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CENOMANIAN CEPHALOPODS FROM THE GLAUCONITIC LIMESTONE SOUTHEAST OF ESFAHAN, IRAN

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The Glauconitic Limestone of the area southeast of Esfahan yields a rich Cenomanian cephalopod fauna of Boreal aspect, including species of *Anglonautilus, Stomohamites, Sciponoceras, Idiohamites, Ostlingoceras, Mariella, Hypoturrilites, Turrilites, Scaphites, Puzosia, Austiniceras, Hyphoplites, Schloenbachia, Mantelliceras, Sharpeiceras* and *Acompsoceras*, most of which represent new records for the area. The age of this fauna is unequivocally Lower Cenomanian, and can be correlated in detail at a distance of 5000 km with parts of the northwest European *Hypoturrilites carcitanensis* and *Mantelliceras saxbii* Zones. The material studied includes none of the Upper Albian, Middle and Upper Cenomanian elements recorded from the unit by previous workers. The fauna is numerically dominated by acanthoceratids, in marked contrast to the *Schloenbachia*-dominated faunas of northwestern Europe. This suggests the area lay in the southern parts of the Boreal Realm, where *Schloenbachia* is known to become progressively scarcer, as is supported by proximity to the Zagros line marking the juncture of Asian and Arabian plates.

Key words: Boreal Ammonites, Esfahan, Lower Cenomanian, Glauconitic Limestone.

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INTRODUCTION

Boreal middle Cretaceous ammonite faunas have long been known to be dominated numerically by members of the ammonite families Hoplitidae and Schloenbachiidae, most of which are wholly restricted to the area, which extends from eastern Greenland and Spitzbergen south to the Mediterranean coast of France and east to Transcaspasia and Turkmenistan.

The southern boundary of this province can be shown to be gradational in western Europe (Kennedy and Cobban 1976; Juignet and Kennedy 1977) with hoplitids and schloenbachiids becoming scarcer south-

wards, and mingling with mesogean elements in areas such as the Alpes-Maritimes and Provence. Rich hoplitid faunas are known from classic localities such as Escragnolles and Gourdon, whilst in the Cenomanian stray *Hyphoplites* are known from Cassis (on the Mediterranean coast) and it's predecessor, the late Albian *Discohoplites* is even recorded from North Africa. Traced eastwards, however, this mingling of faunas terminates abruptly, and Boreal and Mesogean fauns are sharply separated along a belt which corresponds to the line of closure of the Tethys. This tectonic juxtaposition of faunas is best illustrated in Iran and the adjacent areas of the USSR. Hoplitids are abundant in the Albian of Transcaspasia, the Kopet-Dag and between the southern shores of the Caspian and the Crimea, (Semenov 1899; Sinzov 1909, 1915; Glazunova 1953*a*—*b*; Owen 1973), and *Schloenbachia* has a similar distribution. In Iran, the suture between Asian and Arabian plates lies along the tectonic discontinuity marked by the Zagros (e.g. Takin 1972) and the distribution of Cretaceous faunas is thus of great importance in deciphering the history of the area.

In the south, entirely Tethyan faunas with *Knemiceras* and other pseudoceratites have long been known from the coastal Fars, Hamiran, Gachsaran and elsewhere (e.g. Spath 1923—1943, James and Wynd 1965). To the north, Spath (1923—1943:242) recorded the presence of *Schloenbachia* south of Esfahan some fifty years ago, but only recently has the range of Boreal elements present in the area been recognised. Seyed-Emami *et al.* (1971) recorded *Leymeriella*, *Hoplites dentatus* and a number of other more widely occurring Albian species, and also noted the presence of *Hyphoplites falcatus* and *Schloenbachia varians* amongst other ammonites from the Cenomanian southeast of Esfahan. Alvai-Naini (1972) subsequently noted and figured *Leymeriella* from the Djan region, whilst Stocklin *et al* (1965) and Stocklin and Nabavi (1971) record *Schloenbachia* from the Tabas area, and there is a record from the Sarvak Formation on the north-eastern flank of the Kabir Kuh Range near the Iraq/Iran border (James and Wynd 1965:2213).

The richest Cenomanian faunas, from southeast of Esfahan, come from the Tabas area, and there is a record from the Sarvak Formation a minor discontinuity on the Albian *Beaudanticeras* Shale (see schematic section in fig. 1). Published faunal lists from this unit (Seyed-Emami *et al.* 1971:17—25, Table 1) comprise the following: *S. (Scaphites) simplex*, *S. (S.) obliquus*, *S. (S.)* aff. *equalis*, *Turrilites costatus*, *T. scheuchzerianus*, *Ostlingoceras puzosianum*, *Mariella bergeri*, *Anisoceras perarmatum*, *Lechites moreti*, *Hamites (Stomohamites)* cf. *charpentieri*, *Pleurohoplites* cf. *renauxianus*, *Hyphoplites curvatus*, *H. pseudofalcatus*, *Schloenbachia varians*, *S. ventriosa*, *Mantelliceras mantelli*, *M. hyatti*, *Acanthoceras rhotomagense*, *Calycoceras naviculare*, *C. gentoni* and *Mortoniceras* sp.

This range of fauna includes Upper Albian, Lower, Middle and Upper

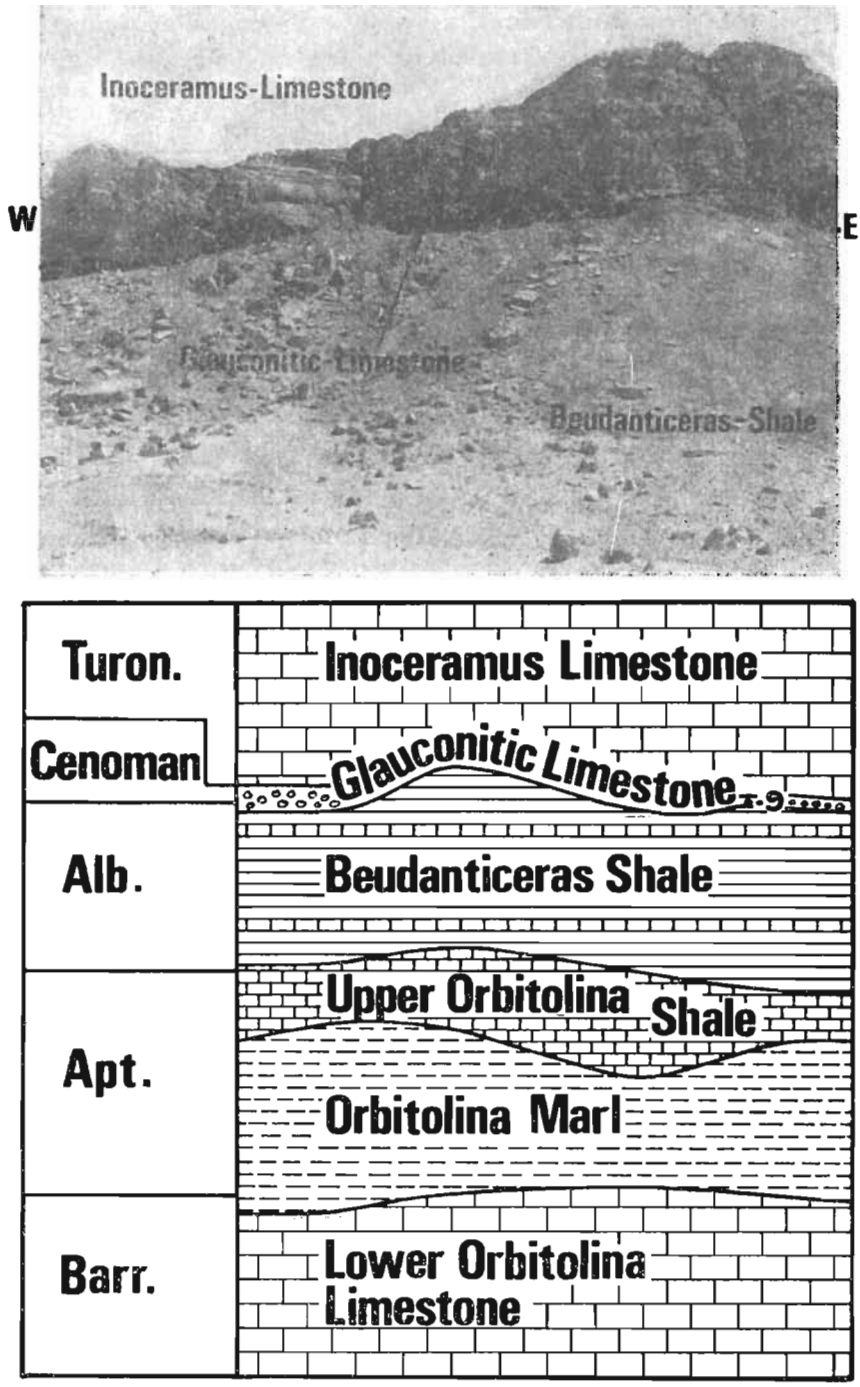

Fig. 1. Field photograph and schematic section of the mid-Cretaceous succession in the Kolah-Qazi Mountains.

Cenomanian marker species, and indicates the Glauconitic Limestone to be an incredibly condensed unit, as well as having a markedly Boreal faunal aspect, although unfortunately, there is no systematic account of the assemblage.

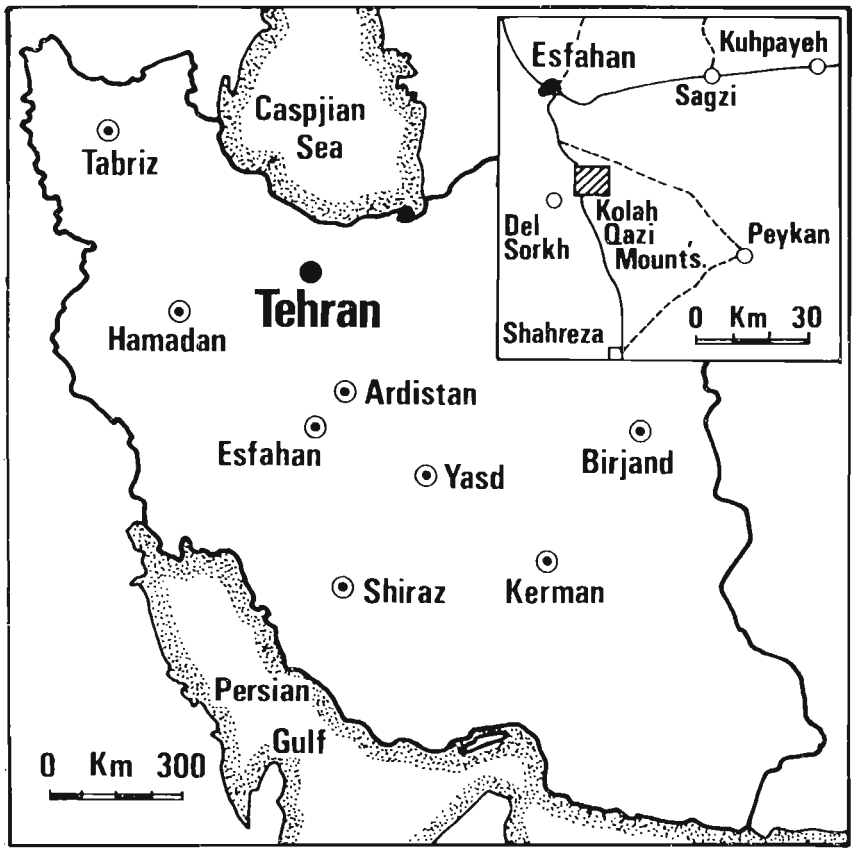

Fig. 2. Locality maps showing the provenance of the material studied.

In the present paper, we have tried to place the faunas of the Glauconitic Limestone on an objective basis by providing full illustration of the material available to us. The account is based upon over 100 specimens, collected from the Kolah-Qazi Mountains, south-east of Esfahan (fig. 2); our discussion of the age and affinities of the fauna is given in a concluding section, following the systematic work.

Location of specimens. — The following abbreviations are used to indicate the source of specimens mentioned in the text:

BMNH British Museum (Natural History), London.
GSM Geological Museum Collections, London.
OUM University Museum, Oxford.
GSI Geological Collections, Esfahan.

Dimensions. — Dimension of specimens are given in millimetres, in the following order: Diameter (D), Whorl breadth (Wb), Whorl height (Wh), and breadth of umbilicus (U). Figures in parentheses refer to dimensions as a percentage of the diameter. The term Rib Index applied to hetermomorphs is the number of ribs in a length equal to the whorl height measured at the mid point of the region of the rib count.

Suture terminology. — The suture terminology of Wedekind (1916; see Kullman and Wiedmann 1970) is followed in the present work:
Is = Internal lobe with septal lobe; U = Umbilical lobe; L = Lateral lobe; E = External lobe.

Techniques. — Specimens were photographed on Kodak Pan F 35 mm film, ASA rating 50, using a Pentax reflex camera with 1:2/55 super-Takumar lens. All specimens were coated with Ammonium Chloride sublimate prior to photography.

Preservation. — Many of the specimens described are distorted and abraded, whilst some retain recrystallised shell, or have a coating of calcareous or ferrigineous deposits. Sutures are in consequence poorly visible, and on many specimens are corroded even when exposed. Whorl sections and suture lines are therefore of limited value and are not illustrated.

SYSTEMATIC PALAEONTOLOGY

Phylum **Mollusca**
Class **Cephalopoda** Cuvier, 1797
Subclass **Nautiloidea** Agassiz, 1847
Order **Nautilida** Agassiz, 1847
Superfamily **Nautilaceae** de Blainville, 1825
Family **Cymatoceratidae** Spath, 1927

Genus *Anglonautilus* Spath, 1927

Type species: *Nautilus undulatus* J. Sowerby, 1813 by the original designation of Spath 1927: 21.

Discussion. — We follow Teichert *et al.* (1964: K453) in maintaining *Anglonautilus* as a distinct genus of Cymatoceratidae; Wiedmann (1960: 173 et. seq.) regarded it as a junior synonym of *Pseudocenoceras* Spath, 1927 which was in turn treated as a subgenus of *Angulithes* Montfort, 1808.

Occurrence. — The genus ranges from Hauterivian to Cenomanian and has been recorded from Europe (England to the Crimea); the specimen described below represents the first record from Iran.

Anglonautilus undulatus J. Sowerby, 1813
(pl. 1:1)

1813 *Nautilus undulatus* J. Sowerby: pl. 40, upper figure
1853 *Nautilus undulatus* J. Sowerby; Sharpe: 15, pl. 5, fig. 4 a—c.
1927 *Anglonautilus undulatus* (J. Sowerby); Spath: 21.
1951 *Anglonautilus undulatus* (J. Sowerby); Wright and Wrigt: 12.

1956 *Anglonautilus undulatus* (J. Sowerby); Kummel: 430, pl. 26:20.
1960 *Angulithes (Pseudocenoceras) undulatus* (J. Sowerby), 1813; Wiedmann: 176.
1964 *Angulithes undulatus* (J. Sowerby); Teichert *et al.*: K453, fig. 334, 3a—b.

Material. — One specimen, GSI 1.

Description. — The specimen is an almost wholly septate internal mould with a maximum diameter of 95 mm. The relative proportions are as follows:

	D	Wb	Wh	Wb:Wh	U
GSI 1	80.7	34.3 (62)	46.8 (58)	1.07	—
	54.3	50 (63)	?31.0(57)	1.1	—

Although quite badly damaged, the specimen shows involute coiling, with a small umbilicus (blocked by sediment) and a depressed subquadrate whorl section with the greatest breadth just outside the umbilical shoulder. The shoulder itself is rounded, the inner flanks swollen, outer flanks flattened and venter broadly rounded.

The specimen appears to have been smooth up to a diameter of ca. 50 mm. Beyond this ornament comprises broad, fold-like undulations on the mould, which strengthen with increasing diameter. These are weak on the flank, but strengthen and pass backwards across the ventrolateral shoulder to form a deep ventral sulcus. No details of growth lines or finer ornament are preserved.

The suture is gently flexed, with broad shallow lateral and external lobe. The siphuncle is dorsal, subcentral.

Discussion. — Depressed whorl section, siphuncle position and coarse ventral folds characterise *A. undulatus* very distinctively. *Pseudocenoceras largilliertianum* (d'Orbigny) (1840:86, pl. 18; Kummel 1956:385, pl. 10:3—4) and *Pseudocenoceras dorsoplicatis* Wiedmann (1960:176 = *Nautilus largilliertianus* Sharpe *non* d'Orbigny 1853:16, pl. 6:2 only) both develop the same type of fold, but are compressed with flattened sides and venter, a larger open umbilicus, more flexuous suture line and dorsal siphuncle.

Occurrence. — This species ranges from Aptian to Lower Cenomanian in both England and France; the present record represents the first occurrence in Iran.

Subclass **Ammonoidea** Zittel, 1884
Order **Lytoceratida** Hyatt, 1889
Suborder **Ancyloceratina** Wiedmann, 1966
Superfamily **Ancyloceratacea** Meek, 1876
Family **Hamitidae** Hyatt, 1900

Genus *Stomohamites* Breistroffer, 1940

Type species: *Hamites virgulatus* Brongniart, 1822 by orignal designation (Breistroffer 1940: 156).

Discussion. — Recent authors have treated *Stomohamites* as both an independent genus and as a subgenus of *Hamites*. *Hamites* sensu stricto ranges from the Lower Albian *Douvilleiceras mammilatum* Zone to the *Stoliczkaia dispar* Zone of the Upper Albian, whilst *Stomohamites* derives from *Hamites* and ranges from Upper Albian to Upper Cenomanian; Lower Turonian records of the genus are probably a result of some workers' reference of the *Sciponoceras gracile* zone to this stage.

In general, *Stomohamites* are more densely ribbed than *Hamites*, and have collared apertures, although there are also sutural differences, for in *Hamites* U_2 is small and not symmetrically bifid like the much larger L, whilst in *Stomohamites* L and U_2 are of similar size and bifid.

Occurrence. — *Stomohamites* first appears in the Upper Albian and ranges well into the Upper Cenomanian. The geographic distribution includes Europe, North Africa, Angola, Mozambique, Zululand, Madagascar, the United States (Texas, Oklahoma, Colorado) and northern Australia.

Stomohamites simplex (d'Orbigny, 1842)
(pl. 1: 5)

1842 *Hamites simplex* d'Orbigny: 550, pl. 134: 12—14.
1956 *Hamites simplex* d'Orbigny; Sornay: fiche 18.
1971 *Stomohamites simplex* (d'Orbigny); Kennedy: 6, pl. 1: 1—8.
1972 *Stomohamites* cf. *simplex* (d'Orbigny); Cobban and Scott: 44, pl. 13: 5—10, pl. 17: 3—4.
1977 *Stomohamites simplex* (d'Orbigny); Juignet and Kennedy: 51, pl. 1: 8, 9, 10 (with synonymy).

Types. — d'Orbigny based the species *simplex* on a series of specimens from the phosphatic fossil bed of the Craie de Rouen at Rouen (Seine Maritime), Sornay (1956) recognised eight of these syntypes and designated a lectotype.

Material. — One specimen GSI 2.

Description. — The specimen is an internal mould and consists of a wholly septate fragment of a curved early part and following straight shaft, the maximum whorl height being 8.2 mm. The whorl section is a compressed oval (whorl breadth to height ratio is 0.89), and the expansion rate low. Ornament consists of strong, straight, sharply rounded ribs; the rib index being 5—6. The ribs are strong on the flanks, recti- to faintly prorsiradiate on the shaft but rursiradiate on the hook. They pass straight across the venter without diminution, but are of much reduced strength on the dorsum, although they do not show obvious duplication.

Discussion. — Only relatively few other Cenomanian species of *Stomohamites* have been described. The best known of these is the Upper Albian to Lower Cenomanian *S. duplicatus* (Pictet and Campiche), a densely ribbed form with seven or eight ribs in a distance equal to the whorl height. This species shows a tendency for ribs to efface and become merely striae on the dorsum. Rather finely ribbed *Stomohamites* described by Collignon (1928, 1964) from the Cenomanian of Madagascar may be intermediate between *S. simplex* and the Lower Cenomanian *S. duplicatus*.

Occurrence. — D'Orbigny's types come from the Middle Cenomanian *T. costatus* Zone fauna of the Rouen Fossil Bed, on Mont Saint Catherine, Rouen (Seine Maritime), and the species occurs at the same horizon at many localities in Normandy and Sarthe.

