

## Some early Middle Jurassic ammonites of Tethyan affinities from the Aalenian of southern England

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**ABSTRACT** - The ammonites of the early Middle Jurassic Aalenian Stage in Britain are dominated by the family Graphoceratidae, whose habitat was predominantly in extra-Alpine Europe. New collections, particularly from the Scissum Bed and Zone exposed in temporary sections near Burton Bradstock, Dorset, contain however a significant proportion of Mediterranean Tethyan elements, some of which are described. They include *Erycites* cf. *fallifax* Arkell and *E. exulatus* sp. nov. of the subfamily Erycitinae Spath, 1938; *Hammatoceras lorteti* (Dumortier), *H.* cf. or aff. *procerinsigne* Vacek, *Planammatoceras planinsigne* (Vacek) [M] and *P. tenellum* sp. nov. [m] (from the Murchisonae Zone of Horn Park) of the Hammatoceratinae Hyatt, 1867; *Csernyeiceras verpillierense* (Roman & Boyer) of the Haugiinae Buckman, 1905; and *Tmetoceras scissum* (Vacek) in several transients from Lower to Upper Aalenian. These species occupy important positions in the evolutionary histories of their families, which are discussed.

**KEY WORDS:** Jurassic, Aalenian, Dorset, Scissum Bed, ammonites, Tethyan, biostratigraphy, systematics.

### INTRODUCTION

The ammonite biostratigraphy of the Aalenian must be one of the most intensively studied and best understood of any Stage of the Jurassic. Detailed successions have been worked out at localities ranging widely across Europe, beginning with the classical early work of Buckman in Dorset (1887-1907), recently brought up to date by the present authors (Callomon & Chandler 1990), and extending via northern Germany (Hoffmann 1913, Althoff 1940), Swabia (Rieber 1963), eastern France (Contini 1969-70, Caloo 1970, -71) to Iberian and Betic Spain (Ureta Gil 1983, -85; Linares, Ureta & Sandoval 1989). Illustrations of stratigraphically less extensive or less well-controlled collections are to be found in almost innumerable other works. The evolutionary homotaxis of the dominant elements of the faunas, the Graphoceratidae, across the whole of this large area is remarkable. It has therefore been used as the biostratigraphical base for a standard chronostratigraphy that is almost everywhere immediately applicable. This is shown in Figure 1. (Although there is general agreement on the sequence of stratigraphical units in this scale, agreement on many points of nomenclature has still to be worked out, as have formal typological definitions in boundary stratotype sections). More locally, biostratigraphical subdivision can be taken even further. The number of

the ultimate units, the distinguishable ammonite faunal horizons, that could be recognized in the northern Jura by Contini was twelve. In Dorset it is currently sixteen.

Nevertheless, this impressive picture of the ammonite biostratigraphy was until recently highly incomplete. It is strongly biased through the dominance, both in numbers and persistence, of the one family, the Graphoceratidae, in what happened to be, historically, the cradle of classical biostratigraphy and biochronology in extra-Alpine northern Europe. In Britain, Germany and the Jura, the Graphoceratidae make up 95% or more of the Aalenian faunas. The remainder provided intriguing glimpses of an alternative culture living "somewhere else". There were therefore indications of bioprovincialism in Aalenian ammonites as in those of other Stages, but it seemed to be much less important. The Graphoceratidae, although dominant in the north, did extend over the Mediterranean as far as North Africa, Sicily, the Italian Apennines and the Balkans. The clear-cut, mutually exclusive, faunal segregations found in the Upper Jurassic, enshrined in the traditional division of the world into Boreal and Tethyan Realms, seemed to be lacking. The exotic minor elements of the faunas were therefore regarded as curiosities. As the Graphoceratidae were

Zones	Subzones	English faunal horizons <sup>5</sup>
<i>Graphoceras concavum</i>	<i>G. formosum</i>	Aa-15,16
	<i>G. concavum</i>	Aa-13,14
<i>Brasilia bradfordensis</i> 4	<i>B. gigantea</i>	Aa-11,12
	<i>B. bradfordensis</i>	Aa-8,9,10
<i>Ludwigia munchisonae</i>	<i>L. munchisonae</i>	Aa-6,7
	<i>L. obtusiformis</i>	Aa-5
	<i>L. haugi</i> 3	Aa-4
<i>Tmetoceras scissum</i> 2	<i>L. comptum</i>	Aa-3
	<i>L. lineatum</i>	Aa-2
<i>Leioceras opalinum</i> 1	<i>L. opalinum</i>	Aa-1

Figure 1. - Zonal classification of the Aalenian in Britain.

Notes on Figure 1.

1. Brauns 1865, based on northern Germany. The holotype of the index came however from an unknown horizon in Franconia. It is lost, and there are as yet neither topotypes nor a neotype. The attachment of the name *opalinum* to these early forms, well known and abundant almost everywhere else, including northern Germany, is therefore conventional. A typical example is illustrated in the *Treatise* (Arkell 1957, p.L263, fig.298.4). Buckman, on the contrary, believed that the type horizon of *L. opalinum* lay higher, in the Scissum Zone. He therefore renamed the forms of the Opalinum Zone *L. opaliniforme*. His *opaliniforme* hemera, or Opaliniforme Zone, is therefore a synonym of Opalinum Zone.
2. Neumayr 1871, and Buckman. Partly replaced by a Comptum Zone by Contini (1969), following biostratigraphical indications of Rieber (1963) and Gabilly (Gabilly & Rioult 1974): Lineatum Subzone left by him as a faunal horizon or Subzone in the Opalinum Zone.
3. An alternative subzonation sometimes used in Germany is based on a succession of *Staufenia*. The boundaries of the Opalinoides, Sinon, Sehndensis and Stauffensis Subzones differ considerably from those given here, however, the last-mentioned reaching well up into the Bradfordensis Zone.
4. Used until recently only as a Subzone of the Murchisonae Zone, but the faunas are so distinctive and widely recognizable that promotion to full zonal status seems justified.
5. Callomon & Chandler, 1990.

sufficiently abundant to solve the main geological problems of stratigraphical correlation, problems arising from bioprovincialism did not excite much interest.

Bioprovincialism becomes important, however, in attempts to solve the biological problems of the ammonites themselves. Leading amongst these problems is that of working out the pattern of evolution as basis for phylogenetic classification. From this can follow discussions of diversities, rates of turnover and extinction. Finally come speculations on causes - the relationships between evolution and environment, currently a popular topic in palaeobiology, ammonites included.

The difficulties in the Aalenian have been largely circumstantial. Known localities yielding good Tethyan faunas have been few. Either material was relatively abundant and well-preserved but stratigraphically doubtful, or it was well localized stratigraphically but confined to isolated horizons, without obvious ancestors or descendants. The most famous example of the former is the fauna from the highly condensed succession in the Venetian Alps

around Lake Garda and Cap San Vigilio described by Benecke (1865) and Vacek (1886). It was for a long time almost the sole arbiter of the Tethyan Aalenian, but even in his reanalysis of 1956, Arkell (p.176) deduced the probable ages of the forms represented by correlation and analogy rather than from primary stratigraphical evidence, of which there was effectively none. Ironically, perhaps, for an equally long time the best examples of the latter case, of faunas from isolated horizons, lay in Buckman's descriptions (1887-1929) of the exotic elements in the faunas of Dorset: genera such as *Asthenoceras*, *Vacekia*, *Bredya*, *Haplopleuroceras*, *Fontannesia*, *Planammatoceras*, *Eudmetoceras*, *Euaptetoceras*, *Abbasites* and *Tmetoceras* itself.

Since then there has been considerable progress, largely through the careful study of new successions. In Europe, the most notable additions have been in Hungary (Geczy 1966-7) and Spain (Ureta, 1983, - 85; Linares, Ureta & Sandoval, 1989). A number of the genera listed above, as well as others such as *Erycites* and *Zurcheria*, have acquired ranges within the Aalenian. Perhaps even more important, some

genera previously thought to be characteristic of the overlying Bajocian, such as *Stephanoceras*, have had their ranges extended downwards into the Aalenian. Several previously held views on phyletic roots have had to be modified and some cryptogenic genera can now be assigned to their proper phyletic places. Finally, probably the strongest new impulse has come from the New World, in which rich faunas presumed to be of Aalenian age have been described along the length of the Eastern Pacific rim, from Alaska to the southern Andes (see e.g. Westermann 1964; Imlay 1973; Westermann & Riccardi 1972). These pose an additional problem. The Graphoceratidae are wholly absent in the Pacific and even the primary attempts at correlation with the European standard are dependent on the common presence in both regions of western Tethyan groups. It is especially here that a better knowledge of the Tethyan genera and their ranges is needed.

The present work is prompted by some new discoveries in temporary sections in Dorset, particularly in the Scissum Bed of Burton Bradstock. This, the lowest member of the Inferior Oolite, is usually rather hard and massive. Hence, although one of the most widespread and persistent units in the formation, its faunas, besides the dominant Graphoceratidae, were until now among the least well understood. Pipe-trenches, widening of farm-tracks and ground clearance for holiday caravans in recent years led to extensive excavations of the Scissum Bed at places where it had weathered near the surface. This made it possible to recover large, well-preserved specimens, often complete with test and bodychamber. The fauna turned out to be relatively rich in Tethyan elements, perhaps surprisingly so in view of the high palaeolatitude of Dorset: certainly so in comparison with Lorraine, the Jura and the Franco-Swabian basins. The cause may have been trophic, for besides ammonites, the Scissum Bed, in common with most of the rest of the Inferior Oolite, has a rich and diverse benthos of bivalves, brachiopods and gastropods, as well as the bioturbation of a fauna of vigorous crustaceans. We describe now a number of these new discoveries, together with a few related forms from slightly higher beds. A description of the considerable number of Hammatoceratinae from the Murchisonae-Concavum Zones that have accumulated is beyond the scope of the present work.

## STRATIGRAPHY

The localities from which the present material came all lie within less than a kilometre of the famous coastal section at Burton Cliff, Burton Bradstock: at Freshwater Caravan Park, 400 m NNE of Burton

Freshwater, the mouth of the River Bride (formerly Bredy); and at Manor Farm, on the SW slopes of Burton village. The succession in the Scissum Bed is the same as that at Burton cliff, which is reproduced here in Fig.2.

The term "Scissum-Beds" was first introduced in England by Richardson (1904, p.67) as lithostratigraphical term for beds in the Cotswolds "laid down during the hemera *scissi* - the characteristic ammonite, *Tmetoceras scissum*, being most distinctive but rare." Its use was extended by him to Dorset somewhat later, and his description of Burton cliff (Richardson 1928, p.63 and Fig.4) has formed the basis of all subsequent accounts. The Scissum Zone in any kind of chronostratigraphical sense seems to go back to Neumayr (1871, p.509), albeit for the "Mediterranean" region, especially Cap San Vigilio. It was extended to Britain by Buckman (1898a, Table I) as hemera, and thence transformed into a standard Zone by Arkell (1933, p.189 and 1956, p.34). It corresponds to the Comptum Zone and highest faunal horizon of the Opalinum Zone of Contini (1969). (Zonal boundaries remain formally to be defined, but in any case the range of *Tmetoceras scissum* - its biozone - is irrelevant to its function as zonal index.)<sup>†</sup>

The Scissum Bed at Burton is best seen in the section at the Freshwater Caravan Park. It consists there of two parts, separated by an indistinct parting when weathered, but inseparably welded together when fresh, as in the fallen blocks at Burton Cliff. The lower part (bed 6a in figure 2) is a very fine-grained calcareous sandstone, deeply and intensely burrowed. It is sparsely fossiliferous, the main elements being very large *Camptonectes* and ammonites embedded at all angles, consisting almost wholly of large Leioceratids, *L. opaliniforme* Buckman [M] and [m], preserved as internal moulds. The upper part (bed 6b) grades upwards into an intensely hard, shelly, oolitic and micritic sandy limestone, also intensely bioturbated. Small to medium-sized ammonites are embedded at all angles, but large shells are flat-lying and seem to retain some layering: *Bredya subinsignis* marks a consistent pavement at a level 5-10 cm from the top. The bed is terminated by a sharp erosion-plane, which is somewhat diachronous: at Burton Cliff, the top has been planed off to a level at or just below the *Bredya* level. Most of the Tethyan ammonites described below also came from this level.

