THE *AMOEBOCERAS* ZONATION OF THE BOREAL UPPER OXFORDIAN

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ABSTRACT. The ammonite family Perisphinctidae, on which the standard zonation of the Middle and Upper Oxfordian has hitherto been based, is poorly represented in the Boreal Province. A new scheme is proposed based wholly on the family Cardioceratidae. It has been worked out from extensive collections from a complete section at Staffin, Isle of Skye, with supporting material from East Greenland, the Scottish mainland, Yorkshire, East Anglia, and Dorset. Published evidence indicates that it should be applicable to the whole of the Boreal Province including Canada, Alaska, and the northern U.S.S.R. The Boreal and Sub-Mediterranean standard zonal successions diverge at the base of the Middle Oxfordian. In the Boreal scheme, the Middle Oxfordian now consists of a Densiplicatum Zone, divided into Vertebrale and Maltonense Subzones, and a Tenuiserratum Zone with abundant small *Cardioceras* (*Miticardioceras*), divided into Tenuiserratum and Blakei Subzones. At the base of the succeeding Glosense Zone *Cardioceras* evolved into *Amoeboceras* and this makes a convenient change on which to base the Boreal Middle–Upper Oxfordian boundary. Four principal faunas of *Amoeboceras* delimit successively the Glosense, Serratum, Regulare, and Rosenkrantzi Zones, each, except the Regulare Zone, divisible into two Subzones. To this end it was necessary to review the taxonomy of existing species of Oxfordian *Amoeboceras*. Nineteen species are described, including the type-species, *A. alternans* (v. Buch), and two new species, *A. newbridgense* and *A. koldeweyense*. A new species of early *Ringsteadia*, *R. caledonica*, is described. We also describe the Oxfordian section at Staffin, which is taken to be the type-section for the Zones in the new scheme.

DIFFICULTIES in the way of precise stratigraphical correlations arising from faunal provincialism in the guide-fossils are well known. They become acute in ammonites during the Middle and Upper Oxfordian, and to make progress it is necessary to set up separate schemes of standard ammonite Zones for each province to describe the successions that are to be correlated. In the region under consideration, namely Laurasia north of the Tethys, three ammonite provinces can be distinguished.

The first, largest and most southerly of these provinces is the Sub-Mediterranean Province, including Portugal, northern Spain, most of France up to the southern half of the Paris Basin, the Helvetic Alps, southern Germany and Poland, the peri-Tethyan Balkans, Crimea and Caucasus. In this province a scheme of Oxfordian ammonite Zones and Subzones has been worked out in great detail in the last twenty years and is well described by Cariou *et al.* (1971). It is based on extensive and continuous sections with profuse faunas, consisting mainly of members of the family Perisphinctidae, and has proved itself so reliable that it must now be regarded as the primary standard of reference for the Oxfordian Stage.

The second is the Sub-Boreal Province, occupying a relatively small area which includes Normandy, southern England, the Boulonnais, northern Germany, Pomerania and parts of Poland, and the U.S.S.R. west of the Urals. Unfortunately, on purely historical grounds, it is this area that has provided the zonal schemes that have been erected in the past and that have become deeply entrenched in the literature, e.g. the zonal scheme given in the ammonite *Treatise* (Arkell *et al.* 1957). Even more unfortunately, these schemes had perforce to be based on unconnected faunas from widely scattered localities in successions now known to be highly incomplete with

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major non-sequences. Moreover the ammonites found are a mixture, not only of Sub-Boreal elements indigenous to the province but also of the adjacent provinces which partly overlap: a mixture which changes rapidly in space and time. The literature amply reveals the resulting confusion; in some cases not even the order of the Zones is beyond doubt. Little seems to be gained by yet further attempts to improve or even closely to define this scheme, and although it may remain useful locally for informal purposes it is to be hoped that its application to more general problems of stratigraphy and correlation will decline as the alternatives become clearer.

The third, most northerly and also very large province is the Boreal Province, including Scotland, Greenland, Spitsbergen and the Barents Shelf, the Baltic, northern Poland and Russia, northern Siberia, Alaska, and Canada. In these regions the Oxfordian ammonite faunas consist principally of members of the family Cardioceratidae. Their species have mostly been long known, but a zonal scheme based on them has had to await the results of detailed stratigraphical work. These are now available, from outcrops in East Greenland (Surlyk *et al.* 1973; Sykes and Surlyk 1976), Scotland (Wright 1973; Sykes 1975*a*, *b*), and Yorkshire (Wright 1972), and cored boreholes in the Wash area of eastern England (Gallois and Cox 1977). Extensive new collections, combined with material in the museums and survey collections, form the basis of the new zonal scheme for the Oxfordian of the Boreal Province. This scheme, already published in outline (Sykes and Surlyk 1976), is refined here down to subzonal level and presented with the necessary stratigraphical details and taxonomic revision of the ammonites.

In this work the localities and sections that have yielded material are outlined. Then the Zones and Subzones of the Oxfordian are defined. Finally, the systematics of the relevant ammonites are summarized.

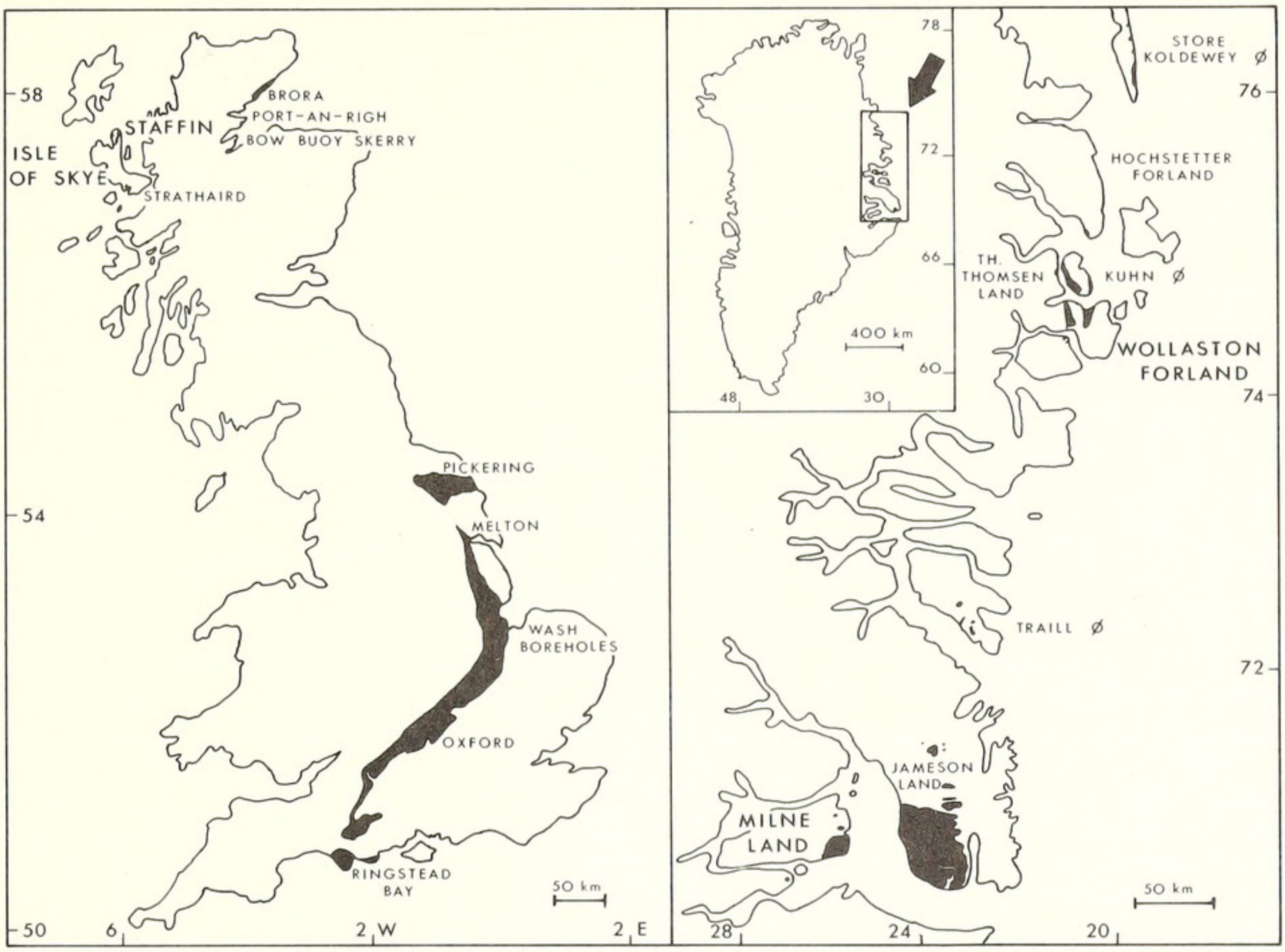
SECTIONS AND LOCALITIES

The outcrops of Upper Jurassic rocks in Britain and Greenland are shown in text-fig. 1, with the names of localities mentioned in the text.

1. North-east Greenland. The Oxfordian outcrops, their lithostratigraphy and ammonites on Wollaston Foreland, Kuhn Ø and Hochstetter Foreland have been recently reviewed by Sykes and Surlyk (1976).

2. East Greenland. The classical descriptions of the successions and faunas of Milne Land by Rosenkrantz (1929), Aldinger (1935), and Spath (1935) have been supplemented through new collections by Callomon (field-seasons 1957–1958), Håkansson *et al.* (1971), and Callomon and Birkelund (1979). The Upper Jurassic succession in Jameson Land was worked out in the field-seasons of 1970–1971 (Surlyk *et al.* 1973). Contrary to what was known previously (Callomon 1961, p. 263), Lower Oxfordian has now been found both in central Jameson Land and on Wollaston Foreland.

3. Western Scotland: Skye. The presence of Upper Oxfordian–Kimmeridgian deposits at Staffin was first shown by MacGregor (1934). Subsequent collections and descriptions were made by the Geological Survey in 1936–1937 (Anderson and Dunham 1966; Turner 1966; Morris 1968; Wright 1973). The beds are poorly exposed on the foreshore of Staffin Bay, mostly below high-water mark and widely covered by boulders of basalt, but their importance as providing probably the best available



TEXT-FIG. 1. Outcrops of Upper Jurassic sediments in Britain and east Greenland with localities mentioned in the text.

section through the Boreal Upper Oxfordian anywhere has been recognized for some time (Torrens and Callomon 1968). A detailed re-examination was therefore made by one of the present authors (Sykes 1975*b*), and the results have been published in summary, with a revision of the lithostratigraphy (Sykes 1975*a*). Some 100 m of richly fossiliferous Middle and Upper Oxfordian shales and siltstones form the upper part of the Staffin Shale Formation, and are chosen as stratotype for most of the zonal scheme described below. They constitute a primary standard of reference, and to help future workers to retrace the succession in the field a more detailed description with numbered beds and prominent field markers is presented here at the end of the paper.

4. Eastern Scotland. The exposures here have also been revisited and redescribed (Sykes 1975*a*, *b*). They yield mainly Lower and Middle Oxfordian faunas, but the presence of higher beds offshore is indicated by beach-boulders and near-travelled glacial erratics on the mainland.

5. Yorkshire. North of the Market Weighton axis Upper Oxfordian is locally present mainly as arenaceous Upper Calcareous Grit, with ammonites that show the formation to be as fragmentary chronologically here as in southern England. Succession summarized by Wright (1972).

6. Humberside. South of the Market Weighton axis the Oxfordian changes to the clays of the Ampthill Clay facies province and a pit worked for cement at Melton

(SE 971271) shows a useful succession across the Middle–Upper Oxfordian boundary, although only a brief description has so far been published (Wright 1972).

7. Southern England. The only major new source of information beyond that summarized previously (Torrens and Callomon 1968) lies in cored boreholes through Ampthill Clay in the area of the Wash (Gallois and Cox 1977), and temporary sections and a borehole near Ampthill (summarized by Callomon in Rood *et al.* 1971) in course of study. Further south, Boreal faunas become rare, to be replaced largely by Sub-Boreal forms, and although there is some progress in the problems of correlation between Sub-Boreal and Sub-Mediterranean Provinces, these are beyond the scope of the present work.

THE AMMONITE ZONES OF THE BOREAL OXFORDIAN

In devising a scheme of standard Zones, we follow the principle of no gaps, no overlaps (Callomon 1965; Callomon and Donovan 1974), which makes Stages, Sub-

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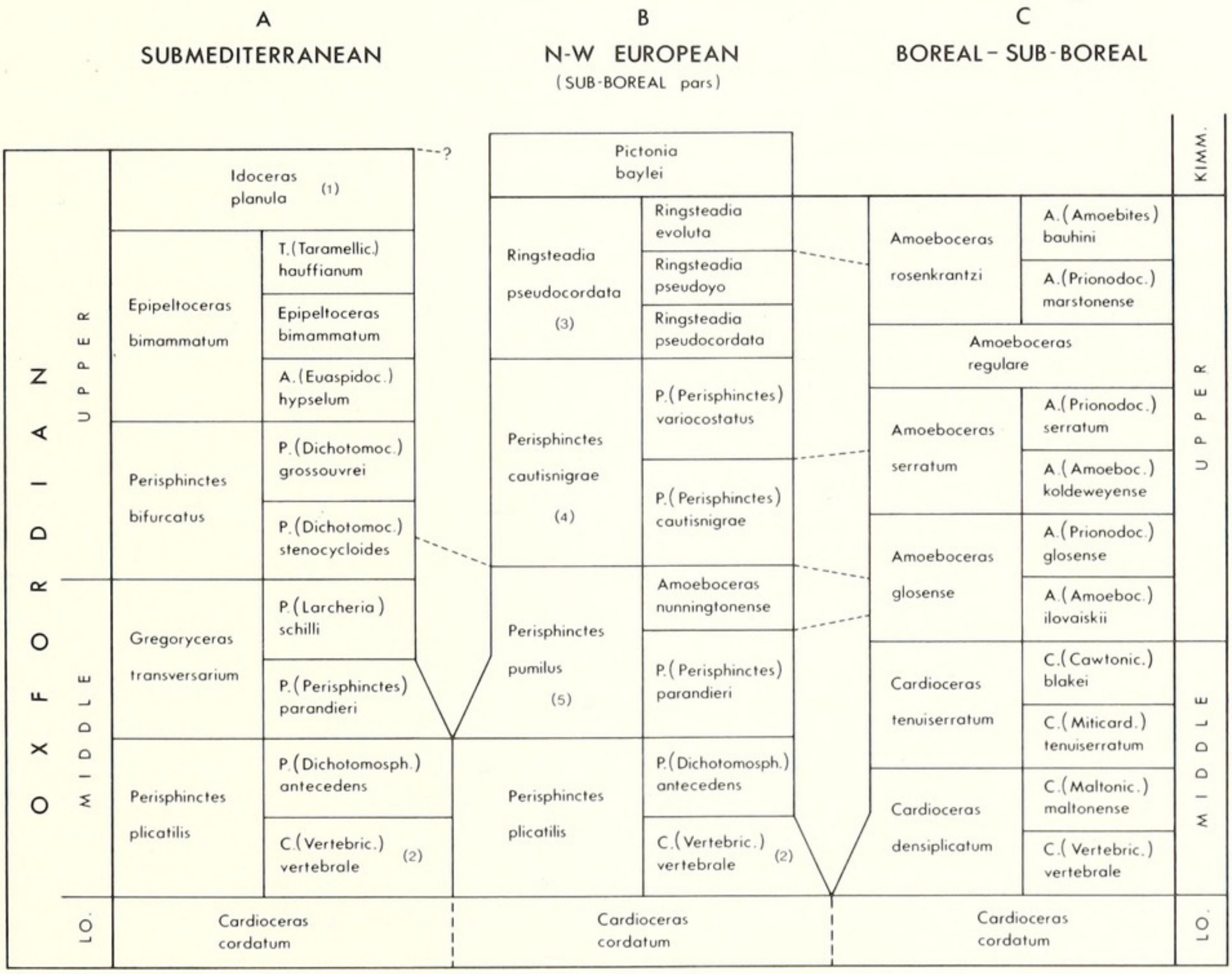
TEXT-FIG. 2. Standard ammonite Zones and Subzones of the Middle and Upper Oxfordian in the three principal faunal provinces.

Notes: (1) Subgenus *Subnebrodites* Spath. (2) Alternatively, *Cardioceras* (*Plasmatoceras*) *tenuicostatum* in those areas or facies in which *Vertebriceras* does not occur. (3) Division into Subzones following Morris (1968). (4) Three Zones based on perisphinctids have been variously proposed in the past to fill this interval. The Decipiens Zone has had to be abandoned, because *Decipia* as a guide-fossil is long-ranging with *D. decipiens* occurring in beds at the bottom not usually included in its nominal Zone, and the Zone as a stratigraphical entity has turned out to be synonymous, more or less, with the Cautisnigrae Zone. There is growing evidence that the fauna of *Perisphinctes variocostatus* occurs above that of *P. cautisnigrae*. (5) The evolution of this nomenclature is complex. (*a*) The Parandieri Subzone was introduced in Britain for the top part of the Plicatilis Zone (Callomon 1960) in an area, in southern England, in which it is followed by a major non-sequence. (*b*) Subsequent work (Enay 1966) showed that the beds of this age fall already into the Transversarium Zone of Oppel 1863. Hence, following the principle that a chronostratigraphic unit be defined by its lowest component, the Parandieri Subzone was transferred into the Transversarium Zone of the Sub-Mediterranean Province, where it still rests, leaving an unfilled gap under the base of the Cautisnigrae Zone. (*c*) Work in other areas (Wright 1972), revealed the presence of a fauna falling into the non-sequence of southern England. This led to the introduction of a Nunningtonense Subzone of the Transversarium Zone as used in England. At about the same time an upper Schilli Subzone was also introduced into the Transversarium Zone of the Sub-Mediterranean Province proper by Cariou *et al.* (1971). This arrangement is clearly unsatisfactory, for it leads to two Transversarium Zones of probably different extent: one with Parandieri and Schilli Subzones in the Sub-Mediterranean Province, and one with Parandieri and Nunningtonense Subzones in the Sub-Boreal Province, in which the zonal index is wholly unknown. A solution to this problem is not easy. To absorb the Nunningtonense Subzone into the Cautisnigrae Zone above as basal Subzone would be unsatisfactory because the latter is already well defined by its base, and its characteristic fauna does not occur in the Nunningtonense Subzone. It would also still leave two Parandieri Subzones below, or a Parandieri Subzone of the Transversarium Zone on the one hand and a Parandieri Zone of the Sub-Boreal Province on the other. To promote the Nunningtonense Subzone to full Zone seems unjustified, as it has been only recognized in Yorkshire. Conversely, to regard it as a horizon in something else leaves unanswered the question of what to call the interval between Plicatilis and Cautisnigrae Zones in column B. It seems desirable therefore *on purely nomenclatural grounds* to find an alternative index for the unit occupying this interval in column B. There is very little choice if the subzonal indices are excluded, for the faunas are poorly known and have few species. *P.* (*Perisphinctes*) *pumilus* Enay, 1966, has now been found repeatedly in England, in Dorset and Huntingdonshire, in beds of Parandieri age, probably the upper part, and it occurs in the Parandieri Subzone of the Jura.

stages, Zones and Subzones a hierarchy of rank, defines each except the lowest unit in the hierarchy in terms of its lowest member, and anchors the whole scheme objectively by defining each unit of lowest rank—Subzone, or if undivided the Zone—by its base in a stratotype (the 'Golden Spike' of authors). The assignment of a unit to a particular rank is largely arbitrary, but we use the following rule of thumb: if a unit can be readily recognized over a very wide area in the field by means of its diagnostic fauna with only a moderately practised eye and a handful of specimens, it ranks as Zone; if it can be differentiated only by comparison with more extensive collections from a more restricted area with reference material in the laboratory it ranks no more than Subzone. Finally, a particular bed marked by a characteristic fauna of purely locally known occurrence we designate an Horizon, an infra-subzonal unit having no formal status. Horizons in this sense represent local biozones (e.g. 'Teilzones')—local for a variety of reasons other than that of interest, which is primarily chronostratigraphical.

The proposed scheme of ammonite Zones and Subzones for all three faunal provinces is shown in text-fig. 2.



LOWER OXFORDIAN

The Lower Oxfordian marks the maximum extent of the 'Boreal Spread' (Arkell 1956), in which the Boreal Cardioceratidae made their strongest and furthest excursion southwards (and some typically Sub-Mediterranean families, e.g. the Aspidoceratidae, made their furthest excursions northwards). The same zonal scheme is therefore currently in common use in all three provinces, even though it should properly be regarded as Boreal. No changes need therefore be considered here: such changes as may become necessary in the future, e.g. in extending the zonation to the areas south of the Tethys, will be made in the Sub-Mediterranean scheme of Zones.

MIDDLE OXFORDIAN

Usage of the terms Middle and Upper Oxfordian has been rather variable. The first attempts to subdivide the Stage introduced Lower and Upper parts only (Arkell 1936*a*), corresponding more or less to the Oxford Clay and Corallian Beds of England, and influenced by the rich succession of ammonites in the former, and the apparent thinness of the latter with its relative paucity of ammonites. As the succession in the Sub-Mediterranean Province was worked out, and the provincial implications more fully appreciated, the picture of the relative time-durations of Lower and Upper divisions was if anything reversed, and a Middle division introduced (Zeiss 1957; Callomon 1964). At first the Middle Oxfordian consisted only of the English Plicatilis Zone, which at the time included parts of what is now placed in the Transversarium Zone. Usage in the Sub-Mediterranean Province has since settled down into a convenient and well-balanced tripartite subdivision, the Middle Oxfordian comprising the Plicatilis and Transversarium Zones.

The subdivision of a separate Boreal scheme of chronostratigraphical units has to be approached independently. Fortunately, within the Boreal Province it is easy to recognize the time-plane corresponding to the base of the Vertebrale Subzone of the Plicatilis Zone, which also defines the base of the Sub-Boreal/Sub-Mediterranean Middle Oxfordian. The Vertebrale Subzone is therefore the lowest Subzone of the lowest Zone in both of what are thereafter diverging zonal columns in the separate Provinces. The tops of the Vertebrale Subzone of the Plicatilis Zone and the Vertebrale Subzone of the Densiplicatum Zone may differ slightly in ages, but as units are defined only by their bases this raises no formal difficulty.

Faunal separation becomes acute in the Antecedens Subzone. In southern England, the Cardioceratidae are quite rare at this level, not exceeding perhaps 10% of the faunas with the balance made up of Perisphinctidae. In Skye, however, *Cardioceras* forms 70% of the fauna. This polarization increases upwards and is maintained well into the Kimmeridgian. The Boreal zonation is therefore based on the evolution of Cardioceratidae. The only other attempt so far at a systematic zonation based on this family is in Poland, where four Zones (Mariae, Bukowskii, Excavatum, and Tenuiserratum) span the Lower and Middle Oxfordian, but no further subdivision has been attempted (Malinowska 1966, 1974; Dembowska and Malinowska 1974). Higher beds in Poland and Russia have been loosely placed in a comprehensive Alternans Zone since the earliest days.

The boundary between Boreal Middle and Upper Oxfordian is now placed between the Tenuiserratum and Glosense Zones. This coincides quite closely with the transition from *Cardioceras* to *Amoeboceras*. The ranges of stratigraphically significant species of ammonites in the reference-sections of Skye are shown in text-fig. 3.

1. *Densiplicatum Zone*

Index: Cardioceras (*Subvertebriceras*) *densiplicatum* Boden, 1911. The index species was fully described and discussed by Arkell (1941, p. lxxvii, 1942, p. 240). His reference to Boden's only figured specimen (from Popilani in Lithuania) as 'the type' may be construed as a lectotype designation. The photograph is reproduced here in Plate 112, fig. 3, along with a typical English example.

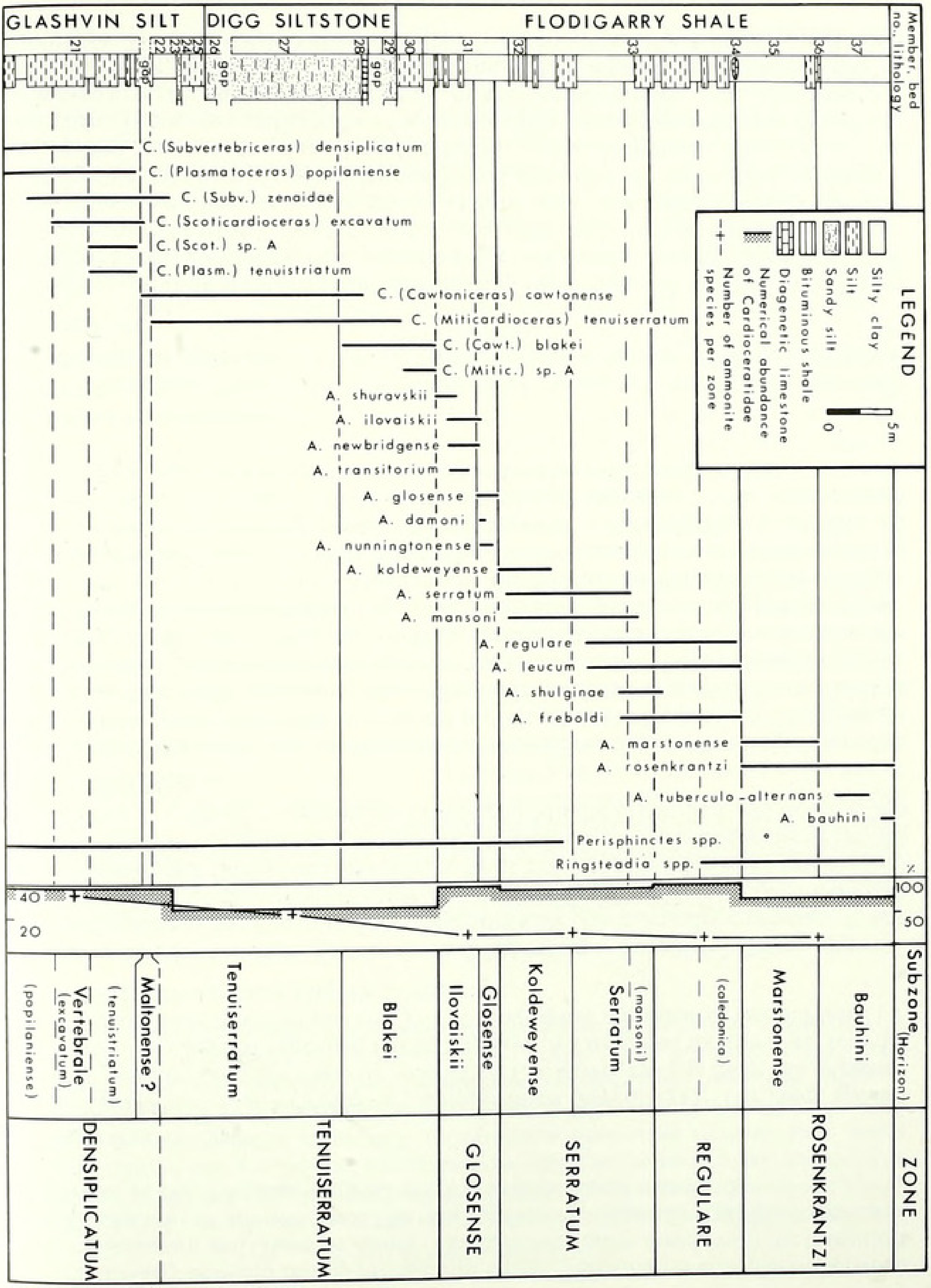
Definition. Subdivided into Vertebrale and Maltonense Subzones. Range approximately the same as the Plicatilis Zone, base identical. Zone broadly equivalent to the Excavatum Zones or Subzones of other authors (e.g. Spath in Anderson and Dunham 1966; Malinowska 1966), but these tend to be of variable ages because of rather loose interpretations of the index species: smooth, keeled, disc-like macroconchs of species of *Cardioceras* occur throughout the Lower and Middle Oxfordian and hence make poor guide-fossils.

