Acta Geologica Polonica, Vol. 52 (2002), No. 3, pp. 307-364

The ammonites of the family Perisphinctidae from the Plicatilis Zone (lower Middle Oxfordian) of the Polish Jura Chain (Central Poland); their taxonomy, phylogeny and biostratigraphy

EWA GŁOWNIAK

Institute of Geology, University of Warsaw, Al. Żwirki i Wigury 93; Pl-02-089 Warszawa, Poland

ABSTRACT:

GŁOWNIAK, E. The ammonites of the family Perisphinctidae from the Plicatilis Zone (lower Middle Oxfordian) of the Polish Jura Chain (Central Poland); their taxonomy, phylogeny and biostratigraphy. *Acta Geologica Polonica*, **52** (3), 307-364. Warszawa.

The Plicatilis Zone of the Submediterranean Middle Oxfordian is redefined and subdivided into three subzones: the Paturattensis Subzone, the Ouatius Subzone and the Arkelli Subzone. Their boundaries are defined by the appearance of the successive perisphinctid species referred to a *Kranaosphinctes-Otosphinctes* lineage. Correlation with other lower Middle Oxfordian zonations is provided. Classification of the studied ammonites is based on the morphological variability in the successive perisphinctid assemblages. The species are assigned to three genera: *Perisphinctes*, *Liosphinctes* and *Neumannia* gen. nov. Microconchs of *Neumannia* gen. nov. and of *Perisphinctes trifidus* (SOWERBY) are described for the first time. The type species of the subgenus *Arisphinctes*, *P. ariprepes* (BUCKMAN), is reassigned to the subgenus *Kranaosphinctes* BUCKMAN, and thus *Arisphinctes* is treated as a younger synonym of *Kranaosphinctes*; *Perisphinctes plicatilis* (SOWERBY) and *Perisphinctes laevipickeringius* ARKELL are reinterpreted and reassigned to the genus *Liosphinctes* BUCKMAN. Two new chronosubspecies, *Perisphinctes ouatius ouatoides* and *Perisphinctes arkelli wysokae* of the subgenus *Otosphinctes*, are distinguished. The *Kranaosphinctes-Otosphinctes* lineage gives rise to the *Perisphinctes-Dichotomosphinctes* lineage at the boundary between the Plicatilis and Transversarium zones. The two other lineages, one of *P. trifidus* (a possible offshoot from the *Kranaosphinctes-Otosphinctes* lineage), and the other of the genus *Liosphinctes*, disappear in the upper Arkelli Subzone of the Plicatilis Zone. Mediterranean roots for all of the three lineages are suggested. The fourth lineage, of *Neumannia* gen. nov., appears in the upper Arkelli Subzone of the Plicatilis Zone as a consequence of an immigration event from the Mediterranean area.

Key words: Perisphinctidae, Ammonoidea, Upper Jurassic, Polish Jura Chain, Taxonomy, Phylogeny, Biostratigraphy.

INTRODUCTION

Although the Submediterranean family Perisphinctidae is one of the ammonite groups critical for biostratigraphic subdivision of the Middle Oxfordian, the succession and evolutionary history of perisphinctid faunas in the lower part of this substage is poorly known. Relatively abundant data from the lower part of the Middle Oxfordian have come from southern England (ARKELL 1935-1939; CALLOMON 1960), whereas in other areas of Western Europe, the Lower-Middle Oxfordian boundary is characterised by condensed or discontinuous

successions, with only scarce and fragmentary material available (e.g. SIEGFRIED 1952, ENAY 1966, HAUERSTEIN 1966, FISCHER & GYGI 1989, MELÉNDEZ & *al*. 1982, MELÉNDEZ 1989, GYGI 1995). The area of the Polish Jura Chain, selected for the present study, is thus of particular importance, containing the most complete succession of lower Middle Oxfordian ammonites in Submediterranean Europe. The fossiliferous and continuous carbonate succession cropping out in this area provides rich and well-preserved material of the family Perisphinctidae, of the Boreal and Subboreal Cardioceratidae, as well as of southern Haploceratacea, making it an important area for biogeographic and biostratigraphic studies. The previous works on Middle Oxfordian perisphinctid ammonites from the Polish Jura Chain dealt either exclusively with their taxonomy, with insufficient stratigraphical resolution (BUKOWSKI 1887; MALINOWSKA 1972a, 1972b), or essentially with perisphinctids from the upper Middle Oxfordian (BROCHWICZ-LEWIŃSKI 1972, 1973, 1976, 1979; BROCHWICZ-LEWIŃSKI & RÓŻAK 1975a, 1975b, 1976).

The aim of the present paper is the presentation of the lower Middle Oxfordian perisphinctid ammonites: their succession, phylogeny, and systematic description. Based on their stratigraphical distribution a zonal scheme for the lower part of the Middle Oxfordian is proposed.

The ammonites of the genus *Platysphinctes* TINTANT from the Plicatilis Zone of the Middle Oxfordian were published previously (GŁOWNIAK 2000).

THE STUDIED SECTIONS

The ammonites were collected in Wysoka Quarry, Ogrodzieniec Quarry and Rudniki Quarry (Text-fig. 1) in the Polish Jura Chain. The quarries are located approximately 30 km south of Częstochowa. The quarries selected for study contain the most complete succession of Oxfordian carbonates in the Polish Jura Chain, ranging from the top of the Callovian, through the Lower Oxfordian, up to the upper Middle Oxfordian. The lower part of the Middle Oxfordian varies in thickness from approximately 2 m in Ogrodzieniec Quarry (Text-fig. 3) to 15 m in Wysoka Quarry (Text-fig. 2). In the area of Wysoka the Middle Oxfordian is developed as bioherms and biostromes that pass laterally into the platy limestones distinguished as Zawodzie beds (RÓŻYCKI 1953). In the Ogrodzieniec Quarry the Middle Oxfordian is developed as marls and thin bedded marly limestones with sponges (Jasna Góra beds) overlaid by the Zawodzie beds.

The nature of the local tectonics made it necessary to collect faunas from several sections in each of the quarries (Text-figs 2-3). The sections were correlated by marker beds.

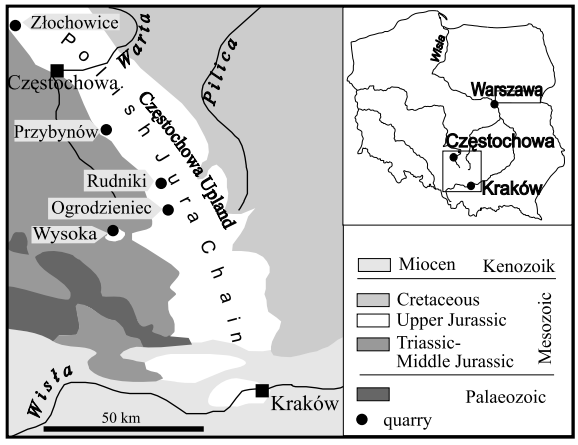

Fig. 1. Geological sketch-map of the Polish Jura Chain showing the locations of the studied quarries

The ammonite species and their location in sections and beds are listed in the Appendix.

CONCEPT OF CLASSIFICATION AND METHODOLOGY

A collection comprising c. 170 perisphinctid specimens, precisely localised in sections (Text-figs 2-3, Appendix), has been studied. Morphological variability recognized in the ammonite assemblages enabled the distinction of successive "groups" comparable to natural biospecific units. The groups consist of microconch species of the subgenus *Otosphinctes* BUCKMAN and corresponding macroconch species of the subgenus *Kranaosphinctes* BUCKMAN from isochronous or nearly isochronous horizons. In every "horizontal" group one microconch species and usually more than one corresponding macroconch species are recognized. The species of the subgenus *Otosphinctes* as interpreted in the present paper are characterised by a wide range of continuous morphological variability in particular horizons, including the final size (Text-fig. 5). The latter varies usually in a unimodal way, except for *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN). The variability of the microconch is recognized on the basis of numerous adult individuals represented in the studied collection by 43% of specimens. The adult and complete macroconchs of the subgenus *Kranaosphinctes*, on which the classification of the latter is based, are less numerous in the studied collection than their corresponding microconchs, being represented by c. 5% of the whole number of individuals. Additionally, abundant juvenile macro-

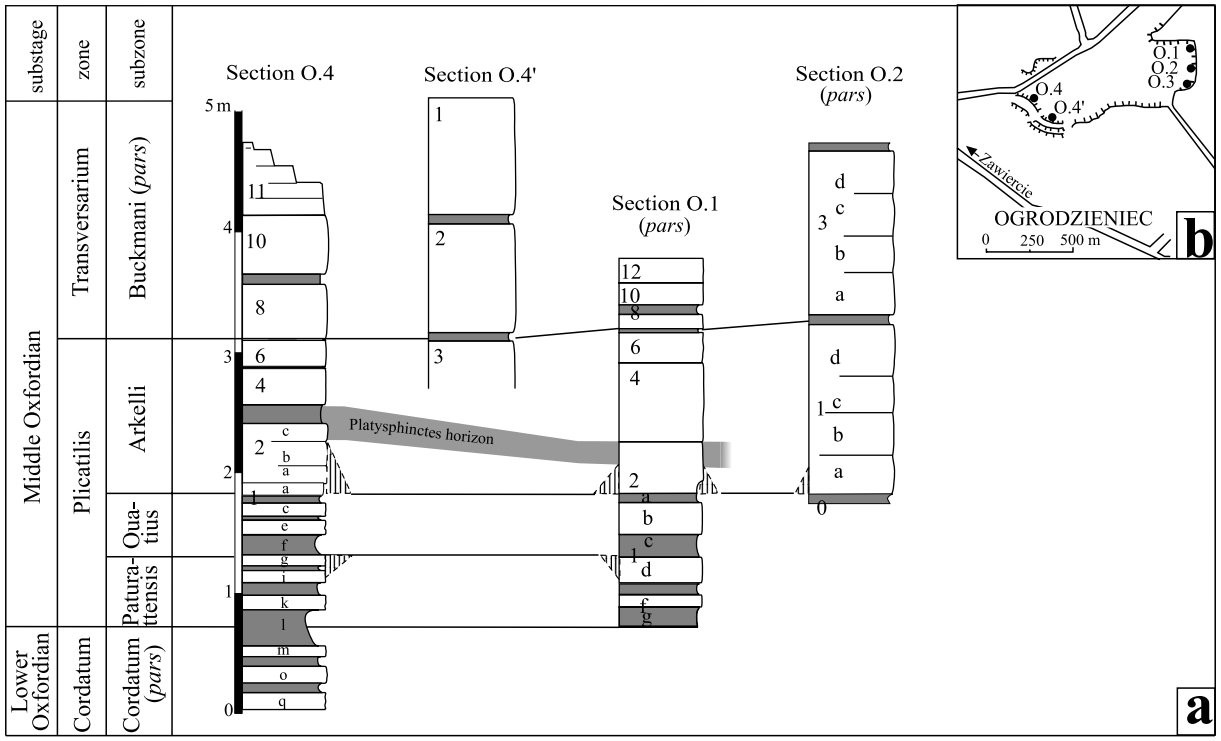

Fig. 3. Correlation of sections from Ogrodzieniec Quarry (a) and their location in Ogrodzieniec Quarry (b); explanations see Text-fig. 2

conchs appear, these being, however, less informative for taxonomic interpretation. The classification of the subgenus *Kranaosphinctes* at specific level is still far from definitive, as the number of specimens available for study, especially adult forms, is still increasing.

Evolutionary changes recognized in the groups of micro- and macroconchs of the subgenera *Otosphinctes* and *Kranaosphinctes* make them the main biostratigraphic tool in the lower Middle Oxfordian, and enable high resolution at subzonal level (Text-fig. 6).

The taxonomic separation of micro- and macroconch counterparts between the two subgenera *Otosphinctes* and *Kranaosphinctes* is applied in the present paper following previous authors (BUCKMAN 1921, 1926; ARKELL 1938, 1939; ENAY 1966; MELÉNDEZ 1989). However, these subgenera, according to the interpretation proposed in the present paper, embrace exclusively the upper Lower Oxfordian-lower Middle Oxfordian forms recognized as a single lineage, and thus their interpretation differs from that of the previous authors (op. cit.). All of the other examples of dimorphism described in the present paper for the first time are interpreted at specific level. The microconchs newly described are assigned either to the species *Perisphinctes trifidus* (SOWERBY) or to the new genus *Neumannia*, both of them hitherto known only by their macroconchs. The genus *Liosphinctes* BUCKMAN described from the studied material remains known exclusively by macroconchs.

The material from the Plicatilis Zone is assigned to three genera: *Perisphinctes* WAAGEN, *Liosphinctes* WAAGEN and *Neumannia* gen. nov. They represent, as interpreted in the present paper, different monophyletic units. This phylogenetic inference, apart from the morphological homogeneity, takes account of the whole of the available data, e.g. the biostratigraphic range and palaeobiogeographic distribution of the species assigned to the genus in question (see *Neumannia* gen. nov. and *Liosphinctes)*.

For biostratigraphic and biogeographic purposes, particular "vertical" morphotypes are distinguished within species or chronosubspecies characterised by a wide range of morphological variability. These morphotypes are labelled with their traditional specific names, e.g. *paturattensis* morphotype or *montfalconensis* morphotype, both assigned herein to a single species, *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL.

PHYLOGENETIC OUTLINE

Perisphinctes (*Kranaosphinctes*) *promiscuus* BUKOWSKI and *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL, the early representatives of the

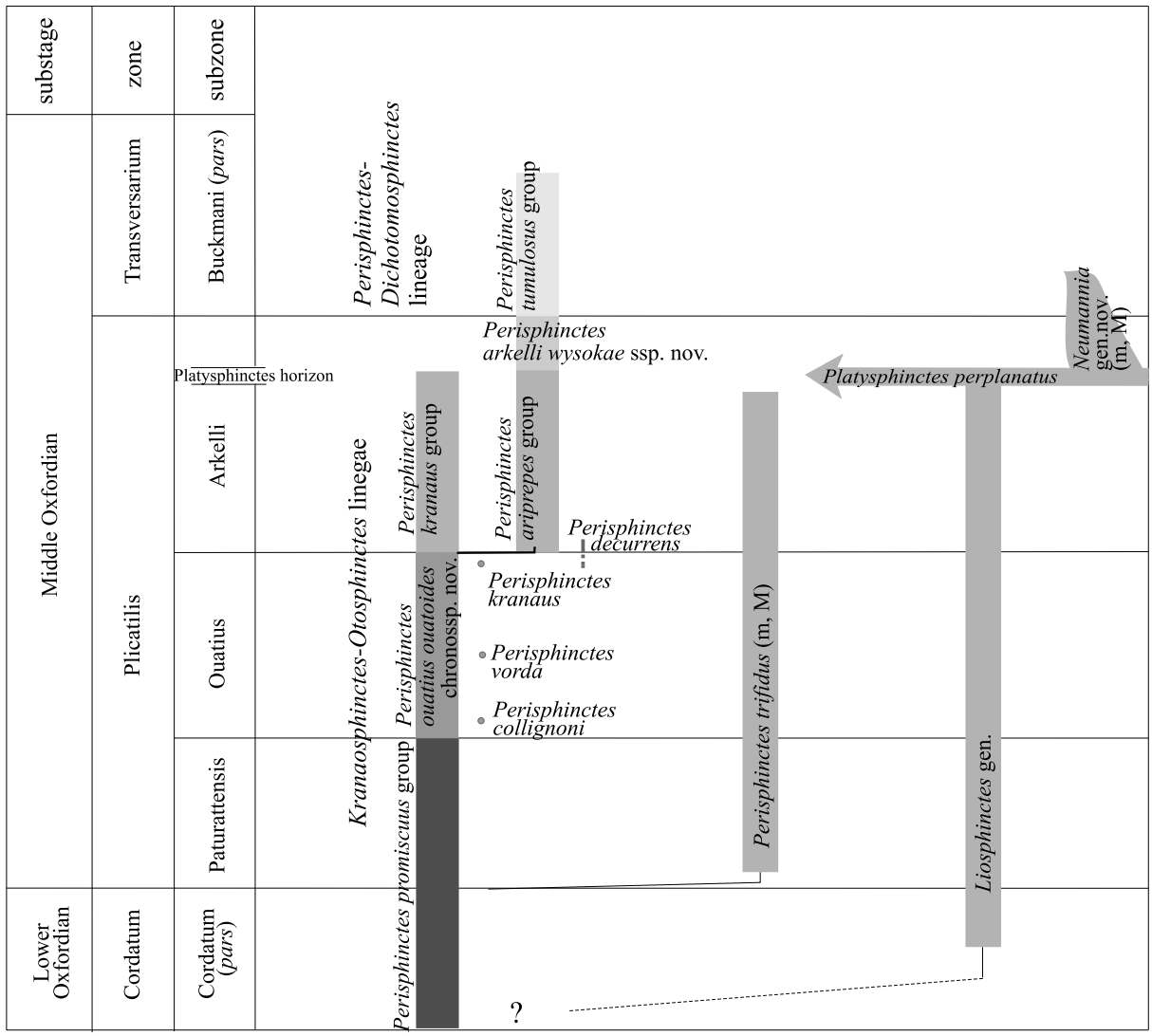

Fig. 4. Phylogeny of perisphinctid ammonites across the Plicatilis Zone and the lower Transversarium Zone. Dots are for single specimens

Kranaosphinctes-Otosphinctes lineage (Text-fig. 4), and *Liosphinctes plicatilis* (SOWERBY), the early representative of the *Liosphinctes* lineage, range up into the Plicatilis Zone of the Middle Oxfordian from the underlying Cordatum Zone of the Lower Oxfordian (Text-fig. 6) (cf. BROCHWICZ-LEWIŃSKI 1981, MATYJA 1977, GYGI 1998). The species *Perisphinctes trifidus* (SOWERBY) (m, M) as interpreted in the present paper, represents a distinct lineage which evolves from the *Kranaosphinctes-Otosphinctes* lineage at the lower boundary of the Plicatilis Zone. Early representatives of all three lineages, with their shell-morphology characterised by fine, dense ribbing, show characters of Mediterranean ammonites, from which they probably originate. The ammonites of Mediterranean affinity make their second appearance in the studied area in the upper Arkelli Subzone of the Plicatilis Zone. These ammonites are treated here as a single lineage of the genus *Neumannia* gen. nov. (Text-fig. 4), and their appearance is interpreted as an immigration event (GŁOWNIAK 2000). *Neumannia* gen. nov. disappears from the study area in the lower part of the Transversarium Zone.

The evolution of the *Kranaosphinctes-Otosphinctes* lineage leads from forms of Mediterranean affinity appearing in the upper Cordatum Zone of the Lower Oxfordian but becoming abundant only in the Paturattensis Subzone of the Plicatilis Zone of the Middle Oxfordian, through the transitional forms appearing in the Ouatius Subzone, to typical Submediterranean forms represented by the "English" species (MELÉNDEZ 1989, p. 210) ranging through the Arkelli Subzone of the Plicatilis Zone. At the boundary

between the Plicatilis and Transversarium zones as interpreted herein, representatives of this lineage disappear, giving rise to the *Perisphinctes-Dichotomosphinctes* lineage characteristic of the Transversarium Zone.

Two other lineages, of *Perisphinctes trifidus* (m, M) and of *Liosphinctes*, disappear from the study area in the Arkelli Subzone of the Plicatilis Zone, although the latter lineage makes its second appearance in the upper Transversarium Zone, being there represented by different species.

MIDDLE OXFORDIAN PERISPHINCTID EVOLUTION THROUGHOUT THE PLICATILIS ZONE

The *Kranaosphinctes-Otosphinctes* lineage is composed of three successive groups of the micro- and macroconchs (Text-fig. 4), comparable to biospecies (see concept of classification and methodology, p. 270): the *Perisphinctes promiscuus* group appearing in the upper Cordatum Zone of the Lower Oxfordian and ranging up higher through the Paturattensis Subzone of the Plicatilis Zone of the Middle Oxfordian; the group consisting of *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* and its macroconchs, ranging through the overlying Ouatius Subzone; and the *Perisphinctes kranaus* group appearing at the boundary between the Ouatius and Arkelli subzones of the Plicatilis Zone and disappearing in the upper Arkelli Subzone. At the boundary between the Ouatius and Arkelli subzones *Kranaosphinctes-Otosphinctes* lineage gives rise to the *Perisphinctes ariprepes* group, which in turn is succeeded in the upper Arkelli Subzone by the group consisting of *Perisphinctes arkelli wysokae* chronossp. nov. and its macroconchs. The latter group gives rise at the lower boundary of the overlying Transversarium Zone to the *Perisphinctes tumulosus* group, comprising the first representatives of the *Perisphinctes-Dichotomosphinctes* lineage.

The *Perisphinctes promiscuus* group (Text-fig. 4) comprises the small, densely ribbed macroconchs *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI, *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI) (its first representatives appearing only in the upper Paturattensis Subzone) and their microconch counterpart *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL. Fine, dense ribbing and a serpenticone shell are the distinctive features of the *P. promiscuus* group, both macro- and microconchs.

At the boundary between the Paturattensis and Ouatius subzones the *P. promiscuus* group is succeeded by small to middle-sized, moderately densely ribbed microconchs constituting the chronosubspecies *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. (Text-fig. 4), the direct descendants of *P.* (*O.*) *paturattensis*. Its presumed macroconch counterparts are *Perisphinctes* (*Kranaosphinctes*) *collignoni* (its late representatives from the Ouatius Subzone), *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN) (its first representatives appearing in the upper Ouatius Subzone) and/or possibly also *Perisphinctes* (*Kranaosphinctes*) *vorda* ARKELL. Each of the latter three species is represented in the studied material from the Ouatius Subzone by one specimen only; accurate recognition of the actual affinities in the group under consideration requires further study. The characters of the shell morphology of *P. ouatius ouatoides* chronossp. nov. and its presumed macroconchs, such as the subquadrate whorl-section [except for *P.* (*K.*) *vorda*] changing only in microconchs to subcircular or oval on the body-chamber, the moderately evolute coiling of the outer whorls and the moderately thick, rarely thick ribbing, are the features which differentiate them from the ancestral *P. promiscuus* group, and show their transitional character to the younger species.

P. ouatius ouatoides ssp. nov. disappears at the boundary between the Ouatius and Arkelli subzones giving rise to the large, moderately thick to thickly ribbed forms of the *Perisphinctes kranaus* group (Text-fig. 4) and the *Perisphinctes ariprepes* group. The former consists of *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN) (its representatives from the Arkelli Subzone), and its microconch counterpart, *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN), the younger chronosubspecies of *P.* (*O.*) *ouatius*. The latter group consists of *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN) and its microconch partner, *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK. Also appearing at the lower boundary of the Arkelli Subzones or possibly somewhat below is *Perisphinctes* (*Kranaosphinctes*) *decurrens* (BUCKMAN), which is distinctly smaller than the macroconchs of the *P. kranaus* and *P. ariprepes* groups but resembles them in whorl-section and rib-thickness. Determination of the possible affinity of this form to either of the two groups requires more material. Both, the *P. kranaus* and *P. ariprepes* groups, and *P.* (*K.*) *decurrens* represent shell morphology of Submediterranean forms: they posses usually a subquadrate whorl-section, evolute coiling (in the *P. ariprepes* group it is moderately evolute only on the inner whorls), and moderately thick to thick ribs.

The *P. kranaus* group disappears in the upper Arkelli Subzone of the Plicatilis Zone, whereas the *P. ariprepes* group gives rise to the microconchs constituting the chronosubspecies *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov. (Text-fig. 4), the successor to *P.* (*O.*) *arkelli arkelli*. The presumed macroconch counterparts of *P.* (*O.*) *arkelli wysokae* chronossp. nov.

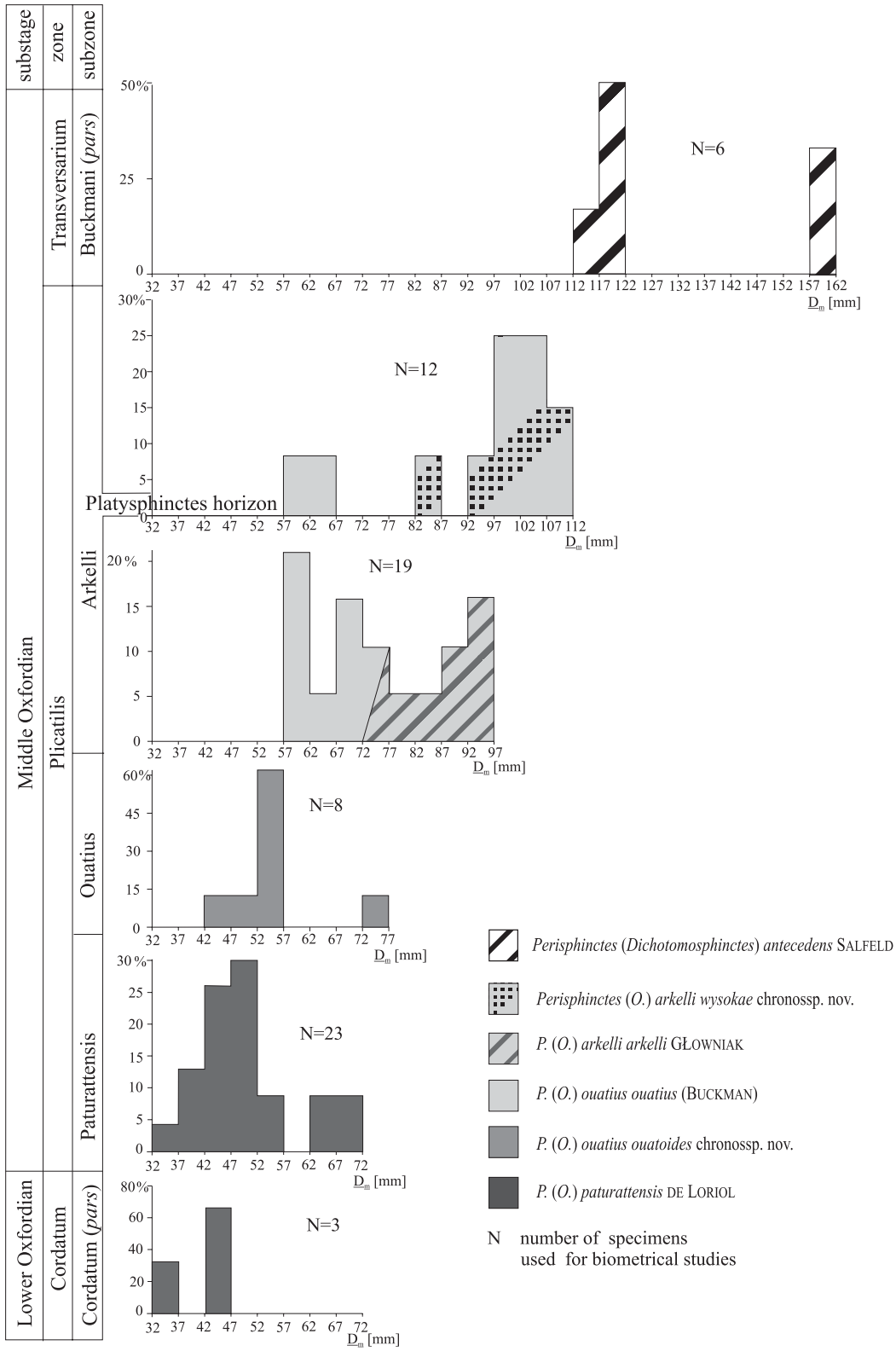

Fig. 5. Size variability in the successive species or subspecies of the subgenus *Otosphinctes* BUCKMAN through the Plicatilis Zone, and in *Perisphinctes* (*Dichotomosphinctes*) antecedens SALFELD from the lower Buckmani Subzone of the Transversarium Zone

are *Perisphinctes* (*Kranaosphinctes*) *maximus* (YOUNG & BIRD) and/or the closely allied *Perisphinctes* (*Kranaosphinctes*) *ingens* (YOUNG & BIRD), forms transitional to the descendant *Perisphinctes* s. str. (CALLOMON 1960). In *Perisphinctes arkelli wysokae* chronossp. nov., the largest and evolutionarily the most advanced *Otosphinctes*, the whorl-section is compressed; coiling is evolute or nearly evolute; the ribs are moderately thick, usually thinner and more densely spaced than in the older chronosubspecies *P.* (*O.*) *arkelli arkelli*.

Perisphinctes (*Otosphinctes*) *arkelli wysokae* chronossp. nov. and its presumed macroconchs disappear at the boundary between the Plicatilis and Transversarium zones, giving rise to microconch *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD and its corresponding macroconch, *Perisphinctes* (*Perisphinctes*) aff. *maximus* (YOUNG & BIRD) and its successor, *Perisphinctes* (*Perisphinctes*) *tumulosus* BUCKMAN. All of these species are referred to herein as the *Perisphinctes tumulosus* group (Text-fig. 4). The appearance of this group marks the main evolutionary event in the studied perisphinctid succession, the appearance of the *Perisphinctes-Dichotomosphinctes* lineage, characterising the Transversarium Zone. The early representatives of *P.* (*D.*) *antecedens,* with their subquadrate to subrectangular whorl-section, moderately evolute to evolute coiling, and moderately thick ribs, resemble the ancestral *P.* (*O.*) *arkelli wysokae* chronossp. nov., differing from them, however, in larger final size and in somewhat denser ribbing. *P.* aff. *maximus*, the earliest macroconch with an initial variocostation of ribs on the body-chamber, resembles its presumed immediate predecessors of the subgenus *Kranaosphinctes*, *P. maximus* and *P. ingens*, in decrease in rib-number per whorl on the last 1.5 -2 whorls, which only in *P.* aff. *maximus* is accompanied with their slow modification. Moreover, it agrees with *P.* (*K.*) *maximus* and *P.* (*K.*) *ingens* in the subquadrate whorl-section and moderately evolute to evolute coiling.

The successive species of the *Kranaosphinctes-Otosphinctes* lineage display throughout the Plicatilis Zone a phyletic size increase. It is best recognized in the microconchs constituting the subgenus *Otosphinctes*. *P.* (*O.*) *paturattensis* of the *P. promiscuus* group from the Paturattensis Subzone varies in maximum diameter ($\underline{D}_m$) from 32 mm to 72 mm (Text-fig. 5). Specimens of $\underline{D}_m$ from 47 mm to 52 mm predominate, comprising 30 % of the material. In its evolutionary successor, *P.* (*O.*) *ouatius ouatoides* chronossp. nov. from the overlying Ouatius Subzone, 60% of the specimens in the studied collection are those with $\underline{D}_m$ between 52 mm and 57 mm (Text-fig. 5), a range which in *P.* (*O.*) *paturattensis* represents only c. 9% of specimens. In *P.* (*O.*) *ouatius ouatoides* chronossp. nov. the whole size variability ranges from 42 mm to 77 mm, but it is discontinuous between 57 mm and 72 mm. In *P.* (*O.*) *ouatius ouatius*, the younger chronosubspecies of *P.* (*O.*) *ouatius* from the Arkelli Subzone of the Plicatilis Zone, specimens ranging from 57 mm to 62 mm are commonest. *P.* (*O.*) *arkelli arkelli*, which overlaps with *P.* (*O.*) *ouatius ouatius* stratigraphically, also overlaps in final size, although its most abundant representatives are distinctly larger, with $\underline{D}_m$ between 92 mm and 97 mm (Text-fig. 5). *P.* (*O.*) *arkelli wysokae* chronossp. nov., in the upper Arkelli Subzone, becomes still larger, with final diameter up to 112 mm (Text-fig. 5). The largest diameters are attained by *Perisphinctes* (*Dichotomosphinctes*) *antecedens* of the *P. tumulosus* group from the Buckmani Subzone of the Transversarium Zone, with final size between 112 mm and 162 mm (Text-fig. 5).

The final size increase also characterises the corresponding macroconchs, although it is less clearly recognized (the number of specimens is too low). The adults of *P.* (*K.*) *promiscuus* of the *P. promiscuus* group (Text-fig. 4) are not much larger than 150 mm. The evolutionarily younger *P.* (*K.*) *collignoni*, from the the Ouatius Subzone of the Plicatilis Zone, attains $\underline{D}_m$ c. 190 mm, and *P.* (*K.*) *vorda* c. 210 mm. A similar size is attained by *P.* (*K.*) *decurrens* from the lower Arkelli Subzone (Text-fig. 4) with $\underline{D}_m$ c. 180 mm. Other species from the Arkelli Subzone are distinctly larger: *P.* (*K.*) *kranaus* of the *P. kranaus* group (Text-fig. 4) with $\underline{D}_m$=510 mm, is the largest macroconch species of the *Kranaosphinctes-Otosphinctes* lineage in the studied collection, whereas *P.* (*K.*) *ariprepes* of the *P. ariprepes* group attains up to 300 mm, but does not show cessation of growth at this diameter. Finally, *P.* (*P.*) aff. *maximus* and its successor, *P.* (*P.*) *tumulosus*, of the *P. tumulosus* group (Text-fig. 4) from the Buckmani Subzone of the Transversarium Zone, attain $\underline{D}_m$=410 mm, and $^*\underline{D}_m$=360 mm respectively; the latter diameter corresponds, however, to an incomplete specimen.

The size increase of the successive groups of the *Kranaosphinctes-Otosphinctes* lineage is accompanied in the macroconchs by an ontogenetic shift in the appearance of particular ornamentation types (for the characteristic of particular ornamentation types – see p. 336). In *P.* (*K.*) *promiscuus* of the *P. promiscuus* group (Text-fig. 4) from the Paturattensis Subzone, type Ia ornamentation extends up to c. 90 mm diameter, in *P.* (*K.*) *collignoni*, from the Ouatius Subzone, up to 110 mm-120 mm, and in *P.* (*K.*) *decurrens*, from the lower Arkelli Subzone, up to 130 mm-140 mm. In all three species type Ia ornamentation appears on the phragmocone, and it is followed on the adult body-chamber by type Ib ornamentation. In *P.* (*K.*) *vorda* from the Ouatius Subzone, the change of ornamentation type, from Ia to

Ib, takes place at c. 135 mm. Both ornamentation types appear on the phragmocone. Type Ib ornamentation characterises late juveniles. The adults are characterised by type II ornamentation, which starts to appear at c. 180 mm diameter, and extends onto the body-chamber. A similar sequence of ornamentation types is observed in *P.* (*K.*) *kranaus* and *P.* (*K.*) *ariprepes*, from the Arkelli Subzone. In *P.* (*K.*) *kranaus*, type Ib ornamentation appears at 110 mm-130 mm diameter, and approximately at the same diameter it appears in *P.* (*K.*) *ariprepes*; type Ic, occurring only in the former species, appears after 190 mm-210 mm, and it extends up to c. 280 mm, where it is followed by type II ornamentation. The latter appears in *P.* (*K.*) *ariprepes* already at c. 200 mm diameter. Type II ornamentation characterises the adults of these species.

Morphological trends in the successive groups of the *Kranaosphinctes-Otosphinctes* lineage also concern changes in the parabolic structures and body-chamber length. The latter characters are best recognized in microconchs. In *P.* (*O.*) *paturattensis* of the *P. promiscuus* group (Text-fig. 4) parabolic ribs and parabolic nodes are common, but also, in the younger representatives of this group, occasionally oblique swollen ribs appear. In the successor, *P.* (*O.*) *ouatius ouatoides* chronossp. nov., typical parabolae are less common and oblique swollen ribs with indistinct parabolic nodes appear frequently. The latter cause irregular rib-spacing resembling shallow constrictions, a feature that is missing in older forms. In *P.* (*O.*) *ouatius ouatius* of the *P. kranaus* group (Text-fig. 4) usually oblique swollen ribs appear and, occasionally, also constrictions on the body-chamber, which are missing in the older species. In *P.* (*O.*) *arkelli arkelli* of the *P. ariprepes* group from the equivalent stratigraphical interval, parabolae are extremely rare, whereas constrictions become commoner. Finally, in the most advanced taxon, *P.* (*O.*) *arkelli wysokae* chronossp. nov., parabolae are absent, whereas rare oblique ribs appear on the inner whorls. Constrictions are also rare, but they become commoner in its phyletic descendant, *P.* (*D.*) *antecedens*.

The length of the body-chamber in *P.* (*O.*) *paturattensis* and in *P.* (*O.*) *ouatius ouatoides* chronossp. nov. from the Paturattensis Subzone and the Ouatius Subzone respectively, is 5/8 of a whorl long. In *P.* (*O.*) *ouatius ouatius* and in *P.* (*O.*) *arkelli arkelli*, both from the Arkelli Subzone, it is also of a 5/8 whorl long, but it occasionally becomes longer, 3/4 of a whorl long. In *P.* (*O.*) *arkelli wysokae* chronossp. nov. from the upper Arkelli Subzone the body-chamber is 3/4 of a whorl long, as it is in the successor *P.* (*D.*) *antecedens*.

In the lower Paturattensis Subzone of the Plicatilis Zone appears *Perisphinctes trifidus* (SOWERBY) (m, M) (Text-fig. 4), arising from the *Kranaosphinctes-Otosphinctes* lineage. *P. trifidus* (m, M) as interpreted in the present paper, is a geographically variable species in the Submediterranean Province. Through almost the whole Plicatilis Zone *P. trifidus* (m, M) retains in the study area more or less stable characters of shell morphology and shell-ornamentation: subrectangular whorl-section, moderately to weakly evolute coiling, changing to evolute or moderately evolute on the outer whorls, thin to moderately thin ribs. This species is the most abundantly represented in the study area in the Paturattensis Subzone, higher up it becomes less numerous, and disappears in the Arkelli Subzone of the Plicatilis Zone. In southern Europe, where it is represented by the densely ribbed *helenae* morphotype as interpreted in the present paper (see the species description, p. 321) it ranges through the Antecedens Zone (sensu MELÉNDEZ 1989). It possibly gives rise to the upper Middle Oxfordian forms of the genus *Sequeirosia* MELÉNDEZ described from Spain (MELÉNDEZ 1989, p. 182). The latter forms do not occur in the area of the Polish Jura Chain.

The early representative of the *Liosphinctes* lineage (Text-fig. 4), *L. plicatilis* (SOWERBY), appears in the Cordatum Subzone of the Cordatum Zone of the Lower Oxfordian (GYGI 1998), but becomes numerous only in the Paturattensis Subzone of the Plicatilis Zone of the Middle Oxfordian. In contrast to the other perisphinctid groups described herein, *Liosphinctes* is represented by macroconchs only. In the *Liosphinctes* lineage, the early forms are thin ribbed, being succeeded upward by more coarsely ribbed ones. In the Paturattensis Subzone the finely and densely ribbed *L. plicatilis* (SOWERBY) predominates, whereas the moderately coarsely ribbed *Liosphinctes* sp. A occurs less commonly. In the Ouatius Subzone the finely ribbed *L. plicatilis* becomes rare, and the moderately coarsely ribbed *Liosphinctes cumnorensis* (ARKELL) becomes abundant. Coexisting with, but less numerous than the latter forms are the moderately thinly ribbed *Liosphinctes* sp. B. At the boundary between the Ouatius and Arkelli subzones *L. plicatilis* and *L. laevipickeringius* disappear. *L. cumnorensis*, the moderately coarsely ribbed form, ranges through the Arkelli Subzone of the Plicatilis Zone and disappears in its upper part. The representatives of the *Liosphinctes* lineage re-appear in the study area in the upper part of the Middle Oxfordian, being there represented by different species. The late representatives of this lineage will be discussed elsewhere.

In the upper Arkelli Subzone of the Plicatilis Zone ammonites of Mediterranean affinity (BROCHWICZ-LEWIŃSKI 1973; BROCHWICZ-LEWIŃSKI & RÓŻAK 1975a, 1976) make their second appearance in the study area (Text-fig. 4). These ammonites are assigned to the new

genus *Neumannia* and they are represented by the species *Neumannia cyrilli* (NEUMANN), *Neumannia* aff. *cyrilli* (NEUMANN), *Neumannia gyrus* (NEUMANN), and their microconch counterparts, which are described for the first time in the present paper, *N.* sp. The species *N. cyrilli* and the closely allied *Neumannia methodii* (NEUMANN) were previously interpreted (BROCHWICZ-LEWIŃSKI 1973) as the possible ancestors of the late Middle Oxfordian genus *Passendorferia* BROCHWICZ-LEWIŃSKI, 1973. Subsequently, BROCHWICZ-LEWIŃSKI & RÓŻAK (1976) reinterpreted the two species and referred them to a single phylogenetical lineage parallel to the lineage of the genus *Passendorferia*. The stratigraphical and palaeontological data presented herein suggest that each of these two genera, *Neumannia* and *Passendorferia*, could represent two successive offshoots of a single Mediterranean lineage. Such an interpretation is supported by the fact that their representatives appear in the study area abruptly, and at different horizons: *Neumannia* appears in the upper Arkelli Subzone of the Plicatilis Zone and disappears in the lower part of the Buckmani Subzone of the Transversarium Zone; *Passendorferia* first appears higher, in the upper part of the Transversarium Zone of the Middle Oxfordian (BROCHWICZ-LEWIŃSKI 1973) and ranges higher up to the Bifurcatus Zone of the Upper Oxfordian as used in the present paper.

Simultaneously with the appearance of the first representatives of the genus *Neumannia* gen. nov., *N. gyrus* and the microconchs *N*. sp., *Platysphinctes perplanatus* TINTANT appears in the study area (Text-fig. 4, see also GŁOWNIAK 2000), but the latter disappears in the upper Arkelli Subzone of the Plicatilis Zone. The occurrence of representatives of *Neumannia* gen. nov. and the accompanying species *P. perplanatus* is interpreted as an immigration event from the Mediterranean area (GŁOWNIAK 2000).

BIOSTRATIGRAPHICAL SUBDIVISION OF THE LOWER MIDDLE OXFORDIAN

Remarks on the proposed zonation

The Submediterranean Middle Oxfordian (Text-fig. 4) as used herein is traditionally divided into the Plicatilis Zone (HUDLESTON 1878) and the Transversarium Zone (OPPEL 1866). Both zonal names are retained in the present paper, however, the zones are redefined, and subdivided by species of the Submediterranean family *Perisphinctidae* STEINMANN (Text-fig. 6). The Plicatilis Zone is subdivided into the Paturattensis Subzone, the Ouatius Subzone and the Arkelli Subzone in ascending order. The subzones are the lineage units, as their boundaries (except for the lower boundary of the Paturattensis Subzone) are defined by successive species of the subgenus *Otosphinctes* BUCKMAN and their corresponding macroconchs of the subgenus *Kranaosphinctes* BUCKMAN (Text-fig. 4). The subzones are additionally characterised by species of the genera *Liosphinctes* BUCKMAN, *Neumannia* gen. nov. and *Platysphinctes* TINTANT. The base of the overlying Transversarium Zone is defined herein at the level of the appearance of the first representatives of the subgenera *Dichotomosphinctes* BUCKMAN and *Perisphinctes* WAAGEN, the evolutionary successors of *Otosphinctes* and *Kranaosphinctes* which at this boundary disappear.

Zonal and subzonal definitions

Stratigraphical ranges of the perisphinctid species and chronosubspecies, and of the morphotypes distinguished within them are shown in Text-fig. 6 (for species distribution and biostratigraphical details of the studied sections see the Appendix).

The Plicatilis Zone

Index taxon: *Liosphinctes plicatilis* (SOWERBY, 1817). The Zone was named by HUDLESTON (1878).

Definition: The base of the Plicatilis Zone and, at the same time, the base of the Middle Oxfordian, is defined in the conventional way (SALFELD 1914) by means of cardioceratid ammonites. The lower boundary of this zone is marked by the last occurrence (LO) of the Lower Oxfordian species of the subgenus *Cardioceras* NEUMAYR & UHLIG, such as *Cardioceras* (*Cardioceras*) *cordatum* (SOWERBY), *Cardioceras* (*Cardioceras*) *ashtonense* ARKELL, *Cardioceras* (*Cardioceras*) *persecans* BUCKMAN and the first occurrence (FO) of the Middle Oxfordian cardioceratid species of the subgenera *Plasmatoceras* BUCKMAN and *Subvertebriceras* ARKELL, such as *Cardioceras* (*Plasmatoceras*) *tenuicostatum* NIKITIN, *Cardioceras* (*Plasmatoceras*) *tenuistriatum* BORISSJAK, *Cardioceras* (*Plasmatoceras*) *popilaniense* BODEN, and *Cardioceras* (*Subvertebriceras*) *densiplicatum* BODEN.

The top of the Plicatilis Zone and the base of the overlying Transversarium Zone, as newly defined here, is drawn at the FO of the species *Perisphinctes antecedens* SALFELD and *Perisphinctes* aff. *maximus* (YOUNG & BIRD) (Text-fig. 6), the first representatives of the subgenera *Dichotomosphinctes* BUCKMAN and *Perisphinctes* WAAGEN respectively, and, simultaneously, at the LO of *P. arkelli wysokae* chronossp. nov., the last

representative of the subgenus *Otosphinctes* BUCKMAN; at this boundary also disappear the macroconchs constituting the subgenus *Kranaosphinctes* BUCKMAN. From the Plicatilis Zone sensu ARKELL (1947) and CALLOMON (1964), the Plicatilis Zone as here defined, differs by exclusion of the beds with *Perisphinctes* (*Dichotomosphinctes*) *antecedens*.

