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The ammonites of the English Chalk Rock
(Upper Turonian)

C. W. Wright

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C. W. Wright

Old Rectory, Seaborough, Beaminster, Dorset DT8 3QY

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Synopsis

The English Chalk Rock fauna of ammonites (Upper Cretaceous, Upper Turonian) is described as an aid to international correlation. It comprises 28 species and subspecies referred to 15 genera. Five new species (*Anisoceras reidi*, *Allocrioceras strangulatum*, *Scaphites diana*, *Otoscapites reidi* and *Lewesiceras woodi*) and 2 new subspecies (*Scaphites geinitzii laevior* and *S. lamberti doylei*) are described. Lectotypes are designated of *Scaphites geinitzii* d'Orbigny, *S. g. intermedius* Scupin, *S. fritschi* Grossouvre [= *S. auritus* Fritsch, non Schlüter] and *Puzosia curvatisulcata* Chatwin & Withers. *Pseudopuzosia* Spath is placed in the synonymy of *Pseudojacobites* Spath.

Introduction

This paper comprises a full description of the ammonite component of the fauna of the Upper Turonian Chalk Rock of southern England, together with some conclusions for correlation. The fauna includes a number of wide-ranging ammonite species and, since they occur together in England in beds representing a relatively short period of time, the fauna is of particular importance as a standard of comparison in a stage in which few abundant ammonite faunas are known.

The individual study of which this paper describes some of the results has been largely overtaken by the International Geological Correlation Programme Project on Mid-Cretaceous Events and the paper is therefore offered in the context of that project.

The Chalk Rock

Above the Cenomanian the English Chalk ceases in general to contain many ammonites and it is only at a few narrow horizons that they are at all common. The best-known of these is the Chalk Rock. It is a variable composite hardground or series of hardgrounds (Kennedy & Garrison 1975 and references therein) up to about 4 m thick, but generally less, occurring in the lower part of the *Holaster planus* Zone, the highest of the three conventional zones of the English Turonian chalk. The upper surface (where it comprises a single bed) and the top of individual hardgrounds (where separate) are irregular, and generally have included in them or immediately above them phosphatized cemented chalk pebbles, often green-coated, and phosphatized fossils. Similar fossils, normally less well preserved and less abundant, may be found lower in the hardgrounds. The fauna is large and varied; its most characteristic elements are lithistid and hexac-

tinellid sponges and aragonitic molluscs – scaphopods, gastropods, bivalves and cephalopods. Woods (1896–97) described and figured many of them and Billinghamurst (1927) described further species of ammonites. In recent years much collecting has been done, particularly at Billinghamurst's locality of Hill End Farm, Hitch Wood near Hitchin, at Reed near Royston and at Kensworth near Luton. A good many new forms have come to light.

Although specimens of ammonites have been collected at various levels in the series of hardgrounds at different localities there is no significant difference in the lists from place to place apart from the abundance of *Baculites undulatus* at Reed and Kensworth and its absence elsewhere. It is therefore reasonable to treat the fauna as a single one, occupying part of the lower part of the *Holaster planus* Zone.

The Chalk Rock occurs in East Anglia and the south Midlands, extending as far west as north Dorset and Wiltshire. Outside this area there may be incipient hardgrounds or beds of nodular chalk that yield the Chalk Rock fauna. Elsewhere specimens of the aragonitic mollusca may occasionally be found in normal chalk of the *Holaster planus* Zone. In Yorkshire several cases are known (Wright 1935) of patches of chalk containing abundant aragonitic gastropods and bivalves apparently protected from dissolution by large ammonite shells that lay above them. It can only be assumed therefore that elements of the Chalk Rock fauna occurred more widely and persistently than in the special conditions under which the hardgrounds were formed.

Systematic descriptions

The following abbreviations are used.

BM	British Museum (Natural History)
coll.	collected by, or collection of
GSM	Geological Survey Museum of the Institute of Geological Sciences
GSP	Geological Survey, Pretoria, South Africa
IGS	Institute of Geological Sciences
MMH	Mineralogical Museum, Copenhagen
SM	Sedgwick Museum, Cambridge
WW	C. W. & E. V. Wright collection

Superfamily TURRILITACEAE Meek, 1876

Wiedmann (1962 : 179; 1969; 1973) has published successive revisions of the classification of Cretaceous heteromorphs, mainly in contrast with that adopted in the *Treatise on Invertebrate Paleontology* (Wright 1957b). A few points, relevant to the present work, are discussed here.

Wiedmann rejects the separation at superfamily level of the Turrilitaceae from the Ancylocerataceae. However, even if, as is probable, the earliest families assigned to the Turrilitaceae (Anisoceratidae and Hamitidae) were derived from one or more ancyloceratine ancestors, the Turrilitaceae represent a renewed radiation based primarily on bifid sutural lobes, in contrast with the trend to trifid lobes in most stocks of Ancylocerataceae.

Wiedmann included in an enlarged family Baculitidae not only the Hamitinae, Baculitinae and Polytychoceratinae but also Ptychoceratinae; moreover his Baculitinae embraced the wholly Lower Cretaceous group of Bochianitinae. There is in fact no good evidence to contradict Spath's (1941 : 659) view that the Baculitidae were derived, by way of *Lechites*, from straightening members of *Hamites*; they constitute a group starting with and retaining bifid lateral lobes. On the other hand the Bochianitidae start (in late Jurassic) and end with trifid lateral lobes.

As to the taxonomic level of the hamitids and baculitids, although the sutures are generally similar the remainder of the morphology is so distinct (with implications for the biology) that by normal ammonite standards family separation is wholly justifiable.

There is much to be said for Wiedmann's reduction of the Nostoceratidae and Diplomoceratidae to subfamilies of Turrilitidae, and this view is adopted here. The former include a wide range of late Upper Cretaceous loosely and tightly coiled forms, many of which closely resemble the

Middle Albian immediate precursors of *Turrilites* and its close allies. The subfamily Diploceratinae, on the other hand, comprises a mixed bag of more or less hamitoid presumed offshoots of the Nostoceratinae.

Family **HAMITIDAE** Meek, 1876

Genus *METAPTYCHOCERAS* Spath, 1926

TYPE SPECIES. *Ptychoceras smithi* Woods, 1896.

The genus comprises small forms, with more or less straight penultimate and final shafts closely pressed together and finely ribbed; the almost smooth, feebly constricted initial shaft is described below for the first time.

The type species was the only one referred to the genus by Spath and he gave no generic diagnosis. Thus it is not clear what he envisaged as the difference between this genus and *Hemiptychoceras* from the Upper Albian which he described the year before (Spath 1925 : 189). *Metaptychoceras* is diagnosed (Wright 1957b : L217) as 'small; much like *Hemiptychoceras* but has fine ribbing of *Stomohamites*', as opposed to *Hemiptychoceras* which has 'ribs as in *Hamites* except on 2nd bend where they tend to be scale-like, as in some *Euptychoceras*'.

Subsequently Wiedmann (1959 : 715) quoted *M. smithi* from his Spanish zone of *Fallotites* (*Ingridella*) *malladae*, the fifth from the base of seven zones into which he divided the Lower Turonian. A species of the genus has also been found in Colombia. Cobban & Scott (1972 : 45) described a new species *Hemiptychoceras reesidei* from the uppermost Cenomanian (*Sciponoceras gracile* horizon) Bridge Creek Limestone of Colorado and referred to 'a smaller but very closely related species' from the basal Turonian with *Watinoceras coloradoense* of South Dakota.

Reviewing all this material it seems that the distinction between *Hemiptychoceras* and *Metaptychoceras* is slight but real. The former is larger, more coarsely ribbed and with constrictions on the penultimate shaft and final bend. The latter is very small, finely ribbed and with no constrictions after the initial shaft. A decision whether these differences justify generic separation must await the discovery of more specimens of these rare forms.

Metaptychoceras smithi (Woods)

Pl. 1, figs 1, 2

- 1896 *Ptychoceras smithi* Woods : pl. 2, figs 1, 2.
 1926 *Metaptychoceras smithi* (Woods) Spath : 81.
 1959 *Metaptychoceras smithi* (Woods); Wiedmann : 715.

HOLOTYPE. SM B4098, from Cuckhamsley Knob.

DESCRIPTION. Small, with two slender, more or less straight and parallel, shafts followed by a closely adpressed hook; there was probably a minute initial coiled spire, but this has not yet been found. The recurved part of the hook is circular in section and rests in a rather deep groove in the dorsum of the shaft; there is a minute 'umbilicus' at the bend. The first shaft is smooth except for an occasional feeble oblique constriction and accompanying fold. Weak oblique ribs begin soon after the first bend and rapidly become radial, low, rounded and dense. In one specimen (BM C79653; Pl. 1, fig. 1) on the later part of the second bend and the beginning of the second shaft they are rursiradiate, sharp and distant; thereafter they are a little coarser, more distant and radial. In another specimen (BM C79658) the ribs have almost disappeared on the bend and only become strong on the latter part of the final shaft. Woods differentiates the species from *Hemiptychoceras gaultinum* (Pictet) by the absence of any coarsening of the ribs on the bend, but the ribbing in the later stages in *M. smithi* seems to be variable and detailed differences are probably unimportant. The suture consists of rather wide and splayed, moderately subdivided and very regularly bifid elements; the external lobe is a little less deep than the first lateral lobe.

OCCURRENCE. The species seems to be rare, but being small may sometimes pass unnoticed. Besides the holotype from Cuckhamsley (SM B4098) there is a specimen (SM B21326) from Lannock Farm, east of Hitchin. Hill End Farm Pit, Hitch Wood yielded to R. E. H. Reid two specimens more complete than the holotype and to R. G. Bromley the juvenile specimen here figured. A specimen was recorded from Burham, Kent by Dibley (1912 : 373).

Family **BACULITIDAE** Meek, 1876

Genus **SCIPONOCERAS** Hyatt, 1894

TYPE SPECIES. *Hamites baculoides* Mantell, 1822.

Sciponoceras appears first in the *dispar-perinflatum* Subzone of the uppermost Albian in England and France. These early forms are not yet well known, since only rather short fragments of internal casts have been found. They seem to be derived directly from a species of *Lechites*, such as *L. communis* Spath, by the almost complete loss of ribs and the strengthening of constrictions. Small fragments of similar forms are found in the early Cenomanian Glauconitic Marl of the Isle of Wight. They may be distinct from the type species, *S. baculoides* (Mantell), but well-characterized specimens have yet to be found.

The Chalk Marl of Sussex and the Isle of Wight has yielded fairly well preserved specimens similar to the type specimens of *S. baculoides* (Kennedy 1971 : pl. 2, figs 1–5), characterized by an oval whorl section, strong and fairly close constrictions with only the faintest of intermediate ribs, strong ventral ribbing just before the aperture and a dorsally-directed aperture with ventral sinus and lateral lappets. By the middle of the Cenomanian in England (the Dorset and Somerset basement beds, Kennedy's *Turrilites acutus* assemblage) there is a species differing from *S. baculoides* mainly in its aperture, which is oblique instead of slightly curved, has only feeble lateral lappets and has a ventral rostrum instead of sinus. In the uppermost Cenomanian with *Metoicoceras* in Europe and the United States occurs *S. gracile* (Shumard), with ribs that become very strong in adults. In the earliest Turonian there is, in England at least, a form which foreshadows the typical *S. bohemicum* described below.

S. bohemicum (Fritsch) retains marked constrictions and an aperture not very different from that of the Cenomanian type species; despite certain other features it can be fairly regarded as a *Sciponoceras*. It is accompanied, however, by an early form of true *Baculites*, also described below, and is probably the last *Sciponoceras*.

Sciponoceras bohemicum (Fritsch)

Pl. 1, figs 3–5; Pl. 7, figs 10, 12

- 1843 *Baculites anceps* Geinitz : 9.
 1850 *Baculites baculoides* Geinitz : 122.
 1872 *Baculites faujassi* Lamarck var. *bohémica* Fritsch : 49; pl. 13, figs 23–25, 29, 30.
 1874 *Baculites baculoides* Geinitz; Geinitz : 195; pl. 35, figs 17–21.
 1875 *Baculites bohemicus* Fritsch; Barrois : 403.
 1876 *Baculites* cf. *bohemicus* Fritsch; Schlüter : 140; pl. 39, figs 1–5.
 1893 *Baculites Faujassi* var. *bohémica* Fritsch & Schlönbach; Fritsch : 80, fig. 63.
 1895 *Baculites Faujassi* var. *bohémica* Fritsch; Jahn : 133; pl. 8, fig. 8.
 1896 *Baculites bohemicus* Fritsch & Schlönbach; Woods : 76; pl. 2, figs 9, 10.
 1908 *Baculites (Lechites) Bohemicus* Fritsch & Schlönbach; Nowák : 348–350.
 1927 *Cyrtochilus bohemicus* (Fritsch & Schlönbach) Billingshurst : 513.
 1951 *Sciponoceras bohemicum* (Fritsch) Wright & Wright : 16.

LECTOTYPE. The original of Fritsch's 1872: pl. 13, fig. 25a, b, c, here designated.

DESCRIPTION. The shell increases very slowly in height and width; it is elliptical in section with the sides tending to become flattened with age.

	Dorsoventral diameter	Transverse diameter
BM C79497	5.5 mm	4 mm
BM C79496	12.5 mm	9.5 mm

The body chamber becomes somewhat triangular in section towards the aperture. During the camerate stage there are on internal casts rather frequent broad shallow constrictions at somewhat irregular intervals. In the early stages they are almost as strong on the dorsum as on the sides and venter, but the dorsal part weakens with age and in many individuals they become almost imperceptible on the inner third of the side. The constrictions run backwards at an angle of about 120° to the long axis of the shell, then curve forward a third of the way up the side to run obliquely at about 40° to the long axis as far as the venter, which they cross in a broad curve with a steep rear and a shallow forward slope. Between the constrictions there are in the early stages two or three low rounded ribs, distinct on the outer third and on the venter. Later they become flattened and indistinctly branched. On the body chamber the ribs are distinct also on the inner part of the sides where they branch from crescentic bullae which are low but perceptible, to strong. At this stage, in the absence of constrictions, the ornament is somewhat like that of the camerate part of contemporary *Baculites undulatus*. At the aperture the dorsum and in fact the whole shell curves inwards, the aperture being directed about 45° dorsally. There are no lappets or collars such as characterize the Cenomanian species of *Sciponoceras*, and the aperture is much like that of *S. gracile* (Shumard).

The suture has rather irregularly bifid elements. The first lateral (external) saddle is much higher than the next one and the umbilical lobe and internal saddle are markedly shorter than the other elements.

REMARKS. Although *S. bohemicum* has been frequently quoted in the literature and has been figured several times there is no satisfactory description of the species. The English Chalk material has yielded many fragments of internal moulds in hard phosphatized chalk which allow an accurate assessment of the ornament to be made. There is good agreement with Fritsch's clear figures and there can be no doubt of the identity of the English with the Czechoslovakian material.

AFFINITIES AND DIFFERENCES. *S. bohemicum* is in many respects close to the uppermost Cenomanian *S. gracile* (Shumard) from which it is probably derived. Typical *S. gracile* differ in having a somewhat less compressed whorl section, in their stronger, more evenly rounded ribs becoming very strong on the body chamber, and in their constrictions that are noticeably less distinct on the sides and dorsum and cross the venter more or less transversely. In *S. bohemicum*, by contrast, the ribs are flat and almost scale-like even on the body chamber; the constrictions are frequently obvious even on the dorsum and cross the venter in an even curve. Some American populations of *S. gracile*, though not those of the English south-west, show variation in the strength of ribs and constrictions and some individuals in their early stages may be difficult to distinguish from *S. bohemicum*.

Specimens from the English Melbourne Rock (e.g. WW 16137–40 from Buckland Limeworks, Surrey, and SM B91099 and B91100 from Folkestone, Kent) that are only slightly later than the uppermost Cenomanian *S. gracile* from Devon have ribbing closely resembling that of *S. bohemicum* and constrictions strong on the inner part of the sides and the dorsum. The only feature linking them with *S. gracile* is the transverse course of the constrictions on the venter. They should probably be treated as a subspecies of *S. bohemicum*.

The Lower and Middle Cenomanian *S. baculoides* (Mantell) has ribs shallow behind and steep in front. They thus resemble the scale-like ribs of *S. bohemicum* but are much stronger, prorsiradiate as they rise near the dorsum and distinctly recurved towards the venter.

From contemporary forms assignable to *Baculites*, *S. bohemicum* is readily distinguished by its frequent and well-marked constrictions, although body-chamber fragments may be difficult to identify.

OCCURRENCE. *S. bohemicum* is widespread and fairly common in both Chalk Rock and nodular facies of the *Holaster planus* Zone of south-eastern England, East Anglia and the midlands. It occurs in northern and central Europe at presumably the same horizon.

Genus *BACULITES* Lamarck, 1799

TYPE SPECIES. *B. vertebralis* Lamarck, 1801, subsequently designated by Meek (1876).

Baculites appears to have been derived from an Upper Turonian *Sciponoceras* by loss of constrictions and further simplification of the aperture. I have seen no undoubted *Baculites* earlier than *B. undulatus* described below. Poorly-preserved and crushed *Sciponoceras*, particularly fragments of body chambers, often look deceptively like *Baculites*.

Baculites undulatus d'Orbigny

Pl. 1, figs 6-8; Pl. 7, fig. 11

- 1850 *Baculites undulatus* d'Orbigny : 19 & 21, no. 21.
 ? 1872 *Baculites undulatus* d'Orbigny ?; Fritsch : 49.
 1895 *Baculites* n. sp. Jahn : 136; pl. 8, fig. 8a-c.
 1913 *Baculites undulatus* d'Orbigny; Roman & Mazeran : 11; pl. 4, figs 6-8.
 1963 *Baculites undulatus* d'Orbigny; Matsumoto & Obata : 28; pl. 8, fig. 4; pl. 9, figs 1-5; pl. 11, figs 2, 3; text-figs 62-71.

DESCRIPTION. Whorl section elliptical, narrowing ventrally with increasing age. The low rounded ribs are rursiradiate dorsally at about 150° but bend forward and become prorsiradiate at about 45° on the ventral three-quarters of the shell, forming a more or less crescentic bulla at the bend. At first the ribs are mainly single but from a (major) diameter of about 10 mm they begin to branch irregularly at or above the bulla. On the body chamber the dorsal part of most ribs becomes weaker, so there can be seen only rounded and well-spaced bullae from which spring sheaves of six or more feeble ribs. The aperture is described from Japanese specimens by Matsumoto & Obata (1963 : 29). The largest fragment seen (Doyle coll. 662) has diameters of 26 and 20.5 mm.

AFFINITIES AND DIFFERENCES. *B. undulatus* is readily distinguished at the camerate stage from the contemporary *Sciponoceras bohemicum* by the absence of constrictions and by the finer and weaker but more numerous ribs. On the body chamber the well-spaced bullae and sheaves of fine secondary ribs are sufficiently characteristic. Although d'Orbigny's types of *B. undulatus*, as figured by Roman & Mazeran (1913), are only small fragments they clearly belong to the same species as the better-preserved English specimens. Presumably the Bohemian specimens described but not figured by Fritsch belong to the same form.

The next earliest true *Baculites* that have been described are Coniacian species from the Pacific (Japan and California), Africa and Europe. *Baculites brevicosta* Schlüter (Coniacian or Lower Santonian of northern Europe), the African and Pacific *C. boulei* Collignon and *B. capense* Woods, and the American *B. asper* all have far more distinct and prominent crescentic bullae than those of *B. undulatus*. There is, however, an intermediate group comprising *B. yokoyamai* Tokunaga & Shimizu, *B. besairiei* Collignon and *B. schenki* Matsumoto. Describing the Californian forms Matsumoto (1959) considered that *B. yokoyamai*, which occurs frequently in Japan in the Coniacian immediately above *Sciponoceras* aff. *bohemicum*, probably includes *B. besairiei* Collignon from Madagascar. These forms appear to have feebler ornament than the present species but similar whorl section and suture. The closely allied *B. schenki* from California is more triangular in section and typically has more strongly tuberculate dorsolateral crescents on the ribs.

B. undulatus could also well have been the source of the Coniacian *Euhomaloceras incurvatum* (Dujardin), characterized by distant, large, round dorsolateral tubercles as well as by the curved body chamber.

