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The oppeliid, perisphinctid and aspidoceratid ammonite faunas of the 'Corallian' Beds (Upper Jurassic) in Cambridgeshire, England

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Abstract: The Upware Limestone Member comprises an enclave of Middle Oxfordian 'Corallian' facies limestone situated on the East Midlands Shelf within the more typical mudrock-dominated sequences of eastern England, and is assigned to the West Walton Formation. Recent deep excavations in the district have revealed the base of the Upware Limestone, not exposed since the last century, resting on a mudrock sequence, the Dimmock's Cote Marl Member. The Upware Limestone and Dimmock's Cote Marl have yielded an unusually common ammonite fauna, including both Boreal (Cardioceratidae) and Tethyan (Perisphinctinae) elements, and rare Tethyian oppeliids and aspidoceratids. Thirteen nominal species of *Perisphinctes* are described and figured, as are one species of *Neocampylites* and one of *Euaspidoceras*. Three distinct assemblages of *Perisphinctes* are recognized in the Upware succession. The faunas are correlated with existing zonations for the Middle Oxfordian of Sub-Boreal and Sub-Mediterranean regions, including sub-subzonal schemes (i.e. 'biohorizons'). Such correlations aid the construction of correlative links between two distinct ammonite provinces and have great potential for resolving some of the outstanding questions of European Middle Oxfordian stratigraphy. The succession is also of great importance within Britain as it is the only known locality to yield faunas that are stratigraphically intermediate between the classic Corallian assemblages of Oxford and the later faunas of the Upper Calcareous Grit of Yorkshire.

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The fossiliferous carbonate succession exposed at Upware, Cambridgeshire, provides a rich, well-localized succession of perisphinctid and cardioceratid ammonites that spans the critical Plicatilis–Transversarium zonal boundary, making this an important area for biogeographical and biostratigraphical studies. The cardioceratids have been the subject of a separate study (Wright & Page 2006); the remaining ammonite fauna is described here. This paper sets the oppeliid, perisphinctid and aspidoceratid faunas of newly exposed beds in the context of the extensive museum collections of similar ammonites collected over many years from higher beds.

The 'Corallian' facies rocks of Upware crop out in a narrow, low-lying ridge that stretches for some 6 km along the eastern side of the River Cam (Fig. 1) and rises only 5 to 10 m above the surrounding fens. The rocks largely consist of relatively soft, poorly cemented limestones, the Upware Limestone of Wright *et al.* (2000) and Wright & Page (2006). Only two exposures remain of those formerly visible and listed by Wright *et al.* (2000). Commissioners' Pit [TL 539 708] is at present well exposed, being actively maintained by the Upware Field Studies Centre, Cambridgeshire County Council. Dimmock's Cote Quarry [TL 545 724] has been worked by the Wicken Lime & Stone Co., though work here is now on a lesser scale than before.

The 'Corallian' succession at the Dimmock's Cote Quarry

The 'Corallian' succession at Upware has long been known for its Middle Oxfordian ammonite fauna, some of which was figured by Arkell (1935–1948). The succession as then understood was described in detail by Kelly (1985). In 1993, quarrying began at a deeper level at Dimmock's Cote Quarry, exposing a 0.6 m thick bed of limestone, the Crinoid Bed of Wright *et al.* (2000), which has yielded numerous *Perisphinctes* spp. and *Cardioceras* spp. Trial holes and drainage ditches in the base of the pit revealed several metres of underlying marls with calcareous concretions that had never been exposed previously at Upware. These were named the Dimmock's Cote Marl by Wright *et al.* (2000). A fauna of *Perisphinctes* spp. and *Cardioceras* spp. which differs in important aspects from that found in the beds above was collected. The faunal succession at Dimmock's Cote Quarry is thus of considerable importance in attempts to unravel the complicated history of the Tethyan perisphinctid and Boreal cardioceratid faunas in the British Middle Oxfordian. Detailed measured sections, faunal lists and a discussion of the manner of deposition of the whole Upware succession were published by Wright *et al.* (2000). A summary of the succession as seen in Dimmock's Cote Quarry is given in Figure 2; the lithologies of the various beds are as follows (informal lithostratigraphic subdivisions in brackets):

Preservation of the Sponge Bed and Crinoid Bed ammonites

As noted by Wright *et al.* (2000), the Sponge Bed and Crinoid Bed together form a tempestite, their fauna

[AQ: 11]

UPWARE LIMESTONE MEMBER		m
(9)	Cream-coloured, soft, fossiliferous, pisolitic oobiomicrite with a rich bivalve-gastropod fauna, and frequent ammonites.	3–5
CORAL BED		
(8)	Coarse, bioclastic, coral-rich limestone seen at the western end of the pit, and containing a prolific bivalve-gastropod-echinoid-coral fauna.	0–0.6
(7)	Grey, relatively soft, marly pisolite, weathering pale cream; echinoids are common in a band near the top.	c 4
CRINOID BED		
(6c)	Pale grey biomicrite containing macroconch perisphinctids and cardioceratids with the phragmocones not infilled; hollow apart from sparry calcite.	0.3
(6b)	Medium grey, coarse biomicrite containing a poorly preserved micrite-infilled ammonite fauna and numerous bivalves and echinoids.	0.3
SPONGE BED		
(6a)	Shelly, argillaceous limestone full of micrite-filled microconch cardioceratid and perisphinctid ammonites, also bivalves and sponges.	0.15
DIMMOCK'S COTE MARL MEMBER		
(5)	Dark grey mudrock with a poorly preserved cardioceratid ammonite/bivalve fauna.	0.6
(4)	Grey, argillaceous limestone containing large perisphinctid fragments.	0.1–0.15
(3)	Dark grey mudrock with occasional bivalves and an impersistent, argillaceous limestone.	1.7
(2)	Grey, argillaceous, spicular, shelly limestone with poorly preserved ammonites and bivalves.	0.3–0.4
(1)	Dark grey mudrock with scattered bivalves and a large perisphinctid preserved in a concretion.	seen to 1.5

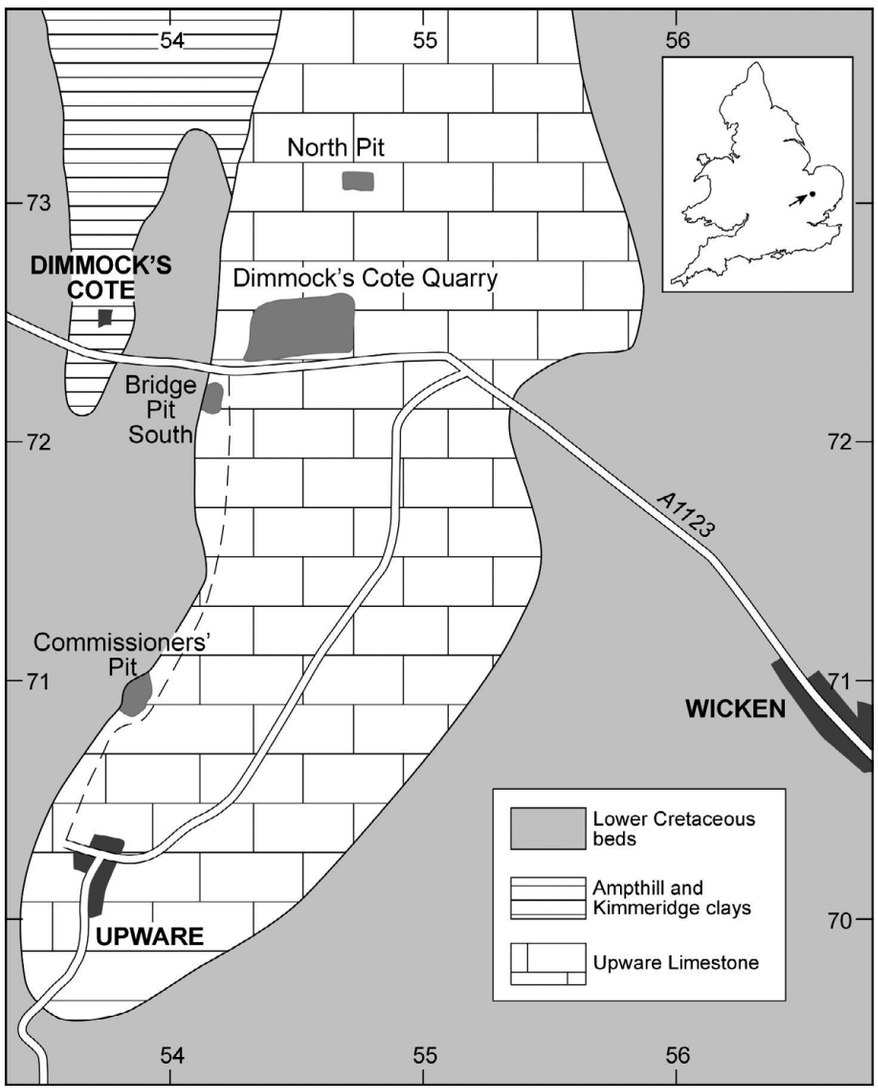


Fig. 1. Geological and topographical map of the Upware area, after Wright & Page (2006), showing locations of quarries exposing the Upware Limestone. National Grid co-ordinates at 1 km spacings.

potentially comprising members of a living population plus deceased individuals suddenly swept together by a storm. As such, many more immature, juvenile ammonites are present than is usual. Also, dissolution of the shells took place while the sediment was still soft, leaving a thin carbonaceous film marking the outline of the shell. Though the specimens are often easily extracted from the matrix, it can be very difficult to make out septa, even with a binocular

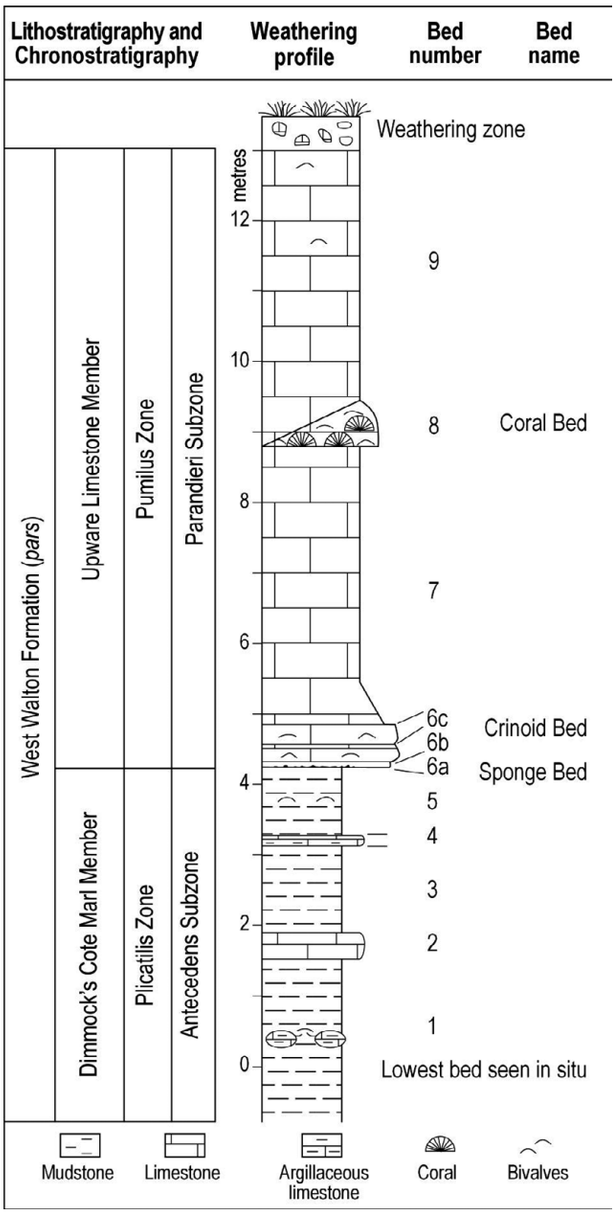


Fig. 2. Summary of the lithological succession at Upware, after Wright *et al.* (2000).

microscope, or, if septa are visible, to decide whether the final ones are crowded, signifying a mature adult. Thus, in the frequent absence of the aperture or of noticeable uncoiling, the adult status of many specimens is uncertain.

Repository of speciments, conventions and localities

All ammonites studied, including those newly collected by the authors, are in the collection of the Sedgwick Museum, Cambridge (CAMSM, abbreviated to SM here). All specimens from the Dimmock's Cote Marl and all the authors' specimens from the Upware Limestone were collected from Dimmock's Cote Quarry, previously known as Bridge Pit North [TL 545 724]. Most previously collected specimens from the Upware Limestone in the Sedgwick Museum collection came from quarries in this area that no longer exist, particularly North Pit [TL 544 728] and Bridge Pit South [TL 542 722]. The pits formerly known as New Pit and Bridge Pit were close together and, according to Arkell (1937*b*), these names were used interchangeably. Both pits seem to have been later subsumed into Dimmock's Cote Quarry. Some specimens were also collected from the quarry near Upware formerly known as South Pit, and now known as Commissioners' Pit [TL 539 708].

Ammonite measurements: whorl height, whorl breadth and umbilical width are given conventionally as proportions of the shell diameter at which measurements were made. Where specimens have bold ribbing, the breadth given is that between high points of the ribs, with the breadth in between ribs given in brackets. The following abbreviations are used:

D (phg) = diameter at final septum

D (ad) = diameter of adult with uncoiling and/or crowding of final septa

D (juv) = diameter of complete juvenile

D (max) = maximum diameter preserved

0.x wh bch = fraction of body-chamber preserved as a proportion of the whorl

rpw = ribs per whorl

Systematic Palaeontology

Order **Ammonoidea** Zittel, 1882

The following sequence of ammonite faunas, listed as 'nominal' species (see discussion below), is recognizable in the Upware district, primarily in Dimmock's Cote Quarry ([M] = macroconch, [m] = microconch):

Beds 7 and 9 (* = specimens in pre-existing Sedgwick Museum collections identified as being from Bed 9 by matrix): *Cardioceras (Maltoniceras) maltonense* (Young & Bird), *C. (Miticardioceras) tenuiserratum* (Oppel)*, *C. (M.)* aff. *sopotense* (Malinowska), *C. (Subvertebriceras) densiplicatum* Boden*, *C. (S.) zenaidae* Ilovaisky*, *Perisphinctes (P.) holtonensis* Buckman [M]*, *P. (P.) chloroolithicus* Gümbel [M]*, *P. (Dichotomosphinctes)* aff. *dobrogensis* Simionescu [m]*, *Aspidoceras* (*Euaspidoceras*) sp. aff. *paucituberculatum* Arkell* and *Neocampylites* sp. aff. *henrici* (d'Orbigny)*.

Beds 6a (Sponge Bed) and 6b–6c (Crinoid Bed): *Cardioceras (Cawtoniceras) cawtonense* (Blake & Hudleston), *C. (Maltoniceras) highworthense* Arkell, *C. (M.) maltonense, C. (Miticardioceras)* aff. *sopotense, C. (Scoticardioceras) excavatum* (J. Sowerby), *C. (Subvertebriceras) densiplicatum, C. (S.) zenaidae, Perisphinctes (P.) parandieri* de Loriol [M], *P. (P.) tumulosus* Buckman [M], *P. (Kranaosphinctes)* sp. aff. *decurrens* Buckman [M], *P. (Dichotomosphinctes) antecedens* Salfeld [m], *P. (D.) buckmani* Arkell [m] and *P. (Otosphinctes)* sp. A [m].

Beds 1–5 (Dimmock's Cote Marl, upper part): *Cardioceras (Cawtoniceras) cawtonense, C. (Miticardioceras) tenuiserratum, C. (M.) sopotense, C. (Subvertebriceras) zenaidae, Neocampylites* sp. aff. *henrici, P. (Kranaosphinctes) ariprepes* (Buckman) [M], *P. (K.)* sp. aff. *maximus* (Young & Bird) [M], *P. (Otosphinctes)* cf. *arkelli* Głowniak [m] and *P. (Otosphinctes)* cf. *ouatius* Buckman [m].

Superfamily **Haploceratoidea** Zittel 1884
Family **Oppelidae** Bonarelli 1894
Subfamily **Ochetoceratinae** Spath 1928
Genus ***Neocampylites*** Callomon 1973

Type species: *Ammonites delmontanus* Oppel 1863, designated by Callomon 1973, p. 1003.
Neocampylites sp. aff. *henrici* (d'Orbigny) (Fig. 13B)

Material. Two specimens from ?Bed 4, Dimmock's Cote Marls (SM X.50139.32, -.62) and three specimens from Bed 9, Upware Limestone (SM J68503, SM J68916, SM X18021), all from Dimmock's Cote Quarry. All specimens are fragments of septate macroconch inner whorls.