The Plicatilis Zone is subdivided here into the Paturattensis, Ouatius and the Arkelli subzones. The subzonal boundaries are defined by the FOs of the successive species of the subgenera *Otosphinctes* and *Kranaosphinctes* (Text-fig. 6).

Distribution: Poland, England, Germany, France, Switzerland, and Spain.

Remarks: In south-west Europe, except for some sections in France (e. g. Beauvoisin), this zone is reduced in thickness due to condensations, or it is missing due to gaps.

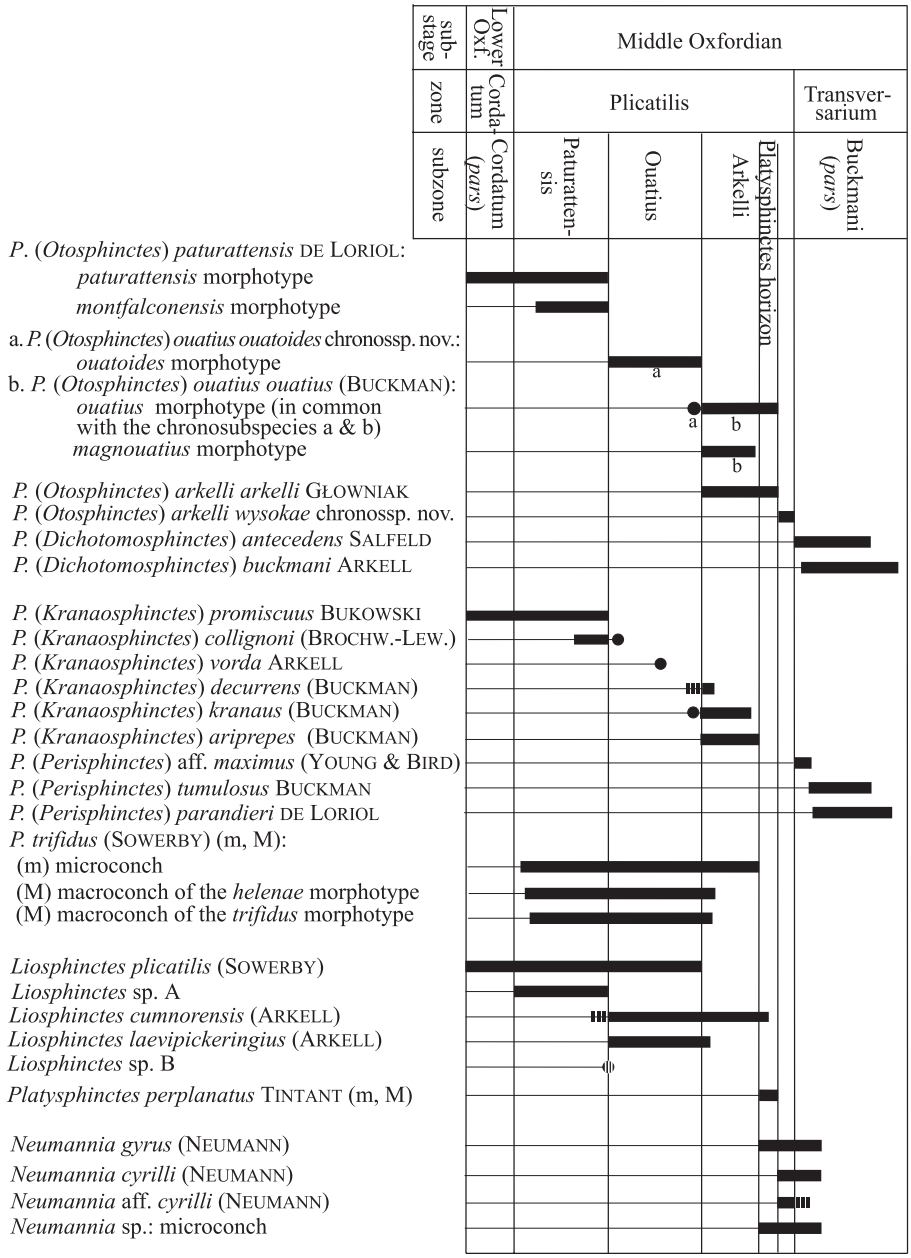

Fig. 6. Ranges of the species and the species morphotypes in the lower Middle Oxfordian and the zonal scheme; dots are for single specimens; dashed bar or dot signify uncertain stratigraphical range; the letters "a" and "b" at the range chart are for *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. and *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN) respectively

Paturattensis Subzone

Index taxon: *Perisphinctes paturattensis* de LORIOL, 1901. The Subzone was named by BROCHWICZ-LEWIŃSKI (1981).

Definition: The base of the Paturattensis Subzone coincides with the base of the Plicatilis Zone and the definition of the latter also defines the base of the Paturattensis Subzone. The top of the Paturattensis Subzone is defined by the FO of *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov., marking the base of the Ouatius Subzone.

P. (*O.*) *paturattensis* (the *paturattensis* morphotype) and *P.* (*K.*) *promiscuus*, characteristic of the Paturattensis Subzone and disappearing at its top (Text-fig. 6), appear already in the underlying Cordatum Subzone of the Cordatum Zone of the Lower Oxfordian (MATYJA 1977, BROCHWICZ-LEWIŃSKI 1981, GYGI 1998). The *montfalconensis* morphotype of *P.* (*O.*) *paturattensis* ranges through the upper Paturattensis Subzone only, and disappears at the top of it (Text-fig. 6). *P.* (*K.*) *collignoni* occurs in the upper part of the Paturattensis Subzone and ranges up to the lower part of the overlying Ouatius Subzone.

P. trifidus (SOWERBY) (m, M), the other characteristic form of the Paturattensis Subzone, composed of microconchs and macroconchs, the latter represented by two morphotypes: the *trifidus* morphotype and the *helenae* morphotype, appears in the lower part of the Paturattensis Subzone and ranges up to the Arkelli Subzone. *Liosphinctes plicatilis* (SOWERBY) ranges up from the Cordatum Subzone of the Cordatum Zone (GYGI 1998), and *Liosphinctes* sp. A appears at the base of the Paturattensis Subzone (Text-fig. 6). The former ranges up into the overlying Ouatius Subzone, the latter disappears at the top of the subzone.

In the upper Paturattensis/lower Ouatius beds appear *Liosphinctes* sp. B and *Liosphinctes cumnorensis* (ARKELL). Throughout the Paturattensis Subzone perisphinctid ammonites are accompanied by abundant *Cardioceras* (*Plasmatoceras*) *tenuicostatum* NIKITIN (MATYJA & GŁOWNIAK 1998).

Distribution: France (Jura, Beauvoisin), Spain, Germany (Frankenalb), Poland, Switzerland.

Remarks: In Western Europe ammonites indicative of the Paturattensis Subzone, if they appear at all, are usually reworked due to condensed sequences and gaps at the boundary of the Lower/Middle Oxfordian.

Ouatius Subzone

Index taxon: *Perisphinctes ouatius* BUCKMAN, 1926.

Definition: The base of the Ouatius Subzone, newly erected herein, is defined by the FO of *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. and its top, coinciding with the base of the Arkelli Subzone is defined by the FO of *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK, 2000.

Perisphinctes (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. is represented by two morphotypes: the *ouatoides* morphotype ranging throughout the subzone, and the *ouatius* morphotype, which first appears in the upper part of this subzone. *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI) is still present in the lower part of the subzone. *Perisphinctes* (*Kranaosphinctes*) *vorda* ARKELL, represented in the studied material by a single specimen, is known only from this substage. In the topmost part of the subzone appears *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN), and possibly *Perisphinctes* (*Kranaosphinctes*) *decurrens* (BUCKMAN). Both of these species range up into the overlying Arkelli Subzone.

Additional taxa worthy of mention are *Perisphinctes trifidus* (SOWERBY) (its microconchs, and the macroconchs of both the *trifidus* and the *helenae* morphotypes), *Liosphinctes plicatilis* (SOWERBY) and *Liosphinctes laevipickeringius* (ARKELL) (see Text-fig. 6).

Distribution: Poland, France, England.

Arkelli Subzone

Index taxon: *Perisphinctes* (*Otosphinctes*) *arkelli* GŁOWNIAK, 2000. The subzone was established by GŁOWNIAK (2000).

Definition: The base of the Arkelli Subzone is defined by the FO of *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK, the older chronosubspecies of *P.* (*O.*) *arkelli* GŁOWNIAK. The top of the Arkelli Subzone, coinciding with the base of the Transversarium Zone, is defined by the FO of *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD and *Perisphinctes* (*Perisphinctes*) aff. *maximus* (YOUNG & BIRD).

P. (*O.*) *arkelli* is represented by two chronosubspecies: *P.* (*O.*) *arkelli arkelli*, ranging through the lower and middle part of the subzone, and *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov. from the upper part of the subzone. *Perisphinctes* (*Otosphinctes*) *ouatius* (BUCKMAN) is represented by *P.* (*O.*) *ouatius ouatius* (BUCKMAN) first appearing in the Arkelli Subzone, with its two morphotypes, the *magnouatius* and the *ouatius* morphotypes (Text-fig. 6). *P.* (*O.*) *ouatius ouatius* ranges through the Arkelli Subzone up to its upper part, but it does not reach the top of it, disappearing in the Platysphinctes horizon (Text-fig. 6). Other characteristic species of the Arkelli Subzone are: *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN), ranging up from the underlying Ouatius Subzone but

becoming numerous only in the Arkelli Subzone, *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN), and *Perisphinctes* (*Kranaosphinctes*) *decurrens* (BUCKMAN) (Text-fig. 6).

In the lower part of the Arkelli Subzone, *P. trifidus*, characteristic of the Paturattensis and Ouatius subzones, disappears as do *L. laevipickeringius* and *L. cumnorensis*, ranging up from the Ouatius Subzone.

In the upper part of the Arkelli Subzone there is the FO of the representatives of *Neumannia* gen. nov.: *Neumannia gyrus* (NEUMANN), *Neumannia* sp., and, somewhat above that of the latter species, the FO of *Neumannia cyrilli* (NEUMANN) and *Neumannia* aff. *cyrilli* (NEUMANN) (Text-fig. 6). All of these species, possibly except for the latter, range up into the lower part of the Buckmani Subzone of the Transversarium Zone. The FO of *N. gyrus* coincides with that of *Platysphinctes perplanatus* TINTANT; the latter species has only a short stratigraphical range and disappears below the top of the Arkelli Subzone.

Distribution: England, France, Spain, Germany, Poland, Switzerland?

Remarks: In most of the sections of south-west Europe, except for e. g. Beauvoisin, the Arkelli Subzone is developed in condensed or discontinuous successions.

Platysphinctes horizon

Index taxon: the genus *Platysphinctes* TINTANT, 1961.

The horizon was defined by GŁOWNIAK (2000). Apart from *Platysphinctes perplanatus* (M, m) TINTANT and NEUMANN's (1907) species of the Mediterranean *Neumannia* gen. nov., *N. gyrus* and *N.* sp., the Platysphinctes horizon yields also a few perisphinctid species ranging up from below: *P.* (*O.*) *arkelli arkelli*, *P.* (*O.*) cf. *ouatius ouatius* (the *ouatius* morphotype), and *L. cumnorensis*. All of the last three taxa have their LO in the Platysphinctes horizon.

Distribution: So far known only in Poland.

Transversarium Zone

Index taxon: *Gregoryceras transversarium* (QUENSTEDT, 1847). The zone was named by OPPEL (1866).

The lower boundary of the Transversarium Zone is redefined here at the FO of *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD and *Perisphinctes* (*Perisphinctes*) aff. *maximus* (YOUNG & BIRD), the corresponding micro- and macroconch. This level is also marked by the LO of *P.* (*O.*) *arkelli wysokae* chronossp. nov., the parent species of *P.* (*D.*) *antecedens*, and the LO of the macroconchs constituting the subgenus *Kranaosphinctes*, which at this level disappear giving rise to *Perisphinctes* s. str. This level corresponds to the major evolutionary event in the Middle Oxfordian perisphinctids, which makes it a useful base to the Transversarium Zone.

The Transversarium Zone is divided into the Buckmani Subzone below, and the Elisabethae Subzone above, based on successive species of the *Perisphinctes-Dichotomosphinctes* lineage (GŁOWNIAK 2000). The Transversarium Zone and its subzones are not discussed here in detail.

Distribution: England, Germany, Switzerland, France, Spain, Poland.

Buckmani Subzone

Index taxon: *Perisphinctes* (*Dichotomosphinctes*) *buckmani* ARKELL, 1936. The Subzone was named by BROCHWICZ-LEWIŃSKI (1976).

The base of the Buckmani Subzone coincides with the base of the Transversarium Zone, and the definition of the latter (see previous section) is applicable here. Close to the base of the Buckmani Subzone, defined by the FO of *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD and *Perisphinctes* (*Perisphinctes*) aff. *maximus* (YOUNG & BIRD), is the FO of *Perisphinctes* (*Dichotomosphinctes*) *buckmani* ARKELL and *Perisphinctes* (*Perisphinctes*) *parandieri* DE LORIOL, which disappear in the upper part of this subzone.

In the lower Buckmani Subzone disappear *N.* sp., *N. gyrus*, *N. cyrilli* and perhaps also *N.* aff. *cyrilli*, all of them ranging up from below.

Distribution: Germany, England, France, Spain, Switzerland, Poland, Bulgaria.

CORRELATIONS

The correlation of the Submediterranean perisphinctid zonation of the lower Middle Oxfordian defined herein, with the zonations as proposed by SYKES & CALLOMON (1979) for north-west Europe and as proposed by CARIOU & MELÉNDEZ (1990) and CARIOU & *al.* (1991) for Submediterranean south-west Europe, based on the perisphinctid taxa ranges (Text-fig. 6) recognized in the study area of the Polish Jura Chain, is shown in Text-fig. 7.

SYKES & CALLOMON (1979) distinguished in the Middle Oxfordian of southern England the Plicatilis Zone and the Pumilus Zone (Text-fig. 7). Following ARKELL (1947) and CALLOMON (1964), they subdivided the Plicatilis Zone into the Vertebrale Subzone below and the Antecedens Subzone above. The Vertebrale Subzone is defined by Boreal cardioceratid species

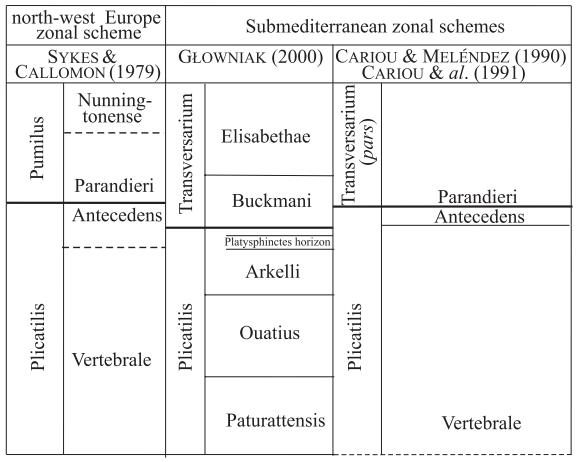

Fig. 7. The correlation of the Plicatilis Zone and the lower Transversarium Zone (sensu GŁOWNIAK 2000) with zonal and subzonal schemes of other authors for Submediterranean Europe and for north-western Europe.

(CALLOMON 1960, 1964) and is characterised additionally by perisphinctid species, e.g. *Liosphinctes plicatilis* (SOWERBY), *Liosphinctes cumnorensis* (ARKELL), *Perisphinctes trifidus* (SOWERBY) and large macroconchs of the subgenus *Kranaosphinctes* BUCKMAN: *Perisphinctes kranaus* (BUCKMAN), *Perisphinctes aripreps* (BUCKMAN) (=*P. cotovui* SIMIONESCU *sensu* ARKELL 1939), *Perisphinctes decurrens* (BUCKMAN), and others. According to the recent studies *L. plicatilis* appears in the upper part of the Lower Oxfordian (GYGI 1998) and ranges through the Paturattensis and Ouatius subzones of the Plicatilis Zone (Text-fig. 6); *P. trifidus*, as interpreted in the present paper, appears in the lower Paturattensis Subzone; *L. cumnorensis* appears at the base of the Ouatius Subzone or perhaps somewhat below and disappears in the Arkelli Subzone of the Plicatilis Zone. The other species previously mentioned appear in the upper Ouatius Subzone or at the base of the Arkelli Subzone (Text-fig. 6), and disappear at different points below the upper boundary of the Plicatilis Zone. The Vertebrale Subzone of ARKELL (1947) and CALLOMON (1964) corresponds to the Paturattensis Subzone, the Ouatius Subzone and the lower Arkelli Subzone of the Plicatilis Zone as defined herein.

Above the Vertebrale Subzone SYKES & CALLOMON (1979) distinguished the Antecedens Subzone. In this subzone the Cardioceratidae become rare, whereas the Perisphinctidae predominate. According to CALLOMON (1960), indicative species for the Antecedens Subzone are *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD and *Perisphinctes* (*Dichotomosphinctes*) *buckmani* ARKELL. In addition, the first *Perisphinctes* s. str. appear in this subzone. *Perisphinctes* (*Otosphinctes*) *arkelli* GŁOWNIAK and the species of the subgenus *Kranaosphinctes* range up from the underlying Vertebrale Subzone. The Antecedens Subzone, thus defined, should be correlated with the upper part of the Arkelli Subzone of the Plicatilis Zone as defined herein (Text-fig. 7) (probably with that part corresponding to the stratigraphical range of *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov., Text-fig. 6) and to the lower Buckmani Subzone of the Transversarium Zone. This correlation based on perisphinctids is additionally supported by the cardioceratids, which become extremely rare in the studied sections in the Arkelli Subzone and in the Buckmani Subzone (MATYJA & GŁOWNIAK 1998). The Antecedens Subzone in southern England is additionally characterised by the genus *Liosphinctes* (cf. CALLOMON 1960), which becomes abundant for the first time, but is represented by different species from those in the Vertebrale Subzone. The representatives of the genus *Liosphinctes* in the Submediterranean sections of the study area disappear in the upper Arkelli Subzone of the Plicatilis Zone (Text-fig. 6), in the interval equivalent to the lower part of the Antecedens Subzone *sensu anglico*.

The Plicatilis Zone in the zonal scheme of SYKES & CALLOMON (1979) includes in its upper part beds with *P.* (*D.*) *antecedens* and *P.* (*D.*) *buckmani* which, in the zonal scheme defined herein, are excluded from this zone (Text-fig. 7).

Above the Plicatilis Zone SYKES & CALLOMON (1979) distinguished the Pumilus Zone with the lower, Parandieri Subzone (CALLOMON 1964), and the upper, Nunningtonense Subzone (WRIGHT 1972). The ammonites of the Parandieri Subzone comprises few species (SYKES & CALLOMON 1979): *Perisphinctes* (*Perisphinctes*) *parandieri* DE LORIOL, *P.* (*D.*) *buckmani*, *P.* (*D.*) cf. *antecedens* (cf. CALLOMON 1964) and, in the upper part of the subzone, *Perisphinctes* (*Perisphinctes*) *pumilus* ENAY. Of these species, the first three occur in the Buckmani Subzone as characterised herein (Text-fig. 6): *P.* (*D.*) *antecedens* appears at the at the base of this subzone, whereas *P.* (*P.*) *parandieri* and *P.* (*D.*) *buckmani* appear somewhat above the base. The fourth species, *P.* (*P.*) *pumilus*, makes its first appearance above the levels where these forms disappear, and ranges in the Elisabethae Subzone of the Transversarium Zone (GŁOWNIAK 1997a, 1997b). It should be noted, however, that in the Elisabethae Subzone the species *P.* (*P.*) *pumilus* overlaps with the subzonal index, *Perisphinctes* (*Dichotomosphinctes*) *elisabethae* DE RIAZ; the latter taxon was not found with *P.* (*P.*) *pumilus* in the upper Parandieri Subzone in England. The Parandieri Subzone as used by SYKES & CALLOMON (1979) corresponds approximately to the upper part of the Buckmani Subzone and to the lower Elisabethae Subzone of the

Transversarium Zone as proposed herein. The upper part of the Elisabethae Subzone in the zonation of the present paper corresponds in the scheme of SYKES & CALLOMON (1979) to the Nunningtonense Subzone. From the latter subzone WRIGHT (1996a, 1996b) figured the index of the Elisabethae Subzone, *P.* (*D.*) *elisabethae*, and other representatives of the subgenus *Dichotomosphinctes* that occur commonly in the Elisabethae Subzone in the study area (GŁOWNIAK 1997a).

In the Submediterranean sections of south-west Europe CARIOU & MELÉNDEZ (1990) and CARIOU & *al*. (1991) distinguished in the lower part of the Middle Oxfordian the Plicatilis Zone and above it the Transversarium Zone (Text-fig. 7). They (op. cit.) divided the Plicatilis Zone into ARKELL's (1947) two subzones: the Vertebrale Subzone and the Antecedens Subzone. In the lower part of the Vertebrale Subzone as characterised by these French and Spanish authors occur e.g. *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL, *Perisphinctes* (*Otosphinctes*) *montfalconensis* DE LORIOL, *Perisphinctes episcopalis* DE LORIOL and *Perisphinctes laisinensis* DE LORIOL. The first two forms are assigned in the present paper to a single species, *P.* (*O.*) *paturattensis* (see p. 326). This species, as thus interpreted, ranges up from the upper Lower Oxfordian (BROCHWICZ-LEWIŃSKI 1981, GYGI 1988) to the Paturattensis Subzone of the Plicatilis Zone of the lower Middle Oxfordian as proposed in the present paper, and disappears at the top of this subzone (Text-fig. 6). The other two taxa, *P. episcopalis* and *P. laisinensis*, have not been recorded in the area of Polish Jura Chain above the lower boundary of the Middle Oxfordian. All of these taxa indicate that the lower part of the Vertebrale Subzone as proposed by CARIOU & MELÉNDEZ (1990) and CARIOU & *al*. (1991) correlates with the upper part of the Lower Oxfordian and with the Paturattensis Subzone of the Plicatilis Zone in the Middle Oxfordian of the present scheme (Text-fig. 7). CARIOU & MELÉNDEZ (1990) and CARIOU & *al*. (1991) characterise the upper part of the Vertebrale Subzone by e.g. *P.* (*O.*) *arkelli*, and draw the upper boundary of this subzone at the LO of this species. This boundary correlates therefore with the upper boundary of the Plicatilis Zone as defined herein. The lower boundary of the Antecedens Subzone of the Plicatilis Zone *sensu* CARIOU & MELÉNDEZ (1990) and CARIOU & *al*. (1991) is defined by the FO of *P.* (*D.*) *antecedens*, and it correlates with the base of the Buckmani Subzone of the Transversarium Zone of the present scheme. The upper boundary of the Antecedens Subzone is defined by the FO of *P.* (*D.*) *buckmani* and *P.* (*P.*) *parandieri*. The Antecedens Subzone, taken as the stratigraphical interval between the FO of *P.* (*D.*) *antecedens* and the FO of *P.* (*D.*) *buckmani* (Text-fig. 6), corresponds to the extremely thin interval in the basal part of the Buckmani Subzone of the present paper (Text-fig. 7). From the Antecedens Subzone CARIOU & MELÉNDEZ (1990) and CARIOU & *al*. (1991) also report *Perisphinctes helenae* DE RIAZ and *Perisphinctes trifidus* (SOWERBY). In the area of the Polish Jura Chain these two forms, interpreted as morphotypes of a single species, *P. trifidus*, have a shorter stratigraphical range than in southern Europe; they range through the Paturattensis and Ouatius subzones, and disappear in the Arkelli Subzone of the Plicatilis Zone.

Following CALLOMON (1988), CARIOU & MELÉNDEZ (1990) and CARIOU & *al*. (1991) define the base of the Transversarium Zone and the bottom of the Parandieri Subzone by the FO of *P.* (*D.*) *buckmani* and *P.* (*P.*) *parandieri.* Accordingly to the taxa ranges recognized in the studied sections of the Polish Jura Chain (Text-fig. 6), this boundary as defined by the French and the Spanish authors falls somewhat above the lower boundary of the Transversarium Zone of the present report, in the lower part of the Buckmani Subzone.

The perisphinctid subzonal scheme for the Plicatilis Zone as proposed by MELÉNDEZ & *al*. (1985) has been subsequently revised (CARIOU & MELÉNDEZ 1990) and it is not discussed here.

PALAEONTOLOGICAL ACCOUNT

Repositories

All specimens are housed in the Museum of the Geology Department of the University of Warsaw, collection no IGPUW/A/36.

Shell terminology

The abbreviations "m" and "M" used in the species description are for microconchs and macroconchs respectively.

Symbols used in the text for shell characters are as follows: **D** – diameter (size); $\mathbf{D_m}$ – maximum diameter of a complete specimen; $\underline{\mathbf{D_m}}$ – maximum diameter of an adult specimen (final size); $\mathbf{*D_m}$ – maximum diameter of incomplete specimen; $\mathbf{D_f}$ – maximum diameter of phragmocone; $\underline{\mathbf{D_f}}$ – maximum diameter of phragmocone of an adult specimen; $\mathbf{*D_f}$ – maximum diameter of an incomplete phragmocone; **U** – umbilical width; **W** – whorl height, **W/U** – whorl height as a fraction of umbilical width; **U/D** – umbilical width as a fraction of diameter; $\overline{\mathbf{W/D}}$ – whorl height as a fraction of diameter. Statistics

used comprise: $\overline{\mathbf{U/D}}$ – mean value of umbilical width as a fraction of the diameter, **W/D** – mean value of whorl height as a fraction of the diameter; **OS** – standard deviation.

Coiling of the shell is classified after GEYER (1961); according to the value of W/U it is referred to evolute, when $W/U \leqslant 0.50$, to moderately evolute, when $0.50 < W/U \leqslant 0.75$, or to weakly evolute, when $0.75 < W/U \leqslant 1.0$.

The rib types are used after ARKELL (1935, vol. 1, p. xxvii-xxix), whereas the mode of rib-division follows ARKELL (1935, vol. 1, p. xviii) and GEYER (1961, p. 14). Primary, secondary and intercalatory ribs are distinguished; the two latter are called ventral ribs. The types of rib-division are referred to as dichotomous (bifurcation) or bidichotomous. In addition, paradischizotomous rib division is distinguished here to describe the style of rib-division where a free-ending intercalatory rib curves inwards at its extremity, approaching the primary rib just below the point of division, thereby giving the impression of an incipient dischizotomy.

Terms and abbreviations for the septal suture, after ARKELL (1934, vol. 1, pp. x, xxx), are as follows: suspensive lobe (N), external lobe (E), and lateral lobe (L).

The terms "parabolic ribs" and "parabolic nodes" are used after ATROPS (1982), A collective names for these structures is "parabolae". In addition, oblique swollen ribs and oblique ribs are distinguished, arising from the primary rib at any point of the whorl-height. A zigzag pattern appears on the venter when two secondary ribs arising from a single primary rib at one whorl-side pass across the venter and join two primary ribs at the opposite whorl-side.

Systematic description

Superfamily Perisphinctaceae STEINMANN, 1890
Family Perisphinctidae STEINMANN, 1890
Genus *Perisphinctes* WAAGEN, 1869

Perisphinctes trifidus (SOWERBY, 1821) (m, M)
(Microconchs: Pl. 10, Fig. 1; Pl. 11, Fig. 4; Pl. 12, Fig. 3; Pl. 13, Fig. 2; Text-figs 8-9)
(Macroconchs: Pl. 10, Figs 2-3; Pl. 11, Figs 1-3; Pl. 12, Figs 1-2, Text-figs 8, 10-11)

Microconchs:

1977. *Perisphinctes* (*Otosphinctes*) nov. sp. ? A; BOURSEAU, p. 49, Text-fig. 17; Pl. 1, Fig. 12.

1977. *Perisphinctes* (*Dichotomosphinctes*) nov. sp. ? A; BOURSEAU, p. 57, Text-fig. 24; Pl. 3, Fig. 7.

Macroconchs:

1821. *Ammonites triplicatus* SOWERBY, p. 167, Pl. 292 (holotype, *V.*).

1821. *Ammonites trifidus* SOWERBY, p. 194 (nom. nov. for *A. triplicatus* 1821 *non* 1815).

1835. *Ammonites triplex* SOWERBY, p. 249 (= nom. nov. for *A. triplicatus* 1821 *non* 1815).

1898. *Perisphinctes helenae* sp. n.; DE RIAZ, p. 15, Pl. 8, Fig. 1 (lectotype, *V.*), Figs 2-3 (syntypes, *V.*).

non 1907. *Perisphinctes helenae* DE RIAZ; SIMIONESCU, p. 202, Pl. 9, Fig. 6.

1920. *Perisphinctes trifidus* SOWERBY; BUCKMAN, p. 27.

1939. *Perisphinctes* (*Arisphinctes*) *helenae* DE RIAZ; ARKELL, p. 149, Text-figs 48-49; Pl. 30. Figs 7, 8 (*V.*); Pl. 31, Figs 1, 3.

1939. *Perisphinctes* (*Kranaosphinctes*) *trifidus* (SOWERBY); ARKELL, p. 165, Text-fig. 52; Pl. 36, Fig. 1 (holotype, *V.*); Pl. 36, Figs 2a-c, 3, 4 (*V.*).

1966. *Perisphinctes* (*Arisphinctes*) *helenae* DE RIAZ; ENAY, p. 413, Text-figs 118-119; Pl. 20, Figs 2 (*V.*), 3 (*V.*), 4.

? 1966. *Perisphinctes* (*Arisphinctes*) *helenae* DE RIAZ; HAUERSTEIN, p. 40. Text-figs 8, 9, 14a; Pl. 3.

non 1972a. *Perisphinctes* (*Arisphinctes*) *cf. helenae* RIAZ; MALINOWSKA, p. 16, Pl. 4, Fig. 1 [=P. (?*Liosphinctes*) sp.]

non 1972a. *Perisphinctes* (*Kranaosphinctes*) *trifidus* (SOWERBY); MALINOWSKA, p. 25, Text-fig. 6; Pl. 2, Fig. 2 (?*P.* (*Kranaosphinctes*) sp.)

non 1972b. *Perisphinctes* (*Arisphinctes*) *cf. helenae* DE RIAZ; MALINOWSKA, p. 181, Text-fig. 5; Pl. 2 (*V.* =?*Passendorferia sp.*).

non 1976. *Kranaosphinctes trifidus* (SOWERBY); BROCHWICZ-LEWIŃSKI & RÓŻAK, Pl. 33 [?*Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN)].

non 1989. *Perisphinctes* (*Arisphinctes*) *helenae* DE RIAZ; MELÉNDEZ, p. 234, Text-fig. 46; Pl. 24, Fig. 1a,b (*V.*).

non 1989. *Perisphinctes* (*Arisphinctes*) *helenae* DE RIAZ; FISCHER & GYGI, Fig. 5-A.

EMENDED DIAGNOSIS: micro- and macroconchs of subrectangular whorl-section. Densicostate to moderately densely ribbed; ribs thin to moderately thin, prorsiradiate. Microconchs middle- to large-sized, constricted, lappeted; moderately evolute, rarely weakly evolute; parabolae common on the adult body-chamber. Macroconchs moderately evolute or weakly evolute on the inner whorls, changing with growth to evolute or moderately evolute. Adult macroconchs coarsely ribbed on the body-chamber, body-chamber whorl-section oval.

MATERIAL: **Microconchs**: Nine specimens: IGPUW/A/36/108 (Pl. 13, Fig. 2), IGPUW/A/36/59

(Pl. 11, Fig. 4), IGPUW/A/36/87, IGPUW/A/36/94, IGPUW/A/36/118, IGPUW/A/36/120 (Pl. 10, Fig. 1), IGPUW/A/36/122 (Pl. 12, Fig. 3), IGPUW/A/36/124, IGPUW/A/36/135. Almost all of the specimens are lappeted. Five specimens are crushed flat or distorted. They come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.2', bed 22; section W.4, bed 16, 17a, 17c; section W.5, bed 1, bed 3; section W.6, bed 28c; and from the Rudniki Quarry (Text-fig. 2, Appendix), section Rd., bed 6. The two specimens of *P.* cf. *trifidus* (m) are from the Wysoka Quarry, section W.4, beds 16 and 17a. **Macroconchs**: Fifteen specimens; eight complete or nearly complete, four with incomplete body-chamber, two phragmocones, one cast of a half-specimen; eight specimens crushed flat or distorted. They come from the Wysoka Quarry (Text-fig. 2, Appendix), section W. 4, bed 17b; W.4III, bed 19; section W.6, beds 27a, 28b and collected loose from beds 27a-27e; section W.6', beds 28 c/d, 28 d/e, and collected loose from beds 27-28; section W.8, bed 2a; section W.9', bed 8.6; section W.9", beds 8.1g, 12b; and from the Ogrodzieniec Quarry (Text-fig. 3, Appendix), section O.1, bed 1a.

DESCRIPTION: **Microconchs**: IGPUW/A/36/108 (Pl. 13, Fig. 2) is a complete, mature specimen, of $\underline{D}_m$=72 mm. The phragmocone ends at $\underline{D}_f$=49 mm; the body-chamber is 5/8 of a whorl. The peristome is provided with lappets. The last ribs on the body-chamber become somewhat flexuous and approximated, indicating maturity. The other eight specimens represent mature individuals, of $\underline{D}_m$ ranging from 50 mm to 71 mm. The phragmocones end in the range of $\underline{D}_f$ from 32 mm to 44 mm. The body-chamber is 5/8 of a whorl, occasionally 3/4 of a whorl.

The whorl-section of the body-chamber (Text-fig. 8) is subrectangular, occasionally with slightly convex whorl-flanks. The coiling is moderately evolute, rarely weakly evolute between 20 mm-40 mm diameter; at larger diameters it changes to moderately evolute. In the adults, with $\underline{D}_m$ from 50 mm to 71 mm $\overline{U/D}$=0.47, (OS=0.03); $\overline{W/D}$=0.30, (OS=0.02), and W_m/U_m ranges from 0.53 to 0.73; the coiling is moderately evolute at this diameter. The ribs are prorsiradiate; they are fine and densely spaced on the phragmocone, and become coarser and more distant on the body-chamber. Near the aperture they are somewhat flexuous. The primary ribs bifurcate. The secondary ribs are less distinct than the primary ribs; they cross the venter straight, except in IGPUW/A/36/59, in which the secondary ribs curve distinctly backwards in the final part of the phragmocone and at the beginning of the body-chamber. The rib-number per whorl (Text-fig. 9) varies from 30 to 37 at a diameter of c. 20 mm. At c. 20 mm to c. 40 mm diameter the rib-number increases approximately by 8 ribs per whorl. Between c. 40 mm and 50 mm-67 mm, the rib-number remains approximately

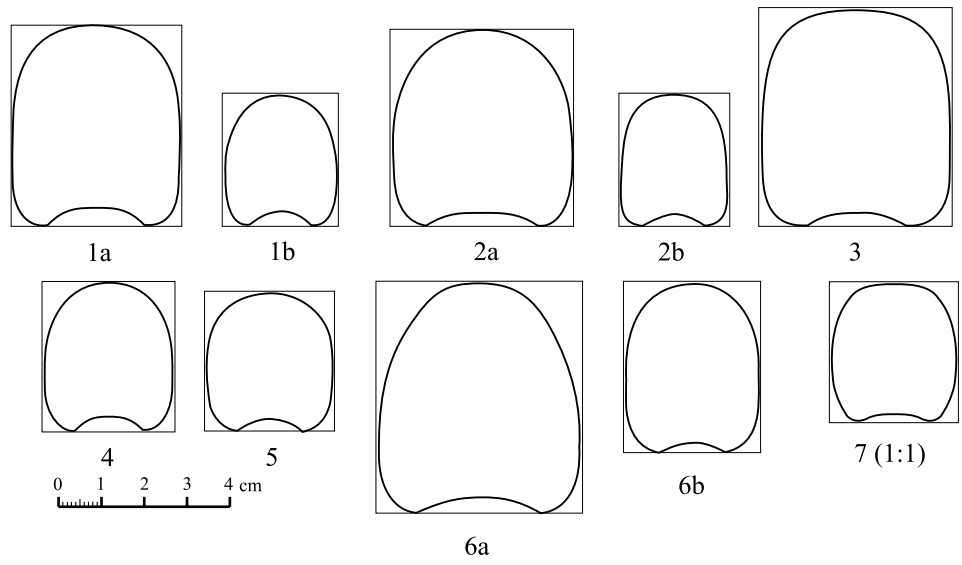

Fig. 8. Whorl-section of *Perisphinctes trifidus* (SOWERBY) (m, M) at a given diameter of the specimen (whorl-sections 1-6 reduced according to the scale drawn on the figure; whorl-section 7 is of natural size): *P. trifidus* (M: *helenae* morphotype): 1. IGPUW/A/36/185 (Pl. 10, Fig. 2), a: D=195 mm, b: D=105 mm; 2. IGPUW/A/36/285 (Pl. 11, Fig. 2), a: D=160 mm, b: D=98 mm; 3. IGPUW/A/36/280 (Pl. 10, Fig. 3), D=200 mm; 4. IGPUW/A/36/191 (Pl. 11, Fig. 1), D=140 mm. *P. trifidus* (M: *trifidus* morphotype): 5. IGPUW/A/36/276 (Pl. 11, Fig. 3), D=120 mm; 6. IGPUW/A/36/190 (Pl. 12, Fig. 2), a: $\underline{D}_m$=235 mm, b: D=140 mm. *P. trifidus* (microconch): 7. IGPUW/A/36/108 (Pl. 13, Fig. 2), $\underline{D}_m$=72 mm

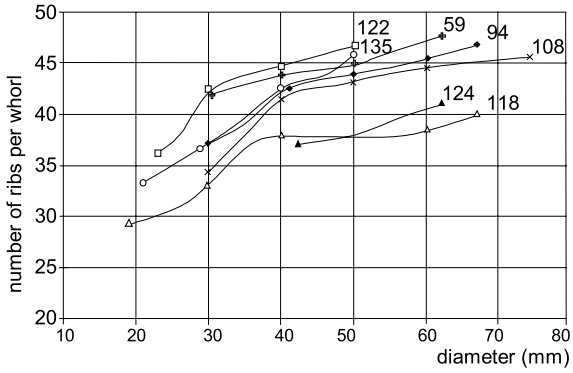

Fig. 9. Rib-density curves of *Perisphinctes trifidus* (SOWERBY) (microconch); the specimens are numbered by only the last component of their full registration numbers

constant or increases maximally by 4 ribs per whorl. Oblique ribs appear commonly on the whorl-flanks. Less commonly there appear blunt parabolic nodes located just above the ventro-lateral margin at the beginning of the body-chamber. In a few specimens the zigzag pattern of the secondary ribs appears on the venter. Constrictions are present on the phragmocone and on the body-chamber. Four to five of them are present on the body-chamber in IGPUW/A/36/108 (Pl. 13, Fig. 2) and in IGP/UW/A/36/122 (Pl. 12, Fig. 3), respectively.

Macroconchs: Two morphotypes are distinguished in the studied material: the *trifidus* morphotype (IGPUW/A/36/189, IGPUW/A/36/190 (Pl. 12, Fig. 2), IGPUW/A/36/196, IGPUW/A/36/213 (Pl. 12, Fig. 1), IGPUW/A/36/267, IGPUW/A/36/276 (Pl. 11, Fig. 3), IGPUW/A/36/279) and the *helenae* morphotype (IGPUW/A/36/185, IGPUW/A/36/191 (Pl. 11, Fig. 1), IGPUW/A/36/200, IGPUW/A/36/217, IGPUW/A/36/280, IGPUW/A/36/285 (Pl. 11, Fig. 2), IGPUW/A/36/286, IGPUW/A/36/299).

IGPUW/A/36/190 (*trifidus* morphotype, Pl. 12, Fig. 2) is a complete, mature specimen, of $\underline{D_m}$=235 mm, and $\underline{D_f}$=140 mm. Its body-chamber occupies one whorl; the peristome is partially crushed. The individual is mature, as indicated by changes of the whorl-section in the final part of the body-chamber from compressed-subrectangular to oval (Text-fig. 8) and by reinforcing of the last few ventral ribs, immediately preceding the aperture. IGPUW/A/36/280 (*helenae* morphotype, Pl. 10, Fig. 3) is an incomplete specimen, with $*D_m$ c. 340 mm; the phragmocone ends at a break at D_f=230 mm; the preserved fragment of the body-chamber is 1/8 of a whorl. IGPUW/A/36/185 (*helenae* morphotype, Pl. 10, Fig. 2) is of $*D_m$=245 mm; the body-chamber starts at D_f=195 mm, it occupies half of a whorl but it is not complete. IGPUW/A/36/280 and IGPUW/A/36/185 are mature or nearly mature individuals. Other specimens, representing both morphotypes, range in D_m from 117 mm to 240 mm; the septation ceases in the range of D_f from 70 mm to c. 180 mm; the body-chamber, if complete, occupies one whorl. The individuals are juvenile, except for IGPUW/A/36/213 (*trifidus* morphotype, Pl. 12, Fig. 1) which shows the middle part of the adult body-chamber.

In both the *trifidus* and *helenae* morphotypes the whorl-section is subrectangular, with flat flanks and rounded ventro-lateral margin and venter (Text-fig. 8). In the final part of the adult body-chamber in IGPUW/A/36/190 (*trifidus* morphotype, Pl. 12, Fig. 2; Text-fig. 8) the venter narrows, the flanks become convergent, and the whorl-section changes to oval. The coiling is moderately evolute, rarely weakly evolute on the inner whorls. With growth the coiling becomes rapidly more evolute, and after c. 100 mm diameter all of the studied specimens are evolute or moderately evolute. Between 60 mm and 66 mm diameter $\overline{U/D}$=0.45 (OS=0.034), $\overline{W/D}$=0.30 (OS=0.027), and W/U varies from 0.59 to 0.84. Between 160 mm and 170 mm $\overline{U/D}$=0.52 (OS=0.032), $\overline{W/U}$=0.27 (OS=0.012), and W/U varies from 0.45 to 0.59. The shell-ornamentation of the macroconchs of *P. trifidus* is characterised by bifurcating ribs. The primary ribs are straight, rectiradiate or somewhat prorsiradiate on the whorl-flanks. They bifurcate on the ventro-lateral margin. Throughout the shell ontogeny of the macroconchs of *P. trifidus* the ribs coarsen gradually on the whorl-flanks, the secondary ribs become associated with intercalatory ribs and the ventral ribs become indistinct. The following types of shell ornamentation are distinguished: type Ia in which the secondary ribs are occasionally associated with an intercalatory rib; type Ib in which every pair of secondary ribs is associated with an intercalatory rib (they may occasionally curve inwards at its extremity giving the impression of trifurcation, which in fact does not appear in this species); additionally, in type Ib ornamentation the ventral ribs become somewhat indistinct; type II ornamentation is characterised by moderately thick primary ribs on the whorl-flanks and by smooth or nearly smooth venter. In both the *trifidus* and *helenae* morphotypes, the ornamentation types, Ia and Ib, appear on the phragmocone, except for IGPUW/A/36/190 (*trifidus* morphotype, Pl. 12, Fig. 2), in which type Ib continues up to the adult body-chamber. In all of the other studied specimens type II ornamentation appears on the adult body-chamber. The diameters at which the successive ornamentation types appear vary between the *trifidus* morphotype and *helenae* morphotype. In the former type Ia ornamentation changes to type Ib between 120 mm and 140 mm; type II ornamentation starts to appear between diameters 180 mm and 230 mm, the exact diameter is not known due to the incompleteness of the specimen IGPUW/A/36/213

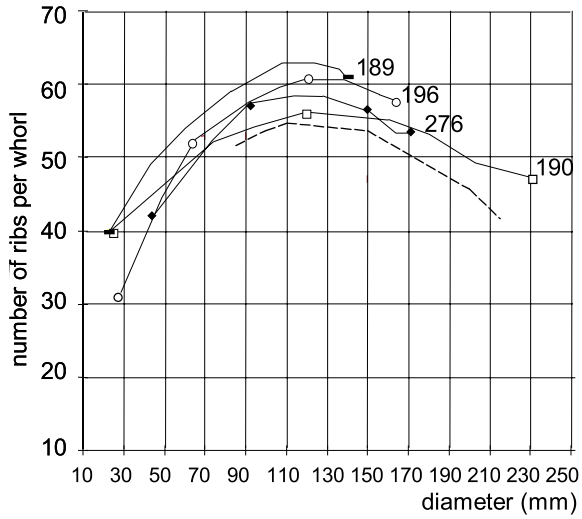

Fig. 10. Rib-density curves of *Perisphinctes trifidus* (SOWERBY) (M: *trifidus* morphotype) (continuous lines) compared to the holotype of *P. trifidus* (SOWERBY) (dashed line); the specimens are numbered by only the last component of their full registration numbers

(Pl. 12, Fig. 1) showing type II ornamentation. In the *helenae* morphotype type Ia ornamentation changes to type Ib usually at 160 mm-170 mm diameter, except in IGPUW/A/36/191 (Pl. 11, Fig. 1), in which it appears already at 120 mm; type II ornamentation occurs on the body-chamber, between 230 mm and 290 mm, the exact diameter is not known due to the incompleteness of the specimen IGPUW/A/36/280 (Pl. 10, Fig. 3) showing it.

