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A REVISION OF THE GENERIC CLASSIFICATION OF THE FAMILY ECHIOCERATIDAE (CEPHALOPODA, AMMONOIDEA) (LOWER JURASSIC)

T. A. Getty

Cumberland House Museum, Portsmouth, England
(formerly University College, London, England)

ABSTRACT

Following a summary of the stratigraphic subdivisions of the *Oxynoticeras oxynotum* and *Echioceras raricostatum* Zones of the Lower Jurassic, a brief outline is given of earlier classifications of the Echioceratidae at generic level. These, mostly sketchy and based on the "Law of Recapitulation," are of mainly historical interest. Evidence is here presented to show that the earliest echioceratid, *Palaeoechioceras*, was probably an offshoot of the asteroceratid, *Epophioceras*, and was the radical from which the other echioceratids were descended. *Gagaticeras* is interpreted as a short-lived branch in the lower *oxynotum* Zone, while *Orthechioceras* is believed to have arisen from *Palaeoechioceras* near the base of the *raricostatum* Zone and to be the immediate precursor of *Echioceras*, which is restricted to the *Echioceras raricostatoides* Subzone. Two main groups of *Echioceras* can be recognized: 1) the typical raricostate forms, and 2) more densely ribbed forms descended from *Orthechioceras*. *Paltechioceras* was derived from the second group at the top of the *raricostatoides* Subzone, and ranges throughout the two upper subzones of the *raricostatum* Zone, giving rise to the smooth *Leptechioceras*, which is restricted to the lower of these. The homeomorphy between *Paltechioceras* and certain Lower Sinemurian arietitids, as well as that between echioceratids and eoderoceratids, is discussed. In the systematic part, several lectotypes and neotypes of echioceratids and related genera are proposed.

INTRODUCTION

BASIS OF PRESENT CLASSIFICATION

In order that a classification may, at least, reflect the phylogeny, it is necessary that it should be based on a firm stratigraphic framework. Only in this way, by isolating discrete units defined by morphological discontinuity at single horizons, these units representing the interbreeding populations, can the evolution of a group be interpreted meaningfully (Howarth, 1958, p. ii, xxii, xxxiv).

Although it is generally agreed that all char-

acters should be taken into consideration when assessing the morphology of a population, it must be realized that not all are of equal taxonomic importance. In the Echioceratidae, for example, the umbilical width of all genera is large and its variation small and within the range of experimental error. This means that the degree of involution is a character which has no taxonomic importance in this family. In this work emphasis is placed on ribbing (rib density and patterns of rib frequency during ontogeny) as a feature of major taxonomic importance at the generic level and this for two principal reasons: 1) the genera recognized on this basis also show differences in whorl proportions and in the form of the whorl and of the ribs, and 2) material which has been crushed (particularly that retrieved from bore holes) can be interpreted more fully.

Detailed treatment of the Echioceratidae is rather uneven, largely because many of the type species are based on single specimens, which are the only known representatives and which are frequently of unknown age. This applies particularly to the material from the Radstock district.

In most cases, however, allied forms have been collected from the thicker and more complete successions of Dorset, Yorkshire, and Raasay, so that some indication of the stratigraphic position is available, providing a framework for constructing a tentative phylogeny of the family.

PREVIOUS WORK

Buckman (1913, p. *v*) proposed the family Echioceratidae to include *Echioceras* Bayle, 1878, and *Gagaticeras* Buckman, 1913. Later (Buckman, 1914, p. 96c), he divided *Echioceras* into several groups, without, however, designating formal names. This scheme was based largely on material collected by the Geological Survey on the island of Raasay (Inverness) (Buckman in Lee, 1920). Between 1914 and 1927 Buckman proposed four genera of Echioceratidae, while Trueman & Williams (1925), in a detailed study of the later members, proposed a further nine genera and subsequently added an additional two (Trueman & Williams MS in Buckman, 1926; Trueman & Williams, 1927). Spath (1925) named two genera, which he believed represented primitive members from the Mediterranean region, but which are here excluded from the family for the reasons given below (p. 25) and (Spath, 1929) replaced a junior homonym of Trueman & Williams, 1927. Crickmay (1928) proposed a new name for forms from British Columbia, which he later regarded as Echioceratidae. Latterly, Spath (1956) proposed a further genus, as did Erben (1956), thus bringing the total of available generic names (excluding those proposed by Spath, 1925) to twenty. This elaborate nomenclature has never been in general use, although used in part by Trueman & Williams (1925; in Richardson, 1929) and Buckman (1930) in the construction of (hypothetical) tables of hemerae. Since 1930 only sporadic use has been made of certain names, most lavishly by Mouterde (1953), who employed five of Trueman & Williams' genera (as well as *Gagaticeras*, *Echioceras*, *Paltechioceras*, and *Leptechioceras*) as subgenera of *Echioceras*. Erben (1956) retained three genera in addition to the four named above, while others (e.g., Lefavrais-Raymond (in Fleury, 1968)) have identified specimens as *Euechioceras*. This use of the nomenclature has been quite uncritical and no reasons given why some names were used and others rejected. This is also the case in Roman (1938), followed by Krimgolts (in Luppov & Drushchits, 1958), where mention is made of only thirteen of the available names.

A brief study of the family was made by Donovan (MS), which formed the basis for the account in the *Treatise on Invertebrate Paleontology* (Arkell, 1957), where the number of genera was reduced drastically (but not sufficiently, according to Schindewolf, 1962, p. 482). Further comments on this revision were given by Donovan (1958). In this present revision, six genera are considered to be valid, while thirteen are rejected as synonyms and three as *nomina dubia*.

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ABBREVIATIONS

The following abbreviations are used for museums and other institutions in which most of the specimens are located. The names of institutions not included in this list are given in full. Unprefixed register numbers refer to specimens in the author's collection.

BM	British Museum (Natural History).
BS	Bayerische Staatssamlung für Paläontologie und Hist.-Geologie, Munich.
GBW	Geologische Bundesanstalt, Vienna.
GPS	Geologische-Paläontologische Institut der Universität, Stuttgart.
GSE	Museum of the Geological Survey of Scotland, Edinburgh.
GSM	Geological Survey Museum, Institute of Geological Sciences, London.
MCZ	Museum of Comparative Zoology, Harvard, Cambridge, Mass.
MHN	Muséum national d'Histoire naturelle, Paris.

The *International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology* (1964) is referred to throughout, for the sake of brevity, as the *Code.*

Type species of genera discussed here are types either by original designation (OD), or monotypy (M) and are abbreviated accordingly. Several species which were regarded as types by monotypy by Donovan (1958) are here interpreted as types by original designation, since the term genotype was originally defined as "the word 'type' in connexion with genera—a given species is the type of a genus" (Schuchert & Buckman, 1905). Although subsequently misused and now banned (*Code*, Recommendation 67A), it ought to be interpreted in its original sense.

STRATIGRAPHY

The classic sections in Dorset, Yorkshire, and Raasay, as well as material from I.G.S.[1] boreholes, have been investigated and the results show that the subzonal scheme proposed by Donovan (in Dean, Donovan, & Howarth, 1961) is probably the best for correlation throughout the Northwest European ammonite province and, therefore, is followed here. The *Echioceras raricostatoides* Subzone, however, is restored in place of the *Echioceras raricostatum* Subzone, the two index species now being considered distinct (see below, p. 13, 14). In addition, the base of the *rarico-*

[1] Institute of Geological Sciences, London.

statum Zone is here defined as the first appearance of *Crucilobiceras*, in accordance with Oppel (1856, p. 56), who cited *Ammonites densinodus* as one of the characteristic species of the zone. Donovan (in Dean, *et al.*, 1961, p. 458) suggested that the base of the zone might be indicated by the first *Paltechioceras*, since this genus was believed to occur in the *Crucilobiceras densinodulum* Subzone of Raasay and part of southern England. The Raasay specimens, however, are probably *Orthechioceras* sp. (see p. 23) and, although occurring at the base of the Pabbay Shales, may belong to a horizon equivalent to Bed 98 (Lang, 1926) in the Black Ven Marls of Stonebarrow, Dorset, i.e., the top of the *densinodulum* Subzone, below the first *Echioceras*. The examples from southern England are densely ribbed, similar to *Paltechioceras favrei* and *P. boehmi* (Prof. Donovan, pers. commun.) and, therefore, quite different from typical *Orthechioceras*. It is possible that the former may represent an early form of *Orthechioceras* and the latter a late form of *Palaeoechioceras*.

Otherwise, the subzones are defined as in Dean, *et al.* (*op. cit.*). The base of the *raricostatoides* Subzone is marked by the first appearance of *Echioceras* and the base of the *Leptechioceras macdonnelli* Subzone by the first appearance of *Leptechioceras*, which is not known to overlap with *Echioceras*. The base of the *Paltechioceras aplanatum* Subzone is indicated by the upper limit of the range of *Leptechioceras*. This is not entirely satisfactory, but the ranges of *Leptechioceras* and *Paltechioceras* overlap completely in places. *Paltechioceras aureolum* (Simpson) occurs in the basal part of the *aplanatum* Subzone in Yorkshire and the index species of the subzone occurs at higher levels here, but elsewhere other species (e.g., *Paltechioceras favrei* and *P. boehmi*) are cited from the *macdonnelli* Subzone as well.

The *Eoderoceras miles* "Zone" (Hoffman, 1948), originally employed for the beds between the *raricostatoides* "Zone" and the *Uptonia jamesoni* Zone of North Germany (Hoffman, 1944; 1948; 1950), was later restricted to the range of *Leptechioceras* (Hoffman, 1964) and thus became a synonym of the *macdonnelli* Subzone. In Yorkshire, however (author's coll.), *Eoderoceras miles* (Simpson) occurs with the highest *Echioceras* (*E. intermedium* (Trueman & Williams)) and ranges through the *macdonnelli* Subzone and most of the *aplanatum* Subzone. If the *miles* Subzone is employed, therefore, it should be used in its original sense, while recognizing that the lower part may, perhaps, be equivalent to the top of the *raricostatoides* Subzone of other localities.

Outside the British Isles, good successions of the *oxynotum* and *raricostatum* Zones are known from North Germany (Hoffman, 1964) and the Jura (Blaison, 1961), where most of the subzones can be recognized, including the *macdonnelli* Subzone, which had not been readily identifiable in published versions of sections on the Continent prior to 1961.

The succession of lower Liassic ammonite zones referred to in this paper is shown in Table 1.

TABLE 1. *Lower Liassic Ammonite Zones and Subzones of Northwestern Europe.*

SUBSTAGE	ZONE	SUBZONE
Lower Pliensbachian	*Uptonia jamesoni*	
	Echioceras raricostatum	*Paltechioceras aplanatum* *Leptechioceras macdonnelli* *Echioceras raricostatoides* *Crucilobiceras densinodulum*
Upper Sinemurian	*Oxynoticeras oxynotum*	*Oxynoticeras oxynotum* *Oxynoticeras simpsoni*
	Asteroceras obtusum	*Eparietites denotatus* *Asteroceras stellare* *Asteroceras obtusum*

EVOLUTION OF THE ECHIOCERATIDAE

Hyatt (1889) considered *Echioceras raricostatum* to have been derived from "*Caloceras carusense*," a species which, for Hyatt, included forms now assigned to *Vermiceras*, *Metophioceras*, *Alsatites*, and *Epophioceras* (the first three being cited in his synonymy of the species and the last being figured by him). Buckman (1898, 1913, 1914) refuted the arietitid origin of the

Echioceratidae, although he considered them to be descended from an unnamed ancestor, which gave rise to the Arietitidae and was intermediate between the Echioceratidae (which he saw as a forerunner of the Hildoceratidae) and the Liparoceratidae. Trueman & Williams (1925-27) did not attempt to postulate ancestors for the lineages they discerned, merely observing that they believed them to have been derived from different stocks. The reason for this is to be seen, presumably, in their statement that "It must be borne in mind that the recapitulation of phylogenetic stages in ontogeny may be obscured by different degrees of acceleration of the several biocharacters. In other words, at a given point in the ontogeny of an ammonite, the several biocharacters . . . have attained certain stages of development, but it does not necessarily follow that in any ancestor the same stages in these characters were similarly associated. . . . It is thus conceivable that in a species in which the ontogenetic characters are all palingenetic, stages may occur in ontogeny differing completely in appearance from any ancestral form" (Trueman & Williams, 1925, p. 702). This undermining of the "Recapitulation Theory" by its avowed proponents is remarkable, but it is not remarkable that the theory was never again applied to ammonites by workers in this country, except for the study of *Promicroceras* by Williams (1927) and of the oxynoticeratids by George (1930), both of whom were influenced by Trueman.

Spath (1923, p. 67) stated that "morphological transitions and especially the stratigraphic occurrence clearly demonstrate the Deroceratid origin of the family Echioceratidae" and later (Spath, 1926, p. 45) mentioned that specimens from Robin Hood's Bay appeared to be transitional between *Promicroceras* and *Gagaticeras*, although he was dubious of the reality of this "lineage" (based on two specimens) and went on to adduce evidence supporting the arietitid origin of the family. Three lines of evidence were proposed: 1) that the suture lines of the Echioceratidae were more similiar to those of arietitids (e.g., *Epophioceras*, *Aegasteroceras*) than to those of eoderoceratids (Spath, 1926, p. 47, 48); 2) that the development of compressed, bisulcate shells, with a tendency to produce oxycone forms, can be matched in the arietitids, but not in the eoderoceratids (Spath, 1926, p. 48); and 3) that juvenile *Gagaticeras* embrace a wide variety of forms, ranging from those with the ventral characters of *Promicroceras* to those resembling juvenile *Paracaloceras*, but that adult *Gagaticeras* resemble each other closely. This juvenile variation was ascribed to environmental factors (and was, therefore, by implication, of no taxonomic value) (Spath, 1926, p. 137, 139). From consideration of these points, Spath concluded that the Echioceratidae were derived from "Arietitids," such as *Paracaloceras* or *Canavarites* (1926, p. 49), which he thought existed in the Mediterranean region, together with *Epophioceras* and "certain evolute Mediterranean genera," at the same time that *Eparietites*, *Asteroceras*, "and their involute derivatives" (i.e., Oxynoticeratidae) existed in Northwest Europe (Spath, 1926, p. 170), thereby explaining the long interval between the occurrence of the arietitids and Echioceratidae in the latter region (Spath, 1925, p. 362). A separate origin was proposed for *Gagaticeras*, however, as a capricorn offshoot of *Parechioceras*, which was believed to have evolved directly from the Lytoceratidae (Spath, 1926, p. 170).

Spath made no further comment on the origins of the Echioceratidae, although he observed (1956, p. 149) that most of the specimens of *Palaeoechioceras pierrei* (Spath) from Stowell Park "were at first taken to represent a late development of *Epophioceras* (of the *Asteroceras stellare* Subzone), though they were much more closely ribbed."

Finally, Schindewolf (1962, p. 481, 482), from a study of the sutural development, concluded that descent from the Alsatitinae (*Paracaloceras*, etc.) was less probable than descent from Arietitinae, such as *Euagassiceras*.