Thomel (1965 and subsequent publications) records it from high in the Lower Cenomanian as well as the Middle Cenomanian of south-eastern France, whilst F. Amedro has shown us specimens from the Middle Cenomanian of the Boullonais. There are also records from Poland (Cieśliński 1959: 35, pl. 3: 7), W. Germany (Windmöller 1881), North Africa (Pervinquière 1907: 83; 1910: 17), Madagascar (? Collignon 1928: 55, pl. 7: 1—3; 1964: pl. 318: 1358; pl. 319: 1370—1372) and northern Australia (Wright 1963: 597—599, pl. 81: 1a—c). An interesting occurrence from a much higher horizon, the *Sciponiceras gracile* zone of Colorado, is recorded by Cobban and Scott (1972: 44, pl. 13: 5—10, pl. 17: 3—4). Their material is crushed, however, and can only be compared with *simplex*.

Family **Baculitidae** Meek, 1876

Genus *Sciponoceras* Hyatt, 1894

Type species: *Hamites baculoide* Mantell (1822: 123, pl. 23: 6, 7) by original designation (Hyatt 1894).

Discussion. — Extensive discussions and diagnoses of *Sciponoceras*, together with details of differences from *Lechites* (from which genus it evolved during late Albian time) and *Baculites* (of which it is the ancestor) are given by Matsumoto (1959), Matsumoto and Obata (1963), Kennedy (1971) and Cobban and Scott (1972).

Only four names have been applied to European Cenomanian species: *S. roto* Cieśliński from the Lower Cenomanian, *S. baculoide* (Mantell), a widely applied name although the type material comes from the Middle Cenomanian, and *S. gracile* (Shumard) which characterises the highest Cenomanian are well authenticated, whilst a fourth name, *S. subbaculoides* (Geinitz) has been used sporadically for fragmentary material, of Lower to Upper Cenomanian age (e.g. Marcinowski 1970, 1974).

Matsumoto, Wright and Kennedy have all discussed the difficulties of recognising the old European species which were all based on poorly localised fragments, but unpublished work by C. W. Wright and W. J. Kennedy suggests that several successive species can be recognised.

Dimorphism has not been described as such within the Baculitidae, but within *Sciponoceras*, it is well known that two distinctive types of aperture are present; the one with coarse ventral ribbing at large sizes, the other, with a delicately ribbed hood, occurs at small sizes (Wright, in Matsumoto 1959, Juignet and Kennedy 1977).

Occurrence. — Passage forms between *Lechites* and *Sciponoceras* occur in the *Stoliczkaia dispar* Zone faunas of the Anglo-Paris Basin, and the genus extends to the Upper Turonian. The geographic range is extensive (Matsumoto 1973: fig. 1) and includes Europe as far west as Transcaspasia, Iran (the present record) and south to the Mediterranean, North Africa, the Middle East, Angola, Zululand, Madagascar, Japan, northern Australia and New Zealand.

Sciponoceras cf. *roto* Cieśliński, 1959

compare: 1959 *Sciponoceras roto* Cieśliński: 39, 75, 89, fig. 14, pl. 4: 10a—c.
1963 *Sciponoceras roto* Cieśliński; Wright: 599.
1971 *Sciponoceras roto* Cieśliński; Kennedy: 10, pl. 3: 7.

Types. — Cieśliński based this species on nine syntype fragments. The original figures are too poor to determine which example best characterises the species, and it would be unwise to designate a lectotype without examining his originals.

Material. — One specimen, GSI 3.

Description. — The specimen is an internal mould of the adult aperture and part of the terminal body chamber with a total length of 22 mm. The whorl section is elliptical and depressed, with a whorl breadth to height ratio of 1.125. Only the ornament associated with the apertural modifications is present. The dorsum is smooth. Ribs arise low on the flank as mere striae, are markedly prorsiradiate and pass obliquely across the flanks, strengthening as they do so. At the ventrolateral shoulder, the ribs flex backwards, and become markedly convex, strengthen, and pass straight across the venter, where they are at their maximum strength. In profile, the ventral ribbing is markedly assymetric, scale-like, with a gently inclined back and steep front face.

Ribbing of this type extends almost to the aperture, with the last definite rib much weakened. Beyond this, the venter projects markedly forwards to form a distinctive cowl which is ornamented by faint striae and folds. A final distinct rib

marks the actual apertural margin, and there is a clear siphonal spout, flanked by convex areas (pl. 1: 4e), the remainder of the aperture, so far as is visible, forming a uniform oval.

Discussion. — Lack of phragmocone and early body chamber render determination of this specimen difficult. Because of its depressed whorl section it is compared to *S. roto*, a species in which the whorl section is circular on the phragmocone; it thus differs markedly from typically compressed species such as *S. baculoide* (Mantell), *S. gracile* (Shumard) and other well-known younger species.

This is the oldest *Sciponoceras* in which the aperture is known. It resembles some apertures of *S. baculoide* (e.g. the coarsely ornamented examples figured by Kennedy 1971: pl. 2: 3*a*—*b*; Juignet and Kennedy 1977: pl. 1: 3a—c, 4a—c, 6a—c), but does not appear to show as distinctive a pair of lateroventral projections on either side of the siphonal 'spout' (e.g. Juignet and Kennedy 1977: pl. 1: 3*b*, *d*) nor as deep a constriction below the aperture (*ibidem*: pl. 1: 3*c*). In these respects it also differs from the Middle Cenomanian *Sciponoceras* aperture figured by Crick (1896: 80, text-fig.) or the distinctly lappeted form of Noetling's figure (1885: pl. 8: 7, 7a). It is also quite different from the finely ribbed *Sciponoceras* apertures seen in one of Mantell's paralectotypes of *S. baculoide* (Kennedy 1971: pl. 2: 5a, lower specimen; Matsumoto and Obata 1963: pl. 2: 1—3).

By virtue of these differences, the present specimen forms a morphological passage form to the simple oblique apertured late Albian *Lechites* (e.g. Spath 1923—1943: text-fig. 667 d—e; pl. 72: 6) from which *Sciponoceras* arose.

Occurrence. — *Sciponoceras roto*, with which we compare our fragment occurs in the Lower Cenomanian of England and Poland.

Family **Anisoceratidae** Hyatt, 1900

Genus *Idiohamites* Spath, 1925

Type species: *Hamites tuberculatus* Sowerby (1818: 50, pl. 216: 5) by original designation (Spath 1925).

Discussion and *occurrence.* — *Idiohamites* is a predominantly Upper Albian genus. A few species have been recorded from the Lower Cenomanian of Western Europe, Madagascar and North Africa, where the genus is a scarce but persistent member of *Hypoturrilites carcitanensis* and low *Mantelliceras saxbii* assemblage Zone faunas. The present material represents the first recorded from Iran. Cobban and Scott (1972) have recorded the genus from the Middle Cenomanian Granenos Shale of Colorado, but their poor specimens (op. cit.: pl. 13: 1—4) may equally be *Anisoceras* which have lost flank tubercles — an extreme of the trend seen in some *Anisoceras* of the *plicatile* group. Dougherty and Powell (1963: 2062) have recorded the genus from the late Cenomanian of Coahuila, Mexico, but we doubt this occurrence at so high an horizon, whilst the Campanian *Idiohamites oronesis* Lewy (1969: 127, pl. 3: 10—11) and *I. circularis* Lewy (1969: 128, pl. 3: 9, fig. 3) are presumably either nostoceratid or diplomoceratid homoeomorphs. Turonian records of *Idiohamites* usually refer to *Allocrioceras* species.

Idiohamites alternatus vectensis Spath, 1939
(pl. 1: 12)

1939 *Idiohamites alternatus* var. *vectensis* Spath: 598.

1971 *Idiohamites alternatus vectensis* Spath; Kennedy: 18, pl. 4: 5, 7, 8, 10, 11, pl. 5: 1a—b, 2a—b, 3, 5, 8, 9 (with synonymy).

1977 *Idiohamites alternatus vectensis* Spath; Juignet and Kennedy: 57, pl. 3: 1a—b, 4 (with synonymy).

Lectotype: BMNH 36585a, from the Lower Cenomanian of Warminster, Wiltshire, designated by Kennedy (1971: 18).

Material. — One specimen GSI 4.

Description. — The specimen consists of a 56 mm. long fragment of an internal mould, most of which is body chamber. The whorl section is a compressed oval, with a whorl breadth to height ratio of 1.16. The ornament consists of sharply rounded distant, straight, essentially rectiradiate ribs; the rib index is 4. Ribs are virtually effaced on the dorsum and weaken somewhat on the venter, being at their strongest on the upper flank and ventrolateral shoulder. Nine complete ribs are preserved, but only two of these bear ventral tubercles. Other ribs simply flatten somewhat over the venter.

Discussion. — *Idiohamites alternatus* is a variable species; as discussed elsewhere (Juignet and Kennedy 1977), the variety *vectensis* with a rib index of 4 (to which our specimen is referred), rather than *alternatus* sensu stricto with a rib index of 6, is the commoner form. The incipient looping of ventral ribs, together with the development of a lateral tubercle seen in some individuals (Juignet and Kennedy *op. cit.*) are both features reminiscent of *Anisoceras*. Numbers of nontuberculate ribs between tuberculate ones is variable in English specimens, from one to five being present. *I. alternatus* is readily distinguished from other Cenomanian species; *I. ellipticus* Spath is a compressed, densely ribbed form in which most of the ribs in the restricted subspecies are tuberculate and markedly flexuous, whilst in the variety *radiatus* Spath, there are five straight ribs in a distance equal to the whorl height. *I. vohipalensis* Collignon (1964: 8, pl. 319: 1366, 1367) has a more circular cross section whilst all ribs bear ventral tubercles and are interrupted on the venter by a groove.

I. alternatus rigida Sornay (1955a: 10, pl. 1: 5, 9, 13) appears to be a synonym of *vectensis*.

Occurrence. — *Idiohamites alternatus alternatus* and var. *vectensis* are constant if scarce members of *Hypoturrilites carcitanensis* assemblage Zone faunas, and occur as a rarity in the suceeding *saxbii* Zone of southern England. They are also known from the *carcitanensis* assemblage Zone of Normandy (Rouen) and Sarthe (Marnes de Ballon). Records from Tunisia and Poland are also of Lower Cenomanian age; the present specimen is the first recorded from Iran.

Idiohamites ellipticus radiatus Spath, 1939
(pl. 3: 2b)

1910 *Hamites alternatus* Mantell, var.; Pervinquière: 181, pl. 1: 27 only.
1939 *Idiohamites ellipticus* var. *radiatus* Spath: 598.
1951 *Idiohamites ellipticus* var. *radiatus* Spath; Wright and Wright: 14.
1955a *Idiohamites ellipticus* var. *radiatus* Spath; Sornay: 11.
1971 *Idiohamites ellipticus radiatus* Spath; Kennedy: 16, pl. 4: 6, 13a—b, 17 (with synonymy).

Lectotype: The original of Pervinquière 1910: pl. 1: 27a—b only, from the Berrouaghia-Aumaule area of Algeria. Designated by Kennedy 1971: 16.

Material. — One specimen, GSI 42, embedded in the matrix infilling the body chamber of a *Schloenbachia*.

Description. — The specimen is only partially exposed, but comprises a strongly curved wholly septate fragment 20 mm long, with a maximum whorl height of

8.5 mm. The whorl section appears to have been markedly compressed, with a narrowly rounded dorsum, gently rounded flanks and flattened venter. Ornament consists of sharply rounded crowded ribs (the rib index is 6—7), straight to faintly flexed, effaced on the dorsum but well developed on flank and venter. Although damaged, many (perhaps a majority) of the ribs bear ventral clavi, and in some, these clavi are seen to be the bases of short septate spines.

Discussion. — This specimen, by its dense rater delicate ribbing and compressed whorl clearly belongs to *I. ellipticus*; the shape of ribs, and the presence of ventral tubercles on most of them suggest the variety *radiatus*, rather than the flexuously ribbed *I. ellipticus ellipticus*. The rib density is closer to that of the restricted from, however. The specimen also differs clearly from the superficially similar *Idiohamites collignoni* Spath, which has alternating tuberculate and non-tuberculate ribs.

Occurrence. — This is a rare form. In addition to the type from Algeria, which can be dated on more precisely than probably Lower Cenomanian, it has been recorded from the *Hypoturrilites carcitanensis* assemblage Zone of Hampshire and Dorset (England). *I. ellipticus ellipticus* has a wider distribution, for we have rare specimens recorded from the *carcitanensis* assemblage Zone of Souance (Eure et Loire) (Juignet and Kennedy 1977: 57), and there is also a record from the Lower Cenomanian of Poland (Cieśliński 1959: 36, pl. 4: 3a—b). In England, *I. ellipticus ellipticus* also occurs as a great rarity in the *Mantelliceras saxbii* assemblage Zone (Kennedy 1971: 16). The present specimen represents the first record of this species from Iran.

Family **Turrilitidae** Meek, 1876

Genus *Ostlingoceras* Hyatt, 1900

Type species: *Turrilites puzosianus* d'Orbigny: 1842 pl. 143: 1, 2 by the original designation of Hyatt 1900.

Discussion. — Probable relationships between *Ostlingoceras* and other genera are disputed (Wright 1957: L221; Dubourdieu 1953: 42; Spath 1923—43: 523; Kennedy 1971: 25). In addition to the restricted subgenus, Breistroffer (1953: 1350) proposed the subgenus *Parostlingoceras* (type species *Turrilites moutonianus* d'Orbigny, 1842) for those species in which ribbings is irregular and tuberculation weak.

Occurrence. — *Ostlingoceras* ranges from the Middle Albian to Lower Cenomanian and has been reported from Europe east to Iran, North Africa, Madagascar, North America and Japan.

Subgenus *Ostlingoceras (Ostlingoceras)* Hyatt, 1900

Ostlingoceras (Ostlingoceras) rorayensis (Collignon, 1964)
(pl. 1: 2)

1964 *Turrilites rorayensis* Collignon: 49, pl. 330: 1479.
1975 *Ostlingoceras (Ostlingoceras) rorayensis* (Collignon); Förster: 186, pl. 6: 7—8; fig. 5.

Holotype: The specimen figured by Collignon; 1964: pl. 330: 1479, from the Lower Cenomanian of Lake Horay, Madagascar.

Material. — One specimen GSI 9.

Description. — The specimen consists of an internal mould of three succesive whorls, partially embedded in matrix. Most of the specimen appears to be body

chamber; the maximum whorl height is 18 mm. Coiling is sinistral, with an apical angle of 20°. The lower whorl sides are flattened, the upper rounded, with sharply rounded upper and lower angles. Ornament consists of an estimated 23 ribs per whorl. These arise at the upper whorl suture, are broad, low and rounded, slightly curved and prorsiradiate. They may extend to the lower whorl angle, but are all markedly weakened or even effaced completely across a spiral depression low on the flanks. Below this, is a row of strong blunt, transversely elongate tubercles, exposed low on the outer whorl face, and equal in number to the ribs. A second row of less elongate, blunt tubercles lies in the lower whorl suture, accommodated in distinct crenulations on the upper face of the succeeding whorl. There is some indication that the tubercles of this lowermost row have resulted from the fusion of a pair of smaller tubercles on the early whorls, but our material is too poor at the smallest diameter preserved to fully confirm or dismiss this view.

Discussion. — Reference of this specimen to *Ostlingoceras rorayensis* is based on comparison with large collections from the Lower Cenomanian of Zululand. These show Collignon's species to be highly variable, especially in terms of the ratio of ribs to tubercles, and the sporadic development of a tubercle at mid flank, just above the spiral depression. Flat whorl sides (rather than inflated) readily separate *O. (O.) rorayensis* from species such as *Ostlingoceras (Ostlingoceras) bechii* (Sharpe) (1857: 66, pl. 26: 13a—b), *O. (O.) brandi* Young (1958: 287, pl. 40: 4, 5, 7), *O. (O.) conlini* Clark (1965: 37, pl. 8: 4; pl. 9: 2, 6) and *O. (O.) davisiense* Young (1958: 289, pl. 39: 29, 34). Of flat-sided species, *O. (O.) sublaevigatum* Wiedmann and Dieni (1968: 79, pl. 15: 4) has virtually smooth flanks. *O. (O.) puzosianum* (d'Orbigny) (1842: 587, pl. 143: 1—2) has 30 straight ribs per whorl and lacks the spiral zone of weakened ribbing low on the outer whorl face. *O. (O.) puzosiforme* Spath (1926b: 432, = *Turrilites puzosianus* d'Orbigny var. in Sharpe 1857, pl. 27: 11) is closely related. In the holotype, ribbing is more oblique, flexuous and delicate than in our specimen, and there is a row of delicate transversely elongated tubercles just below mid-flank.

Occurrence. — This species is common in the Lower Cenomanian of Zululand and Mozambique; The holotype is from Madagascar. The present specimen is the first recorded from Iran.

Genus *Hypoturrilites* Dubourdieu, 1953

(= *Hypoturrilites* Shimizu, 1935 (*nom. nud.*), Spath, 1923—43 (*nom. nud.*); *Turrilites* Wright and Wright, 1951 (*pars.*), *Eohypoturrilites* Scholz, 1973).

Type species: *Turrilites gravesianus* d'Orbigny, 1842: 596, pl. 44: 3—5, by the original designation of Dubourdieu 1953.

Discussion. — Shimizu (1935: 195) proposed the genus *Hypoturrilites* with *Turrilites komatoi* Yabe, 1904 as type species, without, however, providing a diagnosis. The name was validated by Dubourdieu (1953: 55) with *Turrilites gravesianus* as type species.

The ratio of tubercles in the first row to those of the other rows is variable. Generally there are two to three times as many tubercles in the lower than in the first row. In *H. mantelli* (Sharpe, 1857) there are only about five more tubercles in the lower rows than in the first. *H. combense* Renz, 1963 differs from all other species of *Hypoturrilites* in that the number of tubercles in the third and fourth rows differs from that of the second row, which in turn again differs from that of the first row. Ribs may or may not be developed in the genus, and this feature is of uncertain systematic significance.

Hypoturrilites is easily distinguished from other turrilitid genera by the larger and fewer tubercles in the upper row. In 1965, Clark (p. 51, pl. 19: 1—3) described

what he believed to be the earliest representative of this genus, from the Upper Albian Paw Shale of Texas. One of us (WJK) recently restudied the unique holotype, preserved in the Texas Memorial Museum, Austin, and concluded that the specimen was a pathological *Mariella*, confirming previous suspicions (Juignet and Kennedy 1977: 58).

Scholz (1973) erected the subgenus *Hypoturrilites (Eohypoturrilites)* with *Turrilites mantelli* Sharpe (1857: 63, pl. 25: 4, 8a—b) as the type species for early members of the group which are transitional to *Mariella*. As Scholz notes, *H. mantelli* differs from *H. gravesianus* and *H. tuberculatus* in several respects, notably the slight difference in number of tubercles in upper and lower rows (as indicated above) and that the tubercles in the upper row are somewhat elongate. Scholz further describes a subspecies *H. (E.) mantelli submantelli* for Upper Albian specimens in which the tubercles of the upper row are elongate, but tubercles of all rows are similar in number.

In our view, there is no support for retention of Scholz' subgenus for the following reasons:

1. His subspecies *submantelli* has an equal number of tubercles in all rows, and is a *Mariella*.
2. Many of the specimens referred to *submantelli* in his synonymy are of Lower Cenomanian age, and do not precede other *Hypoturrilites* species, rather co-occurring with them.
3. On examining specimens described and identified by Scholz, we conclude that the Albian material is all referrable to *Mariella*. Specimens from the Lower Cenomanian of Lamnay, Sarthe, in the Paris museums identified by Scholz as either *Mariella* or *Eohypoturrilites* and referred to as Vraconnian (!) are all contemporaries, and have been referred to one or other subgenus on the basis of the minutest differences in number and form of tubercles.

In our experience, *Hypoturrilites mantelli* can be readily distinguished from contemporary *Mariella*, and to place it in a separate primitive subgenus of *Hypoturrilites* cannot be supported because it has not, in our view, been shown to be older than other species of the genus.

Occurrence. — *Hypoturrilites* is a predominantly Lower Cenomanian genus, which occurs rarely in the Middle and Lower Upper Cenomanian. Albian records are unacceptable, as we have shown above.