The Leioceratinae in beds 6a and 6b are distinct. The abundant new collections from 6b confirm Rieber's (1963) and Contini's findings (1969-70) that apparently two quite separate groups are present, each dimorphic:

# BURTON BRADSTOCK

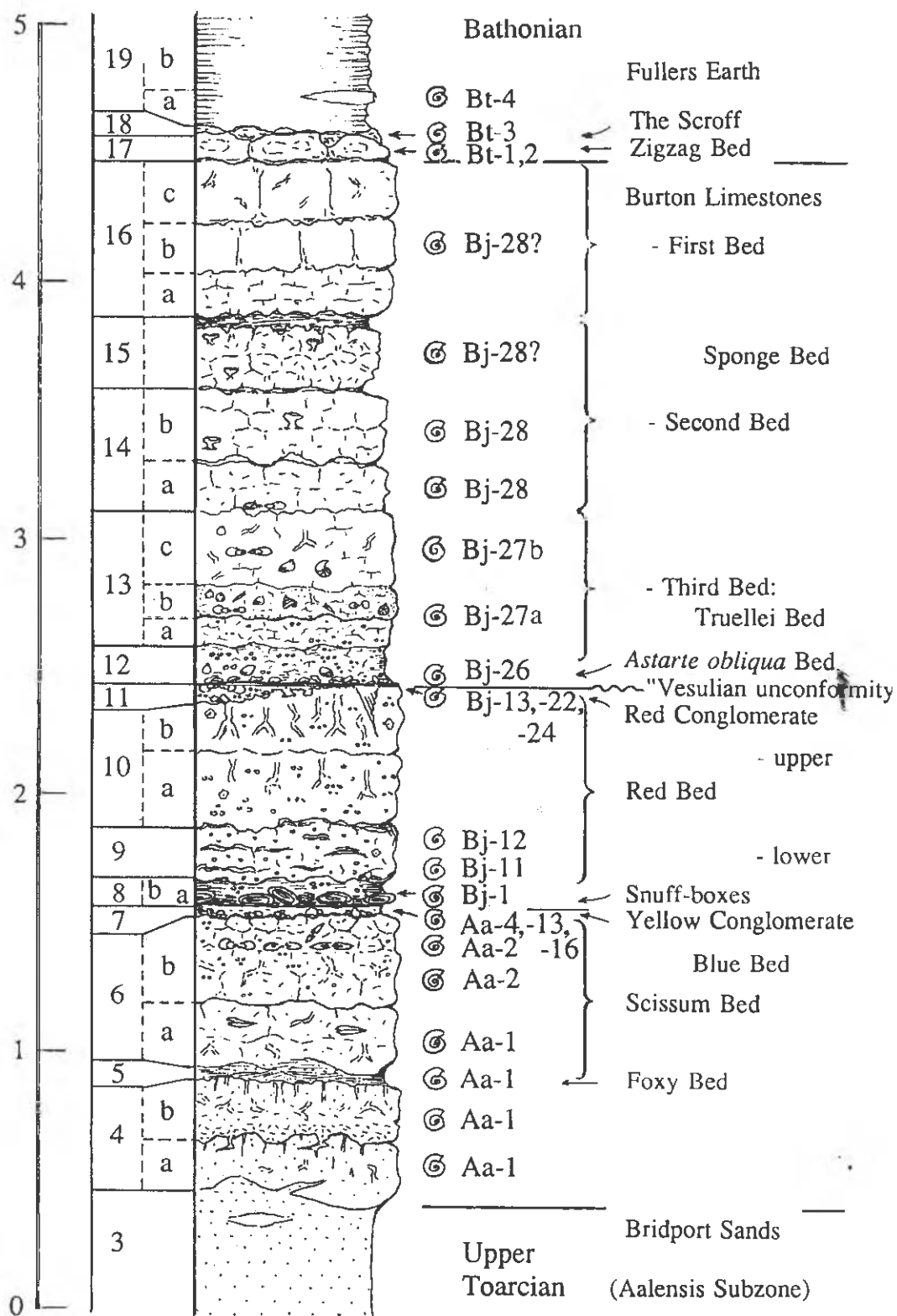


Figure 2. - The section through the Inferior Oolite at Burton Bradstock, Dorset. (Beds 3-11 based on Freshwater Caravan Park, beds 12-19 on Burton Cliff).

Subfamily Leioceratinae Spath, 1936  
Genus **Leioceras** Hyatt, 1867 [= *Lioceras* Bayle, 1878]

*L. (Cypholioceras) lineatum* Buckman, 1899 [M] (incl. *L. grave*, *partitum*, *plectile*, *plicatellum*: type localities and horizons all Burton Bradstock).

*L. (Leioceras) opalinum* Buckman non auctt., nec Reinecke ? [m] (= *L. undulatum* Buckman, 1899).

Subfamily Staufeniinae Maubeuge, 1950  
Genus **Cylicoceras** Buckman, 1899

*C. (Cylicoceras) uncinatum* Buckman, 1899 [M] (incl. *C. unicum*: both types from Burton).

*C. (Costiceras) subcostosum* Buckman, 1899 [m] (= *Amm. opalinus costosus* Quenst., preoccupied), *tortum* Buckman, 1899 [m] (lectotype Suppl. pl.11, figs 1-3; type species of *Rhaeboceras* Buckman, 1899, non Meek, 1876).

*C. (Costiceras) paucicostatum* Rieber, 1963 [m] (type species of *Costiceras* Contini, 1969).

The duality goes back into the Opalinum Zone below, as illustrated by Buckman from his *opaliniforme* hemera, and probably lower, into the Toarcian. Upwards, *Cylicoceras* can be followed effortlessly into *Staufenia*, *Leioceras* into *Ancolioceras*. *Cylicoceras* is relatively rare at Burton Bradstock.

The Leioceratinae of bed 6a appear to differ from those in beds 4 and 5 below only in size, although not enough have yet been collected from bed 4 to quantify this. Such an upward increase in size of what appear otherwise to be very similar forms of *Leioceras* has been noted also in the Opalinum Zone on the Continent. In Swabia, it occurs in the "Opalinuston", up to 100 m thick. In France, it has been formally expressed in terms of two successive faunal horizons or Subzones, those of *L. subglabrum* Buck. below and of *L. opaliniforme* Buck. above. The position of the true *L. opalinum* (Reinecke) itself remains uncertain, for the type material is lost and there appear to be no topotypes on which to base a new interpretation, including its stratigraphical horizon. The Opalinum Zone at Burton is therefore taken to be beds 4-6a inclusive, and the Scissum Zone to be represented by bed 6b only.

## SYSTEMATIC DESCRIPTIONS

Family Phymatoceratidae Hyatt, 1867  
[nom. corr. pro Phymatoidae Hyatt, 1867: ICZN Opinion 575, 1959]

Subfamily Erycitinae Spath, 1928  
Genus **Erycites** Gemmellaro, 1886  
[Type species *Amm. fallax* Benecke, 1865 (non Guéranger),

SD Loczy 1915, p.381; non *Amm. gonionotus* Benecke, des. Roman 1938, p.138]

**Erycites** cf. **fallifax** Arkell, 1957  
(Pl.I, figs 1,2,3)

- cf. 1865 *Ammonites fallax* Benecke (non Guéranger), p.171, pl.6, figs 1-3.  
non 1874 *Ammonites fallax* (Benecke): Dumortier, pl.55, figs 3,4.  
cf. 1886 *Hammatoceras fallax* Benecke: Vacek, p.93, pl.15, figs 1-9 (topotypes)  
cf. 1904 *Erycites fallax* Benecke: Prinz, p.89, pl.25, fig.1  
? 1922 *Erycites sphaeroconus* Buckman: pl.315  
1957 *Erycites fallifax* Arkell, p.L267, fig.308.3a,b (Benecke's fig.1 reproduced: holotype).  
cf. 1966 *Erycites fallifax fallifax* Arkell: Geczy, p.106, pl.30, figs 2-5, pl.31, fig.3  
1966 *Erycites fallifax flexuosus*: Geczy, p.110, pl.31, fig.3  
cf. 1989 *Erycites fallifax* Arkell: Linares, Ureta & Sandoval 1989, pl.1, fig.8

**Material** - One nearly complete adult (RBC 524) and one nucleus (RBC 525). Scissum Bed, Burton Bradstock.

**Type** - Benecke founded the species on the basis of some 40 syntypes. There was no holotype. Only one of his three figures gave a side-view of a complete specimen (Pl.6, fig.1), and this has been taken by some authors to imply that it was the type (e.g. Vacek 1886, p.93 and Geczy 1966, p.108) even though the other two figures were derived from two other syntypes. No confusion has arisen, however, and in any case the matter was settled when Arkell (1957, in the *Treatise* p.L267) renamed the species *E. fallifax*, to resolve the junior homonymy with *Amm. fallax* Guéranger, 1865, and chose Benecke's fig.1 to be holotype of the species, *nomen novum*. The type was said by Vacek to represent an unusually small variant and appears to be lost. According to Hantken in Prinz (1904, p.89) the type-series was kept in Strasbourg, where Benecke was professor. Enquiry at Strasbourg in 1974 elicited the reply from Mlle Marguerite Wolf, conservateur, that the whole of the collection of types was destroyed in a fire in 1967, but that the types of *Amm. fallax* had not been among them. There was evidence that it had remained in Benecke's private collection which was dispersed after his death in 1917 and cannot be further traced. An old plaster-cast has however recently been discovered in the Vacek collection at the Geologische Bundesanstalt in Vienna (JHC 1991). Nevertheless, a neotype may have to be selected.

**Description and comparisons** - Although the species is widespread and locally abundant in the Mediterranean area - Vacek claimed to have had some 700 specimens from San Vigilio - few good specimens have been figured, making it difficult to

assess the considerable variability. A topotype is therefore shown here for comparison in pl.I, fig.2, kindly donated by Sr. Luigi Ambrosi of S. Ambrogio, Verona. It came from the Scissum bed of Capitello quarry, San Vigilio (Sturani 1964, p.9, fig.2, bed s), the top member of the Oolite of San Vigilio, varying from 15 to 65 cm in thickness across the quarry, bounded at top and bottom by sharp erosion planes, and locally packed with ammonites in fresh preservation (observations made in 1988). The topotype is partly deformed, in that the bodychamber has been displaced sideways and is now somewhat askew, but this does not detract from what is otherwise a reliable representation of a typical variant. A terminal adult constriction is still partly preserved on the venter at the end of the bodychamber.

The larger specimen from Burton shares most of the major features of sculpture with the topotype: the adult maximum size; the inflated, involute inner whorls, becoming evolute and compressed on the outer whorl; the dense, sharp, fine ribbing; and the vestigial break in the secondary ribbing on a perfectly round venter. The dimensions are: maximum diameter 85 mm, septate to 67 mm, 0.4 whorl bodychamber preserved, umbilical seam indicating 0.75 whorl bodychamber when complete. At 67 mm: whorl-height  $h$ , 0.37; whorl-breadth  $b$ , 0.40; umbilical width  $u$ , 0.34; 36 ribs per whorl. The principal difference lies in the style of the ribbing, particularly on the bodychamber. The Burton specimens have straighter primaries, more accentuated at the umbilical margin, slightly flexuous, dividing relatively low on the whorl-side. The general impression is still more Hammatoceratid, less Stephanoceratid, than the Mediterranean forms.

