Developmental polymorphism in the Oxfordian ammonite subfamily Peltoceratinae

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ABSTRACT - Developmental polymorphism in ammonites (cf. Matyja 1986) may be clearly seen in the subfamily Peltoceratinae. Among Lower Oxfordian representatives of this subfamily typical tuberculate macroconchs corresponding to the genus *Peltoceratoides* attain up to 520 mm in diameter (i.e. 8.5-9.4 whorls). The microconch genus *Parawedekindia* reaches up to 110 mm in size (i.e. up to 7.4 whorls). The third group (miniconchs), distinguished here for the first time, embraces the smallest lappeted forms, 21.8-27.3 mm in size (i.e. 4.65-5.65 whorls).

The Middle Oxfordian genus *Gregoryceras* organized its life almost exclusively as a microconch. Tuberculate forms, which can be treated as macroconchs, appeared only at the end of phyletic lineage of the genus, due to hypermorphosis.

KEY WORDS: ammonites, Peltoceratinae, developmental polymorphism, Oxfordian.

INTRODUCTION

In 1986 the author presented a new interpretation of variation in final diameter of ammonite shells, giving it the name of the hypothesis of developmental polymorphism. This hypothesis, which is in the opposition to the theory of sexual dimorphism, was exemplified by several Oxfordian representatives of the superfamilies Stephanocerataceae and Haplocerataceae.

New examples supporting the hypothesis of developmental polymorphism, based on the Oxfordian representatives of the subfamily Peltoceratinae (which belong to the so far undiscussed superfamily Perisphinctaceae, the last of three superfamilies of Ammonitina) are presented here. It is important in so far as the Ammonitina are a classic group on which the theory of sexual dimorphism was based (see Callomon 1981).

A basic assumption of the theory of sexual dimorphism in ammonites is that there are forms which differ in size and type of sculpture, but which have identical inner whorls. Occurrence of such forms in pairs resulted in the proposal of sexual explanation for that differentiation (Callomon 1963, 1969, 1981; Makowski 1962, 1963, 1971).\

Occurence of different quantitative relations between morphological forms in the investigated material induced the present author to question the classical theory of sexual dimorphism, and to put forward the hypothesis of the developmental polymorphism. The developmetal polymorphism

hypothesis states that the occurrence of various number of ammonite morphs having identical initial stages of ontogeny, differing in final shell size and morphology, is due to a variation in time needed for sexual maturation of individuals (Matyja 1986 p. 60).

The basic differences between both hypotheses concerns the facts rather than the interpretation. The only difference in the interpretation is in statement that according to the theory of sexual dimorphism forms differing in size represent different sexes, while according to the hypothesis of developmental polymorphism they represent forms differing in time of reaching sexual maturity. One has to note that earlier maturation of the microconch, i.e. that it lives shorter and as a consequence attains smaller size of a shell and earlier stages of morphological development, is accepted de facto by supporters of the theory of sexual dimorphism (compare Kulicki 1974).

If we consider the facts only, the basic question is:
- whether in each case only two groups of forms exist which differ in size but display identical stages of morphological development, as it is postulated by the theory of sexual dimorphism, or
- whether there can be one, two or three such groups as is postulated by the theory of developmental polymorphism.

The analysis of facts forming the basis of the author's hypothesis is presented by Matyja (1986), while its critical evaluation is included in the review by Callomon (1988). New examples supporting it are presented below.

Representatives of the subfamily Peltoceratinae appear in the Athleta Zone of the Upper Callovian and cease in the Bifurcatus Zone of the Middle Oxfordian. The Oxfordian genera belong to two different morphological and temporal groups. The first group consists of the genera *Peltoceratoides*, *Peltomorphites* and *Parawedekindia*, which occur in the Lower Oxfordian. The second group consists of the genus *Gregoryceras* with two subgenera *Pseudogregoryceras* and *Gregoryceras*. The subgenus *Pseudogregoryceras* occurs in the uppermost subzone of the Lower Oxfordian, and the subgenus *Gregoryceras* occurs in the whole of the Middle Oxfordian (Gygi 1977).

