

The Sub-Boreal/Boreal ammonite succession at the Oxfordian/Kimmeridgian boundary at Flodigarry, Staffin Bay (Isle of Skye), Scotland

Bronisław A. Matyja, Andrzej Wierzbowski and John K. Wright

ABSTRACT: This paper describes extensive new collections of ammonites made bed-by-bed across the Oxfordian/Kimmeridgian boundary sequence in the Flodigarry sections at Staffin Bay on the Isle of Skye. The ammonites belong to the Sub-Boreal family Aulacostephanidae and the Boreal family Cardioceratidae, enabling recognition of both the current standard Sub-Boreal and Boreal ammonite zonations. In consequence, it is possible to make a close correlation of these two zonal schemes through the interval studied in Skye. The research has provided new palaeontological data at levels of precision that justify the proposal of the section at Staffin as the site of a potential Global Boundary Stratotype Section and Point (GSSP) for the Oxfordian/Kimmeridgian boundary.

The traditional Oxfordian/Kimmeridgian boundary placed at the Pseudocordata/Baylei zonal boundary of the Sub-Boreal zonal scheme corresponds precisely to the Rosenkrantzi/Bauhini zonal boundary of the Boreal zonal scheme. This level is characterised by the appearance of the first *Pictonia* (*Pictonia flodigarriensis* sp. nov.) together with first *Prorasenia*, replacing an older assemblage of *Ringsteadia*–*Microbiplipes* (Sub-Boreal). It is also characterised by the first occurrence of small-sized *Amoeboceras* (*Plasmatites*) spp., as well as large *Amoeboceras schulginae* Mesezhnikov (Boreal). An alternative level that may be considered as a potential GSSP is the boundary between the Bauhini Zone and the Kitchini Zone of the Boreal zonal scheme, characterised by first occurrence of *Amoeboceras* (*Amoebites*) of the *A. bayi* group. This level corresponds to the Planula/Galar subzonal boundary of the Sub-Mediterranean zonal scheme, and lies close to the currently accepted Oxfordian/Kimmeridgian boundary in the Sub-Mediterranean Province.

KEY WORDS: ammonites, biostratigraphy, Boreal zonation, correlation, Sub-Boreal zonation

The uppermost Oxfordian–lowermost Kimmeridgian deposits exposed at Staffin Bay in the Trotternish region of northern Skye (western Scotland) are among the stratigraphically most complete and richest in ammonites in Britain. They are developed as dark silty and shaly clays with bands of limestone nodules, and are included in the highest part of the Flodigarry Shale Member of the Staffin Shale Formation (Turner 1966; Sykes 1975; see also Sykes & Callomon 1979; Morton & Hudson 1995; Wright 2001). The deposits yield abundant ammonites belonging to two families, the Aulacostephanidae, typical of the Sub-Boreal Province and the Cardioceratidae, typical of the Boreal Province (Wright 1973, 1989; Sykes & Callomon 1979; Birkelund & Callomon 1985; Matyja *et al.* 2004). The co-occurrence of ammonites belonging to these two families is of great importance for the detailed biostratigraphical correlation of the Sub-Boreal and Boreal zonal schemes, and for precise recognition of the Oxfordian/Kimmeridgian boundary.

The Kimmeridgian Stage was defined originally within the Sub-Boreal ammonite succession with its base placed at the base of the Baylei Zone – the lowest ammonite zone of the Kimmeridge Clay in Dorset, southern England (Salfeld 1913, see also Arkell 1947b). Subsequent attempts at identifying the base of the Kimmeridgian Stage elsewhere, within the Boreal and Sub-Mediterranean/Mediterranean ammonite successions, were based on this original definition. However, it has since become apparent that some of the correlations were incorrect, resulting in the location of the Oxfordian/Kimmeridgian boundary at different chronostratigraphic horizons in separate ammonite successions. The difference is especially acute between the Sub-Boreal/Boreal, and the Sub-Mediterranean/

Mediterranean ammonite successions and their corresponding zonal schemes (Schweigert 1995; Matyja & Wierzbowski 1997; Schweigert & Callomon 1997).

It seemed to the present authors that the first step to clarify the correlation problem would be to study a detailed ammonite succession across the Oxfordian/Kimmeridgian boundary in a continuous succession which combined elements of both the Sub-Boreal and Boreal provinces, preferably in the UK. None of the Dorset sections offers such a possibility due to the existence of a stratigraphical gap at the base of the Kimmeridge Clay in that region (see e.g. Arkell 1956), as well as an almost total lack of Boreal ammonites of the family Cardioceratidae. Of the more complete successions in clay facies, that at South Ferriby, Lincolnshire (Cox 2001a) lacks a really good sequence of Boreal ammonites. The sections at Staffin Bay in the Isle of Skye, and especially the best of them at Flodigarry, showing very complete Boreal and Sub-Boreal ammonite successions, form the best natural link between the Sub-Boreal and Boreal ammonite provinces, and the ammonite subdivisions recognised therein. Moreover, the standard ammonite zonal scheme for the Boreal Upper Oxfordian was largely defined at Staffin, and the position of the Oxfordian/Kimmeridgian boundary inferred there (Sykes & Callomon 1979; Birkelund & Callomon 1985; see also Wierzbowski & Smelror 1993). For these reasons we undertook a detailed study of the Flodigarry section at Staffin Bay, carried out under the remit of the Oxfordian/Kimmeridgian Boundary Working Group of the International Subcommittee of Jurassic Stratigraphy of the IUGS. The preliminary results of our study were presented during the 6th International Symposium on the Jurassic System at Mondello, Sicily in



The Sub-Boreal/Boreal ammonite succession at the Oxfordian/Kimmeridgian boundary at Flodigarry, Staffin Bay (Isle of Skye), Scotland

Bronisław A. Matyja, Andrzej Wierzbowski and John K. Wright

ABSTRACT: This paper describes extensive new collections of ammonites made bed-by-bed across the Oxfordian/Kimmeridgian boundary sequence in the Flodigarry sections at Staffin Bay on the Isle of Skye. The ammonites belong to the Sub-Boreal family Aulacostephanidae and the Boreal family Cardioceratidae, enabling recognition of both the current standard Sub-Boreal and Boreal ammonite zonations. In consequence, it is possible to make a close correlation of these two zonal schemes through the interval studied in Skye. The research has provided new palaeontological data at levels of precision that justify the proposal of the section at Staffin as the site of a potential Global Boundary Stratotype Section and Point (GSSP) for the Oxfordian/Kimmeridgian boundary.

The traditional Oxfordian/Kimmeridgian boundary placed at the Pseudocorda/Baylei zonal boundary of the Sub-Boreal zonal scheme corresponds precisely to the Rosenkrantzi/Bauhini zonal boundary of the Boreal zonal scheme. This level is characterised by the appearance of the first *Pictonia* (*Pictonia flodigarriensis* sp. nov.) together with first *Prorasenia*, replacing an older assemblage of *Ringsteadia*–*Microbiplites* (Sub-Boreal). It is also characterised by the first occurrence of small-sized *Amoeboceras* (*Plasmatites*) spp., as well as large *Amoeboceras schulginae* Mesezhnikov (Boreal). An alternative level that may be considered as a potential GSSP is the boundary between the Bauhini Zone and the Kitchini Zone of the Boreal zonal scheme, characterised by first occurrence of *Amoeboceras* (*Amoebites*) of the *A. bayi* group. This level corresponds to the Planula/Galar subzonal boundary of the Sub-Mediterranean zonal scheme, and lies close to the currently accepted Oxfordian/Kimmeridgian boundary in the Sub-Mediterranean Province.

KEY WORDS: ammonites, biostratigraphy, Boreal zonation, correlation, Sub-Boreal zonation

The uppermost Oxfordian–lowermost Kimmeridgian deposits exposed at Staffin Bay in the Trotternish region of northern Skye (western Scotland) are among the stratigraphically most complete and richest in ammonites in Britain. They are developed as dark silty and shaly clays with bands of limestone nodules, and are included in the highest part of the Flodigarry Shale Member of the Staffin Shale Formation (Turner 1966; Sykes 1975; see also Sykes & Callomon 1979; Morton & Hudson 1995; Wright 2001). The deposits yield abundant ammonites belonging to two families, the Aulacostephanidae, typical of the Sub-Boreal Province and the Cardioceratidae, typical of the Boreal Province (Wright 1973, 1989; Sykes & Callomon 1979; Birkelund & Callomon 1985; Matyja *et al.* 2004). The co-occurrence of ammonites belonging to these two families is of great importance for the detailed biostratigraphical correlation of the Sub-Boreal and Boreal zonal schemes, and for precise recognition of the Oxfordian/Kimmeridgian boundary.

The Kimmeridgian Stage was defined originally within the Sub-Boreal ammonite succession with its base placed at the base of the Baylei Zone – the lowest ammonite zone of the Kimmeridge Clay in Dorset, southern England (Salfeld 1913, see also Arkell 1947b). Subsequent attempts at identifying the base of the Kimmeridgian Stage elsewhere, within the Boreal and Sub-Mediterranean/Mediterranean ammonite successions, were based on this original definition. However, it has since become apparent that some of the correlations were incorrect, resulting in the location of the Oxfordian/Kimmeridgian boundary at different chronostratigraphic horizons in separate ammonite successions. The difference is especially acute between the Sub-Boreal/Boreal, and the Sub-Mediterranean/

Mediterranean ammonite successions and their corresponding zonal schemes (Schweigert 1995; Matyja & Wierzbowski 1997; Schweigert & Callomon 1997).

It seemed to the present authors that the first step to clarify the correlation problem would be to study a detailed ammonite succession across the Oxfordian/Kimmeridgian boundary in a continuous succession which combined elements of both the Sub-Boreal and Boreal provinces, preferably in the UK. None of the Dorset sections offers such a possibility due to the existence of a stratigraphical gap at the base of the Kimmeridge Clay in that region (see e.g. Arkell 1956), as well as an almost total lack of Boreal ammonites of the family Cardioceratidae. Of the more complete successions in clay facies, that at South Ferriby, Lincolnshire (Cox 2001a) lacks a really good sequence of Boreal ammonites. The sections at Staffin Bay in the Isle of Skye, and especially the best of them at Flodigarry, showing very complete Boreal and Sub-Boreal ammonite successions, form the best natural link between the Sub-Boreal and Boreal ammonite provinces, and the ammonite subdivisions recognised therein. Moreover, the standard ammonite zonal scheme for the Boreal Upper Oxfordian was largely defined at Staffin, and the position of the Oxfordian/Kimmeridgian boundary inferred there (Sykes & Callomon 1979; Birkelund & Callomon 1985; see also Wierzbowski & Smelror 1993). For these reasons we undertook a detailed study of the Flodigarry section at Staffin Bay, carried out under the remit of the Oxfordian/Kimmeridgian Boundary Working Group of the International Subcommission of Jurassic Stratigraphy of the IUGS. The preliminary results of our study were presented during the 6th International Symposium on the Jurassic System at Mondello, Sicily in



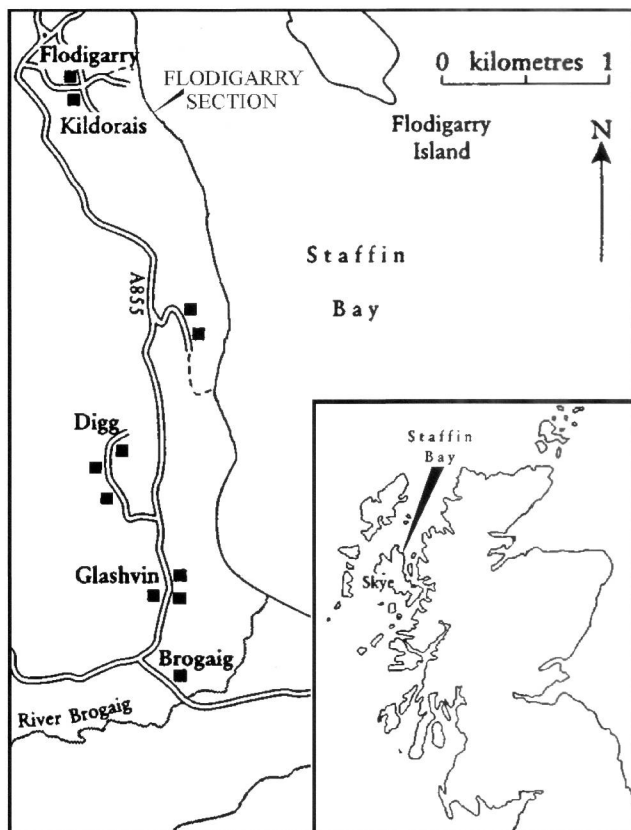


Figure 1 Locality map of Staffin Bay and the Flodigarry section (from Matyja *et al.* 2004).

September 2002, and published in the symposium volume (Matyja *et al.* 2004).

1. General details of the sections studied

The Flodigarry Shale Member outcrops in two restricted areas of foreshore at Flodigarry and Digg in Staffin Bay (Fig. 1). These deposits are exposed on the intertidal rock platform, some areas of shale being obscured by a covering of seaweed and basalt and dolerite boulders. The deposits are cut in a few places by dolerite dykes and sills which show very limited thermally altered zones. The strata generally dip steeply to the west, and are cut by small faults which divide the exposures into numerous tectonic blocks showing some differences in dip. The tectonic complexity is related to the Quirang landslip, which originated in the base of the Palaeocene basalt scarp of Trotternish and which affected the Flodigarry Shale Member deposits of the area of Staffin Bay (Anderson & Dunham 1966; see also Wright 1989).

The importance of the Staffin outcrops for studies of the Oxfordian/Kimmeridgian boundary was first noted by Anderson & Dunham (1966), these authors presenting provisional lists of ammonites and maps of the sections. Morris (1968) collected a substantial number of ammonites from the Flodigarry sections. The subsequent work of Wright (1973) and especially the definitive work of Sykes & Callomon (1979) was largely carried out in the Digg sections to the south (Fig. 1). However, the condition of these small outcrops has deteriorated substantially in recent years, and Kimmeridgian exposures are very limited here, so that subsequent work has been concentrated on the much better Flodigarry sections. Wright (1989) provided the first comprehensive description of the Kimmeridgian sequence here, and the work of Sykes & Callomon (1979) and Wright (1989) was synthesised and

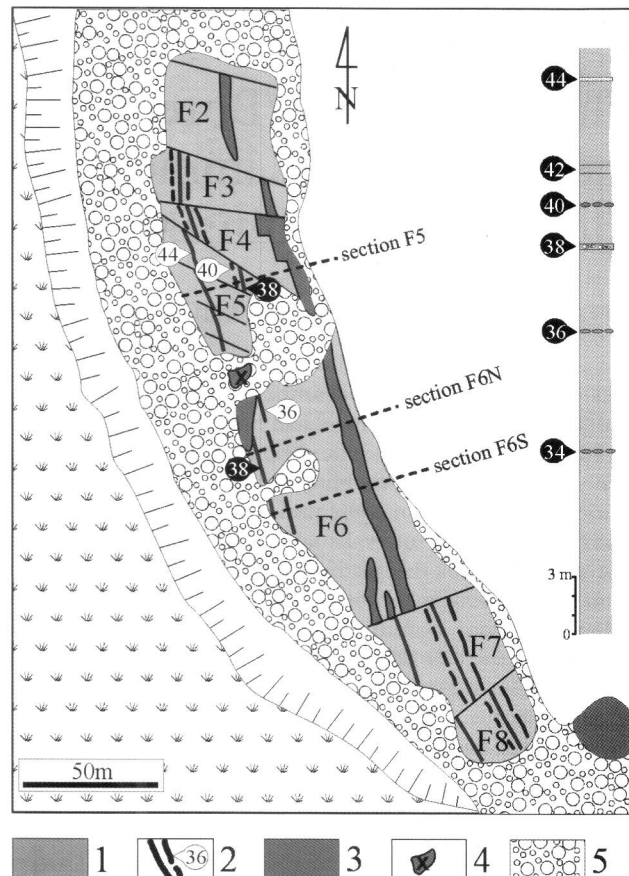


Figure 2 Map of the foreshore at Flodigarry with detailed log: 1—shale; 2—numbered marker beds; 3—dolerite sills; 4—prominent dolerite sill; 5—boulders.

updated by Morton & Hudson (1995), Cox (2001b) and Wright (2001).