The geographic distribution of the genus is wide, including records from many parts of Europe, North Africa, the Middle East, Madagascar, Zululand, southern India, Japan, northern Australia, New Zealand, the United States and Mexico. The present specimens are the first reported occurrence in Iran.

Hypoturrilites gravesianus gravesianus (d'Orbigny, 1842)

(pl. 1: 8)

1814 *Turrilites tuberculatus* J. Sowerby: 169, pl. 74 (non Bosc).
1822 *Turrilites tuberculatus* Mantell: pl. 24: 6 (non Bosc).
1842 *Turrilites gravesianus* d'Orbigny: 596, pl. 144: 3—5.
1960 *Hypoturrilites gravesianus* (d'Orbigny); Chiriac: 460, pl. 3: 30—32.
1971 *Hypoturrilites gravesianus* (d'Orbigny); Kennedy: 21, pl. 6: 11 (*pars*), 12, pl. 10: 4, 5 (with full synonymy).
1974 *Hypoturrilites gravesianus* (d'Orbigny, 1840); Marcinowski: 168, pl. 32: 8a—b, 10.
1974 *Hypoturrilites* aff. *gravesianus* (d'Orbigny 1840); Marcinowski: 168, pl. 32: 9a—b.

?1975 *Hypoturrilites* cf. *gravesianus* (d'Orbigny 1840); Förster: 188, pl. 7: 2.
1977 *Hypoturrilites gravesianus* (d'Orbigny); Juignet and Kennedy: 58, pl. 3: 8 (with synonymy).

Lectotype: d'Orbigny's original specimen (1842: pl. 144: 3—5) from the Cenomanian of Oise, France, by the subsequent designation of Kennedy 1971.

Material. — We have two specimens GSI 5 and 6.

Description. — Both specimens are wholly septate internal moulds; the more complete comprises four successive whorls with a maximum whorl height of 20 mm, the other is one complete whorl of an individual of 16 mm whorl height. The whorl section is markedly depressed and swollen; ornament consists of four rows of tubercles, those of the upper row are large, massive and number 12 per whorl, those in the lower rows are clavate and number 26—30 per whorl. The upper whorl suture is notched to accommodate the lower row, and the upper and lower whorl surfaces are ornamented by a corresponding number of strong radial ribs.

The suture includes a large assymetric E/L.

Discussion. — This well-known species is readily separated from *H. tuberculatus* (Bosc) by its fewer, and larger tubercles in the upper row (10—12 vs. 20) and by the suture line. In *H. gravesianus* the E/L (first lateral) saddle is asymmetric, whereas that of *H. tuberculatus* is symmetrical.

Of other species with similar ornament, there are several based on minute pyritic fragments, and these cannot be usefully compared with our specimens (e.g. *H. schneegansi* Dubourdieu 1953: 63, pl. 4: 34—41), whilst the type material of species such as *Hypoturrilites laevis* Wiedmann (1962: 191, pl. 11: 6, fig. 49) is too poor for positive comment, but may be within the limits of *H. gravesianus*, as may Marcinowski's fragment (1974: 168, pl. 32: 9a—b). The specimen from Mozambique described by Förster (1975: 188, pl. 7: 2) shows what appears to be ribbing on the upper, outer whorl face, which suggests either that it is closer to Collignon's (1964: 13, pl. 320: 1387, 1388) ribbed subspecies *H. gravesianus betaitraensis* or some other ribbed and tuberculate form like *H. nodiferus* (Crick) (1907: 177, pl. 11: 5a—b).

Occurrence. — The species is widespread in the Lower Cenomanian of western Europe (France, Italy, W. Germany, Switzerland), Poland and Yugoslavia, north Africa, Madagascar and Zululand. There are records from higher parts of the Cenomanian in both northern Australia (Wright 1963) and England (Kennedy 1970).

Hypoturrilites carcitanensis (Matheron, 1842)
(pl. 1: 7, 11)

1842 *Turrilites carcitanensis* Matheron: 267, pl. 12: 4.
1850 *Turrilites alpinus* d'Orbigny: 148.
1955b *Turrilites alpinus* d'Orbigny; Sornay, Sornay: fiche 2.
1960 *Hypoturrilites carcitanensis* (Matheron); Chiriac: 459, pl. 3: 29.
1964 *Hypoturrilites carcitanensis* (Matheron); Collignon: 12, pl. 320: 1382—1385.
1971 *Hypoturrilites carcitanensis* (Matheron); Kennedy: 23, pl. 6: 1, 2, 4—10 (with synonymy).
non 1975 *Hypoturrilites carcitanensis* (Matheron); Förster: 187, pl. 7: 1.
1977 *Hypoturrilites carcitanensis* (Matheron); Juignet and Kennedy: 50, pl. 3: 7, 13, 14, 15 (with synonymy).

Holotype: Matheron's original specimen (1842: pl. 12: 4) refigured by Fabre (1940: pl. 5: 7), from the Banc des Lombards, Cassis, Bouches du Rhone, by monotypy. The specimen has subsequently disappeared (G. Thomel, personal communication 1971).

Material. — Two specimens, GSI 7—8.

Description. — Our materials consists of a large, partially septate fragment of three successive whorls and a juvenile of just over two whorls. The coiling is sinistral, with a low apical angle (13—14°). The flanks are flattened, the whorl suture little impressed, and ornament subdued. In the smaller individual (GSI 8), ornament consists of an upper row of eleven small tubercles just above mid flank and two rows of smaller tubercles, approximately 25 in number per whorl. The upper of these rows lies at the lower whorl suture and the tubercles are somewhat elongate, whilst the third row is concealed below the suture. The base of the whorl bears weak ribs. The larger specimen has sixteen tubercles per whorl in the upper row, and twenty-four in the lower two rows, which have begun to coalesce on a bituberculate swelling. In addition, there are short ribs on the upper, outer whorl face, linking the upper suture to the upper row of tubercles in pairs with occasional intercalated ribs between tubercles.

Discussion. — *Hypoturrilites carcitanensis* is a distinctive species, and large collections studied from the lower part of the Lower Cenomanian of both Normandy and southern England (Kennedy 1971, Juignet and Kennedy 1977) suggest that there is continuous gradation from those individuals with strong rounded tubercles in the upper row — *Hypoturrilites morrisii* (Sharpe) (1857: 65, pl. 26: 4—8), to those in which the tubercles are small and pointed as in Matheron's type and our smaller specimen. In some individuals there may be a spiral ridge linking the upper row of tubercles, whilst the arrangement of the lower rows of tubercles is highly variable. These observations lead to the conclusion that *morrisii* is a synonym of *carcitanensis*, and that *H. oberlini* Dubourdieu (1953: 39, pl. 4: 27—30), *Turrilites carcitanensis antsiramensis* Breistroffer (in Fabre 1940: 242, = *T. morrisii* var. *carcitanensis* Collignon 1928—1929: 59, pl. 6: 6), the ribbed *Hypoturrilites morrisiformis* Collignon (1964: 53. pl. 331: 1490) and *H. dubourdieui* Collignon (1964: 53, pl. 331: 1491) are all within the range of variation of *carcitanensis*.

It must be admitted, however, that the European material is from phosphatic basement beds, and that *oberlini*, *morrisiformis*, and *dubourdieui* might merit subspecific separation if they were demonstrated to occur at different levels in expanded sequences. This has still not been fully possible, and we continue to maintain a conservative position.

Occurrence. — *H. carcitanensis* is widespread and frequent in the lowest third of the lower Cenomanian all over southern England and northern France, being the index of the lowest Cenomanian *carcitanensis* assemblage Zone of the area. It is also recorded from the Lower Cenomanian of the south-eastern Paris Basin (Hoffstetter 1936) Sarthe and Provence (Thomel 1955 etc.), W. Germany, Yugoslavia, North Africa, Madagascar, Zululand, Japan, and possibly southern India. The present individuals are the first record of the species from Iran.

Genus *Mariella* Nowak, 1916

(= *Paraturrilites* Breistroffer, 1953; *Hemiturrilites Breistroffer*, 1953; *Paraturrilites* (*Bergericeras*) Wiedmann, 1962).

Type species: *Turrilites bergeri* Brongniart, 1822 by the original designation of Nowak 1916.

Discussion. — Nowak originally separated *Mariella* from *Turrilites* because the latter, as represented by its type species, *Turrilites costatus* Lamarck, 1801 showed a subtrifid lateral lobe (L), whereas the corresponding lobe in *Mariella*, as represented by the type species *Turrilites bergeri* Brongniart, 1822 was bifid.

Spath (1923—43: 510) investigated these differences, and came to the conclusion (as have subsequent workers) that it was difficult to decide when a bifid lobe became

subtrifid, and that certain factors such as ornamentation and direction of coiling affected the detail of the suture line to such an extent that generic separation based solely on such differences was impractical. He accordingly based the generic separation on ornamentation; the main characteristic of *Mariella* being "the equal number and more or less equal size of tubercles of all four or more equidistant rows and their arrangement along more or less oblique ribs" (Spath 1923—43: 510). Obviously there are species which diverge from this and show differentiation of ribbing and tubercles, and these have been treated in varying ways; forms such as *M. essensis* (Geinitz) and *M. cenomanensis* (Schlüter) in which the tubercles of the upper row enlarge or elongate being placed in *Turrilites* by some authors, and indeed they are in some respects morphologically intermediate, if not evolutionary links between the two genera.

Nomenclatorial problems surround the use of *Mariella*, and the name applied to these ammonites varies widely. Breistroffer in 1947 considered *Mariella* to be invalidated as a homonym of *Mariaella* Gray, 1833 (Gastropoda). He proposed the genus *Paraturrilites*, with *Turrilites gresslyi* Pictet and Campiche, 1861 as type species to accommodate these multituberculate turrilitids. As Wright (1957: L222) notes, and as reiterated elsewhere (Kennedy 1971: 27, Juignet and Kennedy 1977) this is an error, as article 56a of the Code states: "Even if the difference between two genus-group names is due to only one letter, these names are not to be considered homonyms". Scholz (1973: 121) claimed that article 58 (1) of the Code contradicts this, and indeed it indicates that names which differ by the combination ae, oe, or e, are considered as "variable spellings". Scholz failed to take the elementary precaution of noting that this article applies only to names in the species group; *Mariella* and *Mariaella* are genus group names, and article 38 does not apply to them.

Occurrence. — *Mariella* has an essentially worldwide distribution in the Upper Albian and Lower Cenomanian.

Subgenus *Mariella (Mariella)* Nowak, 1916
Mariella (Mariella) dorsetensis (Spath, 1926)
(pl. 1: 9)

1857 *Turrilites bergeri* Brongniart; Sharpe: 65, pl. 26: 11 only.
1926b *Paraturrilites dorsetensis* Spath: 429.
1937 *Mariella dorsetensis (Spath)* Spath: 513.
1951 *Paraturrilites dorsetensis* (Spath); Wright and Wright: 16.
1963 *Mariella (Mariella) dorsetensis* (Spath); Renz: 1095, pl. 1: 3.
1964 *Paraturrilites dorsetensis* (Spath); Collignon: 51, pl. 331:1482, 1483.
1977 *Mariella (Mariella) dorsetensis* (Spath); Juignent and Kennedy: 62, pl. 3: 9, pl. 27: 6a—b.

Holotype: BMNH C3834, figured by Sharpe 1867: pl. 26: 11 only, by original designation (Spath 1926b: 429) from the Lower Cenomanian of Chardstock in Devon.

Material: One specimen only, GSI 12.

Description. — The specimen consists of two and a half whorls of a partially septate internal mould with a maximum whorl height of 16 mm. Coiling is sinistral, with an apical angle of 16°. The whorl section is rounded, with a smooth, gently sloping upper outer whorl face, rounded intertubercular region and gently rounded base. The whorl suture is deeply indented.

The upper part of the outer whorl face is quite smooth. Below are four rows of tubercles, three of which are exposed, the fourth being concealed in the crenulate whorl suture. There are nineteen tubercles in the uppermost row, and these are the largest, with a rounded termination and a slight extension towards the upper whorl suture. This row is situated on the upper third of the flank. The second row are

situated on the middle third, and slightly smaller, rounded, and offset from the first row. The third row are separated by an equal distance as are the first and second rows, but are smaller and tend towards the clavate. They lie just above the lower whorl suture, and on the last half whorl, terminate suddenly, being replaced by a narrow sharp spiral ridge where the specimen has suffered minor injury in life. The fourth row are very close to the third, and are markedly clavate. From them arise well-marked radial ribs which extend across the lower whorl surface and are accommodated in corresponding grooves on the succeeding whorl.

Discussion. — Spath separated *M. (M.) dorsetensis* from *M. (M.) lewesiensis* (Spath) by stating that *dorsetensis* lacks an uppermost row of tubercles. In fact, both possess four rows, and the main difference between the two species is that the type of *lewesiensis* has a broad flat upper, outer whorl face and coarse tubercles. So great is the size difference between the type specimens of the two species that we suspect they may simply be juvenile and adult of a single species.

Occurrence. — Lower Cenomanian of England, France, Switzerland, Zululand and Madagascar. The present specimen represents the first record from Iran.

Mariella (Mariella) species undetermined
(pl. 1: 6)

Material. — One specimen GSI 11.

Description. — The specimen is distorted, consisting of three partially septate whorls retaining traces of shell.

Coiling is sinistral, with an apical angle of approximately 10°. The whorl section is rectangular with abruptly rounded corners. Ornament consists of four rows of closely spaced tubercles, the tubercles being equal in number, twenty-four to twenty-five per whorl.

The upper, flat whorl face is ornamented by low radial ribs corresponding to the tubercles in the upper row. These lie at the angle between upper and outer whorl face and are the largest, rounded, with slight spiral elongation. They are separated by a sharply demarcated smooth spiral band from the offset and slightly smaller tubercles of the second row, which show slight oblique elongation. A further smooth, somewhat deeper spiral zone separates this row from the third, again offset and obliquely elongated, but of like size to the tubercles in the third row. The tubercles of the fourth row, again offset slightly, lie in the whorl suture, and are close to the third row, but smaller and produced into clearly demarcated ribs, which extend across the lower whorl surface.

Discussion. — The arrangement and number of tubercles, together with the rectangular whorl section represent a combination of features which we have been unable to match in described *Mariella* species. Similar fragments occur in the Lower Cenomanian of southern England (C. W. Wright, J. M. Hancock Collections), and appear to represent an undescribed form, left in open nomenclature at this time pending collection of better material.

Occurrence. — Lower Cenomanian, *Hypoturrilites carcitanensis* and low *Mantelliceras saxbii* Zones of southern England and Iran.

Mariella (Mariella) aff. *harchaensis* (Dubourdieu, 1953)
(pl. 1: 3)

compare: 1953 *Turrilites harchaensis* Dubourdieu: 53, pl. 4: 14—21.

Material. — One specimen only, GSI 10.

Description. — The specimen consists of three and a half whorls of an individual

retaining much of the shell. Coiling is sinistral, with a low apical angle (10—12°), the shell having a distinctive slender character. The whorl suture is markedly impressed, and the whorl section polygonal. The upper, outer whorl face is flattened and inclined. The outer whorl face is flattened between tubercles, but appear distinctly concave in profile across the line of the tubercles. Upper and lower angles are abruptly rounded. Ornament consists of three rows of tubercles per whorl. There are seventeen tubercles in the upper row; these are blunt, flat-topped, and lie at the angulation between the upper and outer parts of the exposed whorl face. From these tubercles, a subdued rib extends to the upper whorl suture, and sweeps obliquely forwards across the spiral depression on the outer whorl face to meet with similar transversely elongate tubercles just above the whorl suture. There are slightly more tubercles (19—20) in this second row. Below, ribs extend to a third close-set row of tubercles concealed in the whorl suture and housed in notches on the top of the succeeding whorl. On the lower whorl face there are strong rounded radial ribs corresponding to this lower row of tubercles.

Discussion. — There are three turrilitids which show an approach to the distinctive whorl section and tuberculation of the specimen before us; all, unfortunately, are based on minute pyritic individuals from North Africa, so that comparisons are difficult. *'Turrilites' pervinquierei* Diener (1925: 84, = Pervinquière 1907: 98, pl. 4: 13, 14; see also Dubourdieu 1953: 56, pl. 4: 22—27) is known only from individuals with maximum whorl heights of 6 mm; there are 18—21 tubercles per whorl, as in our specimen, but the spiral depression between the first and second rows of tubercles is less pronounced, and a fourth row of tiny tubercles is present.

In *'Turrilites' harchaensis* Dubourdieu (1953: 53, pl. 4: 14—21), the largest individual of which has a whorl height of 5 mm, there are 24—27 tubercles per whorl, and again four rows are present. In *'Turrilites' asselensis* Dubourdieu (1953: 58, pl. 4: 46—48), the disposition of tubercles is closest to that of our specimen, as is the whorl section. The tiny syntypes lack ribs on the outer whorl face, however, have 24—27 tubercles per whorl, and develop a fourth row close to the third and linked to it by a rib.

Because of differences in ornament and the presence of only three rows of tubercles in our specimen (although the third could possibly be derived from the fusion of two closely spaced rows of small tubercles) we would refer to it as *Mariella* (*Mariella*) aff. *harchaensis*, which species it most closely resembles.

Occurrence. — The types of *'T'. harchaensis* are from the Lower Cenomanian of Oued el Harcha, Algeria.

Genus *Turrilites* Lamarck, 1801
(= *Euturrilites* Breistroffer, 1953)

Type species: *Turrilites costatus* Lamarck, 1801 by original designation.

Turrilites specites undetermined
(pl. 1: 10)

Material. — One specimen only, GSI 13.

Description. — The specimen is an internal mould of three whorls of body chamber, with a maximum whorl height of 16 mm. Coiling is sinistral with an apical angle of 14°. Only two rows of twelve tubercles per whorl are visible on the exposed whorl face. The tubercles in the upper row are the larger, and are distinctly conical, whilst those in the lower row are smaller and show slight spiral elongation. At the smallest size visible, there is a suggestion of a tiny, weak clavate tubercle

concealed beneath the whorl suture; otherwise both upper and lower whorl faces are smooth.

Close to the aperture, feeble ribs extend across the base of the whorl, and these bear a weak, third row of tubercles.

Discussion. — This remarkable specimen stands apart from the majority of turrilitids known to us by virtue of the few tubercles per whorl and the presence of only two exposed rows. That the tubercles in all rows are equal in number precludes reference to *Hypoturrilites*, whilst we know of no *Mariella* with such ornament. Amongst *Turrilites*, ornament of this type, and in particular smooth lower and upper whorl surfaces below the whorl suture is seen in several species. There are thus similarities to *Turrilites scheuchzerianus* Bosc (Kennedy and Juignet 1977: 66, pl. 4: 4, pl. 27: 7, with synonymy), especially juveniles at the *'desnoyensi'* stage. Here, the whorls are higher, flatter, and ornament consists of interrupted ribs, 15 to 24 per whorl. In *T. costatus* Lamarck (Juignet and Kennedy *op. cit.*: 63, pl. 3: 15, 18, 19, with synonymy) ornament consists of long ribs and two rows of tubercles below, 19—25 per whorl. In the closely related *T. acutus* Passy (Juignet and Kennedy *op. cit.*: 65, pl. 3: 6, pl. 4: 1, 2, 3, with synonymy) the whorls are lower, with sharp tubercle-ribs above and 2 distinct rows of clavate tubercles below, 15—21 per whorl. All, however, possess the same style of ornament as our specimen, which lead us to suggest it to be a *Turrilites*, although it corresponds to no named species known to us. In consequence, it is left in open nomenclature.

Occurrence. — Lower Cenomanian Glauconitic Limestone southeast of Esfahan.

Family **Scaphitidae** Meek, 1876

Genus *Scaphites* Parkinson, 1811

Subgenus *Scaphites (Scaphites)* Parkinson, 1811

Type species: *Scaphites equalis* J. Sowerby, by the subsequent designation of Meek (1876).

Diagnosis. — See Wiedmann (1965) and Kennedy (1971) for a full diagnosis.