The Lower Oxfordian Peltoceratinae

According to generally accepted opinion, the tuberculate genera *Peltoceratoides* and *Peltomorphites* are considered as macroconchs, while the nontuberculate and lappetted genus *Parawedekindia* represents a microconch. Species in these genera are distinguished on the basis of whorl section, degree of involution, density of ribs and the number of tubercle rows. The discussion presented below is limited only to species representing densely ribbed, planulate forms with only one row of ventrolateral tubercles, i.e. *Peltoceratoides* (d'Orbigny) and nontuberculated *Parawedekindia arduennensis* (d'Orbigny). They are represented by several hundreds specimens in the author's collection housed in the Geological Museum of the Faculty of Geology, University of Warsaw, under the number IGPUW/A/18.

There are several morphological stages of shell development in the above mentioned species (see Fig. 1). Ammonitella stage attains a diameter of 0.9 mm. The shell is initially totally smooth, but later it becomes covered with densely distributed and simple ribs. This stage can attain the diameter 2.7 to 2.85 mm. From this size on, ribs start to form pairs in the dorsolateral part, thus entering the stage of bifurcating ribs typical for the Lower Oxfordian Peltoceratinae. This stage exists to a diameter of 52-68 mm. From this moment on the ribs on the venter become depressed and a more or less visible groove originates; this is so called venter-groove stage. At the diameter of 68-110 mm tubercles, gradually increasing in size, appear on ribs near the ventral margin. The tuberculate stage, develops up to diameter of 300-520 mm, is the final stage.

Morphological modification corresponding with developmental stages of the microconch are superimposed on the stages of shell development presented above. Microconchs never attain the tuberculate stage of development. They develop, however, thickening of ribs near and on the ventral side (Pl. 2, Fig. 2). The stage of thick-venter ribs begins. at the diameter 52-82 mm, and terminates at the final diameter of the microconch i.e. 66-108 mm. The venter-groove stage can be, but is not always, present in microconchs. Before the thick-venter ribs stage the developmental stages of microconchs and macroconchs are identical.

Besides micro and macroconchs, there is another clearly separated group of morphs, which are here defined as miniconchs (Pl. 1, Figs 1-4). Final diameter of their shells is from 21.8 to 27.3 mm. They have identical initial moirphological shell stages to the micro and macroconchs, comparative rib curves (Fig. 3), and what is more, co-occur with them in the same strata (Fig. 4). The sculpture of miniconchs near their aperture show modifications expressed as the appearance of singular ribs (Pl. 1, Figs 1-3), denser rib spacing (Pl. 1, Figs 1,3), rib weakening (Pl. 1, Figs 2,3) or even disappearance in the dorsolateral part of the shell flank (Pl. 1, Fig. 1), while their apertures are equipped with lappets (Pl. 1, Figs 3,4).

The size of miniconchs does not result from variable rates of the shell coiling* (this problem is discussed in Makowski 1971), as they are identical both in micro and macroconchs (Fig. 2). They can not also be interpreted as dwarf forms; two arguments support this opinion. First, miniconchs do not have the thick venter ribs stage typical for microconchs, and if they represent dwarf microconchs they shold have. The second is that the number of septa in miniconchs in corresponding whorls is identical to that of micro and macroconchs (Fig.3), and therefore the tempo of their growth had to be identical. The question of rib density and growth rate was discussed by Matyja (1986, p.42-43) and Dommerques (1988).

Rates of coiling found in the Peltoceratinae equal 2.11-2.40. It follows from the final diameter and rate of coiling (see Fig. 2) that the number of whorls will fluctuate between 4.65 and 5.65 in miniconchs, between 5.95 and 7.4 in microconchs, and between 7.7 and 9.4 in macroconchs.

It seems obvious that the miniconchs, together with two other groups i.e. microconchs and macroconchs, form a polymorphic (more precisely trimorphic) assemblage (Pl. 2). This represents three temporaly different stages of final shell size attainment, corresponding to the mature stage.