The beach outcrops at Flodigarry were re-surveyed in detail for the present work, and the resulting map (Fig. 2) differs to some extent from those maps published previously (Wright 1973, 1989; Morton & Hudson 1995; Wright 2001; Hesketh & Underhill 2002). The interval of Flodigarry Shale Member studied spans bed SS 33 (upper part) to bed SS 45, according to the standard subdivision of the Staffin Shale Formation between Digg and Flodigarry introduced by Sykes & Callomon (1979), and summarised by Morton & Hudson (1995). The three sections chosen for detailed biostratigraphical study in the present paper are situated close together on the foreshore at Flodigarry, where the deposits show only minor tectonic disturbance and are exposed the most completely. Two of the sections are situated in the northern part of the block F6, about 60 and 25 metres south of the prominent sill marked on Figure 2 (coordinates of the middle part of the sections are: N57°39'39.5", W6°14'43.9", and N57°39'40.5", W6°14'45.0"), and denoted herein as F6S, and F6N, respectively (Fig. 2). The third section is situated in the middle part of the neighbouring block F5, 26 metres north of the prominent sill (coordinates of the middle part of the section are: N57°39'42.1", W6°14'46.7"), and is denoted as F5. The present work confirms the general sequence of beds and thicknesses given by Sykes & Callomon (1979), Wright (1989), Morton & Hudson (1995), Cox (2001b) and Hesketh & Underhill (2002), although some smaller differences in thicknesses of particular beds can be noticed (Figs 2, 3). The continuous sequence of deposits comprises predominately silty clays (beds SS 33, 35, 37, 39, 41, 42) and shaly clays and clays (beds SS 38, 43, 45) with thin layers (horizons) of calcareous

doggers or nodules (beds SS 34, 36, 40), and a thin, variably developed, argillaceous sandstone (bed SS 44). The correlation of particular beds between the three sections does not present any difficulties, and this enables the recognition of the complete succession of ammonite faunas in the sequence studied.

The ammonites were collected at 66 levels: among them 34 in measured sections in block F6 (15 levels in section F6S; and 19 levels in section F6N), and 32 levels in block F5, in measured section F5. The position of each level was carefully measured and checked in relation to characteristic lithological horizons, such as the thin sandstone (bed SS 44), the band of limestone nodules (bed SS 36), and the characteristic dark, shaly clay rich in ammonites of the genus *Pictonia* (bed SS 38). Additionally, ammonites were collected at six levels directly below bed SS 36 in the easternmost part in block F7. The thicknesses of beds, and relative position of the ammonite assemblages, were measured to the nearest centimetre by stretching a tape across the steeply inclined beds on the rock platform; the measurements were reduced according to dip values: about 70°–78° for section F5, and from 75°, through about 60°, to about 70° for younger, middle (around bed 37), and older strata (down to bed 33), respectively, for sections F6S, and F6N. The position of the particular ammonite assemblages is given in metres in relation to the positions of bed SS 36 and bed SS 44 in the sections studied. The biostratigraphy of the time-diagnostic ammonites is shown in Figure 3.

2. Genera and species

During latest Oxfordian and earliest Kimmeridgian, the Aulacostephanidae formed a smoothly evolving lineage from *Ringsteadia* through *Pictonia* to *Rasenia* (mostly macroconchs), and from *Microbiplices* to *Prorاسenia* (microconchs) (see Birkelund & Callomon 1985). The Cardioceratidae ranged from the *Amoeboceras regulare* group through the *Amoeboceras rosenkrantzi* group, and then through small-sized forms of the subgenus *Plasmatis* (the *A. bauhini* group) up to the first *Amoebites* (see Birkelund & Callomon 1985).

Specific names in what follows are used in the sense of morphospecies, having vertical ranges, as opposed to isochronous 'horizontal' assemblages thought to represent what had been variable biospecies, phyletic transients in an evolving lineage (see Callomon 1985). Generic names are used in a similarly morphogeneric sense. The dimorphism strongly marked in shell morphology within the Aulacostephanidae is thus similarly expressed morphotaxonomically at the generic and species levels. Changes of generic name for what were most probably merely successive segments of a single lineage, e.g. from *Ringsteadia* to *Pictonia*, may therefore be arbitrary and reflect merely historical conventions. The dividing lines between particular genus rank taxa are placed commonly at the level where the new features typical of the forthcoming taxon become dominant—e.g. the dominance of bullate ribs, recognised as indicative of the oldest *Rasenia* faunas (Birkelund & Callomon 1985). A dominance of new features sometimes appears quite suddenly in the succession. This may have resulted either from a slow rate of sedimentation or accelerated evolutionary transformation. Typical examples in the section studied are the transitions from *Ringsteadia* into *Pictonia* (macroconchs) and *Microbiplices* into *Prorاسenia* (microconchs).

A review of the genus rank taxa of the Aulacostephanidae and Cardioceratidae in the Sub-Boreal and Boreal provinces is given herein in the systematic palaeontology section.

Some 300 aulacostephanids and cardioceratids were collected by the present authors from the Staffin sections. The collection is housed in the University Museum, Oxford, collections ST600 to ST926. The following abbreviations are used in the description of the ammonites: D—diameter of specimen in mm, Wh—whorl height as percentages of D; Ud—umbilical diameter as percentages of D; PR—number of primary ribs per whorl.

3. The standard ammonite chronozones and chronosubzones of the Sub-Boreal Oxfordian/Kimmeridgian boundary succession

3.1. Pseudocordata Zone

Index: *Ringsteadia pseudocordata* (Blake & Hudleston). Holotype from the Westbury Ironstone of Wiltshire, refigured by Buckman (1925b, pls 560A, 560B).

Definition. Subdivided into Caledonica, Pseudoyo, Pseudocordata and Evoluta Subzones. The Zone includes all the British ammonite faunas consisting of *Ringsteadia* and its microconch counterpart (mostly *Microbiplices*, also forms transitional between *Microbiplices* and *Prorاسenia*).

Horizon at Staffin. This zone is represented in the deposits outcropping at Flodigarry from 14.72 m below bed 36 (i.e. down to bed 33) to 1.24 m below bed 36. This means that the total thickness of the zone is about 13.5 m (or even a little more).

3.1.1. Caledonica Subzone

Index: *Ringsteadia caledonica* Sykes & Callomon. Holotype from the top of Bed 33 of the Staffin Shale at Flodigarry, Skye, described and figured by Sykes & Callomon (1979, p. 890, pl. 121, fig. 8).

Definition. Introduced by Sykes & Callomon (1979) as the *caledonica* horizon of the Boreal Regular Zone, and defined as the upper part of the zone at Staffin by Sykes & Callomon. Used as a formal subzone of the Pseudocordata Zone by Wright (1980).

Characteristic fauna and horizon at Staffin. The oldest fauna of *Ringsteadia*, consisting of *R. caledonica*, is found 14.72 m below bed 36. The fauna includes small forms of this genus, representing both macro- and microconchs (75 mm and 30 mm in diameter respectively). Both have irregular, subdued ornament, with numerous flared ribs preceded in some cases by possible weak constrictions. Microconchs have a similar style of ribbing to the macroconchs, but the adults have lappets (Sykes & Callomon 1979). This same fauna has been placed from about 9 m to 3.3 m below bed 36 in the Staffin Bay area by Sykes & Callomon (1979, p. 855, 893, 894). This position in the sections differs markedly from that stated in the present paper, and we were unable to find *R. caledonica* at these higher levels. Moreover, the stratigraphical range of *R. caledonica* as indicated by Sykes & Callomon (1979) corresponds to the stratigraphical range of *R. pseudoyo*, and even partly *R. pseudocordata*, as recognised in the present paper (see Fig. 3).

3.1.2. Pseudoyo Subzone

Index: *Ringsteadia pseudoyo* Salfeld. Holotype from the Marston Ironstone of Wootton Bassett, Wiltshire, described and figured by Salfeld (1917, p. 74, pl. 8, figs 1a, b).

Definition. Introduced by Morris (1968) as the fauna of the "Upper Calcareous Grit" (=Marston Ironstone) of Marston, near Swindon, Wiltshire, and included in the formal correlation table of Sykes & Callomon (1979). *Perispinctes*, *Euaspidoceras* and *Amoeboceras marstonense* Spath are characteristic in addition to the distinctively involute platycone *R. pseudoyo* and *R. spp.*

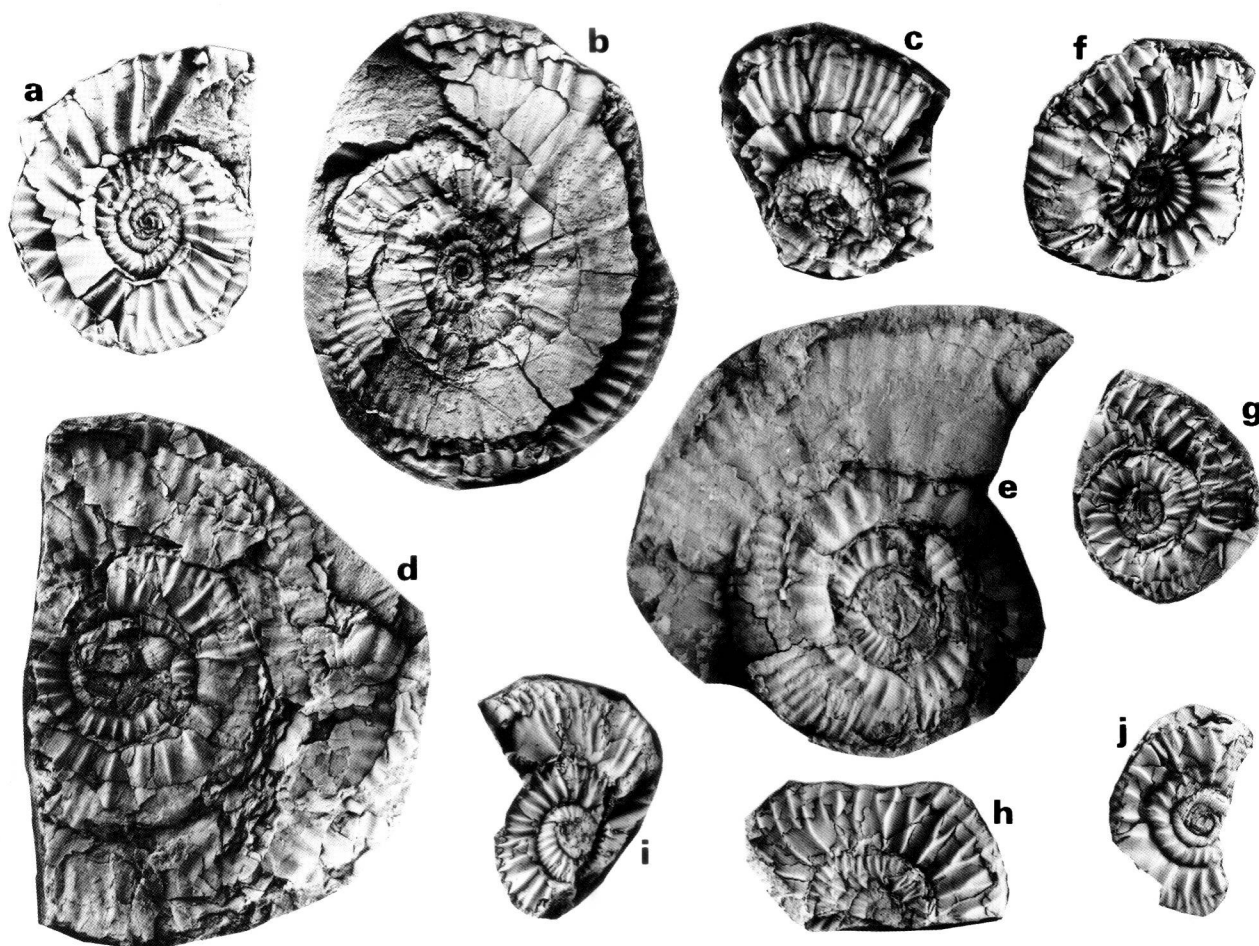


Figure 4 Aulacostephanid ammonites from the Pseudocordata and Baylei zones (all specimens actual size). (a) *Microbiplices microbiplex* (Quenstedt): ST826; Flodigarry, section F6N, bed 33, 13.85 m below bed 36; Pseudocordata Zone, Pseudoyo Subzone. (b) *Ringsteadia* ex gr. *pseudoyo* Salfeld: ST827; Flodigarry, bed 33, about 7.5 m below bed 36; Pseudocordata Zone, Pseudoyo Subzone. (c) *Ringsteadia* sp. showing inner whorls with *Pictonia* type ornamentation: ST828; Flodigarry, section F6S, bed 35, 2.34 m below bed 36; Pseudocordata Zone, Pseudocordata Subzone. (d–e) *Ringsteadia evoluta* Salfeld: Flodigarry, section F6S, bed 35; (d) ST829; 1.4 m below bed 36, Pseudocordata Zone, Evoluta Subzone; (e) ST830; 1.8 m below bed 36, Pseudocordata Zone, Evoluta Subzone. (f–h) *Microbiplices/Prorasenia* transitional form: Flodigarry, section F6S, bed 35, Pseudocordata Zone, Evoluta Subzone: (f) ST831; 1.65 m below bed 36; (g–h) ST832, ST833; 1.4 m below bed 36. (i) *Prorasenia hardyi* Spath: ST834; Flodigarry, section F5, bed 41, 5.7 below bed 44; Baylei Zone, Normandiana Subzone. (j) *Prorasenia bowerbanki* Spath: ST835; Flodigarry, section F7, bed 35, 0.6 m below bed 36; Baylei Zone, Densicostata Subzone, *flodigarriensis* horizon.

Characteristic fauna and horizon at Staffin. The oldest ammonites characteristic of this subzone, *Ringsteadia brandesi* Salfeld and *Microbiplices* sp., were found 13.85 m below bed 36 (i.e. still within bed 33). The *Microbiplices* (Fig. 4a) attain about 40 mm in final diameter, and are moderately evolute (at $D=30\text{--}40$ mm, $Wh=32.5\%$, $Ud=40\text{--}42.5\%$). Up to about $D=25$ mm, they are fairly densely, and somewhat irregularly ribbed, with biplicate, triplicate and intercalatory ribs, and the presence of distinct constrictions ($PR=34\text{--}28$). On the last whorl the ribbing becomes regularly biplicate ($PR=26$). These features show the close similarity of these specimens to *Microbiplices microbiplex* (Quenstedt). A specimen of *Ringsteadia* ex gr. *pseudoyo* found near the top of the subzone at about 7.5 m below bed 36 (Fig. 4b) is characteristically strongly involute (at $D=62$ mm, $Ud=19.3\%$, $Wh=42\%$), showing typical moderately dense, regular ribbing.

3.1.3. Pseudocordata Subzone

Index: as for the Zone.

Definition. Introduced by Morris (1968) for the fauna of the Westbury Ironstone, Wiltshire. Sykes & Callomon (1979, p. 857) added the fauna of the Sandsfoot Grit of Dorset. *Microbiplices* and *Amoeboceras rosenkrantzi* Spath are also

characteristic, in addition to *R. pseudocordata* (Sykes & Callomon 1979; Wright 1998).

Characteristic fauna and horizon at Staffin. *Ringsteadia* cf. *pseudocordata* and *Microbiplices* spp. (including *M. anglicus* Arkell) occur from 7.28 m to 2.34 m below bed 36, i.e. from the uppermost part of bed 33 to the middle part of bed 35. The more evolute *Microbiplices* specimens are generally comparable to the type specimens of *M. anglicus* (see Arkell 1947a, pl. 76, figs 6a, b, 7a, b). Some specimens occurring in this interval still show the dense ribbing and moderately evolute coiling typical of *M. microbiplex* (for instance Sykes & Callomon 1979, pl 121, fig. 15, found about 5 m below bed 36).

3.1.4. Evoluta Subzone

Index: *Ringsteadia evoluta* Salfeld. Holotype from the Osmington Mills Ironstone of Osmington Mills, Dorset, described and figured by Salfeld (1917, p. 84, pl. 12, figs 1a, b).

Definition. Introduced by Morris (1968) for the fauna of the Ringstead Coral Bed of Dorset. Formally defined as such by Sykes & Callomon (1979, p. 857). The definition was expanded by Wright (2003) to include the fauna of the Osmington Mills Ironstone, of which the Ringstead Coral Bed is part.