Discussion. — Wiedmann (1965) has provided a lengthy discussion of the systematics of the genus. Within the restricted subgenus *S.* (*Scaphites*), Wiedmann recognised three lineages, which showed parallel evolutionary trends. In the equalis main stock, including *S.* (*S.*) *simplex* Jukes-Browne, *S.* (*S.*) *obliquus* J. Sowerby and *S.* (*S.*) *equalis* J. Sowerby, ornament consists of ribs alone, which are non-tuberculate, the whorl section being rounded to oval, without lateral bulges covering the umbilicus. In the *similaris* stock, including *S.* (*S.*) *yonekurai* Yabe *S.* (*S.*) *bassei* Collignon and *S.* (*S.*) *hilli* Adkins and Winton, the shell is small, and strong bulges develop to cover the umbilicus in some members. In the *meriani* stock, including *S.* (*S.*) *hungardianus* d'Orbigny, *S.* (*S.*) *meriani* Pictet and Campiche and *S.* (*S.*) *collignoni* Wiedmann, there is a closed umbilicus and conical ventrolateral tubercles.

The recognition of these lineages is, unfortunately, less simple than Wiedmann suggested. As noted previously (Juignet and Kennedy 1977: 67) study of hundreds of *Scaphites* of the *equalis* lineage shows that there is great variability in the relative development of lateral bulges. In our view, the specimen of *S.* (*S.*) *yonekurai* from Rouen figured by Wiedmann and other Cenomanian specimens referred to *yonekurai* by him are mere variants of *S.* (*S.*) *obliquus*, and are not evidence of overlap of the largely Boreal *equalis* lineage with the North-African — Indian — Japanese — Malagassy *similaris* lineage, for the type of *yonekurai* is of Coniacian age. Equally, we are uncertain of the relationships between *S.* (*S.*) *equalis* and *S.* (*S.*) *similaris*

Stoliczka, which could well fall within the variation range of the *equalis* lineage, especially as its actual horizon is not precisely known. *S. bassae* is certainly distinctive, but we have seen intermediates between *S. obliquus* and *S. yonekurai* (sensu Wiedmann, non Yabe) and *S. equalis* and *S. similaris*.

Occurrence. — *Scaphites* appears in the Upper Albian, and ranges to the Upper Campanian. Geographically it is known from North America through western Europe, the USSR, Iran, India and Japan, occurs widely in North, East, West and South Africa, Madagascar, northern Australia and New Zealand.

Scaphites (Scaphites) equalis J. Sowerby, 1813
(pl. 2: 3)

1811 *Scaphites* Parkinson, pl. 10: 10.
1813 *Scaphites equalis* J. Sowerby: 53, pl. 18: 1—3.
1965 *Sc. (Scaphites) equalis* J. Sowerby; Wiedmann: 417, pl. 56: 1—4; figs. 3a, 3b (with full synonymy).
1965 *Sc. (Scaphites) similaris* Stoliczka; Wiedmann: 422 (with synonymy).
1971 *Scaphites (Scaphites) equalis* J. Sowerby; Kennedy: 32, pl. 64: 5a—b, 6a—b.
1977 *Scaphites (Scaphites) equalis* J. Sowerby; Juignet and Kennedy: 68, pl. 4: 6a—c, 7a—c, 11.

Holotype: Sowerby's original specimen (1813, pl. 18: 1—3), BMNH 43986, from the Middle Cenomanian of south-west England.

Material. — One specimen only GSI 25.

Description. — The specimen is a complete adult, with the aperture preserved. The maximum length is 28.5 mm. The coiled early whorls are depressed and involute. Ornament consists of numerous fine primary ribs which bi- or trifurcate at the ventrolateral shoulder and loop across the venter, together with occasional intercalated ribs.

There are eight very strong, distant primary ribs on the body chamber, which branch into up to four finer secondary ribs crossing the venter together with one or more short intercalated ribs, giving a total of 26 ventral ribs.

Discussion. — The strong primary ribs on the body chamber of *S. equalis* readily separate the species from typical *S. obliquus* (although intermediates occur), *S. simplex*, *S. bassei* and *S. yonekurai*, and lack of tubercles separates it from *S. hungardianus*, *S. meriani* and *S. collignoni*. The type of *Scaphites similaris* Stoliczka is more compressed and smaller, with finer, delicate ornament, and long, rather weak ribs on the flanks of the body whorl with 5—6 secondaries. The precise horizon of the type of *S. similaris* and of *Scaphites equalis* var. *turonensis* Roman and Mazerin (a synonym according to Wiedmann 1965: 423) is not known, and we do not believe it is possible to regard them so definitely as members of different species as Wiedmann suggests without seeing further material.

Occurrence. — *S. equalis* is common in the Middle and Upper Cenomanian of England and northern France, especially in Basement Bed facies of south-west England and the Rouen Fossil Bed. There are other records from the Middle-Upper Cenomanian of Bohemia, Poland, many localities in southern France and Spain, and if *S. similaris* is a synonym, Madagascar and Southern India can be added to the list.

Scaphites (Scaphites) obliquus J. Sowerby, 1813
(pl. 2: 4, 5, 11)

1813 *Scaphites obliquus* J. Sowerby: 54, pl. 18: 4—7.
1965 *Sc. (Scaphites) obliquus* J. Sowerby; Wiedmann: 417, pl. 56: 1—4; figs. 3a—b (with synonymy).

pars 1965 *Sc.* (*Scaphites*) *yonekurai* Yabe; Wiedmann: 421, pl. 56: 7, fig. 3d (with synonymy).

1971 *Scaphites (Scaphites) obliquus* J. Sowerby; Kennedy: 33, pl. 63: 2a—b, pl. 64: 2, 3a, b, 4.

1977 *Scaphites (Scaphites) obliquus* J. Sowerby; Juignet and Kennedy: 69, pl. 4: 8a—c, 9a—c, 10a—c, 12a—c.

Lectotype: BMNH 43987a, figured by J. Sowerby 1813: pl. 18: 4—6, from Hamsey, Sussex. Designated by Kennedy (1971: 33).

Material. — Five specimens GSI 22—24 and 26—27.

Description. — All specimens are mature adults, and are either internal moulds or retain traces of shell. Specimens vary from compressed with weak ornament, to depressed with strong ornament. On the coiled portion, there are about twenty primary ribs, which bi- or trifurcate across the venter, where one or two intercalated ribs are added. On the hook, the primary ribs strengthen, but are always denser and weaker than in *S. equalis*, bi- or trifurcating across the venter, with added intercalatories.

Discussion. — Our specimens add little to previous observations on the species (Juignet and Kennedy 1977: 69). There is considerable variation, even in our small sample, from small slender individuals with an open hook (pl. 2: 5), to those with a distinctive 'broken back' appearance (pl. 2: 4), or GSI 27, which shows an umbilical bulge like Wiedmann's *yonekurai* (1965: pl. 56: 7).

Previously (Juignet and Kennedy 1977: 69) there was uncertainty as to the precise relationships of *S. obliquus* and *S. yonekurai*. Since that time it has been possible to re-study Japanese material and successions, and to clarify relative ages.

Contrary to Wiedmann's view (1965), *S. yonekurai* is not an intermediate form between the Late Albian/early Cenomanian *S. hilli* and the Cenomanian or Turonian *S. similaris*; the lectotype, from the *Scaphites* Beds of Opiraushibets, Teshio, Hokkaido, is a later, Coniacian species, and other Cenomanian specimens referred to *yonekurai* by Wiedmann are simply variants of *S. obliquus* rather than the early members of a very long ranging species; the morphological similarities between these specimens are imply an example of heterochronous homoeomorphy, as for instance between some individuals of the Cenomanian *Scaphites equalis*, Turonian *S. pseudequalis* Yabe and *S. ferronensis* Cobban, or the tuberculate Albian *S. meriani* Pictet and Campiche and Campanian *Scaphites hippocrepis* (Dekay).

Occurrence. — *S. obliquus* ranges from Lower to Middle Cenomanian. The species is recorded widely in Western Europe (England, France, W. Germany), Poland, the Balkans, USSR, the Middle East, North Africa, and if *S.* (*S*) *yonekurai* Wiedmann (pars) non Yabe are included, Madagascar, Southern India and South Africa can be added.

Order **Ammonitida** Zittel, 1884
Suborder **Ammonitina** Hyatt, 1889
Superfamily **Desmoceratacea** Zittel, 1895
Family **Desmoceratidae** Zittel, 1895
Subfamily **Puzosiinae** Spath, 1922
Genus *Puzosia* Bayle, 1878

Type species: *Ammonites planulatus* J. Sowerby, 1827 by the original designation of Bayle (1878), non *Ammonites planulatus* Schlotheim 1820: 59, nec *Ammonites planulatus ellipticus* Schuebler in von Zieten 1830: 40). = *Ammonites subplanulatus* Schlüter, 1871.

Diagnosis. — See Wiedmann and Dieni 1968: 110; Kennedy 1971: 34.

Discussion. — In their recent revision of this genus, Wiedmann and Dieni (1968) have placed both *Anapuzosia* and *Mesopuzosia* Matsumoto in synonymy, whilst providing some clarification of the rather confused nomenclature of mid-Cretaceous representatives of the genus.

Occurrence. — Lower Albian to Upper Turonian, world-wide.

Subgenus *Puzosia (Puzosia)* Bayle, 1878

Puzosia (Puzosia) cf. *subplanulata* (Schlüter, 1871)

(pl. 2: 7)

compare: 1871 *Ammonites subplanulatus* Schlüter: 4, pl. 2: 5—7.
1971 *Puzosia subplanulata* (Schluter); Kennedy: 35, pl. 9: 1—2; pl. 10: 3a—b; pl. 50: 5 (with synonymy).

Material. — One specimen only, GSI 15.

Description. — The specimen is a wholly septate disc 105 mm. in diameter, deformed into an ellipse, and retaining much shell material. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
GSI 115	94.5 (100)	32.5 (34)	38.8 (41)	0.84	30.5 (32)

The coiling is evolute, with a broad umbilicus (32% of diameter) of moderate depth, with a vertical wall and abruptly rounded shoulder. The whorl section is compressed (breadth to height ratios measured vary from 0.84 to 0.94 depending on the degree of distortion) with sub-parallel inner flanks, convergent shoulders and an arched venter. There are an estimated six or seven constrictions on the outer whorl. These are markedly prorsiradiate across the umbilical shoulder, convex on the inner flank, flexing backwards across mid-flank, concave on the outer flank, thence flexing forwards and projecting strongly on the ventrolateral shoulders to form a broad ventral peak. On the shell, each constriction is preceded by a strong rounded rib, and followed by a somewhat weaker rib, both extending down to the umbilical shoulder. Between constrictions the inner flanks appear to have been either smooth, or ornamented by little more than striae, but on the outer flank, and across the venter, there are an estimated thirty-five fine, dense ribs. These begin as mere striae, convex at mid-flank, but flex backwards to become markedly concave across outer flank and shoulder, crossing the venter with a broad convex flexure.

Discussion. — Because of distortion it is difficult to identify this specimen with confidence. The general proportions, whorl section, form and number of constrictions all recall, however, *Puzosia subplanulata* (Schlüter), with which it is compared. It differs markedly from the many species reviewed by Wiedmann and Dieni (1968) (q.v.); when compared with specimens of *Puzosia mayoriana* (d'Orbigny) before us, it has fewer constrictions, and fewer, less flexuous ribs.

Occurrence. — *P. subplanulata* ranges throughout the Lower and the Middle Cenomanian of western Europe and elsewhere.

Puzosia (Puzosia) cf. *octosulcata* (Sharpe, 1857)

(pl. 1: 13)

compare: 1857 *Ammonites octo-sulcatus* Sharpe: 42, pl. 19: 3a—b.
1971 *Puzosia (Puzosia) octosulcata* (Sharpe); Kennedy: 36, pl. 13: 3; pl. 14: 1a—b, 2a—b, 3 (with synonymy).

Lectotype: GSM 7761, the original of Sharpe's (1857) pl. 19: 3a—b, from the Lower Chalk of Ventnor, Isle of Wight, by the subsequent designation of Wright and Wright (1951: 37).

Material. — One specimen only, GSI 16.

Description. — The specimen is a broken corroded individual only 18 mm diameter. Coiling is moderately involute, with a slightly compressed whorl section. The flanks are flattened, the venter arched and rounded. The umbilicus is shallow, and comprises 31% of the diameter. No trace of ornament remains, but there are eight rather shallow constrictions on the outer whorl. These are prorsiradiate and very gently flexed across the flanks, and projected forwards across the ventrolateral shoulder to a shallow ventral chevron.

Discussion. — Relatively swollen whorls, together with the number and form of constrictions indicate this poor specimen to be best compared with *P. octosulcata*. Like all other described specimens of that species, it is also characterised by its small size.

Occurrence. — Lower and Middle Cenomanian of southern England, Lower Cenomanian of Madagascar. The present specimen represents the first record from Iran.

Genus *Austiniceras* Spath, 1922

Type species: *Ammonite austeni* Sharpe 1858: 28, pl. 12: 1a—b only, by the original designation of Spath (1922: 127).

Discussion and distribution. — Kennedy (1971: 37) has recently presented a diagnosis of this genus. All known *Austiniceras* to date consist of very large discs, and the early stages are poorly understood. The specimen described here may be a juvenile of the genus, although definite assignation is not possible. *Austiniceras* has a long time range, and is known from Lower Cenomanian to Upper Turonian sediments in western Europe. Collignon (1961) records species from the Coniacian to Campanian of Madagascar. There are also records from Japan and North Africa, and the United States (Texas).

Austiniceras? sp. juv.
(pl. 2: 6)

Material. — One specimen only, GSI 14.

Description. — The specimen is a distorted, largely septate internal mould with the following dimensions:

	D	Wb	Wh	Wb:Wh	U
GSI 14	75.0	—	27.0 (36)	—	27.0 (36)
	66.0	18.5 (28)	22.0 (33)	0.89	26.7 (40)

The coiling is very evolute, with a broad shallow umbilicus. The umbilical wall is low, flattened, with an abruptly rounded shoulder. The whorl section is compressed (breadth to height ratio is 0.89) with flattened sides and a high, narrowly rounded venter. There are four (possibly five) broad, prominent, quite deep prorsiradiate slightly sinuous constrictions per whorl, projected strongly forwards on the ventrolateral shoulder to an acute, sharp ventral peak.

The mould is smooth between constrictions save for fine, dense, crowded, convex prorsiradiate riblets on the ventrolateral shoulders and venter, which are slightly more prominent where traces of shell survive. The suture is intricately subdivided, but too poorly preserved for illustration.

Discussion. — Open coiling, broad umbilicus, form and number of constrictions plus whorl section, all recall the poorly known early whorls of *Austiniceras*, in

particular a specimen of *Austiniceras austeni* in the Sedgwick Museum Cambridge (SMB 82593), where the nucleus is present as an oyster cast. It is, however, eminently possible that one or other of the small European Cenomanian *Puzosia* may prove to be the juvenile of *A. austeni,* and there are also comparisons to be made with that genus.

However, in most *Puzosia* species with so few constrictions these are distinctly sigmoidal (e.g. *P. lata* Seitz, *P. provincialis* (Parona and Bonarelli): see Wiedmann and Dieni 1968).

Superfamily **Hoplitaceae** H. Douvillé, 1890

Following the work of Wiedmann (summarised in Kullman and Wiedmann 1970), the Hoplitaceae are here restricted by the removal of the 'false hoplitids' — the deshayesitids and douvilleiceratids, which are placed in separate superfamilies Douvilleiceratacеae and Deshayesitaceae, by virtue of their independent origins in the Ancyloceratina.

Family **Hoplitidae** H. Douvillé, 1890

Genus *Hyphoplites* Spath, 1922

Type species: *Ammonites falcatus* Mantell (1822: 117, 118, pl. 21: 6, 12) by the original designation of Spath (1922).

Diagnosis. — See Wright and Wright 1949: 481.

Occurrence. — *Hyphoplites* evolved from *Discohoplites* Spath, 1925 during the late Albian, and ranged to the top of the Lower Cenomanian. Middle Cenomanian records, e.g. from southern England, are based upon remanié or derived specimens. The genus is typically Boreal in distribution, extending across western Europe and beyond to Transcaspasia and Iran, as with present specimens and those previously noted by Seyed-Emami *et. al.* (1971). Its soutern limits are Cassis (Fabre 1940) and Provence (Thomel 1965) in southern France, whilst Avnimelech (1965) recorded a solitary specimen from Israel.

Hyphoplites curvatus (Mantell, 1822)
(pl. 2: 1, 9)

1822 *Ammonites curvatus* Mantell: 118, pl. 21: 18.
1949 *Hyphoplites curvatus* (Mantell); Wright and Wright: 488, pl. 31: 1—4 (with synonymy).
1971 *Hyphoplites curvatus* (Mantell); Kennedy: 43, pl. 15: 1, 3a—c (with synonymy).
1977 *Hyphoplites curvatus* (Mantell); Juignet and Kennedy: 75, pl. 6: 12a—b, 14a—b, 15a—b (with synonymy).

Holotype: BMNH 5739, Mantell's original specimen, from the Lower Chalk of Hamsey, Sussex, England.

Material. — Two specimens, GSI 18—19.

Description. — Our specimens are adults, retaining body chambers and traces of shell. The coiling is involute, the whorls slightly compressed, and bearing distinct umbilical, lower and upper ventrolateral tubercles. Small umbilical bullae give rise to groups of three or more bunched falcoid ribs, with two or three ribs intercalated. The dense even ribs link in two's and three's to distinct clavate lower ventrolateral

tubercles, whilst there are prominent clavate upper ventrolateral tubercles. On the last parts of the body chamber, all tuberculation declines markedly.

Discussion. — Typical members of this species differ from *Hyphoplites pseudofalcatus* in having stronger, robust tubercles, and our specimens can be regarded as representative of the not uncommon passage forms between the two. They differ from the similarly tuberculate *H. arausionensis* (Hébert and Munier-Chalmas) in that species lacks delicate flank ribs during early and middle growth (they may appear on adult body chambers), although again, transitional forms are known.

Occurrence. — This species is common in *H. carcitenensis* and *M. saxbii* assemblage Zone faunas in southern England, and has a comparable range in Normandy and Sarthe in northern France. It occurs widely elsewhere in the Lower Cenomanian, in the south-eastern parts of the Paris Basin, in W. Germany, Switzerland, Transcaspasia and central Iran.

Hyphoplites arausionensis arausionensis (Hébert and Munier-Chalmas, 1875)

(pl. 2: 2, 8)

1875 *Ammonites arausionensis* Hébert and Munier-Chalmas: 115, pl. 4: 5 only.

1949 *Hyphoplites arausionensis* (Hébert and Munier-Chalmas); Wright and Wright: 491 (with synonymy).

1949 *Hyphoplites crassofalcatus crassofalcatus* (Semenow); Wright and Wright: 490, pl. 32: 1, 5, 6, 8 (with synonymy).

1971 *Hyphoplites arausionensis arausionensis* (Hébert and Munier-Chalmas); Kennedy: 43, pl. 19: 4 (with synonymy).

1977 *Hyphoplites arausionensis arausionensis* (Hébert and Munier-Chalmas); Juignet and Kennedy: 75, pl. 6: 8, 9, 16a—b.

Lectotype: The original of Hébert and Munier-Chalmas' pl. 4: 5, in the Collections of the Sorbonne, and from the Lower Cenomanian of Gacé (Orne). Designated by Wright and Wright (1949).

Material. — Two specimens, GSI 17 and 22.

Description and discussion. — GSI 22 is a phragmocone 31 mm in diameter; GSI 17 a mature adult 49 mm, in diameter, retaining body chamber. Both specimens are internal moulds with traces of shell. *H. arausionensis arausionensis* is a quadrate-whorled, moderately evolute *Hyphoplites* with prominent umbilical and ventrolateral tubercles but no ribs or only faint, simple ribs, save on the adult body chamber, when tubercles decline and delicate ribs develop (pl. 2: 2a). Typical specimens are readily separable from *H. curvatus*, whilst *H. arausionensis horridus* Wright and Wright is much more depressed and inflated, with spinose tubercles, although there are passage forms between the two.

Hyphoplites arausionensis is a senior synonym of *H. crassofalcatus* Semenow (1899: 199), as discussed by Kennedy (1971).

Occurrence. — This is a relatively common species in *H. carcitanensis* and *M. saxbii* assemblage Zone faunas in England and northern France; there are other records from Orne, Orange (Hébert and Munier Chalmas 1875), various localities in the Basses Alpes, and at Cassis, Bôuches du Rhone. Elsewhere, the species is known from Transcaspasia and Iran.

Hyphoplites arausionensis horridus Wright and Wright, 1949

(pl. 2: 10)

1949 *Hyphoplites crassofalcatus* var. *horridus* Wright and Wright: 491 pl. 31: 10, pl. 32: 7.

