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Phylogeny of the ammonite family Aulacostephanidae Spath, 1924 during the Late Oxfordian and the Early Kimmeridgian in Europe: Main lineages, patterns of evolution and sedimentological to palaeogeographical controls on evolutionary development

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Key words: ammonites, evolution, Late Jurassic, biogeography, faunal turnovers.

Abstract. The evolutionary history of the Aulacostephanidae presented here includes the interval of about 5 Ma of the Late Oxfordian and Early Kimmeridgian ranging from the origin of the family to is maximal development. The development and biogeographical distribution of aulacostephanids in Europe were related mostly to sea-level changes and tectonics. The appearance of the ancestor genus *Decipia* and the following genus *Ringsteadia* was controlled by marine transgressions during the Late Oxfordian which stimulated also the distribution of these ammonites in Subboreal and Submediterranean Europe. The main faunal turnover at the Oxfordian/Kimmeridgian boundary was related to allopatric speciation correlated to separation of the aulacostephanid assemblages: it resulted in the appearance of the main *Ringsteadia–Pictonia–Rasenia* lineage in NW Subboreal Europe and the side-lineages *Ringsteadia–Vielunia–Eurasenia/Involuticeras* and *Ringsteadia–Vineta–Balticeras–Rasenioides* in NE Subboreal and Central Submediterranean Europe. A strong development of the shallow-water carbonate platforms during the Early Kimmeridgian stimulated the development of still another *Pictonia* (*Pomerania*) – *Rasenia* (*Pachypictonia*) lineage. The main faunal turnover correlated to a large transgression at the end of the Early Kimmeridgian resulted in the sudden distribution of the new aulacostephanid faunas over large areas of northern and central Europe, and opened a new stage in the evolutionary development of the family.

INTRODUCTION

The family Aulacostephanidae represents the main constituent of the whole ammonite fauna of the Upper Oxfordian and the Lower Kimmeridgian of NW Europe, and is an important element of the faunas of the coeval deposits of NE and Central Europe. It characterized mostly the Subboreal Province, and has been the basis for the detailed zonal subdivision of that succession. The Subboreal aulacostephanid succession “that has provided the zonal schemes that have been erected in the past, and that have become deeply entrenched in the literature” (Sykes, Callomon, 1979, p. 839) is thus of marked importance for subdivision of this stratigraphical interval. The subdivision as more recently modified (see *e.g.*, Sykes, Callomon, 1979; Birkelund *et al.*, 1983; Birkelund, Callomon, 1985; Matyja *et al.*, 2006; Wright, 2010) is of additional value for stratigraphy as well as for wider stratigraphical correlations, because of the quite common co-occurrence of Aulacostephanidae and ammonites of Boreal and Submediterranean affinity in many European sections (see *e.g.* Wierzbowski *et al.*, 2016). In consequence the formal acceptance of the GSSP of the base of the Kimmeridgian Stage in the Flodigarry section at Staffin Bay on the Isle of Skye in northern Scotland has been based

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markedly on the evolution of ammonites of that family (Matyja *et al.*, 2006; Wierzbowski *et al.*, 2018; Coe, Wierzbowski, 2021). Hence, detailed recognition of the phylogeny of the ammonite family Aulacostephanidae is of crucial importance for stratigraphy, and for stratigraphical correlations of the Upper Oxfordian and the Lower Kimmeridgian in the whole of Europe.

The ammonites of the family Aulacostephanidae originally inhabited during the Late Oxfordian peripheral areas of the Boreal Realm, characterized by unstable environmental conditions of a more shallow-water zone called the "European Archipelago", and corresponding to the Subboreal Province (Fürsich, Sykes, 1977; *cf.* also Sykes, Callomon, 1979). They temporary migrated, however, beyond this area, both northward into the Boreal Province (*e.g.*, Birkelund *et al.*, 1978; Wierzbowski, Smelror, 2020) but also southward into the Submediterranean Province, especially its northeastern to central parts, from central Poland to southern Germany and northern Switzerland, called the German-Polish Subprovince (Matyja, Wierzbowski, 1995). They produced here new lineages of Aulacostephanidae, the descendants of one of them finally colonizing the wide areas of northern and central Europe during the large transgression at the end of the Early Kimmeridgian (Birkelund *et al.*, 1983). Hence, the evolutionary development of the family, as discussed herein, was controlled mostly by changes in the palaeogeography. The varying environmental conditions were either tectonically and/or climatically induced by: changes of sea-level, the formation of shallow-water areas, the opening of new sea-ways, but also by a periodical separation of the formerly uniform sedimentary environments (*cf.* Mesezhnikov, 1969; Wierzbowski *et al*., 2016).

The phylogeny of ammonites of the family Aulacostephanidae shows the intervals when the diversity in the particular lineages (clades) changed markedly – expressed by the appearance or lose of new/old forms. Such intervals of a fairly short duration in the geological scale called "evolutionary faunal turnovers" are discussed in detail at the end of the study. They were possibly attributed to the appearance of pervasive causes – mostly changes in the surrounding environment which influenced the ammonite shell morphology as the consequence of the opening of new adaptive opportunities. Such time-intervals in the development of the discussed ammonite family (but also of other Late Jurassic families, see Atrops, Ferry, 1989; Hantzpergue, 1995) seem to be related to sea-level changes, and at least partly result from orbitally forced climate oscillations (see *e.g.*, Bouila *et al.*, 2008, 2010).

The stratigraphical interval discussed herein includes a number of standard zones and subzones for each of the province successions: for the Subboreal Province – the Cautisnigrae Subzone of the Cautisnigrae Zone corresponding to the old Decipiens Zone of Salfeld (1913), the latter is dropped, however, by British stratigrahers because the genus *Decipia* ranges down here into the older deposits of the Nunningtonense Subzone of the Pumilus Zone (Wright, 1972; Sykes, Callomon, 1979), and the Pseudocordata Zone (Upper Oxfordian), the Baylei Zone and the Cymodoce Zone (Lower Kimmeridgian) as based mainly on ammonites of the family Aulacostephanidae; for the Boreal Province – the Glosense Zone, the Serratum Zone, the Regulare Zone and the Rosenkrantzi Zone (Upper Oxfordian), the Bauhini Zone and the Kitchini Zone (Lower Kimmeridgian) as based on ammonites of the family Cardioceratidae; for the Submediterranean Province – the Bifurcatus Zone and the Hypselum Zone (Upper Oxfordian), the Bimammatum Zone, the Planula Zone, the Platynota Zone, the Hypselocyclum Zone and the Divisum Zone (Lower Kimmeridgian) as based on ammonites of the families Perisphinctidae, Aspidoceratidae and Ataxioceratidae. Although the detailed correlations between some intervals of the indicated zonal schemes are still the subject of discussions, the general correlation chart as shown herein is based on recently published studies showing also the detailed subdivisions of particular zones into subzones and ammonite horizons (see *e.g.*, Matyja *et al.*, 2006; Wright, 2010; Głowniak *et al.*, 2010; Wierzbowski, Rogov, 2013; Wierzbowski, Matyja, 2014; Wierzbowski *et al.*, 2016, 2018; Rogov *et al.*, 2017; Wierzbowski, 2017a, 2020; Wierzbowski, Smelror, 1993, 2020; and earlier papers cited therein).

The evolution of the family Aulacostephanidae during the Late Oxfordian and the Early Kimmeridgian as presented in general outline by Callomon (1980) and Hantzpergue (1989), and more recently by Głowniak (2012) and Enay and Howarth (2019), is discussed in more detail, and supplemented according to Wierzbowski (2017a, b, 2020) and Wierzbowski *et al.* (2018). This study is therefore based partly on material published previously (see especially Wierzbowski, 1970, 2017a, b, 2020; Wierzbowski *et al.*, 2018) – both illustrations of specimens, and their interpretations. Additionally, some of these specimens, the most important for the deciphering of the evolutionary history of the families, are refigured and commented on. The bulk of the specimens discussed is, however, new – especially specimens of Aulacostephanidae from the Polish collections coming from the famous (but no longer existing) quarry at Czarnogłowy (Zarnglaff) in western Pomerania, and from other areas of northern and central Poland: at Barcin in Kujawy area, in the Częstochowa Upland and the Wieluń Upland, and at the south-western and north-eastern margins of the Holy Cross Mts. (Fig. 1), collected and described by the author as well as other geologists (A. Czekalska, J. Gutowski, J. Kutek, B.A. Matyja, A. Radwański, A. Szynkiewicz), but also specimens collected by students during preparation

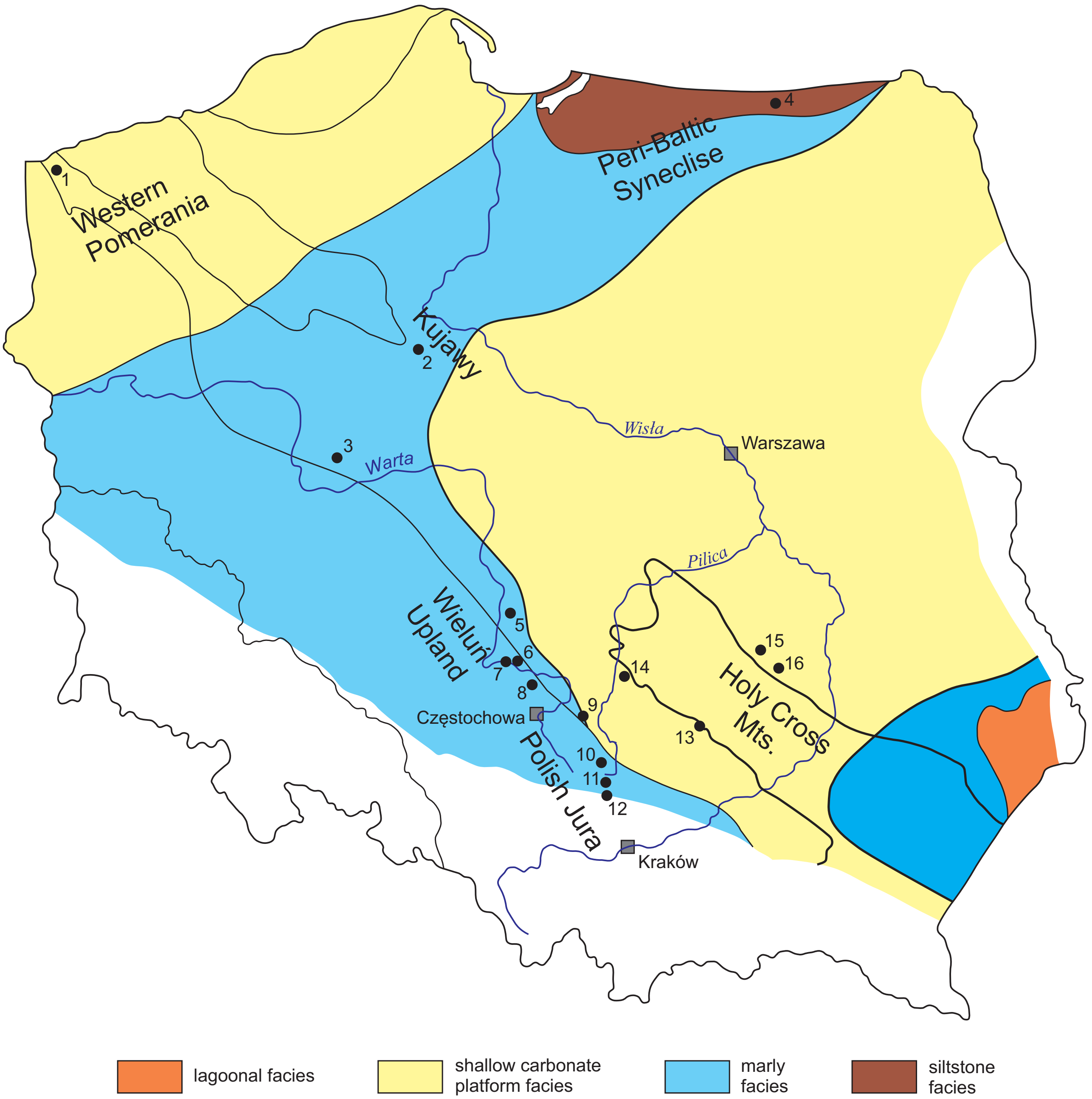

Fig. 1. Palaeogeographical map of the Hypselocyclum Zone (middle Lower Kimmeridgian) of Poland (after Matyja *in*: Matyja *et al.*, 1998) showing the location of the Upper Oxfordian – Lower Kimmeridgian palaeontological sites discussed in the study

Thin lines indicate the present extension of the dicussed Lower Kimmeridgian deposits.

Palaeontological sites: 1 – Czarnogłowy (Zarnglaff); 2 – Wapienno and Bielawy cement-work quarries at Barcin; 3 – Środa IG-1 Borehole; 4 – Bartoszyce IG-1 Borehole; 5 – Burzenin; 6 – "Warta" cement work quarry at Działoszyn; 7 – Lisowice; 8 – Łobodno (Katarowa Góra quarry); 9 – Julianka; 10 – Pradła; 11 – Poręba near Wolbrom; 12 – Trzyciąż; 13 – Małogoszcz cement work quarry; 14 – Góry Mokre near Przedbórz; 15 – Wierzbica cement work quarry; 16 – Iłża

of their Msc. Thesis at the Faculty of Geology, University of Warsaw (J. Niemczynowicz, M. Dunin, M. Skowronek, M. Wojciechowska). A part of the study refers also to specimens of Aulacostephanidae from the U.K. sections on the Dorset Coast in southern England (collected by M. Barski and A. Wierzbowski) and at Staffin Bay, Isle of Skye in northern Scotland discussed before on the occasion of the proposal of the GSSP for the Oxfordian/Kimmeridgian boundary (Matyja *et al*., 2006; see also Wierzbowski *et al*., 2016, 2018). The new ammonites are housed and catalogued in the collection of the Museum of the Geological Faculty of Warsaw University (collection numbers MWG UW ZI/108/1-37; additional illustrated ammonites have come from older collections MWG UW A/27 and MWG UW ZI/84. Some specimens illustrated are also from the collection of the Museum of the National Geological Institute – National Research Institute in Warszawa (MUZ PIG 1120.II). Plaster-casts of some specimens of the old German collections, especially of the Quenstedt (1887–1888) collection, are additionally presented when considering the Submediterranean ammonites of the family. The aim of the study is to provide a full description of the evolution of the Aulacostephanidae in Europe during the Late Oxfordian and Early Kimmeridgian based on material published so far, but also on not yet published material.

THE EVOLUTIONARY HISTORY OF AULACOSTEPHANIDAE

Four main lineages are recognized within the Aulacostephanidae during the Late Oxfordian and Early Kimmeridgian (Callomon, 1980; Wierzbowski 2017b; see Fig. 2): (1) the main lineage, initially existing in the whole Subboreal Province and adjoining parts of the Submediterranean and Boreal provinces, but finally evolving only in the NW part of the Subboreal Province, consisting of *Decipia–Ringsteadia–Pictonia–Rasenia* and its microconch counterparts; (2) the side-branch which evolved in the NE part of the Subboreal Province and the adjoining part of the Submediterranean Province, consisting of *Pictonia* (*Pictonites–Pomerania*) and *Rasenia* (*Pachypictonia)*, and microconch counterparts; (3) the side branch which evolved in the Submediterranean Province and the adjoining part of the NE European Subboreal Province, consisting of *Vielunia–Eurasenia/ Involuticeras* and microconch counterparts; (4) the side-branch which evolved in the Submediterranean Province and adjoining part of the NE European Subboreal Province, but which finally colonized the whole Subboreal Province and adjoining parts of the Boreal Province, consisting of *Vineta–Balticeras–Rasenioides* and microconch counterparts (and leading to *Aulacostephanoides*).

LINEAGE *DECIPIA–RINGSTEADIA–PICTONIA–RASENIA* AND MICROCONCH COUNTERPARTS

Genus *Decipia* Arkell, 1937 (macro- and microconchs) and its allies

The roots of the family Aulacostephanidae are within the perisphinctid genus *Liosphinctes* Buckman, 1925 which gave rise to the earliest genus of the family – *Decipia* (see Callomon, 1980; Głowniak, 2012; Enay, Howarth, 2019). When considered in detail, the transition into the genus *Decipia* from its possible ancestors becomes, however, somewhat speculative, and needs additional comments.

The genus *Decipia* includes both macro- and microconchs differing in size, but revealing similar ornamentation on the outer whorl of microconchs and the middle whorls of macroconchs which consists of widely spaced, in older forms rod-like, but later swollen primary ribs, showing distinctive separation into three or four secondary ribs in bundles or sheaves, and additionally simple ribs on the body chamber of macroconchs. The inner whorls up to about 20 mm are regularly biplicate at or below the middle of the whorl sides and bear well-marked constrictions (Arkell, 1947; see also Wright, 1996). The genus *Decipia* when originally established in England by Arkell (1937) was treated as "a genus distinct from *Perisphinctes* and its many subgenera, and perhaps as worthy of full generic separation as *Pictonia* or *Ringsteadia*, to which it seems to be closely allied".

Ammonites from the English sections which may be treated as possible direct forerunners of the genus *Decipia*, are, however, poorly known. Possibly some phylogenetic relations may be with poorly-known macroconchs placed in *Pseudopomerania* by Wright (1996) which show, however, densely-ribbed biplicate ribbing on the inner whorls remaining up to much larger diameters (at least up to 60 mm diameter) than in the genus *Decipia* where the biplicate ribs occur only in the innermost whorls. More conclusive for interpretation of the possible roots of the genus *Decipia* are results of a recent study of the section at Mikhalenino of the Kostroma District on the Russian Platform. Here, directly below the first find of the genus *Decipia* in NE Europe, referred to as *D.* cf. *decipiens* (Sowerby), occurred a form of microconch ammonite which could be considered as a possible forerunner of the genus. These specimens referred to as *Decipia*(?) *kostromensis* Głowniak *et al*., show some

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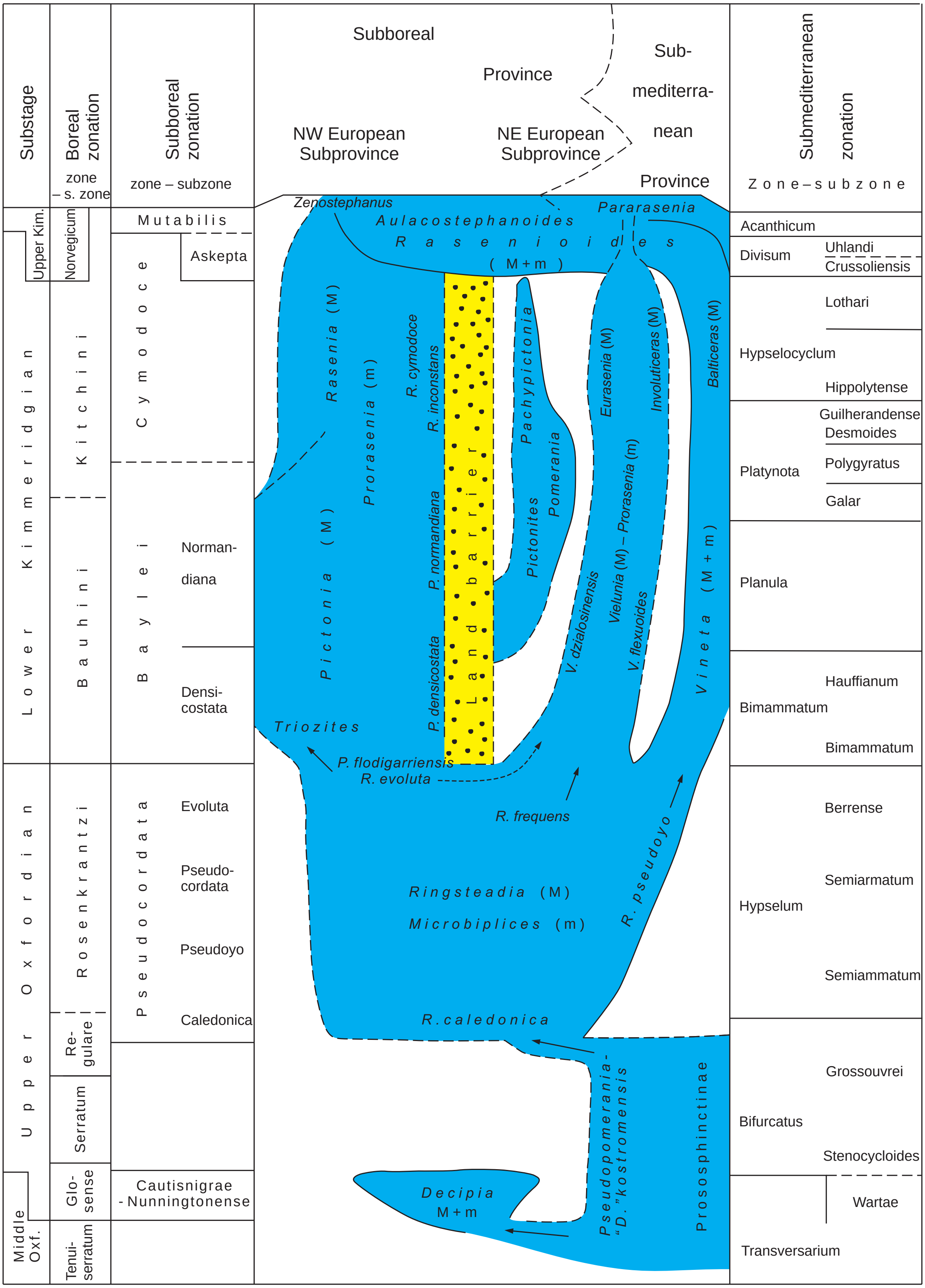
Fig. 2. Phylogeny of the ammonite family Aulacostephanidae during the Late Oxfordian and Early Kimmeridgian in Europe

The stratigrapical intervals are drawn to scale corresponding to the chronostratigraphical time-scale of Hesselbo *et al.* (2020)


Substage
Boreal zonation
zone – s. zone
Subboreal zonation
zone – subzone
Subboreal Province
NW European Subprovince
NE European Subprovince
Sub-mediterranean Province
Submediterranean zonation
Zone – subzone
Upper Kim.
Norvegicum
Mutabilis
Askepta
Lower Kimmeridgian
Kitchini
Cymodoce
Bauhini
Bayle i
Norman-diana
Densi-costata
Upper Oxfordian
Rosenkrantzi
Pseudocordata
Evoluta
Pseudo-cordata
Pseudoyo
Caledonica
Re-gulare
Serratum
Glo-sense
Cautisnigrae - Nunningtonense
Middle Oxf.
Tenui-serratum
Zenostephanus
Aulacostephanoides
Rasenioides (M+m)
Pararasenia
Rasenia (M)
Prorasenia (m)
R. cymodoce
R. inconstans
Land barrier
Pachypictonia
Pomerania
Pictonites
Eurasenia (M)
Involuticeras (M)
Balticeras (M)
Pictonia (M)
P. normandiana
P. densicostata
V. dzialosinensis
Vielunia (M) – Prorasenia (m)
V. flexuoides
Vineta (M + m)
Triozites
P. flodigarriensis
R. evoluta
R. frequens
R. pseudoyo
Ringsteadia (M)
Microbiplices (m)
R. caledonica
Pseudopomerania - "D." kostromensis
Prososphinctinae
Decipia M + m
Acanthicum
Divisum
Uhlandi
Crussoliensis
Lothari
Hypselocyclum
Hippolytense
Guilherandense
Desmoides
Platynota
Polygyratus
Galar
Planula
Hauffianum
Bimammatum
Bimammatum
Berrense
Semiarmatum
Hypselum
Semiammatum
Grossouvrei
Bifurcatus
Stenocycloides
Wartae
Transversarium

features of *Decipia*, like the type of coiling, prorsiradiate ribbing and the presence of trifurcate ribs, but differ in retaining the biplicate ribbing longer, reaching up the middle whorls, and in the occurrence of the trifurcate ribs only on the body chamber, similarly as in the genus *Liosphinctes* (see Głowniak *et al.*, 2010, p. 21, pl. 2: 8, 9). The form thus links phylogenetically the genus *Liosphinctes* with later *Decipia* (Głowniak, 2012). Although *Decipia*(?) *kostromensis* is a microconchiate species, the character of its coiling and ornamentation shows also similarity to those of the inner whorls of poorly known macroconchiate forms of *Pseudopomerania* (Wright, 1996, pl. 3: 1b), which make plausible their close phylogenetic, and thus systematic, relation.

Crucial for the interpretation of the genus *Decipia* is thus its comparison with the genus *Liosphinctes*. Detailed study of the ontogeny of *Liosphinctes* in the Middle Oxfordian, in the area of Submediterranean central Poland, resulted in the recognition of several stages in the development of the ornamentation – from type Ia where the ribs are regularly biplicate, and the intercalatory ribs occur irregularly (this type of ribbing occurs normally in the phragmocone, up to about 100–140 mm diameter); through stage Ib-Ic- where sheaves of three ribs arise indistinctly from the primary ribs, as well as some additional intercalatory ribs appearing; up to stage II where the ribbing consists of blunt single ribs well developed near the umbilicus, but the outer part of the whorl as well as the ventral side become smooth (Głowniak, 2002). The general succession of the ornamentation stages in the genus *Decipia* is similar but the first stage Ia is markedly reduced as it appears only in the innermost whorls. This phenomenon resulted possibly from acceleration (in term of heterochrony) in the morphological development of *Decipia*, which generally shows the disappearance of dense biplicate ribbing at markedly smaller diameters, when compared with older *Liosphinctes* as well as other transitional forms like *Pseudopomerania*.