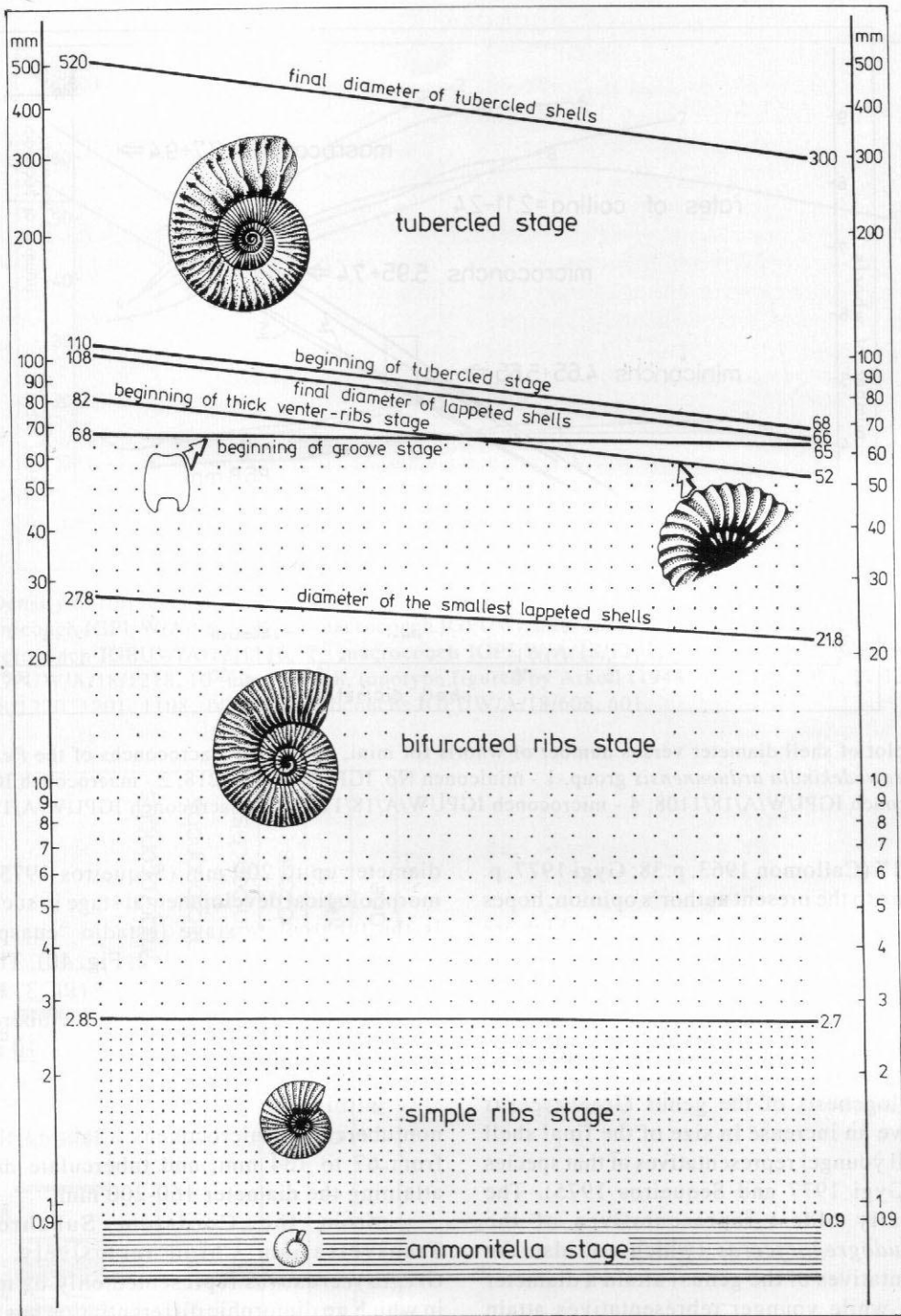* rates of coiling = n/(n-1), where n is a diameter at n whorl

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Fig. 1 - Morphological stages of the *Peltoceratoides constantii - Parawedekindia arduennensis* group.