1971 *Hyphoplites arausionensis horridus* Wright and Wright; Kennedy: 43 (with synonymy).

1977 *Hyphoplites arausionensis horridus* Wright and Wright; Juignet and Kennedy: 76 (with synonymy).

Holotype: GSM 37217, figured by Wright and Wright (1949) as their pl. 31: 10, from the Lower Cenomanian of Ventnor, Isle of Wight, Hampshire, England.

Material. — One specimen, GSI 20.

Description. — The specimen is a slightly distorted adult retaining all the body chamber, with traces of shell preserved. On the phragmocone the whorl section is depressed, with a narrow deep umbilicus. There are ten huge umbilical spines, visible partially embedded in the matrix of the specimen. Faint low simple ribs connect these to strong clavate lower ventrolateral and oblique clavate upper ventrolateral tubercles. The venter is flat, with a broad siphonal groove flanked by distinctive ridges. On the body chamber, all tuberculation declines suddenly especially the umbilical tubercles, leaving the shell ornamented by bunches of fine falcoid ribs lacking ventrolateral tubercles.

Discussion. — All previously figured examples of *Hyphoplites arausionensis horridus* are juveniles. The present specimen is the first described which shows the marked modification of ornament on the adult body chamber; interestingly, this corresponds precisely to the changes seen on the restricted form of the species (e.g. Wright and Wright 1949, pl. 32: 6a—b).

Occurrence. — *H. arausionensis horridus* is rare, accompanying the typical form in *Hypoturrilites carcitanensis* assemblage Zone faunas in southern England and northern France. The specimen described is the first recorded occurrence in Iran.

Family **Schloenbachiidae** Parona and Bonarelli, 1897

The family Schloenbachiidae have their origins in the Upper Albian hoplitids, the type species of *Schloenbachia, S. varians* (J. Sowerby) evolving from several different 'genera' of the currently over-split Hoplitinae (Kennedy 1971: 44, Juignet and Kennedy 1977: 76). As such *Schloenbachia*, like its ancestors, has an entirely Boreal distribution (Juignet and Kennedy 1977: 134 et. seq.) In contrast, all other genera attributed to the family by Wright (1957: L400) and other authors have much wider distributions and are generally rare or absent in the Boreal region, with the exception of the dubious taxa *Saltericeras* and *Praeschloenbachia*. We strongly suspect that, *Schloenbachia* apart, these other genera are quite independently derived, that the family is polyphyletic as currently conceived, and is a mere repository for keeled Cenomanian-Turonian hoplitaceans and acanthocerataceans, linked only by this common feature. If confirmed, the Schloenbachiidae can be assimilated into the Hoplitinae whence *Schloenbachia* arose.

Genus *Schloenbachia* Neumayr, 1875

Type species: *Ammonites varians* J. Sowerby, 1817 by the subsequent designation of H. Douvillé (1890).

Diagnosis. — A highly variable group of medium-sized ammonites; involute and compressed to evolute and highly inflated; carinate, the keel being strong to weak. Compressed forms may be smooth and constricted, although most forms bear umbili-

cal and lower lateral tubercles which may or may not be connected by fine striae or ribs to about twice as many ventrolateral clavi. More inflated forms usually have strong umbilical and lower lateral tubercles, each lower lateral tubercle giving rise to a pair of flexuous ribs, with strong ventrolateral clavi at the end of each rib. With increasing inflation the ribbing breaks down into tubercles only; very inflated forms bear huge upper lateral and smaller lower lateral or umbilical tubercles or septate spines.

Discussion. — The diagnosis indicates the wide variation seen in this genus. Most specimens described to date are internal moulds, when the extremes of ornament are rather reduced, for the tubercles of inflated variants commonly represent the bases of septate spines. Some compressed *Schloenbachia* are almost smooth; others develop puzosii-like constrictions and yet others bear looped hoplitid-like ribs.

This is the commonest genus in the Boreal Cenomanian, and in the Anglo-Paris Basin usually outnumbers the remainder of the ammonite fauna at any given level throughout most of the stage. Large collections from this region indicate very clearly that throughout its range, any contemporary collection represents but a single, rather variable species. The majority of named *Schloenbachia* 'species' are thus no more than variants of a limited number of true species.

Hancock (in preparation) has reviewed and revised the nomenclature of *Schloenbachia*, and his suggestions are followed here. In the Lower Cenomanian, a single species, *Schloenbachia varians* (J. Sowerby) is recognised, and for convenience, a number of intergrading variants are named, from hypernodose *ventriosa* through *varians, tetrammata, subtuberculata and 'subvarians'* to the almost smooth *subplana*. In the Middle Cenomania, members of the genus are referred to *Schloenbachia coupei* (Brongniart), and again, a number of intergrading variants are named, from hypernodose forms through *trituberculata, quadrata*, several unnamed forms to *costata*. Unfortunately, the type of *S. coupei* itself lies away from the common range of variants.

In the Upper Cenomanian, the youngest species of the genus is represented by *Schloenbachia lymense* Spath; none of the variants of this species have, however, received names at this time.

One of the difficulties introduced by recognition of such wide variation is that differences between individuals at either end of the spectrum of intraspecific variation are far greater than differences between comparable regions of the plexus of variation in successive species. Thus *Schloenbachia varians subplana* and *ventriosa* are far easier to distinguish than the hypernodose variants of the Lower Cenomanian *S. varians* and the Middle Cenomanian *S. coupei*, a phenomenon which has led some workers to believe that Brongniart's *Ammonites coupei* was a synonym of Sowerby's *Ammonites varians*.

Hancock (*in litt.*) has noted, however, a number of evolutionary changes which affect the ornament. The easiest to detect is the change in the strength of the umbilical tubercles, which, in any given morphotype tend to become more and more prominent as one ascends the Cenomanian stage. But to use this feature to fix an horizon from a *Schloenbachia* one must compare the specimen with others of comparable inflation and at the same stage of ontogeny.

More obvious are shifts in the general population structure. The proportion of inflated individuals decreases higher in the Cenomanian; in the early Cenomanian forms such as *S. varians varians* are a common element of the *Schloenbachia* population; through the Middle Cenomanian they become decidedly uncommon; in the Upper Cenomanian, inflated forms can still be found but are very rare.

Scholz (1973) introduced the subgenus *Schloenbachia (Praeschloenbachia)* (type species *P. briacensis* Scholz) for what he believed to be passage forms between *Arrhaphoceras* and *Schloenbachia*. His diagnosis, loosely translated, is as follows:

"Primitive *Schloenbachia* derived from *Arrhaphoceras*. The form of the shell resembles that of an *Arrhaphoceras*, the ornamentation comprises strong umbilical and marginal tubercles and weak, broad, flat ribs, irregularly bi-or trifurcating, or simple. In the middle of the outer periphery, there is a distinct keel, but this keel, in contrast to that of *Schloenbachia s. str.*, is broader, round and flattened."

When compared with somewhat older *dispar* Zone *Arrhaphoceras*, *Praeschloenbachia* is indeed transitional to *Schloenbachia*, but as we have noted above, *Schloenbachia* evolves from a series of late "Albian" 'genera', and what Scholz has described is an evolutionary grade which can be found not only in *Arrhaphoceras* derivatives but also those of *Pleurohoplites*, *Callihoplites* and *Lepthoplites*. We figure here, for example (pl. 3: 1) a specimen from the South Dorset *Dispar* Zone ammonite bed which is transitional between *Callihoplites* and *Schloenbachia* in keel development.

Because of the presence of these passage forms in a range of genera, we believe it better to regard *Praeschloenbachia* as a subgenus of *Arrhaphoceras*, pending adequate revision of the late Albian hoplitid complex that is the origin of *Schloenbachia*.

The genus *Saltericeras* Atabekian, 1961 is a synonym of *Schloenbachia*. This taxon was introduced in a rather unsatisfactory manner (Atabekian 1960, Atabekian and Likhadieva 1961), and its validity may be doubted, but nevertheless, Mikhailova (1974), in an interesting discussion of the origins of the Schloenbachiidae, places it in an intermediate position between *Callihoplites* and *Schloenbachia*. Nomenclatural considerations aside, the genus is a junior subjective synonym of *Schloenbachia*; the type species, *Ammonites salteri* Sharpe (1857: 50, pl. 23: 3a—c, 5a—b) is based upon malformed *Schloenbachia varians*. Wright and Wright (1951: 21) suggested that *salteri* might be pathological and indeed, Sharpe's figures both show the distinct assymetry common to such individuals. These malformations may, however, affect very young shells, which then regain perfect symmetry, as with the specimens of *Ammonites renauxianus* Sharpe (*non* d'Orbigny) (Sharpe 1857: 41, pl. 19: 2a—c), = Spath's (1923—1943: 241) *Schloenbachia ecarinata* — or the *Forbesiceras*-like malformations of *Schloenbachia varians subplana — intermedia* which led Wright (1957: L. 402) to suggest that *Forbesiceras* derived from *Schloenbachia*. What the affinities of material like that studied by Mikhailova prove to be must await proper illustration of the specimens.

Occurrence. — *Schloenbachia* is a classic Boreal genus, it's distribution following that of the ancestral hoplitids as recently demonstrated by Owen (1970). It is unknown in the New World, extending no further west than East Greenland, (Donovan 1953, 1954). In Europe, it occurs all over the British Isles, FRG and GDR, Switzerland and Poland. In France, the genus occurs in the north in the type Cenomanian and, to the east, extends down the Rhone as far south as the Alpes-Maritimes. There are records from the Mediterranean coast, at Cassis, but these are doubtful (Kennedy, in preparation). The genus is not known from the western Mediterranean, nor from Spain or points south, i.e. the well-known North African and Madagascan faunas. In the Soviet Union, the genus occurs widely, as far east as Khrebet Pay-Koy on the Kara Sea coast, and as far south east as the Ukraine, the Mangyshlak Peninsula (Transcaspasia) and in Turkmenstan (Kopet Dag). In Iran, Seyed-Emami *et al.* (1971) have recently confirmed Spath's (1923—1943: 242) earlier records of the genus.

Schloenbachia ranges throughout the Lower and Middle Cenomanian, and to the top of the Upper Cenomanian *E. pentagonum* assemblage Zone. There are a number of records from the Upper Albian of both England and France (Kennedy 1971: 45). All the English occurrences can be discounted, whilst records in the Alpes Maritimes (Thomel 1961) are based on the occurrence of derived Albian fossils in Cenomanian deposits (Thomel *in litt.*) The other records by Breistroffer (1936) and Follet (1954) require reinvestigation.

Schleonbachia varians (J. Sowerby, 1817)
(pl. 3: 2—7; pl. 4: 1—5)

1817 *Ammonites varians* J. Sowerby: 169 (pars) pl. 176 uppermost figure, figure in row below, right-hand figure in row below.
1822 *Ammonites varians* var. *subplana* Mantell: 166, pl. 21: 2.
1822 *Ammonites varians* var. *intermedia* Mantell: 166, pl. 21: 5, 7.
1828 *Ammonites varians* var. *tettramata* J. de C. Sowerby: 166, pl. 587: 2.
1853 *Ammonites varians* var. *subtuberculata* Sharpe: 22, pl. 8: 5a—c, 6a—b.
1853 *Ammonites varians* var. *intermedia* Sharpe: 23, pl. 8: 7a—b, (non Mantell, = *S. subvarians* Spath).
1853 *Ammonites coupei* var. *inflata* Sharpe: 24, pl. 8: 1a, 1b (non Brongniart, = *S. ventriosa* Stieler).
1926*a* *Schloenbachia subvarians* Spath: 81.
1926*b* *Schloenbachia subvarians* Spath: 430.
1926*b* *Schloenbachia subvarians aperta* Spath: 430.
1926*b* *Schloenbachia subvarians densicostata* Spath: 430.
1928 *Schloenbachia ecarinata* Spath: 241.

Lectotype: BMNH 43962b, the original of J. Sowerby 1817: pl. 176, top figure (re-figured by Kennedy and Hancock 1977, pl. 3: 1a—b); designated by Spath (1938).

Material. — 30 specimens, GSI 28—56, 63; there are also a few additional fragments embedded in the matrix of other specimens.

Description and discussion. — The suite of specimens before us span a complete range in variation from juveniles (pl. 3: 6) to mature adults (pl. 3: 5) and from almost smooth individuals (pl. 3: 3) to strongly tuberculate variants (pl. 3: 7) As noted in the generic discussion it is convenient to describe these in terms of a small number of named variants and passage forms, whilst in view of the enormous literature and Hancock's pending revision, we have limited our synonymy to the critical citations of the named forms used here.

The assemblage is of typical Lower Cenomanian main plexus forms, chiefly *Schloenbachia varians varians* (J. Sowerby) and *S. varians subtuberculata* (Sharpe) and intermediate varieties, but there are also a few examples of *S. varians subvarians* Spath.

With as many specimens as this, it is possible to date more closely than merely Lower Cenomanian, and this assemblage belongs to the *carcitanensis* Zone. Seven individuals show typical *carcitanensis* Zone ornamentation: 37, 41, 43, 47, 48, 51 and 53. Eight others would probably be *carcitanensis* Zone: 29, 36, 38, 39, 42, 44, 50 and 56. None appear to be from the *saxbii* Zone, let alone any higher horizon.

This assignment to a basal Cenomanian horizon is further supported by the fact that most specimens belong to inflated varieties of *Schloenbachia*, although it is a little curious that none is a *S. varians ventriosa* Stieler, though no. 63 is a very coarsely ribbed *S. varians varians*.

Occurrence. — As for genus.

Superfamily **Acanthocerataceae** Hyatt, 1900
Family **Acanthoceratidae** Hyatt, 1900
Subfamily **Mantelliceratinae** Hyatt, 1900
Genus *Mantelliceras* Hyatt, 1900

Type species: *Ammonites mantelli* J. Sowerby, 1814, by the original designation of Hyatt (1900: 113).

Diagnosis. — See Kennedy (1971) and Juignet and Kennedy (1977) for recent diagnoses.

Discussion. — Although more than fifty species of *Mantelliceras* have been named, there have been few attempts to introduce subgeneric groupings, because of the widespread recognition of the continuous gradation from strongly tuberculate inflated forms to almost non-tuberculate compressed forms at any given stratigraphic level. Recently, however, Thomel (1972) introduced four subgenera, to which can be added *Coulonicera*s Busnardo *et al.*, 1966. As discussed by Juignet and Kennedy (1977: 84) these are all rather unsatisfactory groupings, and at least one subgenus, *Pseudomantelliceras* Thomel, 1972 is a subjective synonym of *Sharpeiceras*, as discussed below. No subgeneric division is used here.

Occurrence. — *Mantelliceras* has a world-wide distribution and appears to be restricted to the Lower Cenomanian. Collignon (1939, 1959, 1964 etc.) has consistently recorded it from his Lower Cenomanian Zone of *Mantelliceras mantelli* and *Calycoceras newboldi*, although the latter is regarded as a Middle Cenomanian species elsewhere in the world. The supposed Upper Albian '*Mantelliceras*' from southern France listed by Thomel (1962, 1968, 1972: 16, pl. 1: 8—12) appears to the *Stoliczkaia*.

Mantelliceras mantelli (J. Sowerby, 1814)
(pl. 6: 1, 3; pl. 8: 4)

1814 *Ammonites mantelli* Sowerby: 119, pl. 55, lower figure only.
1903 *Mantelliceras mantelli* (J. Sowerby); Hyatt: 114.
1971 *Mantelliceras mantelli* (J. Sowerby); Kennedy: 54, pl. 17: 9a—c, pl. 20: 2 (= *M.* aff. *mantelli*); pl. 23: 2a—b (= *M. aff. mantelli*) (with synonymy).
1972 *Mantelliceras* (*Mantelliceras*) *mantelli* (Sowerby); Thomel: 37, pl. 10: 3—12; pl. 11: 1, 7, 8 (non 5—6, = *Mantelliceras* sp. juv.).
1977 *Mantelliceras mantelli* (Sowerby); Juignet and Kennedy: 86, pl. 12: 2a—c, pl. 13: 6a—b; pl. 17: 4a—b (with synonymy).

Lectotype: BMNH 4394a, the original of J. Sowerby 1813: pl. 55, lower figure only, from the Lower Chalk of Ringmer near Lewes, Sussex. Designated by Kennedy 1971: 54.

Material. — Ten specimens, GSI 65—74.

Description. — Our specimens include both wholly septate moulds, specimens with body chamber, and those with traces of shell. Dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U	Ribs
BMNH 43940a (Lectotype)	45.0 (100)	22.8 (50.7)	21.5 (47.8)	1.06	10.5 (23.3)	36
GSI 72	45.0 (100)	22.0 (48)	188 (42)	1.2	— (—)	—
GSI 74	53.0 (100)	22.8 (43)	23.5 (44)	0.97	14.2 (—)	37
GSI 70	68.5 (100)	34.5 (50)	32.0 (47)	1.07	— (—)	41
GSI 66	71.5 (100)	32.5 (45)	— (—)	—	— (—)	41
GSI 69	71.0 (100)	— (—)	28.5 (40)	—	23.2 (33)	40
GSI 68	71.0 (100)	36.0 (51)	32.0 (45)	1.13	— (—)	38?

Our specimens show considerable variation, but as a group are characterised by moderately evolute coiling and a slightly depressed whorl which tends to be octagonal in section. Ornament consists of 36 to 40 rather delicate ribs per whorl, alternating more or less regularly long and short. Long ribs bear umbilical, mid-lateral, lower and upper ventrolateral tubercles, whilst intercalated ribs, which arise quite low on the flanks, bear only ventrolateral tubercles.

Discussion. — Specimens such as GSI 72 (pl. 6: 3) are very close to the lectotype of *M. mantelli*, but show a tendency towards greater inflation and earlier loss of lower

ventrolateral tuberculation. Others, such as GSI 74 (pl. 8: 4) are much more compressed, but retain the tubercles, whilst there are also round-whorled individuals such as GSI 69 (pl. 6: 1), which although delicately ribbed, may be regarded as passage forms to *M. cantianum*.

Occurrence. — *Mantelliceras mantelli* ranges throughout most of the Lower Cenomanian. It's geographic distribution extends from England to most of western Europe, north Africa, India, the USSR and Iran.

Mantelliceras cantianum Spath, 1926
(pl. 5: 3, 5; pl. 7: 4)

1857 *Ammonites navicularis* Mantell; Sharpe: 39, pl. 18: 1, 2 (*non* Mantell).
1926a *Mantelliceras cantianum* Spath: 82.
1971 *Mantelliceras cantianum* Spath; Kennedy: 55, pl. 18: 1a—c; pl. 26: 1a—c, 5 (with synonymy).
1972 *Manteliceras* (*Bunburyiceras*) *cantianum* Spath; Thomel: 46, pl. 14: 1—2.
1972 *Mantelliceras* (*Bunburyiceras*) *budaense* Adkins; Thomel: 46.
1972 *Mantelliceras* (*Bunburyiceras*) *moulinense* Thomel: 47, pl. 14: 3, 4, 9.
?1972 *Mantelliceras* (*Couloniceras*) *couloni ravelense* Thomel: 30, pl. 3: 1, 2.
1977 *Mantelliceras cantianum* Spath; Juignet and Kennedy: 87, pl. 12: 1a—c, 4a—b; pl. 13: 4a—c; pl. 14: 5a—c; pl. 22: 3a—b (with synonymy).

Holotype: BMNH 36934, the original of Sharpe 1857: pl. 18: 1, from the Lower Chalk of Folkestone, Kent, by original designation (Spath 1926a: 82).

Material. — Six specimens, GSI 81—82, 85—88.

Description. — Our specimens are all juveniles, having the following dimensions:

	D	Wb	Wh	Wb:Wh	U	Ribs
BMNH 36834 (Holotype)	117.0 (100)	— (—)	49.0 (42)	—	37 (31.6)	32
BMNH C5027	59.0 (100)	34.0 (57)	26.5 (40)	1.30	16.0 (27)	34
GSI 82	30.8 (100)	— (—)	14.3 (46)	—	7.7 (25)	32
GSI 81	33.5 (100)	19.5 (58)	15.2 (45)	1.30	9.3 (28)	34
GSI 85	54.5 (106)	32.0 (58)	25.0 (46)	1.28	17.0 (31)	30
GSI 86	60.5 (100)	29.0 (48)	23.9 (40)	1.21	19.5 (32)	30

Coiling is moderately evolute, with a deep umbilicus which typically comprises 31—32% of the diameter. The whorl section is depressed (breadth to height ratio varies between 1.21 and 1.30) with the greatest breadth at the lower lateral tubercle. The whorl sides are swollen and rounded, with a flattened venter. Ornament consists of 30 coarse, rounded, alternately long and short ribs per whorl. Long ribs bear prominent umbilical bullae and strong lateral tubercles, whilst all ribs bear distinct slightly clavate ventral tubercles, and a lower ventrolateral tubercle is visible on some specimens at small diameters.