Description. When first seen, between 15 and 20 mm diameter, the shell is smooth. At 25 mm, traces of falcoid secondary ribs are present on the outer half of the whorl side and beyond a spiral raised area, giving an *Oxycerites*-like appearance. The venter has a sharp median keel and very narrow shoulders. The secondary ribs appear to fade by 67 mm diameter and the maximum septate diameter observed is around 75 mm in SM J68916, suggesting a maximum size of at least 100 mm (allowing for half a whorl of body-chamber).

Discussion. The Upware form appears to be different from the species described by Arkell (1943, pp. 265–268) from the 'Elsworth Rock' and the 'St Ives Rock' (West Walton Formation), under the names *O. (O.) canaliculatum* (von Buch) var. *hispidum* (Oppel) (Arkell 1943, pl. 60, figs 1, 2), *O. (Campylites) henrici* (d'Orbigny) (Arkell 1943, pl. 60, figs 3–6) and *O. (Trimarginites) arolicum* (Oppel) (Arkell 1943, pl. 60, fig. 7). Arkell's specimens appear to have stronger ribbed inner whorls and apparently lack the distinctive *Oxycerites*-like secondary ribbing on their middle whorls. Although none of the specimens recorded by Arkell were collected *in situ*, additional and comparable material has now been recovered *in situ* from the Elsworth Rock Member at Papworth Everard (Page 1986). The associated ammonite fauna at Papworth, although stratigraphically condensed, includes many cardioceratids and perisphinctids typical of lower stratigraphic levels than Bed 9, thereby suggesting that the Elsworth Rock *Ochetoceras*, at least, may represent a slightly older species.

Specimen SM X18021 has a broad resemblance to the type of *O. (Neocampylites) henrici* (d'Orbigny 1850) as refigured by Enay & Gauthier *in* Fisher (1994, pl. 73, fig. 5), but the latter has slightly closer secondary ribbing. The type of *O. henrici* is stated to be from the Antecedens Subzone of Précy (Yonne) in France (Enay & Gauthier *in* Fisher 1994) and is therefore of broadly similar age to the Upware species.

Superfamily **Perisphinctoidea** Steinmann, 1890
Family **Perispinctidae** Steinmann, 1890
Subfamily **Perisphinctinae** Steinmann, 1890

Notes on perisphinctid taxonomy. As discussed extensively elsewhere (*e.g.* Callomon 1963, 1981, 1985; Makowski 1963, 1971; Kennedy & Cobban 1976; Lehman 1981; Dommergues *et al.* 1996; Page 2008), ammonite *biospecies* were sexually dimorphic. The dimorphs are primarily separable by size, with large forms (macroconchs) presumed to be female and small forms (microconchs) male. A difference in mature shell ornament is also typical, and the microconchs of the Perisphinctina (sensu Besenov & Michailova 1983; Page 1996) typically have paired lateral apertural projections (lappets) and the macroconchs simple curved apertures. Each dimorph also shows a range of ornament strength and whorl section, with round-whorled, coarse-ribbed and more compressed, finer-ribbed extremes being typical.

In the Perisphinctinae, as in many other ammonoid groups, each of these variants has typically been assigned a different specific name and the two members of dimorphic pairs are often placed in different subgenera. The great variability of perisphinctids in particular expressed by this traditional morphological classification can, however, confuse true biological relationships between the preserved members of a biological population. Taken to its extreme, this traditional approach led to an expression of despair by W. J. Arkell during compilation of his famous monograph of British Corallian ammonites: *"The present study has shown again how ammonite material if sufficiently plentiful, will defeat any attempt at classification, however "natural" and well balanced its author may consider it to be"* (Arkell 1948, p. 380; Callomon 1985, p. 55). Though Arkell was scrupulous in his desire to describe only valid species of ammonite, subsequent ammonite workers have regarded him as a 'splitter' having little regard for the concept of variation within a species (Kennedy 2006). This comment is perhaps a little unkind, as Arkell did, for instance, introduce many new varieties of pre-existing species of cardioceratids to cover such variation in that family. However, he named only two varieties of pre-existing species of *Perisphinctes*, preferring to introduce many new species names for variants within such macroconch 'genera' as *Kranaosphinctes* (including *Arisphinctes*) and *Perisphinctes s.s.*, and microconchs within *Dichotomosphinctes* and *Otosphinctes*. Many of these 'species' are almost certainly simply variants within a single evolving biospecies.

As the reasoning behind the concept of sexual dimorphism in ammonites became increasingly accepted, Cope (1967) was the first to accord dimorphs the same specific name through a lineage of perisphinctids. In this manner, Chandler & Callomon (2009) described a large collection of graphoceratid ammonites from a single horizon in the Aalenian of Dorset, SW England, and showed that this assemblage, which varies considerably in morphology, consists of the macroconchs and microconchs of a single very variable biospecies. A new biospecific name, *Leioceras comptocostosum* Chandler & Callomon, was introduced to encompass this assemblage, with pre-existing morphospecies being regarded as varieties of the new biospecies. Subsequently, Wright (2012) described a fauna of cardioceratids from the Lower Oxfordian of the Isle of Skye, again showing that almost all named morphospecies are simply variants of one biospecies. A similar conclusion was reached concerning a separate population of Lower Oxfordian cardioceratids from North Yorkshire.

Returning to the perisphinctids, surely it should now be possible to abandon Arkell's scheme and introduce a scheme

of transient biospecies, grouping morphospecies and morphosubgenera together into a succession of biological populations. Before introducing a new scheme, however, it is necessary to decide on the extent to which the assemblage of perisphinctids from Upware is likely to be endemic and composed of biologically related animals, i.e. a 'biospecies', or ademic and comprising unrelated specimens brought together by post-mortem drift, with several biospecies likely to be present. Fernandez-Lopez (1995) and Meléndez *et al.* (2009) have proposed criteria whereby these two alternatives can be distinguished. Studies of Sub-Mediterranean perisphinctids by these authors have shown that ademic ammonite assemblages are characterized by a dominance of mature macroconchs with far fewer microconchs and juveniles. Endemic populations, where individuals are likely to be closely related, are typically characterized by a mixed assemblage of macroconchs, microconchs and juveniles, with macroconchs in the minority.

[AQ: 2] Wright & Głowniak (in prep. 2015 show that the perisphinctid fauna of the Upper Oxfordian Clavellata Member (Corallian Group) of Dorset is dominated by macroconchs (50 macroconchs, 16 microconchs), and is likely to be an ademic assemblage in which representatives of a number of biospecies are present. In contrast, the fauna of the Crinoid Bed at Upware is dominated by microconchs (13 microconchs, 9 macroconchs) and is likely to be an endemic assemblage of related specimens.

Given that the fauna of the Crinoid Bed (beds 6b–c), in particular, appears consistent with it being one contemporaneous population, represented by a full range of macroconchs and microconchs that almost certainly all belong to one biospecies, it might be thought that we should introduce one biospecific name for this assemblage. However, only when a number of important criteria are met can this procedure be convincingly applied. Chandler & Callomon (2009) noted that:

(1) The assemblage should be isochronous, something that almost certainly applies to the Upware Crinoid Bed fauna.

(2) There should be sufficient specimens to show a seamless integration of characters between them. This is not the case with the Crinoid Bed fauna, where there are gaps in morphology between groups of specimens that may or may not have been filled in life.

(3) The assemblage to be tested for morphological integration should be adult. As mentioned above, many of the Crinoid Bed microconchs are juvenile or are not sufficiently well preserved to enable the maximum adult size to be determined. Głowniak (2002) has shown how essential it is to have this data, the maximum size of microconchs increasing steadily with time during the Middle Oxfordian. Crinoid Bed macroconchs can also be juvenile, or are frequently poorly preserved, lacking the outermost whorl.

Thus, reluctantly, we eschew the possibility of describing this fauna as a biospecies and, as recommended by Chandler & Callomon (2009), when the criteria are not met, pre-existing morphospecific names are retained. In the present work, the use of subgenera will follow that of Głowniak (2002) and the reader is referred to that work for a definitive discussion of valid perisphinctid subgeneric divisions. Głowniak's (2002) analysis of Polish Middle Oxfordian perisphinctids was based on the recognition of distinct lineages. However, she was dealing with a succession of faunas that is largely older stratigraphically than the Upware succession, living in an area situated much closer to, and liable to the influx of, Mediterranean populations with their separate lineages. We suggest that, at Upware, we are only dealing with one lineage, within which the proportions of the contained morphotypes varied with time. Effectively, this is a succession of biospecies, each evolving from the previous one.

Microconch adults of *Otosphinctes* and *Dichotomosphinctes* complete with aperture are rare in the Upware faunas, and thus maximum size, as used by Glowniak (2002), is not a criterion that can be applied to subdivide the Upware microconchs into successive species and sub-species. However, an attempt has been made to use graphical plots

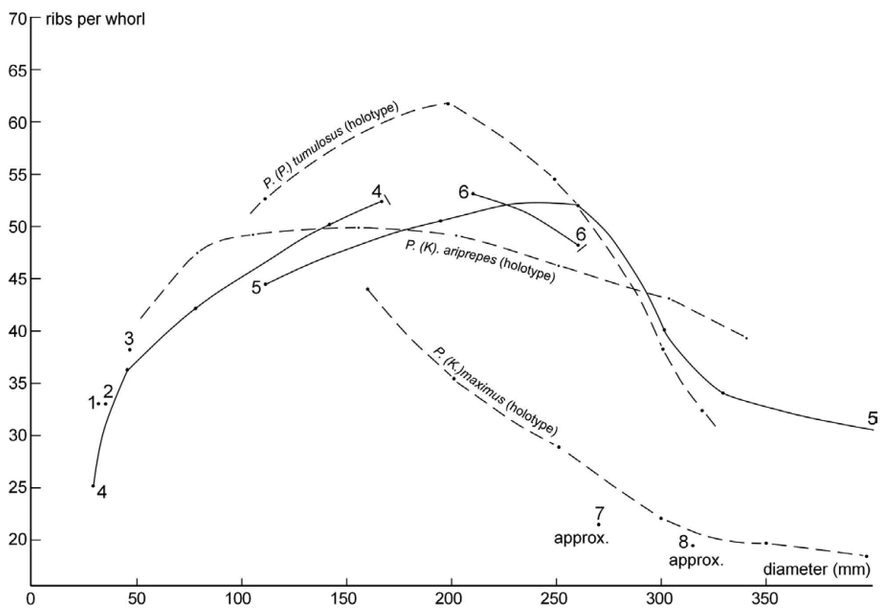
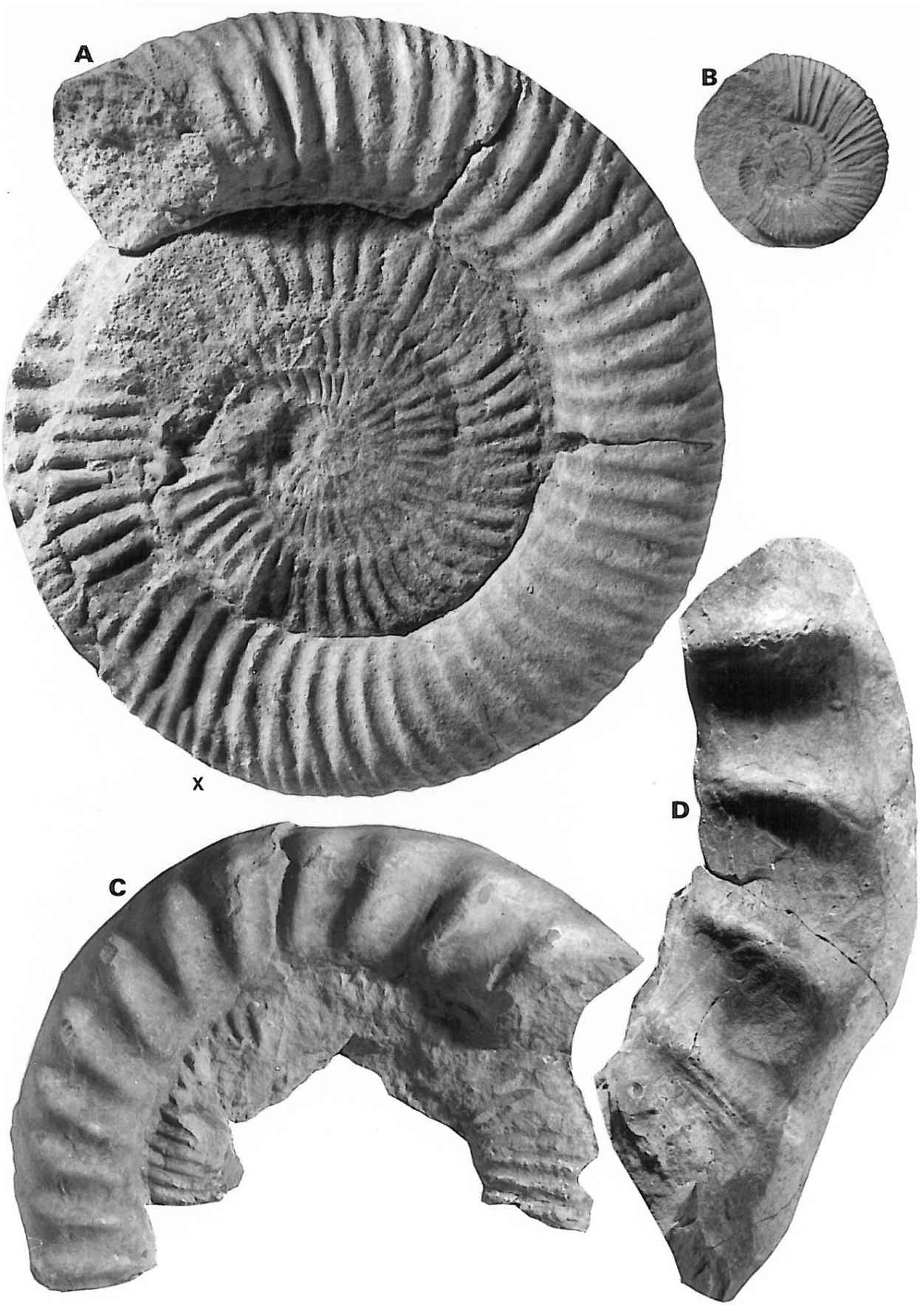


Fig. 3. Rib curves of perisphinctids from the Dimmock's Cote Marl. 1, *Perisphinctes (Otosphinctes)* cf. *ouatius* Buckman; 2–3, *P. (O.)* cf. *arkelli* Głowniak; 4–6, *P. (Kranaosphinctes) ariprepes* Buckman; 7–8, *P. (Perisphinctes)* aff. *maximus* (Young & Bird). 1, SM X.50139.63; 2, SM X.50139.76; 3, SM X.50139.37; 4, SM X.50139.35; 5, SM X.50139.97; 6, SM X.50139.89; 7, SM X.50139.60; 8, SM X.50139.61.


A
B
X
C
D

of dimensions and rib counts of the microconchs to separate distinct morphological groups. Within the macroconchs *Kranaosphinctes* and *Perisphinctes s.s.*, statistical analysis is not possible, and morphospecific variants have been chosen to describe the range of variability present. The rib-density, including the rate of decrease in rib numbers per whorl with increasing shell diameter on variocostate macroconch final whorls, is a useful character for comparison with the macroconchs recorded by Arkell (1935–1948). Graphs representing each successive assemblage are included herein. Some rib numbers have been estimated, as not all specimens show completely preserved whorls. Several juvenile macroconchs have been collected but these are less informative.

Thus, within the whole Upware succession, we describe a series of successive populations, using established subgeneric and specific names to demonstrate the changes in the proportions of these morphotypes with time. The morphospecific names used here should only be taken as guides, the nature of the variation of the assemblage being more diagnostic as illustrated by the figured specimens.

Genus ***Perisphinctes*** Waagen 1869
Subgenus ***Perisphinctes*** Waagen 1869
Type species. *Ammonites variocostatus* Buckland 1836, designated by Arkell 1937, p. liii.

Perisphinctes (Perisphinctes) tumulosus Buckman
(Fig. 10C,D,F)

1927 *Perisphinctes tumulosus* sp. nov.; Buckman, pl. 714.
1936*b Perisphinctes (Perisphinctes) tumulosus* Buckman; Arkell, pp. 166, 173.
1938 *Perisphinctes (Perisphinctes) chloroolithicus* (Gümbel); Arkell, pl. 18, figs 1a, b, 5a, b, text fig. 25.

Material. Six specimens, SM X.50139.79, -.86, -.90, -.91, -.94, -.96, from the Upware Limestone, Crinoid Bed (beds 6b–c), all showing portions of the body-chamber, with the inner ribbing poorly seen.

