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On the typological basis of *Perisphinctes* Waagen, 1869 and the leading modern ammonite superfamily Perisphinctoidea Steinmann, 1890

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Abstract. A re-examination of the type specimen of *Ammonites biplex* Sowerby, 1821 shows that the reasons previously given for rejecting this species as the type species of Perisphinctes, to be replaced by Amm. variocostatus Buckland, 1836 (Hemming, 1954), were unfounded. Fortunately, the replacement, based on a macroconch type, is a better representative of the genus than its originally validly designated microconch, *Ammonites biplex*. The decision in Opinion 303 (Hemming, 1954) is therefore a good one but arrived at for the wrong reasons. It should be left unchanged.

INTRODUCTION

The perisphinctids constitute arguably the most important group of Jurassic ammonites, to judge by the profusion of their record in the rocks, their systematic and morphological diversities, their phylogenetic fecundity and the enormous literature they have generated. They are today formally encompassed in the superfamily Perisphinctoidea Steinmann, 1890 whose taxonomic structure has itself evolved historically from the purely morphological one of von Buch in 1832, via one of the earliest attempts to introduce Darwinian evolutionary concepts into invertebrate palaeontology by Waagen in 1869, to the predominantly phylogenetic classifications attempted today as reflected in the masterly review by Arkell in the ammonite volume of the *Treatise* (Arkell *et al.*, 1957). The Perisphinctoidea of modern times are regarded as a single clade of high rank having a monophyletic origin somewhere in the early Bajocian of the early Middle Jurassic, branching repeatedly in both time and space and persisting in some lineages recognizably at least into the Hauterivian of the Early Cretaceous, a duration of some 40 Ma.

Standing quite apart from this historical development of our ideas of the palaeobiological classification of a group of once living organisms is the historical development of its nomenclature according to the Linnéan canon as enshrined today in the *International Code of Zoological Nomenclature* (4th edition, 1999, effective from the beginning of 2000). The constraints this imposes can create the turgid thickets of confusion in the literature to be unravelled, something with which many of us are so familiar. From such confusion the perisphinctids are far from exempt. The cause lies in the interpretation of the fundamental taxonomic unit both of biology and nomenclature, the taxon of the *species*. It is a truism

[1] The following manuscript was unfinished on the death of John Callomon in 2010. It appears that it was largely completed, and it is published here as left by the author with the addition of data supplied by John Callomon by e-mail to J.K.W. in 2009.

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to recall how this has itself evolved since the time of Linnaeus and continues to evolve in the realm of molecular genetics today. So the conceptual diagnosis of an ammonite species has also evolved since the time of Waagen. It is the purpose of this note to review briefly the historical development of one important example, that of the type species of *Perisphinctes* and thereby of all the higher taxa built upon it. The conclusion is that we have arrived at the right outcome – but for the wrong reasons. Things should be left as they are.

HISTORICAL

The taxon *Perisphinctes* was created by Waagen in 1869 (p. 248) as a subgenus of his also newly-founded genus *Stephanoceras*, as follows:

"5) **Stephanoceras**. To this I assign the C o r o n a t e n, P l a n u l a t e n, M a c r o c e p h a l e n and (?) O r n a t e n (...)

The genus may be readily further subdivided into several groups that differ fairly consistently among themselves. I can distinguish:

a. The [members of] S t e p h a n o c e r a s proper: (...)

b. Another group for which I would like to propose the subgeneric name P e r i s p h i n c t e s, characterized in its juvenile stages (...) by lappets ['Ohren'] on its peristome and the possession, at least on its early whorls, of clearly developed constrictions (...) To this subgenus belong all the true Planulaten [*sic*] of the middle and upper Jurassic, with additionally *Per. anceps* [*Reineckeia* today], *astierianus* [*Spiticeras*]" *etc*.

THE TYPE SPECIES OF PERISPHINCTES

There was, as customary at the time, no designation of a type species, only a syntypic series: the Planulati. This was one of a number of such groups referred to by Waagen and widely accepted at the time, those of von Buch (1832). His was the first comprehensive attempt to classify the already bewildering profusion of species of ammonites, then still included *faute de mieux* in the single Linnéan-style genus *Ammonites*, into more cohesive groups based on shared morphological characters of their shells rather than those of single 'typical' individuals. These groups he termed families. Setting aside ## I, Goniatites and II, Ceratites, that resulted in 12 Families of species in the single genus *Ammonites* (!). In particular, in VII. Planulati (p. 144), he lists explicitly ten species, some with synonyms. These taxa, although nominally valid, have proved to be of variable quality in subsequent attempts to interpret them. But they include (with modern generic assignments) # 3. *Amm. mutabilis* Sow. [*Aulacostephanus*, Kimmeridgian], 5. *Amm. plicatilis* Sow. [*Perisphinctes*, Oxfordian], 6. *Amm. giganteus* [*Titanites*, Portlandian], 8. *Amm. biplex Sow*. [*Perisphinctes*, Oxfordian], 9. *Amm. bifurcatus* [*Dichotomoceras*, Oxfordian], 10. *Amm. parkinsoni* Sow. [*Parkinsonia*, Upper Bajocian]. The syntypic series of species that Waagen had in mind for his *Perisphinctes* of 1869 was therefore broad but quite clearly defined.

