Kennedy, W.J., Cobban, W., and Larson, N.L. 2010. *Scaphites* of the "*nodosus* group" from the Upper Cretaceous (Campanian) of the Western Interior of North America. *Bulletin of the American Museum of Natural History* 342: 1–242.

Lehmann, U. 1981. *The Ammonites: Their Life and Their World*. 246 pp. Cambridge University Press, New York.

Maeda, H. 1993. Dimorphism of Late Cretaceous false-puzosiine ammonites, *Yokoyamaoceras* Wright and Matsumoto, 1954 and *Neopuzosia*, 1954. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series* 169: 97–128.

Majewski, W. 2000. Middle Jurassic concretions from Częstochowa (Poland) as indicators of sedimentation rates. *Acta Geologica Polonica* 50: 431–439.

Makowski, H. 1962. Problem of sexual dimorphism in amonites. *Palaeontologia Polonica* 12: 1–92.

Mangold, C. and Rioult, M. 1997. Bathonien. *In*: E. Cariou and P. Hantzpergue (eds.), Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations paralléles et distribution des invertébres et microfossiles. *Bulletin du Centre de Recherche Elf-Exploration et Production* 17: 134–139.

Matyja, B.A. and Wierzbowski, A. 2000. Ammonites and stratigraphy of the uppermost Bajocian and Lower Bathonian between Częstochowa and Wieluń, Central Poland. *Acta Geologica Polonica* 50: 191–209.

Matyja, B.A. and Wierzbowski, A. 2001. Palaeogeographical distribution of early Bathonian ammonites of the *Asphinctites–Polysphinctites* group. *Hantkeniana* 3: 89–103.

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.

Parent, H. 1997. Ontogeny and sexual dimorphism of *Eurycephalites gottschei* (Tornquist) (Ammonoidea) of the Andean lower Callovian (Argentine–Chile). *Geobios* 30: 407–419.

Parent, H. 1998. Upper Bathonian and lower Callovian ammonites from Chacay Melehué (Argentina). *Acta Palaeontologica Polonica* 43: 69–130.

Parent, H., Scherzinger, A., and Schweigert, G. 2008. Sexual phenomena in Late Jurassic Aspidoceratidae. Dimorphic correspondence between *Physodoceras hermanni* (Berckhemer) and *Sutneria subeumela* Schneid, and first record of possible hermaphroditism. *Palaeodiversity* 1: 181–187.

Rollier, L. 1911. *Le faciès du Dogger ou oolithique dans le Jura et les régions voisines*. 352 pp. Georg & Cie., Zürich.

Shea, E.K. and Vecchione, M. 2002. Quantification of ontogenetic discontinuities in three species of oegopsid squids using model II piecewise linear regression. *Marine Biology* 140: 971–979.

Schairer, G. 1994. *Polysphinctites polysphinctus* Buckman aus dem "Parkinsonien-Oolith" von Segenthal. *Mitteilungen der Bayerischen Staatssammlung für Palaontologie und Historische Geologie* 34: 159–162.

Schloenbach, U. 1865. Beiträge zur Paläontologie der Jura- und Kreide-Formation im nordwestlichen Deutschland. *Palaeontographica* 13: 147–192, 267–332.

Schlögl, J., Rakus, M., Mangold, C., and Elmi, S. 2005. Bajocian–Bathonian ammonite fauna of the Czorsztyn Unit, Pieniny Klippen Belt (Western Carpathians, Slovakia); its biostratigraphical and palaeogeographical significance. *Acta Geologica Polonica* 55: 339–359.

Schweigert, G. 1997. Die Ammonitengattungen *Simocosmoceras* Spath und *Pseudhimalayites* Spath (Aspidoceratidae) im süddeutschen Oberjura. *Stuttgarter Beiträge zur Naturkunde B* 246: 1–29.

Steinmann, G. 1890. Cephalopoda. *In*: G. Steinmann and L. Döderlein (eds.), *Elemente der Paläontologie*, 344–475. Engelmann, Leipzig.

Sturani, C. 1971. Ammonites and stratigraphy of the "Posidonia alpina" beds of the Venetian Alps (Middle Jurassic, mainly Bajocian). *Memorie Instituto Geologico e Mineralogico de la Universita Padova* 28: 1–190.

Torrens, H.S. 1987. Ammonites and stratigraphy of the Bathonian rocks in the Digne-Barrême area (South-Eastern France, Dept. Alpes de Haute Provence). *Bolletino de la Societa Paleontologica Italiana* 26: 93–108.

Verma, H.M. and Westermann, G.E.G. 1973. The Tithonian (Jurassic) ammonite fauna and stratigraphy of Sierra Catorce, San Luis Potosi, Mexico. *Bulletin of American Paleontology* 63: 107–320.

Welch, B.L. 1937. The significance of the difference between two means when the population variances are unequal. *Biometrika* 29: 350–362.

Westermann, G.E.G. 1958. Ammoniten-Fauna und Stratigraphie des Bathonien NW-Deutschland. *Beihefte zum Geologischen Jahrbuch* 32: 1–103.

Westermann, G.E.G. 1964. Sexual-Dimorphismus bei Ammonoideen und seine Bedeutung für die Taxionomie der Otoitidae (einschliesslich Spharoceratinae; Ammonoidea; M-Jura). *Palaeontographica A* 124: 33–73.

Westermann, G.E.G. 1969. Proposal: classification and nomenclature of dimorphs at the genus-group level [with discussion]. *In*: G.E.G. Westermann (ed.), *Sexual Dimorphism in Fossil Metazoa and Taxonomic Implications (IUGS, Series A1)*, 233–238. Schweizerbart, Stuttgart.

Westermann, G.E.G. and Callomon, J.H. 1988. The Macrocephalitinae and associated Bathonian and Early Callovian (Jurassic) ammonoids of the Sula Islands and New Guinea. *Palaeontographica A* 203: 1–90.

Westermann, G.E.G., Hudson, N., and Grant-Mackie, J. 2002. New Jurassic Ammonitina from New Zealand: Bathonian–Callovian Eurycephalitinae. *New Zealand Journal of Geology and Geophysics* 45: 499–525.

Wetzel, W. 1950. Fauna und Stratigraphie der Württembergica-Schichten insbesondere Nord-deutschlands. *Palaeontographica A* 99: 61–120.

Zatoń, M. 2010a. Bajocian–Bathonian (Middle Jurassic) ammonites from the Polish Jura. Part 1: Families Phylloceratidae, Nannolytoceratidae, Sonninidae, Strigoceratidae, Oppeliidae and Lissoceratidae. *Palaeontographica A* 292: 65–113.

Zatoń, M. 2010b. Bajocian–Bathonian (Middle Jurassic) ammonites from the Polish Jura. Part 2: Families Stephanoceratidae, Perisphinctidae, Parkinsonidae, Morphoceratidae and Tulitidae. *Palaeontographica A* 292: 115–213.