Measurements. SM X.50139.91 (not figured): D (ad) *c.* 280 mm; at 265 mm, 0.21, 0.28 (0.20), 0.58, ribs *c.* 48 at 88 mm, *c.* 53 at 140 mm, *c.* 59 at 210 mm.

SM X.50139.96 (Fig. 10C,D): D (phg) 350 mm, D (ad) 460 mm; at 370 mm, 0.20, 0.34 (0.23), 0.65; ribs *c.* 58 at 75 mm, *c.* 60 at 192 mm, *c.* 44 at 305 mm, *c.* 17 at 450 mm.

Description. Giant forms, some mature at around 460 mm diameter (Fig 10C,D) with just over half a whorl of body-chamber (septate to around 350 mm). The maximum size is very variable, and two specimens (SM X.50139.91, -.94; Fig. 10F) are apparently mature at only 300 mm, as is the holotype (Buckman 1927, pl. 714). The inner whorls are typically evolute, closely, sharply and regularly ribbed, with only faint, infrequent constrictions present. There are typically around 53 to 60 ribs on the final whorl before variocostation begins. There is then only a steady fall in the rib curve from 60 rpw at 200 mm to 20 rpw at 460 mm (Fig. 6).

The whorl section is flat sided up to 200 mm, when a rounded whorl section develops. Secondary ribs initially persist at this stage, as variocostation develops, but suddenly fade, and the venter becomes flat and smooth. The early part of the body chamber has widely spaced primary ribs and a rectangular section with a flattened venter. The final part of the body chamber, towards the mature aperture, develops a rounder section with more frequent ribs (Fig. 10C,D). This change in SM X.50139.94 (Fig. 10F) begins at about 220 mm; it is the coarsely ribbed stage that is much shorter in this specimen.

Remarks. The rib curve of the Upware specimens (Fig. 6) matches that of *P. tumulosus* quite closely. There is much less resemblance to *P. parandieri* de Loriol (*e.g.* Arkell 1938, text figs 28, 30, 31) and the neotype (Enay 1966, pl. 6). Though there is a similar ventral flattening of the whorl just before the end of septation so that the whorl breadth here is twice the whorl height, the ridge-ribs on the outer whorl are not as bold as in *P. parandieri* and are much more numerous.

Perisphinctes (Perisphinctes) parandieri de Loriol
(Fig. 11A–D)

1899 *Perisphinctes de Riazi* Siemiradzki (*nom. nov*. for *P. subrota* de Riaz, 1898, p. 31, pl. 14, *non* Choffat, 1893).
1903 *Perisphinctes parandieri* de Loriol, *pars*, pl. 7 (lectotype selected by Buckman, 1924, pl. 511B), *non* pl. 8.
1927 *Martelliceras orientale* Buckman, pl. 736A, B.
1939 *Perisphinctes (Perisphinctes) parandieri* de Loriol; Arkell pp. 95, 97, text figs 28, 30, 31.
1963 *Perisphinctes (Perisphinctes) parandieri* de Loriol; Malinowska, pp. 157–158, pls 39, 40.
1966 *Perisphinctes (Perisphinctes) parandieri* de Loriol; Enay, pp. 357–363, pl. 5, figs 1–2.

Material. Two specimens (SM X.50139.92, -.95) from the Upware Limestone, Crinoid Bed (beds 6b–c).

Measurements. SM X.50139.92 (Fig. 11A,B); D (max) *c.* 300 mm. D (phg) 215 mm; at 230 mm, 0.14, 0.30 (0.25), 0.67; ribs 53 at 150 mm, 54 at 180 mm, *c*. 38 at 230 mm, *c*. 31 at 255 mm.

Fig. 4. *P. (Otosphinctes)* and *P. (Kranaosphinctes)* from the Dimmock's Cote Marl. (**A**) *Perisphinctes (Kranaosphinctes) ariprepes* (Buckman) [juv. M]; SM X.50139.35; largely complete specimen lacking the last quarter of a whorl of body-chamber; natural size. (**B**) *Perisphinctes (Otosphinctes)* cf. *arkelli* Głowniak. [?m]; SM X.50139.50; no suture visible; natural size. (**C**) *Perisphinctes (Kranaosphinctes)* aff. *ariprepes* Buckman, trans. to *Perisphinctes (P.) tumulosus* (Buckman) [M]; SM X.50139.89; specimen largely complete including aperture. End of phragmocone not preserved. ×0.5. (**D**) *Perisphinctes (Kranaosphinctes)* aff. *maximus* (Young & Bird) [M]; SM X.50139.61; fragment of body-chamber including aperture; ×0.7. Note: On this and following similar figures, the end of the phragmocone is marked by an X. Specimens that are wholly septate and portions of non-septate body-chambers are described as such in the plate descriptions; in all other cases, the presence and extent of suture lines cannot be determined.

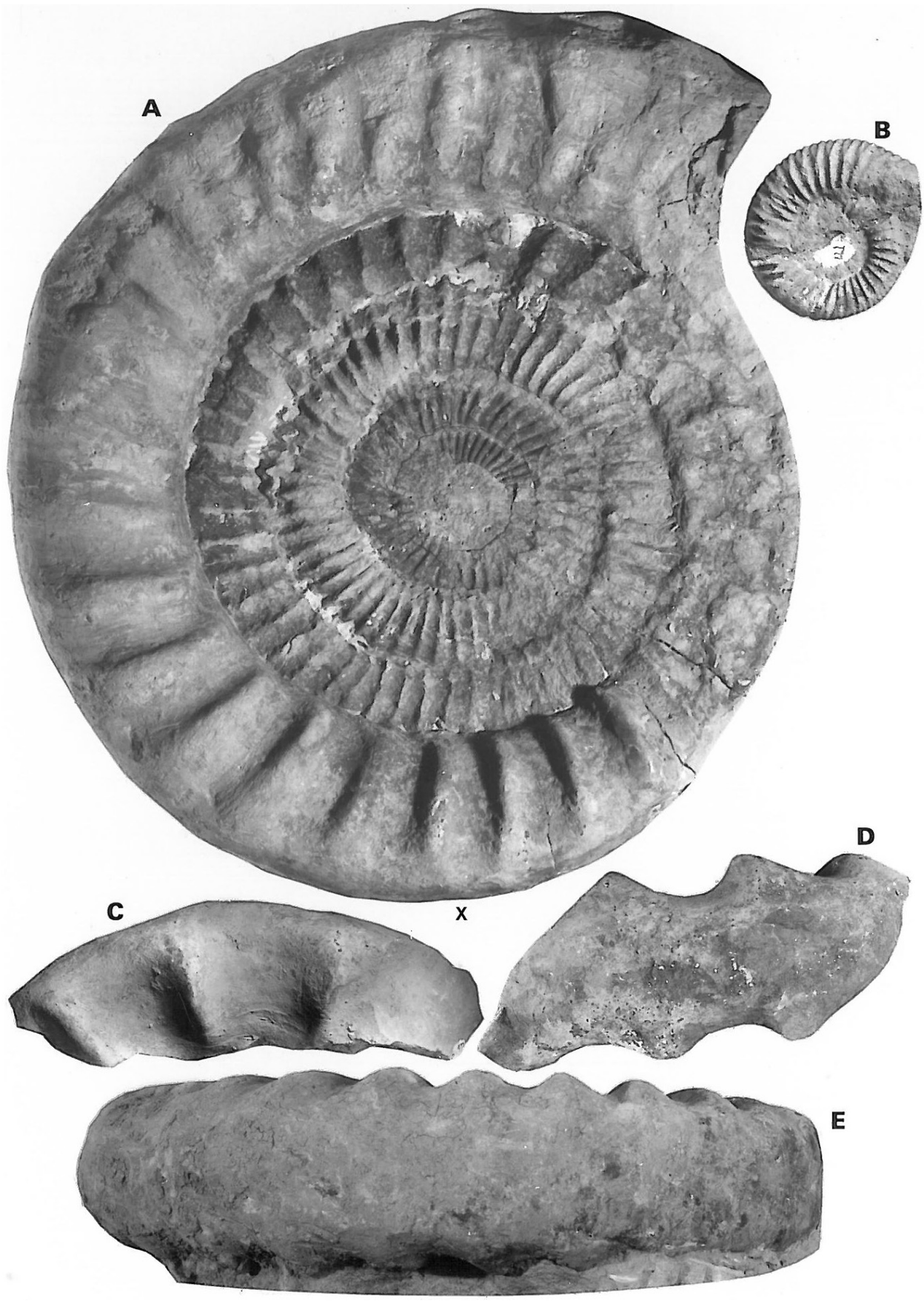


Fig. 5. *P. (Otosphinctes)* and *P. (Kranaosphinctes)* from the Dimmocks Cote Marl. (**A, E**) *Perisphinctes (Kranaosphinctes) ariprepes* (Buckman) [M]; SM X.50139.97; almost complete specimen, aperture broken away, inner whorls slightly crushed, Bed 1; ×0.41. (**B**) *P. (Otosphinctes)* cf. *ouatius* Buckman, SM X.50139.63. (**C, D**) *Perisphinctes (Kranaosphinctes)* aff. *maximus* (Young & Bird) [M]; SM X.50139.60; fragment of body-chamber; ×0.50.

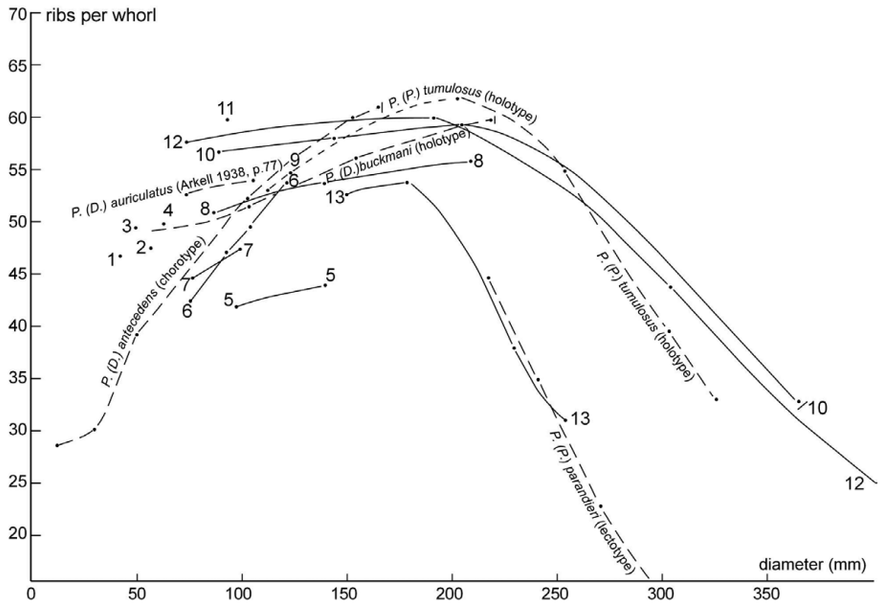


Fig. 6. Rib curves of perisphinctids from Bed 6 the Upware Limestone, Dimmock's Cote Quarry. 1, 3–4, 11, *P. (Dichotomosphinctes) buckmani* Arkell. 2, *P. (Otosphinctes)* sp. 5, *P. (Kranaosphinctes)* aff. *decurrens* Buckman. 6–7, 9, *Perisphinctes (D.) antecedens* Salfeld. 8, 10, 12, *P. (P.) tumulosus* Buckman. 13, *P. (P.) parandieri* de Loriol. 1, SM X.50139.53; 2, SM X.50139.26; 3, SM.X.50139.47; 4, SM.X.50139.71; 5, SM X.50139.28; 6, SM X.50139.87; 7, SM X.50139.44; 8, SM X.50139.91; 9, SM X.50139.29; 10, SM.X.50139.94; 11, SM X.50139.42; 12, SM X.50139.96; 13, SM X.50139.92.

Description. Large forms, mature at over 350 mm diameter. The innermost whorls are not well exposed in the present specimens, but the rib curve appears to rise gently up to 180 mm, when it falls off rapidly (Fig. 6). The early whorl is relatively compressed with flat whorl sides (Fig. 11B). Ribbing is typically biplicate, branching at around 80–83% of the whorl height and with a noticeable forward slant when viewed laterally.

Variocostation takes place over half a whorl between 180 and 230 mm diameter and is extreme, producing widely spaced ridge-ribs before the end of septation. These sharp, gently curving ribs may be opposite each other (Fig. 11A), or may alternate in a zig-zag fashion (Fig. 11D). The whorl section at this stage is typically ventrally flattened with a broad, flat venter. Rib numbers plummet to only 17 at around 355 mm diameter (Fig. 6). The rib curve (Fig. 6:13) of SM X.50139.92 (Fig. 11A,B) matches very closely that of the lectotype.

Discussion. De Loriol (1903) figured two specimens as the new species *P. parandieri*. According to Arkell (1939, p. 106), these are so distinct from each other that they cannot be conspecific. Buckman (1924, pl. 511B) designated de Loriol's specimen with coarser ribbing on the inner whorls (de Loriol 1903, pl. 7) as lectotype. Enay (1966, pl. 5, fig. 3) designated the finely ribbed variant as "morphotype densicosté".

Perisphinctes (Perisphinctes) chloroolithicus (Gümbel)
(Figs 11G, 13E, 14B,D)

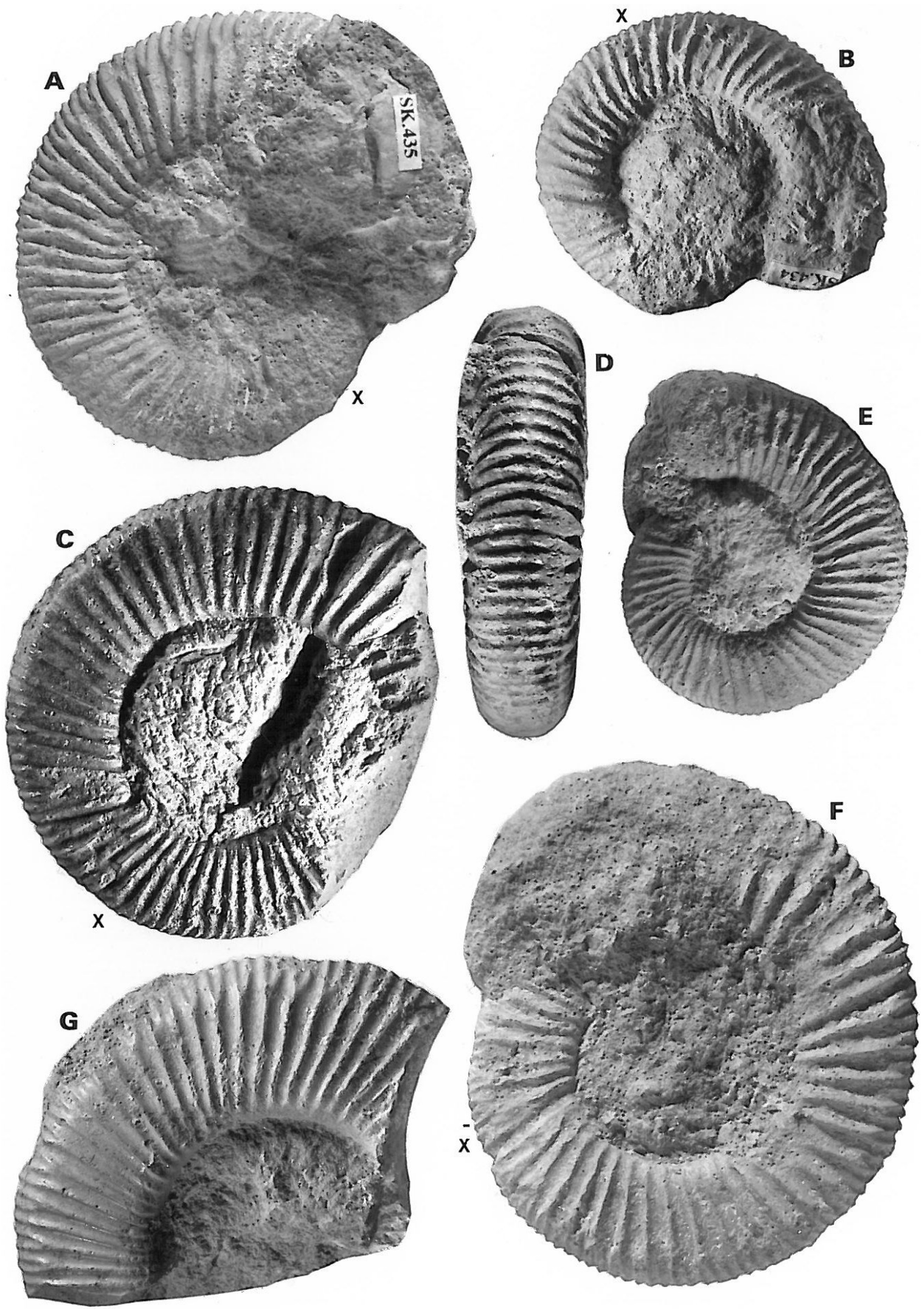
1865 *Ammonites chloroolithicus* Gümbel, p. 49.
1891 *Perisphinctes chloroolithicus* Gümbel, p. 121.
1912 *Perisphinctes chloroolithicus* (Gümbel); Klebelsberg, p. 197, pl. 18, figs 4a, b.
1930 *Perisphinctes chloroolithicus* (Gümbel); Dorn, p. 131, pl. 4, figs 1–3.
1938 *Perisphinctes (Dichotomosphinctes) buckmani* Arkell; Arkell, pl. 14, fig. 2.
1938 *Perisphinctes (Perisphinctes) chloroolithicus* (Gümbel); Arkell, pp. 95–104, pl. 18, figs 1–7, pl. 19, fig. 4, text figs 26, 27.
1966 *Perisphinctes* cf. *chloroolithicus* (Gümbel); Enay, pp 363–366, pl. 5, figs 4a, b.