Intercalated ribs arise below mid-flank, and all ribs cross the venter without diminution or interruption.

Discussion. — These small specimens, by their coarse, robust ornament, depressed whorls and prominent lateral tubercles which dominate over the umbilical, clearly fall into *Mantelliceras cantianum* Spath. Differences from other coarsely ornamented species are discussed by Juignet and Kennedy (1977: 88), what is interesting in our present collection is a suite of specimens which show somewhat denser ribbing and/or weaker turberculation (pl. 5: 6). Although still depressed, these specimens are morphologically gradational towards *Mantelliceras mantelli* (J. Sowerby). They closely resemble the specimen described and figured by Matsumoto *et al.* (1969: 256, pl. 28:

1a—d). Dimensions of Matsumoto's specimen and our own forms, also best referred to as *Mantelliceras* aff. *cantianum*, are as follows:

	D	Wb	Wh	Wb:Wh	U	Ribs
GK H5610	07.5 (100)	37.2 (38)	38.2 (3)	0.97	29.5 (34)	40
(after Matsumoto	88.3 (100)	41.0 (46)	36.5 (41)	1.12	26.5 (30)	39
et al. 1969)	68.0 (100)	35.0 (51)	30.5 (45)	1.14	14.0 (28)	37
GSI 84	45.0 (100)	22.5 (54)	18.9 (42)	1.19	14.5 (32)	34
GSI 80	61.5 (100)	30.5 (50)	25.0 (40)	1.22	— (—)	39?
GSI 79	64.0 (100)	28.2 (44)	25.5 (40)	1.10	20.5 (32)	42

Occurrence. — *Mantelliceras cantianum* ranges throughout the Lower Cenomanian and is known widely in southern England, northern France, Sarthe, south to the Alpes Maritimes, and also Texas, Japan and Iran (the present records).

Mantelliceras tenue Spath, 1926

1859 *Ammonites mantelli* J. Sowerby; Picted and Campiche: 200 (*pars.*) pl. 26: 3a—b.
1926*b* *Mantelliceras tenue* Spath: 427, 430.
1971 *Mantelliceras tenue* Spath; Kennedy: 60, pl. 20: 6, pl. 23: 3 (with synonymy).
1977 *Mantelliceras tenue* Spath; Juignet and Kennedy: 80, pl. 16: 1a—b; pl. 19: 4; pl. 22: 5a—b.

Holotype: The original of Pictet and Campiche (1859, pl. 26: 3a—b), by monotypy (Spath 1926*b*: 430).

Material. — One specimen, GSI 75.

Description. — The specimen is a partially septate internal mould retaining some shell. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U	Ribs
GSI 75	72.0 (100)	28.0 (39)	27.0 (38)	1.04	23.2 (32)	34
	55.3 (100)	26.5 (48)	21.5 (3)	1.23	18.0 (33)	32

The whorl section is depressed, polygonal, with the greatest breadth at the mid-lateral tubercle, when developed. The umbilicus is of moderate depth with a vertical wall and abruptly rounded shoulder. The flanks are flattened, with rounded shoulders and venter in intercostal section and an angular costal section. There are 34 ribs on the outer whorl, alternately long and short. Long ribs arise at the umbilical seam, and develop small umbilical bullae, whence arise strong, straight, slightly prorsiradiate ribs with variably developed mid-lateral tubercles, smaller lower ventrolateral tubercles, which decline as diameter increases, and are lost on the last quarter whorl, together with persistent upper ventrolateral clavi which are linked across the venter by a strong rounded rib. Intercalated ribs arise low on the flank, and bear only lower and upper ventrolateral tubercles. They show a similar ventral development to the long ribs.

Discussion. — The style of ornament of this specimen is identical with that shown in Pictet and Campiche's protograph, and although the ribbing is sparser in the holotype, there can be little doubt of its assignation to the species. *Mantelliceras tenue* combines the general whorl form of *Manteliceras mantelli* with greater evolution and stronger ribbing. It differs from *Mantelliceras cantianum* in the much more angular and less depressed whorl section.

Occurrence. — Lower Cenomanian, *H. carcitanensis* and *M. saxbii* Zones of England, northern France, Sarthe, the Alpes-Maritime and Switzerland.

Mantelliceras costatum (Mantell), 1822
(pl. 5: 1)

1822 *Ammonites mantelli* var. *costata* Mantell: 113—114, pl. 21: 9 only.
1926b *Mantelliceras costatum* (Mantell); Spath: 431.
1951 *Mantelliceras costatum* (Mantell); Wright and Wright: 24.
1964 *Mantelliceras callomoni* Collignon: 99, pl. 352: 1559.
1971 *Mantelliceras costatum* (Mantell); Kennedy: 57, pl. 19: 1a—b, 2a—c (with synonymy).
1977 *Mantelliceras costatum* (Mantell); Juignet and Kennedy: 88, pl. 13: 1a—c, 2a—b; pl. 14: 4; pl. 17: 3a—c (with synonymy).

Lectotype: BMNH C5028, the original of Mantell 1822: pl. 21: 9, designated by Kennedy 1971: 57.

Material. — Nine specimens, GSI 64, 92—95, 102—104, 106.

Description. — Our specimens comprise of group of typically slightly compressed *Mantelliceras* with whorl breadths varying from 0.83 to 1.0. Coiling is moderately evolute, the umbilicus comprising 28—31% of the diameter, and of moderate depth. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U	Ribs
GSI 64	127.0 (100)	49 (39)	57.2 (45)	0.86	35 (28)	—
GSI 92	125.0 (100)	44.5 (36)	49.5 (40)	0.90	37 (30)	38?
GSI 93	97.0 (100)	38.8 (40)	41.5 (43)	0.93	— (—)	39?
GSI 94	103.0 (100)	39.5 (28)	42.5 (41)	0.93	31 (30)	36
GSI 95	113.0 (100)	37.8 (33)	45.5 (40)	0.83	35.5 (31)	38
GSI 102	66.0 (100)	31.5 (48)	31.5 (48)	1.0	20.5 (31)	39

The umbilical wall is low and sloper outwards, with a rounded shoulder, rounded sides with the greatest breadth close to mid-flank, and a somewhat flattened venter. Ornament consists of strong ribs, 36 to 38 per whorl, generally regularly alternating long and short. Long ribs bear umbilical bullae which decline markedly in relative strength as size increases. They pass straight across the lower whorl sides, flex slightly across the upper, and decline somewhat in strenght. Up to a diameter of 30 mm. a weak lower ventrolateral tubercle is present; beyond this, there are only strong, blunt clavate ventral tubercles joined across the venter by a strong rib.

Shorter ribs, arising low on the flank are intercalated singly, or sometimes in two's. They have a similar ventral and ventrolateral development to the long ribs.

Discussion. — Early loss of lower ventrolateral tubercles, absence of a lateral tubercle and decline in umbilical bullae, together with style, strength and density of ribbing all compare well with the lectotype of *M. costatum*, suggesting reference to Mantell's species. Also present in our collections, and separated from *Mantelliceras costatum* on the basis of somewhat flatter sides, a narrower venter and generally more slender whorls, are a suite of specimens (GSI 96, 98—101, 105) which also lack lateral and lower ventrolateral tubercles (pl. 6: 2, 4, 5). We refer to these specimens as *Mantelliceras* aff. *costatum*; morphologically they form a transitional series to *Mantelliceras* of the *saxbii* (Sharpe) and *ventnorense* Diener groups (see Kennedy and Hancock 1971). Dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U	Ribs
GSI 98	81.2 (100)	31.5 (39)	39.0 (48)	0.81	19.5 (24)	39
GSI 99	76.0 (100)	— (—)	34.5 (45)	—	17.8 (23)	42
GSI 100	74.5 (100)	28.0 (38)	35.0 (47)	0.8	18.1 (24)	37

Occurrence. — *Mantelliceras costatum* is known from *Hypoturrilites carcitanensis* and *Mantelliceras saxbii* Zone faunas of southern England, northern France, Sarthe, and Madagascar. The present material constitutes the first record of the species from Iran.

Mantelliceras ventnorense Diener, 1925
(pl. 7: 3)

1857 *Ammonites feraudianus* Sharpe: 51, pl. 23: 6a—c (*non* d'Orbigny).
1925 *Mantelliceras ventnorense* Diener: 170.
1971 *Mantelliceras ventnorense* Diener; Kennedy, 62, pl. 26: 2a—c (with synonymy).

Holotype: GSM 7759, from the Lower Chalk of Ventnor, Isle of Wight, figured by Sharpe 1857: pl. 23: 6a—c.

Material. — One specimen GSI 113.

Description. — The specimen is a largely septate juvenile, having the following dimensions:

	D	Wb	Wh	Wb:Wh	U	Ribs
GSI 113	36.7 (100)	13.8 (38)	17.0 (46)	0.81	8.2 (22)	40

Coiling is moderately evolute, with a small shallow umbilicus. The whorls are compressed (whorl breadth to height ratio is 0.81) with the greatest breadth close to mid-flank. The sides are flattened, converging to a narrow venter, rounded between ribs, but flattened costally. Ornament comprises 40 ribs on the outer whorl. Approximately half of these are long, arising from weak umbilical bullae, with one or two intercalated ribs arising low on the flank, and some long ribs bifurcating. The ribs are prorsiradiate, markedly flexuous, and bear only small clavate ventral tubercles which are connected across the venter by broad rounded ribs.

Discussion. — Although more densely ribbed than the poorly preserved holotype of Diener's species, this specimen shows the characteristic lack of lateral tubercles and flexuous ribs, as do those individuals referred to the species by Fabre (1940: 236, pl. 8: 5) and Collignon (1964: 87, pl. 347: 1547).

Occurrence. — *H. carcitanensis* and *M. saxbii* Zones of England, northern France, Sarthe, Provence and Madagascar. The species has not been previously recorded from Iran.

Mantelliceras saxbii (Sharpe), 1857
(pl. 7: 5)

1857 *Ammonites saxbii* Sharpe: 45, pl. 20: 3a—b.
1971 *Mantelliceras saxbii* (Sharpe); Kennedy and Hancock: 437, pl. 47: 1—5, pl. 80: 1—4; pl. 82: 2, 4, 7 (with synonymy).
pars 1972 *Mantelliceras* (*Submantelliceras*) *saxbii* (Sharpe); Thomel: 15? *non* pl. 1: 1, 5—6; *non* pl. 1: 8—12 (= *Stoliczkaia* spp.); *non* pl. 1: 13?; *non* pl. 2: 3.
non 1972 *Mantelliceras saxbii paucicostatum* Thomel: 20, pl. 1: 7.
pars 1972 *Mantelliceras* (*Submantelliceras*) *hyatti* Spath; Thomel: 21, pl. 6: 1—2; *non* pl. 7: 10—11 (? = *M. costatum*).
pars 1972 *Mantelliceras* (*Mantelliceras*) *batheri* Spath; Thomel: 40, *non* pl. 9, 1—2 (? = *M. costatum*).
1977 *Mantelliceras saxbii* (Sharpe); Juignet and Kennedy: 97, pl. 19: 1a—c.

Lectotype: GSM 7763, the original of Sharpe 1857: pl. 20: 3a—b, from the Lower Chalk of Ventnor, Isle of Wight, Hampshire, Designated by C. W. and E. V. Wright, 1951: 38.

Material. — GSI 107.

Description. — The specimen is a wholly septate internal mould having the following dimensions:

	D	Wb	Wh	Wb:Wh	U	Ribs
GSI 107	45.5 (100)	16.5 (36)	20.0 (45)	0.82	11.9 (26)	38

Coiling is moderately evolute, with a small, shallow umbilicus (26% of diameter). The sides are flattened, with convergent ventrolateral shoulders and a flattened venter. Ornament consists of 38 ribs on the outer whorl. There are sixteen weak umbilical bullae, from which ribs arise singly, or, rarely, in pairs. Long ribs are low, narrow and rounded, straight and prorsiradiate to mid-flank, but flexed slightly and broadened across the outer flank. There are no discrete lower ventrolateral tubercles, but whorl profile changes and ribs broaden across the ventrolateral shoulder to distinct clavate ventral tubercles, linked across the venter by a broad rib. Between one and three intercalated ribs arise at various points on the flank, and follow a similar course to the long ribs, with a comparable ventrolateral and ventral development.

Discussion. — This specimen falls close to topotypes of *Mantelliceras saxbii*; differences in proportions and rib density when compared to the lectotype in part being a reflection of size differences. Also present in our collections are a series of more inflated individuals (GSI 97, 110—112; pl. 5: 4; pl. 8: 5) corresponding to specimens described by Kennedy and Hancock (1971, pl. 79: 5a—b; pl. 82: 4—5) as *M.* aff. *saxbii*. These specimens are morphologically transitional towards *M.* aff. *costatum* discussed above.

Occurrence. — *Manteliceras saxbii* Zone of western Europe. Inflated individuals referred to as *M.* aff. *saxbii* occur widely in the preceeding *H. carcitanensis* Zone. Not previously recorded from Iran.

Mantelliceras aff. *couloni* (d'Orbigny, 1840)

(pl. 5: pl. 7: 2)

compare 1840 *Ammonites mantelli* J. Sowerby; d'Orbigny: 340, pl. 54: 1—3 (*non* J. Sowerby).
1850 *Ammonites couloni* d'Orbigny: 147.
1937 *Mantelliceras couloni* (d'Orbigny); Collignon: 56, 57, pl. 9: 1a—c.
1977 *Mantelliceras couloni* (d'Orbigny); Juignet and Kennedy: 95, pl. 17: 5 (with synonymy).

Material. — Three specimens, GSI 89—91.

Description. — Our specimens comprise two juveniles and one mature adult. Dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U	Ribs
GSI 91	143.0 (100)	51.5 (36)	58.7 (81)	0.88	43.0 (30)	34
GSI 90	87.2 (100)	36.5 (42)	36.5 (42)	1.0	24.0 (28)	34

Coiling is relatively evolute, with an umbilicus of moderate width. During middle growth, the whorl section is compressed (breadth to height ratio 0.88), with convex sides and a flattened venter. There are 34 ribs per whorl, of which nearly half are long, arising from umbilical bullae of variable strength. The ribs are straight to faintly convex, prorsiradiate, strong and rounded, and bear strong, sharp, clavate ventral tubercles between which the venter is concave in costal section. One, or rarely two intercalated ribs arise at or about mid-flank, and have a similar ventrolateral and ventral development to the long ribs.

In the adult specimen related to the juveniles described above, there are similarly strong ventral clavi, but here accompanied by distinct blunt lower ventrolateral tubercles which are retained to a diameter of over 80 mm, whilst all tuberculation declines markedly on the adult body chamber.

Discussion. — These specimens compare well with English material referred to as *M.* aff. *couloni* (Kennedy and Hancock 1971: pl. 82: 1a—b), and can also be matched

with topotypes in the Paris Museums, all of which differ from the lectotype of *M. couloni* (see Juignet and Kennedy 1977: 95 for an outline of the confusion surrounding the type material of the species) in much greater inflation and less pronounced clavi.

Occurrence. — The stratigraphic distribution of *M. couloni* is poorly documented. In England and France, true *couloni* and forms like those described here appear to characterise levels close to the boundary of the *Hypoturrilites carcitanensis* and *Mantelliceras saxbii* Zones.

Genus *Sharpeiceras* Hyatt, 1903

Type species: *Ammonites laticlavius* Sharpe (1855: 31, pl. 14: 1a—b), by the original designation of Hyatt (1903: 111).

Diagnosis. — See Matsumoto *et al.* (1969), Kennedy (1971), and Thomel (1972) for recent diagnoses of this genus.

Discussion. — *Sharpeiceras* is a highly distinctive genus reaching a large size, and characterised by high whorls in which all ribs are commonly of similar length, and bear umbilical, mid-lateral, lower and upper ventrolateral tubercles, the latter sometimes merging into a horn.

The genus appears in the lowest Cenomanian in England and France, and has no obvious ancestors. Very small specimens before us from southern Africa show that at diameters of less than 10 mm, species lack a mid-lateral tubercle, and that *Sharpeiceras* is yet another mantelliceratinid with *'Submantelliceras'* nuclei; it appears that some of the minute pyritic specimens which occur in clay facies in North Africa and Madagascar may prove to be juveniles of this genus. In particular, *Sharpeiceras falloti* (Collignon) (1931: 41, pl. 4: 9—12) juveniles are virtually identical with *Acanthoceras* (*Mantelliceras*) *pervinquierei* Collignon (1931: 42 = *'Acanthoceras' villei* Pervinquière 1907: 300 (*pars*), pl. 16: 14—15 (*non* Coquand)), suggesting that *Mantelliceras* (*Pseudomantelliceras*) Thomel, 1972, of which *M. pervinquierei* is type species, may prove to be a subjective synonym of *Sharpeiceras*. *Tlanhualiloceras* Kellum and Minz (1962) is a further synonym (Matsumoto *et al.* 1969).

Occurrence. — *Sharpeiceras* is restricted to the lower two-thirds of Lower Cenomanian, the *carcitanensis* and *saxbii* assemblage Zones and their equivalents. It has a widespread distribution, extending from England to northern and southern France, W. Germany, Poland, Spain, North Africa, the Middle East, Iran, Mozambique, Angola, Zululand, Madagascar, southern India, Tibet, Japan, Mexico, Texas and Peru.

Sharpeiceras laticlavium (Sharpe, 1855)
(pl. 8: 1, 2)

1855 *Ammonites laticlavius* Sharpe: 31, pl. 14: 1a—b.
1903 *Sharpeiceras laticlavium* (Sharpe); Hyatt: 111.
1971 *Sharpeiceras laticlavium* (Sharpe); Kennedy: 64, pl. 27: 1a—c; pl. 28: 1 (with synonymy).
1972 *Sharpeiceras laticlavium* (Sharpe); Thomel: 50, pl. 15: 1; pl. 16: 1.
1972 *Sharpeiceras laticlavium* (Sharpe) var. *macambiquensis* (Choffat); Thomel: 51.
1977 *Sharpeiceras laticlavium* (Sharpe). Juignet and Kennedy: 99, pl. 10: 1, 2a—b (with synonymy).

Holotype: By monotypy, Sharpe's original specimen (1855: pl. 14: 1a—b), GSM 7755, from the Lower Chalk (Cenomanian) of Bonchurch, Isle of Wight.

Material. — Four specimens, GSI 57—60.

Description. — Our specimens range from a wholly septate juvenile 69 mm in diameter to a large disc which is still wholly septate at a diameter of over 200 mm. All are distorted to varying degress, but relative proportions are as follows:

	D	Wb	Wh	Wb:Wh	U	Ribs
GSI 57	68.5 (100)	21.6 (32)	30.0 (44)	0.72	19.0 (27)	35?
GSI 58	113.0 (100)	31.0 (27)	42.0 (37)	0.74	34.5 (36)	36
GSI 60	125.0 (100)	43.5 (35)	52.0 (42)	0.83	47.0 (38)	34
at	93.5 (100)	32.0 (34)	35.0 (37)	0.91	31.5 (34)	33
GSI 59	204.0 (100)	— (—)	79.0 (38)	—	79.0 (38)	32?

The wide scatter of the relative proportions are in large part a reflection of the post-mortem deformation of specimens.

Coiling is very evolute, with a compressed whorl section, the greatest breadth being at the mid-lateral tubercle, with flattened sides, ventrolateral shoulders and venter. Ornament consists of up to 36 ribs per whorl, the number decreasing slightly as size increases. Virtually all ribs are long, with only a few intercalated low on the flank. Most arise singly from umbilical bullae, although there are occasional paired ribs. Ribs are straight, narrow and prorsi- to rectiradiate; all bear a transversely elongated mid-lateral tubercle, conical lower ventrolateral and clavate upper ventrolateral tubercle. The intertubercular area of the venter is distinctly flattened and smooth during early growth, although low ribs connecting clavi occur in our larger individuals.