Distribution. Greenland: the top Mudderbugt Member of the Charcot Bugt Sandstone of Milne Land (Callomon 1961; Callomon and Birkelund 1979, faunas 5–7); Olympen Formation of central Jameson Land (Birkelund *et al.* 1971) and southern Traill Ø (Putallaz 1961). Western Scotland: parts of the Glashvan Silt, Tobar Ceann Siltstone, and Scaladal Sandstone Members of Skye. Eastern Scotland: the Zone includes the transgressive *Rhaxella* spiculites (Ardassie Limestone Member) and glauconitic siltstone (Port-an-Righ Ironstone Member) of the Moray Firth basin (Sykes 1975*a*). England: classified in the Plicatilis Zone. The characteristic Cardioceratidae extend as far as the Terres Noires of the Basses Alpes in southern France (Bourseau 1977), the Moscow Basin (Ilovaisky 1904), northern Siberia (Kniazev 1976), Alaska and Wyoming (Reeside 1919), and the Canadian Rockies (Whiteaves 1903).

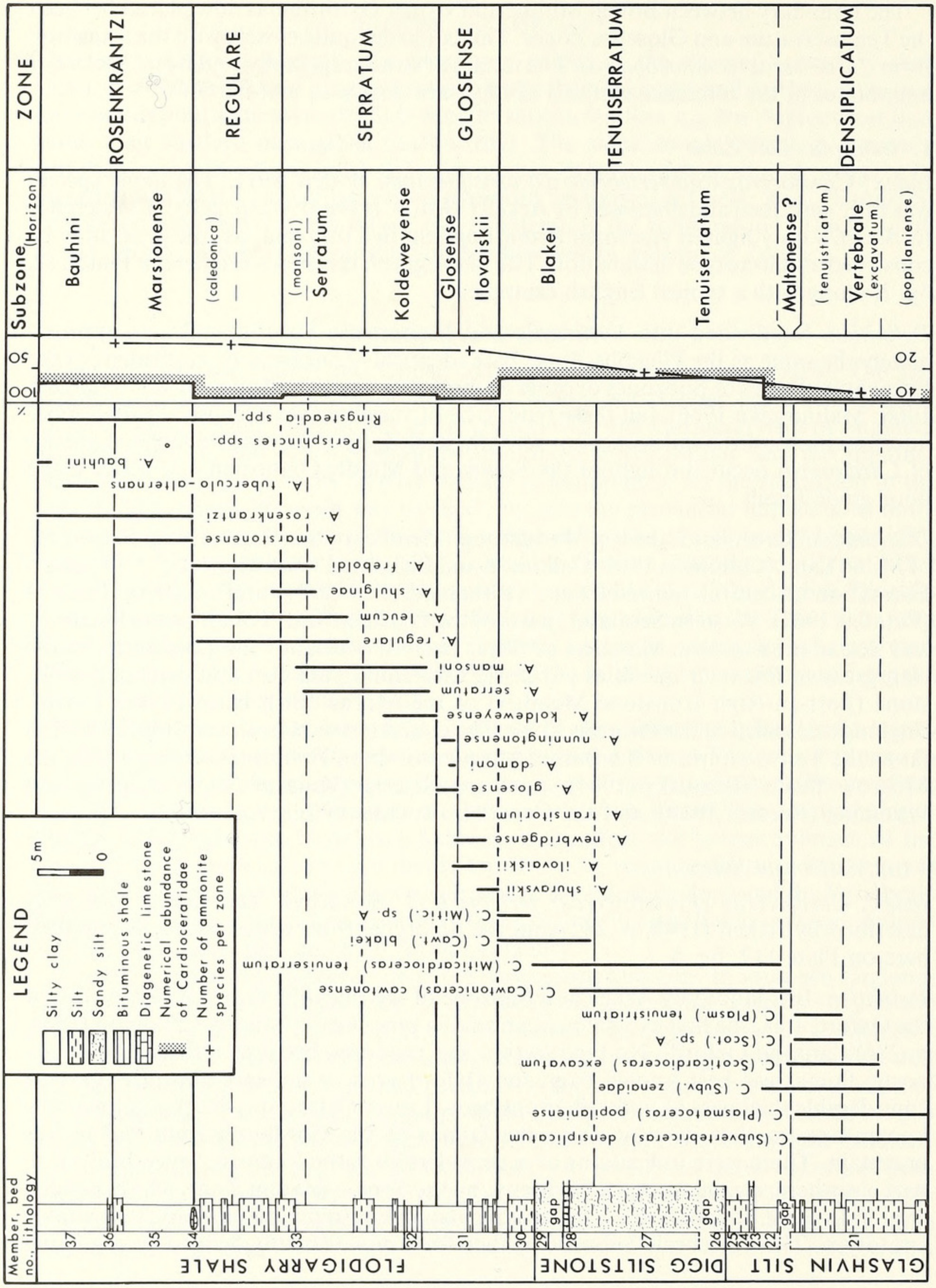
1 (*a*) *Vertebrale Subzone*

Index: *Cardioceras* (*Vertebriceras*) *vertebrale* (J. Sowerby). The species was fully described by Arkell (1942, p. 242) and the holotype, from near Oxford, is refigured here on Plate 112, fig. 5.

Definition. Introduced by Arkell as a Subzone of the Plicatilis Zone (1947*a*, p. 48) for the Oxford area, the first explicit indication of a type-locality was by Callomon (1964, p. 286): 'around Oxford'. No type section was proposed because, although the diagnostic fauna was best known from the Oxford area, it appears abruptly above a considerable thickness of unfossiliferous beds (Lower Calcareous Grit) of imprecisely known age, so that its relation to the faunas of the Cordatum Zone below was uncertain. There were indications of a considerable faunal non-sequence bridged in part elsewhere, e.g. in northern Germany, by the Tenuicostatum Zone. The expanded section in Skye, in which the Cordatum Zone is fully represented, makes a suitable stratotype. The Vertebrale Subzone is, therefore, now formally defined as beginning



TEXT-FIG. 3. Ranges of stratigraphically significant ammonites in the Middle and Upper Oxfordian of Staffin, Skye.



TEXT-FIG. 3. Ranges of stratigraphically significant ammonites in the Middle and Upper Oxfordian of Staffin, Skye.

5·4 m above the base of bed 21 of the Staffin Shale Formation at Staffin as described in the section given below.

Characteristic fauna and horizons. The differences between the forms of *Cardioceras* in the Cordatum and Densiplicatum Zones are most clearly seen in the style of the secondary ribbing. In the earlier forms the secondaries sweep forward strongly at the ventrolateral shoulders but persist and run continuously into the finely serrated ventral keel. In the later forms ventrolateral shoulders bearing accentuated secondaries tend to be separated from the more coarsely serrated keel by smooth margins with at most vestigial ribbing. In the Vertebrale Subzone strongly-ribbed forms (*Subvertebriceras*, *Vertebriceras*) predominate among the microconchs. The cordate forms of the Cordatum Subzone become rare. The macroconchs tend to be large and smooth (*Scoticardioceras*, *Goliathiceras*) and hence not diagnostic.

There is also a group of small, compressed, evolute, finely and densely ribbed forms of the subgenus *Plasmatoceras*, present already in the Cordatum Zone and probably evolved independently from *Scarburgiceras*. This group may or may not co-occur with *Subvertebriceras*, depending apparently to some extent on lithofacies, for *Plasmatoceras* predominates in clays and silts, *Subvertebriceras* in arenaceous facies. The systematic position of *Plasmatoceras* has been in some doubt. The type and only specimen of the type-species, *P. plastum* Buckman, 1925 (pl. 607) was described and not too well figured alongside a very similar-looking specimen, the type and only specimen of another species, *Plasmatites crenulatus* Buckman, 1925 (pl. 608). Both specimens bore identical and rather cryptic labels, which were interpreted by Arkell (1941, p. lxxvii), but left the localities and horizons of origin uncertain. The additional material in the British Museum was no more conclusive. The difficulty was that *P. crenulatus* seems to be without doubt a true *Amoeboceras s.s.* close to *A. bauhini* (Oppel), probably from the Baylei Zone, which occurs near the surmized locality, or possibly from uppermost Upper Oxfordian immediately below. The inference was that *Plasmatoceras* was similarly a late *Amoeboceras*. New evidence from a collection of ammonites, including one indubitable bodychamber of *P. plastum*, in the same preservation as the type (collected by the Geological Survey in 1887 (IGS Jr1947b–d) and bearing the label 'brickyard 1 mile west of Wooton Bassett') shows that the locality inferred by Arkell is without doubt in the Cordatum Zone, probably Costicardia Subzone. Arkell's interpretation of *Plasmatoceras*, as given in the *Treatise*, is therefore correct.

In the thick type-section in Skye the Subzone can be further subdivided into three informal horizons (see text-fig. 3). From below: (i) *popilaniense* horizon: the lowest 3 m of the Subzone are dominated by small *C.* (*Plasmatoceras*) *popilaniense* Boden, without either *C.* (*Cardioceras*) or *C.* (*Scoticardioceras*); (ii) *excavatum horizon*: 4 m above the base sees the incoming of *C.* (*S.*) *excavatum* (Sowerby) with abundant *C.* (*Subvertebriceras*) *densiplicatum*, *zenaidae* Ilovaisky and *sowerbyi* Arkell; (iii) *tenuistriatum horizon*: from 7 m above the base the fauna is characterized by small *C.* (*P.*) *tenuistriatum* Borissiak and *tenuicostatum* (Nikitin).

Distribution. At Port-an-Righ and Bow Buoy Skerry the Vertebrale Subzone is thin, but representatives of the *popilaniense* horizon can be recognized near the top of the

Shandwick Siltstone Member. The well-preserved fauna of the Port-an-Righ Ironstone Member at both these localities belongs to the *excavatum* horizon, although at Bow Buoy Skerry the upper part of the member is of *tenuistriatum* horizon age. At Brora the Ardassie Limestone Member belongs to the *tenuistriatum* horizon, explaining Buckman's difficulty (1925, p. 49) in matching the fauna with English forms. In Strathaird, Isle of Skye, only the *excavatum* horizon can be recognized. The *excavatum* horizon can now also be recognized in an important section at Warboys, north-north-west of Cambridge. There, a thin black clay (Callomon 1968, p. 289, bed 9) resting non-sequentially on Bukowskii Subzone was formerly assigned to Upper Oxfordian on the basis of poorly-preserved ammonites resembling *Amoeboceras* that could not be matched with any comparable material then available. When crushed, *Plasmatoceras* and *C. sowerbyi* may be hard to distinguish from *Amoeboceras*. The *tenuistriatum* fauna has not been recorded from Britain before but is well known from the Heersum Beds near Hannover (Siegfried 1952), the Czestochowa area of Poland (Brochwicz-Lewinski 1976), and the Jura (Enay 1966, p. 248).

1 (*b*) *Maltonense Subzone*

Index: *Cardioceras* (*Maltoniceras*) *maltonense* (Young and Bird). The holotype is lost, and no suitable topotype has come to light, so a specimen from Highworth, Wiltshire, has been designated neotype by Arkell (1941), refigured here on Plate 113, fig. 1.

Definition. The base of the Maltonense Subzone is defined by the appearance of *C.* (*Maltoniceras*) and the top by the appearance of *C.* (*Miticardioceras*). Such a subzone is necessary to define the interval yielding *C.* (*Maltoniceras*) and *C.* (*Scoticardioceras*) but without *C.* (*Miticardioceras*). Unfortunately, the foreshore at this level at Staffin is boulder strewn and poorly exposed. It is therefore proposed that the type locality should be the foreshore at Port-an-Righ, Ross-shire, in eastern Scotland (text-fig. 1). The Maltonense Subzone fauna is found in the top bed of a prominent red-weathering nodular ironstone unit (the Port-an-Righ Ironstone Member of Sykes (1975*a*)). The characteristic elements include *C.* (*Maltoniceras*) *maltonense*, *vagum* Ilovaisky, *schellwieni* Boden (*non* Arkell), *C.* (*Cawtoniceras*) *cawtonense* (Blake and Huddleston), and *C.* (*Subvertebriceras*) *zenaidae*, before *C.* (*Miticardioceras*) *tenuiserratum* appears near the base of the overlying Port-an-Righ Siltstone Member. Perisphinctids are also abundant at this level, including *P.* (*Dichotomosphinctes*) cf. *antecedens* Salfeld and *P.* (*Arisphinctes*) *vorda* Arkell. The Boreal Maltonense Subzone and the Sub-Boreal Antecedens Subzone largely coincide (see text-fig. 2), as the overlap of the areal distribution of the Cardioceratidae and the Perisphinctidae probably reaches its maximum during this time. The tops, however, probably do not coincide, as *C.* (*Miticardioceras*) appears to come in some way below the base of the Sub-Mediterranean Parandieri Subzone.

Distribution. East Greenland: Traill Ø (Putallaz 1961). Skye: Staffin, between beds 21 and 22; Strathaird, the Scaladal Sandstone Member, upper part, 20 m+ (Sykes 1975*a*). Eastern Scotland: Port-an-Righ. England: usually described under Antecedens Subzone (see Callomon 1960); that of Yorkshire recently reviewed by Wright (1972). The Wash boreholes: beds 8–10 (Gallois and Cox 1977). Canada: the southern

Rockies (*C.* (*C.*) *canadense* Whiteaves; see Frebold 1957). Russia: Moscow basin (*C. vagum* Ilovaisky, 1904).

2. *Tenuiserratum Zone*

Index: *Cardioceras* (*Miticardioceras*) *tenuiserratum* (Oppel). The specimen from the Argovian Jura figured by Oppel (1863, pl. 53, fig. 2*a–c*), referred to by Arkell (1941, p. 237) as holotype, is now designated lectotype. It is kept at the ETH, Zürich, and is refigured here as Plate 113, fig. 2. The species was first used as index of a Zone by Malinowska (1966) for the northern parts of Poland in which Cardioceratidae predominate, but later (e.g. Malinowska 1776) it appears only as joint index with *Perisphinctes chloroolithicus* in a way that indicates a temporal extent for the Zone differing considerably from that defined here and based possibly in part on a miscorrelation. The Zone is subdivided into Tenuiserratum and Blakei Subzones. Equivalent to the upper part of the Antecedens Subzone and most if not all of the Parandieri Subzone of the Sub-Boreal/Sub-Mediterranean Provinces.

2 (*a*). *Tenuiserratum Subzone*

Index: as for the Zone.

Definition and characteristic fauna. The base of the Subzone is marked by the appearance of small, almost smooth button-like species retaining little besides subdued widely spaced lateral nodes and a finely crenulate keel, of which *C. tenuiserratum* appears to be a microconch and *C.* (*Miticardioceras*) *mite* Buckman (1923, pl. 375) a macroconch. They tend to have been overlooked in the past, and dismissed merely as nuclei or juveniles of *Maltoniceras*, but although there is some range of variability of ornament the maximum adult size is a remarkably constant character. At Staffin these forms occur commonly throughout beds 23–30, at some of the higher levels in extreme abundance. These beds are therefore designated stratotype of the Zone, and the Subzone is defined by its base, bed 23. Other forms include *C.* (*Maltoniceras*) *schellwieni* and *C.* (*Cawtoniceras*) *cawtonense* ranging up from below; rare *C.* (*Subvertebriceras*); and *Perisphinctes* (*Dichotomosphinctes*) cf. *antecedens* Salfeld.

Distribution. *C. tenuiserratum* makes a most useful stratigraphical marker over a very wide area. Eastern Greenland: Kosmocerasdal Member of the Kap Leslie Formation of Milne Land (Callomon and Birkelund 1979, fauna 8), with *C. cawtonense*, *C. maltonense*, and *C.* (*Maltoniceras*) *bodeni* Maire as well as the index (Sykes Collection). Skye: Staffin. Eastern Scotland: Port-an-Righ Siltstone Member, Port-an-Righ. Eastern and Southern England: Melton, near the base; St. Ives, near Huntingdon, the St. Ives Rock—cf. *C.* (*M.*) *schellwieni* Arkell (non Boden) and *C.* (*M.*) *brightoni* Arkell, *partim* (1941, pl. LI, fig. 11; 1942, pl. LII, figs. 17, 18); Upware, north-east of Cambridge, in Corallian facies, common but unlocalized (Sedgwick Museum); the Wash boreholes: Ellsworth Rock Series (= West Walton Beds of Gallois and Cox 1977), beds 11–16, and Ampthill Clay, beds 1–4; Ampthill: throughout the Oakley Beds, Ellsworth Rock Group, some 6 m of irregularly-bedded silts and siltstones with *Exogyra* lumachelles and lenticles of serpulite resting with sharp boundary on a remanié bed of concretions containing the fauna of the Vertebrale Subzone, and overlain by typical dark pyritic Ampthill Clay; Worminghall, near

Oxford: the Worminghall Rock—a bed of siltstone in the Oakley Beds which yielded the type of *Miticardioceras mite* Buckman. Western France: Poitou, where it characterizes a distinct horizon (Cariou 1966, fauna 2); Eastern France: Talant, near Dijon (Maire 1938); The French, Ledonian, and Argovian Jura (Petitclerc 1916; Enay 1966; de Loriol 1902; Oppel 1863). Northern Germany: near Hanover (Arkell 1941, p. 238). South Germany: Saxony; north of the Bohemian massif (Bruder 1885). Moravia, south of the Bohemian massif (Uhlig 1881) and Galicia, the Pennine klippen belt (Neumayr 1871). Northern and Southern Poland (Malinowska 1976). Moscow Basin: including the forms described as *C. zieteni* Rouillier (Ilovaisky 1904, refigured by Arkell 1941, p. 233, text-fig. 83.3, 4.). The true *zieteni* is much more inflated and although it may belong to this group, the name is best kept separate for the time being.

2 (*b*). *Blakei Subzone*

Index: *Cardioceras* (*Cawtoniceras*) *blakei* Spath. The holotype (IGS 72203) was figured by Spath (1935, pl. 13, fig. 4) and is refigured here as Plate 113, fig. 3.

Definition. The subzone is marked by the incoming of the youngest *Cardioceras* fauna, characterized by *C. blakei*, with its widely spaced primary ribs and almost wholly separated secondaries. Type-locality: Staffin, base 7·7 m above the base of bed 27 in the Digg Siltstone Member, rising through bed 30 of the Flodigarry Shale Member and into the lower part of bed 31. Here the fauna consists of *C.* (*Cawtoniceras*) *blakei*, aff. *intercalatum* Arkell, *C.* (*Maltoniceras*) *vagum* Ilovaiskii, *C.* (*Miticardioceras*) *tenuiserratum* and sp., and *Perisphinctes* (*Dichotomosphinctes*) spp. At the top, bed 30, more strongly-ribbed forms occur, including *C.* (*Cawtoniceras*) cf. *ogivale* (Buckman) and individuals transitional to *Amoeboceras ilovaiskii* (M. Sokolov) and *A. newbridgense sp. nov.*

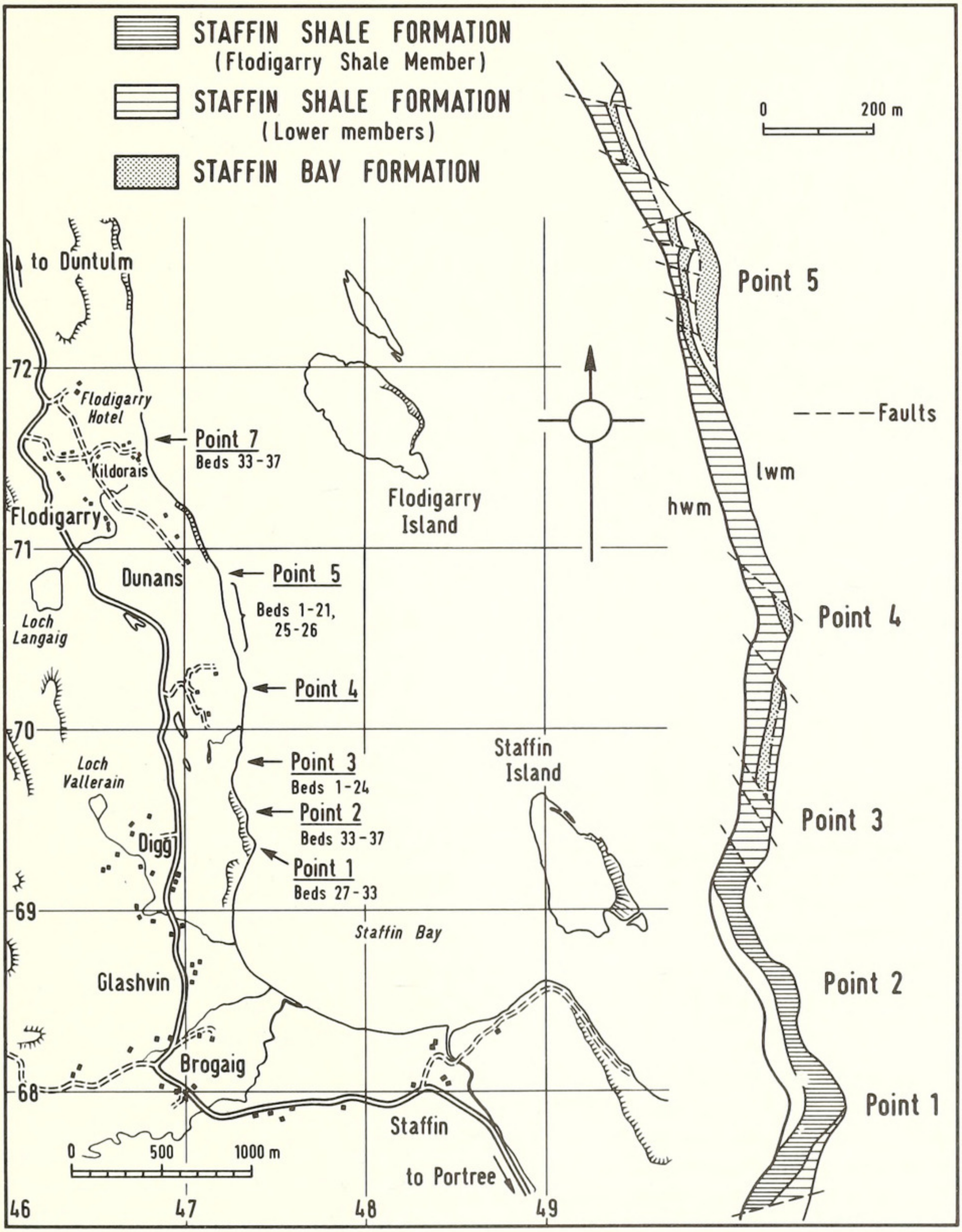
Distribution. The Subzone has not yet been very widely recognized because southwards Cardioceratidae are rapidly replaced by Perisphinctidae, giving a '*Cardioceras* gap' between the last forms of the Tenuiserratum Subzone and the first *Amoeboceras* of the Upper Oxfordian. The Blakei fauna is clearly recognizable in the Wash boreholes, beds 5–14 (Gallois and Cox 1977). The index species occurs 4 m above the base of the Ampthill Clay, with more strongly ribbed forms a further 4 m above. 12 m of clays with perisphinctids then separate these forms from the first *Amoeboceras*. A similar gap appears to be present in the lower Ampthill Clay of Ampthill, and in Poland and France, although the ranges of *Amoeboceras* are still little known there.

UPPER OXFORDIAN

In the Boreal succession, the principal faunas of *Amoeboceras* allow the Upper Oxfordian to be divided into four Zones: Glosense, Serratum, Regulare, and Rosenkrantzi Zones (Sykes and Surlyk 1976). These Zones may now be subdivided into six Subzones, with the recognition of three further informal horizons.

3. *Glosense Zone*

Index: *Amoeboceras* (*Prionodoceras*) *glosense* (Bigot and Brasil). The protograph of



TEXT-FIG. 4. Map showing the principal outcrops of Middle and Upper Oxfordian in Staffin Bay, Skye.

the holotype, which has been destroyed, is reproduced here as Plate 115, fig. 9. The systematics of this species are discussed fully below.

Definition. Subdivided into Ilovaiskii and Glosense Subzones. Corresponds roughly to the Alternoides Zone of Russian authors, but as there are serious systematic uncertainties attached to the name *Ammonites alternoides* Nikitin, its use as index is best avoided. Its characteristic fauna includes both *Decipia decipiens* (J. Sowerby) and spp., and the Cardioceratidae of the *Trigonia clavellata* Beds of Dorset, so that it is also equivalent to the lower part of the Cautisnigrae Zone of the Sub-Boreal Province as well as the Decipiens Zone of authors, a zone whose supposed position in the succession has oscillated.

3 (*a*). *Ilovaiskii Subzone*

Index: *Amoeboceras* (*Prionodoceras*) *ilovaiskii* (M. Sokolov 1929) (*non* Arkell 1945) (= *A. pseudocaelatum* Spath, 1935, obj.). The protograph of the holotype is reproduced here as Plate 113, fig. 4.

Definition and characteristic fauna. Type-locality Staffin, base near the bottom of bed 31 in the Flodigarry Shale Member. The fauna consists there of *A. ilovaiskii*, *A. transitorium* Spath, *A. newbridgense* sp. nov., *A. shuravskii* (D. Sokolov), *Decipia* sp., and *Perisphinctes* sp. These first faunas of *Amoeboceras* are characterized by dense ribbing on the outer whorl that curves strongly forward giving them a considerable resemblance to *Cardioceras* (late *Scarburgiceras*) of the Cordatum Zone, with which they may be and have been confused in the past when material is not well preserved: the uncertainties attaching to *Ammonites alternoides* are of this kind. Inner whorls are typically those of *Amoeboceras*, however, with straight dense ribbing on fairly flat whorlsides rising to quadrate ventrolateral shoulders.

Distribution. Greenland: higher parts of the Kosmocerasdal Member of Milne Land (Callomon and Birkelund 1979, faunas 9 and 10), in which the specimens reach what is probably normal size, around 60 mm diameter, compared with only about 20 mm in eastern England. Western Scotland: Staffin, 1–2 m. North Yorkshire: found in the discontinuous Newbridge Beds at the base of the Upper Calcareous Grit Formation. The lower part of the overlying Spaunton Sandstone yields a fauna characterized by *A. nunningtonense* Wright (1972), a species only sporadically encountered elsewhere in the Glosense Subzone. Its position is between the well-known faunas of the Sub-Boreal Parandieri Subzone and Cautisnigrae Zone, a position long thought to be represented by a major gap in the classical successions of southern England. To fill this gap Wright (1972) created a Nunningtonense Subzone for the fauna, which includes typical and abundant *Decipia*. The Sub-Boreal scheme of Zones has since had to be modified and the precise arrangement is not resolved, but the Sub-Boreal column is where the Nunningtonense Subzone belongs (see text-fig. 2). In the Boreal succession *A. nunningtonense* is rare and ranges from the upper part of the Ilovaiskii Subzone through possibly to the base of the Serratum Zone. Although this establishes the correlation of the Boreal and Sub-Boreal successions, other species of *Amoeboceras* seem more appropriate as zonal indicators in the Boreal succession. Southern Yorkshire: Melton. Eastern England: the clays of the Lower Ampthill Clay with an assemblage consisting almost only of *Decipia* and *Perisphinctes*, encountered in boreholes round the Wash and in Norfolk (Gallois and Cox 1977, beds 11–14), are followed by a fauna of well-preserved but diminutive *Amoeboceras* (bed 15). They include *A. ilovaiskii*, *A. transitorium*, and *A.* cf. *newbridgense* and constitute the '*A.* aff. *pseudocaelatum* fauna' obtained from temporary exposures at Long Stanton, Cambridgeshire, and recorded by Arkell (1937*a*). U.S.S.R., Moscow basin: a comparable succession is found (Ilovaisky 1904; Nikitin 1916; Sazonov 1957)—beds B–C (2 m) of Miatshkovo with *C. tenuiserratum* and *C.* (*Subvertebriceras*) *zenaidae* Ilovaiskii of the Tenuiserratum Zone are followed by bed D (0.8 m) with *A. ilovaiskii*. *Amoeboceras* of this age is also figured by D. Sokolov (1912) from the Petchora (pl. III, fig. 1).