The rib-thickness and rib-density vary between the two morphotypes. In the *helenae* morphotype the ribs are thin to moderately thin, densely to moderately densely spaced on the whorl-flanks. The rib-number increases from 30-40 per whorl at c. 30 mm (Text-fig. 11) to 60-70 ribs per whorl at 160 mm-170 mm; at diameters greater than 160 mm-170 mm the number of ribs decreases, reaching 50-55 ribs per whorl at 240 mm diameter, and 35 ribs per whorl at 340 mm. In the *trifidus* morphotype the ribs are moderately thin, moderately densely to densely spaced on the whorl-flanks. The rib-number per whorl increases from 30-40 per whorl at c. 30 mm, to 56-65 at c. 120 mm diameter (Text-fig. 10); after a diameter of 120 mm the rib-number decreases, first slowly and, after c. 140 mm diameter more rapidly, decreasing to 47 ribs per whorl at 230 mm.

The septal suture of formula EL=L=N appears in both morphotypes between 95 mm and 110 mm. At larger diameters it changes: firstly to EL=N>L at 120 mm in IGPUW/A/36/196, and then to N>EL>L at 160 mm in IGPUW/A/36/213 (Pl. 12, Fig. 1) (the two latter specimens are of the *trifidus* morphotype). The pattern of septal suture N>EL>L, appears also in the specimens of the *helenae* morphotype, IGPUW/A/36/191 (Pl. 11, Fig. 1) at 130 mm diameter and in IGPUW/A/280 (Pl. 10, Fig. 3) at 230 mm diameter. The septal suture N>EL=L appears in the studied material exclusively in the *helenae* morphotype, in the specimen IGPUW/A/36/185 (Pl. 10, Fig. 2), at D=180 mm.

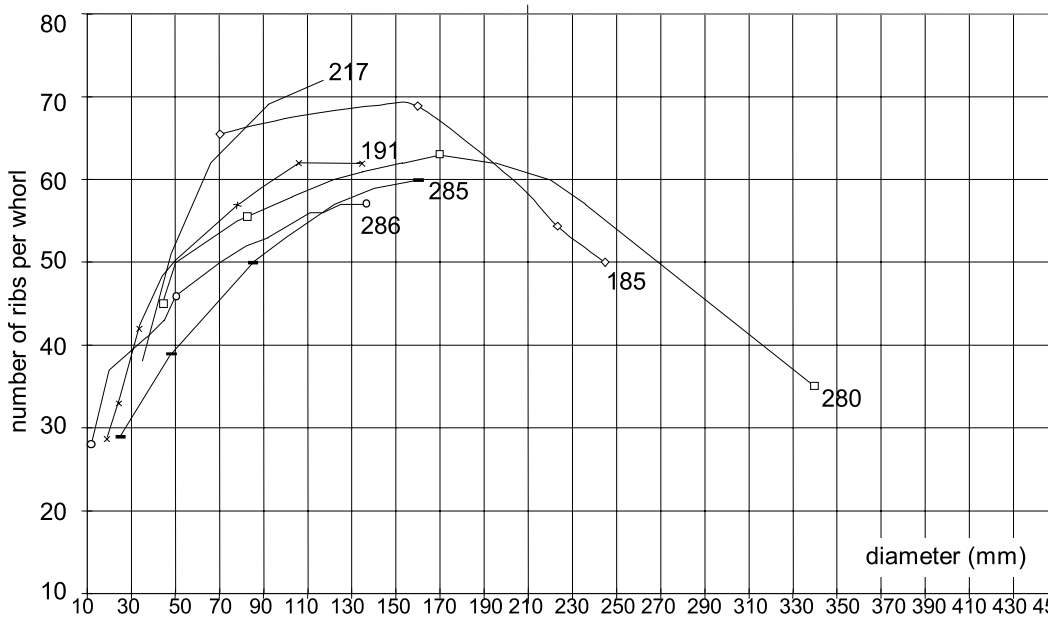

Fig. 11. Rib-density curves of *Perisphinctes trifidus* (SOWERBY) (M: *helenae* morphotype); the specimens are numbered by only the last component of their full registration numbers

DISCUSSION: The microconch counterparts of the species *Perisphinctes trifidus* (SOWERBY) are described here for the first time. Two specimens from southern France: *Perisphinctes* (*Otosphinctes*) nov. sp. ?A (BOURSEAU 1977, Pl. 1, Fig. 12) and *Perisphinctes* (*Dichotomosphinctes*) nov. sp. ?A (BOURSEAU 1977, Pl. 3, Fig. 7) are assigned to *P. trifidus* (see the synonymy). The BOURSEAU specimens agree with the studied specimens in compressed whorl-section, weakly evolute coiling, fine, prorsiradiate ribs, and appearance of parabolae. The microconchs of *P. trifidus*, with their dense ribbing on the inner whorls and subrectangular whorl-section of the body-chamber resemble *Perisphinctes auriculatus* ARKELL (see ARKELL 1935, vol. 1, Pl. B, Fig. 3a,b; 1938, vol. 4, p. 77-78, Pl. 14, Fig. 5, Pl. 17, Figs 4, 7, 8). The microconchs of *P. trifidus* differ from ARKELL's species in sharper and more prorsiradiate ribs on the whorl-flanks and in straight projection of the secondary ribs on the venter (in ARKELL's species the secondary ribs are curved forward).

P. trifidus (m, M), as interpreted in the present paper is a geographically variable species, with the *helenae* morphotype predominating to the south of the Submediterranean Province, in France and Spain, and with the *trifidus* morphotype predominating to the north, in southern England. This suggests the subspecific diversity of the species. In the Polish material these two morphotypes intergrade, indicating the intermediate character of the studied population. The *helenae* morphotype and the *trifidus* morphotype, commonly referred to two separate species, *P. trifidus* (SOWERBY) and *Perisphinctes helenae* DE RIAZ (e.g. ARKELL 1939, ENAY 1966, HAUERSTEIN 1966, MELÉNDEZ 1989), agree in a subrectangular whorl-section at equivalent growth stages, and in the coiling, which is moderately evolute or weakly evolute, changing to evolute or to moderately evolute on the middle and outer whorls. In addition, these two morphotypes agree in the mode of rib-density changes, characterised by decrease in the rib number per whorl through the type Ib and type II ornamentation. The less densely ribbed *trifidus* morphotype is linked to the more densely ribbed *helenae* morphotype by specimens of intermediate rib-density (Text-figs 10-11). The two morphotypes differ in the final size of adults. The adult specimens of the *trifidus* morphotype are of $\underline{D}_m$=235 mm, whereas the largest specimen in the collection of the *helenae* morphotype is of D_m=340 mm and shows no indications of cessation of growth at this diameter. In addition, the representatives of the two morphotypes differ in the diameters at which the equivalent ornamentation types start to occur. In the *trifidus* morphotype type Ib ornamentation starts to appear at 120 mm-140 mm whereas in the *helenae* morphotype, usually at 160 mm-170 mm; some specimens of the latter morphotype show it, however, already at 120 mm.

P. trifidus (m, M) with its shell-ornamentation characterised by bifurcating ribs, thin, to moderately thin primary ribs, densely to moderately densely spaced and prorsiradiate on the whorl-flanks, with the shape of rib-curves and with the mode of rib-density changes, resembles the early species of the subgenus *Kranaosphinctes* BUCKMAN, *Perisphinctes promiscuus* BUKOWSKI and *Perisphinctes collignoni* (BROCHWICZ-LEWIŃSKI), and their corresponding microconchs of the subgenus *Otosphinctes* BUCKMAN, *Perisphinctes paturattensis* DE LORIOL (see the respective descriptions in the present paper). *P. trifidus* (m, M) differs from these species in the subquadrate whorl-section, the less evolute coiling of the inner whorls, the larger diameters at which particular ornamentation types appear, and in the final shell-size, which is larger in the macroconchs of *P. trifidus* than in the species of *Kranaosphinctes* previously mentioned. The microconchs of *P. trifidus* are comparable in size with the largest specimens of *P.* (*O.) paturattensis*, but they differ in that they do not show increase in height and width of the body-chamber that appears at the adult stage of growth in *P.* (*O.*) *paturattensis*.

The lower Middle Oxfordian species *P. trifidus* (m, M) with its bifurcating ribs, thin to moderately thin primary ribs, densely to moderately densely spaced on the whorl-flanks, subrectangular whorl-section, moderately evolute to evolute coiling of shell, and the moderately thickly ribbed adult body-chamber, resembles the species of the upper Middle Oxfordian genus *Sequeirosia* MELÉNDEZ, *S. brochwiczi* (SEQUEIROS) and *S.* n. sp. A., described by MELÉNDEZ (1989, p. 182). The latter author (op. cit., p. 233) noted the similarity between the *helenae* morphotype of *P. trifidus* as interpreted in the present paper, and the genus *Sequeirosia*. This genus groups the upper Middle Oxfordian forms of Mediterranean affinity (ENAY 1966, BROCHWICZ-LEWIŃSKI & RÓŻAK 1976). *P. trifidus* (m, M) with its thin, dense ribs, indicating its affinity to Mediterranean ammonites, could be the ancestor of *Sequeirosia*. The representatives of the latter genus are, however, missing in the upper Middle Oxfordian of the study area.

The macroconchs of *P. trifidus* differ from most of the species of the subgenus *Kranaosphinctes*, except for *P. promiscuus* and *P. collignoni* (see above), in generally less evolute coiling at all stages of growth, thinner ribs more densely spaced on the whorl-flanks, and in the rib-curves and the mode of rib-density changes. In *P. trifidus* the rib-curves are steep, noticeably convex, and more or less symmetrical (Text-figs 10-11); the rib number per whorl increases rapidly in the range of diameters corresponding to type Ia ornamentation, and it decreases markedly

through the diameters corresponding to type Ib and II ornamentation; in *Kranaosphinctes* the rib-curves are flattened and asymmetrical; the rib-number per whorl usually increases through the type Ia and Ib ornamentation, and decreases through the type II ornamentation, or it decreases gently throughout type Ib, type Ic and type II ornamentation. The septal suture of *P. trifidus* and of the species of the subgenus *Kranaosphinctes* is usually different, except for the formula N>EL>L, which is recognized in both of these forms.

The septal suture formula N>EL>L also appears in some specimens of the genus *Neumannia* gen. nov. From the species of the latter genus *P. trifidus* differs in less evolute coiling at equivalent stages of growth, the subrectangular whorl-section, lack of simple ribs, and in the shell-ornamentation of the adult body-chamber: in *P. trifidus* the ribs on the adult body-chamber are not accentuated at the ventro-lateral margin, whereas they are in *Neumannia* gen. nov.

From the species of the genus *Liosphinctes* BUCKMAN, *P. trifidus* differs in the subrectangular whorl-section as compared to oval in *Liosphinctes*, the more evolute coiling, and in the lack of the non-bifurcating ribs that are common in *Liosphinctes*. In addition, *P. trifidus* differs in the distinctly ribbed body-chamber whorl-flanks, compared to the almost smooth whorl-flanks in *Liosphinctes*. These two forms differ generally in septal suture. One of the septal sutures, however, EL=L=N, is present in both *P. trifidus* and the genus *Liosphinctes*. The other patterns of septal sutures are different in the two compared forms.

OCCURRENCE: Macroconchs: England, Poland, Germany, France, Spain. Microconchs: France and Poland. The species *P. trifidus* (m, M) ranges from the Paturattensis Subzone to the Arkelli Subzone of the Plicatilis Zone (Text-fig. 6); macroconchs disappear in the lower part of the subzone, microconchs range up somewhat higher and disappear below the Platysphinctes horizon of the Arkelli Subzone.

Subgenus *Otosphinctes* BUCKMAN, 1926

TYPE SPECIES: *Otosphinctes ouatius* BUCKMAN (1926, Pl. 649, Figs 1, 2); see also ARKELL (1936, p. 43; 1938, p. 93, Pl. 17, Fig. 5 a-g).

EMENDED DIAGNOSIS: microconchs small to middle sized; coiling moderately evolute, rarely evolute or weakly evolute; whorl-section circular, subquadrate, subrectangular or oval. Ribs bifurcating. Parabolae present. Peristome provided with lappets.

REMARKS: Small microconchs from the upper part of the overlying Transversarium Zone, such as *Perisphinctes siemiradzkii* ENAY, 1966, *P. anguiculus* ENAY, 1966, *P. vermicularis* LEE, 1905, and *Perisphinctes nectobrigensis* MELÉNDEZ, 1989, referred to the subgenus *Otosphinctes* by other authors (ENAY 1966, MELÉNDEZ 1989), are excluded from the synonymy of this subgenus. *Otosphinctes*, as interpreted in the present paper, represents microconch counterparts of the species of the subgenus *Kranaosphinctes* BUCKMAN, 1921 with which it is limited stratigraphically to the upper Cordatum Zone of the Lower Oxfordian and the Plicatilis Zone of the Middle Oxfordian.

Perisphinctes (*Otosphinctes*) *paturattensis* DE LORIOL, 1901 (Pl. 1, Figs 3-5; Pl. 2, Figs 1, 4-5; Pl. 3, Fig. 1; Text-figs 5, 12-13)

1901. *Perisphinctes paturattensis* sp. n.; DE LORIOL, p. 23; Pl. 2, Figs 2-6; Pl. 2, Figs 4, 4a (lectotype).
1901. *Perisphinctes montfalconensis* sp. n.; DE LORIOL, p. 27; Pl. 2, Figs 7 (lectotype), 8, 9.
1930. *Perisphinctes paturattensis* LORIOL; DORN, p. 164; Pl. 35 (11), Figs 2a, 2b.
1966. *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL; ENAY, pp. 432, 447, Figs 123-(3-9), 133; Pl. 25, Fig. 3 (lectotype).
1966. *Perisphinctes* (*Otosphinctes*) *montfalconensis* DE LORIOL; ENAY, p. 432, Fig. 123-1, p. 449; Pl. 25, Figs 1, 2.
?1976. *Nebrodites* (? *Enayites*) sp.; BROCHWICZ-LEWIŃSKI & RÓŻAK, Pl. 35, Fig. 3.
1977. *Perisphinctes* (*Otosphinctes*) *montfalconensis* DE LORIOL; BOURSEAU, p. 38, Text-figs 12, 14; Pl. 1, Fig. 1; Pl. 2, Figs 8, 11.
1977. *Perisphinctes* (*Otosphinctes*) sp. gr. *montfalconensis* DE LORIOL; BOURSEAU, p. 41, Text-figs 17-18; Pl. 1, Figs 5, 8.
1977. *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL; BOURSEAU, p. 42, Fig. 13; Pl. 1, Figs 4, 7, 9-11; Pl. 4, Figs 2, 7.
1981. *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL; BROCHWICZ-LEWIŃSKI, p. 235, Pl. 3, Figs 2, 3.
1982. *Perisphinctes* (*Otosphinctes*) cf. *paturattensis* DE LORIOL; MELÉNDEZ, SEQUEIROS, BROCHWICZ-LEWIŃSKI, Pl. 2, Fig. 2 (*V.*).
1982. *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL; MELÉNDEZ, SEQUEIROS, BROCHWICZ-LEWIŃSKI, Pl. 5, Fig. 3 (*V.*).
1982. *Perisphinctes* (*Otosphinctes*) sp. ex gr. *paturattensis* DE LORIOL; MELÉNDEZ, SEQUEIROS, BROCHWICZ-LEWIŃSKI, Pl. 5, Fig. 4 (*V.*).
1982. *Perisphinctes* (*Otosphinctes*) *montfalconensis* DE LORIOL; MELÉNDEZ, SEQUEIROS, BROCHWICZ-LEWIŃSKI, Pl. 5, Fig. 2 (*V.*).

1982. *Perisphinctes* (*Otosphinctes*) ex. gr. *montfalconensis* DE LORIOL; MELÉNDEZ, SEQUEIROS, BROCHWICZ-LEWIŃSKI, Pl. 2, Fig. 3 (*V.*).

1989. *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL; MELÉNDEZ, pp. 252; 270, Fig. 52; Pl. 36, Figs 2-4, ?5, 6, 7, *V.*).

1989. *Perisphinctes* (*Otosphinctes*) *montfalconensis* DE LORIOL; MELÉNDEZ, pp. 259, 273; Text-fig. 53; Pl. 36, Figs 8-10 (*V.*).

MATERIAL: Twenty-nine specimens; fifteen lappeted, eleven with lappets broken away. In addition two specimens with incomplete body-chamber, one specimen representing half-whorls, and six lappeted whorl-fragments classified as *P.* (*O.*) cf. *paturattensis.*

The specimens of *P.* (*O.*) *paturattensis* and of *P.* (*O.*) cf. *paturattensis* representing the *paturattensis* morphotype (see below) come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.6, bed 26b, bed 27a (four specimens); 27b, 28a (three specimens), 28b, 28c (three specimens); section W.6', beds 27 (a–e), 28h, 29, 30 (two specimens), section W.4, bed 18, 19a; section W.4III, bed 20, 21 (two specimens), section W.9", bed 8.1g; from Rudniki Quarry (Text-fig. 2, Appendix), section Rd., beds 10, 12, 14 (two specimens); from Ogrodzieniec Quarry (Text-fig. 3, Appendix), section O.4, bed 1p.

The specimens of *P.* (*O.*) *paturattensis* and of *P.* (*O.*) cf. *paturattensis* representing the *montfalconensis* morphotype (see below) come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.6, bed 27a, 28a; section W.6', bed 27 (a-e); section W.4, bed 18.

DESCRIPTION: The specimens represent mature individuals, as indicated by approximation of the last ribs on the body-chamber, noticeable enlarging of the body-chamber in width and height, and by a peristome provided with lappets. The phragmocones of the studied specimens end at diameters between 24 mm and 47 mm; the body-chamber is 5/8 of a whorl; the final size of the specimens $\underline{D}_m$ varies from 32 mm to 72 mm (Text-fig. 5). The specimens of $\underline{D}_m$ from 42 mm to 47 mm and from 47 mm to 52 mm represent, respectively, 26% and 30% of specimens from the Paturattensis Subzone of the Plicatilis Zone (Text-fig. 5). Smaller specimens, between 32 mm and 37 mm and between 37 mm and 41 mm represent 4.3% and 13.1% of specimens respectively. Larger specimens, of $\underline{D}_m$ 52 mm-57 mm, 62 mm-67 mm, and 67 mm-72 mm diameters, are represented in each of these classes by 8.7% of specimens. Specimens of $\underline{D}_m$ from 57 mm to 62 mm are lacking in the studied material.

Based on the size variability recognized in the studied material, two size morphotypes are distinguished: the smaller, *paturattensis* morphotype, and the larger, *montfalconensis* morphotype. The specimens of the *paturattensis* morphotype are of $\underline{D}_m$ from 34 mm to 55 mm (85% of specimens in the studied group); the specimens of the *montfalconensis* morphotype are of $\underline{D}_m$ from 62 mm to 72 mm (15% of specimens in the studied group).

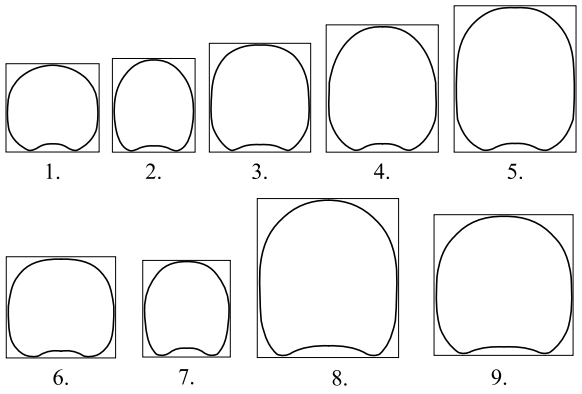

Fig. 12. Whorl-sections of the specimens of the subgenus *Otosphinctes* BUCKMAN (natural size) at a given diameter; *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL, *paturattensis* morphotype: 1. IGPUW/A/36/57 (Pl. 1, Fig. 5), $\underline{D}_m$=49 mm; 2. IGPUW/A/36/75 (Pl. 2, Fig. 4), $\underline{D}_m$=41 mm; 3. IGPUW/A/36/71 (Pl. 3, Fig. 1), $\underline{D}_m$= 55 mm; *montfalconensis* morphotype: 4. IGPUW/A/36/72 (Pl. 1, Fig. 3), $\underline{D}_m$=68 mm. *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov.: 5. IGPUW/A/36/117 (Pl. 7, Fig. 3), $\underline{D}_m$=75 mm. *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov.: 6. IGPUW/A/36/116 (holotype) (Pl. 4, Fig. 1), $\underline{D}_m$=53 mm. *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN): 7. IGPUW/A/36/91 (Pl. 6, Fig. 2), D=51 mm. *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK: 8. IGPUW/A/36/96 (holotype), $\underline{D}_m$=88 mm. *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov.: 9. IGPUW/A/36/140 (holotype, Pl. 14, Fig. 4), $\underline{D}_m$=100 mm; 10. IGPUW/A/36/146 (Pl. 15, Fig. 1), D=91 mm

The whorl-section (Text-fig. 12) of the body-chamber in the studied specimens of both morphotypes is circular to oval. The coiling is usually moderately evolute; occasionally it becomes weakly evolute in the *paturattensis* morphotype, or nearly evolute in the *montfalconensis* morphotype. In the *paturattensis* morphotype, at $\underline{D}_m$ from 36 mm to 55 mm, $\overline{U/D}$=0.46 (OS=0.03), $\overline{W/D}$=0.31 (OS=0.02) and W_m/U_m ranges from 0.58 to 0.71 (occasionally 0.81 and 0.94). In the *monfalconensis* morphotype, at $\underline{D}_m$ c. 70 mm, U_m/D_m=0.50, W_m/D_m=0.26-0.28, and W_m/U_m=0.51 to 0.56.

Shell-ornamentation consists of bifurcating ribs. The ribs are thin, rarely moderately thin, densely spaced and prorsiradiate on the whorl-flanks of the phragmocone and somewhat coarser, not sharp on the body-chamber. At the end of the phragmocone and on the body-chamber the primary ribs become S-shaped on the upper part of the whorl-flanks and the secondary ribs pass across the venter with a backward inflexion. The ventral ribs com-

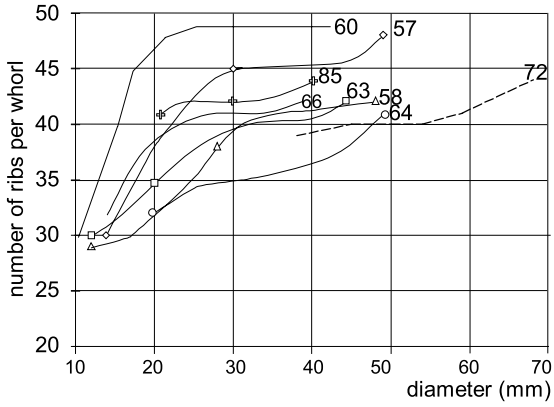

Fig. 13. Rib-density curves of *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL; continuous lines are for the *paturattensis* morphotype, dashed line is for the *montfalconensis* morphotype; the specimens are numbered by only the last component of their full registration numbers

monly form a zigzag pattern. Each zigzag pattern ends in a free ending half-rib, appearing on one side of the whorl. It resembles a simple rib, which in fact does not appear in this species.

The rib-number per whorl (Text-fig. 13) increases from c. 30 per whorl at a diameter of c. 10 mm, to 35-48 per whorl between 20 mm and 30 mm. After these diameters the rib-number per whorl remains constant nearly to the end of the last whorl, except for the final part of the body-chamber where it increases due to the approximation of the last ribs. The rib-density curves rise up steeply between c. 10 mm and 25 mm, and again near the final diameter, where the ribs become approximated on the whorl-flanks. At intermediate diameters the rib-curves become nearly flat.

Parabolae are common in the *paturattensis* morphotype. In the *montfalconensis* morphotype oblique swollen ribs commonly appear, whereas typical parabolae are rare. Parabolae and oblique ribs, appear in the two morphotypes in the final part of the phragmocone and continue nearly to the end of the body-chamber. They disappear on the last 1/8 of a whorl before the aperture. Constrictions are rare. Usually there are two constrictions on the last whorl: one in the final part of the phragmocone, and the other at the peristome.

DISCUSSION: The *paturattensis* morphotype and the *montfalconensis* morphotype, commonly assigned to separate species (DE LORIOL 1901, ENAY 1966, BOURSEAU 1977, MELÉNDEZ 1989), intergrade in whorl-section, mode of coiling, character of ribbing, length of body-chamber and in the presence of parabolic structures; they can be accommodated in a single species, *P.* (*O.*) *paturattensis*. Both morphotypes intergrade almost continuously in final size (Text-fig. 5). The *paturattensis* morphotype, represented by smaller forms, appears more commonly in the studied material of *P.* (*O.*) *paturattensis* than the *monfalconensis* morphotype.

The morphological variability of *P.* (*O.*) *paturattensis* in a single horizon concerns final size, rib-density and rib-number per whorl, and parabolic ribs. These characters change in the following way:

- the difference in size between the smallest and the largest specimen from a single horizon reaches 32 mm of diameter but does not exceed it;
- the rib-number per whorl differs by up to c. 8 ribs per whorl at the end of the phragmocone between the most and the least densely ribbed specimen from a single horizon;
- the number of parabolic ribs varies from 1 to 6 on the last whorl; specimens which do not possess parabolic ribs, but oblique swollen ribs, are also present.

Other characters, such as the whorl-section of the body-chamber (usually circular, rarely oval) and the coiling (usually moderately evolute, rarely weakly or nearly evolute) do not vary significantly in *P.* (*O.*) *paturattensis*.

The morphological trends in *P.* (*O.*) *paturattensis* through its stratigraphical range are as follows:

- increase in final size; the upper Lower Oxfordian specimens in the studied collection are of $\underline{D}_m$ between 32 mm and 37 mm, and 42 mm and 47 mm (Text-fig. 5); the specimens from the Paturattensis Subzone of the Plicatilis Zone of the Middle Oxfordian vary in $\underline{D}_m$ from 36 mm in the lower part of the subzone to 72 mm in the upper part of the subzone.
- decrease in number of parabolic ribs, with oblique swollen ribs becoming commoner.
- predominance of finely and densely ribbed specimens in the lower, compared to moderately thin ribbed specimens in the upper part of the stratigraphical range of the species.

From the Spanish specimens of *P.* (*O.*) *paturattensis* (see MELÉNDEZ 1989), the Polish specimens of *paturattensis* morphotype differ in larger final size, slightly coarser ribbing of the inner whorls, weaker backward inflexion of the ribs on the outer whorl, and in less numerous constrictions on the outer whorl. These differences may result from geographic variation of *P.* (*O.*) *paturattensis*. It is also possible, however, that Spanish material may be slightly older stratigraphically, as it comes from the condensed beds spanning the Lower-Middle Oxfordian.

The fine, dense ribbing and circular whorl-section of *P.* (*O.*) *paturattensis*, suggests the Mediterranean affinity of this species.

OCCURRENCE: France, Spain, Switzerland, and Poland. It appears in the Cordatum Subzone of the

Cordatum Zone of the Lower Oxfordian, and ranges up higher throughout the Paturattensis Subzone of the Plicatilis Zone of the Middle Oxfordian. The *montfalconensis* morphotype is limited stratigraphically to the upper part of the Paturattensis Subzone of the Plicatilis Zone (Text-fig. 6).

Perisphinctes (*Otosphinctes*) *ouatius ouatius* (BUCKMAN, 1926)
(Pl. 5, Fig. 3; Pl. 6, Figs 2-3; Pl. 9, Figs 1-2; Text-figs 5, 12, 14)

1926. *Otosphinctes ouatius* sp. nov.; BUCKMAN, Pl. 649, Figs 1-2 (holotype, *V.*).
1936. *Perisphinctes* (*Dichotomosphinctes*) *ouatius* (BUCKMAN); ARKELL, p. 43.
1938. *Perisphinctes* (*Dichotomosphinctes*) *ouatius* (BUCKMAN); ARKELL, p. 93; Pl. 17, Fig. 5 a-g (holotype, *V.*); Pl. 17, Figs 6 (*V.*), ? 1, 2, 10.
1938. *Perisphinctes* (*Dichotomosphinctes*) *magnouatius* sp. nov.; ARKELL, p. 94; Pl. 17, Fig. 9 (holotype, *V.*); Pl. 17, Figs ? 11-12.
1952. *Perisphinctes* (*Dichotomosphinctes*) *ouatius* (BUCKMAN); SIEGFRIED, p. 310, Pl. D, Fig. 2.
1966. *Perisphinctes* (*Dichotomosphinctes*) *magnouatius* ARKELL; ENAY, p. 462; Pl. 27, Fig. 8.
1975 b. *Perisphinctes* (*Otosphinctes*) sp.; BROCHWICZ-LEWIŃSKI & RÓŻAK, Text-fig. 1; Pl. 1, Fig. 1.
1977. *Perisphinctes* (*Otosphinctes*) *cf. magnouatius* ARKELL; BOURSEAU, p. 45, Text-figs 15-16; Tab. 9; Pl. 2, Fig. 7.
1977. *Perisphinctes* (*Otosphinctes*) sp. gr. *magnouatius* ARKELL; BOURSEAU, p. 46 (*pars*), Text-fig. 18; Tab. 10; Pl. 1, Fig. 3, *non* Fig. 2 [?*P.* (*O.*) *ouatius ouatoides* DE LORIOL].

MATERIAL: Twelve complete specimens, and four specimens unsuitable for biometric studies, classified as *P.* (*O.*) cf. *ouatius ouatius*. Two size morphotypes are distinguished in the studied material (see below): the *ouatius* morphotype (six complete and three incomplete specimens) and the *magnouatius* morphotype (six complete and one incomplete specimen).

The specimens of *P.* (*O.*) *ouatius ouatius* and of *P.* (*O.*) cf. *ouatius ouatius* representing the *ouatius* morphotype come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.4III, bed 2; section W.5, beds 3, 5b; section W.8, bed 4; section W.9, bed 10 (two specimens) and 14a; from the Rudniki Quarry (Text-fig. 2, Appendix), section Rd., bed 3; from Przybynów (Text-fig. 1).

The specimens of *P.* (*O.*) *ouatius ouatius* and of *P.* (*O.*) cf. *ouatius ouatius* representing the *magnouatius* morphotype come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.8, bed 10; W.9, beds 9 and 10 (three specimens); W.9", bed 12a; W.5, bed 1.

DESCRIPTION: The specimens are lappeted and they represent adult individuals. Their phragmocones end at $\underline{D}_f$ from 35 mm to 51 mm; the body-chamber is 5/8 to 3/4 of a whorl. The specimens range in final size ($\underline{D}_m$) from 57 mm to 73 mm. The size distribution in the studied group is bimodal (Text-fig. 5). The specimens of $\underline{D}_m$ ranging from 57 mm to 62 mm and those of $\underline{D}_m$ from 67 mm to 72 mm represent 21% and 15.8% respectively of the specimens from the lower Arkelli Subzone in the studied material (of both chronosubspecies *P.* (*O.*) *ouatius ouatius* and *P.* (*O.*) *arkelli arkelli* GŁOWNIAK) . The specimens of $\underline{D}_m$ from 62 mm to 67 mm and of $\underline{D}_m$ from 72 mm to 77 mm are less numerous (5.3% and 10.5% respectively).

Based on the bimodal size distribution in the studied group, two morphotypes are distinguished in *P.* (*O.*) *ouatius ouatius*: the smaller, *ouatius* morphotype and the larger, *magnouatius* morphotype. The limit of final size between them is arbitrary taken at $\underline{D}_m$=66 mm.

The whorl-section in both morphotypes is subquadrate to subcircular on the phragmocone, and sub-

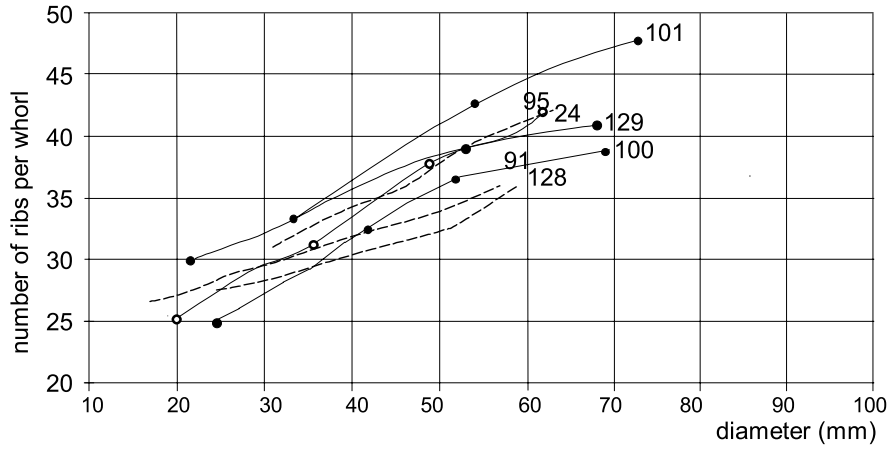

Fig. 14. Rib-density curves of *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN); dashed lines are for the *ouatius* morphotype, dotted lines are for the *magnouatius* morphotype; the specimens are numbered by only the last component of their full registration numbers

quadrate, with rounded venter and margins, or occasionally subcircular, on the body-chamber (Text-fig. 12). The coiling of all of the studied specimens is moderately evolute, occasionally evolute throughout ontogeny. At a final diameter from 55 mm to 73 mm $\overline{U/D}$=0.49, (OS=0.03), $\overline{W/D}$=0.29 (OS=0.02), and W_m/U_m usually ranges from 0.55-0.68, occasionally it is 0.50 and 0.71. The ribs vary from moderately thick in the *magnouatius* morphotype to thick in the *ouatius* morphotype.

The ribs are generally straight and somewhat prorsiradiate on the whorl-flanks, except for the final part of the phragmocone and the beginning of adult body-chamber, where the ribs curve backward on the upper half-flank and on the venter, and become S-shaped. On the last quarter-whorl of the body-chamber in both morphotypes the primary ribs again become straight and somewhat prorsiradiate, and the secondary ribs pass straight across the venter. The latter character appears in both morphotypes. The *ouatius* morphotype is generally less densely ribbed than the *magnouatius* morphotype, especially on the middle and outer whorls; on the inner whorls these two groups strongly overlap in rib-density. In the *ouatius* morphotype the rib-number per whorl (Text-fig. 14) is c. 28 per whorl at D=20 mm; it increases to 32-35 ribs per whorl at D=50 mm, and then to 37 at $\underline{D_m}$ from 57 mm to 59 mm. The rib-density curves are gently inclined up to c. 50 mm diameter, and rise up more steeply near the final diameter. In the *magnouatius* morphotype (Text-fig. 14) the rib-number per whorl ranges between 25 and 30 at D=20 mm; it increases noticeably up to 36-42 ribs per whorl at D=50 mm; at larger diameters it changes only slightly, reaching 39-48 at $\underline{D_m}$ from 67 mm to 72 mm. The rib-density curves of *magnouatius* morphotype are somewhat convex upward.

The oblique swollen ribs and, rarely, parabolic ribs with blunt parabolic nodes appear in the final part of the phragmocone and at the beginning of the adult body-chamber in both morphotypes. They disappear in the final part of the body-chamber, a quarter of a whorl before the aperture. Oblique ribs are rarely present on the phragmocone. The zigzag pattern of the ventral ribs is common on the body-chamber. It finishes with the free-ending secondary rib, which sometimes tends to join the pair of secondary ribs, giving an impression of trifurcation (IGPUW/A/36/91 Pl. 6, Fig. 2), which, in fact, does not appear in this subspecies. Constrictions number 1-2 on the body-chamber; on the phragmocone they are usually absent. IGPUW/A/36/128 (Pl. 6, Fig. 3) differs from the other specimens in the collection in possessing a constricted phragmocone.

DISCUSSION: In the studied material the *ouatius* morphotype and the *magnouatius* morphotype, previously assigned to separate species (ARKELL 1938, SIEGFRIED 1952, ENAY 1966, BOURSEAU 1977) are accommodated in a single species *Perisphinctes* (*Otosphinctes*) *ouatius* (BUCKMAN). The two morphotypes agree in the whorl-section, coiling, and parabolic structures. They intergrade in respect of the rib-density (Text-fig. 14) and final size, showing, however, bimodal distribution of the latter (Text-fig. 5).

The morphological variability of *P.* (*O.*) *ouatius ouatius* in any single horizon concerns final size, rib-number per whorl, number of parabolic and oblique ribs, and number of constrictions. They change as follows:

- final size difference between the smallest and the largest specimen from a single horizon reaches c. 15 mm diameter;
- rib-number per whorl reaches c. 5 ribs per whorl at an equivalent diameter, between the least and the most densely ribbed specimen;
- the number of parabolic ribs and/or oblique swollen ribs varies from one to four on the last whorl;
- constrictions vary from zero to four on the inner whorls, and from zero to two on the body-chamber.

Morphological trends through the stratigraphical range of *P.* (*O.*) *ouatius ouatius* are as follows:

- densely ribbed specimens predominant in the lower part of the range of the subspecies, whereas in the upper part they become succeeded by the specimens with a lower number of ribs per whorl;
- small specimens, of $\underline{D_m}$ from 53 mm to 61 mm, become succeeded by larger ones, of $\underline{D_m}$ from 61 mm to 66 mm;
- oblique swollen ribs or/and parabolic ribs become less frequent upward, and are occasionally absent in the specimens from the top of the stratigraphical range of the chronosubspecies.

P. (*O.*) *ouatius ouatius* differs from *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. in the presence of constrictions, a body-chamber which does not enlarge noticeably in height and width in the final part, and in the generally larger final size (Text-fig. 5, see details in the discussion of *P.* (*O.*) *ouatius ouatoides* chronossp. nov., p. 332).

P. (*O.*) *ouatius ouatius* differs from *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK in the subquadrate, or, occasionally, subcircular whorl-section of the body-chamber, the usually less evolute coiling, the appearance of backward inflexion of ribs at the end of the phragmocone and at the beginning of the body-chamber, which in *P.* (*O.*) *arkelli arkelli* occurs only at the end of the body-chamber; in the oblique swollen ribs and/or parabolae, which are rare in *P.* (*O.*) *arkelli arkelli*; and in the generally smaller final size, except for some specimens which overlap in size with *P.* (*O.*) *arkelli arkelli* (Text-fig. 5).

OCCURRENCE: England, Germany, and Poland. *P.* (*O.*) *ouatius ouatius* appears at the base of the Arkelli Subzone of the Plicatilis Zone, and ranges up higher to the Platysphinctes horizon of the Arkelli Subzone, where it disappears. The *magnouatius* morphotype of *P.* (*O.*) *ouatius ouatius* appears at the base of the Arkelli Subzone of the Plicatilis Zone, and is limited stratigraphically to the lower and middle part of the subzone (Text-fig. 6).

Perisphinctes (*Otosphinctes*) *ouatius ouatoides* chronossp. nov.

(Pl. 4, Figs 1-2; Pl. 6, Fig. 1; Pl. 7, Fig. 3; Text-figs 5, 12, 15)

? 1977. *Perisphinctes* (*Otosphinctes*) sp. gr. *magnouatius* ARKELL; BOURSEAU, p. 46, Text-fig. 18; Tab.10; Pl. 1, Fig. 2 (without synonymy).

? 1977. *Perisphinctes* (*Otosphinctes*) nov. sp.? aff. *sorlinensis* DE LORIOL; BOURSEAU, p. 48, Text-fig. 17; Pl. 2, Fig. 6.

HOLOTYPE: IGPUW/A/36/116 (Pl. 4, Fig. 1) from the Ouatius Subzone of the Plicatilis Zone of the Wysoka Quarry (Text-fig. 2, Appendix), section W.4, collected loose from beds 17a-c.

PARATYPES: IGPUW/A/36/81 (Pl. 4, Fig. 2), IGPUW/A/36/62, IGPUW/A/36/111, IGPUW/A/36/114 (Pl. 6, Fig. 1), IGPUW/A/36/115, IGPUW/A/36/117; all of them complete or nearly complete. Additionally two poorly preserved specimens referred to as *P.* (*O.*) cf. *ouatius ouatoides* chronossp. nov.

The specimens of *P.* (*O.*) *ouatius ouatoides* chronossp. nov. and *P.* (*O.*) cf. *ouatius ouatoides* chronossp. nov. represented by the *ouatoides* morphotype (see below) come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.4, beds 17b (two specimens) and 17c; W.8, bed 1e; W.4III, bed 10; and from Ogrodzieniec Quarry (Text-fig. 3, Appendix), section O.1, bed 1c and bed 1a. The specimen of *P.* (*O.*) *ouatius ouatoides* chronossp. nov. representing the *ouatius* morphotype (see below) come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.4, bed 17c.

DERIVATION OF NAME: The name "*ouatoides*" indicates the affinity to *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN).

DIAGNOSIS: Microconchs; small to middle-sized; coiling moderately evolute; whorl-section subquadrate, changing on the body-chamber to subcircular or oval. Ribs moderately thick, occasionally thick. Body-chamber 5/8, rarely 3/4 of a whorl; enlarging in height and width in the final part of the last whorl. Parabolae and oblique swollen ribs common. Peristome lappeted.

DESCRIPTION: The holotype is a complete, mature specimen of $\underline{D}_m$=53 mm; with the phragmocone up to $\underline{D}_f$=34 mm. The body-chamber is 5/8 of a whorl. The peristome is lappeted. The maturity of the holotype is indicated by the approximation of the last seven ribs and their flexuous inflexion on the body-chamber. Moreover, the body-chamber enlarges in width and height close to the aperture, which is distinctive character of the final stage of growth in this species. The paratypes are mature individuals. The septa are not perfectly exposed, except in IGPUW/A/36/81 (Pl. 4, Fig. 2), IGPUW/A/36/114 (Pl. 6, Fig. 1) and IGPUW/A/36/117 (Pl. 7, Fig. 3). In the first two specimens the phragmocone ends at $\underline{D}_f$=36 mm and the body-chamber is 5/8 of a whorl; in the latter specimen the phragmocone ends at $\underline{D}_f$=46 mm and the body-chamber is 3/4 of a whorl. The specimens range in maximum diameter $\underline{D}_m$ from 46 mm to 55 mm, and occasionally reach 75 mm (Text-fig. 5). 62% of the specimens collected from the Ouatius Subzone of the Plicatilis Zone are those of $\underline{D}_m$ from 52 mm to 57 mm (Text-fig. 5). Smaller specimens, of $\underline{D}_m$ from 42 mm to 51 mm, and the larger specimens, from 72 mm to 77 mm, are represented in each of these two classes by 12.5% of individuals. Specimens of intermediate final size, from 57 mm to 72 mm, are absent from the studied group.

Two morphotypes are distinguished in the studied material: the *ouatoides* morphotype and the *ouatius* morphotype. The *ouatius* morphotype, represented in the studied group by IGPUW/A/36/114 (Pl. 6, Fig. 1), is of $\underline{D}_m$=55 mm. The *ouatoides* morphotype, represented in the studied collection by the holotype and seven paratypes, ranges in $\underline{D}_m$ from 46 mm to 53 mm, occasionally to 75 mm.

The whorl-section (Text-fig. 12) in the two morphotypes is subquadrate on the phragmocone, and it changes to subcircular or, rarely, to oval on the body-chamber. The coiling is moderately evolute, rarely, in the *ouatoides* morphotype, weakly evolute on the inner whorls. On the outer whorl it becomes moderately evolute in all of the studied specimens. In the holotype, at $\underline{D}_m$=53 mm, U/D=0.44, W/D=0.31, and W/U=0.70. In the paratypes, at $\underline{D}_m$ from 49 mm to 55 mm, U/D ranges from 0.43 to 0.49, W/D ranges from 0.28 to 0.30, W/U ranges from 0.58 to 0.62.

The ribs bifurcate. The primary ribs vary from moderately thick, moderately densely spaced in the *ouatoides* morphotype, to thick, distantly spaced in the *ouatius* morphotype (IGPUW/A/36/114, Pl. 6, Fig. 1). They are straight, rarely arched forward, prorsiradiate on the whorl-flanks. In the final part of the phragmocone and

on the body-chamber they curve backward on the upper half-flank and on the venter. The latter character is more distinct in the *ouatoides* morphotype than in the *ouatius* morphotype. The secondary ribs are weaker than the primary ribs. They pass across the venter with a backward sweep, and usually form a zigzag pattern.

In the *ouatoides* morphotype rib-number is 29-32 per whorl at a diameter of 20 mm (Text-fig. 15), then it increases to 37-41 per whorl at $\underline{D}_m$=50 mm, and to c. 40-44 ribs per whorl at the final diameters $\underline{D}_m$=53 mm and $\underline{D}_m$=75 mm. In the *ouatius* morphotype the rib-number is 25 per whorl at a diameter of c. 20 mm (Text-fig. 15), at larger diameters it increases to 32 at D=50 mm, and then to 34 at $\underline{D}_m$=55 mm. The rib-density curves of both morphotypes rise up gently.