OCCURRENCE. In England *B. undulatus* is known only from a few localities, Reed in Hertfordshire and Kensworth.

Family ANISOCERATIDAE Meek, 1876

Genus *ANISOCERAS* Pictet, 1854

TYPE SPECIES. *Anisoceras saussureanum* Pictet.

Anisoceras reidi sp. nov.

Fig. 1; Pl. 1, fig. 15

TYPES. The holotype is BM C79487 (WW, *ex* Reid coll.) from Hitch Wood; a paratype is GSM 117001 (trans. from St Albans City Museum, *ex* Morison coll.) from Luton Railway Cutting.

NAME. For Mr R. E. H. Reid.

DESCRIPTION. The section is compressed and the venter only slightly flattened; the height increases rather rapidly. The ribs are fairly dense, low and rounded, irregularly with and without ventrolateral spines, of which low flat bases alone appear on the internal mould. The ribs with tubercles are doubled across the venter. The ribs are slightly bowed forward at midflank and are thus weakly biconcave. First and second lateral saddles of the suture and lateral and umbilical lobes are basically bifid but the lobes are irregularly asymmetric (Fig. 1); indeed the lateral lobe in the holotype is obviously bifid on the left side but almost trifid on the right. The third lateral saddle is distinctly narrower than the others.

REMARKS. R. E. H. Reid collected a single specimen of what appears to be a true *Anisoceras*, although superficially it resembles some contemporary *Allocrioceras*. Hitherto *Anisoceras* has been only doubtfully represented above the Cenomanian and it is already rare in the uppermost part of that stage. Schlüter (1872) described and figured from the uppermost Turonian two species that belong to this family, *Ancyloceras paderbornense* (1872 : 97; pl. 30, figs. 1, 2) and *A. cuvieri* (1872 : 97; pl. 30, figs 3, 4). The former, though not typical of *Anisoceras*, may be referred provisionally to that genus; it differs from *A. reidi* by its lateral tubercles and less regular and more distant ventrolateral tubercles. *A. cuvieri* (Schlüter) is perhaps best referred to *Allocrioceras* (see below). Although like *Anisoceras reidi* it has no lateral tubercles, it has ventrolateral ones only on every fifth or sixth rib, which is more prominent than the rest; moreover the ribs are slightly sinuous and more prorsiradiate than in the present species. Most *Allocrioceras* are distinguishable by their sharper ribs and tubercles and simpler sutures. However, the two new species of *Allocrioceras* described below have in their later stages rounded ribs and septate tubercles that leave flat spine bases on the internal moulds as in *Anisoceras*; their sutures are also complex in

Plate 1

× 1 (Figs 1–2, 4–5 × 2)

Metaptychoceras smithi (Woods) (p. 284). Hitch Wood.

Fig. 1. Coll. R. E. H. Reid. BM C79653, × 2. Fig. 2. R. G. Bromley coll. C.146, × 2.

Sciponoceras bohemicum (Fritsch) (p. 285). Hitch Wood.

Fig. 3a, b. J. C. Doyle coll. Figs 4a, b, 5. Coll. R. E. H. Reid. BM C79496, C79507, both × 2.

See also Pl. 7, figs 10, 12.

Baculites undulatus d'Orbigny (p. 287). Reed.

Figs 6, 7, 8. J. C. Doyle coll. See also Pl. 7, fig. 11.

Allocrioceras angustum (J. de C. Sowerby) (p. 290). Hitch Wood.

Figs 9, 10. R. E. H. Reid coll. BM C79489, C79488. Fig. 11a, b. Specimen showing aperture. J. C. Doyle coll. 382.

Allocrioceras strangulatum sp. nov. (p. 291). Hitch Wood.

Figs 12, 14a, b. Paratypes, J. C. Doyle coll. 477, 352. Fig. 13a, b. **Holotype**, coll. R. E. H. Reid. BM C79490. See also Pl. 2, fig. 1.

Anisoceras reidi sp. nov. (above). Hitch Wood.

Fig. 15a, b. **Holotype**, coll. R. E. H. Reid. BM C79487. See Fig. 1, p. 290, for suture.



old age. The main distinguishing features of *A. reidi* then are the doubling of the tuberculate ribs as they cross the venter and the length and narrowness of the second and third lateral saddles in the suture.

Of earlier species of *Anisoceras* the Upper Albian and Lower Cenomanian *A. campichei* Spath is perhaps closest to *A. reidi*, but it has sharper and more distant ribs which meet regularly in pairs at the ventrolateral tubercles.

OCCURRENCE. Only two undoubted specimens are known, from Hitch Wood and the Luton railway cutting.



Fig. 1 Suture of *Anisoceras reidi* sp. nov., $\times 2$.

Genus *ALLOCRIOCERAS* Spath, 1926

TYPE SPECIES. *Allocrioceras woodsi* Spath, 1926, = *Hamites angustus* J. de C. Sowerby, 1850.

Spath attributed this genus to his family Phlycticrioceratidae. The nominate genus of that family is with little doubt derived from *Allocrioceras* but differs from it and from most other hamitoid genera in having a siphonal row of tubercles. *Prophlycticrioceras* Clark from the Upper Albian of Texas seems to be an analogue rather than a direct ancestor. A little-known Coniacian genus *Boehmoceras* Riedel, 1931, doubtfully attributed to the same family, has an entire rounded keel and clearly does not belong here. Although *Allocrioceras* constitutes a fairly distinct group of species it does not have any characters of such importance as to justify its separation from the Anisoceratidae. Phlycticrioceratidae, if necessary as a taxon at all, are best regarded as a subfamily of Anisoceratidae and as including only the nominate genus.

Allocrioceras includes some species that are apparently regularly coiled in one plane and others that are rather irregular and generally rather helicoid, with the shell so twisted that the dorsoventral axis is at an angle greater than 90° to the axis of the spire. The ribs are normally single, regular or variable in strength, and in most species the majority carry ventrolateral tubercles. Constrictions may be present. The saddles of the suture are more or less regularly bifid. The lateral and umbilical lobes are asymmetric and not so obviously bifid as in some allied genera.

Allocrioceras is first known from the top of the Cenomanian in Britain and the U.S.A. (*A. annulatum* (Shumard)). It may have been derived from *Idiohamites* of the group of *I. alternatus* (Mantell).

Allocrioceras angustum (J. de C. Sowerby)

Pl. 1, figs 9–11

1850 *Hamites angustus* J. de C. Sowerby, in Dixon : 346; pl. 29, fig. 12.

1850 *Hamites geinitzii* d'Orbigny : 215.

1876 *Crioceras ellipticum* Mantell sp.; Schlüter : 164; pl. 43, figs 1, 2 (*non* 1872 : 100; pl. 30, figs 11, 12).

1896 *Crioceras ellipticum* (Mantell); Woods : 84; pl. 3, figs 8–10.

1927 *Allocrioceras* aff. *ellipticum* (*non* Mantell) Woods sp.; Billingham : 517; pl. 16, fig. 4a–c.

1939 *Allocrioceras woodsi* Spath : 598.

1951 *Allocrioceras woodsi* Spath; Wright & Wright : 15.

DESCRIPTION. Coiled more or less regularly in a loose open spire, with the dorsoventral axis of the shell oblique to the axis of the spire. The body chamber levels out and uncoils, so that the last

part may be almost straight. The section is oval, with a flat venter emphasized by the outwardly-directed ventrolateral spines present on all the ribs or on alternate ones. The ribs are alternately strong and weak and the tubercles on the weak ones, if present, are feebler than those on the strong ribs; the difference is sometimes marked (e.g. BM C33429). The ribs are fairly sharp and separated by distinctly wider interspaces; they may be radial, prorsiradiate or rursiradiate, varying with the coiling. The aperture has a flat striated margin, parallel with the ribs. The suture has moderately indented, squarish saddles, more or less symmetrically divided by lobules, and bifid lobes, the lateral and umbilical slightly asymmetrical. The first lateral saddle is the widest and the second lateral the narrowest of the three that are present.

AFFINITIES AND DIFFERENCES. *A. angustum* closely resembles its predecessor and presumed ancestor *A. annulatum* (Shumard). It differs in its less symmetrical and more irregular coiling, by its slightly irregular ribs, alternately strong and weak, by the feebleness or absence of tubercles on the weaker ribs and by the slightly to moderately compressed whorl section. No doubt in a series of specimens collected throughout the Turonian the variation in these characters would be found to be continuous, but *A. annulatum* is known in this country only from the uppermost Cenomanian with *Metoicoceras* and *Neocardioceras* and in the United States from that and slightly earlier horizons, whereas *A. angustum* occurs much later.

Woods (1896) recognized that Sowerby's *Hamites angustus* was the common Chalk Rock species but identified both, incorrectly, with Mantell's *Idiohamites ellipticus*, a Lower Cenomanian species with much more compressed section and more rounded ribbing. *Idiohamites alternatus* (Mantell), also Lower Cenomanian, is more distantly and coarsely ribbed and tuberculate. C. F. Römer (1870 : 322; pl. 37, fig. 10) figures as *Hamites ellipticus* a fragment with distant blunt ribs and apparently no tubercles; although he said that Dixon's *H. angustus* was 'probably synonymous', this seems unlikely.

OCURRENCE. This is one of the commonest Chalk Rock species and is also known from the *Holaster planus* chalk in its nodular and normal facies, occurring even in Yorkshire.

Allocrioceras strangulatum sp. nov.

Pl. 1, figs 12-14; Pl. 2, fig. 1

1876 *Crioceras ellipticum* (Mantell); Schlüter : pl. 30, figs 11, 12 (*non* 1876 : pl. 43, figs 1, 2).

TYPES. The holotype is BM C79490 (WW coll.), the paratypes BM C79508 (WW coll.) and Doyle coll. 352 and 477, all from Hitch Wood.

NAME. 'Constricted.'

DESCRIPTION. Coiled in a moderately open, slightly helical spiral, perhaps irregular in the early stages. Section compressed oval. Constrictions are present but are sparse and rather feeble on the outer whorls. The ribs are rather fine and sinuous, almost biconcave, with paired ventral tubercles, rather close together on each rib; occasionally two ribs join at the ventrolateral tubercle. The ribs and tubercles are sharp on the early whorls but become blunter later, the tubercles then being slightly elongated spirally, instead of transversely as on the early part, and in some cases septispinate.

AFFINITIES AND DIFFERENCES. The compression, constrictions, sinuous ribs and the closeness of the ventral tubercles on the early whorls readily distinguish this species from *A. angustum* or *A. annulatum*. The English specimens compare well with Schlüter's *Crioceras ellipticum* (1876 : pl. 30, figs 11, 12) from the Turonian of Lengerich, in section, coiling, rib curve and tuberculation; despite the apparent absence of constrictions in the German specimen it is presumably the same species.

OCURRENCE. In England it is known only from Hitch Wood and Kensworth, where it is rare. It occurs also in Germany.

Allocrioceras billinghursti Klinger

Pl. 2, figs 2, 3a, b

1874 *Helicoceras ellipticum* (Mantell); Geinitz : 194; pl. 35, figs 14–16.1927 *Allocrioceras* sp. ind. Billinghurst : 617; pl. 16, fig. 7a, b.1976 *Allocrioceras billinghursti* (Wright MS) Klinger : 32; pl. 9, fig. 2a, b; text-fig. 7b.

TYPES. Klinger merely designated as holotype 'Geinitz pl. 35, fig. 16'. The originals of Geinitz' figs 14 and 15 and of Billinghurst's pl. 16, fig. 7a, b (BM C32298), which were cited in Klinger's synonymy, as well as the latter's Zululand specimens GSP Z1598 and Z2069, are paratypes.

MATERIAL. The following English specimens were cited in drafts of the present paper from which Klinger presumably took the specific name: BM C78510, C79650–2 (WW *ex* Reid coll.), BM C79505–6 (WW *ex* Bromley coll.), all from Hitch Wood; A. Wainwright coll. J62 from Kensworth and R. Bromley coll. C158 from Reed.

DESCRIPTION. Coiled in an open, apparently more or less regular helical spire; markedly torticone, with the long diameter of the whorl section oblique to the axis of the spire. The ribs are almost vertical if fragments are placed so that the axis of the spire would be vertical. They are strong and well spaced, fairly sharp at first but becoming more rounded later. The main ribs bear rather strong spines, which on later parts of the shell become septate so that only flat spine bases are seen on internal moulds. Between the main ribs there are one or two that are weaker on the venter; in the early stages such ribs carry spines but later they are untuberculate. The suture is florid at later growth stages but still has the wide, more or less parallel-sided and equal saddles typical of *Allocrioceras*.

AFFINITIES AND DIFFERENCES. The stronger ribs in the early stages and the more helical and strongly torticone coiling serve to distinguish this species from contemporary members of the genus. Some specimens of the uppermost Cenomanian and basal Turonian *A. annulatum* (Shumard) approach the present species in these respects but are not so torticone and have much weaker ventrolateral spines. A few specimens of *A. billinghursti* (e.g. BM C33430) have rather finer, closer and more regular ribs than the typical form and thus are closer to *A. angustum*. Large fragments like BM C79510 and Geinitz' specimens resemble many nostoceratids in the swung ribs and coiling, but the suture remains typical of *Allocrioceras* and has no resemblance to the nostoceratid type with deeply dissected, overhanging and narrow-based first lateral saddle.

OCCURRENCE. In England in the Chalk Rock of Hitch Wood, Kensworth and Reed; in the Turonian of Saxony and in the Lower Coniacian of Zululand.

Allocrioceras (?) cf. *cuvieri* (Schlüter)cf. 1872 *Ancylloceras cuvieri* Schlüter : 97; pl. 30, figs 3, 4.

DESCRIPTION. A single specimen in J. C. Doyle's collection, comprising two fragments of compressed, more or less criocone early whorls with maximum whorl height of 11 mm and breadth of 8.5 mm, seems to compare best with Schlüter's species, founded on a specimen from the 'Cuvieri-Pläner' of Salzgitter. The English specimen has regular prorsiradiate rounded ribs, six in a distance corresponding to the larger diameter, with slight but distinct bullate ventrolateral tubercles; the ribs at first are interrupted on the venter but later cross it transversely, while the tubercles weaken. An enlarged rounded rib is visible at the anterior end of the larger fragment.

AFFINITIES AND DIFFERENCES. The German holotype is at its smaller end nearly twice the diameter of the English specimen and exact comparison is therefore impossible. It has prominent ventrolateral tubercles on the periodic enlarged ribs but it is not clear whether there were also tubercles on the minor ribs. The English specimen somewhat resembles *Allocrioceras strangulatum* sp. nov. (p. 291) in peripheral view but the prorsiradiate ribs, rounded from an early stage of growth, readily distinguish it.

The periodic enlarged ribs are unlike anything seen in other species of *Allocrioceras* but the present form is probably best placed in this genus.

OCCURRENCE. Chalk Rock of Kensworth.

Genus *NEOCRIOCERAS* Spath, 1921

This genus was based on an unidentified form allied to, but according to Shimizu (1933 : 15) distinct from, *Crioceras spinigerum* Jimbo, 1894, but that species was subsequently designated as type by Diener (1925 : 192). This is an apparently criocone form, perhaps with initial whorls not in one plane, with fine close ribs on some of which there are midlateral and on others ventrolateral tubercles, the latter alternating on the venter. Other species with more or less straight shafts, that had from time to time been referred to *Neocrioceras*, were rightly separated from the typical species as a distinct subgenus *Schlueterella* Wiedmann (1962 : 205) with type species *Ancyloceras pseudoarmatum* Schlüter, 1872; Wiedmann doubted indeed whether the two subgenera were of the same phylogenetic origin. Subsequently Collignon (1969 : 47) described a new genus *Christophoceras*, with a type species based on a magnificent body chamber with straight shaft and final hook, that is undoubtedly a synonym of *N.* (*Schlueterella*). The form described below is very similar to Collignon's.

Subgenus *SCHLUETERELLA* Wiedmann, 1962

Neocrioceras (*Schlueterella*) *multinodosum* (Schlüter)

Pl. 2, figs 4, 5

1872 *Hamites multinodosus* Schlüter : 106; pl. 32, figs 1, 2.

DESCRIPTION. The English material comprises a small but uncrushed specimen (GSM 108903), apparently at the stage where the shell has just straightened after a bend, and a very small fragment of a slightly larger specimen (Doyle coll. 469). The section is oval. There are periodic rectiradiate ribs which bear prominent spines high up on the sides, joined by looped riblets to prominent paired ventral spines, similarly joined across the venter by looped riblets. Between these major ribs there are slightly less strong ones, seven in number in this small fragment, with small but distinct ventrolateral and ventral spines similar in position to those on the major ribs.

AFFINITIES AND DIFFERENCES. The English specimen figured in Pl. 2, fig. 5 is at about the same growth stage as the holotype of *Neocrioceras* (*S.*) *sanushibense* Wright & Matsumoto (1954 : 121; pl. 7, fig. 5a, b) from the Upper Santonian of Japan, but differs in having a more compressed section and seven as opposed to three or four intermediate minor ribs, which moreover do not tend to join at the ventrolateral tubercles. All the characters suggest the association of the English specimens with Schlüter's crushed and fragmentary holotype of *H. multinodosus*; at a considerably later growth stage than the English material this has five minor ribs between the major ones; taking into account the Campanian *N.* (*S.*) *pseudoarmatum* (Schlüter) which has only one or two intermediate ribs (Schlüter 1872 : 99; pl. 31, figs 1-3; 1876 : pl. 43, figs 5-9) one would expect the number to decrease from early to later stages in phylogeny.

The periodic enlarged ribs with looped riblets between the tubercles on shoulder and venter distinguish *Neocrioceras* from most species of the otherwise rather similar *Pseudoxybeloceras*. However, *Ancyloceras lineatum* Gabb and *Oxybeloceras petrolense* Anderson, referred by Matsumoto (1959 : 162) to *Pseudoxybeloceras*, have occasional major ribs of *Neocrioceras* type. Indeed the present form is particularly interesting in that its abundant straight minor ribs strongly recall the ribs of *Pseudoxybeloceras* (cf. Wright & Matsumoto 1954 : text-figs 9-12). The two genera are now both known to range from Upper Turonian to Campanian and one is probably derived from the other. If the decrease in the number of minor ribs between each pair of major ones from seven in the Turonian *N. multinodosum* to three or four in the Santonian *N. sanushibense* and one or two in the Campanian *N. pseudoarmatum* is taken to indicate that the enlarged major

ribs were a new feature when the genus first arose, then *Neocrioceras* was derived from *Pseudoxybeloceras* rather than the reverse.

OCCURRENCE. Single fragments each from Reed, Hitch Wood and north Germany.

Family **TURRILITIDAE** Meek, 1876

Subfamily **NOSTOCERATINAE** Hyatt, 1894

Howarth (1965 : 371–374) has reviewed the classification of this family and in particular Wiedmann's (1962) drastic reduction of the three most widely used genera to the status of synonyms of *Cirroceras* Conrad, 1868. I agree with Howarth that *Cirroceras*, which I accepted as senior synonym of *Didymoceras* Hyatt, 1894 (Wright 1957b), should be treated as a *nomen dubium*, and I also accept his conclusion that *Bostrychoceras* and *Didymoceras* are best regarded as synonymous.

Genus **DIDYMO CERAS** Hyatt, 1894

TYPE SPECIES. *D. nebraskense* Hyatt.

Didymoceras (including *Bostrychoceras* Hyatt, see Howarth 1965) was long regarded as an Upper Senonian genus; earlier species with similar coiling and ribbing were referred, by Billingshurst (1927 : 513) for example, to *Hyphantoceras*, whose type species has very irregular coiling and different ornament. In fact there is a series of species beginning with *D. thomasi* (Pervinquieré) from the Upper Cenomanian of Algeria and continuing to the Campanian forms with whorls regularly in contact until the body chamber, which become increasingly U-shaped, and have regular dense ribbing. The main differences between species lie in the apical angle, the numbers, angle and curve of the ribs and the numbers and form of constrictions. These early *Didymoceras* differ little from Middle Albian *Proturrilitoides*, from survivors of which they were presumably derived, except in the pendent, incipiently U-shaped body chamber. By the Campanian, however,

Plate 2

× 1

Allocrioceras strangulatum sp. nov. (p. 291). Hitch Wood.