3 (*b*) *Glosense Subzone*
Index: as for the Zone.

Definition and characteristic fauna. Type section, Staffin: Flodigarry Shale Member, bed 31, 2·95–4·50 m above the base. Besides the index, *A. damoni* Spath and *A. nunningtonense* occur. In Yorkshire the latter prevails in the upper Spaunton Sandstone, but in Skye, where the Subzone is in any case thin, it is not common enough to establish a characteristic horizon. Southwards the perisphinctids of the overlapping Sub-Boreal fauna come in: *P.* (*P.*) aff. *strumatus* Buckman, *P.* (*Arisphinctes*) aff. *osmingtonensis* Arkell, *P.* (*Pseudarisphinctes*) *damoni* Arkell, *Decipia decipiens*, and *D. lintonensis*.

Distribution. Despite its thinness in Scotland and eastern England this is the most widely recognizable Subzone. Greenland: Jacobsstigen Member, Th. Thomsens Land, and Bernbjerg Formation, Wollaston Foreland (Sykes and Surlyk 1976); Milne Land, Pecten Sandstone, especially in its reduced western outcrop (Callomon and Birkelund 1979, fauna 11). Staffin: 1·5 m in bed 31. Yorkshire: Spaunton Sandstone, passing into Ampthill Clay at Melton. Eastern England: Boxworth Rock (Sedgwick Museum). Southern England: remanié and lenticular Upper Calcareous Grit resting on Coral Rag at Cumnor, Oxford (Oxford University Museum, Morris Collection) and near Abingdon (old collections); Steeple Ashton, Wiltshire; and *A. glosense* and *A. damoni* (the type) occur in the *Trigonia clavellata* Beds of the Dorset coast. Normandy: Sables de Glos (the type of *A. glosense*). Hence the Glosense Subzone is equivalent to parts at least of the Cautisnigrae Zone in the south, and the Nunningtonense Subzone in Yorkshire.

4. *Serratum Zone*
Index: *Amoeboceras* (*Prionodoceras*) *serratum* (J. Sowerby). The neotype is refigured here as Plate 117, fig. 1; systematic treatment below.

Nomenclature. The first use of this species as a zonal index was by Davies (1916) to label the beautifully preserved drift assemblage of *Amoeboceras* of eastern England derived from the Ampthill Clay. The position of this assemblage in the succession was not known. It also included large Perisphinctidae of the group of *P. variocostatus* (Buckland) but whether these occurred at precisely the same level as *A. serratum* was not known. Arkell (1937*a*) placed the whole fauna in the Middle Ampthill Clay as a single Variocostatus Zone, to include at the same time the Dorset *T. clavellata* Beds. He subsequently referred to the drift assemblage as the *prionodes* fauna (1947, p. 356), which he thought included *P. variocostatus*, and finally as the *variocostatus* cum *serratum* fauna (1956). Spath (1935) introduced a zone of *Ringsteadia anglica* and *A. serratum* for the Pecten Sandstone of Milne Land.

Definition and characteristic fauna. Subdivided into Koldeweyense and Serratum Subzones. The most typical species are *A. koldeweyense* sp. nov., *A. serratum*, and *A. mansoni* Pringle, characterized by dense straight ribbing on rather flat whorlsides, the ribs accentuated or swelling almost into tubercles at the umbilical margin, at mid height, and at the angular ventrolateral shoulders: innermost whorls and macroconch bodychambers smooth. The type-section of both Subzones is at Staffin where, as now defined, the Serratum Zone is then partly equivalent to the Variocostatus Zone of Anderson and Dunham (1966), the Mansoni Zone of Morris (1968) and the Cautisnigrae and Pseudocordata Zones of Wright (1973).

4 (*a*) *Koldeweyense Subzone*

Index: *Amoeboceras koldeweyense* sp. nov.

Definition. Type-locality Staffin, bed 31, 4·5 m above the base, to bed 33, 3·2 m above base, characterized by the appearance of the distinctive index in which the inner whorls are completely smooth to a much later stage than in other species. The longer-ranging *A. serratum* and *A. mansoni* already occur but as minor elements; also *P.* (*Dichotomoceras*) cf. *bifurcatus*.

Distribution. This new fauna is known principally from Staffin, where it is extremely abundant in the top of bed 31, 10 m above the base of the Flodigarry Shale Member. North-east Greenland: Store Koldewey Ø, Kløft I Formation in part (Ravn 1911). Eastern England: occasional specimens from glacial drift, derived from Ampthill Clay.

4 (*b*) *Serratum Subzone*

Index: as for the Zone.

Definition. Type-section Staffin, bed 33, middle part, 3·2–9·0 m above the base. Characterized by *A. serratum* and *mansoni* as principal elements, without *A. koldeweyense*; less common are *A. shulginae* Mesezhnikov and *A.* cf. *freboldi* Spath, while *A. regulare* Spath and *A. leucum* Spath make their first appearance, although they dominate in the Regulare Zone above. At Staffin *Perisphinctes sp.* and *Euaspidoceras* have also been found. *A. mansoni* dominates there in the upper part of the Subzone and this may be designated an informal *mansoni* horizon.

Distribution. Greenland: Bernbjerg Formation, Wollaston Foreland and Jacobsstigen Member, Th. Thomsens Land (Sykes and Surlyk 1976); upper part of the Pecten Sandstone, Milne Land(?). Scotland: Staffin, 5·8 m. Yorkshire: *A.* aff. *serratum* recorded from the Snape Sandstone (Wright 1972) but the presence of *Ringsteadia* at the same level suggests Regulare Zone. Eastern England: probably about 10 m in the Wash boreholes; elsewhere in the Ampthill Clay of the region, but known almost exclusively from concretions found in glacial drift. Southern England: in the area in which the Middle Oxfordian is developed in Corallian facies, the *serratum* fauna is practically unknown, the most southerly occurrence so far being at Cumnor, near Oxford, or possibly Red Down, Highworth (Arkell 1947, p. 353). The absence most probably reflects the well-known major non-sequences in the Upper Oxfordian. On the Dorset coast the Red Beds at the top of the *Trigonia clavellata* Beds, which define the Cautisnigrae Zone and have yielded *Amoeboceras glosense* of the Boreal Glosense Zone, are separated by some 5 m of Sandsfoot Clay from the next overlying zoneable formation, the Sandsfoot Grit, which yields *Ringsteadia* of the Pseudocordata Zone. The Sandsfoot Clay seems to have yielded no diagnostic ammonites and must therefore still be classed in the Cautisnigrae Zone, but it may well be equivalent to the Serratum Zone of the north. Russia: Petchora (Sokolov 1912, pl. III, fig. 4; Mesezhnikov 1967, pl. 5). Canada: the Serratum Zone can now be recognized in the Fernie Group of the Rocky Mountains and foothills (Frebold *et al.* 1959).

5. *Regulare Zone*

Index: *Amoeboceras* (*Prionodoceras*) *regulare* Spath. The holotype from Novaya Zemlya, is refigured as Plate 118, fig. 9.

Definition. Characterized by moderately evolute, densely, and regularly ribbed *Amoeboceras* resembling spoked wheels, including *A. regulare*, *freboldi* Spath, *leucum* Spath, and *schulginae* Mesezhnikov, and lacking the more discoidal forms with smooth body-chambers of the *A. serratum* group. They represent the next evolutionary stage away from *Cardioceras* towards the *Pleuroceras*-like late forms. Type-locality Staffin, bed 33, about 9·5 m above the base, to the base of bed 35. The thick shales of bed 33 are rather featureless so that the boundary cannot be tied to any easily recognizable marker-bed but has to be located by means of the ammonites.

The Zone is not at present further divisible, but its upper part is characterized by the common occurrence of a new species of *Ringsteadia*, *R. caledonica* sp. nov., which first appears 2·7 m below bed 34, and is the oldest *Ringsteadia s.s.* known from Britain. The upper part of the Zone may therefore be designated the *caledonica* horizon.

Nomenclature. The fauna as found at Skye is strikingly similar to that figured by Mesezhnikov (1967) from Siberia, for which he created a Ravni Zone (1967, 1976) based on *A. ravni* Spath as index, a species defined apparently only by its holotype which came from 'East Coast of Scotland (Shandwick?)'. Re-examination of the outcrops near Shandwick revealed no beds higher than Tenuiserratum Zone (Sykes 1975*a*), so that the position of *A. ravni* remains problematical, and unsuitable as a zonal index.

Distribution. Greenland: Bernbjerg Formation of Wollaston Foreland, 50 m; shales above the Pecten Sandstone of Milne Land; part at least of the Hareelv Formation of southern Jameson Land. Staffin: 6 m. Northern North Sea, Brent-Cormorant fields: borings (Callomon 1975). East England: drift *ex* Ampthill Clay (the type of *A. leucum*). Northern Siberia: Kheta/Boyarka rivers. Novaya Zemlya: the types of *A. regulare* and *freboldi*. Arctic Canada: Mackenzie King Island (*A. freboldi*: Frebold 1961, pl. 3, figs. 2, 3) and northern Yukon (*A. regulare*: Frebold 1977, pl. 3, fig. 6). *Ringsteadia caledonica* sp. nov. is close to *R. flexuoides* (Quenstedt) which occurs in southern Germany and the Jura in the Bimammatum Zone, Hypselum Subzone.

6. *Rosenkrantzi Zone*

Index: *Amoeboceras* (*Prionodoceras*) *rosenkrantzi* Spath. The holotype, from Wollaston Foreland, is refigured as Plate 120, fig. 3.

Nomenclature. New Zone, equivalent at Staffin to the Anglica Zone of Anderson and Dunham (1966) and the Pseudocordata Zone with *A*. aff. *marstonense* of Wright (1973).

Definition. Subdivided into Marstonense and Bauhini Subzones.

6 (*a*) *Marstonense Subzone*

Index: *Amoeboceras* (*Prionodoceras*) *marstonense* Spath.

Definition and characteristic fauna. Marked by the incoming of *A*. *marstonense* and *A*. *rosenkrantzi*, involute compressed forms with accentuated secondary ribs twisting sharply forwards at the ventrolateral shoulder of the whorlside and strongly densely crenulated keels. Type-locality Staffin, bed 35. *R*. *caledonica* still occurs in the lower part, and *R*. *pseudocordata* throughout.

Distribution. Greenland: Bernbjerg Formation, Cardiocerasdal and Rødryggen areas of Wollaston Foreland; Milne Land, shales of the Bays Elv Member above the Pecten Sandstone; Southern Jameson Land, Hareelv Formation (Spath 1935, pl. 13, fig. 5). Scotland: Staffin, 6 m. Southern England: Marston, near Swindon in ironstones similar to those of Westbury (the type of *A*. *marstonense*, and associated fauna of *Ringsteadia pseudoyo*). Canada: Mackenzie King Island (Frebold 1961).

6 (*b*) *Bauhini Subzone*

Index: *Amoeboceras bauhini* (Oppel).

Definition. Characterized by the incoming of diminutive species of the group of *A*. *bauhini*, including *A*. *praebauhini* Salfeld and *A*. *tuberculatoalternans* (Nikitin), in which the ribbing tends to bend backwards on ascending the whorlside before twisting sharply forward at the ventro-lateral shoulders. *A*. *rosenkrantzi* persists, as does *Ringsteadia* cf. *pseudocordata*. Type-locality Staffin, beds 36–37.

Distribution. Greenland: shales and glauconites above the Pecten Sandstone of Milne Land. Scotland: Staffin, 5·5 m, the only locality at which the Subzone has so far been clearly characterized. Southern England: characteristic ammonites occasionally found in beds of the Pseudocordata Zone, although rare. Southern Germany: the type of *A*. *bauhini*, from '*β*-Kalke' of Hundsrück, precise age not known, but probably from the Planula Zone. Russia: Petchora.

Correlation of the Rosenkrantzi Zone. There is considerable overlap in both provinces between Boreal *Amoeboceras* and Sub-Boreal *Ringsteadia*, so that a closer correlation should be possible at this level. Although continuous sections in southern England are almost non-existent it is evident that the Pseudocordata Zone encompasses a succession of distinguishable *Ringsteadia* faunas. These are (*a*) the fauna from the Upper Calcareous Grit of Marston, north-east of Swindon, which yields mainly the involute disc-like forms of the group of *R*. *pseudoyo* Salfeld and *A*. *marstonense*;

(*b*) the fauna of the Westbury Ironstone, with giant, moderately evolute but compressed forms of the group of *R. pseudocordata*, various other perisphinctids, but apparently no *Amoeboceras*; and (*c*) the fauna of the Ringstead Coral Bed, with *R. evoluta* and *A.* cf. *bauhini*. The *Ringsteadia* species of fauna (*b*) are also found in the Sandsfoot Grit of Dorset, where they are associated with *A.* cf. *rosenkrantzi*. These three faunas are the basis of a subdivision of the Pseudocordata Zone proposed by Morris (1968), who placed the Pseudoyo Subzone above the Pseudocordata Subzone because he found a specimen of *R. pseudoyo* between Sandsfoot Grit and Ringstead Coral Bed near Ringstead. The position of *A. marstonense* in the succession at Staffin suggests that the Marstonense Subzone is equivalent to both Pseudoyo and Pseudocordata Subzones of the Pseudocordata Zone, but the material of *Ringsteadia* from Staffin is not sufficient to establish the order of the Subzones independently. The occurrence of *R. caledonica* in the top part of the Regulare Zone of Staffin indicates that the *Ringsteadia* species of the Sandsfoot Grit, the lowest in Dorset, are not the oldest, and that there is a faunal non-sequence there.

KIMMERIDGIAN

From the base of the Kimmeridgian upwards the distinction between Boreal and Sub-Boreal Provinces becomes blurred as the Pictoniinae spread northwards. A common zonal scheme based on *Pictonia*, *Rasenia*, and *Aulacostephanus* has been widely used. The Kimmeridgian Stage is defined by its lowest Zone, the Baylei Zone, stratotype at Ringstead, Dorset, in the *Rhactorhynchia inconstans* Bed (Arkell 1947*a*, p. 44, bed 26). This bed can be correlated precisely with the easily recognizable base of bed 38 in the Staffin section. The base of the Baylei Zone is used formally to 'close' the Boreal Upper Oxfordian by defining the base of the Kimmeridgian Stage at the same level in both Boreal and Sub-Boreal Provinces. The common forms of *Pictonia* found in the *R. inconstans* Bed both in Dorset and around Swindon are *P. densicostata* (Salfeld MS.) Buckman 1925, pl. 533, not *P. baylei* Tornquist, which is a member of the slightly younger fauna of 'degenerated perisphinctids' with characteristic irregular ribbing described by Tornquist (1896) and usually referred to under the name *P. normandiana* Tornquist. Provincial separation from the Sub-Mediterranean Province persists into the Kimmeridgian. Although the base of the Sub-Mediterranean Kimmeridgian is taken conventionally to lie at the top of the Planula Zone, the precise correlation of this level with that of the type succession remains open and may be uncertain by as much as a whole ammonite Zone.

SYSTEMATIC DESCRIPTIONS

Species definitions. The zonation of the Boreal Oxfordian is based on the evolutionary steps of one family, the Cardioceratidae, with two genera, *Cardioceras* and *Amoeboceras*. The former has been monographed repeatedly and needs no further discussion: the basis for reference is the work by Arkell (1935–1948). The latter genus has been described so far only piecemeal, the principal difficulty lying in the lack of reliable stratigraphy.

In deciding the taxonomic principles to be followed, the choice is between 'horizontal' and 'vertical' classifications. In the former, to be successful one needs collections level by level large enough to assess variability of a probable biospecies. Given sufficient stratigraphic refinement, successive biospecies would be seen to change subtly as a whole; and any recognizable change in successive populations can be reflected in the nomenclature, be it at specific level, or chronologically subspecific level, or even by a chronologically serial index, e.g. α, β, . . . There is then considerable morphological overlap between successive populations, and this raises the practical problem in attempting to identify new material, say from a new locality: any single specimen might qualify for one of several names, depending on its precise age. But to determine the age is usually the purpose of trying to name it! In a vertical classification a nominal taxon is defined purely morphologically. The field-information is plotted as a range-chart, constantly changing as new material is discovered. A population at one level may then be broken up into an assemblage of morphospecies, which may seem artificial and unnatural, but makes it possible to communicate new information and to identify new material before trying to decide its precise age. At the same time, the morphological range of what one thinks to have been a biospecies at any one level may be expressed by reading off the names of the morphospecies recorded at that level on the range-chart. In the genus *Amoeboceras* attempts to classify horizontally are particularly difficult, for intraspecific variability seems to be unusually large. Dimorphism is not always clearly discernible (see below), and there is a tendency towards repeated close homoeomorphy over a restricted range of morphologies. Small collections, particularly of microconchs, from scattered localities are hard to identify. Despite all the new information that has been obtained, most of our material is still of this kind. The number of collections of Upper Oxfordian *Amoeboceras* from single horizons numerous and well-preserved enough to attempt a biospecific analysis of variability is perhaps three: faunas 9 and 11 from the Glosense Zone of Milne Land, eastern Greenland, and the fauna of the Koldeweyense Subzone of Staffin. The only fauna with extensive and well-preserved material is that of the *A. serratum* group from the glacial drift of eastern England, but it is probably not all of the same age. Nor is this peculiar to *Amoeboceras*: despite the extensive previous treatments, the classification of *Cardioceras* is also essentially vertical. It is still too early for a comprehensive treatment of *Amoeboceras*, and certainly beyond the present paper. We follow an essentially vertical, 'conventional' classification for the time being, and confine ourselves to a review of those selected aspects relevant to the stratigraphy.

Superfamily STEPHANOCERATACEAE Neumayr, 1875
Family CARDIOCERATIDAE Siemiradzki, 1891
Subfamily CARDIOCERATINAE Siemiradzki, 1891
Genus AMOEBOCERAS Hyatt, 1900

Type species. Ammonites alternans von Buch, 1831. A number of additional generic names are available for members of this group. Whether adequate or useful depends on the taxonomic principles to be followed. For the present purposes it suffices to treat the existing names as all subgeneric within the single genus *Amoeboceras*. Those based on Oxfordian species are as follows:

Amoeboceras Hyatt, 1900, *s.s.*

Type species. Ammonites alternans von Buch, 1831. Small strongly-ribbed microconchs still resembling *Vertebriceras* of the Lower Oxfordian; discussed further below. Bifurcatus or Bimammatum Zones of Germany and the Jura.

Prionodoceras Buckman, 1920

Type species. Prionodoceras prionodes Buckman, 1920. Large macroconchs becoming smooth on the adult bodychamber. Subj. syn. of *Amoeboceras serratum* (J. Sowerby) discussed further below, q.v. Suitable for all macroconchs of the Upper Oxfordian; type-species from the Serratum Zone.

Plasmatites Buckman, 1925

Type species. Plasmatites crenulatus Buckman, 1925. Small microconchs with dense straight wiry ribbing, of the group of *A. bauhini* (Oppel). The type came from Wiltshire, exact locality not known, and may be

Kimmeridgian, Baylei Zone, although latest Upper Oxfordian cannot be ruled out. Neither generic nor specific names have been used since their creation, although they may become useful for members of the *bauhini* group when better understood. The relation between *Plasmatites* and homoeomorphic Lower Oxfordian *Plasmatoceras* has been already discussed above (p. 847). No attempt will be made in what follows to assign species systematically to subgenera.

Dimorphism. Like the rest of the Cardioceratidae, *Amoeboceras* is in general strongly dimorphic. To pick out macro- and microconch partners is not easy because of the considerable variability of the dimorphs. A satisfactory pairing will have to await the collection of much more material at almost every level. No attempt will be made to try to introduce a consistent and comprehensive taxonomy in either of the two systems at present in use. If separate specific names already exist for what may well be simply dimorphic partners, they will not necessarily be united. New names will not be introduced for the other member of what is thought to be a dimorphic pair, in which only one has been so far named. The dimorphic status of a specimen, or morphospecies as defined by its type specimen, may, however, be indicated by the symbols [m] or [M] as usual.

List of species. The following forty-nine species of *Amoeboceras*, listed alphabetically, have been recorded from beds probably of Upper Oxfordian age. The order of species in the systematic part essentially follows stratigraphical succession.

A. alternans (v. Buch, 1831).
A. alternoides (Nikitin, 1878) (p. 147) (possibly a Lower–Middle Oxfordian *Cardioceras*).
A. arkelli Mesezhnikov, 1967 (p. 115) (*nom. nov. pro A. ilovaiskyi* Arkell, 1945, p. 350, *non* Sokolov, 1929).
A. bauhini (Oppel, 1863).
A. crenulatum (Buckman, 1925) (pl. 618) (possibly Lower Kimmeridgian).
A. damoni Spath, 1935.
A. dorsoplanatum (Rouillier, 1849) (p. 364, pl. L, fig. 88).
A. excentricum (Buckman, 1924) (pl. 464).
A. franconicum Spath, 1935 (p. 15) (*pro Cardioceras excavatum*, Dorn, 1930, pl. 19 (35), fig. 2*a*, *b*).
A. freboldi Spath, 1935.
A. glosense (Bigot and Brasil, 1904).
A. grumanticum (D. Sokolov, 1931) (in Sokolov and Bodylevsky 1931, p. 87, p. 16, fig. 4).
A. ilovaiskii (M. Sokolov, 1929) (= *A. pseudocaelatum* Spath, 1935, obj.) (*non* Arkell, 1945).
A. koldeweyense sp. nov.
A. leucum Spath, 1935.
A. lineatum (Salfeld, 1915) (p. 182; lectotype pl. 17, fig. 10*a–d* here designated; = *Ammonites alternans lineatus* Quenstedt, 1887, pl. 91, fig. 23 refigured).
A. lorioli (Oppenheimer, 1907) (p. 239, pl. 21, fig. 3).
A. mansoni Pringle, 1936.
A. marchense Spath, 1935 (= *Cardioceras* aff. *excavato*, Crick, 1898, pl. 18, figs. 9–10; an isolated [m] from glacial drift).
A. marstonense Spath, 1935.
A. neischli (Dorn, 1916) (p. 101, text-fig. 3; refigured by Dorn, 1930, pl. 18 (34), fig. 28).
A. newbridgense sp. nov.
A. novosselkense (Davitashvili, 1926) (p. 286, pl. 5, figs. 1, 2).
A. nunningtonense Wright, 1972.
A. ovale (Quenstedt, 1845) (p. 96, pl. 5, fig. 8).
A. pectinatum Mesezhnikov, 1967 (p. 124, pl. 4, fig. 2).
A. pinguis (Rouillier, 1849) (p. 362, fig. 109).
A. praebauhini (Salfeld, 1915) (p. 178; lectotype, pl. 17, fig. 5 designated here. IGS 26054, ex drift, Norfolk).
A. prionodes (Buckman, 1920) (pl. 155).
?*A. quadratolineatum* (Salfeld, 1915) (p. 186; = *Ammonites alternans quadratus* Quenstedt, 1845, pl. 5, fig. 7, refigured by Salfeld as pl. 17, fig. 22).
A. quadratum (J. Sowerby, 1813) (p. 52, pl. 17, fig. 3. Discussed by Arkell 1948, p. 394).
A. rasoumowskii (Rouillier, 1849) (p. 360, pl. L, fig. 90).
A. ravni Spath, 1935 (p. 17, pl. 4, fig. 4. Mentioned above, p. 855).

A. reclinatoalternans (Nikitin, 1916) (p. 41, pl. 2, fig. 14).
A. regulare Spath, 1935.
A. reichenbachense (Salfeld, 1915) (p. 172, pl. 17, fig. 2).
A. rosenkrantzi Spath, 1935.
A. schlosseri (Wegele, 1929) (p. 33 (127), pl. 28 (4), fig. 8).
A. serratum (J. Sowerby, 1813).
A. schulginae Mesezhnikov, 1967.
A. shuravskii (D. Sokolov, 1912).
A. simplex Spath, 1935 (p. 22; = *Cardioceras bauhini*, Nikitin 1916, pl. 1, fig. 8) (*non* Mesezhnikov and Romm, 1973, = *A. mesezhnikovi* Sykes and Surlyk, 1976, *nom. nov.*).
A. subcordatus (d'Orbigny, 1845) (p. 434, pl. 34, figs. 6, 7).
A. superstes (Phillips, 1871) (p. 332, pl. 15, fig. 21).
A. transitorium Spath, 1935.
A. transversum (Quenstedt, 1887) (p. 826, lectotype, designated here, pl. 91, fig. 11; refigured Salfeld 1915, p. 170, pl. 17, fig. 1).
A. truculentum (Buckman, 1927) (pl. 704).
A. tuberculatoalternans (Nikitin, 1878).

Location of specimens. The repository of specimens is indicated by the following abbreviations:

BM	British Museum (Natural History), London. BM/RMS: R. M. Sykes collection, now in the BM
BU	Geology Department, University of Birmingham
ETH	Eidgenössische Technische Hochschule, Zürich
GGU	Geological Survey of Greenland collections, Copenhagen
GSC	Geological Survey of Canada collections, Ottawa
IGS	Institute of Geological Sciences collections, London
IGSE	Institute of Geological Sciences collections, Edinburgh
JHC	J. H. Callomon collection, 1957–8
JKW	J. K. Wright collection, Chelsea College, London
MGUH	Geological Museum of the University of Copenhagen (formerly MMH)
OUM	Oxford University Museum
RMS	R. M. Sykes collection
RS	Riksmuseum, palaeontological collections, Stockholm
WM	Woodend Museum, Scarborough

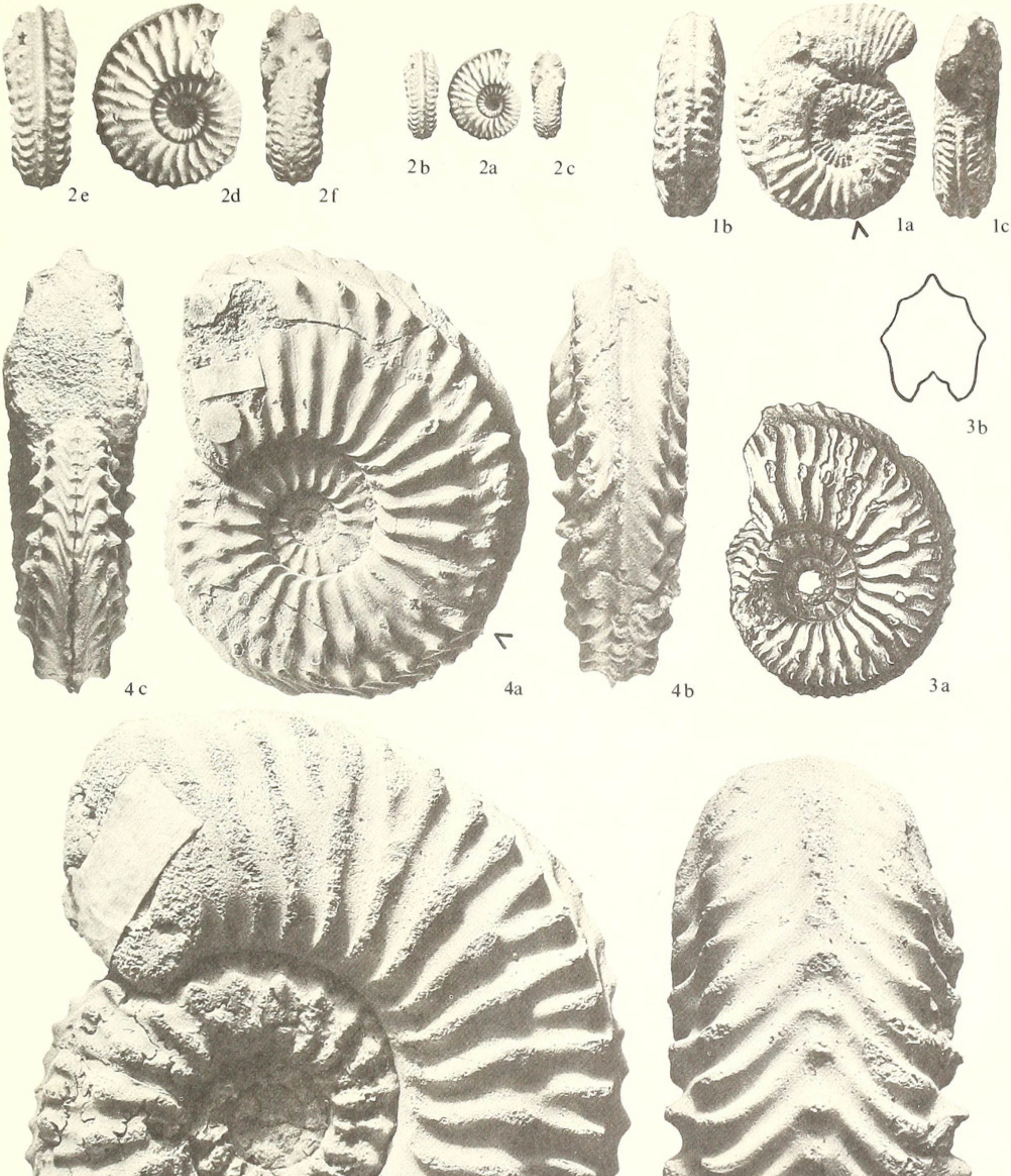
Measurement of dimensions. D, diameter (mm); Wh, Wb, whorl-height and breadth as fractions of D; Ud, umbilical diameter as fraction of D; P, number of primary ribs per whorl. S/P, ratio of secondary to primary ribs.

