

Time Changes of Oxfordian Ammonite Fauna of the Polish Jura Chain; Some Reflections

by

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Summary. Reversible and irreversible time changes in an ammonite shell size, dimensions, ornamentation and presumably sutures, known to occur in *Glochiceras* [34], are also found in contemporaneous Oxfordian groups, such as perisphinctids. Periods of the maximum size reduction, the *Tenuicostatum-Antecedens* and *Bifurcatus-Bimammatum* junction beds, coincide with the sharpest changes in the composition of ammonite faunas, whereas the changes appear markedly smaller or almost none in periods of limited shell-size oscillations. Changes in the shell size and morphology appear at least partly related to external factors. The changes may partly explain the "overweight" of the taxa of the Submediterranean and Subboreal provinces in comparison with other provinces.

Introduction

The paper deals with ammonite fauna of the Oxfordian of the Polish Jura Chain. In the last few years it has been possible to collect well-preserved material from several horizons of the Oxfordian. In the course of the study of the specimens some interesting observations concerning time changes in this ammonite fauna could be made. The studies were greatly facilitated by Enay's [13] monograph of Oxfordian perisphinctids from France and by papers on contemporaneous ammonite fauna of the Polish Jura Chain recently published by Malinowska [25—26].

The study on time changes in any fauna greatly depends on the time scale available. The Submediterranean and NW-European zonation recently applied in France [12—14], England [8, 10, 32], FRG [33], Spain [4] and in Poland [5, 21] appeared useful for the present purpose.

Previous studies on time changes in Jurassic Ammonite faunas

In attempts to explain time changes in Jurassic Ammonite faunas Waagen, Gemmellaro and Neumayr began to look for the succession of similar species and to connect these species into lineages, i.e. to trace evolutionary changes [34]. Further studies showed that the situation was much more complex. Besides changes of this

type Siemiradzki [29] found changes in the ammonite spectrum, which result from the recruitment of new elements from other provinces, e.g. *Cardioceratidae* from more northerly areas to the Oxfordian basin of southern Poland.

The problem of the dependence of ammonite ornamentation on environmental conditions was touched by Spath [31], according to whom "like other mollusc shells these ornamented ammonites often bear the stamp of their local habitat although the animals inhabiting these shells may be assumed to have been identical". If it is the case, then certain simultaneous trends in changes of ammonite shells of different ammonite groups inhabiting the same region may be expected.

A number of authors have noted remarkable differences in the mean size of ammonite shells of different ages [3]. It was Różycki [28] who reported a certain tendency for the mean size of shells to increase during the Neuvisian and Argovian. Arkell [1] regarded the adult maximum size of shell as a good specific characteristic which forced him to interpret the appearance of the Oxfordian giant perisphinctid fauna in Submediterranean Europe in terms of migration from more southern areas [2]. The possibility of an increase of the maximum shell size and the resulting or accompanying changes in ornamentation were evidenced in *Creniceras-Glochoceras* and *Perisphinctes* faunas by Ziegler [34] and Enay [13], respectively. The former study showed that these size changes may be reversible, on the contrary to some changes in the shell morphology.

Thus, it may be stated that changes in a given ammonite community may result from: (1) evolution of species, (2) immigration of new elements from other areas and (3) the influence of environmental factors on a number of morphological features, including the shell size, the length of the final body chamber, the complexity of sutures, the whorl outline [34] and the density and strength of the sculpture [13]. It should be noted that there is a possibility to distinguish artificial species genera or series on the basis of changes induced by factors (2) and (3).

Sexual dimorphism in ammonites [23, 9] gave an invaluable clue to the analysis of changes in ammonite faunas, as recognition of dimorphic pairs makes it necessary and possible to analyse changes in both micro- and macroconchs and to apply tests of mutual consistency. This was already shown by Enay [13].

Changes in Oxfordian perisphinctid faunas of Polish Jura Chain

The lowermost Oxfordian from the Częstochowa-Żarki area, Polish Jura Chain (the *Cordatum* and lower *Plicatilis* Zones) yields numerous small microconchs of the *Prososphinctes mazuricus* groups and their macroconchs, *P. claromontanus* group. There also occur some microconchs of *Alligaticeras* and fragments of fairly large macroconchs representing the ancestors or early *Kranaosphinctes*.

The *Kranaosphinctes promiscuus* group first appear at the base of the *Antecedens* Subzone, where they are represented by forms attaining ca. 180 mm in size and with body chamber over a whorl long. They are accompanied by some macroconchs already referable to *Arisphinctes* and *Sphaerosphinctes*. Microconchs are repre-

nted by minute *Otosphinctes* and early *Dichotomosphinctes*, 40—100 mm in diameter, and minute *Passendorferia czenstochovensis* (Siem.). Generally, the sculpture and shape of these specimens are strictly similar to those of perisphinctids from the *Bifurcatus-Bimammatum* junction beds. All the specimens are relatively small-sized, with very long body chambers moderately to markedly evolute and ornamented with innumerable, coarse, round-crested ribs. On purely morphological premises it is possible to place some of them in species and genera known from the uppermost *Bifurcatus*-lowermost *Bimammatum* beds, such as *Microbiplices*, *Orthosphinctes*, *Progeronia*, and vice versa.

From the base of the *Antecedens* Subzone, there is a distinct trend of the ultimate size of microconchs to increase [8, 13]. This is shown best by the series proposed by Enay [8], p. 857; the maximum shell size given in brackets): *Otosphinctes ouatius* or *O. Monfalconensis* (ca. 60 mm) → *O. magnouatius* (80 mm) → *Dichotomosphinctes ptoides* (ca 100 mm) → *D. antecedens* (150—180 mm) → *D. wartae* (160—180 mm). Close to the end of the *Antecedens* Subzone there appear giant microconchs, *D. buckmani* and *D. dobrogensis*, about 200 mm or more in diameter. A similar trend seems to be observable in macroconchs. Macroconchs of the *Kranaosphinctes prominiscus* group increase in size up to 220—240 mm and are soon followed by *K. trifidus*, over 400 mm in size. References in the literature and fragmentary specimens indicate that soon appear giant *Kranaosphinctes*, *Arisphinctes* and early *Perisphinctes* s. st., up to 500 mm in size or more. The size increase is accompanied by a tendency to develop finer and denser ribbing of microconchs and inner whorls of macroconchs [13], a shorter final body chamber, and an increased complexity of sutures.