Parabolic ribs with blunt parabolic nodes, and swollen oblique ribs are common in the *ouatoides* morphotype and less common in the *ouatius* morphotype. They appear at the end of the phragmocone and on the first part of the body-chamber, and disappear 1/8 of a whorl before the aperture. Constrictions are usually absent, with the exception of the apertural constriction. Structures resembling shallow constrictions appear rarely as a result of the appearance of swollen ribs causing irregular rib-spacing on the whorl-flanks (IGPUW/A/36/81, Pl. 4, Fig. 2).

DISCUSSION: *Perisphinctes* (*Otosphinctes*) *ouatius* (BUCKMAN) is divided into two chronosubspecies: *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov., from the Ouatius Subzone of the Plicatilis Zone, and *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN) from the Arkelli Subzone. *P.* (*O.*) *ouatius ouatoides* chronossp. nov. is generally smaller than *P.* (*O.*) *ouatius ouatius* (Text-fig. 5), ranging in $\underline{D}_m$ from 42 mm to 57 mm (occasionally 75 mm); whereas *P.* (*O.*) *ouatius ouatius* ranges in $\underline{D}_m$ from 57 mm to 77 mm (Text-fig. 5).

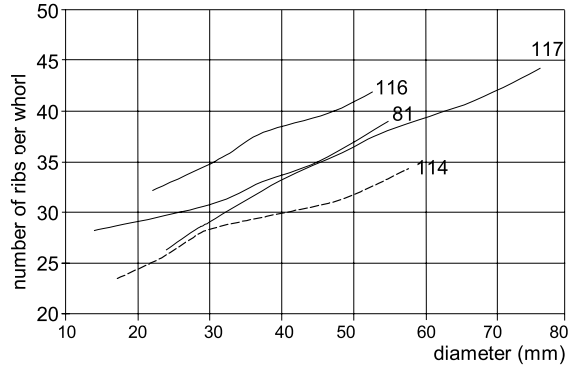

Fig. 15. Rib-density curves of *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov.; continuous lines are for the *ouatoides* morphotype, dashed line is for the *ouatius* morphotype; the specimens are numbered by only the last component of their full registration numbers

P. (*O.*) *ouatius ouatoides* chronossp. nov. differs from *P.* (*O.*) *ouatius ouatius* in enlargement of the body-chamber in width and height in its final part, in weakly evolute coiling appearing rarely on the inner whorls, and in lack of constrictions except for the apertural constriction.

Through distinct enlargement of the adult body-chamber and the appearance of parabolae. *P.* (*O.*) *ouatius ouatoides* chronossp. nov. resembles *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL. It overlaps in final size with the latter species (Text-fig. 5). *P.* (*O.*) *ouatius ouatoides* chronossp. nov. differs from *P.* (*O.*) *paturattensis* in moderately thick to thick ribbing, the lower number of ribs on the inner and middle whorls (Text-figs 13, 15), and the subquadrate whorl-section (Text-fig. 12) of the phragmocone and usually also of the body-chamber.

OCCURRENCE: Poland, and possibly France. *P.* (*O.*) *ouatius ouatoides* chronossp. nov. ranges from the bottom to the top of the Ouatius Subzone of the Plicatilis Zone. The *ouatius* morphotype of *P.* (*O.*) *ouatius ouatoides* chronossp. nov. is limited to the top of the stratigraphical range of the subspecies (Text-fig. 6); it ranges, however, higher, into the overlying Arkelli Subzone of the Plicatilis Zone, where it characterises, together with the *magnouatius* morphotype, *Perisphinctes* (*Otosphinctes*) *ouatius ouatius.*

Perisphinctes (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK, 2000
(Pl. 14, Figs 2-3; Text-figs 5, 12, 16)

1938. *Perisphinctes* (*Dichotomosphinctes*) *rotoides* RONCHADZÉ; ARKELL, p. 90, Text-fig. 23-3; Pl. 16, Figs 1a,b; 2a,b; 3a,b; 5; 7 (*V.*); ? Pl. 16, Figs 4a,b; 6a,b.
1966. *Perisphinctes* (*Dichotomosphinctes*) *rotoides* RONCHADZÉ; ENAY, p. 467 (*pars*), Text-figs 137-1, 137-2, 138-1; Pl. 27, Fig. 10 a-c.
1977. *Perisphinctes* (*Dichotomosphinctes*) *rotoides* RONCHADZÉ; BOURSEAU, p. 51, Text-fig. 20; Pl. 1, Fig. 6; Pl. 4, Figs 3, 8.
2000. *Perisphinctes* (*Otosphinctes*) *arkelli* sp. nov. GŁOWNIAK, p. 153 (*pars*), Text-fig. 10; Pl. 5, Figs 1 (holotype), 2, 3 only.

HOLOTYPE: IGPUW/A/36/96 (GŁOWNIAK 2000, Pl. 5, Fig. 1) from the lower Arkelli Subzone of the Plicatilis Zone of the Wysoka Quarry (Text-fig. 2, Appendix), section W.9", bed 12a.

PARATYPES: Eight lappeted specimens: IGPUW/A/36/92 (Pl. 14, Fig. 3), IGPUW/A/36/97 (Pl. 14,

Fig. 2), IGPUW/A/36/103 (GŁOWNIAK 2000, Pl. 5, Fig. 2), IGPUW/A/36/104, IGPUW/A/36/105, IGPUW/A/36/138 (GŁOWNIAK 2000, Pl. 5, Fig. 3), IGPUW/A/36/306, IGPUW/A/36/792. Six of them are complete; one specimen is broken and represented by half-whorls, the other one has a damaged phragmocone. Four specimens are crushed flat. They come from the Wysoka Quarry (Text-fig. 2), section W.4III, bed 2; W.5, bed 4b; W.8, bed 11 (three specimens); W.9", beds 12b and 16 (two specimens).

DERIVATION OF NAME: In honour of W. J. ARKELL, the eminent student of the Middle Oxfordian perisphinctids.

DIAGNOSIS: Microconchs. Shell robust, whorl-section of body-chamber oval, coiling evolute to moderately evolute. Ribs moderately thick to thick on inner whorls, thick on body-chamber. At the end of the body-chamber the ribs curve backwards on whorl-flanks and venter. Parabolae rare, zigzag pattern of ventral ribs common on body-chamber. Oblique ribs occur rarely on phragmocone. Adult body-chamber 5/8 or 3/4 of a whorl. Peristome constricted, provided with lappets.

DESCRIPTION: The holotype is a lappeted specimen, of $\underline{D}_m$=88 mm. The septa are not perfectly exposed and the end of the phragmocone is not discernible. A detailed description of the holotype is provided by GŁOWNIAK (2000). The paratypes are mature specimens. The phragmocones end at $\underline{D}_f$ from 45 mm to 60 mm; the body-chamber is 5/8 or 3/4 whorl-long. The specimens range in $\underline{D}_m$ from 72 mm to 95 mm (Text-fig. 5). 16% of the specimens of *P.* (*O.*) *arkelli arkelli* (accounted as a fraction of all the specimens of the latter and *P.* (*O.*) *ouatius ouatius* subspecies from the lower and middle Arkelli Subzone of the Plicatilis Zone) are of $\underline{D}_m$ from between 92 mm-97 mm; 10,5% are of $\underline{D}_m$ from between 72 mm-77 mm and from between 87 mm-92 mm, respectively; 5.3% are of $\underline{D}_m$ ranging in between 77 mm-82 mm and 82 mm-87 mm, respectively.

The whorl-section (Text-fig. 12) of the body-chamber is oval, with rounded venter and margins; the height of the body-chamber slightly exceeds its width. The inner whorls are subquadrate or subcircular. The coiling is evolute to moderately evolute throughout ontogeny. In the paratypes and in the holotype, at $\underline{D}_m$ ranging from 72 mm to 95 mm, $\overline{U/D}$=0.52 (OS=0.02), $\overline{W/D}$=0.26 (OS=0.01), and W_m/U_m ranges at these diameters from 0.46 to 0.54. The ribs on the phragmocone vary from moderately thick and moderately densely spaced to thick and distantly spaced. On the body-chamber they are thick; in all of the studied specimens they are distantly spaced. The ribs are slightly prorsiradiate on the whorl-flanks, except for near the final aperture, where they curve backwards. The ribs bifurcate. The secondary ribs pass straight across the venter or, near the final aperture, curve slightly backwards. The rib-number per whorl (Text-fig. 16) is 24-32 per whorl at 30 mm; it increases to 29-38 per whorl at D=50 mm, and then, to 41-43 at the final diameter $\underline{D}_m$ from 70 mm to 90 mm. The rib-density curves (Text-fig. 16) show noticeable variation in rib-number per whorl on the inner and middle whorls, and a relatively uniform rib-density on the outer whorl. Oblique ribs appear rarely on the inner whorls; parabolae occur rarely on the body-chamber and disappear a quarter of a whorl before the aperture. On the venter of the body-chamber the zigzag pattern of the ribs commonly appears. Constrictions are usually missing, except for the peristomal one.

DISCUSSION: *Perisphinctes* (*Otosphinctes*) *arkelli* GŁOWNIAK is divided in the present paper into two chrono-subspecies: *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK from the lower and middle Arkelli Subzone, and *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov., which ranges through the upper Arkelli Subzone. *P.* (*O.*) *arkelli arkelli* is less densely ribbed on the body-chamber and, rarely, also on the inner whorls. It has a more robust shell, and its adult stage of growth is marked by backward inflexion of the ventral ribs preceding the aperture, whereas in *P.* (*O.*) *arkelli wysokae* chronossp. nov. it is marked by a slightly forward sweep of the ventral ribs near the aperture. Moreover, *P.* (*O.*) *arkelli arkelli* possesses rare parabolae, absent in *P.* (*O.*) *arkelli wysokae* chronossp. nov., and a usually shorter body-chamber (5/8 to 3/4 of a whorl as compared to 3/4 of a whorl in the latter species). Both subspecies overlap in final size between 82 mm and 97 mm, however, *P.* (*O.*) *arkelli arkelli* is usually smaller, ranging in $\underline{D}_m$ between 72 mm and 82 mm (Text-fig. 5).

P. (*O.*) *arkelli arkelli* differs from *P.* (*O.*) *ouatius ouatius*, as interpreted herein, in the oval whorl-section, as compared to subquadrate, or, rarely, subcircular in the latter subspecies; the somewhat more evolute coiling on the outer whorl; and in the rare appearance of parabolae and/or oblique ribs, which are commoner in *P.* (*O.*) *ouatius ouatius*. Both forms overlap in final size in the range of diameters 72 mm-77 mm, *P.* (*O.*) *arkelli arkelli* is, however, usually larger than *P.* (*O.*) *ouatius ouatoides* chronossp. nov. and reaches $\underline{D}_m$ up to 97 mm (see Text-fig. 5). Both forms resemble each other in moderately thick to thick ribs, rib-density per whorl, and in body-chamber length.

OCCURRENCE: England and Poland. The chronosubspecies ranges from the bottom of the Arkelli Subzone of the Plicatilis Zone up to the Platysphinctes horizon of

the Arkelli Subzone, where it makes its last occurrence (Text-fig. 6).

Perisphinctes (*Otosphinctes*) *arkelli wysokae* chronossp. nov.
(Pl. 14, Figs 1, 4; Pl. 15, Figs 1-3; Text-figs 5, 12, 16)

1938. *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD; ARKELL, p. 83 (*pars*), Text-fig. 19 (3); Pl. 15, Fig. 5 only.
1966. *Perisphinctes* (*Dichotomosphinctes*) *rotoides* RONCHADZÉ; ENAY, pp. 467; 471 (*pars*), Text-fig. 137-5; Pl. 27, Fig. 11a,b only.
1976. *Perisphinctes* (*Dichotomosphinctes*) *rotoides* RONCHADZÉ; BROCHWICZ-LEWIŃSKI, Pl. 3, Fig. 2.
1981. *Perisphinctes* (*Dichotomosphinctes*) *rotoides* RONCHADZÉ-*transitional form to P.* (*D.*) *antecedens* SALFELD; BROCHWICZ-LEWIŃSKI, Pl. 4, Fig. 1a,b.
2000. *Perisphinctes* (*Otosphinctes*) *arkelli* sp. nov. GŁOWNIAK, p. 153 (*pars*), Text-fig. 10; Pl. 5, Fig. 4 only.

HOLOTYPE: IGPUW/A/36/140 (Pl. 14, Fig. 4) from the upper Arkelli Subzone of the Plicatilis Zone of the Wysoka Quarry (Text-fig. 2, Appendix), section W.9, bed 16 (a-b).

PARATYPES: Ten specimens: IGPUW/A/36/88, IGPUW/A/36/141 (Pl. 14, Fig. 1), IGPUW/A/36/142 (Pl. 15, Fig. 3), IGPUW/A/36/144 (GŁOWNIAK 2000, Pl. 5, Fig. 4), IGPUW/A/36/145, IGPUW/A/36/146 (Pl. 15, Fig. 1), IGPUW/A/36/147, IGPUW/A/36/304 (Pl. 15, Fig. 2), IGPUW/A/36/309, IGPUW/A/36/310, IGPUW/A/36/408. Except for IGPUW/A/36/304 (Pl. 15, Fig. 2), in which a quarter of a whorl of the body-chamber is broken away, all of the specimens are complete. Lappets are preserved in three specimens. The paratypes come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.5, beds 5b, 6a, 6b (two specimens), and 6c; W.5', bed 6b/7a; W.9, bed 16a, and from the Ogrodzieniec Quarry (Text-fig. 3, Appendix), sections O.2, bed 1d; O.4', bed 3. Two specimens assigned to *P.* (*O.*) cf. *arkelli wysokae* chronossp. nov. come from the Wysoka Quarry, section W.4, bed 12.

DERIVATION OF NAME: The name refers to the type locality of the chronosubspecies.

DIAGNOSIS: Microconchs. Shell moderately compressed, with subrectangular or oval whorl-section. Ribs moderately thick to thin, prorsiradiate on whorl-flanks. Ventral ribs almost as strong as primaries, marking a shallow forward sinus on body-chamber. Oblique ribs appear on inner whorls. Constrictions rare. Body-chamber 3/4 of a whorl. Peristome lappeted.

DESCRIPTION: The holotype is a complete, mature specimen, with $\underline{D}_m$=100 mm. The phragmocone is slightly crushed flat. It ends at $\underline{D}_f$=90 mm. The body-chamber is 3/4 of a whorl. The peristome is provided with lappets. The paratypes are mature individuals; their phragmocones end at $\underline{D}_f$ ranging from 52 mm to 76 mm; the body-chamber is 3/4 of a whorl. The peristomes are constricted and lappeted. In IGPUW/A/36/146 (Pl. 15, Fig. 1) the peristome is preceded by deep, flexuous constriction bordered by two swollen ribs, followed towards the aperture by three flexuous ribs. The last of these gives rise to an oblique, swollen rib immediately preceding the apertural constriction. The lappets are broken away in this specimen. The maturity of the paratypes is also indicated by the approximation of the last few ribs on the body-chamber.

The studied specimens range in $\underline{D}_m$ from 84 mm to 112 mm (Text-fig. 5). 25% of specimens of *P.* (*O.*) *arkelli wysokae* chronossp. nov. (accounted as a fraction of all the specimens of both *P.* (*O.*) *arkelli wysokae* chronossp. nov. and *P.* (*O.*) *ouatius ouatius* chronosubspecies from the upper Arkelli Subzone of the Plicatilis Zone) are of $\underline{D}_m$ from 97 mm to 107 mm; 17% of them are of $\underline{D}_m$ from 107 mm to 112 mm; 8.3% range in $\underline{D}_m$ from 82 mm to 87 mm and from 92 mm to 97 mm respectively. There are no specimens in the studied material of $\underline{D}_m$ from 87 mm to 92 mm.

The whorl-section of the holotype (Text-fig. 12) is compressed-suboval. In paratypes it is compressed, subrectangular or oval. The coiling is evolute to moderately evolute throughout ontogeny. In the holotype, at $\underline{D}_m$=100 mm, U_m/D_m=0.54, W_m/D_m=0.25, W_m/U_m=0.45. In the paratypes, at $\underline{D}_m$ ranging from 84 mm to 110 mm, $\overline{U/D}$=0.54 (OS=0.03), $\overline{W/D}$=0.25 (OS=0.02), and W_m/U_m ranges from 0.40 to 0.55. The ribs are moderately thick to thin and sharp, moderately densely to densely spaced on the whorl-flanks, slightly prorsiradiate. They bifurcate. The secondary ribs, almost as distinct as the primaries, form a shallow sinus towards the aperture on the body-chamber. The rib-number per whorl (Text-fig. 16) ranges from 31 to 40 at a diameter of c. 30 mm; it increases to 35-46 at D=50 mm, and to 45-53 per whorl at D=90 mm, and finally, to 47-55 per whorl at a diameter of c. 100 mm. Oblique ribs appear exclusively on the inner whorls, where they number 1-2 per whorl. Constrictions number 1-2 per whorl; they appear on the inner whorls, rarely on the outer whorl.

DISCUSSION: *P.* (*O.*) *arkelli wysokae* chronossp. nov. differs from *P.* (*O.*) *arkelli arkelli* GŁOWNIAK in the more compressed whorl-section, the appearance of thin-ribbed specimens, with sharp, densely spaced ribs on the

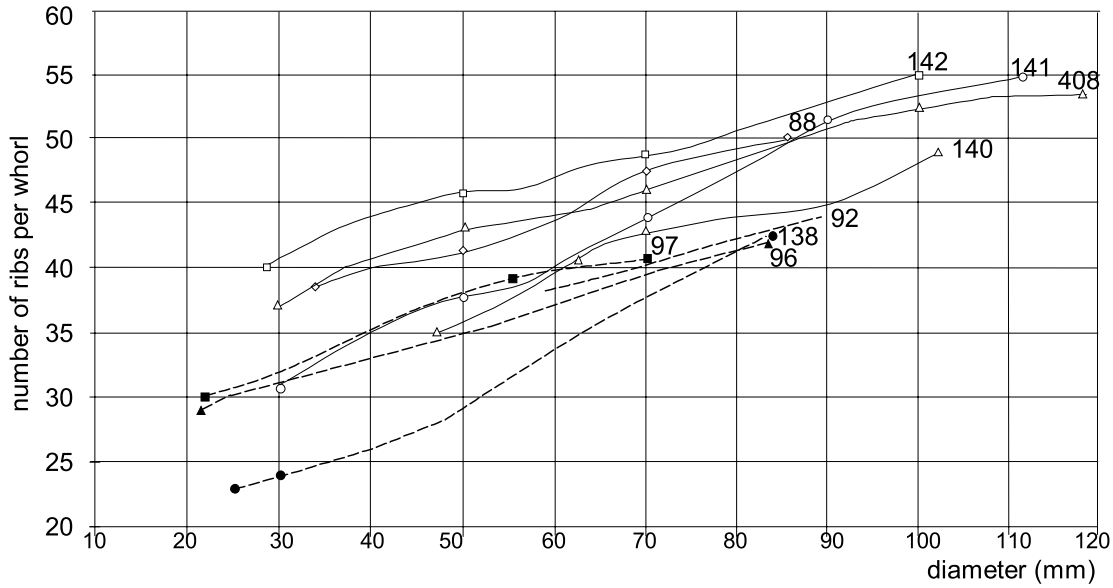

Fig. 16. Rib-density curves of *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK (dashed lines) and *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov. (continuous lines); the specimens are numbered by only the last component of their full registration numbers

whorl-flanks, the slightly forward sweep of the secondary ribs in the final part of the body-chamber, the lack of parabolae and in the larger final size (Text-fig. 5).

P. (*O.*) *arkelli wysokae* chronossp. nov. shows affinity to *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD. The two forms agree in the mode of coiling and whorl-section; they both show a shallow sinus towards the aperture on the venter, and they overlap in rib-density. The two forms differ in final size: *P.* (*O.*) *arkelli wysokae* chronossp. nov. ranges from 82 mm to 112 mm, and *P.* (*D.*) *antecedens* ranges from 112 mm to 162 mm (Text-fig. 5).

OCCURRENCE: Germany, France, and Poland. It appears in the Platysphinctes horizon in the upper Arkelli Subzone of the Plicatilis Zone, and disappears at the top of the subzone (Text-fig. 6).

Subgenus *Kranaosphinctes* BUCKMAN, 1921

TYPE SPECIES: *Kranaosphinctes kranaus* BUCKMAN, 1921. The holotype of type species is figured by BUCKMAN (1921, vol. 3, Pl. 243) and by ARKELL (1939, vol. 5, Pl. 38, Fig. 1a,d).

SYNONYMY: *Cymatosphinctes* BUCKMAN, 1923; *Arisphinctes* BUCKMAN, 1924. The type species of *Cymatosphinctes* BUCKMAN is *Perisphinctes* (*Cymatosphinctes*) *cymatophorus* (BUCKMAN, 1923), the holotype of which is figured by BUCKMAN (1923, vol. 5, Pl. 450) and by ARKELL (1935, vol. 1, Pl. A, Fig. 2; 1939, vol. 5, Text-fig. 56, Pl. 37, Fig. 5). The type species of *Arisphinctes* BUCKMAN, 1924 is *Perisphinctes* (*Arisphinctes*) *ariprepes* (BUCKMAN, 1924), the holotype of which is figured by BUCKMAN (1924, vol. 5, p. 33, Pl. dxi) and by ARKELL (1935, vol. 1, Pl. A, Fig. 4; 1939, vol. 5, Pl. 24, Fig. 5a,b). ARKELL (1939, vol. 5, p. 126) synonymised *Perisphinctes* (*Arisphinctes*) *ariprepes* (BUCKMAN, 1924) with *Perisphinctes cotovui* SIMIONESCU, 1907 and designated SIMIONESCU's species as the type species of the subgenus *Arisphinctes*. ARKELL's synonymy is not accepted herein.

EMENDED DIAGNOSIS: Macroconchs. Whorl-section subquadrate or subrectangular, rarely circular on phragmocone; on adult body-chamber subrectangular, compressed or depressed, rarely oval. Coiling evolute, rarely moderately evolute on inner whorls. Ribs thick to moderately thick, rarely thin, bifurcating. Secondary ribs associated with intercalatory ribs. Adult body-chamber with thick, not variocostate ribs on whorl-flanks, and with smooth or nearly smooth venter. Last ribs on body-chamber approximated on whorl-flanks; ventral ribs preceding aperture distinctly marked.

REMARKS: *Perisphinctes ariprepes* (BUCKMAN, 1924), designated by BUCKMAN (1924) as the type species of the subgenus *Arisphinctes* BUCKMAN, 1924, is assigned in the present paper to the subgenus *Kranaosphinctes* BUCKMAN, 1921. *Perisphinctes kranaus* (BUCKMAN, 1921), the type species of the subgenus *Kranaosphinctes*, and *P. ariprepes*

resemble each other in shell-morphology and ornamentation. The two forms display but minor differences, consisting mainly of the mode of rib-density changes. The separation of the two species, *P. ariprepes* and *P. kranaus*, between two subgenera, seems to be unjustified.

To the subgenus *Kranaosphinctes*, as interpreted in the present paper, are assigned the "English" species (see MELÉNDEZ 1989 p. 210) representing the typical Submediterranean forms described originally by BUCKMAN (1921, 1924), ARKELL (1939), and BROCHWICZ-LEWIŃSKI (1979); and also BUKOWSKI's (1887) species of Mediterranean affinity, recognised herein as the direct predecessors of the species previously mentioned (see chapter on phylogeny, p. 311). NEUMANN's (1907) species of Mediterranean affinity (BROCHWICZ-LEWIŃSKI 1973, BROCHWICZ-LEWIŃSKI & RÓŻAK 1975a), broadly referable to the Submediterranean subgenus *Kranaosphinctes* (ENAY 1966; BROCHWICZ-LEWIŃSKI 1973, 1979; BROCHWICZ-LEWIŃSKI & RÓŻAK 1975a; MELÉNDEZ 1989), are assigned in the present paper to a new genus, *Neumannia* gen. nov. (see p. 354). The Indian forms, that are morphologically close to *Kranaosphinctes*, viz. *Pachyplanulites* SPATH, 1930 and *Germanosphinctes* ARKELL, 1935, and both synonymised by ARKELL (1939, vol. 5, p. lx-lxii) with *Kranaosphinctes*, are excluded from the synonymy of this subgenus.

Kranaosphinctes, as interpreted here, represents macroconch counterparts of the species of the subgenus *Otosphinctes* BUCKMAN, with which it is limited stratigraphically to the upper Cordatum Zone of the Lower Oxfordian and the Plicatilis Zone of the Middle Oxfordian.

ONTOGENETIC ORNAMENTATION TYPES: The shell ornamentation of the subgenus *Kranaosphinctes*, as interpreted in the present paper, consists of bifurcating ribs. Throughout shell ontogeny the secondary ribs become associated with intercalatory ribs on the venter, the ventral ribs become indistinct, whereas the ribs on the whorl-flanks remain distinct and thicken as the shell-diameter increases. The following types of ornamentation are distinguished:

Type Ia: the secondary ribs, usually somewhat less distinct than the primary ribs, may be occasionally associated on the venter with an intercalatory rib.

Type Ib: the intercalatory ribs appear regularly on the venter; every pair of the secondary ribs is associated with one intercalatory rib. Here and there a free-ending intercalatory rib may curve inwards at its extremity, thereby tending to give an impression of trifurcation, which in fact does not appear in any of the species studied. The ventral ribs become indistinct.

Type Ic: every pair of secondary ribs becomes associated with two intercalatory ribs. The primary ribs strengthen all along the whorl-flanks. The ribs on the venter are faint and indistinct.

Type II: the primary ribs become thick and distant on the whorl-flanks; they are distinct all along the whorl-flank, and they disappear entirely above the ventro-lateral margin; the venter is smooth.

In the species *P.* (*K.*) *promiscuus* BUKOWSKI, *P.* (*K.*) *collignoni* (BROCHWICZ-LEWIŃSKI) and *P.* (*K.*) *decurrens* (BUCKMAN) type Ia ornamentation appears on the whorls of the phragmocone and is succeeded on the adult body-chamber by type Ib ornamentation, which is the final shell-ornamentation in these species. In the species *P.* (*K.*) *kranaus*, *P.* (*K.*) *ariprepes* and *P.* (*K.*) *vorda* ARKELL types Ia and Ib ornamentation appear successively on the whorls of the phragmocone, in *P.* (*K.*) *kranaus* they are succeeded by type Ic ornamentation. Type II ornamentation appears in these species on the last whorl of the phragmocone and continues on the adult body-chamber or, in *P.* (*K.*) *vorda*, it appears only on the body-chamber.

PHYLOGENETIC CHANGES OF ORNAMENTATION: The approximate ranges of shell-diameter in which the particular ornamentation types start to appear do not differ significantly between the species which overlap stratigraphically and, therefore, they alone do not distinguish them. The ranges of diameters show, however, a progressive shift towards larger diameters in the species from successive stratigraphical horizons. Hence, the diameter at which the ornamentation types appear are considered in the discussion on the evolution of this subgenus (see p. 311).

THE SEPTAL SUTURE: In *P.* (*K.*) *kranaus* and in *P.* (*K.*) *ariprepes*, on their middle and outer whorls, the suspensive, external and lateral lobes are of different length. The longest is the suspensive lobe and the shortest is the lateral lobe (N>EL>L). This formula of septal suture is the one on which BUCKMAN (1921) founded the subgenus *Kranaosphinctes*. In full-grown individuals of *P.* (*K.*) *kranaus* from the studied collection, after a diameter of 260 mm the umbilical lobe shortens, and at 290 mm it becomes approximately as long as the external lobe (EL≈N>L). Later in ontogeny, the umbilical and the external lobes shorten, and finally, at 390 mm diameter, all three lobes are of equal length (EL≈N≈L). At about this diameter the septa become approximated, indicating that the specimen is full-grown.

The septal suture of formula N>EL>L recognized in both *P.* (*K.*) *kranaus* and *P.* (*K.*) *ariprepes* demonstrates that BUCKMAN's (1921, 1924) idea that these two species could be discriminated by means of their sutures, is not justified. The septal suture of formula N>EL>L appears also in some species of the genus *Neumannia* gen. nov.

and in a few specimens of *Perisphinctes trifidus* (SOWERBY) (m, M) (see p. 326).

Perisphinctes (*Kranaosphinctes*) *promiscuus* BUKOWSKI, 1887
(Pl. 1 Figs 1-2; Pl. 3, Fig. 3; Text-figs 17-18)

1887. *Perisphinctes promiscuus* n.f.; BUKOWSKI, p. 137 (*pars*), Pl. 29, Fig. 1 (lectotype, *V.*), ? Fig. 2, *non* Pl. 28, Fig. 1 (*V.*).
1977. *Perisphinctes* (*Kranaosphinctes*) *cyrilli* NEUMANN, 1907; MATYJA, p. 50, Text-fig. 6; Pl. 7, Fig. 6.
1998. *Perisphinctes* (*Kranaosphinctes*) aff. *cyrilli* NEUMANN, 1907; GYGI, p. 10 (*pars*), Pl. 13, Fig. 4, only, *non* Pl. 10, Fig. 1.

MATERIAL: Three incomplete specimens, two of them are crushed flat on the phragmocones. Additionally, a loose fragment of the body-chamber, and an incomplete phragmocone, classified as *P.* (*K.*) cf. *promiscuus*.

The material comes from the Wysoka Quarry (Text-fig. 2, Appendix), section W.6, beds 27a, 28b, 28c. The specimens of *P.* (*K.*) cf. *promiscuus* comes from section W.4, bed 18.

DESCRIPTION: IGPUW/A/36/281 shows a crushed, incomplete phragmocone of $*D_f$=85 mm and a cast of the 1/3 of a whorl, incomplete body-chamber. The body-chamber ends at $*D_m$ c. 150 mm. IGPUW/A/36/282 (Pl. 1, Fig. 2) is of $*D_m$=148 mm; the phragmocone is up to D_f=95 mm; the body-chamber is 3/4 of a whorl, incomplete. These two incomplete specimens are probably mature, and their final sizes are probably not far from their actual maximum diameters. IGPUW/A/36/288 is a juvenile specimen, of $*D_m$=75 mm; the phragmocone is of D_f=65 mm; the body-chamber is 1/4 of a whorl, incomplete. IGPUW/A/36/373 (Pl. 3, Fig. 3) is a half-whorl fragment of the adult body-chamber.

The whorl-section of the phragmocone and of the juvenile body-chamber is circular. The whorl-section of the adult body-chamber is not known due to the poor state of preservation. The coiling is evolute, except for the inner whorls, up to diameters between 60 mm and 70 mm, which are moderately evolute to evolute. At diameters between 90 mm and 100 mm U/D ranges from 0.50 to 0.54, W/D is 0.27 and W/U ranges from 0.48 to 0.50; coiling at this diameter is evolute. The ribs are thin, densely spaced on the whorl-flanks,

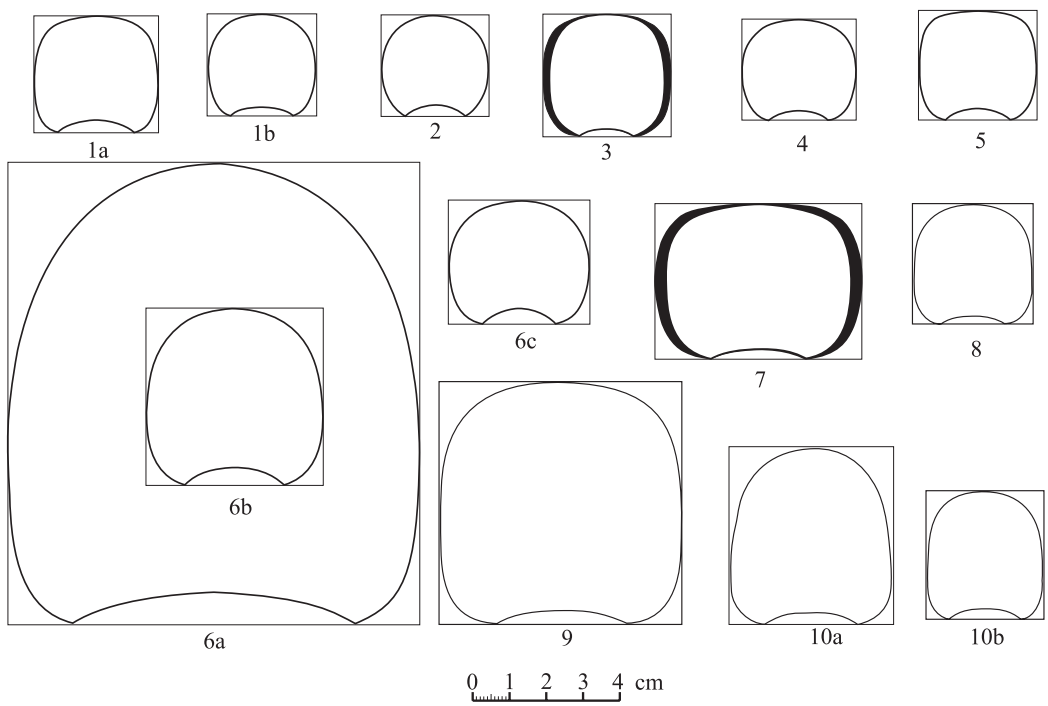

Fig. 17. Whorl-section of the subgenus *Kranaosphinctes* BUCKMAN, at a given diameter; *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI): 1. IGPUW/A/36/260, a: D=130 mm, b: D=110 mm; 2. IGPUW/A/36/263 (Pl. 2, Fig. 2), D=102 mm. *Perisphinctes* (*Kranaosphinctes*) *decurrens* (BUCKMAN): 3. IGPUW/A/36/273 (Pl. 3, Fig. 2), D=140 mm. *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN): 4. IGPUW/A/36/251 (Pl. 5, Fig. 2), D=130 mm; 5. IGPUW/A/36/212 (Pl. 4, Fig. 3), D=150 mm; 6. IGPUW/A/36/219 (Pl. 6, Fig. 4), a: $\underline{D_m}$=510 mm, b: D=220 mm, c: D=130 mm; 7. IGPUW/A/36/205, D=200 mm. *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN): 8. IGPUW/A/36/233, D=135 mm; 9. IGPUW/A/36/202 (Pl. 13, Fig. 1), D=295 mm. *Perisphinctes* (*Kranaosphinctes*) *vorda* ARKELL: 10. IGPUW/A/36/275 (Pl. 13, Fig. 3), a: D=211 mm, b: D=150 mm

bifurcating. Type Ia ornamentation (see ontogenetic ornamentation types, p. 336) appears on the phragmocone up to a diameter of c. 90 mm in IGPUW/A/282 (Pl. 1, Fig. 2). After this diameter type Ib appears on the body-chamber. The ribs are moderately thick and distant on the whorl-flanks and blunt on the venter. Although the specimens show no unequivocal characters indicating cessation of growth, the thick and distantly spaced ribs appearing on the body chamber indicate that they probably represent mature individuals. Type Ib then represents the ornamentation of the adult stage of growth in *P. promiscuus*. The rib-number increases from 40-45 at 20 mm-30 mm diameter, to 45-48 per whorl at c. 50 mm in IGPUW/A/36/281 and IGPUW/A/36/ 288 (Text-fig. 18); then it remains constant or decreases insignificantly up to 90 mm in these specimens. At diameters greater than c. 90 mm, corresponding to the appearance of type Ib ornamentation, the rib-number diminishes noticeably. It decreases to c. 30 ribs per whorl in IGPUW/A/36/281 at 150 mm and to 46 ribs per whorl in IGPUW/A/36/282 at this diameter.

Parabolic ribs, numbering 1-2 per whorl, and parabo lic nodes appear on the inner whorls of the phragmocone.

DISCUSSION: NEUMANN (1907, p. 37) assumed that the three syntypes of *Perisphinctes* (*Kranaosphinctes*) *promiscuus* (see BUKOWSKI 1887, Pl. 28, Fig. 1, Pl. 29, Figs 1, 2) differed at specific level. As lectotype of the species *P.* (*K.*) *promiscuus*, NEUMANN (1907) designated the smaller syntype of BUKOWSKI (1887, Pl. 29, Fig. 1). One of the larger syntypes of BUKOWSKI (1887, Pl. 28, Fig. 1) he compared to the holotype of *Neumannia gyrus* (NEUMANN, 1907) (see NEUMANN 1907, Pl. 3, Fig. 11a,b), and this syntype is synonymised in the present paper with the species *N. gyrus* (see the discussion on the latter species, p. 358 and also on *P.* (*K.*) *collignoni,* p. 339).

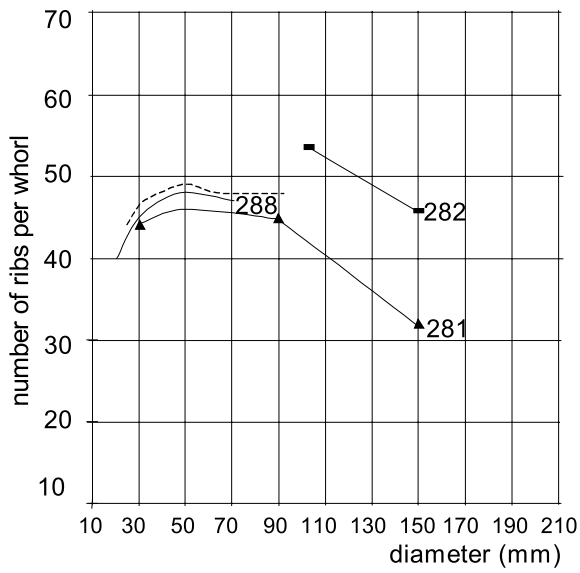

Fig. 18. Rib-density curves of *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI compared with the rib-density curve of the lectotype of *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI (dashed line); the specimens are numbered by only the last component of their full registration numbers

The specimens from the Lower Oxfordian of the Holy Cross Mountains assigned by MATYJA (1977, Pl. 7, Fig. 6) to the Middle Oxfordian species *Neumannia cyrilli* (NEUMANN, 1907), and the Lower Oxfordian specimens from Herznach in the Swiss Jura assigned by GYGI (1988, Pl. 13, Fig. 4) to *Neumannia* aff. *cyrilli*, are put into the synonymy of *P.* (*K.*) *promiscuus*. Both specimens agree with BUKOWSKI's species in thin, dense ribbing on the inner whorls, the evolute coiling, the presence of parabolae and in the reduction of the rib-number per whorl at diameter greater than c. 90 mm (Text-fig. 18). Their rib-curves are markedly convex and almost symmetrical. In *N. cyrilli*, to which MATYJA's and GYGI's specimens from the Lower Oxfordian were originally assigned, the rib-number per whorl (Text-fig. 30) decreases slowly at diameters greater than c. 130 mm, and the rib-density curves are smoothly convex or flattened and asymmetrical.

The ornamentation of *P.* (*K.*) *promiscuus*, especially its fine and dense ribbing of the inner whorls, evolute coiling, and the reduction of the rib-number per whorl by c. 100 mm diameter, indicates its affinity to the Mediterranean ammonites. It strongly resembles the specimens described from southern Europe: *Perisphinctes* (*Kranaosphinctes*) sp. ind. of SAPUNOV (1976, Pl. 2, Fig. 2a,b) and *Nebrodites* (*Passendorferia*) sp. of BROCHWICZ-LEWIŃSKI & RÓŻAK (1976, Pl. 36, Fig. 1a, b) from the Oxfordian of Bulgaria, as well as *P.* (*Kranaosphinctes*) cf. *decurrens* (BUCKMAN) (MELÉNDEZ 1989, p. 217, Pl. 21, Fig. 2) from Spain.

P. (*K.*) *promiscuus* differs from *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI) in thinner ribbing, smaller adult size, and in the smaller diameter at which type Ib ornamentation appears (for details see discussion on *P.* (*K.*) *collignoni,* p. 339). The two species, however, have the same circular whorl-section, and resemble each other in a general outline.

OCCURRENCE: Poland, Switzerland, ?Bulgaria, ?Spain. The species appears in the upper part of the Cordatum Zone of the Lower Oxfordian and ranges up to the Paturattensis Subzone of the Plicatilis Zone of the Middle Oxfordian (Text-fig. 6).

Perisphinctes (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI, 1979)
(Pl. 2, Figs 2-3; Text-figs 17, 19)

1975b. "*Kranaosphinctes* of the *K. promiscuus group*"; BROCHWICZ-LEWIŃSKI & RÓŻAK, Pl. 4, Fig. 2 (holotype of *Kranaosphinctes collignoni* BROCHWICZ-LEWIŃSKI, 1979, *V.*).

1979. *Kranaosphinctes collignoni* sp. nov.; BROCHWICZ-LEWIŃSKI, p. 168 (*pars*), Text-fig. 1 only, *non* Pl. 1 [*V.*, *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN)], *non* Pl. 2 [*V.*, *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN)].

MATERIAL: Three specimens, one with complete body-chamber, all from the Wysoka Quarry (Text-fig. 2, Appendix), section W.4III, bed 21; section W.4, bed 18; and section W.9", bed 8.6.

DESCRIPTION: IGPUW/A/36/794 (Pl. 2, Fig. 3) is a complete specimen of $\underline{D}_m$=193 mm. The phragmocone ends at $\underline{D}_f$=112 mm; the body-chamber is one whorl long; the peristome is constricted and associated with a swollen rib. The specimen represents a mature individual, as indicated by the approximation of ribs on the last quarter of the body-chamber, and by the changes of the whorl-section in the final part of the body-chamber, into compressed-oval. IGPUW/A/36/260 is an incomplete, possibly mature specimen of $*D_m$=180 mm; the phragmocone is of D_f=117 mm, it is somewhat crushed; the body-chamber is 3/4 of a whorl, incomplete. IGPUW/A/36/263 (Pl. 2, Fig. 2) is an incomplete, juvenile specimen of $*D_m$=100 mm; the phragmocone is of D_f=80 mm; the preserved body-chamber is half a whorl, and ends at a fracture.

The whorl section is circular or subquadrate on the phragmocone (Text-fig. 17). On the body-chamber it is circular, and in the final part it changes to compressed-oval (IGPUW/A/36/794, Pl. 2, Fig. 3), which suggests that this specimen is mature. The coiling is evolute, except for inner whorls up to a diameter of c. 60 mm, where it is evolute to moderately evolute. At D=60 mm U/D ranges from 0.50 to 0,53, W/D ranges from 0.23 to 0.28, and W/U ranges from 0.47 to 0.57; the coiling is evolute to moderately evolute. At $\underline{D}_m$=193 mm in IGPUW/A/36/794 (Pl. 2, Fig. 3) U/D=0.52, W/D=0.26, W/U=0.49; the coiling is evolute. The ribs are moderately thin, fairly densely spaced on the whorl flanks. They bifurcate. Type Ia ornamentation (see ontogenetic ornamentation types, p. 336) appears on the phragmocone, up to c. 110 mm-120 mm. After this diameter type Ib ornamentation appears on the adult body-chamber. In IGPUW/A/36/794 (Pl. 2, Fig. 3), the ventral ribs become weak and faint on the second half of the body-chamber and, finally, fade away almost entirely. The rib-number per whorl (Text-fig. 19) increases from 40 at 30 mm diameter, to a maximum 60 ribs per whorl between 110 mm and 120 mm. Beyond these diameters, corresponding approximately to the appearance of type Ib ornamentation, the rib number per whorl decreases, and reaches 46 per whorl at 180 mm diameter in IGPUW/A/36/794 (Pl. 2, Fig. 3). In the latter specimen the last ribs are approximated, which indicates its maturity. The rib-curves of the study specimens are approximately symmetrical, and have steeply inclined flanks.

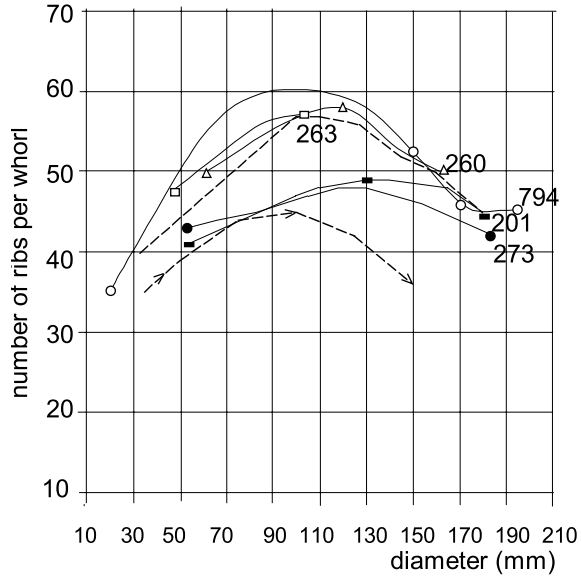

Fig. 19. Rib-density curves of *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI) (lines with white symbols) and *Perisphinctes* (*Kranaosphinctes*) *decurrens* (BUCKMAN) (lines with black symbols) compared with the rib-density curve of the holotype of *P.* (*K.*) *collignoni* (dashed line) and the type specimen of *P.* (*K.*) *decurrens* (dashed line with arrows); the specimens are numbered by only the last component of their full registration numbers

Parabolae appear occasionally on the inner whorls.