Material. Three specimens: SM J359 (North Pit), SM J374 'South Pit', SM J3836 'New Pit', from Bed 9 by matrix, plus numerous inner whorl fragments not identifiable as micro or macroconchs; SM J380 ('Bridge Pit'), SM J41877 and SM X. 50139.39 (Dimmock's Cote Quarry).

Measurements. SM J359 (Fig. 11G): D (phg) 150 mm; at 153 mm, 0.26, 0.20, 0.52; ribs *c.* 61 at 93 mm, 57 at 153 mm.

SM J3836 (Fig. 14B); D (max) 353 mm; ribs 60 at 180 mm, 50 at 200 mm, 47 at 250 mm, 30 at 300 mm, 17 at 353 mm.

Description. Gümbel's holotype comprises only the inner whorls (Arkell 1938). These are densely ribbed, the rib curve rising rapidly from 30 rpw at 40 mm to 60–64 rpw at 160 mm (Fig. 12). Both Arkell (1938) and Enay (1966) considered the holotype to be the inner whorls of a coarsely ribbed, macroconch *Perisphinctes s.s.* On this interpretation, variocostation sets in rapidly, changing through simple, coarse primary ribs to bold, wedge-shaped ribs over a quarter of a whorl (Fig. 14B). Specimen SM J374 (Figs 13E and 14D) has the extremely wide, cuneiform and even flat topped ribs on the late phragmocone and early body chamber that distinguishes *P. chloroolithicus* from *P. parandieri* (Arkell 1938, p. 98). The ribbing on the mature stage of *P. parandieri* is much more pointed (Fig. 11D) and curves gently forward (Fig. 11B), without a marked wedge shape (Arkell 1939, p. 106). The rib curve of SM J3836 (Fig. 12:16) matches quite closely that of *P. chloroolithicus* as interpreted by Enay (1966).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SK.435
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G
X

Remarks. The species as interpreted here includes the variants from Upware and Normandy with extremely coarse ribbing on the body-chamber described by Arkell (1938, pp. 96, 97). Specimens from the Headington Shell Bed with less coarse ribbing on the body-chamber, described by Arkell (1938) as *P. chloroolithicus*, are included here in *P. tumulosus.*

Perisphinctes (Perisphinctes) holtonensis Buckman
(Figs 13A and 14A,C)
1927 *Dichotomosphinctes holtonensis* sp. nov.; Buckman pl. 715.
1939 *Perisphinctes (Arisphinctes) maximus* (Young & Bird); Arkell, p. 117.
1939 *Perisphinctes parandieri* de Loriol; Arkell, text-fig. 32.
1966 *Perisphinctes (Perisphinctes) andelotensis*; Enay, pp. 366–371, pl. 9, figs 1a, b, 2a–c.
1966 *Perisphinctes (Perisphinctes)* aff. *andelotensis*; Enay, pp. 366–371, pl. 9, figs 3a, b.
?1995 *Perisphinctes (Dichotomosphinctes) dobrogensis* Simionescu; Gygi, pp. 34, 36, fig. 15.

Material. Four specimens: SM J363 (North Pit), SM J371 (?North Pit), SM J383 ('Bridge Pit'), SM X.50214 (Bridge Pit South), by matrix from Bed 9.

Measurements. SM X.50214 (Fig. 13A); D (phg-juv) 121 mm, D (max) 180 mm; at 160 mm, 0.23, 0.24 (0.22), 0.57; ribs 50 at 115 mm, 51 at 129 mm, *c*. 44 at 180 mm.

SM J363 (Fig. 14A,C); D (max) 180 mm; at 156 mm, 0.21, 0.28 (0.25), 0.61; ribs 40 at 180 mm.

Description. Buckman's holotype has the inner whorls poorly preserved. The present specimens show that the rib curve rises gently from 50 rpw at 60 mm to 56–60 rpw at 120 mm (Fig. 12). The stage of coarse primary ribbing separating the dense ribbing of the inner phragmocone from the coarse, wedge-shaped ribbing of the body-chamber is long, at least half a whorl, giving the rib curve a very gentle inverted U shape (Fig. 12:7 and 14). The downturn of the curve starts at between 120 and 140 mm, much earlier than in other species of *Perisphinctes s.s*. All the Upware specimens are situated on the graph very close to the line of Buckman's holotype.

Remarks. *P. holtonensis* is distinguished from *P. parandieri* by the earlier onset of variocostation. Arkell (1939, p. 111) could find nothing to separate *P. holtonensis* from *P. parandieri*, but unfortunately he mis-plotted the rib curve of *P. holtonensis* in his text-figure 108. The rib curve of *P. holtonensis* is much shallower than Arkell thought. Because of this, specimen SM J363, considered by Arkell to belong to *Arisphinctes* (=*Kranaosphinctes*), fits quite nicely as the inner whorls of *P. holtonensis*. The rib curve of Enay's *P. (P.) andelotensis* also matches that of the holotype of *P. holtonensis* very closely. The specimen figured as a *Dichotomosphinctes* by Gygi (1995) has modified ribs suggestive of an immature or incompletely preserved *Perisphinctes s.s*. Its rib curve matches very closely that of SM X.50214 (Fig. 13A).

Subgenus *Kranaosphinctes* Buckman 1924
Type species. *Kranaosphinctes kranaus* Buckman 1921, pl. 243.
Perisphinctes (Kranaosphinctes) ariprepes (Buckman)
(figs 4A,C and 5A,E)
1924 *Arisphinctes ariprepes* sp. nov.; Buckman, p. 33, pl. 511A, B.
1939 *Perisphinctes (Arisphinctes) cotovui* Simionescu; Arkell, p. 126 (pars), figs 39–43; pl. 24, figs 3, 4, 5a, b; pl. 25, fig. 3 only, *non* text-figs 41, 42; pl. 25, fig. 1a–f.
2002 *Perisphinctes (Kranaosphinctes) ariprepes* (Buckman); Głowniak, pp. 344, 345, pl. 13, fig. 1, text-figs 17, 22 (contains full synonomy).
2006*b* *Perisphinctes (Kranaosphinctes) ariprepes* (Buckman); Głowniak, pp. 191–192.

Material Four specimens from the Dimmock's Cote Marl: a large, complete specimen 415mm in diameter (SM X.50139.97) from Bed 1, a smaller specimen, 260 mm maximum diameter and thus a possible juvenile macroconch (SM X.50139.89) from beds 2 or 3, a nearly complete juvenile macroconch showing the inner whorls from beds 2 or 3 (SM X.50139.35), and a smaller body-chamber fragment (SM X.50139.48) from Bed 3.

Measurements. SM X.50139.35 (Fig. 4A): D (phg-juv) 110 mm, D (max) 167 mm; at 147 mm, 0.24, –, 0.56; ribs 26 at 28 mm, 37 at 45 mm, 43 at 80 mm, 51 at 140 mm, 53 at 167 mm.

SM X.50139.97 (Fig. 5A,E): D (max) 415 mm; at 335 mm, 0.23, 0.25 (0.21), 0.64; ribs 45 at 110 mm, 51 at 195 mm, 53 at 260 mm, 41 at 300 mm, 35 at 330 mm, 31 at 415 mm.

Description. SM X.50139.97 has half a whorl of mature body-chamber at 415 mm (Fig. 5A). It is septate to 315 mm, the last quarter of a whorl of body-chamber having broken away, making its maximum original diameter *c*. 470 mm. The specimen is a typical *Kranaosphinctes*, showing a gradual development of variocostation from a diameter of around 190 mm, some one and a half whorls before the final mature aperture. The inner whorls are regularly and sharply ribbed and variocostation develops by a gradual increase in the spacing of the primary ribs (Fig. 3). There is an associated decrease in sharpness, the ribs becoming more massive

Fig. 7. *P. (Otosphinctes)* and *P. (Dichotomosphinctes)* from Bed 6 of the Upware Limestone of Dimmock's Cote Quarry. All natural size. (**A**) *Perisphinctes (Dichotomosphinctes) buckmani* Arkell [m]; SM X.50139.27. (**B**) *Perisphinctes (Otosphinctes)* sp. A [m]; SM X.50139.26. (**C, D**) *Perisphinctes (Dichotomosphinctes) buckmani* Arkell [m]; SM X.50139.42. (**E**) *Perisphinctes (Dichotomosphinctes) buckmani* Arkell [m]; SM X.50139.71; an almost complete whorl of body-chamber. (**F**) *Perisphinctes (Dichotomosphinctes) antecedens* Salfeld [m]; SM X.50139.44; body-chamber present but aperture broken away. (**G**) *Perisphinctes (Dichotomosphinctes) buckmani* Arkell [m]; SM X.50139; fragment of body chamber.

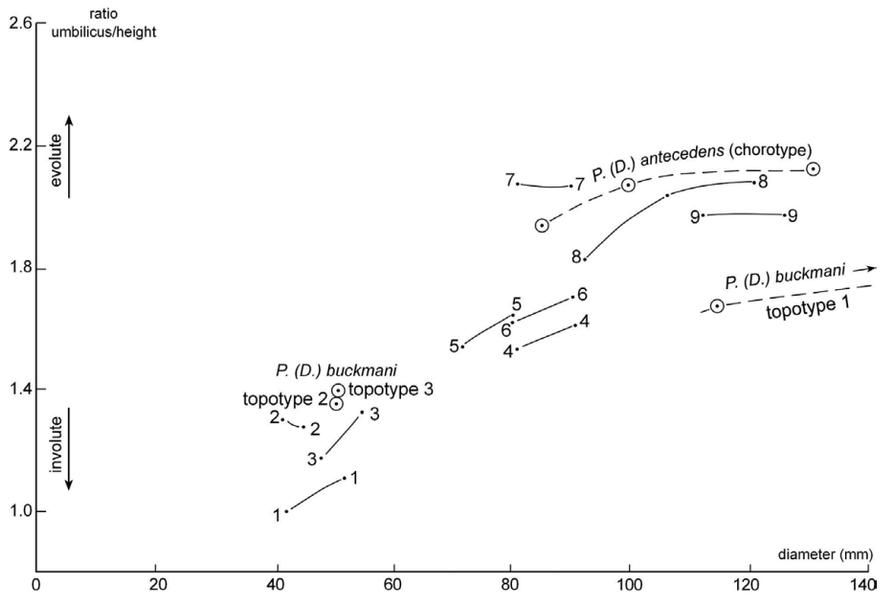


Fig. 8. Plots of umbilicus/whorl height ratios for *P. (Dichotomosphinctes)* spp. from Bed 6 of the Upware Limestone of Dimmock's Cote Quarry. 1–5, *P. (D.) buckmani* Arkell. 6–9, *P. (D.) antecedens* Salfeld. 1, SM X.50139.47; 2, SM X.50139.53; 3, SM X.50139.71; 4, SM X.50139.42; 5, SM X.50139.27; 6, SM X.50139.44; 7, SM X.50139.88; 8, SM X.50139.87; 9, SM X.50139.29.

but not changing their basic shape. Towards the mature aperture, the ribs become slightly closer. Secondary ribs are absent on the final whorl, which has a distinctive flattened venter (Fig. 5E). A single specimen, 167 mm in diameter (septate to around 115 mm), appears to represent an almost complete juvenile macroconch (Fig. 4A). Ribbing is strong, and although dominantly biplicate, some triplicate ribs are present. The apparent forward curve of the ribs on the figured specimen is due to partial crushing of the body chamber. SM X.50139.89 may be a juvenile macroconch, being preserved to around 260 mm diameter, but septate to 200 mm, with wedge-shaped ribbing beginning at about 230 mm (Fig. 4C).

Remarks. The macroconchs are typical of a number of large *Kranaosphinctes* figured (as *Arisphinctes*) by Arkell (1939), including *P. (K.) cotovui* Simionescu (the holotype of which is now considered to be from the Upper Oxfordian Bimammatum Chronozone; J.H. Callomon, personal communication, 2005) and *P. (A.) ingens* (Young & Bird). All these forms have relatively close-ribbed body-chambers but, in the absence of good stratigraphical control on the source level of most specimens, discussions on synonymies and correlations are problematic. Głowniak (personal communication, 2007) has noted that the wedge-shaped ribs of SM X.50139.89 are more characteristic of *Perisphinctes s.s.* than *Kranaosphinctes*. This specimen thus marks a transition from the former into the latter subgenus. However, its rib curve is closer to that of *Kranaosphinctes* than *Perisphinctes s.s.* (Fig. 3:6). The rib curves of the Dimmock's Cote Marl macroconchs thus match quite well those of *P. ariprepes* as figured by Głowniak (2002, fig. 22), but the Upware specimens have bolder ribs and a steeper downturn of the rib curve at larger dimensions, more indicative of *Perisphinctes s.s*.

Perisphinctes (Kranaosphinctes) aff. *maximus* (Young & Bird) (Figs 4D and 5C,D)

1828 *Ammonites maximus* sp. nov.; Young & Bird, 2nd edition, p. 255 (no figure).
1914 *Perisphinctes parandieri* de Loriol; Salfeld, p. 238, pl. 13, fig. 5.
1924 *Arisphinctes maximus* Young & Bird; Buckman, pl. 512 (holotype figured).
1939 *Perisphinctes (Arisphinctes) maximus* (Young & Bird); Arkell, pp. 112–118 pl. 19, figs 1–3, pl. 20, figs 1–4, pl. 21, fig. 2, pl. 22, figs 1, 2, pl. 25, fig. 4, text figs 34, 35.
1972 *Perisphinctes (Arisphinctes) maximus* (Young & Bird); Malinowska, pp. 182–184, pl. 3.

Material. Two body-chamber fragments (SM X.50139.60, -.61) of a macroconch perisphinctid from the Dimmock's Cote Marl, probably from Bed 4.

Description. These body chamber fragments (Figs 4D and 5C,D) are close to *P. (K.) ariprepes*, but have more widely spaced primary ribs on the body-chamber than occur in *P. (D.) ariprepes*. The fauna of the highest Dimmock's Cote Marl thus includes specimens with this widely spaced rib style and a more rounded mature whorl section.

Remarks. The widely spaced ribbing and rounded whorl section suggest a comparison with *P. (A.) maximus* (Young & Bird), specifically specimens figured by Arkell (1939, pl. 19, figs 3 and pl. 20, figs 1, 2, 4). With more complete, accurately located material, it may be possible to define a discrete transient species at this level.

Perisphinctes (Kranaosphinctes) sp. aff. *decurrens* Buckman (Fig. 10E)

1923 *Kranaosphinctes decurrens* sp. nov.; Buckman, pl. 449.
1939 *Perisphinctes (Kranaosphinctes) decurrens* Buckman; Arkell, pl. 38, fig. 4; pl. 39, figs 1–6; text-fig. 62.
1963 *Perisphinctes (Kranaosphinctes) decurrens* Buckman; Malinowska, p. 155, pl. 33, igs 157a, b.
1977 *Perisphinctes (Kranaosphinctes) decurrens* Buckman; Matyja, pl. 7, fig. 7.