The genus *Decipia* occurs commonly in the NW European part of the Subboreal Province. The stratigraphical range of the genus *Decipia* corresponds here to the Cautisnigrae Subzone of the lower part of the Cautisnigrae Zone, as well as to some upper parts of the underlying Pumilus Zone, especially those corresponding to the Nunningtonense Subzone. The stratigraphical range of the genus *Decipia* corresponds moreover to that of the Boreal Glosense Zone. The genus is not known from the upper part of the Subboreal Cautisnigrae Zone corresponding to the Variocostatus Subzone, and the Boreal Serratum Zone (see *e.g.*, Sykes, Callomon, 1979; Wright, 1972, 1996, 1997, 2016; Wright, Powell, 2008; Page *et al.*, 2015). In the NE European part of the Subboreal Province, the genus *Decipia* has been recognized in the Glosense Zone, whereas its possible forerunner, *Decipia*(?) *kostromensis* occurs in the lowermost part of this Zone – in the lower part of the Ilovaiskii Subzone along with Submediterranean ammonites indicative of the upper part of the Transversarium Zone, in the Elisabethae Subzone (Głowniak *et al.*, 2010).

The stratigraphical and phylogenetical position of *Decipia*(?) *kostromensis* having been more widly established, it becomes a matter of some importance to discuss the phylogenetical positions of some Submediterranean forms of Prososphinctinae (see Głowniak, 2012, fig. 27) coming from a similar stratigraphical interval – *i.e.* from the Transversarium Zone and the lower part of the Bifurcatus Zone in central Poland. These forms include: the *Liosphinctes* (?) *cracoviensis* (Siemiradzki) group, *Liosphinctes* (?) *berlieri* (Loriol) (see Brochwicz-Lewiński, 1972, pl. 10, 11, 14; Głowniak, Wierzbowski, 2007, figs 21, 22), and even some forms referred to as “*Liosphinctes decipiens*” by Brochwicz-Lewiński (1972, pl. 15). Whereas the bulk of typical *Liosphinctes* species as discussed above occurs in the older deposits of the Plicatilis Zone (see Głowniak, 2002), these younger forms which occur rarely in central Poland, show an even larger similarity to *Decipia*, because of the occurrence of three or even four ribs in sheaves at fairly small diameters, and the markedly reduced interval of occurrence of dense biplicate ribbing in the inner whorls. It is not clear, however, if these ammonites coming from central Poland are strictly phylogenetically related with the discussed forerunners of *Decipia*, such as those of the *Decipia*(?) *kostromensis* type, or represent an independent, parallel branch.

On the other hand, there existed other groups of ammonites which also show some features of *Decipia* but represent separate branches of the Prososphinctinae and inhabited different Submediterranean-Mediterranean areas, such as the genus *Larcheria* Tintant, 1961. The genus *Larcheria* reveals, moreover, nearly the same stratigraphical range as the genus *Decipia* being known from the topmost part of the Transversarium Zone, and the lowermost Bifurcatus Zone – as correlated with the Wartae Subzone (see Głowniak, 2006, and earlier papers cited therein). The genus *Larcheria* shows a wide geographical distribution and spread around the marginal carbonate platforms of Submediterranean Western Europe, and further south along the margin of the Indo-East African Province (Marchand *et al.*, 1982; Krishna *et al.*, 1995). The genera *Decipia* and *Larcheria* are treated as representing the closely related and coeval end-members of parallel lineages – the Subboreal one and the Submediterranean-Mediterranean one, coming both of the same ammonite stock of Prososphinctinae (Głowniak, 2012, fig. 27). The development of similar but geographically isolated parallel lineages coming from a single stock, and existing during the same fairly short geological time of their evolutionary history suggests strong interrelations between the evolution of the groups and the changing environmental conditions. This, resulted possibly from the special trait of these ammonites which was their ability to rapid colonize new areas under unstable environmental conditions (Główniak, 2012).

Genus *Ringsteadia* Salfeld, 1913 (macroconchs) and microconch counterparts (*Microbiplices* Arkell, 1936 and its allies)

There is not known in the fossil record a continuous transition between the genera *Decipia* and *Ringsteadia.* Although evidently related, these two groups are separated by a stratigraphical interval, corresponding to the Boreal Serratum Zone and the Subboreal upper Cautisnigrae Zone corresponding to the Variocostatus Subzone, where these ammonites do not occur. This special character of their distribution was recognized both in NW European and NE European parts of the Subboreal Province, and adjoining Boreal and Submediterranean areas (see *e.g.*, Wright, 1973, 2010; Sykes, Callomon, 1979; Wright, Powell, 2008; Główniak *et al.*, 2010; Wierzbowski, Matyja, 2014). The first ammonite of the genus *Ringsteadia* – *R. caledonica* Sykes et Callomon appears not before the upper part of the Boreal Regulare Zone, and marks the base of the Subboreal Pseudocordata Zone (Sykes, Callomon, 1979). The ammonites occurring directly below the first occurrence of *R. caledonica* and/or in deposits correlated with those at the base of the Pseudocordata Zone bear a large similarity to those referred to as *Decipia*(?) *kostromensis* which preceded the appearance of the older genus *Decipia* (see Wierzbowski, Matyja, 2014, p. 60, 68, pl. 3: 5; Wierzbowski *et al.*, 2015, fig. 8i). A similarity between the form which gave rise to the much older genus *Decipia* and that which precedes the appearance of the genus *Ringsteadia* and is treated as its forerunner, both bearing “primitive” features of ancestors such as the dense biplicate ribbing, suggests a repeated origination of lineages from less specialized forms, in a way characteristic of the iterative evolution (Wierzbowski *et al.*, 2018; see also Wierzbowski, 2017b). This type of evolution may act on the unspecialized forms, after extinction of one group, when the conditions favorable to formation of the more specialized group arose again.

The inner whorls of *Ringsteadia caledonica* have irregular ornamentation consisting of biplicate and intercalatory ribs, replaced thereafter by more numerous secondaries with very common constrictions bordered by flared ribs. The weakly evolute microconchs with lappets attain about 30–45 mm in diameter, and reveal irregular subdued ribbing, but the primaries on the last whorl are generally more stout. The macroconch, about 75 mm in diameter, shows highly involute coiling of the last whorl (at 60 mm diameter, the whorl height is 47% and the umbilical diameter is 21% of diameter), with strongly developed secondary ribs with the secondary/primary ribs ratio equaling about 3 or somewhat more (Sykes, Callomon, 1979, p. 890–893, pl. 121: 8–13). The species shows similarity to representatives of the genus *Decipia* (especially in the inner whorls), but it differs in the generally smaller size of both micro and macroconchs, and the involute coiling of the outer whorls of macroconchs. *Ringsteadia caledonica* reveals, however, a similar type of dimorphism when compared with that of the genus *Decipia* – represented by similarly ornamented micro and macroconchs at comparable diameters, differing only in shell size and the presence of lappets in the microconchs. In the term of heterochrony (see *e.g*., Landman, Geyssant, 1993) the observed ontogenic shifts may be classified as examples of progenesis – *i.e.* the attaining of maturity at an earlier stage in the morphological development in microconchs, and of hypermorphosis – *i.e.* attaining of maturity at an later stage of the morphological development in macroconchs. They may be classified also as an example of heterochronic development of progenesis as understood by Matyja (1986, p. 41) where the rates of growth and morphological transformation are the same in both the forms, but the progenetic form reaches its maturity earlier, and is characterized by shorter longevity, smaller final size, and an earlier morphological stage at maturity.

The younger ammonite faunas of the genus *Ringsteadia* are widely recognized in southern England where they are subdivided in their succession into three levels treated as subzones (sometimes also as faunal horizons – see Sykes, Callomon, 1979; Wright, 1997, 2010): the Pseudoyo Subzone, the Pseudocordata Subzone, and the Evoluta Subzone. The same subzones are recognized also in the Staffin Bay section on the Isle of Skye, northern Scotland (Matyja *et al.*, 2006; Wierzbowski *et al.*, 2006, 2018) which suggests the uniform character of the ammonite succession everywhere. The changes in ammonite faunas are characterized by a different proportion in the occurrence of the involute *R. pseudoyo* group, the moderately involute to evolute *R. brandesi* group, and the evolute *R. marstonensis* group in the Pseudoyo Subzone and the Pseudocordata Subzone – with a general dominance of the involute to evolute forms in the former, and the preponderance of the moderately evolute and evolute forms in the latter; in the Evoluta Subzone a smaller share of the strongly involute forms is noted, whereas the bulk of the species corresponds to the moderately involute forms of *R. frequens* and the evolute *R. evoluta*; moreover, the morphospecies have been recognized in each group of ammonites on the basis of differences in whorl section and/or strength of ribbing (Wright, 2010). Similar morphologically ammonite faunas occur also in Central and NE European areas – in Poland, Germany, and Russia where, however, partly for the historical reasons, partly because of some subtle differences in ornamentation and coiling, other names of species have been introduced – but their correlation with the English counterparts makes no difficulty (see *e.g.*, Głowniak, Wierzbowski, 2007; Głowniak *et al.*, 2010; Wierzbowski, Matyja, 2014, and earlier papers cited therein).

The ammonites of the genus *Ringsteadia* discussed herein were collected (Pl. 1: 1, 2; Pl. 2: 1; Pl. 3) from the uppermost part of the Pseudocordata Zone – the Evoluta Subzone of the Osmington Mills Ironstone Mbr., exposed at Black Head, Dorset Coast, southern England. They are belonging to four species: *Ringsteadia pseudoyo* Salfeld, *R. frequens* Salfeld, *R. marstonensis* Salfeld, and *R. evoluta* Salfeld, each of them showing well developed morphological features. The description of these specimens is given in detail because it illustrates well the differentiation of the youngest fauna of *Ringsteadia* during the latest Oxfordian in Europe. It is the case of *R. pseudoyo* which shows the strongly evolute coiling of the innermost whorls up to about 20–30 mm diameter and the sparsely placed prorsiradiate primaries in inner whorls [also other specimens of this species from the same locality described by Wright (2010, p. 26, pls. 5: 3; 7: 4) show “moderately strong well-spaced primaries and secondaries developed at 35 mm”]. At larger diameter the coiling becomes strongly involute, and the ribbing initially stays dense, and then gradually fades, beginning from the primary ribs in the middle of the whorl-height, but the secondaries remained strongly developed at least up to 100 mm diameter (Pl. 3: 1A): these features result in quite distinctive position of the species in the collection studied. On the other hand, the specimen of *Ringsteadia frequens* Salfeld, about 90 mm in diameter (Pl. 1: 2), represented by the phragmocone, is evolute in its inner parts (up to about 60 mm diameter), but the last part of the phragmocone shows already moderately involute coiling. The ribbing is fairly strong: the primaries are markedly prorsiradiate, and their number per whorl oscillates from 28 at 45 mm diameter to about 25 at 90 mm diameter, but the secondaries appearing at about a half of the whorl height tend to disappear already at 70 mm diameter. The most evolute specimens belong to the species *Ringsteadia marstonensis* Salfeld (Pl. 2: 1) and *R. evoluta* Salfeld (Pl. 1: 1), and strictly correspond to description of these species at comparable diameters, *e.g.* the holotype of *R. marstonensis* illustrated by Salfeld (1917, pl. 11: 1a, b) and *R. evoluta* by Wright (2010, pl. 8: 3–5). The specimen studied of the former species is 145 mm in diameter consisting of the phragmocone and an initial part of the body chamber, that of the latter is about 150 mm in diameter and shows a large part of the body chamber preserved. These two specimens show the evolute coiling of the inner whorls with some widening of the whorl height at a distance about half a whorl before the end of the phragmocone which results in similar sizes of whorl height and the umbilicus diameter at that point indicating the coiling at the evoluteness/involuteness boundary, but the last part of the shell reveals the succeeding marked uncoiling. The ribbing is generally coarse (number of primaries per whorl oscillates between 23–29 at 30–145 mm diameters), but the secondary ribs begin to fade out at about 100 mm diameter at the last part of the phragmocone. The specimen of *R. evoluta* shows additionally the irregularity of ribbing connected with development of strong constrictions; moreover, a special feature of this specimen is a very dense ribbing of the innermost whorls (at 20 mm diameter the number of primaries per whorl attains about 35).

The corresponding microconchs of all the younger *Ringsteadia* species are quite different from those of the older *R. caledonica*, and are normally referred to as different “species” of the genus *Microbiplices* or *Microbiplices/Prorasenia* transitional forms. The microconch succession has been especially well recognized in the Polish Jura sections of central Poland (Wierzbowski, Matyja, 2014), but also in the Staffin Bay sections of northern Scotland (Wierzbowski *et al.*, 2018; see also Matyja *et al.*, 2006). It begins with the dominance of forms showing very densely ribbed inner whorls and the initial part of the outer whorl, up to about 20–25 mm diameter, with common biplicate ribs, and a fairly involute coiling of the body-chamber, as in *Microbiplices procedens* (Oppenheimer) (Pl. 2: 4) and *M. guebhardi* (Oppenheimer). These are successively replaced in the stratigraphical succession by forms where the very dense biplicate ribbing is observed only up to about a few mm in diameter, being less densely ribbed and more evolute thereafter, like *Microbiplices microbiplex* (Quenstedt) (Pl. 2: 2, 3), and *M. anglicus vieluniensis* Wierzbowski et Matyja, which is very close to *M. anglicus anglicus* Arkell. Whereas the microconchs *M. procedens* correspond to the strongly involute and densely ribbed macroconchs of the *Ringsteadia pseudoyo* group (Pl. 1: 3, 4), the more evolute *M. microbiplex* and *M. anglicus* may be correlated with more evolute and more coarsely ribbed species of the genus *Ringsteadia* (Wierzbowski, Matyja, 2014).

The extreme variability seen in the ammonite genus *Ringsteadia* and its microconchs shown by the presence of numerous morphospecies co-occurring at successive stratigraphical levels, has been interpreted commonly as representing “merely the intergrading variants of a single biospecies” (Wright, 2010, p. 24). However, this refers mostly to older forms of the Pseudoyo and Pseudocordata subzones, whereas the ammonite fauna of the Evoluta Subzone is “quite distinctive” and shows “a substantial range in variation of shell shape… not as marked as in earlier subzones” (Wright, 2010, p. 18). The differences between the particular species reveal here some specific trends observed during their ontogenic development. Such a range of morphological features, recognized in the Evoluta Subzone as discussed above, makes the species closer to the real biological entities, and thus the ideal forerunners of the new side branches emerging in particular areas due to the speciation processes. This is especially the case with the irregularly ribbed *Ringsteadia evoluta* Salfeld which can be treated as the forerunner of the genus *Pictonia* in the main aulacostephanid lineage. On the other hand, some related forms along with those similar to *Ringsteadia frequens* possibly gave rise to the side branch beginning with the genus *Vielunia*, whereas those related to *Ringsteadia pseudoyo* possibly gave rise to the side branch with the genus *Vineta* (see also discussion below at the detailed description of the indicated side branches of Aulacostephanidae). These interpretations indicate a special position of the genus *Ringsteadia* in the phylogenetical development of the Late Oxfordian to Early Kimmeridgian aulacostephanids.

In the ontogeny of the discussed macroconchs of *Ringsteadia* species, the ribbing of the inner whorls is usually more dense and biplicate, whereas that of the following whorls becomes more distant, and the number of secondary ribs markedly increases. On the other hand, the corresponding microconchs (*Microbiplices* and *Microbiplices – Prorasenia* transitional forms) show very early deviation in their ontogeny from that shown by macroconchs: the dense biplicate ribbing is observed mostly on the innermost whorls (especially in late forms), and it is followed by the loosely spaced triplicate and biplicate ribs with some intercalatories, which generally are similar to those of *Ringsteadia*, but appear at markedly smaller diameters. The final specific ornamentation observed at some late microconchs is composed of widely-bifurcated ribs occurring on the last whorl and ranging up to the final aperture with lappets (*e.g.*, Matyja *et al.*, 2006; Wright, 2010; Wierzbowski *et al.*, 2018).

The development of the discussed micro and macroconchs may be compared in terms of heterochrony (*cf.* Wierzbowski *et al.*, 2018). This is expressed by "normal" hypermorphosis in *Ringsteadia* macroconchs, similar to that of older *Decipia*. On the other hand, the microconchs (*Microbiplices* and *Microbiplices – Prorasenia* transients) show markedly smaller end-size and earlier offset, resembling thus somewhat progenesis in the categories of heterochrony, but with acceleration in ornamentation development. Additionally, a special type of ribbing composed of widely-bifurcated ribs at the end of the shell is observed: this new feature is recognized in forms more advanced in morphology like *Microbiplices microbiplex.* Interestingly, there exist some intermediate specimens close to *M. microbiplex* which show still the presence of triplicate ribs up to end of the last whorl and the final aperture (*e.g.* those referred erroneously to as "*Prorasenia*" by Schairer and Schlampp, 2003, pl. 2: 2, 12, 13, from southern Germany), without the stage of the widely-bifurcate ribs. This type of development of small-sized microconchs, as based on the *Microbiplices microbiplex* morphology, appeared so successful an adaptation for changing environmental conditions that it was adopted, but in slightly modified form, by all the younger microconchs in the whole Aulacostephanidae (*cf.* Birkelund, Callomon, 1985). It may be treated as a special adaptation appearing to be associated with a more unstable environment.

Genus *Pictonia* Bayle, 1878 (macroconchs – subgenera: *Pictonia* Bayle, 1878, and *Triozites* Buckman, 1924) and microconch counterparts (some *Prorasenia* Schindewolf, 1925)

The appearance of the genus *Pictonia* in the NW European Subboreal succession represents one of the main turnovers in the phylogeny of the Aulacostephanidae which suddenly follows the decline of an older smoothly evolving segment of the *Ringsteadia* lineage. This defines the base of the Subboreal Baylei Zone correlated with the base of the Kimmeridgian. The full succession of the *Pictonia* faunas is, however, not represented in any of the sections of southern-middle England. Everywhere there a stratigraphical gap associated with a marked change in the character of sedimentation above the youngest beds with *Ringsteadia evoluta* Salfeld, and below the oldest preserved deposits with *Pictonia densicostata* Salfeld is recognized. This occurs: at the boundary of the Sandsfoot Formation and the so-called Inconstans beds of the lowermost part of the Kimmeridge Clay Formation in Dorset, and at the boundary of the Ampthill Clay Formation and the Kimmeridge Clay Formation at South Ferriby. A larger gap including even beds with *Pictonia densicostata* occurs also in the sections of Normandy in northern France (see *e.g.*, Arkell, 1956; Ahmed, 1987; Hantzpergue, 1989; Wignall, 1990; Cox, 2001; Wright, 2010). The only sections which are complete and show the transition from the *Ringsteadia* faunas to the *Pictonia* faunas, including the occurrence of the earliest one of *Pictonia flodigarriensis* Matyja, Wierzbowski, Wright, are those of Staffin Bay, Isle of Skye, in northern Scotland (Matyja *et al*., 2006; Wierzbowski *et al.*, 2006, 2016). The distribution of ammonites in that succession and their characteristics have been recently presented in detail by Wierzbowski *et al.* (2018), and these observations are briefly summarized below.

The typical *Pictonia* macroconchs, attributed herein to the nominative subgenus, comprises fairly large ammonites, ranging up to about 200 mm in diameter, and showing strongly evolute coiling with mostly biplicate ribbing on the inner whorls. This type of ribbing is undoubtedly of the "primitive" perisphinctoid character (Salfeld, 1917, p. 73). The two oldest species *P. flodigarriensis* and *P. densicostata*, known from the Densicostata Subzone of the lower part of the Baylei Zone, reveal such biplicate ribbing up to about 40–50 mm diameter (see *e.g.*, Matyja *et al.*, 2006, fig. 5a–d; Wierzbowski *et al.*, 2018, fig. 6, pl. 1: 7). In younger species like *P. normandiana* (Tornquist) and *P. baylei* Salfeld/*P. normandiana* of the Normandiana Subzone of the upper part of the Baylei Zone, the biplicate ribbing is still visible on the inner whorls, but it disappears already at about 20–30 mm diameter (see *e.g.*, Matyja *et al.*, 2006, fig. 5f–i; Wierzbowski *et al.*, 2018, pl. 1: 8). The following whorls of all these species of *Pictonia* show more distant, biplicate and polyplicate ribbing with periodical occurrence of swollen (flared) ribs bordering deep constrictions. At larger diameters this ornamentation fades out.

There exists, however, another group of ammonites, occurring in the Densicostata Subzone, which show large affinities with *Pictonia*, but differ in the presence of bold, rather distant biplicate ribbing on the inner whorls with some intercalatory ribs and a lack of marked constrictions and/or flared ribs. These ammonites, compared with *Triozites* Buckman, 1924 resemble in their character of ribbing the inner-middle whorls of *Ringsteadia evoluta*, but their general S-shaped curve and outer whorl tending to be smooth, already at a diameter 60–70 mm, indicate that they are closer to *Pictonia* (see Wright, 2010). They should be possibly separated at the subgeneric level, and have been referred to as *Pictonia* (*Triozites*) *seminudata* Buckman (see Wierzbowski *et al.*, 2018, pl. 1: 4–6).

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). These ammonites generally of small size (up to a few cm in diameters) reveal dense biplicate ribbing on the innermost whorls only. Soon thereafter appear loosely spaced biplicate and triplicate ribs (which become fairly thick on middle whorls), followed by widely bifurcating ribs ranging up to the aperture with lappets, similarly as in older *Microbiplices*.

When interpreting the evolutionary changes in the developmental timing of the discussed ammonites some general opinions in relation to the recognized types of heterochronic variations can be given (see also Wierzbowski *et al.*, 2018). It is important to note that some of these features 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 the dense biplicate ribbing up to about 20–30 mm diameter (Matyja *et al.*, 2006, p. 402, fig. 4C; see also Pl. 1: 1 herein). The early *Pictonia* ammonites like *P. flodigarriensis* and *P. densicostata* with densely placed biplicate ribbing of the inner whorls, persisting up to fairly large diameters, represent the same, but a more advanced, trend of heterochrony. It may be classified as the paedomorphic result of neoteny according to Landman and Geyssant (1993), when the later adult shows strongly accentuated "primitive" features of the ancestor. On the other hand, late *Pictonia* ammonites like *P. baylei* and *P. normandiana* show a markedly limited interval of occurrence of biplicate ribbing on the inner whorls revealing thus the beginning of reversion of the tendency of heterochrony which is developed especially strongly in the still younger genus *Rasenia* (see Wierzbowski *et al.*, 2018).

The overall variability of ammonites coming from the Densicostata Subzone in southern England related to the species *Pictonia densicostata* (and thus referred to the nominative subgenus herein) and *P. seminudata* (of the subgenus *Triozites*) was discussed recently by Wright (2010). This revealed a very large spectrum of features of all these specimens both in character of ribbing and presence of constrictions, which resulted in recognition of only two main groups indistinctly outlined about the two indicated morphospecies. The forms grouped around *P. seminudata* (and treated herein as subgenus *Triozites* Buckman, 1924) seem additionally to represent a special "transitional" member between *Ringsteadia* and *Pictonia*, being closer in early stages of ontogeny to those commonly recognized in older *Ringsteadia*.

The microconchiate counterpart of *Pictonia* generally corresponds to the morphotype of *Prorasenia* which reveals a very short interval with biplicate ribs on the innermost whorls, and the presence of swollen triplicate ribs on the middle to initial part of the outer whorl. 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*. Thus, the appearance of similar ribbing in microconchs referred to as *Prorasenia* at markedly small shell diameters may be interpreted in term of heterochrony as a consequence of their faster rate of development – which is the acceleration; this is followed by a special development of the widely-bifurcated ribs on the body-chamber, not encountered in its ancestors, similarly as in their forerunner – *Microbiplices*.

The changes in faunal character of Aulacostephanidae are well correlated with changes of the depositional environment – as stimulated by the tectonic movements which occurred in large areas of northern Europe at the Oxfordian/Kimmeridgian boundary (Enay, 1980; Wierzbowski, 2010; Wierzbowski *et al.*, 2016; see also comments herein at the end of the study). The consequence of the geographic separation of NE and NW parts of the Subboreal Province was the allopatric speciation which occurred in Aulacostephanidae inhabiting these areas. The appearance of the genus *Pictonia* in NW European areas was thus the consequence of such a speciation, and the further evolution of the NW European Aulacostephanidae lineage stayed here with limited contact with the parallel lineages of that family which evolved in NE and Central European areas (see also discussion below).

Genus (and subgenus) *Rasenia* Salfeld, 1913, and its microconch counterpart (some *Prorasenia* Schindewolf, 1925, and akin forms)

The succession of macroconchs of the nominative subgenus is characteristic of the Subboreal Cymodoce Zone of NW Europe. It is well known and was studied in detail by Birkelund *et al.* (1978, 1983) in the Subboreal sections of southern England, but its earliest member *Rasenia* (*Rasenia*) *inconstans* Spath is described also from the Staffin Bay area in northern Scotland (Matyja *et al.*, 2006). Additionally, the whole succession is recognized and commented by Birkelund and Callomon (1985) in East Greenland.

The early members of Subboreal *Rasenia*, like *R. inconstans* and *R. cymodoce*, are recognized moreover in the Submediterranean Province: mostly in north Aquitaine (Hantzpergue, 1989), but also markedly towards south-east in central Poland (Wierzbowski, 2020, pl. 6: 1). Such is a newly discovered specimen coming from north-eastern margin of the Holy Cross Mts., central Poland, described herein (Pl. 2: 6). It belongs to *Rasenia* (*Rasenia*) *inconstans* and is about 95 mm in diameter being represented mostly by the body chamber with typical ribbing consisting of short swollen primaries and numerous secondaries (the ratio of primaries to secondaries is 4.2). The ribbing tends to disappear at about 90 mm diameter, as primaries become thinner and non-bullate, which seems to indicate the specimen is fully grown. The specimen shows evolute coiling (at 93 mm diameter, the whorl height is 31.2%, and the umbilical diameter is 35.3% of the specimen diameter).