EXPLANATION OF PLATE 112

Figs. 1, 2. *Amoeboceras* (*Amoeboceras*) *alternans* (von Buch) [m]. 1, neotype, White Jura α, Lochen, near Balingen, Swabia. Complete adult, natural size. (Tübingen, Quenstedt Coll. 1887, pl. 91, fig. 6; Salfeld, 1915, pl. 16, fig. 6. Photo: courtesy J. Wendt.) 2, former syntype, White Jura α, Stuifenberg, near Göppingen, Swabia. (von Buch Coll., Humboldt Museum, Berlin, HUB.C.448.1.) 2*a*–*c*, natural size; 2*d*–*f*, ×2.

Figs. 3, 4. *Cardioceras* (*Subvertebriceras*) *densiplicatum* Boden [m]. 3, lectotype, from Popilani, Lithuania (Boden, 1911, pl. 1, fig. 14). 4, typical complete adult from near Oxford, with test largely preserved (OUM J4069; previously figured by Arkell 1942, pl. 52, fig. 4*a*, *b*).

Fig. 5. *Cardioceras* (*Vertebriceras*) *vertebrale* (J. Sowerby) [m]. Holotype, Marcham, near Abingdon, Berks. (OUM J3000). Short arrows here and subsequently mark the onset of bodychamber. Note the uncoiling umbilical seams in the adults of figs. 1, 4, and 5.



SYKES and CALLOMON, *Amoeboceras*, *Cardioceras*

Amoeboceras alternans (v. Buch, 1831)

Plate 112, figs. 1, 2

1831 *Ammonites alternans* von Buch, pl. 7, fig. 4 (two figures) and text in legend.
1858 *Ammonites alternans* von Buch; Quenstedt, pl. 73, fig. 10.
1887 *Ammonites alternans* von Buch; Quenstedt, pl. 91, figs. 6, 14.
1895 *Ammonites alternans* von Buch; Woodward, p. 155, fig. 68 (= von Buch's figures redrawn).
1915 *Cardioceras alternans* (von Buch); Salfeld, p. 161 (synonymy partim), pl. 16, figs. 3, 4 (= von Buch's figured specimen refigured), 6, 7 (= Quenstedt 1887, figs. 6, 14 refigured).
1931 *Cardioceras alternans* (von Buch); Dorn, p. 81, pl. 19 (35), fig. 5 (*non* 3, 4).
1931 *Cardioceras subcordatum* (D'Orb.); Dorn, p. 79, pl. 19 (35), fig. 7 (*non* 6).
1957 *A.* (*Amoeboceras*) *alternans* (von Buch); Arkell, p. L306, fig. 375.5 (= Quenstedt 1887, fig. 6 refigured).
1977 *Amoeboceras alternans* (von Buch); Ziegler, pl. 1, fig. 7.

Type series. Von Buch's text cites the species as 'common in S. Germany, from Bamberg (Franconia) to Switzerland'. His collection contains numerous specimens, all nuclei, from Streitberg in Franconia, and Stuifenberg and Lochen near Balingen in Swabia. The original description was accompanied by two figures of what seemed to be a single specimen seen in side and ventral views, said to be from Lochen. However, Salfeld (1915) concluded that the figures were probably based on two specimens, both of which he refigured photographically. Moreover, the locality cited originally seemed to be in error, for the specimens in question carried a label in von Buch's handwriting stating 'Streitberg', a locality also favoured by matrix and preservation. No lectotype was ever designated. The first modern reviser of the species was Salfeld. The name *alternans* had come to be applied to a wide range of forms of varying ages, far from the type locality. It had become synonymous with what would now be called *Amoeboceras* from the Upper Oxfordian. There are two main difficulties: the inadequacy of the remaining type material, barely identifiable nuclei, unsupported by any subsequent better topotypes; and uncertainties of stratigraphy. Moreover, von Buch's syntypes themselves included several species, so that a restricted interpretation of the species could vary according to the lectotype chosen. Guided by the traditional German view of the species, Salfeld divided von Buch's syntypes into two groups: one of three specimens (including the two thought to be the basis of von Buch's figure) for which the name *alternans* was retained, the other included at least seven specimens from Streitberg and Lochen, which were identified as belonging to *Ammonites ovalis* Quenstedt, 1845. This restricted interpretation has been widely followed, and indicates that the lectotype should be selected from the first group.

EXPLANATION OF PLATE 113

Fig. 1. *Cardioceras* (*Maltoniceras*) *maltonense* (Young and Bird) [M]. Neotype, Highworth Limestones, Highworth, Wilts. The last septa are approximated. (Arkell Coll., OUM J2983.)

Fig. 2. *C.* (*Miticardioceras*) *tenuiserratum* (Oppel) [m]. Lectotype, Birmensdorfer Schichten, Birmensdorf, Aargau. No sutures are visible, but part at least of the outer whorl is bodychamber. (Moesch Coll., ETH Zürich, Ve S.4; Oppel, 1863, pl. 53, fig. 2*a–c*.)

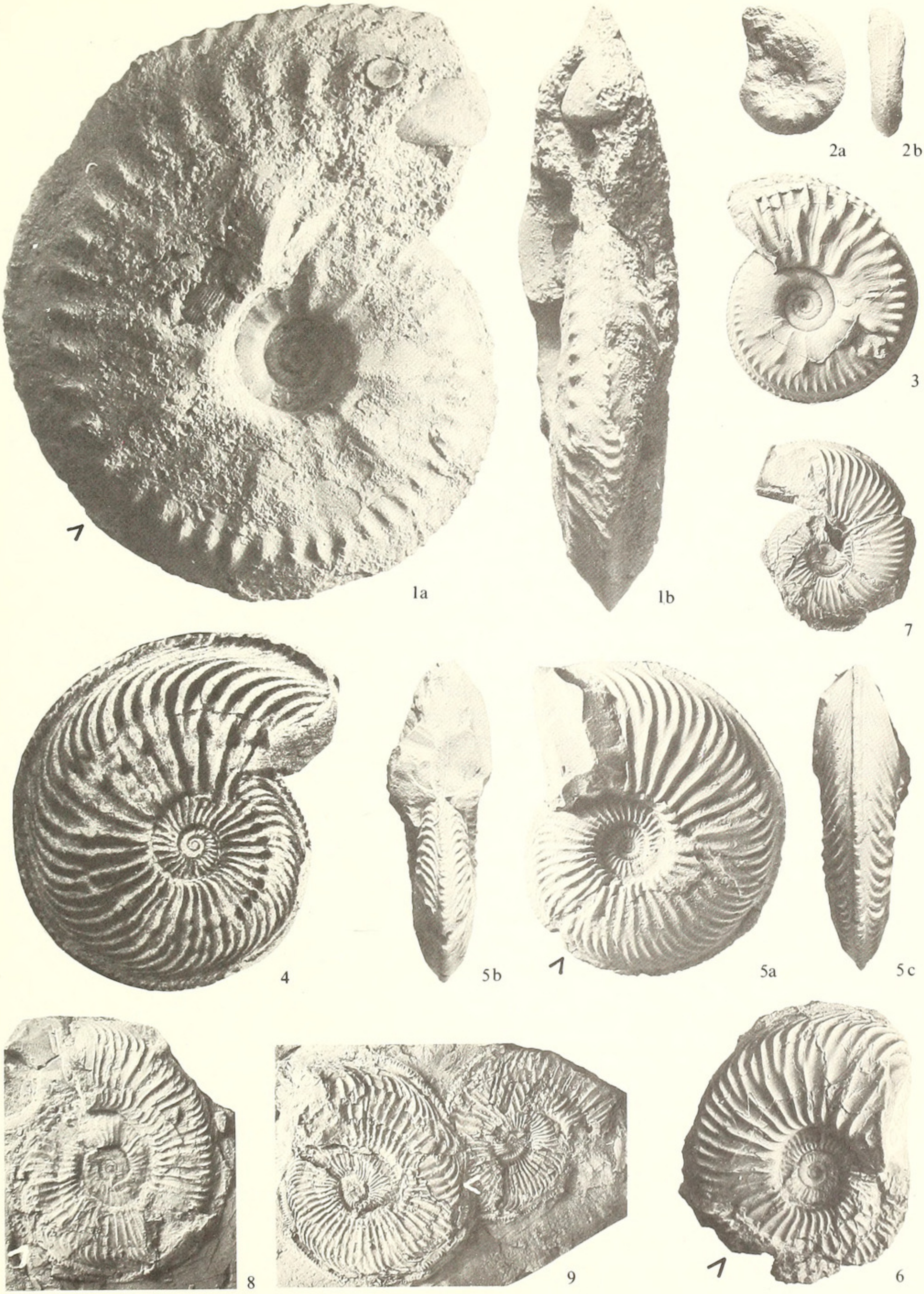
Fig. 3. *C.* (*Cawtoniceras*) *blakei* Spath [m]. Holotype; cast of an impression in a calcareous concretion from glacial drift ex Ampthill Clay. Complete adult with some of the final peristome preserved (IGS 72203).

Fig. 4. *Amoeboceras ilovaiskii* (M. Sokolov) [M]. Protograph of holotype, from near Moscow (Ilovaisky 1904, pl. 11, fig. 7; slightly enlarged).

Figs. 5–7. *A. glosense* (Bigot and Brasil). Fauna from a layer of concretions at Melton, North Humberside. 5, juvenile [M] with test preserved on inner whorls (F. Whitam Coll., Hull; cast in BM). 6, idem (RMS/BM C.80413). 7, adult [m] with half a whorl bodychamber (RMS/BM C.80414).

Fig. 8. *A. nunningtonense* Wright [m]. Staffin, Flodigarry Shale Member, bed 31, 3·5 m above the base, boundary between Ilovaiskii and Glosense Subzones (RMS/BM C.80411).

Fig. 9. *A.* cf. *glosense* (Bigot and Brasil) [m]. Fine-ribbed variety. Staffin, bed 31, 3·0 m above the base (RMS/BM C.80412).



SYKES and CALLOMON, *Amoeboceras*, *Cardioceras*

Unfortunately, the two syntypes figured by von Buch and Salfeld appear to be lost. The collections at the Humboldt University were searched by Dr. J. Helms in 1974, who reported that only the third syntype assigned to *A. alternans* by Salfeld (1915, p. 164) survives, a nucleus 14 mm in diameter, from Stuifenberg. It is figured here on Plate 112, fig. 2. It is inadequate to define a species, lacking any part of the adult stage on which taxonomy now heavily depends. Were it now selected as lectotype, following the *Rules*, the interpretation of this species would be permanently in doubt. A neotype would be excluded as long as a syntype continued to exist. The relevant clauses in Art. 75 have been somewhat ambiguous, with a strong presumption (in 75 (c) (3)) that a neotype is ruled out unless 'all of the original type-material . . . be lost or destroyed'. The Secretary of the Commission (Mr. R. V. Melville) has informed us that the wording of this Article will be amended in a proposed new version of the *Rules* (see Melville 1977). This will state that when a lectotype has been designated out of an original type-series all the remaining members of that series automatically cease to have any special status beyond that also tenable by other specimens not originally syntypes, e.g. topotypes. Should the lectotype be subsequently lost, no special attention need be paid to any surviving specimens originally members of the type-series in looking for a neotype.

We therefore propose the following solution to the problem of *A. alternans*:

Lectotype. The syntype figured by Salfeld (1915) as Plate 16, fig. 3*a*, *b*, presumed to be the basis at least in part of the figure given by von Buch; now presumed lost. Hence, all other syntypes may be stripped of status. *Proposed Neotype*. The specimen in the Quenstedt Collection (1887, pl. 91, fig. 6) in Tübingen, refigured by Salfeld (1915, pl. 16, fig. 6) and Arkell (1957, *Treatise*). It is refigured on Plate 112, fig. 1*a*–*c*. It is a complete adult, 31 mm in diameter, a typical microconch, from Lochen. It clearly shows the specific characters: small size; evolute, quadrate, moderately inflated whorl-section; coarse ribbing, biplicate or with alternating simple flexuous primary and intercalatory secondary ribs, resembling *Vertebriceras* of the Lower Oxfordian; and a fully differentiated and finely crenulate keel.

We propose to take this case to the ICZN for final validation.

Age and distribution. The exact age of *A. alternans* in southern Germany remains somewhat uncertain. Most of the material in the collections comes from soft marls ('Impressa-Mergel') of the White Jura and in successions that tend to be obscured by slumping of overlying harder limestones or disturbed by the presence of diapir-like calcareous reefs. The biofacies of the marls are somewhat peculiar, with restricted faunas, among which the ammonites are relatively rare and almost always preserved only as nuclei, which are not closely datable. Many authors seem agreed that the two species *A. alternans* and *A. ovalis* occur in succession across the α/β boundary. This boundary is probably a lithological one and diachronous, but in places in which the lowest β beds have yielded ammonites they seem to establish that *A. ovalis* occurs in the Hypselum Subzone of the Bimammatum Zone (Dorn 1930–1931). The age of *A. alternans* is thus probably Bifurcatus Zone. Attempts to recognize the species further afield have met with two difficulties. Either specimens that resemble the types are similarly well preserved but came from beds also of uncertain ages (Moscow, Petchora); or they occur in Boreal clay facies, are crushed flat (Britain), and have been recorded under a different name. A specimen that seems close is shown here on Plate 116, fig. 8 as *A. glosense* [m], from the Pecten Sandstone of Milne Land, eastern Greenland, Glosense Subzone of the Glosense Zone; and as the general resemblance of *A. ovale* is to the microconchs of the overlying *A. serratum*, the succession *A. alternans*—*A. ovale*, Bifurcatus—Hypselum Zones of the Sub-Mediterranean Province may have its equivalents in the succession *A. damoni/glosense* [m]—*A. serratum* [m], Glosense—Serratum Zones in the Boreal Province (text-fig. 2). It seems safest, however, to restrict the use of the names *alternans* and *ovale* to the more southerly province for the time being.

Amoeboceras ilovaiskii (M. Sokolov, 1929)

Plate 113, fig. 4; Plate 114, fig. 5; Plate 115, fig. 8

1904 *Cardioceras* cf. *alternans* (von Buch); Ilovaisky, p. 272, pl. 11, fig. 6 (refigured here, Pl. 113, fig. 4).
1929 *Cardioceras ilovaiskii* M. Sokolov, p. 29.
1935 *Amoeboceras* (*Prionodoceras*) *pseudocaelatum* Spath 1935, p. 19 (= *Cardioceras ilovaiskii* M. Sokolov, obj.).
1937*a* *Amoeboceras* aff. *pseudocaelatum* Spath; Arkell, p. 65, pl. 3, figs. 6, 9.
1957 *Cardioceras ilovaiskii* M. Sokolov; Sazonov, p. 137, pl. 18, fig. 2.

Type material. Holotype (monotype) figured by Ilovaisky (1904); Moscow, Miatchkovo, bed D.

Dimensions. Holotype: D 54·0, Wh 0·45, Ud 0·24, P 31; Arkell 1937*a*, pl. 3, fig. 9: D 15·3, Wh 0·40, Wb 0·29, Ud 0·33, P 31.

Diagnosis. Small to medium-sized *Amoeboceras* with rectiradiate primary ribbing. Lateral tubercles feeble or absent and secondaries strongly projected forward from the furcation point. Umbilical and ventro-lateral tubercles absent.

Description. The holotype is quite distinctive with rather straight primaries ending in small tubercles half-way up the whorl-side. Bifid secondaries appear above the tubercles and are slightly weaker at their bases. They immediately project evenly but strongly forward in a characteristic manner. In small specimens from eastern England the secondary ribs are also very fine.

Discussion. Ilovaisky's original figure was renamed *Cardioceras ilovaiskii* by M. Sokolov in 1929. Spath (1935), unaware of Sokolov's paper, added a second new name for the same specimen, *A. pseudocaelatum*, which must now lapse. Subsequently Arkell (1945*a*) created *A. ilovaiskyi* as a new species based on Ilovaisky's plate 11, fig. 7. This is thus a junior homonym of *A. ilovaiskii* (M. Sokolov) and has been renamed *A. arkelli* by Mesezhnikov (1967). Arkell (1937*a*) referred all the small Long Stanton microconchs to *A. ilovaiskii*, but on re-examination of the material *A.* cf. *transitorium* and *A. newbridgense* are also present. The rare macroconchs, identified by him as *A. truculentum*, show much more projected ribbing on the outer whorl and may also belong to *A. ilovaiskii*. In the Moscow area *A. ilovaiskii* occurs in bed D1 of Ilovaisky (1904), immediately above beds with abundant *C.* (*M.*) *tenuiserratum*. This situation is strongly reminiscent of the succession both at Staffin and in eastern England.

Range. A. ilovaiskii characterises its Subzone but may range up into the lower part of the Glosense Subzone.

Distribution. Eastern England: Ampthill Clay (Long Stanton; North Wooton and Gedney boreholes). Yorkshire: Newbridge Beds (Laysthorpe Quarry); Spaunton Sandstone (Newbridge Quarry). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Central East Greenland: Milne Land, fauna 9 (GGU 137845, 234051). U.S.S.R.: Novosselki near Moscow.

Amoeboceras shuravskii (D. Sokolov)

Plate 114, fig. 6

1912 *Cardioceras shuravskii* D. Sokolov, p. 37, pl. 2, figs. 4–6 [M].
1912 *Cardioceras* cf. *quadratoides* Nikitin; D. Sokolov, p. 39, pl. 2, figs. 7–8 [m].
1916 *Cardioceras alternans* var *f* Nikitin, p. 8, pl. 1, fig. 3 [m].
cf. 1966 *Amoeboceras subcordatum* (Salfeld, *non* d'Orbigny); Malinowska, pl. 2, fig. 6 [m].
1972 *Amoeboceras* sp. Wright, pl. 13, figs. 2–3; pl. 14, fig. 1 [m?].

Type material. Sokolov (1912) does not indicate a holotype, but his plate 2, fig. 4 [M], from the Petchora, was designated lectotype by Mesezhnikov (1967, p. 125).

Dimensions	D	Wh	Wb	Ud	P
Lectotype	103	0·47	0·34	0·21	—
Sokolov 1912, pl. 2, fig. 8	35	0·41	0·37	0·28	
Nikitin 1916, pl. 1, fig. 3	42	0·40	0·30	0·30	22
Wright 1972, pl. 13, fig. 3	52	0·40	—	0·30	31

Diagnosis. Medium-sized *Amoeboceras* with strong, low-density ribbing. Primaries rectiradiate or slightly prorsiradiate, bifid secondaries turn gently forward from faint lateral tubercles. No umbilical or ventro-lateral tubercles.

Description. *A. shuravskii* shows a quadrate section. The inner and middle whorls are strongly ribbed with no sign of a smooth inner stage. The strong primaries are slightly prorsiradiate and follow a straight to slightly flexuous course until they are raised into faint lateral tubercles two-thirds of the way across the whorl-side. From here bifid secondaries are projected forward. On the outer whorl of macroconchs the ribbing fades and becomes more strongly projected near the smooth or faintly striate body chamber.

Discussion. The low-density projected ribbing differentiates *A. shuravskii* from *A. transitorium*, and it does not have the angular secondaries of *A. glosense*. Macroconchs differ from *Amoeboceras* of the *serratum* group in the absence of trituberculate middle whorls and the greater projection of the secondaries on the outer whorl. *A. shuravskii* is easily recognized by its bold, spaced ribbing. It is the earliest species of *Amoeboceras* at Staffin appearing in the lower part of bed 31 of the Flodigarry

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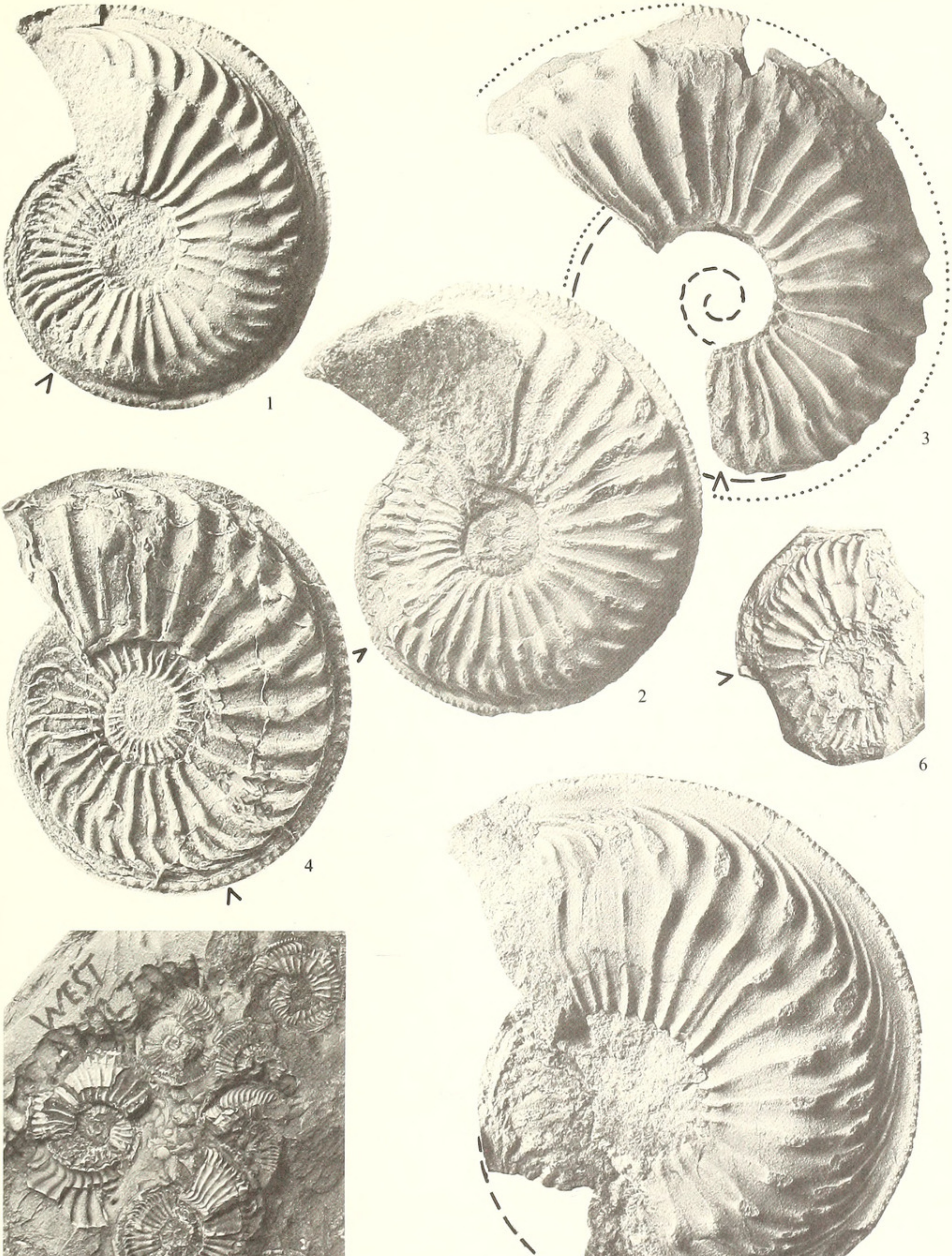
EXPLANATION OF PLATE 114

Figs. 1–4. *Amoeboceras transitorium* Spath [m]. Topotypes, Ilovaiskys Dal, Milne Land; upper Kosmocerasdal Member, Kap Leslie Formation (Callomon and Birkelund 1979, fauna 9). 1, typical variant with test and hence keel preserved on the bodychamber (JHC/TB Coll. 1977; MGUH 14775). 2, involute variant (RMS/BM C.80409). 3, 4, coarse-ribbed variants with prominent mid lateral tubercles (RMS/BM C.80408 and JHC 1683).

Fig. 5. *A. ilovaiskii* (M. Sokolov) [M]. Horizon and locality as figs. 1–4 (JHC/TB Coll. 1977; MGUH 14774).

Fig. 6. *A.* cf. *shuravskii* (D. Sokolov) [m]. Staffin, bed 31, 1·0 m above the base; Ilovaiskii Subzone (RMS/BM C.80410).

Fig. 7. *A. newbridgense* sp. nov. [m] (arrow) and sp. cf. *ilovaiskii* [m] (small nuclei). Ampthill Clay, West Walton Highway borehole, Norfolk (Gallois and Cox 1977, bed 15; p. 217, Bh 3C; IGS FR 1398). (Photos: figs. 1, 5, courtesy J. Aagaard, Copenhagen; 7, IGS.)



SYKES and CALLOMON, *Amoeboceras*

Shale Member (see text-fig. 3). Similar forms occur in the middle of bed 31, but show low-density keel serrations and well-spaced primary ribbing characteristic of *C.* (*Cawtoniceras*) *blakei* and *C.* (*C.*) *ogivale* (S. Buckman).

Range. A. shuravskii is most abundant in the Ilovaiskii Subzone, but ranges up into the basal Glosense Subzone.

Distribution. Yorkshire: Spaunton Sandstone (Laysthorpe and Newbridge Quarries, JKW, BM/RMS). Scotland: Flodigarry Shale (Staffin, BM/RMS). U.S.S.R.: Moscow area; Petchora basin; Siberia. Poland: Miedzychod borehole.