The Middle Oxfordian Peltoceratinae - genus *Gregoryceras*

The problem of the identification of ancestors of the genus *Gregoryceras* is still not solved. Some authors derive it from the genus *Parawedekindia*, while others from the genus *Mirosphinctes* (see Gygi 1977, p. 514-515). Leaving aside the question of which of these opinions are true, it is important for our consideration that in both cases the genus *Gregoryceras* is derived from microconch genera. It so happens because representatives of this genus have morphological characters of shell corresponding, in the family Aspidoceratidae to which they belong, to microconchs, i.e. they do not develop a tuberculate stage. No differentiation into micro and macroconchs, to be expected on the grounds of sexual dimorphism,
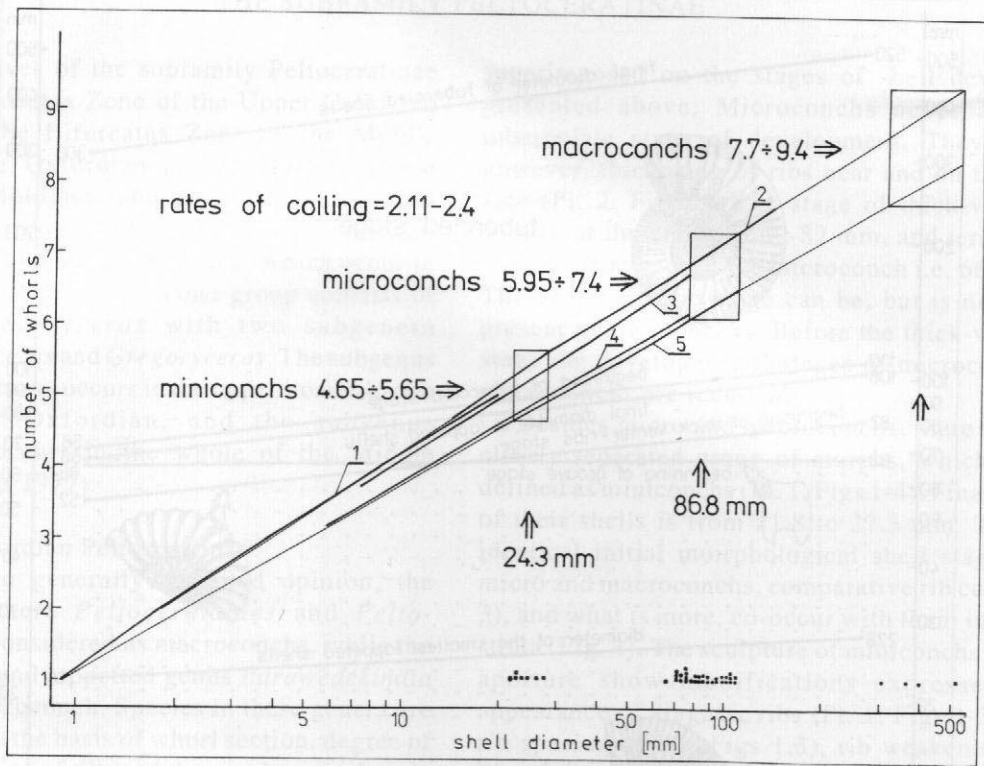
number of whorls

macroconchs 7.7÷9.4 ⇒

rates of coiling = 2.11–2.4

microconchs 5.95÷7.4 ⇒

miniconchs 4.65÷5.65 ⇒

86.8 mm

24.3 mm

shell diameter [mm]

Fig. 2 - A plot of shell diameter versus number of whorls for mini, micro and macroconchs of the *Peltoceratoides constantii - Parawedekindia arduennensis* group. 1 - miniconch No. IGPUW/A/18/1218, 2 - macroconch IGPUW/A/18/601, 3 - microconch IGPUW/A/18/1108, 4 - microconch IGPUW/A/18/1195, 5 - macroconch IGPUW/A/18/608

has been noted [**] (Callomon 1963, p.38; Gygi 1977, p. 307). According to the present author's opinion, hopes that we will in the future find macroconchs which are presently classified in other genera are futile. We know well what the macroconchs look like in the genus *Gregoryceras* because they exist, the only problem is that they can not be used as "a couple" from the theory of sexual dimorphism.

In the phylogenesis of the genus *Gregoryceras* one can observe an increase in size of the final shell diameter in still younger representatives of that species (see data in Gygi 1977 and Sequeiros 1975). The stratigraphically oldest representatives of the subgenus *Pseudogregoryceras* (which are also the oldest representatives of the genus) attain a diameter up to 67 mm, while younger representatives attain diameter from 70 to 140 mm [***]. On the other hand, specimens which belong to *Gregoryceras foquei* (Kilian) occurring in the Bifurcatus Zone attain a

diameter up to 200 mm (Sequeiros 1975). The final morphological developmental stage in such specimens is the tuberculate stage (estadio "euaspidoceras" - Sequeiros 1975, p.171. Pl. 2, Fig. 40). The specimen illustrated in the present paper (Pl. 3, Fig.2) has a diameter of about 170 mm, and the tuberculate stage has been attained at a size of about 110 mm.