**Ages** - These are so far the only specimens of the group found in Britain, and hence we know it from only a single horizon, in the lower Scissum Zone. In the Mediterranean region it has some range. Geczy (1966) has distinguished a series of successive transients, as subspecies: *E. fallifax fallifax* (upper Comptum Zone or Subzone, see fig.1) - *E. fallifax excavatus* (Opalinoides Subzone, equivalent to the lowest, Haugi Subzone of the Murchisonae Zone) - *E. fallifax flexuosus* (the same, somewhat higher) - *E. fallifax arkelli* (?Concavum Zone). In Spain, Linares, Ureta and Sandoval (1989) give the genus *Erycites* almost exactly the same range, although they do not subdivide it further into species. A typical example of *E. fallifax* s.s. has recently been described also from the Comptum Subzone in the southern Beaujolais (Rhône) by Elmi & Rulleau (1993, pl.2, fig.3). That the genus as a whole ranges upwards is known to be the case also in Britain, where a specimen of *Erycites partschi* Prinz was already figured by Buckman (1921, pl.246). Its probable horizon, as deduced from several subsequent finds, is Aa-8, lowest Bradfordensis Zone.

The other species described by him, *E. sphaeroconus*, is said to have the whole of its last whorl, maximum diameter only 30 mm, consisting of bodychamber. Its horizon is also unknown, although at the place at which it was found, Marston Road Quarry (Buckman 1893, p.490), the Scissum Bed is well represented. It is best regarded as an indeterminable juvenile *Erycites* s.s. and its name treated as a *nomen dubium*.

The type horizon of *E. fallifax* at Cap San Vigilio appears to be firmly dated as upper Comptum Subzone (see also Linares et al. 1989, p.198). The *Leioceras comptum* found in intimate association with *E. fallifax* and *Tmetoceras scissum* (confirmed in 1988), including the specimens figured by Vacek, appears to be correctly identified, as confirmed by Rieber (1963). The Dorset specimens would seem therefore to be slightly older. Perhaps this would explain their slightly more "ancestral" morphology.

Forms that are most probably ancestral have been abundantly described from the Mediterranean region. Two that are worth citing are *E. subquadratus* Geczy (1966, p.95, pl.27, fig.1) from the topmost Toarcian, which has already the tightly involute coiling of *E. fallifax* in its inner whorls but retains hammatoceratid ribbing on its bodychamber as in the specimens from Dorset; and thence *E. elaphus* Merla (1934, p.25, pl.4, fig.5), from the *Dumortieria meneghini/pseudoradiosa* Zone.

#### *Erycites exulatus* sp. nov.

(Pl.II, figs 1,2)

?1874 *Ammonites gonionotus* Benecke; Dumortier 1874, pl.56, fig.5 only (from La Verpilliere).

?1886 *Hammatoceras* (*Erycites*) *barodiscus* Gemmellaro, p.205, partim (syntypes in Palermo).

**Material** - Holotype, Pl.II, fig.2 (RBC 528), paratype I, pl.II, fig.1; paratypes II (RBC 536) and III (RBC 537), not figured, and a septate nucleus possibly belonging to this species: all macroconchs.

#### Description - Measurements:

	HT (Pl.II, fig.2)		PT I (Pl.II, fig.1)		PT II		PT III	
Max.diameter (mm)	138		105		140		110	
septate diameter (mm)	85		91		80		65	
bodychamber (whorl) (p: peristome)	0.8, p		0.8, p		0.8, p		0.85, p	
Diameter (mm)	125	85	100	65	125	85	100	65
whorl-height, $h$	0.34	0.39	0.31	0.36	0.34	0.36	0.32	0.37
whorl-breadth, $b$	0.35	0.45	0.35	0.51	0.36	0.44	0.38	0.51
umbilicus, $u$	0.39	0.31	0.42	0.40	0.40	0.36	0.41	0.36
Number of ribs	28	24	34	30	30	27	29	28

Comparison of pls. II and I shows that the new species mirrors *E. fallifax* in all major features of

morphology, with consistent small differences. *E. exulatus* is bigger - c. 140 mm against c. 95 mm - and much more strongly and coarsely ribbed. The adult bodychamber retains strong hammatoceratid ribbing to the end, unlike that in *E. fallifax* which modifies strongly and fades. The nucleus appears to be sphericonic as in *E. fallifax*, from which it may be indistinguishable; and the specimen shown in Pl.I, fig.3 may belong to *E. exulatus* rather than to *E. fallifax*. Septal sutures are barely visible but appear to be typically complex.

*Comparisons* - There are very few figures in the literature that resemble the present forms at all closely. The nearest seems to be the one given by Dumortier, although it is incomplete. It may have additional direct relevance through its place of origin, La Verpillière. There appears to be no detailed stratigraphy at this locality (cf. Arkell 1956, p.103), but it is one of the few to have yielded some of the other forms now being described from the Scissum Bed of Dorset, such as "*Hammatoceras*" *verpillierense* (see below).

The closest match may turn out to be with *Erycites barodiscus* Gemmellaro. We are indebted to Dr Stefano Cresta (Rome) for showing us some photographs of the type material in Palermo. There appear to be at least three syntypes, which resemble the Dorset forms in most respects - size, coarseness of ribbing and bodychambers. As Gemmellaro never completed the projected monograph of the faunas of Monte San Giuliano and gave no figures, his species was not taken up by subsequent authors. Its name has been ignored in the hundred years since. Neither were the indications of stratigraphy sufficiently detailed to permit comparisons of age with the precision needed in the present context. It seems best therefore to regard the name of the Sicilian species as a *nomen oblitum* for the time being and not to let it introduce uncertainty into the description of well-localized new material from another very distant locality, Dorset.

*Erycites* aff. *exulatus* sp. nov.  
(Pl.I, fig.4)

*Material* - One complete phragmocone (RBC 526).

*Description and comparisons* - Measurements: maximum diameter 122 mm, septate to 120 mm, bodychamber just beginning, umbilical seam indicating a former bodychamber of 0.85 whorl, which, with a spiral half-whorl constant of 1.27 would have given an adult diameter of 175 mm. Dimensions: at 120 mm,  $h = 0.30$ ,  $b = 0.32$  and  $u = 0.47$ . Ribs: 28 at 120 mm, 31 at 80 mm, 31 at 50 mm. No septal sutures visible.

There is a strong overall resemblance to *E. exulatus*

in the general style of ribbing, but the shell was even bigger and the inner whorls are strikingly more evolute. In this respect there is some similarity with *E. gonionotus* (Benecke) (1865, p.172, pl.7, fig.3), but this is outweighed by other differences. In *E. gonionotus* the coverage of the flanks of the inner whorls is so light that the secondary ribbing is partly visible. This is also the case in the specimens figured under the name by Vacek (1886, pl.16, fig.10, a nucleus) and Geczy (1966, pl.29, fig.3). In the English specimen the secondary ribbing, as well as being coarser, is fully covered on the inner whorls. Lastly, there is no guarantee that either Benecke's figured lectotype or Geczy's Hungarian specimen came from the Scissum Zone. They could be older.

One of the characters that remains to be explored more closely, in both the Erycitinae and the Hammatoceratinae, is the significance and intraspecific variability of the involuteness of the coiling. In some descendants, e.g. *Sonninia* s.s., material is sufficient to leave no doubt that the umbilical width, usually the most direct measure of "involuteness", can vary enormously. This could be the case in *Erycites*; and the possibility that the present specimen is merely an extreme variant of *E. exulatus* cannot be ruled out. Much more material would be needed before we could tell.

*General remarks on Erycites*. At the generic level, *Erycites* occupies by common consent a central position in the phylogeny of the ammonites of the Middle and Upper Jurassic. Its roots as an independent lineage lie somewhere in the Phymatoceratidae in the Upper Toarcian, for the very typical *E. elaphus* was already fully differentiated from *Hammatoceras* s.s. in the Tethyan Pseudoradosa/Meneghini Zone, immediately above the Insigne Zone (equivalent to the lowest part of the NW European Levesquei Zone). It persisted with little change at least into the Bradfordense Zone of the Upper Aalenian (*E. partschi*, *intermedius*) or even the Concavum Zone (Linares, Ureta & Sandoval 1989). But it branched at least three times. One branch had already separated in the Scissum Zone: *Spinammatoceras* - *Malladaites* - *Zurcheria* (and *Haplopleuroceras*?) (Linares & Sandoval 1986, Fernandez-Lopez, Mousterde & Rocha 1989). For this branch, as clear an example of proterogenetic evolution as could be wished for, the name Zurcheriinae Hyatt 1900 would be available. The second branch led in the Murchisonae Zone to *Abbasites*, with the involute sphericonic coiling already seen in *E. fallifax*, and thence presumably to *Docidoceras* - *Emileia* of the Otoitidae, all the Sphaeroceratidae, etc. The third branch led to *Stephanoceras* of the Stephanoceratinae not later than the Murchisonae Zone, for typical *St. longalvum* (Vacek) (often still referred to as *Docidoceras*) occurs

already in the Bradfordensis Zone of Portugal (JHC coll. 1987). It seems fully justified therefore to revive the subfamily Erycitinae Spath 1928 for at least the main stem of *Erycites*, to differentiate it from the Hammatoceratinae.

At the specific level, it is perhaps a little puzzling that the new material from Dorset should be so similar overall to its contemporaries in the Tethys, and yet so different in some respects, mainly size. Could this be a reflection merely of geographic subspeciation? Are the Dorset forms representatives of *Erycites* that have been exiled (banished, *exulati*) to the bioprovincial periphery of Durnovaria, as in the days of Imperial Rome? If so, they lived rather well.

Subfamily Hammatoceratinae Buckman, 1887  
Genus *Hammatoceras* Hyatt, 1867

*Hammatoceras lorteti* Dumortier, 1874  
(Pl.III, fig.1)

1874 *Ammonites lorteti* Dumortier, p.262, pl.54, figs 1,2 (holotype by monotypy).

**Material** - One complete phragmocone (RBC 529), and some fragments. Scissum Bed, Burton Bradstock.

**Description** - Within even a quite narrowly acceptable range of variability, the resemblance of the Dorset specimen to the holotype is astonishing: the photograph of the type is reproduced on pl.III, fig.2, and pl.IV, fig.2. The high keel, coiling and nodose ribbing are all typical of *Hammatoceras* s.s. The Dorset specimen has a diameter of 165 mm with about a tenth of a whorl of bodychamber. The complete adult must therefore have exceeded 200 mm in diameter. Its dimensions are: at 100 m:  $h = 0.29$ ,  $b = 0.21-0.25$ ,  $u = 0.47$ ; at 100 mm:  $h = 0.30$ ,  $b = 0.24-0.29$ ,  $u = 0.33$ . The holotype has a diameter of 151 mm, but there are no indications whether it retains any bodychamber. It differs from the Dorset specimen mainly in having 4-6 fewer ribs per whorl.

**Comparisons** - The name *lorteti* has been widely used but none of the specimens figured under the name is exactly like the type, in retaining the characteristic tubercles to such large diameters. The first to use the name was Vacek himself (1886, pl.16, figs 5-9) for material from San Vigilio. His specimens were renamed *Hammatoceras subinsigne vaceki* by Prinz (1904). But *Hammatoceras vaceki* was preoccupied by Brasil (1895), used for a species from the Murchisonae Zone of Normandy whose holotype (pl.2, figs 1,2) he compared with Vacek's *H. planinsigne* rather than with *H. lorteti*, which is not mentioned. A second attempt to rename Vacek's forms was made by Roman & Boyer (1923, p.32), unaware

of Prinz's attempt. They introduced *Hammatoceras vaceki* "nov. sp." for a species whose syntypes included Vacek's figured specimens and four specimens in their own collection from the Rhone valley. This name is thus doubly preoccupied. The homonymy was resolved by Elmi (1963, p.89) who renamed Roman & Boyer's species *Planammatoceras romani* "nom. mut." [nom. nov.] and took as type one of Roman & Boyer's specimens. Vacek's specimens are therefore at best paratypes of *H. romani* (Elmi, 1963) and are not very closely related to *H. vaceki* Brasil, 1895.