Fig. 1. Closely-ribbed specimen with occasional looped ribs. Paratype, J. C. Doyle coll. 358. See also Pl. 1, figs 12–14.

Allocrioceras billingshursti Klinger (p. 292). Hitch Wood.

Fig. 2. The species is always twisted so that both right and left ventrolateral tubercles are visible in this view. Coll. WW. BM C79510. Fig. 3. Later whorls with blunt ribs, coll. R. G. Bromley. BM C79505.

Neocrioceras (Schlueterella) multinodosum (Schlüter) (p. 293).

Fig. 4. Hitch Wood. Doubtful fragment. J. C. Doyle coll. 469. Fig. 5a, b. Reed. Body-chamber fragment, coll. C. J. Wood. GSM 108903.

Hyphantoceras reussianum (d'Orbigny) (p. 297). Hitch Wood.

Fig. 6. End of camerate part and regular pendent body chamber, J. C. Doyle coll. 1288. Fig. 7. Irregular body chamber with expanded aperture, coll. WW. BM C79478. See also Pl. 7, figs 4, 6.

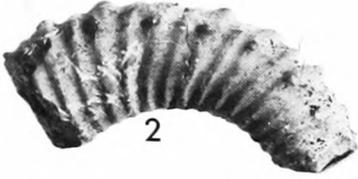
Didymoceras saxonicum (Schlüter) (p. 296).

Figs 8, 9a, b. Hitch Wood. Fig. 8 shows reversal of direction of ribs between the first and second preserved whorls. Coll. R. E. H. Reid. BM C79491, C79492. Fig. 10. Hitch Wood. Body chamber of sinistral individual. Coll. WW. BM C79476. Fig. 11. Hitch Wood. Body chamber of dextral individual showing penultimate and ultimate constrictions. J. C. Doyle coll. 647. Fig. 12. Cuckhamsley Knob. Specimen with unusually fine ribs. SM B4253. See also Pl. 7, fig. 5.

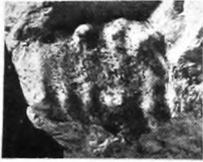
Photograph: Fig. 2 by BM.



1



2



4



5a



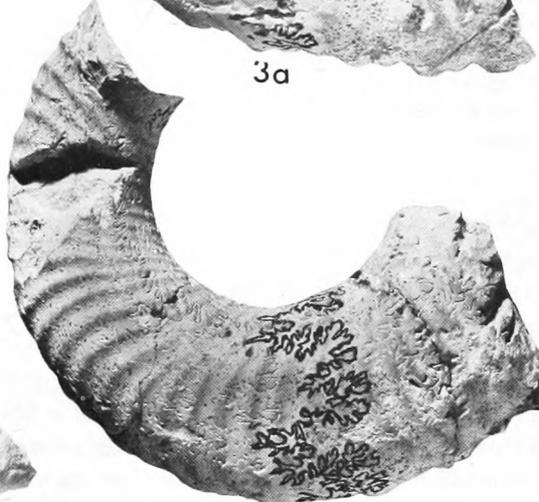
5b



12



3a



3b



6



7



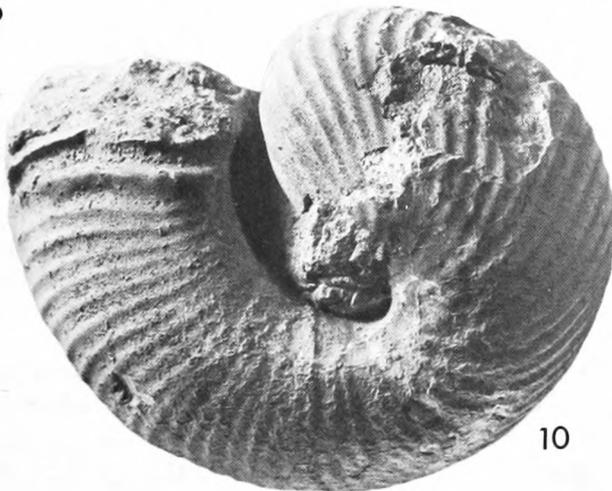
8



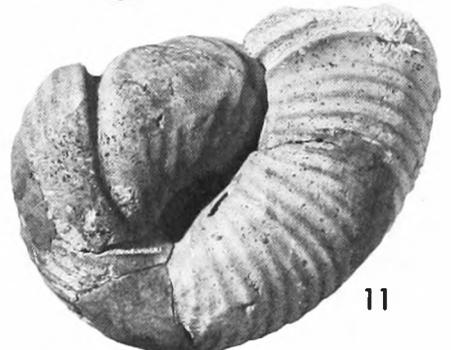
9b



9a



10



11

additional forms appear in which the last few whorls before the body chamber become uncoiled and may be more or less regularly bituberculate. These include the type species of the genus; among such species probably lies the origin of *Nostoceras* with regular bituberculate ribbing (Howarth 1965 : 372–374). *Eubostrychoceras* Matsumoto (1967 : 332), created for the pre-Campanian species, I would now regard as unnecessary, but it might reasonably be employed as a subgenus.

Didymoceras saxonicum (Schlüter)

Pl. 2, figs 8–12; Pl. 7, fig. 5

- 1840 *Turrilites undulatus* Mantell; Geinitz : 42; pl. 13, fig. 1 only.
 1841 *Turrilites polyplocus* F. A. Römer : pl. 14, fig. 2 only.
 1843 *Turrilites polyplocus* Römer; Geinitz : 67; pl. 13, fig. 1.
 1846 *Turrilites polyplocus* Römer; Geinitz : pl. 12, fig. 3.
 1850 *Turrilites Geinitzii* d'Orbigny : 216.
 1870 *Turrilites polyplocus* F. A. Römer; C. F. Römer : 321; pl. 36, fig. 1.
 1872 *Turrilites Geinitzii* d'Orbigny; Schlüter : 113; pl. 35, fig. 10.
 1874 *Turrilites polyplocus* F. A. Römer; Geinitz : 195; pl. 36, figs 1–3.
 1875 *Turrilites saxonicus* Schlüter : 30.
 1876 *Turrilites saxonicus* Schlüter; Schlüter : 135.
 1895 *Turrilites saxonicus* Schlüter; Kossmat : 143.
 1896 *Heteroceras* sp. Woods : 75; pl. 2, figs 6–8.
 1922 *Heteroceras woodsii* Kitchin : 49.
 1927 *Hyphantoceras woodsii* (Kitchin) Billinghurst : 517; pl. 16, figs 5, 6.
 1962 *Cirroceras* (*Cirroceras*) *indicum saxonicum* (Schlüter) Wiedmann : 203.

DESCRIPTION. Coiled in a sinistral or dextral spire with a wide umbilicus and with the whorls in contact until the slightly pendent U-shaped body chamber. The whorl section in the early stages is round, subquadrate or slightly oval but becomes increasingly oval with age. There are two or three oblique constrictions to a whorl; on the internal mould they are rather deep with rounded edges but on the shell they have sharp collars. On the later whorls they are strongly undercut and towards the end the front collar is directed backwards over the constriction. The shell increases suddenly in cross section after each constriction. Between constrictions there are fine, regular, sharp or rounded, single or branching ribs, separated by slightly wider interspaces. The density of ribbing varies between individuals but there are normally about 90 ribs to a whorl, many branched low on the side. The ribs and constrictions are always oblique and on most of the shell are directed forwards from the upper margin, but in some individuals they are directed backwards for a few whorls and then change direction (Pl. 2, fig. 8). On the more oval later whorls the ribs are very sinuous. The pendent body chamber turns up at the end and has a final constriction with sharp collars. The siphuncle is in the middle of the outer side of the whorl. The suture has rather florid bifid elements; the first lateral lobe is the widest and undercuts the first lateral (external) saddle, reaching almost to the siphuncle on one side and the umbilical lobe on the other. A small fragment of the early stages (BM C79470) from the *Holaster planus* Zone of the Guildford bypass indicates a shell with a right-angled bend in one plane followed by three more or less straight shafts, up to 9 mm long, joined by right-angled bends in another plane. This fragment links with the specimen figured in Pl. 7, fig. 5 and suggests that the species had irregular and possibly heterostrophic early whorls. To the best of my knowledge no normally-coiled initial whorls of the species have been found.

AFFINITIES AND DIFFERENCES. The much later (Campanian) *D. polyplocus* has more inflated whorls than *D. saxonicum*, no constrictions, straighter ribs, a freer pendent body chamber and no sudden change in whorl section at the end of the spire. The Coniacian *D. indicum* (Stoliczka) appears to have distinctly less oblique and stronger ribs and a more acute apical angle than *D. saxonicum*, with a consequential narrower umbilicus. Kossmat (1895 : 143) recognized the close similarity of the two forms and it may be that *D. saxonicum* should be treated as a subspecies of *indicum*. Indeed Wiedmann (1962 : 202) treated these two, with *elongatum* of Whiteaves, as subspecies of a

variable long-ranging species. I am not yet satisfied that this is justified and prefer to maintain the three as distinct species for the present.

NOMENCLATURE. Geinitz' (1839) specimen of '*Turrilites undulatus*' was referred by Römer (1841) to his species *polyplocus*, but since Geinitz described it from areas, such as Strehlen, noted for their Turonian faunas it presumably belongs to the present species. D'Orbigny's (1850 : 216) species *geinitzii* was based only on one of Geinitz' specimens (1840 : pl. 13, fig. 3); later Geinitz (1874 : 195) stated that this specimen was too badly preserved for specific determination, an opinion which the illustration supports. Schlüter (1872 : pl. 35, fig. 10) figured a specimen as *T. geinitzii* d'Orbigny, but Geinitz in 1874 said that this was not the same species as d'Orbigny's *T. geinitzii*, based on Geinitz' own badly-preserved example. In the light of his statement the name cannot be regarded as validated by Schlüter's description of good and identifiable material, as might otherwise have been the case. *T. geinitzii* must therefore be treated as a *nomen dubium*, being based only on unidentifiable material. Schlüter recognized this and (1875 : 30) named the species *Turrilites saxonicus*, represented in his figure of 1872 (pl. 35, fig. 10). He used the same name in a later part of his monograph (Schlüter 1876 : 135), where he gave a synonymy that largely agrees with that given above, but under '1841 *Turrilites polyplocus* Ad. Römer' he cited 'pl. 14, fig. 1 (non! fig. 2).' This is the reverse of what would accord with the rest of his synonymy and is presumably a mistake.

OCCURRENCE. Abundant in Hertfordshire, Bedfordshire and Buckinghamshire but rare elsewhere in England. It occurs also in north and south Germany and in Czechoslovakia.

Genus *HYPHANTOCERAS* Hyatt, 1900

TYPE SPECIES. *Hamites reussianus* d'Orbigny, 1850.

Shorn of the species now referred to *Didymoceras*, *Hyphantoceras* is a well-circumscribed genus, characterized by loose and frequently irregular coiling in three dimensions, distant main ribs, thin and high with two to four flare-like tubercles, with or without fine feeble intermediate ribs. The suture is florid and similar to that of *Didymoceras*.

H. reussianum is the earliest known species. It could well have been derived from some early species of *Didymoceras* by loosening of the coiling, loss of the constrictions and development of flared main ribs perhaps from the collars of *Didymoceras*. Later species differing in coiling and details of the ribbing range into the Santonian.

Hyphantoceras reussianum (d'Orbigny)

Pl. 2, figs 6, 7; Pl. 7, figs 4, 6

- 1840 *Hamites plicatilis* Mantell; Geinitz : 41; pl. 12, fig. 4; pl. 14, fig. 2.
- 1841 *Hamites plicatilis* Sowerby; F. A. Römer : 94; pl. 14, fig. 7.
- 1843 *Hamites plicatilis* Sowerby; Geinitz : 8; pl. 5, fig. 2.
- 1843 *Turrilites polyplocus* var. Geinitz : 8; pl. 5, fig. 4.
- 1845 *Hamites plicatilis* Sowerby; Reuss : 23; pl. 7, figs 5, 6.
- ? 1845 *Turrilites Astierianus* d'Orbigny; Reuss : 24; pl. 7, fig. 7.
- 1846 *Hamites armatus* d'Orbigny; Geinitz : 304; pl. 12, fig. 3.
- 1850 *Hamites reussianus* d'Orbigny : 216.
- 1861 *Anisoceras Reussianum* (d'Orbigny) Pictet & Campiche : 76.
- 1870 *Helicoceras annulifer* C. F. Römer : 320; pl. 36, fig. 2.
- 1872 *Heteroceras Reussianum* (d'Orbigny) Schlüter : 109; pl. 32, figs 13–21; pl. 33, fig. 1.
- 1872 *Helicoceras armatus* d'Orbigny; Fritsch : 47; pl. 13, fig. 16; pl. 14, figs 8, 17 only.
- 1874 *Helicoceras Reussianum* d'Orbigny; Geinitz : 193, pl. 35, figs 11, 12.
- 1889 *Helicoceras Reussianum* Geinitz; Fritsch : 71, text-fig. 44.
- 1896 *Heteroceras Reussianum* (d'Orbigny); Woods : 74; pl. 2, figs 3–5.
- 1900 *Hyphantoceras Roissyanum* (Schlüter); Hyatt : 587.
- 1910 *Heteroceras reussianum* (d'Orbigny); Crick : 347; pl. 27, fig. 3.

1913 *Hamites* sp.; Roman & Mazeran : 19; pl. 4, fig. 19.

1951 *Hyphantoceras reussianum* (d'Orbigny); Wright & Wright : 18.

? 1957a *Hyphantoceras* cf. *reussianum* (d'Orbigny); Wright : 806; pl. 54, fig. 2a, b.

DESCRIPTION. More or less irregularly coiled; some specimens consist of a fairly regular open or tightly coiled conical helix, with a pendent U-shaped body chamber (Pl. 2, fig. 6); occasionally the helix is cylindrical (Schlüter 1872: pl. 32, fig. 18); in other cases the coiling is very irregular, especially in the later stages (Pl. 2, fig. 7). The cross section increases very slowly. The early stages of *H. reussianum* are similar (BM C79471 from Sparsholt, Berkshire) to the heterostrophic initial whorls of *H. reflexum* (Quenstedt) that have been figured (Fritsch 1872 : pl. 14, figs 14–16, 18). The major ribs at most growth stages are thin, high and distant on the body chamber and normally carry four fairly distinct tubercles, but at earlier stages they may have four, two or no tubercles. Between them is a variable number of ribs or striae. The suture is very similar to that of *D. saxonicum*.

AFFINITIES AND DIFFERENCES. On the early whorls the major ribs may be closer than on the later but even on whorls only 2 mm high (BM C79471) there are two or three intermediaries, a feature which clearly distinguishes the species from *H. reflexum*, as Schlüter eventually (1876 : 166) concluded. *H. flexuosum* (Schlüter), which is of slightly later date than *H. reussianum*, differs in having less differentiated major and minor ribs and, apparently, no tubercles. Some loosely coiled specimens (e.g. Pl. 7, fig. 4), show no major ribs, at least on internal moulds, on considerable lengths of shell. These are probably fragments of aberrant specimens of the present species.

OCCURRENCE. *H. reussianum* is widespread in England and occurs both in the Chalk Rock and nodular facies and also occasionally in the normal *Holaster planus* Zone chalk of Lincolnshire and Yorkshire, from which several large U-shaped body chamber fragments have come. Abroad it is widely distributed in northern and central Europe and a probable example is recorded from New Zealand (Wright 1957 : 806; pl. 54, fig. 2a, b).

Family SCAPHITIDAE Meek, 1876

The family apparently originates early in the Upper Albian and by the Cenomanian a variety of species of two groups, one involute and without lappets (Scaphitinae), the other evolute and with lappets (Otoscapitinae), is widespread in most parts of the world. The case for maintaining these as subfamilies (Wright 1953) despite Wiedmann's objections (1965) is being made in a separate paper. Only a very few species, however, seem to survive the end of the Cenomanian and it is not until the latter part of the Turonian that either stock becomes abundant again. The Scaphitinae begin at this time to radiate and during the Coniacian and Santonian there is great expansion in the number of species. The particular interest of the late Turonian forms described below is that they are beginning to foreshadow some of this expansion; the origins of several Coniacian species can be clearly seen among variants of the *Scaphites geinitzii* group.

Subfamily SCAPHITINAE Meek, 1876

Several species and subspecies are distinguished below among the Chalk Rock fauna, but they are all closely related and a case could be made for treating most of them as variants of *Scaphites geinitzii*.

Genus SCAPHITES Parkinson, 1811

TYPE SPECIES. *S. equalis* J. Sowerby, 1813.

Scaphites geinitzii d'Orbigny

(For synonymy see under the subspecies.)

DESCRIPTION. The size varies from about 20 to about 60 mm in greatest length and the maximum thickness ranges from about 35% to about 50% of the length. The density of ribbing is also variable. On the spire the ribs are normally slightly sinuous and the primaries split half to two-thirds of the way up the side into two to four secondaries. On the shaft and hook the primaries give rise to three to five secondaries. On the later part of the shaft and on the hook the point of branching is raised into a more or less distinct tubercle which varies from a feeble bulla in the compressed forms to a prominent one in inflated specimens. Normally these tubercles number between six and nine and there are no distinct umbilical ones. Inflated and compressed forms are equally involute; the beginning of the shaft conceals up to half or even more of the small umbilicus. The suture is relatively simple with rather regularly bifid lateral saddles and lobes.

REMARKS. The name *Scaphites geinitzii* was first published by d'Orbigny in the *Prodrome* (2, 1850 : 214) as follows:

* 58. *Geinitzii*, d'Orb., 1847. Espèce voisine du *Scaphites obliquus*, mais pourvue de plis tuberculeux externes. *Scaph. aequalis*, Geinitz (non Sowerby). France, Villedieu (Loire-et-Cher); Dresde, Strehlen.

The asterisk indicates that d'Orbigny had specimens in his own collection. Monsieur J. Sornay has with great kindness sent me plaster casts of three specimens, labelled as from Strehlen, in the d'Orbigny collection, which he reports contains no *Scaphites* from Villedieu.

Opinion 126 of the International Commission on Zoological Nomenclature ('Opinions and Declarations' 1, Sec. B, Facsimile Edition, London, 1958) lays down that the 'Prodrome' should be regarded as containing preliminary diagnoses and that the adequacy of the diagnosis is for the systematist to assess in each case. The diagnosis of *Scaphites geinitzii* differentiates the species from two earlier ones and refers to the characteristic outer tubercles. The name is certainly in common use for the abundant and widespread tuberculated Upper Turonian *Scaphites* of Europe. It seems reasonable to hold that the words of the description coupled with the mention of Strehlen and the survival in the d'Orbigny collection of Strehlen specimens amount to an adequate diagnosis.

Of d'Orbigny's three specimens, all more or less crushed, two clearly belong to the species generally known as *Scaphites geinitzii*. The third is either a different species, resembling Yabe's *Yezoites planus* (1910 : 167; pl. 18, fig. 14), or, more probably, a pathological specimen of *S. geinitzii*. I designate as **lectotype** a complete but distorted specimen, one of two numbered 7197, of which a plaster cast is here figured (Pl. 3, fig. 1).

A further nomenclatorial complication arises from the fact that Römer described (1841 : 86; pl. 13, fig. 4) as *Ammonites cottae* a specimen that, despite Wiedmann's (1965 : 430) reference to it as *S. (Otoscapites) cottae* (Römer), seems to me to be the spire of *S. geinitzii*. This conclusion has been reached by most subsequent authors, but none has taken the consequential step of reviving Römer's name in preference to *geinitzii*. In order to stabilize accepted usage an application to conserve the name *geinitzii* will be made to the International Commission on Zoological Nomenclature.

It is important to ascertain where the type lies in the rather wide range of forms included in *S. geinitzii*. The specimen figured in Pl. 3, fig. 2 closely resembles the lectotype in whorl section, rib density and form of tubercles. It may safely be regarded as typical of the species. This specimen is the original of Woods (1896: pl. 3, fig. 6).