The relationships of the Echioceratidae, according to the present interpretation, are shown in Figure 1. *Palaeoechioceras* is regarded as the ancestral form, descended from *Epophioceras*, which it closely resembles in sutural development and general morphology, as Spath (1925, 1926) has already shown. The presence, near the base of the *Oxynoticeras simpsoni* Subzone in Robin Hood's Bay, of forms similar to *Palaeoechioceras pierrei* (Spath) (1264/1) (but less densely ribbed than that species and, on the other hand, more compressed and with sharper

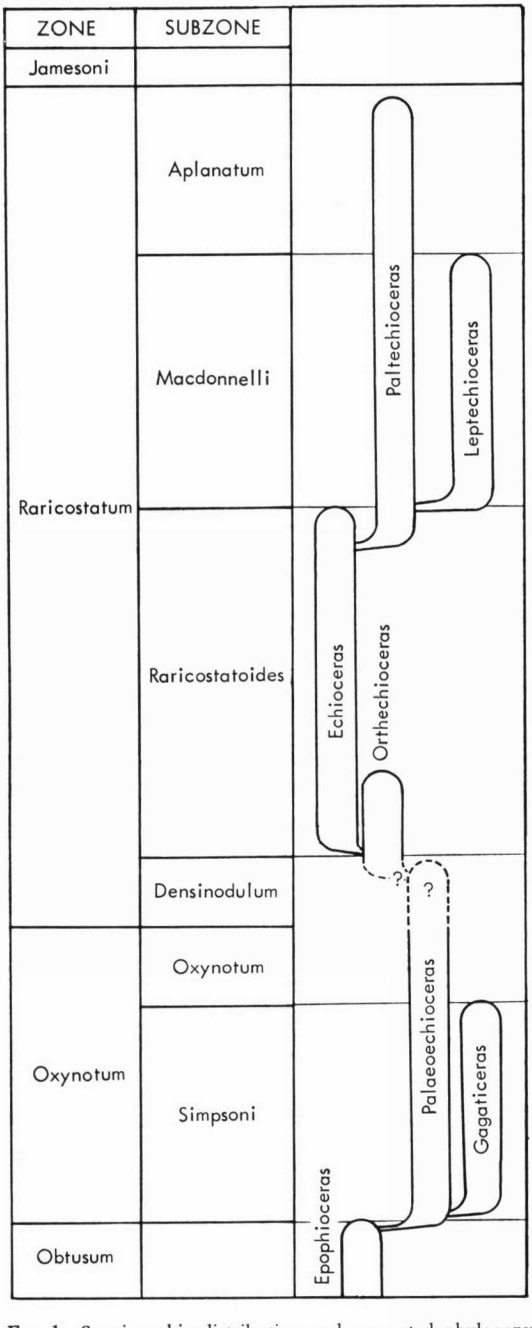

FIG. 1. Stratigraphic distribution and suggested phylogeny of the Echioceratidae. The upper limits of the ranges of *Epophioceras, Palaeoechioceras,* and *Echioceras* are uncertain, as is the lower limit of the range of *Orthechioceras.* (Stratigraphical subdivisions after Dean, Donovan, and Howarth, 1961.)

ribs than *Epophioceras*) associated with nuclei indistinguishable from *P. spirale* (Trueman & Williams) lends support to this hypothesis. Moreover, the occurrence of *Epophioceras* and *Oxynoticeras* together in the same bed at Champfromier (Bovier, 1931, p. 268), if correctly identified, suggests that *Epophioceras* ascends into the *Oxynoticeras oxynotum* Zone, at least locally, thus obviating the necessity of explaining long gaps in the evolutionary sequence. Even if Bovier's identification is at fault, *Epophioceras* is known to occur in the *stellare* Subzone in Dorset (Lang, 1926) and at the corresponding horizon in Robin Hood's Bay (L. Bairstow, pers. commun.), while it may also occur in the *Eparietites denotatus* Subzone (Prof. Donovan, pers. commun.), so that the interval involved is not a long one.

Hyatt's original hypothesis, therefore, was correct at least in essentials (if Hyatt's interpretation of *Caloceras carusense* as his figured specimen is accepted), although based on a now discredited theory of ammonite evolution.

The earliest Echioceratidae are known in abundance only from Northwest Europe, suggesting that the family evolved in this area rather than in the Mediterranean region. This assumption removes the large scale diachronism between the Mediterranean and Northwest European faunas envisaged by Spath (1926, p. 170), which would preclude the possibility of correlating the deposits of these two regions. The faunas cited by Spath (1926) from the Mediterranean were not collected with any stratigraphical precision, while more recent collecting has been hampered by the complicated structure, rapid facies changes, condensed sequence, and poor preservation of the material, as well as by the fact that much collecting is done without the aim of studying the fine stratigraphy of small units, but rather to elucidate the general geology of selected areas. For these reasons, knowledge of the Mediterranean faunas is still relatively meagre and interpretation of the ammonite records is based largely on comparisons with the Northwest European faunas (see Hölder, 1964; Donovan, 1958).

Palaeoechioceras is connected by a series of intermediates with *Gagaticeras*, an offshoot that is restricted to the *simpsoni* Subzone of Robin Hood's Bay and equivalent beds in North Germany (Hoffmann, 1944, 1964) and France (Mou-

terde, 1953; Maubeuge, 1953, 1955, 1966; Berthe & Nouet, 1961; Poujol, 1961; Blaison, 1961). The evidence from Stowell Park (Spath, 1956) and Gloucester Gas Works (Trueman & Williams, 1927), however, suggests that *Palaeoechioceras* persists into the *oxynotum* Subzone, while the record of *Paltechioceras* from the *densinodulum* Subzone of southern England (Donovan in Dean, *et al.*, 1961, p. 458) may refer to late forms of *Palaeoechioceras*, from which *Orthechioceras* is thought to have evolved (see p. 14). The latter, like *Palaeoechioceras*, possesses a short initial smooth stage, followed by a widely ribbed stage, but while *Palaeoechioceras* becomes close-ribbed and compressed, *Orthechioceras* remains widely ribbed throughout and becomes quadrate with a subsulcate venter. *Orthechioceras* is believed to have given rise to *Echioceras* by loss of the sulci and increase of the ribbing on the innermost whorls to produce the characteristic concave rib frequency curve diagnostic of *Echioceras*.

The earliest *Echioceras* are densely ribbed throughout and the typical raricostate forms are probably an offshoot of this group. Both raricostate and nonraricostate forms coexisted throughout the *raricostatoides* Subzone in Robin Hood's Bay and on Raasay, although at the former locality the highest forms are nonraricostate and densely ribbed, showing a superficial similarity to *Paltechioceras* (see p. 23).

Paltechioceras is believed to have evolved from such densicostate, late *Echioceras*, rather than from *Orthechioceras*, because of the presence of these intermediate forms, as well as because the latter is not known from beds higher than the base of the *raricostatoides* Subzone (unless the Radstock examples have been derived from higher levels). Similarly, forms intermediate between *Paltechioceras* and *Leptechioceras* indicate that the former is ancestral to *Leptechioceras*, early variants of which (*L. meigeni* (Hug)) are weakly ribbed throughout, with the typically smooth *L. macdonnelli* (Portlock) becoming dominant later. Not only does *Paltechioceras* overlap with the last *Echioceras*, but it extends higher in the sequence than *Leptechioceras* and is the last survivor of the family. The early *Paltechioceras* of the *macdonnelli* Subzone are predominantly densely ribbed and such forms persist into the *aplanatum* Subzone, where they are accompanied by the subzonal index species and its allies, together with less densely ribbed forms, such as *Paltechioceras aureolum* (Simpson). The prolific *Paltechioceras* fauna of the Radstock district is, perhaps, largely derived from beds of *aplanatum* Subzone age, although this is not susceptible of proof.

A feature of *Paltechioceras* is the occurrence of "looped" ribs, which sometimes fade out into areas of smoothly undulating test. There appears to be no consistent pattern in the development of these ribs and whether they are to be regarded as "abnormalities" linked with the extinction of the group, or, more probably, whether they merely represent local damage to the mantle is uncertain (see p. 21). Both in the Jura (Blaison, 1961) and at Robin Hood's Bay a considerable facies change occurs within the *aplanatum* Subzone, without any apparent effect on the *Paltechioceras* fauna. It is possible that the extinction of the genus (and the persistence of the associated eoderoceratids) was due to unknown predators, the nonspinous Echioceratidae being preferred as food to the more heavily armored eoderoceratids.

HOMEOMORPHY BETWEEN THE ECHIOCERATIDAE AND ARIETITIDAE

Prior to 1924, the carinate, sulcate Echioceratidae, now referred to *Paltechioceras*, were usually identified as *Arietites* or *Vermiceras* and this usage has persisted in some quarters, largely as a result of regarding these names as "sack names" for all Lower Lias ammonites with carinate, sulcate venters, irrespective of their other characters.

Among the Arietitidae, however, only a small number of genera can be confused with Echioceratidae. By far the greatest confusion lies between *Paltechioceras* and certain Arietitinae (*Metophioceras* and *Vermiceras*), although other cases occur (e.g., *Gagaticeras* and *Aegasteroceras*; *Gagaticeras* and *Metarnioceras*). Small species of *Aegasteroceras* resemble *Gagaticeras* in having a

"capricorn" type of ribbing but, in *Aegasteroceras*, the inner whorls are carinate and the keel is lost in the later stages, while in *Gagaticeras* the converse is true and, in many cases, a keel is never developed. The "capricorn" ribs of small *Aegasteroceras* are stronger and more distant than the ribbing of *Gagaticeras*, and the ribs are very much swollen on the flanks and flattened on the venter, features which are not seen in *Gagaticeras*. *Gagaticeras* can be readily distinguished from *Metarnioceras* Spath, 1925, not only by the different sutural development in the two forms, as Spath (1925, p. 362) already noted, but also by the compressed, flat-sided whorls of *Metarnioceras*, with an initial smooth stage giving way to strong, straight ribs, which are conspicuously geniculate on the shoulder, where they are projected and rapidly die out. The venter is fastigate and the keel is bordered by smooth or feebly subsulcate bands. The holotype of the type species of *Metarnioceras* (figured only in ventral view) was destroyed by enemy action in 1942 and no other examples of the species are known. The specimen referred to by Spath (1925, p. 360, footnote) as resembling *Ammonites neera* Reynès, 1879 (BM C33581) is here figured for comparison with *Gagaticeras* (Pl. 1, fig. 10a,b). The only dateable specimens of *Metarnioceras* are from the *Arnioceras semicostatum* Zone of the Dorset Coast (Lang, 1924), the Stowell Park Borehole (Spath, 1956) and Redcar, Yorkshire (*Ammonites Pauli* Dumortier in Tate & Blake, 1876, pl. 6, fig. 5 (*non* Dumortier) BM C17880, and author's coll.), which fact, together with the morphological differences noted above, is sufficient to indicate that the genus is distinct from the later *Gagaticeras*, contrary to the statement in Guérin-Franiatte (1966, p. 355).

With regard to the homeomorphy between *Paltechioceras* and the Arietitinae, it has already been shown by Schindewolf (1962) and Bremer (1965) that the two are most readily distinguished by the different development of the suture line. In *Metophioceras* and *Vermiceras* the U_1 lobe is bipartite, leading to the formation of two internal saddles of unequal size, while in *Paltechioceras* U_1 is undivided, so that there is only one internal saddle (Fig. 2). The umbilical lobes of the Arietitinae are markedly retracted, which is not the case in *Paltechioceras*, and this feature is a useful means of differentiation when the internal suture cannot be seen. Finally, the whole suture line in the Arietitinae is often more elaborately frilled than in *Paltechioceras*, although this is a variable feature.

These sutural differences are accompanied by differences in the overall morphology, particularly in that *Paltechioceras* possesses more compressed whorls, with more inflated flanks and, at least on the outer whorls, a trigonal, virtually tricarinate, whorl section. *Metophioceras* and *Vermiceras*, on the other hand, have quadrate, flat-sided whorls. The former is bisulcate, corresponding to *Paltechioceras*, but its keel is tall and conspicuous. These differences also allow *Paltechioceras* to be distinguished from isolated, large body-chambers of *Arnioceras*. *Paltechioceras* and *Metophioceras* may also be distinguished by the dense, fine ribbing of the inner whorls of the former, in contrast to the initial smooth stage of the latter.

In *Vermiceras scylla* Reynès, which is, at the most, feebly sulcate, the morphological resemblances to *Orthechioceras* are much stronger and only the longer initial smooth stage of the former and its bipartite U_1 lobe serve to separate the two.

SYSTEMATIC DESCRIPTIONS[1]

Superfamily PSILOCERATACEAE Hyatt, 1867
Family ECHIOCERATIDAE Buckman, 1913

The members of this family range throughout the *Oxynoticeras oxynotum* and *Echioceras raricostatum* Zones and are characterized by their serpenticone whorls, which are usually subcircular in cross section, becoming either depressed or compressed in some genera. The ornament consists of strong, simple ribs, usually straight, but in some forms projected on the shoulder. In species from the *oxynotum* Zone they pass over the venter without interruption and a keel is not always developed, while in later forms a keel is invariably present and the ribs die out on the

[1] Synonyms are treated in smaller type following discussion of each valid genus.

venter, which is tabulate or fastigate and, in *Paltechioceras*, usually conspicuously bisulcate.

The suture is simple, consisting of broad lobes and saddles, weakly incised, except in some more evolute species where the elements are rather narrower and more elaborately frilled. In all forms, however, the development is the same and results in the formation of five principal lobes (*E*, *L*, U_2, U_1, *I*). Of these, U_1 is always undivided and usually the same depth as U_2, while *L* tends to be bifid, or to have an equal number of accessories. Development of U_3 may not occur and identification of this lobe in most cases is doubtful, because of its small size. The umbilical lobes are only weakly retracted, if at all (Fig. 2).

Genus PALAEOECHIOCERAS Spath, 1929

[*nom. nov. pro Protechioceras* Trueman & Williams, 1927 (*non* Spath, 1925)]

Type Species (OD).—*Protechioceras spirale* Trueman & Williams, 1927, p. 248, pl. 28, fig. 6.

Holotype.—Original of Trueman & Williams, *loc. cit.* GSM 51475. Refigured herein, Pl. 1, fig. 2.

Type Locality.—Gloucester Gas Works, Gloucestershire, England.

Type Stratigraphic Occurrence.—Upper Sinemurian (*?oxynotum* Zone, *oxynotum* Subzone). Not collected *in situ*.

Derivation of Name.—παλαιός = old; ἔχις = adder; κέρας = horn.

Discussion.—The characteristic features of this genus are its depressed globose, initially smooth nucleus, becoming ornamented by blunt, widely spaced ribs, persisting to about 5 mm. diameter and then becoming more evolute and rapidly more densely ribbed. At about the same diameter a week keel develops and the ribs become projected on the shoulder, where they either die out or are continued as chevrons over the venter, sometimes with the development of secondary chevrons. A collection of topotypes (GSM Zd. 3075-3105), the majority nuclei, shows considerable variation in the size at which the densicostate stage is initiated and also in the form of the venter, which may be rounded or flattened with or without a keel. These nuclei can be matched by similar small specimens from the base of the *simpsoni* Subzone of Robin Hood's Bay. A larger specimen from this locality (1264/1, Pl. 1, fig. 1a, b) is more strongly ribbed than the type and does not possess a keel until about 15 mm diameter, which is the start of the outer whorl. The inner whorls are not preserved. The slender, compressed, slightly fastigate whorls and blunt ribs, fading on the shoulder into faint ventral chevrons, indicate the affinity of this specimen with *Palaeoechioceras*, although in lateral view it closely resembles *Epophioceras*.

The Yorkshire specimens can be accurately dated, by their association with *Oxynoticeras simpsoni* (Simpson), to the base of the *simpsoni* Subzone. The Gloucester specimens, however, were collected from spoil tips, but the other ammonites from these tips included *O. oxynotum* (Quenstedt), *Cheltonia accipitris* (J. Buckman), *Eoderoceras (?) ignotum* (Trueman & Williams), *Paracymbites dennyi* (Simpson) and *Angulaticeras* sp., an assemblage which, as a whole, suggests the *oxynotum* Subzone, although *P. dennyi* and *Angulaticeras* occur also at higher horizons (Donovan, 1961, 1966).

A number of previous records of *Palaeoechioceras* have been concealed by misidentifications. Geyer (1886, p. 255, pl. 3, fig. 14) described and figured a typical *Palaeoechioceras* sp. as "*Arietites* cf. *Quenstedti* Schafhäutl sp." In the description, he emphasized that weak secondary ribs were present, which were projected on the venter, forming a right angle on the keel. Spath (1956, p. 150) identified this species as *Parechioceras (?)*, but in that genus secondary ribbing is not present and the ribs do not pass over the keel. The specimen figured as *Parechioceras?* sp. ind. cf. *quenstedti* (Schafhäutl) Geyer (Spath, 1956, pl. 9, fig. 14) appears to be a crushed *Palaeoechioceras*. Similarly, *Arietities geyeri* Siemiradzki, 1923 (*nom. nov. pro Arietities* sp. ind. aff. *nodotianus* Geyer, 1886, pl. 3, fig. 16) appears to be a *Palaeoechioceras*, rather than a *Leptechioceras*, although this cannot be proved without the specimen.