Summing up:

- within the genus *Gregoryceras* exist both nontuberculate microconchs attaining the diameter from 67 to 134 mm, and tuberculate macroconchs attaining the diameter 160-200 mm,

- from the Cordatum Subchron to the Transversarium Chron inclusively, the genus *Gregoryceras* was represented only by microconchs in which no dimorphic differentiation has been found,

- tuberculate macroconchs appear only at the end of the phyletic lineage.

[**] suggestion by Gygi (1977, p. 507), that the final size difference of the shell observed between *Gregoryceras (Pseudogregoryceras) iteni* Jeannet and *G. (P.) tiechei* Jeannet can be expression of sexual dimorphism is not convincing as the latter species is know only from unique specimen.

[***] within the described trend toward increase of diameter in phylogeny, Gygi (1977, p. 490) observed opposite tendency in *G.transversarium* (Quenstedt): from 110-115 mm in Vertebrale or lower Antecedens Subzone to about 80 mm in Transversarium Zone.
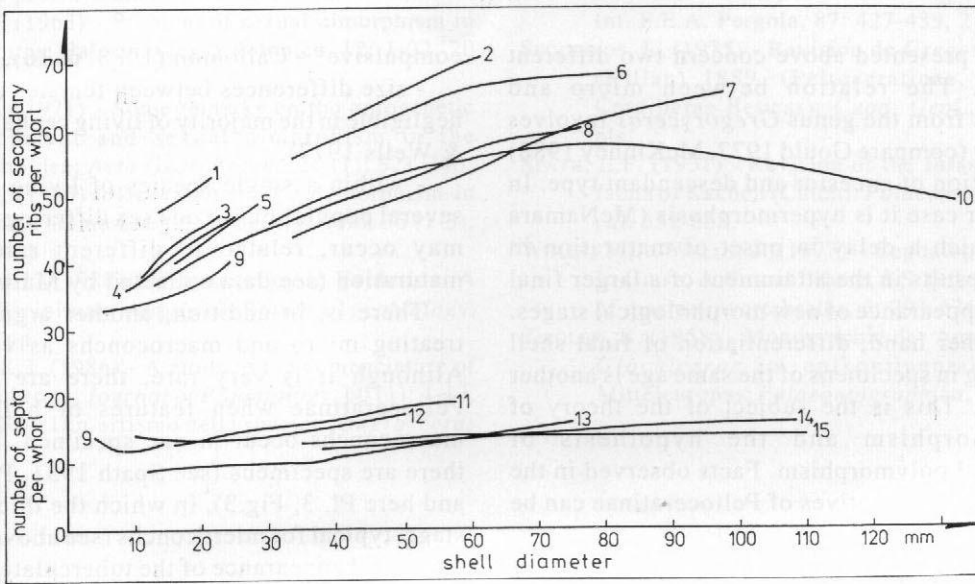
Fig. 3 - Density of ribs and density of septa curves of the *Peltoceratoides constantii - Parawedekindia arduennensis* group. 1 - miniconch IGPUW/A/18/1219, 2 - macroconch IGPUW/A/18/1221, 3-5 miniconchs IGPUW/A/18/1146, 1145, 1147, 6 - microconch IGPUW/A/18/1116, 7 - macroconch IGPUW/A/18/1202, 8 - microconch IGPUW/A/18/490, 9 - miniconch IGPUW/A/18/1218, 10 -macroconch, topotype figured by Arkell (1944, Text-fig. 101), 11-13 - microconchs IGPUW/A/18/1220, 1201, 1108, 14-15 - macroconchs IGPUW/A/18/608, 601.
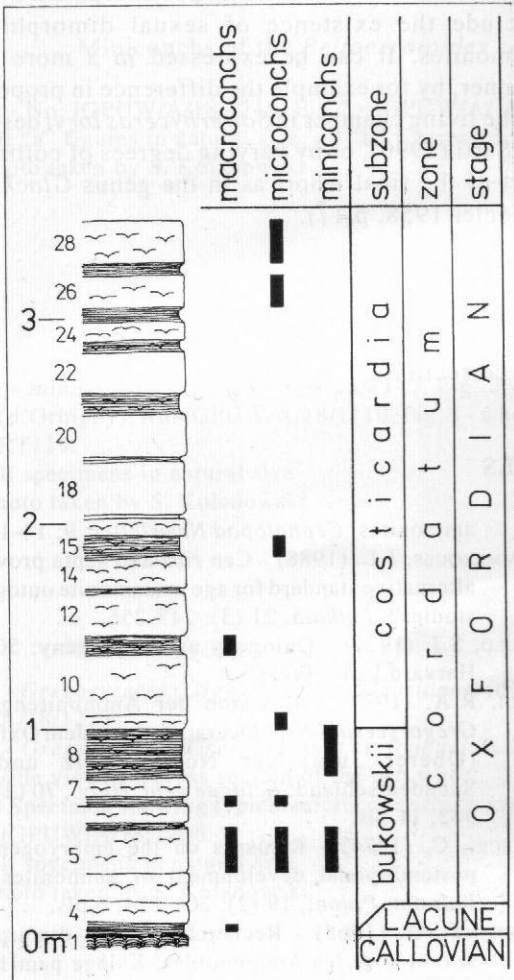