DISCUSSION: The specimen of *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI) figured by BROCHWICZ-LEWIŃSKI & RÓŻAK (1975, Pl. 4, Fig. 2) is the holotype of BROCHWICZ-LEWIŃSKI's species. The two other specimens of *P.* (*K.*) *collignoni* figured by BROCHWICZ-LEWIŃSKI (1979, Pls. 1, 2) differ from the holotype of the species in the whorl-section, rib-thickness, and in the mode of rib-density changes; they are not conspecific in the opinion of the present author. One of these specimens (BROCHWICZ-LEWIŃSKI 1979, Pl. 1) is assigned here to the species *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN) (see the discussion,

p. 345), and the other (BROCHWICZ-LEWIŃSKI 1979, Pl. 2) is assigned to *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN) (see the discussion, p. 343).

BROCHWICZ-LEWIŃSKI (1979) synonymised with *P.* (*K.*) *collignoni* the syntype of *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI figured by BUKOWSKI (1887, Pl. 28, Fig. 1). The latter specimen, however, is a larger form: at its maximum diameter of 170 mm, is still not a full-grown individual, whereas the full grown specimens of *P.* (*K.*) *collignoni*, the holotype (BROCHWICZ-LEWIŃSKI & RÓŻAK 1975b, Pl. 4, Fig. 2) and IGPUW/A/36/794 (Pl. 2, Fig. 3), are of $\underline{D}_m$=218 mm and $\underline{D}_m$=193 mm respectively. The syntype of *P.* (*K.*) *promiscuus* (BUKOWSKI 1887, Pl. 28, Fig. 1) is synonymised in the present paper with *Neumannia gyrus* (NEUMANN, 1907).

P. (*K.*) *collignoni* resembles *P.* (*K.*) *promiscuus* in circular whorl-section, dense ribbing on the inner whorls, ornamentation of the adult body-chamber corresponding to type Ib, and in the mode of rib-density changes, which is characterised in both species by reduction of the rib-number per whorl at diameters corresponding to the appearance of type Ib ornamentation. *P.* (*K.*) *collignoni* differs from *P.* (*K.*) *promiscuus* in its larger final size: in the former species $\underline{D}_m$ ranges from 193 mm to 218 mm, whereas in the latter species it is approximately 150 mm. In *P.* (*K.*) *collignoni* the rib-number per whorl start to decrease at larger diameters, c. 120 mm-130 mm, whereas in *P.* (*K.*) *promiscuus* at c. 100 mm.

Similar characters of ribbing and mode of rib-density changes to those in *P.* (*K.*) *collignoni* also appear in *Perisphinctes* (*Kranaosphinctes*) *decurrens* (BUCKMAN). In the latter species, however, the ribs are thicker and less densely spaced on the inner and middle whorls than in *P.* (*K.*) *collignoni.* Additionally, in *P.* (*K.*) *decurrens* the rib-number decreases at diameters greater than 130 mm-140 mm as compared to 120 mm-130 mm in *P.* (*K.*) *collignoni.*

OCCURRENCE: Poland. It ranges through the upper Paturattensis Subzone and the lower Ouatius Subzone of the Plicatilis Zone.

Perisphinctes (*Kranaosphinctes*) *decurrens* (BUCKMAN, 1923)
(Pl. 3, Fig. 2; Text-figs 17, 19)

1923. *Kranaosphinctes decurrens* sp. nov.; BUCKMAN, Pl. 449 (*V.*).
1939. *Perisphinctes* (*Kranaosphinctes*) *decurrens* BUCKMAN; ARKELL, p. 175; Text-figs 61, 62; Pl. 38, Fig. 4 (*V.*); Pl. 39, Fig. 5a, b (holotype, *V.*); Pl. 39, Figs 1-4 (*V.*).
1939. *Perisphinctes* (*Kranaosphinctes*) aff. *decurrens* BUCKMAN; ARKELL, p. 175; Pl. 39, Fig. 6a, b (*V.*).

MATERIAL: Two complete specimens; one is crushed flat, the other has crushed flat phragmocone. Both are from the Wysoka Quarry (Text-fig. 2, Appendix), section W.4III, bed 5; section W.4, bed 16.

DESCRIPTION: IGPUW/A/36/273 (Pl. 3, Fig. 2) is a complete, possibly mature specimen of $\underline{D}_m$=185 mm. The phragmocone ends at $\underline{D}_f$=130 mm, the septa are imperfectly exposed. The body-chamber is nearly one whorl. The aperture is constricted and associated with an oblique rib. The body-chamber possesses 5 constrictions, including the apertural one; they appear every quarter of a whorl. The number of constrictions suggests that the specimen is full-grown. IGPUW/A/36/201 is a specimen of D_m=180 mm; the suture is not exposed, and the beginning of the body-chamber cannot be recognised.

The body-chamber whorl-section is subquadrate and it changes in the final part of the whorl to oval in IGPUW/A/36/273 (Text-fig. 17). The phragmocone is crushed flat. The coiling is evolute, except for the inner whorls of IGPUW/A/36/201, which are moderately evolute. At a diameter of 60 mm U/D ranges between 0.50-0.52, W/D ranges between 0.25-0.27, and W/U ranges between 0.48-0.53; the coiling is evolute to moderately evolute. At a diameters between 165 mm and 175 mm U/D ranges between 0.55-0.59, W/D ranges between 0.23-0.24, W/U ranges between 0.39-0.43; the coiling is evolute. The ribs are moderately thick, and moderately densely spaced on the whorl-flanks; they bifurcate. Type Ib ornamentation appears on the body-chamber after 130 mm-140 mm diameter. The ventral ribs become less distinct on the second half of the body-chamber, they remain, however, distinguishable to the aperture. The rib-number (Text-fig. 19) increases slowly, from 40 per whorl at c. 50 mm diameter, to a maximum 49 ribs per whorl at 130 mm-140 mm. After these diameters, corresponding to the appearance of type Ib ornamentation, the rib number reduces to 42-45 ribs per whorl at c. 180 mm. Constrictions number 1-2 on the phragmocone, and 5 on the body-chamber in the specimen IGPUW/A/36/273 (Pl. 3, Fig. 2).

DISCUSSION: *P.* (*K.*) *decurrens* differs from *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN) in the mode of rib-number changes: in *P.* (*K.*) *decurrens* the rib-number per whorl reduces noticeably after c. 130 mm-140 mm diameter, at which type Ib ornamentation appears, whereas in *P.* (*K.*) *kranaus* the rib-number per whorl remains approximately constant, or decreases but slightly in the range of diameters corresponding to the appearance of type Ib ornamentation, and decreases noticeably at diameters greater than 190 mm-210 mm, corresponding to the appearance of type Ic. *P.* (*K.*)

decurrens is smaller than *P.* (*K.*) *kranaus*: the mature individual of *P.* (*K.*) *decurrens* has $\underline{D}_m$=185 mm, and of *P.* (*K.*) *kranaus* has $\underline{D}_m$=510 mm.

P. (*K.*) *decurrens* differs from *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ–LEWIŃSKI) in the subquadrate whorl-section, thicker and more distant ribs, and in the reduction of the rib-number per whorl at larger diameters (see also the discussion, p. 339).

OCCURRENCE: Poland, England. It occurs in the beds of unprecised stratigraphical position, representing the topmost Ouatius Subzone or lower Arkelli Subzone of the Plicatilis Zone and ranges through the lower Arkelli Subzone (Text-fig. 6).

Perisphinctes (*Kranaosphinctes*) *vorda* ARKELL, 1939
(Pl. 13, Fig. 3; Text-figs 17, 20)

1939. *Perisphinctes* (*Arisphinctes*) *vorda* sp. nov.; ARKELL, p. 154, Text-figs 49-51; Pl. 32, Figs 1 (*V.*), 2 a, b (holotype, *V.*), 3 (*V.*), 4 (*V.*), Pl. 34, Figs 1 (*V.*), 2 (*V.*) (with synonymy).
1953. *Perisphinctes* (*Arisphinctes*) *vorda* ARKELL; CALLOMON, p. 84 (*pars*), the specimen from the Shell Pebble Bed, only (*V.*).

MATERIAL: One incomplete specimen from the Wysoka Quarry (Text-fig. 2, Appendix), section W.4, bed 17 (a-c).

DESCRIPTION: IGPUW/A/36/275 (Pl. 13, Fig. 3) is probably a mature individual of *D_m=211 mm; the body-chamber starts at $\underline{D}_f$=165 mm and it is half-whorl long, but incomplete. The septa are imperfectly exposed.

The whorl-section is subrectangular on the phragmocone and oval on the body-chamber (Text-fig. 17). The coiling is evolute throughout ontogeny. With growth the umbilicus widens somewhat, and the whorl height decreases slightly. Between 100 mm and 200 mm diameter U/D increase from 0.50 to 0.59, W/D decrease from 0.25 to 0.23, and W/U decrease from 0.50 to 0.38. The ribs are moderately thick; they are almost rectiradiate on the whorl-flanks of the phragmocone, and somewhat prorsiradiate on the body-chamber. At 135 mm diameter, when the venter of the phragmocone appears for the first time, the ornamentation corresponds to type Ib (see otogenetic ornamentation types, p. 336). Type II ornamentation appears on the body-chamber at 180 mm, after a constriction. The rib-number per whorl (Text-fig. 20) increases from 28 to 52 between diameters of 30 mm and 130 mm; then it remains approximately constant up to 170 mm, and subsequently decreases to 48 ribs per whorl at 210 mm diameter. The constrictions number 2-3 per whorl on the phragmocone, and 2 on the half-whorl of the body-chamber. The septal suture is not recognised.

DISCUSSION: *P.* (*K.*) *vorda* resembles *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN) in the mode of the rib-number changes: the rib-number per whorl decreases in these two species at relatively large diameters, corresponding to the appearance of type II ornamentation. In *P.* (*K.*) *vorda* the whorl-section of the body-chamber, however, is oval, whereas in *P.* (*K.*) *ariprepes* it is subquadrate.

OCCURRENCE: England, Poland. The Ouatius Subzone of the Plicatilis Zone (Text-fig. 6).

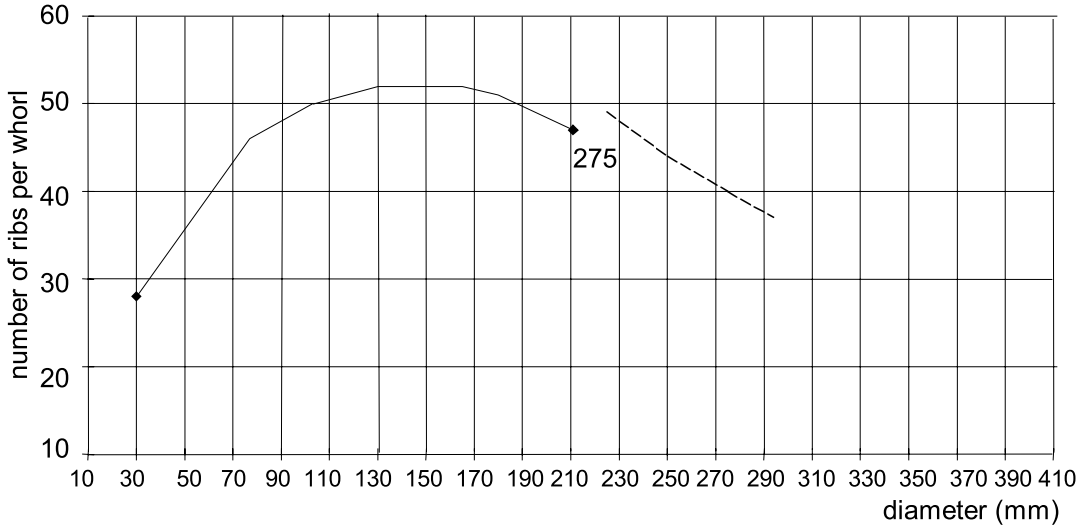

Fig. 20. Rib-density curve of *Perisphinctes* (*Kranaosphinctes*) *vorda* ARKELL (continuous line) compared to the holotype of *P.* (*K.*) *vorda* ARKELL (dashed line); the specimen is numbered by only the last component of its full registration number

Perisphinctes (*Kranaosphinctes*) *kranaus* (BUCKMAN, 1921)
(Pl. 4, Fig. 3; Pl. 5, Figs 1-2; Pl. 6, Fig. 4; Text-figs 17, 21)

1921. *Kranaosphinctes kranaus* nov.; BUCKMAN, Pl. 243 A, B (holotype, *V.*).
1923. *Cymatosphinctes cymatophorus* nov.; BUCKMAN, Pl. 450 A, B (holotype, *V.*).
1935. *Perisphinctes* (*Cymatosphinctes*) *cymatophorus* BUCKMAN; ARKELL, p. xii; Pl. A, Fig. 2 (holotype).
1939. *Perisphinctes* (*Kranaosphinctes*) *cymatophorus* (BUCKMAN); ARKELL, p. 168, Text-figs 55-60; Pl. 37, Figs 1-5 (*V.*).
1939. *Perisphinctes* (*Kranaosphinctes*) *kranaus* BUCKMAN; ARKELL, p. 174 (*pars*), Text-fig. 61; Pl. 38, Fig. 1a-d (holotype, *V.*) only, *non* Pl. 38, Fig. 2a,b (*V.*, =*P.* (*Kranaosphinctes*) sp.).
1979. *Kranaosphinctes collignoni* sp. nov.; BROCHWICZ-LEWIŃSKI, p. 168 (*pars*), Text-figs 1, 2; Pl. 2 only (*V.*).
1982. *Kranaosphinctes kranaus* BUCKMAN; MELÉNDEZ, SEQUEIROS, BROCHWICZ-LEWIŃSKI, p. 176, Pl. 6.
1989. *Kranaosphinctes kranaus* BUCKMAN; MELÉNDEZ, p. 214, Text-fig. 43, Pl. 21; Fig. 1a,b.

MATERIAL: Nine specimens, variably preserved, some crushed flat on the phragmocone; one specimen with a complete, adult body-chamber. Two whorl fragments assigned to *P.* (*K.*) cf. *kranaus.* All specimens come from the Wysoka Quarry (Text-fig. 2, Appendix), sections W.4, beds 16, 17c; W.4III, beds 3, 4; W.5, bed 3, and one specimen collected loose from beds 1-3; W. 8, bed 6 (the specimen of *P.* (*K.*) cf. *kranaus*); W.9', bed 8.2a (the specimen of *P.* (*K.*) cf. *kranaus*) and bed 8.2c; W.9", bed 16.

DESCRIPTION: IGPUW/A/36/219 (Pl. 6, Fig. 4) is a mature individual of $\underline{D}_m$=510 mm; the phragmocone ends at $\underline{D}_f$=410, and the last septa are approximated. The body-chamber occupies half a whorl, and is complete. The peristome is damaged. The specimen is full-grown, as indicated by approximation of the last few ribs, by the ventral ribs becoming prominent near the aperture and forming a sinus convex forward, and by changes of whorl-section in the final part of the body-chamber to compressed-oval. IGPUW/A/36/203 (Pl. 5, Fig. 1), IGPUW/A/36/205, and IGPUW/A/36/212 (Pl. 4, Fig. 3) are incomplete, late juvenile or mature individuals of $*D_m$ ranging from 215 mm to 300 mm. IGPUW/A/36/212 (Pl. 4, Fig. 3) is an incomplete phragmocone of $*D_m$=300 mm; in the other two specimens the body-chamber starts at D_f 140 mm and 200 mm respectively, it occupies 5/8 of a whorl but is incomplete. Other specimens are middle to late juveniles; they range in D_m from 123 mm to 190 mm; the phragmocones end at D_f from 80 mm to 130 mm. The body-chamber, when complete, is one whorl long.

The whorl-section (Text-fig. 17) is circular or subquadrate on the middle whorls of the phragmocone. On the outer whorl of the phragmocone and on the body-chamber it remains subquadrate or occasionally changes to depressed-subrectangular or to oval. Near the aperture, in a full-grown specimen IGPUW/A/36/219 (Pl. 6, Fig. 4), the whorl-section changes to compressed-oval, and the venter becomes narrow and convex (Text-fig. 17). The coiling is evolute, except for the inner whorls where it is occasionally moderately evolute. At D=60 mm $\overline{U/D}$=0.60 (OS=0.02), $\overline{W/D}$=0.25 (OS=0.03), W/U varies from 0.44 to 0.53; the coiling is evolute to moderately evolute. Between 215 mm and 280 mm diameter $\overline{U/D}$=0.58 (OS=0.03), $\overline{W/D}$=0.22 (OS=0.01), W/U varies from 0.37 to 0.40; the coiling is evolute. In the specimen IGPUW/A/36/219 (Pl. 6, Fig. 4), at $\underline{D}_m$=510 mm, U/D=0.58, W/U=0.20 and W/U=0.34. The ribs are moderately thick to thick, straight, rectiradiate or slightly prorsiradiate on the whorl-flanks; bifurcating. Type Ia ornamentation (see ontogenetic ornamentation types, p. 336) appears on the inner whorls of the phragmocone, up to 110 mm-130 mm diameter. After this diameter type Ib ornamentation appears on the middle whorls of the phragmocone. Type Ic ornamentation appears after 190 mm-210 mm diameter, on the outer whorls of the phragmocone. After 280 mm diameter, half a whorl before septation ceases, type II ornamentation appears and continues on the adult body-chamber. Close to the aperture the secondary ribs become prominent on the venter, and form a conspicuous sinus convex forward. The rib-number (Text-fig. 21) increases from 25-33 per whorl at 30 mm, to c. 40-43, occasionally to 53 per whorl, at 80 mm diameter. From c. 80 mm to 110 mm-130 mm the rib-number per whorl remains approximately constant, or diminishes insignificantly. After 110 mm-130 mm the rib-number reduces slowly, and after 190 mm-210 mm more rapidly, reaching c. 35 per whorl at 280 mm-290 mm diameter. The studied specimens differ in the rib-number per whorl on the middle whorls. The most densely ribbed specimen possesses 13 ribs per whorl more than the less densely ribbed specimen at comparable diameters. On the last one or two whorls of the phragmocone the rib-number per whorl decreases and becomes similar in all of the study specimens. Parabolic nodes appear occasionally in IGPUW/A/36/272. Constrictions number 1-2 per whorl, rarely 5 on the last whorl in IGPUW/A/36/203 (Pl. 5, Fig. 1). They are shallow and wide. The septal suture of formula N>EL>L appears at 185 mm and at 260 mm diameter (IGPUW/A/36/205; IGPUW/A/36/212 Pl. 4, Fig. 3). In the mature individual IGPUW/A/36/219 (Pl. 6, Fig. 4) the septal suture is EL≈N>L at 290 mm, and at 390 mm, near the end of the phragmocone, it changes to EL≈N=L.

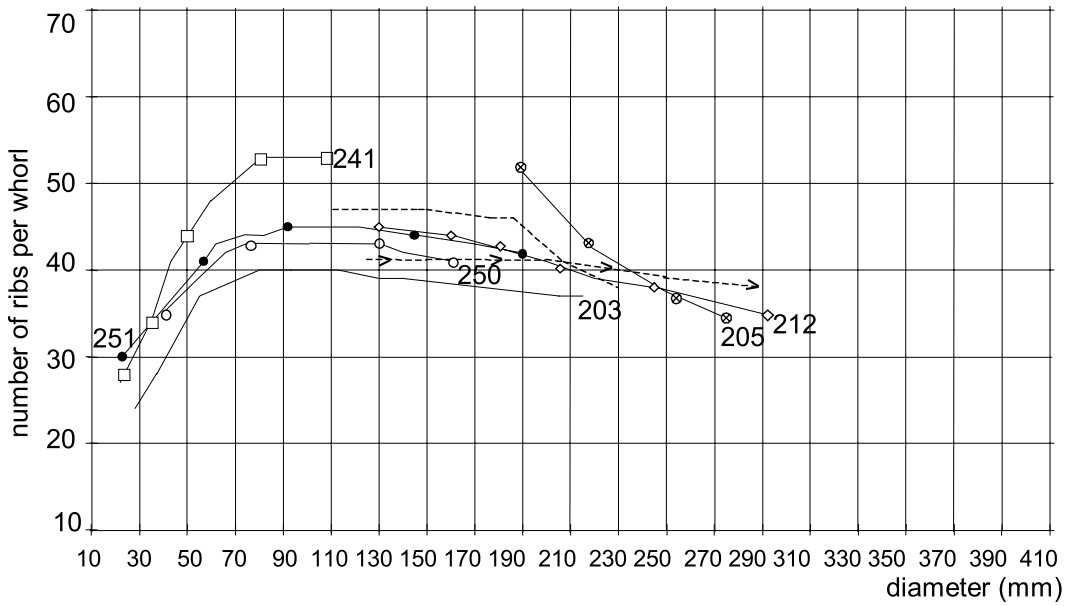

Fig. 21. Rib-density curves of *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN) and *P.* (*K.*) cf. *kranaus* (BUCKMAN) (IGPUW/A/36/241) compared with the rib-density curve of the holotype of *P.* (*K.*) *kranaus* (BUCKMAN) (dashed line with arrows) and of the holotype of *Perisphinctes* (*Kranaosphinctes*) *cymatophorus* (BUCKMAN) (dashed line); the specimens are numbered by only last component of their full registration numbers

DISCUSSION: *Perisphinctes* (*Cymatosphinctes*) *cymatophorus* (BUCKMAN) (BUCKMAN 1923, Pl. 450 A, B, holotype) is synonymised here with *P.* (*K.*) *kranaus*; it agrees with the latter species in the coiling of the whorls, subquadrate whorl-section, and in the moderately thick ribs. Additionally, the diameters at which the successive types of ornamentation appear in the two species overlap. Although the holotype of *P.* (*C.*) *cymatophorus* (BUCKMAN 1923, Pl. 450 A, B) is slightly more densely ribbed on the middle whorls (up to c. 190 mm diameter) than the holotype of *P.* (*K.*) *kranaus* (BUCKMAN 1921, Pl. 243 A, B, see also Text-fig. 21 in the present paper), the rib-density curves of the larger material of *P.* (*K.*) *kranaus* encompasses the rib-density of both forms. ARKELL (1939, p. 175) assumed the more incised septal suture in *P.* (*C.*) *cymatophorus* than in *P.* (*K.*) *kranaus* to be a fundamental difference between these two forms. As is shown herein, the septal suture is incised in the juveniles of *P.* (*K.*) *kranaus*, and simplifies in the adults. Therefore, the degree of incision of the septal suture cannot be used to discriminate these two forms as separate species.

P. (*K.*) *kranaus* differs from *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN), as interpreted herein, in the mode of rib-density changing (Text-figs 21-22): in *P.* (*K*) *kranaus* rib-density curves start to descend at diameters greater than c. 130 mm, corresponding to the appearance of type Ib ornamentation, and continue through type Ic and II ornamentation; in *P.* (*K.*) *ariprepes* the rib-number per whorl remains constant or increases insignificantly through the type Ia and Ib ornamentation and it does not decrease significantly until c. 200 mm diameter, where the type II ornamentation appears. The rib-density curves are flat and asymmetrical in *P.* (*K.*) *kranaus* compared to moderately convex in *P.* (*K.*) *ariprepes* (Text-figs 21-22). The two forms resemble each other in the coiling, rib-thickness, whorl-section, and possibly also in the final size (see details in the discussion on *P.* (*K.*) *ariprepes*, p. 345).

P. (*K.*) *kranaus* differs from *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI (see the description in the present paper, p. 337), with which it was synonymised by SIEGFRIED (1952), in the larger final size of adults [510 mm in *P.* (*K.*) *kranaus*, and c. 150 mm in *P.* (*K.*) *promiscuus*], and in ribs that are moderately thick to thick in *P.* (*K.*) *kranaus* and thin, densely spaced in *P.* (*K.*) *promiscuus*; additionally these two species differ in the rib-density curve, which is flat and asymmetrical in *P.* (*K.*) *kranaus* and convex, steeply sloping and approximately symmetrical in *P.* (*K.*) *promiscuus*.

OCCURRENCE: England, Germany, Spain, and Poland. The species appears in the topmost part of the Ouatius Subzone, ranges up to the overlying Arkelli Subzone of the Plicatilis Zone, and disappears in its upper part (Text-fig. 6).

Perisphinctes (*Kranaosphinctes*) *ariprepes* (BUCKMAN, 1924)
(Pl. 13, Fig. 1; Text-figs 17, 22)

1914. *Perisphinctes biplex* DE LORIOL; SALFELD, p. 235, Pl. 11, Fig. 1.
1924-1925. *Arisphinctes ariprepes* sp. nov.; BUCKMAN, p. 33, Pl. 511 A, B, C (holotype, *V.*).
1935. *Perisphinctes* (*Arisphinctes*) *ariprepes* (BUCKMAN); ARKELL, p. xii, Text-fig. 1; Pl. A, Fig. 4 (holotype, *V.*).
1935. "*Perisphinctes* (*Arisphinctes*) of the *ariprepes* group"; ARKELL, Pl. A, Fig. 1 a, b.
1939. *Perisphinctes* (*Arisphinctes*) *cotovui* SIMIONESCU; ARKELL, p. 126 (*pars*), Figs 39-43; Pl. 24, Figs 3, 4, 5 a, b (holotype of *Arisphinctes ariprepes* BUCKMAN, *V.*); Pl. 25, Fig. 3 only, *non* Text-figs 41, 42; Pl. 25, Fig. 1a-f [*V.*, *Perisphinctes trifidus* (SOWERBY)].
1966. *Perisphinctes* (*Arisphinctes*) *cotovui* SIMIONESCU; HAUERSTEIN, p. 28; Text-figs 4-5; Tab. 2; Pl. 1.
1972 b. *Perisphinctes* (*Arisphinctes*) cf. *cotovui* SIMIONESCU; MALINOWSKA, p. 177, Figs 3, 4; Pl. 1, Figs 1, 2. (*V.*)
1975 b. *Perisphinctes* (*Kranaosphinctes*) of the *K. promiscuus* group; BROCHWICZ-LEWIŃSKI & RÓŻAK, Pl. 5, Fig. 1 (*V.*)
1976. *Kranaosphinctes promiscuus* (BUKOWSKI); BROCHWICZ-LEWIŃSKI & RÓŻAK, Pl. 32 (*V.*).
? 1977. *Perisphinctes* (*Arisphinctes*) sp. gr. *cotovui* SIMIONESCU; BOURSEAU, p. 64, Text-fig. 27; Pl. 5, Fig. 5a,b; Pl. 6, Fig. 1.
1979. *Kranaosphinctes collignoni* sp. nov.; BROCHWICZ-LEWIŃSKI, p. 168 (*pars*), Text-fig. 1; Pl. 1 only (paratype, *V.*).

MATERIAL: 13 specimens, complete or incomplete, mostly distorted or crushed flat; all from the Wysoka Quarry (Text-fig. 2, Appendix), section W.4III, bed 4; section W.9, beds 10, 11; section W.9", beds 12a, 12b, 16, 18.

DESCRIPTION: IGPUW/A/36/202 (Pl. 13, Fig. 1) is an incomplete specimen of $*D_m$=310 mm; the body-chamber starts at D_f=250 mm, but the last septa are still not approximated at this diameter. The body-chamber occupies half a whorl and is incomplete. The specimen represents a close to mature individual. The other specimens in the collection represent early to late juvenile individuals; they range in D_m from 85 mm to 217 mm, the septation ceases in the range of D_f from 60 mm to 140 mm; the body-chamber, if complete, is one whorl long.

The whorl-section is subquadrate, with rounded margins (IGPUW/A/36/275 and IGPUW/A/202, Text-fig. 17), and remains as such throughout ontogeny. The coiling of the specimens is evolute, except for the inner whorls, up to c. 100 mm, where it is moderately evolute to evolute. From 140 mm to 165 mm diameter $\overline{U/D}$=0.54 (OS=0.04), $\overline{W/D}$=0.23 (OS=0.02) and W/U ranges from 0.39 to 0.49; the coiling is evolute. At D_m=310 mm in the specimen IGPUW/A/36/202 (Pl. 13, Fig. 1) U/D=0.60, W/D=0.21, W/U=0.36; coiling is evolute. The ribs are moderately thick, and moderately densely spaced on the whorl-flanks. Type Ia ornamentation (see ontogenetic ornamentation types, p. 336) changes to type Ib ornamentation between 120 mm and 145 mm diameter; type II ornamentation is recognised as early as at c. 205 mm (IGPUW/A/202, Pl. 13, Fig. 1). The rib-number per whorl (Text-fig. 22) increases from c. 30 at 30 mm diameter to 48-53 ribs per whorl at 120 mm-140 mm. Between 120 mm-140 mm and c. 200 mm the number of ribs remains approximately constant, or increases

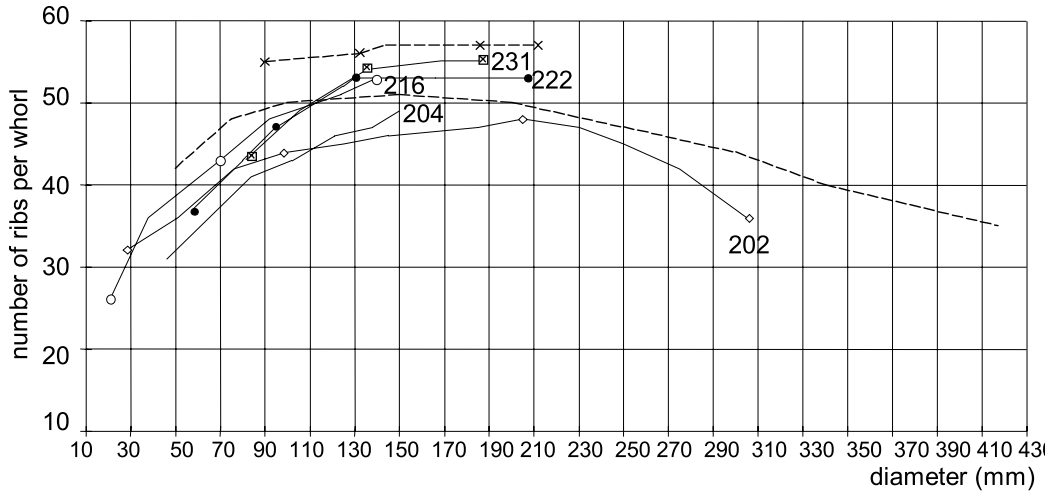

Fig. 22. Comparison of rib-density curves of *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN) (continuous lines) with the holotype of *P.* (*K.*) *ariprepes* (BUCKMAN) (dashed line), and with the specimen no Kl. 16/33 (dashed line marked with crosses) [paratype of *Kranaosphinctes collignoni* (BROCHWICZ-LEWIŃSKI 1979, Pl. 1)]; the specimens of *P.* (*K.*) *ariprepes* (BUCKMAN) are numbered by only the last component of their full registration numbers

insignificantly. After c. 200 mm the ribs become more widely spaced and less numerous per whorl, and they decrease in number to 35 ribs per whorl at 310 mm. The rib-density curve is flat and low, with gently sloping flanks. The constrictions number 2-3 per whorl on the phragmocone and on the body-chamber. The septal suture is of formula N>EL>L at D=135 mm in IGPUW/A/36/233, and at D=225 mm in IGPUW/A/36/202 (Pl. 13, Fig. 1).

DISCUSSION: ARKELL (1939, p. 126) synonymised *P.* (*K.*) *ariprepes* with the Romanian species *Perisphinctes cotovui* SIMIONESCU, 1907 (see SIMIONESCU 1907, Pl. 4, Fig. 3, Pl. 7, Fig. 1: lectotype). The ARKELL's synonymy is not accepted herein. *P.* (*K.*) *ariprepes* differs from SIMIONESCU's species in less evolute coiling and the subrectangular whorl-section.

P. (*K.*) *ariprepes*, as interpreted herein, resembles *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN). These two forms show similar, evolute coiling, except for the inner whorls which are moderately evolute to evolute in *P.* (*K.*) *ariprepes*, and only occasionally become moderately evolute in *P.* (*K.*) *kranaus.* They show similar whorl-section (Text-fig. 17), which is subquadrate on both the phragmocone and body-chamber. In *P.* (*K.*) *kranaus*, however, the whorl-section can, additionally, be circular on the phragmocone, and oval or depressed-subquadrate on the body-chamber, which never occurs in *P.* (*K.*) *ariprepes.* The two species resemble each other in the character of ribbing, which is moderately thick in *P.* (*K.*) *ariprepes* and moderately thick to thick in *P.* (*K.*) *kranaus*; as well as in the shell-diameters at which ornamentation types appear in ontogeny (type Ib starts to appear at 120-145 mm in *P.* (*K.*) *ariprepes* and at 110-130 mm in *P.* (*K.*) *kranaus*). The two species are both large-sized: the largest specimen of *P.* (*K.*) *ariprepes* in the studied collection is of $^{*}D_{m}$=310 mm, but it is incomplete and not full-grown; the specimens of *P.* (*K.*) *kranaus* is of $\underline{D_{m}}$=510 mm, it is complete and full grown. The two species differ in the mode of rib-density changes (Text-figs 21-22): in *P.* (*K.*) *ariprepes* the rib-density curves descend at diameters greater than c. 200 mm, whereas in *P.* (*K*) *kranaus* they start to descend, first slowly, then more rapidly, already at c. 130 mm (see also the discussion on p. 343).

P. ariprepes was designed as the type species of BUCKMAN's (1924) subgenus *Arisphinctes*. *P. ariprepes* is, however, morphologically close to *P. kranaus*, the type species of the subgenus *Kranaosphinctes* BUCKMAN. The separation of these two forms between two subgenera seems to be unjustified.

Into the synonymy of *P.* (*K.*) *ariprepes* is put herein Kl.16/33, the paratype of *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI) (see BROCHWICZ-LEWIŃSKI 1979, Pl. 1). This specimen differs distinctly from other type specimens of *P.* (*K.*) *collignoni* in a subquadrate whorl-section, moderately evolute coiling of the inner whorls, and evolute coiling of the middle and outer whorls, and in the appearance of type Ib ornamentation at 140 mm diameter. In addition, the rib-number per whorl in Kl. 16/33 (Text-fig. 22) remains constant in the range of diameters corresponding to type Ib ornamentation, in which it agrees with *P.* (*K.*) *ariprepes*, and differs from *P.* (*K.*) *collignoni.*

OCCURRENCE: England, France, Germany, and Poland. The species ranges through the Arkelli Subzone of the Plicatilis Zone, and it disappears in its upper part, below the upper boundary of the subzone (Text-fig. 6)

Genus *Liosphinctes* BUCKMAN, 1925

TYPE SPECIES: *Liosphinctes apolipon* BUCKMAN, 1925; the holotype figured by BUCKMAN (1925, vol. 5, Pl. 566) and by ARKELL (1939, vol. 5, Pl. 35, Fig. 3 a, b).

EMENDED DIAGNOSIS: Shell constricted, discoidal. Whorl-section oval or high-oval, rarely subrectangular on phragmocone. Coiling weakly evolute on inner whorls, changing to evolute on last whorl of adults. Ribs mostly bifurcating, occasionally branching into three or four secondary ribs; paradischizotomous rib-divisions rarely appear. Secondary ribs associated with 1 or 2 intercalatory ribs. Division points obscure, situated at 3/4 or 4/5 of the height of the whorl-flank. Adult body-chamber smooth on upper half flank and on venter, with blunt ribs on umbilical margin persisting up to final aperture.

REMARKS: The material herein presented, and that previously studied (ARKELL 1939, CALLOMON 1960, ENAY 1966) shows that the representatives of *Liosphinctes*, among them *Liosphinctes plicatilis* (SOWERBY) and *Liosphinctes laevipickeringius* (ARKELL), referred to this genus for the first time, form a uniform, distinctive group of the Middle Oxfordian macroconchs, which is treated as a single phylogenetic lineage in the present paper. This is at variance with the opinion of ARKELL (1939), who regarded *Liosphinctes* as "an arbitrary group-designation within the large subgenus *Arisphinctes*" (ARKELL 1939, vol. 5, p. LIX), and of GEYER (1961), who put *Liosphinctes* into the synonymy of *Kranaosphinctes* BUCKMAN (see the comparative description, p. 346).

In the opinion of the present author, the Middle Oxfordian genus *Platysphinctes* TINTANT is closely allied to *Liosphinctes*. Contrary to the view of BROCHWICZ-LEWIŃSKI (1972), who put *Platysphinctes* into the synonymy of *Liosphinctes*, these two forms are assigned in the present paper to separate genera. Determination of their relationship requires further study.

ONTOGENETIC ORNAMENTATION TYPES: The genus *Liosphinctes* possesses bifurcating and non-bifurcating ribs. In the course of ontogeny the secondary ribs become associated with the intercalatory ribs on the venter and the primary ribs become indistinct on the upper half-flank of the whorl and on the venter. On the adult body-chamber they almost disappear and the body-chamber becomes nearly smooth. The ornamentation types in the ontogeny of the genus *Liosphinctes* are as follows:

Type Ia: the ribs bifurcate regularly; the division-points are somewhat indistinct; they are situated at 4/5 or 3/4 of the height of the whorl-flank. The intercalatory ribs appear irregularly.

Type Ib: the secondary ribs become regularly associated with the intercalatory ribs; the primary ribs on the whorl-flanks become indistinct on the upper half-flank. Occasionally, paradischizotomous rib-division appears, or sheaves of 3 or 4 ribs that arise indistinctly from the primary rib. The rib-division is situated at 3/4 of the height of the whorl-flank. The division points are indistinct.

Type Ic: the secondary ribs are associated with 2 intercalatory ribs. Sheaves of 3 ribs associated with one intercalatory rib appear. The ribs are faint on the upper half-flanks and on the venter. This ornamentation type appears irregularly in the species studied.

Type II: the ribs fade almost entirely away on the venter and on the whorl-flanks, except near the umbilical margin, where they form blunt ridges and persist as such up to the aperture. Type II ornamentation is representative for mature individuals.

Two modes of appearance of successive ornamentation types in the course of ontogeny is recognized in the studied material. In *L. plicatilis*, *Liosphinctes* sp. A, and *Liosphinctes cumnorensis* (ARKELL) type Ia ornamentation appears at or nearby at the end of the phragmocone, whereas types Ib, Ic and type II ornamentation appear successively on the body-chamber, after each 1/3 of a whorl. In *L. laevipickeringius* and *Liosphinctes* sp. B types Ia, Ib and, occasionally, also type Ic ornamentation appear successively on the phragmocone; type II ornamentation is presumed to appear on the body-chamber, however, this was not studied in the two latter species due to the incompleteness of the specimens.

SEPTAL SUTURE: In the studied material the septal sutures are recognised in *L. plicatilis* and *L. laevipickeringius*. In both species half of the whorl before septation ceases the suspensive lobe is longer than the lateral lobe (N>L); the external lobe is not exposed. In *L. plicatilis*, towards the end of the phragmocone, the suspensive lobe shortens, and finally, when the septa become approximated, all three lobes are of equal length (EL=L=N). This occurs at $\underline{D}_f$ =126 mm. In the species *L. laevipickeringius* the septal suture, up to a preserved diameter of 167 mm shows all of the three lobes to be of equal length (EL=L=N).

COMPARATIVE DESCRIPTION: The genus *Liosphinctes* differs from the subgenus *Kranaosphinctes* BUCKMAN of the genus *Perisphinctes* WAAGEN in the oval whorl-section, as compared to subquadrate or subrectangular, compressed or depressed, in *Kranaosphinctes*; weakly evolute coiling of the inner whorls, compared to evolute to moderately evolute in *Kranaosphinctes*; presence of non-bifurcating ribs, absent in *Kranaosphinctes*; ribs becoming indistinct on the upper half of the whorl-flank in *Liosphinctes*, but not in *Kranaosphinctes*; the almost smooth body-chamber in the adult stage of growth of *Liosphinctes*, and the distinctly ribbed adult body-chamber of *Kranaosphinctes*.

The species of the genus *Liosphinctes* differ from *Perisphinctes trifidus* (SOWERBY) (m. M), as interpreted in the present paper, in generally less evolute coiling at the equivalent stages of growth; the whorl-section, usually oval in *Liosphinctes*, subrectangular in *P. trifidus*; the non-bifurcating ribs characteristic of *Liosphinctes*, but absent in *P. trifidus*; ribs that are indistinct on the upper half-flank in *Liosphinctes*, but not in *P. trifidus*. The septal suture is different in the two forms, except for the septal suture of formula EL=L=N, which is found in both of them.

From *Neumannia* gen. nov. *Liosphinctes* differs in whorl-section, coiling and shell-ornamentation (for details see the comparative description on p. 354).

The genus *Liosphinctes* and the closely allied *Platysphinctes* TINTANT are both characterised by the appearance of bifurcating and non-bifurcating ribs; loss of distinctness of ribs on the upper half-flank of the whorl; nearly smooth adult body-chamber; constricted shell. *Liosphinctes* is, however, less evolute on the inner whorls than *Platysphinctes*, and more evolute on the outer whorls; the whorl-section is usually oval in *Liosphinctes*, and rectangular or trapezoidal, rarely oval in *Platysphinctes*; the final size of adults is larger in *Liosphinctes* than in *Platysphinctes* (see also GŁOWNIAK 2000).

Liosphinctes plicatilis (SOWERBY, 1817)
(Pl. 16, Figs 1-2; Pl. 17, Figs 1-2; Text-figs 23-24)

1817. *Ammonites plicatilis*; J. SOWERBY, p. 149, Pl. 166 (holotype, *V.*).
non 1898. *Perisphinctes plicatilis* SOWERBY; DE RIAZ, p. 9, Pl. 1; Pl. 2, Figs 1(a, b)-3.
non 1898. *Perisphinctes cf. plicatilis* SOWERBY; DE RIAZ, p. 9, Pl. 2, Fig. 4; Pl. 4, Figs 1, 2; Pl. 5.
1904. *Perisphinctes plicatilis* (SOWERBY); HEALEY, p. 55, Pl. 9, Figs 1, 2 (holotype)
1907. *Perisphinctes plicatilis* SOWERBY; NEUMANN, p. 26, Tab. 1, Fig. 3a, b.
non 1930. *Perisphinctes plicatilis* SOWERBY; DORN, p. 146, Pl. 6, Fig. 1.
1939. *Perisphinctes* (*Arisphinctes*) *plicatilis* (SOWERBY); ARKELL, p. 145, Fig. 41 (*pars*); Pl. 29, Fig. 1a-c (holotype), Fig. 3 a, b (*V.*) [*non* Pl. 29, Fig. 2 a–b (*V.*)].
1952. *Perisphinctes* (*Arisphinctes*) *plicatilis* (SOWERBY); SIEGFRIED, p. 304, Pl. F, Fig. 1, 1a.
1966. *Perisphinctes* (*Arisphinctes*) *plicatilis* (SOWERBY); ENAY, p. 416, Fig. 117; Pl. 19, Fig. 2.
1966. *Perisphinctes* (*Arisphinctes*) *plicatilis* (SOWERBY); HAUERSTEIN, p. 46, Figs 10-11; Tab. 5; Pl. 4.
1966. *Perisphinctes* (*Arisphinctes*) *elisabethae* DE RIAZ; HAUERSTEIN, p. 52, Figs 12, 13, 14c; Pl. 5 (without the synonymy).
? 1977. *Perisphinctes* (*Arisphinctes*) cf. *plicatilis* (SOWERBY); BOURSEAU, p. 66, Fig. 29; Pl. 5, Figs 1a-b, 2a-b.
1989. *Perisphinctes* (*Arisphinctes*) *plicatilis* (SOWERBY); FISCHER & GYGI, Fig. 4 D.
1989. *Perisphinctes* (*Arisphinctes*) *plicatilis* (SOWERBY); MELÉNDEZ, p. 229, Fig. 46 (*pars*); Pl. 23, Fig. 2 only (*V.*) [*non* Pl. 23, Fig. 1 a, b (*V.*)].
1998. *Perisphinctes* (*Arisphinctes*) *plicatilis* (SOWERBY, 1817) (M); GYGI, p. 12, Pl. 14, Fig. 4, Text-fig. 9, Tab. 6.
1998. *Perisphinctes* (*Arisphinctes*) sp. gr. *plicatilis* (SOWERBY, 1817) (M); GYGI, p. 13, Pl. 2, Fig. 4; Text-fig. 10; Tab. 7.
non 1972a. *Perisphinctes* (*Arisphinctes*) *plicatilis* (SOWERBY); MALINOWSKA, p. 18 [14], Fig. 2; Pl. 5, Fig. 1a,b.
non 1972b. *Perisphinctes* (*Arisphinctes*) *plicatilis* (SOWERBY); MALINOWSKA, p. 184, Figs 3, 8; Pl. 4, Figs 1, 2 (*V.*).

MATERIAL: Eight specimens: seven with complete or incomplete body-chamber and one incomplete phragmocone. All come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.6, bed 26a, 28c; section W.6', bed 28d; section W.4III, beds 6, 10, 20, 21; and section W.4, bed 17a. Four whorl-fragments, classified as *Liosphinctes* cf. *plicatilis*, come from the Wysoka Quarry, section W.4III, bed 20 and were collected loose from the beds 6-20; section W.6, bed 28c; and section W.9", bed 8.1 a-c.