Characteristic fauna and horizon at Staffin. *Ringsteadia evoluta* Salfeld occurs together with forms transitional between *Microbiplices* and *Prorاسenia* from 1.8 m to 1.24 m (possibly also 1.1 m) below bed 36. The specimens of *Ringsteadia*, mostly 60–70 mm in diameter, but also 140 mm and 230 mm, are characterised by fairly evolute coiling (Ud=44%–48%), and fairly strong and distant ribbing (PR=23–26), and compare well with *R. evoluta* (Fig. 4d, e).

3.1.5. Pseudocordata/Baylei zone boundary

The dividing line between *Ringsteadia* and *Pictonia* is discussed in the systematics section of this paper. Based on the choice made there, the boundary between the Pseudocordata Zone and the Baylei Zone, i.e. the boundary between the Sub-Boreal Oxfordian and Kimmeridgian, lies in the 0.16 m thick interval between the highest occurrence of *Ringsteadia* (1.24 m below bed 36) and the first occurrence of *Pictonia* (1.08 m below bed 36). Such a position of the Oxfordian/Kimmeridgian boundary as inferred from distribution of the aulacostephanid ammonites is at least 1 m lower than previously assumed (cf. Birkelund & Callomon 1985, pp. 16–17).

3.2. Baylei Zone

Index: *Pictonia baylei* Salfeld. Holotype from the Lower Kimmeridgian Calcaires coquilliers of Normandy, described and refigured by Hantzpergue (1989, p. 214, pl. 21a). Gallois (2005) gives details of the Normandy Kimmeridgian sections.

Definition. Introduced by Salfeld (1913, p. 423) for the fauna of *Pictonia* spp. found on the Dorset coast characterising the lowest Zone of the Kimmeridgian Stage. Arkell (1933) noted the presence of the typical species of *Pictonia* in the Inconstans Bed, the basal bed of the Kimmeridge Clay Formation traceable at many localities across England from Dorset to Yorkshire. Most subsequent authors (i.e. Sykes & Callomon 1979, p. 857; Birkelund & Callomon 1985, p. 17; Schweigert & Callomon 1997, p. 43; Cox 2001a, p. 123) have placed the base of the Baylei Zone immediately below the appearance of *Pictonia densicostata* (Salfeld MS) Buckman, the characteristic species of the Inconstans Bed. However, on the Dorset coast, the lower boundary of the Baylei Zone as so defined corresponds to the major non-sequence at the base of the Inconstans Bed (see e.g. Arkell 1956). Below, in the Osmington Mills Ironstone Member (which includes the Ringstead Coral Bed), fairly abundant specimens of *Ringsteadia evoluta* Salfeld are known to occur indicating the uppermost part of the Pseudocordata Zone: these consist almost exclusively of heavily-ribbed forms having nothing in common with *Pictonia densicostata*. Thus, the acceptance of the Baylei Zone as the lowest subdivision of the Kimmeridgian Stage as recognised on the Dorset coast led to the problem from the very beginning of the location of the precise boundary between Oxfordian and Kimmeridgian, there being a morphological gap between *Ringsteadia* and *Pictonia* in Dorset. It should also be remembered that a marked hiatus must occur at the junction of the Pseudocordata and Baylei zones, i.e. at the boundary of the Oxfordian and Kimmeridgian, in many other English sections (see e.g. Wignall 1990; Cox 2001a). At Staffin, the first occurrence of *Pictonia* is represented by *Pictonia flodigarriensis* sp. nov. *P. densicostata* appears at Flodigarry well above *P. flodigarriensis*, indicating that the sections at Staffin Bay are much more complete than the English sections (see also Matyja et al. 2004). We propose to distinguish the *flodigarriensis* biohorizon as the lowest level of the Baylei Chronozone. The reason for such a re-definition of the Baylei Zone is that it gives the zone a larger correlation potential, and the Staffin section where the re-definition is made becomes suitable as the candidate for the GSSP.

Two or three informal faunal horizons have been recognised previously in the Baylei Zone (see Birkelund & Callomon 1985; Hantzpergue 1989; Schweigert & Callomon 1997). These are the *densicostata*, *baylei* and *normandiana* horizons (the two latter were often treated together). According to present work, a further horizon is present, at the base of the Baylei Zone – the *flodigarriensis* horizon. However, a formal subdivision of the Baylei Zone into two Subzones seems now practicable and useful, and the zone is here divided as follows: the Densicostata Subzone below, and the Normandiana Subzone above (Fig. 3).

Characteristic fauna and horizon at Staffin. The total range of the Baylei Zone as marked by occurrence of ammonites of the genus *Pictonia* in the sections at Flodigarry is from 1.08 m below bed 36 (i.e. from uppermost part of bed 35) to 3.73 m below bed 44 (i.e. to the lowermost part of bed 43), which indicates that the zone is about 10 metres thick.

3.2.1. Densicostata Subzone

Index: *Pictonia densicostata* (Salfeld MS) Buckman. Holotype from the Inconstans Bed of Ringstead Bay, Dorset, figured by Buckman (1924, pl. 533).

Definition. Type locality Flodigarry, upper part of bed 35, 1.08 m below bed 36, to bed 39, between 0.2 and 1.8 m below bed 40. The Densicostata Subzone is characterised by occurrence of the macroconch species *Pictonia flodigarriensis* and *P. densicostata* associated with microconchs resembling *Prorاسenia bowerbanki* Spath.

Characteristic fauna at Staffin. The oldest typical representatives of the genus *Pictonia* occurring from 1.08 m below bed 36 to 0.2 m above bed 36 are distinguished herein as a new species *Pictonia flodigarriensis*, described more fully in the systematic section (see Fig. 5a–c). Morphologically, the species occupies an intermediate position between the last representatives of *Ringsteadia* and the previous oldest known species of *Pictonia*, *P. densicostata*, being especially close to the latter, and thus placed in the genus *Pictonia*.

An assemblage of microconchs collected from the same sections and levels as *P. flodigarriensis* corresponds generally to *Prorاسenia bowerbanki* (see Spath 1935, p. 43, pl. 14, figs 3a, b (holotype), pl. 13, figs 3a, b; see Fig. 4j). They attain a final diameter ranging from about 30 mm to 40 mm, and show the aperture with lappets. Coiling is markedly evolute. The innermost whorls up to 5–6 mm diameter are smooth. Thin, dense ribs then appear which show a high point of furcation covered by the younger whorls. At 8–10 mm diameter or slightly later, the ribbing becomes more distant (PR=17–20). The ribs are biplicate and triplicate, becoming heavier and more pointed, with the point of division lowering to below the mid flank of the whorl. The last stage of ornamentation, sometimes preceded by a poorly marked constriction, consists of biplicate ribs showing a similar low point of furcation. This ribbing occupies the last whorl or half-whorl up to the aperture (PR=30).

Abundant specimens of *Pictonia densicostata* were collected from about 0.9 m above bed 36 to the tough, shaly clay of bed 38. The specimens may exceed 120 mm in diameter, and show densely ribbed inner and middle whorls (PR=36–40 at about 40 mm diameter) with about two secondaries per primary, and flared ribs following constrictions. The ribbing fades on the outer whorl (Fig. 5d). In their character, these specimens agree closely with specimens of *P. densicostata* from southern England; the holotype and specimens usually attributed to that species (see e.g. Spath 1935, pl. 8, figs 4a, b; see also Birkelund & Callomon 1985, p. 32; Schweigert & Callomon 1997, p. 39). The microconchs present in this stratigraphic interval are all of the *Prorاسenia* type, about 30 mm in diameter, smooth up to 5 mm diameter, followed by ribbing which soon becomes distant and coarse (at D=15–20 mm, PR=15–20). The

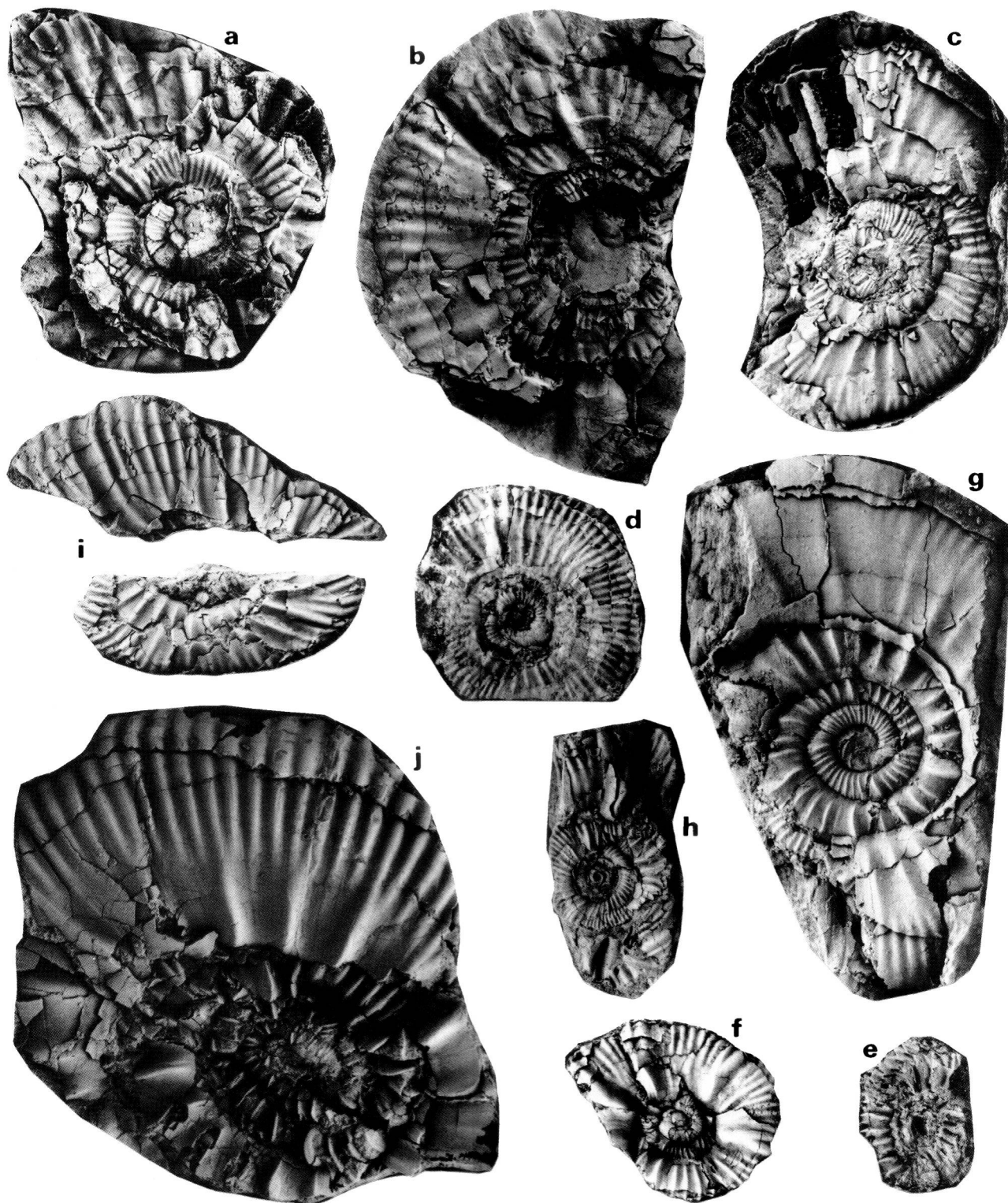


Figure 5 Aulacostephanid ammonites from the Baylei Zone (all specimens actual size). (a–c) *Pictonia flodigarriensis* sp. nov.: Flodigarry, Baylei Zone, Densicostata Subzone, *flodigarriensis* horizon: (a) ST836; section F6N, bed 35, 0.39 m below bed 36 – paratype; (b) ST837; section F7, bed 35, 0.52 m below bed 36 – paratype; (c) ST838; section F6N, bed 35, 1.08 m below bed 36 – holotype. (d) *Pictonia densicostata* Buckman: ST839; Flodigarry, section F5, bed 38; Baylei Zone, Densicostata Subzone. (e) *Prorasenia* cf. *bowerbanksi* Spath: ST840; Flodigarry, section F5, bed 38; Baylei Zone, Densicostata Subzone. (f, h–i) *Pictonia baylei* Salfeld/normandiana (Tornquist): Flodigarry, section F5, Baylei Zone, Normandiana Subzone: (f) ST841; uppermost part of bed 39, 6.6 m below bed 44; (h) ST843; bed 41, 5.7 m below bed 44, (i) ST844; two pieces of the same specimen, bed 43, 3.73 m below bed 44. (g) *Pictonia normandiana* (Tornquist): ST842; Flodigarry, section F5, bed 41, 5.8 m below bed 44; Baylei Zone, Normandiana Subzone. (j) *Rasenia inconstans* Spath: ST845; Flodigarry, section F5, bed 44, Cymodoce Zone, *inconstans* horizon.

specimens are, however, badly crushed and flattened (Fig. 5e), precluding their precise identification (*Prorasenia* cf. *bowerbanksi* Spath).

3.2.2. Normandiana Subzone

Index: *Pictonia normandiana* Tornquist. Lectotype, designated by Schweigert & Callomon 1997, p. 40) from the

Lower Kimmeridgian Calcaires coquilliers of Normandy, described and refigured (as *P. thurmanni* (Contejean)) by Hantzpergue (1989, p. 224, pl. 25d).

Definition. Type locality Flodigarry, from bed 39, between 0.2 and 1.8 m below bed 40, to bed 43, between 3.73 and 2.25 m below bed 44. The Normandiana Subzone is characterised by occurrence of the macroconchs *Pictonia bayleilnormandiana* showing more distant ribbing, already at fairly small diameters, and sometimes more strongly flared ribs. The characteristic microconchs are less well known, but seem related, at least partly, to *Prorrasenia hardyi*.

Characteristic fauna at Staffin. The youngest specimens of *Pictonia* come from section F5 – from 6.6 m to 3.73 m below bed 44 (i.e. from the upper part of bed 39 to the lowermost part of bed 43). The specimens are smooth up to 5 mm diameter, followed by dense biplicate ribbing continuing to about 12–18 mm, rarely 25 mm, diameter. Thereafter, the primary ribs become more distant (PR=about 20). The secondary ribs are as strongly developed as the primaries, with about three secondary ribs per primary. Strong flared ribs with well marked ventral collars follow constrictions. Most *Pictonia* from this interval are small and incomplete, not exceeding 45 mm diameter. Figure 5f shows a specimen about 40 mm in diameter, with half a whorl of body chamber. At the end of the specimen three successive flared ribs are much more closely spaced than the flared ribs occurring on the inner whorls. This does not mean, however, that the specimen is fully grown (see e.g. a large specimen of *Pictonia baylei* illustrated by Hantzpergue 1989, pl. 23b which shows irregularly spaced flared ribs on the inner and middle whorls).

These youngest specimens of *Pictonia* from the Flodigarry sections (see also Fig. 5h–i) may be compared with the inner whorls of *Pictonia baylei* and *P. normandiana*. These two species are very close each other, differing mostly in the persistence of secondary ribs to larger diameters in *P. normandiana*, as well as in the more involute coiling of the latter. Hantzpergue (1989) preferred to allocate such specimens to *P. thurmanni* (Contejean), but Schweigert & Callomon (1997) preferred to retain *P. normandiana* formally mainly to distinguish it from *P. thurmanni* on biostratigraphic grounds, designating the lectotype referred to above, and the present authors agree with this proposal. However, the small, incomplete specimens of *Pictonia* from the Flodigarry sections cannot be assigned unequivocally to either of the two species, and they are referred herein to as *Pictonia bayleilnormandiana*.

Two larger specimens of *Pictonia*, collected in section F5 from a limestone concretion of bed 40, and from bed 41, about 5.8 m below bed 44 (Fig. 5g), are closely comparable with the lectotype of *Pictonia normandiana*. They show marked collars and flared ribs in the inner whorls (from about 18–20 mm diameter), but these are not present at diameters greater than 45 mm. The bold primary ribs (PR=25–26 at D=50–85 mm) regularly divide into three secondary ribs with occasional intercalatories. This style of ribbing continues to the maximum diameter preserved (80–95 mm), at which point a third to about half of a whorl of body chamber is preserved. Coiling is strongly evolute on the inner whorls, and weakly evolute on the outer whorls.