The relief provided by von Buch's subdivision of *Ammonites* was temporary. The next step was taken by Siemiradzki (1898–1899) in an attempt to bring order into what had become a bewildering jungle of species in the now fully-fledged genus *Perisphinctes*. His final catalogue lists more than 400 species, ranging in ages from Bajocian in the Middle Jurassic to the basal Cretaceous. He subdivided this array in turn into six groups according to criteria that tried to combine morphological similarities with temporal relationships, *i.e.* in a tentative phylogenetic taxonomy. These groups he gave the rank of subgenera within *Perisphinctes*, which he retained at full generic level. This left him with the nominal subgenus *P. (Perisphinctes)* reduced to only 85 species, but neither he nor any of his predecessors designated a type species.

This gap was filled by Buckman (1920, p. 26). After considering the possible candidates according to how closely they fitted Waagen's specification of the morphological features characteristic of the genus, he selected *Amm. biplex* J. Sowerby, 1821 to be the type species of *Perisphinctes*.

But that was not the end of the story. There were misgivings as to the interpretation of the type species because of alleged imperfections of its type specimens (see below). These led Arkell (1951) to apply to the *International Commission on Zoological Nomenclature* (ICZN) to suppress under its plenary powers *Amm. biplex* as type species of *Perisphinctes* in favour of *Amm. variocostatus* Buckland, 1836. The application was successful and the latter species was declared to be the type species in the Commission's Opinion 303 (Hemming, October 1954). There the matter rests today, codified in the ammonite *Treatise* (Arkell *et al*., 1957) and accepted by all taxonomists since. But what were the alleged shortcomings of *Amm. biplex* and are they real?

THE TYPE SPECIMEN OF AMM. BIPLEX J. SOWERBY, 1821

Sowerby founded his species on a series of apparently four specimens (1821, pl. 293, figs 1–4), although in the brief text (p. 168) he cites explicitly and describes only two, his figs 1, 2. Of these, fig. 1 is that of a tolerably complete shell of many whorls (reproduced here in Plate 1, Fig. 1),

fig. 2 that of a mere fragment of a whorl. His text leaves little doubt that they came from different sources and collectors, out of the Chalky Boulder Clay of Suffolk – the smaller (fig. 2) explicitly from Barrow, between Newmarket and Bury St Edmunds. Both survive in the Natural History Museum, nos. 43989a (fig. 1), b (fig. 2). [*N.b.*, Arkell (1947) recorded the specimen number as 43898; John Callomon's photograph of the specimen label clearly shows it to be 43989].

The first redescription was by Siemiradzki (1898, p. 265). He had been sent plaster casts by H.B Woodward of the two syntypes, of which he figured the larger photographically at natural size in right-lateral view (in which the spiral of coiling opens clockwise) on his pl. 25, fig. 41. Its diameter is 160 mm. By coincidence, the smaller syntype fits quite closely into the gap of the missing portion of the outer whorl. This led Siemiradzki to assert that both syntypes were merely parts of a single specimen. The need to specify a lectotype therefore did not arise. More seriously, he states categorically that 'the' specimen consists entirely of septal chambers, *i.e.* that it is at least in part the phragmocone of an originally much larger shell.

The next description was by Maud Healey (1904). She had direct access to the original specimens and gave an excellent photographic image, now in left-lateral view, of the large syntypes on her pl. 10, fig. 1. Dismissing on grounds of matrix and morphology Siemiradzki's claim that the two syntypes were merely parts of the same specimen, the large shell was explicitly designated 'the "type" specimen', *i.e.* lectotype. She gave a description of it that is hard to improve or augment. In particular, she reports correctly that about three-quarters of the outer whorl consist of bodychamber, filled with a 'hard, yellowish, compact matrix' as against the inner whorls, which are uncrushed and filled with crystalline calcite. The re-crystallised test is preserved over much of the shell. There is some distortion of the outer whorl, but only in the sense of some displacement from its expected position resulting from diagenetic shrinkage in the septarian claystone concretion in which the specimen had been originally preserved. Miss Healey's description establishes Sowerby's species as based on an excellent type specimen, nearly complete and closely interpretable. The only residual uncertainty lay in its stratigraphical origins. This uncertainty had led the name *Amm. biplex* being applied to specimens from over a wide range of strata. It seemed to have become regarded as the zone fossil of the Upper Kimmeridge Clay because it shares with the *Pavloviae* found there the character of strong, purely biplicate secondary ribbing. To make the point she figured also a typical *Pavlovia pallasioides* (microconch) from the Hartwell Clay in the eponymous Zone near Oxford. Her guess was also that the age of *P. biplex* was Kimmeridgian, 'but the horizon from which it came must remain doubtful'. She went on: "In cases like this, it is perhaps wisest to abandon the name altogether, or at least restrict it to the abnormal specimen to which it was first attached."