DESCRIPTION: IGPUW/A/36/154 (Pl. 16, Fig. 2) is a complete, full-grown specimen, of $\underline{D_m}$=195 mm. The phragmocone ends at $\underline{D_f}$=126 mm, and shows the approximation of the last septa. The body-chamber is 7/8

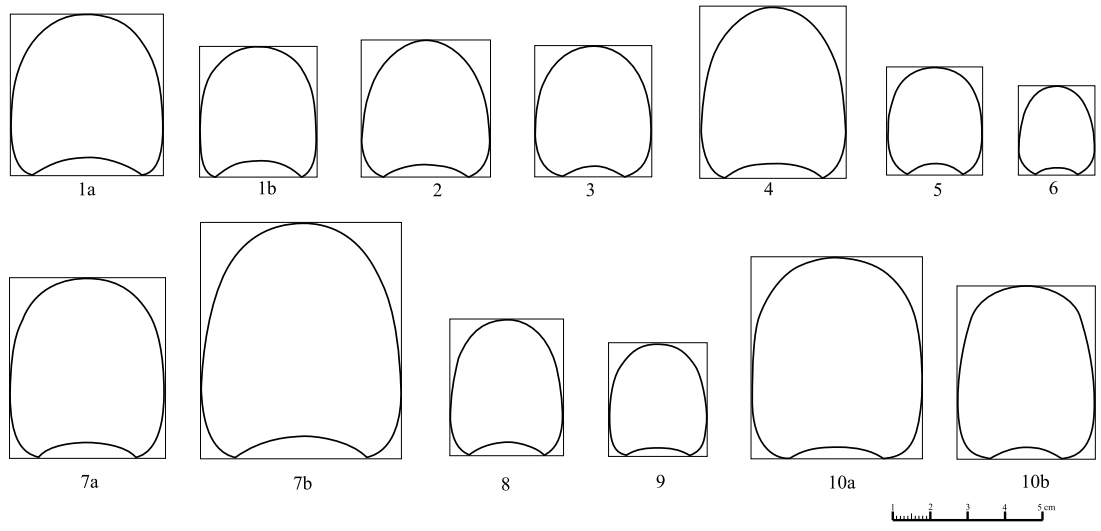

Fig. 23. Whorl-section of the genus *Liosphinctes* BUCKMAN, at a given diameter; *Liosphinctes laevipickeringius* (ARKELL): 1. IGPUW/A/36/162 (Pl. 18, Fig. 1), a: D=130 mm, b: D=100 mm; *Liosphinctes* sp. B: 2. IGPUW/A/36/163 (Pl. 18, Fig. 2), D=125 mm; *Liosphinctes plicatilis* (SOWERBY): 3. IGPUW/A/36/152 (Pl. 17, Fig. 2), D=140 mm, 4. IGPUW/A/36/154 (Pl. 16, Fig. 2), D=180 mm, 5. IGPUW/A/36/164 (Pl. 16, Fig. 1), D=92 mm, 6. IGPUW/A/36/165 (Pl. 17, Fig. 1), D=75 mm; *Liosphinctes* sp. A: 7. IGPUW/A/36/179 (Text-fig. 25), a: D=120 mm, b: D=180 mm; 8. IGPUW/A/36/174 (Pl. 18, Fig. 3), D=120 mm; *Liosphinctes cumnorensis* (ARKELL): 9. IGPUW/A/36/182, D=90 mm, 10. IGPUW/A/36/180 (Text-fig. 27), a: D=230 mm, b: D=180 mm

of a whorl. IGPUW/A/36/152 (Pl. 17, Fig. 2) and IGPUW/A/36/153 are nearly complete specimens, of D_m=170 mm and D_m=175 mm, respectively. The phragmocone ends at D_f=110 mm in IGPUW/A/36/152, and the body-chamber occupies 7/8 of the last whorl. In IGPUW/A/36/153 the septa are not exposed and the end of the phragmocone is not discernible. These two specimens are probably nearly mature, and their final diameters are possibly not far from the actual maximum diameters. Other specimens represent early to late juveniles. They range in D_m from 112 mm to 120 mm; the phragmocones end at D_f between 90 mm and 107 mm; the body-chamber, when complete, is one whorl long. IGPUW/A/36/159 is an incomplete phragmocone of $^*D_f$=80 mm.

The whorl-section (Text-fig. 23) of the phragmocone is high-oval, rarely subrectangular. The whorl-section of the adult body-chamber is high-oval. The coiling is weakly evolute on the inner whorls. After c. 70 mm diameter it changes to moderately evolute, and subsequently, on the adult body-chamber, to evolute or nearly evolute. Between 60 mm-70 mm and 100 mm-130 mm diameter $\overline{U/D}$ increases from 0.41 to 0.46 (OS=0.02), $\overline{W/D}$ decreases from 0.33 (OS=0.03) to 0.29 (OS=0.02), and W/U decreases from between 0.72-0.87 to 0.55-0.75. Between 150 mm and 170 mm U/D ranges from 0.51 to 0.55, W/D ranges from 0.25 to 0.27, and W/U ranges from 0.45 to 0.54. The ribs are fine and densely spaced on the phragmocone. They are prorsiradiate, straight or slightly flexuous on the whorl-flanks. Type Ia ornamentation (see ontogenetic ornamentation types, p. 346) appears on the phragmocone up to a diameter of 130 mm. At the beginning of the adult body-chamber, after the constriction, type Ib ornamentation appears. After a constriction at 170 mm diameter, type II ornamentation appears on the last quarter of the adult body-chamber. The rib-number is 40-50 per whorl at a diameter of c. 30 mm (Text-fig. 24). The ribs then increase in number and reach a maximum 70-80 ribs per whorl between 110 mm and 150 mm diameter. At diameters greater than 110 mm-150 mm, corresponding to type Ib and type II ornamentation, the rib-number per whorl decreases to 60 ribs per whorl at 190 mm. IGPUW/A/36/165 (Pl. 17, Fig. 1) differs from the other specimens in the collection in attaining the maximum rib number per whorl already at a diameter of 70 mm. At diameter greater than 70 mm the rib-number per whorl decreases in this specimen.

Constrictions are shallow. They number 2-4 on the phragmocone and 3-4 on the body-chamber. The septal suture at D=100 mm shows the suspensive lobe longer than the lateral lobe (N>L); the external lobe is not exposed at this diameter. Towards the end of the phragmocone the suspensive lobe shortens, and finally, at $\underline{D_f}$=126 mm all three lobes are of equal length (EL=L=N). The septa are approximated at this diameter.

DISCUSSION: *Ammonites plicatilis* SOWERBY (see SOWERBY 1817, vol. 2, p. 149, Pl. 146) is assigned here to the genus *Liosphinctes* BUCKMAN and not to the genus *Perisphinctes* WAAGEN as is commonly the case (e.g. ARKELL 1939; ENAY 1966; MELÉNDEZ 1989; MALINOWSKA 1972a, 1972b). *L. plicatilis* represents all the characters of shell morphology that characterise the genus *Liosphinctes*, such as: loss of ribbing on the adult body-chamber, frequent appearance of constrictions, high-oval whorl-section, weakly evolute coiling of the inner whorls and evolute or nearly evolute coiling of the last whorl in adults.

From the synonymy of *L. plicatilis* are excluded herein the following specimens: the one of DORN (1930), in which coiling is evolute at all growth stages, the ribs are moderately coarse and sharp, and moderately densely spaced on the whorl-flank; the specimen of MALINOWSKA (1972a), which is evolute at all growth stages, possesses a subquadrate whorl-section, and a shell that is not constricted, and with ribs that do not fade on the outer whorl but actually become prominent at its peripheral margin; the specimen of MALINOWSKA (1972 b), which has a subrectangular whorl-section, is moderately evolute at all growth stages, and in which the ribs remain distinct on the whorl-flanks; one of the specimens of MELÉNDEZ (1989, Pl. 23, Fig. 1a, b), which is moderately evolute at all growth stages, and in which the ribs remain distinct on the whorl-flanks.

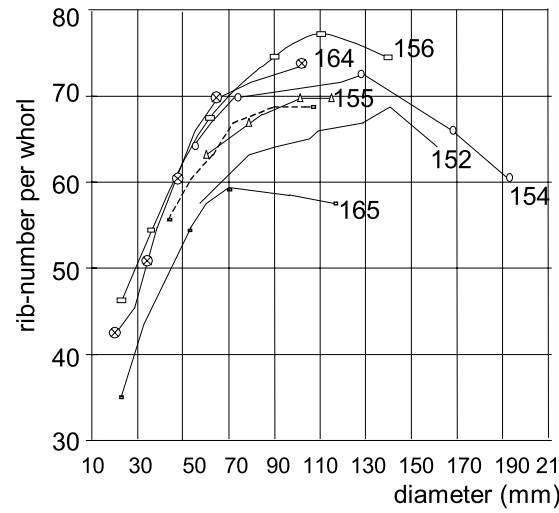

Fig. 24. Rib-density curves of *Liosphinctes plicatilis* (SOWERBY) compared with the rib curve of the holotype of *L. plicatilis* (SOWERBY) (dashed line); the specimens are numbered by only the last component of their full registration numbers

Of the species of the genus *Liosphinctes*, *L. plicatilis* possesses the finest and the most densely spaced ribs. It resembles *Liosphinctes* sp. A. and *Liosphinctes cumnorensis* (ARKELL) in the mode of ornamentation changes through ontogeny: type Ia ornamentation extends in all of the three species to the end or nearly to the end of the phragmocone, whereas types Ib, Ic and type II ornamentation appear successively on the body-chamber. *L. plicatilis* is, however, smaller than *L.* sp. A and *L. cumnorensis*, with the final size 190 mm as compared to c. 270 mm in *L.* sp. A and c. 240 mm in *L. cumnorensis*; it is also more densely ribbed on the inner whorls than the two latter species (see Text-figs 24, 26, 28).

OCCURRENCE: England, Germany, France, Spain, Switzerland, and Poland. It ranges through the Paturattensis and the Ouatius subzones of the Plicatilis Zone (Text-fig. 6).

Liosphinctes laevipickeringius (ARKELL, 1939)
(Pl. 18, Fig. 1; Text-figs 23, 26)

1939. *Perisphinctes* (*Arisphinctes*) *laevipickeringius* sp. nov.; ARKELL, p. 142 (*pars*), Fig. 46; Pl. 30, Figs 4 (*V.*), 5 a, b (holotype, *V.*); ? Pl. 30, Figs 1-3 (*non* Pl. 30, Fig. 6, Pl. 33, Fig. 6).

1960. *Perisphinctes* (*Liosphinctes*) *laevipickeringius* ARKELL; CALLOMON, p. 192.

? 1966. *Perisphinctes* (*Liosphinctes*) *laevipickeringius* ARKELL; ENAY, p. 420, Text-fig. 120.

MATERIAL: Three specimens; one is an incomplete phragmocone from the Wysoka Quarry (Text-fig. 2, Appendix), section W.4III, bed 10, the second specimen is complete, it comes from Złochowice north of Częstochowa (Text-fig. 1), the third is a poorly preserved specimen referred here to *L.* cf. *laevipickeringius*, from the Wysoka Quarry, section W.8, bed 2a.

DESCRIPTION: IGPUW/A/36/162 (Pl. 18, Fig. 1) is an incomplete phragmocone of a possibly late juvenile individual, of $*D_f$=167 mm. IGPUW/A/36/358 is a complete, late juvenile individual of D_m=160 mm. The phragmocone ends at D_f=100 mm; the body-chamber occupies one whorl.

The whorl-section on the phragmocone and on the body-chamber is oval (Text-fig. 23), almost as thick as high. The venter is moderately wide and gently rounded. The coiling is weakly evolute up to a diameter of c. 65 mm. Then, it changes to moderately evolute. In IGPUW/A/36/162 (Pl. 18, Fig. 1), at diameters between c. 65 mm and 167 mm, U/D increase from 0.45 to 0.46, W/D decrease from 0.32 to 0.30, and W/U decrease from 0.75 to 0.65. The ribbing is coarse. The primary ribs divide at 4/5 whorl-height, and the division-points are obscure. The ventral ribs make a forward sweep on the venter, where they are interrupted, forming a smooth band. Type Ia ornamentation (see ontogenetic ornamentation types, p. 346) appears on the phragmocone up to 100 mm diameter, and then it is followed by type Ib ornamentation. The latter is characterised in *L. laevipickeringius* by the common appearance of sheaves of three ribs arising indistinctly from the primary rib. After a diameter of 130 mm type Ic ornamentation appears, and it extends up to the end of the incomplete phragmocone in IGPUW/A/36/162 (Pl. 18, Fig. 1). The free-ending intercalatory ribs commonly curve inward at their extremities, and the ventral ribs resemble sheaves of four ribs, or sheaves of three ribs with an associated intercalatory between. The ribs become faint on the upper whorl-flank and on the venter as the diameter increases. After the constriction at c. 150 mm they are low and blunt ridges on the whorl-flanks, and on the venter they fade away almost entirely. The ribs increase in number (Text-fig. 26) from c. 40 per whorl at 60 mm diameter to a maximum 45-48 ribs per whorl at 110 mm-130 mm. After this diameter, corresponding approximately to the appearance of type Ic, the rib-number remains constant or decreases insignificantly. At diameters greater than 150 mm, in the interval with type II ornamentation, the rib-number per whorl decreases. At 167 mm, in IGPUW/A/36/162, there are 43 ribs per whorl. The rib-density curves are low and flat. There are 1-2 constrictions per whorl on the phragmocone in IGPUW/A/36/162 (Pl. 18, Fig. 1), and 4 on the body-chamber in IGPUW/A/36/358. The septal suture is of formula EL=L=N at a diameter of 167 mm in IGPUW/A/36/162 (Pl. 18, Fig. 1).

DISCUSSION: *L. laevipickeringius* is the most coarsely ribbed and has the thickest whorl-section of all the studied species of the genus *Liosphinctes*. A similarly thick whorl-section also characterises *Liosphinctes* sp. B, however, in contrast to this species, *L. laevipickeringius* possesses a broader venter and less convergent flanks. The two species resemble each other in the mode of rib-density changes: it remains constant through type Ia, type Ib and most of type Ic ornamentation, and it decreases at the diameters corresponding to the end of type Ic ornamentation. From *Liosphinctes* sp. A *L. laevipickeringius* differs in the more robust shell, thicker and less densely spaced ribs and in less convergent flanks.

OCCURRENCE: England, ?France, and Poland. It ranges through the Ouatius Subzone and the lower Arkelli Subzone of the Plicatilis Zone (Text-fig. 6).

Liosphinctes sp. A
(Pl. 18, Fig 3; Text-figs 23, 25, 26)

MATERIAL: Four specimens; one with a nearly complete body-chamber; the other two are incomplete phragmocones, the fourth is a poorly preserved specimen referred here to *L.* cf. sp. A. The material comes from the Wysoka Quarry (Text-fig. 2, Appendix), section W.2', bed 22, and from the Ogrodzieniec Quarry (Text-fig. 3, Appendix), section O.4, bed 1j and 1l. *L.* cf. sp. A comes from the Wysoka Quarry, section W.4, bed 18 (a-c).

DESCRIPTION: IGPUW/A/36/179 (Text-fig. 25) is a nearly complete specimen, of $\underline{D}_m$=270 mm. The phrag-

Fig. 25. *Liosphinctes* sp. A: IGPUW/A/36/179; Wysoka, W.2' bed 22, $\underline{D}_m$=270 mm, $\underline{D}_f$=190 mm, reduced × 0.6. Arrow indicates end of the phragmocone

mocone ends at $\underline{D}_f$=190 mm; the body-chamber occupies 3/4 of a whorl. The peristome is broken away. The last septa on the phragmocone are not approximated, however, type II ornamentation appearing on the last half-whorl of the body-chamber indicates that the specimen represents a mature individual. IGPUW/A/36/173 and IGPUW/A/36/174 (Pl. 18, Fig. 3) are incomplete phragmocones, with $^*D_f$ =140 mm and $^*D_f$ =130 mm respectively. The whorl-section on the phragmocone is oval (Text-fig. 23), flat-sided, with the maximum thickness at 1/3 of the whorl-height, or it is subrectangular with gently rounded flanks and venter and rounded margins. The body-chamber is oval, somewhat higher than wide. The coiling is weakly evolute up to c. 90 mm; then it changes to moderately evolute, and after 140 mm diameter it becomes evolute. At 60 mm diameter U/D ranges from 0.41 to 0.45, W/D range from 0.31 to 0.35, and W/U ranges from 0.75 to 0.84. At $\underline{D}_m$=270 mm in IGPUW/A/36/179 (Text-fig. 25) U/D=0.57, W/D=0.24, and W/U=0.42. The ribs are moderately thick. Type Ia ornamentation (see ontogenetic ornamentation types, p. 308) appears on incomplete phragmocones, maximally up to 140 mm diameter. After c. 115 mm diameter intercalatory ribs occur with every second or third pair of secondary ribs. Type Ib ornamentation is recognised in IGPUW/A/36/179 (Text-fig. 25) on the final part of the phragmocone, after 175 mm diameter, where the venter first appears from beneath the outer whorl. It continues on the first quarter of the body-chamber, where it is followed after the constriction at 230 mm by type Ic ornamentation. After 245 mm diameter type II ornamentation appears on the last quarter of the body-chamber. The rib number per whorl (Text-fig. 26) increases from c. 45 at 30 mm diameter to c. 60 at 110 mm. Between 110 mm and c. 160 mm, in the range of diameters still corresponding to type Ia ornamentation, the rib-number per whorl remains approximately constant. Then, in the range of diameters corresponding to types Ib, Ic and II ornamentation, it decreases. At 270 mm diameter there are about ten ribs per whorl fewer than at a diameter of 160 mm. Constrictions number 1-2 per whorl on the phragmocone, and 3 on the body-chamber. They are shallow.

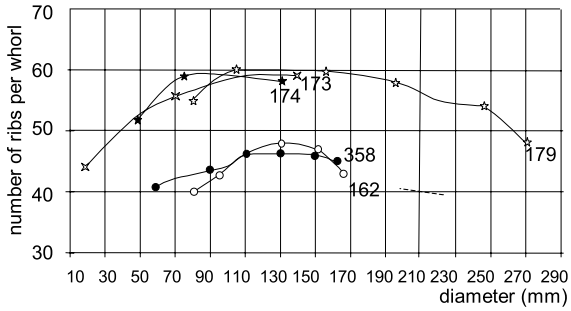

Fig. 26. Rib-density curves of *Liosphinctes* sp. A (lines marked with stars) and *Liosphinctes laevipickeringius* (ARKELL) (dot lines) compared with the rib-density curve of the holotype of *L. laevipickeringius* (ARKELL) (dashed line); the specimens are numbered by only the last component of their full registration numbers

DISCUSSION: *Liosphinctes* sp. A resembles *Liosphinctes plicatilis* (SOWERBY) and *Liosphinctes cumnorensis* (ARKELL) in the mode of ornamentation changes through ontogeny (see p. 346). It differs from *L. plicatilis* in its larger final size and in less densely ribbed inner whorls. From *L. cumnorensis* it differs in thinner and more densely spaced ribs on the inner whorls of the phragmocone up to c. 70 mm diameter. From *Liosphinctes laevipickeringius* (ARKELL) *Liosphinctes* sp. A differs in a less robust whorl-section, more convergent whorl-flanks, and in finer and more densely spaced ribs. The rib-density curves of both species are parallel, but that of *L.* sp. A corresponds to the lower rib-number per whorl at equivalent diameters (Text-fig. 26).

OCCURRENCE: Poland. The Paturattensis Subzone of the Plicatilis Zone (Text-fig. 6).

Liosphinctes sp. B
(Pl. 18, Fig. 2; Text-figs 23, 28)

MATERIAL: One complete specimen, from the Wysoka Quarry (Text-fig. 2, Appendix), section W.4III, bed 12.

DESCRIPTION: IGPUW/A/36/163 (Pl. 18, Fig. 2) is a middle or late juvenile, of D_m=132 mm. The phragmocone ends at D_f=77 mm; the body-chamber is nearly one whorl long.

The whorl-section is oval (Text-fig. 23), with narrow and high-rounded venter, almost as thick as high. The maximum whorl-thickness is at 1/4 of the whorl-height. The shell is thick. The umbilicus is deep. The coiling is at first weakly evolute, and on the last whorl it changes to moderately evolute. Between 68 mm and 130 mm diameter U/D increases from 0.44 to 0.46, W/D decreases from 0.34 to 0.30, and W/U decreases from 0.77 to 0.65. The ribbing is moderately thin; it becomes thicker on the body-chamber. The ribs are distinctly prorsiradiate on the whorl-flanks, slightly flexuous on the body-chamber. The ribs bifurcate. The secondary ribs arise at 2/3 of the whorl-height; the division-points are obscure. The secondary ribs pass across the venter following the direction of the primary ribs. They are thick and rounded,

and remain clearly visible up to the end of the body-chamber. On the final part of the phragmocone, after 73 mm diameter, where the venter first appears from beneath the outer whorl, the ornamentation is of type Ib (see ornamentation types, p. 346). It continues to the end of the body-chamber. Every pair of secondary ribs is associated with one, and after 120 mm diameter, occasionally, with two intercalatory ribs. The distinctive feature is the appearance of paradischizotomous rib-division on the body-chamber and, rarely, sheaves of three or four ribs, arising indistinctly from the primary rib. The ribs increase in number (Text-fig. 28) from 53 per whorl at 60 mm diameter to 57 at c. 80 mm. At diameters from c. 80 mm to 132 mm, corresponding to type Ib ornamentation, the rib-number is constant, at 57 per whorl. Constrictions number 3 on the body-chamber. They are shallow and flexuous.

DISCUSSION: *Liosphinctes* sp. B differs from other species of the genus *Liosphinctes* in a thick and oval whorl-section, distinctly convergent flanks, narrow, high-rounded venter, and in a deep umbilicus. Moreover, it possesses paradischizotomous rib-division, which is not known in the other studied species. Type Ib ornamentation appears already at c. 73 mm diameter, whereas in all the other species of the genus *Liosphinctes* it appears at larger diameters.

OCCURRENCE: Poland. The specimen comes from a bed of undetermined stratigraphical position belonging to the upper Paturattensis Subzone or the lower Ouatius Subzone of the Plicatilis Zone (Text-fig. 6)

Liosphinctes cumnorensis (ARKELL, 1939)
(Text-figs 23, 27, 28)

1939. *Perisphinctes* (*Liosphinctes*) *cumnorensis* sp. nov.; ARKELL, vol. 5, p. 163 (*pars*), Text-figs 53, 54; Pl. 35, Fig. 1a-c only (holotype, *V.*); ? Pl. 34, Fig. 3a, b.

MATERIAL: Four specimens with complete or incomplete body-chamber. Their phragmocones are crushed flat; in some specimens the body-chamber is also crushed flat. The specimens come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.5, bed 2 and bed 4b, and from the Rudniki Quarry (Text-fig. 2, Appendix), section Rd., bed 4. IGPUW/A/36/180 (Text-fig. 27) was collected loose in the Wysoka Quarry. Additionally, some poorly preserved whorl-fragments, classified as *Liosphinctes* cf. *cumnorensis* (ARKELL), come from the Wysoka Quarry, section W.4, where they were collected loose from beds 16-17.

DESCRIPTION: IGPUW/A/36/180 (Text-fig. 27) is a nearly complete, probably mature individual, of $*D_m$=240 mm. The phragmocone ends at D_f=170 mm, and the septa are imperfectly exposed at this diameter; the body-chamber is 3/4 of a whorl, incomplete. IGPUW/A/36/181 is an incomplete, late juvenile specimen, of D_m=186 mm. The phragmocone ends at D_f=120 mm; a fragment of the last whorl of the phragmocone is broken away; the body-chamber is one whorl long, complete. IGPUW/A/36/182 and IGPUW/A/36/177 are juvenile individuals, of $*D_m$=115 mm and D_m=138 mm, respectively. The phragmocone ends at D_f=100 mm in IGPUW/A/36/182, and the body-chamber is 1/4 of a whorl, incomplete. In IGPUW/A/36/177, in which the septa are not exposed, the beginning of the body-chamber is not discernible.

The whorl-section of the phragmocone and of the body-chamber is oval (Text-fig. 23), moderately compressed. The maximum whorl-thickness is about mid-flank. In IGPUW/A/36/180 (Text-fig. 27) the whorl-section of the first 3/8 of the body-chamber is slightly trapezoidal, probably due to the partial crushing flat of the specimen, and oval in the second 3/8. The coiling changes from weakly evolute to moderately evolute on the inner and middle whorls. At diameters between 105 mm and 116 mm U/D ranges from 0.41 to 0.43, W/D ranges from 0.30 to 0.33, and W/U ranges from 0.61 to 0.79. In IGPUW/A/36/180 (Text-fig. 27) the coiling becomes evolute on the body-chamber; at 240 mm diameter U/D=0.58, W/D=0.24, and W/U=0.41. The ribbing is moderately coarse. The ribs are prorsiradiate on the whorl-flanks; occasionally, slightly flexuous on the phragmocone. The primary ribs bifurcate at 3/4 of the whorl-height; the division-points are somewhat indistinct. The ventral ribs remain visible up to c. 190 mm diameter and then fade away. Type Ia ornamentation (see ontogenetic ornamentation types, p. 346) occurs to the end of the phragmocone, up to a diameter of 170 mm. Type Ib then appears, and extends on the first half of the body-chamber, up to 190 mm diameter in IGPUW/A/36/180 (Text-fig. 27). The primary ribs bifurcate, and the division-points are slightly indistinct. Ventral ribs are also indistinct, but remain discernible up to 190 mm. After the constriction at 190 mm, type II ornamentation appears. It occurs on the second half of the body-chamber in IGPUW/A/36/180 (Text-fig. 27). The ribs (Text-fig. 28) increase in number from c. 40 per whorl at 30 mm diameter to maximally 56-66 between 110 mm and 140 mm. After these diameters the number of ribs remains more or less constant, and after c. 170 mm, approximately where type Ib appears, it decreases slowly, reaching c. 50 ribs per whorl at 240 mm. Constrictions are shallow, numbering 1-2 on the inner whorls, and 3 on the body-chamber.

Fig. 27. *Liosphinctes cumnorensis* (ARKELL): IGPUW/A/36/180 (specimen donated by Dr. H. Matyja); Wysoka, collected loose, *D_m=240 mm, D_f=170 mm, reduced × 0.75. Arrow indicates end of the phragmocone

DISCUSSION: *L. cumnorensis* differs from other representatives of the genus *Liosphinctes* in the moderately coarse ribbing. Additionally, type Ib ornamentation appears in this species at 150 mm-170 mm diameter, that is at the largest diameter among other species of the genus *Liosphinctes*.

OCCURRENCE: England, and Poland. First appears in the upper Paturattensis Subzone or lower Ouatius Subzone, and ranges higher up to the Arkelli Subzone. It disappears in the Platysphinctes horizon (Text-fig. 6).

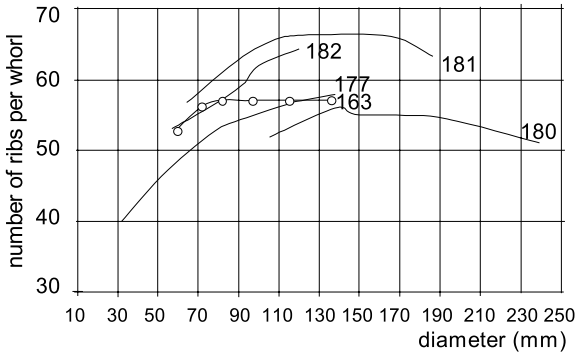

Fig. 28. Rib-density curves of *Liosphinctes cumnorensis* (ARKELL) and *Liosphinctes* sp. B (dot line); the specimens are numbered by only the last component of their full registration numbers

genus *Neumannia* gen. nov.

TYPE SPECIES: *Perisphinctes cyrilli* NEUMANN, 1907. The holotype (NEUMANN 1907, Pl. 4, Fig. 12a) is from the Middle Oxfordian of Četechovice in Moravia; it is stored at the Geological Institute of the University of Vienna, collection of J. NEUMANN.

DERIVATION OF NAME: In honour of Johann NEUMANN, the Austrian palaeontologist who described the species referred to as the genus *Neumannia* sp. nov. in the present paper.

DIAGNOSIS: Dimorphic. Densicostate; with bifurcating ribs and occasional simple ribs. Ribs rectiradiate, moderately thin to thin in macroconchs; thin in microconchs. Coiling evolute in macroconchs, occasionally on the inner whorls moderately evolute; moderately evolute in microconchs. Whorl-section of phragmocone circular in micro- and macroconchs, occasionally subquadrate in macroconchs. Whorl-section of adult body-chamber oval in both morphs, in macroconchs also subquadrate or depressed-subrectangular. Adult body-chamber in macroconchs smooth on venter and distinctly ribbed on whorl-flanks, with ribs somewhat pronounced on ventro-lateral margin.

REMARKS: *Neumannia* gen. nov. comprises species of Mediterranean affinity (ENAY 1966, BROCHWICZ-LEWIŃSKI 1973, BROCHWICZ-LEWIŃSKI & RÓŻAK 1976) described by NEUMANN (1907). It groups the macroconchs and their corresponding microconchs; the latter are described for the first time in the present paper.

ONTOGENETIC ORNAMENTATION TYPES: The shell ornamentation of the macroconchs of *Neumannia* gen. nov. is characterised by bifurcating ribs, with occasional simple ribs. The changes of shell-ornamentation consist in the appearance of intercalatory ribs on the venter in the later stages of ontogeny, in loss of distinctness of the ventral ribs, and in thickening of the ribs and their more distant spacing on the whorl-sides, which becomes clear on the adult body-chamber. The following ornamentation types are distinguished:

Type Ia: the secondary ribs, usually less distinct than the primary ribs, may be occasionally associated with an intercalatory rib

Type Ib: every pair of secondary ribs is associated with one intercalatory rib; the ventral ribs become indistinct.

Type II: the ribs on the whorl-flanks are thick; they are pronounced on the ventro-lateral margin but they disappear above it; the venter is smooth.

In two of the studied species, *Neumannia gyrus* (NEUMANN) and *Neumannia cyrilli* (NEUMANN), type Ia and type Ib ornamentation appear successively on the whorls of the phragmocone, and in the final part of the phragmocone is succeeded by type II ornamentation. The latter continues on the adult body-chamber. In the species *N.* aff. *cyrilli* type Ia ornamentation continues up to the end of the phragmocone, and is immediately succeeded by type II ornamentation on the adult body-chamber.

THE SEPTAL SUTURE: Septal sutures are poorly exposed in the studied material, except in the case of one specimen of *Neumannia gyrus* (NEUMANN). On the middle whorls of this species, the suspensive, external and lateral lobes are of different length: the longest is the suspensive lobe and the shortest is the lateral lobe (N>EL>L).

COMPARATIVE DESCRIPTION: *Neumannia* gen. nov. differs from the genus *Passendorferia* BROCHWICZ-LEWIŃSKI, 1973 in the smaller number of simple ribs; and in the body-chamber, distinctly ribbed on the whorl-sides and smooth on the venter in *Neumannia* gen. nov. and distinctly ribbed also on the venter in *Passendorferia*. The other characters, such as evolute coiling throughout ontogeny; circular whorl-section of the whorls of the phragmocone and oval of the body-chamber; thin to moderately thin ribs on the whorl-flanks; appearance on the body-chamber of ribs accentuated on the ventro-lateral margin, are similar in the two genera.

From the subgenus *Kranaosphinctes* BUCKMAN the macroconchs of *Neumannia* gen. nov. differ in the lack of parabolae; occasional appearance of simple ribs; thin to moderately thin ribs on the whorl-flanks and moderately thick or thick in *Kranaosphinctes*; primary ribs on the body-chamber accentuated on the ventro-lateral margin

in *Neumannia* gen. nov. but not in the subgenus *Kranaosphinctes*; usually circular whorl-section of the phragmocone in *Neumannia* gen. nov. In the subgenus *Kranaosphinctes* the whorl-section is usually subquadrate or subrectangular, except for *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI, in which, in contrast to the other species, it is circular. From the latter species, *Neumannia* gen. nov. differs in the lack of parabolae and the larger final size of adults. The rib-density in *Neumannia gyrus* (NEUMANN) decreases throughout the type Ib, Ic and type II ornamentation, in which this species resembles most of the species of the subgenus *Kranaosphinctes.* From the latter subgenus *N. gyrus* differs, however, in the thin primary ribs, densely spaced on the whorl-flanks. The septal suture of formula N>EL>L, recognized in *Neumannia* gen. nov., appears also in *Kranaosphinctes.* The latter subgenus shows, however, other suture patterns, not recognised in *Neumannia* gen. nov.

The species of the genus *Neumannia* gen. nov. differ from *Perisphinctes trifidus* (SOWERBY) in more evolute coiling at all stages of growth; circular, rarely subquadrate whorl-section on the phragmocone (in *P. trifidus* it is subrectangular); rare presence of simple ribs, lacking in *P. trifidus*; ribs on the body-chamber, accentuated on the ventro-lateral margin in *Neumannia* gen. nov. but not in *P. trifidus*. The septal suture of formula N>EL>L appears in the two compared forms; in *P. trifidus*, however, the other formulae also appear, which is not recognized in *Neumannia* gen. nov.

From the genus *Liosphinctes* BUCKMAN the genus *Neumannia* gen. nov. differs in the circular, rarely subquadrate whorl-section of the phragmocone and the oval, subquadrate, or depressed-subrectangular whorl-section of the body-chamber (in *Liosphinctes* the whorl-section of both the phragmocone and body-chamber is oval); usually evolute coiling, which is weakly evolute to evolute in *Liosphinctes*; occasional appearance of simple ribs, absent in *Liosphinctes*; lack of the non-bifurcating ribs characteristic of *Liosphinctes*. In *Neumannia* gen. nov. the body-chamber is distinctly ribbed on the whorl-flanks whereas in *Liosphinctes* it is almost smooth on the upper half-flank.

Neumannia sp.
the microconch allied to the species *Neumannia cyrilli* (NEUMANN, 1907), *Neumannia* aff. *cyrilli* (NEUMANN, 1907), and/or *Neumannia gyrus* (NEUMANN, 1907)
(Pl. 8, Figs 1, 4; Text-fig. 31)

MATERIAL: Two nearly complete specimens, with the peristomes broken away. They come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.5, bed 5a and from the Ogrodzieniec Quarry, section O.1, bed 8.

DESCRIPTION: IGPUW/A/36/421 (Pl. 8, Fig. 4) and IGPUW/A/36/422 (Pl. 8, Fig. 1) represent complete, mature specimens of $\underline{D}_m$=75 mm and $\underline{D}_m$=69 mm, respectively. The phragmocone ends at $\underline{D}_f$=49 mm in IGPUW/A/36/421, and at $\underline{D}_f$=40 mm in IGPUW/A/36/422; the body-chambers are 3/4 and 7/8 of a whorl respectively. The maturity in these specimens is indicated by changing of the whorl-section from circular on the phragmocone to oval on the body-chamber, and by approximation of the last ribs (IGPUW/A/36/422, Pl. 8, Fig. 1).

The coiling is moderately evolute at all stages of growth. At 30 mm diameter U/D=0.50, W/D=0.30, W/U=0.60 in the two specimens. At 60 mm in IGPUW/A/36/422 (Pl. 8, Fig. 1) U/D=0.51, W/D=0.27, W/U=0.55. At 75 mm in IGPUW/A/36/421 (Pl. 8, Fig. 4) U/D=0.52, W/D=0.27, W/U=0.52. The ribs are fine, straight, rectiradiate or nearly rectiradiate on the whorl-flanks, bifurcating. On the body-chamber in IGPUW/A/36/422 (Pl. 8, Fig. 1) simple ribs appear. The rib-number is 35-40 per whorl at 20 mm diameter. After this diameter the rib-number increases noticeably, up to 55-62 per whorl at 70 mm. Constrictions number 2-4 per whorl on the phragmocone, and 2 on the body-chamber. The septal suture is imperfectly exposed.

DISCUSSION: The circular whorl-section, moderately evolute coiling, the appearance of fine, dense ribbing, and the occurrence of simple ribs in the studied specimens indicate that *Neumannia* sp. is the microconch partner of *Neumannia cyrilli* (NEUMANN), *Neumannia* aff. *cyrilli* (NEUMANN) and/or *Neumannia gyrus* (NEUMANN). The actual dimorphic pairs are, however, not possible to recognize, due to the small number of specimens.

In the circular whorl-section of the phragmocone and in the fine, dense ribbing, the microconchs herein described resemble the early representatives of the subgenus *Otosphinctes* BUCKMAN: *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL (see p. 326). The microconchs of *Neumannia* gen. nov. differ from the latter in the compressed-oval whorl-section of the adult body-chamber and in the lack of parabolae.

OCCURRENCE: Poland. They range from the Platysphinctes horizon in the Arkelli Subzone of the Plicatilis Zone to the lower Buckmani Subzone of the Transversarium Zone (Text-fig. 6).

Neumannia cyrilli (NEUMANN, 1907)
(Pl. 9, Fig. 3; Text-figs 29-30)

1907. *Perisphinctes Cyrilli* n. f.; NEUMANN, p. 39, Pl. 4, Fig. 12a.
1966. *Perisphinctes* (*Kranaosphinctes*) *cyrilli* NEUMANN, 1907; ENAY, p. 433, Text-fig. 124; Pl. 18, Fig. 2.
1982. *Kranaosphinctes* cf. *cyrilli* (NEUMANN, 1907); MELÉNDEZ, SEQUEIROS, BROCHWICZ-LEWIŃSKI, p. 176, Pl. 3.
1989. *Kranaosphinctes cyrilli* (NEUMANN, 1907); MELÉNDEZ, p. 219, Text-fig. 44; Pl. 22, Fig. 1a,b.
non 1972a. *Perisphinctes* (*Kranaosphinctes*) cf. *cyrilli* NEUMANN; MALINOWSKA, p. 24, Text-fig. 3; Pl. 11, Fig. 4.
non 1972b. *Perisphinctes* (*Kranaosphinctes*) *cyrilli* NEUMANN; MALINOWSKA, p. 190, Text-figs 6, 11; Pl. 8, Figs 1, 2.

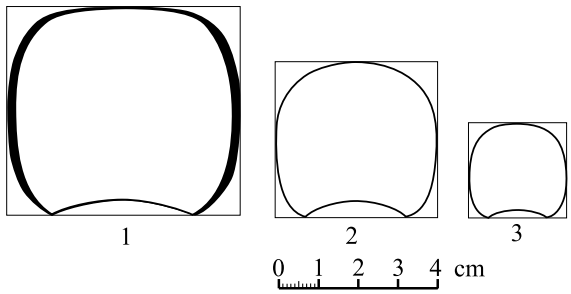

Fig. 29. Whorl-section of the genus *Neumannia* gen. nov. at a given diameter; *Neumannia cyrilli* (NEUMANN): 1. IGPUW/A/36/254 (Pl. 9, Fig. 3), D=240 mm. *Neumannia gyrus* (NEUMANN): 2. IGPUW/A/36/255 (Pl. 8, Fig. 3), D=165 mm; 3. IGPUW/A/36/252 (Pl. 7, Fig. 2), D=98 mm

MATERIAL: Five specimens: four with complete or nearly complete body chamber, and one incomplete phragmocone; all from the Wysoka Quarry (Text-fig. 2, Appendix), section W.5, beds 5b and 7b; section W.9', bed 22; and section W.9II, bed 4.

DESCRIPTION: IGPUW/A/36/254 (Pl. 9, Fig. 3) is a wholly septate specimen of $*D_m$=262 mm, representing possibly a mature individual. The other specimens are late juveniles; they range in D_m from 120 mm to 160 mm; the phragmocones end at D_f from 85 mm to 95 mm; the body-chamber, when complete, is one whorl long.

The whorl-section of the phragmocone is circular up to c. 100 mm diameter, then becomes subquadrate, and at c. 240 mm depressed-subrectangular (Text-fig. 29), slightly wider than high. The coiling is moderately evolute to evolute up to 70 mm, occasionally, up to 120 mm diameter. Then it changes to evolute. At diameters between 60 mm and 70 mm, U/D ranges from 0.48 to 0.55, W/D ranges from 0.23 to 0.27, and W/U ranges from 0.42 to 0.53. At diameters between 120 mm and 155 mm U/D ranges from 0.51 to 0.58, W/D ranges from 0.23 to 0.27, and W/U ranges from 0.39 to 0.53. At 250 mm in IGPUW/A/36/254 (Pl. 9, Fig. 3), U/D=0.58, W/D=0.23, and W/U=0.39. The ribs are moderately coarse, densely to moderately densely spaced on the whorl-flanks; they bifurcate. Type Ia ornamentation (see ontogenetic ornamentation types, p. 316) appears on the inner and middle whorls of the phragmocone, up to c. 160 mm. After this diameter, on the phragmocone in IGPUW/A/36/254 (Pl. 9, Fig. 3) type Ib ornamentation occurs, and after c. 240 mm, a quarter of whorl before the phragmocone at a break,

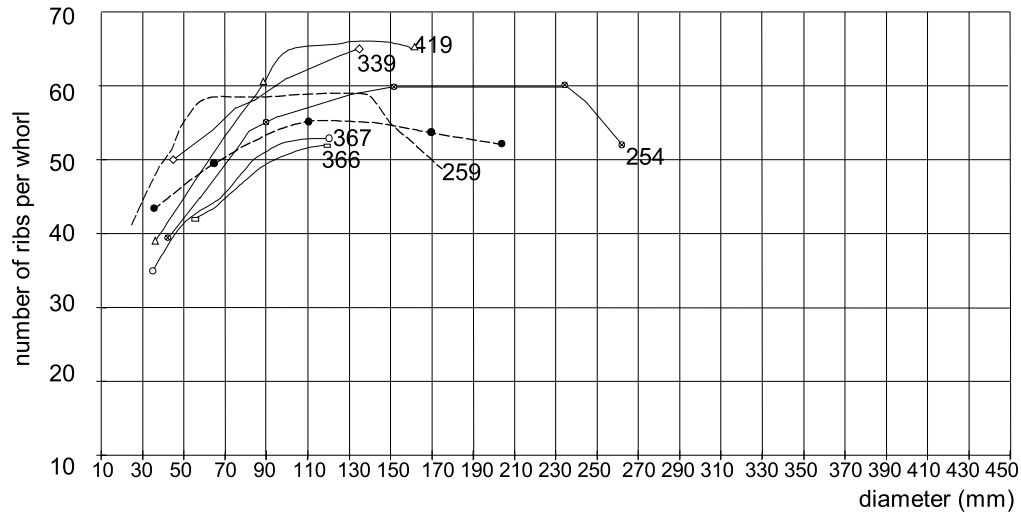

Fig. 30. Rib-density curves of the *Neumannia cyrilli* (NEUMANN) (continuous lines) and *Neumannia* aff. *cyrilli* (NEUMANN) (dashed line) compared to the holotype of *Neumannia cyrilli* (NEUMANN) (dashed line with dots); the specimens are numbered by only the last component of their full registration numbers

the ventral ribs become indistinct, and the primary ribs strengthen on the whorl-flanks. These characters correspond to type II ornamentation. The end of the phragmocone and the body-chamber are broken away in this specimen. The rib-number (Text-fig. 30) is c. 42 per whorl, occasionally attains 51 per whorl at 50 mm diameter. After this diameter the rib-number increases noticeably, and at 100 mm reaches 50-65 per whorl. Between 100 mm and 150 mm the rib-number per whorl remains constant or increases insignificantly. In IGPUW/A/36/254 (Pl. 9, Fig. 3, Text-fig. 30), showing the most complete rib-density curve, the rib-number remains constant, numbering 60 per whorl between 150 mm and 240 mm diameter. After 240 mm diameter the rib-number decreases to 52 per whorl at 262 mm. Constrictions are shallow, numbering 1-2 per whorl. The suture is imperfectly exposed.

DISCUSSION: In contrast to the holotype of the species *N. cyrilli* (see NEUMANN 1907, Pl. 4, Fig. 12a) the studied specimens lack the simple ribs.

OCCURRENCE: Četechovice in Moravia, France, Spain, and Poland. It ranges from the top of the Arkelli Subzone of the Plicatilis Zone to the lower Buckmani Subzone of the Transversarium Zone (Text-fig. 6).

Neumannia aff. *cyrilli* (NEUMANN, 1907)
(Pl. 8, Fig. 2, Text-fig. 30)

MATERIAL: Two specimens consisting of complete or incomplete body-chambers and crushed or partially abraded phragmocones. All from the Wysoka Quarry (Text-fig. 2, Appendix), section W.5, one from bed 6b, and the other collected loose from beds 4-7.

DESCRIPTION: IGPUW/A/36/259 (Pl. 8, Fig 2) is an incomplete, possibly mature individual, of $*D_m$=175 mm. The phragmocone ends at D_f=140 mm. The last half-whorl of the phragmocone is abraded, and the septa are imperfectly exposed. The body-chamber is half a whorl, and the second part of it is broken away. IGPUW/A/36/420 is a complete, juvenile individual, of D_m=110 mm; the phragmocone ends at D_f=65 mm, the body-chamber occupies one whorl.