Amoeboceras transitorium Spath

Plate 114, figs. 1–4

cf. 1916 *Cardioceras alternans* var *e* Nikitin, p. 8, pl. 1, fig. 4.
1935 *Amoeboceras* (*Prionodoceras*) *transitorium* Spath, p. 17, pl. 1, fig. 8 [M].
1935 *Amoeboceras* (*Prionodoceras*) aff. *pseudocaelatum* Spath, p. 19, pl. 2, fig. 4 [m].
cf. 1937*a* *Amoeboceras* aff. *pseudocaelatum* Spath; Arkell, p. 65, pl. 3, figs. 7, 10, 12.
cf. 1966 *Amoeboceras ovale* (Quenstedt); Malinowska, p. 795, pl. 1, fig. 2a [m].

Type material. Holotype in the Mineralogisk Museum, Copenhagen, MGUH 231, from Milne Land, East Greenland.

Dimensions. Holotype: D 90, Wh 0·47, Wb 0·34, Ud 0·27; Plate 114, fig. 2: D 68, Wh 0·42, Ud 0·27, P 32.

Diagnosis. Strongly ribbed *Amoeboceras* with rectiradiate to slightly rursiradiate primary ribbing and lateral tubercles.

Description. The inner and middle whorls of *A. transitorium* carry strong ribs of variable density. The primaries are rectiradiate to slightly rursiradiate. Umbilical tubercles are always lacking, but bullate lateral tubercles are often well developed in forms showing low-rib density. Secondary ribs are short and usually weak at their base but are then raised into ventro-lateral tubercles. On the inner and middle whorls projection of the secondaries is minimal but increases as the ribbing fades on the outer whorl of macroconchs.

Discussion. Examination of the holotype shows that it is deformed. The side figured by Spath shows unduly projected ribbing, which on the reverse is markedly rursiradiate. Further collecting in the coastal ravines of eastern Milne Land has shown that *A. transitorium* is the dominant species at this locality and typical macroconchs are figured here (Pl. 114, figs. 1–4). Having established the position of *A. transitorium* and its microconch in Milne Land, one can find very similar but even smaller *Amoeboceras* microconchs at exactly the same stratigraphic level in eastern England (where Arkell (1937*a*) included them within *A.* aff. *pseudocaelatum*) and northern Poland (Malinowska 1966). Since size is the only difference between these two groups of specimens they are here included in the same species.

A. transitorium is closely related to *A. ilovaiskii*, and represents one of the few cases in which enough material is available from a single horizon to give an idea of variability. This is not the case in *A. ilovaiskii*, and so the names are kept separate for the time being.

Range. A. transitorium characterizes the Ilovaiskii Subzone, but may range up into the basal Glosense Subzone in Yorkshire.

Distribution. Eastern England: Ampthill Clay (Long Stanton; North Wooton, West Walton, and Gedney boreholes). Yorkshire: Spaunton Sandstone (Nunnington, Snape Hill, Laysthorpe, and Newbridge Quarries, OUM J4462, J18805, BM/RMS). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Central East Greenland: central and north-east Milne Land (Callomon and Birkelund 1979, fauna 8; GGU 137845, 137865, 234035; JHC 1686, 1712, BM/RMS).

Amoeboceras newbridgense sp. nov.

Plate 114, fig. 7; Plate 115, figs. 2–7

cf. 1904 *Cardioceras cordatum* (J. Sowerby); Ilovaisky, p. 266, pl. 10, fig. 30.
1937*a* *Amoeboceras* aff. *pseudocaelatum* Spath, Arkell, p. 65, pl. 3, figs. 8, 11, [m].
1948 *Amoeboceras* (*Prionodoceras*) sp. aff. *alternoides* (Nikitin), Arkell, p. 395, text-fig. 136 (small specimen) [m].
cf. 1966 *Amoeboceras alternans* (von Buch); Malinowska, p. 795, pl. 1, figs. 8*a*, *b* [m].
1972 *Amoeboceras* sp., Wright, pl. 14, fig. 2.

Type material. Holotype, [m] (RMS/BM C. 80407; pl. 4, fig. 3) and 2 paratypes (figs. 4, 5) from Newbridge Quarry, Pickering, North Yorkshire.

Description. The higher cherty beds of the Upper Calcareous Grit at Newbridge Quarry, thought to represent a local development of the Spaunton Sandstone, abound in a small characteristic species found only sporadically elsewhere and hence suggesting restriction to a short time interval in a bed developed only locally, or a tie to a peculiar biofacies, as in the older, homeomorphic *Plasmatoceras* of the Lower–Middle Oxfordian. Adult diameters are typically only around 30 mm, and the coiling is evolute. The primary ribbing is somewhat variable, between flexuously prosiradiate (Pl. 115, figs. 6, 7) and straight to rectiradiate (fig. 3), but always fine and very dense, with even finer and denser very short secondaries confined to the region of the ventrolateral shoulder high on the whorl-side. Although so plentiful, the material is all crushed and distorted, and it is with some reluctance that we select Plate 115, fig. 3 as holotype. None of the material is fit to give measurements. The specimen shown in Plate 115, fig. 2 is much better preserved but comes from a faunal assemblage in which it is present only as a minor constituent.

Discussion. The finer ribbing and smaller size differentiate *A. newbridgense* from *A. shuravskii*. *A. nunningtonense* is also bigger with usually more flexuous ribbing; and *A. ilovaiskii* is much more involute, with secondary ribs that are longer and much more strongly projected. The closest similarity is with what are taken to be the inner whorls of *A. glosense*, seen in nuclei, and this species may well be the macroconch partner, in part, of *A. newbridgense*. The latter may, however, include the microconchs of a number of other species.

Range. A. newbridgense ranges throughout the Glosense Zone but is commonest near the middle.

Distribution. Dorset: *Trigonia clavellata* Beds (Ringstead; OUM J4108). Eastern England: Ampthill Clay (bed 15 of the Wash boreholes; drift, Alconbury, Hunts., BM C. 73734). Humberside: Melton pit. Yorkshire: Spaunton Sandstone and equivalents (Laysthorpe, Newbridge, Nunnington, and Snape Hill Quarries: JKW and RMS/BM). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). East Greenland: beds with *A. transitionis* in Milne Land (GGU 137845, 137865; BM/RMS). Poland: Paslek borehole.

Amoeboceras nunningtonense Wright

Plate 113, fig. 8

cf. 1911 *Cardioceras nathorsti* Lundgren; Ravn p. 487, pl. 35, fig. 10.
cf. 1916 *Cardioceras alternans* var. *b*, Nikitin, p. 8, pl. 1, fig. 6.
1972 *Amoeboceras* (*Amoeboceras*) *nunningtonense* Wright, p. 261, pl. 13, figs. 1 (holotype), 4 (paratype).

Type material. Holotype (WM M27) and one paratype (WM M28), from Laysthorpe Quarry, North Yorkshire.

Dimensions. Holotype: D 58, Wh 0·38, Ud 0·33, P 46; Paratype: D 43, Wh 0·38, Ud 0·31, P 40; Plate 113, fig. 8 (Staffin): D 37, Wh 0·38, Ud 0·32, P 48.

Diagnosis. Medium-sized flexously ribbed *Amoeboceras*. Primaries are dominant with secondaries irregular in both style and length. Non-tuberculate.

Description. A. nunningtonense [m] shows an oval section with rounded ventro-lateral shoulders. It is rather evolute and shows distinct uncoiling of the umbilical seam in mature specimens. Ribbing is fine and characteristically flexous with primaries the dominant element. In general their trend is rectiradiate, but they show a prominent sweep forward just below mid flank. The secondaries are highly irregular including short ribs, long ribs, bifid pairs and intercalatories. The ribbing becomes crowded near the aperture in mature specimens. Occasionally individuals show completely

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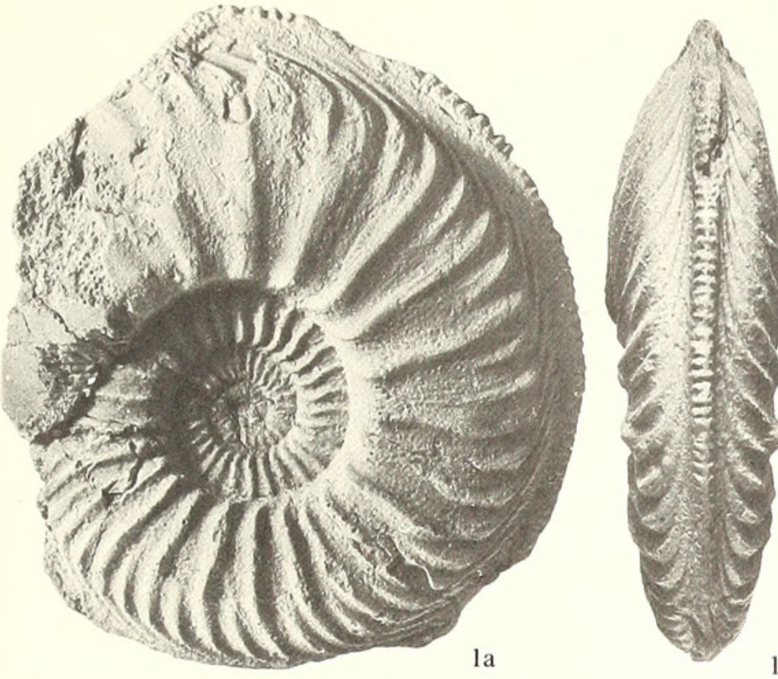
EXPLANATION OF PLATE 115

Fig. 1. *Amoeboceras glosense* (Bigot and Brasil) [M]. Dorset, the Red Beds of the *Trigonia clavellata* Beds, Osmington; Glosense Zone and Subzone. Evolute variant with test preserved; no sutures visible, but part of the last whorl is bodychamber (JKW Coll., Chelsea College; cast in BM).

Figs. 2–7. *A. newbridgense* sp. nov. [m]. 2, pyritic specimen with some of the adult bodychamber and test preserved. Ampthill Clay, bed 15, West Hill, Old Fordey Farm, 3 km north of Mepal, Cambridgeshire [TL 542749](IGS Coll. 1951, FD 2094). 3, holotype, Upper Calcareous Grit, Newbridge Quarry, Pickering, north Yorkshire: the chert-beds in the higher parts of the quarry, equivalent to the Spaunton Sandstone (RMS/BM C.80409). 4, paratype, evolute variant, horizon same as 3 (JKW U/2/113). 5, paratype, unusually large variant, horizon same as 3 (JKW U/2/20; previously figured Wright 1972, pl. 14, fig. 2). 6–7, various more or less fragmentary topotypes (JKW U/2/87, 105).

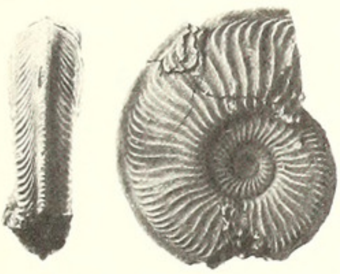
Fig. 8. *A.* cf. *ilovaiskii* (M. Sokolov) [m]. Typical nuclei of the '*Amoeboceras* aff. *pseudocaelatum*' fauna of the Fenland Ampthill Clay, bed 15; Gedney Drove End borehole (Gallois and Cox 1977, Bh 4A; FR 1549; photo: courtesy IGS).

Fig. 9. *A. glosense* (Bigot and Brasil) [M]. Protograph of the holotype, lost, from Glos, Calvados (Bigot and Brasil 1904, pl. 1, fig. 13).



1a 1b

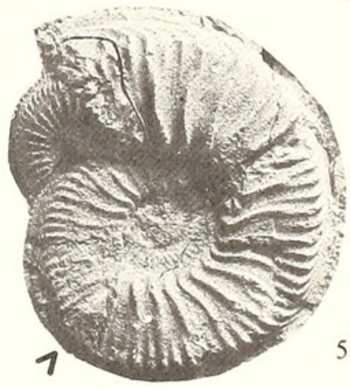
6



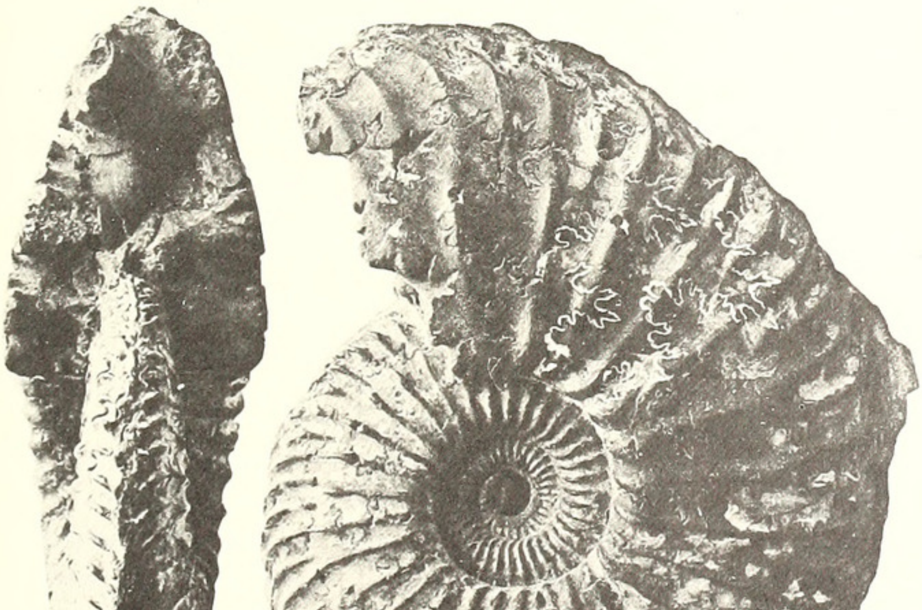
2b 2a 2c

3

4



5



9b 9a

7

8

SYKES and CALLOMON, *Amoeboceras*

smooth inner whorls (Ravn 1911, plate 35, fig. 10), whilst younger forms show fading of the ribbing near the centre of the whorl-side. Macroconch not yet identified.

Discussion. In general this species is abundant in the Glosense Subzone, especially in the Upper Calcareous Grit of Yorkshire. Very occasionally specimens occur in the Koldeweyense Subzone, before the closely related *A. freboldi* appears in the Serratum Subzone. A specimen from the Transversarium Zone (Schilli Subzone) near Poitiers, north-west France (collection, Geol. Inst. Univ. Poitiers) also shows considerable resemblance to this species. *A. nunningtonense* shows finer ribbing than the later *A. freboldi*, and does not show the characteristically flattened ribbing of the latter species. It is consistently bigger than *A. newbridgense*.

Range. *A. nunningtonense* characterizes the Glosense Subzone. However, in Yorkshire it is abundant in the upper part of the Ilovaiskii Subzone, whilst at Staffin it may range up into the Koldeweyense Subzone.

Distribution. Eastern England: Ampthill Clay (drift of Alconbury, BM C. 73737, 73746; North Wooton and Gedney boreholes, IGS). Yorkshire: Spaunton Sandstone (Laysthorpe, Newbridge, and Nunnington Quarries (WM M27–M28; OUM J18791, J18794, J18800, J18807). Scotland: Flodigarry Shale Member (BM/RMS). Central East Greenland: Pecten Sandstone (central Milne Land, GGU 137838/12). North-east Greenland: Muslingebjerg Member (Hochstetter Foreland). U.S.S.R.: Moscow basin.

Amoeboceras glosense (Bigot and Brasil)

Plate 113, figs. 5–7, 9; Plate 115, figs. 1, 9; Plate 116, figs. 1–3, 6–10

1904 *Cardioceras alternans* var. *glosensis* Bigot and Brasil, p. 17, pl. 1, fig. 17 [M].
1916 *Cardioceras alternoides* (Nikitin); Nikitin, p. 6, pl. 1, fig. 1 [m].
cf. 1930 *Cardioceras* cf. *nathorsti* Lundgren; Frebold, p. 75, pl. 26, fig. 1.
cf. 1932 *Cardioceras alternoides* (Nikitin); Pakuckas, pl. 19, 71, pl. 1, fig. 1.
1937 *Amoeboceras* (*Prionodoceras*) *glosense* (Bigot and Brasil); Arkell, p. 48 (first use of name at specific rank) (*non* pl. 12, figs. 3, 4, = *A. damoni*).
1976 *Amoeboceras glosense* (Bigot and Brasil); Sykes and Surlyk, fig. 5D.

Type material. Single specimen from the Sables de Glos, Lisieux, Normandy, figured by Bigot and Brasil (1904, pl. 1, fig. 13). This holotype, kept in Caen University Museum, was destroyed during World War II. However, the protograph gives a clear indication of the nature of the species.

Dimensions	D	Wh	Wb	Ud	P	S/P
Holotype	88	0·48	0·33	0·25	28	—
GGU 137838/6	34	0·48	0·27	0·24	37	1·34
GGU 137838/7	46	0·42	0·27	0·22	30	—
MGUH 14128 (Pl. 116, fig. 1)	71	0·45	0·16	0·24	32	1·21
MGUH 14779 (Pl. 116, fig. 6)	36	0·48	0·28	0·25	30	1·58
MGUH 14777 (Pl. 116, fig. 3)	49	0·48	0·28	0·24	28	1·63

In the above table S/P represents the ratio of secondary to primary ribs. All except the holotype come from one assemblage in the Pecten Sandstone of Milne Land.

Diagnosis. Medium-sized *Amoeboceras* with prorsiradiate primary ribbing. Lateral tubercles poorly developed. Secondaries show slight turn forward from the furcation point and then a second turn forward on the ventro-lateral shoulder to make a characteristic angle. Keel high and strongly crenulate.

Description. Since the holotype has been destroyed and no topotypes appear to have been found, the species is redescribed here. This is now possible with the aid of a fine collection from the Pecten Sandstone of central Milne Land, housed in the Institut for Historical Geology and Palaeontology, Copenhagen. The fauna is dominated by macroconch *A. glosense* in which the earliest primaries are rectiradiate and raised just above the mid flank into poorly developed elongate tubercles. The ribbing is weaker immediately above the tubercles, but strengthens again as irregular secondaries turn slightly forward. With growth the ribbing becomes more prorsiradiate and at about 40–50 mm diameter begins to fade in the mid flank area. At roughly the same size the whorl section begins to change from slightly quadrate with ventrolateral shoulders to a more arched, sagittate form. The ribbing continues to fade on the outer whorl, whilst at the same time becoming more projected in an even curve reminiscent of *A. ilovaiskii*. The body-chamber may be smooth, striate, or very faintly ribbed.

Variation. The principal variable is the strength of the ribbing on the outer whorl and the diameter at which fading begins. Strongly ribbed individuals usually show more inflated whorl-sections and in terms of whorl height, number of primary ribs and ribbing pattern show a gradation towards *A. damoni*.

Discussion. The present species includes forms often identified in the past with *A. alternoides* (Nikitin, 1878), index of an Alternoides Zone of some authors (e.g. Voronets 1962). The interpretation of Nikitin's species is highly uncertain. The only figured specimen from the original indefinite type-series came from Miatchkovo, where the species is said to be common in the Cordatum Zone (albeit *sensu lato*). No type has ever been selected, and the figure is poor; but in so far as it is interpretable, it differs significantly from specimens subsequently figured by Nikitin (1916), and from *A. glosense*. The specimen taken by later authors to represent the species (1916, pl. 1, fig. 1) does resemble *A. glosense* and is supposedly from Mniovniki, but in the text to this material Nikitin states that although *A. alternoides* had been found once in the true *alternans* beds of Miatchkovo, it was unknown in the *alternans* beds of Mniovniki. The implication is that *A. alternoides* (Nikitin, 1916), although resembling *A. glosense*, is a *Cardioceras* from the Lower or Middle Oxfordian. Subsequent use of this name in the U.S.S.R. has often been for *Cardioceras* of the 'Zenaidae Zone' (Sokolov 1912; Sazonov 1957, 1965). However, other Soviet authorities, including Mesezhnikov (1967), regard it as an *Amoeboceras*. The true affinities of *A. alternoides* await clarification pending a re-examination of Nikitin's original material.

Material from the *Trigonia clavellata* Beds of Dorset was ascribed to *A. glosense* by Arkell (1937), or compared by him with *A. alternoides* (Arkell, 1948). The majority of Dorset forms are more strongly ribbed with longer secondaries and more sloping whorl-sides than in *A. glosense*, and these have been renamed *A. damoni* by Spath (1943). A transitional specimen is figured here on Plate 115, fig. 1. In comparing Dorset material with the holotype of *A. glosense* it has to be remembered that the former almost always retains the test, with high keel, whereas the latter was an internal cast. *A. glosense* is easily distinguished from *A. ilovaiskii* by its angular secondaries. The presumed microconch is illustrated in Plate 116, figs. 8, 9. Its resemblance to *A.*

alternans has already been noted above. Most of the Staffin material is also microconch, but is more finely ribbed (Plate 113, fig. 9).

Range. *A. glosense* is limited to the Glosense Zone, and is commoner in the upper part.

Distribution. Normandy: Sables de Glos (Lisieux). Dorset: *Trigonia clavellata* Beds (Ringstead OUM J1568, J4103). Oxfordshire: Upper Calcareous Grit (Cumnor, OUM J18121). Eastern England: Ampthill Clay (drift, Alconbury; North Wooton and Gedney boreholes). Humberside: Melton Pit. Yorkshire: Spaunton Sandstone (Laysthorpe, Newbridge, and Snape Hill Quarries, OUM 18979, J18802, J4459, J1562; JKW; RMS). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Central-east Greenland: the Pecten Sandstone of Milne Land (GGU 137838) and more rarely the shales below. Jameson Land: Hareelv Formation (GGU 143011/1–2). North-east Greenland: Jakobsstigen Member (Th. Thomsens Land, GGU 139311/1; Bernbjerg Formation, Cardiocerasdal, Wollaston Foreland, GGU 139447/1, 139465/1). U.S.S.R.: Novaya Zemlya (loose).

Amoeboceras damoni Spath

Plate 116, figs. 4, 5

1888 *Ammonites serratus* J. Sowerby; Damon, pl. 15, fig. 5 [M].
1937 *Amoeboceras* (*Prionodoceras*) *glosensis* (Bigot and Brasil); Arkell, p. 48, pl. 12, figs. 3–4 (holotype refigured).
1943 *Amoeboceras* (*Prionodoceras*) *damoni* Spath, p. 117.
1948 *Amoeboceras* (*Prionodoceras*) sp. aff. *alternoides* (Nikitin); Arkell, p. 395, text-fig. 136 (larger specimen) [M].
1948 *Amoeboceras* (*Prionodoceras*) *glosensis* (Bigot and Brasil); Arkell, p. 400, text-fig. 138 [m].
1976 *Amoeboceras damoni* Spath; Sykes and Surlyk, fig. 5c.

Type material. Holotype (Damon Collection, BM C.3305), from the *T. clavellata* Beds, Dorset.

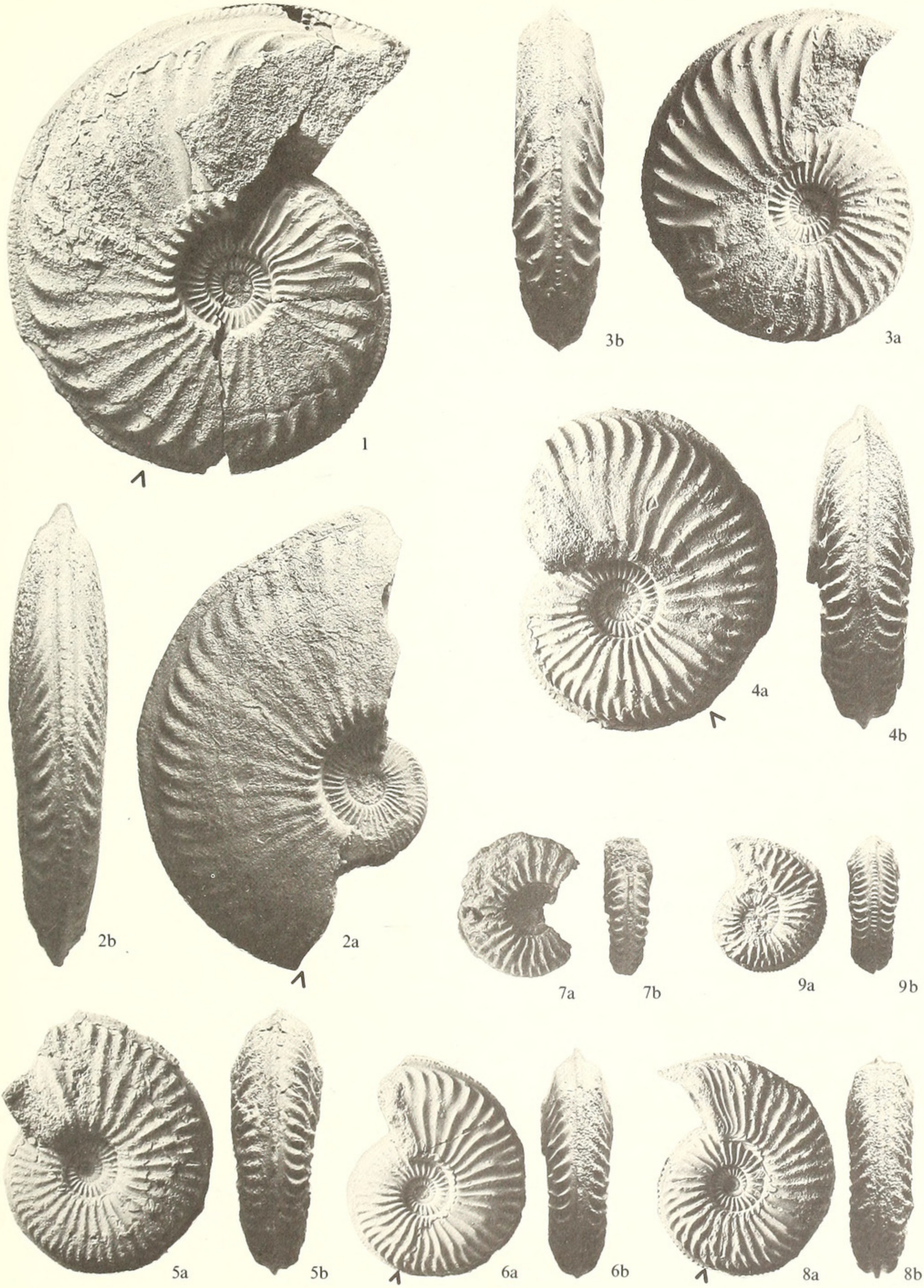
Diagnosis. Closely related and gradational to *A. glosense*, but more inflated with stronger, more spaced ribbing and more prominent lateral tubercles.

Dimensions. GGU 137838/4 (Pl. 116, fig. 5): D 38, Wh 0·49, Wb 0·34, Ud 0·25, P 30, S/P 1·78; MGUH 14130 (Pl. 116, fig. 4): D 51, Wh 0·49, Wb 0·24, Ud 0·33, P 31, S/P 1·81; GGU 137838/2: D 66, Wh 0·50, Wb 0·21, Ud 0·30.

EXPLANATION OF PLATE 116

Figs. 1–3, 6–10. *Amoeboceras glosense* (Bigot and Brasil). 1, nearly fully-grown [M] (MGUH 14128). 2, extremely finely and densely ribbed and compressed variant, [M] (MGUH 14776). 3, more coarsely ribbed variant; juvenile [M], with some bodychamber (MGUH 14777). 6, another juvenile [M] (MGUH 14779). 7, a coarse-ribbed nucleus, wholly septate, resembling *A. alternans* (see Pl. 112, fig. 2) (JHC 1708). 8, a complete adult [m] (cf. fig. 6) also resembling *A. alternans* (see Pl. 112, fig. 1) (MGUH 14129). 9, another [m] (MGUH 14780).

Figs. 4, 5. *A. damoni* Spath [M]. 4, juvenile (MGUH 14130); 5, nucleus (MGUH 14778). These forms are more inflated, round-whorled, strongly and flexuously ribbed than *A. glosense*, and have lateral tubercles. All except fig. 7 from Pecten Sandstone, locality west of Kronen, Milne Land (coll. E. Håkansson 1970; photos: courtesy J. Aagaard, Copenhagen). Fig. 7 from the east coast of Milne Land.