That *Perisphinctes* s. st. originate from *Arisphinctes* was shown by Enay [13] and Hauerstein [18]. Most probably the former evolved from the *Arisphinctes maximus-ingens* group via the transitory *Perisphinctes chloroolithicus-parandieri* group. Early *Arisphinctes* are known from the lower *Antecedens* Subzone, characterized by rich and differentiated *Kranaosphinctes* fauna. However, the Polish early *Kranaosphinctes* appear very close to the *Kranaosphinctes cyrilli-methodii* group comprising Mediterranean species roughly referable to the English genus *Kranaosphinctes* Buckman (see [13], p. 590). Microconchs of these Mediterranean *Kranaosphinctes* may be assumed to belong or are closely allied to the *Passendorferia czenstochovensis-birmensdorfensis* group, comprising late representatives of *Mutationsreihe* des *P. alligatus* of Siemiradzki [30]. These groups, Mediterranean *Kranaosphinctes* and early *P. czenstochovensis-birmensdorfensis* are assumed to give rise to the *Passendorferia* group including idoceratids of the late *Plicatilis-Bifurcatus* zones [7]. If it is the case then the ancestors of *Arisphinctes* should be looked for elsewhere. It was mentioned above that the basal part of the *Antecedens* Subzone yields numerous *Otosphinctes-Dichotomosphinctes*. The evolutionary series of Enay (see above) clearly show that this fauna gave rise to later giant *Dichotomosphinctes*, which are sexual counterparts of *Arisphinctes* and the *Perisphinctes* proper. Therefore, macroconchs of these early *Otosphinctes-Dichotomosphinctes* were to give rise to the *sphinctes-Perisphinctes* faunas. These ancestral macroconchs may be

Comment to the ammonites illustrated

Some ammonites of paleontological importance are shown in Plates I—IV. In their descriptions the following abbreviations were used: *D* — diameter, *D Ph* — diameter of phragmocone, *H* — height of whorl, *T* — whorl thickness, *U* — umbilical diameter

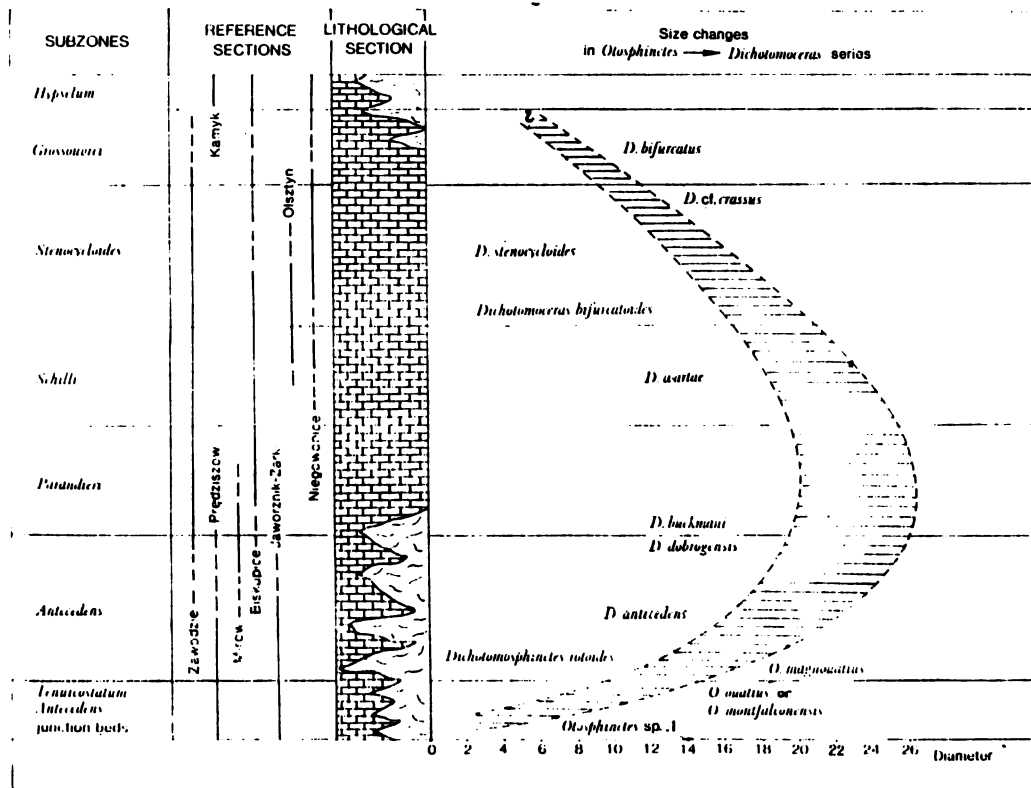


Figure. Time changes in the shell size of ammonites of the *Otosiphinctes* series.

preferable to the English (proper) stock of *Kranaosphinctes* or, which seems more probable, represent early *Arisphinctes*. In either case, in the late *Plicatilis* Zone (or even earlier) Mediterranean and Submediterranean lineages were well separated.

The *Transversarium-Bifurcatus* zones seem to display a trend to reduce the shell size gradually. Such conclusion may be drawn from the analysis of the sequence of microconchs. The late *Transversarium* (*Schilli* Subzone) yields microconchs of the *D. wartae* group, 180—160 mm in size, i.e. smaller than the *D. buckmanidobrogensis* fauna. The early *Bifurcatus* (*Stenocycloides* Subzone) yields descendants of the former, *Dichotomoceras bifurcatoides-stenocycloides* group, 180—150 mm or less in size. This group is gradually replaced by smaller forms of the *D. cf. crassus* group ca. 120 mm, and those in turn by still smaller forms of the *D. bifurcatus* group (100—70 mm, and even less than 50 mm at the end of the *Bifurcatus* Zone). The macroconch fauna of this age is still little known, but a similar trend may be noted. Sexual dimorphs of the *D. wartae* group (*P. cuneicostatus* — ? *martelli* — ? *cautisnigrae*), attaining 350—460 mm in size, are replaced by dimorphs of the *D. bifurcatoides-stenocycloides* group (*P. cf. panthieri*), some of which are smaller than their ancestors. The *Dichotomoceras cf. crassus* fauna presumably matches macroconchs of the *P. variocostatus* group which are less than 300 mm in size. And finally the presumable macroconchs of *D. bifurcatus* attain about 220 mm in size. Here presumably belong small-sized macroconchs recently placed by Malinowska [26] in *P. (Dichotomoceras) crassus* Enay. It should be noted that this trend to reduce the shell size in faunas of the *Bifurcatus* Zone was independently found by R. Enay's team (Enay, pers. inf.).