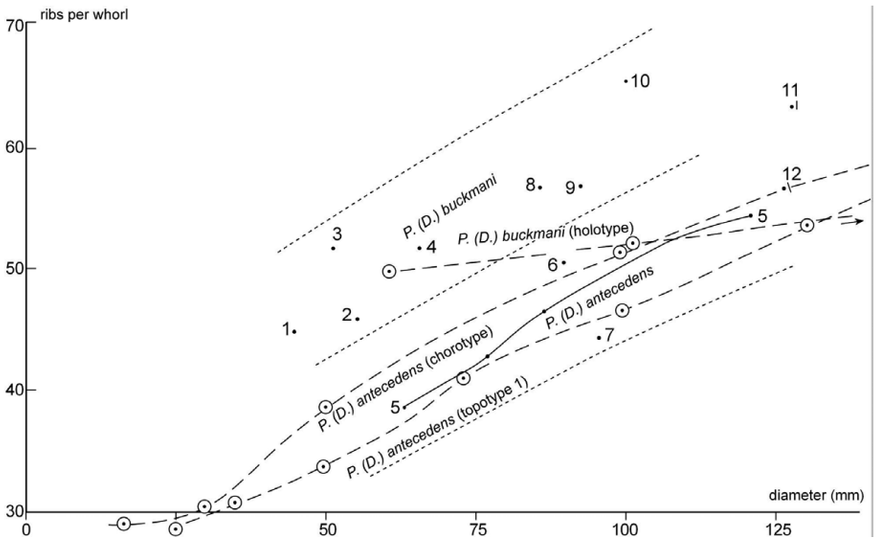


Fig. 9. Rib curves and rib counts for *P. (Dichotomosphinctes)* spp. from Bed 6 of the Upware Limestone of Dimmock's Cote Quarry. 1–4, 8–10, *P. (D.) buckmani* Arkell. 5–7, 11–12, *P. (D.) antecedens* Salfeld. 1, SM X.50139.53; 2, SM X.50139.70; 3, SM X.50139.47; 4, SM X.50139.71; 5, SM X.50139.87; 6, SM X.50139.88; 7, SM X.50139.44; 8, SM X.50139.27; 9, SM X.50139.42; 10, SM X.50139.69; 11, SM X.50139.34; 12, SM X.50139.29.

Material. One largely complete juvenile specimen (SM X.50139.28) and one body-chamber fragment (SM X.50139.36) from the Upware Limestone, Crinoid Bed (beds 6b–c).

Measurements. SM X.50139.28 (Fig. 10E): D (phg-juv.) 107, D (max) 138 mm, 0.6 wh bch; at 91 mm, 0.27, 0.32, 0.55; ribs 42 at 97 mm, *c*. 44 at 140 mm.

Description. The juvenile specimen (Fig. 10E) is well preserved, showing features characteristic of *Kranaosphinctes*, with bold primary ribbing, much less prominent bifurcating secondaries, a depressed whorl section and prominent, prorsiradiate constrictions with marked interruption of the ribbing. Constrictions are frequent, three or four per whorl, though not deep. Each is followed by a strong, simple rib whose trend is then followed by that of the primary ribbing. The whorl section is depressed, being 18 mm high at 70 mm diameter, with the whorl breadth 23 mm. Sutures are thin and difficult to make out, but the last septum in this specimen appears to be at 107 mm. The maximum preserved diameter of 140 mm appears to be close to the maximum diameter achieved by this juvenile; the last two ribs, visible on the reverse of the specimen, are both simple, but no aperture is preserved. Specimen SM X.50139.36 (not figured) is a body-chamber fragment from close to the aperture of an individual some 250–300 mm in diameter. It shows coarse, regularly spaced primary ribs passing strongly over the venter as simple ribs and with biplicate secondaries.

Remarks. SM X.50139.28 is comparable with specimens identified as *P. (K.) decurrens* by Arkell (1939), particularly the specimen illustrated in his plate 39, figure 4. This latter specimen has the markedly prorsiradiate primary ribbing that is particularly prominent at 120 mm in diameter in our specimen. However, Arkell's specimen has predominantly triplicate secondaries at this diameter, whereas almost all secondaries bifurcate in the Upware specimen. Another specimen of *P. (K.) decurrens* (Arkell 1939, pl. 39, figs 6a,b), though having much more rectiradiate ribbing than SM X.50139.28, does have predominantly biplicate secondaries at 120–130 mm.

It must be admitted that the rib curve of the Upware specimen (Fig. 6:5) does not have the falling off between 100 and 150 mm that characterizes *P. decurrens* (Arkell 1939, fig. 61) and is more like that of *P. (K.) kranaus* (Buckman). However, none of the specimens of *P. (K.) kranaus* figured by Arkell (1939, pl. 38), though prosiradiate to some extent, have markedly prorsiradiate ribbing. [AQ: 3]

SM X.50139.36, a whorl fragment of whorl height 62 mm, has coarse secondary ribbing passing strongly over the venter close to the aperture in the manner of *P. (K.) bullingdonense* Arkell. Arkell's species came from the Antecedens Subchronozone, so a close match with the Upware specimens from the lower Parandieri Subchronozone is not to be expected. Głowniak (personal communication, 2007) has noted the similarity of SM X.50139.28 to the inner whorls of some *Perisphinctes s.s.* from Poland. A further interesting new species of *Kranaosphinctes* was reported from the Antecedens Subchronozone by Callomon (1960).

Subgenus ***Otosphinctes*** Buckman, 1926

Type species. *Otosphinctes ouatius* Buckman, 1926, pl. 649, figs 1, 2.

Perisphinctes (Otosphinctes) cf. *ouatius* (Buckman) (Fig. 5B)

1926 *Otosphinctes ouatius* sp. nov.; Buckman, pl. 649, figs 1, 2.

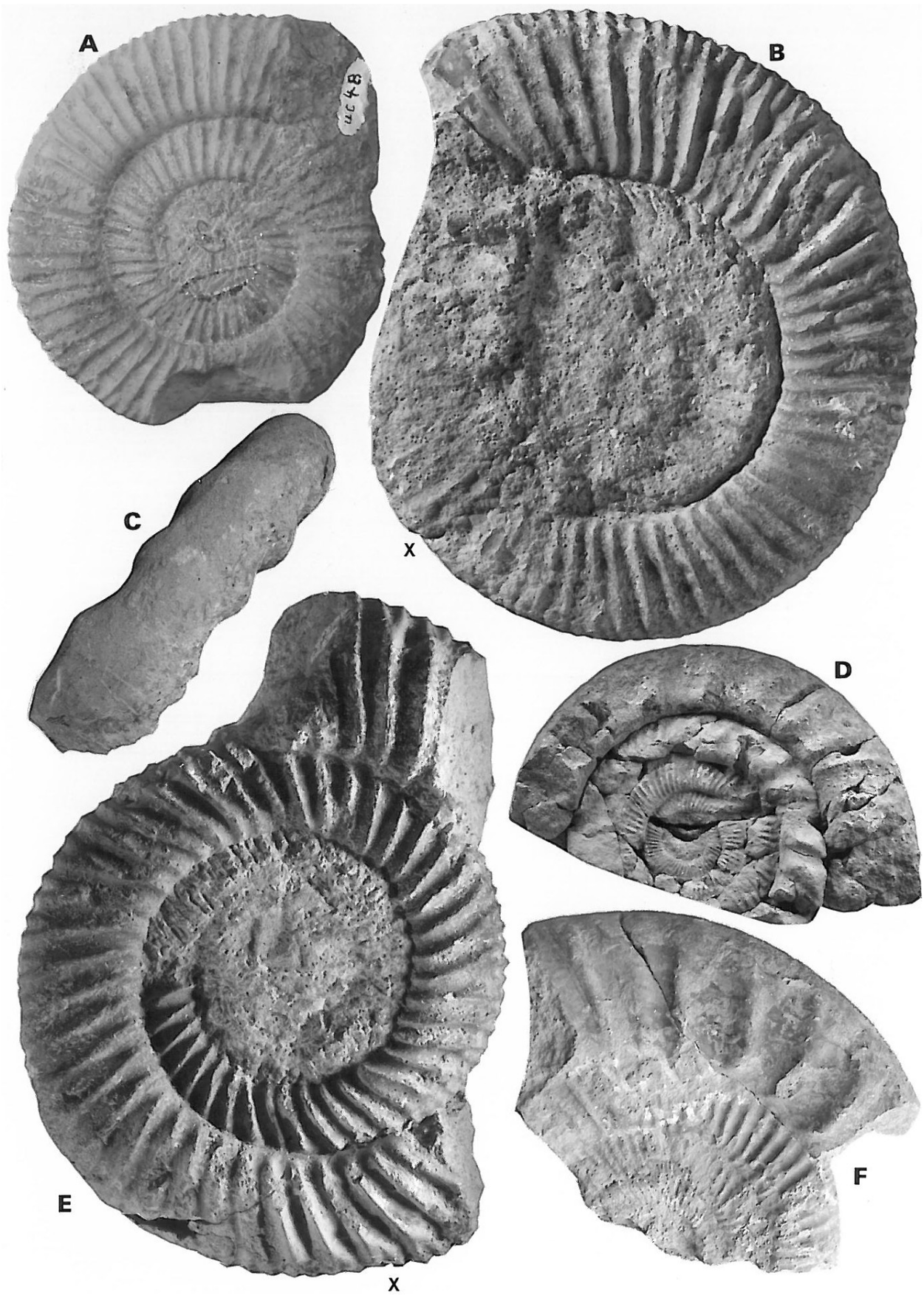
1938 *Perisphinctes (Dichotomosphinctes) ouatius* (S. Buckman); Arkell, pp. 93–94, pl. 17, figs 1, 2, 5, 6, 10.

2002 *Perisphinctes (Otosphinctes) ouatius ouatius* (Buckman 1926); Głowniak, pl. 5, fig. 3; pl. 6, figs 2–3; p. 9, figs 1–2; text-figs 5, 12, 14 (includes detailed synonomy).

Material. Two specimens (SM X.50139.57, -.63) from beds 2–4 of the Dimmock's Cote Marl.

Measurements. SM X.50139.63 (Fig. 5B): D (max) 36.5 mm; at 34 mm: 0.29, 0.37 (0.32), 0.47; 33 ribs.

Description. The specimens consist of internal moulds of parts of the inner whorls, well preserved in calcareous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concretions, but not showing sutures. The primary ribs are sharp, initially trifurcating, then bifurcating regularly after 25 mm diameter. The secondaries pass strongly over the venter with a slight forward sweep. A deep constriction is present in SM X.50139.63, followed by an oblique simple rib. The whorl section of this specimen is circular; that of the other specimen is slightly depressed, subquadrate.

Remarks. The presence of the deep constriction distinguishes the present species from *P. (O.) ouatius ouatoides* Głowniak. The circular to depressed whorl section distinguishes *P. (O.) ouatius ouatius* from *P. (O.) arkelli arkelli* Głowniak, the latter having an oval whorl section. However, there is considerable variation in the whorl section of Plicatilis Chronozone *Otosphinctes* (Głowniak 2002) and, in order to be certain of identifications, it is necessary to have adult specimens complete with aperture, something not present in any of the Upware *Otosphinctes*.

Perisphinctes (Otosphinctes) cf. *arkelli* Głowniak
(Fig. 4B)
1938 *Perisphinctes (Dichotomosphinctes) rotoides* Ronchadze; Arkell, pp. 90–93, pl. 16, figs 1–5, 7.
2000 *Perisphinctes (Otosphinctes) arkelli* sp. nov.; Głowniak, p. 153 (*pars*), text-fig. 10, pl. 5, figs 1–3.
2002 *Perisphinctes (Otosphinctes) arkelli arkelli* chronosubsp. nov.; Głowniak, p. 332, pl. 14, figs 2–3, text fig. 16.

Material. Four specimens (SM X.50139.25, -.37, -.50, -.76) from beds 2–4 of the Dimmock's Cote Marl.

Measurements. SM X.50139.76 (not figured): D (max) 37 mm; at 37 mm: 0.32, 0.27, 0.41; *c*. 35 ribs.

Description. The figured specimen (SM X.50139.50) is largely complete with body-chamber, the inner septate whorls being crushed; the specimen is thus probably immature. The ribbing is fine, moderately dense, bifurcating regularly, and passing strongly over the venter. The whorl section is oval. An oblique simple rib is present, with no noticeable constriction.

Remarks. This species is distinguished from *P. (O.) ouatius* by the absence of constrictions, combined with the slightly compressed, oval whorl section. It is distinguished from *P. (O.) arkelli wysoka* Glowniak by the presence of the oblique simple rib. Głowniak (2000) has pointed out that Arkell (1938) incorrectly allocated these microconchs to *P. (D.) rotoides* Ronchadze, now regarded as a Transversarium Chronozone *Dichotomoceras*. One specimen figured by Arkell (1938, pl. 16, fig. 6) as *P. rotoides* is 100 mm+ in diameter. It was allocated to *P. (O.) arkelli arkelli* by Głowniak (2002). However, we consider that such specimens should be allocated to *P. (O.) arkelli wysokae*, and that *P. (O.) arkelli arkelli* should be used for specimens of 80–95 mm maximum diameter. Głowniak (personal communication, 2007) has noted that the presence of parabolic nodes in this specimen means that it is quite close to *P. ouatius*.

Perisphinctes (Otosphinctes) sp. A (Fig. 7B)
?1977 *Perisphinctes (Otosphinctes)* sp. A. Matyja, pl. 8, fig. 7.

Material. Three fragmentary microconchs (SM X.50139.26, -.73, -.84) from the Upware Limestone, Sponge Bed (Bed 6a).

Measurements. SM X.50139.26 (Fig. 7B): D (max) 66 mm, sutures indistinct; 0.3 wh bch; at 59 mm; 0.28, 0.35, 0.50; ribs *c.* 48.

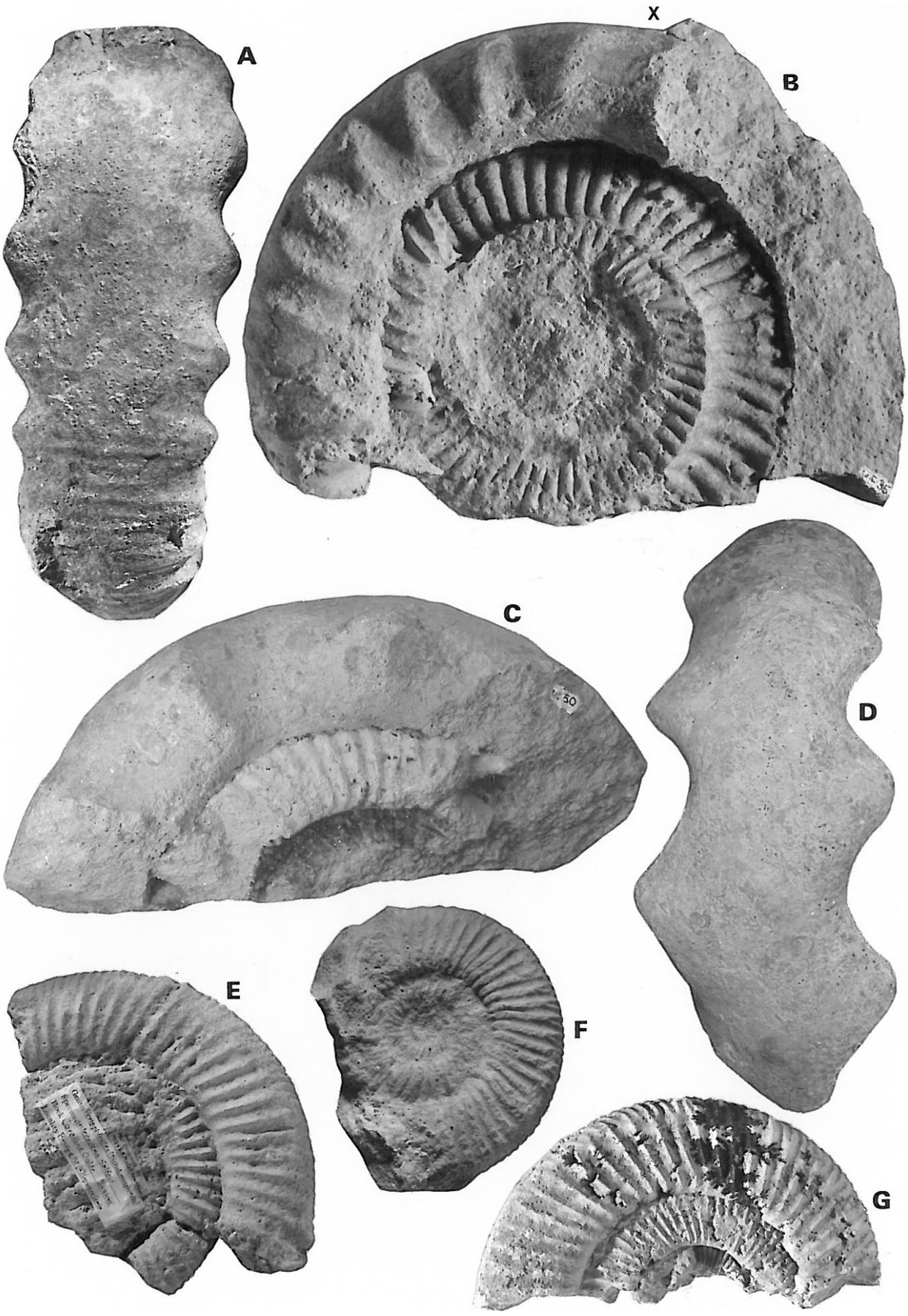
SM X.50139.73 (not figured): D (max) 42 mm, entirely septate. At 35 mm, 0.33, 0.36, 0.46; ribs 18 per half whorl at 42 mm.