Examination of the figures in the literature and of a fairly large number of specimens from the English Chalk Rock suggest that this variable species should be widely drawn. The stock seems to include in the Upper Turonian a range of forms differing in degree of inflation, density of ribbing and strength of ribs and tubercles. By the beginning of the Coniacian the variation is discontinuous and a number of good species can be separated. These are foreshadowed in the Upper Turonian material but most of it cannot be separated into distinct species. Subspecies however can be usefully distinguished in some cases and a limited number are established below. In all of these subspecies the degree of involution, the general pattern of ribs and tubercles and the direction of the ribbing on the shaft remain noticeably constant.

Apart from the subspecies here described there occurs in Germany (e.g. Schlüter 1872 : pl. 23, figs 2, 13) and Czechoslovakia an inflated form in which the ventrolateral tubercles become increasingly prominent and clavate. This is probably a slightly later offshoot of *S. g. intermedius* Scupin and leads directly to the Lower Coniacian *S. meslei* Grossouvre, which, *pace* Sturm (1901 : 61), followed by Scupin (1913 : 101), is not the same as *S. kieslingwaldensis* Langenham & Grundey (see p. 303).

OCCURRENCE. *S. geinitzii* is recorded from the Zone of *Terebratulina lata* in this country, probably therefore from the horizon of *Collignoniceras woollgari* (as in Germany – Schlüter 1876 : 221) but good specimens are not known. It is abundant in the Zone of *Holaster planus*. It also ranges in England into the Zone of *Micraster cortestudinarium* (lower Coniacian) and in France (Aude) into the middle Coniacian. The occurrences in Saxony and Czechoslovakia were reviewed in an important paper by Prescher (1963).

Scaphites geinitzii geinitzii d'Orbigny

Pl. 3, figs 1–4, 6–7; Pl. 7, fig. 9

- 1840 *Scaphites aequalis* Sowerby; Geinitz : 40.
 1841 *Scaphites costatus* Mantell; F. A. Römer : 90.
 1841 *Ammonites Cottae* F. A. Römer : 86; pl. 13, fig. 4.
 1850 *Scaphites Geinitzii* d'Orbigny : 214.

Plate 3

× 1

Scaphites geinitzii d'Orbigny (above).

Fig. 1. Upper Turonian, Strehlen, Saxony. Plaster cast of crushed lectotype. Musée d'Histoire Naturelle, Paris, 7197; d'Orbigny coll. Figs 2, 6, 7. Chalk Rock, Cuckhamsley Knob. Fig. 2 original of Woods 1896: pl. 3, fig. 6, 6a. Coll. Montague Smith. SM B4206, B4221, B4215. Fig. 3a, b. Hitch Wood. Coll. C. J. Wood. GSM 108884. Fig. 4. Hitch Wood. Coll. WW. BM C79475. See also Pl. 7, fig. 9.

Scaphites pseudoaequalis Yabe (p. 305). Cuckhamsley Knob.

Fig. 5. Original of Woods 1896: pl. 3, fig. 5, 5a. Coll. Montague Smith. SM B4205. See also Pl. 7, fig. 1.

Scaphites geinitzii laevior subsp. nov. (p. 302).

Fig. 8. Reed. **Holotype**, SM B594. Fig. 9. Cuckhamsley Knob. Paratype, coll. Montague Smith. SM B4208. See also Pl. 7, fig. 7.

Scaphites kieslingwaldensis Langenhan & Grundey (p. 303).

Fig. 10. Cuckhamsley Knob. Coll. Montague Smith. SM B4212. Figs 11a, b, 12a, b. Hitch Wood. Coll. R. E. H. Reid. Fig. 11, broad-ventered form retaining the sinuous ribs of *S. geinitzii* on the spire. BM C79579. Fig. 12, form with weak tubercles on the hook. BM C79485.

Scaphites lamberti doylei subsp. nov. (p. 304). Hitch Wood.

Fig. 13. **Holotype**, coll. R. E. H. Reid. BM C79486.

Scaphites diana sp. nov. (p. 304).

Fig. 14a, b. Hitch Wood. Paratype, coll. R. E. H. Reid. BM C79515. Fig. 15. Cuckhamsley Knob. **Holotype**, coll. Montague Smith. SM B21299. Fig. 16a, b. Hitch Wood, Paratype, J. C. Doyle coll. 645.

Otoscapites reidi sp. nov. (p. 307).

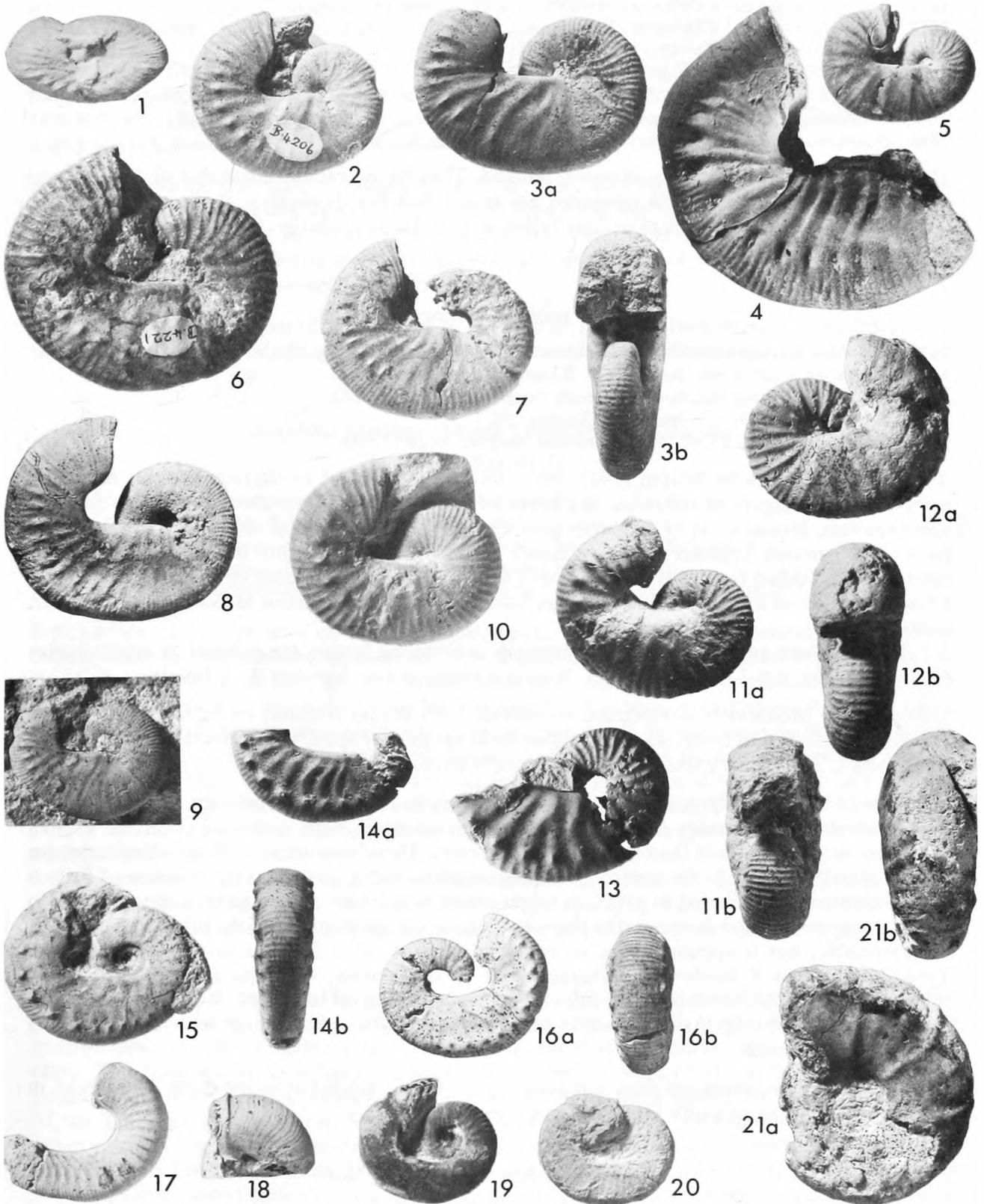
Fig. 17. Medmenham. Paratype, coll. R. E. H. Reid. BM C79498. Fig. 18. Hitch Wood. Paratype, coll. WW. BM C79511. See also Pl. 7, fig. 8.

Otoscapites bladenensis (Schlüter) (p. 305). *Holaster planus* Zone.

Fig. 19. Mickleham bypass. Original of Wright & Wright 1945: pl. 5, fig. 1a–c (as *Scaphites auritus*). Coll. WW. BM C79517. Fig. 20. Guildford bypass. Original of Wright & Wright 1945: pl. 5, fig. 2a, b (as *S. auritus*). Coll. WW. BM C79518.

Lewesiceras woodi sp. nov. (p. 312). Hitch Wood.

Fig. 21a, b. **Holotype**, coll. R. E. H. Reid. BM C79509. See also Pl. 6, fig. 6.



- 1855 *Ammonites wiltonensis* Sharpe : 53; pl. 23, fig. 10.
 1870 *Scaphites Geinitzii* d'Orbigny; C. F. Römer : 320; pl. 35, fig. 6.
 1872 *Scaphites Geinitzii* d'Orbigny; Schlüter : 75; pl. 23, figs 14–16 only.
 1872 *Scaphites Geinitzii* d'Orbigny; Fritsch : 42; pl. 13, fig. 12a–c only.
 1874 *Scaphites geinitzi* d'Orbigny; Geinitz : 191; pl. 35, figs 1–4.
 1889 *Scaphites geinitzi* d'Orbigny; Fritsch : 71, fig. 43.
 1895 Übergangsform zwischen *Scaphites* cf. *Geinitzi* var. *Lamberti* Grossouvre und *Scaphites Geinitzi* d'Orbigny; Jahn : 138; pl. 8, fig. 2a–d.
 1896 *Scaphites Geinitzi* d'Orbigny; Woods : 81; pl. 3, figs 6, 7 only.

DESCRIPTION. Compressed to moderately inflated. The ribs are rather coarse and slightly sinuous on the spire. On the shaft the primaries are broad and flat, branching at prominent pointed ventrolateral tubercles into three or four rather distant fine secondaries. On the hook the primary ribs are less flattened.

Scaphites geinitzii intermedius Scupin

- 1872 *Scaphites Geinitzii* var. *binodosus* Römer; Fritsch : 42; pl. 14, fig. 13a, b.
 1891 *Scaphites geinitzii* var. *binodosa* A. Römer; Jahn : 180, figs 1–5.
 1907 *Scaphites Geinitzi* var. nov. *intermedia* Scupin : 696 (*nom. nud.*).
 1913 *Scaphites Geinitzi* var. *intermedia* Scupin : 98.
 1934 *Scaphites geinitzi* d'Orb. var. *intermedia* Scupin; Andert : 400.

TYPE. The references by Scupin (1907 : 696, 704) are insufficient to characterize this form and since there is no figure or reference to a previous figure or description the name at this date is a *nomen nudum*. However, in 1913 Scupin gave a long description of this variety and of the typical form of *S. geinitzii*, together with a reference for *intermedia* to a figure of Jahn's. The name is therefore established from this date. Scupin's description is by no means clear but he apparently knew a number of specimens from various localities which he regarded as belonging to his var. *intermedia*.

I designate here as **lectotype** of the subspecies *intermedius* Scupin the original of Jahn's figures (1891 : 180, 181, figs 1–5, described as '*Scaphites Geinitzii* var. *binodosa* A. Römer').

DESCRIPTION. Moderately compressed to inflated with strong rounded or bullate ventrolateral tubercles on shaft and hook, sometimes also on latter part of spire, and distinct umbilical bullae on the shaft. The primary ribs are only moderately strong.

REMARKS. Scupin rightly regarded his variety as a transitional form between typical *geinitzii*, with ventrolateral tubercles only, and *lamberti* Grossouvre, with umbilical tubercles as well which are more prominent than the ventrolateral ones. Those specimens with umbilical tubercles approximately as large as the ventrolateral ones, such as the *S. geinitzii* var. *binodosa* of Fritsch (which Grossouvre included in his *S. lamberti*), were treated by Scupin as transitional between *geinitzii intermedius* and *lamberti*. On the sole basis of the proportions of the tubercles this might be reasonable, but it appears to be more useful to take other features into account as well. Typical Coniacian *S. lamberti* are characterized by very coarse, well-separated secondary ribs, springing on the shaft and hook in pairs from the ventrolateral tubercles. *S. g. intermedius* has closer and finer ribbing than this, as do all *S. geinitzii*, with at least three secondaries to each ventrolateral tubercle.

OCCURRENCE. This subspecies does not occur in the Chalk Rock but seems to be widespread in the Upper Turonian of south Germany and Czechoslovakia.

Scaphites geinitzii laevior subsp. nov.

Pl. 3, figs 8, 9; Pl. 7, fig. 7

- 1872 *Scaphites Geinitzii* d'Orbigny; Schlüter : pl. 23, figs 21 and ? 22 only.
 1895 *Scaphites Geinitzi* d'Orbigny; Jahn : 133; pl. 8, fig. 3a–d.

TYPES. The holotype is SM B594 from Reed, and paratypes are SM B4208, 21298 and 21300 from Cuckhamsley, and IGS Zr 7788 from Kensworth.

NAME. 'Smoother'.

DESCRIPTION. The density of the ribs on the spire is as much as twice that of the typical subspecies; the primary ribs on the shaft are less flattened and the ventrolateral bullae on the hook are thin and reduced. The greater rib density is owing partly to an increased number of primaries and partly to each primary being split into secondaries.

AFFINITIES AND DIFFERENCES. *S. planus* Roman & Mazeran (1913 : 13; pl. 4, figs 15–17) is a compressed and fine-ribbed form of the *geinitzii* group but the few small specimens on which the species was based are so poorly preserved that it is impossible to make out their characters adequately. If further material indicates that they are identical with *S. geinitzii laevior* the sub-specific name should be changed to *planus*.

OCCURRENCE. This is a rather rare form in the Chalk Rock of Berkshire, Hertfordshire and Bedfordshire and in the *H. planus* Zone of Surrey; it occurs also in Germany.

***Scaphites kieslingwaldensis* Langenhan & Grundey**

Pl. 3, figs 10–12

- 1891 *Scaphites kieslingwaldensis* Langenhan & Grundey : 9; pl. 1, fig. 1.
 1897 *Scaphites binodosus* Römer; Fritsch : 37, fig. 20.
 1901 *Scaphites kieslingwaldensis* Langenhan & Grundey; Sturm : 61; pl. 3, fig. 8.
 1913 *Scaphites kieslingwaldensis* Langenhan & Grundey; Scupin : 101.
 1934 *Scaphites kieslingwaldensis* Langenhan & Grundey; Andert : 402; pl. 19, fig. 5.

DESCRIPTION. This species is an inflated development of *S. geinitzii* with rounded rather than bullate ventrolateral tubercles on shaft and hook. Both the spire and the shaft are very inflated, the thickness being from 25% to 30% greater than in *S. geinitzii*; the whorl section of the spire may be almost circular; the venter of the hook is broad and in some examples nearly flat. Distinct rounded ventrolateral tubercles, varying in position from a half to two-thirds up the side, appear on the hook but are not in all cases clearly defined on the shaft. On the spire the primary ribs are rather thin and high, normally rectiradiate, rarely slightly sinuous and branch into two or three secondaries. On the shaft they are broad and blunt, varying in strength from weak to very prominent and, after a more or less distinct ventrolateral tubercle, each gives rise to three moderately strong secondaries.

The holotype has twice been refigured photographically. Fritsch's figure (1897 : 37, fig. 20) gives a clear idea of the species, but that of Sturm (1901 : pl. 3, fig. 8), perhaps the most accessible, is much retouched and gives a false impression of sharpness and narrowness of primary and secondary ribs.

AFFINITIES AND DIFFERENCES. The inflated members of the *geinitzii* group have generally in the past been referred to F. A. Römer's Campanian *S. binodosus*, which is bigger, less inflated and has ventrolateral tubercles already on the spire, while on the shaft they form a row of close prominent clavi. The Campanian *S. inflatus* Schlüter differs from *binodosus* only in having less clavate tubercles and in being more inflated, but the tubercles on the spire readily distinguish it from any of the Turonian group. Sturm, Scupin and Andert all treated *S. kieslingwaldensis* as a senior synonym of *S. meslei* Grossouvre, but that species has distinctly clavate ventrolateral tubercles on shaft and hook. Moreover, both *S. meslei* and *S. lamberti* Grossouvre, which does have rounded ventrolateral tubercles, are less inflated and have coarser ribbing than *S. kieslingwaldensis*. However, it may well turn out if more material becomes available that *lamberti* and *meslei* should be treated as subspecies of *kieslingwaldensis*. It is close to *geinitzii* and it is difficult to draw the line between the variable forms of the two species.

REMARKS. There is considerable variation in the appearance of these small inflated *Scaphites*, deriving mainly from variation in the straightness or sinuosity of the ribs and the position on the flanks of the ventrolateral tubercles. There also seems to be a tendency for earlier forms to have distinct tubercles only on the hook, while later examples have them also on the shaft, but too few specimens from different localities and horizons are known for one to be sure. For the present I would regard all these variable specimens as belonging to a single species.

OCCURRENCE. Rather rare in the Chalk Rock of Berkshire and Hertfordshire; it occurs also in central and northern Europe.

Scaphites lamberti Grossouvre

1894 *Scaphites Lamberti* de Grossouvre 241: pl. 32, figs 1, 5.

DESCRIPTION. A coarsely ribbed form with prominent bullate or circular ventrolateral and bullate umbilical tubercles on the shaft and hook. The ventrolateral tubercles may appear already on the last part of the spire. The ribs on the shaft are very strong and for the most part give rise to pairs of coarse, distant secondaries. The nominate subspecies, from the Coniacian, has strong umbilical tubercles and does not occur in England.

Scaphites lamberti doylei subsp. nov.

Pl. 3, fig. 13

? 1872 *Scaphites* sp.? Schlüter: 76; pl. 23, figs 23–25.

1934 *Scaphites lamberti* Grossouvre; Andert: 402; pl. 19, fig. 4a, b.

HOLOTYPE. BM C79486 from the Chalk Rock of Hitch Wood.

NAME. For Mr J. C. Doyle.

DESCRIPTION. The ribbing is similar to that of the typical Coniacian subspecies but with relatively feeble umbilical tubercles. Although this form is transitional between the more closely ornamented specimens of *S. kieslingwaldensis* and *S. lamberti* it has the characteristic ribs and general aspect of the latter.

AFFINITIES AND DIFFERENCES. *S. g. intermedius* is a comparable form but combines distinct umbilical tubercles with rather fine ventral ribbing. The spire figured by Jahn (1895: pl. 8, fig. 1a–d) as *S. cf. geinitzii* var. *lamberti* Grossouvre, from the Priesen Beds, seems to be a good deal more inflated and to have tubercles earlier than the English form. Schlüter's *Scaphites* sp. (1872: pl. 23, figs 23–25) may perhaps be referable to this subspecies. On the other hand, the figures give the impression of clavate ventrolateral tubercles; if they are accurate, the specimen probably belongs to a parallel subspecies of *S. meslei* Grossouvre.

OCCURRENCE. It appears to be rare in the English Chalk Rock; the single undoubted specimen comes from Hitch Wood.

Scaphites diana sp. nov.

Pl. 3, figs 14–16

TYPES. The holotype is SM B21299; paratypes are SM B4225, B4239, B21301, BM C79515, J. C. Doyle coll. 645 and GSM 108906–7.

NAME. From Diana of Ephesus, the 'many-breasted mother'.

DESCRIPTION. A compressed to slightly inflated and evolute *Scaphites* with sinuous primary ribs on the shaft and about twelve pointed ventrolateral tubercles on the shaft and hook. On the spire the ribbing is rather irregular; the distant, low, regular rounded and sinuous primaries split high up on the sides into two low secondaries which cross the venter with a forward bend.