Along with the phenomenon of the size reduction there are distinct changes in the whorl shape and ornamentation. The most distinct change takes place at the base of the *Bifurcatus* Zone, where rib-curves of microconchs and of inner whorls of macroconchs become U-shaped. Such rib-curves are typical of the *Dichotomoceras* and *Perisphinctes variocostatus* groups (i.e., the type specimen of *Perisphinctes* s. st. and its close allies). This change results from ribs being more crowded on the innermost whorls and somewhat more loosely spaced thereafter. It is accompanied by some decrease in the number of ribs and a change in their appearance — they become more prominent and sharper-crested [13]. A forward sweep of secondaries, typical of *D. wartae*, is retained in *D. bifurcatoides-stenocycloides* and even emphasized in *D. bifurcatus*. From the base of the *Grossouvrei* Subzone there is a further reduction in the number of ribs and an increase in their strength. It seems possible to distinguish two principal types of sutures in the *Dichotomoceras* fauna of the *Bifurcatus* Zone: one closer to *Dichotomosphinctes*, and the other, bifurcatus-type, markedly simplified (Cariou, pers. inf.). It is of vital importance to state whether or not these types represent stages of simplification of sutures. It should be noted that the small-sized conchs of *D. bifurcatus* also display markedly simplified sutures.

The decrease in the shell size is also accompanied by changes in its shape. The transition from *Arisphinctes* to *Perisphinctes* s. st. [1, 13] seems to be related to a more sudden transition from ornamentation common for both micro- and macroconchs

to that typical of macroconchs. This seems to result from the shell size reduction and along with a further progress of this phenomenon anomalous forms appear. Such are some small-sized macroconchs of the *P. variocostatus* group, having the final body chamber of the width, height and ribbing which look as if taken from a macroconch twice as large. However, along with a further decrease in size the proportions are restored. The problem whether or not the small-sized macroconch of *Perisphinctes* s.st., cited from the *Antecedens* Subzone [13], corresponds to an earlier phase of the size reduction is of vital importance here.

Changes in the shell size and remodelling of the sculpture of this *Arisphinctes* *Perisphinctes* fauna are accompanied by similar changes in cooccurring perisphinctid. The changes are well-marked in microconchs *Subdiscosphinctes*. Close to the lower *Bifurcatus* boundary there is a transition from the *Subdiscosphinctes kreutzii-richi* group (*m*) to *S. cracoviense* (*m*), which is marked by a change from isocostate to variocostate ribbing. This is reflected by a change from steeply rising rib curves of the former [13, 6] to the initially even steeper rising and thereafter broadly convex rib curves of the latter group (*S. cracoviense* (Siem.), *S. sp. ex. gr. rhodanicus* Dumort., *S. sp. A*; see [6], Figs. 3—4). It may also be noted that the ribbing of *Subdiscosphinctes* recorded from the *Stenocycloides* Subzone is somewhat sharper and less densely spaced than that of its earlier representatives. Close to the end of this subzone this genus recedes; none of its representatives has been found either in the *Grossouvrei* Subzone or in the early *Bimammatum* Zone in Poland so far.

Several problems concerning this *Subdiscosphinctes* fauna remain open. The *Schilli* and/or *Stenocycloides* Subzones yield macroconchs not exceeding 300 mm in diameter and microconchs having 140—160 mm and occasionally less in diameter. Recently Malinowska [25] described a number of macroconchs of *Subdiscosphinctes* markedly exceeding 300 mm in size. Two such forms are at the author's disposal. Although their accurate position is not known, it may be inferred that they are derived from the lower *Transversarium* or the uppermost *Plicatilis* Zone. This would be confirmed by the find of giant microconchs of that genus in the lower part of Zawodzie section, in strata older than the *Schilli* Subzone. The problem of the origin of *Subdiscosphinctes* (formerly *Lithacoceras*) was previously discussed [6]. Subsequent studies on the faunas of the *Plicatilis* Zone gave some early macroconchs and a number of small, relatively highly evolute microconchs of *Subdiscosphinctes*. However, it is still an open question whether or not there is a continuity between *P. mazuricus-consociatus* and the above *Subdiscosphinctes* fauna.

The *Transversarium* and *Bifurcatus* Zones also yield some late *Arisphinctes* (of the *pickeringius* group) and *Liosphinctes*. These specimens also display the above phenomena of the size reduction and sculpture changes. However, dimorphism in these genera is still poorly known. *Arisphinctes* seems to pass the *Bifurcatus* *Bimammatum* boundary giving rise to *Pseudorthosphinctes*. One of us (W.B.-L.) [6] is not so sure as he used to be about dimorphism in *Liosphinctes*. He had followed Enay [13] regarding *Platysphinctes* as a microconch, whereas it may represent a small-sized macroconch. Similarly, the forms identified as microconchs of *Liosphinctes decipiens* (see [5], Pl. VIII, Fig. 2; Pl. XV) are characterized by the final body

amber over a whorl long and may represent "dwarvish" macroconchs. This see be also the case of *Decipia decipiens* in Malinowska [26]. Thus the microconchs *Liosphinctes* are still to be identified. Moreover, it remains an open question whether these presumable miniature macroconchs from the *Tenuicostatum-Antecedens* and late *Bifurcatus-Bimammatum* series represent ancestors and descendants of the *Liosphinctes* proper, respectively. Such an interpretation seems plausible. Malinowska [24] reports "*Platysphinctes*" from the *Bimammatum* Zone of the Polish Jura Chain. The fate of this evolutionary line appears difficult to assess but it is not improbable that along with a new phase of an increase in the shell size comes *Lithacoceras* sensu Geyer [15].