Fig. 4 - Distribution of polymorphs of the *Peltocertoides constantii - Parawedekindia arduennensis* group in the Wrzosowa section.

The facts presented above concern two different phenomena. The relation between micro and macroconchs from the genus *Gregoryceras* involves heterochrony (compare Gould 1977, McKinney 1988) as it is a relation of ancestor and descendant type. In our particular case it is hypermorphosis (McNamara 1986), in which a delay in onset of maturation in descendant results in the attainment of a larger final size and the appearance of new morphological stages.

On the other hand, differentiation of final shell size occurring in specimens of the same age is another phenomenon. This is the subject of the theory of sexual dimorphism and the hypothesis of developmental polymorphism. Facts observed in the unitemporal representatives of Peltoceratinae can be summed up and generalized as follows:

- it is possible for the co-occurrence of three groups of morphs in ammonites differing clearly in the diameter of the shell and in the type of sculpture, but having identical early ontogenetic stages,

- there can exist also only one group of morphs in ammonites.

Both cases allow us to suppose that shell size has nothing to do with a particular sex. Mini, micro and macroconchs may be regarded as separate populations of one species, which attained maturity at various time. The shell size is then a function of the time which elapsed between hatching of the ammonitella, and the maturation stage.

It is worth remembering that: "analogy wiyh living forms should be trated as suggestive, never compulsive" - Callomon (1988, p. 16), but also that:

- size differences between females and males are negligible in the majority of living cephalopods (Wells & Wells 1977),

- within a single species of living cephalopods, several populations of one sex differing in a body size may occur, related to different rates of sexual maturation (see data collected by Matyja 1986).

There is, in addition, another argument against treating micro and macroconchs as various sexes. Although it is very rare, there are cases in the Peltoceratinae when features of both micro and macroconchs occur in one specimen. For example, there are specimens (see Spath 1931, Pl. 54, Fig.4a; and here Pl. 3, Fig.3), in which the thick-venter ribs stage, typical for microconchs (see above) is followed by a rapid appearance of the tuberculate stage typical for the macroconch. According to the hypothesis of developmental polymorphism, this would only mean that animal entered the reproduction stage for the second time, while according to the theory of sexual dimorphism it would mean a change of sex.

Finally, one has to stress that acceptance of the hypothesis of developmental polymorphism does not exclude the existence of sexual dimorphism in ammonites. It can be expressed in a more subtle manner, by for example the difference in proportions of the living chamber in *Sowerbyceras loryi* described by Sarti (1990), or by varying degrees of coiling of a part of the final whorl as in the genus *Glochiceras* (Ziegler 1958, p.17).

ACKNOWLEDGEMENTS

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EXPLANATION OF THE PLATES

Plate 1
Miniconchs of the *Peltoceratoides constantii - Parawedekindia arduennensis* group.

