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Notes on the evolution of the ammonite families Aulacostephanidae and Cardioceratidae and the stratigraphy of the uppermost Oxfordian and lowermost Kimmeridgian in the Staffin Bay sections (Isle of Skye, Northern Scotland)

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Key words: stratigraphy, ammonites, Oxfordian/Kimmeridgian boundary, evolution, heterochrony.

Abstract. Detailed study of all the ammonite collections gathered by the authors in the Staffin Bay sections has resulted in minor changes in the distribution of ammonite taxa, and slight modification of the position of the Oxfordian/Kimmeridgian boundary. Most significant is the discovery of *Pictonia* (*Triozites*) cf. *seminudata* which results in the placing of the stage boundary 0.16 m below the level formerly proposed. This study discusses the evolution of the Subboreal family Aulacostephanidae, and the Boreal family Cardioceratidae, indicating changes in the patterns of individual development in the evolution of both families in terms of heterochrony. The Oxfordian/Kimmeridgian boundary interval shows major morphological changes in both ammonite families which were released from phylogenetic constraints by heterochrony, closely related to changes in environmental conditions.

INTRODUCTION

The uppermost Oxfordian and lowermost Kimmeridgian deposits which crop out in the sections at Staffin Bay, northern Skye (Northern Scotland) – especially at Flodigarry and Digg hamlets, comprise a remarkably complete succession very rich in ammonites, and proposed as the potential stratotype (GSSP) of the base of the Kimmeridgian (Matyja *et al.*, 2004, 2006; Wierzbowski *et al.*, 2006, 2016). The succession generally corresponds to that described in older studies of the area of Staffin Bay (Anderson, Dunham, 1966; Sykes, Callomon, 1979; Wright, 1989, 2001; Morton, Hudson, 1995; Hesketh, Underhill, 2002), but some differences in thicknesses of particular beds can be noticed. Details of the succession, especially well seen at Flodigarry, are discussed in these papers but additional comments related to the distribution of the ammonites, and their stratigraphical interpretation, are given herein. These are based on the careful study of all the ammonite collections gathered by the authors, with special attention to newly obtained specimens, and/or revised older determinations. This study has resulted in minor changes in the distribution of a few ammonite taxa, and some stratigraphical reinterpretation (Figs 1–3). No major change is proposed in the position of the Oxfordian/Kimmeridgian boundary, compared with previous interpretations (Wierzbowski *et al.*, 2016: fig. 2).

Study of the sequence of faunas of the ammonite families Aulacostephanidae Spath, 1924, and Cardioceratidae Siemiradzki, 1891 by several authors has resulted in several presentations of the evolutionary history of these two fami-

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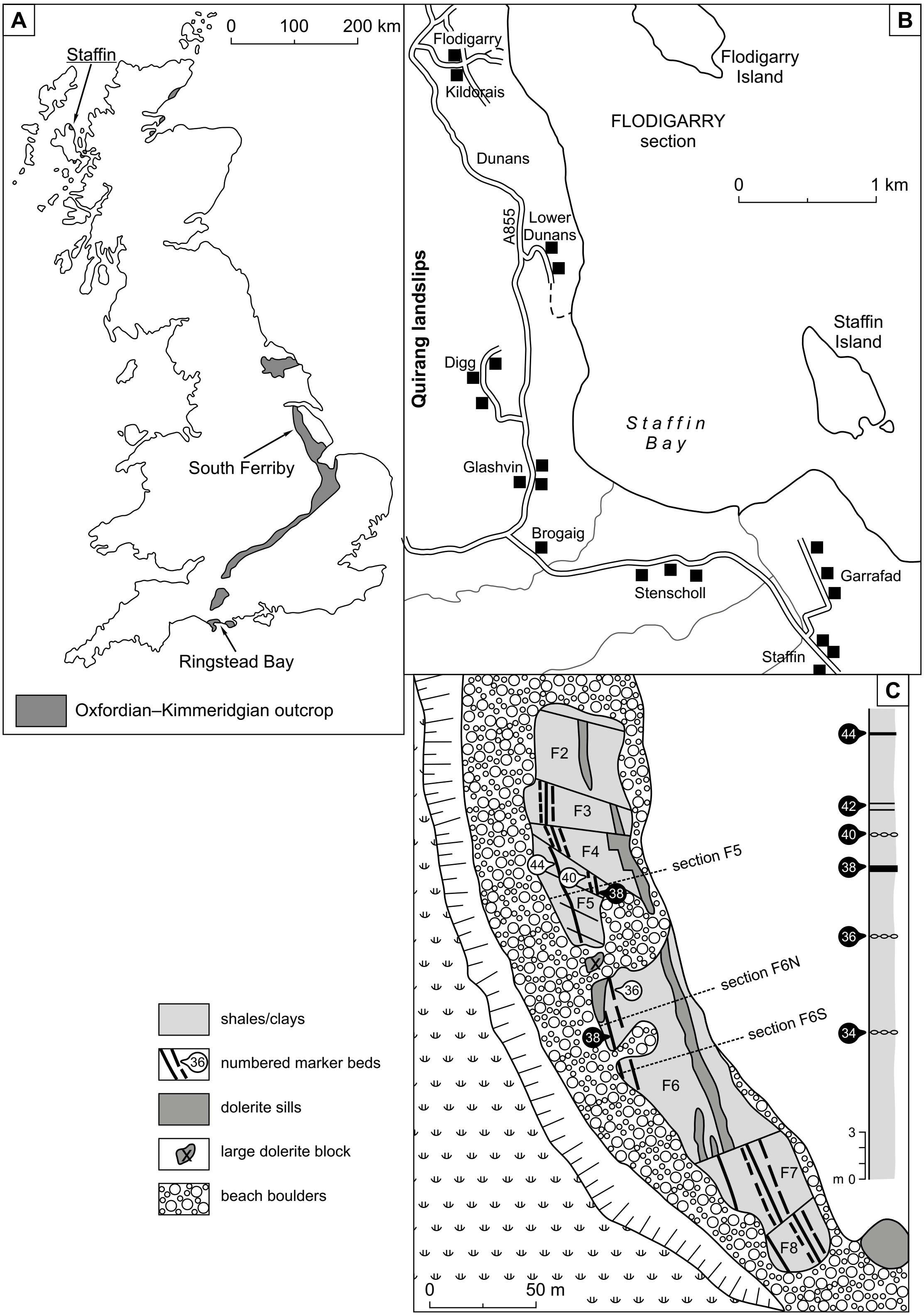

Fig. 1. B. Location map of Staffin Bay (the inset A shows the position of the area in Northern Scotland and the most important Oxfordian/Kimmeridgian boundary outcrops in U.K.); C. Map of the foreshore at Flodigarry showing the position of the sections studied (after Wierzbowski *et al.*, 2006)

Fig. 2. View along the beach at Flodigarry showing the position of bed 36

A. General view of the foreshore at Flodigarry, showing the position of the large boulder (arrowed); **B.** View looking north along the beach at Flodigarry showing the marker limestone bed 36 and the large boulder; **C.** Limestone bed 36 lies which were dominant in the Subboreal and Boreal provinces of NW Europe during the Late Oxfordian and Early Kimmeridgian. The evolution of the family Aulacostephanidae as presented in general outline by Callomon (1980) and Hantzpergue (1989), is discussed herein in more detail, and partly modified according to Wierzbowski (2017). The evolution of the Jurassic family Cardioceratidae was discussed by Callomon (1985), but the detailed pattern of changes concerning the development of the lineage during the latest Oxfordian – earliest Kimmeridgian as given herein is slightly different, and presents the supplemented and modified interpretation of Wierzbowski and Rogov (2013).

This study refers mostly to specimens of Aulacostephanidae and Cardioceratidae collected from the sections at Staffin Bay, Isle of Skye in Northern Scotland. The phylogenies of both the Aulacostephanidae and the Cardioceratidae in the Staffin Bay sections have been discussed previously on the occasion of the proposal of the GSSP for the Oxfordian/Kimmeridgian boundary (Matyja *et al*., 2006; see also Wierzbowski *et al*., 2016). However, this is supplemented in the present work using information from specimens from older collections made in 1998, 2001 and 2003, all at the disposal of the authors, and not discussed in detail previously. Some of these are illustrated and described herein (Pls 1, 2). A summary of the accepted classification scheme of the ammonites studied is given in Appendix 1, and a list of the newly determined and revised ammonites in the collection is given in Appendix 2.

AMMONITE STRATIGRAPHY

The zones and subzones as used herein are chronozones (chronosubzones) distinguished according to the convention widely accepted for the Jurassic System: “this is to take only the adjectival, specific part of the Linnéan bionomen of the index and to write it in non-italicized form with initial capital letter, and similarly to capitalize the word “Zone” (Callomon, 1984: p. 623). The ammonite zonations used in the proposed stratotype section are based on both Subboreal Aulacostephanidae, and Boreal Cardioceratidae and this enhances the correlation potential of the section.

Both the specific and generic names (including those used for dimorphic forms), are used here in the morphogeneric sense in order to cover the “vertical” range in similar morphologies present. Such an approach is purely descriptive and “fully conscious”, because the detailed relations between the particular morphs described herein takes into account the presence of natural “horizontal” assemblages of morphotypes, and makes possible the recognition of the general evolutionary directions in the particular lineages.

AULACOSTEPHANIDAE

The biostratigraphical classification based on the evolution of the Aulacostephanidae is shown in Fig. 3. The uppermost Oxfordian Subboreal Pseudocordata Zone can be subdivided into the Caledonica Subzone, the Pseudoyo Subzone, the Pseudocordata Subzone and the Evoluta Subzone (Wright, 2003, 2010) – based on an evolutionary sequence of ammonites of the genus *Ringsteadia* (macroconchs), and corresponding microconchs of the genus *Microbiplices,* followed by *Microbiplices – Prorasenia* transitional forms. The lowermost Kimmeridgian Subboreal Baylei Zone, with subdivisions based on ammonites of the genus *Pictonia* and microconch counterparts (*Microbiplices – Prorasenia* transitional forms, and *Prorasenia*), includes the lower Densicostata Subzone (with basal *flodigarriensis* horizon overlain by the *densicostata* horizon) and upper Normandiana Subzone. The basal part of the Cymodoce Zone, the *inconstans* horizon, is distinguished on the basis of ammonites of the genus *Rasenia* (see Matyja *et al.*, 2006; Wierzbowski *et al.*, 2016).

