Sexual dimorphism in the Bathonian morphoceratid ammonite Polysphinctites tenuiplacatus

HORACIO PARENT and MICHAL ZATOŃ

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Asphinctites tenuiplacatus [M] and Polysphinctites secundus [m] from the Asphinctites tenuiplacatus 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 tenuiplacatus [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.

Horacio Parent [parent@fceia.unr.edu.ar], Laboratorio de Paleontología, IFG-FCEIA, Universidad Nacional de Rosario, Pellegrini 250, 2000 Rosario, Argentina.
Michał Zatoń [mzaton@wnoz.us.edu.pl], University of Silesia, Faculty of Earth Sciences, Department of Palaeontology and Stratigraphy, ul. Będzinska 60, 41-200 Sosnowiec, Poland.

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Introduction

Sexual dimorphism is virtually universal in living and fossil cephalopods. 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 tenuiplacatus (Brauns, 1865) and the microconch Polysphinctites secundus (Wetzel, 1950) from the Early Bathonian P. tenuiplacatus Zone, are commonly assumed or suggested to conform...
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; Dp, diameter at adult peristome; Ds, diameter at last adult septum; H1/D, whorl height ratio; H2/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: Kowdorza 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 Wierzowski 2000; Zatoń 2010a, b; Gedl and Kaim 2012). In Kowdorza 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 *Aspinctites tenuiplicatus* (Brauns, 1865) and *Polysphinctites 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.

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
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, H1/D, H2/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, H1, H2, 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 (K₀, K₁, and K₂) for the post-neo-
pionic shell are considered (see Figs. 3B, 4A–E): K₀; 3 < D ≤ 20 mm, most adult microconchs have their last septum at
about D = 20 mm; K₁; 20 < D < 37 mm, the largest micro-
conch has D = 36.7 mm; K₂; D ≥ 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, H₁/D,
H₂/D and P by means of the Welch (1937) modification of
the t-Student test. The t-Student test is valid for small sam-
ple sizes and produces acceptable results from samples showing
a bell-shaped distribution, not necessarily normally distrib-
uted. 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 para-
metrical comparison of the growth curves of shell dimensions
(U, H₁, H₂, 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 chrono-
zones 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 re-
spects, 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, 5F,
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 (K₀) of both dimorphs are statistically
identical, although there could be a statistically significant
difference in W/D. Nevertheless, this difference in the pro-
portions of the whorl section does not seem to be biologi-
cally significant, for they are originated by some few atypi-
cal 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 K₁ is signifi-
cant for U/D, H₁/D and W/D but not clearly for H₂/D. This
non-significant difference is not surprising for H₂/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 macro-
conchs with significant differences. Both dimorphs show an
increase of rib density towards the adult body chamber, but
in microconchs from smaller size (Fig. 4E). L₁b is signifi-
cantly longer in females than in males (see Table 1, Fig. 4F).

Discussion.—The working hypothesis for testing sexual di-
morphic 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 mor-
phologic comparisons are in accord with the hypothesis, as
shown in Figs. 4 and 5. The results of the statistical evalu-
ation of sexual dimorphic correspondence, considering the
differences due to intraspecific variation, confirm the re-
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 Grossouwiria secunda sp. nov.; Wetzel 1950: 79.
Asphinctites tenuiplicatus (Wetzel); Dietze et al. 1997: 12, pl. 2: 1–8, pl. 3: 1–3 (with synonymy).

Asphinctites (Asphinctites) tenuiplicatus (Brauns); Mangold and Riout 1997: pl. 16: 7.

Polysphinctes secundus (Brauns); Kopik 1998: pl. 6: 5.

Asphinctites tenuiplicatus (Brauns); Matyja and Wierzbowski 2000: 207, pl. 7: 4, 5.

Asphinctites polycanthus secundus (Brauns); Matyja and Wierzbowski 2000: 207, pl. 7: 3.

Asphinctites tenuiplicatus secundus (Brauns); Matyja and Wierzbowski 2001: pl. 1: 1–8, pl. 2: 4, 5, 9, 10.

Asphinctites polycanthus secundus (Brauns); Matyja and Wierzbowski 2001: pl. 2: 1–3, 6–8.

Asphinctites tenuiplicatus (Brauns) [M and m]; Zatoń 2010b: 163, pl. 13E–I, text-figs. 11B, C, 15, 16A–E.