**Age** - The type of *H. lorteti* came also from the condensed iron-ore deposits of La Verpillière (Isère). The Dorset specimen serves therefore now firmly to establish the age of the species as (lower) Scissum Zone, Lineatum Subzone.

*Hammatoceras* cf. or aff. *procerinsigne* Vacek  
(Pl.V, fig.1)

cf. 1886 *Hammatoceras procerinsigne* Vacek, p.89 [33], pl.14, figs 11,12 (lectotype, here designated)

**Material** - One complete adult (RBC 531) and a fragment. Scissum Bed, Burton Bradstock.

**Description** - Maximum diameter 150 mm, septate to 95 mm, nearly 0.9 whorl bodychamber, peristome partly preserved. Dimensions: at 130 mm:  $h = 0.32$ ,  $b = 0.21$ ,  $u = 0.42$ ; at 90 mm:  $h = 0.33$ ,  $b = 0.27$ ,  $u = 0.44$ . Ribs: at 150 mm, 36; 100: 34; 60: 32; 40: 30; 25: 23; 15: 16. The characteristic features are relatively small size; the evolute coiling, especially on the inner whorls; the compressed whorl-section; and the persistence of tubercles into the middle whorls up to diameters around 60 mm. The keel on the phragmocone is floored and high, but not excessively so, very much as shown by Vacek. On the bodychamber it is only quite moderately prominent, leaving only a somewhat acutely fastigate carina on the internal mould.

**Comparisons and discussion** - Of all the forms illustrated by Vacek, his *H. procerinsigne* comes closest to the Dorset form in size, coiling and sculpture. The main difference lies in the density of the ribbing in the tuberculate stage, which also persists to relatively large diameters.

The question arises of generic assignment. The present form also has many of the features of what is today placed in a separate genus *Planammatoceras* (see below). The characteristics of its type species are the involute, compressed coiling on the inner whorls and the dense, rather fine ribbing with subdued primaries on the middle and outer whorls, a tuberculate stage, if present, being confined to the innermost



whorls. The outer whorls of the Dorset specimen could therefore be well placed in *Planammatoceras*, but the inner whorls not. Except for the much higher density of ribbing, their affinities appear to lie closer to *H. lorteti*, and we prefer to regard the present specimen as being more closely related to the group of the latter for the time being. Whether it might in fact be merely an extreme variant of the same species remains once again an open question that only more material could resolve.

Vacek's illustrations do give the impression that three distinct groups are represented at San Vigilio: (a) the group of *H. lorteti* (= *romani* Elmi) and *procerinsigne*, as discussed above; (b) the group of *H. planinsigne* and *tenuinsigne*, placed by common consent into *Planammatoceras*; and (c) the group of *H. subinsigne* (Oppel), today placed in *Bredya* (see below). That apparently both groups (a) and (b) are separately recognizable also in Dorset is shown in the next section. Group (a) has not so far been given a separate generic name. It could be accommodated under the names either of its probable ancestors or descendants. The only plausible name available among the latter could be *Parammatoceras* Buckman, 1925, as interpreted by Elmi (1963). His *P. boyeri* and *P. auerbachense* from the Murchisonae Zone seem to belong to the same group as *H. lorteti*. But the type of *Parammatoceras*, *P. obiectum*, from the upper Bradfordensis Zone, is rather different. We prefer therefore to retain the name from below, *Hammatoceras* itself.

#### Genus *Planammatoceras* Buckman, 1922

##### *Planammatoceras planinsigne* (Vacek, 1886) [M] (Pl.IV, fig.1)

- 1886 *Hammatoceras planinsigne* Vacek, p.89 [33], pl.13, figs 1 (lectotype), 2-6.  
 ? 1923 *Hammatoceras tenuinsigne* Vacek: Roman & Boyer, p.33, pl.7, fig 1.  
 ? 1963 *Planammatoceras planiforme* (Vacek): Elmi, p.82, pl.11, fig.1a,b.  
 1982 *Planammatoceras* (*P.*) *planinsigne* (Vacek): Westermann & Riccardi, p.19, text-fig.3 (lectotype refigured).

**Material** - One complete phragmocone (RBC 530), from the Scissum Bed of Burton.

**Description** - Maximum diameter 220 mm, wholly septate; estimated diameter of complete adult 350 mm. Dimensions at 210 mm:  $h = 0.35$ ,  $b = 0.18$ ,  $u = 0.38$ ; at 120 mm:  $h = 0.39$ ,  $b = 0.22$ ,  $u = 0.36$ . The test has been largely lost and the innermost whorls have been broken, so that all that can be seen of the ribbing is its impression on the internal mould. But it clearly consisted of very subdued primaries and dense, fine secondaries that persisted, even on the inner whorls

already at 45 mm diameter. The keel was high and sharp, as shown in all of Vacek's figures and in the photograph of the lectotype, and hollow and floored on the phragmocone. The Dorset specimen agrees with the lectotype in almost all details. The latter was also still wholly septate, at a diameter of 150 mm, so the species was a large one. The septal suture also has the typically high complexity, with long, multiply incised spidery lobes densely covering almost the whole of the whorl-side.

**Discussion** - The forms from the Scissum Zone differ only in detail from the type-species of the genus, *P. planiforme* (Buckman 1922, pl.356), which probably came from the Murchisonae Zone and Subzone. New finds range upwards into the lower Bradfordense Zone. The specimen figured under this name by Elmi, together with another referred to in the text, appears also to have come from the Murchisonae Subzone and could equally well be assigned either to *planiforme* or to *planinsigne*. It seems therefore that these forms of *Planammatoceras* ranged almost unchanged at least from lower Scissum to lower Bradfordense Zones, making the genus a well-defined independent phyletic entity. A similar range is cited in Spain (Linares et al. 1989).

##### *Planammatoceras tenellum* sp. nov. [m] (Pl.VI, fig.2a,h)

- 1886 *Hammatoceras tenerum* Vacek, p.90 [34], pl.12, fig.5.5a only  
 1887 *Hammatoceras* (?) *tenerum* Vacek: Haug, p.128, pl.5, fig.7a,b

**Material** - The holotype only (RBC 533), from Horn Park quarry, bed 3c, horizon Aa-7, Murchisonae Zone and Subzone (Callomon & Chandler 1990, p.90, fig.3).

**Description** - Maximum diameter 43 mm, complete phragmocone with the beginnings of the bodychamber; internal cast, no test preserved. Coiling evolute, compressed, with acutely carinate venter, the keel not floored and hollow. Dimensions: at 40 mm,  $h = 0.32$ ,  $b = 0.21$ ,  $u = 0.44$ . The ribbing is dense, subdued and relatively delicate (tenellate), the primaries bifurcating irregularly at the shallow umbilical edge or remaining simple with intercalatory secondaries; ribs about 26 per whorl on the outer whorl, 35 at diameter 25 mm. The septal sutures are well incised but relatively simple and well-spaced, with long ventral and lateral lobes ( $E > L$ ), only vestigial accessory lobes and the simplest of short umbilical lobes, barely retracted. The last two sutures are at best only slightly approximated but show a simplification indicating adult maturity. Assuming a former length of bodychamber of three quarters of a

whorl, the complete adult would have been about 65 mm in diameter. Size and suture therefore point strongly to a microconch, and the non-tuberculate, compressed, sharply keeled coiling strongly suggests the microconch of *Planammatoceras planiforme*.

**Comparisons** - The present specimen matches in almost all details one of the four syntypes of *Hammatoceras tenerum* from San Vigilio, the one shown in Vacek's pl.12, fig.5, as well as the topotype figured by Haug. The second syntype figured by Vacek (fig.4) is significantly different. The septal suture, shown at a diameter of 55 mm, has the same plan as that of the Dorset specimen but is much more incised, with strongly retracted umbilical lobe. There is no indication whether it is the last, and its complexity suggests not. The ribbing has also wholly faded. One cannot therefore exclude the possibility that the specimen is merely the nucleus of what was a much larger specimen, presumably then a macroconch. A lectotype has not so far been unambiguously designated. Geczy (1966, p.55) states *en passant* that "Au cours de sa morphogénèse le type perd complètement son ornementation...", suggesting Vacek's figure 4, and tentatively assigns his fig.5 to a new subspecies *szoerenyiae* whose type (Geczy, pl.10, fig.4) is however quite different. To avoid further confusion we stabilize Geczy's intention by now formally designating Vacek's fig.4 lectotype of *H. tenerum*, even though it leaves the interpretation of this species somewhat uncertain. It is then a logical step to introduce a new name for those specimens whose morphological interpretation as well as age are not in doubt.

The apparent rarity of the microconchs of both the Erycitinae and Hammatoceratinae more generally is something of a mystery. The exception is the genus *Bredya*, whose undoubted microconchs are common and well documented (see below).

#### Genus *Bredya* Buckman

[Type species *Bredya crassornata* Buckman, 1910; = *Amm. subinsignis* Oppel, 1856 (subj.)]

[= *Pseudammatoceras* Elmi, 1963, type species *Amm. subinsignis* Oppel, 1856]

#### *Bredya subinsignis* (Oppel) [M] and [m]

The species has been exhaustively described by Senior (1977), who designated a lectotype and discussed the numerous synonyms. The new collections from the Scissum Bed include several specimens, but they add little to what was known before and we cite the species here only to complete the list of Hammatoceratinae from the Scissum Bed. It seems there is a level 5-10 cm below the top of the bed at which the species forms a layer, for several

were found *in situ*.

Senior used the same name for the forms both of the Opalinum and Scissum Zones. The lectotype of *B. subinsignis* in the Oppel collection came from the "Torulosus-Schichten" of Swabia, lowest Opalinum Zone. The holotype of *B. crassornata* came from the Scissum Bed of Burton Bradstock. The microconch, with lappets, appears not to have been given a separate name in the past. The main areas of distribution seem to lie in the more temperate shelf-seas away from the Tethys - Europe and the southern Andes (Hillebrandt & Westermann 1985) - which may account for one of the generic characteristics, a relatively simple septal suture compared with those of the other Lower Aalenian Hammatoceratids.

Subfamily Haugiinae Buckman, 1905 (p.cxcviii)

Genus *Csernyeiceras* Geczy, 1966 (p.83)

[Type species *Hammatoceras verpillierense* Roman & Boyer, 1923]

#### *Csernyeiceras verpillierense* (Roman & Boyer, 1923)

(Pl. VI, fig.1; pl. VII, fig. 1a-c; pl. VIII, fig. 1a-c)

? 1886 *Oppelia subaspidoides* Vacek, partim, p.84 [28], pl.10, fig.7 only

1923 *Hammatoceras verpillierense* Roman & Boyer, p.34, pl.8, fig.1 (holotype by monotypy, reduced x 0.88)

1963 *Euapetoceras verpillierense* (Roman & Boyer): Elmi, p.73.

1966 *Hammatoceras* (*Csernyeiceras*) *verpillierense* (Roman & Boyer): Geczy, p.83, pl.22; pl.41, fig.2

**Material** - Two complete phragmocones (RBC 341, 534), an incomplete phragmocone showing inner whorls, and fragments; all from the Scissum Bed of Burton.