It should be noted that these tendencies are also displayed by Mid-Oxfordian aspidoceratids. They (*Passendorferia zieglerei* and *P. cf. uptonoides*) are markedly larger than the early *Kranaosphinctes promiscuus* group and the small-sized *Passendorferia resiformis* known from the late *Bifurcatus* Zone, but much smaller than the giant *Kranaosphinctes* from the late *Antecedens* times. An analysis of ribbing shows that it is finest and most densely spaced in the case of *P. zieglerei* and becomes progressively coarser and more loosely spaced towards the end of the *Bifurcatus* Zone. Only a few complete microconchs of this group were found. Recently A. Bittner found a complete megalomorph (76 mm in size) with all the features of *P. birmensdorfensis* Moesch at Zawady, Polish Jura Chain (see cooccurring fauna in [26]) in the *hilli-Stenocycloides* junction beds. This megalomorph is almost twice as large as *P. czenstochovens* and *P. birmensdorfensis* known from the lower *Antecedens* and *Grossouvrei* Subzones, respectively. Recent collecting gave also a number of perisphinctids referable to "*Perisphinctes*" *birmensdorfensis* Oppenheimer (nomen nudum) from the uppermost *Bifurcatus*-lower *Bimammatum* strata (Pl. IV, Photo 2). These are small-sized microconchs with loosely spaced, coarser, round-crested ribs and relict parabolic nodes-resembling swellings spaced along the final body whorl. Their macroconchs are still to be identified.

In the case of aspidoceratids, some fragments of giant macroconchs (*Paraweledonia*) and accompanying microconchs (*Peltoceratoides*; about a dozen centimeters in diameter) were recorded in the *Cordatum* Zone. However, they soon disappeared. The *Tenuicostatum-Antecedens* junction beds reveal almost no aspidoceratids. Giant aspidoceratids are reported again from the late *Antecedens*-early *Parandieri* subzones (*Euaspidoceras paucituberculatum* and its allies, over 400 mm in size). Towards the end of the *Bifurcatus* Zone smaller (up to 300 mm in size) *E. oegir* and small, heavily tuberculated forms transitional to *E. hypselum* begin to prevail. The lower part of the *Bimammatum* Zone yields small (up to 150 mm in size) *E. hypselum* and *E. schwabi* and their allies.

The *Bifurcatus-Bimammatum* junction beds yield an assemblage of small perisphinctids, which is still poorly known. This assemblage comprises "dwarvish" *Perisphinctes* (*Dichotomoceras*) *bifurcatus* (Qu.), less than 50 mm in size, ancestors of *Microbiplices*, early *Orthosphinctes*, some involute perisphinctids roughly referable to *Ringstedia*, highly evolute "*Perisphinctes*" *birmensdorfensis* Oppenheimer (nomen nudum) and its allies, a.o. The genus *Perisphinctes* s. st. undoubtedly disappears

but the question remains open whether or not it gives rise to any other one. A transition from *P. bifurcatus* to *Microbiplices* [13] seems improbable, but this should be verified by the taxonomic position of the sexual dimorphs of the latter, which are still to be identified. Generally, this perisphinctid assemblage represents a maximum reduction in the shell size and from the base of the *Bimammatum* Zone a certain trend to increase the shell size is marked again.

After a time, large perisphinctids begin to prevail once more. Higher horizons of the *Bimammatum* Zone yield large macroconchs of *Decipia* sensu Enay [13], *Liticoceras* sensu Geyer [15], *Pseudorthosphinctes* sensu Enay [13], micro- and macroconchs referable to *Progeronia*, various *Orthosphinctes*, *Ringsteadia*, "*Perisphinctes*" cf. *acer* Neumayr, and others. The large forms are generally close in appearance to those from the upper *Plicatilis-Transversarium* zones and some specimens can easily be placed in taxa typical of these zones. *Platysphinctes* of Malinowska and *Perisphinctes wartae* of Koerner [19] are good examples. There are no reliable records of macroconchs with cuneicostate ribbing of the final body chamber, typical of the *Perisphinctes* proper, and microconchs with highly densicostate, fine ribbing of the *Subdiscosphinctes kreutzii-richei* (m) group. And a morphological type appearing here for the first time is that of *Ringsteadia*.

The above trends should be also reflected by changes in other ammonite groups, but, unfortunately, the data are still insufficient. The genus *Glochiceras*, thanks to the pioneer study of Ziegler [34], is the only exception here. Its representation with the mean size of 30 (22—43) mm in the *Transversarium* Zone decreases with time, attaining 24 (18—28) mm on the average in the *Bimammatum* Zone [34]. The size reduction in *Glochiceras* is correlated with an increase in the length of the final body chamber (from 2/3 to 7/8 of the whorl) with some changes in the sub-peristomal whorl section and with a simplification of sutures.

To sum up, the *Tenuicostatum-Antecedens* junction beds seem to display a period of size reduction in perisphinctids. From the base of the *Antecedens* Subzone perisphinctids increase in size to attain their maximum in late *Antecedens-Parandensis* times. This is followed by another period of initially gradual reduction in the shell size, which becomes fairly rapid since the beginning of the *Grossouvrei* Subzone. The second period of the minimum shell size is attained close to the end of the *Bifurcatus* Zone and is followed by another period of an increase in the shell size. This phenomenon of changes in the shell size seems to be of oscillatory nature and the above-outlined main phases presumably represent the net result of a number of smaller-scale oscillations.

The phenomenon of the shell-size changes presumably results in or is accompanied by changes in the shell shape and ornamentation and in the complexity of sutures, hence it appears to be of remarkable importance for the taxonomy of ammonites. Generally, ammonites from different periods of miniaturization are very similar to one another in shell size, shape, dimensions, ornamentation and in simplified sutures. This seems to be also the case with ammonites from different periods of gigantism. Thus the phenomenon appears to be a potential source of serious taxonomic obstacles, particularly for attempts to restore evolutionary series.

Previous studies [34, 13] and the above analysis imply a reversibility of some changes in the shell morphology, size, ornamentation and in the complexity of faunas. This phenomenon makes it difficult to distinguish between possible immigrants from other ammonite provinces and "endemic" elements of the Submediterranean province. Some remarks on the possible paleobiogeographic importance of the above phenomena are given below.

Previous analyses [18, 13] showed "accelerated" evolution of perisphinctids in the *Plicatilis* Zone. Recently Kutek *et al.* ([21]), p. 575 found "a very abrupt change in ammonite faunas, marked by the appearance of new genera, subgenera "groups of species" at the base of the *Bimammatum* Zone. It follows that these two most abrupt changes in the composition of the Oxfordian ammonite faunas coincide with the above-discussed periods of size reduction. In turn, the changes of composition of ammonite faunas appear markedly smaller or almost none during periods of limited oscillations in shell size — as, for example, changes at the *Plicatilis-Parandieri* and *Bimammatum-Planula* boundaries.