On the other hand, the occurrences of NW European Subboreal *Rasenia* (*Rasenia*) are placed deep in the Boreal Province down to Svalbard and the Barents Sea area (Wierzbowski, 1989; Wierzbowski, Smelror, 2020, and earlier papers cited therein). Such a wide distribution of the early members of the genus and subgenus (and locally also the preceeding late representatives of *Pictonia*) reflects the temporary migrations which could be tectonically and/or climatically induced (*cf.* Birkelund *et al.*, 1983; Hantzpergue, 1989, 1995; Wierzbowski, 2020).

The genus *Rasenia* follows the genus *Pictonia*, and the transition between them in the succession is gradual and the boundary purely arbitrary (Birkelund, Callomon, 1985). Although the main feature of the genus is the appearance of bullate ribs, the oldest species – *Rasenia inconstans* Spath and *R. cymodoce* (d'Orbigny) show the innermost whorls up to about 20 mm diameter always very densely ribbed resembling the inner whorls of their ancestors. Moreover, the first representatives of *R. inconstans* with heavy bullate ribs occur together with specimens with non-bullate ribs on the outer whorls being close to *Pictonia*, showing thus the wide lateral variation at a single biospecies level. Still younger *Rasenia* species, like *Rasenia involuta* Spath and *R. evoluta* Spath, close the succession of the faunas of the nominative subgenus corresponding to the Subboreal Cymodoce Zone in the NW part of the Subboreal Province. They show very strongly bullate ribs from very small diameters, but the outer whorl sometimes tends to be smooth, or shows the presence of thinner, elongated, biplicate or single ribs.

The microconchs of *Rasenia* are less commonly known that the macroconchs. Several specimens attributed to the genus *Prorasenia* were described by Mesezhnikov (1984, pl. 4) from the peri-Polar Ural Mts., Russia, and some, correlated with older group of macroconchs, from East Greenland (Birkelund, Callomon, 1985, pl. 12: 4, pl. 18: 4, ? 3, 5, 6) and Spitsbergen (Wierzbowski, 1989, pl. 19: 1, 2). These older microconchs show commonly the presence of biplicate ribs (sometimes possibly also triplicate) on the outer whorl, resembling thus *Prorasenia* from the Subboreal and Submediterranean areas of Europe (*cf.* Geyer, 1961), but are generally of larger sizes, attaining usually about 40 mm, but occassionally even 60–80 mm in final diameter. The younger *Rasenia* microconchs described *e.g.* by Birkelund *et al.* (1983), corresponding to *R. evoluta* and *R. involuta* macroconchs, consist predominantly of two variants. The first one includes larger forms (40–80 mm in diameter), showing the presence of biplicate ribs on the outer whorl (Birkelund *et al.*, 1983, fig. 4: C, D; fig. 5: A–C). The second variant is smaller, and it reveals numerous secondary ribs up to the final peristome with lappets (Birkelund *et al.*, 1983, fig. 3C, D).

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

The detailed interpretation of the evolutionary process which led from *Rasenia* s.s. to younger rasenoidal ammonites is generally outside the scope of this study. It is worth noting, however, that its earliest stage was related with formation of *Zonovia* Sazonov, 1960 showing an incipient smooth band at the ventral side of the phragmocone of macroconchs (see *e.g.*, Birkelund, Callomon, 1985). The species *Rasenia involuta* and some variants of *R. evoluta* of the lineage in question seems to be close to *Zonovia* (see Birkelund *et al.*, 1978).

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 latter gave rise to another lineage of aulacostephanids beginning with *Zenostephanus* (older *Xenostephanus*, see Arkell, Callomon, 1963) which developed during the early Late Kimmeridgian in the high-latitude Boreal areas (see *e.g.*, Mesezhnikov, 1969, 1984; Rogov, Poulton, 2015; Wierzbowski, Smelror, 2020). The descendants of *Rasenia* s.s. might also encompass, after Borrell (2014), some forms previously attributed (Ziegler, 1962; see also *e.g.*, Callomon, 1980; Birkelund *et al.*, 1983; Birkelund, Callomon, 1985) to the subgenus/genus *Aulacostephanus*, excluding a group placed around the type species of *Aulacostephanus* – *A. pseudomutabilis* (de Loriol). Such an interpretation results in the splitting of the original range of *Aulacostephanus* into two separate subgenera/genera: *Aulacostephanus* and *Aulacostephanoceras* (see Enay, Howarth, 2019), the former deriving from the genus *Rasenioides*, the latter possibly from *Rasenia* ss. (see Borrell, 2014).

LINEAGE *PICTONIA (PICTONITES–POMERANIA)–RASENIA (PACHYPICTONIA)*

Genus *Pictonia* – subgenera: *Pictonites* Mesezhnikov, 1969 and *Pomerania* Arkell, 1937

The first ammonites of the genus *Pictonia*, compared with Subboreal representatives of the *Pictonia* (*Pictonia*) *densicostata* group of the NW European areas, were reported from the lower part of the Submediterranean Hauffianum Subzone (upper part of the Bimammatum Zone) of the Lower Kimmeridgian together with Boreal cardioceratid ammonites of the subgenus *Plasmatites* in the “upper Amoeboceras layer” in the Wieluń Upland in central Poland (Matyja, Wierzbowski, 1997, p. 87, pl. 5: 6–11; see also earlier papers cited therein). A similar assemblage of aulacostephanid ammonites has been discovered also in the coeval stratigraphical horizon in the quarries at Barcin in Kujawy area, northern Poland, as reported herein for the first time. It consists of fragmentarily preserved ammonites of the genus *Pictonia* close to *P. densicostata* and numerous microconchs of *Prorasenia bowerbanki* Spath. The ammonite assemblage discussed is comparable to that of the Densicostata Subzone of the Baylei Zone of the Subboreal lowermost Kimmeridgian of NW Europe.

The representative of a different group of *Pictonia* associated with *Pictonia* (*P.*) *densicostata* (Matyja, Wierzbowski, 1997, pl. 5: 5) were discovered in still younger deposits of the lowermost part of the Planula Zone (*matyjai* horizon) in the Wieluń Upland. The specimen in question, 45 mm in diameter, consists of the phragmocone (? up to 35 mm diameter) and a fragment of the body-chamber (Pl. 2: 5). It can be safely attributed to *Pictonia* (*Pictonia*) as shown by the irregular ribbing, the collared constrictions, and fading of ribbing on the outer whorl. It differs, however, from the *Pictonia* (*Pictonia*) *densicostata*, occurring mostly in older deposits in the Wieluń Upland (Matyja, Wierzbowski, 1997, p. 87), in its having a smaller number of primary ribs (about 25 per whorl) and a larger number of secondaries (the primary/secondary rib ratio is about 3.0). This specimen resembles *Pictonia normandiana* Tornquist (see Tornquist, 1896; also Birkelund, Callomon, 1985, p. 30, pl. 10: 1–6; pl. 11: 1–3, with synonymy given), although it is of smaller size as indicated by the earlier fading of its ornamentation at about 40 mm diameter. Thus it is referred to as *Pictonia* (*Pictonia*) aff. *normandiana* Tornquist. The occurrence of this form near the base of the Submediterranean Planula Zone suggests the correlation of that level with the base of the Normandiana Subzone of the Baylei Zone of the Subboreal lowermost Kimmeridgian of NW Europe.

The occurrences of the NW European Subboreal *Pictonia* faunas in the Submediterranean succession indicates that these ammonites have been able to migrate temporarily into the areas of Central Europe – such as central Poland (Matyja, Wierzbowski, 1997), but also southern Germany, where similar forms have been described as *Pictonia praeperisphinctoides* by Schweigert and Callomon (1997). These ammonites may have given rise to the local aulacostephanid side branch lineage which developed in the NE European part of the Subboreal Province and in adjoining areas of the Submediterranean Province during the earliest Kimmeridgian, possibly as the result of the peripatric speciation within the group of the founders of *Pictonia*.

This well-documented appearance of a new ammonite lineage refers to *Pictonia perisphinctoides* (Wegele) and another Submediterranean *Pictonia* species – *P. thurmanni* (Contejean), both being similar to Subboreal species *Pictonia* (*Pictonia*) *normandiana* Tornquist. These ammonites are known from the Submediterranean Planula Zone in France, southern Germany and central Poland (Hantzpergue, 1989; Schweigert, Callomon, 1997; Wierzbowski, 2017a), which may be correlated with some parts of the Normandiana Subzone of the upper part of the Subboreal Baylei Zone. The special feature of *Pictonia perisphinctoides* is the coarse curved triplicate ribbing of the outer whorl which is, however, poorly visible in the holotype of the species, described originally as *“Rasenia” perisphinctoides* by Wegele (1929, pl. 10: 2a, b), because of its fairly small size. Such ribbing is well seen in another specimen of

Wegele (1929, pl. 10: 1a, b) referred originally to as "*Rasenia dacquei*", and treated for a long time as a separate species, but which represent the outer whorl of *P. perisphinctoides* (see Schweigert, Callomon, 1997, p. 45; see also Wierzbowski, 2017a, p. 81). A similar development of the ornamentation on the outer whorl shows another, somewhat younger, species of *Pictonia* of the same lineage described as *Pictonia kuiaviensis* Matyja et Wierzbowski. This species was originally described from the Galar Subzone at Barcin in the Kujawy area, northern Poland, and was based mostly on small-sized specimens, but also on a fragment of the outer whorl referred originally as "*Rasenia* aff. *daquei*", being very similar to the outer whorl of *P. perisphinctoides*, as discussed above (Matyja, Wierzbowski, 2002, pl. 1: 4–11 and 12, respectively). The same species has been identified in a similar stratigraphical position in the borehole in the Peri-Baltic Syneclise (Wierzbowski *et al.*, 2015, fig. 9k), and at Julianka quarry in the Częstochowa Upland in central Poland (Matyja, Wierzbowski, 2006), where it is represented by several small-sized specimens associated with a *Prorasenia* microconch. The microconchs corresponding to the macroconchs discussed are generally poorly recognized. The oldest macroconchs of *P. perisphinctoides* group, possibly have their counterparts in forms similar to *Prorasenia hardyi* Spath (see Schweigert, Callomon, 1997; Wierzbowski, 2017a).

The development of the ornamentation of the discussed ammonites from *P. perisphinctoides* to *P. kuiaviensis*, although very similar to the genus *Pictonia*, differs in the appearance of stronger ribbing at larger diameters, not known in the nominative subgenus, and deserve thus a separate subgenus name. Such was the original proposal of Meseshnikov (1969) who distinguished the name *Pictonites* with the type species – *Pictonia* (*Pictonites*) *perisphinctoides* (Wegele) for the evolute forms from southern Germany, showing fairly regular ornamentation which continues on the outer whorl. Such a taxonomical interpretation of the discussed group of ammonites differs from that given recently by Enay and Howarth (2019) who recognized *Pictonites* as a younger synonym of the name *Pictonia.*

The crucial aspect of recognition of the subgenus *Pictonites* is strictly related to the phylogenetical position of another somewhat enigmatic taxon – *Pomerania* Arkell, 1937. The ammonites originally described by Dohm (1925) from the Upper Jurassic of Western Pomerania, in the quarry at Czarnogłowy (Zarnglaff), were compared by him with the genus *Pictonia.* Such an interpretation was questioned by Arkell (1937) who introduced a new name *Pomerania* (with the type species *Pomerania dohmi* as based on specimens attributed by Dohm to the species *Pictonia baylei* – see Dohm, 1925, p. 32, pl. 5: 6), and proposed it as a new subgenus of the genus *Decipia.* Although there exists some similarity in ornamentation of the middle and outer whorls between *Decipia* and *Pomerania*, the stratigraphical positions of these two ammonite taxa are quite different, however. Still another interpretation of *Pomerania* suggesting its possible relation to *Lithacosphinctes*, *i.e.* the macroconch of the widely treated *Orthosphinctes* of the Ataxioceratinae (see Enay, Howarth, 2019), is also difficult to accept. Although there exists some similarity in ornamentation of the outer whorl of *Pomerania* and *Lithacosphinctes* shown in the presence of large swollen primary ribs, which has resulted in the past in the erranaceous reference of some *Orthosphinctes*-like ammonites to the genera *Decipia* and/or *Pomerania* (see Enay, 1966; Wierzbowski, 1978), the ornamentation of the inner whorls of these two groups of ammonites is markedly distinct.

Geyer (1961) recognized that the Lower Kimmeridgian ammonites placed in the genus *Pachypictonia* by Schneid (1940) are related to the genus *Pomerania,* and tentatively distinguished the genus *Pomerania* with two subgenera *Pomerania* and *Pachypictonia*, indicating the relation of the former to the genus *Pictonia*, and the latter to the genus *Rasenia.* A similar opinion was expressed by Kutek (1968). There exist a number of species which may be placed in the subgenus *Pomerania* as described mostly by Schneid (1940) from southern Germany. Some of them were subsequently described also from central Poland and Switzerland (Kutek, 1968; Gygi, 2003), showing thus their wide distribution in the Submediterranean areas.

Although the quarry at Czarnogłowy, the *locus typicus* of *Pomerania* ammonites, is nowadays completely flooded, there exists a number of specimens coming from that locality, and preserved in Polish, and especially in German collections. A few ammonites from the collections of the Museum of the Polish Geological Institute-National Research Institute (1120.II., collected by A. Czekalska), and the Museum of the Faculty of Geology of the University of Warsaw (collected by J. Kutek, collection ZI/108) come from grey marls and limestones ["blue-gray marly unit" of Czekalska, Krygowski (1957)], corresponding approximately to beds 13–18 of Wilczyński (1962) who was the last student working in the quarry. It is the type level of *Pomerania* (*i.e.*, *Pictonia* after Dohm, 1925) as well as some of the "*Rasenia*" ammonites as described by Dohm (1925) and Wilczyński (1962). The specimens at the author disposal are mostly phragmocones and immature forms – but all of them reveal a marked similarity in ornamentation of their inner and middle whorls preserved.

According to Geyer (1961), the bulk of large specimens of *Pomerania* from Czarnogłowy quarry (see *e.g.*, Dohm, 1925, pl. 5: 6; pl. 7: 3; pl. 8: 3; pl. 9: 6) belongs only to one species which is *Pictonia schmidti* Dohm, and then the name *Pomerania dohmi* Arkell distinguished as the type species of the subgenus would appear as its younger subjective synonym. This suggestion, however, is difficult to accept because even the two mentioned species seem to differ markedly – both in their final size, and in the density of ribbing of the inner whorls (see also comments below). The details of ornamentation are, however, poorly visible in the illustrations of the specimens, and revision of the whole B. Dohm's collection preserved in the Museum in Greifswald in Germany is necessary. The comments given below are related to the specimens coming from the Polish collections.

A unique specimen (Pl. 4) was collected by A. Czekalska at Czarnogłowy and was referred to by her as *Pictonia* sp. from the lower part of grey-blue marly unit (after the description on the label in the Museum of the Polish Geological Institute – National Research Institute in Warszawa; see also location *in*: Czekalska, Krygowski, 1957, fig. 7). It consists of the phragmocone (up to 255 mm diameter), and a half of the whorl belonging to the body chamber up to 310 mm in diameter: the whole specimen could have attained about 350 mm in diameter. The specimen shows fairly dense ribbing in the inner whorls [PR (primary rib number) is about 30–32 at D (diameter) = 60–140 mm], which becomes less dense at larger diameters (PR = 26–28 at D = 190–255 mm, and 23 at 310 mm) with secondary ribs attaining 3–4 per one primary rib as visible on the last whorl preserved. The characteristic feature of the specimen is the continuity of a similar type of ornamentation consisting of primary and secondary ribs, resembling strongly that of *Pictonia* (*Pictonites*), up to especially large diameters. Such a development of ornamentation differs from that shown by the bulk of the species of *Pomerania* from Czarnogłowy as described by Dohm (1925), including *Pictonia* (*Pomerania*) *dohmi* (Arkell) (see Dohm, 1925, pl. 5: 6), *P.* (*P.*) *latecosta* Dohm (see Dohm, 1925, pl. 9: 6) and *P.* (*P.*) *robusta* Dohm (see Dohm, 1925, pl. 7: 3), which show the outer whorl covered with loosely placed primary ribs and the virtual absence of the secondaries already at relatively smaller diameters. The only species which seems to be related to the discussed specimen of Czekalska is *Pictonia* (*Pomerania*) *schmidti* Dohm (see Dohm, 1925, pl. 8: 3), attaining very large size (about 510 mm in diameter), and showing the appearance of the single ribs at least from about 380 mm diameter on the last whorl; although the ornamentation of the inner whorls of the species is poorly known, the character of coiling and fairly dense ribbing seem to be close to those of the discussed specimen.

Another specimen from Czarnogłowy (Pl. 5: 1) is represented by a phragmocone about 180 mm in diameter with loosely spaced elongated primary ribs (about 20 ribs per whorl at 120–180 mm diameter), and fairly numerous secondaries [SR/PR (secondary/primary rib ratio) is about 3.0 at D = 70–180 mm] which tend to disappear at about 180 mm diameter, and a very weakly evolute coiling. It resembles very much *Pictonia* (*Pomerania*) *consobrina* (Schneid) which is possibly conspecific with *P.* (*P.*) *armillata* (Schneid) (see Schneid, 1940, pl. 7: 1 and pl. 6: 5; see also Geyer, 1961); both of them because of the elongated primary ribs should be interpreted as belonging to the subgenus *Pomerania* (and not *Pachypictonia* as interpreted by Geyer, 1961); the species is reported from the Platynota Zone of southern Germany

The specimen referred to as "*Rasenia trimera*" by Wilczyński (1962, p. 67; pl. 4: 2) from Czarnogłowy bed 13 is an incomplete phragmocone about 130 mm in diameter which may be interpreted as related to *Pictonia* (*Pomerania*) *albinea* (Oppel). Still another specimen from Czarnogłowy (Pl. 5: 3), about 100 mm in diameter and representing an incomplete phragmocone, is also similar in type of coiling and density of ribbing to *P. albinea.* It differs, however, from that species in its shorter and more coarsely developed primaries, resembling very much the "*Pictonia adelpha*" of Schneid (1940, p. 83, pl. 2: 2). Although the latter has been included into synonymy of *P. albinea* by Geyer (1961, p. 121) its ornamentation is more of a rasenoid type, and thus becomes closer to *Rasenia* (*Pachypictonia*).

The fragmentarily preserved specimen coming from the upper part of the Planula Zone at Lisowice, Wieluń Upland (Pl. 5: 2) is also very similar to *Pictonia* (*Pomerania*) *albinea*: the very characteristic features of the specimen are the coiling which is at the involutneness/evoluteness boundary, and the ribbing consisting of fairly long primaries, and very numerous secondaries (the secondary/primary rib ratio is 4.0 at about 90 mm diameter) which are separated by an indistinctly developed smooth spiral band, seen also in the holotype of *P. albinea* originally described from southern Germany (see Oppel, 1863, pl. 50: 3a, b; Schneid, 1940, pl. 6: 3). This is possibly the oldest well documented stratigraphical occurrence of that species. Additionally, very close, if not conspecific with that species is *Pictonia mesezhnikovi* Głowniak *et al.* (see Głowniak *et al.*, 2010, p. 23, pl. 5: 14, pl. 7: 2) described from an upper part of the Baylei Zone from the Russian Platform.

The recently discussed assemblage of ammonites from the Platynota Zone of the Holy Cross Mts., central Poland, by Wierzbowski (2020, p. 226–228, pl. 4, pl. 5: 1), as based on the collection of Kutek (1968, pls. 8: 3, 9), includes large specimens attaining well above 250–300 mm in final diameter, showing strongly evolute coiling, and distant ribbing whose character changes markedly during ontogeny: the ribbing of the inner whorls is composed of strongly prorsiradiate primaries, becoming shorter and swollen on the middle whorls (from about 120 mm to 150 mm diameter) with secondary ribs attaining 3–4 per one primary, and then successively replaced by sparsely placed cuneiform single ribs on the outer whorl. The two species distinguished in the Platynota Zone of central Poland include *Pictonia* (*Pomerania*) *dohmi* (Arkell), closely comparable with its holotype – "*Pictonia baylei*" of Dohm (1925, pl. 5: 6) from Czarnogłowy (Zarnglaff) quarry, being the type species of *Pomerania*, and *P.* (*Pomerania*) *albinea* (Oppel). These two species show the phylogenetically advanced development of the ornamentation within the subgenus *Pomerania* as revealed in the occurrence of more swollen primary ribs on the middle whorls resembling the ornamentation of later *Pachypictonia*.

Summarizing, beside the overall affinities between *Pomerania* and *Pictonites*, the main difference is in the larger final size and in the occurrence of bold coarse single, straight or wedge-shaped ribs on the body chamber in the former, not developed in *Pictonites*. Moreover, *Pictonites* occurs mostly in older deposits (Planula Zone) than *Pomerania*, which is known especially from the Platynota Zone. Thus, the general statement may be given that "after the dominance of *Pictonites* forms, the appearance of successively larger, and attaining later maturity macroconchs of the *Pomerania* type has been attained" (Wierzbowski, 2020, p. 234). This indicates that the name *Pictonites* Mesezhnikov, 1969 must not be treated a younger synonym of *Pomerania* Arkell, 1937, as the two names correspond to morphs somewhat different in final growth which attained their maturity at different times, and could be treated as representing separate subgenera.

It should be remembered, however, that a single species – *Pictonia constricta* Schneid referred previously to the subgenus *Pictonites* (Wierzbowski, 2017a; Wierzbowski, Głowniak, 2018) ranges somewhat higher in the Submediterranean succession up to the basal part of the Hypselocyclum Zone. This form differs, however, from *P. perisphinctoides*, the type species of the subgenus, in its much shorter primary ribs, which are more strongly accentuated, and commonly separated from the secondaries by a smooth spiral band, especially well seen in the type specimens of the species, and a very close, possibly conspecific, *P. tereticornis* (see Schneid, 1940, pl. 14: 1–4). These features, as well as a tendency of the secondary ribs to disappear at larger diameters are not recognized in older *Pictonites*, but resemble somewhat younger *Pachypictonia* or even *Rasenia* (see Wierzbowski, 2017a, p. 42, pl. 9: 1a, b; see also Kutek, 1968, pl. 1 : 3; Wierzbowski, Głowniak, 2018, fig. 6 ; see also the comment by Wierzbowski, 2020). This suggests a possible direct evolutionary transition between forms similar to *Pictonites* and *Pachypictonia*–*Rasenia* which could represent a local side-branch in the discussed lineage developed due to the peripatric speciation.

Genus *Rasenia*:
subgenus *Pachypictonia* Schneid, 1940

The ammonites of the subgenus *Pachypictonia* originally distinguished on the basis of *Pachypictonia indicatoria* Schneid (see Schneid, 1940, pl. 8: 1–3) differ from those of the *Pictonites*–*Pomerania* type in their having markedly shorter and swollen primary ribs in the inner whorls, resembling the Subboreal subgenus *Rasenia*. They show, moreover large sizes (about 200–400 mm in diameter as stated in Polish specimens), and reveal the development of a special ornamentation on the outer whorl consisting of extremely heavy cuneiform ribs. They were described from southern Germany above all by Schneid (1940) from the northern Frankonian Alb, and Jura Mts of the northern Switzerland by Gygi (2003), but also from central Poland by Kutek (1968), and were recently discussed by Wierzbowski (2020). The Polish specimens came from the shallow-water carbonate deposits of the south-western margin of the Holy Cross Mts. and adjoining areas, especially from the upper part of the Platynota Zone, and the lowermost Hypselocyclum Zone (see Kutek, 1968, pl. 10; Wierzbowski, Głowniak, 2018, fig. 5C, D; Wierzbowski, 2020, pls. 5: 2; 7: 1, 2), and represent the following "German" species: *Rasenia* (*Pachypictonia*) *peltata* (Schneid), *R.* (*Pachypictonia*) cf. *perornatula* (Schneid), *R.* (*Pachypictonia) balteata* (Schneid). Additionally, the described herein specimens (Pl. 6: 1) of *R.* (*P.*) *perornatula* Schneid and other forms of *Pachypictonia* coming from the north-eastern margin of the Holy Cross Mts. (Gutowski, 1992, pl. 5: 5; 1998, pl. 2: 2) belong to the same assemblage. It should be remembered that *Pachypictonia* (*P. peltata*) was described also from an upper part of the Baylei and possibly a lower part of the Subboreal Cymodoce zones of the Russian Platform (see Głowniak *et al.*, 2010, p. 25, pl. 7: 1), showing thus a wide distribution of the *Pachypictonia* ammonites in the NE European part of the Subboreal Province.