Four microconchs occurring from the middle part of bed 41 to the lowermost part of bed 43 attain from 35 mm to 43 mm in diameter and show the aperture with lappets. The innermost whorls are smooth. Dense ribbing occurs between 5 mm and about 8 mm, but soon thereafter coarse, distant, triplicate ribs appear. The secondary ribs are clearly visible beneath the overlapping whorl. Between 20 to 30 mm diameter the ribbing becomes biplicate, and the point of furcation is still low. The best preserved specimens (5.70 m (Fig. 4i) and about 4.2 m

below bed 44) show markedly prorsiradiate ribbing, which becomes dense at the end of the last whorl, with a fairly high whorl section. These features are typical of *Prorrasenia hardyi* Spath (see Spath 1935, p. 40, pl. 15, figs 5a, b).

3.3. Cymodoce Zone

Index: *Rasenia cymodoce* (d'Orbigny). Lectotype indicated by Tornquist (1896, p. 11), and figured by Arkell (1933, pl. 39, figs 4a, b), from Dompierre sur Mer (Charante-Maritime), Aquitaine (see Hantzpergue 1989).

Definition. Formal definition of the base of the zone is yet to be established. The most complete section so far described in England is in the banks of the Fleet lagoon, Weymouth, extending from the Wyke Siltstone upwards (Birkelund *et al.* 1978). The lowest part of the zone is marked by the *inconstans* horizon which was first identified in East Greenland (Birkelund & Callomon 1985). This horizon is the lowest one showing the dominance of ammonites with bullate ribs typical of the genus *Rasenia*.

Characteristic fauna and horizon at Staffin. Specimens found in the highest part of the Flodigarry sections include three representatives of the genus *Rasenia*, occurring in the middle and upper part of bed 43, 2.25 m, and 0.59 m below bed 44, as well as in bed 44. The specimens show the finely ribbed inner whorls and bullate ribs appearing thereafter (from about 20 mm diameter) typical of *Rasenia*. The secondaries are usually hidden by the overlapping whorl. The larger two specimens (0.59 m below bed 44, and from bed 44 – see Fig. 5j), although fragmentarily preserved, are about 80–100 mm in diameter, and still show the presence of nearly straight, rather weakly bullate primary ribs. The character of ribbing and the coiling of these specimens indicate their close similarity to *Rasenia inconstans* Spath (see Birkelund & Callomon 1985, pp. 33–35, pl. 12, figs 1–4; pl. 13, figs 1–5; pl. 14, figs 1–4; see also specimens illustrated by Spath (1935) and put into synonymy of the species by Birkelund & Callomon (1985). The microconchs found in the Flodigarry sections associated with *R. inconstans* are represented by two specimens of *Prorrasenia* found 2.25 m below bed 44.

The boundary between the Baylei and Cymodoce zones must lie lower than the occurrences of these specimens of *Rasenia*, and above the last occurrence of *Pictonia* (3.73 m below bed 44). This means that the boundary in question lies within the 1.48 m thick interval between 3.73 m and 2.25 m below bed 44, i.e. in lower part of bed 43. The overlying part of bed 43, and bed 44, are thus assigned to the *inconstans* horizon of the Cymodoce Zone. The occurrence of *Rasenia cf. evoluta* Spath in bed 43 at Flodigarry, as indicated by Wright (1989, 2001), seems rather unlikely, as *R. evoluta* is indicative of the upper part of the Cymodoce Zone (see Birkelund *et al.* 1983).

4. The standard ammonite chronozones and chronosubzones of the Boreal Oxfordian/Kimmeridgian boundary succession

4.1. Regulare Zone

Index: *Amoeboceras regulare* Spath. Holotype from Novaya Zemlya refigured by Sykes & Callomon (1979, pl. 118, fig. 2).

Definition. The Regulare Zone of the Upper Oxfordian in the Boreal zonal scheme is characterised by the occurrence of evolute, densely and regularly ribbed *Amoeboceras* of the *A. regulare* group (Sykes & Surlyk 1976; Sykes & Callomon 1979).

Characteristic fauna and horizon at Staffin. This zone has yielded typical representatives of *A. regulare* from 13.85 m (close to the base of the sections studied) to 9.93 m below bed 36 (Fig. 3). These specimens are between 40 and 50 mm in diameter, and bear fine, wiry, rectiradial ribs which are non-tuberculate. Sykes & Callomon (1979) noted the presence of more strongly ribbed and even mildly tuberculate forms at this level, referring these to *A. freboldi* Spath, *A. cf. leucum* Spath and *A. cf. schulginae* Mesezhnikov. All these may be taken as representatives of the *A. regulare* group.

Sykes & Callomon (1979, pl. 119, fig. 5) record "*A. cf. regulare* Spath (m) – late form transitional to *A. marstonense* Spath" 8.2 m below bed 36. The first specimens of *A. marstonense*, indicative of the lower part of the overlying Rosenkrantzi Zone, have been found by the present authors between about 7.50 m and 7.28 m below bed 36. Thus both their records and those of Sykes & Callomon (1979) agree in the placing the boundary between the Regular and Rosenkrantzi zones through the interval from 9.93 m to 7.50 m below bed 36, i.e. in the upper part of bed 33. However, it is clear that the position of the boundary between these zones as drawn at the base of bed 35 in the Staffin Bay area by Sykes & Callomon (1979, p. 855, text-fig. 3) and by Wright (2001, fig. 5.15) is drawn too high when compared with data presented herein.

4.2. Rosenkrantzi Zone

Index: *Amoeboceras rosenkrantzi* Spath. The holotype, from Wollaston Foreland, Greenland, was refigured by Sykes & Callomon (1979, pl. 120, fig. 3).

Definition. Subdivided into the Marstonense and Rosenkrantzi Subzones. The Rosenkrantzi Zone was defined originally by Sykes & Surlyk (1976) as the range zone of the index-species. Sykes & Callomon (1979) divided it into two subzones, a lower Marstonense Subzone defined by the co-occurrence of *A. marstonense* Spath and *A. rosenkrantzi*, and an upper Bauhini Subzone with *A. rosenkrantzi* and *A. (Plasmatites) bauhini* (Oppel). Subsequently, the latter was treated as an independent Zone corresponding to the lowermost zone of the Boreal Kimmeridgian (see the description of the Bauhini Zone below). There then appeared the problem of the classification of the stratigraphical interval characterised by the occurrence of *A. rosenkrantzi* well above the upper range of *A. marstonense* and below the appearance of representatives of the *A. bauhini* group. This interval was distinguished as the Rosenkrantzi Subzone by Wright (2003) (see also Matyja *et al.* 2004).

Characteristic fauna and horizon at Staffin. The lower part of the zone is characterised by profuse *A. marstonense*. The middle part of the zone is characterised by the occurrence of *A. cf. leucum* Spath. This occurs 6.34 m below bed 36, in the upper part of the Marstonense Subzone, and it possibly continues upwards to about 3.5 m below bed 36 – i.e. into the lower part of the Rosenkrantzi Subzone. At a level 1.17 m below bed 36, *A. rosenkrantzi* co-occurs already with the first representatives of the subgenus *Plasmatites*, indicating the presence of the Bauhini Zone (see below). The total thickness of the Rosenkrantzi Zone in the Flodigarry sections is thus about 6.35–6.85 m, extending from 7.5 m to 1.2 m below bed 36.

4.2.1. Marstonense Subzone

Index: *Amoeboceras marstonense* Spath. Holotype from the Marston Ironstone of South Marston, Wiltshire, described and figured by Spath (1935, p. 20, pl. 4, figs 5a, b).

Definition. Introduced by Sykes & Callomon (1979) for the *Amoeboceras* fauna of bed 35 of the Staffin Shale at Staffin. Re-defined by Wright (2003) as that part of the Rosenkrantzi Zone containing abundant *A. marstonense* ranging from about

8 m to about 5 m below bed 36. The stratigraphical range of *A. marstonense* as recognised here is from about 7.50 m below bed 36 (i.e. the uppermost part of bed 33) to 5.25 m below bed 36 (i.e. lowermost part of bed 35). Thus, the Marstonense Subzone is at minimum 3 m thick.

Characteristic fauna at Staffin. Specimens collected 7.28 m below bed 36 show more distant, blunter ribbing, with a markedly more backward course of the secondary ribs compared with older *A. regulare*. The point of division of the ribs lies about the mid-height of the whorl, and is accentuated with a small tubercle. These features indicate close relation of the specimens in question with *A. marstonense*. Figure 6a shows a more densely ribbed variety.

A further distinctive *Amoeboceras* fauna occurs in section F6N in the uppermost part of bed 33, 6.34 m below bed 36 (Fig. 6b). It consists mostly of coarsely ribbed specimens (at D=31–46 mm, PR is about 20) showing weakly involute coiling (Ud=29–31%). The primary ribs are markedly prorsiradial and terminate in a prominent lateral tubercle at about 2/3 of the whorl height; the secondary ribs are curved, and strongly accentuated at the ventrolateral margin. A more or less pronounced smooth spiral band runs at the mid-height of the whorl dividing the primary and secondary ribs. These very characteristic specimens were first recognised in the Staffin Bay area, possibly at the same level, "in the middle of bed 35", by Sykes & Callomon (1979, p. 888, pl. 120, fig. 1). These authors considered that they represented a coarsely ribbed variant of the microconch of *A. rosenkrantzi*. However, the specimens in question differ from typical representatives of *A. rosenkrantzi* in several features: the crescent shape of the secondary ribs, the very coarse ornamentation, and the presence of a smooth spiral band. They are very close to *A. leucum*, as emended by Mesezhnikov (1967, pp. 118–120, pl. 1, fig. 3, and pl. 3, figs 2–3), and hence are referred herein to that species. *A. leucum* occurs along with typical forms of *A. rosenkrantzi* 6.34 m below bed 36. The youngest specimens of *A. marstonense* occur 5.25 m below bed 36 (Sykes & Callomon 1979, pl. 119, figs 6–7).

4.2.2. Rosenkrantzi Subzone

Index: as for the zone.

Definition. Introduced by Wright (2003) for the upper part of the Rosenkrantzi Zone containing an abundance of *A. rosenkrantzi* without *A. marstonense* and/or ammonites of the *Amoeboceras (Plasmatites)* group. This specific fauna ranges from about 3.5 m below bed 36 (see Sykes & Callomon 1979, pl. 119, fig. 10; pl. 120, figs 2a, b) to 1.65 m below bed 36. The minimum thickness of the Rosenkrantzi Subzone is thus 1.85 m.

Characteristic fauna at Staffin. The most typical forms of *A. rosenkrantzi*, being close to its lectotype (Spath 1935, pl. 12, fig. 4; see also Sykes & Callomon 1979, p. 888), make their appearance in the Marstonense Subzone (see above), and continue through the Rosenkrantzi Subzone into the overlying Bauhini Zone (see below). The specimens show moderately dense ribbing (PR is about 30–35) consisting of weakly prorsiradial or rectiradial primaries terminating in a feeble tubercle at about the mid-height of the whorl. The secondaries show a more or less pronounced backward curve, and are accentuated at the ventrolateral margin. The keel is distinctly crenulated, and bordered by smooth bands. The more complete specimens may be divided into macroconchs (showing a weakly ornamented outer whorl from about 85 mm in diameter), and microconchs (strongly ornamented and showing a more loosely coiled outer whorl), e.g. a specimen, about 50 mm in diameter, found together with a macroconch in section F6/S at 1.65 below bed 36.

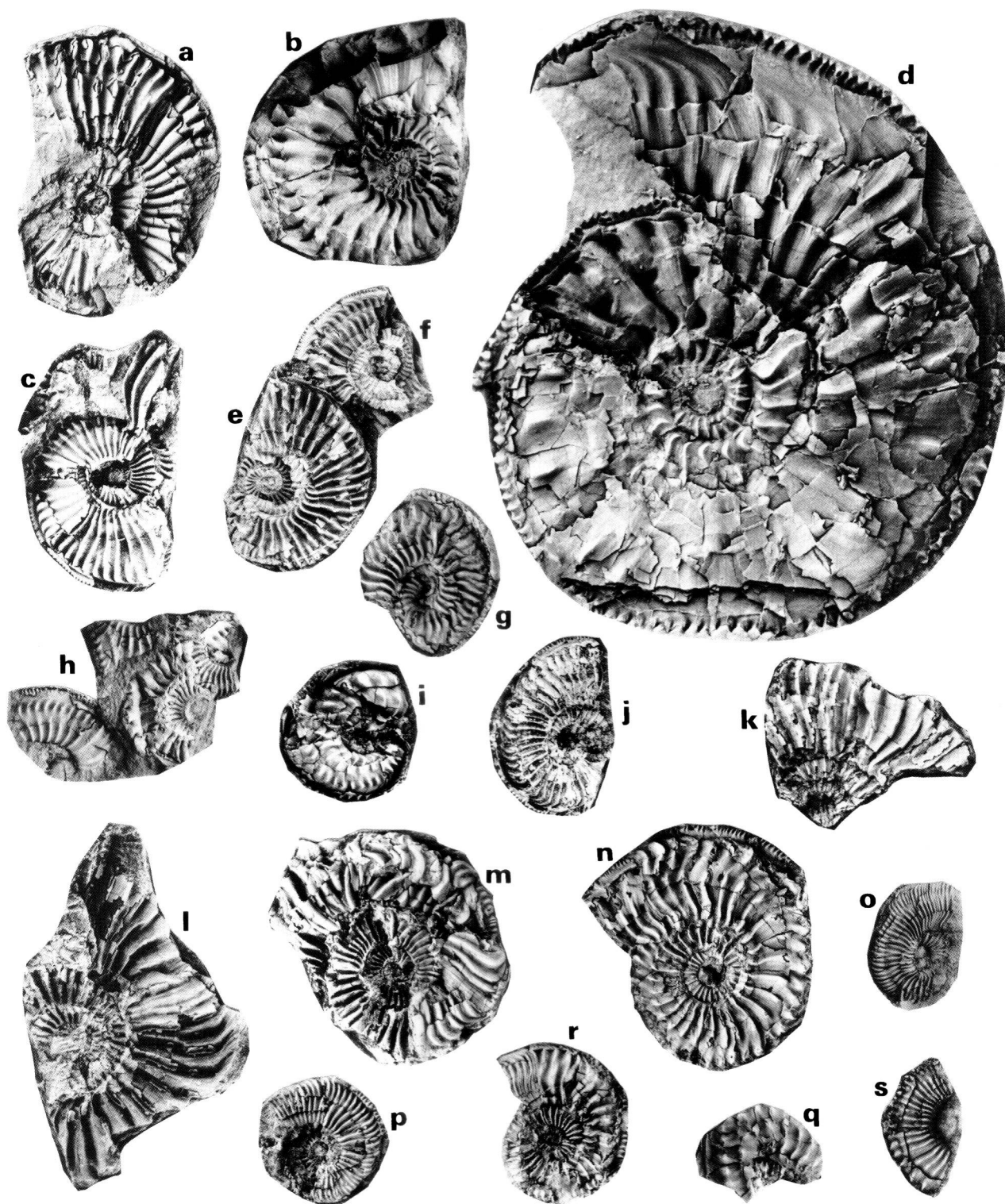


Figure 6 Cardioceratid ammonites from the Rosenkrantzi, Bauhini and Kitchini zones (all specimens actual size). (a) *Amoeboceras marstonense* Spath: ST846; Flodigarry, bed 33, about 7.5 m below bed 36; Rosenkrantzi Zone, Marstonense Subzone. (b) *Amoeboceras leucum* Spath emend. Mesezhnikov: ST846; Flodigarry, section F6N, uppermost part of bed 33, 6.34 m below bed 36; Rosenkrantzi Zone, Marstonense Subzone. (c, e) *Amoeboceras rosenkrantzi* Spath; Flodigarry: (c) ST848; basal part of bed 37; Bauhini Zone; (e) ST850; section F6N, uppermost part of bed 35, 1.17 m below bed 36; Bauhini Zone. (d) *Amoeboceras schulginae* Mesezhnikov: ST849; Flodigarry, section F6S, basal part of bed 37, 0.17 m above bed 36; Bauhini Zone. (f) *Amoeboceras (Plasmatites) praebauhini* (Salfeld): ST851; Flodigarry, section F6N, uppermost part of bed 35, 1.17 m below bed 36; Bauhini Zone. (g) *Amoeboceras (Plasmatites)* aff. *bauhini* (Oppel): ST852; Flodigarry, section F6S, uppermost part of bed 35, 0.6 m below bed 36; Bauhini Zone. (h, i, q) *Amoeboceras (Plasmatites) bauhini* (Oppel); Flodigarry: (h) ST853; section F5, uppermost part of bed 37, 9.02 m below bed 44; Bauhini Zone; (i) ST854; upper part of bed 37; Bauhini Zone; (q) ST861; section F5, bed 41, 5.7 m below bed 44; Bauhini Zone. (j, o–p) *Amoeboceras (Plasmatites) lineatum* (Quenstedt): Flodigarry, section 5: (j) ST855; upper part of bed 37, 9.80 m below bed 44; Bauhini Zone; (o) ST859; bed 41, 5.66 m below bed 44; Bauhini Zone; (p) ST860; bed 41, 5.7 m below bed 44; Bauhini Zone. (k–n) *Amoeboceras* aff. *schulginae* Mesezhnikov: (k–l) ST856; fragments of the same specimen, Flodigarry, section F5, lower part of bed 39, 7.96 m below bed 44; Bauhini Zone; (m) ST857; Flodigarry, section F5, lower part of bed 39, 7.96 m below bed 44; Bauhini Zone; (n) ST858; Digg, the same level as specimens k–m. (r) form transitional between *Amoeboceras bauhini* (Oppel) and *Amoeboceras bayi* Birkelund and Callomon: ST862; Flodigarry, section F5, bed 42, 4.79 m below bed 44. Kitchini Zone, Subkitchini Subzone, *bayi* horizon. (s) *Amoeboceras (Amoebites) bayi* Birkelund and Callomon: ST863; Flodigarry, section F5, bed 42, 4.79 m below bed 44. Kitchini Zone, Subkitchini Subzone, *bayi* horizon.