Description.—Macroconch/female: Inner whorls moderately evolve with oval, slightly higher than wide whorl section (W/H1 = 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 prosiradiate, 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, prosiradiate 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: (°), no n-significant, if probability > 0.05; (*) significant, if probability < 0.05. The comparison of mean values of diameter is given only for indicating the homogeneity 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; H1/D, whorl height ratio; H2/D, ventral (or apertural) whorl height ratio; LBc, length of body chamber; P, rib density, number of primary ribs per half-whorl; U/D, umbilical width ratio; W/D, whorl width ratio.

<table>
<thead>
<tr>
<th></th>
<th>Macroconchs (females)</th>
<th>Microconchs (males)</th>
<th>Means difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n m min max s CV n m min max s CV</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lb½</td>
<td>9 137 360 440 24 6%</td>
<td>11 278 255 310 17 6%</td>
<td></td>
</tr>
<tr>
<td>K0: 3 mm &lt; D ≤ 20 mm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>17 140 7.0 19.7 4.44</td>
<td>33 16.9 6.8 20.0 3.32</td>
<td>(*)</td>
</tr>
<tr>
<td>U/D</td>
<td>7 0.44 0.38 0.49 0.04 9%</td>
<td>33 0.46 0.41 0.50 0.02 4%</td>
<td>(*)</td>
</tr>
<tr>
<td>H1/D</td>
<td>7 0.36 0.30 0.40 0.03 8%</td>
<td>32 0.32 0.28 0.40 0.03 9%</td>
<td>(*)</td>
</tr>
<tr>
<td>H2/D</td>
<td>5 0.29 0.27 0.31 0.01 3%</td>
<td>8 0.26 0.24 0.28 0.02 8%</td>
<td>(*)</td>
</tr>
<tr>
<td>W/D</td>
<td>6 0.35 0.30 0.40 0.04 11%</td>
<td>21 0.28 0.22 0.36 0.03 11%</td>
<td>(*)</td>
</tr>
<tr>
<td>P</td>
<td>3 12 10 14 2.00 17%</td>
<td>25 13 11 15 1.38 11%</td>
<td></td>
</tr>
<tr>
<td>K1: 20 mm &lt; D &lt; 37 mm</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>D</td>
<td>18 29.4 21.2 36.5 4.52</td>
<td>74 25.7 20.1 36.7 3.82</td>
<td>(*)</td>
</tr>
<tr>
<td>U/D</td>
<td>18 0.39 0.35 0.43 0.02 5%</td>
<td>74 0.47 0.42 0.52 0.02 4%</td>
<td>(*)</td>
</tr>
<tr>
<td>H1/D</td>
<td>18 0.37 0.32 0.40 0.02 5%</td>
<td>73 0.32 0.27 0.42 0.02 6%</td>
<td>(*)</td>
</tr>
<tr>
<td>H2/D</td>
<td>8 0.27 0.23 0.35 0.04 15%</td>
<td>24 0.27 0.24 0.33 0.02 7%</td>
<td>(*)</td>
</tr>
<tr>
<td>W/D</td>
<td>12 0.33 0.27 0.42 0.04 12%</td>
<td>33 0.24 0.19 0.31 0.03 13%</td>
<td>(*)</td>
</tr>
<tr>
<td>P</td>
<td>18 13 10 15 1.43 11%</td>
<td>67 15 12 21 1.18 12%</td>
<td>(*)</td>
</tr>
<tr>
<td>K2: D ≥ 37 mm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>37 12 10 15 1.43 11%</td>
<td>67 15 12 21 1.18 12%</td>
<td>(*)</td>
</tr>
<tr>
<td>U/D</td>
<td>37 0.41 0.30 0.54 0.06 15%</td>
<td>37 0.41 0.30 0.54 0.06 15%</td>
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<tr>
<td>H1/D</td>
<td>35 0.34 0.27 0.44 0.05 15%</td>
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<td>H2/D</td>
<td>12 0.26 0.21 0.34 0.04 15%</td>
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<tr>
<td>W/D</td>
<td>20 0.25 0.19 0.32 0.04 16%</td>
<td>20 0.25 0.19 0.32 0.04 16%</td>
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</tr>
<tr>
<td>P</td>
<td>31 16 10 21 3.10 19%</td>
<td>31 16 10 21 3.10 19%</td>
<td></td>
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</table>
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 Rioul...
Microconchs, males.

8-2715.


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 superfam-ily 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 Polyosphinctites 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 Polyosphinctites can be arranged in two species conforming a single Early Bathonian lineage, to which the genus name Polyosphinctites (= Asphinctites as a junior synonym) should correspond. Thus, the species is described as Polyosphinctites tenuiplicatus (Brauns, 1865) [M and m].

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

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