#### Dimensions

	Diameter, D/mm	<i>h</i>	<i>b</i>	<i>u</i>
RBC 341 (Pl. VI, fig.1)	max. 250;			
	at 240;	0.47	0.16	0.23
	180;	0.46	0.16	0.21
	125;	0.46	0.18	0.19
RBC 534 (Pl. VII, fig.1)	max. 240;			
	at 240;	0.42	0.15	0.26
	170;	0.42	0.16	0.25
	120;	0.43	0.18	0.25
RBC 535 (Pl. VIII, fig.1)	max. 120;			
	at 120;	0.48	0.17	0.23

**Description and comparisons** - The species is large. There is no evidence as to the length of the bodychamber, but assuming it to have been 0.5-0.75 whorls, the unusually high spiral half-whorl constant of around 1.5 would extrapolate to an adult maximum diameter of 370-450 mm. The keel is very high and

razor-sharp, hollow, with a broad flat floor giving the internal cast of the phragmocone a tabulate venter (see pl. VIII, fig. 16, lower edge). The ribbing fades in mid-height on the whorl-side, leaving the dense, straight primaries and secondaries accentuated at the umbilical and external margins respectively. Occasionally the secondaries divide again high on the whorl-side, giving short, irregular tertiaries. And perhaps most interestingly, the test shows distinct traces of spiral strigation (see pl. VIII, fig. 1a). The septal sutures are only partially discernible but agree in dense spidery complexity with that shown in Geczy's pl. 41, fig. 2, and appear to have similarly long, broad-based external lobes. They must be among the most complex of any ammonite. The long, thin ancillary lobelets of second, third and even fourth rank fill almost all the space available. The tips of principal lobes run well into the stems of the preceding lobes, and ancillary lobes totally fill all saddles. There is no part of the whorl-side not covered by sutures.

The agreement between the Dorset, French and Hungarian specimens is very close, indicating that the variability of the species is quite small. But except for the presence of a septocarinate keel, these forms have almost nothing in common with their contemporary Hammatoceratinae. Going back in time, they do, however, bear a striking resemblance to *Haugia* of the upper Middle Toarcian Variabilis Zone, such as the splendid *Haugia variabilis*, *jugosa*, *beani* and *phillipsi* from France illustrated by Gabilly (1976, pls. 11-15), or the *Haugia grandis* from the Cotswolds already figured by Buckman (1890, pl. 24, pl. 25 fig. 1). The size, coiling, sculpture, high hollow keel and characteristic complex suture are already all there (Buckman 1889, pl. A, figs 34, 48). There cannot be much doubt that the roots of *Csernyeiceras* lie in *Haugia*, even if the two are currently still separated by a considerable faunal gap. But the very discovery of *Csernyeiceras* itself has shown the danger of attaching any great weight to faunal gaps. Such gaps are negative evidence at best and vulnerable to quite modest increases in collections, as the present example has shown. To underline the independent phyletic position of *Csernyeiceras*, we have revived the subfamily Haugiinae. Going forward in time, it seems a plausible hypothesis to see in *Csernyeiceras* the roots of the hitherto cryptogenic family Strigoceratidae. This was already proposed and examined by Geczy (1966, p. 84), who drew particular attention to the close similarities in the characteristic basic plan of the septal sutures. The tall septocarinate venter of the majority of the Strigoceratidae has always been regarded as one of their leading characters. Precise details of the connection remain unclear, because two plausible routes of descent are

rather distinct: through *Praestrigitites praenuntius* (sic) Buckman (1924, pl. 466), the earliest, from the upper Bradfordensis Zone (probably horizon Aa-11), on the one hand; or through "*Oppelia*" *subaspidoides* Vacek (precise age unknown) or *Hebetoxyites clypeus* Buckman (1924, pl. 496A only) of the early Laeviuscula Zone, horizon Bj-8, on the other (see Geczy 1967, p. 222). But much later still, all the characters of *Csernyeiceras* strikingly reappear in *Strigoceras dorsocavatum* (Quenstedt) (1886, pl. 69, fig. 6) of the Lower Bathonian. The last known member of the Strigoceratidae is a *Phlycticeras* from the Upper Callovian. *Csernyeiceras* seems therefore partly to fill a gap in what is beginning to appear to have been a long lineage going back from the top of the Middle Jurassic to the ancestors of *Haugia* in the Lower Toarcian.

Age - The Dorset forms are firmly dated to the lower Scissum Zone. The type from Verpillière came from condensed Lower Aalenian and could also be from the Scissum Zone. The precise age of the Hungarian material is similarly uncertain. New records from the neighbourhood of Lyon in the Rhône valley are firmly assigned to the Comptum Subzone (Elmi & Rulleau 1993, p. 154). But a second specimen from the Jura cited by Elmi (1963, p. 77) seems to be securely dated as Murchisonae Zone and Subzone. The species has therefore been recorded over some range in the Lower Aalenian.

Family Hildoceratidae Hyatt, 1867  
Subfamily Tmetoceratinae Spath, 1936

Genus *Tmetoceras* Buckman, 1892

*Tmetoceras scissum* (Benecke, 1865)  
(Pl. V, figs 2, 3; pl. VI, fig. 3; pl. VIII, fig. 2, 3, 4)

- 1865 *Ammonites scissus* Benecke, p. 170, pl. 6, fig. 4 (lectotype des. Roman 1938; lost)
- 1874 *Ammonites regleyi* (Thollière MS) Dumortier, p. 119, pl. 31, figs 8, 9.
- 1883 *Cosmoceras hollandae* Buckman, p. 141, pl. 1, fig. 2a, b (lectotype), pl. 2, fig. 2a, b.
- 1886 *Simoceras scissum* (Benecke): Vacek, p. 103, pl. 16, figs 15-17.
- 1892 *Tmetoceras scissum* (Benecke): Buckman, p. 273, pl. 48, figs 1-10.
- 1904 *Parkinsonia* (*Tmetoceras*) *scissa* (Benecke): Prinz, p. 130, pl. 16, fig. 2, pl. 20, fig. 3 (both refigured by Geczy 1967).
- 1905 *Tmetoceras circulare* Buckman, p. clxx (type Buckman 1892, *vide sup.*, pl. 48, figs 1-3)
- 1933 *Tmetoceras scissum* (Benecke): Arkell, pl. 33, fig. 4, 4a.
- 1964 *Tmetoceras scissum* (Benecke): Westermann, p. 428, pl. 72, figs 1, 2.
- 1967 *Tmetoceras scissum* (Benecke): Geczy, p. 160, pl. 35, figs 3-7; pl. 64, figs 73, 74.
- 1990 *Tmetoceras scissum* (Benecke): Callomon & Chandler, pl. 1, fig. 1a, b.

*Discussion* - *Tmetoceras* is fairly common in the Scissum Bed and there is abundant material in the collections. Complete, well-preserved specimens are rather rarer, however, because of the hardness of the rock as ordinarily met with. We take this opportunity merely to illustrate some good new specimens that have become available.

The genus *Tmetoceras* and its relation to other groups have received lengthy discussion in the past, most recently by Geczy (1967). It was, and still is, something of a curiosity, for it stands well apart from any of its contemporaries both in morphology, distribution and evolution. There were the usual early attempts to distinguish separate species on the basis of morphological differences. But when material was abundant, as in the case of the collection from San Vigilio studied by Vacek, these species all appeared to intergrade. Stratigraphical information indicated that the genus did have some range but was insufficiently precise to see whether there were any systematically detectable changes with time. The general conclusions were that in Europe at least, the assemblages from any one horizon were monospecific; that the variability within one isochronous assemblage was large, larger than the differences between successive assemblages; that the genus was therefore of little value as biochronological guide-fossil, even though it had its "acme" in one zone, the Scissum Zone; and hence that one might as well use the one name, *T. scissum*, for the lot.

Further progress should now be possible on two counts. Firstly, as stratigraphically precisely dated assemblages are becoming available, the changes of morphology with time should be reassessed. The precise characterization of successive transients could be important in correlating the Aalenian of the East Pacific margins, from Alaska to the Andes, with the European standards. *Tmetoceras* is abundant, for instance, in Alaska (Westermann 1964). We make a start by indicating the "vertical" position of English material in the systematic nomenclature explicitly. One of the ways in which the *Rules of Nomenclature* allow this to be done is to treat successive transients as (chrono-)subspecies within the species-group. This would however mean the introduction of new (trivial) names that would forever be in possible conflict with existing names (see synonymy) of taxa of uncertain age, and vulnerable to differences of opinion between authors. Instead we prefer to use the existing Linnéan name *T. scissum* for all forms, as is the current practice, and to indicate the transient by an additional infra-subspecific label, that of its faunal horizon as listed previously (Callomon & Chandler 1990; and see Fig.1). The known range in Britain is therefore Aa-2 to Aa-13, lower Scissum to lower Concavum Zones.

Secondly, account must be taken of the fact that

*Tmetoceras* is dimorphic. The first example clearly to be demonstrated was in Alaska: *T. kirki* Westermann, 1964 [M] - *T. tenue* Westermann [m] of the Upper Aalenian. (For consistency, Westermann introduced a new subgeneric name *Tmetoites* for the microconch.) The macroconchs have a size-range of c.45-60 mm, the microconchs c.20-30 mm. The microconchs have clearly-developed lappets. Both dimorphs are isocostate, with minor modification of the ribbing near the end of the adult bodychamber, so that maturity can be easily recognized. Except for the lappets, the dimorphism is thus inconspicuous. No specimens with lappets have so far been figured in Europe, which is probably the reason why dimorphism has escaped notice. We have seen fragments of bodychambers with well-developed lappets in the Scissum Bed at Burton Bradstock, and it seems that the dimorphism in *T. scissum* takes the same form as in *T. kirki*.

The three specimens on Pl.VIII appear to be microconchs of transient Aa-2, Scissum Zone. They are essentially complete, as indicated by the umbilical seams, but unfortunately the actual peristomes have been lost. Fig.4 shows a specimen that raises several interesting questions. It has a terminal constriction and the last five septa are strongly approximated. There can be little doubt, therefore, that it is a complete adult. Yet the bodychamber occupies only a quarter of a whorl, compared with the half whorl that is more usual. This must be the shortest bodychamber in an ammonite yet found. Together with the simplicity of the septal suture, does this indicate a passive mode of life similar to that of some heteromorphs? Was the shell only partly external?

Pl.V, fig.2 is somewhat younger: Aa-6, Murchisonae Zone and Subzone. It appears to be a macroconch, with a broad, shallow terminal constriction and a simple sinuous peristome on the obverse side. It bears a strong resemblance to three of the specimens figured by Geczy (1967, pl.35, figs 3-5), all of which are clearly also macroconchs. Unfortunately, their precise age is unknown, but could be the same. This transient may therefore turn out to have a distinct and easily recognizable morphology. Pl.VI, fig.5c represents a second specimen from the lower Concavum Zone, Aa-12/13, the youngest form so far found in Britain. It is very similar to the one described by us previously (1990, pl.1, fig.1a,b) of the same age. Both are very evolute with broad ventral smooth band and, by analogy, probably microconchs.

## CONCLUSION

The Tethyan ammonites of the Aalenian occupy a key position in the evolutionary history of many important Middle Jurassic lineages whose roots, long

regarded as cryptogenic, are beginning to emerge in the Toarcian. The difficulties in past attempts to unravel these phyletic histories have been largely stratigraphic. In the Tethys, where these ammonites are dominant, the successions consist largely of highly incomplete or condensed pelagic limestones. Fossils are often sparse, poorly preserved or hard to extract. In extra-Tethyan Britain, in contrast, the stratigraphy is now well understood, fossils are abundant and

well-preserved, but Tethyan ammonites are relatively rare. Persistent collecting over the years has however yielded enough of them to contribute significantly to our understanding of their evolution. With the help of the new material described in this account, some venerable Tethyan species are now fully characterized for the first time - on the basis of collections from Dorset.

## ACKNOWLEDGMENTS

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## EXPLANATION OF THE PLATES

All figures natural size except where stated. Asterisks mark onset of bodychamber, where visible.