Published data on interpretation of the uppermost Oxfordian to lowermost Kimmeridgian stratigraphy of the Aulacostephanidae in the Staffin Bay sections is supplemented herein by four newly observed occurrences:

1. Moderately well preserved specimens of *Ringsteadia pseudocordata* (Blake et Hudleston) in the basal part of bed 35 in the Flodigarry section somewhat above the previous records of the species, but in beds still attributed to the Pseudocordata Subzone (Pl. 1: 2; see Matyja *et al.*, 2006);
2. Discovery of *Ringsteadia frequens* Salfeld – a species commonly occurring in the Evoluta Subzone of the Pseudocordata Zone in southern England (see Wright, 2010), in bed 35 (from 1.26 to 1.9 m below bed 36; Pl. 1: 3) in the Flodigarry section in the stratigraphical interval correlated with the topmost part of the Pseudocordata Zone;
3. Poorly preserved specimens referred to as *Pictonia* (*Triozites*) cf. *seminudata* (Buckman) – discovered in bed 35 (from 1.24 to 0.45 m below bed 36; Pl. 1: 4–6) in

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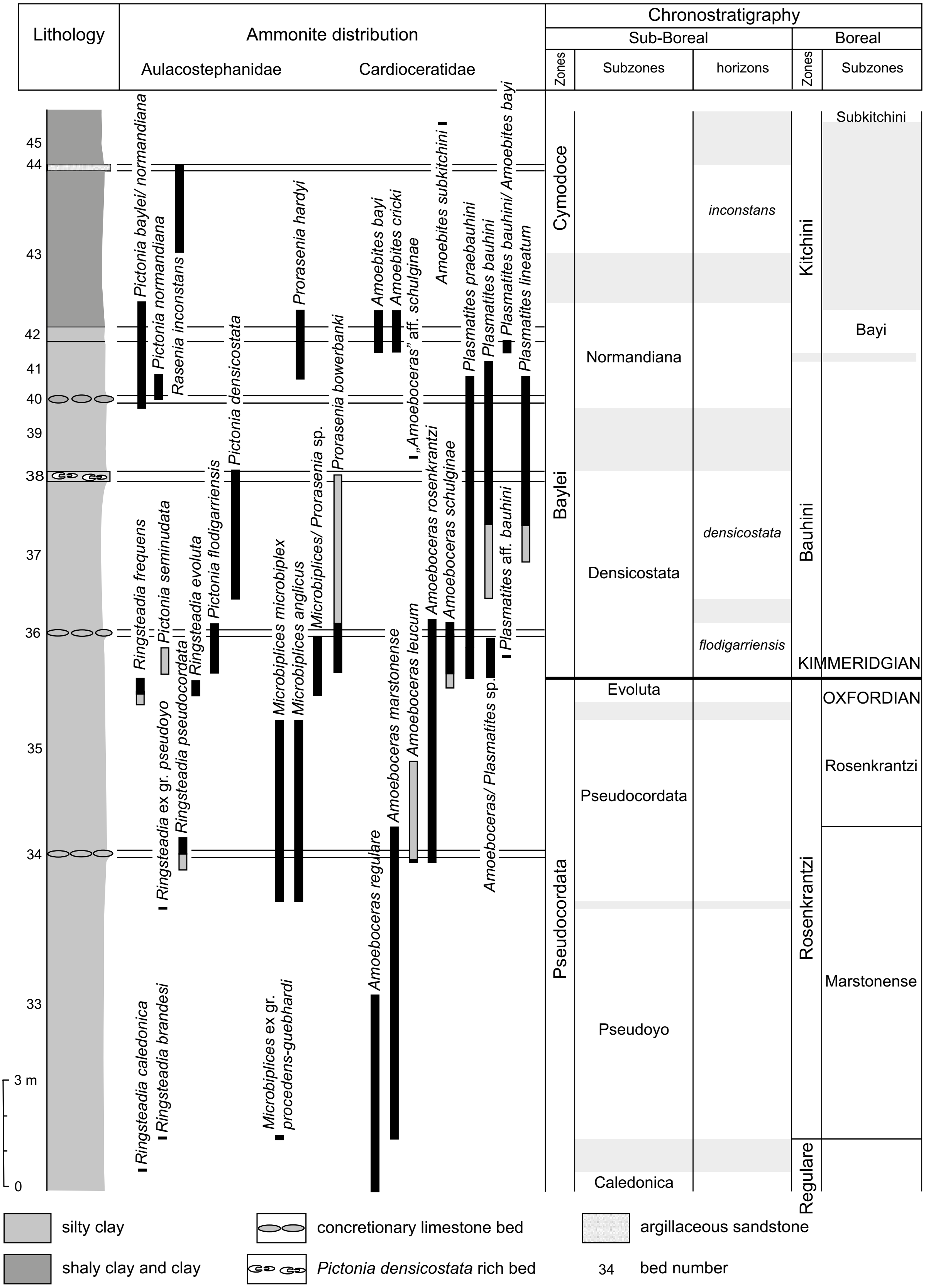
Fig. 3. Distribution of ammonites in the Flodigarry section, Staffin Bay, Isle of Skye – the proposed GSSP of the base of the Kimmeridgian Stage as supplemented herein (modified from Matyja *et al.*, 2006; Wierzbowski *et al.*, 2016);

Ammonite distribution column – grey bars are referred to cf. species; chronostratigraphy column – grey blocks indicate the intervals of uncertain correlation


Lithology
Ammonite distribution
Aulacostephanidae
Cardioceratidae
Chronostratigraphy
Sub-Boreal
Boreal
Zones
Subzones
horizons
Zones
Subzones
45
44
43
42
41
40
39
38
37
36
35
34
33
3 m
0
Pictonia baylei/ normandiana
Pictonia normandiana
Rasenia inconstans
Pictonia densicostata
Prorasenia hardyi
Prorasenia bowerbanki
Amoebites bayi
Amoebites cricki
„Amoeboceras" aff. schulginae
Amoebites subkitchini
Plasmatites praebauhini
Plasmatites bauhini
Plasmatites bauhini/ Amoebites bayi
Plasmatites lineatum
Ringsteadia frequens
Pictonia seminudata
Ringsteadia evoluta
Pictonia flodigarriensis
Microbiplices microbiplex
Microbiplices anglicus
Microbiplices/ Prorasenia sp.
Amoeboceras marstonense
Amoeboceras leucum
Amoeboceras rosenkrantzi
Amoeboceras schulginae
Plasmatites aff. bauhini
Ringsteadia ex gr. pseudoyo
Ringsteadia pseudocordata
Amoeboceras regulare
Amoeboceras/ Plasmatites sp.
Ringsteadia caledonica
Ringsteadia brandesi
Microbiplices ex gr. procedens-guebhardi
Cymodoce
Baylei
Pseudocordata
Normandiana
Densicostata
Evoluta
Pseudocordata
Pseudoyo
Caledonica
inconstans
densicostata
flodigarriensis
Kitchini
Bauhini
Rosenkrantzi
Regulare
Subkitchini
Bayi
KIMMERIDGIAN
OXFORDIAN
Rosenkrantzi
Marstonense
silty clay
shaly clay and clay
concretionary limestone bed
Pictonia densicostata rich bed
argillaceous sandstone
34 bed number

the Flodigarry section. This it is possibly the stratigraphically most important discovery. *P. seminudata* is common in the *densicostata* horizon of the Baylei Zone in southern England (Wright, 2010). Its occurrence in the *flodigarriensis* horizon 1.24 m below bed 36 suggests the placing of the lower boundary of the Baylei Zone (and the base of the Kimmeridgian) should be located 0.16 m below the level formerly accepted. Thus *Pictonia* (*Triozites*) *seminudata* can be accepted as another indicator species, along with *Pictonia flodigarriensis*, for the basal part of the Baylei Zone – the *flodigarriensis* horizon of the Densicostata Subzone;

4. Transitional forms of *Microbiplices – Prorasenia* in the uppermost part of bed 35 up to base of bed 36 in the Digg section indicate a somewhat larger stratigraphical range than previously indicated (Matyja *et al.*, 2006).

CARDIOCERATIDAE

The biostratigraphical classification based on the evolution of the family Cardioceratidae is also shown in Fig. 3. The uppermost Oxfordian Boreal Rosenkrantzi Zone spans the stratigraphical range of the last ammonites of the genus *Amoeboceras*. The lowermost Kimmeridgian Bauhini Zone is defined by occurrence of small-sized ammonites of the genus *Plasmatites.*

Amoeboceras – Plasmatites intermediates. The most important new information is the recognition of the occurrence of forms intermediate between *Amoeboceras rosenkrantzi* Spath, and the first *Plasmatites* – such as *Plasmatites praebauhini* (Salfeld) (Pl. 2: 6, 7) and *P. lineatum* (Quenstedt). These forms show special development of the ventral side on the inner whorls where the secondary ribs continue up onto the keel, thus beginning to adopt a feature common in the genus *Plasmatites*, and which is paedomorphic in character when compared with older *Amoeboceras* (see discussion chapter on the evolution of the Cardioceratidae). This special morphological character of the oldest assemblage of the *Plasmatites* group of ammonites is thus remarkable and of marked stratigraphical importance. However, no detailed study on the distribution of particular morphs in the succession studied at Staffin Bay has ever been carried out.