Buckman (1920), familiar with Healey's account, expressed no reservations as to the quality of the specimen and hence its suitability to characterize a perfectly good type species of *Perisphinctes*. He refers to a sketch of its septal suture-line sent to him by W.D. Lang but does not figure it. From his descriptive remarks it seems however doubtful whether it had been taken from the type specimen, for in this no septal sutures worthy of note are discernible.

Finally, the case was re-examined by Arkell (1937, 1947) in the course of his monography of the ammonites of the English Corallian Beds, leading to his application to the ICZN (1951) to have the type species of *Perisphinctes* shifted from *P. biplex* to *P. variocostatus*. Although he refigured the type (1947, p. 362, text-fig. 126, left-lateral view) the image had been provided for him by the British Museum. He does not appear to have actually handled the specimen itself. His conclusions were strongly influenced by selective parts of the description by Miss Healey, "(...) who had shown that it was a much-distorted and incomplete (*sic*) specimen from the Glacial Drift", her conclusion derived from a study of it having been "In cases like this, it is perhaps wisest to abandon the name altogether, or at least to restrict it to the abnormal specimen to which it was first attached (...)" He failed to pick up what had been Miss Healey's probably most important observation, that contra Siemiradzki, most of the outer whorl consisted of bodychamber, and that "incomplete" amounted to no more than the lack of a quarter-whorl of that bodychamber. Arkell's subsequent discussions indicate that he regarded the specimen as no more than the [septate?] inner whorls of a contemporary much larger, strongly variocostate *P. variocostatus*, "The holotype of this species [*P. biplex*] is a distorted fragment of inner whorls, not identifiable specifically (...) "As to its age, he recalled that it was Blake (1904) who had proposed the source to have been "Upper Corallian", Ampthill Clay [Upper Oxfordian, subboreal Cautisnigrae Zone], contrary to a level somewhere in the Kimmeridge Clay as supposed by Miss Healey. And it was this stratigraphical uncertainty and the confusion in interpretations it had engendered in the literature that was the basis of Miss Healey's suggestion "to abandon the name [*biplex*] altogether", not the shortcomings of the specimen to which it was attached. Arkell concluded 'I therefore interpret *Perisphinctes* (*s.s.*) by *P. variocostatus* (Buckland, 1836) and use this almost equally time-honoured name for the common Drift "variocostate", to which in my opinion the holotype (*sic*) of *P. biplex* belongs (...)'. This was the basis of Arkell's appeal to the ICZN (1951), upheld in Opinion 303 (Hemming, 1954). He was followed without further

comment by Enay (1966, p. 339) in what is certainly the most authoritative revision of the genus *Perisphinctes* to have appeared since, and there the matter rests. It was a fortunate outcome and *P. biplex* does indeed "belong" to *P. variocostatus* (see below) but not in the sense Arkell had in mind.

That *P. biplex* and *P. variocostatus* are very likely microconch and macroconch of the same biospecies was demonstrated in the only section through the beds in question which I have been able to examine, in a (now infilled) deep railway cutting 2 km west of Bluntisham, near Huntingdon, 90 km north of London [UK grid reference TL 345 750]. It exposed some 3–4 m of Ampthill Clay, overlain with typical Pleistocene "Boulder Clay". Some of the beds were highly fossiliferous and packed with ammonites, crushed but unambiguously identifiable. There were present *Amoeboceras serratum* (J. Sowerby) together with *P. variocostatus* [M] and *P. biplex* [m], confirming the supposition that *P. variocostatus* and *P. biplex* were strictly contemporaneous and occur together with *A. serratum*.