### Plate I

Figs 1,3. - *Erycites* cf. *fallifax* Arkell. 1a,b: adult, test largely preserved with umbilical seam indicating former extent of bodychamber of 0.75 whorl, estimated maximum diameter 96 mm (RBC 524, David Sole Coll.). 3a,b: nucleus (RBC 525). Both Scissum Bed, Freshwater Caravan Park, Burton Bradstock. Fig.2. - *Erycites fallifax* Arkell. Complete adult, internal cast, with part of terminal constriction and peristome preserved on the venter; somewhat distorted, the bodychamber displaced obliquely outwards (JHC 1240, leg. Luigi Ambrosio). Topotype, Scissum Bed, Capitello quarry, Cap San Vigilio. Fig.4. - *Erycites* aff. *exulatus* sp.nov. Complete phragmocone, umbilical seam indicating 0.75 whorl former bodychamber, estimated maximum diameter 150-160 mm (RBC 525). Scissum Bed, near top, Manor Farm, Burton Bradstock.

### Plate II

Figs 1,2. - *Erycites exulatus* sp.nov. 1a,b,c: paratype I, complete adult with test and peristome preserved. A *L. opalinum* is embedded in the matrix (RBC 527, David Sole coll.). 2a,b: holotype, nearly complete adult, test preserved, peristome partly preserved on the obverse side as indicated, transposed. Another *L. opalinum* embedded in the matrix. (RBC 528). - Both specimens from the Scissum Bed, at Freshwater Caravan Park and Manor Farm respectively.

### Plate III

Figs 1,2. - *Hammatoceras lorteti* (Dumortier). 1: complete phragmocone with test preserved (RBC 529, David Sole coll.). For side view, see pl.IV, fig.2. Scissum Bed, Freshwater Caravan Park, Burton Bradstock. 2: Dumortier's original figure of the holotype, side view (1874, pl.54, fig.1): for section, see pl.VI, fig.4. Condensed ironstones, La Verpillière (Isère), 28 km ESE of Lyon.

### Plate IV

Fig.1a,b. - *Planammatoceras planinsigne* (Vacek). Complete phragmocone, internal cast, x 0.76. Note remains of high, sharp keel at point of emergence of last whorl (RBC 530). Scissum Bed, Freshwater Caravan Park. Fig.2. - *Hammatoceras lorteti* (Dumortier). Ventral view of specimen on pl.III, fig.1.

### Plate V

Fig.1a,b. - *Hammatoceras* cf. or aff. *procerinsigne* Vacek. Complete adult with test preserved on inner whorls (RBC 531, David Sole coll.). Scissum Bed, Freshwater Caravan Park, Burton Bradstock. Fig.2a,b. - *Tmetoceras scissum* Benecke Aa-6 [M]. Complete adult with peristome (RBC 509). Quarry Hill, Chideock, bed 4 (Callomon & Chandler 1990, p.91, fig.2), Murchisonae Zone and Subzone, horizon of *Ludwigia patellaria* (Aa-6). Fig.3a,b. - *Tmetoceras scissum* Benecke Aa-2 [M?]. Complete adult with simple peristome on obverse side. (RBC 510). Locality and horizon as fig.1.

### Plate VI

Fig.1. - *Csernyeiceras verpillierense* (Roman & Boyer). Complete phragmocone, x 0.76, test partly preserved (RBC 341). Scissum Bed, Freshwater Caravan Park, Burton Bradstock. Fig.2a,b. - *Planammatoceras tenellum* sp.nov. [m]. Holotype, complete phragmocone, internal cast (RBC 533). Horn Park, bed 3c, Murchisonae Zone and Subzone, horizon Aa-7 (Callomon & Chandler 1990, p.92, fig.3). Fig.3a,b. - *Tmetoceras scissum* (Benecke) Aa-12/13 [m?]. Nearly complete adult, former extent deduced from umbilical seam, test preserved, no sutures visible (RBC 532). Horn Park, bed 5c, Concavum Zone and Subzone. Fig.4. - *Hammatoceras lorteti* (Dumortier). Dumortier's figure of the cross-section of the holotype: cf. pl.III and pl.IV, fig.2.

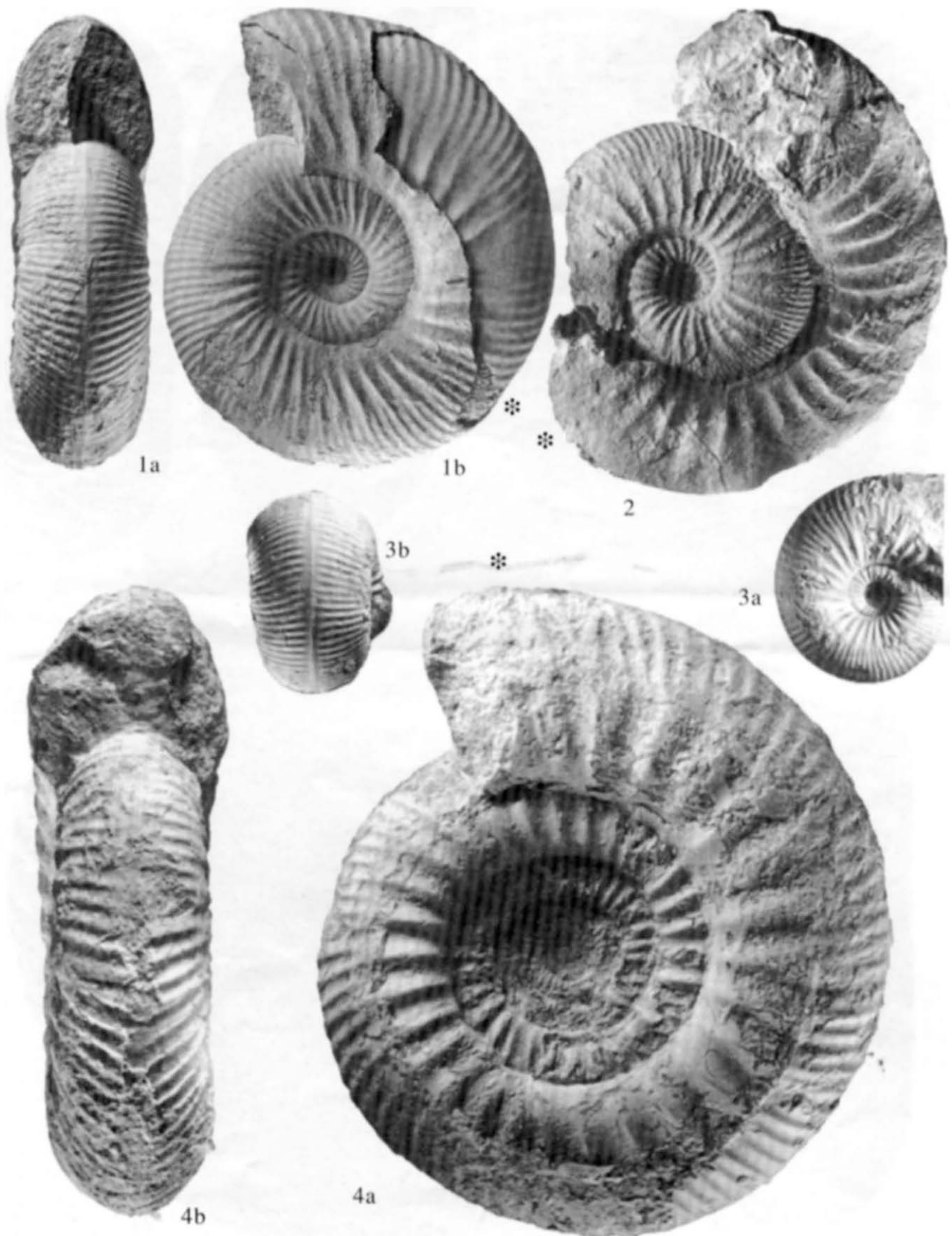
## Plate VII

Fig. 1a-c. - *Csernyeiceras verpillierense* (Roman & Boyer). Complete phragmocone, x 0.76, test partly preserved (RBC 534). Note the razor-sharp keel. Scissum Bed. Freshwater Caravan Park, Burton Bradstock.

## Plate VIII

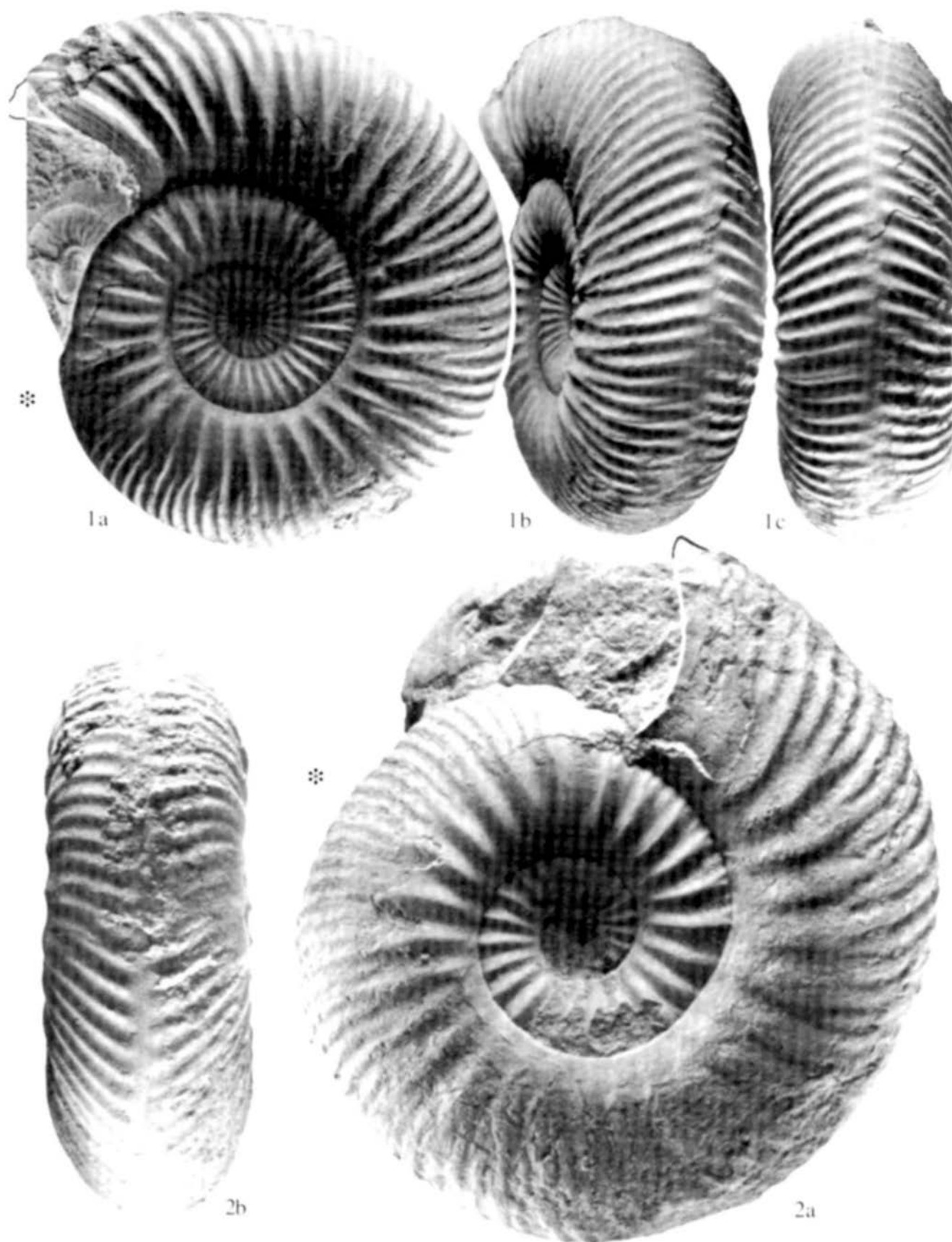
Fig. 1a-c. - *Csernyeiceras verpillierense* (Roman & Boyer). Septate inner whorls, test partly preserved (RBC 535, David Sole coll.). Note the hint of strigation on the whorl-side (1a), the high, sharp keel at the point of emergence of the exposed whorl, and the broad, tabulate venter on the internal cast made by the floor of the hollow keel (1b, 1c, bottom). The second ammonite in the matrix is a *Cylicoceras* (*Costiceras*) *subcostosum* (Buckman) [m]. Scissum Bed. Freshwater Caravan Park, Burton Bradstock. Figs 2-4. - *Tmetoceras scissum* (Benecke) Aa-2 [m]. Three complete adults. Note the very short bodychamber in 4a (RBC 512, David Sole coll.). (2a,b: RBC 514; 3a,b: RBC 517). Locality and horizon as fig.1.