Paleobiogeographic reflections

The first contribution to the problem of the paleobiogeography of the Oxfordian perisphinctid faunas was made by Siemiradzki [29], according to whom the Polish, Arabian and French basins were the center of evolution of a number of series of perisphinctids and the difficulties in the recognition of the series resulted from the migration of open-ocean ("Indian") and other species into these basins. More elaborated evolutionary series were subsequently given by the same author [30], Konchadzé [27] and others.

The opposite interpretation was given by Arkell ([2] p. 610), who, assuming the ultimate shell size as a specific characteristic, interpreted the appearance of Oxfordian faunas of large perisphinctids in Central and Northern Europe as the result of "a return of Tethyan faunas". This was questioned by Callomon, according to whom in the time of the Callovian-Oxfordian Boreal Spread "there was an unusually extensive northward migration of some Tethyan elements" (Callomon, *ibid.* [17], p. 134) as far as East Greenland. Subsequently, the analysis of Cariou [11] showed that "it is exaggerated to speak of a Tethyan migration, as the *Perisphinctidae* (and other Tethyan families) were rather autochthonous in Central and North Europe... and the large movements of ammonite faunas have mostly been made by the Boreal families which transgress towards the south". In this way we returned to Siemiradzki [29, 30], who tried to distinguish continuous Callovian-Kimmeridgian evolutionary series of perisphinctids and found southward migration of cardioceratids.

The extent of migration of perisphinctids within the Tethyan Realm remains controversial. Recent paleobiogeographic analyses (see [11] and the references therein) showed remarkable provinciality of Oxfordian perisphinctids, but boundaries between the provinces are of gradational nature [17].

The Oxfordian assemblage of the Polish Jura Chain mostly consists of Submediterranean elements, with some admixtures of Tethyan, Subboreal and Boreal

ones. There seem to be no greater differences with respect to assemblages known from southern France, FRG and southern USSR [20]. The above changes in perisphinctid assemblages presumably took place on the whole area of the Submediterranean province and certainly in SE France (Enay, pers. inf.).

The most characteristic Submediterranean and Subboreal forms include *Perisphinctes* s. st., *Decipia*, *Ringsteadia*, etc. Accurate relationships of such a perisphinctid assemblage with those known from other provinces are still difficult to assess because of the time scales for the latter regions being far less detailed. Despite modern stratigraphic works in a number of extra-Submediterranean areas the Submediterranean zonation still comprises the maximum number of easily distinguishable zones and subzones (especially for the Oxfordian). This is related to the apparent "overweight" of the Submediterranean taxa. This relative enrichment of the Submediterranean ammonite assemblage and (? resulting) apparent dissimilarity of the assemblage may be interpreted in terms of environmental effects on the shell morphology if the above premise of Spath [31] and the above conclusions are valid. A time sequence of environmental changes would lead to a sequence of changes in the environmentally dependent shell morphology. Different sequences of environmental events would of course lead to a different "ornamentational" sequence, i.e. to the origin of different "morpho-" fauna.

Immigrants to the Submediterranean province were presumably also affected by the changes. There is a relative enrichment of "Submediterranean-Subboreal cardioceratid assemblages in numbers of both genera and species in comparison with the Boreal assemblages. Quantitatively, there are a few times more cardioceratid taxa in the former than in the latter region.

It seems possible to distinguish two principal lineages among the Submediterranean perisphinctids: (1) series of idoceratids, comprising the Mediterranean *Kranaosphinctes* group, descendant *Passendorferia*, and forms transitional to *Nebrodites herbichi-teres* and some *Idoceras* [7], and (2) series of Submediterranean-Subboreal perisphinctids, comprising *Perisphinctes* s. st., its ancestors, *Arisphinctes* and descendants, if any, as well as the corresponding microconchs (*Dichotomoceras*, *Dichotomosphinctes* and *Otosphinctes*). There are some more troublesome genera and species groups, such as Mediterranean *Arisphinctes* and *Dichotomosphinctes* of [13], presumably closer to the 1st series, and some Submediterranean *Liosphinctes* and *Arisphinctes pickeringius*, closer to the 2nd group rather.

It appears difficult to restore the actual position of such groups as *Arisphinctes plicatilis* or the genus *Subdiscosphinctes*. Their affiliation will not be known until their origin is explained but they seem to be closer to the 1st series.

The *Arisphinctes-Perisphinctes* s.st. (M) assemblage appears to be limited to the Submediterranean and Subboreal provinces and any extra-Submediterranean-Subboreal records of it should be tested by identifying the corresponding microconchs. However, there are numerous records of microconchs or even series of microconchs outside these regions, e.g. [4]. The actual position of the microconch should be verified by the position of their macroconchs. Such an analysis may

able one to estimate the extent to which the ornamentation of micro- and macroconchs has been susceptible to environmental factors.

Anyhow, the origin of the genus *Perisphinctes* s. st. appears to result from certain changes in the Oxfordian perisphinctid assemblage, taking place over the areas of Submediterranean and Subboreal provinces. It seems to be a final result of a cycle of size changes. If a narrow interpretation of this genus is accepted, this name should be applied to *Perisphinctes variocostatus* (Buckl.) and its allies, characterized by a U-shaped initial part of the rib-curve, prominent, loosely-spaced, very sharp-crested ribs on inner whorls, etc., and to the corresponding microconchs. In such case, the stratigraphic range of this genus would be confined to the *Bifurcatus* Zone, and all the earlier *Perisphinctes* sensu Arkell and Enay would be placed in *Martelliceras* Schindewolf. It should be noted that the ornamentation of the final body chamber of the *Perisphinctes* type is nothing unusual among Upper Jurassic perisphinctids and it is repeated by some unrelated early Kimmeridgian forms of the genus *Progeronia* Arkell ([36], Pl. 8, Fig. 3, Pl. 9).

Possible causes of time changes

The causes of spreads of Boreal faunas are still unknown. The Boreal elements, as cardioceratids, appear to be independent of climate, as these Boreal forms could live in areas of carbonate deposition situated within the Oxfordian coral belt.

The faunal differences between Oxfordian subzones were partly related by Callomon [8] to some ecological factors. Subsequently, changes in the share of particular families in the ammonite spectrum were shown by Ziegler [35] to be dependent on a number of environmental factors including the depth and temperature of water (but see the objections of Geyer [16]).