The ammonites figured by Kellaway & Wilson (1941, pl. 9, fig. 3-5) as *Plesechioceras* are all referable to *Palaeoechioceras*, although less densely ribbed than the type species. The original of their pl. 9, fig. 5 (GSM 62458) is distinguishable from *Plesechioceras* by the development of secondary ribs, which are projected on the shoulder and, in places, transgress the keel to give it a faintly crenulate appearance. The nu-

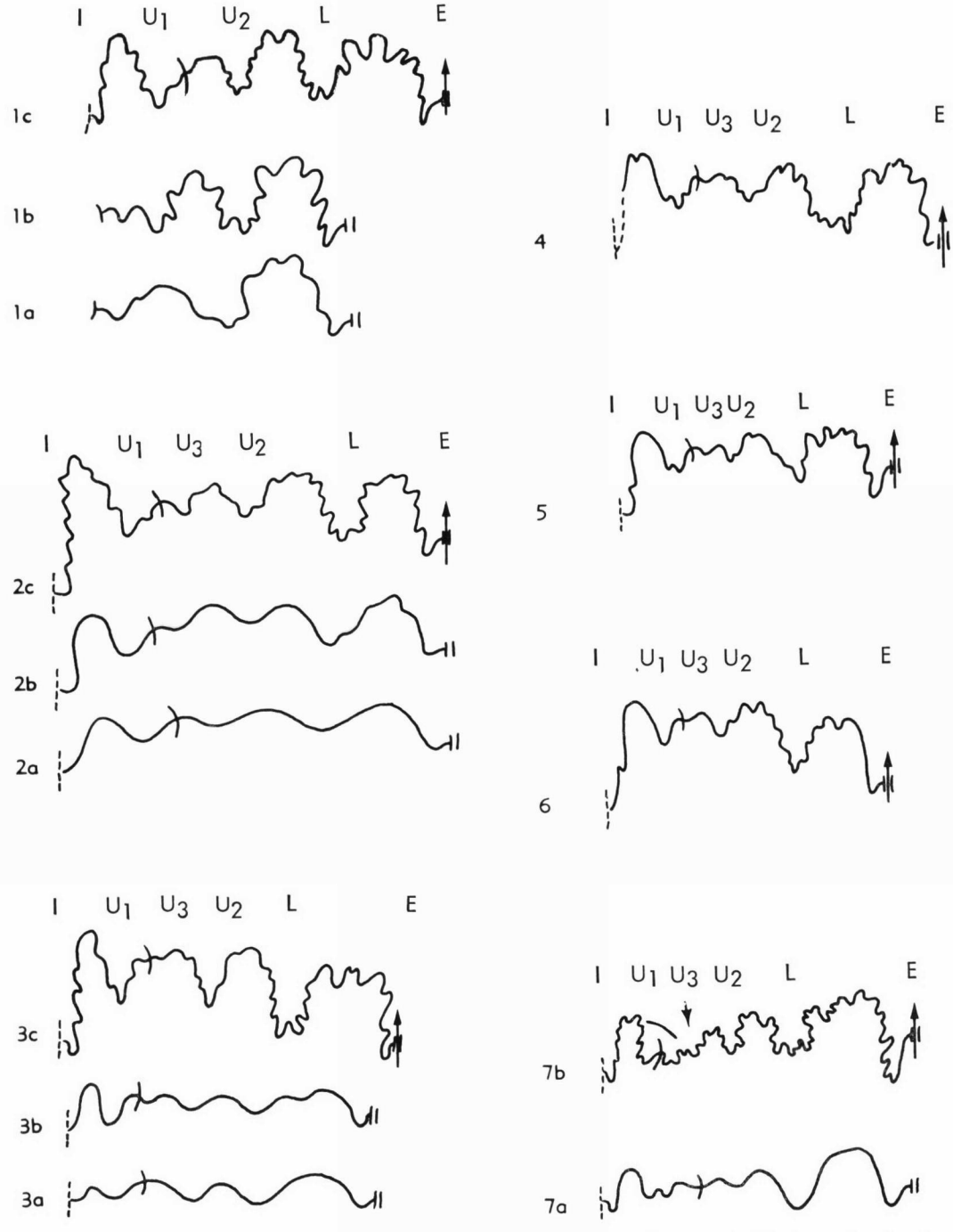

FIG. 2. Suture lines of representative Echioceratidae and of the genus *Vermiceras* (Arietitidae).——*1. Gagaticeras gagateum* (Young & Bird); *1a, D* = 8 mm; *1b,* D = 13 mm; *1c, D,* unknown (after Spath, 1925).——*2. Echioceras raricostatum* (Zieten); *2c, H* = 3.5 mm (after Schindewolf, 1962).——*3. Paltechioceras elicitum* Buckman; *3c, D* = 38 mm, *H* = 6 mm (after Bremer, 1965).——*4. Orthechioceras recticostatum* Trueman & Williams (after Trueman & Williams, 1925).——*5. Echioceras carusense* (d'Orbigny), lectotype; *D* = 18 mm, *H* = 3.5 mm (Getty, n).——*6. Gagaticeras coynarti* (d'Orbigny), lectotype; *D* = approx. 17 mm, *H* = 4 mm (Getty, n).——*7. Vermiceras spiratissimum* (Quenstedt); *7b, H* = 7 mm (after Schindewolf, 1962). [*D* = diameter of shell; *H* = whorl height.]

cleus of this specimen is not well preserved, but that of the original of figure 4 (GSM 62459) is indistinguishable from nuclei of *Palaeoechioceras* from Gloucester Gasworks, while the nucleus of the third specimen (GSM 62460), as seen in lateral view, is also typical of *Palaeoechioceras*, with the smooth initial stage being succeeded by a stage with strong, blunt, distant ribs, giving way to finer denser ribs. All three were collected from a well sinking, together with *Oxynoticeras* and *Bifericeras*, suggesting an *oxynotum* Subzone age.

Genus HYPECHIOCERAS Spath, 1956

Type Species (OD).—*Hypechioceras pierrei* Spath, 1956, p. 149, pl. 9, fig. 13a, b.

Holotype.—Original of Spath, *loc. cit.*, GSM Bj 4196. Refigured here (Pl. 1, fig. 6a,b).

Type Locality.—Stowell Park (Borehole) near Northleach, Oxon, England.

Type Stratigraphic Occurrence.—Upper Sinemurian. *Oxynotum* Zone, *oxynotum* Subzone.

Derivation of Name.—*ὑπό* = below; for "—*echioceras*" see above.

Discussion.—The holotype is the only well-preserved specimen, the syntypes being smaller and crushed in the shale. The venter of the inner whorls is not exposed, but, after the initial smooth stage, the inner whorls are ornamented by blunt, distant ribs, gradually giving way to denser, finer ribbing. Up to ca. 8 mm diameter, the rib densities of *Palaeoechioceras spirale* (Trueman & Williams) and *Hypechioceras pierrei* overlap, but thereafter the former becomes the more densely ribbed, although in both species the increase in rib density is rapid. At the start of the outer whorl of the holotype of *H. pierrei* the ribs are seen to be projected on the shoulder and die out against the feeble sulci bordering the low keel. The whorl is compressed, slightly tabulate, but becomes fastigate and, while the keel persists to the end, the sulci are lost. In view of the disparity in size of the types of *P. spirale* and *H. pierrei* (maximum diameters, respectively, 14 mm and 31 mm), little weight can be attached to the comment by Spath (1956, p. 149) that the peripheries of the two species are "probably" distinct and the similarity of ornament and general aspect do not warrant their generic separation.

Hypechioceras pierrei was believed by Spath (1956) to be the same as *Ammonites hierlatzicus* von Hauer in Reynès (1879, pl. 44, fig. 23-26) (*non* von Hauer, 1856). The original of Reynès' figure cannot be found (Donovan, 1955, p. 34). The examples figured by Geyer (1886, pl. 3, fig. 1, 2) are from the von Hauer Collection and differ from the lectotype of *A. hierlatzicus* von Hauer (here designated as the original of von Hauer, 1856, pl. 7, fig. 4-6; GBW 3034/1), which is not an echioceratid, although its precise affinities are uncertain. Its florid sutures and weakly sigmoidal ribs, tending to be fasciculate in places, suggest that it may be a hildoceratid. The original of Geyer, 1886, pl. 3, fig. 2 (GBW 3034/2) is similar in size to the holotype of *H. pierrei*, but possesses a more densely ribbed nucleus and a less densely ribbed outer whorl. It is also quadrate, compressed, with a prominent shoulder and carinate, bisulcate venter. The inner whorls of the other specimen figured by Geyer (1886, pl. 3, fig. 1; GBW 3034/3) are not visible, but, at a size corresponding to the outer whorl of *H. pierrei*, it it much less densely ribbed than the latter and, although not sulcate at this diameter, the venter is tabulate, with a prominent keel. The outer whorl is carinate, bisulcate, and there can be no doubt that the specimens figured by Geyer (1886) are *Paltechioceras*.

Genus GAGATICERAS Buckman, 1913

Type Species (OD).—*Ammonites gagateus* Young & Bird, 1828, p. 255, pl. 12, fig. 7.

Holotype.—Original of Young & Bird, *loc. cit.*, WM 104. Refigured by Buckman, 1913, pl. 78.

Type Locality.—Robin Hood's Bay, near Whitby, Yorkshire, England.

Type Stratigraphic Occurrence.—Upper Sinemurian, *oxynotum* Zone, *simpsoni* Subzone.

Derivation of Name.—γαγάτης = jet (with reference to the inner whorls being ornamented by ribs "like a row of jet beads") (Young & Bird, 1828).

Discussion.—*Gagaticeras* is retained in the Echioceratidae, notwithstanding its close similarity to the eoderoceratid *Promicroceras*, not only because of its simple suture, with an undivided U_1 lobe, but also because of the occurrence of transitional forms between *Palaeoechioceras* and *Gagaticeras*. Near the base of the *simpsoni* Subzone at Robin Hood's Bay, a thin discontinuous limestone (Tate & Blake, 1876, "*Oxynotus* Beds" bed 28) contains a series of forms connecting *Palaeoechioceras* sp. (1264/1, author's coll.) to *Gagaticeras neglectum* (Simpson) by way of *G. exortum* (Simpson), which is the most abundant form. The changes involved are increase in whorl width relative to whorl height, producing first a rounded and then a depressed whorl section, an increase in the rib density of the inner whorls, and the development of rursiradiate ribs on the middle whorls. These features are seen in specimens from the underlying bed (1270/1, author's coll.; Pl. 1, fig. 9, and 1264/2, author's

coll.; Pl. 1, fig. 5a,b) which are accompanied by numerous *Palaeoechioceras* nuclei.

Gagaticeras neglectum is also similar to *Echioceras carusense* (d'Orbigny) [lectotype here designated as the original of Pl. 1, fig. 8, herein (d'Orbigny Coll. 1475A/1, Muséum natl. d'Histoire Nat., Paris) = original (?) of *Ammonites carusensis* d'Orbigny, 1844, pl. 84, fig. 3-5], which has a similar rib frequency curve, but which is more slender, the outer whorls being fastigate, with a prominent keel against which the ribs abut. The ribs are projects into chevrons on the earlier whorls where there is no keel. Intercalary ribs are not infrequent.

Gagaticeras neglectum appears to be the root stock and longest ranging species, at least in Yorkshire. It is closely related to *G. coynarti* (d'Orbigny) (lectotype here designated as the original of Pl. 1, fig. 4a,b, herein (MHN, d'Orbigny Coll. no. 1474) = original *(partim)* of *Turrilites coynarti* d'Orbigny, 1843, p. 181, pl. 42, fig. 4-7), in which the ribs die out completely on the flattened, depressed venter of the outer whorl, a feature never observed at this stage in the abundant Yorkshire *Gagaticeras* spp.

The type species has a wide geographic distribution, but in Yorkshire its range is restricted to a single horizon near the base of the range of *Gagaticeras neglectum*. In North Germany (Hoffman, 1944) it is found with other *Gagaticeras* spp. in a conglomeratic ironstone and its range elsewhere is unknown.

Gagaticeras is widely distributed in Northwest Europe, occurring in northern England (where the *simpsoni* Subzone is well developed) and also in North Germany, Franconia (Zeiss, 1965), the borders of the Paris Basin (Maubeuge, 1953, 1955, 1966; Mouterde, 1953) and the borders of the Massif Central as far south as Lyon (Mouterde, 1953) and the Jura (Blaison, 1961). It has never been recorded outside this region, however, despite Arkell's identification (1956, p. 185) of *Ammonites althii* Herbich (1878, pl. xx E, fig. 1) as *Gagaticeras*, this species being apparently *Euagassiceras*, similar to *Ammonites defossus* Simpson, in Buckman, 1913 (*non* Simpson, 1843). The identification by Hölder (1964, p. 39) of *Aegoceras planicosta* in Geyer (1886, pl. 3, fig. 20) as *Gagaticeras*, following Buckman, 1913, is also erroneous; the specimen is an eoderoceratid, as the suture shows, perhaps a *Promicroceras*. That this absence of *Gagaticeras* from the Alpine area is not due to absence of beds of *simpsoni* Subzone age is suggested by the specimens of *Oxynoticeras simpsoni* figured by Geyer (1886, pl. 2, fig. 12, 13, as *O. oxynotum*). Geyer's collection was destroyed in World War II, however, and these specimens no longer exist. They were renamed *O. oxynotum* var. *hierlatzicum* von Pia (1914).

Genus PARECHIOCERAS Buckman, 1914

TYPE SPECIES (OD).—*Aegoceras* (?) *finitimum* Blake, 1876, p. 273, pl. 6, fig. 9.

HOLOTYPE.—Original of Blake, *loc. cit.*, SM J 3280. Refigured by Buckman, 1914, pl. 100A.

TYPE LOCALITY.—Robin Hood's Bay, near Whitby, Yorkshire.

TYPE STRATIGRAPHIC OCCURRENCE.—Upper Sinemurian, *oxynotum* Zone, *simpsoni* Subzone.

DERIVATION OF NAME.—παρά = beside, close by.

DISCUSSION.—The genus was originally proposed to include forms with a suture and nucleus similar to *Gagaticeras*, but in which the keel is developed at an early stage and connects the peripheral chevrons of the ribs. Development of the keel, however, is a feature of the late growth stages and occurs sporadically among different forms, including those with the typical "bead-like" ribs of *Gagaticeras gagateum* (*G. funiculatum* Buckman, 1919). For this reason generic separation of *Gagaticeras* and *Parechioceras* is not maintained.

Of the species included in *Parechioceras* by Buckman (1914), only *P. neglectum* (Simpson) is an ally of the type species and is so similar to *Gagaticeras* that no useful purpose is realized by placing them in different genera.

The others were:

a) *Turrilites boblayei* d'Orbigny (lectotype here designated as the original of Pl. 1, fig. 3, herein (MHN, d'Orbigny Coll. no. 1472A/1) = original (*partim*) of *T. boblayei* d'Orbigny, 1843, p. 178, pl. 41, fig. 1-4), which is a *nomen dubium*.

b) *Ammonites charpentieri* Schafhäutl, 1847 (lectotype designated by Böse, 1894, p. 728, as the original of Schafhäutl, 1851, pl. 16, fig. 22 only. Since the original figure is uninterpretable, the lectotype (B.S. AS. IX, 23) is now refigured, Pl. 2, fig. 6). This species is a member of *Leptechioceras* and corresponds to *Leptechioceras meigeni* (Hug) *sensu* Donovan (1958). The lectotype of *L. meigeni* was designated by Andrusov, 1931, p. 144, as the original of Hug, 1899, pl. 11, fig. 2, and is, therefore, a senior objective synonym of *Echioceras hugi* Buckman (1914, p. 96c). The action of Buckman in renaming the original of Hug, 1899, pl. 11, fig. 2, cannot be regarded as his having "virtually" designated as the lectotype of *L. meigeni* the original of Hug, 1899, pl. 11, fig. 3, in effect, by a process of elimination as

Donovan (1958, p. 22) contended [*Code*, Art. 74 (c)]. The original of Hug, 1899, pl. 11, fig. 3, does not, therefore, have type status and is a typical example of *L. charpentieri*. This specimen can no longer be found at Geneva (Dr. E. Lanterno, pers. commun.).

c) *Parechioceras haueri* Buckman, 1914, p. 96c. (Lectotype here designated as the original of Pl. 1, fig. 11, herein (Hauer Coll. GBW, no number, being that one of the (three) syntypes which formed the outline of von Hauer, 1856, pl. 16, fig. 10-12). As Spath (1925, p. 362) has already pointed out, this species is an *Echioceras* and is hardly to be distinguished from *Echioceras raricostatoides*. The lectotype has never been entire and the inner whorls of the figure were probably supplied from the smallest syntype.

d) *Ammonites pauli* Dumortier, 1867, p. 163, pl. 29, fig. 5, 6. This is also an *Echioceras* and occurs with *Echioceras laevidomum* at the base of the *raricostatoides* Subzone in Robin Hood's Bay, Yorkshire.

Genus ECHIOCERAS Bayle, 1878

Type Species (M).—*Ammonites raricostatus* Zieten, 1831, p. 18, pl. 13, fig. 4 (I.C.Z.N. Opinion 324).

Neotype.—Original of Pl. 1, fig. 7a,b, herein, here designated. Allmendinger Coll. GPS, no number.

The original of Zieten's figure has not been traced, despite attempts by Donovan (1958, p. 18), Hölder (pers. commun.) and by the author. Accordingly, a presumed topotype from Pliensbach (the nearest outcrop of Lias β_2 to Boll) is now selected as the neotype. It is the closest match with Zieten's figure and with that of Quenstedt (1845, pl. 4, fig. 3) that could be found among the material from the vicinity of Boll.

Type Locality.—Pliensbach near Boll, Württemberg.

Type Stratigraphic Occurrence.—Schwarzer Jura β_2.

Derivation of Name.—ἔχις = adder; κέρας = horn.