Description. This is an evolute form, moderately densely ribbed in the early whorls, but becoming quite densely ribbed later. The primary ribs are strong, noticeably prorsiradiate, and bifurcate regularly into secondaries. The secondaries do not carry on the prorsiradiate trend, but cross the venter in a much more rectiradiate manner. The figured specimen, SM X.50139.26 (Fig. 7B), shows a marked, strongly prorsiradiate constriction.

Remarks. These very distinctive specimens, with their markedly depressed whorl section and prorsiradiate ribbing, appear to match very few species figured by previous workers. The best match is with *P. (O.)* sp. A of Matyja (1977), which has similar bold, prorsiradiate primary ribbing, but is slightly more evolute.

Subgenus ***Dichotomosphinctes*** Buckman 1926
Type species. *Perisphinctes antecedens* Salfeld 1914, designated by Buckman 1926, pl. 650.
Perisphinctes (Dichotomosphinctes) antecedens Salfeld
(Figs 7F and 10A,B)
1914 *Perisphinctes* cf. *Wartae* Bukowski, *mutatio antecedens* Salfeld, p. 239, pl. 12, fig. 3.
non 1926 *Dichotomosphinctes antecedens* Buckman, pl. 650 (*P. buckmani* Arkell).
1936*a Perisphinctes (Dichotomosphinctes) antecedens* Salfeld; Arkell, p. xlv, Pl. D.
1938 *Perisphinctes (Dichotomosphinctes) antecedens* Salfeld; Arkell, pp. 83–90, pl. 14, fig. 6; pl. 15, figs 1–6; pl. 16, fig. 8.

Fig. 10. *Otosphinctes, Dichotomosphinctes* and *Perisphinctes s.s*. from Bed 6 of the Upware Limestone of Dimmock's Cote Quarry. (**A**) *Perisphinctes (Dichotomosphinctes) antecedens* Salfeld, SM X.50139.87, x0.68. (**B**) *Perisphinctes (Dichotomosphinctes)* antecedens *Salfeld* [m]; SM X.50139.29; body-chamber including modified ribbing close to the aperture, natural size. (**C, D**) *Perisphinctes (P.) tumulosus* Buckman [M]; SM X.50139.96; poorly preserved adult specimen with modified ribbing close to the aperture; **D** shows the reduction in whorl thickness in the last quarter of a whorl up to the aperture; x0.17. (**E**) *Perisphinctes (Kranaosphinctes*) aff. *decurrens* (Buckman) [juv. M]; SM X.50139.28; largely complete specimen with fragments of body chamber preserved; natural size. (**F**) *Perisphinctes (P.) tumulosus* Buckman, SM X.50139.94; ×0.34.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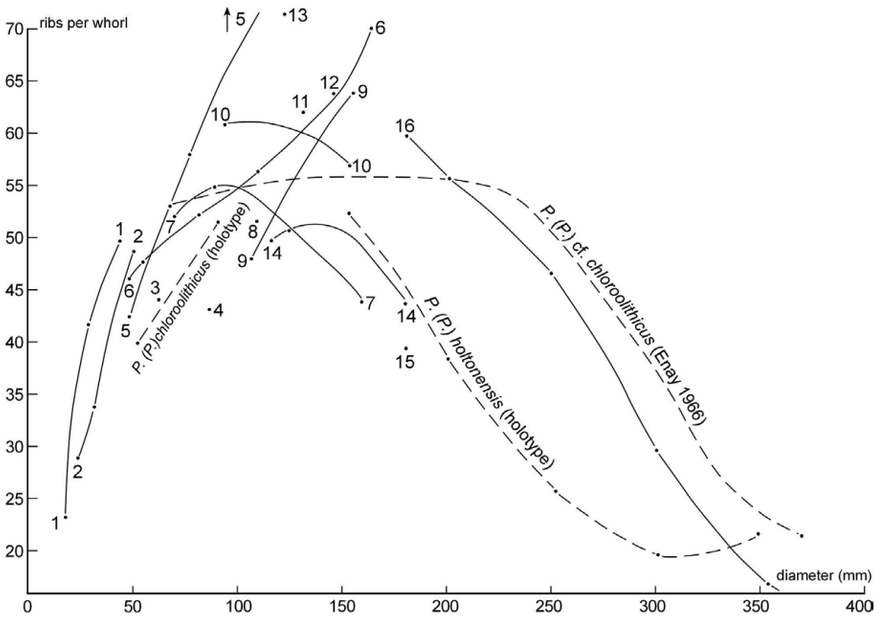


Fig. 12. Rib curves of perisphinctids from the Upware Limestone, Bed 9. 1–6, 9, 11, 12–13, *Perisphinctes (Dichotomosphinctes*) aff. *dobrogensis* Simionescu; 7–8, 14–15, *P. (P.) holtonensis* Buckman; 10, 16, *P. (P.) chloroolithicus* Gümbel. 1, SM J382 ('New Pit'); 2, SM J53029 (Padney); 3, SM J349 (South Pit); 4, SM J18240 ('Bridge Pit'); 5, SM X.50139.40 (Dimmock's Cote Quarry); 6, SM J20256 (Bridge Pit North); 7, SM J371 (?North Pit); 8, SM J383 ('Bridge Pit'); 9, SM J48645 (Bridge Pit North); 10, SM J359 (North Pit); 11, SM J380 ('Bridge Pit'); 12, SM X.50139.39 (Dimmock's Cote Quarry); 13, BMNH C89588 (Bridge Pit North); 14, SM X.50214 (Bridge Pit South); 15, SM J363 (North Pit); 16, SM J3836 ('New Pit').

2006*b Perisphinctes (Dichotomosphinctes) antecedens* Salfeld; Głowniak, pp. 186–189, fig. 12.
2007 *Perisphinctes (Dichotomosphinctes)* cf. *antecedens* Salfeld; Głowniak & Wierzbowski, pp. 77–79, figs 40/1–2.

Material. Six specimens from the Upware Limestone, Crinoid Bed (beds 6b–c): SM X.50139.29, -.34, -.43, -.44, -.87, -.88.

Measurements. SM X.50139.29 (Fig. 10B): D (max-ad) 123 mm; at 100 mm, 0.27, 0.26, 0.57; ribs *c*. 55 at 125 mm.

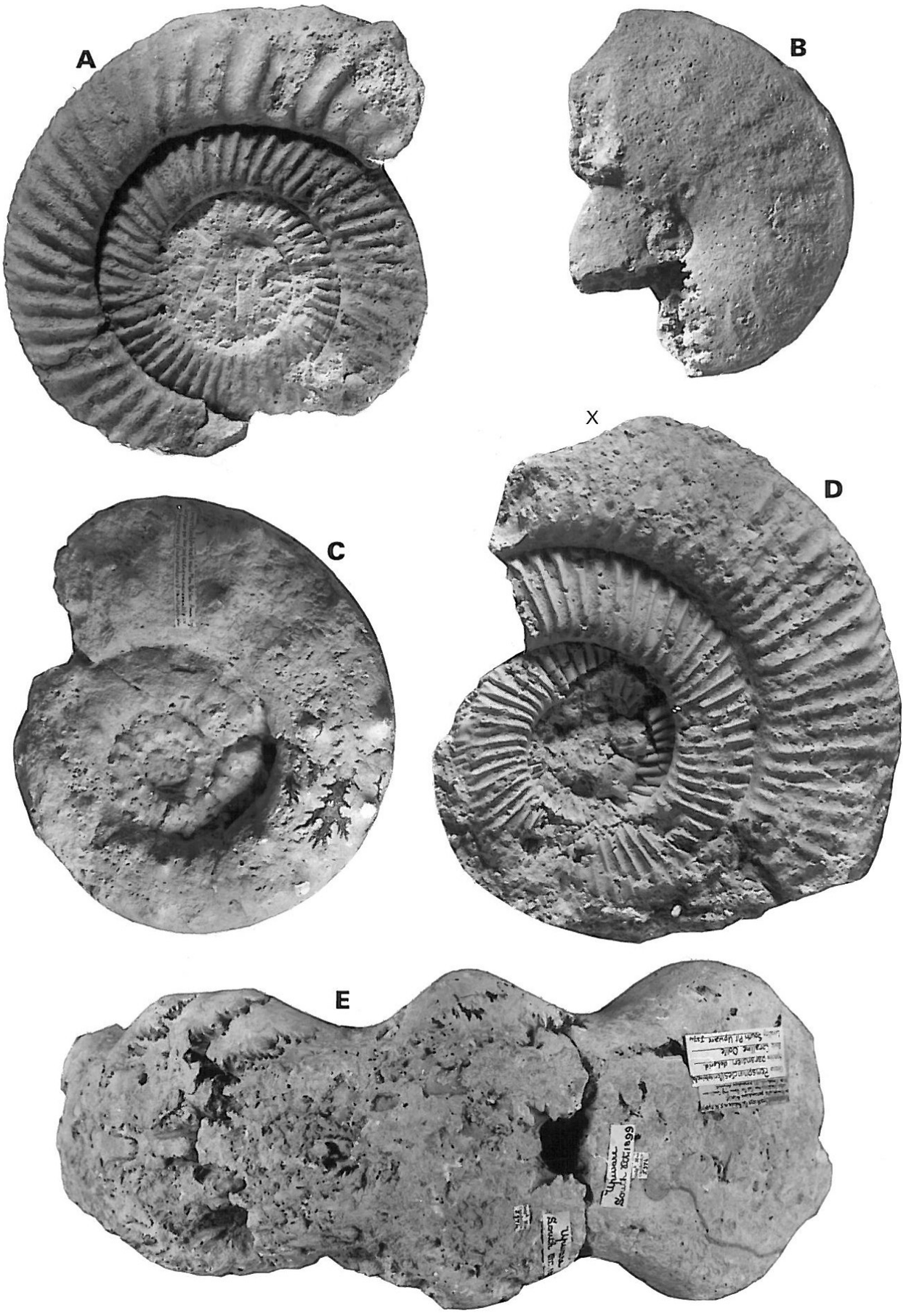
SM X.50139.44 (Fig. 7F): D (phg-?juv) 60 mm, D (max) 95 mm; 0.75 wh bch; at 91 mm, 0.28, 0.25, 0.47; ribs *c.* 45 at 79 mm; 47 at 93 mm.

SM X.50139.88 (not figured): D (max) 122 mm. D (phg-ad) 105 mm; 0.25 wh bch; at 122 mm, 0.26, 0.23, 0.53; at 92 mm, 0.29, 0.26, 0.53; ribs 42 at 79 mm, 45–46 at 92 mm, 54 at 122 mm.

Description. The specimens are sharply ribbed to the end, with predominantly bifurcate ribs with some intercalatories. The furcation point is at 75% to 80% of the whorl height. Some specimens show secondaries with a slight forward curve. Constrictions are occasionally present. The mature size is around 125–140 mm with the rib count increasing from 43 rpw at 65 mm to 55 at 125 mm (Fig. 6:6–7 and 9). Although no lappet is preserved, one specimen (SM X.50139.29, Fig. 10B) shows some simplification of ribbing close to the mature aperture. The whorl section is typically rectangular with flattened sides, and the venter is broadly rounded. All specimens are characteristically evolute (Fig. 8:1–5), and are less densely ribbed than *P. buckmani* (Fig. 9).

Discussion. The holotype, refigured by Arkell (1936*a*, pl. D, fig. 3), is more evolute, with slightly higher bifurcation points and more markedly rectiradiate ribbing than is present in most specimens of *P. (D.) antecedens* as usually interpreted (Arkell 1938, pl. 15, figs 1–6). The Upware specimens match the range of Arkell's specimens almost exactly. Specimen SM X.50139.29 (Fig. 10B) also resembles *P. (D.) auriculatus* Arkell, although the type of that species is slightly larger (150 mm). *P. auriculatus* is from Bed 6 at the Lamb and Flag Quarry, Kingston Bagpuize, near Oxford (Callomon 1960; Arkell 1938, 1948). Bed 6 at the Lamb and Flag Quarry is also the type horizon of the macroconch *P. (K.) kingstonensis* Arkell which, although having comparable inner whorls to those of the fauna of Bed 6 at Dimmock's Cote Quarry (e.g. Arkell 1939, pl. 32, fig. 8, pl. 33, fig. 3), includes quite a different mature morphology, being relatively closely ribbed to the end (Arkell 1939, pl. 32, fig. 7). This morphology may therefore suggest a lower stratigraphic level for *P. (D.) auriculatus s.s*. The specimen of *P. antecedens* figured by Głowniak & Wierzbowski (2007, fig. 40/1) is very close to one of those figured here (Fig. 10A).

Fig. 11. *Perisphinctes s.s*. and *Dichotomosphinctes* from the Upware Limestone. (**A, B**) *Perisphinctes (P.) parandieri* de Loriol [M]; SM X.50139.92; top of Bed 6b, Dimmock's Cote Quarry; inner whorls preserved as a mould, end of phragmocone and first quarter of body-chamber well preserved, ventral view of this part of the whorl in **B**; ×0.5. (**C, D**) *Perisphinctes (P.) parandieri* de Loriol; Bed 6, Dimmock's Cote Quarry; SM X.50139.95; x0.39. (**E**) *Perisphinctes (Dichotomosphinctes)* aff. *dobrogensis* Simionescu [m]; SM J48645; matrix of Bed 9, Bridge Pit North; specimen includes at least a third of a whorl of body-chamber and modified ribs close to the aperture; ×0.5. (**F**) *Perisphinctes (D.)* aff. *dobrogensis* Simionescu [?m]; SM J53029; matrix of Bed 9, 'The Dolveis, Padney'; no suture visible; natural size. (**G**) *Perisphinctes (P.) chloroolithicus* (Gümbel) [M]; SM J359; matrix of Bed 9, North Pit; completely septate inner whorls; ×0.45; partially figured (as *P. (D.) buckmani*) by Arkell (1938, pl. 14, fig. 2).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Perisphinctes (Dichotomosphinctes) buckmani Arkell (Fig. 7A, C–E, G)

?1938 *Perisphinctes (Dichotomosphinctes) buckmani* sp. nov. Arkell, p. 79, pl. 14, figs 1a, b, 3a, b; pl. 17, figs 13a–c.

1963 *Perisphinctes (Dichotomosphinctes) dybowskii* Siemiradzki; Malinowska, pp. 66, 153, pl. 32, fig. 154, pl. 33, fig. 160.

1966 *Perisphinctes (Dichotomosphinctes) buckmani* Arkell; Enay, p. 478, pl. 28, fig. 5, pl. 29, figs 1, 2.

1972 *Perisphinctes (Dichotomosphinctes) buckmani* Arkell; Malinowska, pp. 186, 187, pl. 5.

?1977 *Perisphinctes (Dichotomosphinctes) dybowskii* Siemiradzki; Matyja, pl. 8, fig. 8.

1990 *Perisphinctes (Dichotomosphinctes) antecedens* Salfeld; Gygi, p. 183, pl. 5, fig. 4.

2006*b* *Perisphinctes (Dichotomosphinctes) buckmani* Arkell; Głowniak, pp. 189–190, fig. 13.

2007 *Perisphinctes (Dichotomosphictes)* cf. *buckmani* Arkell; Głowniak & Wierzbowski, pp. 79–82, figs 42/1–3.

Material. Eight specimens (SM X.50139.27, -.41, -.42, -.47, -.53, -.69, -.70, -.71) from the Upware Limestone, Crinoid Bed, (beds 6b–c), Dimmock's Cote Quarry.

Measurements. SM X.50139.27 (Fig. 7A): D (phg-?ad) 57 mm, D (max) 84 mm; 0.66 wh bch; at 82 mm, 0.29, 0.26, 0.46; ribs *c*. 55 at 85 mm.

SM X.50139.42 (Fig. 7C,D): D (phg-?ad) 66 mm, D (max) 95 mm; 0.66 wh bch; at 89 mm, 0.28, 0.30, 0.49, ribs *c.* 59 at 90 mm.