Discussion. — Distortion gives rather disparate appearances to our specimens, GSI 60 in particular appearing unduly evolute. In spite of this complicating factor, all specimens are linked by the high whorls, dense ribbing and style of tuberculation which typifies Sharpe's species.

The closest forms known as large specimens are *S. indicum* (Kossmat), which has fewer ribs than *laticlavium* at comparable diameters, and has lost the mid-lateral tubercle. Other species differ in their coarser ornament (*S. occidentale* Benavides — Cáceres, *S. florencae* Spath (= *S. tlahualiloense* (Kellum and Mintz)) and development of horns (*S. vohipalense* Collignon, *S. kongo* Matsumoto, Muramoto and Takahashi) or more evolute coiling (*S. schlueteri* (Hyatt)).

Species based on pyritic nuclei are more difficult to compare, but our smaller specimen shows *Sharpeiceras falloti* (Collignon) to be relatively coarsely ribbed and tuberculate by comparison, and *S. piveteaui* (Collignon) (1928—1929: 37, pl. 3: 18, 18a) to be more densely ribbed with many short ribs and a rounded whorl.

Occurrence. — *Sharpeiceras laticlavium* is a very widespread species. The type comes from the Isle of Wight, Hampshire, and there are other specimens from Sussex and Kent, where the species occurs as a rarity in *H. carcitanensis*, and possibly *M. saxbii* assemblage Zone faunas. In France, the species has long been known from the lower part of the Lower Cenomanian. We have seen specimens from the Boullonais, Haute Normandie, Rouen and Sarthe, whilst Thomel has recorded the species from south-eastern France. Elsewhere it is known from W. Germany, North Africa, the Middle East, Mozambique, Zululand, Madagascar, Angola, Texas and Mexico and occurs widely in Iran.

Sharpeiceras florencae Spath, 1925
(pl. 8: 3)

1904 *Acanthoceras laticlavium* (Sharpe); Douvillé: 239, pl. 31: 3.
1925 *Sharpeiceras florencae* Spath: 108, pl. 37: a—d.
1933 *Sharpeiceras florencae* Spath; Collignon: 67, pl. 6: 5.
1959 *Sharpeiceras* cf. *florencae* Spath; Matsumoto: 71; fig. 28.
1962 *Tlahualiloceras tlahualiloense* Kellum and Mintz: 276, pl. 6: 7: 1—2; pl. 8: 1.

Holotype: Spath's original specimen (1925: pl. 37: a—d) from the Lower Cenomanian of Maputoland.

Material. — One specimen only, GSI 61.

Description. — The specimen is a partially septate internal mould with traces of shell. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U	Ribs
GSI 61	115.0 (100)	37.8 (33)	44.5 (39)	0.85	43.0 (37)	22
	88.5 (100)	32.0 (36)	34.5 (39)	0.92	34.0 (38)	21

The coiling is very evolute, the upper ventrolateral tubercles of the early whorls being exposed and housed in notches in the umbilical wall of the later whorls. The umbilicus is broad and of moderate depth, the wall subvertical, with a rounded shoulder. The whorl section is compressed (breadth to height ratios vary from 0.85 to 0.92, in part a reflection of slight distortion), the greatest breadth being at the mid-lateral tubercle. The sides and venter are flattened.

Ornament consists of 21—22 ribs per whorl. All are long, arising at the umbilical seam as low broad swellings, which develop into well marked bullae at the umbilical shoulder. From these bullae, strong, straight recti- to slightly prorsiradiate ribs extend across the flanks. They bear well- developed, radially elongate mid-lateral tubercles, conical lower ventrolateral and prominent clavate upper ventrolateral tubercles. There is a deep concave ventral area between clavi, on which the ribs are effaced.

Discussion. — This specimen stands apart from other *Sharpeiceras* in our collection by virtue of its lower rib density, coarser ornament and lower expansion rate. In these respects it closely resembles *Sharpeiceras florencae* Spath, although bearing even fewer ribs than the holotype. Specimens from the type area of northern Zululand in our own collections show rib densities down to eighteen per whorl at comparable diameters, suggesting the specimen to be within the range of intraspecific variation of the species.

Occurrence. — *S. florencae* characterises the lower part of the Lower Cenomanian in Zululand, and is also known from southern England, Iran, Madagascar, Texas and Mexico.

Subfamily **Acanthoceratinae** Hyatt, 1903

Genus *Acompsoceras* Hyatt, 1903

Type species: *Ammonites bochumensis* Schlüter (1871: 1, pl. 1: 1—4; pl. 2: 1) by the original designation of Hyatt (1903: 111).

Diagnosis. — The genus has been recently diagnosed by Kennedy (1971: 67) and Thomel (1972: 101).

Discussion. — Casey (1965) showed that *Pseudacompsoceras* Spath, 1925 (type species *Pseudacompsoceras vectense* Spath 1925: 192; = *Ammonites coupei* var. Sharpe 1853: pl. 19: 1a—c) referred to the Schloenbachiidae by Wright (1957) comprised merely the coarsely ornamented species of *Acompsoceras*, from which it is inseparable generically or subgenerically.

Cobban (1971) proposed the genus *Paracompsoceras* (type species *Paracompsoceras landesi* Cobban 1971: 10, pl. 2: 24—26; pl. 6; pl. 7, pl. 8; pl. 9: 5—8; figs. 9—11) for late Cenomanian acanthoceratids which had *Acompsoceras*-like smooth body whorls, but nuclei which were strongly ribbed, and like *Acanthoceras*, bore long and short ribs, the long ribs with umbilical, lower and upper ventrolateral and siphonal tubercles, the short ribs with ventrolateral and siphonal tubercles only. The suture (Cobban 1971: fig. 10) does not show the same deep incision as some *Acompsoceras*,

although showing the same tendency to subphylloid folioles. The genus was regarded as a homoeomorph of *Acompsoceras*, and presumably derived independently from earlier endemic U.S. Interior *Acanthoceras* species. Some *Acompsoceras* from Sarthe, France, before us have similar lateral ornament and tuberculation to *P. landesi*, as well as bearing siphonal clavi; so marked are these similarities that we believe *Paracompsoceras* may be a junior subjective synonym of *Acompsoceras* rather than an independent homoeomorphic development.

Occurrence. — This is usually a rather rare genus. It appears in *carcitanensis* Zone faunas in southern England, and ranges well into the Middle Cenomanian; it has also been recorded from the lower parts of the Upper Cenomanian. The geographic distribution encompasses southern England, the Boullonais, Haute Normandie, Rouen, Sarthe, the Basses-Alpes, W. Germany, Poland, North Africa, the Middle East, Zululand, Madagascar, Texas and the U.S. Western Interior. The present material represents the first record from Iran.

Acompsoceras sp. indet.
(pl. 7: 1)

Material. — One specimen only, GSI 62.

Description. — The specimen is a distorted internal mould of a wholly septate shell with the following dimensions:

	D	Wb	Wh	Wb:Wh	U
GSI 62	144.5 (100)	45.0 (31)	64.0 (44)	0.70	34.5 (24)
	102.5 (100)	34.5 (34)	47.5 (46)	0.73	25.5 (25)

Coiling is moderately involute, with compressed, high whorls (breadth to height ratio is around 0.70), the greatest breadth being just below mid-flank. The umbilicus is shallow, with a low wall and rounded shoulder. The flanks are flattened, and converge to abruptly rounded shoulders. The venter is relatively broad, and flat.

Approximately twenty feeble umbilical bullae give rise to low, faint, straight, prorsiradiate ribs, whilst other ribs intercalate on the flank, giving a total of approximately forty-five ribs on the outer whorl. Narrow at their origin, the ribs broaden on the outer flank, and terminate as small clavate ventral tubercles; the venter is flat between these tubercles, with a faint siphonal swelling in places.

The suture, imperfectly exposed, is intricately subdivided, with phylloid folioles.

Discussion. — Because of poor preservation, full determination of this specimen is not possible. Whorl section, ornament and coiling all suggest that it is an *Acompsoceras*; there are several named forms with comparable feeble dense ribs, including *Acompsoceras essendiense* (Schlüter) *madjeurensis* Pervinquière (1907: 306, pl. 17: 6, 7), *A. tenue* Collignon (1964: 109, pl. 357: 1572—3; pl. 358: 1574), *A. sahnii* Collignon (1964: 111, pl. 358: 1575—1576) and *A. catzigrasae* Collignon (1964: 112, pl. 358: 1577). Without better material no adequate comparisons can be made with the Iranian form.

Occurrence. — The species compared to the Iranian specimen are from the Lower Cenomanian of England, France, North Africa and Madagascar.

DISCUSSION

Age of the fauna

Although previous workers have recorded Upper Albian (e.g. *Mortoniceras, Pleurohoplites renauxianus*), to Upper Cenomanian ammonites (e.g. *Calycoceras naviculare*), the material described above is wholly and

unequivocally of Lower Cenomanian age. The most detailed subdivisions proposed for this substage are in western Europe, and have been summarised by Kennedy (1971), Hancock and Kennedy (1971), Kennedy and Hancock (1977) and Juignet and Kennedy (1977), whilst range charts of critical species in western Europe and the Cenomanian stratotype area are given by Kennedy and Juignet (1975) and Juignet (1974, 1977). From these sources it is clear that the faunas described here characterise the lower parts of the Lower Cenomanian of western Europe, the *Hypoturrilites carcitanensis* Zone, and also the transitional interval to the succeeding *Mantelliceras saxbii* Zone. The *Sharpeiceras*, *Idiohamites*, *Sciponoceras* and inflated *Mantelliceras* in particular are indicative of the *H. carcitanensis* Zone, but the common occurrence of more compressed predominantly ribbed *Mantelliceras* (*M.* aff. *costatum*, *M.* aff. *couloni*, *M. ventnorense*) is a feature of the *M. saxbii* Zone. We would suggest that either the Glauconitic Limestone at Kolah-Quazi spans the zonal boundary, or that it is a condensed equivalent of part of these two zones. There is no evidence in the material before us for the presence of earlier Albian or later Middle to Upper Cenomanian elements, and this is confirmed by analysis of the *Schloenbachia* population present, which also indicates a low Lower Cenomanian horizon. We can only await full description and illustration of faunas described by previous workers to either confirm or dismiss the much wider dating of the Glauconitic Limestone previously suggested.

Composition of the Fauna

The generic composition of the material before us may be summarised as follows (total number of specimens = 113):

	%
Anglonautilus	0.88
Stomohamites	0.88
Sciponoceras	0.88
Idiohamites	1.76
Ostlingoceras	0.88
Mariella	2.65
Hypoturrilites	3.53
Turrilites	0.88
Scaphites	5.30
Puzosia	1.76
Austiniceras?	0.88
Hyphoplites	4.42
Schloenbachia	26.54
Sharpeiceras	3.53
Mantelliceras	43.36
Acompsoceras	0.88

Objective estimates of generic composition of Cenomanian faunas are only available for England and northern France (Juignet and Kennedy 1977), where *Schloenbachia* constitutes an overwhelming proportion of

faunas, often in excess of 90% of any given collection. The only levels known to us where *Mantelliceras* is dominant are in the Basement Bed of the Wilmington Sands at Wilmington in Devon (Kennedy 1970) and in some of the coarse clastic facies of the Lower Cenomanian of Sarthe. We do not know if these exceptions are merely a reflection of differences in age, or a result of environmental conditions leading to the relative exclusion of *Schloenbachia* from sandstone facies. A more probable explanation is to be found in the view that the Iranian faunas correspond to those of more southerly parts of the western European area, where *Schloenbachia* is known to become scarcer, although it is perhaps surprising that a collection of this size contains no Mesogean elements, even as rarities.

Given the known proximity of the Esfahan faunas to the Zagros line, a geographical interpretation of the difference in generic composition when compared to those of England and northern France is the more likely explanation.

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GŁOWONOGI Z WAPIENIA GLAUKONITOWEGO POŁUDNIOWOWSCHODNIEGO ISFAHANU, IRAN

Streszczenie

W pracy przedstawiono faunę głowonogów z cenomańskiego Wapienia Glaukonitowego odsłoniętego na obszarze południowowschodniego Isfahanu (Iran). W skład tej fauny, mającej wyraźnie borealny charakter wchodzą gatunki *Anglonautilus, Stomohamites, Sciponoceras, Idiohamites, Ostlingoceras, Mariella, Hypoturrilites, Turrilites, Scaphites, Puzosia, Austiniceras, Hyphoplites, Schloenbachia, Mantelliceras, Sharpeiceras* i *Acompsoceras*, których większość notowana jest po raz pierwszy na tym obszarze. Zbadana fauna jest jednoznacznie dolnocenomańskiego wieku i daje się dokładnie korelować na dystansie około 5000 km z wycinkami zon *Hypoturrilites*

carcitanensis i *Mantelliceras saxbii* północnozachodniej Europy. W opracowanym materiale nie stwierdzono obecności żadnego z głównogów górnoalbskich, środkowo- i górnocenomańskich wzmiankowanych z Wapienia Glaukonitowego przez wcześniejszych autorów. Pod względem ilościowym zbadana fauna zdominowana jest przez akantoceratydy, w przeciwieństwie do równowiekowych faun północnozachodniej Europy, w których przeważają przedstawiciele *Schloenbachia*. Wskazuje to na położenie Isfahanu w południowej części strefy borealnej, charakteryzującej się stopniowym zanikiem *Schloenbachia*. Położenie takie potwierdza także bliskość linii tektonicznej Zagros, łączącej płytę azjatycką z arabską.

EXPLANATION OF THE PLATES 1—8

Plate 1

1. *Anglonautilus undulatus* (J. Sowerby). GSI 1, ×0.76.
2. *Ostlingoceras (Ostlingoceras) rorayensis* (Collignon) GSI 19, ×0.76.
3. *Mariella (Mariella)* aff. *harchaensis* (Dubourdieu). GSI 10, ×0.76.
4. *Sciponoceras* cf. *roto* Cieśliński. GSI 13, ×1.5.
5. *Stomohamites simplex* (d'Orbigny). GSI 12, ×0.76.
6. *Mariella (Mariella)* species undetermined. GSI 11, ×0.76.
7, 12. *Hypoturrilites carcitanensis* (Matheron). GSI 11, ×0.76.
8. *Hypoturrilites gravesianus* (d'Orbigny). GSI 15, ×0.76.
9. *Mariella (Mariella) dorsetensis* (Spath). GSI 12, ×0.76.
10. *Turrilites*, species undetermined. GSI 13, ×0.76.
11. *Idiohamites alternatus* (Mantell) *vectensis* Spath. GSI 4, ×0.76.
13. *Puzosia (Puzosia)* cf. *octosulcata* (Sharpe). GSI 16, ×0.76.

Plate 2

1, 9. *Hyphoplites curvatus* (Mantell), transitional towards *H. pseudofalcatus* (Semenow). GSI 18 and 19, ×0.76.
2, 8. *Hyphoplites arausionensis arausionensis* (Hébert and Munier-Chalmas). GSI 17 and 21, ×1.
3. *Scaphites (Scaphites) equalis* (Sowerby). GSI 25, ×1.5.
4, 5, 11. *Scaphites (Scaphites) obliquus* (Sowerby) GSI 23, 24, 26, ×1.5.
6. *Austiniceras*? sp. juv. GSI 14, ×0.76.
7. *Puzosia (Puzosia)* cf. *subplanulata* (Schluter). GSI 15, ×0.76.
10. *Hyphoplites arausionensis arausionensis* (Hébert and Munier-Chalmas). GSI 17 and 21, ×0.76.

Plate 3

1. *Callihoplites* aff. *vraconensis* (Pictet and Campiche) specimen showing transitional features towards *Schloenbachia varians* J. Sowerby). OUM K4865, from the late

Albian *Dispar* Zone Ammonite Bed the top of the Upper Greensand, Dorsetshire Gap, Dorset.

2—7. *Schloenbachia varians* (Sowerby). 2 is GSI 42, a transitional form between *subtuberculata* (Sharpe) and *subvarians* (Spath), with a specimen of *Idiohamites ellipticus* (Mantell) *radiatus* (Spath) in the aperture. 3 is close to *subvarians* Spath; 4 corresponds to *intermedia* (Mantell); 5 and 7 are *varians sensu stricto*; 6 is a *subtuberculata* (Sharpe).

Plate 4

1—5. *Schloenbachia varians* (Sowerby). 1 is GSI 49, and corresponds to *S. varians subvarians* Spath; 2 is GSI 31, and is a passage form between varians and *subtuberculata*; 3 is GSI 63, a *subvarians* Spath and 4 and 5 are *S. varians subtuberculata* (Sharpe), GSI 43 and 48.

Plate 5

1. *Mantelliceras costatum* (Mantell). GSI 94.
2. *Mantelliceras* aff. *oculoni* (d'Orbigny). GSI 90.
3, 5. *Mantelliceras cantianum* Spath. GSI 86 and 82.
4. *Mantelliceras* aff. *saxbii* (Sharpe). GSI 112.
6. *Mantelliceras* aff. *cantianum* (Spath). GSI 79.

Plate 6

1. *Mantelliceras mantelli* (Sowerby), slightly transitional to *cantianum* Spath. GSI 69.
2, 4, 5. *Mantelliceras* aff. *costatum* (Sharpe), GSI 100, 101, 98.
3. *Mantelliceras mantelli* (Sowerby). GSI 72.

Plate 7

1. *Acompsoceras* sp. indet. GSI 62, ×0.53.
2. *Mantelliceras* aff. couloni (d'Orbigny). GSI 91, ×0.76.
3. *Mantelliceras ventnorense* (Diener). GSI 113, ×0.76.
4. *Mantelliceras cantianum* (Spath). GSI 81, ×0.76.
5. *Mantelliceras saxbii* (Sharpe). GSI 107, ×0.76.

Plate 8

1, 2. *Sharpeiceras laticlavium* (Sharpe). 1 is GSI 60, ×0.8; 2 is GSI 57, ×0.76.
3. *Sharpeiceras florencae* Spath. GSI 61, ×0.76.
4. *Mantelliceras mantelli* (Sowerby). GSI 74 a compressed variant, ×0.76.
5. *Mantelliceras* aff. *saxbii* (Sharpe). GSI 97, ×0.76.