Discussion.—Bayle (1878) cited the type species as *Echioceras rarecostatum (sic)* Zieten sp. and later (Bayle, 1879, p. 34) he explained that the name was a replacement for *Ophioceras* Hyatt, 1867 (*non* Barrande, 1865 = *Ophidioceras* Barrande, 1867 (objective synonym)) and stated explicitly that the type species was *E. (Ammonites) rarecostatus (sic)* Zieten. The specimen figured by Bayle was subsequently renamed *Arietites raricostatoides* Vadasz (1908, p. 373) and regarded (incorrectly) as the genotype by Buckman (1914, p. 96c) and by Trueman & Williams (1925, p. 708). This misinterpretation of the type species was accepted by Roman (1938, p. 91), followed by Krimgolts (in Luppov & Drushchits, 1958), a misuse rectified by the I.C.Z.N. (Opinion 324), acting on a proposal by Arkell (1951).

The action by Haug (1894, p. 411, note) in designating *Ammonites raricostatus* Zieten as the type species of *Caloceras* Hyatt, 1870, is wholly invalid, since this species was not one of those originally included in *Caloceras* by Hyatt (1870, p. 22, 29). The designation by Buckman (1912, p. *vii*) of *Ammonites torus* d'Orbigny is the first valid designation of the type species of *Caloceras*, which is not, therefore, a senior synonym of *Echioceras*.

As matters stand at the present, *Acanthopleuroceras* Hyatt (in Zittel, 1900, p. 578) is a junior subjective synonym of *Echioceras*, since the nominal type species, *Ammonites natrix* Schlotheim, 1820, is a species of *Echioceras* (Quenstedt, 1885, p. 185; Jaworski, 1931, p. 134, pl. 6, fig. 11). This state of affairs is the result of Hyatt's having based *Acanthopleuroceras* on the species misidentified by Zieten (1830, p. 5, pl. 4, fig. 5) as *A. natrix* Schlotheim. An application has been made to the I.C.Z.N. to use the plenary powers to stabilize the name *Acanthopleuroceras* in conformity with current usage (Getty, 1970).

The lectotype of *Echioceras raricostatoides* (Vadasz) (designated by Buckman, 1914, p. 96d) can no longer be found in the Bayle Collection, École des Mines, Paris, so that a topotype from Seichamp near Nancy, Lorraine, is now selected as the neotype (École des Mines, Paris, Puzos Coll. B14, 7, larger specimen; Pl. 1, fig. 12, herein). Comparison of the neotype of *E. raricostatoides* with that of *E. raricostatum* shows that the latter increases rapidly in width, producing a depressed whorl at small diameters, with a flattened venter and low keel, but no sulci, and remains depressed to its maximum diameter of 34 mm, where the whorl width is 10 mm. On the other hand, the whorls of *E. raricostatoides* remain subcircular to a much larger size and the venter becomes slightly fastigate, with a low keel and no sulci. At 47 mm diameter it has a whorl

width of 10.5 mm, while a specimen of *E. raricostatum* from Nürtingen (GPS, no number) has a width of 14 mm at this size. Both species have a similar umbilical width throughout and, up to ca. 40 mm diameter, that of the neotype of *E. raricostatoides* is close to that of Bayle's figure, but at larger diameters the two diverge slightly. The inner whorls of both neotypes are densely ribbed, although the nucleus of the type of *E. raricostatum* has been destroyed, and there is a decrease in the rib frequency with size in both. In *E. raricostatoides*, if Bayle's figure is accurate, there is an increase in frequency on the outer whorl at more than 50 mm diameter, and this species is slightly more densely ribbed than *E. raricostatum* at more than 30 mm diameter. The ribs of the latter are sharper and more prominent than those of *E. raricostatoides* and form pronounced geniculae on the shoulder. These differences can be observed in the smaller specimen of *E. raricostatoides* in the Puzos collection, which is of a similar size to the neotype of *E. raricostatum*, and are considered here to be sufficient to separate the two species.

Donovan (1958, p. 16) has already pointed out that *Echioceras* includes not only the typical raricostate species, but also species which are densely ribbed throughout and do not show a distinct raricostate stage. In these forms, however, the rib frequency curve is of the same shape as those of the raricostate forms, showing the very characteristic downwardly convex curve resulting from the decrease in the number of ribs per whorl in the middle stages, followed by an increase on the outer whorls. This pattern of rib frequency serves to distinguish *Echioceras* from other members of the family in those cases where the whorls have been crushed or the ventral characters are not visible (Fig. 3, 4).

The lowest horizons of the *raricostatoides* Subzone on the Dorset and Yorkshire coast are characterized by a preponderance of nonraricostate species of *Echioceras*, although in Dorset, rare examples of *Echioceras raricostatoides* also occur. Higher beds at these localities show a tendency for raricostate forms to replace the nonraricostate, but in Dorset the section is terminated at this point by a non-sequence and in Yorkshire the highest beds of the *raricostatoides* Subzone are characterized by the nonraricostate *E. intermedium*, perhaps transitional to *Paltechioceras* (see below, p. 19). In the Stowell Park Borehole (Spath, 1956) the lowest foot of the *raricostatoides* Subzone contains forms identified as *E. aeneum* and *E. raricostatoides*, the latter persisting alone into the upper beds of the subzone, while in the Upton Borehole (Melville, 1963), where the subzone is thinning out against the "London Platform," only *E. raricostatoides* is recorded. At Witney (Donovan in Poole *et al.*, 1969) the subzone is unproved, the beds ascribed thereto yielding only Eoderoceratidae and, therefore, more probably belonging to the *densinodulum* Subzone.

Sections in Allt Fearns on Raasay do not expose the lowest 100 feet or so of the *raricostatum* Zone. The lowest Echioceratidae recorded are from Locality 7 (Lee, 1920). The specimens from Locality 1 are on the downthrow side of the Beinn na Leac Fault (Lee MS) and the equivalent beds on the other side of the fault are not identifiable with certainty. Although the discontinuity of the outcrop makes the succession difficult to decipher, the lowest exposures of the *raricostatoides* Subzone now visible in this section yield *Echioceras aeneum*, *E. laevidomum*, and their allies, similar to those from the base of the *raricostatoides* Subzone of Yorkshire and Dorset. On Raasay these forms have a considerable range, at about the middle of which is an horizon with *E. raricostatum*. *E. raricostatoides* replaces the nonraricostate forms at higher levels, but the highest exposed beds of the subzone have yielded *E. boreale* Buckman (holotype, GSE 2398, now figured, Pl. 2, fig. 1a,b), a nonraricostate form.

Although the sections in the Jura show that *Echioceras quenstedti* appears below the first *E. raricostatum* and *E. raricostatoides* (Blaison, 1961), they do not otherwise show the alternation of raricostate and nonraricostate forms seen in Britain. They do, however, show the overlap of *E. raricostatum* with *E. raricostatoides*. In Swabia (Söll, 1956) the latter species ranges throughout the subzone, but the former is restricted to the highest beds below the nonsequence at the base of the *jamesoni* Zone, while in the Jura, near Lons-le-Saunier (Blaison, 1961), *E. raricostatum* occupies a distinct horizon below *E. raricostatoides*. In North Germany (Hoffman, 1950, 1964) *E. raricostatoides* is characteristic of the lower part of the subzone, together with *E. microdiscum* (= *E. raricostatum* ?) and its allies in

places, although it is the latter which seem to persist into the upper beds of the subzone (e.g., at Barrien).

The overlap of raricostate and nonraricostate forms, together with the similar overlap of *Echioceras raricostatum* and *E. raricostatoides*, renders it difficult to subdivide the *raricostatoides* Subzone on anything other than a local basis, so that it is here retained as a single unit.

Echioceras is widespread throughout Northwest Europe and extends through the Alps and Carpathians into Turkey, the Crimea, and Caucasus (Bremer, 1965; Muratov, *et al.*, 1960; Nutsubidze, 1966; Gasanov, 1967). It is also recorded

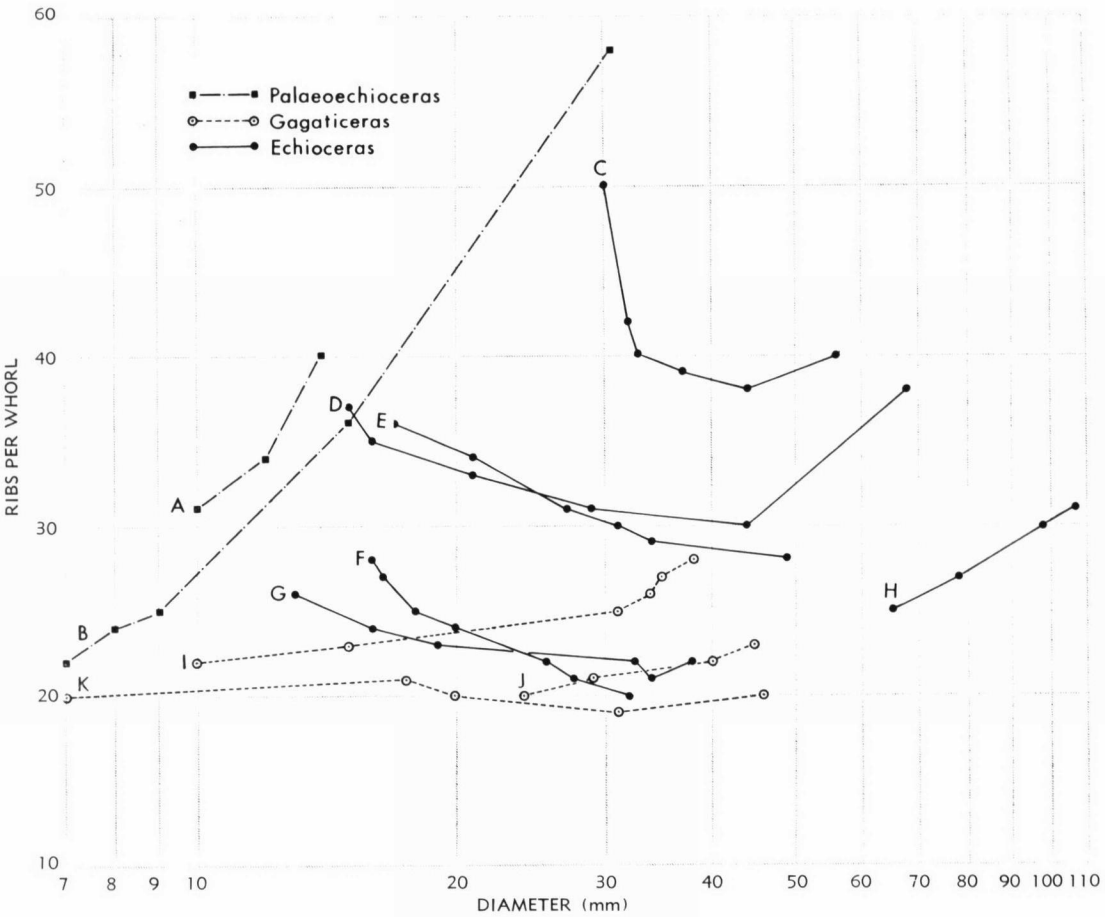

FIG. 3. Rib density curves of *Palaeoechioceras, Gagaticeras,* and *Echioceras.*

A. Palaeoechioceras spirale (Trueman & Williams), holotype. (Type species of *Palaeoechioceras.*)

B. Palaeoechioceras pierrei (Spath), holotype. (Type species of *Hypechioceras.*)

C. Echioceras intermedium (Trueman & Williams), topotype (original of Pl. 3, fig. 1).

D. Echioceras quenstedti (Schafhäutl), lectotype.

E. Echioceras aeneum Trueman & Williams, holotype.

F. Echioceras raricostatum (Zieten), neotype. (Type species of *Echioceras.*)

G. Echioceras raricostatoides (Vadasz), neotype.

H. Echioceras deciduum (Hyatt), lectotype. (Type species of *Pleurechioceras.*)

I. Gagaticeras finitimum (Blake), holotype. (Type species of *Parechioceras.*)

J. Gagaticeras gagateum (Young & Bird), holotype. (Type species of *Gagaticeras.*)

K. Gagaticeras neglectum (Simpson), holotype.

from the Canadian Arctic (Frebold, 1960), Mexico (Erben, 1956), and Peru (Douglas, 1921). Although Schindewolf (1957) considered that the forms described by Erben had been misidentified, they seem to represent typical *Echioceras* of the raricostate group.

Genus PLEURECHIOCERAS Trueman & Williams, 1925

Type Species (OD).—*Ophioceras deciduum* Hyatt, 1867, p. 76 (*nom. nov. pro Ammonites raricostatus* Zieten, von Hauer, 1856, p. 24 (*partim*), pl. 6, fig. 1-3 (*non* Zieten, 1831).

Lectotype.—The original of von Hauer (*loc. cit.*) was designated as the lectotype by Donovan (1958, p. 17). This specimen is here refigured (Pl. 3, fig. 2a-c) and is the only remaining syntype in the Hauer Collection. GBW, VI, 1-3.

Type Locality.—Adneth, Salzburg, Austria.

Type Stratigraphic Occurrence.—Adneth Limestone, Upper Sinemurian, *raricostatum* Zone.

Derivation of Name.—πλευρά = rib.

Discussion.—This genus was proposed to include those Echioceratidae in which the initial densicostate stage is followed by a raricostate stage, but which develop an elevated outer whorl, on which the ribbing increases somewhat in density. These features are well seen in the lectotype of the type species. The so-called "genotype" from Radstock, renamed *Pleurechioceras typicum* Buckman (1927, pl. 695), is, however, a typical *Echioceras quenstedti* (Schafhäutl). Of the two other species originally included in this genus, *P. intermedium* Trueman & Williams is based on a crushed example from Robin Hood's Bay, almost certainly from near the base of Bed 4 of the "*Oxynotus* Beds" of Tate & Blake (1876, p. 73). This bed has yielded crushed specimens identical with the holotype, as well as much better preserved material (Pl. 3, fig. 1a, b), which shows that this species does not possess a raricostate stage, although the rib frequency decreases in the middle stages, and that the outer whorl, although higher than wide, is subquadrate, with a flattened, subsulcate venter. The ribs on the inner whorls are sharp and straight, but become rursicline and irregular on the outer whorl, tending to fade out into striae. The other species, *P. congruens* Trueman & Williams, comprises the outer whorl and fragmentary inner whorls of a form with a subquadrate whorl section and carinate, sulcate venter. The ribs are strong and straight throughout. The holotype of this species is very close to *Orthechioceras* sp. (see below, p. 23). On the other hand, Trueman & Williams (1925) excluded *Echioceras fastigatum* Trueman & Williams from this genus, although noting that this species was close to *P. deciduum* (Hyatt), in their sense.

In view of the failure of Trueman & Williams to interpret *Pleurechioceras* according to the type species (i.e., to employ the name for those raricostate *Echioceras* in which the outer whorl becomes fastigate), thereby creating confusion, together with the fact that the diagnostic features first appear only in the latest growth stages, the "genus" is not now separated from *Echioceras*.

Genus LEPTECHIOCERAS Buckman, 1923

Type Species (OD).—*Ammonites macdonnelli* Portlock, 1843, p. 134, pl. 29A, fig. 12. Refigured Wright, 1880, pl. 37, fig. 3, 4.

Type.—The specimen figured by Portlock (1843) was borrowed by Wright (1881, p. 301) and never returned (Director, Geological Survey of Ireland, pers. commun.). It cannot now be traced at the British Museum (Natural History) or at the Geological Survey Museum and must be presumed lost (Donovan, 1954, p. 37).

The specimen erroneously supposed to be from Larne, Northern Ireland, which was figured as the "genotype" by Buckman (1923, pl. 443; refigured by Dean, Donovan and Howarth, 1961, pl. 67, fig. 6a,b (BM C41756) is labelled "Cheltenham" and cannot, therefore, be a topotype. There is no *raricostatum* Zone at Larne, however (Cretaceous rocks rest directly on beds of Hettangian age), so that Portlock's record of *Ammonites macdonnelli* from this locality must be due to confusion with *Psiloceras*. Unfortunately there are no known examples of Portlock's species from Northern Ireland and Buckman's "genotype" may be taken to typify *Leptechioceras faute de mieux*.

The "genotype" differs from Wright's figure in that the inner whorls of the latter are more densely ribbed and the outer more conspicuously ornamented, although in these features the "genotype" is more similar to Portlock's figure. Wright (1881) considered this to be poor, but his figures are frequently inaccurate themselves.

Type Locality.—(?) Larne, Co. Antrim, Northern Ireland.

Type Stratigraphic Occurrence.—(?) Ballintoy Marls, upper Sinemurian.

Derivation of Name.—λεπτός = thin.