Changes of the ultimate shell size were previously linked by Ziegler with some inherent trends as "the sediments involved give no clues concerning the changes" ([34], p. 231). However, the fact that the changes may take place simultaneously in unrelated groups makes it difficult to accept such an explanation and seems to emphasize the importance of some external stresses.

The coincidence of the "replacement" of Boreal elements by giant Tethyan perisphinctids with the appearance of coral reefs, i.e., with an amelioration of climate was noted by Callomon ([8], p. 198). Actually, the earlier phase of gigantism coincides with the development of large fringe reefs from NE margins of the Holy Cross Mts. [22], which are undoubtedly older than the late *Bifurcatus* Zone (*Perisphinctes bifurcatus* Qu. was recently found in a direct encapping of the reef at Bałtów, the Holy Cross Mts.). However, the Cząstochowa (Polish Jura Chain) sections and particularly *Bifurcatus-Bimammatum* sections displaying the phase of ammonite-shell-size reduction show no changes in lithology (here we are indebted to Dr. A. Gaździcki and Dr. J. Liszkowski for microfacial analyses).

Thus it may be tentatively concluded that the size changes in ammonite faunas appear to be at least partly related to some hitherto unidentified environmental factors, which were changing over the large part of the Submediterranean and Subboreal provinces.

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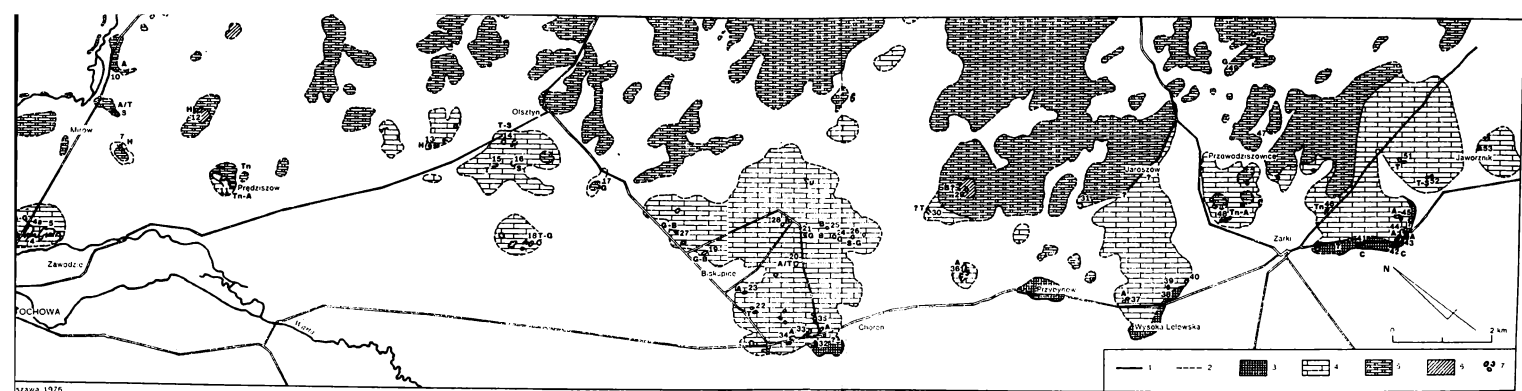


Figure. Oxfordian of the Częstochowa area, Polish Jura Chain (outline of outcrops and main lithological types, partly after S. Z. Różycki, Z. Mosoczy and others)

1 — outcrops of Callovian, 2 — outcrops of Oxfordian; main lithological types: 3 — spongy limestones with marly intercalations, 4 — platy limestones, 5 — massive limestones, 6 — chalky limestones; 7 — quarries, zones and subzones of Oxfordian: C — Cordatum Zone, Tn — Tenuicostatum beds, A — Antecedens Zone, T — Transversarium Zone, S — Stencycloide, Subzone of Bifurcatus Zone, G — Grossourei Subzone of Bifurcatus Zone, B — Bimammatum Zone

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Брохвич-Левиньски, З. Ружак, Замечания о временной изменчивости аммонитовой фауны Оксфорда на территории Польской Юры

содержание. Обратимые изменения в максимальном диаметре раковины, размерах, орнаментации и степени осложнения лопастной линии, известные у аммонитов рода *Glochiceras* и. [34], обнаружены также у их современников из семейства *Perisphinctidae*. Периоды максимальной редукции величины, соответствующие переходным слоям между биоэонами: *micostatium* и *Antecedens*, а также *Bifurcatus* и *Bimammatum*, совпадают с периодами наибольших изменений в составе аммонитовой фауны Оксфорда. Одновременно периодам незначительных изменений величин раковины соответствуют незначительные изменения в составе аммонитовой фауны. В некоторой степени эти изменения являются вероятно вызванными внешними факторами. Независимо, рассматриваемые изменения, хотя бы частично могут выяснять причину резкого преобразования количества Оксфордских таксонов известных Субсредиземноморской и Суббореальной провинции над количеством таксонов обнаруженных в других провинциях.