AFFINITIES AND DIFFERENCES. This rather uncommon species is readily distinguished from all subspecies of *S. geinitzii* by the open umbilicus, which is hardly occluded at all by the beginning of the shaft, and by the sinuous primaries, curling back to the abundant ventrolateral tubercles. On the shaft and hook the primaries are markedly flattened and sinuous, curving back to the small but distinct ventrolateral tubercles and then branching into three to five secondaries which cross the venter transversely. The evolute spire and the ribbing on the spire somewhat resemble that of contemporary *Otoscaphtes* but the tubercles are very distinct. *S. compressus* d'Orbigny from the Lower Coniacian of France (Sornay 1956) is similar and is probably a direct descendant of *S. diana*. It differs primarily in having finer and denser ribbing on the spire, and, above all, a prominent row of rounded umbilical tubercles on the shaft.

OCCURRENCE. Rather rare in the Chalk Rock of Cuckhamsley, Berkshire, Hitch Wood and Reed, Hertfordshire and Underwood Hall, Cambridgeshire.

Scaphites pseudoaequalis Yabe

Pl. 3, fig. 5; Pl. 7, fig. 1

1896 *Scaphites geinitzi* d'Orbigny; Woods : 81; pl. 3, figs 5, 5a only.

1910 *Scaphites pseudoaequalis* Yabe : 163; pl. 15 (1), figs 1-3.

DESCRIPTION. Small inflated *Scaphites* with well-spaced, slightly recurved primary ribs, splitting on the outer third of the side into two to four secondaries which run straight across the venter. On the shaft both primaries and secondaries become relatively stronger and more distant. On the hook the outer ends of the primaries project slightly and almost form ventrolateral tubercles. There is a wide constriction and a very strong flat-topped collar before the aperture. Of the external suture all the major elements are distinctly bifid except for the second lateral lobe.

AFFINITIES AND DIFFERENCES. The only comment that Woods made on his single specimen of this species was that 'in one small specimen the aperture of the shell has a projecting lip'. However, his specimen is rather distinct in proportions as well as in the aperture and is readily separated from all forms of *S. geinitzii*, particularly by the absence of any distinct ventrolateral tuberculation on the shaft.

OCCURRENCE. Yabe's specimens from the *Scaphites* Beds of Hokkaido are probably of Lower Coniacian date. Woods' specimen came from Cuckhamsley (SM B4205) and two more have since been found by M. J. Oates at Kensworth (including GSM 115259).

Subfamily **OTOSCAPHITINAE** Wright, 1953

This subfamily was erected for *Worthoceras* Scott and (*pace* Wiedmann, 1965) its derivative *Otoscaphtes* Wright, small lappeted scaphitids more evolute and with a simpler suture and ornament than their unlappeted contemporaries. They range from low in the Upper Albian to the Coniacian and it is only in the latter stage that they exhibit any significant tuberculation. *Worthoceras* is known in the Upper Albian only from Texas but in the Cenomanian and Turonian it is widespread in North America and occurs in Europe, north Africa and New Zealand. *Otoscaphtes*, arising in the Cenomanian, extends the range of the subfamily to include eastern Asia, New Zealand and California.

Genus **OTOSCAPHITES** Wright, 1953

TYPE SPECIES. *Ammonites* (?) *bladenensis* Schlüter.

Otoscaphtes bladenensis (Schlüter)

Pl. 3, figs 19, 20

1871 *Ammonites* (?) *bladenensis* Schlüter : 30; pl. 10, figs 5, 6.

1872 *Scaphites auritus* Schlüter : 77; pl. 23, fig. 9 only.

- 1875 *Ammonites Bladenensis* Schlüter; Barrois : 188.
 1875 *Scaphites auritus* Schlüter; Geinitz : 192; pl. 35, fig. 10.
 1925 *Scaphites bladenensis* (Schlüter) Diener : 197.
 1945 *Scaphites auritus* Schlüter; Wright & Wright : 126; pl. 5, figs 1, 2.
 1951 *Scaphites bladenensis* (Schlüter); Wright & Wright : 13.
 1953 *Otoscaphtes bladenensis* (Schlüter) Wright : 475.
 1957a *Otoscaphtes bladenensis* (Schlüter); Wright : 807.
 1965 *Scaphites (Otoscaphtes) bladenensis* (Schlüter); Wiedmann : 430; pl. 58, figs 2-4, 6.

LECTOTYPE. The original of Schlüter's (1871) pl. 10, figs 5, 6 (Wright 1957a : 807).

DESCRIPTION. Rather small with a very evolute spire, a short straight or curved shaft and a hook; the ends of the lappets overlap the spire. The whorl section of the spire is moderately compressed with gently convex sides and a narrowly rounded venter; there may be rather strong bifurcating sigmoid ribs, which bend forward slightly on the venter, giving the appearance of a *Deshayesites*, or the primaries may only be visible on the inner half of the side. Towards the end of the spire the umbilical shoulder, hitherto rounded, becomes sharper and on the shaft and hook it is distinctly angular; between it and the dorsal impression there is a distinct flat bevel. The sides of the shaft are flat and on shaft and hook the ribbing is weak and irregular; very feeble rounded or flat primary ribs spring at a forward angle from the umbilical shoulder, quickly straighten and run radially to the ventrolateral shoulder where they may break into very feeble fine riblets or continue as obscure folds over the venter. At least in some specimens the periphery of the shaft and hook is not evenly curved but is made up of a series of short straight lengths. The aperture is preceded by a marked constriction and a high collar, vertical behind and sloping in front; there are long, parallel-sided lateral lappets, slightly turned up.

AFFINITIES AND DIFFERENCES. When my brother and I described two Surrey specimens as *Scaphites auritus* (Wright & Wright 1945), we included in a single species all the specimens figured by Schlüter (1872) as *S. auritus* and also those figured in the same year by Fritsch and described homonymously as *S. auritus*. Grossouvre (1894 : 243) had already renamed Fritsch's specimens *S. fritschi*, distinguishing them from Schlüter's *S. auritus* on the grounds that the ribs were less flexuous and more distant on the inner part of the side. In fact Schlüter's three specimens are all different; only one of them has close flexuous ribs (1872 : pl. 23, figs 7, 8) and this specimen is closely paralleled by one of Fritsch's (1872 : pl. 13, fig. 14). The other specimens on Fritsch's pl. 13 are poorly preserved or consist only of the spire, while his pl. 14, fig. 12 represents a lappeted *Scaphites* of normal type. The *Otoscaphtes* figured by Jahn (1895 : pl. 8, fig. 5a-d) as *S. fritschi* Grossouvre is incomplete and does not help to clarify the characters of that species, if indeed it belongs to the same species as Fritsch's specimens. By distinguishing the various forms and by designating lectotypes appropriately it is possible to make sensible use of all the available names. I have already designated as type of *Ammonites* (?) *bladenensis* Schlüter the original of his pl. 10, figs 5, 6. Wiedmann has (1965 : 429) pointed out that of Schlüter's three specimens of '*S. auritus*' only that figured in his pl. 23, fig. 9, is identical with *bladenensis*. Wiedmann also designated as lectotype of *Scaphites auritus* Schlüter the original of his pl. 23, figs 5, 6; this species is characterized by its sharp umbilical tubercles from which spring directly bundles of three straight ribs. I do not agree with Wiedmann that Schlüter's third specimen belongs to the same species; indeed he points out that in this, the 'presumed paratype', there are no tubercles. This specimen, as Wiedmann says, is identical with the original of Fritsch's pl. 13, fig. 14, which I hereby designate as lectotype of *Scaphites auritus* Fritsch, a homonym of *S. auritus* Schlüter, and thereby of its replacement nominal species *S. fritschi* Grossouvre. This same species, *S. fritschi*, is characterized by rather sinuous, very fine and close ribs on the shaft and slightly coarser ribs on the hook which at first branch into two or three secondaries but are finally single; it is probably closer to *O. reidi* sp. nov. (see p. 307) than it is to *O. bladenensis*.

O. reidi has a further distinctive type of ribbing consisting of very distinct but fine prorsiradiate primaries, each giving rise two-thirds up the side to two to four very fine secondaries that cross the venter almost transversely. *O. awanuiensis* Wright from New Zealand has a well-rounded whorl section even on the shaft, but rather depressed and coronate on the spire, and fine rather

distant primary ribs branching regularly into three secondaries on both spire and shaft. It is not, however, 'undoubtedly Upper Turonian' as I stated in 1954; Mr H. Wellman subsequently sent me a well-preserved specimen which was found in association with *Hypoturrites* and *Scaphites* cf. *equalis* Sowerby of Cenomanian date. Henderson (1973) described and figured further Cenomanian material.

The Japanese Coniacian *O. puerculus* (Yabe) (1910 : pl. 15) and its var. *teshioensis* (Yabe), with spire rather like that of *O. bladenensis*, have prominent primary ribs on the shaft which extend to the ventrolateral shoulder before subdividing; in the var. *teshioensis* there are distinct ventrolateral tubercles at the point of branching. *O. minutus* (Moreman), from the basal Turonian of the western interior of the U.S.A., has a whorl section much like that of *O. awanuiensis*, but much weaker ribs on shaft and hook and lappets splayed sideways. *O. arnaudi* (Grossouvre) is at once distinguished from all other species by having very sinuous branching ribs of more or less the same type on spire, shaft and hook.

OCCURRENCE. *O. bladenensis* appears to be widely distributed in England and rather common in places, mainly in the nodular facies of the *Holaster planus* Zone in Kent and Surrey, but it also occurs rarely in the Chalk Rock of Hitch Wood. It occurs in Germany and Czechoslovakia.

Otoscaphtes reidi sp. nov.

Pl. 3, figs 17, 18; Pl. 7, fig. 8

1957a *Otoscaphtes* sp. ('third undescribed European form') Wright : 807.

TYPES. The holotype is IGS Zr7952 from High Wycombe. Paratypes are BM C79498 (WW ex Reid coll.) from Medmenham, BM C79511-4 (WW coll.) and Doyle coll. 228 from Hitch Wood, and IGS Zr 7789 (Payne & Hogg coll.) from Kensworth.

NAME. For Mr R. E. H. Reid.

DESCRIPTION. The spire has weak, well-spaced, rounded ribs that branch indistinctly. The shaft is flat-sided with broadly rounded venter and is rather long; very distinct sharp primary ribs leave the sharp umbilical shoulder at a forward angle of about 45° forming a very slight tubercle at the edge; a quarter of the way up the side they turn sharply to a radial direction; at midflank they break into two or three fine close and slightly sinuous secondaries which, with occasional intercalatories, cross the venter transversely. The hook expands rather rapidly until it is as wide as or wider than high, with rather flattened venter; here the primary ribs are sinuous and the secondaries more numerous and finer, in some parts absent. The apertural margin is well shown in the holotype and has the typical constriction, collar and long lateral lappets of *Otoscaphtes*.

AFFINITIES AND DIFFERENCES. None of the species distinguished above under *O. bladenensis* have ribbing on the shaft like that of *O. reidi*. *O. bladenensis* itself is more compressed and has very feeble, blunt, rounded and more or less radial primaries on the shaft with fine almost obsolete secondaries. The specimen figured by Yabe (1910 : pl. 15, fig. 24), described as *O. puerculus* var. *teshioensis*, has a close resemblance to *O. reidi* but is characterized by ventrolateral tubercles lacking in *O. reidi*. *O. puerculus* itself, if interpreted solely by the lectotype (Jimbo 1894 : pl. 21, fig. 4, selected by Matsumoto, 1963 : 44), would seem to be very distinct from *O. reidi*, but Tanabe (1975) has recently demonstrated an evolutionary series in *O. puerculus* in presumed Middle Turonian, of which the earlier members (e.g. his pl. 10, figs 1, 2) are close to *O. reidi*. However, these *O. puerculus* seem to have a much less flat-sided shaft with sharper and more crescentic primary ribs and less distinct and regular secondaries than *O. reidi*.

OCCURRENCE. Chalk Rock of Buckinghamshire, Hertfordshire and Bedfordshire.

Family **DESMOCERATIDAE** Zittel, 1895Subfamily **PUZOSIINAE** Spath, 1922Genus **PUZOSIA** Bayle, 1878

TYPE SPECIES. *Puzosia subplanulata* (Schlüter).

It has been held that true *Puzosia* did not survive the end of the Cenomanian, and Turonian forms have consequently been attributed to *Austiniceras* or some other genus. However, several good species of the genus have been described from the Turonian of various parts of the world; most were referred to by Matsumoto in his paper on the Puzosiidae of Hokkaido and Saghalien (1954). Too few specimens have been collected yet for distinctions to be drawn with certainty or for time-ranges to be worked out for the various species.

Puzosia curvatisulcata Chatwin & Withers

Pl. 4, fig. 4; Pl. 7, fig. 3

- ? 1898 *Puzosia gaudama* (Forbes); Kossmat : 115; pl. 16, fig. 2a, b only.
 1909 *Puzosia curvatisulcata* Chatwin & Withers : 68; pl. 2, figs 1-4.
 1913 *Puzosia gaudemaris* Roman & Mazeran : 19; pl. 2, figs 1, 1a, 2, 2a.
 1922 *Austiniceras* (?) *curvatisulcatum* (Chatwin & Withers) Spath : 128.
 1951 *Austiniceras* (?) *curvatisulcatum* (Chatwin & Withers); Wright & Wright : 19.
 1954 *Puzosia orientale* Matsumoto : 74; pl. 13, figs 1, 2a, b.
 ? 1954 *Puzosia orientale kossmati* Matsumoto : 75.
 ? 1959 *Puzosia intermedia orientalis* Matsumoto; Matsumoto : 16; pl. 4, fig. 1a-c.

TYPES. The two syntypes, BM C12229a and b, from the Chalk Rock of Marlow, are probably fragments of one individual. In case of doubt, I select the larger fragment (C12229a) as **lectotype**.

DESCRIPTION. Probably very large; the largest Chalk Rock specimen seen has a diameter of about 160 mm and the holotype of *P. gaudemaris* figured by Roman & Mazeran (1913 : pl. 2, fig. 1, 1a) has a diameter of 180 mm, but a fragment (BM C79656) from the *Holaster planus* Zone that probably belongs to this species is still septate at an estimated diameter of about 380 mm. Moderately compressed, the whorl thickness varying from 70% to 80% of whorl height; the greatest breadth is at about one-third of the whorl height. The umbilical wall is steep but rounded; the sides are flatter on early and more rounded on later whorls. On internal moulds there are visible five or six constrictions to a whorl, radial or slightly prorsiradiate on the inner part then curving moderately far forward and crossing the venter in a rounded arc. The strength of the constrictions varies slightly with age and between individuals. Fine, weak ribs are visible on the outer part of the sides and on the venter on internal moulds. On the shell the constrictions have a strong rib in front and many of the intermediate ribs arise on the umbilical shoulder even at small diameters.

AFFINITIES AND DIFFERENCES. The specimen figured in Pl. 4, fig. 4 (BM C79501) was identified by Matsumoto as 'closely allied to the inner whorl of *Puzosia* (s.s.) *orientale* Matsumoto [= *P. gaudama* Kossmat 1898, *non* Forbes] from Japanese Neogyliakian: Turonian; also resembling *P. curvatisulcata* Chat. & With. which has a more strongly impressed constriction and *P. mulleri*

Plate 4

× 1

Lewesiceras mantelli Wright & Wright (p. 310). Hitch Wood.

Figs 1a, b, 2, 3. Coll. R. E. H. Reid, BM C79481, C79500, C79480. See also Pl. 6, figs 4-5.

Puzosia curvatisulcata Chatwin & Withers (above). Blount's Farm Pit, Marlow.

Fig. 4. Coll. R. E. H. Reid. BM C79501. See also Pl. 7, fig. 3.

Pseudojacobites farmeryi (Crick) (p. 313). Hitch Wood.

Fig. 5. Coll. C. J. Wood. IGS Zr 7977. See also Pl. 5, fig. 1a, b (same specimen) and Pl. 6, figs 2-3.

See Fig. 2, p. 313, for suture.



1a



1b



2



3



4b



4a



5

Gross., which is more compressed'. Better English material is now available than the two poorly-preserved fragments figured by Chatwin and Withers. Allowing for even a modest amount of variation in the strength of the constrictions and the proportion of height to breadth of whorl, both of which seem to change with growth, it seems to me impossible to maintain the specific distinction of *P. orientalis* and *P. curvatisulcata*. At the most it may be desirable to distinguish a Lower Turonian subspecies *P. c. orientalis* from an Upper Turonian *P. c. curvatisulcata*, but I doubt it. *P. intermedia kossmati* Matsumoto seems to differ sufficiently, in its more extreme forward bending of the ribs and constrictions on the outer part of the sides and in the sharper, denser ribbing, to be treated as a distinct subspecies of *curvatisulcata*. *P. intermedia* Kossmat I would treat as a distinct species on the basis of the precocious appearance of long ribs already at a diameter of 55 mm and their falcoid course. *P. gaudemaris* Roman & Mazeran cannot in my view be distinguished from *P. curvatisulcata*.

OCCURRENCE. Rather rare in the Chalk Rock of Blount's Farm pit, Marlow, Hitch Wood and Kensworth; occurs also in the Upper Turonian of Uchaux, France and the Lower Turonian of southern India, Japan and California.

Family PACHYDISCIDAE Spath, 1922

Genus *LEWESICERAS* Spath, 1939

TYPE SPECIES. *Ammonites peramplus* Mantell, 1822.

Lewesiceras is characterized by its strong but irregular ribbing on the early whorls, the ribs bent forward ventrolaterally, with constrictions and umbilical tubercles; the ornament tends to weaken on later whorls except for distant bar-like primary ribs. The sutures are well spaced with minutely frilled elements and widely splayed lobes.

The Turonian *Ammonites peramplus* Mantell was long regarded as typical of the family Pachydiscidae, but Spath rightly separated as *Lewesiceras* the Turonian species with strongly ribbed and tuberculate inner whorls from the restricted *Pachydiscus* of the Campanian and Maastrichtian. Houša (1967) has reviewed *Lewesiceras* and distinguished two groups previously included in it, *Menabonites* and *Tongoboryoceras*; the latter occurs in the Chalk Rock (see p. 316).

The genus ranges probably from the Cenomanian (*Lewesiceras* ? sp. from Algeria, figured as *Pachydiscus* sp. – Pervinquièrre 1910 : 37; pl. 3, figs 1, 2) to the Upper Turonian and perhaps Coniacian.

Lewesiceras mantelli Wright & Wright

Pl. 4, figs 1–3; Pl. 6, figs 4, 5

- 1850 *Ammonites prosperianus* d'Orbigny; J. de C. Sowerby : 359; pl. 27, fig. 22.
 1853 *Ammonites peramplus* Mantell; Sharpe (*pars*) : 26; pl. 10, figs 2, 3a, b only.
 1870 *Ammonites peramplus* Mantell; C. F. Römer : 319; pl. 35, fig. 5.
 1872 *Ammonites peramplus* Mantell; Schlüter : 31; pl. 10, figs 7–14.
 1872 *Ammonites peramplus* Mantell; Fritsch : 38; pl. 8, fig. 4 only.
 1874 *Ammonites peramplus* Mantell; Geinitz : 189; pl. 34, figs 5, 6, ? 4.
 1896 *Pachydiscus peramplus* (Mantell) Woods : 79.
 1913 *Pachydiscus peramplus* Mantell (Sowerby); Roman & Mazeran : 14; pl. 1, fig. 2 only.
 1913 *Pachydiscus vaju* Stoliczka; Roman & Mazeran : 16; pl. 1, figs 5–9.
 1926 *Pachydiscus cricki* Spath : 82 (*non* Kossmat 1898).
 1927 *Pachydiscus sharpei* Spath; Billingshurst : 514; text-fig. 2a–c.
 1951 *Lewesiceras mantelli* Wright & Wright : 20.
 1952 *Lewesiceras mantelli* Wright; Collignon : 84 (republished 1955 : 78).
 1958 *Lewesiceras peramplus* (Mantell); Drushchitz, Michailov & Eristavi : pl. 52, fig. 2a–c.
 1959 *Lewesiceras peramplum* (Mantell); Najdin & Shimanskij : 185; pl. 12, fig. 4a–c; pl. 13, fig. 4a, b.
 1964 *Lewesiceras romani* Sornay : 183, text-figs 1–4.
 1967 *Lewesiceras mantelli* Wright & Wright; Houša : 26; pl. 4, fig. 3 only; pl. 5, figs 1–4; ? pl. 6, figs 1–4.
 1967 *Lewesiceras lenesicense* Houša : 35; pl. 8, figs 1–7.