SYKES and CALLOMON, *Amoeboceras*

Description. To date *A. damoni* has been described only from the *T. clavellata* Beds of Dorset. Very good matches of this species accompany *A. glosense* in the Pecten Sandstone of central Milne Land. Whilst showing many similarities with *A. glosense*, *A. damoni* possesses much stronger ribbing. On the inner whorls the primaries are slightly rursiradiate and show prominent lateral tubercles. The secondary ribs are longer, more numerous and more regularly biplicate than *A. glosense*. In over-all shape *A. damoni* is characterized by its marked inflation, often with maximum whorl thickness near the umbilical margin. It is usually more involute than *A. glosense* with a greater whorl height.

Discussion. The distribution of *A. glosense* and *A. damoni* is interesting. In the Dorset *T. clavellata* Beds *A. damoni* [M] is the dominant element; in the Pecten Sandstone of central Milne Land, *A. glosense* [M] is very common, whilst in the Flodigarry Shale Member finely ribbed *A. glosense* [m] predominate. This distribution may reflect facies control but it is also possible that the three assemblages may be slightly different in age.

Range. *A. damoni* is usually found in the Glosense Subzone, but may possibly range up into the Serratum Zone.

Distribution. Dorset: *T. clavellata* Beds (Bran Point, OUM J4102, J4106–4107). Wiltshire: ?*T. clavellata* Beds (Steeple Ashton, BM C.78919). Cambridgeshire: Boxworth Rock, Boxworth (SM J53007). Yorkshire: Ampthill Clay (Melton). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Central-east Greenland: Pecten Sandstone (central Milne Land, GGU 137838). North-east Greenland: Bernbjerg Formation (Cardiocerasdal, Wollaston Foreland, GGU 139465/2). U.S.S.R.: Moscow area; Popilany.

Amoeboceras koldeweyense sp. nov.

Plate 117, figs. 5, 6; Plate 118, figs. 1, 2

1911 *Cardioceras alternans* (von Buch), Ravn, p. 36, fig. 1 [m].
1911 *Cardioceras* sp. Ravn, p. 488, pl. 35, fig. 11 [m].
cf. 1916 *Cardioceras alternans* vars. *a*, *b* Nikitin, p. 8, pl. 1, figs. 5, 7 [m].

Type material. Holotype, [m] (BM C.80416), figured Plate 118, fig. 1, and three paratypes. From Staffin, Serratum Zone, Koldeweyense Subzone.

Etymology. Named after Store Koldewey, north-east Greenland, whence the species was first figured.

Dimensions. Holotype [m]: D 54, Wh 0·39, Ud 0·26; Staffin, bed 33, average of 20 specimens [m]: D 41, Wh 0·42, Ud 0·25.

Diagnosis. Small to medium-sized *Amoeboceras* of the *serratum* group. Inner and locally middle whorls smooth, thereafter acquiring firstly short ventro-lateral, and then short umbilical ribs. Finally, lateral tubercles appear and tri-tuberculation may develop near the aperture.

Description of holotype. The inner whorls are completely smooth to a diameter of 30 mm, when the specimen acquires short, feeble, projected secondary ribbing. At 35 mm short umbilical nodes appear which are soon connected by rectiradiate primaries to an elongated lateral tubercle. On the outer whorls this trituberculate ribbing style becomes slightly prorsiradiate with weaker areas both above and below the lateral tubercle.

Variation. A collection of over 100 complete specimens from a single level in bed 33 at Staffin may be divided into four groups as follows:

1. Small forms (average mature diameter 33 mm) show smooth inner whorls up to 25 mm, when moderately projected secondaries appear followed by feeble primaries near the aperture (see Pl. 117, fig. 5).
2. Slightly larger forms ($d_{av.}$ = 41 mm) are similar to group 1, but show trituberculate ribbing near the aperture.
3. In the next group ($d_{av.}$ = 44 mm) faint to moderate trituberculation appears earlier on the body chamber at about three quarters of the end diameter.
4. Finally the most strongly ribbed forms display onset of trituberculate ribbing at about half the final diameter, although still retaining the protracted smooth inner whorls. The holotype falls within this group.

Rare macroconchs show similar variation from completely smooth forms to those with strongly trituberculate ribbing extending well onto the outer whorl. That the macroconchs and microconchs belong to the same species is strongly suggested by the distribution of the four morphological groups:

	Group 1	Group 2	Group 3	Group 4
	%	%	%	%
Microconchs	30	20	40	10
Macroconchs	27·5	10	60	2·5

Variation also occurs in the density of the primary ribbing.

Discussion. A. koldeweyense is distinguished from other members of the *serratum* group by its smooth inner whorls together with slightly prorsiradiate, generally low-density ribbing. Occasional densely-ribbed trituberculate forms are difficult to distinguish from the later *A. mansoni.* However, the latter species rapidly acquires lateral tubercles after the smooth stage, whereas *A. koldeweyense* shows a protracted middle stage with only umbilical and ventro-lateral swellings.

Range. A. koldeweyense is limited to its own subzone.

Distribution. Eastern England: Ampthill Clay (drift) BU 1903, BM C17552. Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Central-east Greenland: Pecten Sandstone (central Milne Land, GGU 137879). North-east Greenland: Kløft I Formation (Store Koldewey, MGUH 231b, 778–780, 782); Muslingebjerg Member (Hochstetter Forland, MGUH unnumbered).

Amoeboceras serratum (J. Sowerby)

Plate 117, figs. 1–4

1813 *Ammonites serratus* J. Sowerby, p. 65, pl. 24 [M] (2 figures).
1915 *Cardioceras serratum* (J. Sowerby); Salfeld, p. 172, pl, 18, figs. 1–2 [M] (neotype).
1920 *Prionodoceras prionodes* S. Buckman, pl. 155 [M].
1924 *Prionodoceras excentricum* S. Buckman, pl. 464 [M].
1927 *Prionodoceras truculentum* S. Buckman, pl. 704 [M].

1943 *Amoeboceras* (*Prionodoceras*) *serratum* (J. Sowerby); Spath, text-fig. 1 [M].
cf. 1959 *Cardioceras* (*s.l.*) sp. indet. 3, p. 27, Frebold, Mountjoy and Reed, p. 27, pl. 1, fig. 2 [M].
1965 *Amoeboceras serratum* (J. Sowerby), Sazonov, p. 44, pl. 5, fig. 1; pl. 6, fig. 1 [M].
cf. 1967 *Amoeboceras* (*Prionodoceras*) *shuravskii* (D. Sokolov); Mesezhnikov, pl. 5, figs. 1, 4 [m], 2 [M].
1976 *Amoeboceras serratum* (J. Sowerby), Sykes and Surlyk, fig. 5E [m].

Type material. Both syntypes figures by J. Sowerby in 1813, the lower figure designated lectotype by Arkell (1937*a*), are lost (Dr. M. K. Howarth, in litt. 1975). Hence the specimen figured by Salfeld (1915, pl. 18, fig. 2) and designated neotype by Arkell (1937, p. 50) stands. This specimen is located in the I.G.S. London, No. 26059. It came from glacial drift, derived from Ampthill Clay, of eastern England.

Dimensions		D	Wh	Wb	Ud	P
Neotype	[M]	87	0·47	0·29	0·23	—
Buckman 1920, pl. 155	[M]	190	0·43	0·32	0·23	—
Buckman 1924, pl. 464	[M]	175	0·43	0·30	0·25	—
,, body chamber starts at		91	0·51	0·33	0·17	—
Buckman 1927, pl. 704	[M]	175	0·44	0·39	0·23	—
,, body chamber starts at	[M]	53	0·46	0·40	0·29	—
BU 1901 (Pl. 116, fig. 4)	[m]	49	0·42	0·24	0·28	33

Diagnosis and description. Smooth innermost whorls are followed by strong, rectiradiate primaries. The furcation point is high and the short secondaries are either rectiradiate or slightly prorsiradiate. Umbilical, lateral, and ventro-lateral tubercles are present on the middle whorls. In macroconchs ornament fades gradually on the outer whorls to leave only faint secondaries before the onset of the smooth body-chamber: adults medium to large. Gerontic secondary ribbing may reappear near the aperture. In section the whorl-sides converge gently towards the venter, with a marked increase in slope across the ventro-lateral shoulders. The microconch is figured for the first time (see Pl. 117, fig. 2).

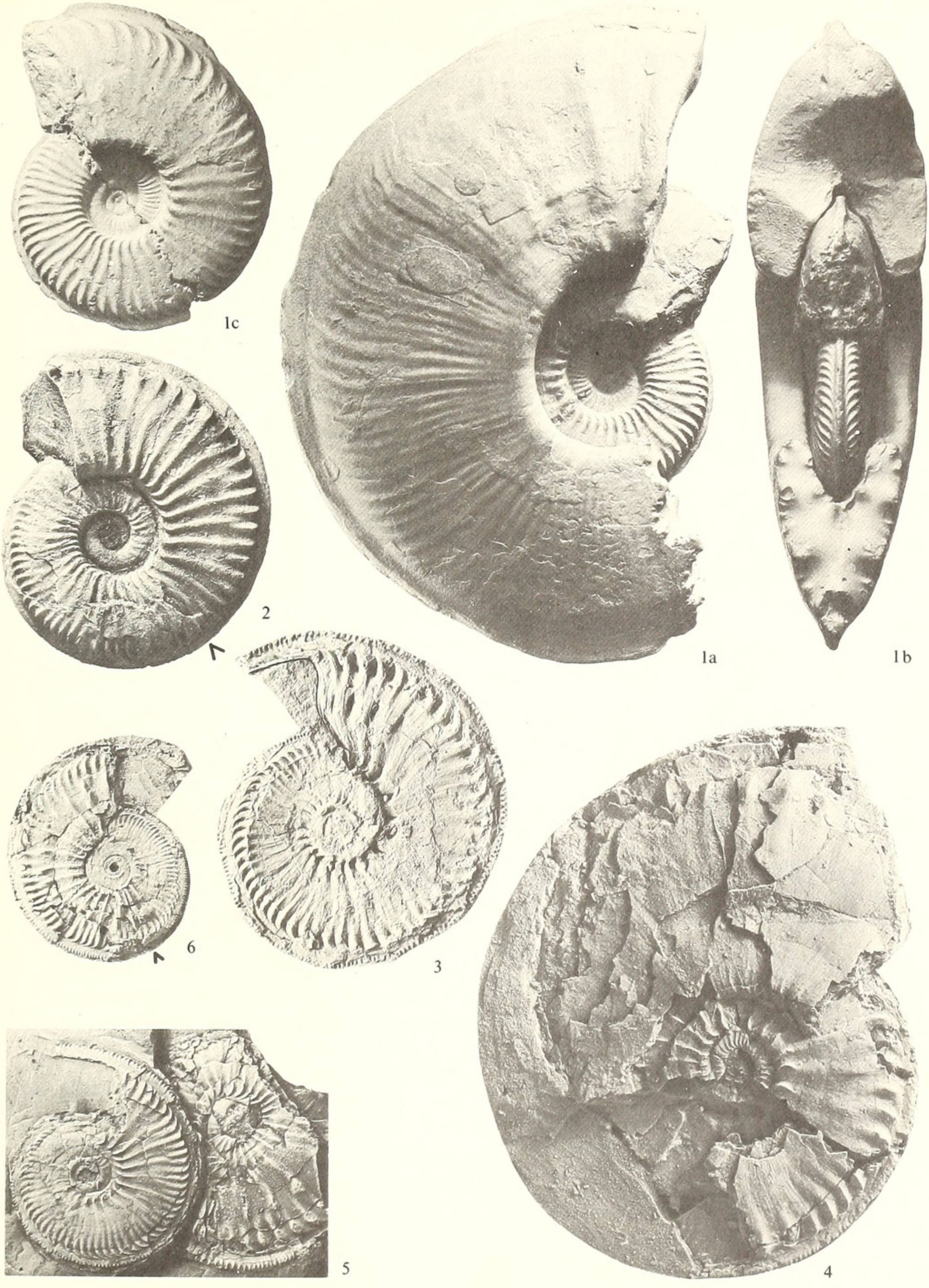
Variation. The principal variation, as in the earlier *A. koldeweyense*, is the strength of the ribbing. The most typical examples are those figured by Sowerby (1813, upper figure) and Spath (1943, text-fig. 1), but almost the whole range of variation occurs in the drift macroconch series *A. excentricum*, *A. prionodes*, *A. serratum*, *A. truculentum*, which show progressively stronger ribbing, and which may all be united under *A. serratum*. A typical macroconch is figured from Staffin as Plate 117, fig. 4 and bears considerable resemblance to Sowerby's (1813) upper figure. Microconchs vary from the moderately ribbed form described above to those with strong lateral tubercles.

EXPLANATION OF PLATE 117

Figs. 1, 4. *Amoeboceras serratum* (J. Sowerby) [M]. 1, neotype, glacial drift ex Ampthill Clay; photo of a plaster-cast (courtesy S. A. Baldwin) (IGS 26059). 1*c*, inner whorls. 4, coarse-ribbed variant (cf. *A. truculentum* Buckman). Staffin, Serratum Zone, Koldeweyense Subzone, bed 33, 5·5 m above the base (RMS/BM C.80417).

Figs. 2, 3. *A. serratum* (J. Sowerby) [m]. 2, adult: compare with fig. 1*c*; glacial drift ex Ampthill Clay (BU 1901). 3, negative impression, Staffin, Serratum Zone, same horizon as fig. 4 (RMS/BM C.82046).

Figs. 5, 6. *A. koldeweyense* sp. nov. [m]. Fine and densely ribbed paratypes with test preserved. Staffin, same level as fig. 4 (RMS/BM C.80415, C.82047).



SYKES and CALLOMON, *Amoeboceras*

Discussion. Considering the population as a whole, *A. serratum* is distinguished from *A. koldeweyense* by its shorter smooth stage and rectiradiate ribbing. *A. mansoni* shows denser ribbing and a longer smooth stage. Macroconchs resemble *A. regulare* [M], although this latter species does not show an initial smooth stage and has sharper, finer ribbing on the middle whorls.

Range. A. serratum ranges throughout its own zone.

Distribution. Eastern England: Ampthill Clay (Gedney borehole; drift of many localities; IGS 26059, OUM J4465–4467, J14463, J14618–14622, J14658, J14823–14824, J16014, J19496, BU, a large collection). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Central-east Greenland: Pecten Sandstone (north-east Milne Land, BM/RMS). North-east Greenland: Bernbjerg Formation (Cardiocerasdal, Wollaston Foreland, GGU 139447/2, 139449/1, 139466/1, 139467–139468); Jakobsstigen Member (Th. Thomsens Land, 139311/2); Kløft I Formation (Store Koldewey, MGUH 231, 793). U.S.S.R.: Moscow and Petchora Basins. Canada: Fernie Group, Miette, Alberta (GSC 13893).

Amoeboceras mansoni Pringle

Plate 118, fig. 3

1936 *Amoeboceras* (*Prionodoceras*) *mansoni* Pringle, p. 309, pl. 13 [m].
1936 *Amoeboceras* (*Prionodoceras*) aff. *superstes* (Phillips); Pringle, pl. 14 (upper figure) [M].

Type material. Holotype in the Institute of Geological Sciences, Edinburgh, No. M638d, figured by Pringle (1936, pl. 13, upper figure). Also three paratypes, Nos. M628d, M3309g, and M3310g. From glacial drift, Plaidy, Aberdeenshire.

Dimensions. Holotype: D 52, Wh 0·48, Wb 0·25, Ud (0·48); Plate 118, fig. 3: D 56, Wh 0·42, Ud 0·27, P 49.

Diagnosis. A medium-sized *Amoeboceras* of the *serratum* group which shows a long smooth inner stage and is characterized by dense ribbing.

Description. Pringle (1936) gave a detailed description of the holotype which is smooth up to 30 mm. The species is characterized by its high rib-density, of up to fifty primaries on the outer whorl.

Discussion. In its protracted smooth early stages, *A. mansoni* resembles *A. koldeweyense*. However, this feature is here more irregular—in some forms primary ribbing may be present on the second whorl and then fade completely, only to return on the middle whorls. The rectiradiate nature of the ribbing also serves to differentiate the two species. *A. mansoni* is more densely ribbed than *A. serratum*.

Closer study of large collections from Staffin reveals that three successive faunas can be distinguished. The earliest is dominated by *A. koldeweyense* and the second by *A. serratum*. The densely ribbed *A. mansoni*, whilst occurring in all three faunas, is most common in the upper part of the Serratum Subzone. This level can thus be described informally as the *mansoni* horizon.

Range. A. mansoni ranges throughout the Serratum Zone.

Distribution. Scotland: Flodigarry Shale Member (Staffin, BM/RMS); drift of Plaidy, Aberdeenshire (IGSE M628d, M638d, M3309g, M3310g). North-east Greenland: Bernbjerg Formation (Cardiocerasdal, Wollaston Foreland, GGU 139450/3, 139466/3).

Amoeboceras regulare Spath

Plate 118, figs. 4, 9, 10; Plate 119, figs. 1, 2, 4, 5

1930 *Cardioceras* cf. *nathorsti* Lundgren; Frebold, p. 75, pl. 26, figs. 2 [m], 3 (lectotype) [M].
1935 *Amoeboceras* (*Prionodoceras*) *regulare* Spath, p. 25.
1967 *Amoeboceras* (*Prionodoceras*) *regulare* Spath; Mesezhnikov, p. 117, pl. 1, fig. 2 [m?].
cf. 1967 *Amoeboceras* (*Prionodoceras*) *shuravskii* (D. Sokolov); Mesezhnikov, p. 125, pl. 6, fig. 3 [m, M].
cf. 1967 *Amoeboceras* sp. indet., Frebold, p. 21, pl. 3, fig. 6.
cf. 1973 *Amoeboceras* cf. and aff. *rasenense* Spath; Surlyk, Callomon, Bromley and Birkelund, p. 48, pl. 1, figs. 6–7 [m].
cf. 1975 *Amoeboceras* (*Amoeboceras*) cf. *ovale* (Quenstedt); Callomon, p. 380, fig. 3c [m].

Type material. Three syntypes; lectotype [M] and paralectotype (allotype) [m] now designated (Stockholm, RM Mo1224, Mo2580), from Novaya Zemlya; refigured here as Plate 118, figs. 9, 10.

Dimensions. Holotype (Pl. 118, fig. 9): D 64, Wh 0·47, Ud 0·23, P 37; Mesezhnikov 1967, pl. 1, fig. 2: D 40, Wh 0·45, Ud 0·24, P 29; Plate 118, fig. 4: D 38, Wh 0·42, Ud 0·25, P 36.

Diagnosis. Medium sized *Amoeboceras* with fine, wiry ribbing. Inner whorls strongly ribbed with rectiradiate primaries and secondaries, the latter turning forward sharply on the ventro-lateral shoulder. Non-tuberculate.

Description of holotype. Only the very earliest whorl is smooth, and it quickly develops sharp, fine, dense, ribbing. The primaries, first seen at 30 mm, are rectiradiate with only the faintest of lateral tubercles situated just under half-way up the whorl-side. The secondaries are long and straight turning forward sharply on the ventro-lateral shoulder.

Discussion. In the present work *A. regulare* is restricted to non-tuberculate forms and is accompanied by the mildly tuberculate *A. shulginae* and *A. leucum*. Macroconchs show identical inner whorls. Fading of the ribbing commences in the centre of the whorl-side at about 35 mm diameter, although short umbilical and ventro-lateral ribs persist until about 55 mm. Usually the body-chamber is smooth although approximated secondaries and locally even primaries may reappear near the aperture. The rostrum is shorter than in the microconchs.

A. freboldi contrasts with the present species in showing fewer primaries and much blunter ribbing. In *A. rosenkrantzi* the ribbing is more rursiradiate and has a tendency to fade in the centre of the whorl-side. *A. regulare* differs from the *serratum* group in that the ribbing is sharper, denser, more wiry, and never trituberculate, although the macroconchs often bear a close resemblance to each other (compare Pl. 119, fig. 1 with Pl. 117, fig. 4).

Range. A. regulare occurs rarely in the Serratum Subzone and ranges to the top of the Regulare Zone.

Distribution. Scotland: Flodigarry Shale Member (Staffin BM/RMS). Northern North Sea: Well 211/21-1. Central-east Greenland: Hareelv Formation (Astartekløft, southern Jameson Land; GGU 138134/1-11, 143004, 143014). North-east Greenland: Bernbjerg Formation (Cardiocerasdal, Wollaston Foreland; GGU 139449/2, 139453/1, 139479, 139480/1). U.S.S.R.: Kheta River, northern Siberia; Besimennaja Bay, Novaya Zemlya. Canada: northern Yukon (GSC 20367).

Amoeboceras leucum Spath emend. Mesezhnikov

Plate 119, fig. 2

1904 *Cardioceras alternans* (von Buch), Ilovaisky, p. 272, pl. 11, fig. 7 [?m] (= *Amoeboceras arkelli* Mesezhnikov).
1904 *Cardioceras* cf. *bauhini* (Oppel); Ilovaisky, p. 273, pl. 11, fig. 2 [m].
cf. 1930 *Cardioceras* cf. *nathorsti* var *robusta* Pompeckj; Frebold, p. 34, pl. 8, fig. 2 [m] (= *Amoeboceras nigrum* Spath).
1935 *Amoeboceras* (*Prionodoceras*) *leucum* Spath, p. 22, pl. 5, fig. 3 [m].
cf. 1935 *Amoeboceras* (*Prionodoceras*) *nigrum* Spath, p. 25.
1945 *Amoeboceras* (*Prionodoceras*) *ilovaiskyi* Arkell, p. 350.
1967 *Amoeboceras* (*Prionodoceras*) *arkelli* Mesezhnikov, p. 115, (nom. nov.).
1967 *Amoeboceras* (*Prionodoceras*) *leucum* Spath; Mesezhnikov, p. 118, pl. 1, fig. 3; pl. 3, figs. 2–3; pl. 4, fig. 5 [m, M].

Type material. Holotype only (IGS 72211). From glacial drift of eastern England.

Dimensions. Holotype: D 50, Wh 0·38, Ud 0·34; Mesezhnikov 1967, pl. 3, fig. 2: D 69, Wh 0·39, Wb 0·31, Ud 0·33, P 32; Mesezhnikov 1967, pl. 3, fig. 3: D 73, Wh 0·41, Wb 0·29, Ud 0·31.

Diagnosis. A medium-sized, evolute *Amoeboceras* of the *regulare* group. The ribbing resembles *A. regulare* except that lateral tubercles are present and occasionally umbilical and ventro-lateral ones as well.

Description. *A. leucum* is characteristically rather evolute with only the innermost whorl smooth. The middle whorls show sharp, rectiradiate primary ribs which become slightly flexuous on the outer whorl. Faint lateral tubercles are usually present and the ribbing may be slightly trituberculate on the body chamber. Near the aperture the ribbing simplifies and becomes more flexuous.

EXPLANATION OF PLATE 118

Figs. 1, 2. *Amoeboceras koldeweyense* sp. nov. 1, holotype, [m], with long ventral rostrum on the adult peristome and characteristic smooth inner whorls. Staffin, Koldeweyense Subzone, bed 33, 8·0 m above the base (RMS/BM C.80416). 2, paratype, [M], same horizon (RMS/BM C.82048).

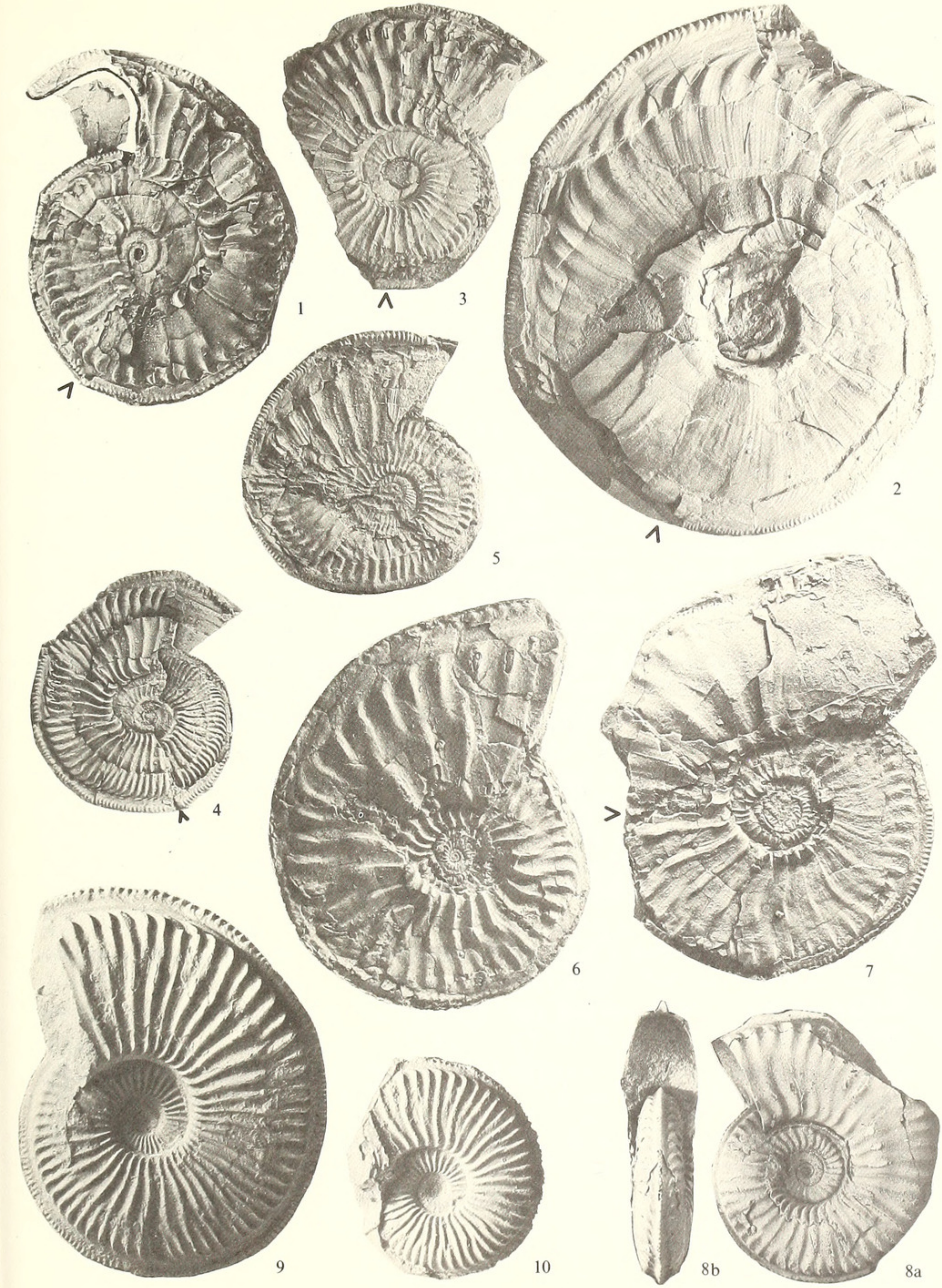
Fig. 3. *A. mansoni* Pringle [m]. Complete adult, Staffin, Serratum Zone, *mansoni* horizon; bed 33, 14·0 m above the base (RMS/BM C.80418).

Fig. 4. *A.* cf. *regulare* Spath [m]. Complete adult, an early fine-ribbed variant. Staffin, Serratum Subzone, bed 33, 11·0 m above the base (RMS/BM C.80419).

Fig. 5. *A.* cf. *schulginae* Mesezhnikov [m]. Staffin, Regulare Zone, bed 33, 16·5 m above the base (RMS/BM C.80422).