SYSTEMATIC SUMMARY

Superfamily **Perisphinctoidea** Steinmann, 1890
Family **Perisphinctidae** Steinmann, 1890
Subfamily **Perisphinctinae** Steinmann, 1890
(in Steinmann & Döderlein, p. 441; as subfamily of Stephanoceratidae Neumayr, 1875)

The reference is to a page in Steinmann & Döderlein's general textbook on palaeontology, all of which is presented under joint authorship with the exception of the last section, the Vertebrata, which are explicitly ascribed to Döderlein. The assignment to a family-group taxon is firm, but I have been unable to find any evidence to support the attribution to Steinmann as sole author as given above, following Arkell in the *Treatise* (Arkell *et al*., 1957, p. L313). In his record-cards made in preparation for the *Treatise*, Arkell attributed authorship jointly to both authors. Family-group taxonomy in pre-*Treatise* times was haphazard. References to 'die Perisphinctiden' by the first major classifier, Siemiradzki (1898–1899), seemed sufficient. Subsequent authors, *e.g.* Hyatt (1900), Schindewolf (1925), Spath (1931) and even Arkell (1938), while referring now to Perisphinctidae or -inae in correct form and sense, never cited an author for the family-group taxon: it seemed unnecessary. Perhaps it is.

Genus *Perisphinctes* Waagen, 1869

Type species – *Ammonites variocostatus* Buckland, 1836 by subsequent designation in ITZN Opinion 303 (Hemming, 1954).

Perisphinctes biplex (J. Sowerby, 1821)
Pl.1: 1–4; Pl.2: 4

1821	*Ammonites biplex* J. Sowerby, 3, p. 168, pl. 293, figs 1, 2.
1898	*Perisphinctes biplex* (Sowerby); Siemiradzki, p. 265, pl. 25, fig. 41 (cast of type refigured).
1904	*Perisphinctes biplex* (Sowerby); Healey, p. 54, 57, pl. 10, figs 1, 2 (lectotype refigured, left-lateral view).
1920	*Am. biplex* Sowerby; Buckman, p. 26 (type species selected).
1937	*Perisphinctes biplex* (Sowerby); Arkell, p. lii.
1947	*Perisphinctes* (*Perisphinctes*) *biplex* (J. Sowerby); Arkell, p. 361, text-fig. 126 (lectotype refigured, left-lateral view, BM(NH) 43989a).
1947	*Perisphinctes* (*Perisphinctes*) *variocostatus* (Buckland); Arkell, pl. 76, figs 1a, b.
1951	*Am. biplex* Sowerby; Arkell, p. 191.
? 1847	*Am. biplex* Sowerby; d'Orbigny, p. 509, pl. 192, figs 1, 2 only (as *Am. biplex* in the legend but included in *Am. plicatilis* Sowerby in the text; specimen never redescribed).
non 1860	*Am. biplex* Sowerby; Damon, pl. 9, fig. 9 (a *Pavlovia* from the Upper Kimmeridge Clay; reproduced unchanged in later editions of 1864, 1880, 1888).
non 1922	*Perisphinctes biplex* (Sowerby); Buckman, pl. 282 (a nucleus of a *Perisphinctes* sp. indet. [M] from the earlier Middle Oxfordian).

Lectotype – Sowerby, pl. 293, fig. 1, designated by Healey (1904, p. 57); protograph reproduced here in Pl.1: 1. It was drawn at × 0.67 in right-lateral view and seems to have been reversed in lithography, for the resemblance is closest to the left-lateral aspect of the shell (Pl.1: 3) shown, for comparison also reversed, in Pl.1: 2.

Description – Healey's description needs few further comments. The specimen differs in details of preservation as seen from its two sides (Pl.1: 3–4), which may have been the cause of the divergent interpretations. The last septum is clearly visible at the arrow marked in the right-lateral view (Pl.1: 4) and is followed by a quarter of a whorl of the infill in brown mudstone of the former bodychamber, the test having become detached. Following the break, the final quarter-whorl of shell preserved is also filled with mudstone and has been slightly displaced from its proper position by a thin calcitic septarian intrusion of diagenetic origin. The expression of the ribbing is however undamaged. The bodychamber extended therefore over at least three-quarters of a whorl, as Miss Healey had reported. The maximum diameter of the shell is 163 mm, septate to 100 mm. To the practiced eye, the last few ribs in Pl.1: 4 show a slight approximation and modification in swing, perhaps even a shallow constriction at the

very end, suggesting that the final peristome had been very close. The secondary ribbing remains strictly dichotomous to the end, with no loss of strength. All these features indicate unambiguously that the specimen is that of a nearly complete, adult microconch *Perisphinctes*, typical of the genus. The only perhaps significant data to be added to previous descriptions are those of the ontogenetic development of the ribbing density, a character much used in perisphinctid taxonomy in the form of rib-density curves. The values as ribs per whorl at successive shell-diameters are: at 20 mm: c.34; 40: c.39; 60: 44; 80: 46; 100: 51; 125: 55.