TYPE. *L. mantelli* was a *nom. nov.* for *Pachydiscus cricki* Spath, 1926 (*non* Kossmat, 1898), of which the holotype by monotypy is BM 88587, the original of Sharpe, 1853 : pl. 10, fig. 3a, b.

DESCRIPTION. Small (c. 90 mm diameter) to moderate in size, rather involute, the section depressed and coronate in the young but becoming higher with growth, varying from inflated and rounded on the body chamber to slightly compressed. To a diameter of 50 to 60 mm the umbilicus is surrounded by large and prominent laterally-directed spines (rounded tubercles on internal moulds) on the edge of the vertical umbilical wall, commonly six or seven to a whorl. The first distinct tubercle normally appears at a diameter of 11 mm and the second at 15 mm. From each spine branch two or three ribs, frequently with a marked constriction in front of the strongest. Shorter ribs are irregularly intercalated. All ribs tend to be weak on the inner part of the side and strongest on the shoulder where they may be angulate or rarely almost form tubercles (Pl. 4, fig. 2). Specimens with the more angulate shoulders naturally have a squarer whorl section than the normal ones. The ribs curve forward strongly and the more prominent ones, particularly those associated with constrictions, form distinct tongue-shaped ridges on the venter.

From a diameter of about 60 mm the whorl is as high as wide, the umbilical spines become weaker and the ribs become more equal and less prominent. The last large spine normally appears at a diameter of about 65 mm, at which stage only the inner part of the ribs remain. At greater diameters there is normally little ornament except very weak umbilical bulges and faint swellings on the venter, but in some cases the ribs may persist ventrally to slightly greater diameters.

The sutures are well spaced and do not interlock; the saddles are plump, subquadrate and regularly and minutely frilled; the lateral lobes are rather wide and irregularly trifid; the external lobe is little more than half as long as the first lateral.

Specimens occur rarely with up to eleven umbilical spines (e.g. IGS 7981 from Hitch Wood and Zr 9329 from Kensworth – see Pl. 6, fig. 4); in fact in such specimens the number of umbilical tubercles is normal on the inner whorls and the excess number only arises at the beginning of the body chamber. The original of d'Orbigny's 1840 : pl. 100, figs 1, 2 is perhaps such a form. A few specimens are known (e.g. BM 88709; Pl. 6, fig. 5) with stronger, sharper and more regular ribs, resembling those of some *Nowakites* or even *Canadoceras*.

AFFINITIES AND DIFFERENCES. Distinction from the earlier *L. peramplum* is difficult because that species is known mainly from very large, badly-preserved specimens. An individual of 60 mm diameter from the *Inoceramus labiatus* Zone of Wharram, North Humberside (WW 9311, *ex* Stainforth coll.) accords reasonably well with the small *L. peramplum* figured by Houša from the Lower Turonian of Czechoslovakia (1967 : pl. 1, figs 1, 2) and is intermediate between the inner whorls of the Upper Albian *Eopachydiscus laevicanaliculatum* (Römer) and the Upper Turonian *L. mantelli*. Compared with the latter it has somewhat more compressed and flatter-sided whorls, weaker umbilical tubercles, feebler constrictions and stronger and more regular intermediate ribs.

L. plicatum Houša (1967 : 32; pl. 7, figs 1–4) differs from the contemporary *L. mantelli* in being more compressed and in having denser ribs that persist with the juvenile sinuous character to a later stage. Certain undescribed Yorkshire specimens (WW 9310, 9313, *ex* Stainforth coll.) may be the inner whorls of *L. plicatum*.

L. sharpei (Spath, 1926 : 82) was based on one of Sharpe's figures of *Ammonites peramplum* (1853 : pl. 10, fig. 1a, b only). This figure, reduced to half natural size, is of a large but incomplete, rather compressed *Lewesiceras* with twelve weak umbilical bulges on the last-preserved whorl, but no other ornament; the inner whorls are missing. The specimen is quite unfit for the diagnosis of a species in this genus; it has not been traced and its precise horizon is unknown. *L. sharpei* (Spath) should be treated as a *nomen dubium*. Wright & Wright (1951 : 20) were wrong to include the original of Sharpe's pl. 10, fig. 2 in *L. sharpei*; it is in fact a typical *L. mantelli*.

The abundant Uchaux examples identified by Roman & Mazeran (1913) as *Pachydiscus vaju* (Stoliczka) and described as a new species *L. romani* by Sornay (1964) seem to be typical examples of *L. mantelli*; the stated grounds for distinction from *L. mantelli* were the more depressed whorl section and more numerous, rounded and prominent umbilical tubercles, but in these and all

other features the Uchaux specimens fall within the range of *L. mantelli*. *P. vaju* itself is a Santonian species and probably a *Nowakites*.

The Malagasy *L. beantalyense*, *L. sornayi* and *L. tongoboryense* described by Collignon (1952, = 1955) all have much more rounded whorl sections than *L. mantelli* and have been separated from *Lewesiceras* by Houša (1967) as *Tongoboryoceras* (see p. 316), while the Indian *Pachydiscus anapadensis* Kossmat and the Malagasy *L. masiaposense* Collignon, both referred to *Lewesiceras* by Collignon (1952), are characterized by strong ventrolateral tubercles joined across the venter by fine looped ribs and have been placed by Houša in a new genus *Menabonites*.

Houša's (1967) *L. lenesicense* is based on small specimens, all figured enlarged, which are typical *L. mantelli*. His far larger specimens attributed to *L. mantelli*, many figured much reduced, may well belong to this species, but English material of the size of his largest specimens has not been found. That his interpretation of *L. mantelli* differs from mine can also be seen from a comparison of the specimens figured in the literature that are referred by each of us to this species, as indicated in our synonymies. However, some of the references to early nineteenth-century authors given in Houša's synonymy but omitted from mine may well refer to *L. mantelli*.

NOMENCLATURE. This species is widely quoted as *L. cricki* (Spath). Collignon (1952 : 84, = 1955 : 78) objected, since the two species belong to different genera, to the renaming of the species because of the prior existence of *Pachydiscus cricki* Kossmat. He ignored however the fact that Spath established his species not as *Lewesiceras cricki* but as *Pachydiscus cricki*; such a primary homonym must under the Rules be renamed.

OCCURRENCE. This is the commonest and most widespread ammonite in the Chalk Rock and indeed in the rest of the *Holaster planus* Zone, occurring even in Lincolnshire and Yorkshire. It is widely distributed in Europe, being recorded usually as *Ammonites* or *Pachydiscus peramplus*. It also occurs in the *Terebratulina lata* Zone (WW 14054 from the Guildford bypass, Surrey).

***Lewesiceras woodi* sp. nov.**

Pl. 3, fig. 21; Pl. 6, fig. 6

1973 *Pseudopuzosia* sp., Birkelund : 141; pl. 12.

TYPES. The holotype is BM C79509 (WW *ex* Reid coll.) from the Chalk Rock of Hitch Wood; paratypes are BM C20239 from the Chalk Rock of Aston Rowant, Oxfordshire, C79504 (WW coll.) presumably from the *Holaster planus* Zone and probably from Kent, and C79520 (Gaster coll.) from the *H. planus* Zone of Malling Hill, Lewes; also Birkelund's specimen MMH 12836, from Särödal, Sweden.

NAME. For Mr C. J. Wood.

DESCRIPTION. Rather compressed with distinctly flat subparallel sides and a low rounded venter. The ornament on the inner whorls is very feeble. There are eight or nine well-marked constrictions, radial on the inner part of the side, then curving forward but crossing the venter with only a slight bend. Behind each is a moderately strong rib, steep in front and shallow behind, raised into a slight bulla on the umbilical shoulder. Between constrictions there are two to four very feeble broad irregular ribs.

AFFINITIES AND DIFFERENCES. This species is obviously a *Lewesiceras* derived from the main stock by reduction of the umbilical tuberculation and the ribbing. In these respects it resembles the inner whorls of *Pseudojacobites* and *Tongoboryoceras* but is readily distinguished by its relative compression, flatter sides, strong forward bend of the constrictions and main ribs on the ventrolateral shoulders and by the well-spaced sutures typical of *Lewesiceras*. Birkelund's Särödal specimen has these sutures and, though more than twice as big as any of the English specimens, exhibits the characteristic features of *L. woodi*.

OCCURRENCE. Rare in the Chalk Rock of Hertfordshire and Oxfordshire, in the *H. planus* Zone of ? Kent and Sussex and in the Upper Turonian of Särödal, Sweden.

Genus *PSEUDOJACOBITES* Spath, 1922
[*Pseudopuzosia* Spath, 1926; *Rotalinites* Shimizu, 1935]

TYPE SPECIES. *Pachydiscus farmeryi* Crick, 1910.

Moderately evolute, inflated with strong constrictions, behind each of which is a strong rounded rib springing from an umbilical bulla, and weak irregular intermediate ribs. On the outer whorls there are strong ventrolateral and siphonal tubercles. The sutures interlock to a slight extent and have long narrow highly-divided bifid saddles and trifold lobes (Fig. 2).

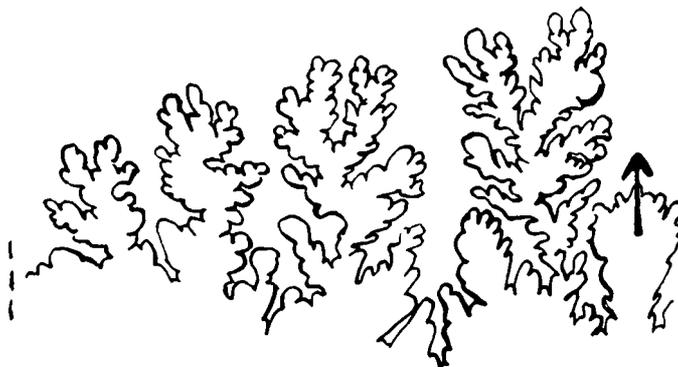


Fig. 2 Suture of *Pseudojacobites farmeryi* (Crick), $\times 2$.

Study of two well-preserved specimens collected in recent years has surprisingly demonstrated that the holotype of *Desmoceras marlowense* Noble, the type species of *Pseudopuzosia* Spath, consists of the inner whorls of a specimen of *Pachydiscus farmeryi* Crick, the type species of *Pseudojacobites* Spath.

The genus is readily distinguished from *Lewesiceras* not only by the ventrolateral and siphonal tubercles on the outer whorls but also by the more depressed whorl section, straighter ribs and constrictions and the interlocking sutures with longer and narrower elements (cf. Fig. 2 and Pl. 5, fig. 1). The tubercles and the weaker, less regular ribbing distinguish *Pseudojacobites* from *Tongoboryoceras*.

Pseudojacobites ranges from Upper Turonian to Coniacian. The Santonian attribution of a species from Texas is doubtful. The genus is widespread but apparently always rare, occurring in Madagascar, southern India, Japan and Texas as well as England.

Pseudojacobites farmeryi (Crick)

Fig. 2; Pl. 4, fig. 5; Pl. 5, fig. 1; Pl. 6, figs 2, 3

- 1910 *Pachydiscus farmeryi* Crick : 345; pl. 27, figs 1, 2.
1911 *Desmoceras marlowense* Noble : 398, text-figs 1, 2.
1922 *Pseudojacobites farmeryi* (Crick) Spath : 121.
1926 *Pseudopuzosia marlowense* (Noble) Spath : 80.
1954 *Pseudopuzosia marlowensis* (Noble); Matsumoto : 113, text-fig. 5.

TYPES. The holotype, by monotypy, is BM C12220 from the *Holaster planus* Zone of Boswell, Lincolnshire; the holotype of *Desmoceras marlowense* Noble is GSM 25456.

DESCRIPTION. Moderately evolute whorl section, increasing very sharply, wider than high and widest at the umbilical shoulder, with long, very slightly convex umbilical wall, slightly flattened sides and broadly rounded venter. There are eight constrictions well marked on the internal

mould, shallow and prorsiradiate on the umbilical wall, rectiradiate on the inner part of the side then curving very slightly forward to cross the venter in a very shallow arc or even transversely. Immediately behind the constriction and following the same course is a prominent well-rounded rib with a distinct large rounded-bullate tubercle on the umbilical shoulder. On the shell (partly preserved in GSM 108896) there is no constriction and the rib is stronger with a more bullate tubercle.

From a diameter of about 45 mm, both on mould and shell, a broad rounded ventrolateral tubercle appears irregularly on main and intermediate ribs, becoming increasingly strong with growth producing a squarish whorl section. Slightly later, there appears on the mould behind each constriction a low rounded tubercle on either side of the siphuncle; on the shell even at this stage there was probably a single transversely elongated siphonal tubercle.

REMARKS. Although the holotype of *Desmoceras marlowense* (Pl. 6, fig. 2a, b) is worn in places and scraped in others, it is by no means as poor a specimen as has been believed. It had in fact been coated with layers of varnish and casting compounds so that its details became obscured. Now cleaned, it can be seen to coincide in all respects with the corresponding stages of the well-preserved specimen figured in Pl. 5, fig. 1. The earliest traces of ventrolateral tubercles can just be seen on the abraded final part of the specimen.

Crick's holotype of *P. farmeryi*, once allowance is made for the lateral crushing and the fact that the specimen is a composite mould, compares very well with the original of Pl. 5, fig. 1. Further support for the identification of these specimens is provided by GSM 108896, which matches the holotype of *marlowense* and also has preserved a pseudomorph of part of the shell showing intermediate ribs like those of the holotype of *farmeryi*.

AFFINITIES AND DIFFERENCES. *Pseudojacobites* seems to be rare wherever it occurs and only a handful of foreign specimens is known – a few *P. rotalinus* (Stoliczka) from the Coniacian of south India and Madagascar, two specimens of *P. ankobensis* Collignon (1965) and two of *P. masiaposensis* (Collignon, 1965) from the Upper Turonian of Madagascar, and the holotype of *P. texanus* Matsumoto (1966) probably from the Turonian of Texas.

Of these *P. masiaposensis* (Collignon) (1955 : pl. 1, fig. 1; 1965 : pl. 380, fig. 1644) is very close to its contemporary *P. farmeryi*. It differs only in having much larger and more prominent tubercles, particularly the umbilical ones, and in its sharper and more regular doubled ribs on the venter. *P. ankobensis* Collignon (1965 : 10; pl. 380, fig. 1643), another contemporary, apparently has a more precocious development of the ventrolateral and siphonal tubercles, but the umbilical ones are perhaps smaller than in *P. masiaposensis*.

Plate 5

× 1 (Figs 8, 10 × 2)

Pseudojacobites farmeryi (Crick) (p. 313). Hitch Wood.

Fig. 1a, b. Coll. C. J. Wood. IGS Zr 7977. See also Pl. 4, fig. 5 (same specimen) and Pl. 6, figs 2–3.

See Fig. 2, p. 313, for suture.

Subprionocyclus neptuni (Geinitz) (p. 319). Hitch Wood.

Figs 2a, b, 3a, b. Coll. R. E. H. Reid. BM C79519, C79655.

Subprionocyclus branneri (Anderson) (p. 320). Hitch Wood.

Fig. 4. Coll. WW. BM C79477. Figs 5a, b, 6a, b. Coll. R. E. H. Reid. BM C79483, C79482.

Subprionocyclus hitchinensis (Billinghurst) (p. 318).

Figs 7–10. Hitch Wood. Fig. 7, Coll. R. E. H. Reid. BM C79472. Figs 8–10, Coll. WW. BM C79495, × 2; C79484, × 1; C79654, × 2. Fig. 13. *Holaster planus* Zone, Guildford bypass. Coll. Mrs Suggate. BM C79474.

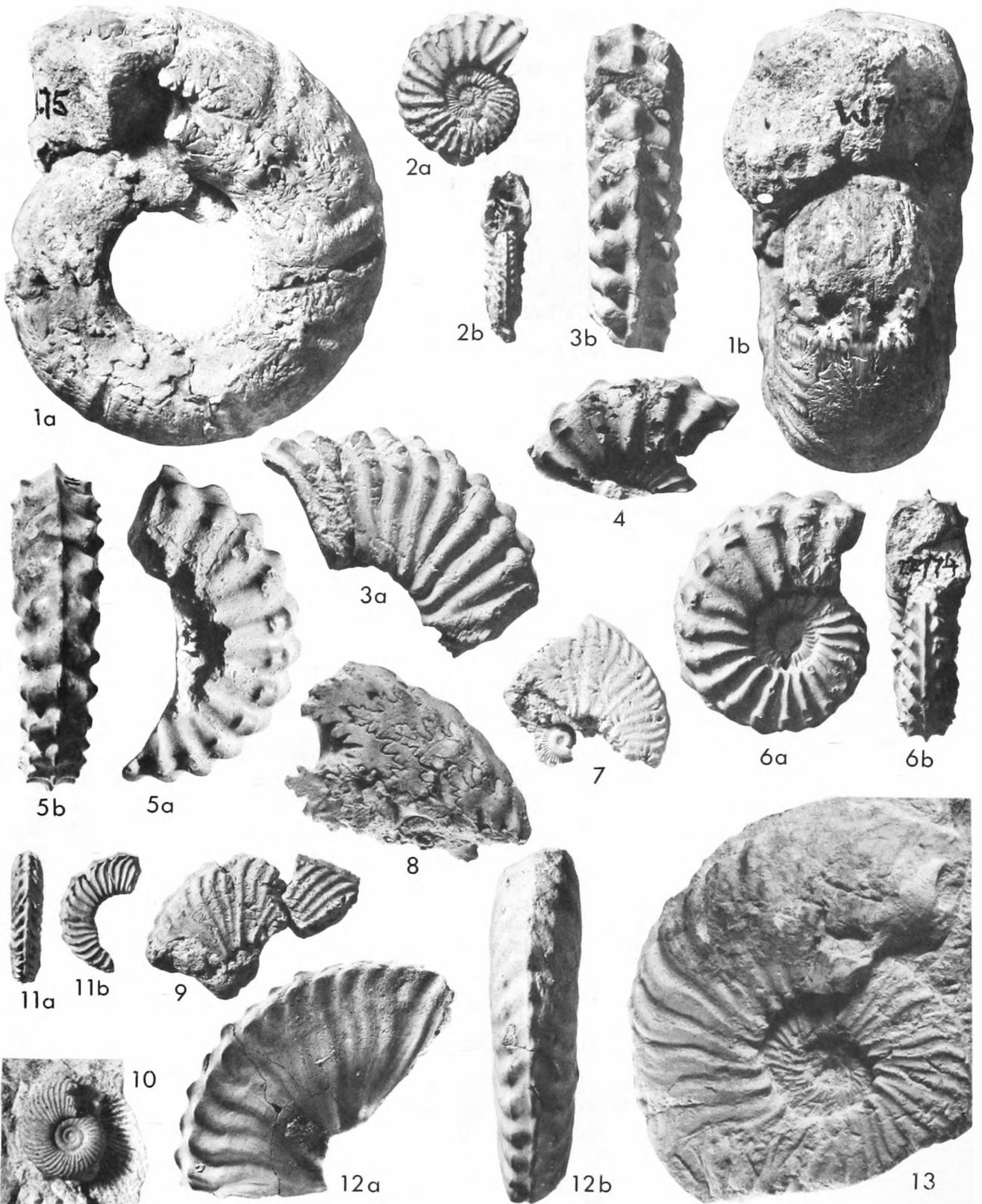
Subprionocyclus sp. (p. 320). Reed Quarry, near Royston.

Fig. 11a, b. Coll. C. J. Wood. GSM 108932.

Subprionocyclus normalis (Anderson) (p. 321). Hitch Wood.

Fig. 12a, b. Coll. WW. BM C79494. See also Pl. 7, fig. 2.

Photographs: Figs 5b and 12a by BM.



The Coniacian *P. rothalinus* (Stoliczka) has a more circular whorl section, has ten or more, rather than eight, primary ribs, which are more regular and prominent, and loses the fine secondary ribs at a diameter probably of about 45 or 50 mm, after which there are a few irregular coarse secondaries.

P. texanus Matsumoto has a comparatively high whorl section, regular well-marked secondaries nearly as strong as the primaries and rather small tubercles.

Menabonites anapadensis (Kossmat) from the Coniacian of south India much resembles *Pseudojacobites masiaposensis* in its depressed whorl section and the ventrolateral tubercles on the outer whorl, but has no siphonal tubercles (see above, p. 312).