The whorl-section is circular on the phragmocone and on the juvenile body-chamber. On the adult body-chamber in IGPUW/A/36/259 (Pl. 8, Fig. 2) it changes to oval. The coiling is moderately evolute to evolute up to 60 mm diameter, then it becomes evolute. At 60 mm U/D ranges from 0.45 to 0.50, W/D=0.25, W/U ranges from 0.50 to 0.55. At 160 mm in IGPUW/A/36/259 (Pl. 8, Fig. 2) U/D=0.54, W/D=0.24, W/U=0.45. The ribbing is fine and dense on the phragmocone and in the beginning of the body-chamber, where it still represents type Ia ornamentation (see ontogenetic ornamentation types, p. 354). On the second half of the adult body-chamber in IGPUW/A/36/259 (Pl. 8, Fig. 2) type II ornamentation appears: the ribs become strong on the whorl-flanks, accentuated on the ventro-lateral margin, above it they fade away entirely, leaving the venter smooth. The rib-number (Text-fig. 30) is 40-43 per whorl at 30 mm; then it increases rapidly reaching c. 60 ribs per whorl at 70 mm. Between 70 mm and 140 mm diameter the rib-number per whorl remains approximately constant or slightly decreases. After 140 mm the rib-number decreases more rapidly, reaching 49 per whorl at $*D_m$=175 mm in IGPUW/A/36/259 (Pl. 8, Fig. 2).

DISCUSSION: *N.* aff. *cyrilli* differs from *N. cyrilli* in the oval whorl-section of the body-chamber, as compared to depressed-subrectangular in *N. cyrilli*; in fine and densely spaced ribs on the whorls of the phragmocone; in type Ia ornamentation being present up to the end of the phragmocone and on the beginning of the body-chamber, and being followed by type II ornamentation on the second half of the body-chamber. In *N. cyrilli* type Ib ornamentation appears already on the phragmocone and type II ornamentation appears on the final part of the phragmocone and on the body-chamber. The final size of *N.* aff. *cyrilli* is possibly smaller than in *N. cyrilli*; in the former species the body-chamber starts at $\underline{D_f}$=140 mm, whereas in the latter one, at *D=262 mm the phragmocone ends at a break.

OCCURRENCE: Poland. It ranges in the upper part of the Arkelli Subzone of the Plicatilis Zone and possibly in the lower part of the Buckmani Subzone of the Transversarium Zone (Text-fig. 6).

Neumannia gyrus (NEUMANN, 1907)
(Pl. 7, Figs 1-2; Pl. 8, Fig. 3; Text-fig. 29, 31)

1887. *Perisphinctes promiscuus* n.f.; BUKOWSKI, p. 137, Pl. 28, Fig. 1 (syntype, *V.*).
1907. *Perisphinctes gyrus* n.f.; NEUMANN, p. 37, Tab. 3; Fig. 11a, b.
1952. *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI; SIEGFRIED, p. 310, Tab. G, Fig. 1 (without synonymy).
1995. *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI; GYGI, p. 31, Figs 12-13; Tab. 4 (without synonymy).

MATERIAL: Seven specimens; two of them have incomplete phragmocones and incomplete body-chambers, the

others are complete or nearly complete. The specimens come from the Wysoka Quarry (Text-fig. 2, Appendix), section W.5, beds 4c, 5b; section W.5', bed 7b; section W.8, bed 13; section W.9', bed 22; and from the Ogrodzieniec Quarry (Text-fig. 3, Appendix), section O.2, bed 2; and section O.4', bed 3.

DESCRIPTION: IGPUW/A/36/357 (Pl. 7, Fig. 1) is an incomplete, mature specimen, of $*D_m$=210 mm. It shows approximation of the septa at $\underline{D_f}$=150 mm. The body-chamber is 3/4 of a whorl, with the middle quarter of the body-chamber broken away, and with last quarter crushed flat. IGPUW/A/36/255 (Pl. 8, Fig. 3) is of $*D_m$=210 mm, and represents possibly a mature individual. The phragmocone ends at D_f=170 mm, the body-chamber is half a whorl, incomplete. The other specimens in the collection are juveniles. They range in D_m from 113 mm to 160 mm, their body-chambers start at D_f ranging from 75 mm to 132 mm, and, if complete, they occupy one whorl. The whorl-section is circular on the inner whorls of the phragmocone, subquadrate on the outer whorl of the phragmocone, and subrectangular on the body-chamber. The coiling is evolute to moderately evolute up to c. 70 mm; at larger diameters it changes to evolute. At c. 70 mm U/D=0.48-0.53, W/D=0.25-0.30, W/U=0.43-0.56. At c. 160 mm U/D=0.55-0.59, W/D=0.22-0.24, W/U=0.38-0.43. The ribs are moderately thin and sharp, straight and rectiradiate. They are densely spaced on the phragmocone, and become distant on the body-chamber. The ribs bifurcate. Type Ia ornamentation (see ontogenetic ornamentation types, p. 316) appears on the inner and middle whorls of the phragmocone, up to the diameter 120 mm-130 mm. After these diameters, on the outer whorl of the phragmocone and on the beginning of the body-chamber, type Ib ornamentation appears. After 180 mm-190 mm diameter, a quarter of whorl before the body-chamber ends due to the fracture in IGPUW/A/36/255 (Pl. 8, Fig. 3), type II ornamentation appears: the ventral ribs fade away, and the ribs on the whorl-flanks become strong and ridge-like, accentuated on the ventro-lateral margin, and fading away entirely above it, leaving the venter completely smooth. The rib-number (Text-fig. 31) is 37-43 per whorl at 30 mm. Then it increases: first rapidly, reaching 40-50 ribs per whorl at 50 mm diameter, and then slowly, reaching 48-55 ribs per whorl at c. 100 mm diameter, and then remains constant. After the diameter 110 mm-120 mm the rib-number per whorl lowers. At the diameter 185 mm-200 mm there are 42-47 ribs per whorl. The constrictions appear occasionally, except IGPUW/A/36/252 (Pl. 7, Fig. 2), in which there appear on the phragmocone 1-2 constrictions per whorl. The suture is N>EL>L at D=115 mm and at $\underline{D_f}$=150 mm in IGPUW/A/36/357 (Pl. 7, Fig. 1).

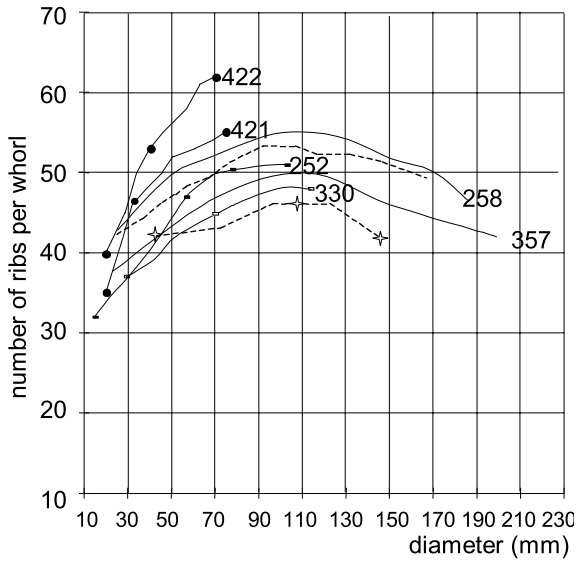

Fig. 31. Rib-density curves of *Neumannia gyrus* (NEUMANN) (dashed line is for the holotype of *N. gyrus*, and of *Neumannia* sp. (microconchs) (IGPUW/A/36/421, IGPUW/A/36/422). Rib-density curves of the syntype of *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI (1887, Pl. 28, Fig 1) is also given (dashed line with stars); the specimens are numbered by only the last component of their full registration numbers

DISCUSSION: NEUMANN (1907) hesitated to treat the syntype of *Perisphinctes promiscuus* BUKOWSKI (see BUKOWSKI 1887, Pl. 28, Fig. 1) as conspecific with *N. gyrus*, due to the incompleteness and distortion of the last whorl in BUKOWSKI's syntype. In the opinion of the present author, the cast of the phragmocone and the outer whorl of the syntype of *P. promiscuus* (BUKOWSKI 1887, Pl. 28, Fig. 1) allow its specific identification. BUKOWSKI's syntype agrees with *N. gyrus* in moderately thin and sharp ribs, straight and rectiradiate on the phragmocone; in reduction of rib-number per whorl at diameters greater than 110 mm (Text-fig. 31), corresponding approximately to the appearance of type Ib ornamentation, and in evolute coiling. In addition, in BUKOWSKI's syntype, at 160 mm diameter U/D=0.54, W/D=0.54, W/U=0.50, in which it agrees with *N. gyrus* (see also the discussion on p. 338 and p. 339).

OCCURRENCE: Germany, Switzerland, Czech Republic, and Poland. It appears in the Platysphinctes horizon in the Arkelli Subzone of the Plicatilis Zone, and ranges up to the lower Buckmani Subzone of the Transversarium Zone (Text-fig. 6).

CONCLUSIONS

1. Taxonomic and phylogenetic interpretation of the perisphinctids from the lower Middle Oxfordian is based on the variability of the successive ammonites assemblages recognized in the Submediterranean sections of the Polish Jura Chain.

2. The species are assigned to the genera *Perisphinctes* WAAGEN, *Liosphinctes* BUCKMAN and to the new Mediterranean genus, *Neumannia* (m, M); these genera, as interpreted in the present paper, represent single phylogenetical lineages.

3. Two microconch morphs are described for the first time; one of them is assigned to the genus *Neumannia* gen. nov. and the other to the species *Perisphinctes trifidus* (SOWERBY).

4. *P. trifidus* (m, M) as interpreted herein, is a geographically variable species.

5. *Perisphinctes ariprepes* (BUCKMAN), the type species of the subgenus *Arisphinctes* BUCKMAN, is reassigned to the subgenus *Kranaosphinctes* BUCKMAN, and thus the former subgenus is treated as a younger synonym of the latter.

6. *Perisphinctes plicatilis* (SOWERBY) and *Perisphinctes laevipickeringius* ARKELL are reinterpreted herein, and reassigned to the genus *Liosphinctes*.

7. The successive groups of micro- and macroconch counterparts of the subgenera *Otosphinctes* and *Kranaosphinctes* respectively, are distinguished; these "groups" are comparable to natural biospecific units and their succession is recognized as a single lineage.

8. The *Kranaosphinctes-Otosphinctes* lineage disappears at the boundary between the Plicatilis and Transversarium zones giving rise to the species of the *Perisphinctes-Dichotomosphinctes* lineage.

9. Of the other lineages recognized in the study area, the *Liosphinctes* lineage and the *P. trifidus* lineage disappear in the upper Plicatilis Zone; almost simultaneously appear immigrant species of the Mediterranean genus *Neumannia* gen. nov. and *Platysphinctes perplanatus* TINTANT.

10. The Plicatilis Zone of the Middle Oxfordian is subdivided in the present paper into three subzones: the Paturattensis Subzone below, the Ouatius Subzone and the Arkelli Subzone above; the subzonal boundaries are defined by the appearance of the successive species of the *Kranaosphinctes-Otosphinctes* lineage.

11. The boundary between the Plicatilis and Transversarium zones is redefined in the present scheme, and marked at the level of disappearance of the last species of the subgenera *Otosphinctes* and *Kranaosphinctes*, and appearance of the first species of the subgenera *Dichotomosphinctes* BUCKMAN and *Perisphinctes* s. str: *Perisphinctes antecedens* SALFELD and *Perisphinctes* aff. *maximus* (YOUNG & BIRD) respectively; this level is marked by distinct morphological change in the perisphinctid succession.

12. The Plicatilis Zone as proposed herein is stratigraphically shorter than the Plicatilis Zone in the schemes for north-west Europe (SYKES & CALLOMON 1979) and for south-west Europe (CARIOU & *al*. 1991); the two latter schemes include in the upper part of the Plicatilis Zone the beds with *P*. (*D*.) *antecedens*, which are excluded from this zone in the scheme defined herein.

Acknowledgements

This monograph is a part of my Ph.D. thesis completed at the University of Warsaw. I am deeply indebted to my supervisor, Professor A. WIERZBOWSKI, University of Warsaw, for his valuable discussions in the course of my studies on the Middle Oxfordian perisphinctids, and his comments on this paper.

I thank the reviewers, Professor J. H. CALLOMON and Dr. J. K. WRIGHT, the journal referees, for their constructive criticism. I am grateful to Mr. C. J. WOOD, Croydon for his valuable comments and corrections improving the final version of this paper. I also wish to thank Dr. K. PAGE, English Nature, Exeter, Dr. H. SUMMESBERGER, Natural History Museum, Vienna, and to Professor J. TRAMMER, University of Warsaw, who helped to improved the final version of this paper. The photographs of ammonites were taken by Mr. S. KOLANOWSKI. The financial support of the KOPIPOL Foundation is acknowledged.

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Manuscript submitted: 10th May 2001
Revised version accepted: 15th May 2002

APPENDIX

BIOSTRATIGRAPHICAL DETAILS OF THE STUDIED SECTIONS

In the study area the lower boundary of the Plicatilis Zone is recognised in section W.6', at the top of bed 30 (Text-fig. 2) and in section O.4 in the upper part of bed 1l (Text-fig. 3).

The base of the Paturattensis Subzone in the Wysoka Quarry is recognized in section W.6', at the top of bed 30 (Text-fig. 2); and in the Ogrodzieniec Quarry in section O.4, in the upper part of bed 1l (Text-fig. 3).

The base of the Ouatius Subzone is recognised in the Wysoka Quarry in section W.4, at the bottom of bed 17a (Text-fig. 2).

The base of the Arkelli Subzone appears in the Wysoka Quarry in section W.9", at the bottom of bed 12a (Text-fig. 2).

The Platysphinctes horizon is recognised in the Wysoka Quarry in sections W.5, W.8, W.9, W.9', W.9" (Text-fig. 2, see also GŁOWNIAK 2000) and in sections O.1, O.4 (Text-fig. 3).

The base of the Transversarium Zone is recognised in the Wysoka Quarry (Text-fig. 2) in section W.4, at the bottom of bed 11; W.5, at the bottom of bed 7a; W.5', at the bottom of bed 7a; W.9, at the bottom of bed 18; and W.9', at the bottom of bed 20. In the Ogrodzieniec Quarry (Text-fig. 3) the base of the Transversarium Zone lies in sections O.1, at the bottom of bed 8; O.2, at the bottom of bed 2; and in O.4, at the bottom of bed 7.

AMMONITE CONTENT AND DISTRIBUTION IN THE STUDIED SECTIONS

Section W.2' (Text-fig. 2)

bed 22: *Perisphinctes trifidus* (SOWERBY) (m); *Liosphinctes* sp. A.

Section W.4

(*pars*, Plicatilis Zone and the lower Transversarium Zone only, Text-fig. 2)

bed 5b: *Perisphinctes* (*Perisphinctes*) *tumulosus* BUCKMAN.

bed 11: *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD (four specimens).

bed 12: *Perisphinctes* (*Otosphinctes*) cf. *arkelli wysokae* chronossp. nov. (two specimens).

bed 16-17: *Liosphinctes* cf. *cumnorensis* (ARKELL).

bed 16: *Perisphinctes trifidus* (SOWERBY) (m) (two specimens); *P.* cf. *trifidus* (SOWERBY) (m); *Perisphinctes* (*Kranaosphinctes*) *decurrens* (BUCKMAN), *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN).

bed 17c: *P.* (*O.*) *ouatius ouatoides* chronossp. nov. (*ouatius* morphotype and *ouatoides* morphotype); *P. trifidus* (SOWERBY) (m); *P.* (*K.*) *kranaus* (BUCKMAN).

bed 17b: *P.* (*O.*) *ouatius ouatoides* chronossp. nov. (two specimens of *ouatoides* morphotype); *P. trifidus* (SOWERBY) (M: *trifidus* morphotype) (two specimens).

bed 17 (a-c): *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. (*ouatoides* morphotype); *Perisphinctes* (*Kranaosphinctes*) *vorda* ARKELL.

bed 17a: *P. trifidus* (SOWERBY) (m); *P.* cf. *trifidus* (SOWERBY) (m), *Liosphinctes plicatilis* (SOWERBY).

bed 17 (a-c): *P.* (*O.*) *ouatius ouatoides* chronossp. nov.; *P.* (*K.*) *vorda* ARKELL.

bed 18 (a-c): *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL (*paturattensis* morphotype: one specimen, and *montfalconensis* morphotype: one specimen); *Liosphinctes* cf. sp. A; *Perisphinctes* (*Kranaosphinctes*) cf. *promiscuus* BUKOWSKI, *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI).

bed 19a: *P.* (*O.*) *paturattensis* DE LORIOL (*paturattensis* morphotype).

Section W.4III (Text-fig. 2)

bed 2: *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN) (*ouatius* morphotype); *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK.

bed 3: *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN).

bed 4: *P.* (*K.*) *kranaus* (BUCKMAN); *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN) (two specimens).

bed 5: *Perisphinctes* (*Kranaosphinctes*) *decurrens* (BUCKMAN).

bed 6: *Liosphinctes plicatilis* (SOWERBY).

bed 10: *Perisphinctes* (*Otosphinctes*) cf. *ouatius ouatoides* chronossp. nov. (*ouatoides* morphotype); *L. plicatilis* (SOWERBY); *Liosphinctes laevipickeringius* (ARKELL).

bed 12: *Liosphinctes* sp. B.

bed 19: *Perisphinctes trifidus* (SOWERBY) (M: *helenae* morphotype).

beds 6-20: *L.* cf. *plicatilis* (SOWERBY) (collected loose).

bed 20: *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL (*paturattensis* morphotype); *L. plicatilis* (SOWERBY); *L.* cf. *plicatilis* (SOWERBY).

bed 21: *P.* (*O.*) *paturattensis* DE LORIOL (*paturattensis* morphotype: two specimens); *L. plicatilis* (SOWERBY); *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI).

Section W.5

(Text-fig. 2; see also GŁOWNIAK 2000, Text-fig. 3)

bed 9: *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD.

bed 8: *P.* (*D.*) *antecedens* SALFELD (five specimens); *Perisphinctes* (*Dichotomosphinctes*) *buckmani* ARKELL (two specimens); *Perisphinctes* (*Perisphinctes*) *tumulosus* BUCKMAN.

beds 8-9: *P.* (*D.*) *buckmani* ARKELL (collected loose).

bed 7b/8: *P.* (*D.*) *buckmani* ARKELL.

bed 7b: *P.* (*D.*) *antecedens* SALFELD (six specimens); *P.* (*D.*) *buckmani* ARKELL; *Neumannia cyrilli* (NEUMANN).

bed 7a: *P.* (*D.*) *antecedens* SALFELD (thirteen specimens); *Perisphinctes* (*Perisphinctes*) aff. *maximus* (YOUNG & BIRD) (three specimens).
beds 7-8: *P.* (*P.*) aff. *maximus* (YOUNG & BIRD) (collected loose)
bed 6c: *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov.
bed 6b: *P.* (*O.*) *arkelli wysokae* chronossp. nov. (two specimens); *Neumannia* aff. *cyrilli* (NEUMANN).
bed 6a: *P.* (*O.*) *arkelli wysokae* chronossp. nov.
bed 5b: *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN) (*ouatius* morphotype); *P.* (*O.*) *arkelli wysokae* chronossp. nov. (two specimens); *Neumannia gyrus* (NEUMANN); *Neumannia cyrilli* (NEUMANN) (top of the bed 5b).
bed 5a: *Platysphinctes perplanatus* (m, M) TINTANT; *Neumannia* sp. (microconch) (top of bed 5a).
bed 4c: *P. perplanatus* (M) TINTANT; *N. gyrus* (NEUMANN) (top of bed 4c).
bed 4b: *P. perplanatus* (m) TINTANT; *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK; *Liosphinctes cumnorensis* (ARKELL).
beds 4-7: *N.* aff. *cyrilli* (NEUMANN) (collected loose).
bed 3: *Perisphinctes trifidus* (SOWERBY) (m); *P.* (*O.*) cf. *ouatius ouatius* (BUCKMAN) (*ouatius* morphotype), *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN).
bed 2: *Liosphinctes cumnorensis* (ARKELL).
bed 1: *P. trifidus* (SOWERBY) (m); *P.* (*O.*) cf. *ouatius ouatius* (BUCKMAN) (*magnouatius* morphotype).
beds 1-3: *P.* (*K.*) *kranaus* (BUCKMAN) (collected loose).

Section W.5' (Text-fig. 2)

bed 9: *Perisphinctes* (*Dichotomosphinctes*) cf. *buckmani* ARKELL.
bed 8/9: *Perisphinctes* (*Perisphinctes*) aff. *maximus* (YOUNG & BIRD).
bed 8: *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD; *P.* (*D.*) *buckmani* ARKELL; *P.* (*P.*) aff. *maximus* (YOUNG & BIRD).
bed 7/8: *P.* (*D.*) *antecedens* SALFELD.
bed 7b: *Neumannia gyrus* (NEUMANN); *P.* (*D.*) *antecedens* SALFELD (two specimens); *P.* (*P.*) aff. *maximus* (YOUNG & BIRD).
bed 7a/b: *P.* (*D.*) *buckmani* ARKELL.
bed 7a: *P.* (*D.*) *antecedens* SALFELD (four specimens); *P.* (*P.*) aff. *maximus* (YOUNG & BIRD) (two specimens).
bed 6b/7a: *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov. (two specimens).

Section W.6 (Text-fig. 2)

bed 26b: *Perisphinctes* (*Otosphinctes*) cf. *paturattensis* DE LORIOL (*paturattensis* morphotype).
bed 26a: *Liosphinctes plicatilis* (SOWERBY).
bed 27 (a-e): *Perisphinctes trifidus* (SOWERBY) (M: *trifidus* morphotype) (collected loose).
bed 27a: *P.* (*O.*) *paturattensis* DE LORIOL (*paturattensis* morphotype: four specimens, *montfalconensis* morphotype: one specimen); *P. trifidus* (SOWERBY) (M: *helenae* morphotype); *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI.
bed 27b: *P.* (*O.*) *paturattensis* DE LORIOL (*paturattensis* morphotype).
bed 28a: *P.* (*O.*) *paturattensis* DE LORIOL (*paturattensis* morphotype: three specimens); *P.* (*O.*) cf. *paturattensis* DE LORIOL (*montfalconensis* morphotype); *Liosphinctes plicatilis* (SOWERBY).
bed 28b: *P.* (*O.*) *paturattensis* DE LORIOL; *P. trifidus* (SOWERBY) (M: *helenae* morphotype); *P.* (*K.*) *promiscuus* BUKOWSKI.
bed 28c: *P.* (*O.*) *paturattensis* DE LORIOL (*paturattensis* morphotype: two specimens); *P.* (*O.*) cf. *paturattensis* DE LORIOL (*paturattensis* morphotype); *P. trifidus* (SOWERBY) (m); *Liosphinctes plicatilis* (SOWERBY) (two specimens); *L.* cf. *plicatilis* (SOWERBY); *P.* (*K.*) *promiscuus* BUKOWSKI (two specimens).

Section W.6' (Text-fig. 2)

bed 27 (a-e): *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL (*montfalconensis* morphotype); *P.* (*O.*) cf. *paturattensis* DE LORIOL (*paturattensis* morphotype).
bed 28h: *P.* (*O.*) cf. *paturattensis* DE LORIOL (*paturattensis* morphotype).
bed 28d/e: *Perisphinctes trifidus* (SOWERBY) (M: *trifidus* morphotype).
bed 28d: *Liosphinctes plicatilis* (SOWERBY).
bed 28c/d: *P. trifidus* (SOWERBY) (M: *trifidus* morphotype).
beds 27-28: *P. trifidus* (SOWERBY) (M: *helenae* morphotype) (collected loose).
bed 29: *P.* (*O.*) cf. *paturattensis* DE LORIOL (*paturattensis* morphotype); *Cardioceras* (*Plasmatoceras*) sp.
bed 30: *P.* (*O.*) *paturattensis* DE LORIOL (*paturattensis* morphotype).

Section W.8
(Text-fig. 2, see also GŁOWNIAK 2000, Text-fig. 3)

bed 13: *Neumannia gyrus* (NEUMANN).
bed 12: *Platysphinctes perplanatus* (m, M) TINTANT.
bed 11: *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK (three specimens).
bed 10: *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN) (*magnouatius* morphotype).
bed 6: *Perisphinctes* (*Kranaosphinctes*) cf. *kranaus* (BUCKMAN).
bed 4: *Perisphinctes* (*Otosphinctes*) cf. *ouatius ouatius* (BUCKMAN) (*ouatius* morphotype).
bed 2a: *Perisphinctes trifidus* (SOWERBY) (M: *helenae* morphotype); *Liosphinctes* cf. *laevipickeringius* (ARKELL).
bed 1e: *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. (*ouatoides* morphotype).

Section W.9

(Text-fig. 2; see also GŁOWNIAK 2000, Text-fig. 3)

bed 20: *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD.

bed 18: *P.* (*D.*) *antecedens* SALFELD (two specimens).

bed 16 (a-b): *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov.

bed 16a: *P.* (*O.*) *arkelli wysokae* chronossp. nov.

bed 14a: *Platysphinctes perplanatus* (m, M) TINTANT; *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN) (*ouatius* morphotype).

bed 11: *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN) (two specimens).

bed 10: *P.* (*O.*) *ouatius ouatius* (BUCKMAN) (two specimens of *ouatius* morphotype; three specimens of *magnouatius* morphotype); *P.* (*K.*) *ariprepes* (BUCKMAN) (two specimens).

bed 9: *P.* (*O.*) *ouatius ouatius* (BUCKMAN) (*magnouatius* morphotype).

Section W.9'

(Text-fig. 2; see also GŁOWNIAK 2000, Text-fig. 3)

bed 22: *Neumannia gyrus* (NEUMANN); *Neumannia cyrilli* (NEUMANN) (two specimens).

bed 20: *Perisphinctes* (*Perisphinctes*) aff. *maximus* (YOUNG & BIRD).

bed 16: *Platysphinctes perplanatus* (m) (TINTANT).

bed 8.6: *Perisphinctes trifidus* (SOWERBY) (M: *trifidus* morphotype).

bed 8.2a: *Perisphinctes* (*Kranaosphinctes*) *cf. kranaus* (BUCKMAN).

bed 8.2c: *P.* (*K.*) *kranaus* (BUCKMAN).

Section W.9"

(Text-fig. 2; see also GŁOWNIAK 2000, Text-fig. 3)

bed 20: *Platysphinctes perplanatus* (m, M) TINTANT.

bed 18: *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN).

bed 16: *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK (two specimens); *P.* (*K.*) *kranaus* (BUCKMAN); *P.* (*K.*) *ariprepes* (BUCKMAN) (three specimens).

bed 12b: *P.* (*O.*) *arkelli arkelli*; *P.* (*O.*) cf. *ouatius ouatius* (BUCKMAN) (*ouatius* morphotype); *P.* (*K.*) *ariprepes* (BUCKMAN); *Perisphinctes trifidus* (SOWERBY) (M: *helenae* morphotype).

bed 12a: *P.* (*O.*) *ouatius ouatius* (BUCKMAN) (*magnouatius* morphotype); *P.* (*O.*) *arkelli arkelli* GŁOWNIAK; *P.* (*K.*) *ariprepes* (BUCKMAN).

bed 8.6: *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI).

bed 8.1a-c: *Liosphinctes* cf. *plicatilis* (SOWERBY).

bed 8.1g: *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL (*paturattensis* morphotype); *P. trifidus* (SOWERBY) (M: *helenae* morphotype).

Section W.9II (Text-fig. 2)

bed 4: *Neumannia cyrilli* (NEUMANN).

bed 5: *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD.

bed 7: *P.* (*D.*) *antecedens*.

Section O.1

(*pars*, the Plicatilis and the lower Transversarium Zone only, Text-fig. 3; see also GŁOWNIAK 2000, Text-fig. 3)

bed 8: *Neumannia* sp. (microconch); *Perisphinctes* (*Dichotomosphinctes*) cf. *antecedens* SALFELD.

bed 3: *Platysphinctes perplanatus* (m) TINTANT.

bed 2 (top): *P. perplanatus* (m, M) TINTANT.

bed 1a: *Perisphinctes* (*Otosphinctes*) cf. *ouatius ouatoides* chronossp. nov. (*ouatoides* morphotype); *Perisphinctes trifidus* (SOWERBY) (M: *helenae* morphotype).

bed 1c: *P.* (*O.*) *ouatius ouatoides* chronossp. nov. (*ouatoides* morphotype).

Section O.2

(*pars*, the Plicatilis Zone and the lower Transversarium Zone only, Text-fig. 3)

bed 2: *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD (ten specimens); *Neumannia gyrus* (NEUMANN).

bed 1d: *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov.

Section O.4

(Text-fig. 3; see also GŁOWNIAK 2000 Text-fig. 3)

bed 7: *Perisphinctes* (*Dichotomosphinctes*) *antecedens* SALFELD.

bed 3: *Platysphinctes perplanatus* (m, M) TINTANT.

bed 2c: *P. perplanatus* (m, M) TINTANT.

bed 1j: *Liosphinctes* sp. A.

bed 1l: *L.* sp. A; *Cardioceras* (*Plasmatoceras*) *tenuicostatum* (NIKITIN) (top of bed).

bed 1m: *Cardioceras* (*Cardioceras*) *persecans* BUCKMAN, *C.* (*C.*) *ashtonense* ARKELL.

bed 1p: *Perisphinctes* (*Otosphinctes*) cf. *paturattensis* DE LORIOL (*paturattensis* morphotype).

Section O.4' (Text-fig. 3)

bed 3: *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov.; *Neumannia gyrus* (NEUMANN).

Section Rd. (Text-fig. 2)

bed 3: *Perisphinctes* (*Otosphinctes*) cf. *ouatius ouatius* (BUCKMAN) (*ouatius* morphotype).

bed 4: *Liosphinctes cumnorensis* (ARKELL).

bed 6: *Perisphinctes trifidus* (SOWERBY) (m).

bed 10: *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL (*paturattensis* morphotype).

bed 12: *P.* (*O.*) cf. *paturattensis* DE LORIOL (*paturattensis* morphotype).

bed 14: *P.* (*O.*) *paturattensis* (*paturattensis* morphotype); *P.* (*O.*) cf. *paturattensis* (*paturattensis* morphotype).

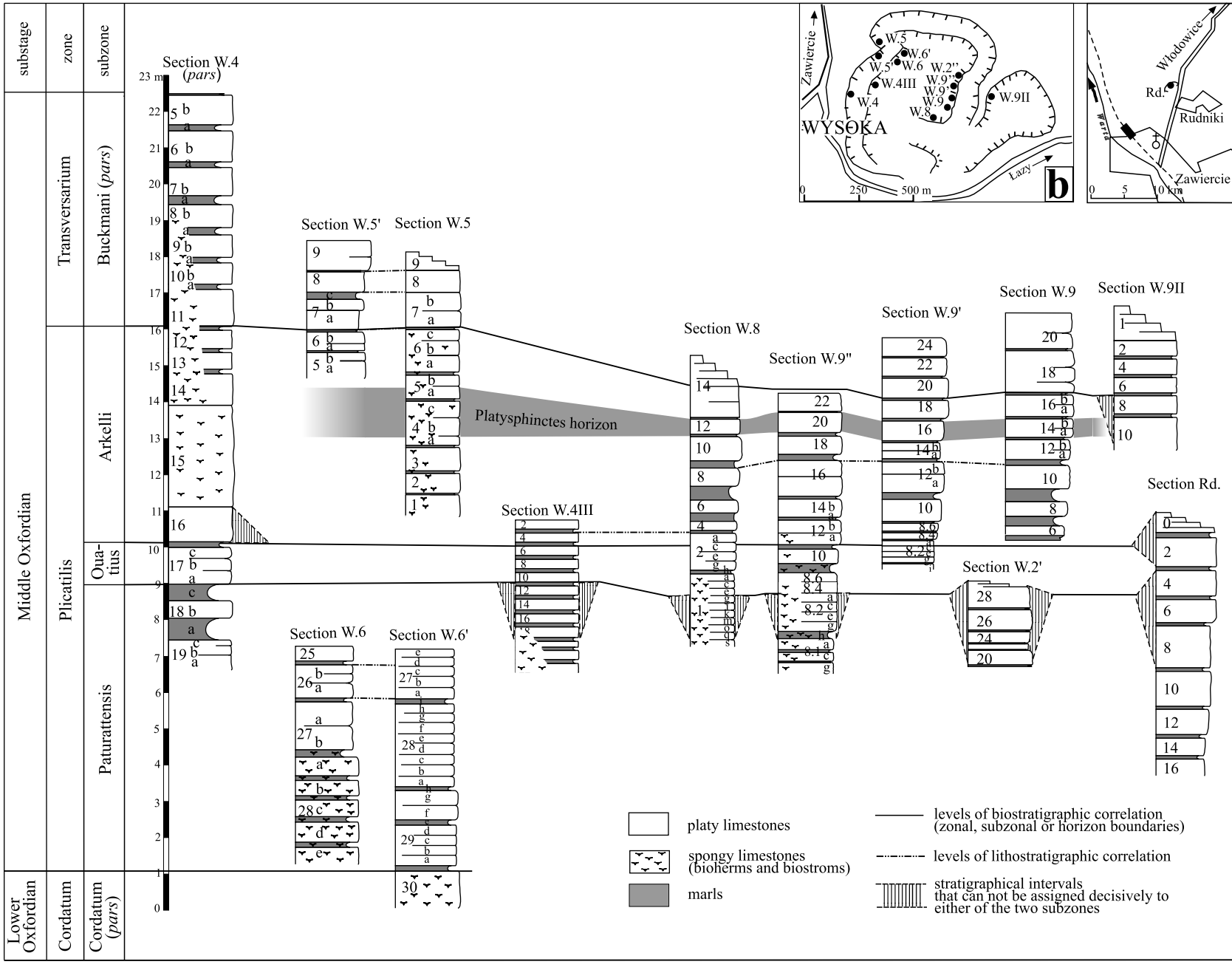

Fig. 2. Correlation of sections from Wysoka Quarry and from Rudniki Quarry (a) and their location in Wysoka Quarry (b) and in Rudniki (c)

PLATE 1

1-2 – *Perisphinctes* (*Kranaosphinctes*) *promiscuus* BUKOWSKI, 1887
1 – IGPUW/A/36/288; Wysoka, W.6, bed 28c; 2 – IGPUW/A/36/282; Wysoka, W.6, bed 28c

3 – *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL, 1901 (*montfalconensis* morphotype); IGPUW/A/36/72; Wysoka, W.6, bed 27a

4-5 – *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL, 1901 (*paturattensis* morphotype)
4 – IGPUW/A/36/63; Wysoka, W.4III, bed 21; 5 – IGPUW/A/36/57; Wysoka, W.6, bed 28c

Arrow indicates end of the phragmocone; all figures are natural size

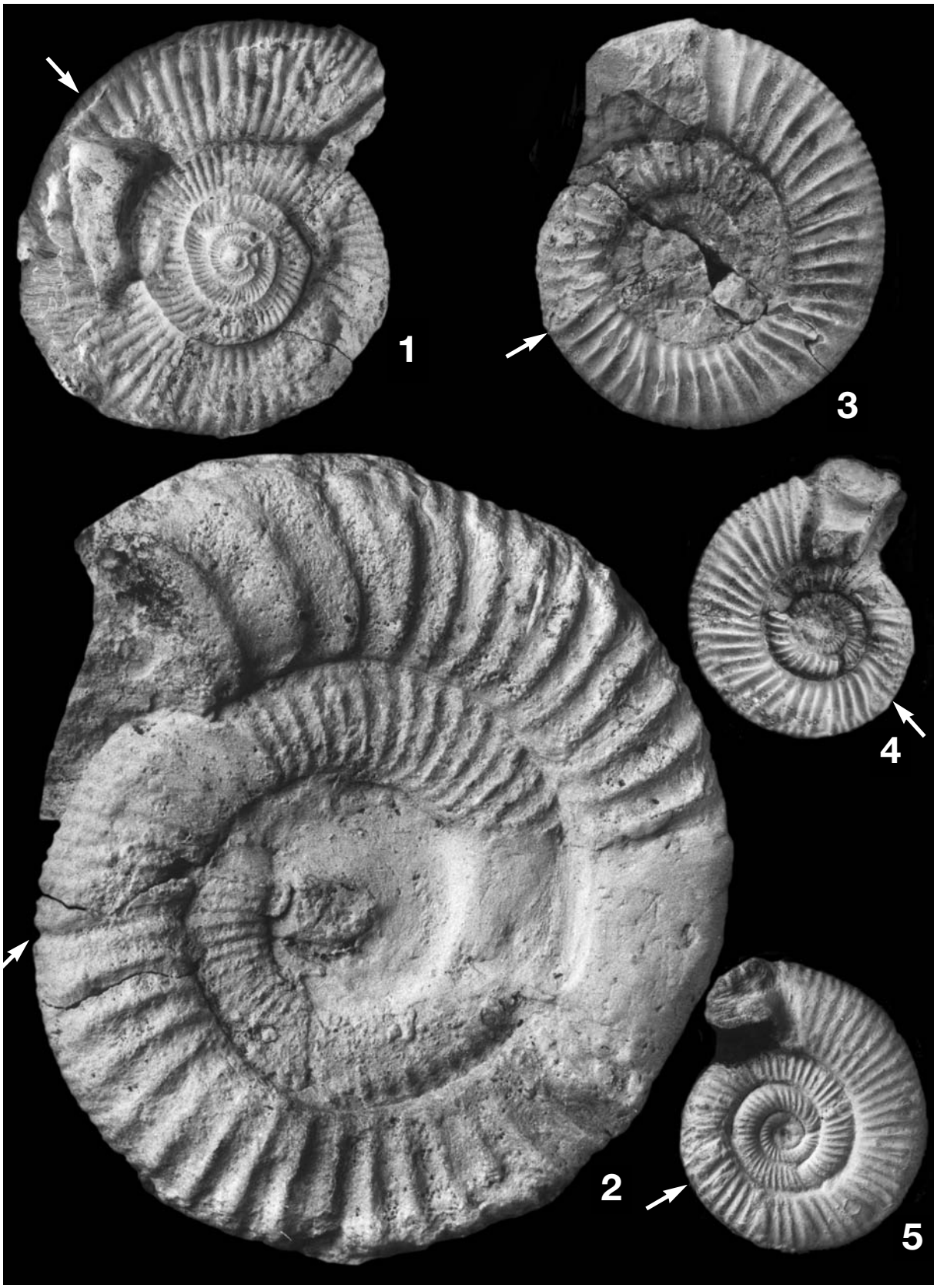
1
3
4
2
5

PLATE 2

1 – *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL, 1901 (*montfalconensis* morphotype)
IGPUW/A/36/80; Wysoka, W.6', bed 27

2-3 – *Perisphinctes* (*Kranaosphinctes*) *collignoni* (BROCHWICZ-LEWIŃSKI, 1979)
2 – IGPUW/A/36/263; Wysoka, W.4, bed 18
3 – IGPUW/A/36/794; Wysoka, W.9", bed 8.6, $\underline{D}_m$=193 mm; $\underline{D}_f$=112 mm

4-5 – *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL, 1901 (*paturattensis* morphotype)
4 – IGPUW/A/36/75; Wysoka, W.6, bed 27a
5 – IGPUW/A/36/67; Wysoka, W.6, bed 28a

Arrow indicates end of the phragmocone; besides fig. 3, which is × 0.7, all figures are natural size

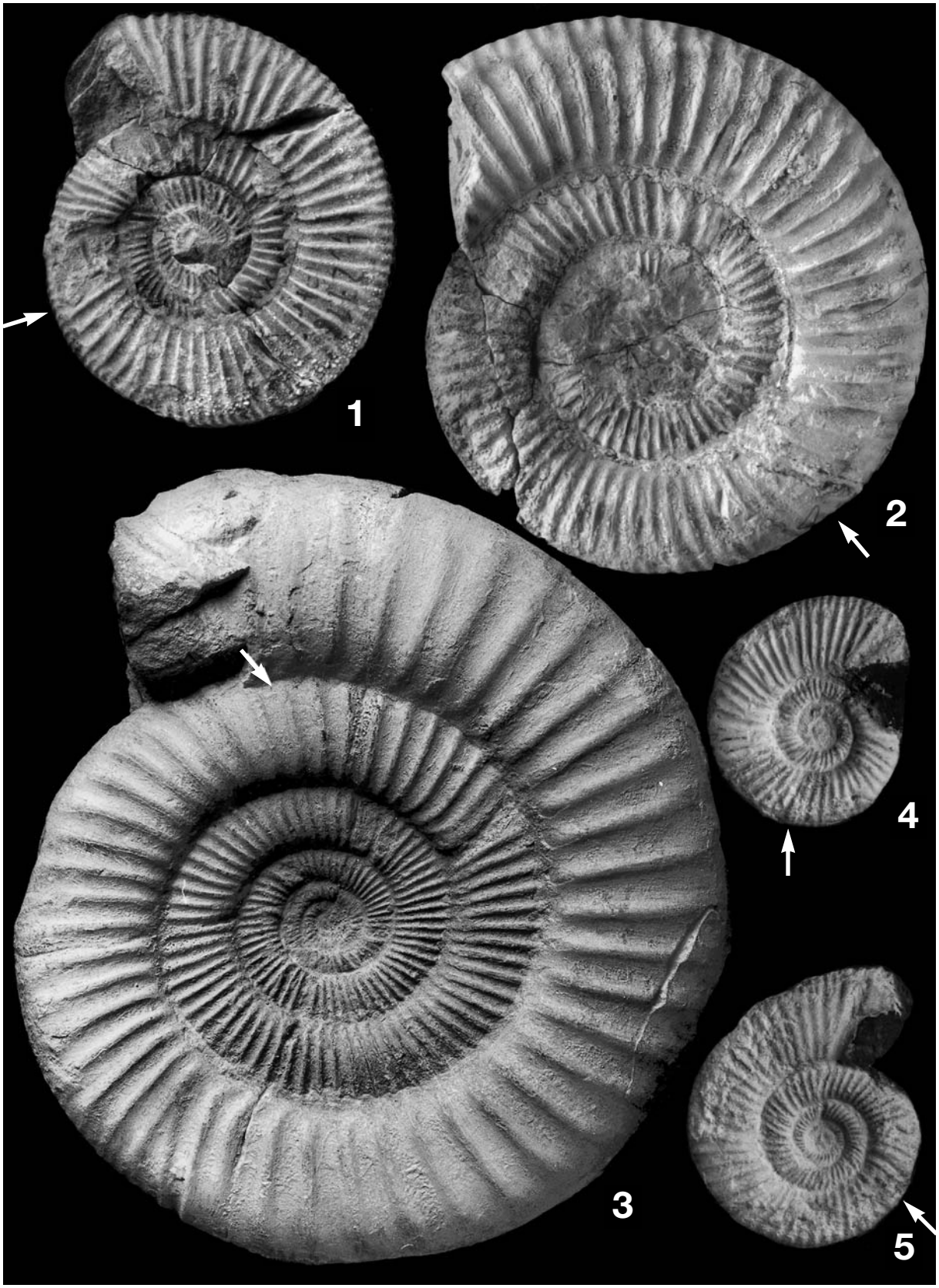
1
2
3
4
5

PLATE 3

1 – *Perisphinctes* (*Otosphinctes*) *paturattensis* DE LORIOL, 1901 (*paturattensis* morphotype) IGPUW/A/36/71; Wysoka, W.6, bed 27b

2 – *Perisphinctes* (*Kranaosphinctes*) *decurrens* (BUCKMAN, 1923) IGPUW/A/36/273; Wysoka, W.4, bed 16, $\underline{D}_m$=185, $\underline{D}_f$=130 mm

3 – *Perisphinctes* (*Kranaosphinctes*) cf. *promiscuus* BUKOWSKI, 1887 IGPUW/A/36/373; Wysoka, W.4, bed 18

Arrow indicates end of the phragmocone; besides fig. 2, which is × 0.75, all figures are natural size