In the left-lateral view (Pl.1: 3), the shell in the neighbourhood of the last septum retains some of the test, so no septal sutures are visible. On the last segment the test has been stripped off. It had however been somewhat crushed on this side, which was probably the upper side as the shell lay on the seafloor, and fragments of the strongly ribbed test had left curved imprints in the infill that give the impression of having been those of parts of the vaulted septa of the phragmocone - hence perhaps the idea that the specimen was wholly septate and merely the inner whorls of a much larger forms, such as macroconch *P. variocostatus*.

Another closely similar specimen is shown in Pl.2: 5–6, reproduced from Arkell (1947), pl. 76, figs 1a, b (BM(NH) 19582b), also from glacial drift. Somewhat smaller than the type of *P. biplex*, it is also an adult microconch of 110 mm diameter retaining half a whorl of bodychamber, septate to 80 mm. It too was identified by Arkell without further comment as *P. variocostatus*.

Comparisons – Pl.2: 4 shows the type of *P. biplex* next to the holotype of *Dichotomoceras dichotomum* Buckman, 1920 (pl.139A–C) (Pl. 2: 1–3), both reduced. The diameter of the *D. dichotomum* holotype is 146 mm and it is septate to 83 mm, with 0.8 whorl bodychamber. It is hard to see any significant difference between the two shells on even the narrowest interpretations. The final septa are at least here clearly visible: relatively simple and approximated. A paratype (Buckman 1920, pl. 139D, E) agrees in all details: maximum diameter 150 mm, septate to 90 mm, with 0.8 whorl bodychamber. It also shows a slight weakening and approximation of the last five or so ribs, leading to what was almost certainly the final, plain peristome. This shows no signs of even the incipient onset of a lappet. *D. dichotomum* could therefore be justifiably regarded as a subjective junior synonym of *P. biplex*. No-one has ever regarded *D. dichotomum* as other than what is today recognized to be a microconch and its antidimorphic macroconch is also undoubtedly *Per. variocostatus*. This was implicitly recognized by Arkell and his claim that the type of *P. biplex* 'belongs' to *P. variocostatus* is correct – but not for the reasons he gave.

Generic taxonomy – Conventional classification of *Perisphinctes* has in the past generated its fair share of additional nominal genus-group taxa, most commonly in the form of subgenera, to express differences in what were regarded as taxonomically significant characters of one kind or another. In some cases the origins of the differences were biogeographic, reflecting endemic segregation; in others, phyletic evolution that had occurred during unrecorded gaps in the biostratigraphical record. Most trivially, subgenera were merely groupings of morphospecies that are no more than variants of isochronous biospecies. In the *Treatise* (Arkell *et al*., 1957), the tally of generic tax ranging from Upper Callovian to Upper Oxfordian in the Perisphinctinae stood at 20. This has grown in the following half-century by another 16. Whatever one chooses make of this jungle, one convention that continues to be useful is to retain at nominally subgeneric level the distinction between macro- and microconchiate dimorphs. This distinction leads back to the type specimens of the type-species on which the subgenera are based. The commonest difficulty in trying formally to combine two existing antidimorphic nominal species into one as biospecifically synonymous lies in the requirement that the types should be strictly isochronous, *i.e.* to have come from beds of precisely the same ages as far as this can be geologically determined. This implies, strictly speaking, from the same bed at the same locality. And in the older literature, this is rarely possible. In the present case, therefore, it remains useful to retain *P*. (*Perisphinctes*) *variocostatus* and *P*. (*Dichotomoceras*) *dichotomus* as separate nominal taxa in the Subboreal Province.

The interpretation of *Dichotomoceras* has however come to be stretched to include an important group of more or less contemporary but biogeographically segregated perisphinctids endemic in the Submediterranean Province to the south. Its leading taxon is "*Dichotomoceras*" *bifurcatus* (Quenstedt), based on *Amm. biplex bifurcatus* Quenstedt, 1847 (p. 163; lectotype 1849, pl. 12, figs 11 a, b, refigured 1888, pl. 101, fig. 9, both figures reversed). A cast of it is refigured here in Pl.3: 1–3, also at × 0.67 (taken from Enay, 1966, pl. 33, figs 1a–c). The type came from Nusplingen in the southern Swabian Alb and the species is common in the White Jura from Franconia through the Jura into the Paris Basin. It is a striking form, which was formally acknowledged by Beurlen (1925) in making it the type species of a new genus *Divisosphinctes*. Following extensive studies of its biostratigraphy in the Jura, it was also made index-species of the *Divisosphinctes bifurcatus* Zone by Enay (1964, p. 494) as the lowest Zone in the standard chronozonation of the Submediterranean Upper Oxfordian.