4.3. Bauhini Zone

Index: *Amoeboceras* (*Plasmatites*) *bauhini* (Oppel). Holotype from Hundsrück, Swabia, White Jura Beta; cast figured by Sykes & Callomon 1979, pl. 121, fig. 3.

Definition. The base of this zone is defined in the present paper by the appearance of small-sized *Amoeboceras* of the subgenus *Plasmatites*. This definition of the base of the Bauhini Zone, and thus the base of the Boreal Kimmeridgian, as presented herein, differs a little from that given by Wierzbowski & Smelror (1993, pp. 233, 242). These authors placed an interval of co-occurrence of the last *A. rosenkrantzi* together with the first *A. (Plasmatites)*, such as *A. praebauhini* Salfeld, still in the Rosenkrantzi Zone. The Bauhini Zone was restricted to the total range of *A. bauhini* together with small-sized *A. schulginae* (= *A. aff. schulginae* as treated herein). On the other hand, the definition of the base of the Bauhini Zone accepted here is close to that given originally by Sykes & Callomon (1979, p. 856) who defined the Bauhini Subzone as "characterised by incoming of diminutive species of the group of *A. bauhini*". They indicated overlapping of the range of the group with that of *A. rosenkrantzi* (see also Matyja *et al.* 2004).

The Bauhini Zone as defined herein thus may be informally subdivided into two parts: (1) the lowermost part characterised by appearance of first *A. (Plasmatites)* such as *A. praebauhini*, and with the occurrence of typical large *A. schulginae* and the last representatives of *A. rosenkrantzi*; (2) the major part of the zone characterised by the occurrence of various *A. (Plasmatites)*, including *A. bauhini*, and a form similar to *A. schulginae*, but differing in its smaller final size, and referred to as *A. aff. schulginae*, which occurs in a thin faunal horizon in the lower part of bed 39.

The major part of the Bauhini Zone in the Flodigarry sections corresponds to the range of closely allied forms of the subgenus *Plasmatites* including *A. bauhini*, *A. praebauhini* and *A. lineatum* (Quenstedt). These are recognised from the lower/middle parts of bed 37 (from about 2 m (possibly even 0.88 m) above bed 36) to the lower and middle parts of bed 41 (from about 1 m above its base). The range of the Bauhini Zone is from 1.17 m below bed 36 to 5.5 m below bed 44, indicating a thickness for the zone of at least 9 m.

Characteristic fauna and horizon at Staffin. At Flodigarry, the sole initial microconch representative is *A. (Plasmatites) praebauhini*, which first appears in the uppermost part of bed 35, from 1.17 m to 1.04 m below bed 36. The specimens are 20–30 mm in diameter, moderately densely ribbed (at D=25 mm, PR=33 – see Fig. 6f). The secondary ribs are curved backwards and accentuated at the ventro-lateral edge, from where they continue onto the crenulated keel. The specimens are very similar to the lectotype of *A. (P.) praebauhini* – see Salfeld (1915, pl. 17, figs 5a,b). Another specimen of *Plasmatites* found in section F6S about 0.60 m below bed 36 is more coarsely ribbed (PR=25). It is about 25 mm in diameter and shows rectiradiate primaries and markedly rursiradiate secondaries (Fig. 6g). Some uncoiling observed at the end of the shell suggests the specimen was fully grown. The specimen is referred to as *A. (P.) aff. bauhini* (Oppel) as it differs from typical representatives of *A. bauhini* in the somewhat lower point of division of the ribs, the lack of a smooth lateral band, and in somewhat more involute coiling.

Abundant representatives of the *Plasmatites* group occur in the upper part of bed 37 (9.8 m to 9.02 m below bed 44) through bed 38 up to the lower and middle parts of bed 41, 5.5 m below bed 44. The specimens are 25–35 mm in diameter, except the youngest ones which are 15–25 mm in diameter. Most common are specimens of *A. bauhini*, recognised in all

the faunas listed above (Fig. 6h, i and q). The specimens compare well with the holotype (Salfeld 1915, pl. 17, fig. 5), as well as with other specimens of this species (see e.g. Schweigert 1995, text-figs 1f–g; Schweigert & Callomon 1997, pl. 1, figs 1–26). They show coarse ribbing, with the primary ribs accentuated or bearing small tubercles above the mid-height of the whorl, and separated by a smooth spiral band from the short secondaries.

Another group of microconch specimens is less strongly ribbed, showing more numerous and less differentiated ribs. It comprises *A. (P.) praebauhini* and *A. (P.) lineatum*, forms which are indistinctly separated from *A. bauhini* – see Matyja & Wierzbowski (1988, pp. 424–427, pl. 2; 1997, p. 99, pl. 5, figs 1–4). These specimens are well represented in the Flodigarry sections (Fig. 6j, o–p) covering nearly the whole interval of occurrence of *A. bauhini* from 9.8 m to 5.66 m below bed 44. To the same group of more densely ribbed *Plasmatites* could be attributed specimens referred to as *Amoeboceras* cf. *bayi* Birkelund & Callomon by Wright (1989, figs 4G–J) from bed 39 at Flodigarry. These specimens show the projected secondary ribs continuing up to the keel characteristic of *A. (P.) lineatum*. Hence, this assemblage ranges from the lower part of bed 37 to the lower part of bed 41, taking into account the records of *A. bauhini* about 2 m above the base of bed 37 by Birkelund & Callomon (1985, p. 17).

The lowermost part of the Bauhini Zone in the Flodigarry sections yields two additional macroconch species. It contains the last representatives of *A. rosenkrantzi*, which ranges up into the lowermost part of bed 37 (Fig. 6c, e). In addition, the first typical large representatives of *A. (Amoeboceras) schulginae*, are present possibly occurring already at 1.44 m below bed 36 (*A. cf. schulginae*), but well recognised from 1.04 m and 0.61 m below bed 36 and 0.17 m above bed 36. A similar, small, incomplete specimen, found at the base of bed 37 in the Staffin Bay area, was referred to as *Amoeboceras* cf. *tuberculatoalternans* (Nikitin) by Sykes & Callomon (1979, pp. 889–890, pl. 121, fig. 7). These more coarsely ribbed and trituberculate *Amoeboceras* (see Fig. 6d) are discussed further under systematic palaeontology below, as are smaller specimens referred to here as *A. aff. schulginae* occurring in bed 39 (Fig. 6k–n).

4.4. Kitchini Zone

Index: *Amoeboceras kitchini* Salfeld, from the Kimmeridge Clay of Eathie, Cromarty, Scotland. Lectotype designated and figured by Birkelund & Callomon (1985, p. 21, fig. 6).

Definition. Characterised by a wide variety of *Amoebites* species listed by Birkelund & Callomon (1985, p. 20) and Wierzbowski & Smelror (1993, p. 247), including *A. bayi* Birkelund & Callomon and *A. subkitchini* Spath.

Characteristic fauna and horizon at Staffin. *A. (Amoebites) bayi* and *A. (A.) cricki* Salfeld appear in the upper part of bed 41 and in bed 42, from 4.99 m below bed 44 upwards. The largest of the specimens are about 30–40 mm in diameter (without aperture preserved) and show on the outer whorl the presence of looped ribs (Fig. 6s). They may be referred to easily as *A. (Amoebites) bayi*, being very close to the specimens of the type-series of that species (Birkelund & Callomon 1985, pl. 1, figs 1–12). Smaller specimens show dense ribbing and poorly marked ventral sulci along the keel, and may be compared with *A. (Amoebites) cricki*, well characterised by its lectotype (Salfeld 1915, pl. 19, figs 2a–c; see also Birkelund & Callomon 1985, p. 16). It seems that the two forms in question are very close each other, and may even appear conspecific (see Atrops *et al.* 1993, p. 221). Similar specimens from the Flodigarry sections attributed to *A. bayi* and *A. cricki*, from beds 41–42, were illustrated by Wright (1989, figs 4A–B, and 4C–F).

The boundary between the Boreal Bauhini and Kitchini zones runs through the 0.8 m interval between the last occurrence of the *A. bauhini* group and the first occurrence of *A. bayi*. However, specimens transitional in character between *A. (Amoebites) bayi* and *A. (Plasmatites) bauhini* are also known from the immediately overlying interval 4.99 to 4.6 m below bed 44. The specimens in question are two small-sized ammonites – one attaining 18 mm in final diameter found 4.99 m below bed 44, and another 28 mm in final diameter found 4.79 m below bed 44 (Fig. 6r). They show rather distant and coarse ribbing which becomes much more dense and weaker at the aperture. The small size of the specimens, and the slightly backward course of the secondary ribs, show the affinity of these specimens with the *A. bauhini* group, whereas weakening of the secondary ribs at the keel indicates affinity with *A. bayi* (see Birkelund & Callomon 1985, p. 15; Atrops *et al.* 1993, pp. 220–222; Schweigert 2000, p. 205). Thus, it may be suggested that the boundary in question could run rather in the upper part of the 0.8 m interval indicated.

The occurrence of *A. bayi* and *A. cricki* from 4.99 m to 3.81 m below bed 44 characterises the lowermost part of the Kitchini Zone. This corresponds to the *bayi* horizon of the lower part of the Subkitchini Subzone (see Wierzbowski *et al.* 2002; see also Wierzbowski & Smelror 1993). The youngest specimens found in the lowermost part of bed 43, from 4.21 m to 3.81 m below bed 44, are either moderately to coarsely ribbed showing the presence of looped ribs, and thus referred to as *A. (Amoebites) cf. bayi*, or more densely ribbed, and compared with *A. (A.) cf. cricki*. A single indeterminate specimen of *Amoebites* was found 2.86 m below bed 44.

Beginning from bed 44 upwards, ammonites become “disappointingly few and badly preserved” (Wright 1989, p. 270). A single fragmentarily preserved specimen showing the development of ventrolateral nodes typical of *A. (Amoebites) subkitchini* found 1.37 m above bed 44 is indicative of the higher part of the Subkitchini Subzone of the Kitchini Zone (Wierzbowski & Smelror 1993, p. 247) (see also specimens illustrated by Birkelund & Callomon (1985, pl. 2, figs 1–7; pl. 3, figs 1–11).

5. Correlation between the Boreal, Sub-Boreal and Sub-Mediterranean zonal schemes

5.1. Correlation of the Boreal and Sub-Boreal zonal schemes

The ammonite succession in the Flodigarry sections on the Isle of Skye is possibly the most complete and fossiliferous of all the sections available through the Boreal and Sub-Boreal uppermost Oxfordian and lowermost Kimmeridgian, thus making possible close correlation of the Boreal and Sub-Boreal zonal schemes. The numbers of specimens of the families Cardioceratidae and Aulacostephanidae are nearly equal, comprising for the uppermost Oxfordian, 40 specimens of Cardioceratidae and 49 of Aulacostephanidae; for the Bauhini Zone plus the corresponding part of the Baylei Zone, 81 and 88 specimens respectively; and for the Kitchini Zone plus the corresponding parts of the Baylei and Cymodoce zones, 22 and 20 specimens respectively. These data differ markedly from those calculated for corresponding stratigraphical intervals in other areas of the Sub-Boreal and Boreal provinces. In southern England most of the ammonites belong to the Aulacostephanidae, whereas the Cardioceratidae are rare (see Sykes & Callomon 1979). In central East Greenland (see Birkelund & Callomon 1985) and in cores from the Norwegian Sea offshore Norway (Wierzbowski *et al.* 2002) there is a marked

dominance of the Cardioceratidae over the Aulacostephanidae (in cores from the latter the ratio of specimens is 3:1). In Spitsbergen and in cores from the Barents Sea almost all specimens belong to the Cardioceratidae (see Yershova 1983; Wierzbowski & Smelror 1993), but there is a single level in the Cymodoce Zone where the Aulacostephanidae occur commonly (Wierzbowski 1989).

Detailed analysis of the Boreal and Sub-Boreal ammonites in the sections studied at Flodigarry indicates that the Sub-Boreal Pseudocordata Zone corresponds to a part of the Boreal Regular Zone plus the whole Rosenkrantzi Zone (as defined herein). The Caledonica Subzone plus a part of the Pseudoyo Subzone of the Pseudocordata Zone corresponds to the upper part of the Regular Zone. This is shown by the co-occurrence of ammonites typical of these Sub-Boreal subzones with *Amoeboceras regulare* indicative of the Regular Zone (Figs 3, 7).

The rest of the Pseudoyo Subzone, and possibly at least a part of the Pseudocordata Subzone, is equivalent to the Marstonense Subzone of the Rosenkrantzi Zone. Such a correlation results from co-occurrence of ammonites such as *Ringsteadia* ex gr. *pseudoyo*, *R. cf. pseudocordata* and *Microbiplipes anglicus* together with *Amoeboceras marstonense*. In the Flodigarry sections, these occur from the upper part of bed 33, about 1.5 m below its top, to the lowermost part of bed 35, about 0.75 m above its base. This corresponds well with data from southern England where the stratigraphical ranges of *Ringsteadia pseudoyo*, *R. pseudocordata*, and *Amoeboceras marstonense* partly overlap (see e.g. Wright 1998, 2003). Also, in the South Ferriby section in northern England, *R. pseudocordata*, *A. cf. marstonense* and *A. rosenkrantzi* are recorded together from the stratigraphical interval corresponding to the Pseudocordata Subzone (Schweigert & Callomon 1997, text-fig. 9; Cox 2001a, p. 123).

Some of the upper part of the Pseudocordata Subzone, plus the Evoluta Subzone of the Pseudocordata Zone (Sub-Boreal) may be correlated with the Rosenkrantzi Subzone of the Rosenkrantzi Zone (Boreal). This is shown by the co-occurrence of *Ringsteadia evoluta*, *Microbiplipes anglicus*, and forms that are transitional between *Microbiplipes* and *Proraseria*, together with *Amoeboceras rosenkrantzi* in the upper part of bed 35, from 2.34 m to 1.24 m below bed 36.

In the Sub-Boreal zonal scheme, the boundary between the Oxfordian and Kimmeridgian corresponds to the boundary between the Evoluta Subzone of the Pseudocordata Zone and the Densicostata Subzone of the Baylei Zone as re-defined in the present study (see section 3.2). This is placed between 1.24 m and 1.08 m below bed 36 at Flodigarry. In the Boreal zonal scheme, the Oxfordian/Kimmeridgian boundary corresponds also to the boundary between the Rosenkrantzi Subzone of the Rosenkrantzi Zone and the Bauhini Zone as defined herein (see section 4.3) (Fig. 7). This is placed 1.17 m below bed 36 at Flodigarry. It appears, thus, that the Oxfordian/Kimmeridgian boundary both in Sub-Boreal and the Boreal zonal schemes is placed exactly (or almost exactly) at the same level in the Flodigarry sections (Fig. 3).