Plasmatites biohorizons. Study of the morphology of the ammonite genus *Plasmatites* in the lowermost Kimmeridgian of the Moscow Syneclise of the Russian Platform, and in Western Siberia, has resulted in the recognition of several smaller scale biostratigraphic units (biohorizons) in the Bauhini Zone (Rogov, 2016, 2017). Some of these biostratigraphic units were correlated by Rogov (2016, 2017) with parts of the Staffin Bay succession based on the ammonites occurring here. It is important to clarify the taxonomic and biostratigraphical premises for such correlations, and to discuss the possibilities of informal subdivision of the Bauhini Zone in the Staffin Bay sections.

The oldest assemblage of ammonites in the Staffin Bay sections which are transitional between *Amoeboceras* and *Plasmatites* seems to correspond to the oldest assemblage of the Bauhini Zone in Russia recognized as the *zieteni* biohorizon (Rogov, 2016, 2017). The species *Plasmatites zieteni* (Rouillier) which is typical of the assemblage in Russia has the outer part of the whorl between the secondary ribs and the keel smooth, showing a transitional character between *Amoeboceras* and *Plasmatites.* This feature also occurs in some specimens from the Staffin Bay sections discussed above. However, *P. zieteni* differs from the Staffin Bay specimens in several other features (such as *e.g.* the character of coiling), and represents thus a separate form.

It is clear that the specimens referred to "*Amoeboceras*" (= *Plasmatites*) *bauhini* (Oppel) from the Staffin Bay sections by Sykes and Callomon (1979, pl. 121: 4, 5) cannot be placed in the synonymy of *P. zieteni* as suggested by Rogov (2016) because of there are differences in morphology, and especially because the specimens occur in a much younger position in the Bauhini Zone than that proposed for the *zieteni* biohorizon. The Staffin specimens come from the middle and upper parts of the Bauhini Zone, 5 metres above the base of bed 37 after Sykes and Callomon (1979, see explanations to their plate 121). Similar specimens are illustrated by Matyja *et al.* (2006: figs. 6h, i) and Wright (1989, figs 4K–M), and see Pl. 2: 9, 10. These represent an assemblage of forms very close to the holotype of *Plasmatites bauhini* (Oppel), but they differ from it in having the secondaries faintly linked up to the crenulations on the keel, with only a tendency for the ribbing to disappear along the keel at the ventral side. Also close is the form "*Amoeboceras*" (=*Plasmatites*) *gerassimovi* Kalacheva et Mesezhnikov (see Pl. 26: 3–8 in Mesehnikov *et al.*, 1989). This has sometimes been compared with *Plasmatites bauhini* (Oppel) (see Głowniak *et al.*, 2010, p. 20, pl. 4: 9–11) in the sections of the Russian Platform.

Although there are no clear grounds for distinguishing precisely defined faunal horizons on the basis of the stratigraphical ranges of particular species of the genus *Plasmatites* in the Staffin Bay sections, some differences in the distribution of some morphotypes in the succession may be recognized. Forms transitional between *Amoeboceras* and *Plasmatites* occur in the lowermost part of the Bauhini Zone, where also *Plasmatites praebauhini* is common. The species *P. bauhini* and *P. lineatum* occur commonly in the middle-upper parts of this zone (the latter illustrated by Matyja *et al.*, 2006: figs 6h–j; and Wright, 1989: figs 4G–J

– these incorrectly allocated to *Amoeboceras bayi* Birkelund et Callomon). On the other hand, there appear also some forms, showing smooth part of the whorls close to the ventral side which are somewhat similar to *P. gerassimovi* (see Pl. 2: 9, 10). The latter may represent the initial stage of development of the new forms, transitional between *Plasmatites* and *Amoebites.*

Klimovae biohorizon. Some comments are also necessary on the nature of the *klimovae* biohorizon recognized in the middle and upper parts of the Bauhini Zone in western Siberia by Rogov (2016). The species *Amoeboceras ?klimovae* Rogov is based on the specimen of "*Amoeboceras ravni* Spath" as illustrated by Mesezhnikov (1967: p. 116, pl. 1: 1), and treated as its holotype. This species occurs along with *Amoeboceras schulginae* Mesezhnikov in the Levaya Boyarka section in northern Siberia, somewhere at the transition between the Rosenkranzti and the Bauhini zones (*cf.* Wierzbowski, Rogov, 2013: p. 1088). Rogov (2016) placed additionally in the synonymy of *A. klimovae* the form described as "*Amoeboceras* aff. *schulginae* Mesezhnikov" by Matyja *et al.* (2006: p. 401, fig. 6k–n) from bed 39 of the Skye sections corresponding to some upper parts of the Bauhini Zone. The latter shows, however, a quite different character on the ventral side where the secondary ribs "may continue with some weakening onto the crenulated keel", whereas in the holotype of *A. klimovae* the keel is evidently bordered from the secondary ribs by very well developed ventral sulci. Such forms with well-developed ventral sulci have never been found at Flodigarry. Thus, because of its stratigraphical position and difference in morphology, the form "*A.* aff. *schulginae* Mesezhnikov" of Matyja *et al.* (2006) cannot be treated as conspecific with *Amoeboceras* ? *klimovae* Rogov, and there are no data to distinguish the *klimovae* biohorizon in the Staffin Bay sections.

THE EVOLUTIONARY HISTORY OF AMMONITES AT THE OXFORDIAN/KIMMERIDGIAN BOUNDARY

AULACOSTEPHANIDAE

Three principal ammonite assemblages can be recognized in the succession studied: (1) the oldest one composed of several successive ammonite faunas represented by macroconchs of the genus *Ringsteadia* and the corresponding microconchs placed in the genus *Microbiplices*, and the appearance thereafter of *Microbiplices – Prorasenia* transitional forms; (2) a middle assemblage characterised by macroconchs of the genus *Pictonia*, and the corresponding microconchs of the *Microbiplices – Prorasenia* transitional forms and the genus *Prorasenia*; (3) the youngest, only fragmentarily represented, characterized by the genus *Rasenia.*

Ringsteadia – Microbiplices and their ancestors. The first ammonite of the genus *Ringsteadia – R. caledonica* Sykes et Callomon makes its appearance not before the upper part of the Boreal Regulare Zone, and marks the base of the Subboreal Pseudocordata Zone (Sykes, Callomon, 1979). For a long time the species was known only from the Staffin Bay sections on Isle of Skye in Northern Scotland (Sykes, Callomon, 1979: pl. 121: 8–13), but recently has been discovered in the same stratigraphical position in north-eastern Poland – in the Bartoszyce IG 1 core from the Peri-Baltic Syneclise (Wierzbowski *et al.*, 2015: fig. 8j–l). In the core in question, this ammonite is directly preceded in the Subboreal succession by another form, closely related to *Decipia*(?) *kostromensis* (Wierzbowski *et al.*, 2015, fig. 8i). The latter bears the "primitive" features of its ancestors such as dense biplicate ribbing occurring not only in the phragmocone, but also in a large part of the body-chamber. A very similar form was also discovered in the coeval deposits of the Submediterranean succession at the base of the Hypselum Zone in the Polish Jura of central Poland (Wierzbowski, Matyja, 2014: p. 68, pl. 3: 5). This form, similar to that which gave rise to the much older *Decipia* lineage near the boundary of the Middle and Late Oxfordian, could be thus treated as the forerunner of the new *Ringsteadia* lineage (Wierzbowski, 2017). Such a repeated origination of lineages with a generally similar morphology, evolving from less specialized forms, is generally characteristic of iterative evolution. This type of evolution may act on the unspecialized forms, after extinction of one group, when the conditions favorable for the flourishing of the more specialized group arose again.

The following *Ringsteadia* faunas may be seen in the succession at Flodigarry in Staffin Bay, (Fig. 3) from its base (but note that the oldest *R. caledonica* fauna has not been studied):

1. *Ringsteadia pseudoyo* Salfeld and *Ringsteadia brandesi* Salfeld and corresponding microconchs of *Microbiplices* ex gr. *procedens* (Oppenheimer) – *guebhardi* (Oppenheimer) and *M. microbiplex* (Quenstedt) (Matyja *et al.*, 2006: fig. 4a, b) ;
2. *Ringsteadia pseudocordata* (Blake et Hudleston) (Pl. 1: 2), and *Microbiplices microbiplex* and *M. anglicus* Arkell;
3. *Ringsteadia evoluta* Salfeld and *R. frequens* Salfeld associated with *Microbiplies – Prorasenia* transitional forms (Matyja *et al.*, 2006: fig. 4d–h; Wierzbowski, Matyja, 2014; also some new information given herein, see Figs 4, 5, also Pl. 1: 1, 3).