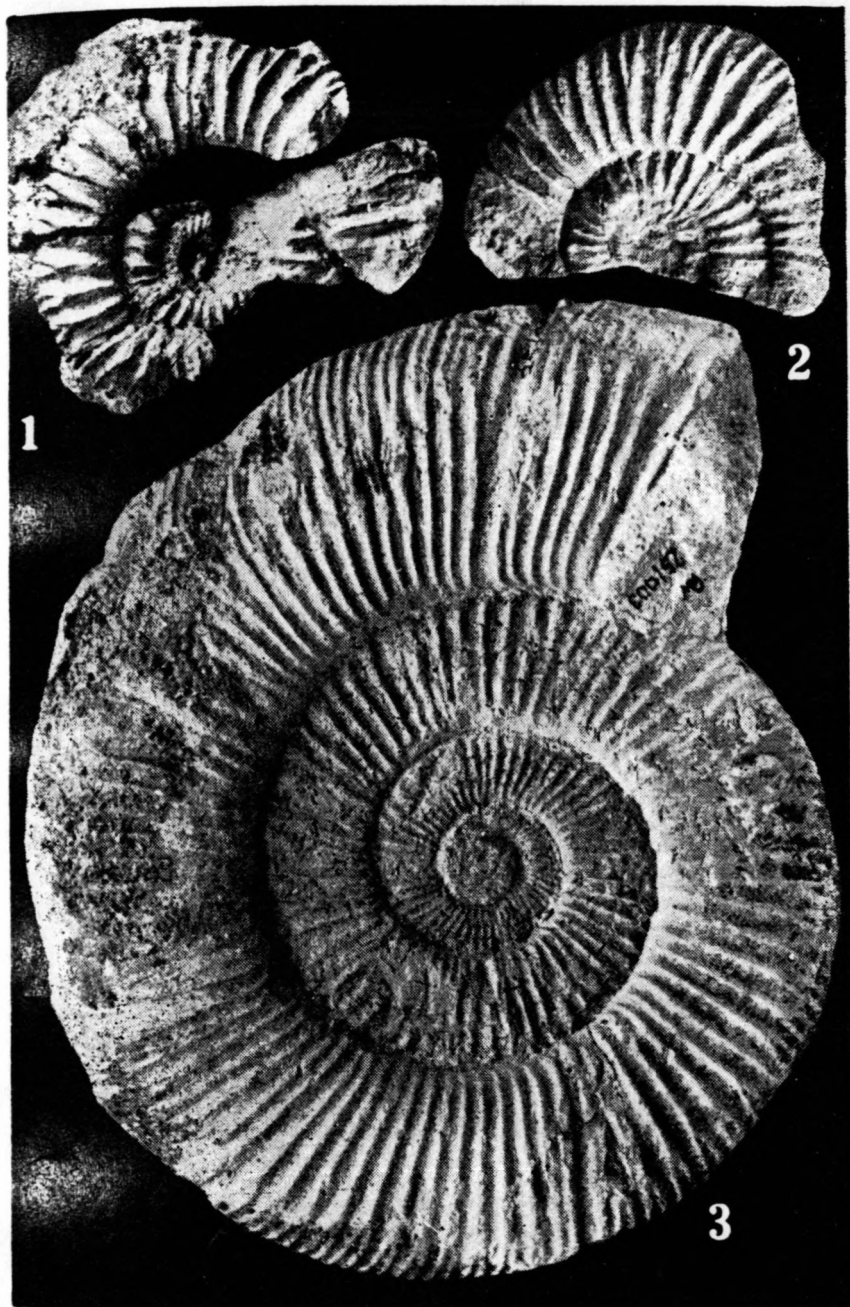


Photo 1. *Microbiplices* sp.; Br 05/273, Zawodzie at Częstochowa, the *Bifurcatus* Zone, *Grossouvrei* Subzone; D_{max} — 55 mm, H/D — 0.28, T/D — ca. 0.34, U/D — 0.49

Photo 2. *Perisphinctidae* (? *Idoceratinae* sp. et gen. indet.); Br 05/045, Zawodzie at Częstochowa, the *Transversarium* Zone, *Grossouvrei* Subzone; D_{max} — 66 mm, ? complete

Photo 3. *Perisphinctes* (*Dichotomoceras*) *bifurcatoides* Enay; Br 25/003, Skrajnica near Olsztyn, Częstochowa; D_{max} — 145, D_{Ph} — 90 mm, H/D — 0.30, U/D — 0.48, D — 109 mm, H/D — 0.30, T/D — 0.30, U/D — 0.47

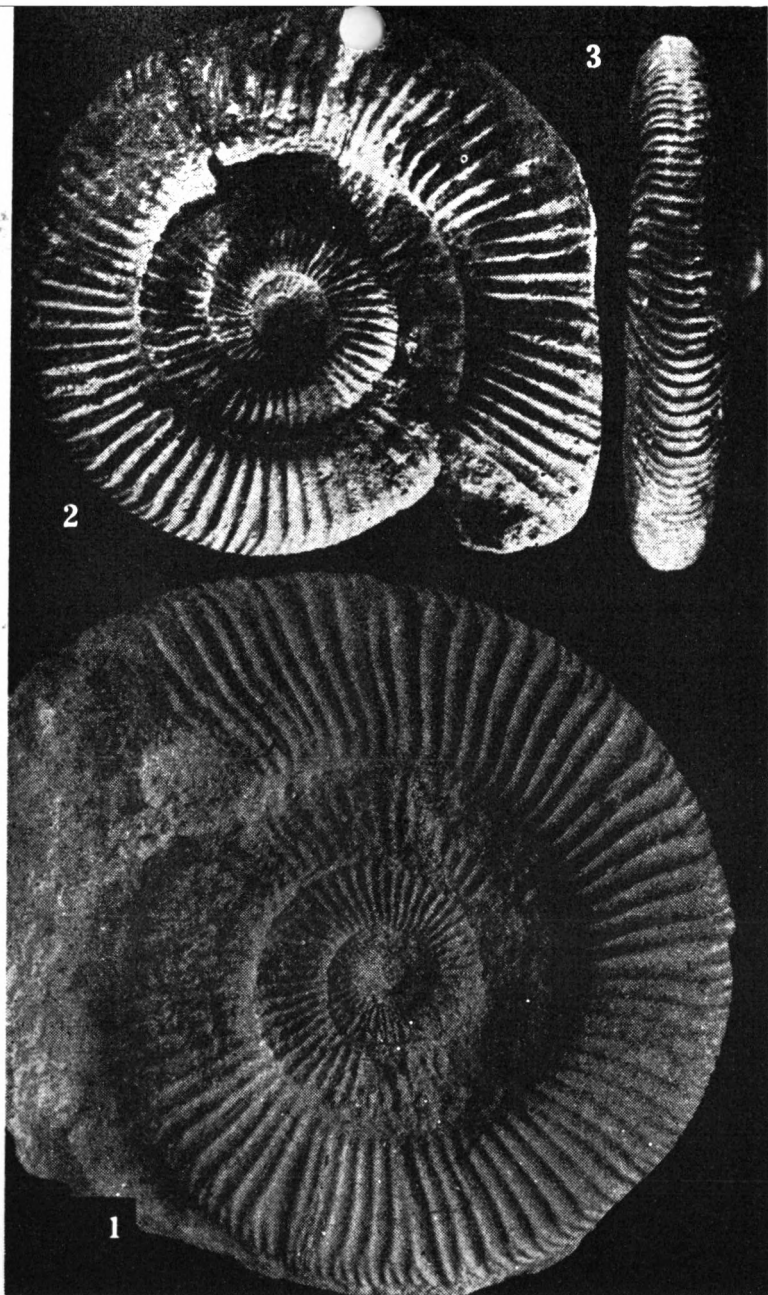


Photo 1. *Perisphinctes (Dichotomosphinctes) wartae* Buk.; Br 02/208, Zawodzie at Częstochowa, the Transversarium Zone, Schilli Subzone; D_{\max} — 162 mm; almost complete