Discussion.—Buckman proposed this genus without comment or diagnosis, although the type species was a member of his earlier group of Echioceratidae, characterized as "carinate, periphery fastigate" (Buckman, 1914, p. 96c). Trueman & Williams (1925, p. 708) defined the genus as including "forms with relatively thin whorls

and acute, often subsulcate, venters; they are probably derived from closely costate forms, but ribs are usually lost on the outer whorl." As with most other genera, Trueman & Williams grouped a wide variety of different forms in the genus and seem to have experienced difficulty in separating it from *Paltechioceras*. *Plesechioceras comptum* Trueman & Williams is much more similar to *Leptechioceras macdonnelli* than to the other species placed by them in *Plesechioceras* (=*Paltechioceras*). *Leptechioceras planum* Trueman & Williams with its low whorls, ornamented by conspicuous dense ribbing, and with a somewhat tabulate venter, is clearly a *Paltechioceras*. *Leptechioceras* is interpreted here as those Echioceratidae in which the outer whorls, at least, are compressed and fastigate and in which the whorl height is relatively large with respect to the diameter, as compared with *Paltechioceras*. In addition, the ribbing becomes reduced in strength on the middle or outer whorls and may be lost entirely, although in such cases low plicae may reappear on adult body-chambers. This is apparently the case with *Echioceras subobsoletum* Buckman, 1914, p. 96c (holotype GSE 2421), here figured for the first time (Pl. 2, fig. 9a,b), which is a fragmentary outer whorl that can be matched in large examples of *L. macdonnelli* from the same locality (e.g., T4488[D]).

Until the type of *Leptechioceras nodotianum* (d'Orbigny) can be defined, there will be some uncertainty whether this species is a junior synonym of *L. macdonnelli*.

In Yorkshire and Raasay, the earliest *Leptechioceras* are ribbed throughout, although the ribs on the outer whorls are reduced in strength. The later forms, however, become smooth at an early stage, as in *Leptechioceras macdonnelli*. This, together with records of slender species of *Paltechioceras* (e.g., *Paltechioceras favrei*) from the *macdonnelli* Subzone, suggests that *Leptechioceras* evolved from such slender *Paltechioceras* by way of *L. charpentieri* (Schafhäutl), or an allied form.

The geographic distribution of *Leptechioceras* is more restricted than that of *Echioceras*. Although occurring widely over most of northwest Europe, it is very rare in North Germany (Hoffmann, 1950, 1964), but is known from the Alps and Carpathians (references in Arkell, 1956) and also from parts of southern France (Rocquefort, 1934; Bernet-Rollande, 1968; Fleury, 1968). Outside Europe it seems to be represented only in Mexico (Erben, 1956, see below) and perhaps in Peru, if *Caloceras newberryi* (Hyatt, 1889, p. 151, fig. 24, 26) (MCZ, type not traced) is related to *Leptechioceras nodotianum*, as Hyatt suggested.

?Genus PSILECHIOCERAS Erben, 1956

Type Species (OD).—*Echioceras* (*Psilechioceras*) *glabrum* Erben, 1956, p. 318, pl. 39, fig. 19.

Holotype.—Original of Erben, *loc. cit.*, Inst. Geol. Mexico 773.

Type Locality.—Cuesta del Viejo (Cu 6), near Huayacocotla, Veracruz, Mexico.

Type Stratigraphic Occurrence.—"Unit with *Echioceras burckhardti*," Huayacocotla Formation, Upper Sinemurian, *raricostatum* Zone, (?)*raricostatoides* Subzone.

Derivation of Name.—ψιλός = smooth.

Discussion.—The features cited by Erben (1956) to distinguish *Psilechioceras* from *Echioceras* were the "subtriangular-rounded" whorl section, the loss of ornament at about 21 mm diameter and the rapid increase in whorl height. It was also said (*op. cit.*, p. 319) that the inner whorls were sparsely ribbed, producing a raricostate stage. Examination of a squeeze on the inner whorls of a cast of the holotype, however, shows them to be densicostate, with no trace of a raricostate stage, and, moreover, it is impossible to determine whether the absence of ornament on the remnant of the outer whorl, or its sagittate whorl section, are original features, or whether they are the result of the weathering and erosion to which the specimen seems to have been exposed. For these reasons the affinity of *Psilechioceras* is doubtful. The "unit" in which it was found is characterized by species referred to *Echioceras* and probably contemporaneous with the *raricostatoides* Subzone of Northwest Europe. Erben, however (*op. cit.*, p. 320), cited *Leptechioceras pumilum* Trueman & Williams as *Psilechioceras*, so that this genus is perhaps to be interpreted as a synonym of *Leptechioceras*, notwithstanding its apparently low horizon, and the relatively broad whorl width, which suggest that it may be merely a worn *Echioceras*. It might be added here that the only unequivocal record of *Leptechioceras* in Mexico is *Leptechioceras* aff. *L. nodotianum* Reynès *non* d'Orbigny, since *L. alvarezi* Erben (1956, p. 325, pl. 39, fig. 20) is a costate, carinate, bisulcate form comparable with *Paltechioceras favrei* (Hug).

Genus PALTECHIOCERAS Buckman, 1924

Type Species (OD).—*Paltechioceras elicitum* Buckman, 1924, pl. 483.

Holotype.—Original of Buckman, *loc. cit.*, BM C41751.

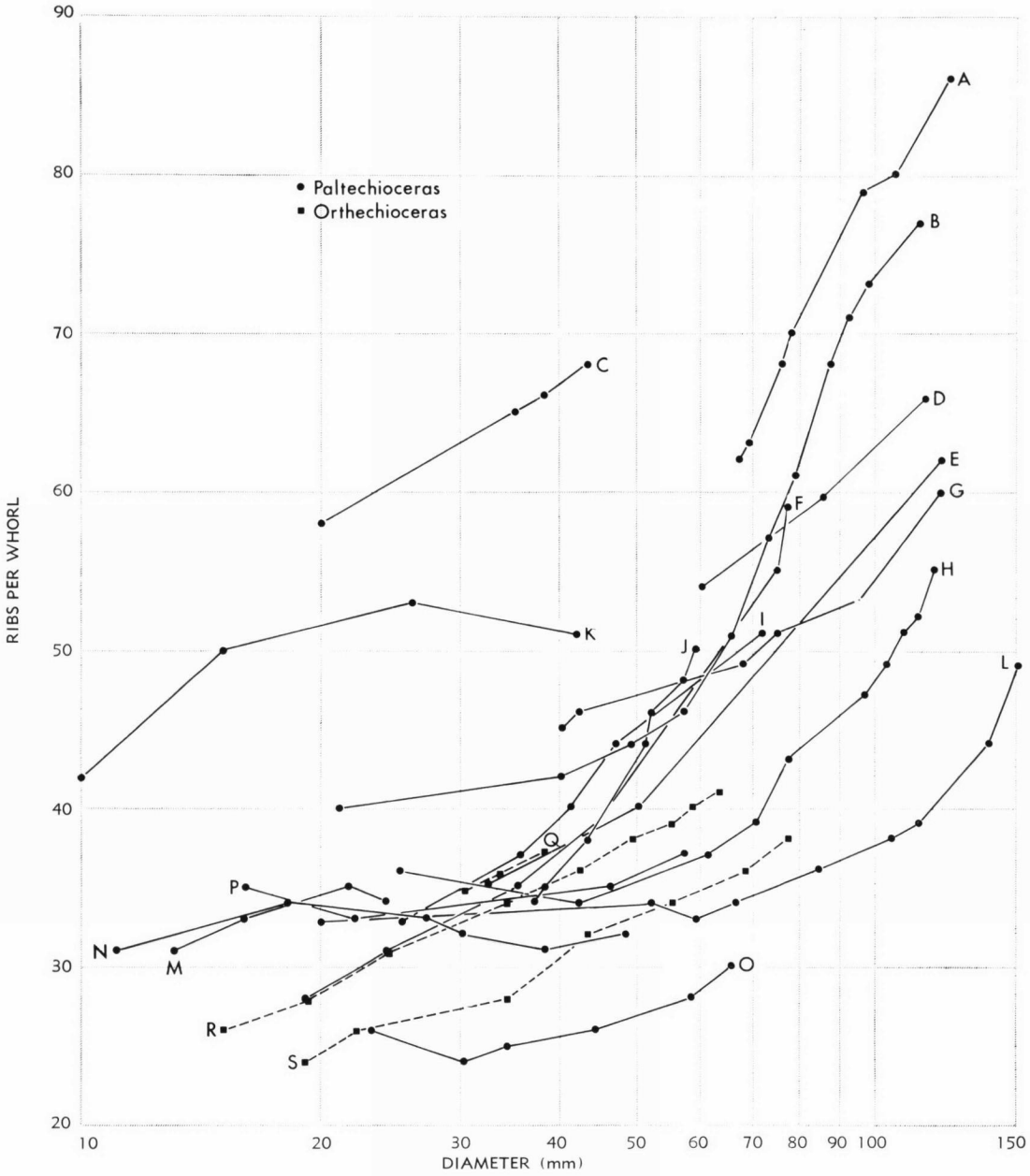

FIG. 4. Rib density curves of type specimens of *Paltechioceras* and *Orthechioceras*.

A. Paltechioceras tardecrescens (van Hauer), lectotype.

B. Paltechioceras nobile (Trueman & Williams), holotype. (Type species of *Euechioceras*.)

C. Paltechioceras delicatum (Buckman), holotype. (Type species of *Plesechioceras*.)

D.[1] *Paltechioceras angustilobatum* (Trueman & Williams), holotype. (Type species of *Stenechioceras*.)

E. Paltechioceras ebriolum Trueman & Williams, holotype.

F. Paltechioceras aplanatum (Hyatt), holotype.

G. Paltechioceras flexicostatum (Trueman & Williams), holotype. (Type species of *Vobstericeras*.)

H. Paltechioceras dignatum Trueman & Williams, holotype.

I. Paltechioceras variabile (Trueman & Williams), holotype. (Type species of *Kamptechioceras*.)

[1] This curve represents the estimated median in an uncertain range of about four ribs/whorl.

TYPE LOCALITY.—Radstock Grove Quarry, Kilmersdon Road, Radstock, Som., England.

TYPE STRATIGRAPHIC OCCURRENCE.—"Armatus Bed," remanié base of the *jamesoni* Zone.

DERIVATION OF NAME.—παλτός = hurled.

DISCUSSION.—Proposed without comment, the name was used by Trueman & Williams (1925, p. 728-729) for a small group of compressed, carinate, bisulcate Echioceratidae, separated from very similar forms on the grounds that they were "probably derived from different stocks of presulcate forms" (Trueman & Williams, 1925, p. 707), evidence of this being their more complex suture and "stouter and narrower" *(sic)* whorls. Measurement of the inner whorls of the holotype is not possible, so that whatever interpretation is placed on the diagnosis given by Trueman and Williams, comparison with their other genera is not possible, while the sutures figured by Trueman & Williams (1925, p. 705) do not indicate that those of *Paltechioceras*, in their sense, are in fact more complex than those of allied forms. Trueman and Williams (p. 706) emphasized the presence of a deep notch in the *E/L* saddle as a feature of distinction, but this is seen in other of their genera, except where masked by frilling of the saddle. The several genera proposed by these authors for compressed, carinate, bisulcate species are now united under the name of *Paltechioceras*, not only for these reasons, but also because the types of the type species are, in the main, from the remanié base of the *jamesoni* Zone of the Radstock district or, in the case of *Plesechioceras* (see below, p. 20), from the condensed limestone facies of the Rhône Valley, so that almost nothing is known of their stratigraphic distribution, similar forms being apparently absent from the thicker sections in Yorkshire and on Raasay. Material from boreholes is crushed and fragmentary, not always safely determinable, and difficult to compare with the Radstock specimens. Emphasis is placed here on the rib frequency as a diagnostic character, as well as whorl proportions, although there is a tendency for the more densely ribbed forms to be more slender than those that are more coarsely ribbed.

The rib frequency curves of the species here included in *Paltechioceras* form a ramifying plexus at diameters of less than about 40 mm, but at larger diameters three broad morphological groups can be recognized (Fig. 4):

a) Very densely ribbed, with a rapid increase. Whorls slender. (*P. delicatum*, *P. boehmi*.)

b) Less densely ribbed than the previous, but also with a rapid increase in density. (*P. tardecrescens*, *P. nobile* (= *P. insigne*), *P. aplanatum*.)

c) Less densely ribbed than (b), with a markedly less rapid increase in density and, in general, rather stouter whorls. (*P. aureolum*, *P. dignatum*, *P. elicitum*, *P. flexicostatum*, *P. favrei*.)

How far these purely morphological differences are reflected stratigraphically is uncertain.

In Yorkshire, the earliest examples referred to this genus occur at the top of the *raricostatoides* Subzone, with *Echioceras intermedium* Trueman & Williams. They differ from the latter by being more densely ribbed at all stages and in lacking the marked decline in rib density in the middle stages. Their closest resemblance is to *Paltechioceras planum* (Trueman & Williams), which, in the I.G.S. boreholes at Stowell Park (Spath, 1956), Upton (Melville, 1963), and Witney (Poole, *et al.*, 1969) occurs in the *macdonnelli* Subzone, accompanied by *P. boehmi* (Hug) and *P. favrei* (Hug). These last persist into the lower part of the *aplanatum* Subzone. Records of *P. aureolum* (Simpson) from the *macdonnelli* Subzone of the Witney Borehole may be mis-

FIG. 4. *(Continued from facing page.)*

J. Paltechioceras aplanatum (Hyatt) (= *Metechioceras tardecrescens* Trueman & Williams, holotype, type species.)

K. Paltechioceras boehmi (Hug), lectotype.

L. Paltechioceras elicitum Buckman, holotype. (Type species of *Paltechioceras*.)

M,N. Paltechioceras aureolum (Simpson), holotype *(M)* (=*Echioceras regustatum* Buckman, holotype *(N)*).

O. Paltechioceras studeri (Hug), holotype.

P. Paltechioceras regulare (Trueman & Williams), holotype. (Type species of *Echioceratoides*.)

Q. Orthechioceras simile (Trueman & Williams), holotype. (Type species of *Homechioceras*.)

R. Orthechioceras radiatum Trueman & Williams, holotype.

S. Orthechioceras reticostatum Trueman & Williams, holotype. (Type species of *Orthechioceras*.)

[*E, H, L,* and *O* comprise *Paltechioceras sensu* Trueman & Williams, 1925.]

identified, as Donovan (1958) had earlier defined this species as forms "with low rib frequency, increasing only slowly with growth" and said that the Swiss examples never attained more than 50 mm diameter.

There is an interval, corresponding to the entire *macdonnelli* Subzone, separating the first *Paltechioceras* from the horizon of *Paltechioceras aureolum* in Robin Hood's Bay. Large examples from this bed ("*jamesoni* Zone," bed 60 of Tate and Blake, 1876) are typical *Paltechioceras* (Pl. 5, fig. 4), but the inner whorls, where the keel is developed without furrows, resemble *Echioceras* and a specimen at this stage was named *Echioceras regustatum* Buckman (1914, p. 96c; holotype (GSM 26439) here figured, Pl. 5, fig. 3). The most obvious difference from *Echioceras* is in the rib frequency, which in *P. aureolum* initially rises to 31 to 35 ribs at about 25 mm diameter and then decreases to 26 to 31 ribs at about 35 to 40 mm diameter, before rising steadily again. The largest topotype has 45 ribs at 95 mm diameter.

It seems probable that the true *Paltechioceras aureolum* (Simpson) evolved from *P. favrei* (Hug) and gave rise to *P. aplanatum* (Hyatt), which occurs in the upper part of the *aplanatum* Subzone at Robin Hood's Bay and elsewhere appears to be confined to this subzone. The abundant *Paltechioceras* fauna found in the reworked "Armatus Bed" of Radstock may be derived from deposits of this subzone, since its constituent species are morphologically very close to *P. aplanatum*.

Paltechioceras is the most widely distributed member of the Echioceratidae, being recorded from the American Cordillera (Lupher, 1941), Mexico (Erben, 1956), Northwest Europe, and the Mediterranean regions, including the Pyrenees and North Africa (Dubar, 1925, 1954; Bremer, 1965; Andrusov, *et al.*, 1965). The inclusion of *Arietites rotticus* (Rothpletz) in the Echioceratidae by Jaworski (1933) was an error, since Rothpletz's species is a *Metophioceras* (Guérin-Franiatte, 1966). *Paltechioceras* does not, therefore, extend into the East Indies.

Genus PLESECHIOCERAS Trueman & Williams, 1925

Type Species (OD).—*Echioceras delicatum* Buckman, 1914, p. 96c, *nom. nov. pro Amm. tardecrescens* von Hauer, Dumortier, 1867, p. 170, pl. 31, fig. 3-5 (*non* von Hauer, 1856).