Description. The primary ribbing is fine, almost always bifurcating on the phragmocone, but with occasional simple ribs. The rib density increases from 40–50 at 50 mm to 60 at 100 mm (Fig. 6). Numerous simple ribs are present on the later body chamber. Constrictions are well seen in Figure 7C (SM X.50139.42) and faint in Figure 7E (SM X.50139.71), one per whorl. Coiling is quite involute for a *Dichotomosphinctes*, the ratio of umbilicus to whorl height varying from 1 to 1.4 at 50 mm, increasing to 1.8 at 80 mm (Fig. 8). The whorl section is sub-quadrate, slightly convergent.

Remarks. The holotype of *P. buckmani* (Arkell, 1938, pl. 14, figs 1a, b) is a specimen of great size for a microconch (215 mm) with a nearly complete whorl of body-chamber and with little uncoiling or approximation of the ribbing close to the aperture. This suggests that it is more likely to be a juvenile macroconch rather than a microconch. The rib curve rises only gently (Fig. 9), much more typical of the inner whorls of a macroconch. However, additional specimens figured by Arkell (1938, pl. 14, fig. 3, pl. 17, figs 13a–c) are probable medium-sized microconchs and the species has been interpreted by continental authors as such; this approach is followed here. Specimens of *P. (D.)* cf. *buckmani* figured by Głowniak & Wierzbowski (2007) are septate to a maximum of 90 mm, with maximum sizes of 120–130 mm, though probably still immature. Specimens figured by Głowniak (2006*b*) and Malinowska (1972) both have maximum diameters just over 160 mm, and this seems to be a preferred maximum diameter for the species. The specimen figured by Gygi (1990) is over 200 mm in diameter, and again probably an immature macroconch.

In the Crinoid Bed fauna, *P. (D.) buckmani* appears to be distinguished from *P. (D.) antecedens* by its distinctly smaller size (D-phg averaging 61 mm compared with D-phg 106 mm for *D. antecedens* from the same bed). However, this is clearly a preservational factor (see discussion on preservation in Section 1), one specimen of *P. (D.) buckmani* being 100 mm + in diameter (Fig. 7G). *P. (D.) buckmani* is more flat-sided and involute than *P. (D.) antecedens*, as shown in the plot of umbilicus/height ratio (Fig. 8). However, the specimen of *P. (D.) antecedens* shown in Figure 7F (SM X.50139.44), as plotted in Figure 8 (6), is intermediate in this respect, being involute in the inner whorls, but becoming round-whorled and coarsely ribbed on the outer body chamber. It clearly plots in the *antecedens* field in Figure 9 (7). The main distinguishing features are thus that, firstly, *P. (D.) antecedens* is round-whorled and does not have the flat, convergent sides of *P. (D.) buckmani*. Secondly, *P. (D.) antecedens* is less densely ribbed than *P. (D.) buckmani*; at 80 mm, the former has about 45 rpw, whereas most specimens of the latter have 55–60 rpw. This feature is quite clear in the rib density plot (Fig. 9). *P. (O.) arkelli wysokae* is similarly less densely ribbed, and more evolute, with less convergent sides. *P. (D.) buckmani* (figured as *P. (D.) dybowskii* Siemiradzski) occurs in Poland along with *P. (O.)* sp. A in the 'Grey Limestone', close to the Plicatilis–Transversarium chronozonal boundary (Matyja 1977). Three specimens, regarded as immature microconchs, were figured by Głowniak & Wierzbowski (2007). These specimens match those figured here very closely, particularly in density of ribbing and degree of involution.

Perisphinctes (Dichotomosphinctes) aff. *dobrogensis* Simionescu (Figs 11E,F and 13D)

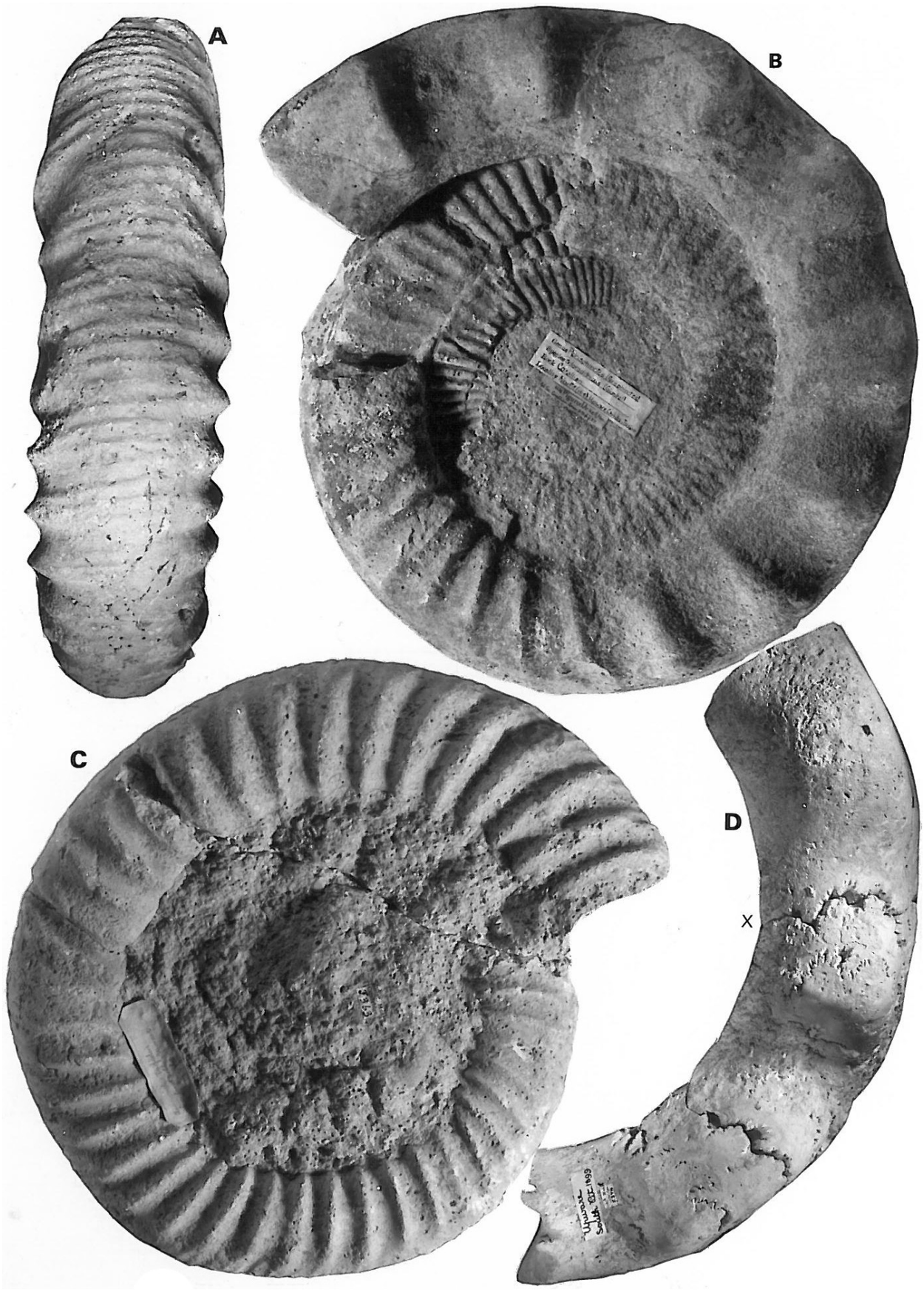
1907 *Perisphinctes dobrogensis* sp. nov.; Simionescu, p. 157, pl. 3, fig. 2, (lectotype), pl. 5, fig. 4.

1938 *Perisphinctes (Dichotomosphinctes) buckmani* Arkell, p. 80, fig. 19.

1966 *Perisphinctes (Dichotomosphinctes) dobrogensis* Simionescu; Enay, p. 481, pl. 29, figs 3–5, text figs 140, 145.

1995 *Perisphinctes (Dichotomosphinctes) dobrogensis* Simionescu; Gygi, pp. 34, 36, fig. 14 only.

Fig. 13. Ammonites from the Upware Limestone, all in the matrix of Bed 9. (**A**) *Perisphinctes (P.) holtonensis* Buckman. [?M]; SM X.50214; Bridge Pit South; body-chamber nearly complete but specimen?immature macroconch; ×0.46. (**B**) *Neocampylites* sp. aff. *henrici* (d'Orbigny) [M]; SM 18021; Bridge Pit North; completely septate inner whorls; natural size. (**C**) *Aspidoceras (Euaspidoceras)* aff. *pacituberculatum* Arkell [M]; SM J4732; North Pit; completely septate inner whorls, ×0.5. (**D**) *Perisphinctes (Dichotomosphinctes)* aff. *dobrogensis* Simionescu [?m]; SM X.50139.40; Dimmock's Cote Quarry; septate inner whorls with last septum at 110 mm, natural size. (**E**) *Perisphinctes (P.)* cf. *chloroolithicus* Gümbel [M]; SM J374; 'South Pit'; whorl fragment showing the end of the phragmocone and the initial part of the body-chamber; ×0.51.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1995 *Dichotomosphinctes* cf. *dobrogensis* (Simionescu); Beznosov & Mitta, pp. 46, 47, pl. 9, fig. 2.
2007 *Perisphinctes (Dichotomosphinctes)* cf. *dobrogensis* Simionescu; Głowniak & Wierzbowski, p. 82, figs 43/1, 43/2

Material. Seven specimens (SM J349, 'South Pit'; SM J382, 'New Pit'; SM J18240, 'Bridge Pit'; SM J20256 and SM J48645, Bridge Pit North; SM J53029, Padney; SM X.50139.40, Dimmock's Cote Quarry), by matrix from Upware Limestone Bed 9.

Measurements. SM J382 (not figured): ribs *c.* 23 at 21 mm, *c.* 42 at 29 mm, *c.* 50 at 45 mm (septate inner whorls).

SM X.50139.40 (Fig. 13D): D (max) 115 mm, D (phg-?ad) 110 mm; at 70 mm, 0.29, 0.23, 0.50; ribs 42 at 45 mm, 53 at 67 mm, *c.* 58 at 75 mm, *c.* 75 at 105 mm.

SM J48645 (Fig. 11E): D (max) 155 mm; 0.3 wh bch; ribs *c*. 48 at 105 mm, *c*. 64 at 155 mm.

Description. These microconchs appear to mature at around 165 mm with between 65 and 80 ribs on the last whorl of phragmocone (Fig. 12). The ribs modify near the aperture, passing strongly over the venter, but no lappet is preserved (Fig. 11F). Constrictions are only occasionally present. The specimens are very evolute, with bifurcation points visible beneath the umbilical seam of the overlapping whorl (Fig. 13D).

Remarks. The microconchs from Bed 9 closely resemble *P. (P.) dobrogensis* Simionescu *sensu* Enay (1966, e.g. pl. 29, figs 3–5). Similar forms have been frequently referred to *P. (D.) buckmani* Arkell (e.g. Arkell 1938, pl. 14, fig. 2, pl. 17, fig. 3; Enay 1966, pl. 29, fig. 1), but *P. buckmani* is interpreted here as an earlier, more involute microconch. Some doubt exists as to the correct horizon of Simionescu's (1907, p. 157, pl. iii, fig. 2) original Romanian type which could indeed be a homeomorphic Upper Oxfordian form (G. Meléndez, personal communication, 1997). The interpretation of *P. (D.) dobrogensis* here follows Enay (1966) and is consistent with Polish interpretations of the same species (e.g. Matyja & Głowniak 1994; and E. Głowniak personal communication, 1997). The dense ribbing of the outer whorl of specimen SM X.50139.40 (Fig. 13D) matches *P. (D.) elizabethae* de Riaz (Enay 1966), but *P. (D.)* aff. *dobrogensis* is more evolute and less densely ribbed on the inner whorls. In this respect, the Upware specimens are slightly less densely ribbed in the inner whorls than those of *P. (D.) dobrogensis* figured by Głowniak & Wierzbowski (2007); these latter specimens are slightly more involute, not showing bifurcation points in the umbilicus.

P. aff. *dobrogensis* is readily distinguishable from *P. antecedens* by its typically finer ribbing with greater forward sweep of the secondary ribs over the venter and generally more compressed whorl section. More evolute coiling, with bifurcation points visible beneath the umbilical seam, seems to be a variant present in both *P. antecedens* (Głowiak & Wierzbowski 2007, fig. 40/1), and in *P*. aff. *dobrogensis* (SM X.50139.40, Fig. 13D).

Family **Aspidoceratidae** Zittel 1895
Subfamily **Aspidoceratinae** Zittel 1895
Genus ***Aspidoceras*** Zittel 1868
Subgenus ***Euaspidoceras*** Spath 1931

Ammonites perarmatus J. Sowerby, 1822; designated by Spath (1931, p. 326, footnote and pp. 588ff.).

Aspidoceras (Euaspidoceras) sp. aff. *paucituberculatum* Arkell (Fig. 13C)
1892 *Ammonites perarmatus* J. Sowerby; Roberts, p. 56.
1937*b Aspidoceras (Euaspidoceras) paucituberculatum* Arkell; Arkell, p. 454.
1940 *Aspidoceras (Euaspidoceras) paucituberculatum* Arkell; Arkell, pp. 210–215, pl. 45, figs 2–5, pls 46, 47, fig. 74.

Material. Two specimens, comprising wholly septate inner whorls (SM J4732) from 'North Pit' and a giant and incomplete outer whorl (not collected) from Dimmock's Cote Quarry. Matrix indicates Bed 9 in both cases (Upware Limestone).

Description. Giant macroconch forms around 450 mm diameter when complete and septate to around 316 mm. Nucleii are relatively closely ribbed to around 60 mm diameter with paired umbilical and ventrolateral tubercles. Subsequent ornament develops as widely spaced round tubercles, which persist to the end of septation. Ornament on the body-chamber is much reduced and nodes not developed. Microconch not known.

Discussion. This is the first record of *Aspidoceras* from the Parandieri Subzone. The specimens from Upware most closely resemble *A. (E.) paucituberculatum* Arkell, the holotype of which (Arkell 1940, pl. 45, fig. 2) is from Bed 6 of the Highworth Limestone at Hangman's Elm Quarry, Highworth, Wiltshire. The fauna of that level predates *P. (Dichotomosphinctes) antecedens, P. (P.) maximus, Cardioceras (Maltoniceras) maltonense* and *C. (M.) highworthense* in Bed 8 at Highworth, the equivalent of the Crinoid Bed fauna, and therefore suggests that the type of *A. (E.) paucituberculatum* is older than the new specimens from Upware. The ornament of *A. (E.) perarmatum* differs from that of the Upware specimens in that its paired nodes are linked by blunt ribs on the middle whorls.

Fig. 14. *Perisphinctes s.s*. from the Upware Limestone, all in the matrix of Bed 9. (**A, C**) *Perisphinctes (P.) holtonensis* Buckman [M]; SM J363; 'South Pit'; suture indistinct, but shows end of the phragmocone and the initial part of the body-chamber; ×0.72. (**B**) *Perisphinctes (P.) chloroolithicus* Gümbel [M]; SM J3836; 'New Pit'; no sutures visible; ×0.44. Ventral view figured by Arkell (1938, fig. 27). (**D**) *Perisphinctes (P.)* cf. *chloroolithicus* Gümbel [M]; SM J374, matrix of Bed 9; Upware South Pit; ventral view of Figure 13E, ×0.51.

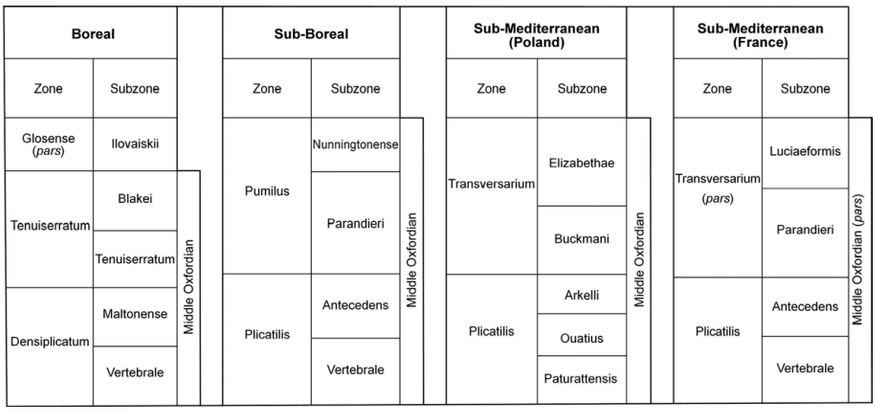

Fig. 15. Correlation of zones and subzones for the Middle Oxfordian of Britain (Boreal and Sub-Boreal), Poland (Sub-Mediterranean) and France (Sub-Mediterranean), after Sykes & Callomon (1979), Głowniak (2006*a*) and Cariou *et al.* (1997). Zones and subzones are used in the sense of Chronozones and Subchronozones, after Callomon (2003). The Middle–Upper Oxfordian boundary is taken higher on the continent than in the UK; above the Transversarium Zone in Poland and higher, above the overlying Bifurcatus Zone, in France.