The lower part of the Sub-Boreal Baylei Zone, distinguished herein as the Densicostata Subzone, plus the lower part of an upper subzone, the Normandiana Subzone, corresponds to the Boreal Bauhini Zone. This is shown by co-occurrence from the uppermost part of bed 35, 1.17 m below bed 36, to the middle part of bed 41 of the *A. bauhini* group, with ammonites of the genus *Pictonia* typifying the Baylei Zone (see also Birkelund & Callomon 1985). The lowermost part of the Densicostata Subzone, newly designated as the *flodigarrienis* horizon (uppermost part of bed 35, 1.08 m below its top, to the lowermost

Western part of the Boreal Province		Sub-Mediterranean Province			Sub-Boreal Province		
Zones	horizons	Zones	Subzones	horizons	horizons	Subzones	Zones
Kitchini (pars)	bayi	Platynota (pars)	Polygyratus	Amoeboceras	inconstans		Cymodoce (pars)
				falcula			
			Galar	wenzeli		Normandiana	
		Planula	Planula	schroederi			
				planula			
Bauhini				proteron			Baylei
				aff. minutum			
				broilii			
				litocerum			
		Bimammatum	Bimammatum		flodigarriensis	Densicostata	
Rosenkrantzi			Hypselum	berrense		Evoluta	
				semimammatum		Pseudocordata	Pseudocordata
						Pseudoyo	
						Caledonica	
Regulare (pars)		Bifurcatus (pars)	Grossouvrei			Variocostatus (pars)	Cautisnigrae (pars)

Figure 7 Correlation of the Boreal and Sub-Boreal zonal schemes with the Sub-Mediterranean zonal scheme.

part of bed 37, 0.2 m above its base), is nearly an exact equivalent of the lowermost part of the Bauhini Zone characterised by the co-occurrence of the first *Amoeboceras* (*Plasmatis*), the last *A. rosenkrantzi*, as well as by the appearance of large *A. schulginae* (from 1.17 m below bed 36 to the lowermost part of bed 37).

The upper part of the Normandiana Subzone of the Baylei Zone contains the *bayi* horizon of the lowermost part of the Boreal Kitchini Zone. This is shown by the co-occurrence of the last representatives of the genus *Pictonia* with *A. bayi*/*A. cricki* in the uppermost part of the interval corresponding to beds 41 and 42 (from 4.99 m below bed 44) to the lowermost part of bed 43 (3.91 m below bed 44). However, the still younger Sub-Boreal biostratigraphical unit recognised in the sections studied (the *inconstans* horizon of the lowermost Cymodoce Zone) cannot be precisely compared with its Boreal equivalent. The *inconstans* horizon is recognised in the upper part of bed 43, from 2.25 m and 0.59 m below bed 44, up to bed 44. It thus occurs between the last occurrence of *A. bayi* (3.91 m below bed 44) indicative of the *bayi* horizon of the lowermost Boreal Kitchini Zone, and the first occurrence of *A. subkitchini* (1.37 m above bed 44) indicative of the upper part of the Subkitchini Subzone of the Kitchini Zone.

The highest Oxfordian zone of the Boreal subdivision of this stage in Siberia is the *Amoeboceras ravni* Zone (see Mesezhnikov 1967, 1984, 1988; Sachs *et al.* 1969a, b). It contains at its base *Amoeboceras regulare*, followed by *A. freboldi*, *A. leucum* Spath emend. Mesezhnikov, *A. schulginae* = "*A. ravni* Spath" and *A. pectinatum* Mesezhnikov. This assemblage is typical of the Regulare Zone plus the Rosenkrantzi Zone of the standard Boreal subdivision, and possibly also of the lowermost part of the Bauhini Zone, based on the ammonites studied at Flodigarry. Mesezhnikov *et al.* (1989, pp. 40–42) later placed in the *Amoeboceras ravni* Zone a fauna consisting of ammonites of the *Amoeboceras bauhini* group described from the Russian Platform, indicating that the whole of the Bauhini Zone could correspond to the lower and middle parts of the *Amoeboceras ravni* Zone. It should be remembered that the ammonites of the subgenus *Plasmatis* (=the *A. bauhini* group) are widely distributed in the Boreal Province, in the Norwegian Sea (Århus *et al.* 1989;

Wierzbowski *et al.* 2002), and Barents Sea areas (Wierzbowski & Århus 1990; Wierzbowski & Smelror 1993), making everywhere a clear distinction of the standard Bauhini Zone of the lowermost Boreal Kimmeridgian.

5.2. Correlation with the Sub-Mediterranean zonal scheme

The correlation of the Boreal and Sub-Boreal zonal schemes with the Sub-Mediterranean one is more difficult and still not clear in many details, although much progress has been made in recent years (see e.g. Matyja & Wierzbowski 1997, 2002, 2003; Schweigert & Callomon 1997, and older papers cited therein).

Amoeboceras rosenkrantzi occurs together with ammonites of the genus *Ringsteadia* (some similar to *R. caledonica*) and *Microbiplices microbiplex* in the *semimammatum* horizon in Central Poland (Matyja & Wierzbowski 1994, pl. 1, figs 11–13). This horizon is situated in the lower part of the Hypselum Subzone of the Bimammatum Zone in the Sub-Mediterranean zonal scheme. The ammonites recorded indicate that this horizon is equivalent to a lower part of the Sub-Boreal Pseudocordata Zone and the corresponding lower part of the Boreal Rosenkrantzi Zone. Still older deposits belonging to the Sub-Mediterranean Grossouvrei Subzone, and thus representing the upper part of the Bifurcatus Zone, have yielded Boreal ammonites in Central Poland comparable with late representatives of the *A. regulare* group (Matyja & Wierzbowski 1994, pl. 1, figs 4–10). An unquestionable representative of the Sub-Boreal genus *Ringsteadia* has been found in deposits of the upper part of the Bifurcatus Zone in southern Germany (Schairer 1989, pl. 3, fig. 6). This suggests that the lowermost part of the Sub-Boreal Pseudocordata Zone, and the corresponding upper part of the Boreal Regulare Zone, correlate with some upper part of the Sub-Mediterranean Bifurcatus Zone (Fig. 7).

The correlation of still younger Sub-Mediterranean biostratigraphical units of the Bimammatum Zone (such as the upper part of the Hypselum Subzone (i.e. the *berrense* horizon), and the Bimammatum Subzone) with the Boreal/Sub-Boreal succession is less clear. The problems are partly related to the scarcity of Boreal/Sub-Boreal ammonites in this part of

the Sub-Mediterranean succession when compared with their common occurrence in the lowermost part of the Bimammatum Zone, but they also result from the generally poor knowledge of ammonite distribution in this Sub-Mediterranean stratigraphical interval (see Schweigert & Callomon 1997, pp. 35–36). However, it should be remembered that the occurrence of the first representatives of *Amoeboceras* (*Plasmatites*), such as *A. praebauhini*, *A. lineatum*, and even forms similar to *A. bauhini*, as well as the first representatives of *Prorاسenia*, are reported from the Bimammatum Subzone in northern Poland and southern Germany (see Matyja & Wierzbowski 1998, p. 40, pl. 1, figs 9–10; Schweigert 2000, p. 205, pl. 1, fig. 8). This indicates that at least part of the Bimammatum Subzone of the Sub-Mediterranean succession correlates with the lowermost part of the Bauhini and Baylei zones, i.e. with the lowermost Boreal/Sub-Boreal Kimmeridgian (Matyja & Wierzbowski 2003).

In Central Poland and southern Germany the upper part of the Sub-Mediterranean Bimammatum Zone, i.e. the Hauffianum Subzone, has yielded fairly abundant ammonites of Boreal and Sub-Boreal affinity – such as *Amoeboceras bauhini*, *A. aff. schulginae*, *Pictonia densicostata* and *Prorاسenia bowerbanki*. These specimens have been found in the middle part of the subzone (Matyja & Wierzbowski 1997, pp. 99–100, pl. 5, figs 1–13; Schweigert & Callomon 1997, pl. 1, figs 1–26, pl. 2, figs 1–2, pl. 5, fig. 2). This allows correlation of the middle part of the Hauffianum Subzone with the lowermost Boreal/Sub-Boreal Kimmeridgian, i.e. with some parts of the Bauhini Zone and the Densicostata Subzone of the Baylei Zone (except their lowermost parts).

In the Planula Zone of the Sub-Mediterranean zonal scheme, ammonites of Boreal/Sub-Boreal affinity are known to occur in the upper part of the Planula Subzone, and in the overlying Galar Subzone. The ammonites from the Planula Subzone, known from southern Germany and northern Poland, represent various forms of the *Amoeboceras bauhini* group (Schweigert 2000, p. 205, pl. 1, fig. 12; Matyja & Wierzbowski 2002, pl. 1 fig. 2), and “Sub-Mediterranean” species of the genus *Pictonia*. The latter, such as *Pictonia perisphinctoides* (Wegele), are similar to the Sub-Boreal species *Pictonia normandiana* – see Hantzpergue (1989, pp. 224, 229) and Schweigert & Callomon (1997, pp. 40, 45, pl. 7, figs 13–14). Thus, they are still indicative of the Boreal Bauhini Zone (of its upper part), and an upper part of the Sub-Boreal Baylei Zone (markedly below its top). On the other hand, Boreal ammonites occurring at the base of the Sub-Mediterranean Galar Subzone, and continuing up through this subzone, in northern Poland and southern Germany, include *Amoebites bayi* and allied forms (Matyja & Wierzbowski 2002, pl. 1, figs 1, 3a, b; Schweigert 2000, p. 206, pl. 1, fig. 13). These indicate that this Sub-Mediterranean subzone correlates already with lowermost part of the Boreal Kitchini Zone.

In the Galar Subzone in northern Poland the last representatives of the Sub-Boreal genus *Pictonia* have been found, distinguished as the new species *Pictonia kuiaviensis* Matyja & Wierzbowski. The species has raseniid-like appearance and represents a form phylogenetically close to the earliest members of the genus *Rasenia*. Thus, it may be treated as indicative of the uppermost part of the Sub-Boreal Baylei Zone (Matyja & Wierzbowski 2002, pp. 416–417, 419–420, pl. 1, figs 4–11, ?12). Hence, the boundary between the Planula Subzone and the Galar Subzone of the Sub-Mediterranean zonal scheme is very close to the boundary between the Boreal Bauhini and Kitchini zones (Schweigert & Callomon 1997, text-fig. 12; Matyja & Wierzbowski 2002, text-fig. 5), but it still runs within the uppermost part of the Sub-Boreal Baylei Zone (Matyja &

Wierzbowski 2002, text-fig. 5). This boundary, well recognised both in the Boreal and in the Sub-Mediterranean succession, and lying fairly close to the currently accepted Oxfordian/Kimmeridgian boundary in the Sub-Mediterranean succession, has a large correlation potential and it may be considered as a candidate level for the Oxfordian/Kimmeridgian boundary (Matyja & Wierzbowski 2002, 2003; Matyja *et al.* 2004).

The occurrence in the lowermost part of the Sub-Mediterranean Platynota Zone in southern Germany, Switzerland, and southern France of the ammonites of the genus *Amoeboceras* grouped around the species of *Amoeboceras* (*Amoebites*) *bayi* (see Atrops *et al.* 1993, pl. 2, figs 1–16), may be treated as indicative of the lower part of the Boreal Kitchini Zone, and possibly still of the upper part of the Sub-Boreal Baylei Zone (see e.g. Matyja & Wierzbowski 2002, 2003).

6. Systematic palaeontology

Superfamily Stephanoceratoidea Neumayr, 1875

Family Cardioceratidae Siemiradzki, 1891

Subfamily Cardioceratinae Siemiradzki, 1891

Genus *Amoeboceras* Hyatt, 1900

Type species. *Ammonites alternans* von Buch, 1831. The oldest members of the genus *Amoeboceras* Hyatt, 1900 include representatives of the nominative subgenus *Amoeboceras* based originally on small strongly-ribbed microconchs, and also representatives of the subgenus *Prionodoceras* (type species *Prionodoceras prionodes* Buckman = *Amoeboceras serratum* Sowerby) comprising large macroconchs with a smooth body chamber (see Sykes & Callomon 1979). The common features of all these Upper Oxfordian forms comprise “tabulate venter, and minutely serrated keel flanked by smooth bands or shallow sulci” (Arkell *et al.* 1957, p. L 306). These features are recognised in representatives of the nominative subgenus, as well as on the inner whorls of large macroconchs. As there exists a considerable variability of the dimorphs within the Upper Oxfordian representatives of *Amoeboceras*, and as the general affiliation of corresponding micro- and macroconchs to a single species does not present serious difficulties (see Sykes & Callomon 1979), the distinction between the subgenera *Amoeboceras* and *Prionodoceras* seems unnecessary. Thus, all the Upper Oxfordian species discussed herein are placed in the nominative subgenus *Amoeboceras*.

Amoeboceras schulginae Mesezhnikov

Fig. 6d

1967 *Amoeboceras* (*Prionodoceras*) *schulginae* Mesezhnikov, p. 123–8, pl. 1, fig. 4; pl. 3, fig. 1; pl. 4, fig. 1.

non 1979 *A. cf. schulginae* Mesezhnikov. Sykes & Callomon, p. 884, pl. 118, fig. 5.

non 1985 *Amoeboceras* (*Amoebites*) aff. *A. (A.) schulginae* Mesezhnikov. Birkelund & Callomon, p. 18, pl. 4, figs 1–3.

Material. Four specimens (ST722, ST725, ST849, ST902) from the top of bed 35 and the base of bed 37 at Flodigarry.

Description. These specimens are large, attaining up to about 110 mm in their final diameter. The primary ribs are strong and distant from the inner whorls up to the first half of the last whorl (PR is about 20). They are markedly accentuated and curved at the umbilical margin, and then rectiradiate or weakly prorsiradiate up to a strong lateral tubercle situated somewhat above the mid-height of the whorl. The secondary ribs are partly placed independently of the primaries. They are

short, almost rectiradiate, and strongly tuberculate at the ventro-lateral shoulders. The keel is coarsely crenulated. On the last half of the outer whorl the ribbing becomes much more dense and weaker, with strongly projected secondaries.

Discussion. These specimens co-occur in the Flodigarry sections with other specimens showing the normal ornamentation of *A. rosenkrantzi*, and the two may be treated possibly in horizontal classification as members of a uniform faunal assemblage. On the other hand, in a more typological approach, the more heavy ribbed forms may be readily compared with *Amoeboceras schulginiae* Mesezhnikov. This latter interpretation is accepted herein. The type specimens of *A. schulginiae* as interpreted by Mesezhnikov (1967), together with specimens of the very close "*Amoeboceras (Prionodoceras) ravni* Spath" sensu Mesezhnikov (1967, pp. 116–117, pl. 1, fig. 1; see also Mesezhnikov 1988, pl. 9, fig. 14), constitute members of a well defined assemblage occurring in the Levaya Boyarka section of North Siberia. This assemblage occurs directly above one containing *Amoeboceras regulare* (see Sachs *et al.* 1969a, p. 24; 1969b, p. 72).

The name *A. schulginiae* has been used in the geological literature as a specific name for *Amoeboceras* of a variety of different ages and differing somewhat in their appearance. These attributions are mostly not accepted here: (1) the specimens referred to as *A. schulginiae* cf. *A. schulginiae* co-occurring with ammonites of the much older *A. regulare* group (see Sykes & Callomon 1979, p. 884, pl. 118, fig. 5) differ mostly from typical representatives of *A. schulginiae* in their weaker ornamentation; (2) the specimens referred to as *Amoeboceras (Amoebites)* aff. *A. schulginiae* by Birkelund & Callomon (1985, p. 18, pl. 4, figs 1–3) found together with *Pictonia* cf. *normandiana*, may represent extremely coarsely ribbed end-members of *Amoeboceras bayi*; (3) the specimens referred to as *Amoeboceras schulginiae* by Wierzbowski & Smelror (1993, pl. 1, fig. 6), as well as by Schweigert (1995, pp. 178–80, figs 1a–e; see also Schweigert & Callomon 1997, p. 6, pl. 2, fig. 1; pl. 5, fig. 3) co-occurring with *Plasmatites* of the *A. bauhini* group, seem the most similar to typical representatives of *A. schulginiae*, but differ mostly in their much smaller end-size (see below).