A very large specimen (Pl. 7) of 330 mm in diameter consisting entirely of the phragmocone has been newly discovered in the Małogoszcz quarry, south-western margin of the Holy Cross Mts., central Poland, at the top of the Hypselocyclum Zone – base of the Divisum zones of the Submediterranean succession, thus in younger deposits than the specimens of *Pachypictonia* discussed above. It shows evolute coiling (at 230 mm diameter, the whorl-height is 35%, and the umbilical diameter is 44% of the specimen diameter, whereas at 310 mm diameter the relevant values are 29%, and 47%, respectively). The sparsely placed bullate primaries (about 20 per whorl in the inner whorls, and 16 on the the outer whorl) split low on the whorl-height into 3–4 secondaries. The roots of the secondaries are seen in the umbilicus, not being covered by younger whorls. The secondary ribs are poorly visible on the outer whorl of the specimen, and successively disappear, and the last fragment of whorl (not illustrated) shows a few sparsely placed single cuneiform ribs. Although the discussed specimen undoubtedly belongs to the subgenus *Pachypictonia*, as shown by its size, and the development of ornamentation, its close comparison with the species described so far is difficult. It resembles *Rasenia* (*Pachypictonia*) *indicatoria* (Schneid) (see Schneid, 1940, pl. 8: 1–3; see also Gygi, 2003, fig. 138) which shows, however, a much earlier disappearance of the secondary ribs, and an earlier appearance of the cuneiform single ribs, representing the final type of ornamentation. The general difference is thus in the much larger size of the discussed specimen of *Pachypictonia* referred herein to as *R.* (*P.*) aff. *indicatoria* (Schneid), which could attain even about 400 mm in diameter, being one of the largest specimens of the subgenus described so far. This very interesting specimen shows also some similarity to the late, very coarsely ribbed, and strongly evolute Subboreal ammonites of the subgenus *Rasenia*, especially *Rasenia* (*Rasenia*) *evoluta* Spath. The typical representatives of *R. evoluta* are, however, markedly smaller in size (maximally about 250 mm), showing moreover the disappearance of the ribbing at fairly small diameters, usually between 110–130 mm, and the following smooth outer whorls corresponding to the end of phragmocone and the body-chamber, sometimes revealing thereafter the re-appearance of the sculpture consisting of blunt, mostly single ribs (see Birkelund *et al.*, 1978, 1983; Birkelund, Callomon, 1985).

Although the *Pachypictonia* ammonites occurred commonly in the NE European part of the Subboreal Province, and adjoining parts of the Submediterranean Province in Central Europe, they occasionally appeared also in other areas marking there a short expansion of their geographical range. Such is the case of the occurrence of a form referred to as "? *Pachypictonia* sp.nov.C" (Birkelund, Callomon, 1985, p. 40–42, pl. 14: 5, 6; 15: 1; 16: 1) from the lower part of the Subboreal Cymodoce Zone in East Greenland. This form resembles *Rasenia* (*Pachypictonia*) *dorsata* (Schneid) and/or *R.* (*P.*) *divergens* (Schneid) from southern Germany (Birkelund, Callomon, 1985; *cf.* Geyer, 1961) although it is markedly more evolute. Also worth noting is that at the same time the Subboreal ammonite *Rasenia* of the main NW European aulacostephanid lineage has expanded temporarily its range into the adjoining Submediterranean European and Boreal Arctic areas (*e.g.*, Hantzpergue, 1979, 1995; Wierzbowski, 1989, 2020; also Pl. 2: 6).

The microconchs corresponding to the macroconchs discussed are generally poorly recognized and were not discussed in detail in relation to their possible microconch counterparts; some suggestion on their affinity with *Prorasenia stephanoides* (Oppel) was given by Birkelund and Callomon (1985, p.40–42) when discussing the occurrence of the forms similar to *Pachypictonia* in the lower Cymodoce Zone of East Greenland.

The development from *Pomerania* to *Pachypictonia* macroconchs was continuous, without any discernible breaks in morphology, as these forms co-occur stratigraphically replacing each other from the Submediterranean middle to upper Platynota Zone to the lowermost Hypselocyclum Zone. This development is especially well-marked in the material studied from the Holy Cross Mts., central Poland where the late species of *Pomerania*, like *Pictonia* (*Pomerania*) *dohmi* and *P.* (*P.*) *albinea* show the presence of bullate, rasenoid ribs on the middle whorls (Wierzbowski, 2020). Such a smooth evolutionary transition resembles that from *Pictonia* (*Pictonia*) to *Rasenia* (*Rasenia*) in the main lineage of the Aulacostephanidae in NW European areas (*cf.* Birkelund, Callomon, 1985). The large-sized representatives such as *Pictonia* (*Pomerania*) and *Rasenia* (*Pachypictonia*) represent forms modified by heterochrony – possibly by the prolongation in the duration of shell growth as controlled by the unstable environmental conditions of the extremely shallow-water environment of the carbonate platforms (Wierzbowski, 2020).

LINEAGE *VIELUNIA – EURASENIA/INVOLUTICERAS* AND MICROCONCH COUNTERPARTS

The lineage evolved in the NE European Subboreal Province and adjoining areas of the Submediterranean Province during the Early Kimmeridgian, and produced quite different forms than those which originated that time in the NW European Subboreal areas. The differences in development of the aulacostephanid ammonite faunas between the two areas was related to the allopatric speciation which resulted from geographical isolation by the emergence of separating land-barriers (Enay, 1980; Wierzbowski, 2010; Wierzbowski *et al.*, 2016).

Genus *Vielunia* Wierzbowski et Głowniak, 2010, and its microconch counterpart (some *Prorasenia* Schindewolf, 1925)

The older macroconchs show some similarity to representatives of *Ringsteadia* from which they evolved at the boundary between the Submediterranean Hypselum and the Bimammatum zones, and the corresponding Subboreal Pseudocordata and Baylei zone boundary. They were in the past commonly confused with the genus *Ringsteadia* (*e.g.*, Wierzbowski, 1970, 1978; Matyja, Wierzbowski, 1997) from which they differ, however, in the stronger development of the secondary ribs – already at smaller diameters, their appearance lower on the whorl side (and in consequence the development of shorter primaries), and their persistence up to larger diameters. These were the reasons they were recognized as belonging to the separate genus *Vielunia* (see Wierzbowski *et al*., 2010). Additionally the microconch counterpart of *Vielunia* is *Prorasenia*, and not *Microbiplices* which is the microconch of the older *Ringsteadia.* It should be mentioned that according to Enay and Howarth (2019) *Vielunia* has been treated as the junior synonym of *Ringsteadia*, but as discussed recently (Wierzbowski, 2020, p. 225) such an opinion "seems inappropriate both from phylogenetic as well as from stratigraphic points of view".

The type species of the genus is *Vielunia dzalosinensis* Wierzbowski et Głowniak while the microconch counterpart is *Prorasenia crenata* (Quenstedt) – both occurring in the Bimammatum Zone and the lowermost Planula Zone in the Wieluń Upland, central Poland (Wierzbowski *et al.*, 2010, p. 70–72, pl. 8: 2; pl. 9: 1–4; pl. 10: 1–5; and the synonymy given therein). The same assemblage was recognized later in northern Poland: in the quarries at Barcin in the Kujawy area (Pl. 6: 2, 3), but also in the Peri-Baltic Syneclise in boreholes (Wierzbowski *et al.*, 2015, fig. 9: d, e, i). The species *V. dzalosinensis* shows well-marked constrictions bordered in front by stronger ribs of the flared type. The primary ribs are markedly prorsiradiate, whereas the secondaries, appearing fairly low on the whorl height, reveal a markedly rectiradiate course already on the inner whorls. The coiling is in the innermost whorls evolute, but soon becomes moderately involute, rarely more involute (the coiling index expressed as whorl height/umbilical diameter ratio ranges usually from 1.1 to 1.7, rarely may attain 2.0–2.2 – see Wierzbowski *et al.*, 2010).

A closely related species is *Vielunia limosa* (Quenstedt) represented by specimens up to about 150 mm in diameter (Quenstedt, 1888, pl. 124: 3; see also Pl. 8: 1, 3; see also Wierzbowski, 2017 a, pl. 9: 5) from the Hauffianum Subzone of the Bimammatum Zone of southern Germany (G. Schweigert, pers. inf.) and the Planula Zone of central Poland. To that very species belong possibly also larger specimens, similar in the middle whorls to *V. limosa.* These reaveal sparsely placed swollen primary ribs, and a smooth outer part of the last whorl at 200–300 mm diameter, like "*Ringsteadia*" cf. *limosa* described by Wierzbowski (1970, pl. 4: 3, pl. 5: 1) from the Planula Zone of the Wieluń Upland, and the close "*Ringsteadia pseudocordata*" of Dohm (1925, pl. 1: 8, 9) from Czarnogłowy quarry.

Forms which are younger stratigraphically, known mostly from the upper part of the Planula Zone and lower to middle parts of the Platynota Zone in southern Germany and Poland, show even stronger secondary ribs (and because of that were compared in the past with *Eurasenia*, see Geyer, 1961), but they still retain elongated primaries of the *Vielunia* type. These include: *Vielunia gothiciformis* (Schneid) (see Schneid, 1939, pl. 9: 12; also Wierzbowski, 2017a, pl. 10: 1, 2, and earlier illustrations from the author's paper cited therein), and *Vielunia conspicua* (Schneid) [possibly also including very similar forms like *Vielunia eucostulata* (Schneid) and *V. sublimosa* (Schneid) (see Schneid, 1939, pl. 10: 1–5), all of them treated as representing a single species by Geyer (1961, p. 97)]. Such is a fragmentarily preserved specimen, showing fairly densely ribbed inner whorls and more loosely placed ribbing with strongly developed secondaries on the body-chamber, referred herein to as *Vielunia* cf. *conspicua* (Schneid), and coming from the uppermost Planula Zone of the Wieluń Upland (Pl. 8: 2). A similar specimen has been found in the collection of A. Czekalska from Czarnogłowy (Pl. 10: 1). Another akin form is heavily ribbed *V. tenuiplexa* (Quenstedt). It was described both from southern Germany and Poland: in the SW margin of the Holy Cross Mts. by Kutek (1968, pl. 9; see also Wierzbowski, 2020, p. 167), and from the lowermost Platynota Zone of the Wieluń Upland (Wierzbowski, 1970, pl. 6; see also Wierzbowski, 2017a, 2020). Similar specimens referred to as *"Ringsteadia marstonensis"* were also described by Dohm (1925, pl. 2: 5, 6) and Wilczyński (1962, pls. 1, 2) from Czarnogłowy quarry in Western Pomerania.

One of the youngest forms comparable morphologically with the subgenus *Vielunia* is *Vielunia attenuata* (Schneid) ranging stratigraphically as high as the lower Hypselocyclum Zone in southern Germany (Schneid, 1940, p. 106, pl. 14: 6) and central Poland (Wierzbowski, Głowniak, 2018, fig. 7). This species was known initially from incomplete specimens, representing parts of the phragmocone, about 140–150 mm in diameter, but a very complete specimen has been discovered recently in the old collection of Dunin (1972) from Pradła, in southern part of the Częstochowa Upland, central Poland. The specimen (Pl. 9) comes from the Platynota Zone, possibly from a stratigraphical interval at the boundary between its lower part (Polygyratus Subzone), and the middle part (Desmoides Subzone). It is about 380 mm in diameter with the final peristome preserved and consists of the phragmocone up to 310 mm diameter and the body-chamber a half of whorl long. The ribbing is represented by elongated primaries (about 22 per whorl at 120 mm diameter) which gradually disappear being preserved only at the umbilicus up to about 220 mm in diameter: the outer whorl is smooth but with a few wide folds. The species although revealing elongated primary ribs in the inner and middle whorls typical of the genus *Vielunia* shows marked similarity in coiling and density of ribbing to large specimens of the genus *Eurasenia*, such as *Eurasenia gothica* (Schneid). The latter (see *e.g.*, Schneid, 1939, pl. 15: 2) differs, however, mostly in the presence of shorter primary ribs, and a more involute coiling at larger diameter (see Geyer, 1961, p. 97–98).

All these forms which are younger stratigraphically, like *V. conspicua*, *V. gothiciformis* and *V. attenuata*, represent late members of the genus *Vielunia*, remaining close in morphology to the younger genus *Eurasenia* with whom have been often compared in the past (*e.g.*, Geyer, 1961), and thus they can be treated as the direct forerunners of that genus (see Wierzbowski, 2017a, p. 80–81).

There exists, however, another branch of the *Vielunia* lineage represented by strongly involute forms, often referred to as "*Ringsteadia*" *flexuoides* (Quenstedt) in the past (see Wierzbowski, 1970) and the closely related *V. caliginosa* (see Wierzbowski *et al.*, 2016). These specimens show the very involute coiling of the inner and middle whorls (the coiling index is commonly attaining 1.60–1.95), changing to less involute coiling of the outer whorl, and rather dense ribbing. Although the type specimen of the species *V. flexuoides* as well as other specimens of that species come from the Bimammatum Subzone of southern Germany (see Jantschke, 2014; see also Pl. 10: 3), very similar specimens have been found in the Planula Zone of the Wieluń Upland, central Poland (Wierzbowski, 1970, pl. 1: 1–3; pl. 2: 1, 2; Wiśniewska-Żelichowska, 1971, pl. 23–25; 26: 1; see Wierzbowski, 2017a, p. 80; see also Pl. 10: 2, 5). This strongly involute species shows markedly developed secondary ribs, appearing fairly low on the whorl sides and continuously preserved even to larger diameters, but the late forms of *V. flexuoides* from the Planula Zone differ, however, from the older ones from the Bimammatum Zone in having a weaker development of the constrictions (Wierzbowski, 1970). A very large specimen, closely related to the species discussed, was described as "*Ringsteadia* cf. *submediterranea*" by Gygi (2003, fig. 27, 28) from northern Switzerland. It is about 205 mm in diameter, representing mostly phragmocone (up to about 180 mm diameter) and a fragment of the body-chamber, but its character of coiling and the type of ribbing are very close to *V. flexuoides*. The general character of coiling and density of ribbing of all the discussed specimens of *Vielunia* resemble very much those of the younger genus *Involuticeras*, especially its more densely ribbed representatives like *I. limbata* (Schneid). The main differences lie in the still more dense ribbing, longer primary ribs and somewhat less involute coiling of the *Vielunia* specimens (*cf.* Geyer, 1961, p. 105; see also Wierzbowski, 2020, p. 225).

The microconchs of the genus *Prorasenia* being the counterparts of the genus *Vielunia* include *Prorasenia crenata* (Quenstedt) as mentioned above, and the co-occurring *Prorasenia bathyschista* Koerner in the Planula Zone, and the still younger *Prorasenia quenstedti* Schindewolf in the Platynota – Hypselocyclum zones (see Wierzbowski, 2017a; *cf*. also Geyer, 1961; Koerner, 1963; Wierzbowski, 1978).

The ammonites of the genus *Vielunia* discussed here are absent in the NW European part of the Subboreal Province, where their coeval counterparts are representatives of *Pictonia* (*Pictonia*). Athough these two genera show many features in common, such as the presence of well-marked constrictions bordered in front by strong ribs of the flared type (well developed in *Pictonia* and older representatives of *Vielunia*), bold ribbing, especially on the middle whorls, and a similar type of microconch, they are generally quite distinct in the type of coiling of the shell, being more involute in *Vielunia*, and strongly evolute in *Pictonia*. The ammonites of the genus *Vielunia* are closer in their type of coiling to older *Ringsteadia*, and possibly represent a "less modified" segment of the lineage coming off *Ringsteadia*, than representatives of *Piconia* strongly changed by heterochrony, and, thus have been called also "the involute analogues of true *Pictonia"* (Wierzbowski, 1994). Nevertheless, even within true assemblages of *Pictonia* are encountered rare forms, such as that described as "*Pictonia* sp indet. B" by Birkelund and Callomon (1985, p. 32, pl. 11: 4) from East Grenland, which shows a large similarity, both in type of the ribbing and character of coiling to *Vielunia*, and which represents either a rare *Vielunia*-type migrant from NE-European Subboreal areas or "merely an extreme variant" of the diversified *Pictonia* assemblage.

Summarizing, the genus *Vielunia* may be treated as a direct descendant of the genus *Ringsteadia* in the SE European part of the Subboreal Province and adjoining areas of the Submediterranean Province in Central Europe, which still preserves some features of the latest forerunners *(cf.* Wierzbowski *et al*., 2016; Wierzbowski, 2017a, b), such as *R. evoluta – R. marstonensis* (in relation to the more evolute representatives of *Vielunia*) and *R. frequens* (in relation to its more involute forms). The transition between *Ringsteadia* and *Vielunia* was rather gradual, although with some acceleration in the development of ornamentation which brought more heavy ribbing in younger forms towards smaller diameters.

Genera *Eurasenia* Geyer, 1961, and *Involuticeras* Salfeld, 1917, and the corresponding microconchs *(Prorasenia*)

Both these genera are closely related, the former generally less involute than the latter, both show the characteristic short swollen primary ribs, and numerous secondaries. The lateral transition between them is also gradual – the most involute forms of the genus *Eurasenia*, which the type species is *Eurasenia rolandi* (Oppel), bear some resemblance to those of the genus *Involuticeras* (Geyer, 1961, p. 92), of which the type species is *Involuticeras involutum* (Quenstedt). Moreover, the appearance of the two genera is nearly coeval, when one takes into account the revision of the taxonomical position of some early forms attributed in the past to the genus *Eurasenia* like *e.g.* "*Eurasenia*" *conspicua* (Schneid) which are closer to late *Vielunia* than to *Eurasenia*: it appears then that both *Eurasenia* and *Involuticeras* are commonly represented in the coeval, well-dated deposits in central Poland (Wieluń Upland and adjoining areas, south-western margin of the Holy Cross Mts.) beginning from some upper parts of the Platynota Zone and the lowermost part of the Hypselocyclum Zone (Kutek, 1968; Wierzbowski, 2017a, 2020; Wierzbowski, Głowniak, 2018). The assemblage of ammonites includes here: *Eurasenia vernacula* (Schneid), *E. rolandi* (Oppel), *E. trimera* (Oppel), *Involuticeras involutum (*Quenstedt), *I. crassicostatum* (Geyer) and *I. limbatum* (Schneid). The common microconch is *Prorasenia*. A similar assemblage of ammonites of the genus *Eurasenia* corresponding to the Hypselocyclum Zone comes also from the north-eastern margin of the Holy Cross Mts., central Poland: it includes two specimens from the environs of Iłża described by Dąbrowska (1983, pls. I, II) as *Eurasenia gothica* (Schneid) and *E. engeli* (Geyer) [the latter possibly being, however, closer to *E. rolandi* (Oppel)], and some additional specimens (Pl. 11: 1; Pl. 12) coming from Wierzbica quarry and corresponding to *Eurasenia vernacula* (Schneid) and *E. trimera* (Oppel) [this latter is an especially large specimen attaining about 220 mm in diameter and still representing the phragmocone, being thus possibly the largest of that species as reported so far].

The new collection of ammonites coming from the uppermost Hypselocyclum Zone and the Divisum Zone in Małogoszcz quarry at the south-western margin of the Holy Cross Mts., central Poland, includes: *Eurasenia rolandi* (Oppel) (Pl. 10: 4), *E. trimera* (Oppel) (Pl. 11: 4, 5) and *E. pendula* (Schneid) (Pl. 11: 2, 3) [this latter finding is additionally commented on below], as well as *Involuticeras involutum* (Quenstedt) (Pl. 14: 2). The microconch counterparts here are ammonites of the genus *Prorasenia*, from some more densely ribbed forms similar to *Prorasenia quenstedti* Schindewolf, to forms less densely ribbed and having coronate whorl sections forms like *Prorasenia witteana* (Oppel) and *Prorasenia stephanoides* (Oppel) (*cf.* Wierzbowski, 1978, p. 321).

Whereas deposits of the more open marine environment and those representing the outer part of the shallow-water carbonate platform of the south-western margin of the Holy Cross Mts., central Poland, show the presence of both *Eurasenia* and *Involuticeras* (see Wierzbowski, 2017a, 2020), the areas of the north-eastern margin of the Holy Cross Mts, representing the inner parts of the shallow-water carbonate platform, have yielded so far only ammonites of the genus *Eurasenia* (see Gutowski, 1992, 1998). The last occurrences of *Involuticeras* in the south-western margin of the Holy Cross Mts. are, moreover, characterized by the presence of especially large sized specimens: like *I. limbatum* (Schneid) attaining about 250 mm in final diameter (Wierzbowski, 2020, pl. 9), or even much larger specimen belonging possibly to the same species (Pl. 13) whose phragmocone is preserved to about 400 mm in diameter. This suggests the distribution of the two groups of ammonites was controlled to some degree by the environmental conditions.

The microconch counterparts are represented by three groups of species: (1) showing evolute coiling, rather dense ribbing with the secondary/primary ribs ratio ranging about 3.0 at the inner whorls, an oval whorl section, and an early onset of biplicate ribs – like *Prorasenia quenstedti*; (2) showing evolute coiling, rather distant and sharp ribbing with the secondary/primary ribs ratio ranging about 3.0–4.0, a coronate whorl section, and the later appearance of biplicate ribs – like *Prorasenia stephanoides*; (3) showing weakly involute coiling, and rather dense ribbing with the secondary/primary ribs ratio between 3.0–4.0 at the inner whorls, and a high-oval whorl section – like *Prorasenia paralepida* (Schneid). They represent possibly the distinct phyletic lineages corresponding to weaker and stronger ornamented macroconchs of *Eurasenia* (groups 1–2; see Wierzbowski, 1978), and *Involuticeras* (group 3), and derived from older, weaker and more strongly ornamented *Vielunia*.

It should be remembered that *Prorasenia paralepida* (Schneid) was treated by Geyer (1961, pl. 5: 10; 8: 4) as belonging to the genus *Rasenioides* who placed in its synonymy two specimens interpreted by Schindewolf (1926, pl. 19: 4, 5) as being close to his *R. transitorius.* This species occupied somewhat isolated position in that genus, however (Geyer, 1961), differing from typical species of *Rasenioides* in its smaller number of secondary ribs and a less involute coiling (see also discussion herein at the description of that genus). These features resulted in interpretation of the species discussed as belonging to *Prorasenia* by Schairer (1969) who reported its occurrence from the middle part of the Platynota Zone. The detailed stratigraphical position of *Prorasenia paralepida* was additionally given recently by Gygi (2003, fig. 158a, b) from northern Switzerland, and Wierzbowski (2017a, pl. 10: 10) from central Poland, as corresponding to a fairly narrow interval between the lower part (Hippolytense Subzone) and the upper part (Lothari Subzone) of the Hypselocyclum Zone.

The genera *Eurasenia* and *Involuticeras* commonly occur in the NE European Subboreal and adjoining Submediterranean areas of Europe – in Germany, France, Switzerland, Czech Republic, Poland, and southern Russia (*e.g.*, Schneid, 1939; Geyer, 1961; Kutek, 1968; Gygi, 2003;

Hrbek, 2014; Rogov *et al.*, 2017; Wierzbowski, 2017a, 2020, and earlier papers cited therein). This suggests that both genera evolved simultaneously and gradually emerged from the two branches of *Vielunia* (discussed above). Consequently their lower boundaries do not represent markedly discernible breaks in morphology in the smoothly evolving lineage – from the evolute to weakly involute *Vielunia* mostly to *Eurasenia*, and from the involute *Vielunia* to *Involuticeras*. Although Enay and Howarth (2019) treated *Involuticeras* and *Eurasenia* as subgenera of the widely treated genus *Involuticeras*, they are interpreted herein as independent genera, according to the traditionally accepted older classifications.

The general development of *Eurasenia–Involuticeras*, and their microconch counterparts (*Prorasenia*), similarly as that of the preceding *Vielunia–Prorasenia*, was thus continuous, without any marked breaks in morphology. The only discernible feature in evolution of macroconchs of the former group is their faster rate of growth, as shown by acceleration in the development of ornamentation.

Also the decline of both genera was approximately coeval and took part at the end of the Early Kimmeridgian, in the uppermost Hypselocyclum Zone and the Divisum Zone corresponding to the Askepta Subzone, correlated also with the upper part of the Cymodoce Zone (Matyja, Wierzbowski, 2000a). In detail, however, the final ranges of the genera differ somewhat between the particular areas which seem to be related to the character of the sedimentary environment; sometimes representatives of the genus *Eurasenia* range higher stratigraphically, like in Aquitaine or in the environs of Ajoie of the Jura Mts. (see Hantzpergue, 1989, 1995; Comment *et al.*, 2015), but in other areas the predominant last occurrences are of the genus *Involuticeras* as recognized in northern Poland and in Tatarstan of central European Russia (Matyja, Wierzbowski, 1998, 2000a; Rogov *et al.*, 2017). In a similar stratigraphical position is observed the sudden appearance of numerous ammonites of the genus *Rasenioides*, gradually followed phylogenetically by *Aulacostephanoides*, representing already another aulacostephanid lineage, recognized over large areas of Europe (see below; also *e.g.*, Birkelund *et al.*, 1983; Matyja, Wierzbowski, 2000a).