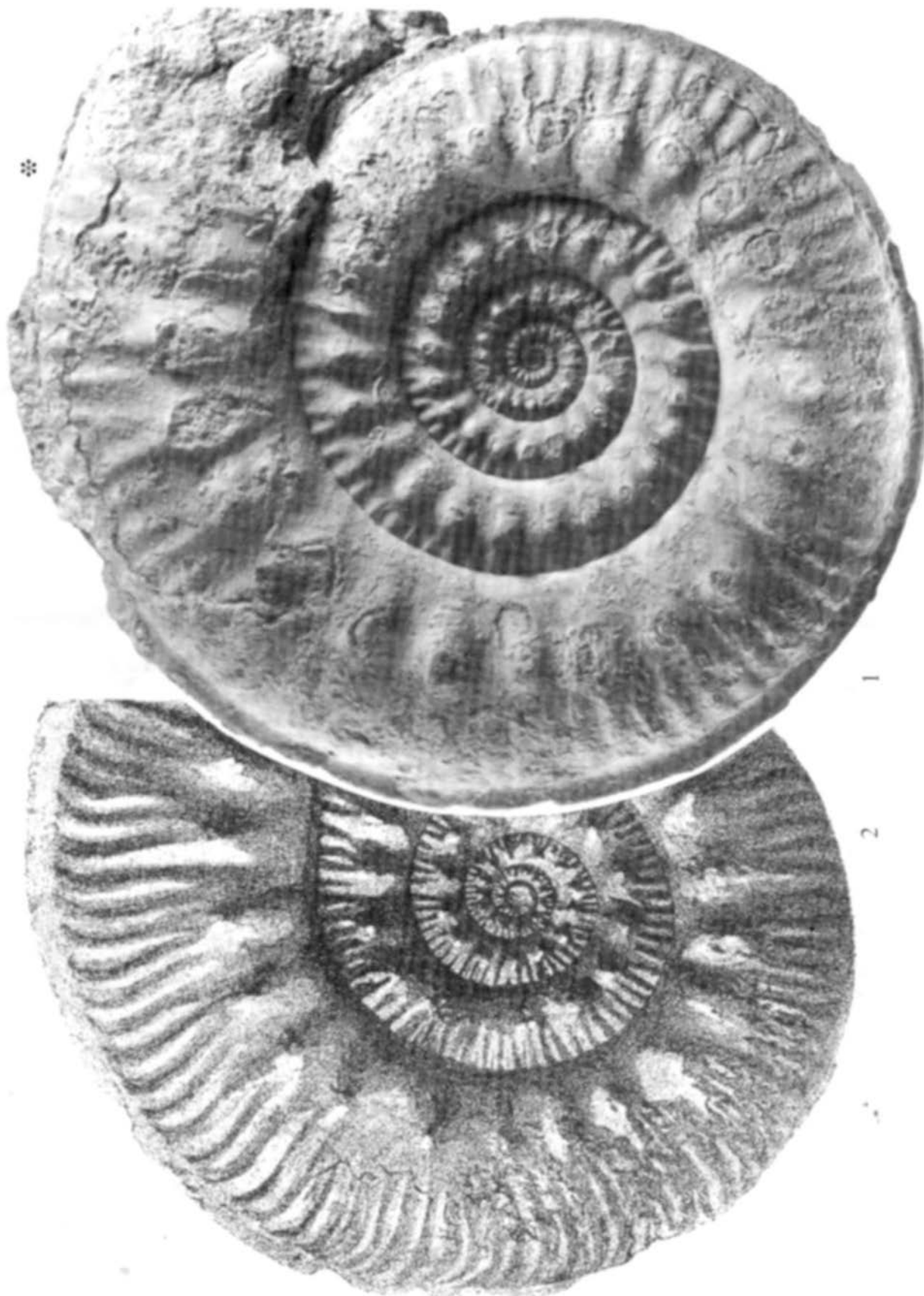
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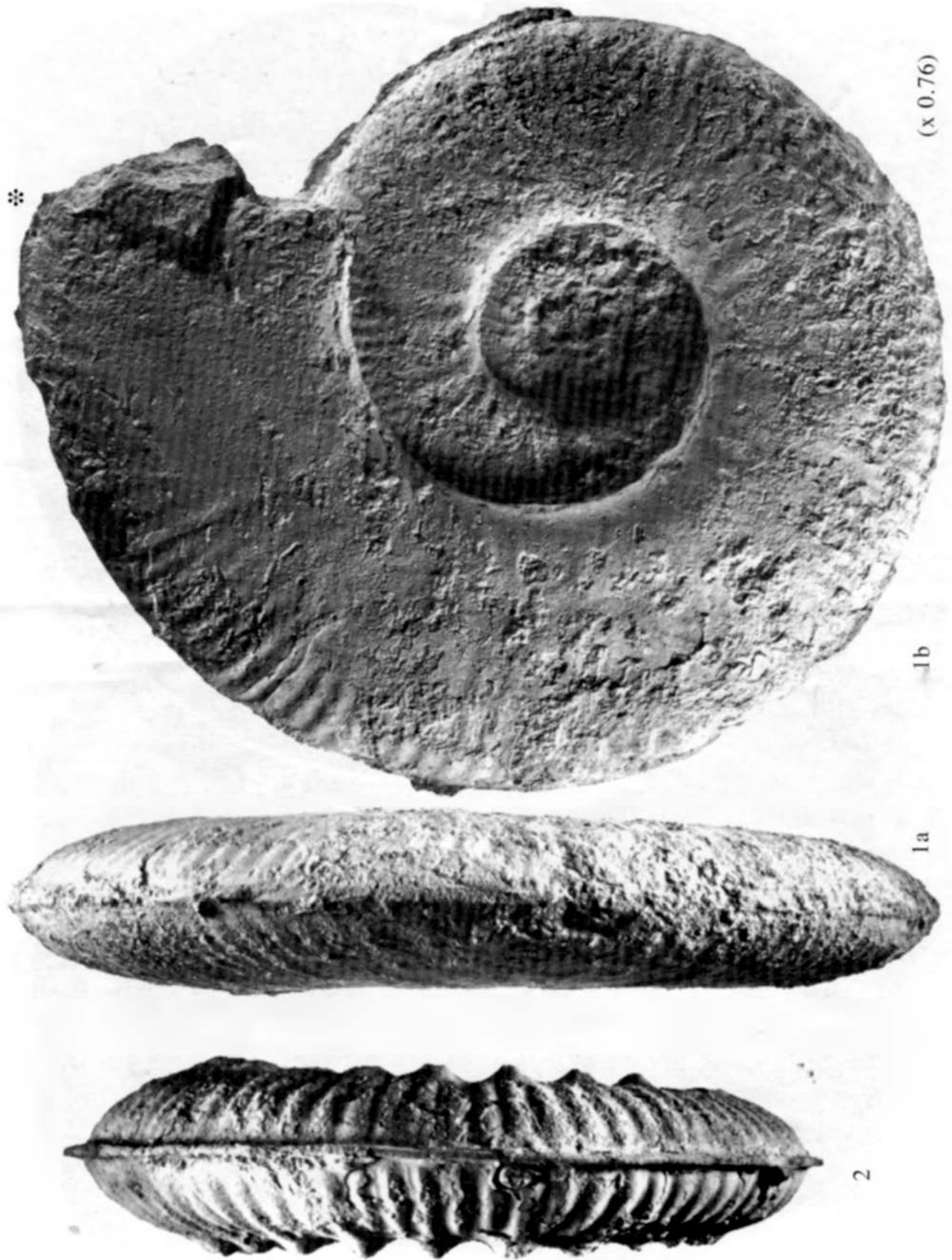
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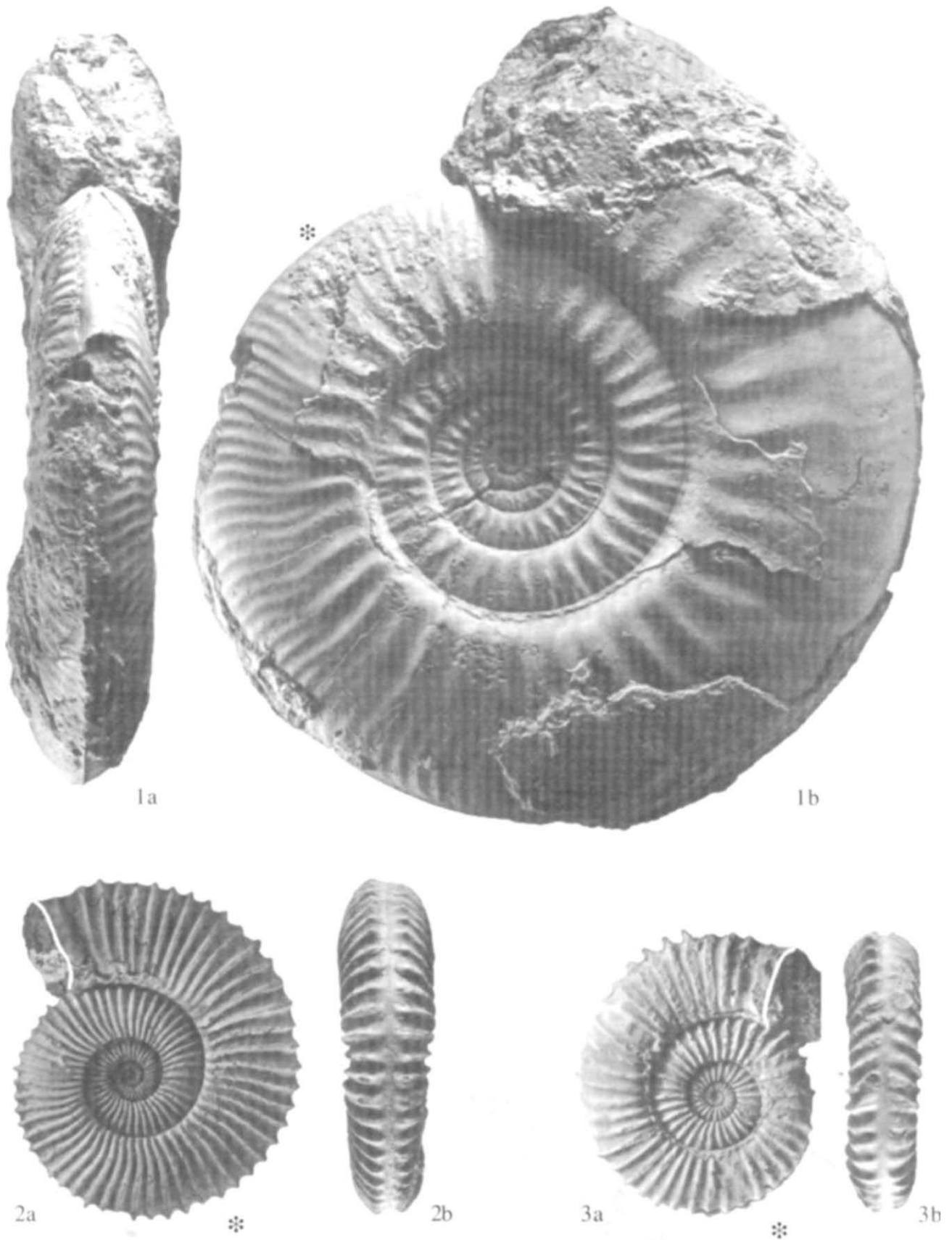
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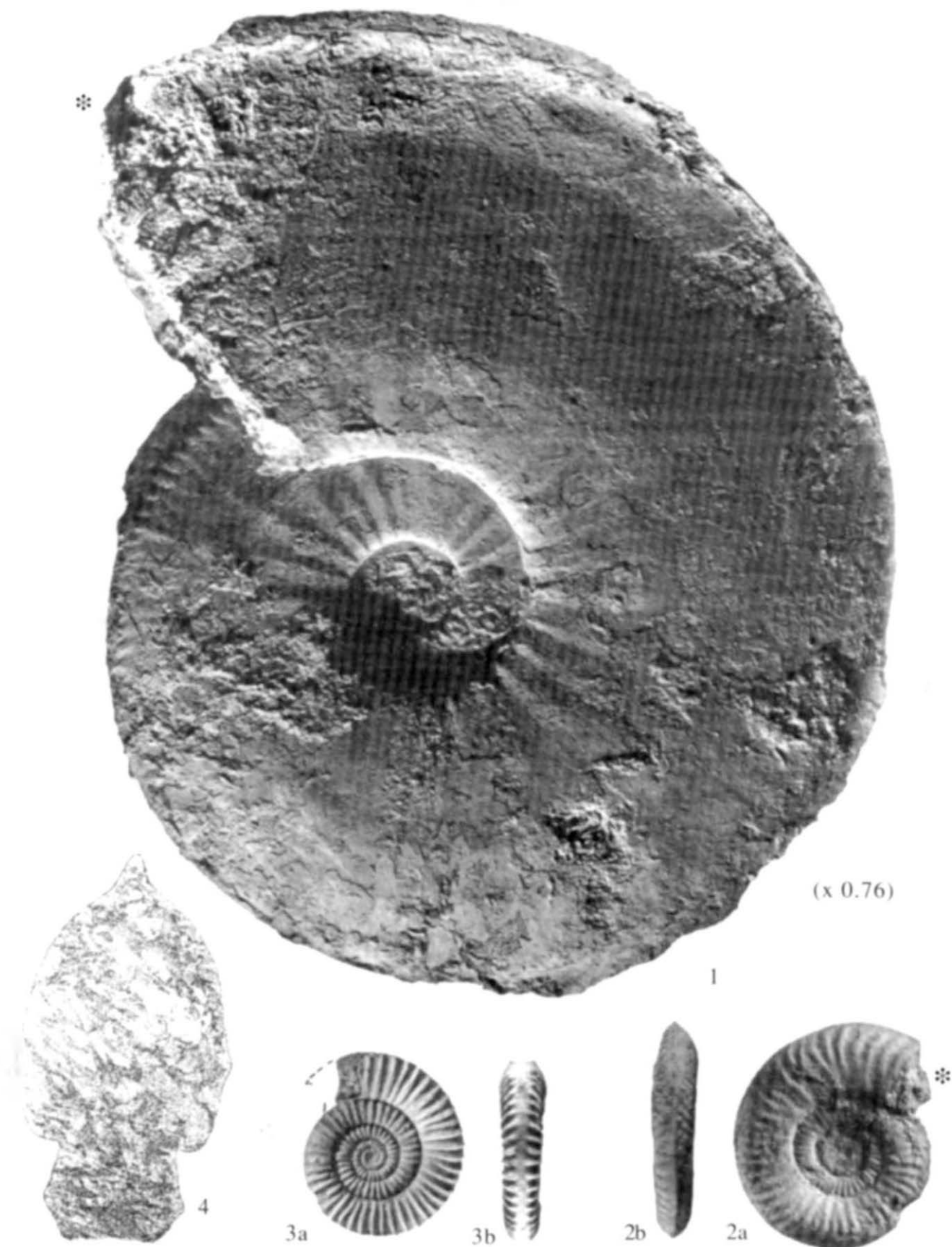
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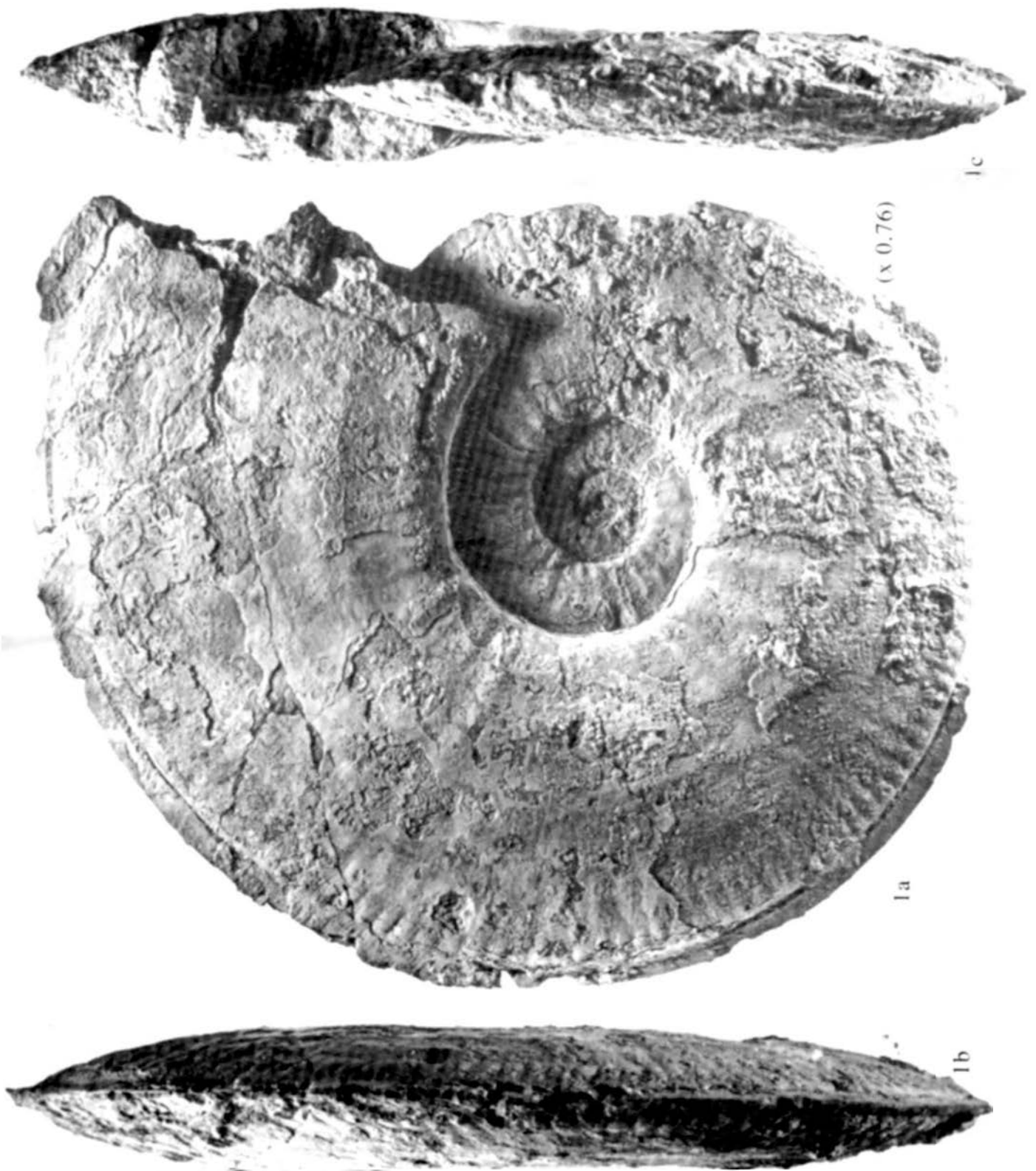