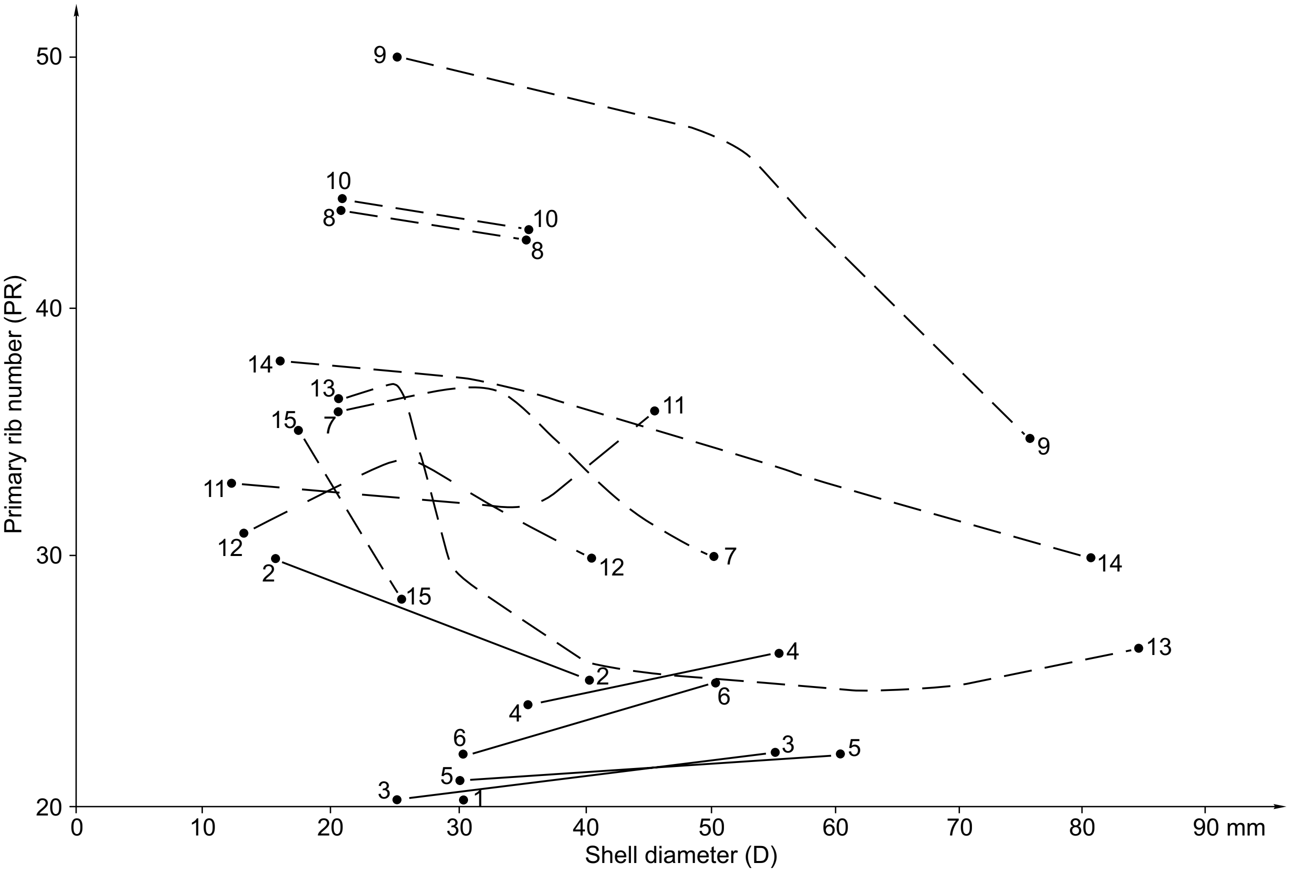


Fig. 4. Number of primary ribs (PR) against shell diameter (D) for macroconchs *Ringsteadia* and *Pictonia* (*Triozites*) (continuous line) and for *Pictonia* (*Pictonia*) (hatched line); all specimens are from the Flodigarry section if not described otherwise

1 – *Ringsteadia* cf. *frequens* Salfeld: section F6S, bed 35 (1.9 m below bed 36), specimen no. MWG UW ZI/94/01; 2 – *R.* cf. *evoluta* Salfeld: section F6S, bed 35 (1.5 m below bed 36), specimen no. MWG UW ZI/94/02; 3 – *R. frequens*: section F6S, bed 35 (1.26 m below bed 36), specimen no. MWG UW ZI/94/03; 4 – *Pictonia* (*Triozites*) cf. *seminudata (*Buckman): section F6S, bed 35 (1.24 m below bed 36), specimens MWG UW ZI/94/04; 5, 6 – *R. pseudocordata* (Blake et Hudleston): section F6/7, bed 35 (lowermost part), specimens no. MWG UW ZI/94/08 and 09; 7, 8 – *Pictonia* ex gr. *flodigarriensis* Matyja *et al.* – *densicostata* Buckman: section F7, bed 35 (0.52 m below bed 36), specimens no. MWG UW ZI/94/06 and 07; 9, 10 – *P. flodigarriensis* Matyja, Wierzbowski et Wright; paratypes: section F7, bed 35 (0.52 m below bed 36), specimen ST 837 (see Matyja *et al.*, 2006, fig. 5b); section F6N, bed 35 (0.39 m below bed 36), specimen ST 836 (see Matyja *et al.*, 2006, fig. 5a); 11 – *P. densicostata* Buckman: section F5, bed 38, specimen ST 839 (see Matyja *et al.*, 2006, fig. 5d); 12 – *Pictonia* ex gr. *normandiana* (Tornquist) – *baylei* Salfeld: section F5, bed 41, 5.9 m below bed 44, specimen no. MWG UW ZI/94/14; 13 – *P. normandiana*: section F5, bed 41, specimen ST 842 (see Matyja *et al.*, 2006: fig. 5g); 14 – *Pictonia densicostata* Buckman: Digg, "*Pictonia bed*" (about bed 38), specimen no. MWG UW ZI/94/21; 15 – *Pictonia* ex gr. *normandiana* (Tornquist) – *baylei* Salfeld: section F5, bed 41, 5.4 m below bed 44, specimen no. MWG UW ZI/94/17

Macroconch members of the lineage show generally rather subtle changes in morphology expressed mostly by changes in the domination of particular morphotypes in the succession – from the dominant involute forms in the oldest fauna, through the increasingly evolute forms in the middle fauna, up to dominant strongly evolute forms which may be strongly constricted in the youngest fauna. Such changes in the *Ringsteadia* ammonite lineage were originally well recognized in southern England (Wright, 2010: fig. 8), which suggest everywhere their uniform character independent of environmental development.

The changes in the microconchs are also subtle, being marked mostly by the dominance of rather weakly and densely ribbed forms in the lower part of the succession and the successive appearance of more strongly, and loosely ribbed forms above (*cf.* Matyja *et al.*, 2006). The whole succession can be thus interpreted as a segment of the smoothly evolved lineage of Aulacostephanidae, and may be easily stratigraphically compared with the Pseudocordata Zone, and its three successive members: the Pseudoyo Subzone, the Pseudocordata Subzone and the Evoluta Subzone (Wright, 2003, 2010).

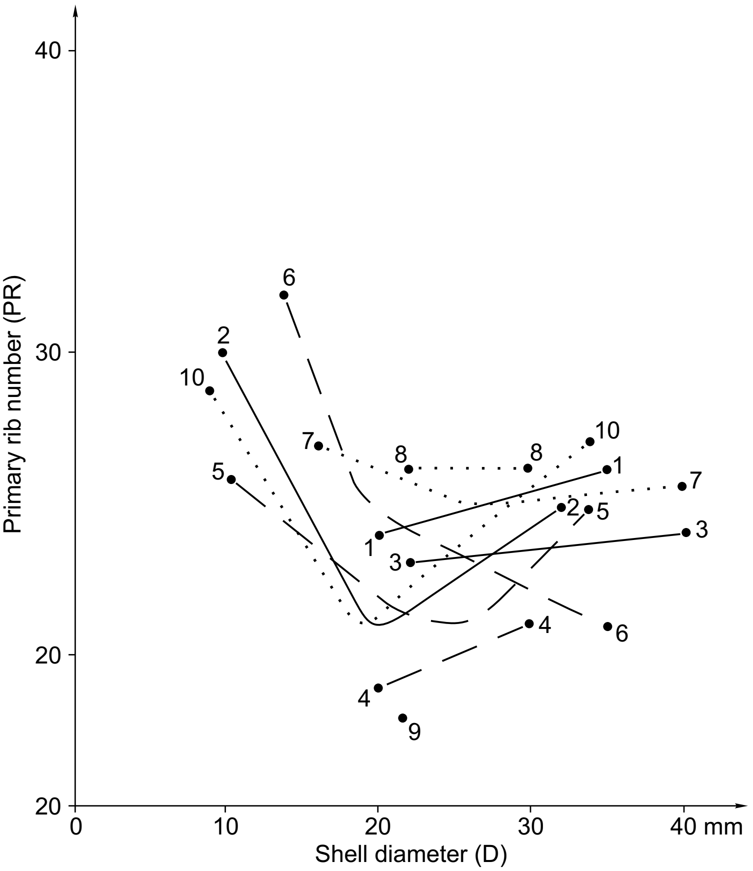


Fig. 5. Number of primary ribs (PR) against shell diameter (D) for microconchs *Microbiplices* (continuous line), *Microbiplices – Prorasenia* transitional forms (hatched line), and *Prorasenia* (stippled line)

Microbiplices cf. *microbiplex* (Quenstedt): 1–3, Flodigarry, lowermost part of bed 35 – from its base up to 0.5 m above, specimens MWG UW ZI/94/10, 11 and 12;

Microbiplices/*Prorasenia* transitional form: 4 – Flodigarry, section F6S, bed 35 (1.4 m below bed 36), specimen ST 832 (see Matyja *et al.*, 2006: fig. 4g); 5, 6 – Digg, bed 35 (0.00–0.15 m below bed 36), specimens no. MWG UW ZI/94/18 and 19;

Prorasenia bowerbanki Spath: 7–9 – Digg, bed 35 (0,00–0.15 m below bed 36), specimens no. MWG UW ZI/94/23, 24, and 25; 10 – Digg, "*Pictonia bed*" (about bed 38), specimen no. MWG UW ZI/94/20

In the ontogeny of the macroconchs of *Ringsteadia* there may be observed the repetition of changes in common in the whole lineage, both in the character of coiling and in character of ribbing. The innermost whorls generally show more evolute coiling than that of the middle-outer whorls; the ribbing on the innermost whorls up to about 15–25 mm diameter varies from quite faint and biplicate, with strong constrictions, to dominant, sharp biplicate ribs. Thereafter, the primary ribs are only boldly developed at the umbilical margin, passing irregularly via a variably developed smooth, spiral band at mid-whorl height into bifurcating and trifurcating secondaries, with frequent intercalated secondaries. The ribbing usually becomes less well developed towards the end of the phragmocone, though some evolute forms retain bold primaries on the body chamber. Most forms retain secondary ribbing near the venter to quite a late stage. Generally the primary rib curves of the *Ringsteadia* macroconchs, showing the relation between the number of the primary ribs per whorl and the diameter of the specimen, are rather flat in their course with noticeable but limited maxima occurring in the innermost whorls, and sometimes also at the end of phragmocone – beginning of the body chamber (Fig. 4).