Fig. 1 - No. IGPUW/A/18/1219, Fig.2 - IGPUW/A/18?1147, Fig.3 - IGPUW/A/18/1146, Fig. 4 - IGPUW/A/18/1145. All "a" figures in natural size, all "b" figures x3
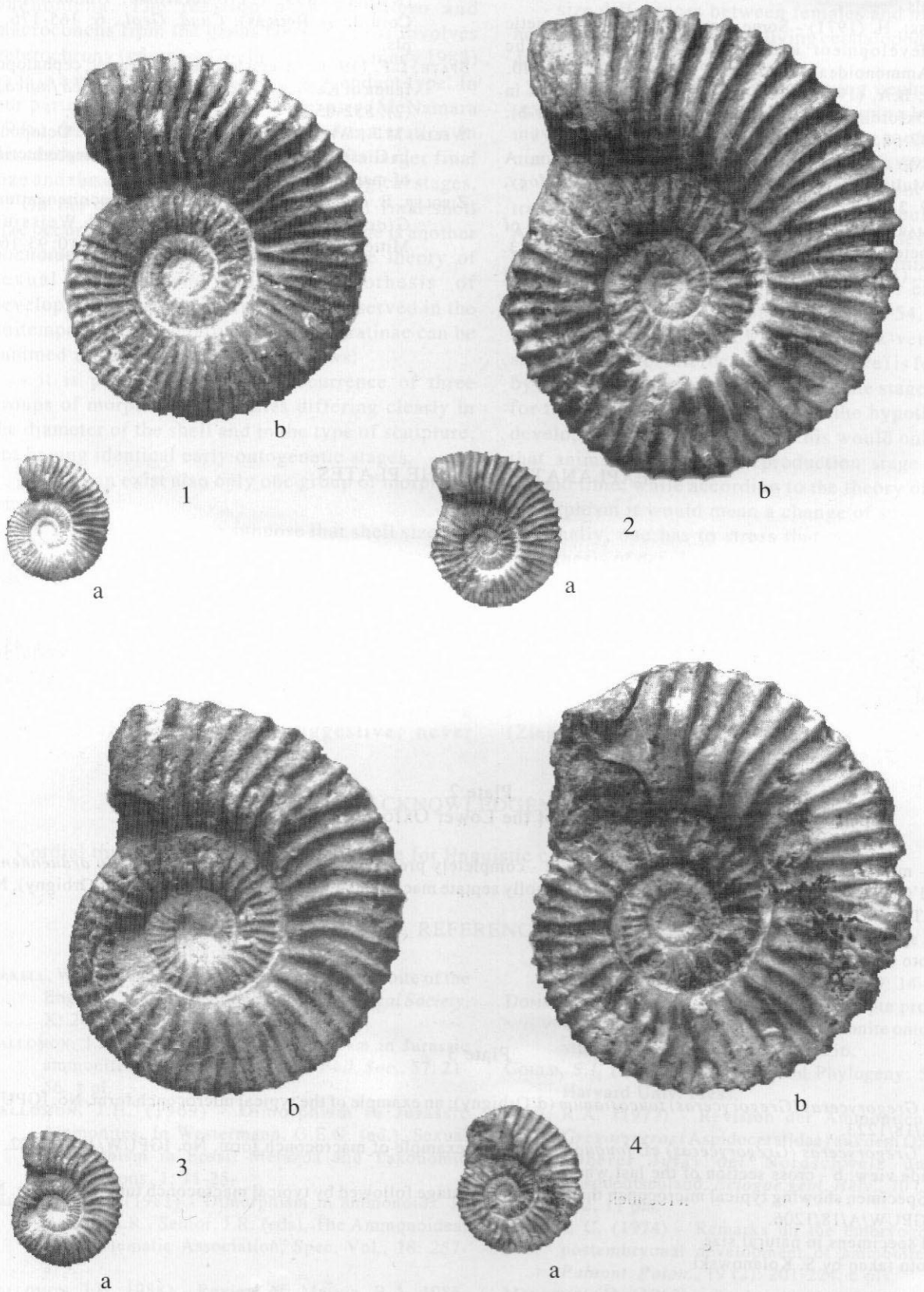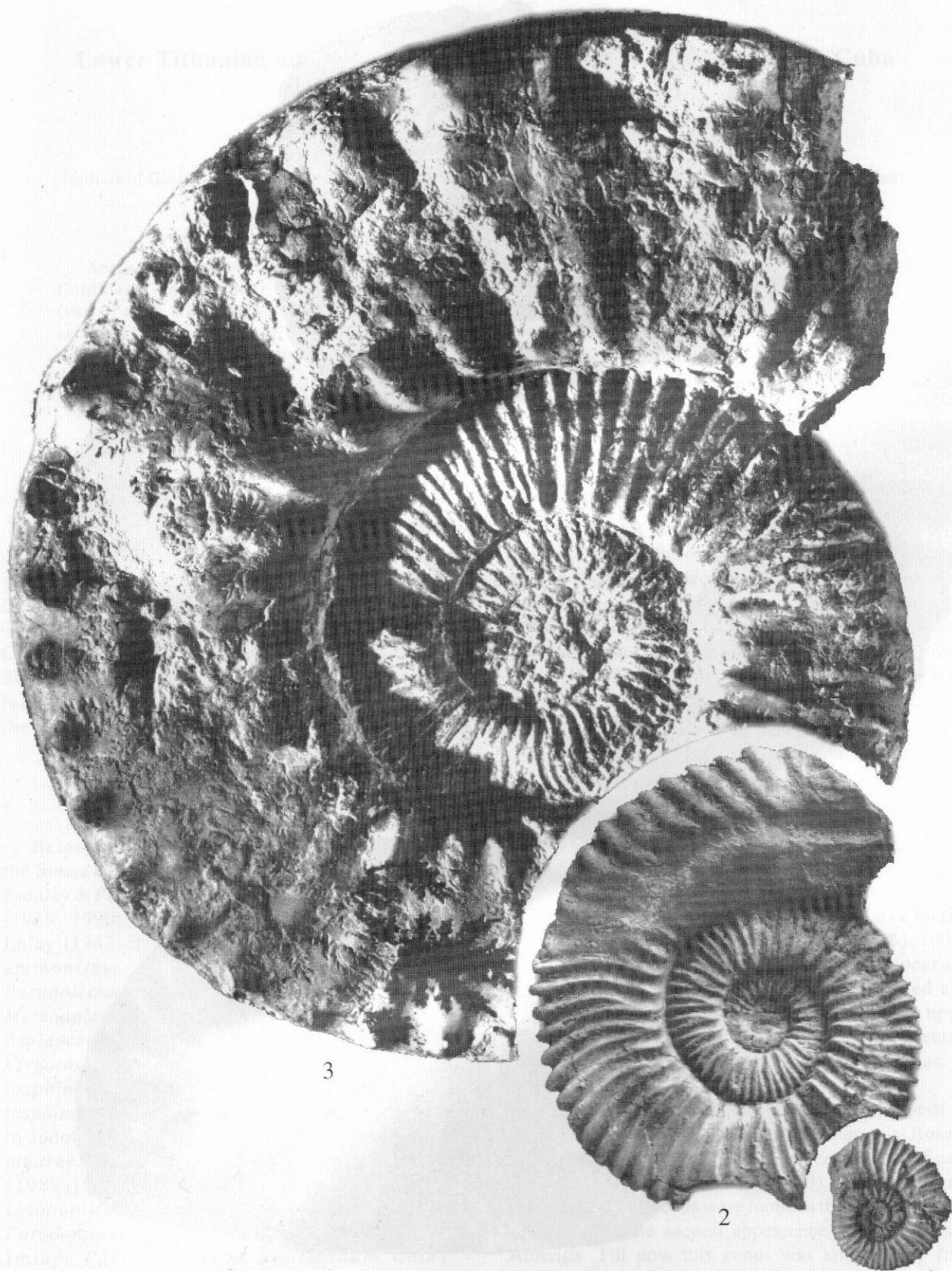Photo taken by S. Kolanowski

Plate 2
Trimorph assemblages of the Lower Oxfordian Peltoceratinae.

Fig. 1 - miniconch - No. IGPUW/A/18/1145, Fig. 2 - completely preserved microconch *Parawedekindia arduennensis* (d'Orbigny), No. IGPUW/A/18/1110, Fig. 3 - wholly septate macroconch *Peltocertoides constantii* (d'Orbigny), No. RT119.
All specimens in natural size
Photo taken by S. Kolanowski

Plate 3

Fig. 1 - *Gregoryceras (Gregoryceras) toucasianum* (d'Orbigny); an example of the typical microconch form. No. IGPUW/A/18/1223.
Fig.2 - *Gregoryceras (Gregoryceras)* cf. *fouquei* (Kilian) an example of macroconch form. No. IGPUW/A/18/1222. a - side view, b - cross section of the last whorl.
Fig. 3 Specimen showing typical microconch thick-venter ribs stage followed by typical macroconch tubercled stage. No. IGPUW/A/18/1206.
All specimens in natural size
Photo taken by S. Kolanowski

Plate 1

Plate 2

Plate 3

2b

2a

1

3