Photo 2. *Perisphinctes waehneri* Siemiradzki (type specimen) = recte *P. (D.) stenocyclotus* Siemiradzki; D_{\max} — 137 mm, ΔPh — 82 mm, D — 111 mm, H/D — 0.29, T/D — 0.22, U/D — 0.50, D — 85 mm, H/D — 0.28, T/D — 0.22, U/D — 0.50; almost complete



Photo 1. *Perisphinctes (Perisphinctes) cuneicostatus* Arkell; Br 05/202, Zawodzie at Częstochowa, the *Transversarium* Zone, *Schilli* Subzone; D_{\max} — 365 mm, D_{Ph} — 255 mm; complete, with peristome

Photo 2. *Perisphinctes (Perisphinctes)* sp.; Br 02/003, Zawodzie at Częstochowa, the *Bifurcatus* Zone, *Grossouvrei* Subzone; D_{\max} — ca. 216 mm, D_{Ph} — 140—160 mm, D — 192 mm, H/D — 0.30, U/D — 0.49, D — 87 mm, H/D — 0.30, U/D — 0.49; almost complete dwarfish macroconch, presumable sexual counterpart of *P. (Dichotomoceras) bifurcatus* (Qu.)

Photo 3. *Perisphinctes (Dichotomoceras) bifurcatus* (Qu.); Ha 24/7a, the *Bifurcatus* Zone, *Grossouvrei* Subzone, upper most part of *Bifurcatus-Bimammatum* junction beds; D_{\max} — 48 mm;

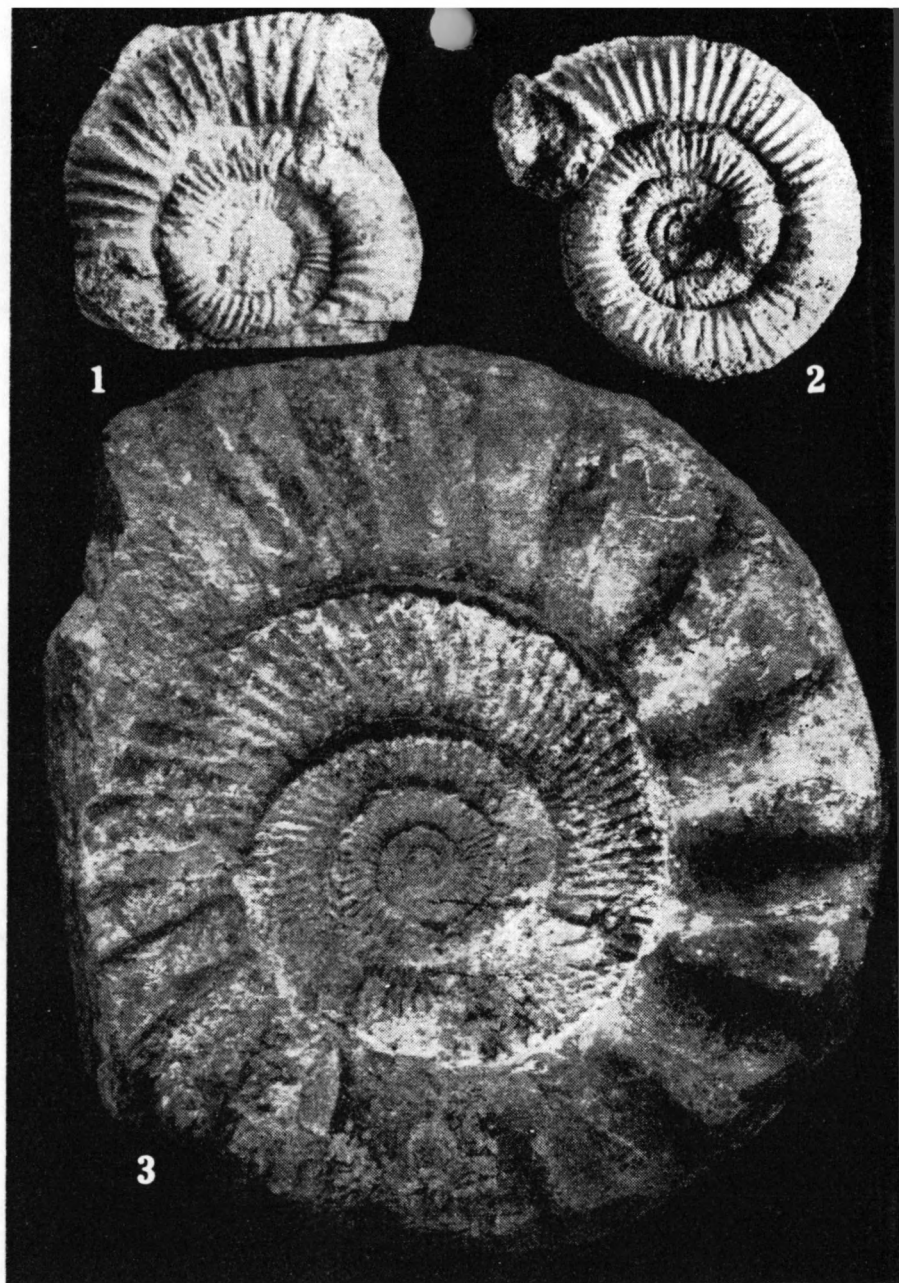


Photo 1. *Passendorferia* cf. *birmensdorfensis* (Oppenh. non Moesch); Br 7/21, Kamyk at Czestochowa, *Bimammatum* Zone, *Hypselum* Subzone; D_{max} — 52 mm, D — 47 mm, H/D — 0.2, TD — 0.30, U/D — 0.50; note swellings-resembling parabolic nodes marked along the fin body chamber

Photo 2. *Passendorferia birmensdorfensis* (Oppenh. non Moesch); Br A19/006, Olsztyn near Czestochowa, *Bimammatum* Zone, *Hypselum* Subzone; D_{max} — 76 mm, H/D — 0.28, U/D — 0.52; complete

Photo 3. *Perisphinctes* (*Perisphinctes*) *cautisnigrae* Arkell; Br 05/201, Zawodzie at Czestochowa, fallen block, the *Transversarium* Zone, *Schilli* Subzone or lowermost *Bifurcatus* Zone; D_{max} —