The corresponding microconchs (*Microbiplices* and *Microbiplices – Prorasenia* transitional forms) show very early deviation in their ontogeny from that shown by the *Ringsteadia* macroconchs. Only in some early forms like *Microbiplices procedens* is the dominant dense biplicate ribbing retained up to somewhat larger diameters, but soon thereafter appear forms like *M. microbiplex* where very dense biplicate ribbing is observed in the innermost whorls only (up to about few mm in diameter). The ribbing appearing then is composed of loosely spaced triplicate and biplicate ribs with some intercalatories, which generally is similar to that of *Ringsteadia*, but often found at smaller diameters (Fig. 5). The final specific ornamentation observed on some younger specimens of *Microbiplices* and on the subsequent *Microbiplices – Prorasenia* transitional forms is composed of widely-spaced bifurcating ribs appearing on the last whorl and ranging up to the final aperture with lappets.

Summarizing, it should be noted that in the evolutionary development of the lineage *Ringsteadia* reveals no changes in the rate of development of morphology, when compared with older *Decipia* macroconchs. On the other hand, the *Microbiplices* microconchs show a smaller final size, and a special development of widely-spaced bifurcating ribs at the end of the shell, not encountered in its ancestors. This feature appeared, however, with some delay in the lineage, in those representatives more advanced in morphology, like *Microbiplices microbiplex* and its allies. Interestingly, there exist some intermediate specimens close to *M. microbiplex* which show the presence of triplicate ribs up to end of the last whorl and the final aperture [*e.g.* those referred erroneously as "*Prorasenia*" by Schairer and Schlampp from southern Germany (2003, pl. 2: 2, 12, 13)], which do not have the final stage of widely-spaced bifurcating ribs.

This type of development of small-sized microconchs as based on the *Microbiplices microbiplex* morphology appeared such a successful adaptation for changing environmental conditions that it was accepted in all but a slightly modified form by all the younger microconchs in the whole Aulacostephanidae – up to the beginning of the Late Kimmeridgian (*cf.* Birkelund, Callomon, 1985).

Pictonia and its microconch counterparts. The macroconchiate genus *Pictonia* comprises fairly large, ranging up to about 200 mm in diameter, aulacostephanid ammonites, generally evolute and planulate, and showing on the inner whorls the "perisphinctoidal" type of ribbing with mostly biplicate ribs and sometimes single intercalatory ribs. On the middle whorls the bold primary ribs pass into more distant, biplicate and polyplicate secondaries. At larger diameters ornamentation fades. The principal characteristic feature of the genus, often encountered, is the periodical occurrence of swollen (flared) ribs bordering deep constrictions, especially common on the middle whorls (Wright 2010, pl. 9: 2, 5). The microconchiate counterparts are some ammonites of the genus *Prorasenia* especially close to the species *Prorasenia bowerbanki* Spath and *P. hardyi* Spath, which show, however, the development of ornamentation markedly different during their ontogeny when compared with that of the *Pictonia* macroconchs (Matyja *et al.*, 2006).

The oldest assemblage of *Pictonia* ammonites discovered in the sections studied at Staffin Bay is very diversified (Fig. 3). These include ammonites referred to as *Pictonia flodigarriensis* Matyja, Wierzbowski et Wright (see Matyja *et al.*, 2006: fig. 5a–c; Fig. 6, herein), and appearing somewhat higher in the succession – *Pictonia densicostata* Buckman (see Matyja *et al.*, 2006: fig. 5d). These two species are characterized by the occurrence of densely placed biplicate ribs in the inner whorls which may persist up to a diameter of about 40–50 mm (Pl. 1: 7; Figs 4, 6). This type of ribbing is undoubtedly of a "primitive" character, and it is close to that of early "*Decipia*"-like ammonites (Wierzbowski, 2017). Interestingly, *P. flodigarriensis* as the older species still shows on its outer whorl some elements of the ornamentation of the middle whorls of its ancestor *Ringsteadia*, whereas the younger *P. densicostata* has smooth outer whorls.

These early *Pictonia* ammonites of the lower part of the Baylei Zone designated as the Densicostata Subzone (Matyja *et al.*, 2006) reveal thus advanced features of heterochrony – which may be classified as the paedomorphic result of neoteny according to Landman and Geyssant (1993), with the later adult showing features of the juvenile of the ancestor. Such an opinion on the appearance of the juvenile stage of ornamentation of ancestor perisphinctids on the later growth stages in *Pictonia* compared with *Ringsteadia* was expressed already by Salfeld (1917: p. 73). Some of these features of heterochrony may be observed already in a few late ammonites of the genus *Ringsteadia* in the upper part of the Pseudocordata Zone which show on their inner whorls dense biplicate ribbing up to about 20–30 mm diameter, resembling very much those of the later genus *Pictonia* (Matyja *et al.*, 2006: p. 402, fig. 4c).

There exists, however, another group of ammonites, which shows similarity to *Triozites* Buckman, 1924 (which is placed in the genus *Pictonia* by Wright, 2010), occurring in a similar stratigraphic position in the Staffin Bay sections to the *Pictonia* discussed above. All these ammonites recently recognized in the upper part of bed 35 (1.24 and 0.45 m below bed 36) of the Flodigarry section show bold, rather distant biplicate ribbing on the inner whorls with some intercalatory ribs (Pl. 1: 4–6; Fig. 4) – somewhat resembling that of the inner-middle whorls of *Ringsteadia evoluta*, but their general S-shaped curve and the tendency for the outer whorl already to be smooth at a diameter of 60–70 mm, suggest that they are close to *Pictonia* (*Triozites*) *seminudata* Buckman.

The overall variability of ammonites related to the species *Pictonia densicostata* and *P.seminudata* was discussed recently by Wright (2010) as based on specimens coming from the *densicostata* horizon of the Densicostata Subzone in southern England. This revealed a very large spectrum of features of all these specimens both in their character of ribbing and the presence of constrictions, which resulted in the recognition of only two main groups based on the two indicated morphospecies. It is important to note that this *densicostata* horizon fauna in southern England rests with a marked break on the strata with an uppermost Pseudocordata Zone fauna (Wright, 2010: fig 8), a gap occupied by the *flodigarriensis* horizon fauna at Flodigarry.

The youngest *Pictonia* ammonites in the Staffin Bay sections have a marked fall in rib density which corresponds to the disappearance of dense biplicate ribbing at somewhat smaller shell diameters (about 20–30 mm) when compared with those of the older part of the succession. The ribbing on the outer whorls is characterized by loosely spaced and short primary ribs with higher number of the secondaries (Pl. 1: 8; Fig. 4). These ammonites have been referred to as *Pictonia normandiana* (Tornquist) and *P. baylei* Salfeld/*P. normandiana* (Tornquist) (see Matyja *et al.*, 2006: fig. 5f–h), and are recognized as indicative of the Normandiana Subzone of the upper part of the Baylei Zone.

The microconch counterparts of the genus *Pictonia* are generally ammonites corresponding to the morphotype of *Prorasenia* Schindewolf, 1925 (see Matyja *et al.*, 2006;

Fig. 6. ***Pictonia flodigarriensis*** **Matyja, Wierzbowski et Wright, paratypes, Flodigarry**

A, B. Specimen ST 837, section F7, bed 35 (0.52 m below bed 36); two imprints of the same side, the phragmocone reaches up to about 80 mm diameter; **C.** Specimen ST 836, section F6N, bed 35 (0.39 m below bed 36); specimens natural size

Pl. 1: 9, 10). These ammonites reveal dense ribbing in the inner whorls, similar to that in the earlier *Microbiplices*, and this is limited to very small shell diameters; thereafter rather loosely-spaced biplicate and intercalatory ribs appear, and then triplicate ribs, with bold widely-spaced primaries. These are followed by more closely-spaced, bifurcating ribs on the body-chamber ranging up to the aperture with lappets. The rib-curve, showing the relation between the number of the primary ribs per whorl and the diameter of the specimen, is thus of U-shaped character (Fig. 5). The triplicate ribs appearing in the middle whorls of *Prorasenia* are fairly thick with the point of division lying below the mid-height, and this type of ribbing is not seen in *Microbiplices.*

Some intermediate microconchs referred to as *Microbiplices – Prorasenia* transitional forms, occurring already in the uppermost part of the Pseudocordata Zone – the Evoluta Subzone, but encountered also in the lower part of the Baylei Zone, reveal the occurrence of a few triplicate swollen ribs just before the appearance of the bifurcate ribs on the body-chamber (Matyja *et al.*, 2006: fig. 4f–h). It should be remembered that thick triplicate ribs are encountered at markedly larger diameters in the middle whorls of some macroconchs – such as late ammonites of the genus *Ringsteadia* and more heavily ribbed *Pictonia.*

Transition between Pictonia and Rasenia. The only form of the genus *Rasenia* found and illustrated in the Staffin Bay area is *Rasenia inconstans* Spath from bed 44 of the Flodigarry section (Matyja *et al.*, 2006: fig. 5j), this being the earliest species of the genus. The succession of the macroconch ammonites of the genus was studied in detail by Birkelund *et al.* (1978, 1983) in the Subboreal sections of southern England, and additionally commented on by Birkelund and Callomon (1985) in East Greenland and Hantzpergue (1989) in North Aquitaine. The genus *Rasenia* succeeds the genus *Pictonia*, and the transition between them in the succession is gradual, thus “the boundaries between genera are purely arbitrary and represent no clearly discernible breaks in the morphological evolution of the group as a whole” (Birkelund, Callomon, 1985: p. 30).

Although the main feature of the genus is the appearance of bullate ribs, the oldest species – *Rasenia inconstans* Spath and *R. cymodoce* (d’Orbigny) always show in the innermost whorls up to about 20 mm diameter very dense ribbing resembling the inner whorls of their ancestors. Moreover, the first representatives of *R. inconstans*, having heavy bullate ribs and occurring together with specimens with non-bullate ribs on their outer whorls and thus being close to *Pictonia*, show thus wide morphological variation at a single biospecies level.