The rasenoid ammonites described above as *Eurasenia pendula* (Schneid) from Małogoszcz quarry at the southwestern margin of the Holy Cross Mts., central Poland, are of some importance for the younger phylogeny of *Eurasenia* and need additional comments. The ammonites (Pl. 11: 2, 3), 74–82 mm in diameter, represent the phragmocone (one of them additionally with the initial part of the body chamber): they are weakly involute (whorl height and umbilical diameter correspond to 34.5–39.0% and 30–34% of the specimen diameter, respectively), and show projected ribbing consisting of rather sparsely placed and short primaries (number of primaries is about 18–20 per whorl) which split markedly below a half of the whorl height into 3–4 long secondaries (the secondary/primary ribs ratio is changing from about 3.8–4.0 in more inner parts of the phragmocone, up to about 3.2 at its end). These specimens are closely comparable with the holotype of *Eurasenia pendula* (Schneid) (see Schneid, 1939, p. 163, pl. 13: 9; Geyer, 1961, p. 96, pl. 9: 7). Although placed in the genus *Eurasenia*, this species differs markedly in its weakly involute coiling from the strongly involute, most typical representatives of the genus, grouped around *E. rolandi – E. vernacula* (see Geyer, 1961, fig. 127). The stratigraphical range of *E. pendula* is not so far precisely recognized. According to Geyer (1961) it ranges from the Hypselocyclum Zone possibly to the Divisum Zone, although the holotype comes even from the Platynota Zone (Schneid, 1939). The specimens discussed herein have been collected in a stratigraphical interval near the boundary between the Hypselocyclum Zone and the Divisum Zone, being thus very close to the latest stratigraphical occurrences of *Eurasenia*, and similar in stratigraphical position to *Eurasenia aulnisa* Hantzpergue and *E. manicata* (Schneid) of Aquitaine (Hantzpergue, 1989, p. 259–270, pls. 31–33). It is worth noting that *E. manicata* whose holotype comes from southern Germany (Schneid, 1939, p. 152, pl. 10: 3) has been recognized earlier (Geyer, 1961) as a younger synonym of *E. pendula*. According to Hantzpergue (1989, p. 266) the range of the species *E. pendula* as interpreted by some authors needs, however, revision [*e.g.*, specimen referred to that species by Schairer (1969, pl. 1: 1) is undoubtedly a representative of *Rasenia* (see Hantzpergue, 1989, p. 249), as is that illustrated by Kutek (1968, pl. 11) – (see Wierzbowski, 2020, p. 232, pl. 6: 1)]. On the other hand, it seems highly probable that the "true" *Eurasenia pendula*, as well as *E. aulnisa* and *E. manicata*, are closely related. This is confirmed by the similar ornamentation of the specimens, including a decrease in the number of secondary ribs with growing diameter, which results even in the appearance of biplicate ribs at larger sizes. These species [as well as *E. trifurcata* (Reinecke) which also shows weakly involute to weakly evolute coiling, but differs from *E. pendula* in a more coarse ribbing] could belong to a special branch of *Eurasenia* leading to *Pararasenia* (see also comments below in the chapter on evolutionary turnovers).

LINEAGE *VINETA–BALTICERAS–RASENIOIDES* AND MICROCONCH COUNTERPARTS

This lineage, in a similar manner to that of *Vielunia–Eurasenia–Involuticeras*, developed during the Early Kimmeridgian due to the allopatric speciation of aulacostephanids in the NE European Subboreal Province and adjoining part of the Submediterranean Province, when being geographically isolated from those of the NW Subboreal Province (see Wierzbowski *et al.*, 2016, and other papers cited therein). The two lineages independently developed here, possibly as the result of the sympatric speciation of corresponding groups of ammonites which showed different environmental preferences. The ammonites of the *Vineta–Balticeras–Rasenioides* lineage explored possibly a more open marine, nectonic, environment, as shown by their wide geographical distribution and occurrence in various deposits, *e.g.* the occurrence of *Vineta* in dark clays in the northern part of the Russian Platform and in limestones in the Polish Jura, southern Germany (Swabian Alb and Franconian Alb), and the Jura Mts. in Switzerland; such a mode of life could explained also the phenomenon of the sudden distribution of *Rasenioides* over wide areas of Europe as the consequence of a marked sea-level rise at the end of the Early Kimmeridgian (*cf.* Hantzpergue, 1995; Matyja, Wierzbowski, 2000a).

Genus *Vineta* Dohm, 1925
(macro- and microconchs)

Macroconchs are involute to strongly involute, initially covered with rather loosely spaced bi- and trifurcate ribs, but these are soon thereafter replaced by dense biplicate ribs with some intercalaries, consisting commonly of markedly prorsiradiate primaries and rectiradiate secondaries which are rather short and persist up to at least about 40–60 mm diameter. At larger diameters the ribs become bi- and trifurcate with common intercalatories, but gradually the primaries tend to disappear, being preserved only at the umbilicus, whereas the secondaries become stronger and more numerous. Such a development of ribbing is recognized in the smaller to medium-sized specimens, such as those of *Vineta streichensis* (Oppel) described by Schweigert and Callomon (1997, p. 24 , pl. 7: 5–9, 11; see also older references given in synonymy) and the medium to larger-sized specimens of *Vineta submediterranea* (Wierzbowski) by Wierzbowski *et al.* (2010, pl. 7, p. 68–69; see also older references given in synonymy; Pl. 14: 1, 5), from the Bimammatum Zone, and the Planula Zone of southern Germany and central Poland. Similar type of ribbing shows also a specimen of *Vineta* referred to as *Ringsteadia* (? *Ringsteadia*) sp. by Wierzbowski (1970, pl. 5: 2) from the Planula Zone of central Poland, which represents an incomplete phragmocone 110 mm in diameter. All these specimens differ markedly in type of ribbing from the involute representatives of the genus *Vielunia*, such as *V. flexuoides* (Quenstedt) encountered in the same beds with which they have been sometimes misinterpreted.

The younger species of *Vineta* known from the upper part of the Planula Zone and the lower part of the Platynota Zone of the same areas, show some differences in the development of the ribbing when compared with the older ones. The specimens of *Vineta striatula* (Schneid), up to about 70–90 mm in diameter, reveal the inner whorls (up to about 40 mm diameter) covered with dense and fairly irregular, bi- and triplicate ribs with some additional intercalatory ribs at the ventral side; a smooth spiral band appearing at a larger diameters separates the primary ribs (preserved in the umbilical area) from the well developed numerous secondaries, although some of the primary ribs retain their original continuity [Schneid, 1939, pl. 16: 5; Geyer, 1961, pl. 22: 1; Wierzbowski, 2017a, pl. 10: 7; it is worth noting that late form of *V. submediterranea* from the Planula Zone (Pl. 14: 5) reveals also some protruding primary ribs observed in the body chamber]. Such a type of ornamentation is shown here in a fragmentarily preserved specimen (Pl. 14: 3) referred to as *V.* cf. *striatula* revealing the densely placed ribs in the last part of phragmocone, and the contrasting ornamentation of the body chamber: somewhat swollen primary ribs seen only at the umbilicus and numerous secondary ribs in the ventrolateral area, separated by a smooth spiral band. Another younger species is *Vineta weinlandi* (Ficher) represented by the larger specimens as shown by its wholly septate holotype 148 mm in diameter (Fischer, 1913, pl. 5: 15; Geyer, 1961, pl. 22: 5), and the specimen showing the phragmocone up to 134 mm diameter with an initial part of the body chamber preserved (Gygi, 2003, fig. 144). The development of ornamentation reveals here the markedly reduced number of the primary ribs, and their rather early disappearance at the middle of the whorl side (from about 80 mm diameter; see Geyer, 1961, pl. 22: 6). Both the discussed younger species of *Vineta* show the deep umbilicus with a fairly steep umbilical wall, and the narrow ventral side of whorls which result in somewhat oxycone character of their whorl section,

The outer whorls of *Vineta* macroconchs become smooth, and some specimens attained giant sizes, even up to about 400 mm in maximum diameter. In that case the ornamentation of the inner whorls is poorly visible. Such large specimens attributed to that genus include several “species” whose relation to those described above is not clear: *Vineta jaekeli* Dohm, recognized as the type of the genus from Czarnogłowy (Zarnglaff) quarry in Western Pomerania, with its lectotype illustrated by Dohm (1925, pl. 4: 4), and a very close specimen described from the Wieluń Upland (Wierzbowski *et al.*, 2010, pl. 8: 1); similar large specimens were described as “*Ammonites vicarius”* by Moesch (1867, pl. 2: 1a, b) and as “*Ringsteadia” magna* by Gygi (2003, figs. 31–33) from the Jura Mts. of northern Switzerland; also as “*Ammonites*” *laevigyratus* of Quenstedt (1888, p. 995, pl. 111: 4, 5;

see also Geyer, 1961, p. 128) from the Swabian Alb of southern Germany; such was possibly also a fragmentarily preserved "*Ammonites*" *cuneatus* of Trautschold (1861, pl. 8: 2a–c) from the Russian Platform (see also the large form referred to as *Vineta jaeckeli* described from this area by Głowniak *et al.*, 2010, pl. 5: 13; pl. 8: 2a, b). All these specimens are known from the Bimammatum Zone (Bimammatum and Hauffianum subzones) to the Planula Zone (and possibly lower Platynota Zone) of the Submediterranean subdivision, and their stratigraphical equivalents.

The microconchs described so far are fairly small, attaining up to about 45 mm in diameter, covered with thin biplicate, and triplicate ribs, replaced by biplicate ribs on the body-chamber, and resembling somewhat much earlier *Microbiplices procedens* which is a microconch of some *Ringsteadia*, such as *R. pseudoyo* (Wierzbowski *et al.*, 2010, pl. 6: 6, 7; Wierzbowski *et al.*, 2015, pl. 9: a–c; Wierzbowski, 2017a, pl. 10: 8; see also Wierzbowski *et al.*, 2016, p. 29). The distinctive character is shown by the unique specimen (Pl. 14: 4A–C) described herein, coming possibly from the Bimammatum Zone at Trzyciąż, near Wolbrom, Cracow Upland. It is about 50 mm in diameter, and fully grown as shown by approximation of the last suture lines at about 30 mm diameter. The coiling is at the involute/evolute boundary: in the phragmocone, at 27 mm diameter, the whorl height and the umbilical diameter equal 37% of the specimen diameter, and these change but a little in the body chamber, at 44 mm diameter, where the whorl height and the umbilical diameter are: 38.5% and 36.5% of the specimen diameter, respectively. The inner whorls are covered with moderately strong, well-spaced, bi- and triplicate ribs whose number per whorl reaches 23 at 15 mm diameter, whereas the secondary/primary rib ratio is 2.6. Above 25 mm diameter, the ribbing becomes very dense, consisting of biplicate ribs whose number per whorl ranges from 33 at 27 mm diameter to about 50 at 44 mm diameter. The specimen discussed resembles very much in its very dense ribbing the well-known specimens of *V. streichensis* of similar size (Oppel, 1863, pl. 66: 3; Nitzopoulos, 1974, pl. 7: 6; Schweigert, Callomon, 1997, pl. 7: 11). It differs from all of them (representing the inner whorls of macroconchs, see Schweigert, Callomon, 1997), however, in its smaller final-size and a less involute coiling of the outer whorl. Most possibly it represents the microconch of *Vineta streichensis* (Oppel).

The systematic position of *Vineta* for a long time became controversial: this taxon was either treated as a closely related to *Ringsteadia* (*e.g.*, Arkell *et al.*, 1957; see also Wierzbowski, 1978), and/or recognized as its subgenus (*e.g.*, Geyer, 1961). The special morphological features of *Vineta* as discussed above, and additionally its different geographical and stratigraphical range when compared with *Ringsteadia*, resulted in the recognition of that taxon as an independent genus (*e.g.*, Enay, Howarth, 2019). A similarity between *Vineta* and strongly involute *Ringsteadia* of the *R. pseudoyo* group (along with their *Microbiplices*-like microconchs), and their occurrence in the stratigraphical succession: *R. pseudoyo*, which although it is more commonly encountered in the lower part of the Pseudocordata Zone continues up to the top of this zone (Wright, 2010; see also comments at the description of the genus *Ringsteadia* herein), where it directly precedes the appearance of *Vineta*, strongly suggest a close phylogenetical relation between the two taxa. The appearance of *Vineta* was coeval with that of the genus *Pictonia* in the NW-European part of the Subboreal Province, and thus the base of the Jaekeli Zone as defined by the occurrence of *Vineta* in the NE-European part of this province (Dohm, 1925; Wilczyński, 1962) may be treated as coeval with the base of the Baylei Zone (see Wierzbowski *et al.*, 2016).

A special feature of the genus *Vineta* remains the occurrence of the very dense and delicate, mostly biplicate ribbing in its inner-middle whorls up to about 40–60 mm in diameter in early representatives of the genus, which especially in the case of giant specimens having poorly preserved inner whorls gives the impression that they are completely devoid of ornamentation (*e.g.*, Dohm, 1925). Such a type of ribbing is possibly of a "primitive" character, and from the point of view of heterochrony is a paedomorphic feature, and suggests a delay in ontogenetic development, to some degree in a similar manner to the coeval *Pictonia*. The similarity in ornamentation of the inner whorls of the genus *Vineta* to those of *Pictonia* was recognized already by Schweigert and Callomon (1997, p. 24). Such was also the reason for a statement on the affinity of early representatives of *Vineta* (treated originally as belonging to the genus *Ringsteadia*, see *e.g.* Wierzbowski, 1978) as representing "the involute analogues of true *Pictonia*" (Wierzbowski, 1994).

Genus *Balticeras* Dohm, 1925

This genus is still poorly known, and its systematic position has become somewhat controversial. It was recognized as a subgenus of *Ringsteadia*, grouping strongly involute forms of that genus (Arkell *et al.*, 1957), and more recently this name has been treated even as a synonym of *Vineta* (Enay, Howarth, 2019). Since its establishment by Dohm (1925, pl. 5: 1), as based on large-sized specimens (about 200 mm in diameter) representing the phragmocone of the type-species *Balticeras pommerania* Dohm, a few new specimens of that genus have been described in detail, however. Such descriptions were given by Gygi (2003, p. 78, figs. 80, 81; p. 134, figs. 153–156) in relation to specimens referred to as *Balticeras pommerania* from the Jura Mts. of northern Switzerland, and recently by Wierzbowski (2017a, p. 83–84, pl. 10: 9; pl. 11: 1a–c), who presented two middle-sized specimens, referred to the new species *Balticeras samsonowiczi* Kowalski emend. Wierzbowski, from the Burzenin area, central Poland. These new descriptions are especially important for the knowledge of the genus because they yield new data on the development of the ornamentation of the inner whorls.

The genus represented by macroconchs, commonly of large sizes, is characterized by very involute coiling in the inner whorls with a narrow umbilicus and by a very steep umbilical wall. The whorl section is discoidal, tending to be oxycone. The ribbing of the inner whorls, from a few centimeters in the specimen's diameter, consists of weak primary ribs (more thin and densely spaced initially, then wider and rather sparsely placed), and much stronger secondaries appearing fairly low on whorl side. In the studied specimens of *B. samsonowiczi* the ribbing on the body chamber, at about 70–80 mm diameter, consists of elongated but fairly short and wide primaries, and long secondary ribs showing some tendency to join the primaries at about one-third of the whorl height (Wierzbowski, 2017a). At larger diameters, coiling becomes weakly involute to weakly evolute, the ornamentation disappears, and the whorls of the giant specimens are completely smooth: such specimens were illustrated by Dohm (1925) and Gygi (2003, see figs. 81, 153 and 155 which represent the phragmocone 390 mm in diameter, and the phragmocone with body chamber about 550 mm in diameter).

There is no doubt that *Balticeras* is very close to *Vineta*. The affinity of both genera is shown by their similar type of coiling, and very close development of ribbing, especially the stronger development of the secondary ribs, and smooth outer whorls. The main differences are in the type of whorl section which in *Balticeras* becomes more oxycone with a steep umbilical wall, and is thus different from that of older *Vineta* which is high-oval, and also in some new features in the development of the ornamentation, such as the appearance of protruding primary ribs in the middle whorls, not represented at a similar position in older species of *Vineta* (although recognized in its youngest ones like *V. striatula* – see Geyer, 1961, pl. 22: 1). Genus *Balticeras* occurs moreover in younger deposits than *Vineta* – newly described specimens from Switzerland and Poland (Gygi, 2003; Wierzbowski, 2017a) come from a similar stratigraphic position – from the upper part of the Hippolytense Subzone to the lowermost part of the Lothari Subzone of the Hypselocyclum Zone. All these observations strongly suggest that *Balticeras* is the direct descendant of *Vineta* in a smoothly evolved aulacostephanid lineage, and the direct forerunner of *Rasenioides*.

Genus *Rasenioides* Schindewolf, 1925
(macro- and microconchs)

Most commonly (*e.g.*, Geyer, 1961; Hantzpergue, 1989; and recently Enay and Howarth, 2019), *Rasenioides* has been treated as closely related to the genus *Rasenia*, and recognized in consequence as a subgenus of *Rasenia*. Such an interpretation is not accepted herein, because *Rasenioides* and *Rasenia* according to the present author belong to different ammonite lineages (Wierzbowski, 2017a, b). Distinction on the genus level of the two taxa was already pointed out by Schindewolf (1925, 1926), and more recently indicated by Birkelund *et al.* [(1983, p. 296): "the fine-ribbed forms and *Rasenia* were following separate evolutionary paths before the top of the Cymodoce Zone and they can now be separated generically; the name *Rasenioides* Schindewolf is available for the fine-ribbed forms – type *R. striolaris* (Reinecke)"].

The genus *Rasenioides* includes a fairly diversified assemblage of ammonites, differing in their final size, to some degree also in the type of coiling, and the development of ornamentation. It is strongly dimorphic, and micro and macroconchs are well differentiated, being usually described under different specific names, but sometimes also placed together into a single biospecies (see *e.g.*, Hanztpergue, 1989). The macroconchs attain from about 100 to 250 mm in diameter; they show a very special type of ornamentation, consisting of tuberculate short primary ribs and very numerous long and fine secondary ribs. The microconchs with lappets, commonly 25–40 mm in diameter, show short swollen primaries with numerous secondaries; the secondary/primary rib ratio ranges to about 8 or less, depending on the species, and on the size of the specimen (see Geyer, 1961; Hantzpergue, 1989). The fine fasciculate ribbing of microconchs differs markedly from that of *Prorasenia* microconchs of other aulacostephanid lineages in the larger number of secondary ribs, which generally increases along with diameter.

Two assemblages of *Rasenioides* differing in morphological features and stratigraphical position can be recognized: the older one generally poorly known composed mostly of microconchs and very rare macroconchs occurring in the Submediterranean Platynota and Hypselocyclum zones, and the younger one well characterized by micro and macroconchs occurring in the uppermost part of the Hypselocyclum Zone and in the Divisum Zone of the Submediterranean subdivision corresponding to the Subboreal Askepta Subzone.

The group of older microconchs of *Rasenioides* includes especially *R. striolaris* (Reinecke) and *R. transitorius* (Schneid), both of them strongly involute and showing the swollen primary ribs in the phragmocone, and the elongated primary ribs in the body chamber (see Schindewolf, 1926, pl. 19: 3; Geyer, 1961, pl. 1: 6; 21: 3; 22: 8). Their stratigraphical position as indicated by Geyer (1961) corresponds to the German "*Weisser Jura Unter und Mittel γ*" which corresponds approximately to the Platynota and Hypselocyclum zones. A similar form was described also from the Środa IG-1 Borehole in northern Poland from the stratigraphical interval at the boundary between the Platynota and Hypselocyclum zones well documented by other ammonites (Malinowska, 1988, fig. 3, pl. 5: 5). The other related but poorly known forms include: *Rasenioides hossingensis* (Fischer) (see Fischer, 1913, pl. 5: 21) being possibly very close to *R. striolaris* and known from the middle part of the Platynota Zone (see Geyer, 1961; Schairer, 1969), and *Rasenioides fascigera* (Quenstedt) (see Quenstedt, 1887, pl. 94: 45) which seems to be close to *R. transitorius* but occurs fairly low in the succession (? German *Weissjura β* which corresponds to the Planula Zone). On the other hand, the microconch described by Gygi (2003, p. 64, fig. 63) as *R. transitorius* differs strongly, however, from the discussed microconchs of *Rasenioides* in its having a weaker development of the primary ribs and their larger number. It comes also from older deposits – the uppermost Planula Zone/lowermost Platynota Zone – the Galar Subzone (Gygi, 2003, fig. 170), and resembles very much in its coiling and ornamentation the inner whorls of the still older *Vineta streichense* (Oppel) from the Hauffianum Subzone of the Bimammatum Zone, as illustrated by Schweigert and Callomon (1997, pl. 7: 5). The specimen of Gygi (2003) should be thus interpreted as a link in the continuous lineage of microconchs in the Submediterranean Platynota and Hypselocyclum zones, between *Vineta streichense* and *R. transitorius/R.fascigera*, followed in turn by *R. striolaris/R.hossingensis*, showing a still larger number of secondaries and somewhat less involute coiling.

The discussed lineage of microconchs includes thus a wide spectrum of forms from the early microconchs of *Vineta* to those of the older assemblage of *Rasenioides*. Such an interpretation makes, however, determination of the systematic position of the particular members of the lineage difficult because of their unclear relation to a spectrum of corresponding but poorly known macroconchs from the late representatives of *Vineta*, through *Balticeras*, up to the early *Rasenioides* (see also comments below).

The unique macroconch of *Rasenioides glazeki* of the older *Rasenioides* assemblage was described by Wierzbowski (2017a, p. 84, pl. 12; Pl. 15: 1A) from the middle part of the Hypselocylum Zone (lowermost part of the Lothari Subzone) of the Burzenin area, central Poland. It attained about 250 mm in size, consisting of a smooth body-chamber at least ¾ of a whorl long, and the ornamented phragmocone up to about 180 mm diameter. The inner whorls of the phragmocone seen partly after preparation of the specimen (Pl. 15: 1B) show involute coiling (at 85 mm diameter, whorl height and umbilical diameter equal 47% and 24% of the specimen diameter, respectively). The ribbing consists of short primaries, and long, but rather massive secondaries; there are about 6 secondary ribs per one primary. The innermost whorls are poorly visible, but short swollen primary ribs are seen at least from about 30 mm diameter. The coiling of the outer whorl (Wierzbowski, 2017a) is strongly involute, and the umbilicus is deep with a steep umbilical wall. The ornamentation of the last whorl of the phragmocone from about 100 mm diameter consists of short swollen primary ribs, which are rather loosely spaced (about 20 primary ribs per whorl), and thin and long secondaries (about 8–10 secondary ribs per one primary). The specimen which is the holotype of *R. glazeki* differs from directly younger *Rasenioides askepta* in its larger size, more involute coiling, steeper umbilical wall, and more massive secondary ribs in the inner whorls. This species, representing possibly the oldest known macroconch of *Rasenioides*, shows some similarity to the older macroconchs of *Balticeras*, like *B. pommerania* Dohm (inner whorls shown by Gygi, 2003, fig. 156) and *B. samsonowiczi* Kowalski emend. Wierzbowski (see Wierzbowski 2017a, pl. 10: 9; pl. 11: 1a–c), but it differs in the presence of the short swollen primary ribs and the long numerous secondary ribs which are typical of the genus *Rasenioides*.

The younger assemblage of *Rasenioides*, both micro- and macroconchs, is described from the Askepta Subzone (and corresponding parts of the Chatelaillonensis Subzone) of Aquitaine, of the so-called "Biome franco-germanique", the transitional area between Subboreal and Submediterranean areas (Hantzpergue, 1989, 1995). The succession recognized consists of several macroconchs associated with corresponding microconchs, and it represents the following three faunal horizons (from below): *Rasenioides askepta* (Ziegler) (M) and *R. lepidulus* (Oppel) (m) – *askepta* horizon; *R. chatelaillonensis* (Morris M.S.) Hantzpergue (M) and *R. lepidulus* (Oppel) (m) – *chatelaillonensis* horizon; *R. discoidus* Hantzpergue (M and m) and *R. ecolisnus* Hantzpergue (M and m) – *discoidus* horizon (Hantzpergue, 1989, 1995; see also Hantzpergue, 1979; Hantzpergue, Debrand-Passard, 1980). The differences between the macroconchs are related to the type of coiling of the inner whorls (less involute to even evolute in *R. askepta* and *R. chatelaillonensis* and very involute in *R. ecolisnus* and *R. discoides*), to the final sizes (much smaller in *R.askepta*), to the whorl section (oval or rectangular), and to the development of ornamentation. The ornamentation commonly follows the pattern typical of the genus; however, in the late species of the lineage the strong ribbing disappears at smaller diameters (*R. ecolisnus* and *R. discoides*). The microconchs of the *R. lepidulus* group corresponding to older macroconchs of the lineage are weakly evolute and show the short, strongly prorsiradiate primaries and the numerous secondary ribs, whereas the younger microconchs are involute, revealing even shorter primaries (Hantzpergue, 1989).

It is worth noting that the *askepta* horizon from Aquitaine, occurring at the base of the discussed younger assemblage of *Rasenioides*, is commonly recognized in other European areas at the narrow stratigraphical interval marking the base of the Askepta Subzone. This horizon, marked by the sudden appearance of ammonites of the genus *Rasenioides*, is well documented in England (Birkelund *et al.*, 1983) and northern Poland (Matyja, Wierzbowski, 1998, 2000a), and possibly in Scotland (Ziegler, 1963), where similar assemblage of ammonites comes from: *R. lepidulus* (Oppel), *R. thermarum* (Oppel) – *R. lepidulus* (Oppel) and *R.* cf. *askepta* (Ziegler).

The common feature of the discussed younger assemblage of *Rasenioides* is the occurrence of forms showing a longer or shorter smooth, or covered with a very weak ornamentation, band in the dorsolateral part of the inner whorls (Hantzpergue, 1989). In some of the species like *Rasenioides moeschi* (Oppel) and *R. thermarum* (Oppel), this stage in development of the ornamentation is especially prolonged, and the first tuberculate primary ribs do not appear before the body chamber. Such forms are especially common in the lowermost and the uppermost parts of the occurrence of the younger assemblage – at the base, and at the top of the Askepta Subzone – where there are known even forms transitional to the genus *Aulacostephanoides* (*cf.* Birkelund *et al.*, 1983 p. 290; Malinowska, 1986, pl. 4:2, see also Wierzbowski *et al.*, 2015, p. 82, fig. 3; Matyja, Wierzbowski, 1998, p. 44, 47, pl. 3: 8; 2000a, fig. 1, fig. 4c).