Holotype.—Original of Dumortier, *loc. cit.*, Muséum d'Histoire naturelle, Lyon. Refigured herein, Pl. 2, fig. 5a-c.

Type Locality.—Nolay (Côte d'Or), France.

Type Stratigraphic Occurrence.—"*Couches à planicosta*" (=*raricostatum* Zone).

Derivation of Name.—πλησίος = close(ly).

Discussion.—Trueman & Williams (1925, p. 707) believed that this genus was perhaps allied to *Echioceratoides*, differing in retaining finer ribs throughout and in the early development of the (always feeble) keel. The type of *Plesechioceras delicatum* differs from all other species of *Paltechioceras* in that it does not attain a sulcate condition, even at the maximum diameter of 58 mm, and in its unusually dense ribbing and slender whorls. As Donovan (1958, p. 24) has already pointed out, however, the earlier initiation of the keel is widespread in *Paltechioceras* and the stage at which the sulci develop varies considerably within a single species. This character, therefore, is not regarded as sufficient ground for separation at the generic level.

Genus EUECHIOCERAS Trueman & Williams, 1925

Type Species (OD).—*Euechioceras nobile* Trueman & Williams, 1925, p. 725, *nom. nov. pro Leptechioceras aplanatum* Hyatt sp.—Buckman, 1924, pl. 482 (*non* Hyatt, 1889). Refigured by Buckman, 1926, pl. 482*.

Holotype.—Original of Buckman, *loc. cit.*, BM C41750.

Type Locality.—Radstock Grove Quarry, Kilmersdon Road, Radstock, Somerset, England.

Type Stratigraphic Occurrence.—"Armatus Bed," remanié base of the *jamesoni* Zone.

Derivation of Name.—Εὖ = well, perfect.

Discussion.—Trueman & Williams (1925, p. 707) distinguished this genus from *Paltechioceras* because of the stouter whorls of the latter, with their stronger ribs, whereas the ribs of the inner whorls of *Euechioceras* were said to be of the same style as those of *Plesechioceras*. *Euechioceras*, as interpreted by Trueman and Williams, included a wide variety of forms, distributed among 14 "species," which show a very considerable overlap, particularly in rib frequency, with the forms placed in *Paltechioceras sensu* Trueman & Williams (Fig. 4). This overlap is here considered sufficient reason for regarding *Euechioceras* as a synonym of *Paltechioceras*.

As well as carinate, bisulcate species, Trueman and Williams (1925, p. 727) included *Ammonites quenstedti* Schafhäutl, 1847 (lectotype here designated as BS AS. IX. 21; original of Schafhäutl, 1851, pl. 17, fig. 24, here refigured (Pl. 2, fig. 7)). It is a species of *Echioceras*, similar to *Echioceras laevidomum* (Quenstedt) (the lectotype of which is now designated as the original of Quenstedt, 1884, pl. 23, fig. 22) (*non* fig. 23, which appears to

be *E. quenstedti*; the specimen is now badly decomposed). *E. quenstedti* has a fastigate, feebly carinate outer whorl, with no trace of sulci.

The ammonites from California figured as *Euechioceras exsolitum* Crickmay (1933) are not echioceratids.

Genus KAMPTECHIOCERAS Trueman & Williams, 1925

Type Species (OD).—*Kamptechioceras variabile* Trueman & Williams, 1925, p. 731, pl. 2, fig. 1.

Holotype.—Original of Trueman & Williams, *loc. cit.*, BM C41749.

Type Locality.—Kilmersdon Colliery Quarry, near Radstock, Somerset, England.

Type Stratigraphic Occurrence.—"Armatus Bed," remanié base of the *jamesoni* Zone.

Derivation of Name.—καμπτός = bent.

Discussion.—Originally separated from *Euechioceras* by Trueman and Williams because of the greater projection and irregularity of the ribs and the different suture (Trueman & Williams, 1925, p. 731), the genus is here placed in synonymy with *Paltechioceras*, since the suture of the holotype (the only specimen) is not markedly different from other species of *Paltechioceras*, while the projection of the ribs can be matched in other forms. Similarly, although the ribbing of *Kamptechioceras* is conspicuously irregular throughout, such irregular ribs are common in *Paltechioceras oosteri* (Dumortier) and also occur in *P. elicitum*, as well as in other species. The irregular ribs are associated with differences in shell texture and there can be little doubt that they are the result of abnormalities in the functioning of the mantle and, therefore, of no taxonomic significance. The rib frequency of *Kamptechioceras variabile* is very similar to that of *P. aplanatum*, which is a much more slender species, however, with a trigonal whorl section.

Genus METECHIOCERAS Trueman & Williams, 1925

Type Species (OD).—*Metechioceras tardecrescens* Trueman & Williams, 1925, p. 706 (*non* von Hauer, 1856).

Holotype.—Original of Blake (in Tate & Blake), 1876, pl. 5, fig. 5. BM C17898. Refigured herein, Pl. 4, fig. 1a, b.

Type Locality.—Robin Hood's Bay, near Whitby, Yorkshire.

Type Stratigraphic Occurrence.—"Upper Conybeari Bed" (="Jamesoni Beds," Bed 59, Tate & Blake, 1876, p. 81).

Derivation of Name.—μετά = in the middle.

Discussion.—Trueman and Williams, when proposing this genus, cited as the type species "*Arietites tardecrescens* Blake, 1876, pl. 5, fig. 5: this specimen is identified by us with *Caloceras aplanatum* Hyatt." Blake (1876, p. 285 and explanation of pl. 5) cited this specimen as "*Arietites tardecrescens* Hauer," so that it is more correctly *A. tardecrescens* von Hauer in Blake, 1876 (*non* von Hauer, 1856). This use by Trueman and Williams of a specimen known to be misidentified is deliberate use of misidentification in designating a type species (*Code*, Art. 70 (b)) and, under the provisions of this Article, Trueman and Williams are considered to have established a new nominal species, with the same name as the misidentified species, in the new nominal genus.

As Trueman and Williams recognized, *Metechioceras tardecrescens* is a synonym of *Caloceras aplanatum* Hyatt, the holotype of which (MCZ 80, figured Buckman, 1926, pl. 640) is from the same horizon and locality. This species is so similar to *Paltechioceras nobile* Trueman & Williams, the type species of Euechioceras, that there can be little doubt that the two are very closely allied, if not conspecific. *Metechioceras* is, therefore, regarded as a synonym of *Paltechioceras*. Both *P. nobile* and *P. aplanatum* are also similar to *Paltechioceras tardecrescens* (von Hauer) lectotype here designated as the original of Pl. 4, fig. 2a, b, herein, being the smaller of the two syntypes remaining in the Hauer Collection; GBW, III, 10-12). The only difference of note between *P. aplanatum* and *P. tardecrescens* is that the latter is slightly more densely ribbed at corresponding diameters, so that their specific distinction is doubtful.

Genus VOBSTERICERAS Trueman & Williams, 1925

Type Species (OD).—*Vobstericeras flexicostatum* Trueman & Williams, 1925, p. 732, pl. 3, fig. 2.

Holotype.—Original of Trueman & Williams, *loc. cit.*, BM C41739.

Type Locality.—Vobster Quarry, south of Kilmersdon, near Radstock, Somerset, England.

Type Stratigraphic Occurrence.—Base of the Lias (="Armatus Bed"), remanié basal *jamesoni* Zone.

Derivation of Name.—From the type locality.

Discussion.—This genus was separated on the grounds that its whorls were narrower than those of other carinate, bisulcate forms and that the ribs possessed a considerable curve (Trueman & Williams, 1925, p. 732). The "narrower" (i.e., lower) whorls in themselves are an insufficient basis for generic separation, while the curved ribs can be matched in *Kamptechioceras* and, to a lesser extent, in some specimens of *Paltechioceras aplanatum*. Curvature of the ribs is also discernible in other *Paltechioceras* species, e.g., *P. delicatum*, so that *Vobstericeras* is not now separated from *Paltechioceras*.

Genus EPECHIOCERAS Trueman & Williams, 1925

Type Species (OD).—*Epechioceras expansum* Trueman & Williams, 1925, p. 722, pl. 3, fig. 6.

Holotype.—Original of Trueman & Williams, *loc. cit.*, BM C41740.

Type Locality.—Clandown Quarry, near Radstock, Somerset, England.

Type Stratigraphic Occurrence.—"Armatus Bed," remanié base of the *jamesoni* Zone.

Derivation of Name.—ἐπί = upon.

Discussion.—The holotype is the only known specimen and is somewhat deformed, but shows densely ribbed inner whorls with a progressive increase in rib frequency on the outer whorl, as in *Paltechioceras delicatum* and *P. boehmi*. It differs from typical *Paltechioceras*, however, in its stout, rounded whorls, with only feeble sulci and low keel. On the other hand, although Trueman & Williams (1925, p. 707) regarded this genus as, probably, a stout derivative of *Echioceratoides*, it differs from the latter, not only in being stouter, but also in having a rib frequency characteristic of *Paltechioceras*, with which genus it is here placed, tentatively, in synonymy. *Orthechioceras* differs in its very much lower rib frequency at all stages, although agreeing with *Epechioceras* in its rounded, subsulcate whorls.

Genus ECHIOCERATOIDES Trueman & Williams, 1925

Type Species (OD).—*Echioceratoides regulare* Trueman & Williams, 1925, p. 720, pl. 4, fig. 2.

Holotype.—Original of Trueman & Williams, *loc. cit.*, BM C41753.

Type Locality.—Kilmersdon Colliery Quarry, near Radstock, Somerset, England.

Type Stratigraphic Occurrence.—"Armatus Bed," remanié base of the *jamesoni* Zone.

Derivation of Name.—*o* (Connective) + εἶδος = form.

Discussion.—This genus was originally proposed for those Echioceratidae in which the initial densicostate stage is followed by one in which the ribs increase in strength, without becoming raricostate, while the whorls are never depressed and the outer whorl is fastigate, with the keel developed at a late stage (Trueman & Williams, 1925, p. 707).

Such a diagnosis is suggestive of *Paltechioceras* and the holotype of *Echioceratoides regulare* is very close in appearance to Yorkshire examples of *Paltechioceras aureolum* (Simpson), particularly to the holotype of *"Echioceras regustatum"* Buckman, 1914. The rib frequency curve of *E. regulare* shows a decrease in frequency at small sizes similar to that seen in *P. aureolum*, followed by a similar rise in frequency from a diameter of about 15 mm. In *P. aureolum* the initial decrease is preceded by a sharp rise in frequency, but the holotype of *E. regulare* is not sufficiently well preserved at the corresponding size to determine the number of ribs. The absence of sulci and the obsolescent keel of *E. regulare* appear to be the result of wear, rather than primary characteristics, and the keel is much more prominent on the last half of the outer whorl, where there are also traces of sulci, than would be expected from the appearance of that part of the venter shown by Trueman & Williams (1925, pl. 4, fig. 2b). The holotype of *E. regulare* is rather more densely ribbed than most examples of *P. aureolum*, but it is felt that this difference is insufficient to separate the two specifically, let alone generically, in view of the range of variation seen in the Yorkshire population.

It is perhaps worthy of note that some typical carinate, bisulcate *Paltechioceras* (e.g., *P. viticola* (Dumortier) and *P. dignatum* (Trueman & Williams) also show a drop in rib frequency in the initial stages, followed by a rapid increase in the number of ribs, to give a curve of quite different appearance from that of *Echioceras*.

Trueman & Williams (1925) included six other species in this genus, of which only *Ammonites viticola* Dumortier (1867, p. 171 (*partim*), pl. 31, fig. 12-13, the original of which cannot be found) resembles *Echioceratoides regulare* in possessing rounded to slightly fastigate whorls, ornamented by straight ribs, which die out on the shoulder and show a marked drop in frequency at about 17 mm diameter, followed by a steady rise. The rib density of *A. viticola*, however, rises from a minimum of 24 ribs at 17 mm diameter to a maximum of 40 at 49 mm, while that of *E. regulare* rises from a minimum of 33 ribs at 17 mm diameter to 37 at 57 mm.

The remaining species placed in the genus by Trueman & Williams are:

a) *Echioceratoides rotundum* Trueman & Williams (1925, p. 721; *nom. nov. pro Ammonites viticola* Dumortier in Reynès, 1879, pl. 24, fig. 1, 2 (*non* Dumortier)). According to Donovan (1955, p. 29), this is a *Vermiceras* (?), but the original cannot be traced.

b) *Arietites favrei* Hug (1899, p. 17, pl. 12, fig. 6; lectotype designated by Trueman & Williams, 1925, p. 721). This is a typical *Paltechioceras*, as Donovan (1958, p. 28-29) has shown.

c) *Echioceras prorsum* Buckman (1914, p. 96c; *nom. nov. pro Ammonites viticola* Dumortier, 1867, pl. 31, fig. 9, 10 only). The blunt, distant ribbing at all stages and rounded venter, with blunt keel suggest that this is an *Epophioceras*.

d) *Ammonites edmundi* Dumortier (1867, p. 163, pl. 39, fig. 3, 4, the original of which cannot be found). This species is here ascribed to *Orthechioceras* (see p. 23).

e) *Ammonites vellicatus* Dumortier (1867, p. 175: lectotype here designated as the original of Dumortier, 1867, pl. 40, fig. 5, 6). The distant blunt ribbing of this species, particularly on the inner whorls, and its rounded whorls, suggest that it may be an *Epophioceras*.

Genus STENECHIOCERAS Buckman, 1927

Type Species (OD).—*Euechioceras angustilobatum* Trueman & Williams, 1925, p. 726.

Holotype.—Original of Trueman & Williams in Buckman, *loc. cit.*, pl. 697, BM C41736.

Type Locality.—Kilmersdon Colliery Quarry, near Radstock, Somerset, England.

Type Stratigraphic Occurrence.—"Armatus Bed," remanié base of the *jamesoni* Zone.

Derivation of Name.—στενός = narrow.

Discussion.—The genus was proposed without comment. The type species had been described by Trueman & Williams (1925, p. 726) as differing from *Euechioceras nobile* in being rather more polygyral, with closely spaced, regular ribs on the inner whorls, becoming more irregular on the outer. The holotype is apparently less densely ribbed at large diameters than *E. nobile*, but is otherwise so very similar that the two are here considered to be conspecific, and separate generic status of "*Stenechioceras*" is not upheld.

Genus ORTHECHIOCERAS Trueman & Williams, 1925

Type Species (OD).—*Orthechioceras recticostatum* Trueman & Williams, 1925, p. 723, pl. 3, fig. 1.

Holotype.—Original of Trueman & Williams, *loc. cit.*, BM C41748.

Type Locality.—Kilmersdon Colliery Quarry, near Radstock, Somerset, England.

Type Stratigraphic Occurrence.—"Armatus Bed," remanié base of the *jamesoni* Zone.

Derivation of Name.—ὀρθός = straight.

Discussion.—*Orthechioceras* is now separated from *Paltechioceras*, although it was considered a synonym by Arkell (1957, p. *L*244), because, as interpreted here, it is clearly distinguishable from *P. elicitum* and its allies and, moreover, is found below *Echioceras* at much lower horizons than *Paltechioceras*. Specimens assigned to the genus have been collected in large numbers from the top of the *densinodulum* Subzone of the Dorset Coast (Black Ven Marls, bed 98 (Lang, 1926, p. 156)), which has yielded forms indistinguishable from *Orthechioceras radiatum* Trueman & Williams (1925, p. 724, pl. 2, fig. 9) (Pl. 5, fig. 1, 2). These are referred to *Orthechioceras*, although the type species is of an unknown horizon, and is closer morphologically to *Paltechioceras*.

As interpreted here, *Orthechioceras* comprises those species which differ from *Paltechioceras* in the greater breadth of the more quadrate whorls, with feeble or non-existent sulci, and ornamented by more distant ribbing. The material from the Black Ven Marls, bed 98, includes a range of forms from stouter, more coarsely ribbed to more slender, and densicostate. *Echioceras elegans* Trueman & Williams (1925, p. 717, pl. 1, fig. 9) apparently belongs to the latter group, while one of the specimens cited by Lang (1926, p. 156) as *Homechioceras* cf. *spiratissimus* (Quenstedt) (BM C26776) is identical with *O. radiatum*. *Euechioceras insolitum* Trueman & Williams (1925, p. 728, pl. 4, fig. 3) (not *in situ*) is apparently a member of the same group, but differs in more conspicuous development of the sulci and higher rib frequency. Some fragmentary specimens from bed 98 possess inner whorls identical with *O. radiatum*, but the outer whorls become compressed and fastigate and at that stage correspond to *Echioceras crassum* Trueman & Williams, the type of which (Trueman & Williams, 1925, p. 719, pl. 1, fig. 6) is a very poorly preserved fragment from the same bed. *O. radiatum* ranges up into bed 99 (the Watch Ammonite Stone), where it is accompanied by the first true *Echioceras*, as well as by *Pleurechioceras congruens* Trueman & Williams (1925, p. 720, pl. 4, fig. 4), which is also a typical *Orthechioceras*.