The correlation of the ammonite faunas of the Upware distract

The perisphinctid faunas of the Upware 'Corallian'

Three

distinct *Perisphinctes* populations can be recognized within the Upware 'Corallian' sequence:

P1. The fauna of the Dimmock's Cote Marl Member consists of microconch species of the subgenus *Otosphinctes* (*P. (O.) ouatius, P. (O.) arkelli*) and large *Kranaosphinctes*-style macroconchs (*P. (K.) ariprepes*) showing a gradual development of variocostation. The presence also in the higher beds of forms comparable to *P. (K.) maximus* and *P. (P.) tumulosus* suggests that this may represent a separate fauna, but insufficient material is presently available to be certain of any stratigraphical distinction, and the recognition of separate faunas (P1a and P1b) must be regarded as provisional.

P2. Bed 6, the basal unit of the Upware Limestone Member, contains species of the microconch subgenus *Dichotomosphinctes* (*P. (D.) antecedens, P. (D.) buckmani*) plus species of the macroconch subgenus *Perisphinctes s.s.* (*P. (P.) parandieri, P. (P.) tumulosus*), which form a second very distinct fauna. The large size of the microconchs, with their rectangular whorl section, is very characteristic of *Dichotomosphinctes*, whereas the rapid development of variocostation and extremely depressed venter around the beginning of the body-chamber in the macroconchs indicates fully developed *Perisphinctes s.s.* Occasional specimens, however, still show the rounded whorl section of the inner whorls more distinctive of *Otosphinctes/Kranaosphinctes.*

P3. In Bed 9 of the Upware Limestone, forms comparable with *P. (D.) dobrogensis* are present, distinguished from *P. (D.) antecedens* by the finer ribbing on the body chamber and the gentle forward swing of the secondaries over the venter. Macroconchs are represented by *P. (P.) chloroolithicus* and *P. (P.) holtonensis*, with onset of variocostation much earlier than in Crinoid Bed (beds 6b–c) specimens.

Position of the Upware faunas within the zonal and subzonal schemes for the Sub-Boreal and Sub-Mediterranean Middle Oxfordian

The subdivision of the English Middle Oxfordian into chronozones and subchronozones, as defined in this Sub-Boreal area, follows Callomon (1960), as modified by Sykes & Callomon (1979). The use of chronozones rather than biozones follows Callomon (2003). Two zones, the Plicatilis and Pumilus zones, are subdivided into the Vertebrale and Antecedens subchronozones, and the Parandieri and Nunningtonense subchronozones, respectively (Fig. 15).

The Vertebrale Subzone is well known. Two distinct faunas are present. In the lower Vertebrale Subchronozone, characterized by the Dorset Preston Grit and the Yorkshire Hambleton Oolite, Upper Leaf (Wright 1997), cardioceratids markedly outnumber perisphinctids. Generally, *Vertebriceras* is rare, *Subvertebriceras, Cardioceras s.s.* and *Scoticardioceras* making up much of the fauna, with perisphinctids represented by *P. (Liosphinctes) plicatilis* (J. Sowerby), *P. (Kranaosphinctes) ariprepes* and *P. (Otosphinctes) ouatius*. In the upper Vertebrale Subzone, characterized by Bed 6 of the Highworth Limestone of Highworth (Arkell 1927) and the Seamer Snake Bed of Yorkshire (Wright 1972; Wright & Rawson 2014), *Kranaosphinctes, Otosphinctes* and *Liosphinctes* occur in abundance, with occasional *P. (Kranaosphinctes) maximus* and *P. (O) arkelli. Scoticardioceras* and *Subvertebriceras* continue. *Vertebriceras* is common around Oxford, but rare elsewhere. Callomon (1960) suggested that *Goliathiceras* and *Aspidoceras* were confined to the subzone, but records from Upware and Yorkshire show that both continue into the Antecedens Subzone, and *Aspidoceras* into the Parandieri Subzone.

Following its introduction by Callomon (1960), the Antecedens Subchronozone has caused problems for subsequent workers (Głowniak 2002). The problem is that the time period represented by Callomon's Antecedens Subchronozone represents the acme of the subgenera *Kranaosphinctes* and its microconch counterpart *Otosphinctes*, and also of *Liosphinctes* spp., which are all very distinct from the subzonal index *P. (D.) antecedens. P. antecedens* is grouped in *Dichotomosphinctes*, and this, with its macroconch counterpart *Perisphinctes s.s.*, represents

only a part of the Antecedens Subchronozone fauna; they only become a dominant element of the fauna in the overlying Parandieri Subchronozone. Thus, beds that have yielded only a few *P. antecedens* must be allocated to the Antecedens Subchronozone, and beds such as the Crinoid Bed, which yield numerous *P. antecedens*, must be allocated to the Parandieri Subchronozone. However, this was a problem inherent in the scheme when it was set up and Callomon (personal communication, 1997) has said that he could see no reason to change the current scheme.

Though Callomon (1960) did not designate a type section for the Antecedens Subchronozone, the Headington Shell Bed in the Beckley Sand Member of Headington or Magdalen Quarry, Oxford (Wright & Cox 2001), may be taken as typical. About equal proportions of *Otosphinctes* [m]*/Kranaosphinctes* [M] and *Dichotomosphinctes* [m]*/Perisphinctes s.s.* [M] are present, *P. (O.) arkelli* and *P (K.) pickeringius* plus *P. (D.) buckmani* and *P. (P.) tumulosus* being prominent (Arkell 1935–1948). Though Callomon (1960) suggested that the Headington Shell Bed might be condensed, with a number of Vertebrale Subchronozone cardioceratids being present, the bulk of the Headington perisphinctids seem undoubtably to give a proper representation of an Antecedens Subchronozone fauna. Even if the Headington Shell Bed is discounted, the fauna of the Highworth Limestone, Bed 8, of Highworth Quarries is very similar (Callomon 1960), with *P. (O.)* spp. and *P. (K.)* spp. plus *P. (D.)* spp. and *P (P.)* spp. all recorded (Arkell 1935–1948).

The situation in the Jura is very similar (Enay 1966). Enay was able to recognize the Antecedens Subchronozone of the Plicatilis Chronozone with abundant *Kranaosphinctes* and *Otosphinctes* in addition to *P. (D.) antecedens*, overlain by the Parandieri Subchronozone with a fauna containing numerous *P. s.s.* and *Dichotomosphinctes*.

Similarly, a mixed fauna is present is the Upper Heersum Beds and Lower Korallenoolith in Germany. From the former, Arkell (1935–1948) recorded numerous species of *Kranaosphinctes*, plus *P. (O.) arkelli, P. (D.) antecedens, P. (D.) buckmani*, and *P. (P.) tumulosus* and *P. (P.) parandieri*, a mixture of forms which is so typical of the Antecedens Subchronozone shell beds around Oxford for instance (Callomon 1960). Głowniak (2006*b*) attempted to confine all records of *Kranaophinctes* and *Otosphinctes* to only a part of the Upper Heersum Beds, with the replacement of these subgenera by *P. (D.) antecedens*, and presumably also by *Perisphinctes s.s.*, in the very highest Heersum Beds. However, even in the overlying Lower Korallenoolith, Arkell recorded *Kranaosphinctes* spp. in addition to *P. (D.) antecedens*. Both the Upper Heersum Beds and the Lower Korallenoolith clearly contain typical mixed Antecedens Subchronozone faunas. Głowniak (2006*a*,*b*) proposed that the disappearance of *Kranaosphinctes/Otosphinctes*, and its replacement by *Dichotomosphinctes/Perisphinctes s.s.*, marked the Plicatilis–Transversarium chronozonal boundary in Europe. This position is clearly untenable, as *Otosphinctes/Kranaosphinctes* occur together with *Dichotomosphinctes/Perisphinctes s.s.* at so many localities in Britain, France and Germany.

In Poland, therefore, Głowniak (2002) was unable to use Callomon's (1960) scheme, as *P. antecedens* and *P. s.s*. are unknown in beds that are apparently equivalent in age to Callomon's Antecedens Subzone. Glowniak (2002) subdivided the Plicatilis Chronozone by means of species of *Otosphinctes* (*P. (O.) patturattensis, P.(O.) ouatius* and *P. (O.) arkelli*). The Polish Arkelli Subzone is almost the direct equivalent of Callomon's Antecedens Subchronozone (Fig. 15), and *P. arkelli* is commonly found in these beds in England. The base of the Polish Transversarium Zone correlates with the lower part of the Pumilus Zone (Fig. 15). It is marked by the incoming in Poland of *P. s.s.* and *Dichotomosphinctes* (Glowniak's Buckmani Subzone).

Concerning the Upware succession, fauna P1 of the Dimmock's Cote Marl may belong to the Antecedens Subchronozone, *Perisphinctes s.s*. apparently making an early appearance alongside *Kranaosphinctes* and *Otosphinctes*. Fauna P2, the Crinoid Bed fauna, with its abundance of *P. s.s.* and *Dichotomosphinctes*, clearly belongs to the Parandieri Subchronozone. There is some indication of a change between Bed 6 and Bed 9, the Crinoid Bed (beds 6b–c) containing the moderately finely ribbed *P. (D.) buckmani* and *P. (D.) antecedens*, with the square-whorled *P. (P.) tumulosus* and *P. (P.) parandieri* as macroconchs, and Fauna P3 from Bed 9 containing the finely ribbed *P. (D.)* aff. *dobrogensis*, with the extremely depressed-whorled *P. chloroolithicus* and P. holtonensis as macroconchs. However, such a distinction is not seen in the Jura (Enay 1966), where densely ribbed *Dichotomosphinctes* spp. occur already in the Antecedens Subchronozone.

The Parandieri Subchronozone is thus marked by a reduction in importance of *Kranaosphinctes* morphs (very few are known), though *Kranaosphinctes*-like forms come into prominence in the later Nunningtonense Subchronozone of the Upper Calcareous Grit of Laysthorpe Quarry, Yorkshire (Wright 1996), as well as in the Upper Oxfordian Cautisnigrae Subchronozone of the Clavellata Formation of Dorset (Arkell 1935, 1937*a*), and in the Pseudocordata Chronozone of the Westbury and Marston Ironstones of Wiltshire (Arkell 1948; Wright 2003). These specimens are now regarded as forming a distinct group within *Perisphinctes s.s.* (Wright & Głowniak, in prep. 2015). [AQ: 4]

The higher part of the Polish Transversarium Chronozone comprises an Elizabethae Subchronozone (index: *P. (D.) elizabethae* de Riaz); although clearly postdating Bed 9 at Upware, there are suggestions that elements of this fauna may be recognizable in the Upper Calcareous Grit of North Yorkshire (Wright 1996, p. 444, pl. 2, figs 2–3, pl. 4, fig. 3) and a tentative correlation of at least the higher part of the Elizabethae Subchronozone with the Boreal Upper Oxfordian Ilovaiski Subchronozone can be proposed (Głowniak 2006*a*).

Biohorizons

The sequence of early Middle Oxfordian ammonite faunas revealed by the new excavations at Upware provides valuable new detailed stratigraphic and taxonomic information. For the first time in Britain, a clear sequence of three or possibly four biohorizons (*sensu* Page 1995) can be recognized at this level (cardioceratid data from Wright & Page 2006).

Plicatilis Chronozone, Arkelli Subchronozone (Central Sub-Mediterranean); Plicatilis Chronozone, Antecedens Subchronozone (Sub-Boreal); Densiplicatum Chronozone, Maltonense Subchronozone (Boreal)

Ia. *P. ariprepes* Biohorizon.

Index: *Perisphinctes (Kranaosphinctes) ariprepes* Buckman.

Reference: Bed 1, Dimmock's Cote Marl Member, West Walton Formation, Dimmock's Cote Quarry, Upware.

Fauna: poorly characterized but includes giant typical *Kranaosphinctes* comparable to the type of *K. ariprepes* (Arkell 1939, pl. 24, figs 5a, b).

Ib. *C. sopotense – P.* aff. *maximus* Biohorizon.

Indices: *Cardioceras (Miticardioceras) sopotense* (Malinowska) and *Perisphinctes (Kranaosphinctes)* sp. aff. *maximus* (Young & Bird).

Reference: beds 2–4, Dimmock's Cote Marl Member, West Walton Formation, Dimmock's Cote Quarry, Upware.

Fauna: *Perisphinctes (Otosphinctes)* aff. *arkelli and P.(O.) ouatius* are common; *P. (Kranaosphinctes)* is frequent, including forms resembling both *P. (K.) ariprepes* Buckman and *P. (K.) maximus* (Young & Bird), and forms close to *P. (P.) tumulosus. C. (M.) sopotense* is abundant with rare *C. (Miticardioceras) tenuiserratum* (Oppel); other cardioceratids include *C. (Cawtoniceras) cawtonense* (Blake & Hudleston) and *C. (Subvertebricereas) zenaidae* (Ilovaisky). Rare *Neocampylites* sp. aff. *henrici* (d'Orbigny).

Transversarium Chronozone, 'Buckmani Subchronozone' (*sensu* Głowniak 2002*) (Sub-Mediterranean); Pumilus Chronozone, Parandieri Subchronozone (Sub-Boreal); Tenuiserratum Chronozone, Tenuiserratum Subchronozone (Boreal)*.

II. *P. tumulosus* Biohorizon.

Index: *Perisphinctes (P.) tumulosus* Buckman.

Reference: beds 6a–c, Upware Limestone Member, West Walton Formation, Dimmock's Cote Quarry, Upware.

Fauna: frequent *P. (P.) tumulosus* and *P. (P.) parandieri* [M], with numerous *P. (D.) antecedens* and *P. (D.) buckmani* [m], rare *P. (Kranaosphinctes)* [M] and *P. (Otosphinctes)* [m], *Cardioceras* spp. including *C. (Scoticardioceras) excavatum* (J. Sowerby), *C. (Maltoniceras) maltonense* (Young & Bird), *C. (M.) highworthense* Arkell, *C. (Cawtoniceras) cawtonense* (Blake & Hudleston), *C. (Subvertebriceras) densiplicatum* Boden, *C. (S.) zenaidae* Ilovaiski and rare *C. (Miticardioceras) sopotense* and *C. (M.) tenuiserratum*.

Transversarium Chronozone, Elizabethae/Luciaeformis subchronozones (Submediterranean); Pumilus Chronozone, Parandieri Subchronozone (Sub-Boreal); Tenuiserratum Chronozone, Tenuiserratum Subchronozone (Boreal)

III. *P.* aff. *dobrogensis–C. tenuiserratum* Biohorizon.

Indices: *Perisphinctes (Dichotomosphinctes)* aff. *dobrogensis* Simionescu and *Cardioceras (Miticardioceras) tenuiserratum* (Oppel).

Reference: Bed 9, Upware Limestone Member, West Walton Formation, Dimmock's Cote Quarry, Upware.

Fauna: *P. (P.) chloroolithicus* is common along with *P. (P.) holtonensis* [M], with *P. (D.)* aff. *dobrogensis. C. (Miticardioceras) tenuiserratum* is common, and other cardioceratids include rare *C. (M.)* aff. *sopotense*, also *C. (Maltoniceras) maltonense, C. (Subvertebriceras) densiplicatum, C. (S.) zenaidae* and *C. (Cawtoniceras) cawtonense.* Rare *Aspidoceras (Euaspidoceras)* sp. aff. *paucituberculatum* Arkell and *Neocampylites* sp. aff. *henrici* (d'Orbigny).

Concluding remarks

The sequence at Upware is instructive as, virtually uniquely, it contains a mixture of Boreal forms and forms that spread from the Sub-Boreal Province into the Sub-Mediterranean Province. It therefore has great potential for aiding the construction of correlative links ('tie lines') between two distinct ammonite provinces, and resolving some of the outstanding questions of European Middle Oxfordian stratigraphy. The succession is also of great importance within Britain as it is the only known locality to yield a sequence of common faunas that are stratigraphically intermediate between the classic Corallian assemblages of Oxford, described by Arkell (1935–1948), and the later faunas of the Upper Calcareous Grit of Yorkshire, described by Wright (1996).

The importance of the Upware faunas in providing such links and increasing the understanding of the nature of the sequence of ammonite faunas in the rather disjointed and locally incomplete sequences of the British Middle Oxfordian cannot be overstated. The new stratigraphical information derived, and the correlations now possible, will significantly aid inter-regional and international studies of the complex history of Middle Oxfordian sedimentation and tectonics in northern and western Europe.

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