In his magisterial review of the perisphinctids of the Oxfordian of the Jura, Enay (1966) then made two changes to the generally accepted generic assignments of the time. First, he abandoned *Divisosphinctes* Beurlen, 1925 as genus in favour of *Dichotomoceras* Buckman, 1920. This by itself

may seem rather strange, for comparing the type of *Divisosphinctes bifurcatus* with that of *Dichotomoceras dichotomum* (Pl. 2) it is not easy to see what they have in common. Second, and largely as the reason for the first change, he enlarged the scope of *Divisosphinctes* to include forms that do resemble *Dichotomoceras* more closely, typified by *D. bifurcatoides* Enay, 1966. The type of this species is shown here in Pl.3: 4 (from Enay 1966, pl. 34, fig. 2, × 0.67). The unifying character in all these versions of *Dichotomoceras* was taken to be the ribbing density on the innermost whorls. Curves of these as function of shell-diameter were shown by Enay for a wide range of specimens (1966, p. 513, fig. 157). In contrast to the rib-curves of most perisphinctids, in which the rib-density per whorl increases more or less steadily with shell-diameter, the innermost whorls of *Divisosphinctes* start with very fine, dense ribbing that then coarsens. The initial part of the rib-curve therefore falls, before rising again on the later whorls. *Divisosphinctes* characterizes the Bifurcatus Zone of the Submediterranean Province at the top of its standard chronzonation of the Middle Oxfordian. Its occurrence is widespread,

[Here the manuscript ends. In notes he prepared for the new edition of the Treatise in 2005, John Callomon included *Divisosphinctes* within *Dichotomosphinctes*. It may be assumed from the above that subsequently, he was coming round to the view that *Divisosphinctes* should be retained as a separate subgenus of *Perisphinctes*. J.K.W.]

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PLATE 1

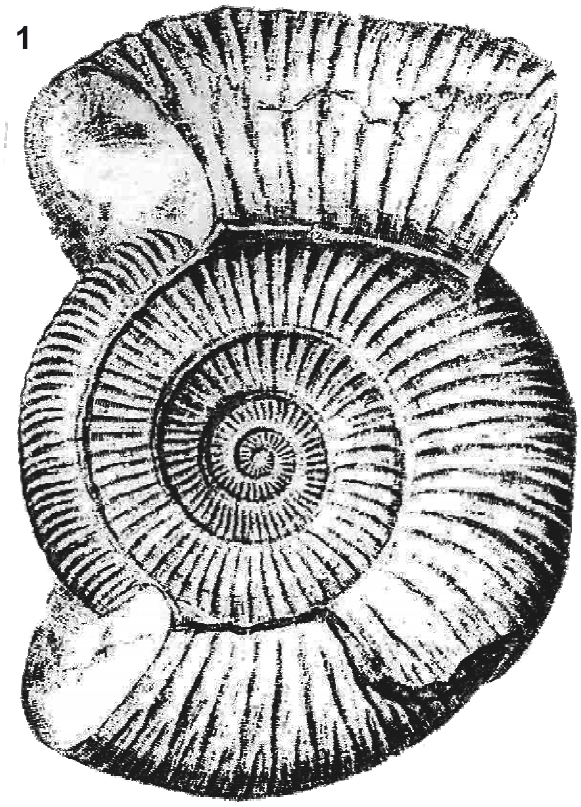
Figs 1–4 *Am. biplex* J. Sowerby, 1821.

Fig. 1. 1 protograph of the lectotype, pl. 293, fig.1.

Fig. 2. Fig. 2 the lectotype (NHM 43989a), left-lateral view, reversed, reduced × 0.67, to compare with the lithographic protograph, which is also reversed.

Fig. 3. Fig. 3 the same, not reversed.

Fig. 4. Fig. 4 the same, right-lateral view. Arrows mark the onset of the bodychambers



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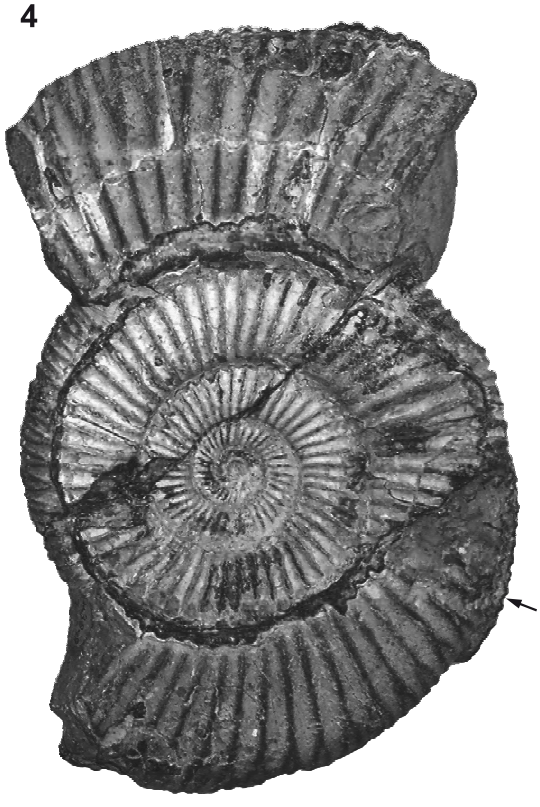