On Raasay *Orthechioceras* is represented by the specimen (GSE 2408) cited by Buckman (in Lee, 1920, p. 18) as "*Echioceras modestum*?" from near the base of the Pabbay Shales of Hallaig Burn, while the crushed specimen (GSE 12732) from the same locality cited by Buckman (*loc. cit.*) and by Trueman & Williams (1925, p. 732) as "*Echioceras* cf. *aplanatum*" (Pl. 2, fig. 8) is more strongly and less densely ribbed than that species and, presumably, is also a member of *Orthechioceras*. These early Echioceratidae from Raasay are probably to be ascribed, like their allies in Dorset, to the topmost beds of the *densinodulum* Subzone, so that the non-sequence at the base of the Pabbay Shales may involve the lower part of the *raricostatum* Zone, as well as the entire *oxynotum* Zone. Two small fragmentary outer whorls found below *Orthechioceras* in the Hallaig Burn (Lee, 1920, p. 17; GSE T3628[D], T3629[D]) are slightly fastigate, carinate, subsulcate, and are presumably also *Orthechioceras*, although this is open to doubt.

Outside the British Isles, *Orthechioceras* is represented only by *Ammonites edmundi* Dumortier (1867, p. 163, pl. 39, fig. 3, 4), the type of which cannot now be traced (Prof. L. David, written commun.). The figure, however, shows a form with subquadrate, feebly sulcate whorls, similar to those of *Orthechioceras recticostatum*. The only record of the stratigraphic position of *Orthechioceras edmundi* is by Blaison (1961), who collected forms identified with this

species from the base of the *raricostatum* Zone at Savagna and Le Pontot, near Lons-le-Saunier (Jura), below the first *Echioceras raricostatoides*.

Trueman and Williams also included in this genus *Echioceras alpinum* Buckman (1914, p. 96c, *nom. nov. pro Ammonites spiratissimus* Quenstedt in von Hauer, 1856 (*non* Quenstedt)) and *Echioceras subquadratum* Buckman (*loc. cit.*; *nom. nov. pro Arietites* cf. *conybeari* Sowerby in Hug, 1899, pl. 12, fig. 4 (*non* Sowerby)). The lectotype of *Echioceras alpinum* is here designated as the larger of the two syntypes of *Ammonites spiratissimus* Quenstedt in von Hauer (1856, pl. 3, fig. 1-3 (*non* Quenstedt)), refigured by Wähner (1888, pl. 26, fig. 1). This specimen was renamed *Epophioceras ultraspiratum* (Fucini) var. *costosa* Vadasz (1908, p. 387). It is now designated as the lectotype of this variety, of which the name *E. alpinum* Buckman is, therefore, a junior objective synonym. *E. ultraspiratum costosum* is not related to *E. ultraspiratum* (Fucini) (lectotype here designated as the original of Fucini, 1902, pl. 12, fig. 4), but is a typical *Alsatites* from the "Gelber Kalk mit *Arietites rotiformis*" of Enzesfeld, from which von Hauer (1856) lists a considerable Hettangian and Lower Sinemurian fauna.

In sharp contrast, *Echioceras subquadratum* is a typical compressed, carinate, bisulcate *Paltechioceras*, which was included in *Orthechioceras* by Trueman and Williams apparently on the basis of poorly preserved material from Raasay and Radstock.

Certain specimens of *Orthechioceras* from the "Watch Ammonite Stone" (bed 99) of the Black Ven Marls have venters similar to those of *Echioceras aeneum* Trueman and Williams and derivation of the latter from *Orthechioceras* is postulated here.

Genus HOMECHIOCERAS Trueman & Williams in Buckman, 1925

Type Species (OD).—*Homechioceras simile* Trueman & Williams in Buckman, 1925.

Holotype.—Original of Trueman & Williams, *loc. cit.*, pl. 609, BM C26775.

Type Locality.—Stonebarrow foot, Charmouth, Dorset, England.

Type Stratigraphic Occurrence.—Black Ven Marls, bed 98 (Lang, 1926, p. 156).

Derivation of Name.—ὁμοῖος = similar.

Discussion.—The holotype is the only example which can be safely assigned to the genus; recent collecting from the type horizon yielded only *Orthechioceras*. Specimens of the latter from the "Watch Ammonite Stone" (Bed 99) match the type of *Homechioceras* fairly closely and it would seem that this genus is a synonym of *Orthechioceras*, differing from other examples only in the more prominent development of the keel, although Arkell (1957, p. L243) considered it a synonym of *Echioceras*. It differs from the latter in its higher rib frequency and strong, distant ribs on the (incomplete) inner whorls. On the other hand, the venter lacks the sulci of *Orthechioceras radiatum*. *Homechioceras simile* may represent a species transitional from *Orthechioceras* to *Echioceras*, as noted above (p. 23).

Trueman and Williams (in Lang, 1926, p. 185) supplied the first description and diagnosis of the genus, emphasizing the early development of the keel as a diagnostic feature. On this basis, they included in the genus *Ammonites raricostatus gracilis* Quenstedt[1] (1856, p. 106, pl. 13, fig. 16) (*non A. gracilis* Münster in Zieten, 1830; *nec* in de Blainville, 1840; *nec. A. gracilis* Simpson, 1843; *nec* Buckman in Murchison, 1844) and *A. raricostatus robustus* Quenstedt (1856, p. 106, pl. 13, fig. 17). These were originally figured in ventral view only and are no longer in the Quenstedt Collection (Dr. F. Westphal, written commun.). It is clear, however, from Quenstedt's later writings (1884, p. 189) that, of the specimens figured by him as *A. raricostatus zieteni* Quenstedt (1884, p. 189, pl. 23, fig. 27-29), the original of fig. 28 is the form which Quenstedt (1856) had understood as *A. raricostatus gracilis* and that the original of fig. 29 is the form which he had understood originally as *A. raricostatus robustus*. The third specimen (*ibid.*, fig. 27) was designated as the lectotype of *A. raricostatus zieteni* Quenstedt by Trueman & Williams (1925, p. 711), but, not only is this last a junior primary homonym of *A. zieteni* Potiez & Michaud, 1838, as well as of *A. zieteni* Rouiller & Vosinsky, 1849, and of *A. zieteni* Oppel, 1853 (and, therefore, invalid), but comparison of a photograph of

[1] *A note on Quenstedt's terminology.*—Hölder (1958) has pointed out that Quenstedt repeatedly disregarded the law of homonymy in his trinomina and has claimed that consequently he did not adhere to the principles of Linnean, binomial, nomenclature in these third names. Later (Hölder, 1972) he considered these names to be covered by the *Code* (Art. 45(d)) and, therefore, to be treated as of subspecific rank. In the Introduction to "Der Jura," however, Quenstedt (1856, p. 17-19) stated explicitly that he was opposed to a strict Linnéan usage and that he preferred to use the species name (under which term he included both binomen and trinomen) more as an adjective to describe both varieties and races. He did not regard these names as competing for priority with names proposed by earlier authors and later in the same work (1857, p. 605) wrote that little attention could be paid to the Principle of Priority (which is the basic principle of binomial nomenclature) (*Code*, Preamble). For this reason alone, because he did not apply the principles of binomial nomenclature, none of Quenstedt's names can be regarded as available (*Code*, Art. 11(c)), irrespective of arguments about their subspecific or infrasubspecific status. The three names under discussion here were first employed by Buckman, 1914, p. 96d, as species of *Echioceras* and for the purposes of the Law of Homonymy are regarded as members of that genus, under Buckman's authorship, with priority from 1914.

the lectotype (Pl. 2, fig. 3a, b) with a cast of the original of fig. 29 (supplied through the courtesy of Dr. Westphal) shows that the two are virtually indistinguishable. Quenstedt's figures, having been restored, are misleading. *A. raricostatus zieteni* cannot replace the prior *A. raricostatus robustus*, as Quenstedt (1884) proposed, so that the correct name for the species hitherto identified as *Echioceras zieteni* (Quenstedt, 1884) is *E. robustum* (Quenstedt, 1856), the neotype of which is here designated as the original of Quenstedt, 1884, pl. 23, fig. 29; refigured Pl. 2, fig. 4a, b). The original of Quenstedt, 1884, pl. 23, fig. 28 is also refigured (Pl. 2, fig. 2a, b).

Neither *Echioceras robustum* (Quenstedt) nor *E. gracile* (Quenstedt, *non* Zieten) resembles *Homechioceras simile*. Both are typical *Echioceras*, the former very close to *E. raricostatum* (Zieten) and the latter more like *E. raricostatoides* (Vadasz).

INCERTAE SEDIS

Spath (1925) proposed two new genera, *Tmaegophioceras* and *Protechioceras*, for Mediterranean species which he believed to be Echioceratidae and these were accepted as such by Arkell (1957). According to Spath (1925, 1926), these forms indicated rich Upper Sinemurian faunas in the Mediterranean and are possibly the "certain evolute Mediterranean genera," which he postulated as associates of *Epophioceras*, persisting throughout the later part of the *Asteroceras obtusum* Zone and the *oxynotum* Zone, while *Eparietites*, *Asteroceras* and *Oxynoticeras* dominated the northwest European faunas (see p. 4). Since the stratigraphy of the deposits in which these Mediterranean genera were found is almost entirely unknown, this can neither be disproved nor confirmed, but the genera in question are excluded from the Echioceratidae on morphological grounds, given below.

The genus *Melanhippites* Crickmay, proposed for problematic forms from British Columbia and subsequently regarded as *Paltechioceras* (Crickmay, 1962), is here considered to be *?Arnioceras* and, accordingly is provisionally retained in the Arnioceratinae, as proposed by Arkell (1957, p. *L*240).

Genus TMAEGOPHIOCERAS Spath, 1925

Type Species (OD).—*Arietites laevis* Geyer, 1886, p. 252, pl. 3, fig. 10.

Lectotype.—Here designated as the original of Geyer, *loc. cit.*, GBW (*teste* Geyer).

Type Locality.—Hierlatz near Hallstadt, Salzkammergut, Upper Austria.

Type Stratigraphic Occurrence.—Adneth Limestone (? Hierlatz Limestone).

Derivation of Name.—τμῆγας = furrow; ὄφις = serpent.

Discussion.—Of the two syntypes in the Geyer Collection, the lectotype was loaned and never returned, while the other is an indeterminable fragment, damaged during World War II (Prof. Dr. R. Sieber, written commun.). No other material is known. The specimen from Monte di Cetona (Fucini, 1902, pl. 12, fig. 7) is corroded, indeterminable, and of unknown affinity. Geyer's figure is of an evolute species, with quadrate, carinate, bisulcate whorls, ornamented by faint and distant ribs. The sparsicostate inner whorls and quadrate outer suggest a similarity with *Orthechioceras*, but the latter is never conspicuously tricarinate and possesses denser ribbing. *Paltechioceras* is much more densely ribbed throughout and the whorls more compressed. The steady increase in the number of ribs/half whorl in *Tmaegophioceras* distinguishes it from *Echioceras*, while no Echioceratidae (except the clearly distinguishable *Leptechioceras*) have such faint ribbing as that of *Tmaegophioceras*. The faint ribbing may be due to erosion of the specimen, in which case an affinity with the Lower Sinemurian Arietitidae is probable. Hyatt (1889, p. 125) included the species in *Tmaegoceras* Hyatt (1889), the type species of which (*Ammonites latesulcatus* von Hauer, 1856) differs in being completely devoid of ribs, and in possessing fewer, more expanded whorls. On the other hand, there is a strong resemblance, in the side view, to *Epophioceras*, although the apertural view, with strong sulci and convergent flanks, is much more similar to Arietitidae.

Genus PROTECHIOCERAS Spath, 1925

Type Species (OD).—*Vermiceras formosum* Fucini, 1902, p. 158, pl. 16, fig. 13.

Lectotype.—Here designated as the original of Fucini, *loc. cit.*, University of Pisa.

Type Locality.—Monte Cetona, Tuscany, Italy.

Type Stratigraphic Occurrence.—Calcari rossi inferiori, Lower Lias.

Derivation of Name.—πρῶτος = first.

Discussion.—The lectotype was removed for safety at the beginning of World War II and not returned, so that it is lost, at least temporarily (Dr. L. Gianelli, written commun.). The figure shows a rather poorly preserved, slender species, in which the most prominent ornament is a series of distant lateral nodes. In places, however, particularly on the penultimate whorl, a number of closely spaced, blunt ribs can be seen in the intervals between the nodes and these latter, in ventral view (Fucini, 1902, fig. 13b), are not as conspicuous as the lateral view (*ibid.*, fig. 13) suggests, although they are brought out in the restored apertural view (*ibid.*, fig. 13a; refigured by Arkell, 1957, fig. 270, 3b). All these figures were retouched and without the specimen, the true nature of these nodes cannot be determined. There is a strong possibility that they represent merely adherent matrix, which has been given prominence by retouching. The blunt keel and such ribbing as is visible suggest that *Vermiceras formosum* may be a member of *Epophioceras*, a genus which is common in the "Calcari grigi," of which the "Calcari rossi" is probably only a local equivalent, since both contain abundant *Arnioceras*, as well as other lower and upper Sinemurian forms (Fucini, 1902). The specimen is quite different from *Paltechioceras*, the only genus of the Echioceratidae which has even a faint resemblance, and is, therefore, here excluded from that family.

The second specimen figured by Fucini (1902, pl. 13, fig. 14) is very badly corroded and indeterminable. Fallot (1937, p. 358) records the species from North Africa, but in the absence of description or figure no reliance can be placed on this identification, and until further material is refigured, the nominal type species must remain a *nomen dubium*.

Genus MELANHIPPITES Crickmay, 1928

Type Species. (OD).—*Melanhippites harbledownensis* Crickmay, p. 61, pl. 3, 4.

Neotype.—Here designated as the original of Crickmay, 1928, pl. 4, fig. d. Crickmay Coll. The holotype, a distorted and extremely poorly preserved specimen, can no longer be found (Dr. C. H. Crickmay, written commun.), so that "Paratype 1," which, in Dr. Crickmay's estimation, shows the typical features of the genus better than the others, is selected as the neotype.

Type Locality.—Parsons Bay, Harbledown Island, Queen Charlotte Sound, British Columbia.

Type Stratigraphic Occurrence.—Harbledown Formation. Sinemurian.

Derivation of Name.—μέλᾶς = dark, ἵππός = horse. From the name "Horses heads" given by local workmen to wave-worn blocks of black argillite (Dr. Crickmay, written commun.).

Discussion.—*Melanippites* Crickmay, 1962, p. 10 (miscorrected transliteration) is an unjustified subsequent emendation (*Code*, Art. 32 (a) ii) and, therefore, is a junior objective synonym of *Melanhippites* (*Code*, Art. 33 (a) ii).

Because of the poor preservation of the former holotype and the disparity in size between it and the syntypes, there will always be a certain element of doubt as to whether they are conspecific. If they are assumed to represent the same species, the rib density as given by Crickmay (1928, text-fig. 2) is intermediate between that of *Paltechioceras elicitum* and that of *P. dignatum* on the middle and outer whorls and very much higher than in these species at less than ca. 40 mm diameter. In this respect, *Melanhippites* resembles *Orthechioceras recticostatum* and this lends support to the contention of Crickmay (1962), supported by Frebold (1970), that *Melanhippites* is a synonym of *Paltechioceras*. There is also a slight resemblance between the sharp, rectiradiate ribbing of the neotype of *Melanhippites* and certain undoubted *Paltechioceras*, from the Adneth Limestone (GBW 211), but the latter are very much more densely ribbed.

On the other hand, ribbing of this nature is much more typical of arietitids and there is a close similarity between *Melanhippites* and the stratigraphically lower *Arniotites* (=*Arnioceras*), the principal difference being the longer initial smooth stage of the latter. The nucleus of *Melanhippites* is not visible in the figured material, but it is costate at a small size. This is true also of species of *Arnioceras* from Italy figured by Fucini (1902, e.g., pl. 16, fig. 1, 7; pl. 20, fig. 5; pl. 22, fig. 4; pl. 26, fig. 13), in which the rib densities are very close to that of *Melanhippites*. The character of the ribbing is also similar in both and the Italian *Arnioceras* cited are all strongly costate by 10 mm diameter. There is,

therefore, a very close resemblance between them and *Melanhippites* and they may be congeneric. The suture line of the neotype of *Melanhippites harbledownensis* has been painted and it is impossible to use it as a means of deciding whether the species is an *Arnioceras* or a *Paltechioceras*.