Still younger *Rasenia* species like *Rasenia involute* Spath, and *R. evoluta* Spath close the succession of faunas of the genus which define the Subboreal Cymodoce Zone in the NW part of the Subboreal Province. The end of the Cymodoce Zone in southern England marks the invasion of quite a different group of aulacostephanids related to the genus *Rasenioides*, and representing another lineage of Aulacostephanidae, whereas the representatives of the genus *Rasenia* “had probably merely migrated further into the Boreal Realm” (Birkelund *et al.*, 1983, p: 296).

The evolution of the macroconch ammonites of the genus *Rasenia* when compared with earlier *Pictonia* indicates the reversion of the tendency of heterochrony observed already in late *Pictonia* towards the peramorphosis, or delaying of maturity, and the faster rate of growth – marking the acceleration in development of the ornamentation.

CARDIOCERATIDAE

The ammonites discussed are represented by two principal faunal assemblages: (1) the older one composed of the last representatives of the genus/subgenus *Amoeboceras* belonging mostly to the *Amoeboceras rosenkrantzi* group (see Sykes, Callomon, 1979), and (2) the younger one of small-sized ammonites of the genus/subgenus *Plasmatites* (see Matyja *et al.*, 2006). The former are indicative of the Rosenkrantzi Zone, the latter of the Bauhini Zone.

Amoeboceras macro and microconchs. The oldest forms discussed here are representatives of *Amoeboceras marstonense* Spath which co-occur with some *Amoeboceras regulare* Spath of the older assemblage in bed 33 (see Wierzbowski, Matyja, 2014) in the Flodigarry section. These are replaced by the last *A. marstonense* which occur together with the first *A. rosenkrantzi* Spath in the topmost part of bed 33 and a lower part of bed 35 (Pl. 2: 1, 2). The younger parts of bed 35 yield a very special fauna of *Amoeboceras* with a characteristic rursiradiate ribbing – represented initially by coarsely ribbed forms referred to *Amoeboceras leucum* Spath (see Matyja *et al.*, 2005), but mostly by *A. rosenkrantzi.* The latter species is represented by a wide spectrum of forms, generally of large size, from about 40–50 mm in microconchs to about 140 mm in macroconchs (*cf.* Sykes, Callomon, 1979; Pl. 2: 3–5), differing mostly in the strength of the ribbing – from moderately strongly ribbed up to very coarsely-ribbed, but generally with short and accentuated secondary ribs. A feature common to all these forms occurs in the ventral side where the serrated keel is flanked by smooth bands or shallow sulci – which is typical of the genus *Amoeboceras.*

Transition between Amoeboceras* and *Plasmatites and the nature of Plasmatites. There is a marked difference between these ammonites of the genus *Amoeboceras* of the *A. rosenkrantzi* group, and the following younger assemblage composed of small-sized representatives of the genus *Plasmatites* which occur already at the topmost part of bed 35 and continue upwards to bed 41. The ammonites of the genus *Plasmatites* attain usually between 15 and 40 mm in diameter only, and they show falcoid ribbing. Some of them show a 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; some show a poor differentiation of primary and secondary ribs. The common feature of all these forms except their small-size, is that the secondary ribs always run up onto the coarsely crenulated keel – which resembles somewhat earlier *Cardioceras* (see Matyja *et al.*, 2006, fig. 6s; Wright, 1989: fig. 4K–M). Crucial for the interpretation of the interrelation between *Plasmatites* and *Amoeboceras* of the *rosenkrantzi* group is thus the study of the ammonite faunas of the stratigraphical interval from the uppermost part of bed 35 up to lowermost part of bed 37 where the both groups co-occur.

Some of the ammonites referred to as *Amoeboceras rosenkrantzi* Spath from the interval in question show a special development of the ventral side which begins to approach that of the genus *Plasmatites.* This is the case with a specimen found in the Flodigarry section, bed 35, 1.17 m below bed 36, in the same fragment of slab as *Plasmatites praebauhini* (Salfeld) (Matyja *et al.*, 2006: fig. 6e, f). The opposite side of this specimen (Pl. 2: 7) shows ornamentation of the inner whorls similar to that of *P. praebauhini* with secondary ribs splitting into thin striae which run up onto the crenulated keel. The outer whorl shows the strongly projected secondary ribs continuing up to base of the keel without any marked longitudinal sulcus.

Another specimen found in the same bed, 0.56 m below bed 36 (Pl. 2: 6), shows also the similarity of its inner whorls to *Plasmatites praebauhini* with similar *Plasmatites* – type of ornamentation of the ventral side, and the outer whorl almost smooth but with weak, and strongly projected secondary ribs near the keel. This is also the case with the specimen illustrated by Sykes and Callomon (1979, pl. 121: 6; p. 888) which "shows inner whorls very close to *A. lineatum* (Quenstedt) [*i.e. Plasmatites lineatum* (Quenstedt) as interpreted herein], but develops normal [*i.e.* similar to *Amoeboceras rosenkrantzi* Spath] outer whorl". The specimens discussed reveal thus features transitional between *A. rosenkrantzi* and *Plasmatites.*

The data strongly suggest that the evolutionary transformation from the last *Amoeboceras* to *Plasmatites* was controlled by heterochrony, and additionally has arisen by paedomorphosis, where the adult resembles the juvenile of the ancestor. The adult morphologies of *Plasmatites* become progressively more paedomorphic – because of their "primitive" ornamentation with some features of its ancestors (especially the character of the ventral side) – thus showing a slower rate of development and being neotenic in character when compared with older *Amoeboceras*. On the other hand, the smaller final sizes of *Plasmatites* resulted possibly from their attaining maturity in an earlier stage of morphological development – thus being progenetic in character (*cf.* Matyja, Wierzbowski, 2000).

The *Plasmatites* ammonites (Pl. 2: 8–10) are recognized generally as microconchs (Sykes, Callomon, 1979), but there always remained the problem of their macroconchs. Somewhat larger specimens, such as late *Amoeboceras rosenkranzti* and the very close *Amoeboceras schulginae*, which shows however coarser ornamentation, may be possibly treated as potential macroconchs, but their stratigraphical range is limited mostly to the lowermost part of the whole range of the genus *Plasmatites* (see Matyja *et al.*, 2006). The only specimens attaining larger sizes which occur at a somewhat higher level, and which are referred to as "*Amoeboceras*" aff. *schulginae*, are known only from a very narrow interval of this range (lowermost part of bed 39 of the Staffin Bay sections , see Fig. 3; Matyja *et al.*, 2006: fig. 6 k–n). Thus the general deficiency of macroconchs becomes a common feature of the *Plasmatites* lineage (Wierzbowski, Rogov, 2013).

Amoebites and its relation to Plasmatites. The replacement of *Plasmatites* by younger cardioceratids of the genus *Amoebites* occurs in bed 41 – in the upper part of the Flodigarry section. This level marks the boundary between the Bauhini Zone and the Kitchini Zone of the Boreal zonal scheme (see Matyja *et al.*, 2006; Fig. 3). It is defined by the appearance of the small-sized *Amoebites bayi* (Birkelund et Callomon) and *A. cricki* (Salfeld) (Wright, 1989: fig. 4C–F). Both of them reveal already the completely different character of the ventral side when compared with older *Plasmatites*, showing the presence of poorly marked ventral sulci along the keel. The evolution of the ammonites of the genus *Amoebites* when compared with earlier *Plasmatites* indicates a reversion of the tendency of heterochrony towards peramorphosis, marking the acceleration in development of the ornamentation.

CONCLUSIONS

Detailed study of the ammonites from the Flodigarry section and the Digg section at Staffin Bay, Isle of Skye, Northern Scotland generally confirms the previous stratigraphical interpretation of the deposits at the Oxfordian/Kimmeridgian boundary (Matyja *et al.*, 2006; see also Fig. 3). Some minor changes, and additional information on the distribution of ammonite taxa as given herein enrich the stratigraphical importance of the Flodigarry section, currently the only candidate for the GSSP of the base of the Kimmeridgian stage. The most important change is related to the finding of the oldest ammonite of the genus *Pictonia* – *Pictonia* (*Triozites*) cf. *seminudata* (Buckman) 0.16 m lower than the previous position of the boundary. The significance is that the boundary between the Pseudocordata

Zone (uppermost Oxfordian) and the Baylei Zone (lowermost Kimmeridgian) in the Subboreal zonal scheme is placed in the very narrow interval between 1.24 and 1.26 m below bed 36 (formerly between 1.09 and 1.24 m). The corresponding boundary between the Rosenkrantzi Zone (uppermost Oxfordian) and the Bauhini Zone (lowermost Kimmeridgian) in the Boreal zonal scheme is placed not higher than 1.17 m below bed 36 (but it may be a little lower; see Matyja *et al.*, 2006). The position of the Oxfordian/Kimmeridgian boundary in both Subboreal and Boreal schemes are practically coeval.

The phylogeny of the ammonites of the Aulacostephanidae and Cardioceratidae has shown some periods when diversity in the particular lineages changed markedly – expressed by the loss of forms or the appearance of new forms. These intervals may be called "faunal turnovers" and have often been applied as useful stratigraphical markers in the past, when substage, and stage boundaries have been founded. Such was the main premise for the original recognition of the Oxfordian/Kimmeridgian boundary which was placed in the Aulacostephanidae (Subboreal) lineage at the boundary of the Pseudocordata Zone and Baylei Zone, corresponding to the marked evolutionary change from the genus *Ringsteadia* to the genus *Pictonia* (see Salfeld, 1913); and in the Cardioceratidae (Boreal) lineage at the boundary of the Rosenkrantzi Zone and the Bauhini Zone, corresponding to the marked evolutionary change from the genus *Amoeboceras* to the genus *Plasmatites* (Matyja *et al.*, 2006; Wierzbowski *et al.*, 2006; see also Wierzbowski, Smelror, 1993).