4

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PLATE 2

Fig. 1–3 *Dichotomoceras dichotomum* S. Buckman, 1920, the holotype of the type species of *Dichotomoceras*, reduced × 0.67 (NHM C.41693), reproduced from Buckman, 1920, pl. 139A–C.

Fig. 4–6 *Perisphinctes biplex* (J. Sowerby), reduced × 0.67. Fig. 4, the holotype in left lateral view. Figs 5–6, reproduced from Arkell 1947, pl 76, figs 1a, b. (figured by Arkell as *P. variocostatus*).

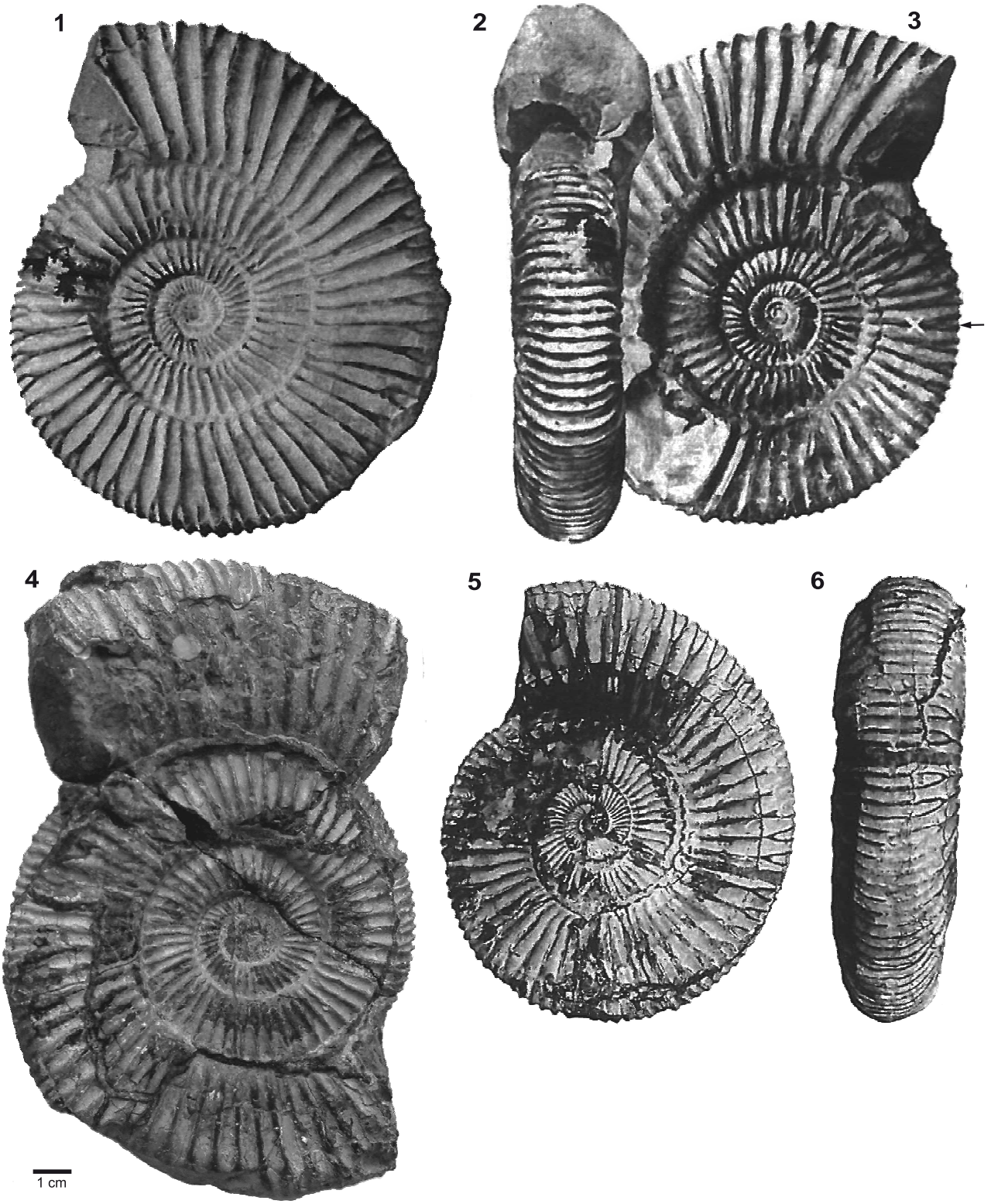
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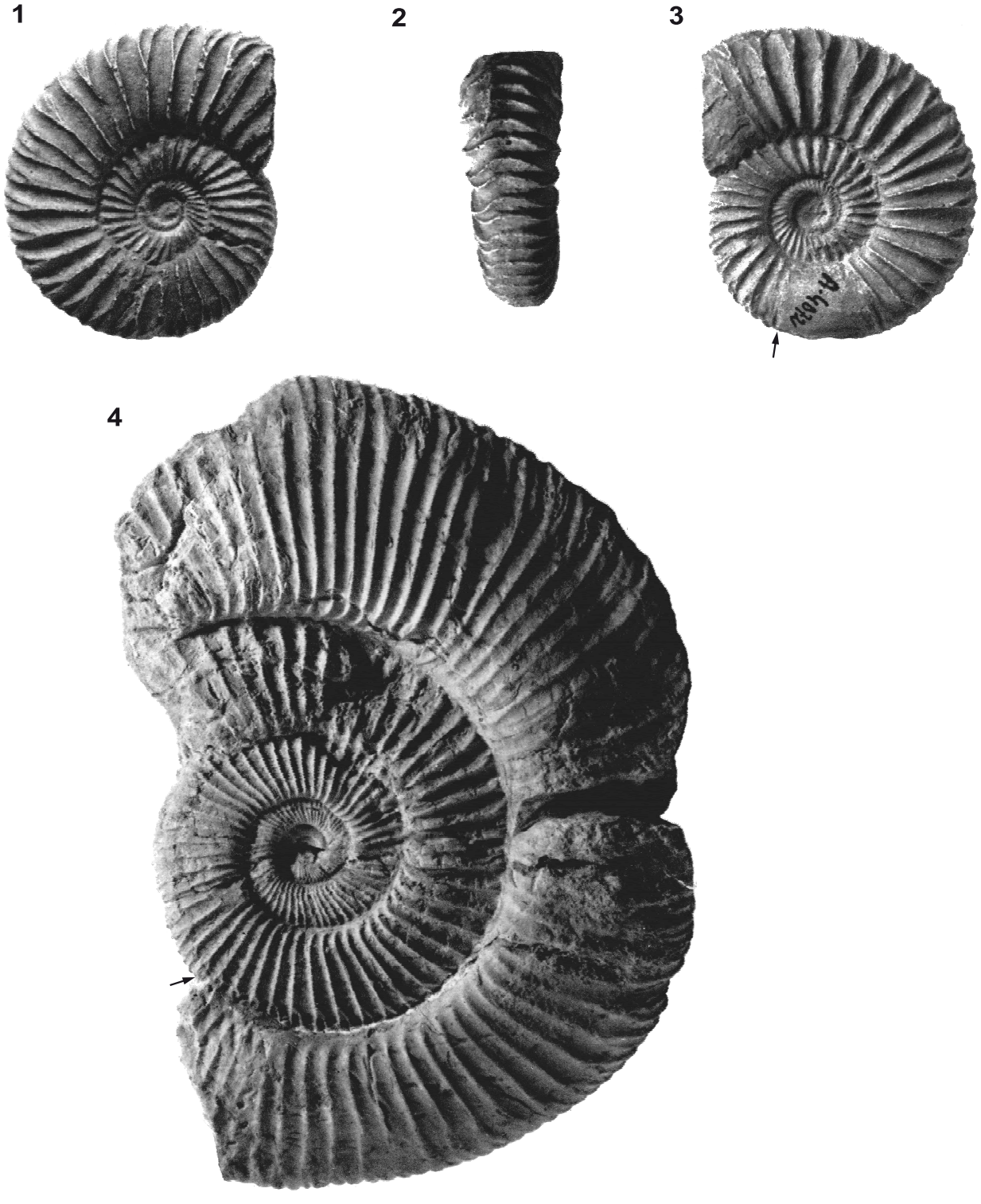
PLATE 3

Fig. 1–3 *"Dichotomoceras" bifurcatus* (Quenstedt), reproduced from Enay (1966, pl. 33, figs 1a–c).

Fig. 4. *"Dichotomoceras" bifurcatoides* Enay, reproduced from Enay, 1966, pl. 34, fig. 2.

Arrows mark the onset of the bodychambers.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