The crushed and generally unsatisfactory nature of the material precludes a firm decision about the taxonomic position of *Melanhippites*, although the weight of the evidence would seem to be in favor of affinity with *Arnioceras*. It is probably best regarded as a *nomen dubium* and allowed to fall into desuetude.

The fact that there is an apparent stratigraphical separation of about 500 feet between beds with *"Arniotites"* (=*Caenisites*) *kwakiutlanus* and *"Arniotites"* (=*?Arnioceras*) *begbei* and beds with *Melanhippites* (Crickmay, 1928, p. 59) does not provide grounds for generic separation, since *Arnioceras* has a similar vertical range in some British sequences (Prof. D. T. Donovan, pers. commun.).

INDEX OF TYPES DESIGNATED

SPECIES	AUTHOR, DATE	TYPE[1]	GENUS	PAGE
alpinus	Buckman, 1914	LT	*Alsatites*	24
boblayei	d'Orbigny, 1843	LT	*"Turrilites"*	12
carusense	d'Orbigny, 1844	LT	*Echioceras*	12
costosus	Vadasz, 1908	LT	*Alsatites*	24
coynarti	d'Orbigny, 1843	LT	*Gagaticeras*	12
formosum	Fucini, 1902	LT TS	*Protechioceras*	25, 26
harbledownensis	Crickmay, 1928	NT TS	*Melanhippites*	26
haueri	Buckman, 1914	LT	*Echioceras*	13
hierlatzicus	von Hauer, 1856	LT	*"Ammonites"*	11
laevidomum	Quenstedt, 1884	LT	*Echioceras*	20
laevis	Geyer, 1886	LT TS	*Tmaegophioceras*	25
quenstedti	Schafhäutl, 1847	LT	*Echioceras*	20
raricostatoides	Vadasz, 1908	NT	*Echioceras*	13
raricostatum	Zieten, 1831	NT TS	*Echioceras*	13
robustum	Quenstedt, 1856	NT	*Echioceras*	25
tardecrescens	von Hauer, 1856	LT	*Paltechioceras*	21
ultraspiratum	Fucini, 1902	LT	*Epophioceras*	24
vellicatum	Dumortier, 1867	LT	*Epophioceras?*	22

[1] Explanation: HT, holotype; LT, lectotype; NT, neotype; TS, type species.

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EXPLANATION OF PLATES

PLATE 1

All photographs natural size, except figs. 2, 4, 5, 8, and 9.

FIGURE

1a, b. *Palaeoechioceras* sp. from *simpsoni* Subzone, Robin Hood's Bay, Yorkshire; author's coll. 1264/1.

2a, b. *Palaeoechioceras spirale* (Trueman & Williams), holotype, *?oxynotum* Subzone, Gloucester Gas Works, ×2; GSM 51475.

3. *Turrilites boblayei* d'Orbigny, lectotype, designated herein, from Lower Lias, zone unknown, Augy-sur-Aubois, near St. Amand (Cher); d'Orbigny Coll. 1472A/1.

4a, b. *Gagaticeras coynarti* (d'Orbigny), lectotype, designated herein, from *?Oxynotum* Zone, Augy-sur-Aubois, near St. Amand (Cher), ×1.5; d'Orbigny Coll. 1474.

5a, b. *Palaeoechioceras* sp., ?transitional to *Gagaticeras* from *simpsoni* Subzone, Robin Hood's Bay, Yorkshire, ×2; author's coll. 1264/2.

6a, b. *Palaeoechioceras pierrei* (Spath), holotype, from *oxynotum* Subzone, Stowell Park Borehole, Oxon; GSM Bj 4196.

7a, b. *Echioceras raricostatum* (Zieten), neotype, designated herein, from Schwarzer Jura β_2 (*raricostatoides* Subzone), Pliensbach bei Boll, Württemberg; GPS, no number.

8a, b. *Echioceras carusense* (d'Orbigny), lectotype, designated herein, from *oxynotum* Zone, Augy-sur-Aubois, near St. Amand (Cher), ×2; d'Orbigny Coll. 1475A/1.

9a, b. *Palaeoechioceras* sp., transitional to *Gagaticeras*, from *simpsoni* Subzone, Robin Hood's Bay, Yorkshire, ×2; author's coll. 1270/1.

10a, b. *Metarnioceras neera* (Reynès) from Yorkshire (?drift); cited by Spath, 1925, p. 360, footnote; BM C33581.

11. *Echioceras haueri* (Buckman), holotype, from *raricostatoides* Subzone, Adneth Limestone, Adneth (Salzburg); GWB 577b.

12. *Echioceras raricostatoides* (Vadasz), neotype, designated herein, from *raricostatoides* Subzone, "Calcaire ocreux," Seichamp, près de Nancy, Lorraine; École des Mines, Paris, Puzos Coll. B14, 7.

PLATE 2

All figures ×0.88.

FIGURE

1a, b. *Echioceras boreale* Buckman, holotype, from *raricostatoides* Subzone, Allt Fearns, Raasay (Inverness); GSE 2398.

2a, b. *Echioceras gracile* Buckman, *ex* Quenstedt, from *raricostatoides* Subzone, Schwarzer Jura β_2, Württemberg, Tübingen; Quenstedt Coll. Ce/5/23/28.

3a,b. *Echioceras zieteni* Buckman, designated as lectotype of *Echioceras zieteni* (Quenstedt *non* Oppel) by Trueman & Williams, 1925, from *raricostatoides* Subzone, Schwarzer Jura β^2, Württemberg, Tübingen; Quenstedt Coll. Ce/5/23/27.

4. *Echioceras robustum* Buckman, *ex* Quenstedt, neo-

type, designated herein, from *raricostatoides* Subzone, Schwarzer Jura β^2, Württemberg, Tübengen; Quenstedt Coll. Ce/5/23/29.

5a-c. *Paltechioceras delicatum* (Buckman), holotype, from *?aplanatum* Subzone, Nolay (Côte d'Or): Dumortier Coll., Mus. d'Hist. nat., Lyon, France.

6. *Leptechioceras charpentieri* (Schafhäutl), lectotype, designated herein, from *macdonnelli* Subzone, Fleckenmergel, Rottachtal bei Tegernsee, Bavaria; BS AS.IX.23.

7. *Echioceras quenstedti* (Schafhäutl), lectotype, designated herein, from *raricostatoides* Subzone, Fleckenmergel. Rochelsee, Bavaria; BS AS.IX.21.

8. *Orthechioceras* sp., from *densinodulum* Subzone, Hallaig Burn, Raasay (Inverness); GSE 12732.

9a, b. *Leptechioceras subobsoletum* (Buckman), holotype, from *macdonnelli* Subzone, Allt Fearns, Raasay (Inverness); GSE 2421.

[Pl. 2, fig. 3 was supplied by Dr. F. Westphal (Tübingen) and Pl. 2, fig. 1, 8, and 9 were supplied by Dr. R. B. Wilson (I. G. S. Edinburgh), to whom the author would like to express his thanks.]

PLATE 3

All figures natural size.

FIGURE

1a, b. *Echioceras intermedium* (Trueman & Williams), topotype, from *raricostatoides* Subzone, Robin Hood's Bay, Yorkshire; author's coll. 1080/1.

2a-c. *Echioceras deciduum* (Hyatt), lectotype, designated by Donovan, 1958, from *raricostatoides* Subzone, Adneth Limestone, Adneth (Salzburg); GBW Hauer Coll. VI, 1-2.

PLATE 4

All figures $\times 0.95$.

FIGURE

1a, b. *Paltechioceras aplanatum* (Hyatt), (holotype of *Metechioceras tardecrescens* Trueman & Williams), from *aplanatum* Subzone ('Upper Conybeari Bed'), Robin Hood's Bay, Yorkshire; BM C17898.

2a, b. *Paltechioceras tardecrescens* (von Hauer), lectotype, designated herein, from *?aplanatum* Subzone, Adneth Limestone, Adneth (Salzburg); GBW Hauer coll. III, 10-12.

PLATE 5

All figures natural size.

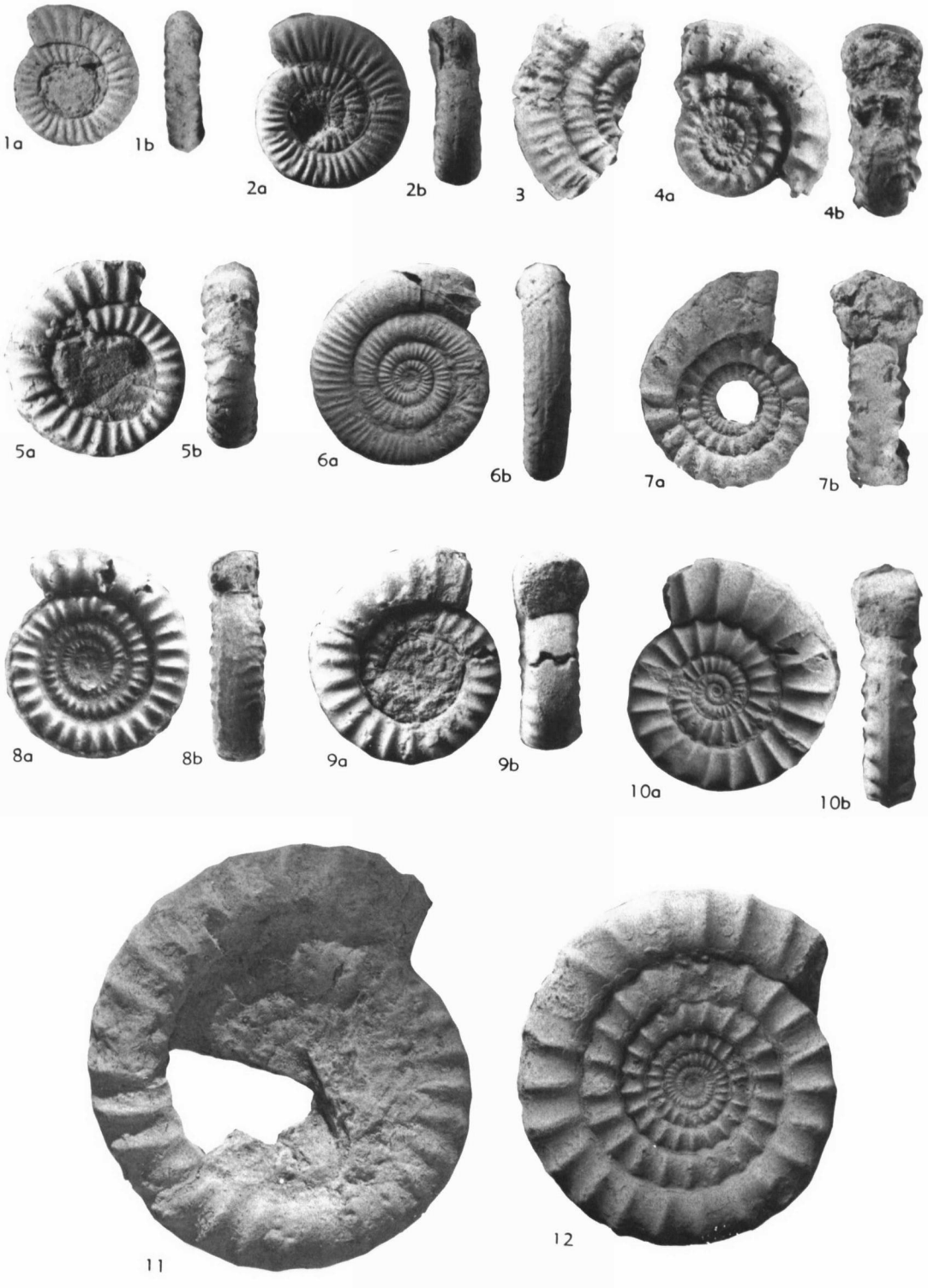
FIGURE

1a, b. *Orthechioceras radiatum* Trueman & Williams, from *densinodulum* Subzone, Stonebarrow foot, near Charmouth, Dorset: author's coll. 1110/1.

2a, b. *Orthechioceras radiatum* Trueman & Williams, from *densinodulum* Subzone, Stonebarrow foot, near Charmouth, Dorset; author's coll. 1116/6.

3a, b. *Paltechioceras aureolum* (Simpson), holotype of *Echioceras regustatum* Buckman, from *aplanatum* Subzone, Robin Hood's Bay, Yorkshire; GSM 26439.

4a, b. *Paltechioceras aureolum* (Simpson), topotype, from *aplanatum* Subzone, Robin Hood's Bay, Yorkshire; author's coll. 1071/1-2.


1a
1b
2a
2b
3
4a
4b
5a
5b
6a
6b
7a
7b
8a
8b
9a
9b
10a
10b
11
12


1a

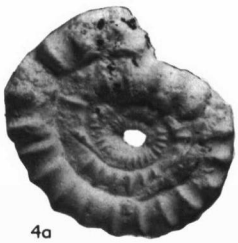

1b


2a


2b


3a


3b


4a


4b


5b


5c


5a


6


7


8


9a


9b

1a

1b

2b

2c

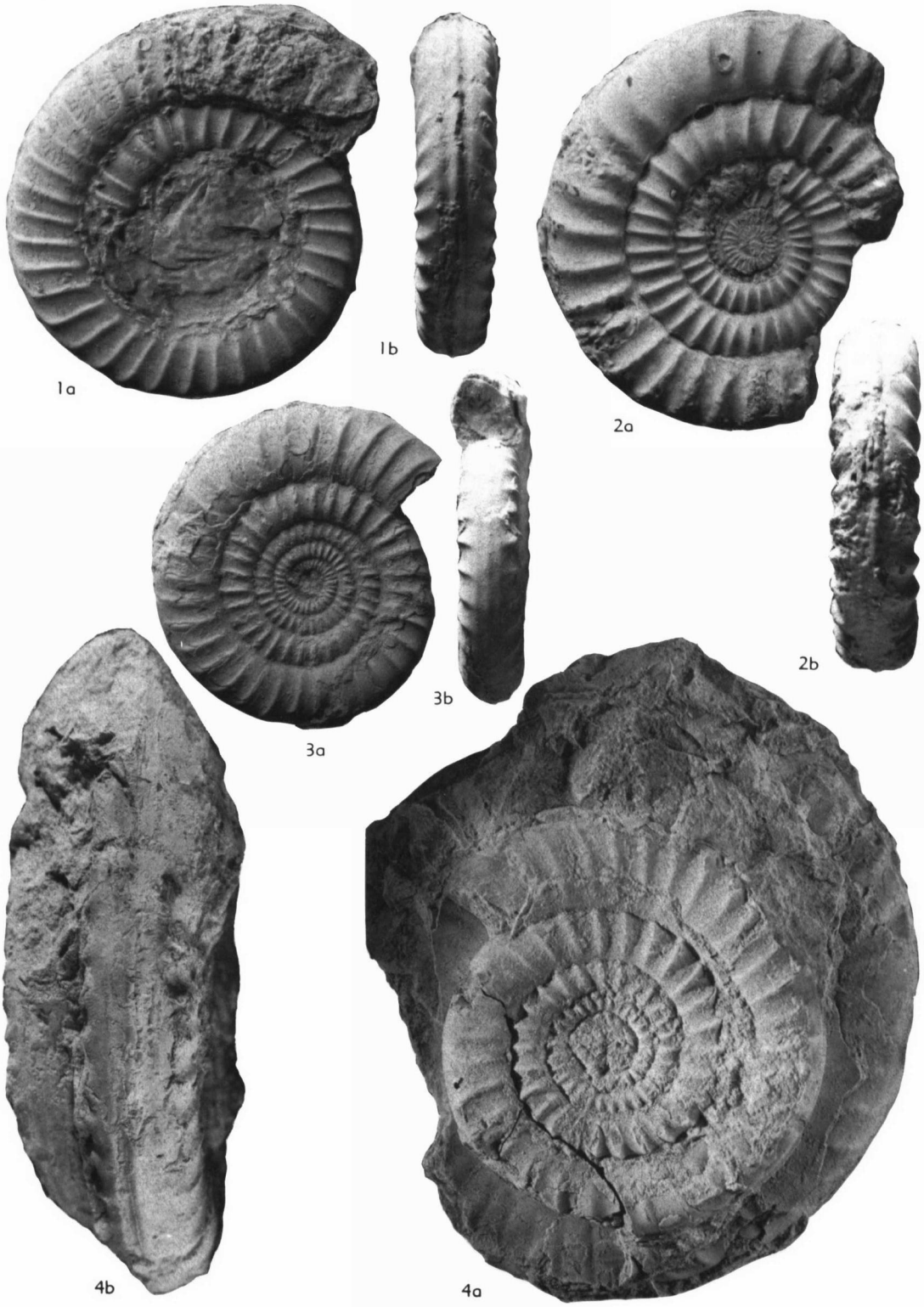
2a

1b

1a

2a

2b


1a
1b
2a
2b
3a
3b
4a
4b