OCCURRENCE. The holotype, BM C12220, from Boswell, Lincolnshire, is from normal chalk recorded as of the *Holaster planus* Zone; the remaining specimens come from the Chalk Rock of Hill End Farm pit, Hitch Wood and Blount's Farm pit, Marlow.

Genus *TONGOBOCYOCERAS* Houša, 1967

TYPE SPECIES. *Lewesiceras tongoboryense* Collignon, 1952.

Houša (1967 : 42) rightly distinguished from *Lewesiceras* a group of species with uniform whorl section and more or less equal primary and secondary ribs. Study of the English specimens of *T. rhodanicum* Roman & Mazeran shows that there are other important generic characters. *Tongoboryoceras* shares with *Pseudojacobites* a complex suture with long and relatively narrow elements compared with those of *Lewesiceras*. The early whorls of *Tongoboryoceras*, moreover, are smooth to a much later stage than those of *Lewesiceras* and the strong constrictions form a marked angle on the venter.

Tongoboryoceras rhodanicum (Roman & Mazeran)

Pl. 6, figs 1, 7

1913 *Pachydiscus rhodanicus* Roman & Mazeran : 18; pl. 1, fig. 10a, b.

1954 *Pseudopuzosia marlowensis* Noble; Matsumoto : 113, text-fig. 6 only.

1967 *Tongoboryoceras rhodanicum* (Roman & Mazeran) Houša : 42.

DESCRIPTION. Rather involute, with depressed whorl section about twice as wide as high, evenly rounded except for the long sloping umbilical wall. There are six to nine irregularly spaced wide constrictions to a whorl, well marked on the internal mould, broadly curved on the sides and crossing the venter with a sharp angle on earlier, more transversely on later whorls. The rib

Plate 6

× 1 (Fig. 4 × 0.4)

Tongoboryoceras rhodanicum (Roman & Mazeran) (above). Kensworth.

Fig. 1a, b. Specimen with beginning of body chamber, coll. P. R. Payne & R. J. Hogg. IGS Zr 9330.

Fig. 7a, b. Inner whorls, coll. M. J. Oates. GSM 115258.

Pseudojacobites farmeryi (Crick) (p. 313).

Fig. 2a, b. Blount's Farm Pit, Marlow. Holotype of *Pseudopuzosia marlowensis* (Noble). GSM 25456.

Fig. 3a, b. Hitch Wood. Coll. C. J. Wood. GSM 108896. See also Pl. 4, fig. 5 and Pl. 5, fig. 1.

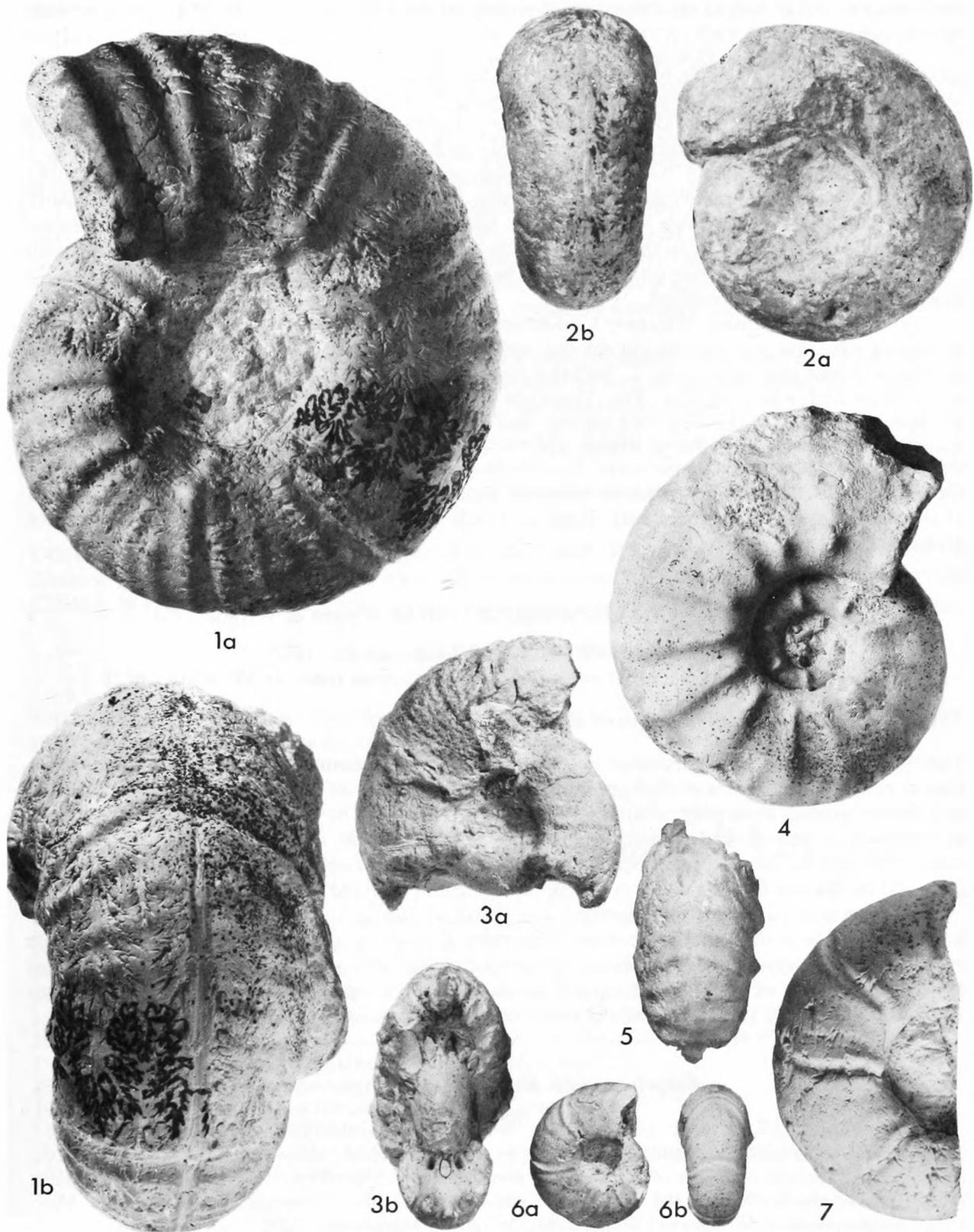
Lewesiceras mantelli Wright & Wright (p. 310).

Fig. 4. Kensworth. Specimen with umbilical tubercles unusually strong and numerous on the body chamber, coll. P. R. Payne & R. J. Hogg. IGS Zr 9329, × 0.4. Fig. 5. Oldbury Hill, Wiltshire. Fragment with unusually strong and regular intermediate ribs. BM 88709. See also Pl. 4, figs 1-3.

Lewesiceras woodi sp. nov. (p. 312). Aston Rowant.

Fig. 6a, b. Paratype. BM C20239. See also Pl. 3, fig. 21.

Photographs: Figs 1-4, 7 by IGS; Figs 5, 6 by BM.



behind each constriction begins to become stronger from a diameter of about 25 mm, at which intermediate ribs first appear. From a diameter of some 75 mm all ribs are strong, broad and rounded, those on either side of the constrictions united on the umbilical shoulder in a large rounded-bullate tubercle.

AFFINITIES AND DIFFERENCES. The inner whorls (e.g. Wainwright coll. J.9 and GSM 115258, *ex* Oates coll.) demonstrate the close relationship with *Pseudojacobites*, but the absence of ventrolateral and siphonal tubercles on the outer whorls and the strong, almost equal ribs distinguish the species and place it in *Tongoboryoceras*. The large Kensworth specimen figured on Pl. 6, fig. 1 (IGS Zr 9330), which agrees well with the holotype, has the beginning of the body chamber preserved at a diameter of 95 mm. The specimen from the Toulmin Smith collection, locality unrecorded (BM 48764), which was figured by Matsumoto (1954 : text-fig. 6) as *Pseudopuzosia marlowensis*, in fact belongs to the present species. It has the prolonged smooth early stage with strong constrictions, angulate on the venter, but the strong intermediate ribs are beginning to appear on the last part preserved.

From the closely related Malagasy Coniacian *T. beantalyense* (Collignon) *T. rhodanicum* differs in having ribs that are slightly curved but not sinuous and much lower and blunter; its constrictions persist to a later stage. *T. tongoboryense* (Collignon) has even more sinuous ribs and a more depressed whorl section. The Turonian *T. donovani* (Collignon) is less depressed than *T. rhodanicum* but is otherwise very similar; the only specimen is too small to show whether the marked feebleness of the ribs persists or not.

OCCURRENCE. Chalk Rock of Kensworth and Blount's Farm pit, Marlow (IGS JM 1354) and chalk immediately above the Chalk Rock at Hitch Wood (IGS Zr 7975); Upper Turonian of Uchaux, France.

Family COLLIGNONICERATIDAE Wright & Wright, 1951

Genus *SUBPRIONOCYCLUS* Shimizu, 1932

[*Oregoniceras* Anderson, (1941 *nom. nud.*) 1958; *Ledoceras* Basse de Ménorval, 1962]

TYPE SPECIES. *Prionocyclus hitchinensis* Billingshurst, 1927.

The type species is at one extreme of a group of closely allied forms with rather a wide morphological range. The ornament changes somewhat with growth, so that fragments of individuals of different growth rates may be difficult to identify. However, by admitting a reasonable degree of variation in density and strength of ribs and tubercles, a satisfactory grouping into a small number of species can be made. Matsumoto (1959) has fortunately reduced to order the species from California and Oregon and it is simple to tie these in with the European species.

The genus is of particular phylogenetic, and therefore stratigraphic, interest since it appears to be the source of a number of the more important Coniacian and later ammonite stocks. The evolute and coarsely-ribbed *S. branneri*, for example, probably gave rise directly to *Protexanites* and *Paratexanites*, of the Texanitinae; *S. normalis*, on the other hand, appears to grade into *Reesidites* and hence to lead to *Barroisiceras* (Barroisiceratinae).

Subprionocyclus hitchinensis (Billingshurst)

Pl. 5, figs 7–10, 13

1927 *Prionocyclus hitchinensis* Billingshurst : 516; pl. 16, figs 1, 2.

1932 *Subprionocyclus hitchinensis* (Billingshurst) Shimizu : 2.

1951 *Prionocyclus hitchinensis* Billingshurst; Wright & Wright : 30.

1954 *Subprionocyclus hitchinensis* (Billingshurst); Wright & Matsumoto : 129.

TYPES. The holotype is BM C32292 from Hitch Wood; paratypes are BM 23156 from the 'Middle Chalk of Kent' and C32293 from Hitch Wood.

DESCRIPTION. Very compressed, the whorl section widest at the umbilical tubercles, the sides flat or slightly convex, subparallel to gently convergent, involute, with steeply rounded to undercut umbilical wall. The ribs are wiry and rounded at first but later tend to be flat, at least on the outer part; they are prorsiradiate and slightly sinuous. In the early stages they are single and more or less equal but later arise in twos and threes from slight umbilical bullae; later still they may be more clearly differentiated into primaries with umbilical bullae and about twice as many branching or intercalated secondaries. The ribs end in more or less distinct ventrolateral thickenings or tubercles; on most specimens there are, at some growth stage, perceptible though feeble inner ventrolateral tubercles, but they are normally absent in the young. The keel on internal moulds is entire at first but later develops weak to strong serrations.

There is some variability in the strength and density of the ribs. Some specimens have rather stronger and more distant ribs with more distinct ventrolateral tubercles; these individuals (e.g. Pl. 5, figs 9, 13) are also rather less involute and have less convergent sides and a flatter venter with a more crenulate keel. Thus they somewhat resemble some specimens of *S. normalis* (Anderson), but their ribs are not as flat or as coarse, at corresponding diameters, as in that species.

The suture has rather narrow, deep and coarsely and irregularly subdivided elements; the first lateral ('external') saddle is marked in some individuals by well-developed 'oblique trifidity' such as characterizes *Diaziceras* and other members of the Barroisiceratinae.

AFFINITIES AND DIFFERENCES. *S. hitchinensis* is readily distinguished from *S. branneri* and *S. neptuni* by its involution and compression, and from *S. normalis* (which it resembles in these features) by its finer and denser ribs, which are also less emphatic and less tuberculate on the shoulders.

OCCURRENCE. *S. hitchinensis* is widespread in the Chalk Rock and the nodular facies of the *Holaster planus* Zone and has even occurred in the normal chalk at this horizon in Devon (BM C79657, WW ex Reid coll.).

Subprionocyclus neptuni (Geinitz)

Pl. 5, figs 2, 3

- 1841 *Ammonites bravaisianus* d'Orbigny : 308; pl. 91, figs 3, 4.
 1842 *Ammonites falcatus* Mantell; Geinitz : 67 (*non* Mantell).
 1850 *Ammonites Neptuni* Geinitz : 114; pl. 3, fig. 3.
 1855 *Ammonites Bravaisianus* d'Orbigny; Sharpe : 52; pl. 23, figs 8, 9.
 1872 *Ammonites Neptuni* Geinitz; Schlüter : 36; pl. 11, figs 2, 5, 7, 8, ?9 only.
 1872 *Ammonites Bravaisianus* d'Orbigny; Fritsch : 29; pl. 8, fig. 5; pl. 16, fig. 4.
 1872 *Ammonites Neptuni* Geinitz; Fritsch : 30; pl. 3, fig. 4 only (*non* pl. 2, fig. 3 *nec* pl. 14, fig. 3).
 1872 *Ammonites Neptuni* Geinitz; Geinitz : 85; pl. 36, fig. 4.
 1874 *Ammonites Neptuni* Geinitz; Geinitz : 280; pl. 62, fig. 4.
 1875 *Ammonites Neptuni* Geinitz; Geinitz : 185; pl. 36, fig. 4.
 1877 *Ammonites Neptuni* Geinitz; Fritsch : 101.
 1896 *Prionocyclus Neptuni* (Geinitz) Woods : 77; pl. 2, fig. 11; pl. 3, figs 1, 2 only.
 1902 *Schloenbachia knighteni* Anderson : 119; pl. 1, figs 1-4; pl. 2, figs 39, 40.
 1902 *Schloenbachia siskiyouensis* Anderson : 119; pl. 1, figs 19, 20.
 1913 *Prionotropis bravaisianus* (d'Orbigny) Roman & Mazeran : 22; pl. 1, figs 13-18.
 1931 *Prionotropis neptuni* (Geinitz) Collignon : 24; pl. 4, figs 1, 2.
 1951 *Prionocyclus neptuni* (Geinitz); Wright & Wright : 30.
 1954 *Subprionocyclus neptuni* (Geinitz) Wright & Matsumoto : 129.
 1958 *Oregoniceras knighteni* (Anderson); Anderson : 264; pl. 24, fig. 5; pl. 33, figs 1, 3 (? *non* fig. 2).
 1958 *Oregoniceras siskiyouense* (Anderson); Anderson : 266; pl. 23, figs 2, 3; pl. 24, figs 1-3.
 1958 *Oregoniceras jillsoni* (Anderson); Anderson : 267; pl. 19, fig. 6.
 1959 *Subprionocyclus neptuni* (Geinitz); Matsumoto : 112; pl. 29, figs 2, 3; pl. 30, figs 2, 3; text-figs 60-63.

LECTOTYPE. The original of Geinitz' figure (1850 : pl. 3, fig. 3) was designated by Matsumoto (1959 : 112).

DESCRIPTION. Moderately but variably involute, rather compressed, the whorl section higher than wide with the sides, at least in costal section, almost parallel for the inner two-thirds or three-quarters, then converging slightly towards the flat to slightly fastigate venter with its distinct keel. The earliest ribs are low and rounded, rising in twos or threes from indistinct umbilical tubercles. Thereafter to a diameter of 16 to 18 mm (the maximum of most Uchaux specimens – see below) they are rather high and narrow, separated by wider interspaces, arising somewhat irregularly at or near the umbilical shoulder singly or in pairs, rarely in threes, from subdued umbilical tubercles or alternately long and short; the specimen shown in Pl. 5, fig. 2a, b has branching ribs on one side and alternately long and short on the other. The ribs are more or less straight but prorsiradiate until a slight inner ventrolateral tubercle at which they bend sharply forward and end in neat outer ventrolateral clavi. The venter is normally smooth. The keel on internal moulds may be apparently entire or weakly to strongly crenulate. The crenulations are well forward of the corresponding ventrolateral clavi. Normally at a diameter of 16 to 18 mm the ribs become more distant and to a variable extent flatter in their outer part; the specimen shown in Pl. 5, fig. 3 (BM C79655) for example retains the characteristic ribbing of the middle stage until the body chamber. The coarse distant ribbing with correspondingly strong tubercles may persist or may be replaced by closer ribs with the inner ventrolateral tubercles weak or absent, the outer ones reduced and the ribs joining the keel in chevrons on the venter.

AFFINITIES AND DIFFERENCES. *S. neptuni* is more involute than *S. branneri* and has more prorsiradiate, closer and wider ribs and weaker tubercles at corresponding diameters. Some individuals with typical *neptuni* inner whorls, however, have a period of growth with ribs and tubercles like those of *branneri*. The coarsely-ribbed adults figured by Matsumoto (1959 : pl. 29, figs 2, 3; pl. 30, figs 2a, b) are somewhat outside the morphological range found so far in the Chalk Rock. *S. hitchinensis* and *S. normalis* are both more involute and compressed than *S. neptuni* and *S. normalis* has flatter and more sinuous ribs at all stages.

A few fragments (Bromley coll. C.151 and GSM 108932 – see Pl. 5, fig. 11a, b) that at first seem very distinct from *S. neptuni* or any other species of the genus are provisionally included here; they are very evolute and have regular single ribs more prorsiradiate, especially in the outer part, than in typical *neptuni* and a rather narrower venter. The specimen from the Unter Pläner of Plauen figured as *neptuni* by Geinitz (1875 : pl. 62, fig. 4) and included by Woods in the synonymy of this species appears to be a *Watinoceras* from the basal Turonian.

NOMENCLATURE. Examination of specimens showing early and middle growth stages demonstrates that *S. bravaisianus* and *S. neptuni* cannot be maintained as separate species. In their paper on the Uchaux fauna, Roman & Mazeran (1913) refigured d'Orbigny's types and their photographs leave little doubt about the synonymy of the two species. In fact none of the presumed syntypes is large enough to provide an adequate diagnosis for a species in this genus; their range of variation is greater than the difference between the lectotypes of *bravaisianus* (Matsumoto & Noda 1966 : 359) and *neptuni*. The prior name is *bravaisianus* but apart from Moreman's (1927 : 96) description of a specimen as *Gauthiericeras* aff. *bravaisi* (d'Orbigny), passing references by Collignon (1931 : 26) and Basse de Ménorval (1959 : 16, 18) and Matsumoto & Noda's paper (1966) the name has been seldom used since 1913, whereas *neptuni* is regularly and widely used. An application will be made to the International Commission on Zoological Nomenclature to conserve the well-known name *neptuni*.

OCCURRENCE. *S. neptuni* is fairly common and widespread in the Chalk Rock and the nodular facies of the *Holaster planus* Zone. It is widely distributed in north and central Europe and occurs also in southern France, north Africa, Madagascar, California and Oregon.

Subprionocyclus branneri (Anderson)

Pl. 5, figs 4–6

1872 *Ammonites Neptuni* Geinitz; Schlüter : 36; pl. 11, fig. 1 only.

1896 *Prionocyclus Neptuni* (Geinitz) Woods : 77; pl. 3, fig. 3 only.

- 1902 *Prionotropis branneri* Anderson : 125; pl. 1, figs 11–16.
 1927 *Prionotropis cristatus* Billingshurst : 515; pl. 16, fig. 3a–c.
 1951 *Collignonicerias cristatum* (Billingshurst) Wright & Wright : 30.
 1954 *Subprionocyclus cristatus* (Billingshurst) Wright & Matsumoto : 129.
 1958 *Prionotropis branneri* Anderson; Anderson : 261; pl. 34, figs 1–3.
 1959 *Subprionocyclus branneri* (Anderson) Matsumoto : 109, text-figs 58, 59.