The patterns of macroevolution of the families of Aulacostephanidae and Cardioceratidae as discussed herein could possibly be attributed to the influence of pervasive causes – mostly changes in the surrounding environment which influenced the ammonite shell morphology as a consequence of the opening of new adaptive opportunities. Although the general development of the two ammonite families followed two smoothly evolving lineages (Birkelund, Callomon, 1985), the stratigraphical interval at the Oxfordian/Kimmeridgian boundary showed major morphological changes in both ammonite families. Their evolution was released from phylogenetic constraints by heterochrony, or changes in the rate of development, and especially by paedomorphosis, with adults resembling the juveniles of their ancestors, especially in the case of the Oxfordian/Kimmeridgian boundary interval.

It is interesting to note that paedomorphosis changed mostly the appearance of the large-sized macroconchs of Aulacostephanidae (*Pictonia* macroconchs) whose growth was determined by their continuous slower rate of development, but also of the Cardioceratidae, realized mostly by the appearance of single, small-sized morphs (*Plasmatites*) – indicating initially a slower rate of development which was completed earlier because of their earlier offset. The microconchs of the Aulacostephanidae from the earlier *Microbiplices*, through the *Microbiplices* – *Prorasenia* transitional forms and up to *Prorasenia* generally showed a faster rate of their development, representing thus quite a different process of heterochrony in attaining their maturity.

It is highly probable that the phylogenetic changes were closely related to changes in environmental conditions stimulated by the tectonic movements which occurred in wide areas of northern Europe at the Oxfordian/Kimmeridgian boundary. These phenomena could have resulted in the activation of marine currents which brought more nutrient-rich waters and increased eutrophication (Wierzbowski *et al.*, 2016; see also Barski, 2018, this issue). Because of the recognition above of the faunal turnover in two independent ammonite lineages in the continuous succession of Oxfordian-Kimmeridgian sediments, the Flodigarry section at Staffin Bay on the Isle of Skye, Northern Scotland is thus a perfect candidate as GSSP for the base of the Kimmeridgian.

Acknowledgements. This study is based on ammonites collected by the authors at Staffin Bay in Skye carried out in successive stays in 1998, 2001, and 2003 (although the first visit in the section by the co-author A.W. together with Nicol Morton was already in 1969!). The largest part of the collection is housed in University Museum Oxford, collections ST 600 to ST 926 and this was presented in our former study (Matyja *et al.*, 2006). The collection discussed herein is housed in Museum of the Faculty of Geology, University of Warsaw (collection number MWG UW ZI/94/01-55), and it is represented mostly by forms which duplicate material in the Oxford collection, not discussed so far in detail (but as it has been shown herein also by some new forms, unfortunately overlooked before). All the details of our study of the Staffin Bay sections were given already by the authors in the Acknowledgements in the former paper (Matyja *et al.*, 2006); however, we express our thanks once more to all the persons and authorities who helped us in the field with special thanks for Scottish Natural Heritage which allowed for carry our studies in the protected area of Trotternish on the Isle of Skye. We are very grateful to editorial referees John Cope, Nicol Morton and Kevin Page who helped very much in improving our manuscript.

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Appendix 1

SUMMARY OF THE CLASSIFICATION SCHEME OF THE AMMONITES STUDIED

Family **Aulacostephanidae Spath, 1924**: genus *Ringsteadia* Salfeld, 1924; genus *Pictonia* Bayle, 1878; genus *Rasenia* Salfeld, 1913

Genus *Ringsteadia* (uppermost Oxfordian, Pseudocordata Zone) with several morphogroups of macroconchs: (1) *R.caledonica* group with *R. caledonica* Sykes et Callomon (Caledonica Subzone), (2) *R. pseudoyo* group with *R. pseudoyo* Salfeld, (3) *R. brandesi* group with *R. brandesi* Salfeld and (4) *R. marstonensis* group with *R. pseudocordata* (Blake et Hudleston), *R. frequens* Salfeld and *R. evoluta* Salfeld; groups 2–4 occur in Pseudoyo Subzone, Pseudocordata Subzone and Evoluta Subzone – with an increased dominance of the succeeding groups towards the younger subzones (see Wright, 2010); microconchs are small-sized forms with lappets, referred to as *R. caledonica* (and corresponding to macroconchs of group 1; see Sykes, Callomon, 1979), and following younger microconchs referred to as *Microbiplices* Arkell, 1936 corresponding to macroconchs of the groups 2, 3 and 4, and represented by *M. precedens* (Oppenheimer)-*guebhardi* (Oppenheimer), *M. microbiplex* (Quenstedt) and *M. anglicus* Arkell (see Wierzbowski *et al.*, 2016, and earlier papers cited therein), but some microconchs transitional between *Microbiplices* and *Prorasenia* as interpreted by Matyja *et al.* (2006) correspond to some macroconchs of the group 4 (Evoluta Subzone).

Genus *Pictonia* (Baylei Zone) with three morphogroups of macroconchs, *i.e.* two of the nominative subgenus: (1) *P. densicostata* group with *P. flodigarriensis* Matyja, Wierzbowski et Wright, and *P. densicostata* Salfeld (Densicostata Subzone), (2) *P. normandiana* group with *P. normandiana* (Tornquist) – *P. baylei* Salfeld (Normandiana Subzone), and the one group of (3) *P. seminudata* group with *P. seminudata* Buckman (Densicostata Subzone) corresponding to the subgenus *Triozites* Buckman, 1924; small-sized microconchs are referred to as *Prorasenia* Schindewolf, 1925 (pars) such as *P. bowerbanki* Spath (corresponding mostly to macroconchs of group 1), and *P. hardyi* Spath (mostly of group 2); additionally some microconchs transitional between *Microbiplices* and *Prorasenia* (especially Densicostata Subzone).

Genus *Rasenia* (Cymodoce Zone) with several succeeding faunas of macroconchs (Birkelund *et al.*, 1978, 1983; Birkelund, Callomon, 1985) – the lowest of them is *Rasenia incostans* Spath, and it is recognized herein; microconch is *Prorasenia* close to *P. hardyi* Spath (see Birkelund, Callomon, 1985).

Family **Cardioceratidae Siemiradzki, 1891**: genus *Amoeboceras* Hyatt, 1900; genus *Plasmatites* Buckman, 1925; genus *Amoebites* Buckman, 1925.

Genus *Amoeboceras* (Upper Oxfordian) with several morphogroups of ammonites: (1) *A. regulare* group with *A. regulare* Spath (Regulare Zone, and lowermost part of the Rosenkrantzi Zone), (2) *A. rosenkrantzi* group with *A. marstonense* Spath, *A. leucum* Spath, *A. rosenkrantzi* Spath and *A. schulginae* Mesezhnikov (Rosenkrantzi Subzone) (see Sykes, Callomon, 1979; Wierzbowski, Rogov, 2013) – which includes both micro and macroconchs (*Prionodoceras* Buckman, 1920).

Genus *Plasmatites* (lowermost Kimmeridgian, Bauhini Zone) includes the diminutive closely related forms such as *P. praebauhini* (Salfeld), *A. bauhini* (Oppel) and *A. lineatum* (Quenstedt) of unclear dimorphic status, sometimes treated as microconchs although there always remained the problem of their macroconch counterpart; the larger forms referred to as "*Amoeboceras*" aff. *schulginae* could be considered as potential macroconchs, although their occurrence is limited to some stratigraphical levels (see Matyja *et al.*, 2006).

Genus *Amoebites* (Lower Kimmeridgian, Kitchini Zone) includes strongly diversified in size in the lineage ammonites: from small-sized ammonites of the *A. bayi* group with *A. bayi* (Birkelund et Callomon) (Lower Kimmeridgian, Bayi Subzone), through large-size *A. subkitchini* group with *A. subkitchini* (Spath) showing small-sized microconchs and large macroconchs (Lower Kimmeridgian Subkitchini Subzone), up to small-sized ammonites of the *A. modestum* group like *A. kitchini* (Salfeld) (Lower Kimmeridgian, Modestum Subzone) – see Wierzbowski, Rogov (2013, and earlier papers cited therein).

Appendix 2

LIST OF ADDITIONAL AMMONITES FROM THE STAFFIN BAY SECTIONS HOUSED IN THE MUSEUM OF THE FACULTY OF GEOLOGY, UNIVERSITY OF WARSAW (COLLECTION NUMBER MWG UW ZI/94/01-55)

FLODIGARRY:

Amoebites cricki (Salfeld), *Amoebites* sp., *Pictonia* sp.; section F5 (bed 42), specimens no. 55a–c

Pictonia ex gr. *normandiana* (Tornquist) – *baylei* Salfeld; section F5, bed 41, 5.4 m below bed 44, specimen no. 17 (Pl. 1: 8)

Plasmatites bauhini (Oppel); section F5 (5.5 m below bed 44; bed 41), specimen 53 (Pl. 2: 9)

Plasmatites bauhini (Oppel); section F5 (5.65 m below bed 44; bed 41), specimen 51

Plasmatites bauhini (Oppel), *Plasmatites lineatus* (Quenstedt); section F5 (5.70 m below bed 44, bed 41), specimens 50 a, b

Pictonia ex gr. *normandiana* (Tornquist) – *baylei* Salfeld; section F5, bed 41, 5.9 m below bed 44, specimen no. 14

Plasmatites bauhini (Oppel); section F5 (5.9 m below bed 44; bed 41), specimen 52 (Pl. 2: 10)

Plasmatites sp.; section F5 (10.1 m below bed 44, upper part of bed 37), specimen 54

Pictonia cf. *densicostata* Buckman; section F5, bed 37 upper part, specimen no. 15a; *Plasmatites praebauhini* (Salfeld), specimen 15b

Pictonia sp., *Prorasenia* sp.; section unknown, bed 37 upper part, specimens no 16a–c; *Plasmatites praebauhini* (Salfeld), specimen 16d

Plasmatites sp.; section F5, bed 37, specimen no. 49

Plasmatites sp.; section F7 (0.3 m below bed 36), specimen 47a; *Pictonia* sp.; section F7, specimen 47b

Plasmatites praebauhini (Salfeld) – *Amoeboceras rosenkranzti* Spath trans. form; section F6S (0.56 m below bed 36), specimen 45 (Pl. 2: 6); *A.* cf. *rosenkrantzi* (0.45 below bed 36), specimen 46