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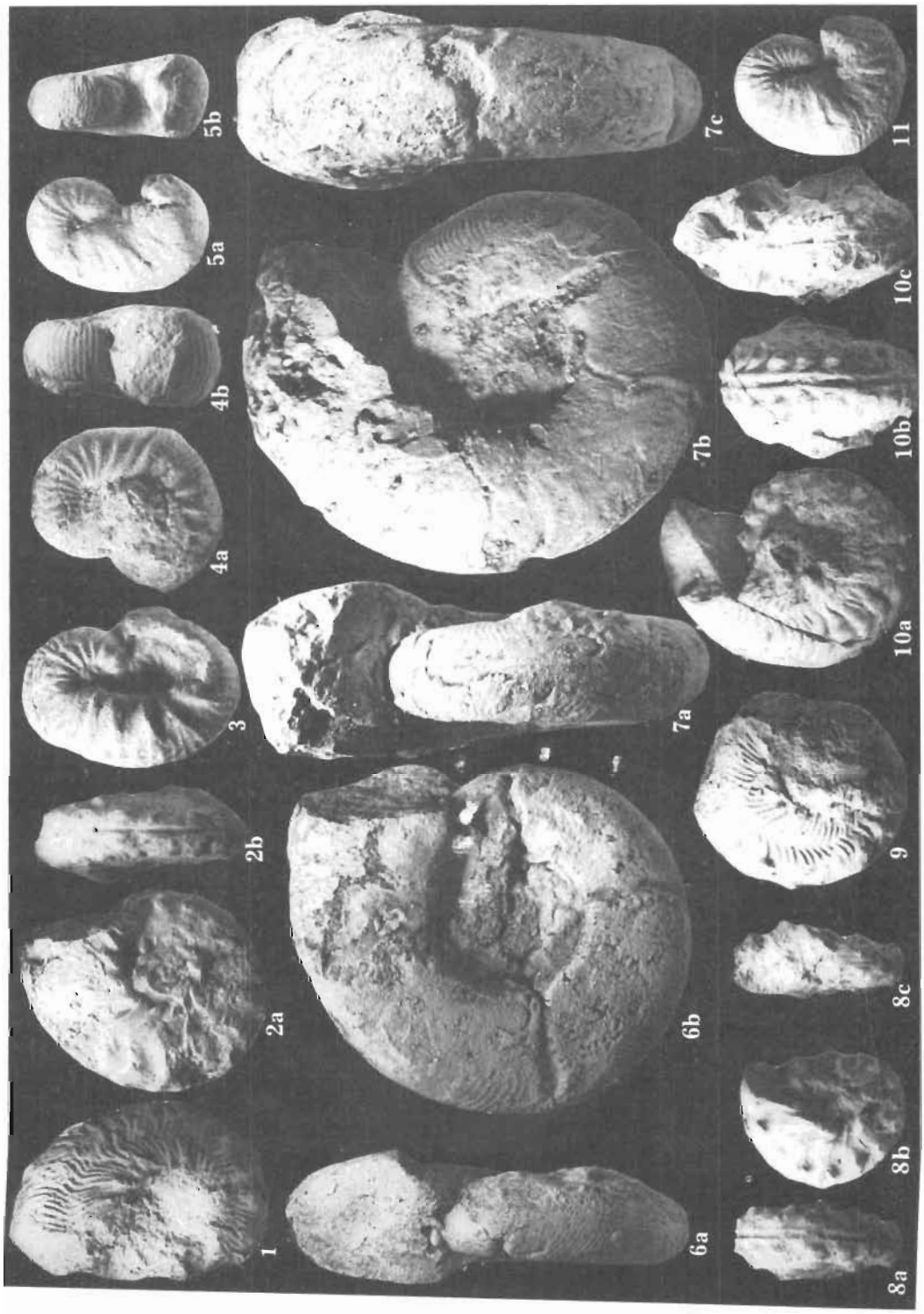
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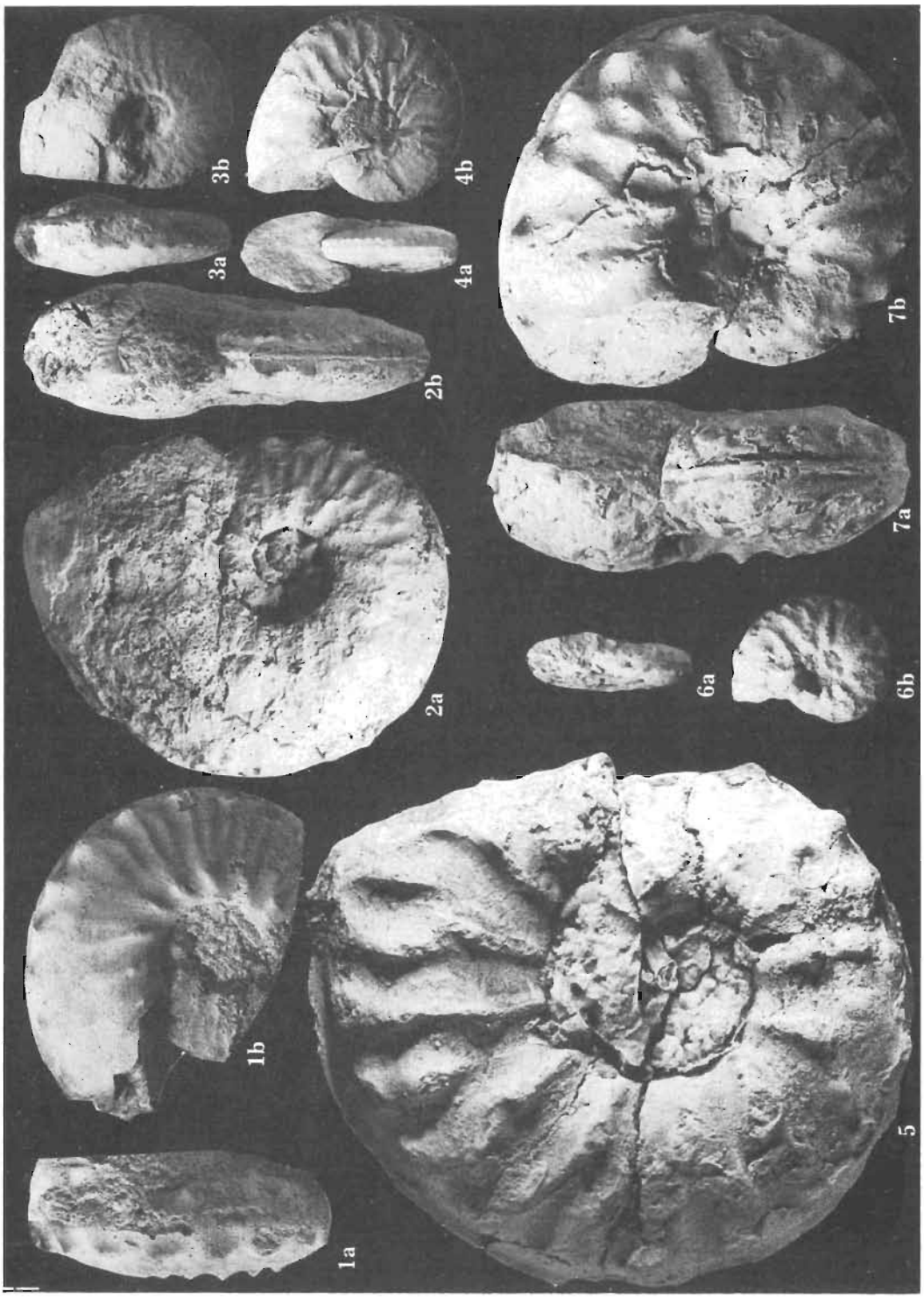
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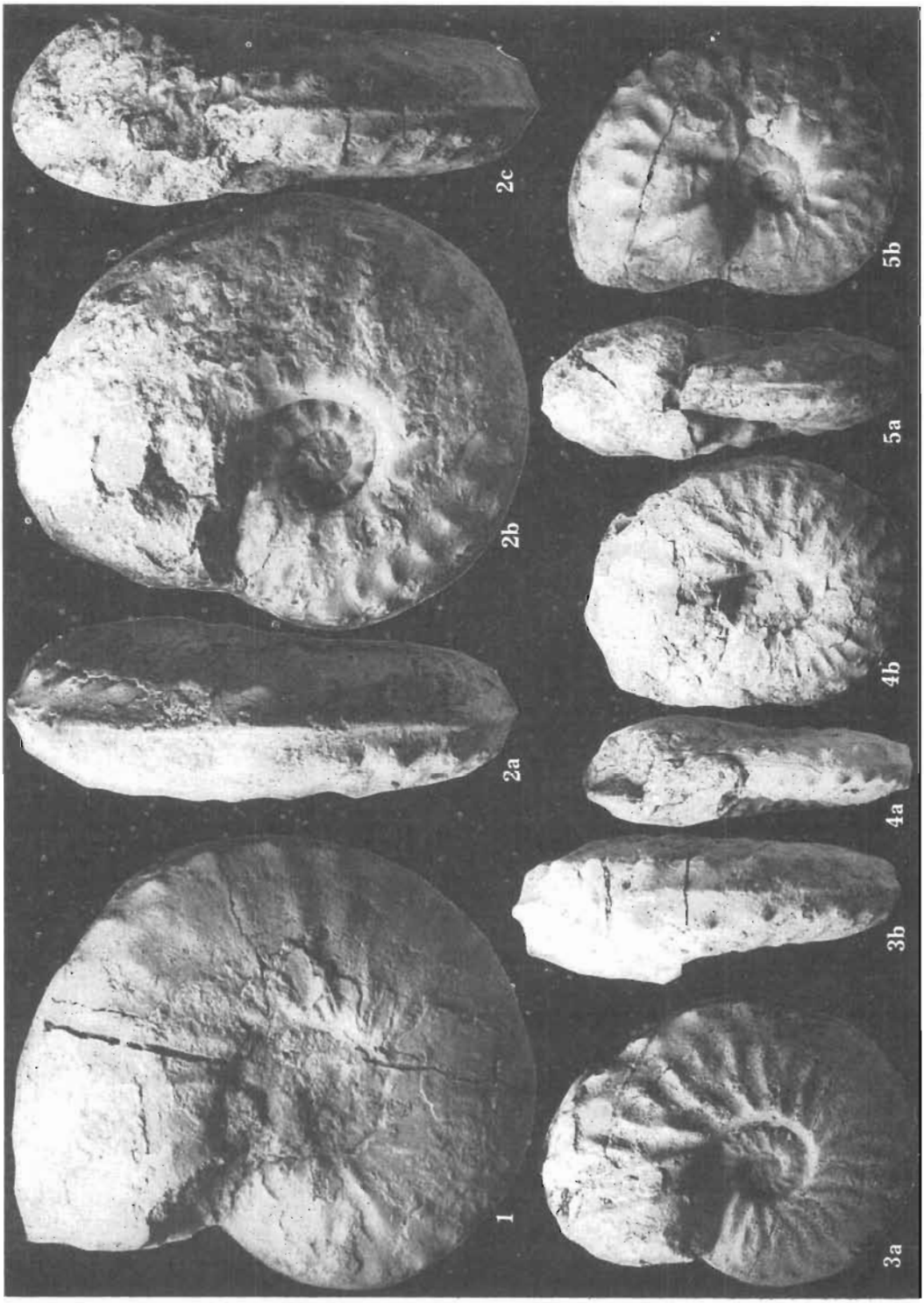
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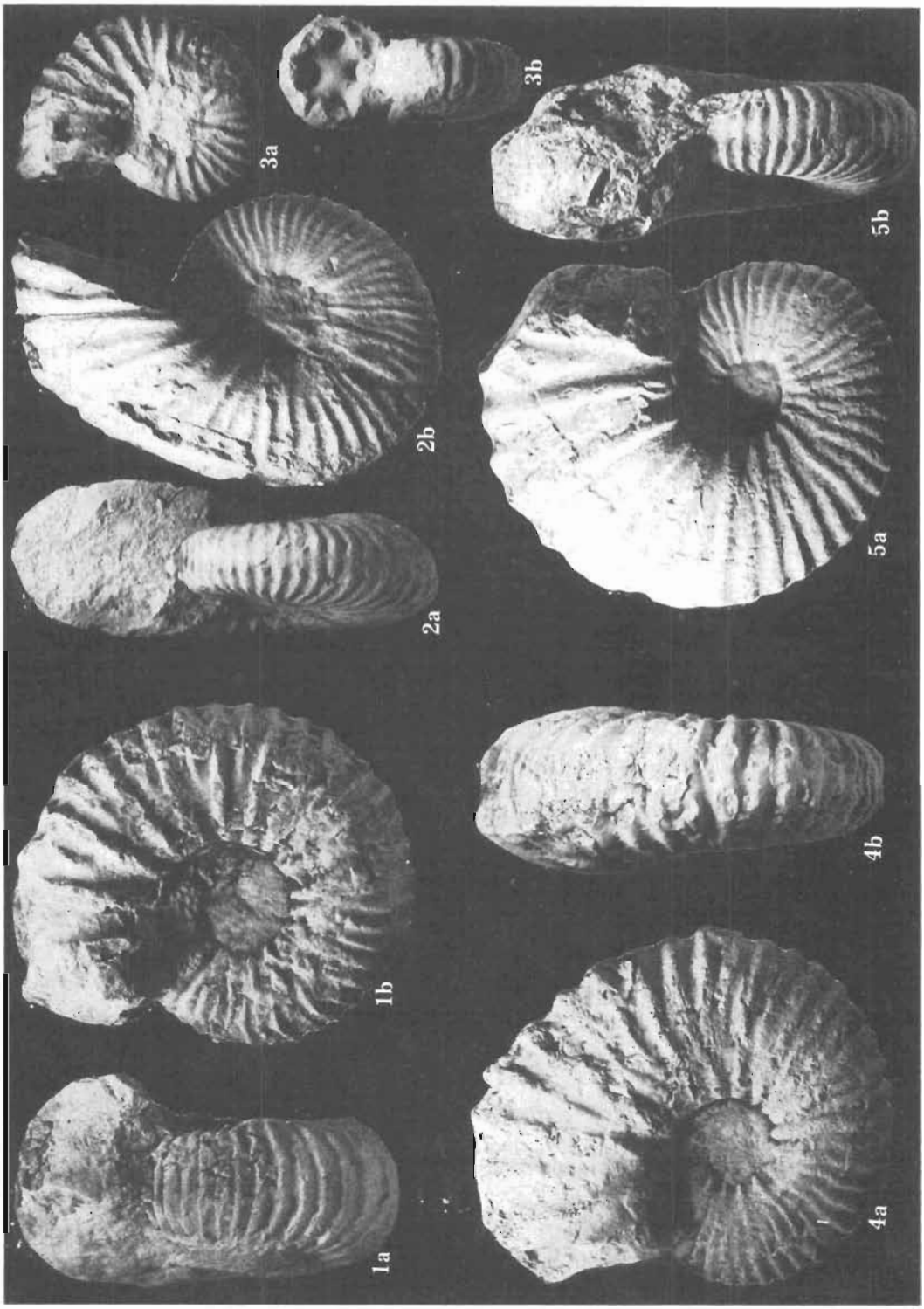
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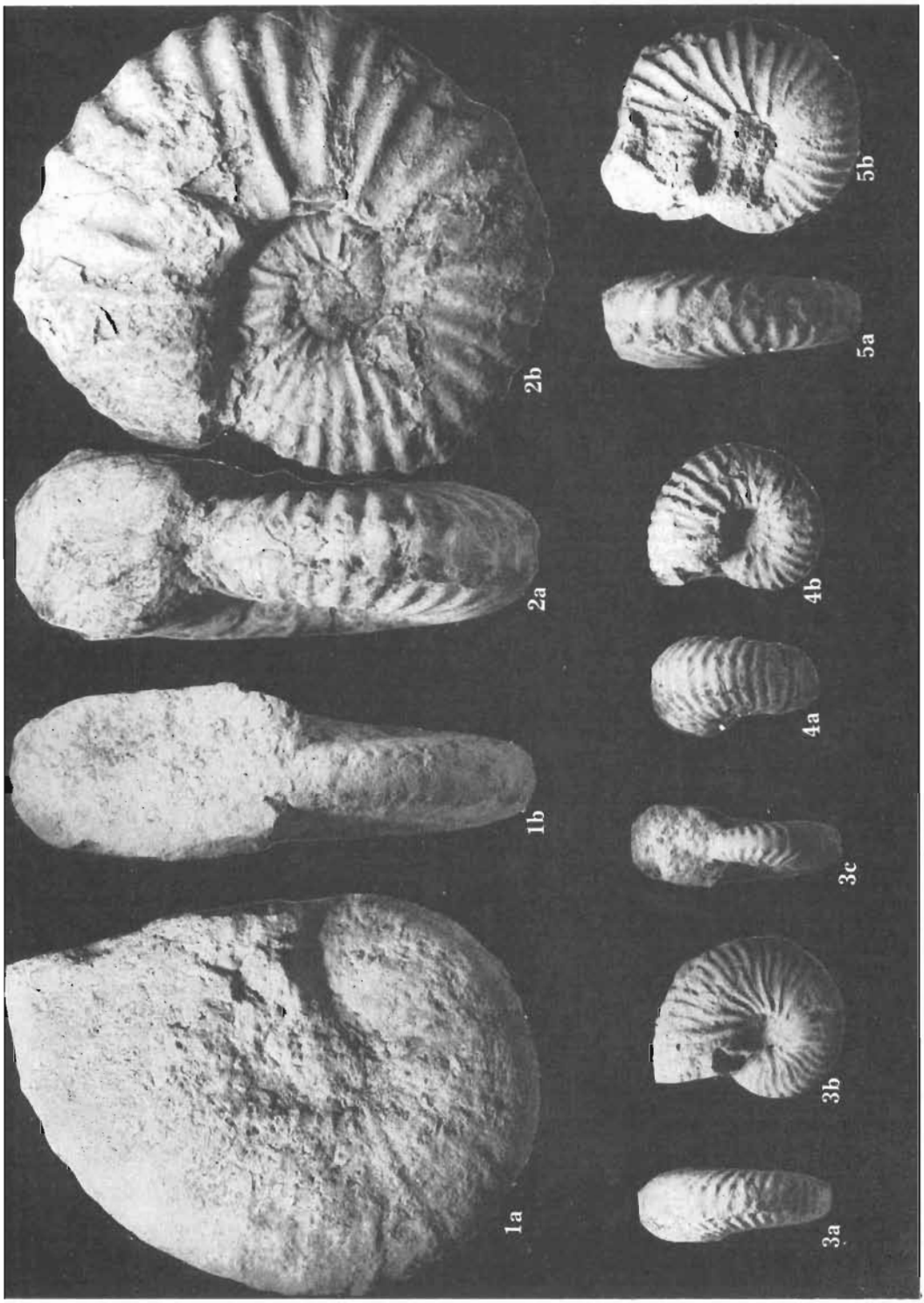
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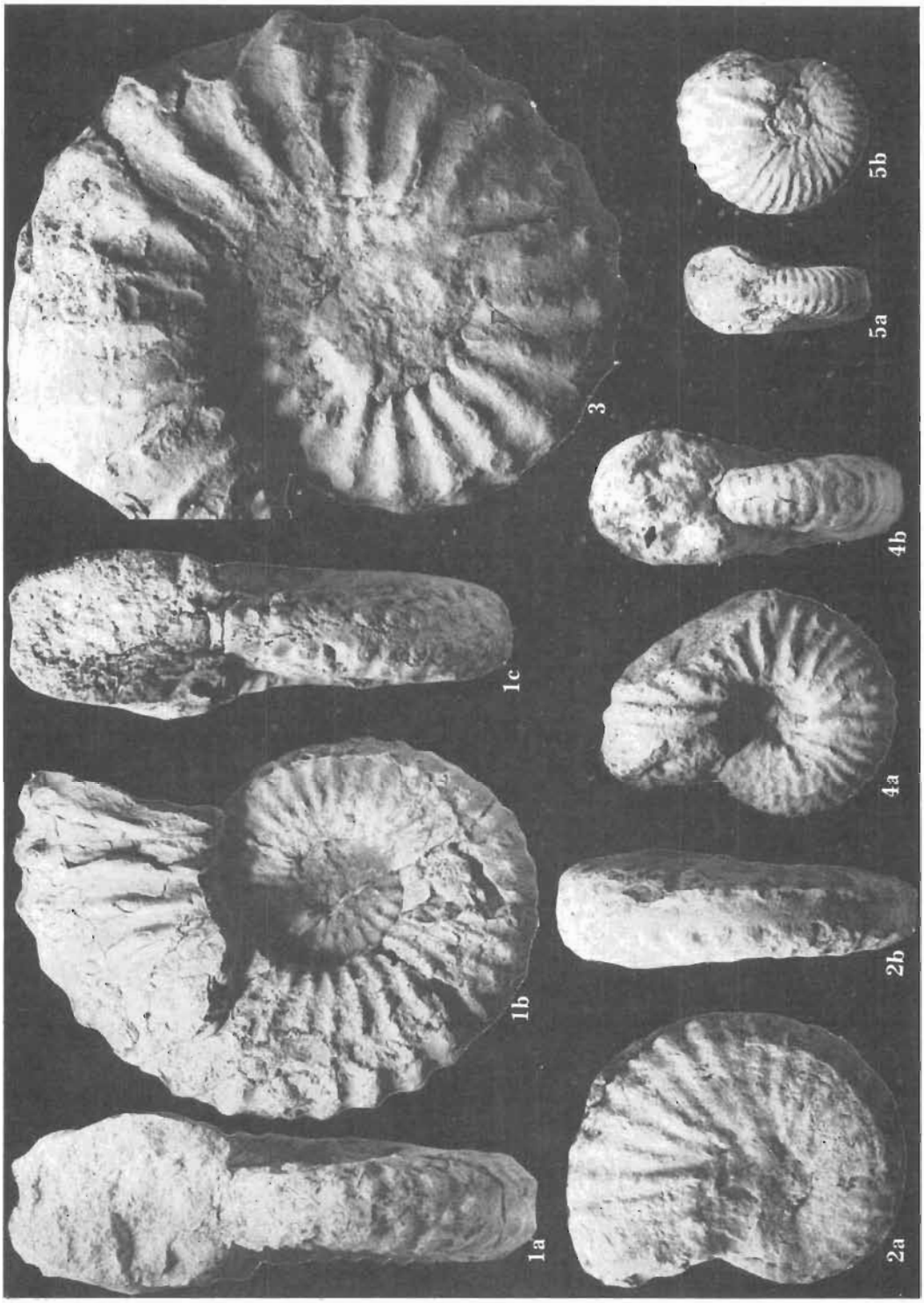
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