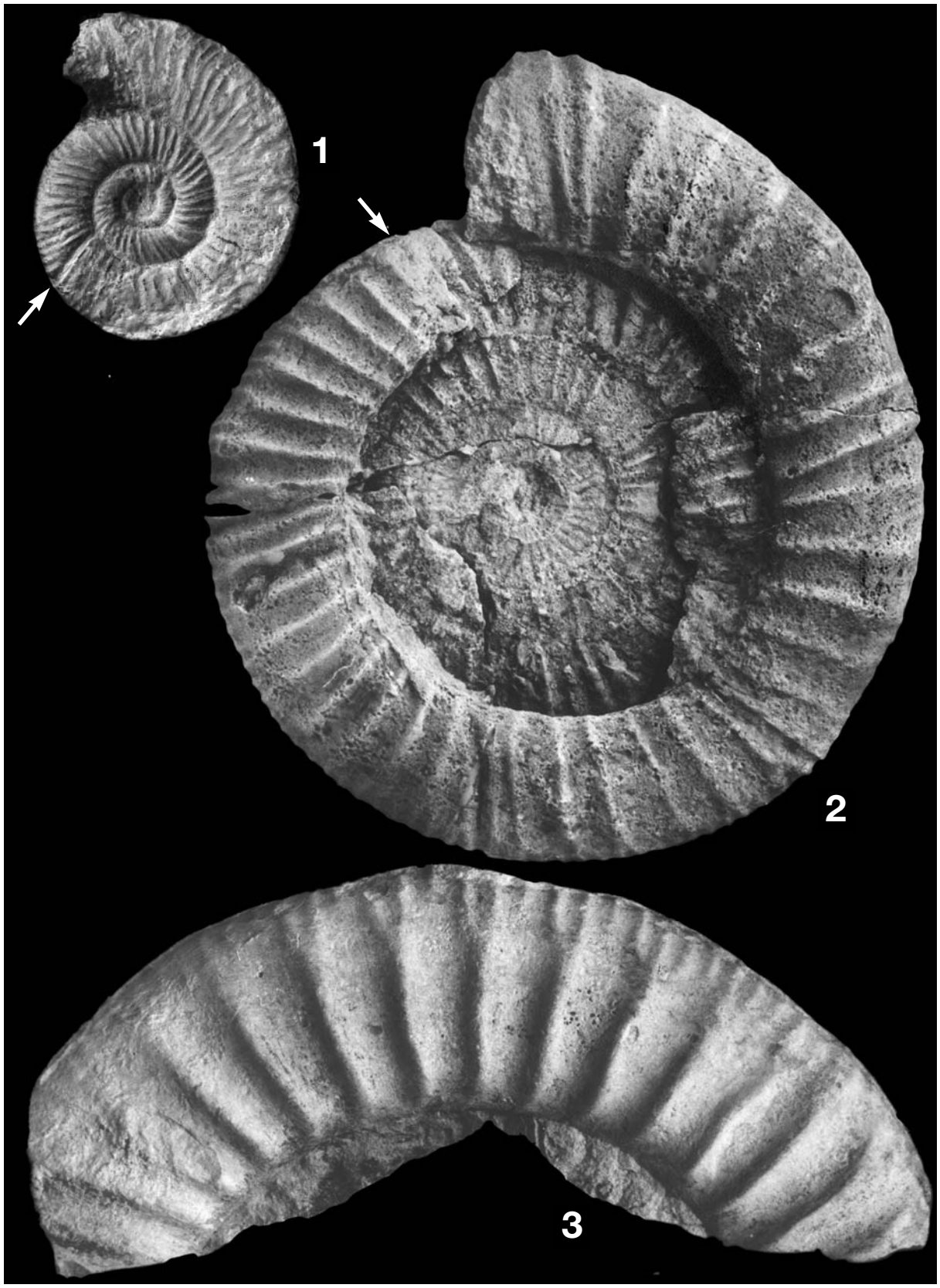
1
2
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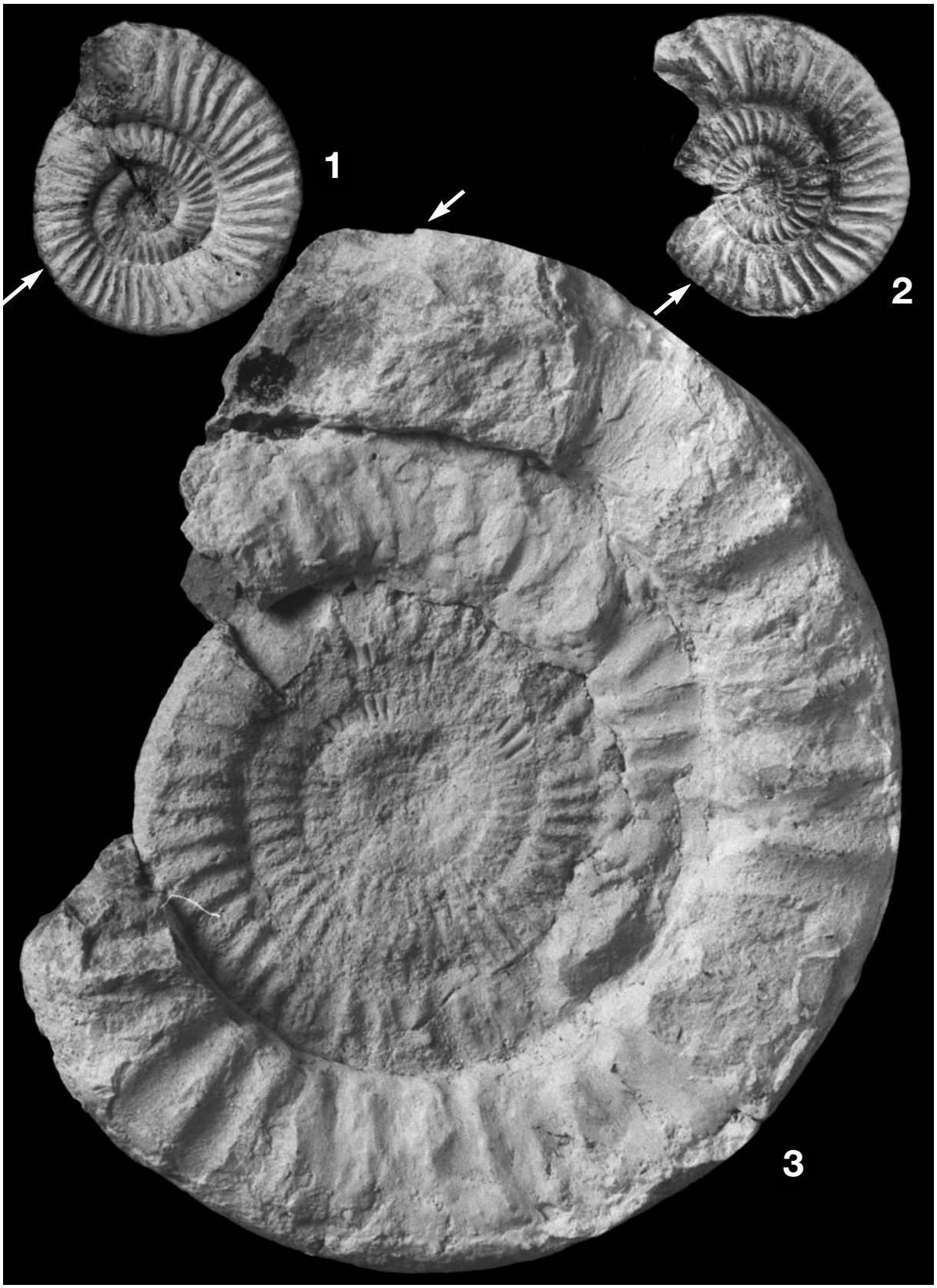
PLATE 4

1-2 – *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. (*ouatoides* morphotype)
1 – IGPUW/A/36/116; holotype, Wysoka, W.4, bed 17 (a-c)
2 – IGPUW/A/36/81; paratype, Wysoka, W.8, bed 1e
3 – *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN) IGPUW/A/36/212; Wysoka, W.9', bed 8.2c, $*D_m$=300 mm, wholly septate

Arrow indicates end of the phragmocone; besides fig. 3, which is × 0.6, all figures are natural size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3

PLATE 5

1-2 – *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN, 1921)
1 – IGPUW/A/36/203; Wysoka, W.4III, bed 4, *D_m=215 mm, D_f=140 mm
2 – IGPUW/A/36/251; Wysoka, W.5, collected loose from beds 1-3, D_m=190, D_f=130

3 – *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN, 1926) (*ouatius* morphotype)
IGPUW/A/36/24; Wysoka, W.5, bed 5b

Arrow indicates end of the phragmocone; besides fig. 3, which is natural size, all figures are × 0.6


1
2
3

PLATE 6

1 – *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. (*ouatius* morphotype)
IGPUW/A/36/114; Wysoka, W.4, bed 17c

2-3 – *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN, 1926) (*ouatius* morphotype)
2 – IGPUW/A/36/91; Wysoka, W.4III, bed 2
3 – IGPUW/A/36/128; Wysoka, W.9, bed 10

4 – *Perisphinctes* (*Kranaosphinctes*) *kranaus* (BUCKMAN, 1921)
4 – IGPUW/A/36/219; Wysoka, W.9", bed 16, $\underline{D}_m$=510 mm, $\underline{D}_f$=410 mm

Arrow indicates end of the phragmocone; besides fig. 4, which is × 0.33, all figures are natural size

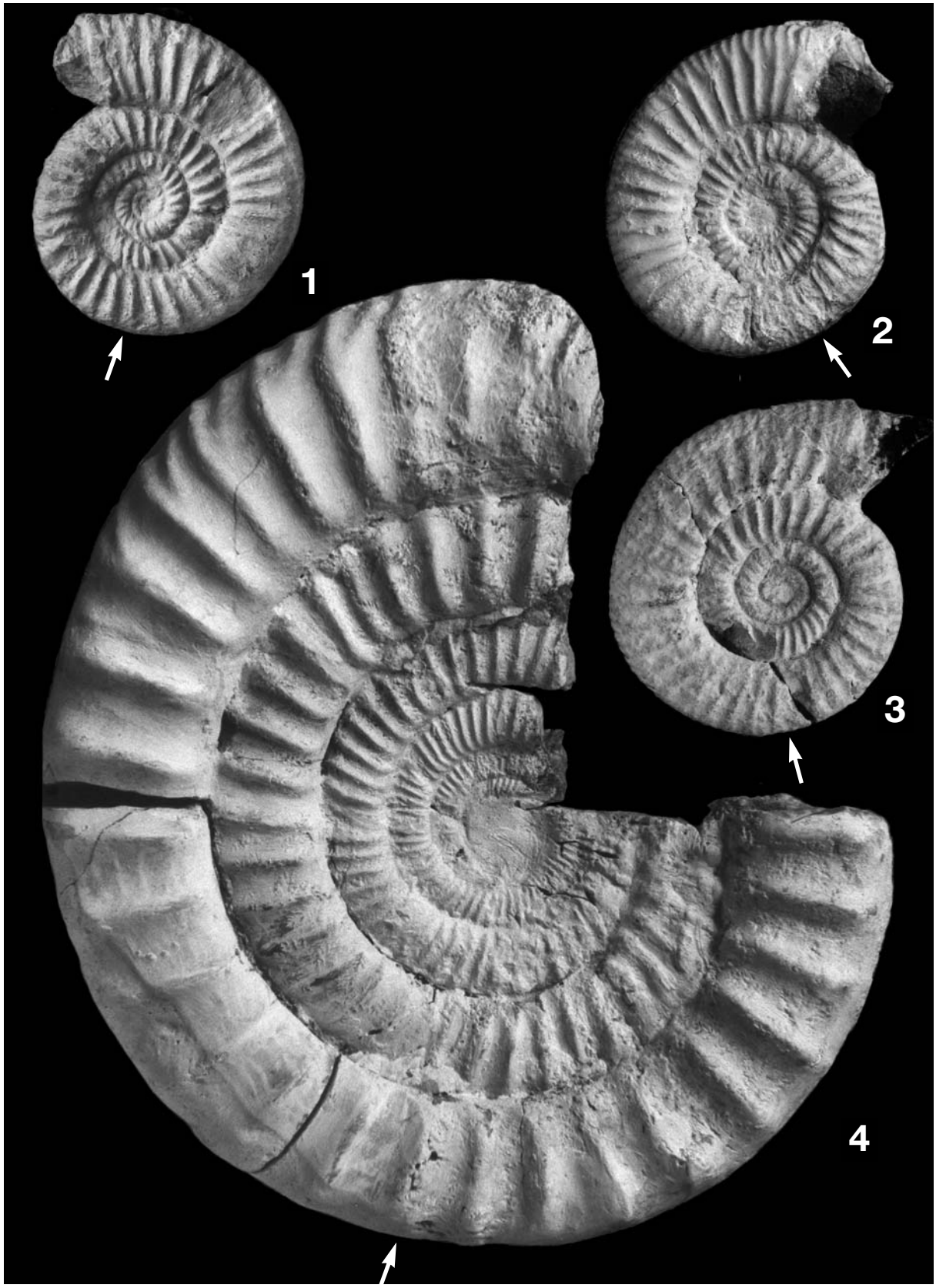
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PLATE 7

1-2 – *Neumannia gyrus* (NEUMANN, 1907)
1 – IGPUW/A/36/357; Ogrodzieniec, O.4', bed 3, only the inner whorls of the specimen up to D=160 mm, $\underline{D_f}$=150 mm
2 – IGPUW/A/36/252; Wysoka, W.5, bed 4c, D_m=160 mm, D_f=125 mm

3 – *Perisphinctes* (*Otosphinctes*) *ouatius ouatoides* chronossp. nov. (*ouatoides* morphotype) IGPUW/A/36/117; Wysoka, W.4, bed 17b

Arrow indicates end of the phragmocone; besides fig. 3, which is natural size, all figures are × 0.6


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PLATE 8

1 – *Neumannia* sp. (microconch)
IGPUW/A/36/422; Ogrodzieniec, O.1, bed 8

2 – *Neumannia* aff. *cyrilli* (NEUMANN, 1907)
IGPUW/A/36/259; Wysoka, W.5, collected loose from beds 4-7, *D_m=175 mm, D_f=140 mm

3 – *Neumannia gyrus* (NEUMANN, 1907)
IGPUW/A/36/255; Wysoka, W.5, bed 5b, *D_m=210 mm, D_f=170 mm

4 – *Neumannia* sp. (microconch)
IGPUW/A/36/421; Wysoka, W.5, bed 5a

Arrow indicates end of the phragmocone; besides figs 1, 4, which are natural size, all figures × 0.6

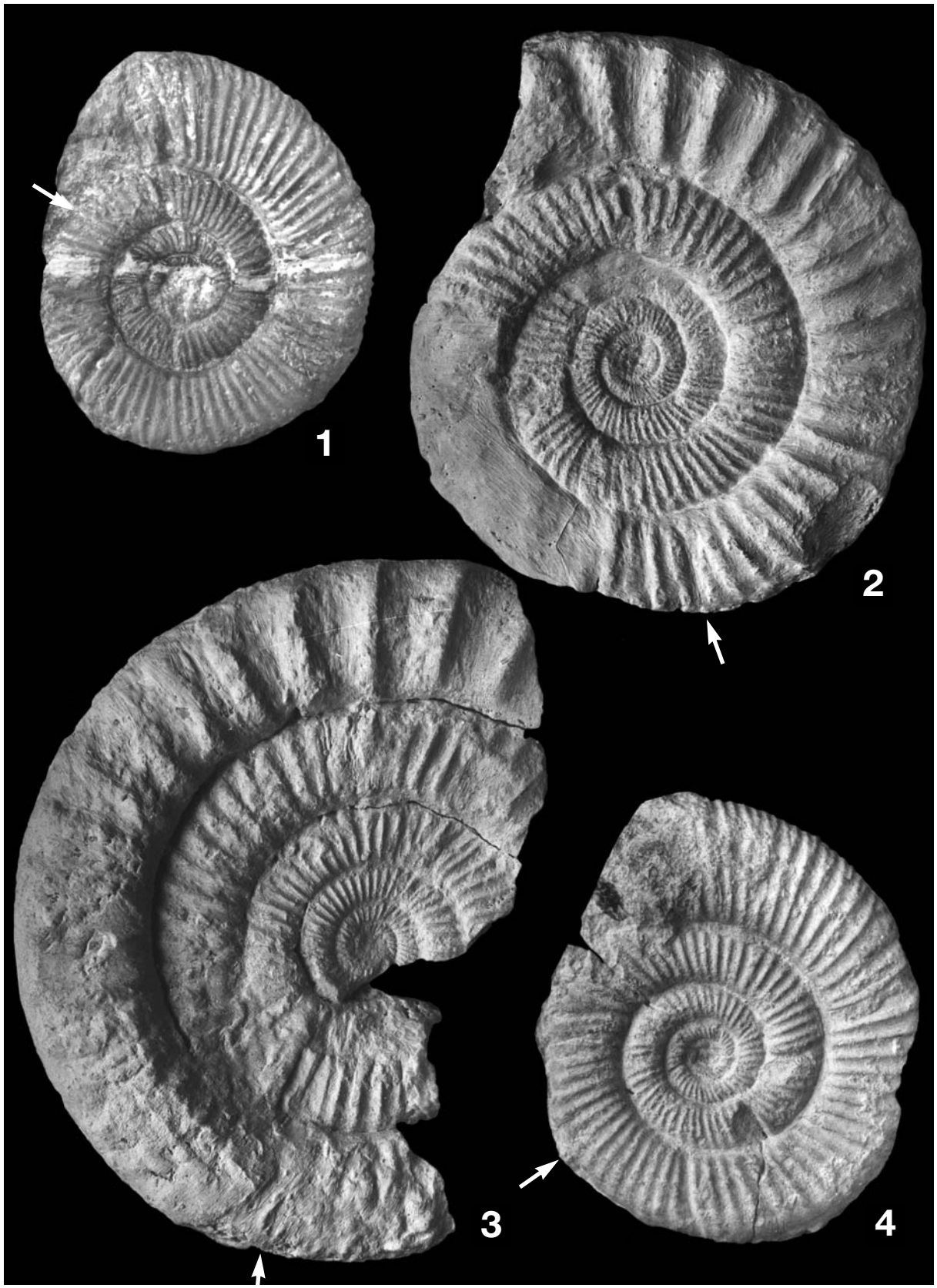
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PLATE 9

1-2 – *Perisphinctes* (*Otosphinctes*) *ouatius ouatius* (BUCKMAN, 1926) (*magnouatius* morphotype)
1 – IGPUW/A/36/100; Wysoka, W.9, bed 10
2 – IGPUW/A/36/129; Wysoka, W.9, bed 10
3 – *Neumannia cyrilli* (NEUMANN, 1907)
IGPUW/A/36/254; Wysoka, W.5, bed 5b, $*D_m$=262 mm, wholly septate

Arrow indicates end of the phragmocone; besides fig. 3, which is × 0.6, all figures are natural size

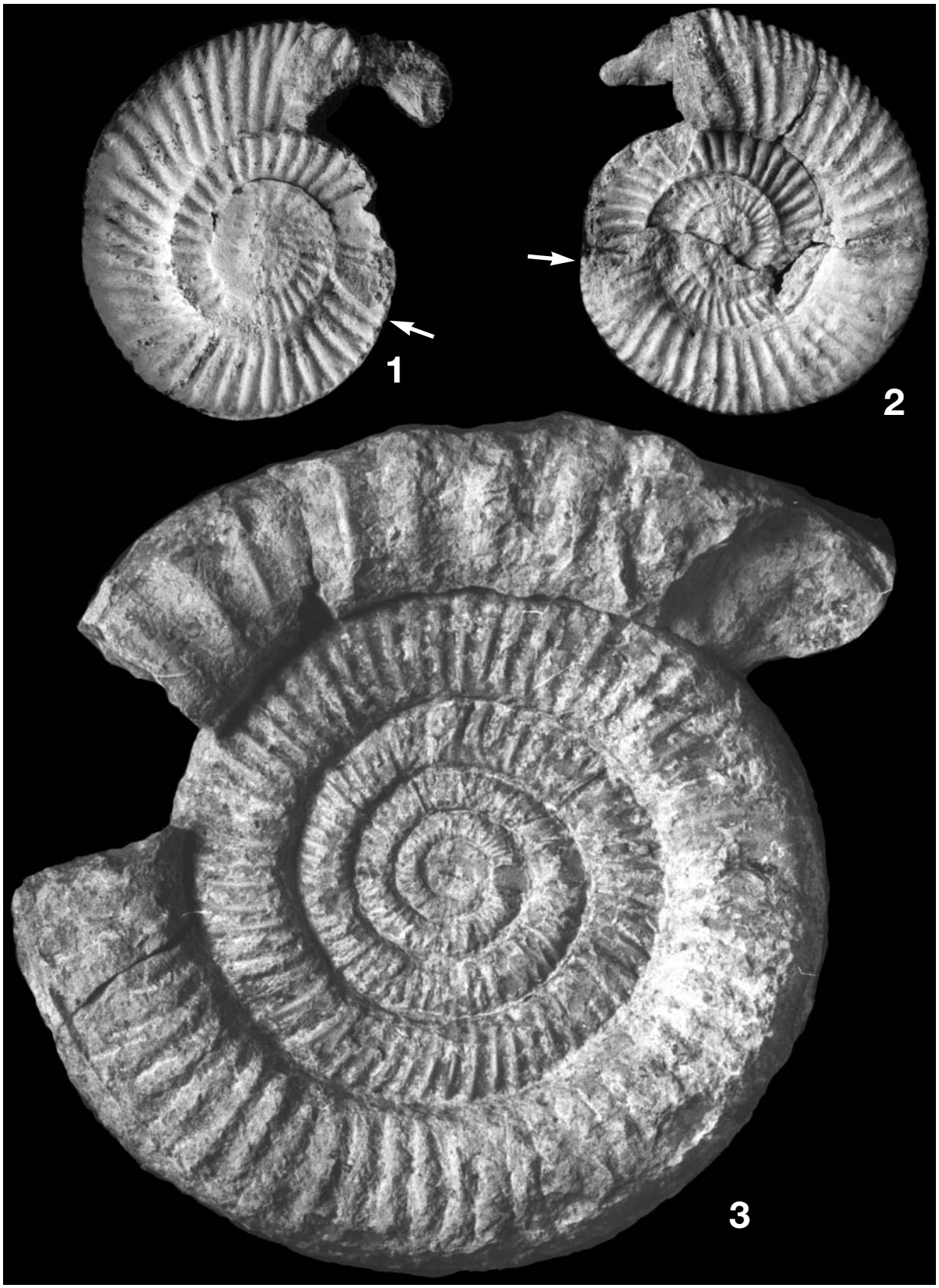
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PLATE 10

1-3 – *Perisphinctes trifidus* (SOWERBY, 1821) (m, M)

1 – IGPUW/A/36/120 (m); Wysoka, W.4, bed 17c, D_f=?; natural size

2 – IGPUW/A/36/185 (M: *helenae* morphotype); Wysoka, W.9", bed 8.1g, $*D_m$=245 mm, D_f=195 mm; × 0.5,

3 – IGPUW/A/36/280 (M: *helenae* morphotype); Wysoka, W.6', beds 27-28 (collected loose), $*D_m$=340 mm, $*D_f$=230 mm; × 0.45

Arrow indicates end of the phragmocone

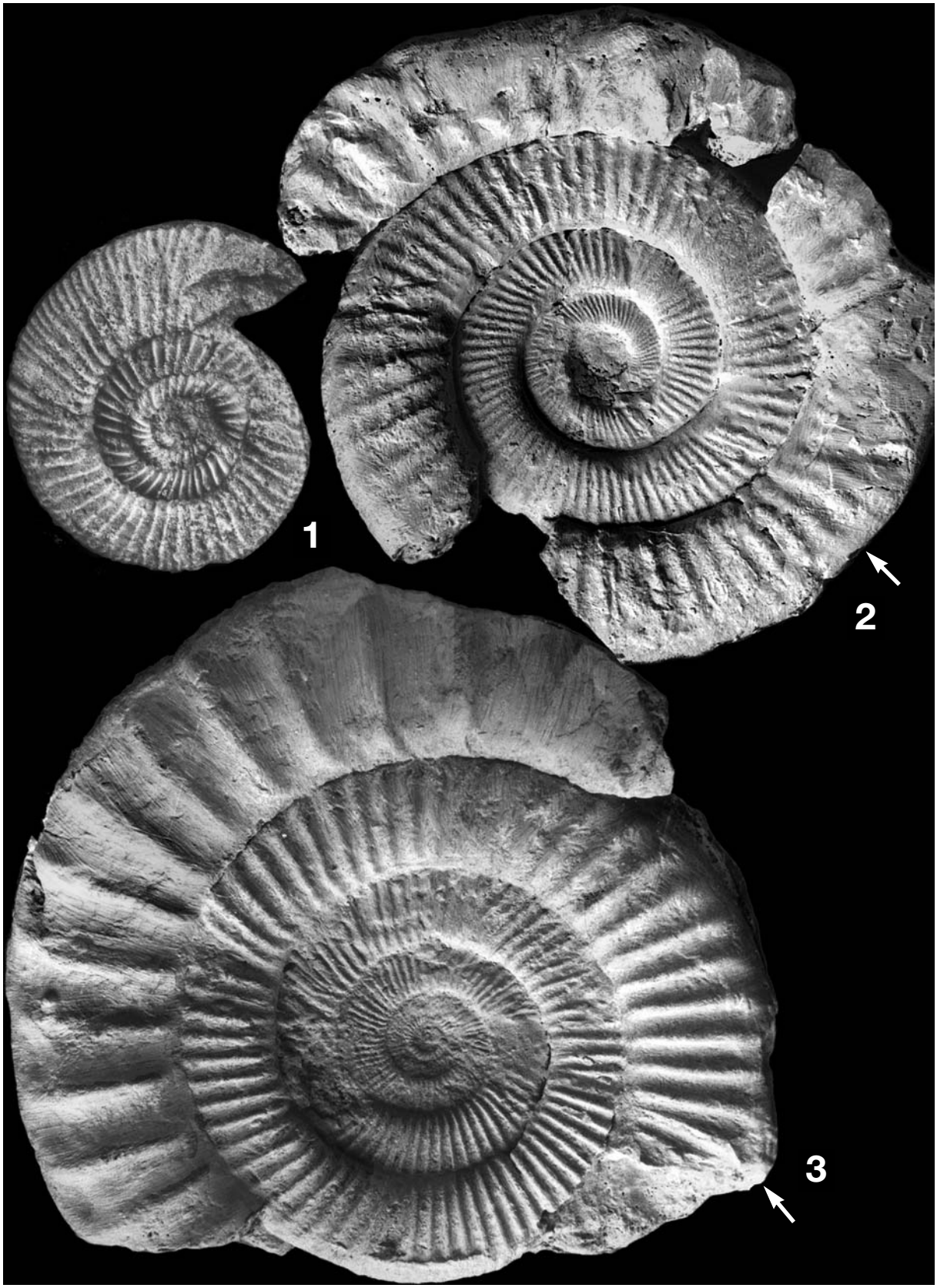
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PLATE 11

1-4 – *Perisphinctes trifidus* (SOWERBY, 1821) (m, M)

1 – IGPUW/A/36/191 (M: *helenae* morphotype); Ogrodzieniec, O.1, bed 1a, D_m=134 mm, wholly septate

2 – IGPUW/A/36/285 (M: *helenae* morphotype); Wysoka, W.6, bed 28b, D_m=165 mm, D_f=97

3 – IGPUW/A/36/276 (M: *trifidus* morphotype); Wysoka, W.4, bed 17b, D_m=170 mm, D_f=105 mm

4 – IGPUW/A/36/59 (m); Wysoka, W.6, bed 28c

Arrow indicates end of the phragmocone; besides fig. 4, which is natural size, all figures are × 0.7

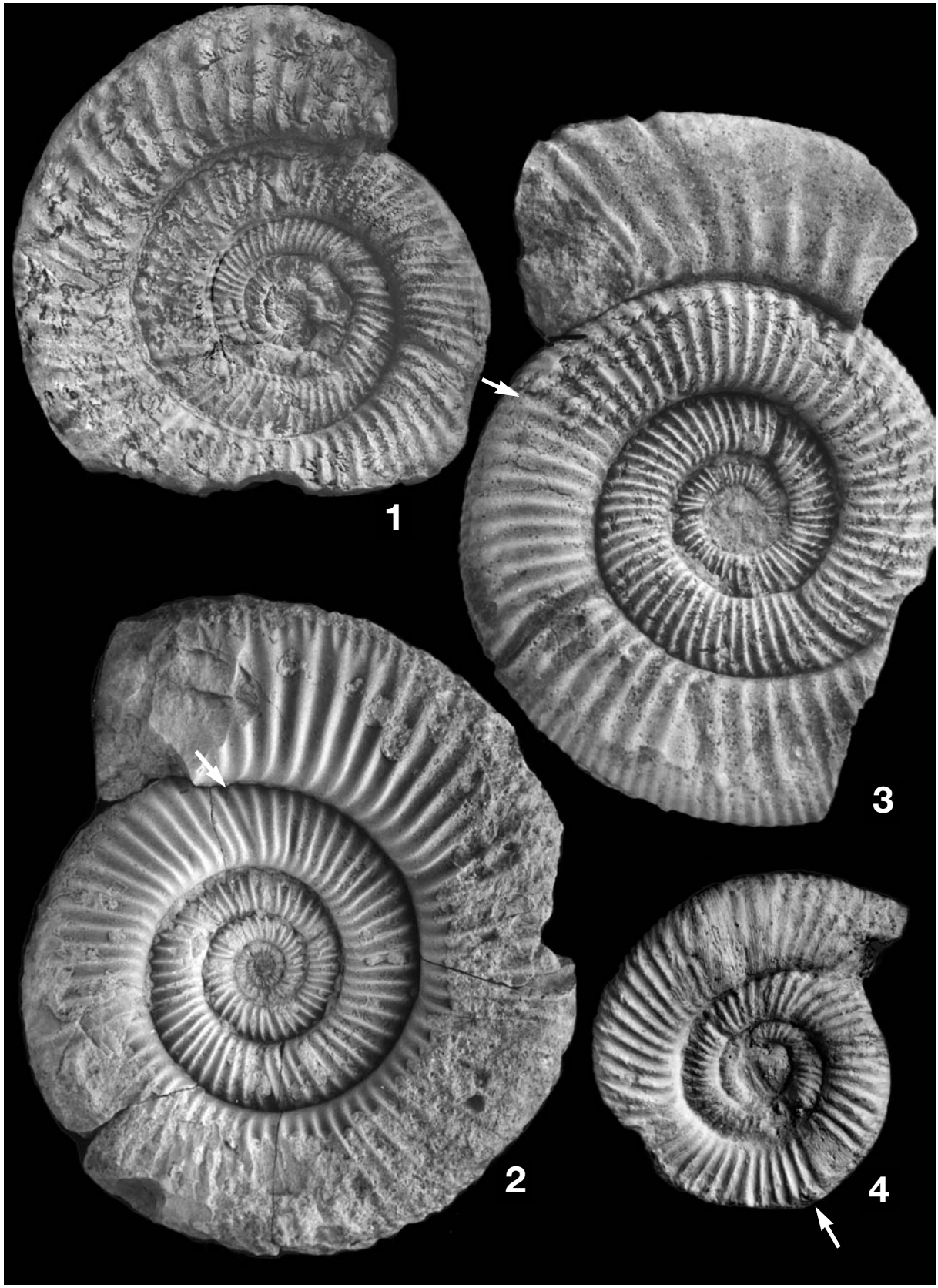
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PLATE 12

1-3 – *Perisphinctes trifidus* (SOWERBY, 1821) (m, M)

1 – IGPUW/A/36/213 (M: *trifidus* morphotype); Wysoka, W.9', bed 8.6, *D_m=240 mm, D_f=180 mm

2 – IGPUW/A/36/190 (M: *trifidus* morphotype); Wysoka, W.6', bed 28c/d, $\underline{D_m}$=235 mm, $\underline{D_f}$=140 mm

3 – IGPUW/A/36/122 (m); Wysoka, W.5, bed 1, D_f=?

Arrow indicates end of the phragmocone; besides fig. 3, which is natural size, all figures are × 0.6

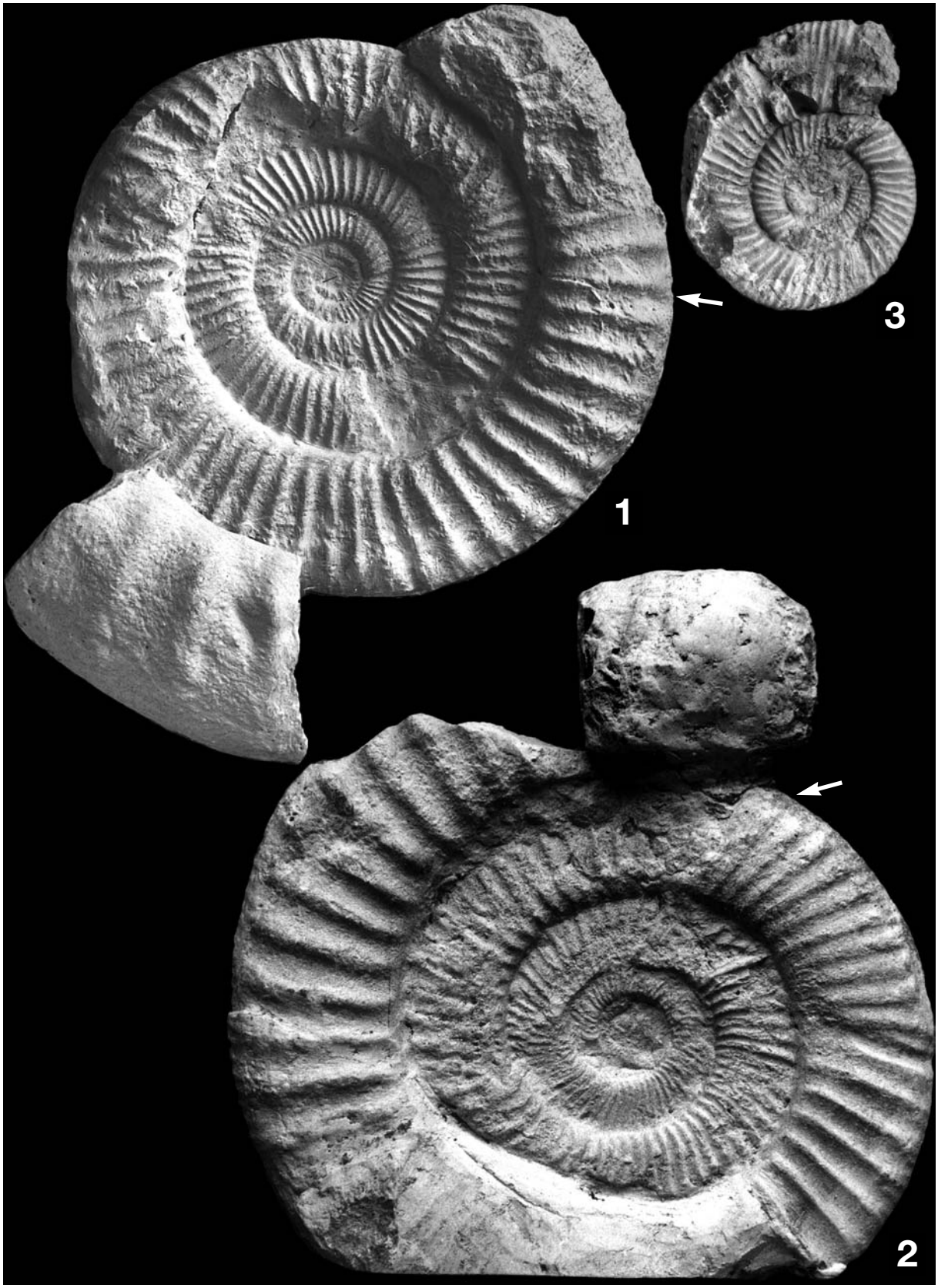
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PLATE 13

1 – *Perisphinctes* (*Kranaosphinctes*) *ariprepes* (BUCKMAN, 1924)
IGPUW/A/36/202; Wysoka, W.4III, bed 4, *D_m=310 mm, D_f=250 mm
2 – *Perisphinctes trifidus* (SOWERBY, 1821) (m, M)
IGPUW/A/36/108 (m); Wysoka, W.4, bed 17a
3 – *Perisphinctes* (*Kranaosphinctes*) *vorda* ARKELL, 1939
IGPUW/A/36/275; Wysoka, W.4, bed 17 (a-c), *D_m=211 mm, D_f=165 mm

Arrow indicates end of the phragmocone; besides fig. 2, which is natural size, all figures are × 0.45


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PLATE 14

1 – *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov.
IGPUW/A/36/141; paratype, Wysoka, W.5, bed 5b
2-3 – *Perisphinctes* (*Otosphinctes*) *arkelli arkelli* GŁOWNIAK, 2000
2 – IGPUW/A/36/97; paratype, Wysoka, W.9", bed 12b
3 – IGPUW/A/36/92; paratype, Wysoka, W.4III, bed 2
4 – *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov.
IGPUW/A/36/140; holotype, Wysoka, W.9, bed 16 (a-b)

Arrow indicates end of the phragmocone; all figures are natural size

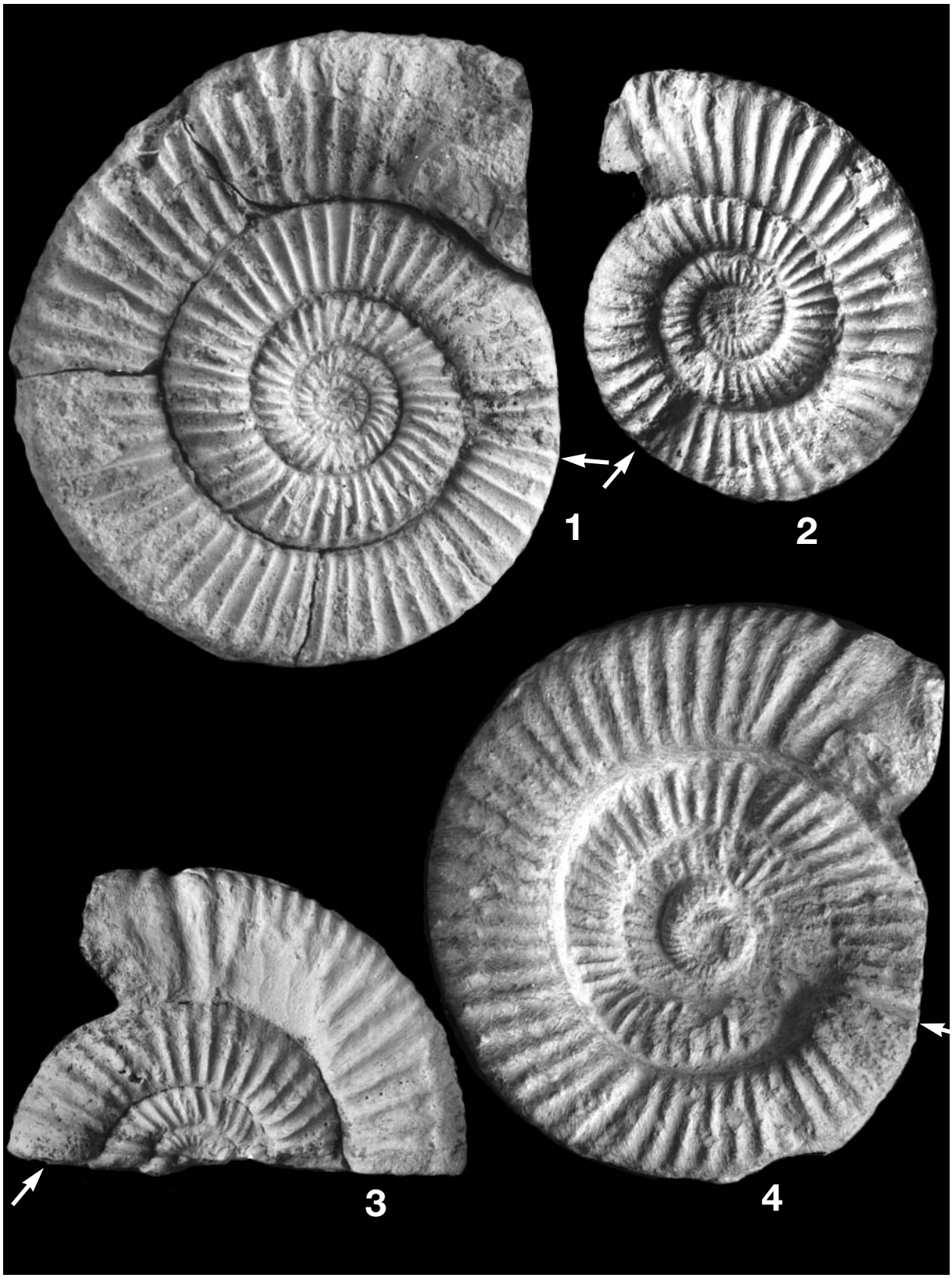
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PLATE 15

1-3 – *Perisphinctes* (*Otosphinctes*) *arkelli wysokae* chronossp. nov.
1 – IGPUW/A/36/146; Wysoka, W.5, bed 6c
2 – IGPUW/A/36/304; Ogrodzieniec, O.2, bed 1d
3 – IGPUW/A/36/142; Wysoka, W.5, bed 5b

Arrow indicates end of the phragmocone; all figures are natural size

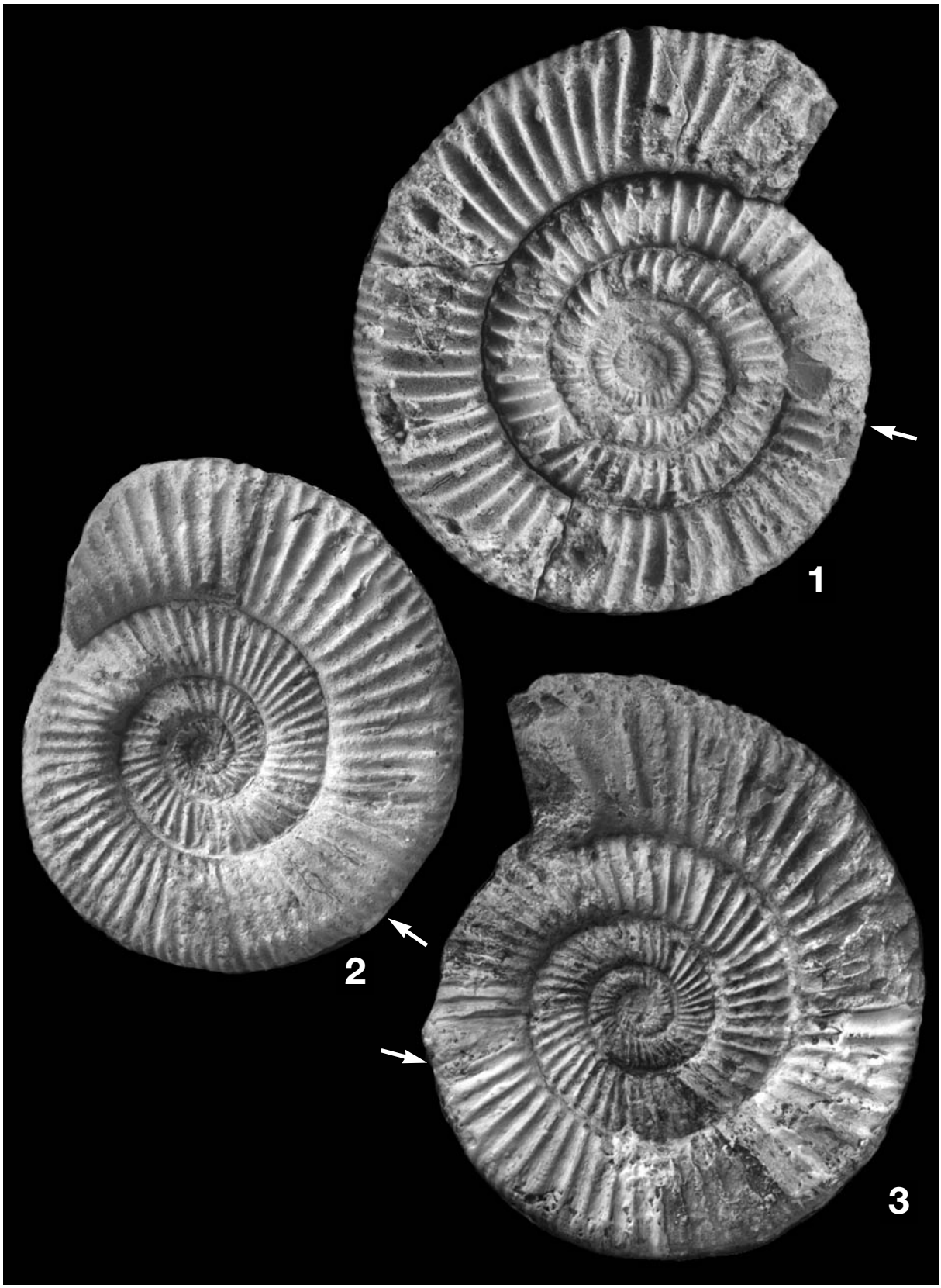
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PLATE 16

1-2 – *Liosphinctes plicatilis* (SOWERBY, 1817)

1 – IGPUW/A/36/164; Wysoka, W.6, bed 28c, wholly septate; natural size

2 – IGPUW/A/36/154; Wysoka, W.4III, bed 20, $\underline{D}_m$=195 mm, $\underline{D}_f$=126 mm; × 0.7

Arrow indicates end of the phragmocone


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PLATE 17

1-2 – *Liosphinctes plicatilis* (SOWERBY, 1817)
1 – IGPUW/A/36/165; Wysoka, W.4III, bed 21, natural size
2 – IGPUW/A/36/152; Wysoka, W.6, bed 26a, D_m=163 mm, D_f=107 mm; × 0.7

Arrow indicates end of the phragmocone


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PLATE 18

1 – *Liosphinctes laevipickeringius* (ARKELL, 1939)
IGPUW/A/36/162; Wysoka, W.4III, bed 10, *D_m=167 mm, wholly septate
2 – *Liosphinctes* sp. B
IGPUW/A/36/163; Wysoka, W.4III, bed 12, D_m=132 mm, D_f=77 mm
3 – *Liosphinctes* sp. A
IGPUW/A/36/174; Ogrodzieniec, O.4, bed 11, *D_m=130 mm, wholly septate

Arrow indicates end of the phragmocon; all figures are × 0.7


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