Pictonia (*Triozites*) cf. *seminudata* (Buckman); section F7, bed 35 (0.45 m below bed 36), specimen no 26 (Pl. 1: 6)

Plasmatites cf. *bauhini* (Oppel); section F6S, bed 35 (0.60 m below bed 36), specimen no 44 (Pl. 2: 8)

Pictonia ex gr. *flodigarriensis* Matyja *et al.* – *densicostata* Buckman; section F7, bed 35 (0.52 m below bed 36), specimens no. 6, 7

Plasmatites sp. and *Amoeboceras* (? *rosenkrantzi*); section F6N (1.08 m below bed 36), specimens 48a, b

Plasmatites praebauhini (Salfeld) – *Amoeboceras rosenkranzti* Spath trans. form; section F6N, bed 35 (1.17 m below bed 36), specimen 43 (Pl. 2: 7)

Pictonia (*Triozites*) cf. *seminudata* (Buckman); section F6S, bed 35 (1.24 m below bed 36), specimens 4a (Pl. 1: 4), 4b (Pl. 1: 5), 5

Ringsteadia frequens Salfeld; section F6S, bed 35 (1.26 m below bed 36), specimen no. 3 (Pl. 1: 3)

Amoeboceras rosenkrantzi Spath; section F6S, bed 35 (1.44 and 1.45 m below bed 36), specimens no 41 (Pl. 2: 3) and 42 (Pl. 2: 4)

Ringsteadia cf. *evoluta* Salfeld; section F6S, bed 35 (1.5 m below bed 36), specimen no. 2 (Pl. 1: 1)

Ringsteadia cf. *frequens* Salfeld; section F6S, bed 35 (1.9 m below bed 36), specimen no. 1

Amoeboceras cf. *rosenkrantzi* Spath; section unknown, bed 35 (about 1.5–2.0 m below bed 36), specimen no. 40

Specimens coming from lowermost part of bed 35 – from its base up to 0.5 m above:

Ringsteadia pseudocordata (Blake et Hudleston), specimens no. 8a (Pl. 1: 2), 8b, and 9

Microbiplices cf. *microbiplex* (Quenstedt), specimen 10–12

Microbiplices cf. *anglicus* Arkell, specimen no. 13

Amoeboceras rosenkrantzi Spath, specimens 31, 32 (Pl. 2: 2), 33 and 35

Amoeboceras cf. *rosenkrantzi* Spath, specimens 38–40

Amoeboceras marstonense Spath; specimen no. 36

Amoeboceras leucum Spath; section F6N, bed 33 (about 0.5 m below bed 34), specimen no. 37

Amoeboceras rosenkrantzi Spath; section F6N, bed 33 (about 0.5 m below bed 34), specimen no. 34 (Pl. 2: 1); section F6S, bed 35 (1.44–1.45 below bed 36), specimens 41 (Pl. 2: 3) and 42 (Pl. 2: 4)

DIGG:

Pictonia densicostata Buckman; "*Pictonia bed*" (about bed 38), specimen no 21 (Pl. 1: 7)

Prorasenia bowerbanki Spath; "*Pictonia bed*" (about bed 38), specimen no 20 (Pl. 1: 10)

Prorasenia bowerbanki Spath; bed 35 (0.00–0.15 m below bed 36), specimens no. (21, 23, 24, and 25 – Pl. 1: 9)

Microbiplices/Prorasenia transitional form; bed 35 (0.00–0.15 m below bed 36), specimens no. 18, 19 and 30

Pictonia sp.; bed 35 (0.00–0.15 m below bed 36), specimens no. 27–29

Plates

PLATE 1

Ammonites of the family Aulacostephanidae of the Staffin Bay sections

Fig. 1. *Ringsteadia* cf. *evoluta* Salfeld; Flodigarry, section F6S, bed 35 (1.5 m below bed 36), specimen MWG UW ZI/94/02

Fig. 2. *Ringsteadia pseudocordata* (Blake et Hudleston); Flodigarry, section 6/7, lowermost part of bed 35 – from its base up to 0.5 m above, specimen no. MWG UW ZI/94/08a

Fig. 3. *Ringsteadia frequens* Salfeld , a part of the last whorl preserved is the body-chamber; Flodigarry, section F6S, bed 35 (1.26 m below bed 36), specimen no. MWG UW ZI/94/03

Fig. 4, 5. *Pictonia* (*Triozites*) cf. *seminudata* (Buckman); Flodigarry, section F6S, bed 35 (1.24 m below bed 36), specimens MWG UW ZI/94/04a and 04b

Fig. 6. *Pictonia* (*Triozites*) cf. *seminudata* (Buckman), a part of the last whorl preserved is the body-chamber; Flodigarry, section F7, bed 35 (0.45 m below bed 36), specimen no. MWG UW ZI/94/26

Fig. 7. *Pictonia densicostata* Buckman, a part of the last whorl preserved is the body-chamber; Digg, "*Pictonia bed*" (about bed 38), specimen no. MWG UW ZI/94/21

Fig. 8. *Pictonia* ex gr. *normandiana* (Tornquist) – *baylei* Salfeld, phragmocone; Flodigarry, section F5, bed 41, 5.4 m below bed 44, specimen no. MWG UW ZI/94/17

Fig. 9, 10. *Prorasenia bowerbanki* Spath; Digg: 9 – a part of the outer whorl preserved is the body-chamber, bed 35 (0.00–0.15 m below bed 36), specimen 25; 10 – "*Pictonia bed*" (about bed 38), specimen no. MWG UW ZI/94/20

All specimens natural size, phragmocone/body-chamber junction is arrowed


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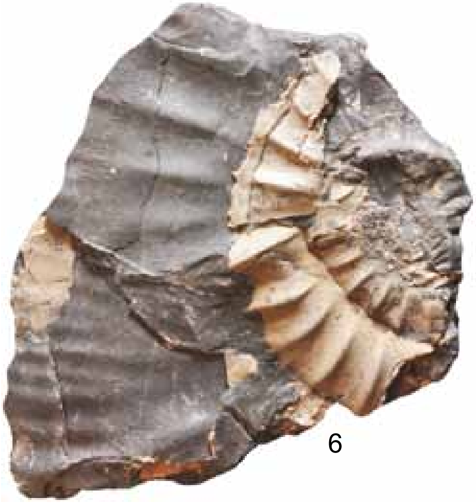
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Andrzej WIERZBOWSKI *et al.* – Notes on the evolution of the ammonite families Aulacostephanidae and Cardioceratidae and the stratigraphy of the uppermost Oxfordian and lowermost Kimmeridgian in the Staffin Bay sections (Isle of Skye, Northern Scotland)

PLATE 2

Ammonites of the family Cardioceratidae of the Staffin Bay sections

Fig. 1, 2. *Amoeboceras rosenkrantzi* Spath; Flodigarry: 1 – section F6N, bed 33 (about 0.5 m below bed 34), specimen no. MWG UW ZI/94/34; 2 – section F6/7, lowermost part of bed 35 – from its base up to 0.5 m above, specimen MWG UW ZI/94/32

Fig. 3, 4. *Amoeboceras rosenkrantzi* Spath; Flodigarry: section F6S, bed 35 (1.44 and 1.45 m below bed 36), specimens no. MWG UW ZI/94/41 and 42

Fig. 5. *Amoeboceras* cf. *rosenkrantzi* Spath; Flodigarry, section F6S, bed 35 (0.45 m below bed 36), specimen no. MWG UW ZI/94/46

Fig. 6. *Amoeboceras rosenkrantzi* Spath – transitional to *Plasmatites praebauhini* (Salfeld), a part of the outer whorl preserved is the body-chamber; Flodigarry; section F6S, bed 35 (0.56 m below bed 36), specimen no. MWG UW ZI/94/45; ×1.5

Fig. 7. *Amoeboceras rosenkrantzi* Spath – transitional to *Plasmatites praebauhini* (Salfeld); Flodigarry, section F6N, bed 35 (1.17 m below bed 36), specimen no. MWG UW ZI/94/43; ×1.5

Fig. 8. *Plasmatites* cf. *bauhini* (Oppel); Flodigarry, section F6S, bed 35 (0.60 m below bed 36), specimen no. MWG UW ZI/94/44

Fig. 9, 10. *Plasmatites bauhini* (Oppel); Flodigarry: 9 – section F5 (5.5 m below bed 44; bed 41), specimen no. MWG UW ZI/94/53; 10 – section F5 (5.9 m below bed 44; bed 41), specimen no. MWG UW ZI/94/52

Figures 1–5 and 8–10 natural size; figures 6, 7 enlarged × 1.5; phragmocone/body-chamber junction is arrowed

PLATE 2


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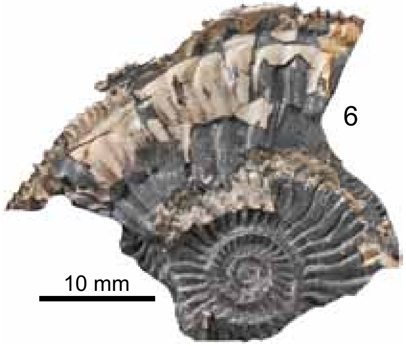

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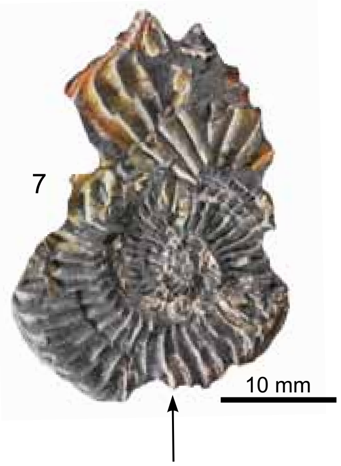

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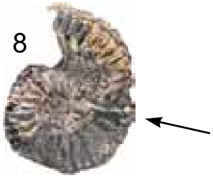
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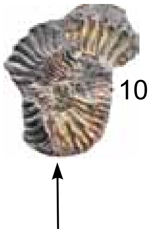
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