Amoeboceras aff. *schulginiae* Mesezhnikov

Fig. 6k–n

1993 *Amoeboceras schulginiae* Mesezhnikov; Wierzbowski & Smelror, pl. 1, fig. 6.

1995 *Amoeboceras schulginiae* Mesezhnikov; Schweigert, pp. 178–180, figs 1a–e.

1997 *Amoeboceras schulginiae* Mesezhnikov; Schweigert & Callomon, p. 6, pl. 2 fig. 1; pl. 5, fig. 3.

Material. Three specimens (ST856, ST857, ST858) from Bed 39 at Digg and Flodigarry.

Description. The specimens attain from 45 mm to 60 mm in final diameter. Coiling is from weakly evolute to weakly involute. The ribbing of the inner and middle whorls, sometimes up to a part of the last whorl, is coarse and distant to moderately dense (PR=25–33 at D=30 mm). The primaries are slightly flexuous, accentuated at the umbilicus, and terminate in a feeble lateral tubercle above the mid-height of the whorl. The secondary ribs are short, rursiradiate in their course, with the development of ventrolateral tubercles. The keel is markedly crenulate. On the outer whorl (or sometimes on its end-part only) the ribs become more densely spaced, without clear differentiation into primaries and secondaries. The ribs here are slightly flexuous, and show the presence of elongated ventrolateral tubercles. There is marked projection

of the ribs on the side of the venter, and they may continue with some weakening onto the crenulated keel.

Discussion. These specimens are very similar in their ornamentation to *A. schulginiae*, showing the typical tri-tuberculation before the final stage of ribbing. They differ, however, from that species in the much smaller final size of the shell, and are referred to herein as *A. aff. schulginiae*. The specimens from the Staffin sections are very similar, and possibly conspecific, with the specimens from the Barents Sea and southern Germany listed in the synonymy above. They co-occur at these localities with *A. (P.) bauhini* (Oppel). At Staffin, *A. aff. schulginiae* occurs at a single level in the lower part of bed 39 at Flodigarry (Fig. 6k–m) and at Digg (Fig. 6n).

Subgenus *Plasmatites* Buckman, 1925

Type species. *Plasmatites crenulatus* Buckman, 1925c (almost surely a younger synonym of *Amoeboceras (Plasmatites) praebauhini* (Salfeld 1915)). Included here are small forms "with dense straight wiry ribbing of the group of *A. bauhini* (Oppel)" – see Sykes & Callomon (1979, p. 858). The ribbing is falcoid. In some specimens there is poor differentiation of primary and secondary ribs. In other specimens there is strong differentiation of primaries and secondaries with feeble tubercles at the end of the primary ribs and a smooth spiral band between primary and secondary ribs. The secondary ribs, raised if not tuberculate on the shoulders, run up onto the coarsely crenulated keel. Ribbing on the outer whorl may be very dense in contrast to the inner whorls where ribbing is usually much more distant. The whorl section varies from lenticulate to oval and even subquadrate/subrectangular (see Salfeld 1915, pp. 178–9; Matyja & Wierzbowski 1988, pp. 425–6, pl. 2; Atrops *et al.* 1993, pp. 219–20, text fig. 2.II).

Small-sized *Plasmatites* attaining 15–40 mm in final diameter have been usually recognised as microconchs (e.g. Sykes & Callomon 1979; Matyja & Wierzbowski 1988) although there always remained the problem of their dimorphic counterpart. Somewhat larger specimens, attaining 40–50 mm in final diameter, referred here to as *Amoeboceras* aff. *schulginiae* (see above) may be considered as potential macroconchs of *A. (P.) bauhini*. Detailed analysis of representatives of Sub-Mediterranean *Plasmatites* by Matyja & Wierzbowski (2000) has shown that their small end-sizes were related to early attainment and long time duration of the mature stage (as shown by crowding of the septae in most or all of the last whorl of the phragmocone).

Subgenus *Amoebites* Buckman, 1925

Type species. *A. akanthophorus* Buckman, 1925a [= *A. kitchini* (Salfeld 1915) subj.]. *Amoebites* "differs from *Amoeboceras* s.s. . . in abandoning mid-lateral tuberculation of primary ribbing and developing instead strongly accentuated secondary ribbing" (Birkelund & Callomon 1985, p. 12). It differs also in the presence of looped ribs on the outer whorl. This type of ornamentation tends to appear already in some more coarsely ribbed forms related to *A. rosenkrantzi*, such as *A. leucum* and *A. schulginiae*. Strongly accentuated secondaries are also common in coarsely ribbed *A. (Plasmatites) bauhini*, which show the presence of a smooth spiral band separating long primary and short secondary ribs (see also Mesezhnikov 1967, p. 123; Birkelund & Callomon 1985, p. 12). The general succession of the species of *Amoebites* was largely established by Birkelund & Callomon (1985), and discussed by other authors (e.g. Wierzbowski & Smelror 1993). It begins with the small-sized *A. (Amoebites) bayi* and continues into generally

larger-sized *A. (Amoebites) subkitchini*, and finishes with the smaller-sized forms of *A. (Amoebites) kitchini* and its allies.

Superfamily Perisphinctoidea Steinmann, 1890

Family Aulacostephanidae Spath, 1924

The ammonite faunas of the family Aulacostephanidae consist of successive members from *Ringsteadia* through *Pictonia* to *Rasenia* (mostly macroconchs) and *Microbiplices* to *Prorاسenia* (microconchs) which formed during the latest Oxfordian and earliest Kimmeridgian a smoothly evolving lineage (see Birkelund & Callomon 1985). Crucial for the stratigraphical problems discussed here is the nature of the transition from *Ringsteadia* to *Pictonia*, and the distinction of the oldest species with the dominant features of *Pictonia*, *Pictonia flodigarriensis* sp. nov. It is also necessary to discuss the transition from *Microbiplices* to *Prorاسenia*, and the occurrence of forms transitional between *Microbiplices* and *Prorاسenia*.

Genus *Ringsteadia* Salfeld, 1913

Type species. *Ammonites pseudocordatus* Blake & Hudleston, 1877. *Ringsteadia* has long, distinct primary ribs on the innermost whorls, most ribs splitting above the mid-height of the whorl, but with some long intercalated secondary ribs. Primary and secondary ribs are equally strong. Deeply incised and relatively wide constrictions may be present. The main stage of ornamentation consists of more loosely spaced and stronger primary ribs, weakening at about the mid-height of the whorl at the point of division. The secondary ribs are more numerous (two to five for each primary), and thinner than the primary ribs. Constrictions are poorly marked, wide and shallow. In specimens attaining large sizes (400 mm+) the ornamentation completely disappears on the outer whorl. The whorl section of the innermost whorls is rounded, that of the middle and outer whorls oval, usually tapering towards the ventral side.

The transition between *Ringsteadia* and *Pictonia* is marked by the retention in some specimens of *Ringsteadia* of dense 'perisphinctoidal' ornament up to somewhat larger diameters compared with the bulk of *Ringsteadia* at the same level. Thus Figure 4c, collected from the uppermost Pseudocordata Sub-zone 2·34 m below bed 36, reveals *Pictonia*-like ornament up to about 17 mm in diameter, when other specimens from this level show similar ornament up to a few millimetres in diameter only. The same phenomenon is even more visible in a younger fauna of *R. evoluta* (F6S, 1·65 m below 36) where irregular ribbing resembling that of *Pictonia* occurs to about 20–30 mm diameter in some specimens.

Genus *Pictonia* Bayle, 1878

Type species. *Pictonia baylei* Salfeld, 1913 [ICZN Opinion 426; = *Pictonia cymodoce* Bayle, 1878 (*non* d'Orbigny, 1850)]. *Pictonia* differs from *Ringsteadia* in being generally more evolute and planulate. Ribbing on the inner whorls of *Pictonia* is of the 'perisphinctoidal' type, generally densely ribbed, with mostly biplicate secondaries and sometimes single intercalated ribs. On the middle whorls the ribbing often becomes more distant, biplicate and polypligate. At larger diameters ornamentation fades, and in most species it is reduced to only dense striae occurring on the body chamber. The principal characteristic feature of the genus is irregularity of ribbing expressed by the periodical occurrence of swollen ribs (flared ribs) bordering deep constrictions, especially strongly developed on the middle whorls (cf. Birkelund & Callomon 1985; Hantzpergue 1989).

The first specimens which show predominantly the characteristic features of *Pictonia* appear in large numbers in the *P. flodigarriensis* faunal horizon distinguished herein as the lowest level of the Baylei Zone.

Pictonia flodigarriensis sp. nov.
(Fig. 5a–c)

?1985. *Pictonia?* sp. indet B; Birkelund & Callomon, p. 32, pl. 11, fig. 4.

Diagnosis. *Pictonia* having the dense ribbing, constrictions and flared ribs characteristic of the genus, with a more regularly ribbed body chamber resembling that of *Ringsteadia*.

Material. The holotype (ST838, Fig. 5c), paratypes (ST836 and ST837, Fig. 5a, b) and seven other specimens (ST683, ST697, ST699, ST701, ST702, ST710, ST721) from the Staffin Shale Formation, uppermost part of bed SS35 to lowermost part of bed SS37 (from 1·08 below bed 36 to 0·2 m above bed 36); lowermost part of the Baylei Zone, *flodigarriensis* horizon.

Derivation of name. From the hamlet of Flodigarry which adjoins the beach section where the type specimens were collected.

Description. The inner whorls show dense ribbing (PR is about 35–45) consisting mostly of biplicate ribs; the point of furcation is located high on the whorl side; stronger accentuated ribs with the character of flared ribs appear at narrow constrictions. Such ornamentation may continue to 15 mm, but often it exists at larger diameters – commonly 20–30 mm, sometimes even 50 mm. On the middle whorls the primary ribs become more distant. The ribbing is mostly triplicate with a number of intercalatory ribs appearing above the mid flank. Flared ribs occur at the well marked constrictions. This ornamentation usually continues up to 50–80 mm diameter. On the last whorl ribbing becomes much more regular, consisting of fairly strong and distant primary ribs, and similarly developed (or somewhat weaker) secondary ribs; the number of secondaries per primary is two to three. The constrictions, if present, are poorly marked here, becoming wide and shallow. This final ornamentation may begin in some specimens a little earlier than in others, i.e. already on the penultimate whorl where it may partly replace the distant and irregular ornamentation of the former stage normally occurring there. The largest specimens attaining about 130–140 mm diameter carry the same type of final ornamentation to the end of the whorl.

The coiling of the inner and middle whorls (phragmocone), showing the irregular *Pictonia*-type ornamentation described above, is strongly evolute. On the other hand, the more regularly ribbed outer whorl corresponding mostly to the body chamber (at least two thirds of it) is much less evolute – from weakly evolute to even weakly involute (at D=70–90 mm, Wh=34–39%, Ud=36–42%), and resembles that of *Ringsteadia*.

Discussion. The species described herein is the oldest species of the genus *Pictonia*. It differs mostly from the closely allied *Pictonia densicostata*, Buckman in having regular strong ornamentation of the outer whorl, and its weakly evolute to weakly involute coiling. Closely similar to *Pictonia flodigarriensis* sp. nov. is a single specimen referred to as *Pictonia?* sp. indet. B by Birkelund & Callomon (1985, p. 32, pl. 11, fig. 4). This specimen reveals an involute body chamber with regular ornamentation, but its inner whorls are not preserved, which precludes unequivocal interpretation.

Genus *Microbiplices* Arkell, 1936

Type species. *Ammonites microbiplex* Quenstedt, 1887–8. According to the original definition (Arkell 1936, p. xli),

Microbiplices comprises forms “with a few coarse, rounded, bifurcating ribs with widely-splayed strong secondaries”. However, this type of ornamentation is characteristic, only of the last whorl up to the aperture as marked by presence of lappets. Several specimens of the type species, *M. microbiplex*, show a different type of ornamentation in the preceding whorl (as well as at the beginning of the last whorl). This consists of fairly thin triplicate, as well as biplicate ribs, with some long intercalatory ribs (see e.g. Arkell 1936, pl. C, fig. 6a–c; Enay 1962, pl. 2, figs 4a–d).

Genus *Prorاسenia* Schindewolf, 1925

Type species. *Prorاسenia quenstedti* Schindewolf, 1925. A change in ornamentation from triplicate ribbing of the inner whorls to biplicate ribbing of the last whorl similar to that seen in earlier *Microbiplices* occurs in representatives of *Prorاسenia*. According to some authors (Schweigert & Callomon 1997) this justifies treatment of the name *Microbiplices* as a junior synonym of *Prorاسenia*. However, in contrast to the similarity in ornamentation of the last whorl, there are marked differences in ornamentation of the penultimate stage. In *Microbiplices* the ribbing is thin, and the point of rib division lies at, or even somewhat above, the mid-height of whorl. In *Prorاسenia* the primary ribs are much thicker, and the point of division lies below the mid-height of the whorl. Thus, in the present paper the two taxa are treated separately.

The transition from *Microbiplices* to *Prorاسenia* is best observed in the upper part of the Pseudocordata Zone where the microconchs occurring here reveal a newer type of ornament. There are three growth stages in *Microbiplices* and *Prorاسenia*: (1) a stage of smooth whorls up to about 4.5–5.5 mm diameter; (2) a stage with biplicate and intercalatory ribs, later changing in ontogeny to triplicate ribs, with deep constrictions and strongly accentuated bordering ribs; (3) a stage with coarse, regularly furcating, biplicate, though sometimes single ribs, occupying a major part of the last whorl up to the aperture. The evolutionary changes appear mostly at the second stage. The primary ribs, initially at the end of the stage, become thicker, and the point of division of the ribs lowers on the whorl side, resulting in the exposure of secondaries of the penultimate whorl at the umbilical margin. Such a style of ribbing appears at the end of the penultimate and at the beginning of the last whorl (from 15–20 mm diameter), and is typical of the genus *Prorاسenia*. However, it follows ‘normal’ thin ribbing of the *Microbiplices* type in the inner whorls. The remainder of the last whorl bears coarse biplicate and single ribs, showing a somewhat lower point of rib furcation than in the outer whorl of typical *Microbiplices*. These specimens are thus intermediate in character between *Microbiplices* and *Prorاسenia* (Fig. 4f–h; see also Sykes & Callomon 1979, pl. 121, fig. 14).

6. Acknowledgements

The results presented in this paper are based on field-work at Staffin Bay in Skye carried out in July 2001 and in June 2003. Most of the ammonites cited here were collected from the Flodigarry section by the present authors. In addition, we thank Dr Julia Bello of the University of Zaragoza and Dr Kevin Page of the University of Plymouth for their help in collecting the fossils in July 2001. Some additional material collected by the present authors during a short visit to Skye in 1998 is also included in the paper. The authors are grateful for financial support enabling the field studies to both the Royal Society and the Faculty of Geology of the University of

Warsaw, who supported the stay in Britain of B. A. Matyja and A. Wierzbowski. We acknowledge also the kind permission from Scottish Natural Heritage to carry out the scientific studies in the protected area of Trotternish on the Isle of Skye, as well as the formal support of our studies by Dr Nicol Morton, chairman of the International Subcommittee of Jurassic Stratigraphy of the International Union of Geological Sciences. We are indebted also to Professor John Callomon and Dr Richard Hesketh for their discussion and comments in their refereeing of this paper.