The discussed differences in morphology of ammonites of the younger and older assemblages of *Rasenioides* might result in serious taxonomical problems. This is the case in the interpretation of the subgenus name *Semirasenia*, originally proposed by Geyer (1961) for the two species *R. moeschi* (Oppel) and *R. thermarum* (Oppel), distinguished by the well-developed band of very weak ornamentation at the umbilical part of the inner whorls (Pl. 15: 2A, B). The scope of the subgenus was subsequently enlarged by Ziegler (1963), assuming that *R. moeschi* represents the macroconch, to include the whole set of macroconchs of the genus *Rasenioides*. It worth noting that according to Enay and Howarth (2019, fig. 68.2b) the holotype of *R. moeschi* is not the macroconch but the microconch. Species showing lack of ornamentation/or very weak ornamentation in some parts of the inner whorls, both micro- and macroconchs, are known commonly, however, in the whole younger assemblage of the *Rasenioides* species (*cf.* Hantzpergue, 1989), thus the name *Semirasenia* fits theoretically to all of them. On the other hand, the type species of the genus *Rasenioides* is just the microconch – *Rasenioides striolaris* (Reinecke) (see Schindewolf, 1925), which is closely related to another species *R. transitorius* Schindewolf; but both of them belong to the older group of the microconch species differing in several features from the younger microconchs (see also comments above). The problem of the taxonomical relation between the older and younger microconchs of *Rasenioides* cannot be thus unequivocally solved at the moment, but it seems possible that the name *Rasenioides* in its original meaning should be reserved in the future to cover a wider scope of microconchs (similarly as the name *Prorasenia*), not necessary related to the macroconchs of the genus *Rasenioides* only. In that case it may appear necessary to replace the name *Rasenioides*, when referring to the *Rasenioides* – type macroconchs and their unequivocal microconchs counterparts, by the genus name *Semirasenia*. The existing separate classification of the micro- and macroconchs of *Rasenioides* at the species level seems, however, the most appropriate distinction for the descriptive purposes at the present, and it is accepted for the time being.

Although the continuous transition between the microconchs of *Vineta* and those of the older assemblage of *Rasenioides* as discussed above seems very probable, detailed data on the development of the corresponding macroconchs of the lineage are still very scarce. Generally the succession of particular characters of the ornamentation, and the differences in final sizes of the microconchs only indicate a tendency to the appearance of swollen primary ribs at larger diameters, originally seen in the older forms of the lineage at the umbilicus: it is correlated with a general tendency to attain the maturity successively at an earlier stage of ontogenetic development. Such a development in terms of heterochrony may indicate the paedomorphosis (and neoteny) which occurs when the younger forms pass through fewer growth stages than the older ones. A different development of characters is observed within the younger assemblage of *Rasenioides* – both micro- and macroconchs. Here, a special character appears which is the dorsolateral smooth band observed in the inner whorls. Its appearance preceeds the occurrence of the very short lateral tuberculate ribs, and the corresponding thin and very numerous secondaries, which differs in character from ribbing observed in the older *Rasenioides* assemblage (*cf.* Geyer, 1961, p. 92–93). If the discussed smooth band corresponded to the interval of very weak ornamentation observed in early-middle whorls in older *Vineta–Balticeras*, the tuberculate ribs appearing thereafter in the younger *Rasenioides* assemblage would be the homologue of the swollen ribs at the umbilicus observed in the middle-outer whorls of these ancestors. Such an approach may indicate that the younger *Rasenioides* assemblage involves a different evolutionary journey than the older one, corresponding to peramorphosis in term of heterochrony, *i.e.* showing a faster rate of ontogenetic development. Agreement is best here between the occurrence of typical rasenioidal thin and numerous secondary ribs at the terminal fragment of the phragmocone in the oldest known macroconch – *Rasenioides glazeki* Wierzbowski (see Wierzbowski, 2017a, pl. 12), and the occurrence of the same type of ribbing at markedly smaller diameters in younger representatives of that genus (see Hantzpergue, 1989). It is worth noting that such a type of evolutionary development of the younger assemblage of *Rasenioides* was proposed by Hantzpergue (1989), although he derived *Rasenioides* from the youngest representatives of *Rasenia.* The phylogenetical continuation of the genus *Rasenioides* as commonly accepted is in the Late Kimmeridgian *Aulacostephanoides–Aulacostephanus* (see *e.g.*, Ziegler, 1962; Hantzpergue, 1989; Borrelli, 2014).

EVOLUTIONARY AMMONITE TURNOVERS

The evolutionary turnovers shown in the phylogeny of the family Aulacostephanidae can be additionally commented on when one considers the development of other ammonite families, especially the Boreal Cardioceratidae, and the Submediterranean Oppeliidae, Perisphinctidae, Ataxioceratidae and Aspidoceratidae occurring in similar stratigraphic positions in the successions studied. The correlation of the ammonite turnovers of all these ammonite groups with changes in the depositional environment, as based on sedimentological data, suggests the specific interaction between the phylogeny of ammonites and the climatic and tectonic factors resulting in sea-level changes and the opening or closing of new/old sea-routes. Such relations between the evolution of the different ammonite lineages and the relative position of sea level were already considered on the occasion of the development of ammonite faunas in the Oxfordian and Kimmeridgian in some European areas which resulted in general statements that the deepest faunal changes occurred during the transgressive tracts (Atrops, Ferry, 1989), and that the "endemism was linked with shallow marine environments of highstand and lowstand system tracks" (Hantzpergue, 1995). This refers also to special adaptations of the aulacostephanids which in general were able to develop in the unstable environmental conditions (Fürsich, Sykes, 1977). All the distinguished evolutionary turnovers (see also Wierzbowski, 2022) are well settled in stratigraphical schemes where they have been often applied in the past for defining chronostratigraphical boundaries.

The Middle/Upper Oxfordian boundary is placed in the Boreal zonal scheme at the base of the Glosense Zone, marking the first turnover discussed herein (Fig. 3), both in the Cardioceratidae lineage – the sudden disappearance of the genus *Cardioceras*, and appearance of the first representatives of the genus *Amoeboceras* (Sykes, Callomon, 1979; Callomon, 1985), and in Aulacostephanidae – the foundation of the whole family with the appearance of the genus *Decipia*, and some closely related forms (Wright, 1996; Wright, Powell, 2008). These changes in ammonite faunas are often associated with the stratigraphical gaps recognized in many sections in the Subboreal Province, but also with the occurrence of "black shales" in other areas – such as some parts of the Russian Platform (Głowniak *et al.*, 2010).

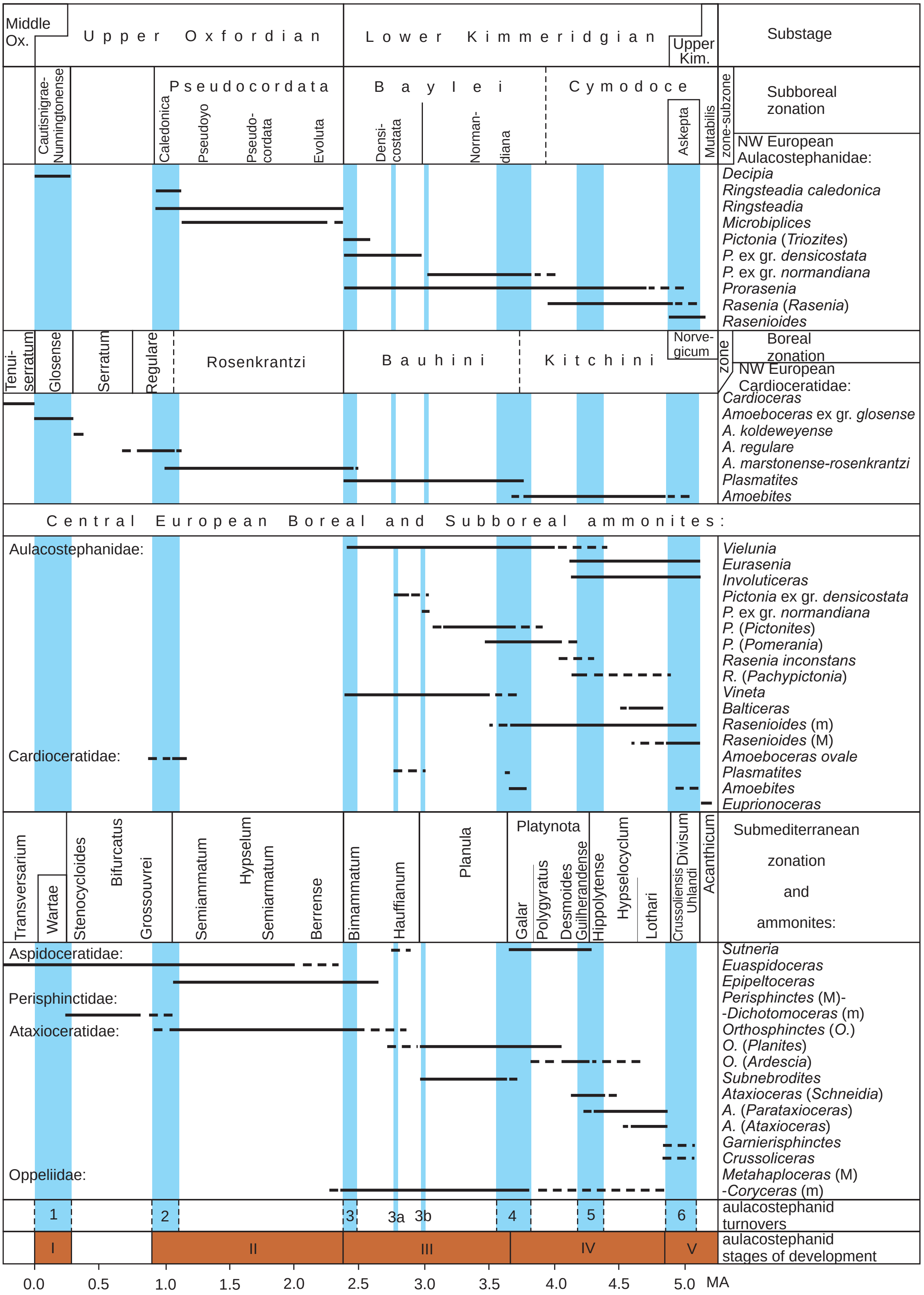
The genus *Decipia* occurs commonly in eastern and northern England, from Oxfordshire to Yorkshire, where it usually appears in the high-energy deposits such as sandstones or sandy limestones of the Upper Calcareous Grit Formation resting usually with a pronounced stratigraphical gap on the deposits of the Middle Oxfordian (see Wright, 1996, 1997). The coeval, more complete mudstones in east Oxfordshire to Cambridgeshire of the Ampthill Clay Formation in east Oxfordshire to Cambridgeshire yielding also *Decipia* ammonites reaveals also some stratigraphical gaps below (Wright, Powell, 2008), or their direct contact with underlying deposits is not well seen (Arkell, 1937, 1947). The genus occurs also in northern Scotland where it was reported together with early *Amoeboceras* of the *A. glosenese* group of the lowermost Glosense Zone at the base of the Flodigarry Shale Member directly above the sharp boundary with the underlying silty-sandy deposits of the Digg Siltstone Member (Wright, 1973; Sykes, 1975). The genus *Decipia* has been reported from the East Greenland (Surlyk *et al.*, 1973, pl. 1: 1; Sykes, Surlyk, 1976: fig 5B) from the deposits which sedimentation was characterized by direct evidence of tectonic activity. All these features suggest the origin of this ammonite genus as a consequence of a rapid evolution under unstable ecological conditions resulting from appearance of intricate facies pattern of the shallow-water environments typical of the Subboreal Province (Fürsich, Sykes, 1977).

A corresponding turnover in the development of the Submediterranean and Mediterranean ammonite faunas was

→

Fig. 3. Stratigraphical ranges of selected species belonging to various ammonite families placed in the background of the Subboreal, Boreal and Submediterranean zonal schemes of the Upper Oxfordian and Lower Kimmeridgian in Europe

The ammonite turnovers (listed in the text) and the stages of the evolutionary development of the Aulacostephanidae are shown in the bottom of the figure where also the chronostratigraphical scale is given (after Hesselbo *et al.*, 2020). All the correlations of zonal schemes are given in relation to the Submediterranean one


Middle Ox.
Upper Oxfordian
Lower Kimmeridgian
Upper Kim.
Substage
Cautisnigrae-Nunningtonense
Pseudocordata
Caledonica
Pseudoyo
Pseudo-cordata
Evoluta
Baylei
Densi-costata
Norman-diana
Cymodoce
Askepta
Mutabilis
zone-subzone
Subboreal zonation
NW European Aulacostephanidae:
Decipia
Ringsteadia caledonica
Ringsteadia
Microbiplices
Pictonia (Triozites)
P. ex gr. densicostata
P. ex gr. normandiana
Prorasenia
Rasenia (Rasenia)
Rasenioides
Tenui-serratum
Glosense
Serratum
Regulare
Rosenkrantzi
Bauhini
Kitchini
Norve-gicum
zone
Boreal zonation
NW European Cardioceratidae:
Cardioceras
Amoeboceras ex gr. glosense
A. koldeweyense
A. regulare
A. marstonense-rosenkrantzi
Plasmatites
Amoebites
Central European Boreal and Subboreal ammonites:
Aulacostephanidae:
Vielunia
Eurasenia
Involuticeras
Pictonia ex gr. densicostata
P. ex gr. normandiana
P. (Pictonites)
P. (Pomerania)
Rasenia inconstans
R. (Pachypictonia)
Vineta
Balticeras
Rasenioides (m)
Rasenioides (M)
Cardioceratidae:
Amoeboceras ovale
Plasmatites
Amoebites
Euprionoceras
Transversarium
Wartae
Stenocycloides
Bifurcatus
Grossouvrei
Semiammatum
Hypselum
Semiarmatum
Berrense
Bimammatum
Hauffianum
Planula
Platynota
Galar
Polygyratus
Desmoides
Guilherandense
Hippolytense
Hypselocyclum
Lothari
Crussoliensis
Uhlandi
Divisum
Acanthicum
Submediterranean zonation and ammonites:
Aspidoceratidae:
Sutneria
Euaspidoceras
Epipeltoceras
Perisphinctidae:
Perisphinctes (M)-
-Dichotomoceras (m)
Ataxioceratidae:
Orthosphinctes (O.)
O. (Planites)
O. (Ardescia)
Subnebrodites
Ataxioceras (Schneidia)
A. (Parataxioceras)
A. (Ataxioceras)
Garnierisphinctes
Crussoliceras
Oppeliidae:
Metahaploceras (M)
-Coryceras (m)
1
2
3
3a
3b
4
5
6
aulacostephanid turnovers
I
II
III
IV
V
aulacostephanid stages of development
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
MA

recognized in south-eastern France. It is reponsible for changes in the Perisphinctidae and Aspidoceratidae from the base of the Schilli Subzone (and the nearly coeval Wartae Subzone) and ranges up into the basal part of the Stenocycloides Subzone, near the boundary of the Transversarium and Bifurcatus zones, and directly corresponds to the transgressive interval according to the recognized "third order transgressive tract" (Atrops, Ferry, 1989). This stratigraphical interval begins with a well-pronounced sequence boundary "O5" both in carbonate platform and adjoining basin successions represented by the hard-ground surface and the associated marly deposits in northern Switzerland (Gygi *et al.*, 1998).

The decline of the genus *Decipia* at the base of the Boreal Serratum Zone corresponds approximately to the Koldeweyense Subzone which is a stratigraphical interval characterized by a marked change in the Cardioceratidae lineage. The subzone shows the occurrence of the special small-sized *Amoeboceras koldeweyense* Sykes et Callomon with very delicate to almost smooth ornamentation of the inner whorls (Sykes, Callomon, 1979), being the oldest member of the subgenus *Amoeboceras* of the *Amoeboceras serratum* group. The appearance of these small-sized specimens was possibly related to changes in the environment which resulted in the evolutionary transformation of shells controlled by heterochrony: either the attaining of earlier maturity due to progenesis, or which seems here more probable, by a slower rate of ontogenetic development (and thus neoteny) when compared with older forms of the lineage (Wierzbowski, Rogov, 2013). It should be remembered that the stratigraphical interval of the Koldeweyense Subzone correlates with some lower parts of the Stenocycloides Subzone of the Bifurcatus Zone which in terms of sequence stratigraphy has corresponded to a very high sea-level of the Late Oxfordian flooding (Atrops, Ferry, 1989). This may suggest that the development of small-sized *A. koldeweyense* took place during maximum transgression as nektopelagic forms, and that the special environmental conditions at that time were responsible also for the decline of *Decipia*.

The second important ammonite turnover is marked by the recovery of the Aulacostephanidae lineage as shown by appearance of the genus *Ringsteadia* at the base of the Subboreal Pseudocordata Zone. The most complete succession of the Pseudocordata Zone is in the Flodigarry Shale Member at Staffin Bay, Isle of Skye, northern Scotland, which begins with beds with *Ringsteadia caledonica* recognized as the Caledonica Subzone (Sykes, Callomon, 1979; Wright, 2003; see also Matyja *et al.*, 2006; Wierzbowski, Matyja, 2014). The species co-occurs here with Cardioceratidae – *Amoeboceras regulare*, including forms similar to *A. marstonense*, which suggests either the topmost part of the Boreal Regulare Zone, and/or the lowest part of the Rosenkrantzi Zone (Wierzbowski, Matyja, 2014, p. 61; Wierzbowski *et al.*, 2018). The same stratigraphical interval, corresponding to the topmost part of the Submediterranean Bifurcatus Zone, in central Poland is marked by the common occurrence of Boreal ammonites of the genus *Amoeboceras* represented both by small-sized *A. ovale* associated with larger-sized *A. marstonense*–*A. freboldi* (Wierzbowski, Matyja, 2014), but also the appearance of the first Tethyan ataxioceratids (mostly *Orthosphinctes*) and the decline of the Submediterranean lineage of *Perisphinctes*. The nearly coeval interval in the borehole Bartoszyce IG-1 in the Peri-Baltic Syneclise in north-eastern Poland showed, besides *A. ovale*, the remarkable occurrence of *Ringsteadia caledonica* (the first recognized outside the U.K., see Wierzbowski *et al.*, 2015, fig. 8j–l).

The ammonites of the genus *Ringsteadia* occur commonly in southern England (Dorset, Wiltshire) in the Sandsfoot Formation, which rests with a marked stratigraphical gap on older deposits. The Sandsfoot Formation shows large lithological variability, resulting from tectonic instability – with frequent uplifts, and localized shallow-water deposits. The unit corresponds to the uppermost Oxfordian and correlates with the Pseudocordata Zone, but *R. caledonica* is missing here (see *e.g.*, Wright, 1986). Towards the east and north the more uniform in character deposits of the Ampthill Clay Formation represent the whole Upper Oxfordian, but the succession of deposits which formerly most completely cropped out at South Ferriby in the East Midlands did not reach the base of the formation (see *e.g.*, Birkelund, Callomon, 1985; and especially Cox, 2001). The unstable environmental conditions possibly had a major impact on the origin of *R. caledonica*, but its patchy occurrence has resulted from the incompleteness of the sedimentary records.

The stratigraphical interpretation of the sections discussed indicates the correlation of the basal part of the Subboreal Pseudocordata Zone with the topmost part of the Boreal Regulare Zone-basal part of the Rosenkrantzi Zone, and additionally with the topmost part of the Submediterranean Bifurcatus Zone, which makes possible a recognition of the evolutionary ammonite turnover when considering the various ammonite lineages. This ammonite turnover is well recognized also in areas corresponding to the Submediterranean Province which do not show any Subboreal and/or Boreal faunal influences, like the area of south-eastern France where it corresponds to the transgressive interval of the "third order transgressive tract" (Atrops, Ferry, 1989). In general the discussed ammonite turnover is shown thus by: (1) appearance of the aulacostephanid genus *Ringsteadia*; (2) beginning of the invasion of the Boreal *Amoeboceras* into the Submediterranean Province which ranges so far southwards as central Poland, southern Germany and northern Switzerland *(e.g.*, Klieberg, 1981; Atrops *et al.*, 1993);

(3) beginning of the invasion of the Tethyan-origin Ataxioceratidae (*Orthosphinctes*) and Passendorferiinae ranging so far northward as central Poland (Wierzbowski, Matyja, 2014); (4) decline of European Submediterranean Perisphinctinae represented by the last *Perisphinctes* (*Perisphinctes*, *Dichotomoceras*) (*e.g.*, Bonnot *et al.*, 2009; Wierzbowski, Matyja, 2014).

The directly younger parts of the Pseudocordata Zone, and of the corresponding Rosenkrantzi Zone (Boreal), as well as of the Hypselum Zone (Submediterranean) of the uppermost Oxfordian, reveal already rather moderate changes in the succeeding aulacostephanid ammonite faunas. An exception is the appearance of microconch *Microbiplices* still in the lower part of the Pseudocordata Zone and its correlatives – mostly the Semimammatum Subzone of the lower part of the Hypselum Zone. This small-sized microconch, showing a very special development of ornamentation (see chapter on evolution of Aulacostephanidae), commonly occurs in the Submediterranean areas from central and southern Poland, and Czech Republic, southern Germany to northern Switzerland and south-eastern France, where several new species and their varietes have been described (*e.g.*, Quenstedt, 1887; Oppenheimer, 1907; Enay, 1962, 1966; Gygi, 2003; Wierzbowski, Matyja, 2014). Remarkable is the co-occurrence here of *Microbiplices* (and *Ringsteadia*) with a very specially developed assemblage of small-sized ("dwarfed") cardioceratids – composed mostly of *Amoeboceras ovale* (representing the continuation of the Boreal invasion from the topmost part of the Bifurcatus Zone), which locally show mass occurrences (in the so called "lower *Amoeboceras* layer"); these ammonites reveal a very low growth rate during ontogeny, as shown by their having a long sector of phragmocone with crowded septa (Matyja, Wierzbowski, 2000b), and can be interpreted as nektopelagic forms (Wierzbowski *et al.*, 2016). Besides, this stratigraphical interval has yielded new aspidoceratids (mostly *Epipeltoceras*) and a diversified assemblage of other Submediterranean ammonites: oppeliids, ataxioceratids, and perisphinctids (*e.g.*, Matyja, Wierzbowski, 2014). Moreover, it shows also the common occurrence of the radiolarian faunas both of Tethyan and the Boreal origin (Smoleń, 2016; Wierzbowski *et al.*, 2016). The interval in question corresponds to a very high sea-level, representing the final stage of the transgression, and it closes the second ammonite turnover.

The third ammonite turnover occurs near the boundary of the Pseudocordata and Baylei aulacostephanid zones in the NW European part of the Subboreal Province where the macroconch genus *Ringsteadia* (and its microconch counterpart *Microbiplices*) is replaced by its phylogenetic descendent – the highly morphologically diversified genus *Pictonia*, including especially its nominative subgenus (and the microconch *Prorasenia*). This turnover corresponds to the boundary of the Oxfordian and Kimmeridgian in the Subboreal zonal scheme (Salfeld, 1913). The boundary has been formally accepted as the global boundary standard of the two stages in question (Wierzbowski *et al.*, 2016, and earlier papers cited therein; Coe, Wierzbowski, 2021). The changes in the Aulacostephanidae lineage have been discussed in detail on account of the GSSP proposal of the Oxfordian/Kimmeridgian boundary which is the Flodigarry section at Staffin Bay on the Isle of Skye, northern Scotland (Matyja *et al.*, 2006; Wierzbowski *et al.*, 2006, 2018; see also discussion herein in the chapter on Aulacostephanidae phylogeny). The same section shows also a continuous succession of the ammonites of the family Cardioceratidae, which reveal the equivalent faunal turnover near the boundary in question, where the genus/subgenus *Amoeboceras* is replaced by a special assemblage of small-sized ammonites of the genus *Plasmatites*. The evolutionary transformation between these genera resembles that between *Ringsteadia* and *Pictonia* in the parallel aulacostephanid lineage, and has been controlled by heterochrony – *Plasmatites* shows a slower rate of development and stays neotenic in relation to older *Amoeboceras*: adult *Plasmatites* ammonites reveal some "primitive" features of their ancestors, such as the continuous ornamentation on the ventral side of whorls (Wierzbowski *et al.*, 2018).

The coeval boundary of the Oxfordian and Kimmeridgian may be also recognized in the NE European part of the Subboreal Province and adjoining parts of the Submediterranean Province at the boundary of the Hypselum and Bimammatum zones where both families Aulacostephanidae and Cardioceratidae show marked phylogenetic changes. These are partly different from those of the NW European area – the lineage of Aulacostephanidae splits here into two new lineages showing the transition between older *Ringsteadia*, and its descendants: the genus *Vielunia*, and the genus *Vineta*, and their microconchs – *Prorasenia* and *Vineta* (m), respectively (see chapter on the phylogeny of Aulacostephanidae), whereas the Cardioceratidae present the same transition from *Amoeboceras* to small-sized *Plasmatites*. The discussed faunal turnover is not recognized so sharply, however, in other families of Submediterranean and Mediterranean origin (Atrops, Ferry, 1989). Here, the changes are observed mostly in Aspidoceratidae, but also Oppellidae, including the common occurrence of the small-sized *Metahaploceras–Coryceras* group (see Wierzbowski *et al.*, 2010). The latter can be interpreted as nektopelagic forms showing a close relation with the occurrence of Tethyan radiolarians (Wierzbowski *et al.*, 2016; Smoleń, 2016).