Figs. 6–8. *A. freboldi* Spath. 6, 7, two incomplete [M]; Staffin, Regulare Zone, bed 33, 16·5 m above the base (RMS/BM C.80423, C.82049a). 8, complete adult [m], glacial drift ex Ampthill Clay (BU 1902).

Figs. 9, 10. *A. regulare* Spath. 9, lectotype, [M], and 10, paralectotype [m]. Besimennaya Bay, Novaya Zemlya; casts from impressions in concretions found in glacial drift (Nordenskjoeld Coll. 1875; RM Stockholm Mo1224, 2580). Both specimens adult and probably nearly complete, although no sutures are visible.



SYKES and CALLOMON, *Amoeboceras*

Discussion. Spath's diagnosis and figure of the holotype give only a sketchy idea of the taxon. A much clearer picture has been provided by Mesezhnikov (1967) who describes the species in detail and figures several fine examples from the Kheta River in northern Siberia. The limited smooth stage and sharp, fine ribbing indicate that *A. leucum* is closely allied to *A. regulare*. These two parameters also differentiate *A. leucum* from trituberculate members of the *serratum* group.

Range. A. leucum ranges from the Serratum Subzone to the Regulare Zone.

Distribution. Eastern England: Ampthill Clay (drift, IGS 72211). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Central East Greenland: Hareelv Formation (Astartekløft, southern Jameson Land, GGU 138134/12–13). Spitzbergen. U.S.S.R.: Moscow area; Kheta River, northern Siberia; Besimennaja Bay, Novaya Zemlya.

Amoeboceras schulginae Mesezhnikov

Plate 118, fig. 5

1961 *Amoeboceras* sp. indet. Frebold, p. 22, pl. 3, fig. 2.
1964 *Amoeboceras* sp. indet. Frebold, p. 98, pl. 47, fig. 5.
1967 *Amoeboceras* (*Prionodoceras*) *schulginae* Mesezhnikov, p. 123, pl. 1, fig. 4; pl. 3, fig. 1; pl. 4, fig. 1 [m, M].

Type material. Holotype [M] in the Museum VNIGRI in Leningrad, No. 24/686, and four paratypes, from northern Siberia.

Dimensions. Holotype: D 98, Wh 0·44, Wb 0·35, Ud 0·30, P 17; Mesezhnikov 1967, pl. 1, fig. 4: D 34, Wh 0·44, Wb 0·35, Ud 0·27; Mesezhnikov 1967, pl. 4, fig. 1: D 92, Wh 0·47, Wb 0·36, Ud 0·21.

Diagnosis. A tuberculate *Amoeboceras* of the *regulare* group closely allied to *A. leucum*. The ribbing is notably spaced and distinctly slender in character.

Description. Sharp, fine primaries typical of the *regulare* group follow the smooth initial whorl. On the holotype the primaries are rectiradiate and well spaced with an elongate lateral tubercle half way up the whorl-side. The outer whorl may be mildly trituberculate, but the ornamentation is notably slender. Near the aperture the ribbing is again simple and approximated. The section is quadrate.

Discussion. A. schulginae is found rarely at Staffin with *A. regulare*, *A. leucum*, and *A. freboldi*. Early forms show more feebly ribbed inner whorls gradational from the *serratum* group. The wiry ribbed inner whorls of *A. schulginae* indicate that it is a further member of the *regulare* group. It is distinguished from *A. leucum* by its spaced and slender trituberculation.

Range. A. schulginae ranges from the upper part of the Serratum Subzone to the lower part of the Regulare Zone.

Distribution. Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Central-east Greenland: Hareelv Formation (Astartekløft, southern Jameson Land, GGU 138134/14). North-east Greenland: Bernbjerg Formation (Cardiocerasdal, Wollaston Foreland, GGU 139480/3). U.S.S.R.: Kheta River, northern Siberia. Canada: Mackenzie King Island (GSC 15130).

Amoeboceras freboldi Spath

Plate 118, figs. 6–8; Plate 119, fig. 3

1930 *Cardioceras* cf. *nathorsti* Lundgren; Frebold, p. 75, pl. 26, fig. 4 [M] (holotype).
1935 *Amoeboceras* (*Prionodoceras*) *freboldi* Spath, p. 25.
cf. 1961 *Amoeboceras* sp. indet., Frebold, p. 22, pl. 3, fig. 3 [m?].
cf. 1964 *Amoeboceras* sp. indet., Frebold, p. 98, pl. 47, fig. 6 [m?].
1967 *Amoeboceras* (*Prionodoceras*) *freboldi* Spath; Mesezhnikov, p. 121, pl. 1, fig. 5; pl. 2, figs. 1–2 [M].
cf. 1975 *Amoeboceras* (*Amoeboceras*) cf. *alternans* (von Buch); Callomon, p. 377, fig. 3A–B [m].
cf. 1976 *Amoeboceras alternans-ovale* group Brochwicz-Lewinski, pl. 4, fig. 9; pl. 8, fig. 1 [?m].
1976 *Amoeboceras freboldi* Spath; Sykes and Surlyk, fig. 5F [M].

Type material. Holotype (Stockholm, RM Mo 2605), from Novaya Zemlya.

Dimensions. Holotype: D 73, Wh 0·41, Ud 0·29, P 28; Mesezhnikov 1967, pl. 1, fig. 5: D 39, Wh 0·45, Wb 0·32, Ud 0·24, P 43.

Diagnosis and description. A medium-sized *Amoeboceras* with strongly ribbed inner whorls. The primaries are strong, well spaced, and characteristically blunt and flattened. They are usually rectiradiate to slightly rursiradiate and flexuous. Only lateral tubercles are present and the ribbing may fade in the centre of the whorl-side. In contrast the secondaries, which tend to bend slightly backwards, are distinctly flattened and blunt. Even at small diameters the thickness of the secondaries may exceed 1 mm compared to only 0·4 mm for the primaries. On the outer whorl the ribbing is straighter and fades slightly in the centre of the whorl side, but then straightens again with the development of feeble lateral tubercles. As in other members of the *regulare* group, early forms show more variable strength of ribbing on the inner whorl and more projected secondaries. Later forms are more rursiradiate and ancestral to *A. marstonense*.

Discussion. *A. freboldi* is an easily recognizable species at localities as widely separated as eastern England, Staffin, Milne Land, and northern Siberia. Its flexuous ribbing bears a resemblance to the earlier *A. nunningtonense*, but the bluntness and low density of the ribbing are features not seen in the older species. The later *A. marstonense* is also similar but shows more rursiradiate ribbing. Some of the more finely ribbed, flexuous forms approach *A. pectinatum* Mesezhnikov.

Range. *A freboldi* is rare in the Serratum Subzone and ranges up to the top of the Regulare Zone.

Distribution. Berkshire: Upper Calcareous Grit (Appleford, OUM J18004, J20226). Eastern England: Ampthill Clay (drift, BU 1902). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Northern North Sea: Well 211/21-1. Central-east Greenland: Pecten Sandstone (north-east Milne Land, BM/RMS). North-east Greenland: Bernbjerg Formation (Cardiocerasdal, Wollaston Foreland, GGU 139450/2, 139453/2, 139466/2, 139469, 139480/2, 139482; Kløft I Formation (Store Koldewey, MGUH, unnumbered). U.S.S.R.: Kheta River, northern Siberia; Besimennaja Bay, Novaya Zemlya. Poland: Czestochowa area. Arctic Canada: Mackenzie King Island GSC 15131.

Amoeboceras marstonense Spath

Plate 119, figs. 6–8

1935 *Amoeboceras* (*Prionodoceras*) *marstonense* Spath, p. 20, pl. 4, fig. 5 [M] (holotype).

Type material. Holotype (IGS 72210), from Marston, Wiltshire; refigured here as Plate 119, fig. 8.

Dimensions. Holotype [M]: D 60, Wh 0·44, Ud 0·26; OUM J14631, topotype [M]: D 91, Wh 0·48, Ud 0·22; Pl. 119, fig. 6 [m?]: D 35, Wh 0·47, Ud 0·23, P 32; Pl. 119, fig. 7 [m]: D 37, Wh 0·46, Ud 0·24, P 29.

Diagnosis. A medium-sized *Amoeboceras* akin to *A freboldi.* The primaries are again blunt and either non-tuberculate or show only a lateral tubercle. The secondaries show a marked swing back from the furcation point before turning forward again high on the ventro-lateral shoulder.

Description. The holotype is strongly compressed, and shows flat whorl-sides with distinct ventro-lateral shoulders. The inner whorls are obscured but at 35 mm straight primaries of low to moderate density are visible. Lateral tubercles are situated just below the centre of the flank, from which bifid secondaries show a distinctive backward curve, before sweeping forward on the ventro-lateral shoulder. At 55 mm the lateral tubercles disappear and the ribbing fades, starting in the middle of the whorl-side. Only weak secondaries remain when the body chamber commences at 60 mm.

Discussion. The material from the Westbury Ironstone of Marston, Wiltshire comprises only macroconchs. However, strongly ribbed microconchs showing little variation are dominant at Staffin. *A. marstonense* is distinguished from the *regulare* group by its low-density blunt ribbing. This feature allies it to *A. freboldi*, from which it differs in showing coarser ribbing. Also the secondaries show a characteristic backward curve, rather than the general flexuosity of *A. freboldi. A. marstonense* is also close to *A. rosenkrantzi*, but the latter species is more sharply and densely ribbed.

Range. A. marstonense ranges throughout its subzone.

Distribution. Wiltshire: Westbury Ironstone (Marston, IGS 72210, OUM J14631). Scotland: Flodigarry Shale Member (Staffin, BM/RMS); Camasunary Siltstone

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EXPLANATION OF PLATE 119

Figs. 1, 4. *Amoeboceras* cf. *regulare* Spath. 1, [M], a variant becoming smooth at intermediate diameters (RMS/BM C.80420). 4, [m], with long rostrum (RMS/BM C.82049b). Staffin, Regulare Zone, 16·5 m above the base.

Fig. 2. *A.* cf. *leucum* Spath [m]. Staffin, same horizon as fig. 1 (RMS/BM C.80421).

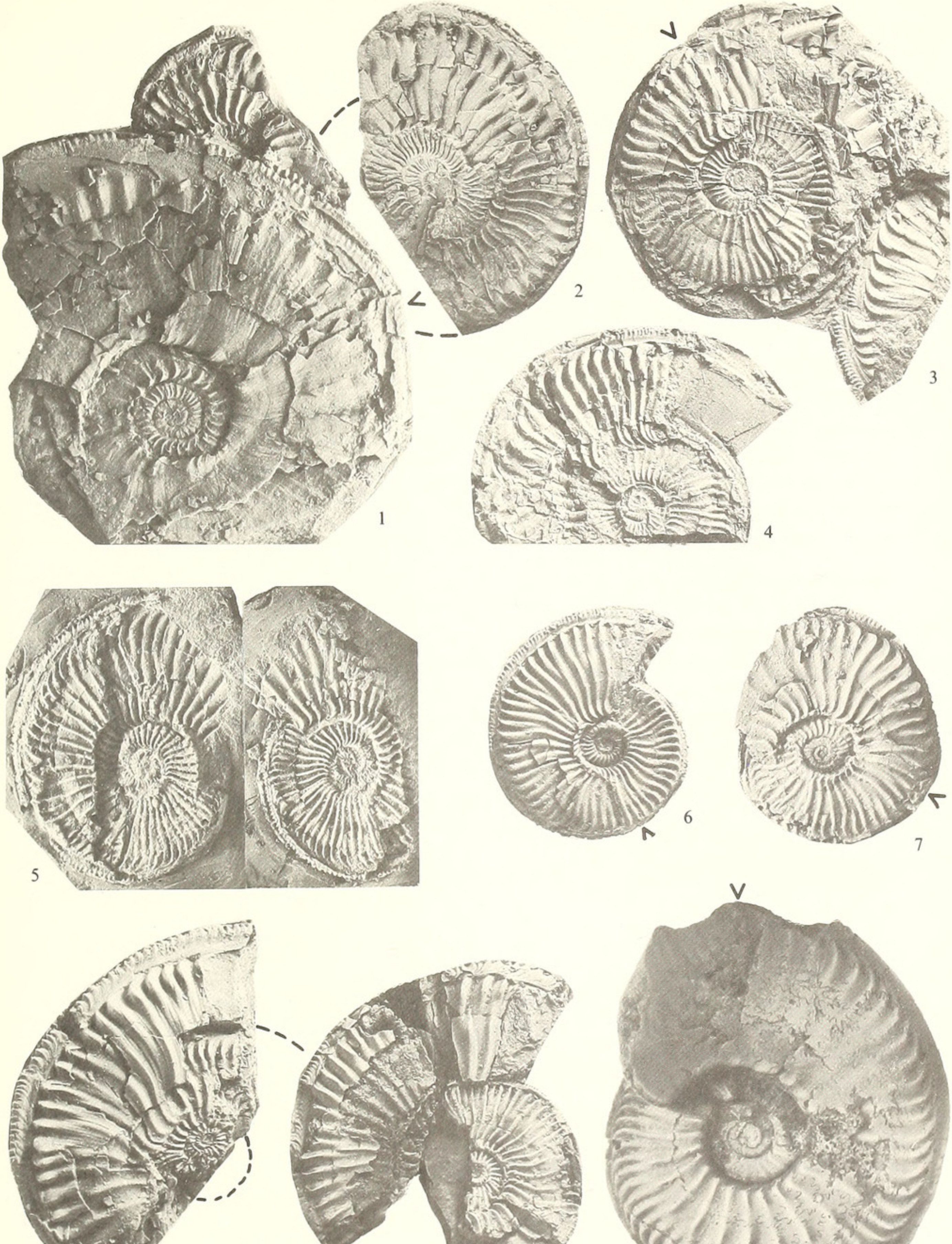
Fig. 3. *A.* cf. *freboldi* Spath [m]. Variant intermediate between *freboldi* and *regulare*. Staffin, same horizon as fig. 1 (RMS/BM C.80423).

Fig. 5. *A.* cf. *regulare* Spath [m]. Late form, transitional to *A. marstonense* Spath. Staffin, bed 33, 20·5 m above the base, 2 m below the top (RMS/BM C.82050).

Figs. 6–8. *A. marstonense* Spath. 6, juvenile?, 7, [m], Staffin, Marstonense Subzone, bed 35, 0·75 m above the base (RMS/BM C.80426, -7). 8, holotype, [M], from ironshot limestone with *Ringsteadia pseudoyo*, Marston, near Swindon, Wilts (IGS 72203; photo: courtesy IGS).

Fig. 9. *A.* cf. *rosenkrantzi* Spath [m]. Staffin, same horizon as figs. 6, 7; complete adult of an early evolute form (RMS/BM C.80425).

Fig. 10. *A. rosenkrantzi* Spath [m]. Staffin, bed 35, 2·5 m above the base; part of a complete adult.



SYKES and CALLOMON, *Amoeboceras*

Member (Strathaird, Isle of Skye, BM/RMS). North-east Greenland: Bernbjerg Formation (Cardiocerasdal, Wollaston Foreland, GGU 139457).

Amoeboceras rosenkrantzi Spath

Plate 119, fig. 10; Plate 120, figs. 1–6

1935 *Amoeboceras* (*Prionodoceras*) *rosenkrantzi* Spath, p. 25, pl. 12, fig. 4, pl. 13, fig. 5 [M].
1961 *Amoeboceras* sp. indet., Frebold, p. 22, pl. 18, fig. 3 [m].
1968 *Amoeboceras* aff. *rosenkrantzi* Spath, Morris MS, p. 214, pl. 24, figs. 1–3, 5–7 [m].

Type material. Two syntypes; lectotype now designated (Spath 1935, pl. 12, fig. 4, MGUH 8192, refigured here, Pl. 120, fig. 3), from Wollaston Foreland, E. Greenland.

Dimensions. Lectotype: D 52, Wh 0·47, Ud 0·22, P 29; Plate 120, fig. 4: D 56, Wh 0·44, Ud 0·27, P 33.

Diagnosis. A medium-sized *Amoeboceras* of the *regulare* group. The strong, wiry primaries are rectiradiate or slightly rursiradiate. The secondaries continue the same trend, only turning forward close to the venter. Lateral tubercles are usually present and may be prominent. Secondaries at the ventro-lateral shoulders strongly accentuated, almost into clavi.

Description. The lectotype is a crushed specimen of the *regulare* group. It is involute and moderately ribbed on the inner whorls. At 26 mm the primaries are rectiradiate and terminate in a feeble lateral tubercle just under half-way up the whorl-side. The long secondaries are notably straight, not turning forward until very near the venter. On the outer whorl the secondaries become slightly rursiradiate and the ribbing fades in the centre of the whorl.

Variation. The most typical form found at Staffin is illustrated in Plate 119, fig. 9, whilst coarsely ribbed specimens such as Plate 120, fig. 1 are confined to a single level in the middle of bed 35 at Staffin. Occasionally forms with smooth or striate inner whorls occur as do feebly ribbed individuals. Some of the later forms show sharply rursiradiate secondaries (Plate 119, fig. 10) and begin to approach the subgenus *Amoebites*.

Discussion. A macroconch *A. rosenkrantzi* is figured for the first time as Plate 120, fig. 2. *A. rosenkrantzi* shows sharper, denser ribbing than *A. marstonense* and *A. freboldi*. The ribbing is more rursiradiate than *A. regulare*, whilst the lack of a spiral smooth band distinguishes it from *A. bauhini* and *A. tuberculatoalternans*. One intermediate specimen shows inner whorls very close to *A. lineatum* (Quenstedt), but develops normal outer whorls (Pl. 121, fig. 6). The small *A. praebauhini* (Salfeld) also seems to be a related species.

Range. A. rosenkrantzi ranges throughout its zone.

Distribution. Dorset: Sandsfoot Grit (Wyke Regis, OUM J22041). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Central-east Greenland: Milne Land, glauconites above Pecten Sandstone (JHC 607, GGU 234068); Jameson Land, Hareelv Formation (GGU 143003). North-east Greenland: Bernbjerg Formation (Cardiocerasdal and Rødryggren, Wollaston Foreland, MGUH 8192, GGU 139472, 139485). Arctic Canada: Mackenzie King Island (GSC 15129).

Amoeboceras bauhini (Oppel)

Plate 121, figs. 1–5

1858 *Ammonites alternans* Quenstedt, p. 595, pl. 74, fig. 6 [m] (holotype).
1863 *Ammonites bauhini* Oppel, p. 210.
1887 *Ammonites alternans quadratus* Quenstedt, p. 827, pl. 91, figs. 18–20, 22 [m].
1912 *Cardioceras bauhini* Oppel; D. Sokolov, pp. 44, 64, pl. 3, figs. 9, 10 [m].
cf. 1915 *Cardioceras praebauhini* Salfeld, p. 178, pl. 17, fig. 5 [m].
1915 *Cardioceras bauhini* (Oppel); Salfeld, p. 180, pl. 18, figs. 3–6 [m].
1929 *Cardioceras bauhini* (Oppel); Wegele, p. 34, pl. 28 (4), fig. 7.

Type material. According to Salfeld, the holotype was redrawn (reversed) as Quenstedt's (1887) plate 91, fig. 19. This specimen was refigured by Salfeld (1915, pl. 18, fig. 3), in Tübingen, and a cast is shown here as Plate 121, fig. 1. From Hundsrück, Swabia, White Jura *β*. Oppel cites the existence of seven further paratypes, unspecified.

Dimensions. Holotype: D 26, Wh 0·37, Wb 0·40, Ud 0·35, P 40; Topotype, Salfeld 1915, pl. 18, fig. 4: D 27, Wh 0·43, Wb 0·43, Ud 0·33, P 42.

Description. The diminutive material from Hundsrück in Swabia is characterized by sharp primaries which curve backwards to a lateral tubercle just over half way up the whorl-side. There is then a marked spiral smooth band before short, tuberculate secondaries appear on the ventro-lateral shoulder. The section is quadrate and depressed, whilst the keel is barely raised above the venter.

Discussion. This miniature German species is particularly abundant at the top of bed 37 at Staffin immediately below the Oxfordian–Kimmeridgian boundary, where it coexists with *Ringsteadia* cf. *pseudocordata*. Apart from the Ilovaiskii Subzone fauna of eastern England this appears to be the only other level in Britain and Greenland to yield diminutive *Amoeboceras* of Franco-German affinities. *A. bauhini* is distinguished from earlier German *Amoeboceras* (*A. alternans*, *A. ovale*, etc.) by the prominent spiral smooth band above the lateral tubercles and denser ribbing. *Plasmatites crenulatus* Buckman, 1925 (pl. 618) seems very close, but its age is not known precisely. *A. bauhini* is clearly a microconch, but the nature of its macroconch partner is still wholly problematical.

Range. A. bauhini seems to be restricted to its Subzone at Staffin. In Milne Land it occurs in thin glauconites between Pecten Sandstone and a greensand of the Baylei Zone, associated with *Ringsteadia*, but in neither place does it appear to range up into the Kimmeridgian.

Distribution. Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Greenland: Milne Land, glauconites with *Ringsteadia* (JHC). Franconia: Malm *β*, Bimammatum Zone, upper Hypselum–Hauffianum Subzones (Wegele 1929). Swabia: Malm *β*. Switzerland: Calcaires de Montchalin.

Amoeboceras cf. *tuberculatoalternans* (Nikitin)

Plate 121, fig. 7

1849 *Ammonites cordatus* var. *pinguis* Rouillier, pl. L, fig. 89 [m].
1878 *Ammonites tuberculatoalternans* Nikitin, p. 150.

cf. 1907 *Cardioceras lorioli* Oppenheimer, p. 239, pl. 2, fig. 3 [m].
cf. 1915 *Cardioceras lorioli* Oppenheimer; Salfeld, p. 169, pl. 16, fig. 12.
1915 *Cardioceras tuberculatoalternans* (Nikitin); Salfeld, p. 162, pl. 17, fig. 4 [m].
1916 *Cardioceras tuberculatoalternans* (Nikitin); Nikitin, p. 10, pl. 1, fig. 9 [m].
1931 *Cardioceras tuberculatoalternans* (Nikitin), Dorn, p. 79, pl. 19, fig. 8 [m].

Type material. Type-series indefinite; lectotype, here designated, the specimen figured by Rouillier (1849, fig. 89), from near Moscow.

Dimensions. Measurement of a representative collection from the Lochenschichten in Tübingen University Museum gave the following average dimensions: D 14·9, Wh 0·43, Wb 0·36, Ud 0·30, P 27.

Description. This is a depressed species of the *alternans* group. The primaries are strongly prorsiradiate and end in lateral tubercles only one-third of the way up the flank. There is then a characteristic spiral band which is either smooth or shows very feeble ribbing before strongly rursiradiate secondaries appear.

Discussion. A. cf. *tuberculatoalternans* is the other miniature species to occur in the Bauhini Subzone at Staffin. It is more depressed than *A. bauhini* and its ribbing is less dense and more flexuous. In the absence of clear sutures it is not possible to decide whether these two species are mature or juveniles.

Range. A. cf. *tuberculatoalternans* occurs at Staffin only in the Bauhini Subzone. In the Sub-Mediterranean Province (Jura, Franconia, Moravia) it occurs in the Hypselum Subzone (Dorn 1931), possibly the upper part.

Distribution. East Greenland: Milne Land, together with *A. bauhini* (JHC). Scotland: Flodigarry Shale Member (Staffin, BM/RMS). Swabia: Lochenschichten. Franconia: Hypselum Subzone of the Bimammatum Zone. Czechoslovakia: Moravian Carpathians (Schwedenschanze). U.S.S.R.: Moscow basin.

Superfamily PERISPHINCTACEAE Steinmann, 1890
Family PERISPHINCTIDAE Steinmann, 1890
Genus RINGSTEADIA Salfield, 1913

Type species: *Ammonites pseudocordatus* Blake and Hudleston, 1877.

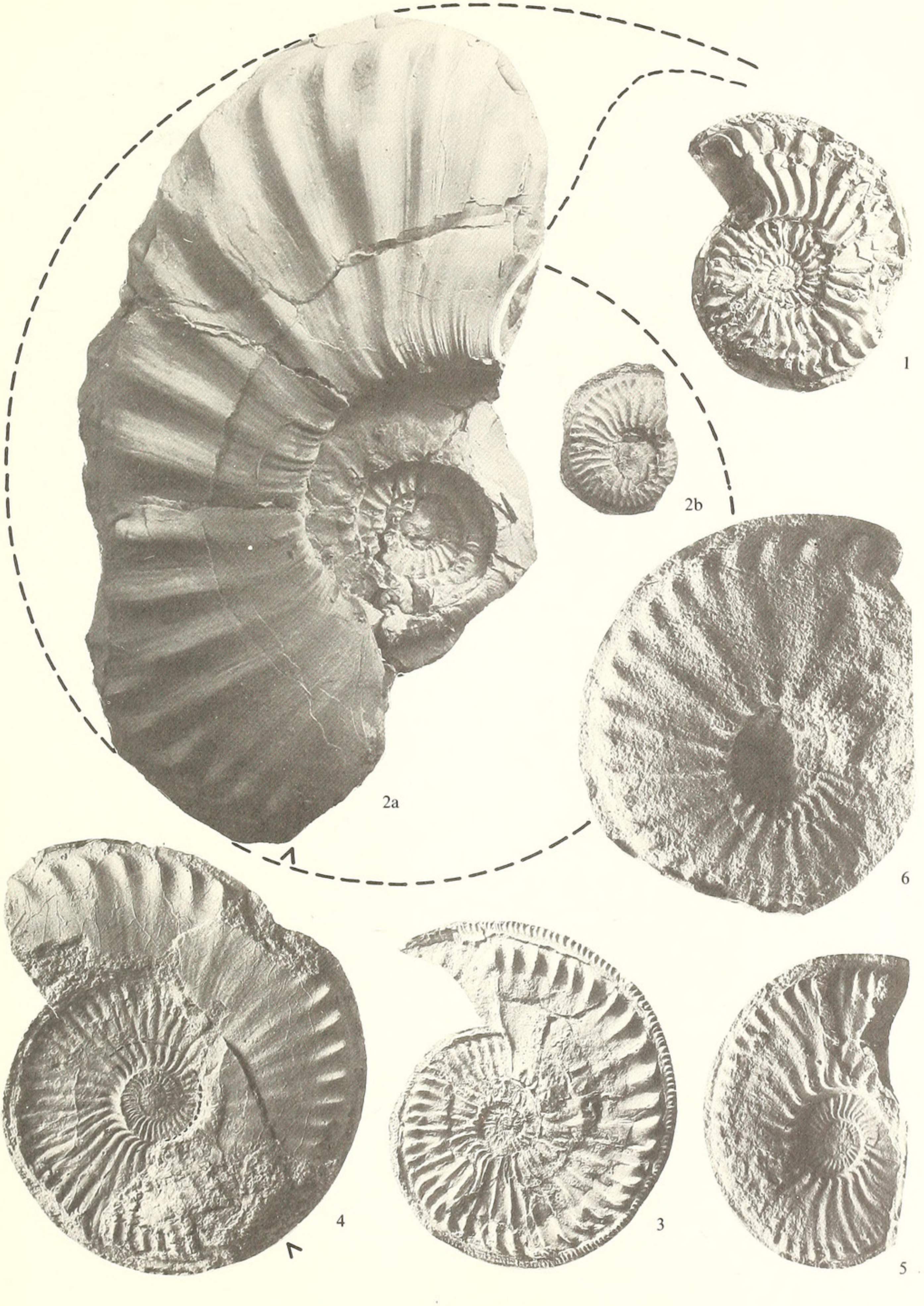
Ringsteadia caledonica sp. nov.