DESCRIPTION. Rather evolute, whorl section more or less rectangular to square, with sharp, high, coarsely crenulate keel. The ribs are typically almost rectiradiate, simple, high and sharply rounded on the inner whorls but increasingly flattened on the outer; they arise near the umbilical seam, form a pinched bulla on the umbilical shoulder and have two regular and prominent ventrolateral clavi; the corresponding siphonal serration on the keel is well forward of the ventrolateral tubercle. In some individuals, however, a few or even a majority of the ribs spring in pairs from umbilical tubercles. Both types of individuals occur together in the English Chalk Rock and it seems doubtful whether subspecific separation, as provisionally suggested by Matsumoto (1958 : 111), is necessary. Some specimens, moreover, have slightly curved and prorsiradiate ribs (e.g. Wainwright coll. J.15). The suture is as might be expected distinctly simpler, with fewer and shallower indentations than in the more involute and compressed members of the genus.

AFFINITIES AND DIFFERENCES. The squarer whorl section and the more nearly rectiradiate distant ribbing with distinct inner and outer ventrolateral tubercles throughout readily distinguish this species from *S. neptuni*. The other species are all much more involute and compressed.

S. branneri foreshadows *Protexanites* in its ribbing and tuberculation but is at once distinguished by the siphonal tubercles being well forward of and higher than the corresponding outer ventrolateral tubercles. At least one specimen of *S. branneri* (Pl. 5, fig. 6a, b) has incipient midlateral tubercles such as appear in many Texanitinae.

OCCURRENCE. *S. branneri* seems to be rather rare in the Chalk Rock except at Hitch Wood and Kensworth. It occurs sparsely in Germany and Oregon and possibly at Uchaux.

Subprionocyclus normalis (Anderson)

Pl. 5, fig 12a, b; Pl. 7, fig. 2

- 1872 *Ammonites Neptuni* Geinitz; Schlüter : 36; pl. 11, figs 3, 4 only.
 1872 *Ammonites* cf. *goupilianus* d'Orbigny; Schlüter : 37; pl. 11, fig. 10.
 1958 *Oregonicerias normale* Anderson : 268; pl. 25, fig. 8, 8a.
 1959 *Subprionocyclus normale* (Anderson) Matsumoto : 118; pl. 29, fig. 1; pl. 31, figs 1–5; text-figs 64–66.
 ? 1962 *Ledoceras massoni* Basse de Ménorval : 871; pl. 22, figs 1–8; pl. 23, fig. 2a; pl. 24, figs 1–5.

DESCRIPTION. Compressed, moderately to very involute and high-whorled with steep to vertical or even undercut umbilical wall and very slightly convex sides. The whorl section is widest just below mid-flank. The venter is flat to fastigate. The ribs, rising singly or in pairs from slight umbilical tubercles or intercalated, are slightly sinuous to falcoid and prorsiradiate, bending forward more sharply at faint inner ventrolateral clavi, which are absent in early and late growth stages, and ending at moderately strong outer ventrolateral clavi. On the body chamber the inner ventrolateral tubercle disappears, the outer one and the ribs become weaker and the venter more fastigate, so that there is great similarity to *Reesidites subtuberculatus* (Gerhardt), *R. minimus* Hayasaka & Fukada and certain *Barroisicerias*. The number of umbilical tubercles and ribs varies widely in the American material and the few English specimens fall at the more densicostate end of the range of variation.

AFFINITIES AND DIFFERENCES. *S. normalis* can be considered a compressed and involute version of *S. neptuni* or a flat and sparsely-ribbed version of *S. hitchinensis*. The Californian population is variable; according to Matsumoto (1959 : 120–1) the ratio of umbilical to total diameter ranges from 15% to 30%, the number of umbilical bullae from 7 to 14 and of ribs from 22 to 35. A

Chalk Rock specimen in A. Wainwright's collection (J.15) has, at a diameter of 40 mm, an umbilicus 22.5% of the total diameter, 15 umbilical bullae and 30 ribs. Some of the characters overlap those of *S. neptuni*, but *normalis* differs in being more compressed and involute, with a narrower umbilicus, more fastigiate venter, weaker ornament, sinuous ribs and a shorter stage in which both inner and outer ventrolateral tubercles are present. Californian specimens apparently have only a steeply sloping umbilical wall, whereas the English specimens have it vertical or undercut. As Matsumoto (1959 : 121) points out the resemblance to *Reesidites* is so close that *S. normalis* may be regarded as phylogenetically intermediate between *S. neptuni* and *Reesidites minimus*. Only the brief appearance of lower ventrolateral tubercles indicates the place of *normalis* in *Subprionocyclus*. Basse de Ménéval's *Ledoceras massoni*, whose holotype is a young Uchaux individual figured at twice natural size, includes specimens with slightly more ribs than the most densely costate Californian specimens figured by Matsumoto (1959), but other features are so similar that even subspecific separation seems unnecessary. The Uchaux and English specimens probably occur at a slightly earlier horizon than the Californian ones and the median point of variation in the populations has probably shifted.

OCCURRENCE. Rare at Hitch Wood and Kensworth. It occurs also in the *Holaster planus* Chalk of Surrey and in France and Germany.

General results and correlations

The fauna of the Chalk Rock, occupying at most a part of the lower half of the *Holaster planus* Zone, is, with its relatively numerous species of ammonites, of considerable importance for

Plate 7

× 1 (Fig. 1 × 3, Fig. 12a × 1.7, Fig. 12b × 1.6)

Scaphites pseudoaequalis Yabe (p. 305). Kensworth.

Fig. 1a, b. Coll. M. J. Oates. GSM 115259, × 3. See also Pl. 3, fig. 5.

Subprionocyclus normalis (Anderson) (p. 321). Kensworth.

Fig. 2. Coll. P. R. Payne & R. J. Hogg. IGS Zr 9331. See also Pl. 5, fig. 12.

Puzosia curvatisulcata Chatwin & Withers (p. 308). Kensworth.

Fig. 3a, b. Coll. P. R. Payne & R. J. Hogg. IGS Zr 7785. See also Pl. 4, fig. 4.

Hyphantoceras reussianum (d'Orbigny) (p. 297).

Fig. 4a, b. Kensworth. Coll. P. R. Payne & R. J. Hogg. IGS Zr 8010. Fig. 6, 1¼ ml (2 km) SW of Dunstable. Closely coiled specimen cited by Woods (1896 : 75). GSM 36955. See also Pl. 2, figs 6-7.

Didymoceras saxonicum (Schlüter) (p. 296). Kensworth.

Fig. 5. Specimen showing the earliest regular whorl, coll. P. R. Payne & R. J. Hogg. IGS Zr 7828. See also Pl. 2, figs 8-12.

Scaphites geinitzii laevior subsp. nov. (p. 302). Kensworth.

Fig. 7a, b. Coll. P. R. Payne & R. J. Hogg. IGS Zr 7788. See also Pl. 3, figs 8-9.

Otoscaphtes reidi sp. nov. (p. 307). High Wycombe.

Fig. 8. Pit behind Broom & Wade factory. **Holotype**, coll. C. J. Wood. IGS Zr 7952. See also Pl. 3, figs 17-18.

Scaphites geinitzii geinitzii d'Orbigny (p. 300). Kensworth.

Fig. 9. Specimen with subdued ornament, coll. P. R. Payne & R. J. Hogg. IGS Zr 7786. See also Pl. 3, figs 1-4, 6-7.

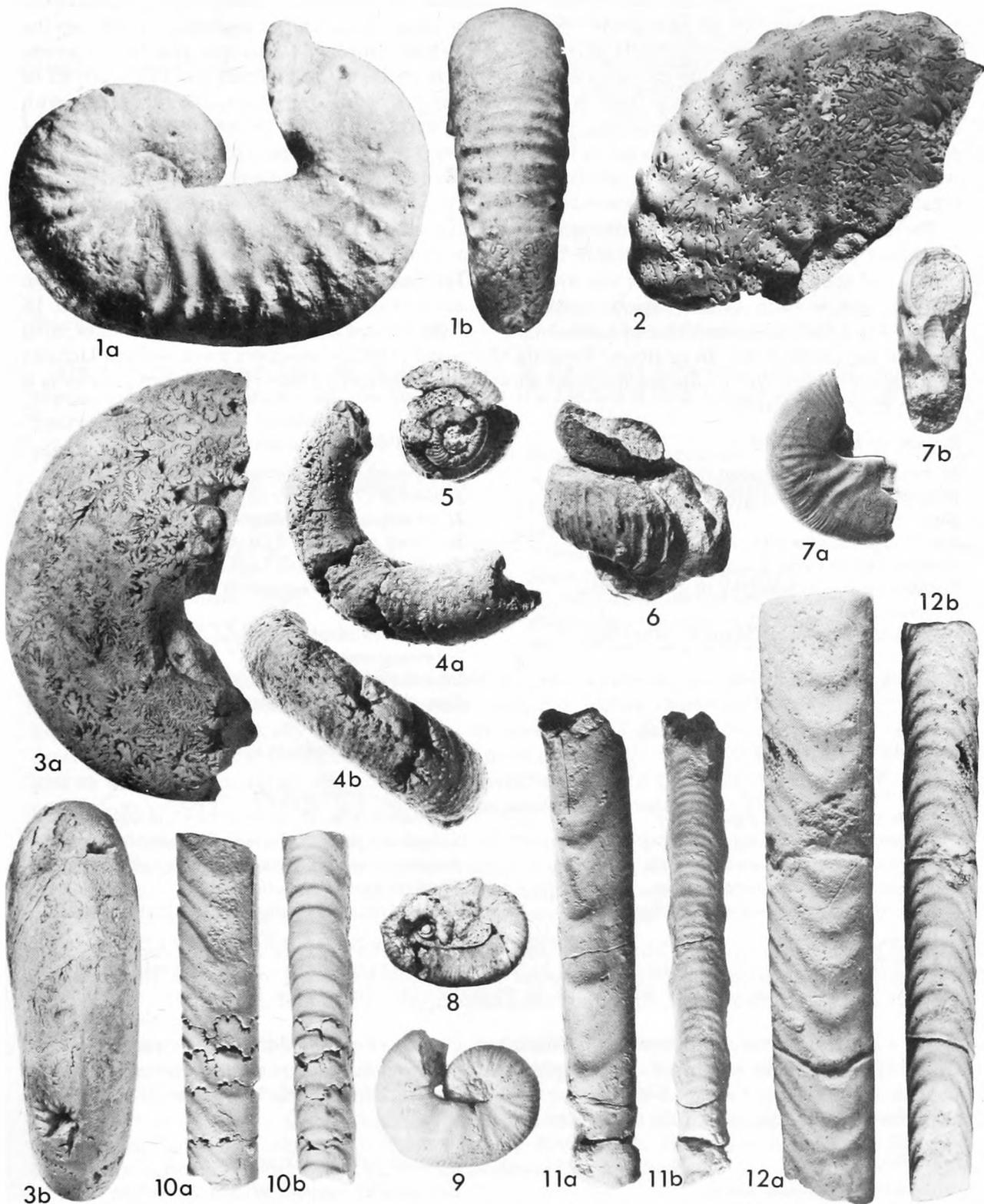
Sciponoceras bohemicum (Fritsch) (p. 285). Kensworth.

Figs 10a, b. Coll. P. R. Payne & R. J. Hogg. IGS Zr 7804. Figs 12a, b. Coll. M. J. Oates. GSM 115260. Fig. 12a, × 1.7. Fig. 12b, × 1.6. See also Pl. 1, figs 3-5.

Baculites undulatus d'Orbigny (p. 287). Kensworth.

Fig. 11a, b. Coll. P. R. Payne & R. J. Hogg. IGS Zr 7803. See also Pl. 1, figs 6-8.

Photographs by IGS, except Figs 2, 4a, b, 5, 6, 7a and 8 by BM.



correlation. As described above, it includes a number of abundant and well-known species as well as various less well known ones and a few genuinely new forms, as listed in the Contents, p. 281.

It is particularly interesting that in various different stocks the beginnings of important evolutionary radiation can be seen at this horizon. For example, *Baculites undulatus*, probably the earliest species of its genus, clearly foreshadows a whole range of Coniacian and later species. The *Scaphites geinitzii* group contains among its many variants the predecessors of a number of Coniacian species. *Lewesiceras* itself is of somewhat restricted morphological range but with *Tongoboryoceras* and *Pseudojacobites*, its presumed derivatives, can be seen as the source of several later genera. *Subprionocyclus* includes *S. branneri* that clearly leads to *Protexanites* and the whole of the Texanitinae, and *S. normalis* that leads to *Reesidites* and thence to the Barroisicercatinae.

There are several European faunas with which that of the Chalk Rock should be compared. The most important is that of Uchaux in south-eastern France, since there also occur there a number of species characteristic of the widespread Tethyan faunas. Unfortunately little is known of the exact horizon of the various ammonite species. Roman & Mazeran (1913) figured 18 species from Uchaux, of which eight, on the basis of the revised determinations given below, also occur in the Chalk Rock. In addition, Basse de Ménéval's (1962) *Ledoceras massoni* from Uchaux is probably a synonym of *Subprionocyclus normalis* and Sornay's (1964) *Lewesiceras romani* is a synonym of *L. mantelli*.

Roman & Mazeran, 1913

Macroscaphites rochatianus d'Orbigny
Hamites gracilis d'Orbigny
Hamites sp.
Baculites undulatus d'Orbigny
Turrilites cf. *costatus* Lamarck
Scaphites aequalis Sowerby mut. *turonensis*
 nov. mut.
Pachydiscus peramplus Mantell (Sowerby)

Pachydiscus vaju Stoliczka
Pachydiscus rhodanicus sp. nov.

Puzosia gaudemarisi sp. nov.
Puzosia sp.
Prionotropis bravaisianus
Prionotropis sp. (pl. 1, figs 18, 19)
Prionotropis sp. (pl. 4, fig. 18)
Acanthoceras deverianum d'Orbigny
Leoniceras groupe de *segne* Solger
Coilopoceras requienianum (d'Orbigny)

Revised determinations

Worthoceras rochatianum (d'Orbigny)
Scalarites (?) *gracilis* (d'Orbigny)
Hyphantoceras reussianum d'Orbigny
Baculites undulatus d'Orbigny
Turrilites cf. *costatus* Lamarck
Scaphites equalis turonensis Roman & Mazeran

Lewesiceras mantelli Wright & Wright and
Lewesiceras sp. indet.

Lewesiceras mantelli Wright & Wright
Tongoboryoceras rhodanicum (Roman &
 Mazeran)

Puzosia curvatisulcata Chatwin & Withers
 indet.

Subprionocyclus neptuni (Geinitz)
Subprionocyclus cf. *normalis* (Anderson)
Subprionocyclus cf. *branneri* (Anderson)
Romaniceras deverianum (d'Orbigny)
Choffaticeras (*Choffaticeras*) sp.
Coilopoceras requienianum (d'Orbigny)

Despite the two apparent Cenomanian survivors (*Turrilites* cf. *costatus* and *Scaphites equalis turonensis*) the *Lewesiceras*, *Tongoboryoceras* and *Subprionocyclus* common to the faunas of Uchaux and the English Chalk Rock indicate a close approximation of date.

The German Scaphiten Pläner has produced specimens of most of the species recorded from the Chalk Rock, but published stratigraphical information is inadequate to determine whether they all come from a restricted horizon or not. Schlüter (1876 : 222) lists from various localities the following species, given here with revised determinations.

Schlüter, 1876

Ammonites peramplus Mant.
Ammonites neptuni Gein.
Ammonites cf. *Goupilianus* d'Orb.
Ammonites Germari Reuss

Revised determinations

Lewesiceras mantelli Wright & Wright
Subprionocyclus neptuni (Geinitz)
Subprionocyclus branneri (Anderson)
Subprionocyclus normalis (Anderson)
Germaniceras germari (Reuss)

<i>Ammonites Bladenensis</i> Schlüt.	<i>Otoscaphtes bladenensis</i> (Schlüter)
<i>Scaphites Geinitzi</i> d'Orb.	{ <i>Scaphites geinitzii geinitzii</i> d'Orbigny <i>Scaphites geinitzii laevior</i> subsp. nov. <i>Scaphites geinitzii</i> aff. <i>intermedius</i> Scupin
<i>Scaphites auritus</i> Schlüt.	{ <i>Otoscaphtes auritus</i> (Schlüter) <i>Otoscaphtes bladenensis</i> (Schlüter) <i>Otoscaphtes fritschi</i> (Grossouvre)
<i>Crioceras ellipticum</i> Mant.	{ <i>Allocrioceras angustum</i> (J. de C. Sowerby) <i>Allocrioceras strangulatum</i> sp. nov.
<i>Helioceras spiniger</i> Schlüt.	?
<i>Helicoceras conradi</i> Mort.	?
<i>Heteroceras reussianum</i> d'Orb.	<i>Hyphantoceras reussianum</i> (d'Orbigny)
<i>Turrilites saxonicus</i> Schlüt.	<i>Didymoceras saxonicum</i> (Schlüter)
<i>Baculites</i> cf. <i>Bohemicus</i> Fr. & Schlönb.	<i>Sciponoceras bohemicum</i> (Fritsch)

Schlüter also figured from this horizon:

<i>Scaphites</i> sp. ?	{ <i>Scaphites lamberti doylei</i> subsp. nov. or <i>Scaphites meslei</i> Grossouvre, subsp. nov.
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The Czechoslovakian Teplitzer beds seem to be somewhat later than the Chalk Rock but precise correlation is impossible on the basis of the literature that I have seen. Fritsch (1899) figures or records the following.

Fritsch, 1889	Revised determinations
<i>Ammonites (Schloenbachia) subtricarinatus</i> d'Orb.	<i>Peroniceras subtricarinatum</i> (d'Orbigny)
<i>Ammonites peramplus</i> Mant.	{ <i>Lewesiceras mantelli</i> Wright & Wright <i>Lewesiceras</i> sp.
<i>Ammonites (Desmoceras) Austeni</i> Sharpe	? <i>Gaudryceras</i> sp.
<i>Scaphites Geinitzii</i> d'Orb.	<i>Scaphites geinitzii</i> d'Orbigny
<i>Helicoceras Reussianum</i> d'Orb.	<i>Hyphantoceras reussianum</i> (d'Orbigny)
<i>Helicoceras polyplocum</i> Rom.	<i>Didymoceras saxonicum</i> (Schlüter)
<i>Baculites undulatus</i> d'Orb.	<i>Baculites undulatus</i> d'Orbigny

From California Matsumoto (1959) recorded *Subprionocyclus neptuni* and *S. normalis* from the Upper Turonian, and said that the former occurred earlier than the latter. Unfortunately, however, a stratigraphically collected series of specimens of *Subprionocyclus* has not yet been described, although California seems to be the most promising area for such a project. These two species occur also in Japan but not enough material seems to be available yet for any refined correlation within the Zone of *Inoceramus teshioensis* (Matsumoto 1971 : 155).

Such evidence as there is points to fairly long ranges for important species such as *Scaphites geinitzii*, *Didymoceras saxonicum*, *Hyphantoceras reussianum*, *Lewesiceras mantelli*, *Subprionocyclus neptuni* and *S. normalis*. Even within the Chalk Rock fauna itself the extent of morphological variation of these species is considerable. Over the whole duration (biochron) of each of these species the mean of the morphological range presumably varied with time, but we are very far from knowing enough of any one population or of the succession of populations in the Upper Turonian to be certain of detailed correlation or to be able to establish refined zonal schemes valid over a wide area.

It is for example possible that evidence will eventually be secured for a zone of *Subprionocyclus normalis* above one of *S. neptuni* or of a subzone of *normalis* within a broad *neptuni* zone. However, even in California and Japan the published evidence does not yet support such an arrangement. What is certain, from the Chalk Rock fauna, is that specimens attributable to *S. normalis* occur with varying forms of *S. neptuni*, *S. branneri* and *S. hitchinensis*. The lesson is that multiplication of zonal or subzonal names based on limited evidence is to be avoided.

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All specimens from the C. W. and E. V. Wright collection (including Mr R. E. H. Reid's ammonites) figured or described here are now in the British Museum (Natural History). The Chalk Rock collection of Mr P. R. Payne and Mr R. J. Hogg and certain of Mr M. J. Oates' ammonites are now in the Institute of Geological Sciences.

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