Similarly as in the Middle/Upper Oxfordian faunal turnovers, that at the Oxfordian/Kimmeridgian boundary is also associated with the occurrence of stratigraphical gaps (see Wierzbowski *et al.*, 2016, and the earlier papers cited therein).

The turnover generaly corresponds to the transition from the transgressive deposits of the high system tract in the terms of sequence stratigraphy, and is placed near the main flooding surface (Coe, 1992; Gygi *et al.*, 1998).

A less distinct ammonite turnover is recognized in the Submediterranean succession at the lowermost part of the Hauffianum Subzone of the Bimammatum Zone. It is related with occurrence in central Poland of the "upper *Amoeboceras* layer" which shows the mass-occurrence of small-sized cardioceratids of the genus *Plasmatites*, but also small-sized oppeliids of the *Metahaploceras*–*Coryceras* group, marking the presence of the *litocerum* horizon (Matyja, Wierzbowski, 1997), and associated with and preceeding the appearance of Tethyan-origin perisphinctids (Passendorferiinae) and ataxioceratids. A very similar assemblage of ammonites has been described also from the Hauffianum Subzone of southern Germany (Schweigert, Callomon, 1997), although the detailed correlation of the sections between the two areas is difficult (see Wierzbowski *et al.*, 2010). This ammonite turnover is reported moreover from the Tethyan succession of south-eastern France where it is defined by the disappearance of the *Epipeltoceras* lineage (Aspidoceratidae) (Atrops, Ferry, 1989). Another minor faunal turnover is recognized near the lower boundary of the Planula Zone of the Submediterranean succession. It is shown *e.g.* in central Poland by the appearance of new perisphinctids (*Passendorferia*) and ataxioceratids (*Subnebrodites*) with some Boreal cardioceratids of the genus *Plasmatites* (Matyja, Wierzbowski, 1997; Wierzbowski *et al.*, 2010; see also comments herein); a similar observation was also made in southern France and eastern Spain where the appearance of the new ataxioceratid subgenus *Planites* of Tethyan origin has been proposed at this level (Meléndez, Atrops, 2006). For the evolutionary development of Aulacostephanidae, both these ammonite turnovers are, however, of smaller importance. Nevertheless they show the migration of NW European origin ammonites of the genus *Pictonia*: these from the Hauffianum Subzone corresponding to the *Pictonia* assemblage of the *P. densicostata* group of the lower part of the Subboreal Baylei Zone (Densicostata Subzone) (see Schweigert, Callomon, 1997; Matyja, Wierzbowski, 1997), and those at the base of the Planula Zone revealing additionally a form similar to *P. normandiana* of the upper part of the Baylei Zone (Normandiana Subzone (see description herein, also Matyja, Wierzbowski, 1997). Their migration into the NE European areas of the Subboreal Province and into central European areas of the Submediterranean Province possibly influenced the development of the indigenous aulacostephanid lineage beginning with *Pictonia perisphinctoides* of the subgenus *Pictonites* in the Planula Zone (see also comments in palaeontological part of the study). Moreover, the discussed stratigraphical interval corresponding to these ammonite turnovers, was characterized by strong development of the radiolarian assemblages in Subboreal areas, especially well characterized in the Peri-Baltic Syneclise of north-eastern Poland but also in some other areas (see Wierzbowski *et al.*, 2015, and references given therein).

The uppermost part of the Planula Zone, and the Galar Subzone (attributed herein to the lowermost part of the Platynota Zone) of the Submediterranean succession shows a marked change in ammonite faunas, corresponding to the fourth major ammonite turnover. This stratigraphical interval represented in some areas of the Submediterranean and NE part of the Subboreal provinces by very shallow-water carbonates, but also by the more open marine deposits with ammonites of the Galar Subzone, reveals here the last migration of the small-sized Boreal cardioceratids of the genus *Plasmatites*, soon replaced by the genus *Amoebites* (Atrops *et al.*, 1993; Schweigert, 2000; Matyja, Wierzbowski, 2002; Matyja *et al.*, 2006). It is also marked in Submediterranean areas by changes in other ammonite families – *e.g.* by decline of some ataxioceratids (*Subnebrodites*) and the flourishing of some aspidoceratids (*Sutneria*) (see Atrops, Ferry, 1989), but also mass-occurrence of small-sized oppeliids of the *Metahaploceras*–*Coryceras* group. The related evolutionary transformation of aulacostephanids included the occurrence of the last *Pictonia* (*Pictonites*) – and possibly the emergence of its direct descendants – the representatives of *Pictonia* (*Pomerania*). Another transformation in aulacostephanids resulted possibly in the transition from the morphology of the *Vineta* – type microconch into that of the *Rasenioides* – microconch type (such as *R. fascigera*). It is worth noting that the discussed stratigraphical interval of the Submediterranean succession corresponds in the NW European Subboreal Province to the uppermost Baylei Zone (see Matyja *et al.*, 2006; Wierzbowski *et al.*, 2018) which directly precedes the evolutionary transition from the genus *Pictonia* to the genus *Rasenia*.

The fifth ammonite turnover occurs in the uppermost part of the Platynota Zone (Guilherandense Subzone) – the base of the Hypselocyclum Zone (*lussasense* horizon) in the Submediterranean areas. In central Poland it corresponds to the replacing of the indigenous "German" Submediterranean lineage of *Pomerania*–*Pachypictonia* aulacostephanids by Submediterranean ataxioceratids and aulacostephanids of the genera *Eurasenia* and *Involuticeras*. A similar phenomenon is known also in northern Aquitaine in western France where Subboreal aulacostephanids (mostly of the genus *Rasenia*) were replaced by Submediterranean ataxioceratids and oppeliids (Hantzpergue, 1989, 1991, 1995; see also Wierzbowski, 2020, p. 194). The same stratigraphical interval in other Submediterranean areas like that of south-eastern France is characterized by changes in other groups of ammonites, especially Ataxioceratidae studied here in detail

(Atrops, 1982): the successive decline of the genus *Orthosphinctes* (subgenus *Ardescia*), and the appearance of the genus *Ataxioceras* (subgenera *Schneidia* and *Parataxioceras*). A Submediterranean ammonite assemblage overdominated by ataxioceratids with rare aspidoceratids of the Guilherandense Subzone has also been described recently from southern Germany (Schweigert, Schlampp, 2020). These faunal changes are correlated with the appearance of the complete flooding surface at the Platynota/Hypselocyclum zone boundary (Atrops, Ferry, 1989).

The succeeding stratigraphical interval in the Submediterranean succession corresponding to the Hypselocyclum Zone marks the come-back of aulacostephanid ammonites. In the Burzenin area of central Poland, the ammonites of the middle part of this zone (near the boundary of the Hippolytense and Lothari subzones) show a remarkable share (near 50%) of aulacostephanids, especially *Eurasenia* and *Involuticeras*, but also some *Balticeras* and *Rasenioides* (Wierzbowski, 2017a). In northern Switzerland (*e.g.*, Gygi, 2003, fig. 170) aulacostephanid ammonites such as *Eurasenia*, *Involuticeras*, *Pachypictonia* and *Balticeras* are described from the middle parts of the Hypselocyclum Zone, near the boundary of the Hippolytense and Lothari subzones. The first macroconch of *Rasenioides* like *R. glazeki* Wierzbowski possibly also emerged here from the *Vineta–Balticeras* lineage.

The sixth major ammonite turnover occurs at the top of the Hypselocyclum Zone – to the Divisum Zone of the Submediterranean zonal scheme, which corresponds to the Subboreal Askepta Subzone correlated either with the topmost part of the Cymodoce Zone or lowermost part of the Mutabilis Zone *sensu lato* (Matyja, Wierzbowski, 2000a). The sudden development of the aulacostephanid genus *Rasenioides* appears to be the main feature enabling the recognition of the basal part of the Askepta Subzone in southern England (Birkelund *et al.*, 1983) and in northern Poland (Matyja, Wierzbowski, 2000a; see also 1998). The same phenomenon is well recognized in Aquitaine, western France, in the Chatelaillonensis Subzone as the *askepta* horizon (Hantzpergue, 1989), marking here the base of a wider stratigraphical interval with dominance of these new Subboreal *Rasenioides* faunas, and the beginning of the new transgressive cycle (Hantzpergue, 1995).

The decline of the shallow-water carbonate platforms marked by the appearance of transgressive deposits was noted commonly in the Submediterranean Province, at the end of the Hypselocyclum Chron: it is observed both in central Poland – in the Holy Cross Mts. area, and in northern Switzerland-south-eastern France in the Jura Mts. This phenomenon placed along the northern Tethyan shelf was possibly also tectonically-controlled (see Kutek, 1994; Wierzbowski, 2020), and had a marked influence on the development of the ammonite faunas. The ammonite faunas which appeared at the top of the Hypselocyclum Zone – the base of the Divisum Zone consisted of new members of the family Ataxioceratidae, such as *Garnierisphinctes* and *Crussoliceras*, whose occurrence was commented on even as “a brutal crisis marked by extinctions, not a real turnover” (Atrops, Ferry, 1989). The phenomenon recognized in the Russian Platform, in Tatarstan of the southern part of European Russia, also shows here the occurrence of the same Submediterranean *Crussoliceras* in deposits transgressively overlying those with Subboreal *Rasenia* (Rogov *et al.*, 2017). It seems thus that the lower part of the discussed major ammonite turnover showed the abrupt arrival of Subboreal *Rasenioides* in the north of Europe, and the new Tethyan-origin Ataxioceratidae in the south.

These migrations resulted in the successive elimination of older ammonite faunas, but some of them – mostly aulacostephanids of the Subboreal genus *Rasenia* and of the Submediterranean genera *Eurasenia* and *Involuticeras* – had continued their existence for some time giving even later, during beginning of the Late Kimmeridgian, an outset to the development of new forms: *Rasenia* to *Zenostephanus* (see *e.g.*, Birkelund *et al.*, 1983; Wierzbowski, Smelror, 2020), and *Eurasenia* to *Pararasenia*. The latter transition is possibly related to the development of a special branch of *Eurasenia* including such forms as *Eurasenia aulnisa* Hantzpergue and *E. manicata* (Schneid) described by Hantzpergue (1989) from the succession of Aquitaine. The corresponding *aulsnisa* horizon and the *manicata* horizon strictly correspond to the *semistriatum* horizon of the Lothari Subzone of the uppermost Hypselocyclum Zone (Matyja, Wierzbowski, 2000a), thus they directly preceed the sudden development of *Rasenioides* indicative of the Askepta Subzone. It should be remembered that such *Eurasenia* species like *E. pendula* (Schneid) and *E. trifurcata* (Reinecke) described herein from the stratigraphical interval at the boundary of the Hypselocyclum Zone and the Divisum Zone in the Holy Cross Mts., central Poland, seem to be closely related to the discussed species from Aquitaine. Some of these species migrated possibly before the end of the Early Kimmeridgian, during the maximum of sea-level rise into peripheral areas lying outside the development of the *Eurasenia* lineage. Then, they evolved possibly into *Pararasenia* Spath, 1925 during the Late Kimmeridgian (see Hantzpergue, 1989, fig. 130; see also Borrelli, 2014: *cf.* also Ziegler, 1962), and successively colonized a wide area of Submediterranean Europe and (?) central America. This is in accordance with the sudden appearance of *Pararasenia* ammonites in the Late Kimmeridgian in many areas, including that of the south-western margin of the Holy Cross Mts., central Poland (Kutek, 1968, pl. 7: 3a, b).

In the higher stratigraphical interval of the Askepta Subzone, the *Rasenioides* ammonite faunas are successively replaced by those transitional to *Aulacostephanoides*; such a transition is widely recognized from southern England and Aquitaine in north-west, through northern Poland, and then to Tatarstan in the southern part of the Russian Platform in the south-east (see *e.g.*, Birkelund *et al.*, 1983; Hantzpergue, 1989, 1995; Matyja, Wierzbowski, 1998, 2000a; Rogov *et al.*, 2017). A possibly late *Rasenioides* corresponding to *R. moeschi* (Oppel) occurs stratigraphically as high as a middle part of the Uhlandi Subzone of the Divisum Zone in the Holy Cross Mts., central Poland (Matyja, Wierzbowski, 2000a; see also herein), a succession dominated by Tethyan-origin ammonites. In the upper part of the stratigraphical interval with *Rasenioides*, in the upper part of the Askepta Subzone, there appears also a new assemblage of small-sized cardioceratid ammonites correlated with the transition between the Boreal Kitchini Zone and the Kochi (=Sokolovi) Zone (see Wierzbowski, Smelror, 1993; Wierzbowski, Rogov, 2013; Wierzbowski *et al.*, 2015). It is composed of more heavily-ribbed small-sized last *Amoebites*, and a very weakly and densely-ribbed group representing possibly the earliest representatives of the genus *Euprionoceras* similar to *E. kapffi* (Oppel) and *E. norvegicum* (Wierzbowski). The occurrence of these cardioceratid ammonites ranging up to the appearance of the first *Aulacostephanoides*, is widely recognized from southern England (Arkell, Callomon, 1963; Birkelund *et al.*, 1983), northern Poland, including Peri-Baltic Syneclise (Wierzbowski *et al.*, 2015), to Tatarstan in southern Russian Platform (Rogov *et al.*, 2017). Their occurrence indicates a very high sea-level and preceeds the beginning of the next aulacostephanid turnover marking the appearance of such Late Kimmeridgian genera like *Aulacostephanoides*, *Pararasenia* and *Zenostephanus* (*e.g.*, Rogov *et al.*, 2017; Wierzbowski, Rogov, 2013; Wierzbowski, Smelror, 2020).

MAIN STAGES OF EVOLUTIONARY DEVELOPMENT OF AULACOSTEPHANIDAE AND SUMMARY

The detailed description of the ammonite faunas of Aulacostephanidae as given above showed that during the Late Oxfordian and the Early Kimmeridgian the development of the family followed a smooth evolutionary path in some stratigraphical intervals and was expressed by fairly sudden evolutionary changes in others. The latter corresponded to ammonite turnovers which denoted the time intervals when particular taxa – mostly of the genus rank have been gained or lost and the diversity of the clades changed markedly. Six major turnovers (1–6), and two of minor scale (3a, 3b) have been distinguished in the discussed evolutionary history of Aulacostephanidae in Europe. These turnovers corresponded also to changes in other ammonite families, and can be summarized as follows:

- **1st major turnover** at the beginning of the family Aulacostephanidae is at the base of the Upper Oxfordian in the Nunningtonense Subzone to the Cautisnigrae Zone interval (Subboreal) marked by appearance and extinction of the genus *Decipia*;
- **2nd major turnover** is marked by appearance of the genus *Ringsteadia* at the base of the Pseudocordata Zone (Subboreal) and transition between the Bifurcatus and Hypselum zones (Submediterranean);
- **3rd major turnover** is marked by splitting (cladogenesis) of the *Ringsteadia* lineage into three major lineages due to the allopatric speciation – that leading to nominative subgenus *Pictonia* (in NW Europe) and those to *Vielunia* and *Vineta* (in NE European and Central European araeas), at the Pseudocordata/Baylei zone (Subboreal) and the Hypselum/Bimammatum (Submediterranean) zone boundaries, corresponding to the Oxfordian/Kimmeridgian boundary;
- **3a and 3b minor turnovers** are marked by short invasions of the NW European Subboreal *Pictonia* into Submediterranean areas – they are recognized in the lowermost part of the Hauffianum Subzone of the Bimammatum Zone, and at the base of the Planula Zone;
- **4th major turnover** is marked by development of the heavily-ribbed last *Pictonia* (*Pictonites*) and *P.* (*Pomerania*) and appearance of the *Rasenioides* microconch type; these changes corresponding also to the occurrence of other more heavily ribbed aulacostephanids are recognized in the uppermost part of the Planula Zone, and in the Galar Subzone in the Submediterranean areas (late *Vielunia*), and in the uppermost part of the Baylei Zone in Subboreal areas (transition between *Pictonia* and *Rasenia*);
- **5th major turnover** is marked by development of the heavily ribbed *Eurasenia* and *Involuticeras* in the Submediterranean areas which successively replaced the older *Pictonia* (*Pomerania*) – *Rasenia* (*Pachypictonia*) assemblage; this phenomenon began already at the boundary of the Platynota and Hypselocyclum Zone, but it continued upwards into the Hypselocyclum Zone;
- **6th major turnover** is marked by a successive decline of the genera *Rasenia*, *Eurasenia* and *Involuticeras*, and a wide development of the genus *Rasenioides* and its migration along the Subboreal to Submediterranean transitional areas; it corresponds stratigraphically to the topmost part of the Hypselocyclum Zone and the Divisum Zone (Submediterranean) and the upper part of the Cymodoce Zone (*sensu lato*) and especially to the Askepta Subzone (Subboreal).

The ammonite turnovers discussed above correspond well to the transgressive phases in the terms of sequence stratigraphy ranging up to the maximum (main) flooding-surfaces – which is in general agreement with the so far proposed relations between the development of the ammonite faunas and sea-level changes during the Late Jurassic. The present study yields, however, some new specific observations on the character of the evolutionary development of Aulacostephanidae (and some other ammonite groups) and their relation to palaeogeography and environmental conditions. These observations make possible the recognition of the main phases of evolutionary development of Aulacostephanidae (see also Wierzbowski, 2022).

The aulacostephanid turnovers (1, 2) were related to transgressions which stimulated the ammonite evolution by unstable ecological factors. The turnovers were generally followed by occurrences of small-sized cardioceratid ammonites interpreted as nektopelagic. Such forms were associated with the common development of the radiolarian faunas and the presence of nutrient-rich waters, and indicated a very high sea-level. These initial stages of aulacostephanid development (I and II, see Fig. 3) include the whole Late Oxfordian.

When considering the stratigraphical interval of the lowermost Kimmeridgian, a marked difference in ammonite faunas and type of sediments is observed between the NW European Subboreal areas (Baylei Zone) and the Central to SE European Submediterranean-Subboreal areas (Bimammatum to Planula zones). The continuous succession of dark silty shales of the Kimmeridge Clay-type facies in the former area is associated with the occurrence of special *Pictonia* ammonites showing marked disturbances in their ontogenetical development. This occurrence is correlated with an almost continuous succession of small cardioceratid ammonites modified by heterochrony (oscillating around widely treated paedomorphosis: mostly slower growth and/or earlier offset) which has been an adaptatation to unstable environmental conditions, such as in the Skye section (Matyja *et al.*, 2006; Wierzbowski *et al.*, 2018). On the other hand, in more southern European areas the deposits are mostly limestones, whereas the intervals with small-sized cardioceratids (also small-sized oppeliids – both interpreted as nektopelagic) with north-western *Pictonia* are encountered sporadically (turnovers 3a, 3b, and initial stage of 4). The intervals with small-sized ammonites reveal commonly the development of radiolarian faunas indicating possibly a high-sea level with nutrient rich waters. Such development of deposits and ammonite faunas is consistent with occurrences of the shelf dysoxic-anoxic events (SDAE) generally characteristic of the Boreal-Subboreal areas especially strongly developed in the northern basins, becoming weaker in southern ones (see Rogov *et al.*, 2020). The dysoxic-anoxic phenomena were especially typical of the Boreal and Subboreal areas during the Late Jurassic, because of a supply of high amounts of dissolved nutrients to the basin due to relatively higher humidity and a high sea-level.

The special palaeogeographical configuration of the two discussed areas, northern and southern ones, during the earliest Kimmeridgian affected the sedimentary environment and the evolutionary development of aulacostephanids begining from the major ammonite turnover 3. This stage of development (III) can be possibly correlated with the "2nd order transgressive cycle" as recognized in northern Switzerland with its base near the Hypselum-Bimammatum zone boundary (Gygi *et al.*, 1998). The different development of aulacostephanids in NW European and NE European areas has resulted, however, mostly from their geographical isolation by the emergence of the separating land-barriers (Enay, 1980; Wierzbowski *et al.*, 2016) which indicates additionally the tectonic constraints of the discussed faunal changes.

The next phase in development of aulacostephanids (IV) begins with ammonite turnover 4 at the top of the Submediterranean Planula Zone, and within the overlying Galar Subzone, and it continues nearly to the top of the Hypselocyclum Zone. This interval has been distinguished in the Submediterranean succession because of its special facies development as the beginning of the "2nd order minor regressive cycle" in terms of sequence stratigraphy (Gygi *et al.*, 1998). It was characterized by strong progradation of the shallow-water carbonate succession, like that of the Holy Cross Mts. in central Poland, which resulted in the appearance of strongly-contrasted facies patterns suitable for the appearance of highly specialized large-sized forms of the *Pictonia* (*Pictonites*) – *P.* (*Pomerania*) *to Rasenia* (*Pachypictonia*) lineage, but also heavily ornamented representatives of *Vielunia* and it descendants (Wierzbowski, 2020; see also comments in palaeontological part of this study). It is worth noting that active current circulation including both Boreal-Subboreal basins in the NW Europe, but also Submediterranean-Subboreal-Boreal areas in central and NE Europe has been recognized from the early Cymodoce Chron, thus corresponding also to the development of the heavily-ribbed aulacostephanids of *Rasenia* (*Rasenia*) and stimulating their migrational routes (Vickers *et al.*, 2020; Wierzbowski, 2020; Wierzbowski, Smelror, 2020).

A disturbance corresponding to the ammonite turnover 5 resulted from the gradual replacing of *Pomerania*–*Pachypictonia* aulacostephanids by Submediterranean ataxioceratids and aulacostephanids of the genera *Eurasenia* and *Involuticeras*, and it has been interpreted as the consequence of a temporary drowning of the shallow-water carbonate platform due to some sea-level rise (see Wierzbowski, 2020). The lineage of *Pictonia* (*Pictonites* and *Pomerania*) to *Rasenia* (*Pachypictonia*) disappeared before the end of the Early Kimmeridgian which was possibly related to changes in sea-current circulation as well as the decline of the central European zone of shallow-water carbonate deposits.

The last phase in the development of Aulacostephanidae (V) begins with ammonite turnover (6), and corresponds to the end of the Lower Kimmeridgian [uppermost Hypselocyclum-Divisum zones (Submediterranean) and Askepta Subzone (Subboreal]. This stratigraphical interval is of strongly transgressive character in Central Europe, and this phenomenon was at least partly tectonically controlled along the northern Tethyan shelf (*e.g.*, Kutek, 1994; see also Wierzbowski, 2020). The overall transgression resulted in the appearance of belts of similar facies: the Kimmeridge Clay-type facies belt dominating in northern Europe was replaced towards the south by marls and limestones of the "facies virgulien" with the oyster *Nanogyra virgula*. These facies showed a strong development of ammonites of the genus *Rasenioides* which commonly occurred in a wide zone of Central and Northern Europe from Aquitaine and southern England in the west (Birkelund *et al.*, 1983; Hantzpergue, 1989) to northern Poland and the Russian Platform in the east (Matyja, Wierzbowski, 2000a; Rogov *et al.*, 2017), replacing to a large extent older aulacostephanids. Similarly as in the earliest Kimmeridgian, this interval is topped with small-sized cardioceratids marking possibly the maximal sea-level rise (see also comments in the chapter on ammonite turnovers). The transgression opened a final stage in aulacostephanid history at the beginning of the Late Kimmeridgian.

Summarizing, after the existence of the primordial genera of Aulacostephanidae – *Decipia* and *Ringsteadia* (stages I and II), the following evolutionary development of the family showed three episodes of marked diversification reflecting the opening up of new possibilities for adaptive divergence. The stages III and V represented episodes of strong radiation marked by the appearance of several new taxa of genus rank, both corresponding to transgressive members of the high-order sedimentary cycles. On the other hand, stage IV, occurring in between and corresponding to a regressive sedimentary member, showed the occurrence of the new endemic lineage of the *Pomerania–Pachypictonia* assemblage (and some heavily ribbed other aulacostephanids), generally related to the major development of shallow-water carbonate deposits.