Plate 121, figs. 8–13

cf. 1966 *Ringsteadia* sp., Wierzbowski, p. 138, pl. 9, fig. 1 [M].
aff. 1888 *Ammonites flexuoides* Quenstedt, p. 969, pl. 107, fig. 15 [M].
aff. 1888 *Ammonites streichensis* Oppel, Quenstedt, p. 966, pl. 107, fig. 6 [M].

EXPLANATION OF PLATE 120

Figs. 1–6. *Amoeboceras rosenkrantzi* Spath. 1, very coarse-ribbed [m]. 2*a*, complete [M] with, 2*b*, nucleus of the same specimen. Staffin, Marstonense Subzone, bed 35, 2·5 m above the base (RMS/BM C.80429, -8). 3, lectotype, [M], Cardiocerasdal, Wollaston Foreland, east Greenland (Rosenkrantz Coll., 1929; MGUH 8192). 4, [M], Bays Elv Member, Kap Leslie Formation, glauconites above the Pecten Sandstone with *Ringsteadia bassettensis* Spath, Visdal, Milne Land (Callomon and Birkelund 1979, fauna 12; JHC 607). 5, [m]?, cast of impression, same horizon and locality (JHC/TB Coll. 1977; MGUH 14773). 6, cast of very coarse-ribbed [M], same horizon (MGUH 14772).



SYKES and CALLOMON, *Amoeboceras*

aff. 1907 *Olcostephanus suberinus* (von Ammon); Oppenheimer, p. 236, pl. 20, fig. 20 [M].
aff. 1925 *Ringsteadia salfeldi* Dorn, p. 531, pl. 18, figs. 1-3 [M].
aff. 1963 *Ringsteadia salfeldi* Dorn; Enay, p. 24, pl. 4, fig. 19*a-c* [M].
aff. 1963 *Ringsteadia flexuoides* (Quenstedt); Koerner, p. 374, pl. 27, fig. 3 [M] (discussion of synonymy).

Type series. Holotype, Plate 121, fig. 8 [M]; paratype Plate 121, fig. 13 [m] both from the upper part of the black silty shales with *Amoeboceras rosenkrantzi* near Kildorais, Staffin (bed 33, top), BM C80819-80820 (W. G. Cordey Collection, 1962). Other paratypes, Plate 121, figs. 9-12 [m], top bed 33, and lowest 3 m of bed 35, BM/RMS.

Description. Maximum diameter of holotype (macroconch) 75 mm. Almost all of the last whorl is bodychamber, and the umbilical seam begins to uncoil the final peristome is largely preserved, simple, and preceded by a broad shallow constriction. Hence the shell seems to be that of a complete mature adult. Although crushed, it seems clear that the whorl-section was involute and compressed, with a whorl-height of *c*. 47% and umbilical width *c*. 21% at 60 mm. The ribbing is subdued and irregular at all diameters, the primaries furcating indistinctly or merging into sheaves of intercalatories at about half whorl-height, the secondaries strengthening on the ventrolateral shoulders *c*. 20 primaries and 77 secondaries on the last whorl. Numerous weak flared ribs, shown by the growth lines on the iridescent aragonitic test to coincide with interruptions of growth, are preceded in some cases by fading of the secondaries suggesting weak constrictions. Thus the last whorl is made up of six successive segmental growth-stages. Septal sutures are not visible.

The microconch has a diameter of 30 mm, and seems to be also a complete mature adult, with final constriction and lacking only the lappet. It too is characterized by subdued, irregular ribbing. Some idea of the variability is given by the other paratypes, all with bodychamber, one of which is only partly crushed (fig. 12) and another of which, slightly larger, shows the lappet (fig. 9).

The species is thus small in both its dimorphs, a characteristic feature in comparison with the large forms of the English Pseudocordata Zone and with the later forms found higher in the Rosenkrantzi Zone, and a feature immediately striking when found in the field. Other macroconch specimens in the OUM (Morris Collection, *Ringsteadia staffinensis* MS) range from about 60 to 110 mm in diameter, but are on the whole more evolute than the holotype.

Discussion. In size and general style of ribbing the macroconchs resemble the first true *Ringsteadia* species that appear abruptly in the Hypselum Subzone of the Bimammatum Zone of the Sub-Mediterranean Province (southern France, southern Germany, southern Poland)—the group of *R. flexuoides* listed in the synonymy, but in this group the ribbing is consistently rather sharper, stronger, and more regular. The Polish specimen listed seems the closest match, although more densely ribbed. The microconchs, however, are quite distinct: their subdued ribbing with dense secondaries stands in strong contrast to the sharp, coarse, biplicate ribbing of the microconchs of most if not all the later *Ringsteadia* species usually placed in the genus *Microbiplices*: *M. microbiplex* (Quenstedt) in the Sub-Mediterranean province. The contrast may be seen by comparison with two typical specimens from higher in the Rosenkrantzi Zone of Staffin shown here in Plate 121, figs. 15, 16, which in turn resemble closely the presumed microconchs of *R. flexuoides* (cf. Enay, 1963, pl. 2, figs. 4, 5).

The microconchs of *R. pseudocordata*, *M. anglicus*, differ mainly in being rather larger and more strongly variocostate, in that the coarse biplicate stage is confined mainly to the adult bodychamber.

Range. Regulare Zone, upper part, *caledonica* horizon in Staffin, bed 33, 2·7 m from the top and upwards into the lowest part of the Rosenkrantzi Zone, Marstonense Subzone, bed 35.

RELATION BETWEEN BOREAL/SUB-BOREAL AND SUB-MEDITERRANEAN *AMOEBOCERAS*

Amoeboceras is essentially a Boreal genus which shows a consistent southerly decrease in its numerical abundance (Sykes 1975*b*). The same typically large species are found both in the Boreal and Sub-Boreal Provinces. *Amoeboceras* is also occasionally found in the Sub-Mediterranean faunas of Portugal, eastern France, Switzerland, southern Germany, Moravia and Poland, but only at certain levels. Despite their rarity they are of potentially great interest as one of the few faunal links making possible a closer correlation of the zonal successions in the different faunal provinces. The Boreal succession having been established, it becomes a matter of some importance to clarify the taxonomic and biostratigraphical positions of the Sub-Mediterranean species of *Amoeboceras*. That this may pose serious problems is immediately indicated by the continued use of a quite separate set of specific names, namely those of the classical species of von Buch (1831), Quenstedt (1845, 1887), and Oppel (1863). Three of these are widely enough distributed to merit further discussion, in ascending order.

A. alternans has already been considered above. It is a small and now identifiably characteristic species. The problem remains its precise age. Most of the records in the literature must be disregarded as too imprecise, either taxonomically or stratigraphically or both, but the residual evidence suggests Bifurcatus Zone, possibly the lower part. This is a part of the column in which uncrushed material is scarce in the Boreal Province, but a comparison with the microconch of *A. glosense* of the Glosense Subzone is encouraging. It would help greatly to know what the macroconchs of *A. alternans* look like, but they have not been found in the facies of most of the areas that have yielded this species. An exception may lie in Franconia, notably a specimen figured by Dorn (1931; *Cardioceras excavatum* (non Sowerby), pl. 19 (35), fig. 1).

A. ovale (Quenstedt, 1845) is similarly known only from microconchs and not closely determinable nuclei. In this case it is the comparable Boreal microconchs which are not too well known, but there is a strong resemblance to [m] of *A. serratum* (J. Sowerby, 1813) (compare the specimen figured here as Pl. 117, fig. 2, with Dorn 1931, pl. 18 (36), figs. 25–27) or of *A. freboldi*. Morphologically, the macroconch could well be *A. franconicum* Spath, 1935 (= *C. excavatum* Dorn, 1931, plate 19 (35), fig. 2) but its precise horizon is again not given, although indicated to be much lower, in the Transversarium Zone. The level at which *A. ovale* is most common appears to be the lower part of the Hypselum Subzone.

A. bauhini seems well localized in the upper part of the Hypselum Subzone of the Bimammatum Zone, occurring together with *Ringsteadia flexuoides* (Quenstedt), and this suggest correlation with the lower part of the Rosenkrantzi Zone, with *R. caledonica*. To judge by Wegele's records (1929) the species may range up as far as the Hauffianum Subzone. In Skye the principal occurrence is in the upper part of the Rosenkrantzi Zone, but whether this slight mismatch at subzonal level is real, reflecting slightly different ranges in the two provinces, remains to be established.

There remains the question of the correlation of the Sub-Mediterranean and Boreal Oxfordian–Kimmeridgian boundaries. This must await a detailed study of the amoeboceratids of the Planula and Baylei Zones, but there are already indications that the boundary in the Sub-Mediterranean Province must be drawn lower than normally accepted, putting most if not all of the Planula Zone into the Kimmeridgian.

SUMMARY AND CONCLUSIONS

1. The rarity of the family Perisphinctidae in the Boreal Province makes correlation with the standard zonal scheme problematic. By contrast the Cardioceratidae are common and make ideal zonal and subzonal indices.

2. A unique section at Staffin, Isle of Skye reveals a complete and richly fossiliferous succession of cardioceratid-bearing shales and siltstones throughout the Oxfordian Stage. This locality is proposed as the stratotype for a new biostratigraphic scheme applicable throughout the Boreal Province.

3. In the Middle Oxfordian two principal faunas (Zones) can be recognized: the older one is dominated by *C.* (*Subvertebriceras*) (Densiplicatum Zone); the younger by *C.* (*Miticardioceras*) (Tenuiserratum Zone).

4. The Middle–Upper Oxfordian boundary is drawn at the top of the Tenuiserratum Zone and marks the evolution of *Cardioceras* into *Amoeboceras*.

5. Four main *Amoeboceras* faunas (Zones) are recognizable in the Upper Oxfordian. The oldest fauna includes forms without umbilical tubercles (Glosense Zone). This is followed by trituberculate species in the Serratum Zone, whilst wiry primary ribbing is the characteristic feature of Regulare Zone *Amoeboceras*. The

EXPLANATION OF PLATE 121

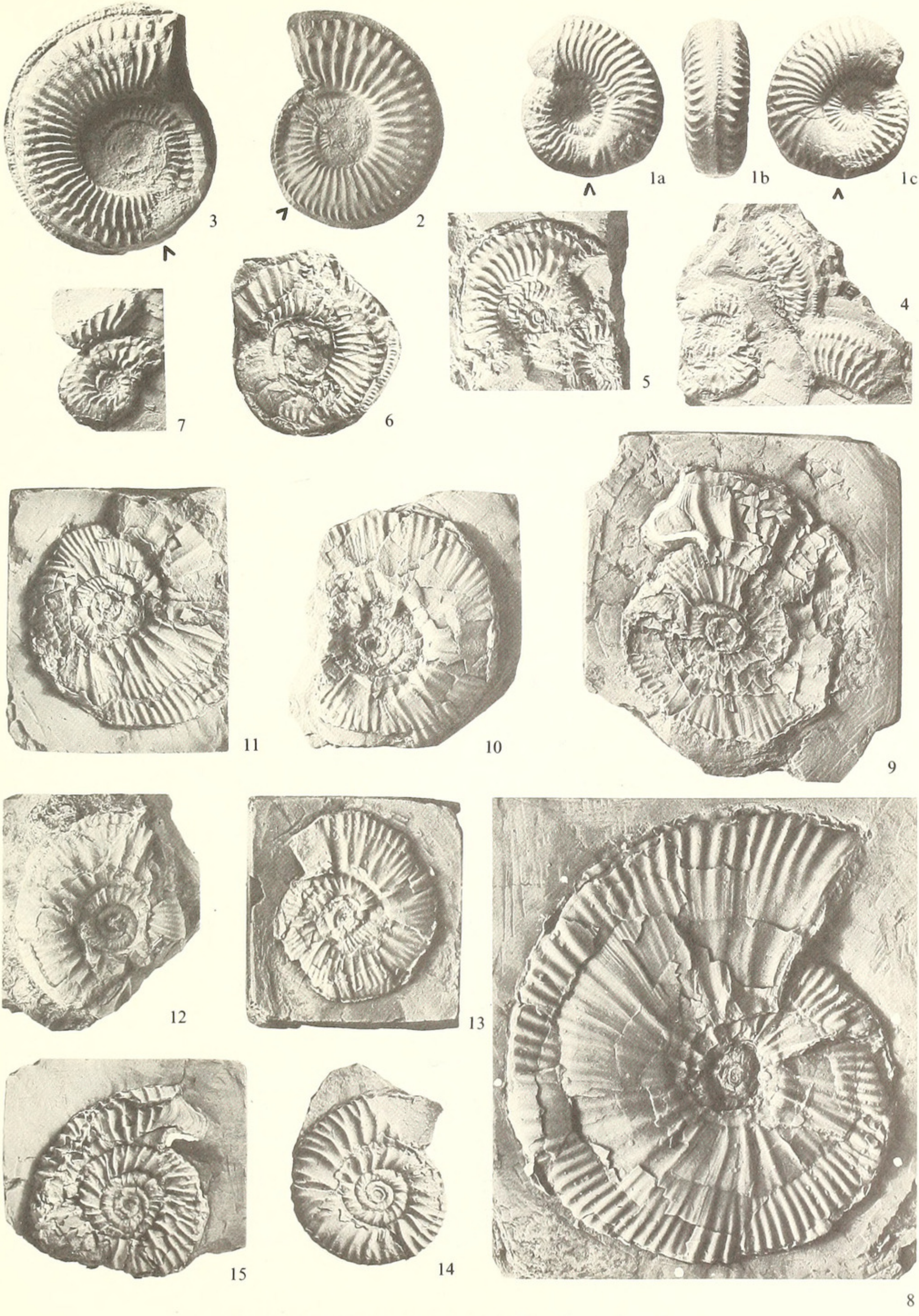
Figs. 1–5. *Amoeboceras bauhini* (Oppel) [m]. 1, cast of holotype (courtesy S. A. Baldwin). White Jura β, Hundsrück, near Balingen, Swabia. (Tübingen, Quenstedt Coll., 1887, pl. 91, fig. 19.) 2, 3, casts of two impressions from the Bays Elv Member, Kap Leslie Formation (Callomon and Birkelund 1979, fauna 13), Bays Bjerge, Milne Land (JHC 836, 636). 4, 5, Staffin, Bauhini Subzone, bed 37, top, 5 m above the base (RMS/BM C.80432a, b).

Fig. 6. *A.* cf. *bauhini* (Oppel) [m]. Form transitional from *A. rosenkrantzi*. Staffin, Bauhini Subzone, bed 37, 3·5 m above the base (RMS/BM C.80433).

Fig. 7. *A. tuberculatoalternans* (Nikitin) [m]. Staffin, Bauhini Subzone, bed 37, base (RMS/BM C.80433).

Figs. 8–13. *Ringsteadia caledonica* sp. nov. 8, holotype, [M], Staffin, Regulare Zone, *caledonica* horizon, bed 33, top (W. G. Cordey Coll. 1962; BM C.80819). White spots indicate discontinuities in shell-growth, preceded by vestigial constrictions. Test preserved, no septal sutures visible. 9, complete adult [m] with lappet; bed 33, 1·7 m from the top (RMS/BM C.80814). 10–12, [m], bed 35, 2·1, 1·0, and 2·7 m above the base (RMS/BM C.80812, -10, -18). 13, paratype of opposite sex to holotype, complete adult with final constriction near the peristome. Bed 33, near the top (W. G. Cordey Coll., 1962; BM C.80820).

Figs. 14–15. *Microbiplices* aff. *anglicus* Arkell [m]. Two complete adults with lappets; Staffin, bed 35, 4·9 and 1·0 m above the base (RMS/BM C.80816, -11).



SYKES and CALLOMON, Jurassic Ammonites

youngest Oxfordian fauna includes morphotypes with rursiradiate ribbing transitional to *Amoebites* (Rosenkrantzi Zone).

6. The regional applicability of the new scheme was checked by use of extensive comparative material from well-documented sections in eastern England, Yorkshire, and east Greenland, and the available evidence suggests that it may be extended to include Canada, and the northern U.S.S.R.

7. The occurrence of the zonal and subzonal indices in southern England and northern France allows correlation between the Boreal and Sub-Boreal Provinces.

8. A taxonomic revision of Upper Oxfordian *Amoeboceras* has been undertaken. Two species, *A. newbridgsense* and *A. koldeweyense*, are new. A new species of *Ringsteadia*, *R. caledonica* is also described.

9. *Amoeboceras* shows relatively little morphological evolution during the Upper Oxfordian. The gross shape stays constant whilst at any one level variation of the ornament is often considerable. Hence large collections are necessary for both taxonomy and biostratigraphy.

10. Only broad stratigraphic and taxonomic comparisons of European and British/Greenlandic *Amoeboceras* can so far be made. Further work on the diminutive European species is necessary fully to comprehend their relationships.

THE TYPE SECTION OF THE STAFFIN SHALE FORMATION

The outcrops of the Staffin Shales occur disjointedly along the western shore of Staffin Bay as shown in text-fig. 4, mainly between low and high watermarks. They are much disturbed and obscured by faulting, land-slips and basalt intrusions, although the tectonics are probably largely trivial, arising mainly from the cambering and slipping of the thick Tertiary lavas which once covered the area, resting on soft clays, as they were cut back by erosion. Precise localities are conveniently referred to a series of reference-points introduced by Anderson and Dunham as Points 1–7 in their large-scale maps of selected exposures (1966, figs. 8–11). Even more detailed maps around Points 1, 2, and 7 were published by Wright (1973). Access to the beach is at a small side-road and farm at Dunans (Point 3), and from side-roads north-east and south-east of Kildorais (Points 5 and 7). Some numbering of beds was introduced by Anderson and Dunham (1966) who treated each exposure separately, and by Turner (1966) who gave no details. By piecing together overlapping partial sections it is now possible to give the almost continuous succession described below, and the beds have therefore been renumbered in sequence from the base of the Staffin Shale Formation upwards.

STAFFIN BAY FORMATION — Thickness, m

Belemnite Sands Member. Lower Callovian, ?Macrocephalus Zone. Calcareous siltstones and sandstones, the top bed glauconitic with belemnites. The only recorded ammonite, *Kepplerites* cf. *keppleri* (Oppel), remains unique.

STAFFIN SHALE FORMATION

Dunans Shale Member. Middle Callovian, Jason Zone and higher?

Type section: foreshore at Point 5 (NG 472708).

1.	Clay, shaly, medium to dark grey, bituminous, with levels of glauconitic silt burrowed by *Chondrites*. *K.* (*Gulielmites*) *medea* Call. abundant at base (Medea Subzone); *K.* (*G.*) *jason* at 0·85 and 1·20 m up (Jason Subzone); higher levels without ammonites. Belemnites abundant in the glauconitic beds. (This bed is not to be confused with similar bituminous shales of the underlying Staffin Bay Formation occurring nearby but full of brackish-water bivalves. Equivalent to Turner's bed 2–3.)	3·25
2.	Shales, laminated, black, bituminous, with *Lingula* and belemnites only.	0·45
3.	Shales, dark grey, bituminous, barren but for occasional belemnites.	3·45

sharp change of facies Thickness, m

Dunans Clay Member. Upper Callovian, Athleta Zone–Lower Oxfordian, Cordatum Zone and Subzone.

Type Section: foreshore at Dunans, midway between Points 3 and 4 (NG 473699). Also extensively exposed in the wave-cut clay platform in the centre of the foreshore at Staffin, although not all the markers of beds 6–20 can be discerned here.

4. Silts and silty clays, light grey-green, the base burrowed by *Chondrites*. Profuse *Bositra buchi* (Roemer) at several horizons. *K.* (*Lobokosmokeras*) *phaeinum* (Buckman), cf. *rowlstonense* (Young and Bird) (Athleta Zone, Phaeinum Subzone; Turner's beds 4a, b). 1·90

5a–c. Two beds (a, c) of carbonate-cemented siltstone ('cementstone') separated by 0·45 m of silty clay (b)—the most prominent marker at Staffin. *Bositra* common throughout, *Kosmoceras* and *Quenstedtoceras* (*Eboraciceras*) spp. from beds (b) and (c), including the holotype of *K. degradatum* (Buckman) (IGS 30450) and topotypes from (c) (Lamberti Zone, Henrici Subzone. Turner's beds 5a–c; Anderson and Dunham's beds 8–10). 0·95

6. Clay, silty, grey-green, with layers of lignitic debris, much bioturbated by *Thalassinoides* and *Chondrites*, and phosphatic nodules. *Bositra* at the base only, succeeded by sporadic nuculacean bivalves belemnites and ammonites: *Kosmoceras* and *Quenstedtoceras* spp. (Lamberti Zone and Subzone); *Cardioceras* (*Scarburgiceras*) (Mariae Zone, Scarburgense Subzone) from 2·20 m upwards (Turner's beds 6–9). 2·55

7. Layer of calcareous, slightly sideritic doggers, weathering reddish (Turner's bed 10). 0·20

8. Clays, as bed 6. *Q. mariae*, *omphaloides*, and *C. scarburgense* in the lower part, *Longaeviceras staffinense* Sykes 2 m above the base. Praecordatum Subzone 3·60 m above the base and upwards (Turner's beds 11–?17). 5·50

9. Layer of doggers, as bed 7. 0·20

10. Silty clays, as bed 6. 1·40

11. Layer of doggers, as bed 7. 0·20

12. Silty clays, as bed 6. Cordatum Zone, Bukowskii Subzone from 0·80 m above base upwards. 2·30

13. Layer of doggers, as bed 7. 0·25

14. Silty clays, as bed 6. 2·70

15. Layer of doggers, as bed 7. 0·20

16. Silty clays, as bed 6. 0·90

17. Layer of doggers, as bed 7. 0·20

18. Silty clays as bed 6. Exact correspondence of beds 12–18 to Turner's bed 18–21 is hard to determine, for the boundary between Praecordatum and Bukowskii Subzones may be variously drawn. Many ammonites from the Bukowskii Subzones were described by Turner (1970). They are characterized particularly by *C.* (*Korythoceras*), the type of *K. korys* Buckman coming from here. 3·90

19. Silty clay, calcareous, harder than the adjacent beds, standing out somewhat on the wavecut platforms as useful marker, in two courses. Costicardia Subzone. 1·50

20. Silty clays, as bed 6, without further markers. Cordatum Subzone from 9·40 m above the base upwards. 12·35

Change of facies, from light grey silty clays to dark grey silts; careful examination of lithologies and removal of seaweed may be necessary to recognize this level.

Glashvin Silt Member. Lower Oxfordian, Cordatum Subzone–Middle Oxfordian, Tenuiserratum Zone and Subzone (text-fig. 3).

Type section: the bulk of the member is exposed south of Point 5 (NG 472708), whence further south beds 4–20 are also exposed. Beds 22–24 in the upper part of the member are best seen in a small cliff at Point 3 (NG 473698) and are only poorly exposed in the boulder-strewn beach between Points 4 and 5. The top of the member, bed 25, is well exposed on the foreshore midway between Points 4 and 5 (NG 472695).

21. Silts, dark grey, with abundant bivalves and ammonites, and subsidiary horizons of light grey-green silty clays as below, or sandy lignitic intercalations; also several cream ash bands, but no easily recognizable markers. Exposures become poor in the upper part of the

Thickness, m

section. The rich faunas of large bivalves in the silts (*Grammatodon*, *Pinna*, *Pleuromya*) contrast sharply with the scattered small *Nuculana* in the clays. Densiplicatum Zone, Vertebrale Subzone from 5·40 m above the base upwards, with horizons dominated by *C.* (*Plasmatoceras*) *tenuistriatum* Borissjak and *popilaniense* Boden. 12·35

gap of unknown but small thickness; base of Tenuiserratum Zone somewhere here

22. Silts, dark grey, with lesser light grey clays, as bed 21: *C.* (*Miticardioceras*) *tenuiserratum* (Oppel) (Tenuiserratum Zone and Subzone) Seen, at Point 3 2·55
23. Sandstone, very fine-grained, silty, forming band in the middle of the cliff at Point 3. 0·10
24. Silt, dark grey, and light clays, as bed 21. 0·80
25. Silts, dark grey, richly fossiliferous. 0·55
Top of the Member is taken at the first bed of light grey fine sandstone seen in the storm beach midway between Points 4 and 5.

Digg Siltstone Member. Middle Oxfordian, Tenuiserratum Zone.

Type Section: base seen clearly between Points 4 and 5 but higher beds quickly become obscured. After a gap the section is resumed on the foreshore south of Point 1 (NG 474694) where the remainder of the unit is exposed. The break between beds 26 and 27 is the only significant gap in the Staffin succession, but to judge by the similarity of lithologies and faunas above and below it is unlikely to be more than a few metres.

26. Sandstones, silty, or sandy silts, light yellow to grey, again rich in bivalves (*Grammatodon*) and ammonites (text-fig. 3). Seen, between points 4 and 5 0·65

gap

27. Sandstone, very fine-grained, or sandy siltstone, yellow to grey, with subordinate dark grey silt. Abundant bivalves (*Grammatodon*) and ammonites. Base of the Blakei Subzone 7·70 m above the base of the exposure. (This bed forms the southern part of bed D_2 of Wright, 1973, fig. 2.) 10·10
28. Nodular sandstone, silty, fine-grained, calcareously cemented. 0·30
29. Silty sandstone as bed 27. (Top of the southern part and base of the northern part of Wright's exposure D_2.) 0·70

major change of facies back to dark shaly clays

Flodigarry Shale Member. Upper Oxfordian–Kimmeridgian.

Type Section: foreshore south of Point 1, as above, for beds 30–32, continued at Point 2 (NG 473696) and exposure D_5 of Wright for beds 33–35. The highest beds 36–37 of the Oxfordian and the overlying beds of the Kimmeridgian continue on the foreshore at Point 7 (NG 468715), exposure F_4 of Wright (1973, fig. 3).

30. Siltstone, dark grey, glauconitic. *Cardioceras* cf. *ogivale* (Buckman) (Blakei Subzone). 2·00
31. Silty clay, medium to dark grey, slightly bituminous, rather poorly exposed in the boulder-strewn beach in the northern part of Wright's exposure D_2. Bivalves very abundant, especially *Trautscholdia* and nuculaceans. Glosense Zone, Ilovaiskii Subzone from 0·60 m above the base; Glosense Subzone from 2·95 m above base; Serratum Zone, Koldeweyense Subzone from 4·50 m above base. 6·20
32. Shale, laminated, bituminous, dark grey, harder than the adjacent beds and forming a marker-ridge in the steeply dipping outcrop. 0·95
33. Silty clays, slightly bituminous, as bed 31. Becoming poorly exposed near the top of the foreshore at the northern end of Wright's D_2, which overlaps slightly with the beds exposed at low watermark at D_5 where the section is continued. Near low watermark the Koldeweyense Subzone is highly fossiliferous, and higher up there are subordinate horizons of siltstone. Serratum Subzone from 12·20 m below the top of the bed; Regulare Zone from 7 m below the top. 20·00

		Thickness, m
34.	Layer of large calcareous doggers.	0·20
35.	Silty clays, slightly bituminous, as bed 31. Rosenkrantzi Zone, Marstonense Subzone from the base upwards.	6·00
36.	Continuous band of carbonate-cemented silty clay, marked on Wright's map as the limestone band below the 'base of the Kimmeridgian' (exposure F_4).	0·35
37.	Silty clays, slightly bituminous, as bed 31. Bauhini Subzone.	5·00
38.	Shale, laminated, hard, black, the bedding-planes strewn with crushed ammonites in chalky preservation: the 'second limestone band' of Wright (1973, p. 453).	0·45
	Oxfordian–Kimmeridgian boundary	
39.	Silty clays with *Amoeboceras* (*Amoebites*) and *Pictonia baylei*: Baylei Zone.	

(Higher beds not recorded: another 20 m of shales and clays rising into the Mutabilis Zone indicated by Wright, p. 455, fig. 4.)

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