7. References

- Anderson, F. W. & Dunham, K. C. 1966. *The geology of northern Skye*. Memoir of the Geological Survey of Great Britain (Scotland).
- Århus, N., Birkelund, T. & Smelror, M. 1989. Biostratigraphy of some Callovian and Oxfordian cores off Vega, Helgeland, Norway. *Norsk Geologisk Tidsskrift* **69**, 39–56.
- Arkell, W. J. 1933. *The Jurassic System in Great Britain*. Oxford: Clarendon Press.
- Arkell, W. J. 1936. A monograph of the ammonites of the English Corallian Beds. *Palaeontographical Society Monograph*, Part 2 **89**, xxxiii–xlvii, 31–42.
- Arkell, W. J. 1947a. A monograph of the ammonites of the English Corallian Beds. *Palaeontographical Society Monograph*, Part 13 **101**, 351–78.
- Arkell, W. J. 1947b. *The geology of the country around Weymouth, Swanage, Corfe & Lulworth: Upper Oxfordian Stage – Corallian Beds*. Memoir of the Geological Survey of Great Britain (England and Wales), 36–63.
- Arkell, W. J. 1956. *Jurassic geology of the World*. Edinburgh and London: Oliver & Boyd.
- Arkell, W. J., Kummel, B. & Wright, C. W. 1957. Mesozoic Ammonoidea. In Moore, R. C. (ed.) *Treatise on Invertebrate Paleontology, Part L, Mollusca 4, Cephalopoda – Ammonoidea*, L80–L490. Boulder, Colorado and Lawrence, Kansas: Geological Society of America & University of Kansas Press.
- Atrops, F., Gygi, R. A., Matyja, B. A. & Wierzbowski, A. 1993. The *Amoeboceras* faunas in the Middle Oxfordian – lowermost Kimmeridgian, Sub-Mediterranean succession, and their correlation value. *Acta Geologica Polonica* **43** (3–4), 213–27.
- Bayle, E. 1878. *Explication de la Carte géologique de France* **4**, (Atlas only published).
- Birkelund, T., Thusu, B. & Vigran, J., 1978. Jurassic-Cretaceous biostratigraphy of Norway, with comments on the British *Rasenia cymodoce* zone. *Palaeontology* **21**, 31–63.
- Birkelund, T., Callomon, J. H., Clausen, C. K., Nøhr Hansen, H. & Salinas, I. 1983. The Lower Kimmeridge Clay at Westbury, Wiltshire, England. *Proceedings of the Geologists' Association* **94** (4), 289–309.
- Birkelund, T. & Callomon, J. H. 1985. The Kimmeridgian ammonite faunas of Milne Land, central East Greenland. *Gronlands Geologiske Undersøgelse* **156**, 1–56.
- Blake, J. F. & Hudleston, W. H. 1877. On the Corallian rocks of England. *Quarterly Journal of the Geological Society of London* **33**, 260–405.
- Buckman, S. S. 1924. *Type ammonites*, Part 49, 41–8, pls 342, 525–36. London & Thame: Published by the author.
- Buckman, S. S. 1925a. *Type ammonites*, Part 50, pp. 49–56, pls. 154, 537–50. London & Thame: Published by the author.
- Buckman, S. S. 1925b. *Type ammonites*, Part 51, pp. 57–64, pls. 179, 259, 440, 513, 531, 551–62. London & Thame: Published by the author.
- Buckman, S. S. 1925c. *Type ammonites*, Part 55, pls 608–21. London & Thame: Published by the author.
- Callomon, J. H. 1985. The evolution of the Jurassic ammonite family Cardioceratidae. *Special Papers in Palaeontology* **33**, 49–90.
- Cox, B. M. 2001a. South Ferriby. In Wright, J. K. & Cox, B. M. (eds) *British Upper Jurassic Stratigraphy (Oxfordian to Kimmeridgian)*, *Geological Conservation Review Series* **21**, 121–6. Peterborough: Joint Nature Conservation Committee.
- Cox, B. M. 2001b. Kildorais. In Wright, J. K. & Cox, B. M. (eds) *British Upper Jurassic Stratigraphy (Oxfordian to Kimmeridgian)*, *Geological Conservation Review Series* **21**, 210–13. Peterborough: Joint Nature Conservation Committee.
- Enay, R. 1962. Contribution à l'étude paléontologique de l'Oxfordien supérieur de Trept. *Stratigraphie et ammonites. Travaux des*

- Laboratoires de G  ologie de la Facult   des Sciences de Lyon, N. S. 8, 7–81.
- Gallois, R. W. 2005. On the Kimmeridgian (Jurassic) succession of the Normandy coast, northern France. *Proceedings of the Geologists' Association* **116**, 33–43.
- Hantzpergue, P. 1989. *Les ammonites kimmeridgiennes du haut-fond d'Europa occidentale: biochronologie, syst  matique,   volution, pal  obiog  ographie*, 1–428. Paris:   ditions du Centre National de la Recherche Scientifique.
- Hesketh, R. A. & Underhill, J. R. 2002. The biostratigraphic calibration of the Scottish and Outer Moray Firth Upper Jurassic successions: a new basis for the correlation of Late Oxfordian–Early Kimmeridgian Humber Group reservoirs in the North Sea Basin. *Marine and Petroleum Geology* **19**, 541–62.
- Hyatt, A., 1900. *Cephalopoda*. In Zittel, K. A. (Ed.) *Textbook of Palaeontology*, 1st English ed., transl. Eastman, C. R., 502–92, figs 1049–1235.
- Matyja, B. A., Page, K. N., Wierzbowski, A. & Wright, J. K. 2004. A potential stratotype for the Oxfordian–Kimmeridgian boundary (Upper Jurassic), Staffin Bay, Isle of Skye, UK: ammonite succession. *Rivista Italiana di Paleontologia e Stratigrafia*, **110**(1), 273–8.
- Matyja, B. A. & Wierzbowski, A. 1988. Two *Amoeboceras* invasions in Sub-Mediterranean Late Oxfordian of Central Poland. In Rocha, R. B. & Soares, A. F. (eds) *2nd International Symposium on Jurassic Stratigraphy* **1**, 421–32. Lisboa.
- Matyja, B. A. & Wierzbowski, A. 1994. On correlation of Sub-Mediterranean and Boreal ammonite zonations of the Middle and Upper Oxfordian: new data from Central Poland. *Geobios M  moire Sp  cial* **17**, 351–8.
- Matyja, B. A. & Wierzbowski, A. 1997. The quest for a unified Oxfordian/Kimmeridgian boundary: implications of the ammonite succession at the turn of the Bimmamatum and Planula zones in the Wielun Upland, Central Poland. *Acta Geologica Polonica* **47** (1–2), 77–105.
- Matyja, B. A. & Wierzbowski, A. 1998. The stratigraphical and palaeogeographical importance of the Oxfordian and Lower Kimmeridgian succession in the Kcynia IG-4 Borehole. *Biuletyn Państwowego Instytutu Geologicznego* **382**, 35–70. [In Polish with English summary.]
- Matyja, B. A. & Wierzbowski, A. 2000. Biological response of ammonites to changing environmental conditions: an example of Boreal *Amoeboceras* invasions into Sub-Mediterranean Province during Late Oxfordian. *Acta Geologica Polonica* **50** (1), 45–54.
- Matyja, B. A. & Wierzbowski, A. 2002. Boreal and Sub-Boreal ammonites in the Sub-Mediterranean uppermost Oxfordian in the Bielawy section (northern Poland) and their correlation value. *Acta Geologica Polonica* **52** (4), 411–21.
- Matyja, B. A. & Wierzbowski, A. 2003. Correlation chart of standard chronostratigraphic ammonite zonations at the Oxfordian/Kimmeridgian boundary. *International Subcommission on Jurassic Stratigraphy Newsletter*, **30**, 25–7.
- Mesezhnikov, M. S., Azbel, A. J., Kalacheva, E. D. & Rotkyte, L. M. 1989. The Middle and Upper Oxfordian of the Russian Platform. *Academy of Sciences of USSR, Stratigraphical Committee Transactions* **19**, 1–158. [In Russian.]
- Mesezhnikov, M. S. 1967. A new ammonite zone of the Upper Oxfordian and the position of Oxfordian and Kimmeridgian boundary in northern Siberia. In Saks, V. N. (ed.) *Problems of paleontological substantiation of detailed stratigraphy of Siberia and Far East*, 110–30. Leningrad: Nauka. [In Russian.]
- Mesezhnikov, M. S. 1984. *Kimmeridgian and Volgian of the North of the USSR*, 1–65. Leningrad: Nedra. [In Russian.]
- Mesezhnikov, M. S. 1988. Oxfordian. In Krymholts, G. Ya., Mesezhnikov, M. S. & Westermann, G. E. G. (eds) *The Jurassic ammonite zones of the Soviet Union. Geological Society of America Special Paper*, **223**, 39–45.
- Morris, N. J. 1968. *Palaeontological and stratigraphical studies in the Upper Jurassic rocks*. Unpublished D. Phil. Thesis, University of Oxford.
- Morton, N. & Hudson, J. D. 1995. Field guide to the Jurassic of the Isles of Raasay and Skye, Inner Hebrides, NW Scotland. In Taylor, P. D. (ed) *Field geology of the British Jurassic*, 209–80. London: Geological Society of London.
- Neumayr, M. 1875. Die ammoniten der Kreide und die Systematik der Ammonitiden. *Zeitschrift der deutsche geologische Gesellschaft*, **27**, 854–92.
- d'Orbigny, A. 1850. R  sum   g  ologique: division des terrains jurassiques en   tages. In d'Orbigny, A. (1842–1851), *Pal  ontologie fran  aise. Terrains jurassiques. C  phalopodes*.
- Quenstedt, F. A. 1887–8. *Die Ammoniten des schwabischen Jura. III. Der Weisse Jura*. Stuttgart.
- Sachs, W. N., Ronkina, Z. Z., Bassov, V. A., Zakharov, V. A., Mesezhnikov, M. S., Schulgina N. J. & Judovny E. G. 1969a. Description of strata and reference section, In Sachs, V. N. (ed.) *Fundamental section of the Upper Jurassic of Kheta River Basin*, 14–63. Leningrad: Nauka. [In Russian.]
- Sachs, W. N., Bassov, V. A., Mesezhnikov, M. S., Ronkina, Z. Z. & Schulgina, N. J. 1969b. Stratigraphical conclusions and correlations. In Sachs, V. N. (ed.) *Fundamental section of the Upper Jurassic of Kheta River Basin*, 64–91. Leningrad: Nauka. [In Russian.]
- Salfeld, H. 1913. Certain Upper Jurassic strata of England. *Quarterly Journal of the Geological Society of London* **69**, 423–32.
- Salfeld, H. 1915. Monographie der Gattung *Cardioceras* Neumayr und Uhlig. I. Die Cardioceraten des oberen Oxford und Kimmeridge. *Zeitschrift der deutschen Geologischen Gesellschaft* **67**, 149–204.
- Salfeld, H. 1917. Monographie der Gattung *Ringsteadia* (gen. nov.). *Palaeontographia* **62** (2), 69–84.
- Schairer, G. 1989. Ammoniten aus dem Braunen und Weissen Jura von Sengenthal. *Mitteilungen der Bayerischen Staatsammlung f  r Pala  ontologie und Historische Geologie* **29**, 109–31.
- Schindewolf, O. H. 1925. Entwurf einer Systematik der Perisphinctiden. *Neues Jahrbuch f  r Mineralogie, Geologie und Pala  ontologie, Abt. B* **52**, 309–43.
- Schweigert, G. 1995. Zum Auftreten der Ammonitenarten *Amoeboceras bauhini* (Oppel) und *Amoeboceras schulginiae* Mesezhnikov im Oberjura der Schw  bischen Alb. *Jahreshefte des Gesellschaft f  r Naturkunde in W  rttemberg* **151**, 171–84.
- Schweigert, G. 2000. Immigration of *Amoeboceras* into the Sub-Mediterranean Upper Jurassic of SW Germany. *GeoResearch Forum* **6**, 203–9.
- Schweigert, G. & Callomon, J. H. 1997. Der *bauhini*-Faunenhorizont und seine Bedeutung f  r die Korrelation zwischen tethyalem und subborealem Oberjura. *Stuttgarter Beitr  ge zur Naturkunde, Serie B* **247**, 1–69.
- Siemiradzki, J. 1891. Fauna kopalna warstw oksfordzkich i Kimerydzkich w okr  gu Krakowskim i przyległych cz  ściach Kr  lestwa Polskiego. *Pami  tnik Akademii Umie  tności w Krakowie Wydział Matematyczno-Przyrodniczy*, **18**, 1–92.
- Spath, L. F. 1924. On the Blake collection of ammonites from Kachh, India. *Palaeontologica Indica*, n. s. **9**, mem. 1.
- Spath, L. F. 1935. The Upper Jurassic invertebrate faunas of Cape Leslie, Milne Land: I. Oxfordian and Lower Kimmeridgian. *Meddelelser om Gr  nland* **99**, 1–82.
- Steinmann, G. 1890. In Steinmann, G. & Doederlein, L. (Eds) *Elemente der Pal  ontologie*. Leipzig, 848 pp.
- Sykes, R. M. 1975. The stratigraphy of the Callovian and Oxfordian stages (Middle–Upper Jurassic) in northern Scotland. *Scottish Journal of Geology* **11** (1), 51–78.
- Sykes, R. M. & Callomon, J. H. 1979. The *Amoeboceras* zonation of the Boreal Upper Oxfordian. *Palaeontology* **22** (4), 839–903.
- Sykes, R. M. & Surlyk, F. 1976. A revised ammonite zonation of the Boreal Oxfordian and its application in northeast Greenland. *Lethaia* **9**, 421–36.
- Tornquist, A. 1896. Die degenerierten Perisphinctiden des Kimmeridge von Le Havre. *Abhandlungen der schweizerischen pala  ontologischen Gesellschaft* **23**, 1–43.
- Turner, J. 1966. The Oxford Clay of Skye, Scalpay, and Eigg. *Scottish Journal of Geology* **2**, 243–52.
- von Buch, L. 1831 *R  cueil des planches des p  trifications remarquables*. 8 plates with legends. Berlin.
- Wierzbowski, A. 1989. Ammonites and stratigraphy of the Kimmeridgian at Wimanfjellet, Sassenfjorden, Spitsbergen. *Acta Palaeontologica Polonica* **34** (4), 355–78.
- Wierzbowski, A. &   rhus, N. 1990. Ammonite and dinoflagellate cyst succession of an Upper Oxfordian–Kimmeridgian black shale core from the Nordkapp Basin, southern Barents Sea. *Newsletters on Stratigraphy* **22** (1), 7–19.
- Wierzbowski, A. & Smelror, M. 1993. Ammonite succession in the Kimmeridgian of southwestern Barents Sea, and the *Amoeboceras* zonation of the Boreal Kimmeridgian. *Acta Geologica Polonica* **43** (3–4), 229–50.
- Wierzbowski, A., Smelror, M. & Mork, A. 2002. Ammonites and dinoflagellate cysts in the Upper Oxfordian and Kimmeridgian of the northeastern Norwegian Sea (Nordland VII offshore area); biostratigraphical and biogeographical significance. *Neues Jahrbuch f  r Geologie und Pala  ontologie Abhandlungen*, **226** (2), 145–64.
- Wignall, P. B. 1990. Depositional history and palaeoecology of the Oxfordian/Kimmeridgian boundary beds at South Ferriby, South

- Humberside. *Proceedings of the Yorkshire Geological Society* **48** (2), 197–208.
- Wright, J. K. 1973. The Middle and Upper Oxfordian and Kimmeridgian Staffin Shales at Staffin, Isle of Skye. *Proceedings of the Geologists' Association* **84** (4), 447–57.
- Wright, J. K. 1980. The Oxfordian Stage. In Cope, J. C. W. (ed.) *A correlation of the Jurassic rocks of the British Isles, Part 2, Middle and Upper Jurassic*. Geological Society of London Special Report **15**, 61–76.
- Wright, J. K. 1989. The Early Kimmeridgian ammonite succession at Staffin, Isle of Skye. *Scottish Journal of Geology* **5** (3), 263–72.
- Wright, J. K. 1998. New stratigraphical and palaeoecological data from the Sandsfoot Formation (Upper Oxfordian) of south Dorset. *Proceedings of the Geologists' Association* **109**, 15–24.
- Wright, J. K. 2001. Staffin. In Wright, J. K. & Cox, B. M. (eds) *British Upper Jurassic Stratigraphy (Oxfordian to Kimmeridgian)*, Geological Conservation Review Series **21**, 201–10. Peterborough: Joint Nature Conservation Committee.
- Wright, J. K. 2003. New exposures of the Ampthill Clay near Swindon, Wiltshire, and their significance within the succession of Oxfordian/Kimmeridgian boundary beds in southern England. *Proceedings of the Geologists' Association* **114**, 97–121.
- Yershova, Y. S. 1983. *Biostratigraphical scheme of the Jurassic and Lower Cretaceous deposits of the Spitsbergen archipelago*, 1–88. Leningrad: Sevmorgeologiya. [In Russian.]

B. A. MATYJA and A. WIERZBOWSKI, Institute of Geology, University of Warsaw, Al. Zwirki i Wigury 93, 02–089 Warszawa, Poland.

J. K. WRIGHT, Department of Geology, Royal Holloway, Egham Hill, Egham, Surrey, TW20 0EX

Manuscript received 19 May 2004. Accepted for publication 4 January 2006.