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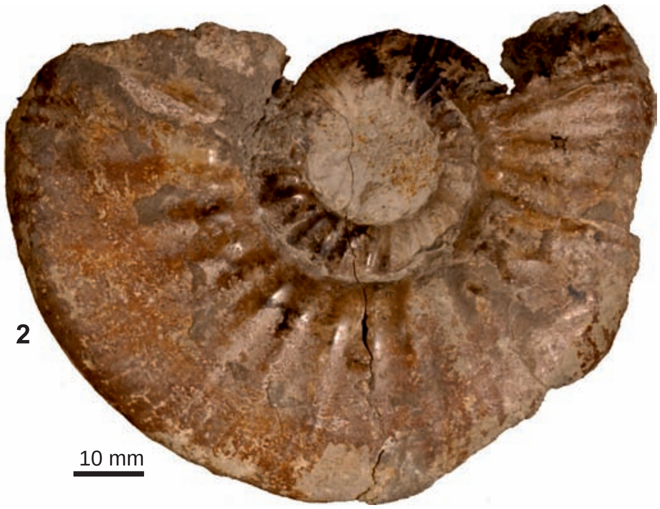
PLATE 1

Fig. 1. *Ringsteadia evoluta* Salfeld; Black Head, Dorset Coast, U.K.; Osmington Mills Ironestone Mbr; Pseudocordata Zone, Evoluta Subzone; MWG UW ZI/108/001 (col. M. Barski)

Fig. 2. *Ringsteadia frequens* Salfeld; Black Head, Dorset Coast, U.K.; Osmington Mills Ironestone Mbr; Pseudocordata Zone, Evoluta Subzone; phragmocone; MWG UW ZI/108/002 (col. A. Wierzbowski)

Fig. 3, 4. *Ringsteadia pseudoyo* Salfeld; Łobodno, Katarowa Góra quarry (beds 10, 11; see Wierzbowski *et al*., 2016), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm.; Hypselum Zone, Semiammmatum Subzone; MWG UW ZI/108/005 and 006 (col. A. Wierzbowski)



Andrzej WIERZBOWSKI – Phylogeny of the ammonite family Aulacostephanidae Spath, 1924 during the Late Oxfordian and the Early Kimmeridgian in Europe: Main lineages, patterns of evolution and sedimentological to palaeogeographical controls on evolutionary development

PLATE 2

Fig. 1. *Ringsteadia marstonensis* Salfeld; Black Head, Dorset Coast, U.K.; Osmington Mills Ironestone Mbr; Pseudocordata Zone, Evoluta Subzone; MWG UW ZI/108/003 (col. A. Wierzbowski)

Fig. 2, 3. *Microbiplices microbiplex* (Quenstedt); Łobodno, Katarowa Góra section (beds 10, 11; see Wierzbowski *et al*., 2016), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm.; Hypselum Zone, Semiammmatum Subzone; MWG UW ZI/108/007 and 008 (col. A. Wierzbowski)

Fig. 4. *Microbiplices procedens* (Oppenheimer); Łobodno, Katarowa Góra section (beds 10, 11; see Wierzbowski *et al*., 2016), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm.; Hypselum Zone, Semiammmatum Subzone; MWG UW ZI/108/009 (col. A. Wierzbowski)

Fig. 5. *Pictonia* (*Pictonia*) aff. *normandiana* Tornquist; Lisowice (Pj 139/140 quarry, bed 1, lowermost part, see. Matyja, Wierzbowski, 1997), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm., Miedzno Chalky Limestone Mbr; Planula Zone, basal part; MWG UW ZI/108/010 (col. A. Wierzbowski)

Fig. 6. *Rasenia* (*Rasenia*) *inconstans* Spath; Wierzbica cement work quarry, north-eastern margin of the Holy Cross Mts., central Poland; Platynota or Hypselocyclum Zone; seen part of the specimen is the body-chamber; MWG UW/A/27/59 (col. J. Gutowski)

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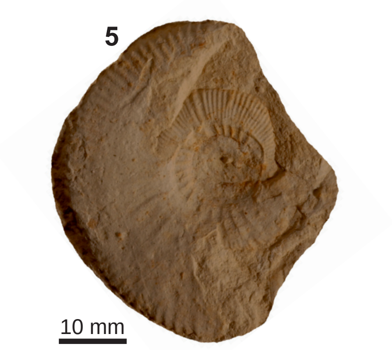

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Andrzej WIERZBOWSKI – Phylogeny of the ammonite family Aulacostephanidae Spath, 1924 during the Late Oxfordian and the Early Kimmeridgian in Europe: Main lineages, patterns of evolution and sedimentological to palaeogeographical controls on evolutionary development

PLATE 3

Fig. 1A, B. *Ringsteadia pseudoyo* Salfeld; Black Head, Dorset Coast, U.K.; Osmington Mills Ironestone Mbr; Pseudocordata Zone, Evoluta Subzone; phragmocone; A, B – both sides of the same specimen; MWG UW ZI/108/004 (col. M. Barski)

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PLATE 4

Fig. 1. *Pictonia* (*Pomerania*) *schmidti* Dohm; Czarnogłowy (Zarnglaff), Western Pomerania, north-western Poland; “blue-gray marly unit” of Czekalska and Krygowski (1957) = beds 13–18 of Wilczyński (1962); MUZ PIG. 1120.II.17 (col. A. Czekalska)

Andrzej WIERZBOWSKI – Phylogeny of the ammonite family Aulacostephanidae Spath, 1924 during the Late Oxfordian and the Early Kimmeridgian in Europe: Main lineages, patterns of evolution and sedimentological to palaeogeographical controls on evolutionary development

PLATE 5

Fig. 1. *Pictonia* (*Pomerania*) *consobrina* (Schneid); Czarnogłowy (Zarnglaff), Western Pomerania, north-western Poland; possibly beds 13–18 of Wilczyński (1962); phragmocone; MWG UW ZI/108/011 (col. J. Kutek)

Fig. 2. *Pictonia* (*Pomerania*) cf. *albinea* (Oppel); Lisowice (Pj 110 quarry, bed 14, see Matyja, Wierzbowski, 1997), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm., Miedzno Chalky Limestone Mbr; Planula Zone, upper part; both fragments belong to the same specimen; MWG UW ZI/108/012 (col. A. Wierzbowski)

Fig. 3. *Rasenia* (*Pachypictonia*) sp. (? *P. adelpha* Schneid); Czarnogłowy (Zarnglaff), Western Pomerania, north-western Poland; "blue-gray marly unit" of Czekalska and Krygowski (1957) = beds 13–18 of Wilczyński (1962); phragmocone; MUZ PIG. 1120.II.21 (col. A. Czekalska)

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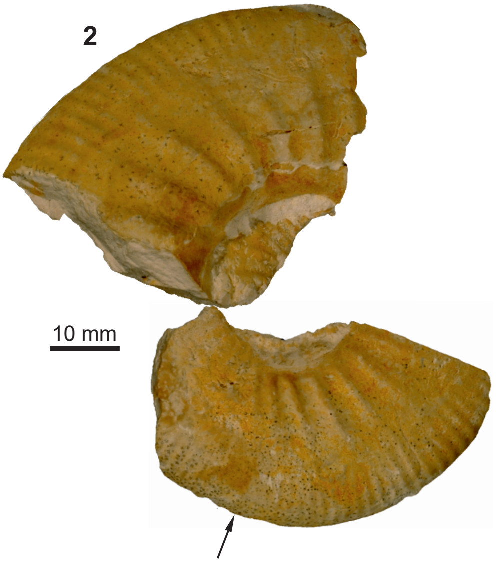

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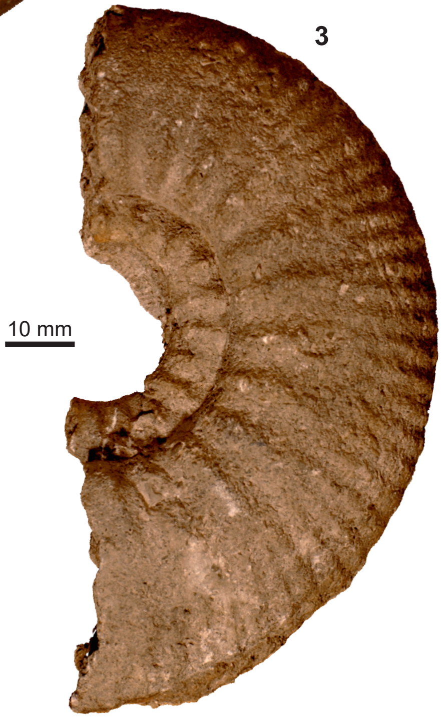

Andrzej WIERZBOWSKI – Phylogeny of the ammonite family Aulacostephanidae Spath, 1924 during the Late Oxfordian and the Early Kimmeridgian in Europe: Main lineages, patterns of evolution and sedimentological to palaeogeographical controls on evolutionary development

PLATE 6

Fig. 1. *Rasenia* (*Pachypictonia*) *perornatula* (Schneid); Wierzbica cement works quarry, north-eastern margin of the Holy Cross Mts., central Poland; uppermost Platynota Zone – lowermost Hypselocyclum zones; phragmocone; MWG UW ZI/108/013 (col. M. Wojciechowska)

Fig. 2, 3. *Vielunia dzialosinensis* Wierzbowski et Głowniak; Bielawy quarry at Barcin; Kujawy region; northern Poland; Częstochowa Sponge Limestone Fm.; Bimammatum Zone;
MWG UW ZI/108/015 and 016 (col. A. Wierzbowski)

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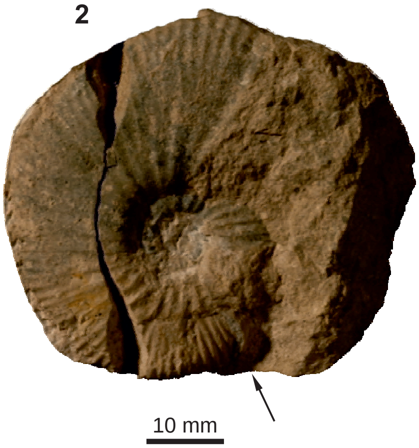

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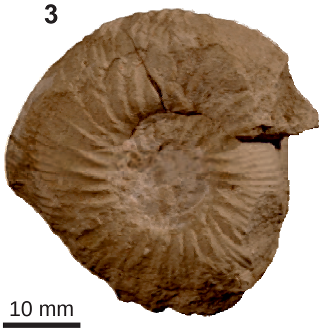

Andrzej WIERZBOWSKI – Phylogeny of the ammonite family Aulacostephanidae Spath, 1924 during the Late Oxfordian and the Early Kimmeridgian in Europe: Main lineages, patterns of evolution and sedimentological to palaeogeographical controls on evolutionary development

PLATE 7

Fig. 1. *Rasenia* (*Pachypictonia*) aff. *indicatoria* (Schneid); Małogoszcz cement work quarry, south-western margin of the Holy Cross Mts., central Poland; Skorków Lumachelle Fm., lowermost part; uppermost Hypselocyclum – lowermost Divisum zones; phragmocone; MWG UW ZI/108/014 (col. A. Wierzbowski)

1

PLATE 8

Fig. 1. *Vielunia limosa* (Quenstedt); Laufen, Swabian Alb, southern Germany; (Impressamergel Fm.; Bimammatum Zone, Hauffianum Subzone – after G. Schweigert pers.inf.); plaster cast of the holotype (*Ammonites limosus* in: Quenstedt, 1888, pl. 124: 3)

Fig. 2. *Vielunia* cf. *conspicua* (Schneid); Działoszyn, “Warta” cement works quarry, Wieluń Upland, central Poland; Pilica Limestone Fm., Wolbrom Limestone Mbr; Planula Zone, upper part; body chamber; MWG UW ZI/108/017 (col. A. Szynkiewicz)

Fig. 3. *Vielunia* cf. *limosa* (Quenstedt); Lisowice (Pj 110 quarry, upper part of the section, rubble; see Matyja, Wierzbowski, 1997), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm., Miedzno Chalky Limestone Mbr; Planula Zone; phragmocone; MWG UW ZI/108/018 (col. A. Wierzbowski)

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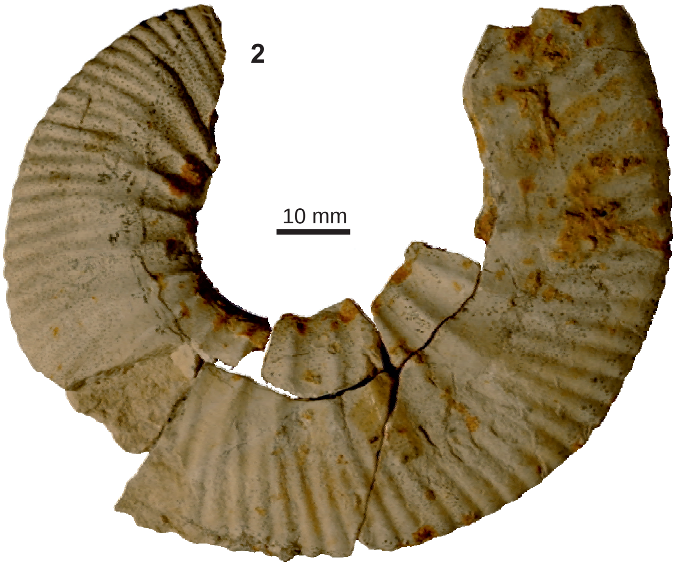

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Andrzej WIERZBOWSKI – Phylogeny of the ammonite family Aulacostephanidae Spath, 1924 during the Late Oxfordian and the Early Kimmeridgian in Europe: Main lineages, patterns of evolution and sedimentological to palaeogeographical controls on evolutionary development

PLATE 9

Fig. 1. *Vielunia attenuata* (Schneid); Pradła, Częstochowa Upland, central Poland; Prusicko Fm.; Platynota Zone, Polygyratus/Desmoides subzones; MWG UW ZI/108/019 (col. M. Dunin)


1
10 mm

PLATE 10

Fig. 1. *Vielunia* cf. *conspicua* (Schneid); Czarnogłowy (Zarnglaff), western Pomerania, north-western Poland; phragmocone; MUZ PIG 1120.II.13 (col. A. Czekalska)

Fig. 2. *Vielunia flexuoides* (Quenstedt); Lisowice (Pj 110 quarry, bed 7, see Matyja, Wierzbowski, 1997), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm., Miedzno Chalky Limestone Mbr; Planula Zone; MWG UW ZI/108/020 (col. J. Graczyk and A. Wierzbowski)

Fig. 3. *Vielunia flexuoides* (Quenstedt); Laufen, Swabian Alb, southern Germany; Impressamergel Fm., Bimammatum Zone – after G. Schweigert pers. inf.; plaster cast of *Ammonites streichenensis* in: Quenstedt, 1888, pl. 107: 6

Fig. 4. *Eurasenia rolandi* (Oppel); Małogoszcz cement work quarry, south-western margin of the Holy Cross Mts., central Poland; Skorków Lumachelle Fm., lowermost part; uppermost Hypselocyclum – lowermost Divisum zones; somewhat distorted, MWG UW ZI/108/029 (col. A. Radwański)

Fig. 5. *Vielunia flexuoides* (Quenstedt); Lisowice (Pj 110 quarry, rubble – lower part of the section, see Matyja, Wierzbowski, 1997), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm., Miedzno Chalky Limestone Mbr; Planula Zone; MWG UW ZI/108/036 (col. J. Graczyk, A. Wierzbowski)

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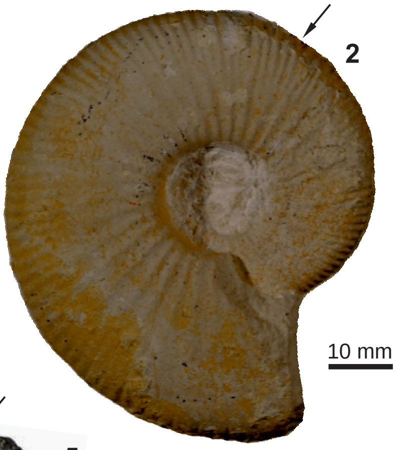

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Andrzej WIERZBOWSKI – Phylogeny of the ammonite family Aulacostephanidae Spath, 1924 during the Late Oxfordian and the Early Kimmeridgian in Europe: Main lineages, patterns of evolution and sedimentological to palaeogeographical controls on evolutionary development

PLATE 11

Fig. 1. *Eurasenia vernacula* (Schneid); Wierzbica cement works quarry, north-eastern margin of the Holy Cross Mts., central Poland; micritic limestones overlying Wierzbica Oolite; Hypselocyclum Zone; MWG UW ZI/108/023 (col. M. Wojciechowska)

Fig. 2, 3. *Eurasenia pendula* (Schneid); Małogoszcz cement work quarry, south-western margin of the Holy Cross Mts., central Poland; Skorków Lumachelle Fm.; Divisum Zone; phragmocones; MWG UW ZI/108/024 and 025 (col. A. Radwański)

Fig. 4. *Eurasenia trimera* (Oppel); Małogoszcz cement work quarry, south-western margin of the Holy Cross Mts., central Poland; Skorków Lumachelle Fm., lowermost part; uppermost Hypselocyclum – lowermost Divisum zones; phragmocone; MWG UW ZI/108/026 (col. A. Radwański)

Fig. 5. *Eurasenia trimera* (Oppel); Małogoszcz cement work quarry, south-western margin of the Holy Cross Mts., central Poland; Skorków Lumachelle Fm., upper part; Divisum Zone, Uhlandi Subzone; phragmocone; MWG UW ZI/108/027 (col. A. Radwański)

1

10 mm

2

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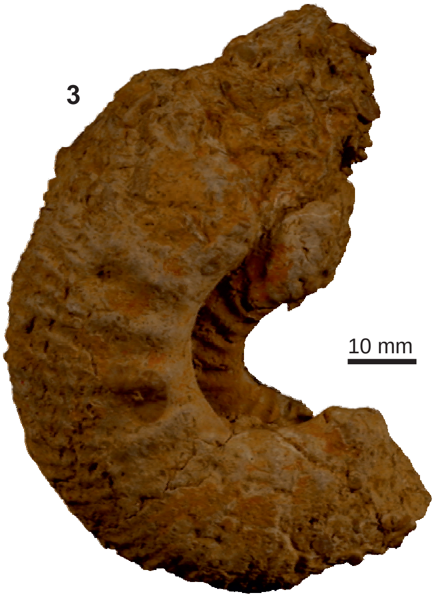

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Andrzej WIERZBOWSKI – Phylogeny of the ammonite family Aulacostephanidae Spath, 1924 during the Late Oxfordian and the Early Kimmeridgian in Europe: Main lineages, patterns of evolution and sedimentological to palaeogeographical controls on evolutionary development

PLATE 12

Fig. 1. *Eurasenia trimera* (Oppel); ? Wierzbica cement work quarry, north-eastern margin of the Holy Cross Mts., central Poland; Platynota–Hypselocyclum zones; phragmocone; MWG UW ZI/108/028

1

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PLATE 13

Fig. 1. *Involuticeras* cf. *limbatum* (Schneid); Góry Mokre, near Przedbórz, south-western margin of the Holy Cross Mts., central Poland; Małogoszcz Oolite Fm.; Platynota Zone, uppermost part – Hypselocyclum Zone, lowermost part; phragmocone; MWG UW ZI/108/030 (col. J. Niemczynowicz)

1

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PLATE 14

Fig. 1. *Vineta submediterranea* (Wierzbowski); Lisowice (Pj 110 quarry, rubble, see Matyja, Wierzbowski, 1997), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm., Miedzno Chalky Limestone Mbr; Planula Zone; MWG UW ZI/108/032 (col. J. Graczyk and A. Wierzbowski)

Fig. 2. *Involuticeras involutum* (Quenstedt); Małogoszcz cement work quarry, south-western margin of the Holy Cross Mts., central Poland; Skorków Lumachelle Fm., lowermost part; uppermost Hypselocyclum – lowermost Divisum zones; phragmocone; MWG UW ZI/108/031 (col. A. Radwański)

Fig. 3. *Vineta* cf. *striatula* (Schneid); Poręba near Wolbrom, Cracow Upland, central Poland; Pilica Fm., Latosówka Marl Mbr., basal part; Planula Zone, uppermost part; MWG UW ZI/108/033 (col. M. Skowronek)

Fig. 4A–C. *Vineta streichense* (Oppel); Trzyciąż near Wolbrom, Cracow Upland, central Poland; Częstochowa Sponge Limestone Fm.; Bimammatum Zone; microconch: A – inner whorls, B – body chamber with the end of phragmocone; C – imprint of the opposite side of the whole specimen; MWG UW ZI/108/034 (col. M. Skowronek)

Fig. 5. *Vineta submediterranea* (Wierzbowski), late form; Lisowice (Pj 110 quarry, upper part of the section, rubble, see Matyja, Wierzbowski, 1997), Wieluń Upland, central Poland; Częstochowa Sponge Limestone Fm., Miedzno Chalky Limestone Mbr; Planula Zone, upper part; MWG UW ZI/108/037 (col. J. Graczyk and A. Wierzbowski)

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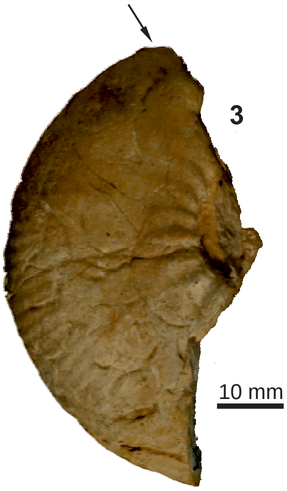

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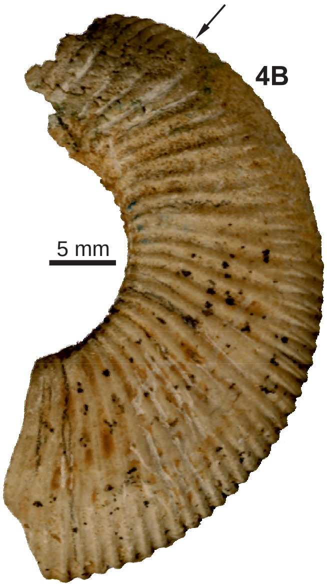
4B



4A

4C

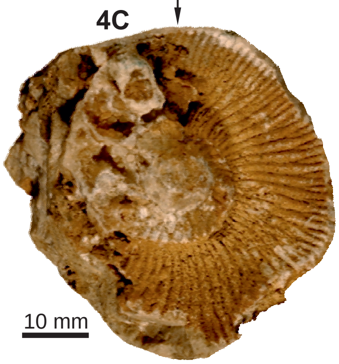


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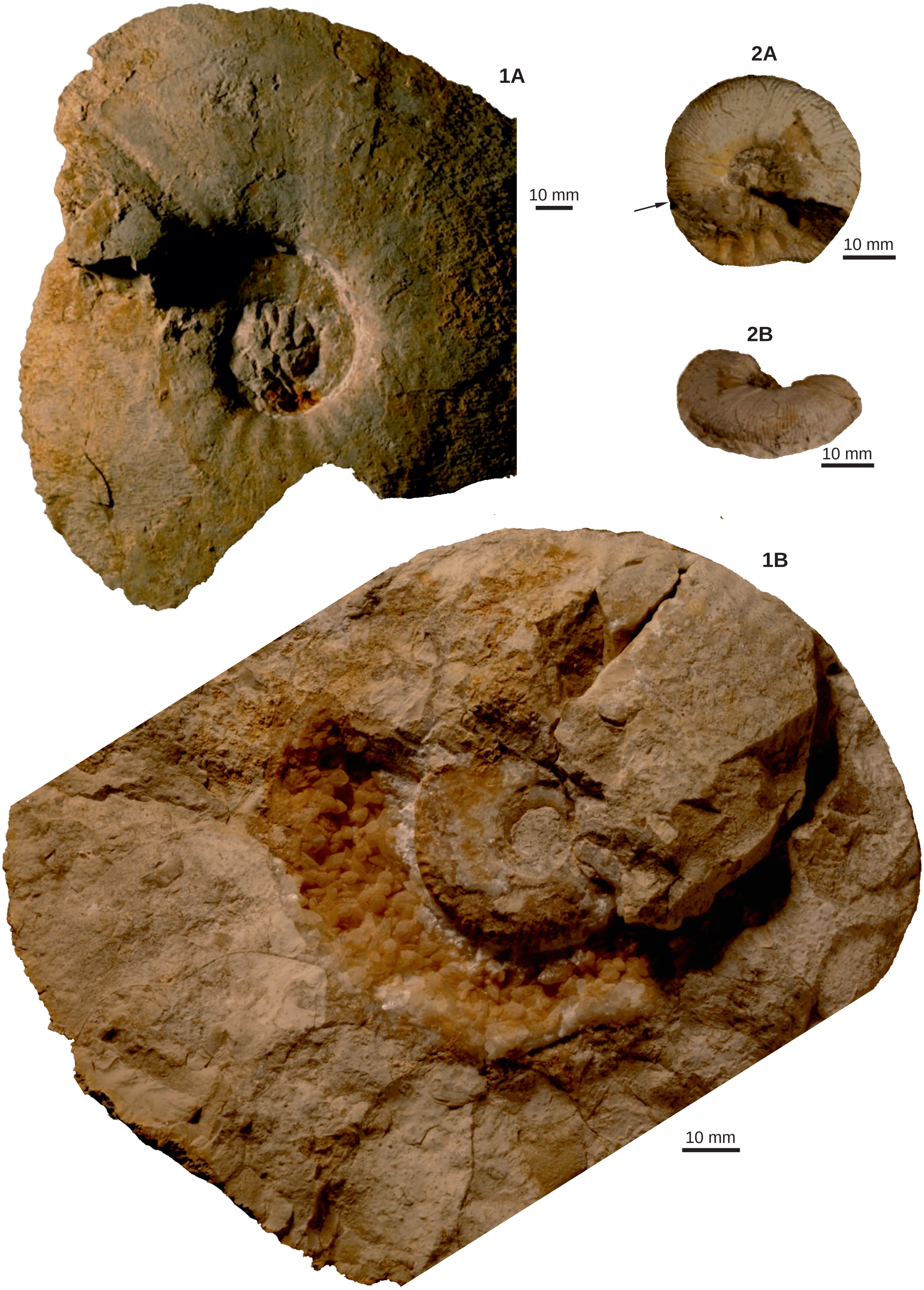
PLATE 15

Fig. 1A, B. *Rasenioides glazeki* Wierzbowski, holotype; Majaczewice near Burzenin, central Poland; Burzenin Fm., Majaczewice Mbr; Hypselocyclum Zone, basal part of the Lothari Subzone; A – phragmocone with part of the body chamber (see Wierzbowski, 2017, pl. 12), B – the view on the inner parts of the same whorls; MWG UW ZI/84/010 (col. A. Wierzbowski)

Fig. 2A, B. *Rasenioides moeschi* (Oppel); Małogoszcz cement work quarry, south-western margin of the Holy Cross Mts., central Poland; Skorków Lumachelle Fm., upper part; ; Divisum Zone, Uhlandi Subzone; A – lateral view, B – ventral view; illustrated by Matyja, Wierzbowski, 2000, fig. 4c; MWGUW ZI/108/035 (col. B. Matyja and A. Wierzbowski)

When recognized the phragmocone/body-chamber boundary is arrowed


1A
10 mm
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2B
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