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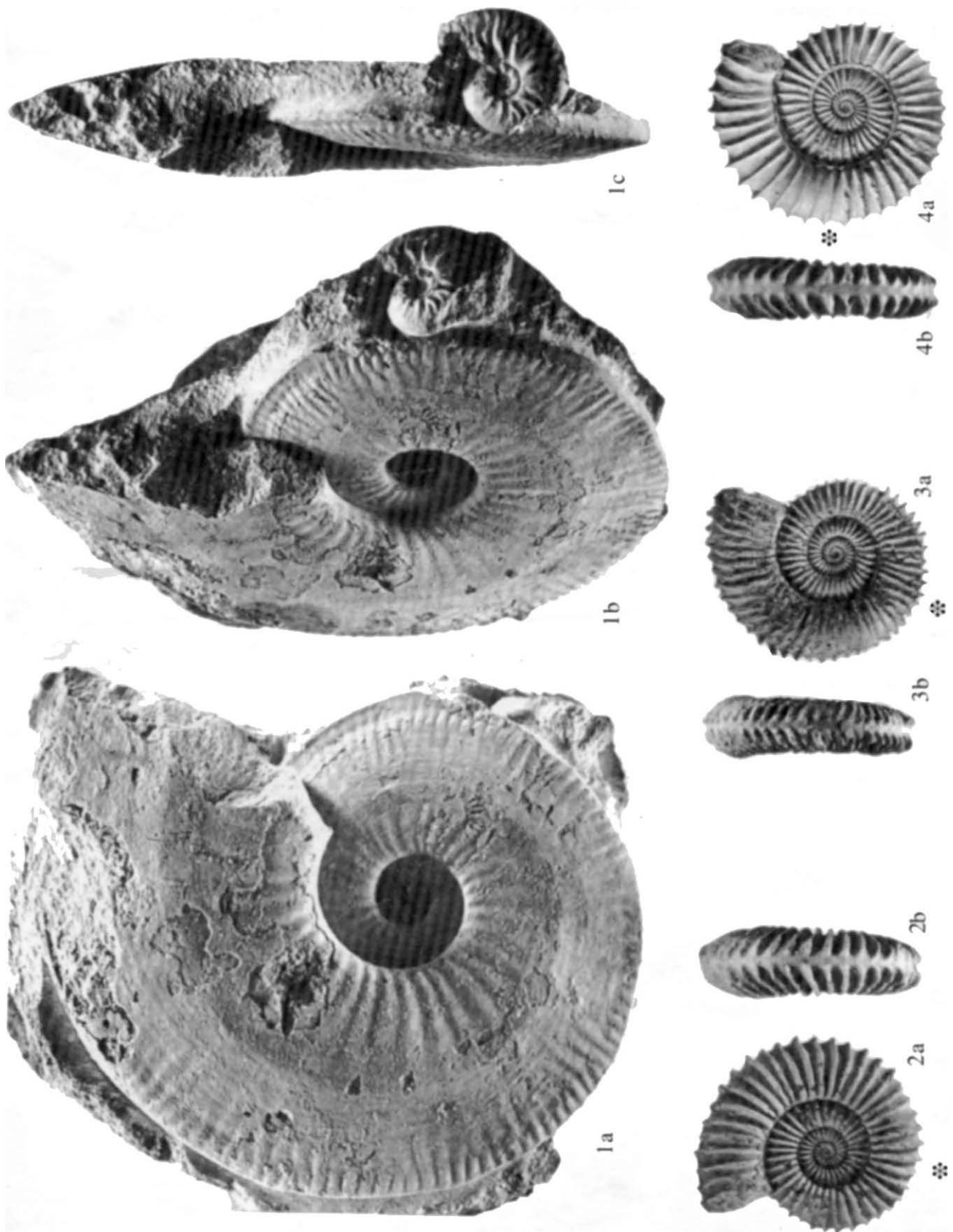


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