

New Passendorferiinae ammonites from the upper Bimammatum Zone (Hauffianum Subzone), lowermost Kimmeridgian of the Wieluń Upland, central Poland, and their biostratigraphic and phylogenetic importance

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Abstract. The new passendorferiid ammonite species *Graefenbergites ingae* sp. nov. along with several other stratigraphically important ammonite taxa are recognized in a very complete succession of the Hauffianum Subzone of the Bimammatum Zone of the lowermost Kimmeridgian present in the Wieluń Upland. This new discovery of ammonites of Mediterranean origin proves the continuation of the *Graefenbergites* lineage known previously only from the basal part of the Hypselum Zone of the uppermost Oxfordian in the Submediterranean Province in Europe, and indicates the appearance of these ammonites on the northern Tethyan shelf during transgressive events. The specimens of *Graefenbergites ingae* described show biplicate and simple ribbing of the inner whorls, followed by trifurcate and polygyrate ribbing on the outer whorls. The new morphological characters on the outer whorls are generally akin to those of the “*Orthosphinctes* group” of the subfamily Ataxioceratinae, but the ornamentation differs from that of the type species of the genus *Orthosphinctes* in some features including development of longer secondaries showing a characteristic forward sweep on the ventral side. This may indicate the origin of some forms of Ataxioceratinae directly from Passendorferiinae.

INTRODUCTION

Objectives. The aim of this study is the presentation of a new Mediterranean-origin ammonite fauna of the subfamily Passendorferiinae occurring in a very complete and highly fossiliferous succession of the upper Bimammatum Zone (Hauffianum Subzone) of the lowermost Kimmeridgian cropping out in the quarries in the Wieluń Upland, central Poland. The ammonite succession in this area has been studied mostly in the past, when numerous active quarries between Raciszyn and Lisowice, along the Warta River, yielded abundant collections of ammonites described in several older papers (Wierzbowski, 1978; Matyja, Wierzbowski, 1997, 2006; Wierzbowski *et al.*, 2010). Progress in knowl-

edge of ammonite phylogeny in relation to the ammonite subfamily Passendorferiinae (*e.g.*, Schairer, Schlapp, 2003; Meléndez *et al.*, 2006, 2009; Enay, Howarth, 2019), however, has resulted in the necessity of revision and re-description of some older palaeontological material. On the other hand, progress in exploitation has resulted in the collection of new ammonite faunas.

This study presents new information on the ammonite faunas of the Hauffianum Subzone, especially at the boundary with the Bimammatum Subzone below, and the Planula Zone above. The corresponding boundaries, having the character of ammonite evolutionary faunal turnovers (*cf.* Wierzbowski, 2022), mark the occurrences of the new ammonite lineages. These resulted from temporary migrations

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of new groups of ammonites of Mediterranean origin and their successive evolutionary development, including especially representatives of the family Perisphinctidae (subfamily Passendorferiinae) and the family Ataxioceratidae (subfamily Ataxioceratinae). The same levels have revealed also the temporary appearance of Boreal and Subboreal ammonites which confirm their distinct transgressive character. The new fauna of Passendorferiinae recognized herein is interpreted as evidence of a wide Mediterranean ammonite dispersion over the northern Tethyan shelf which stimulated the evolutionary development of new groups of ammonites.

Geological setting. The study area of the Upper Jurassic deposits represents a part of the north-western Wieluń Upland of the northern Cracow–Silesian Monocline, which belongs to the Laramian Fore-Sudetic Monocline and consists of gently inclined Permo-Mesozoic strata. The fault pattern recognized in the area of the Wieluń Upland is dominated by two systems: a more latitudinal to WNW–ESE – directed one, and a more oblique NE–SW – directed one, ranging to be more longitudinal (NNE–SSW). Both tectonic directions correspond to strong facies gradients registered in the Upper Jurassic deposits in the study area, and they are represented by a linear development of biohermal complexes of microbial-sponge massive limestones *versus* elongated basins filled with bedded limestones. The latitudinal orientation of the Działoszyn Biohermal Complex during the Late Oxfordian–earliest Kimmeridgian, was bounded by the fault system developed in the substrate at the northern part of the Więcki Elevation (Deczkowski, 1977; Wierzbowski *et al.*, 1983). This biohermal complex was, additionally, cut perpendicularly by the Działoszyn–Kielczygłów Fault Zone having a NNE–SSW direction (see Wierzbowski, 2017, fig. 11) which resulted in the appearance of another branch of bioherms (Trębaczew Biohermal Complex). These large microbial-sponge buildups of the Częstochowa Sponge Limestone Fm., and intervening basins (such as the Pajęczno Interbiohermal Basin and the Wąsosz Interbiohermal Basin filled with micritic limestones and marls of the Pilica Fm.) are actually seen in Raciszyn quarry and the cement works quarry at Działoszyn. The deposits pass laterally towards the north-west into the deeper-water bedded sponge limestones (Miedzno Chalky Limestone Member – see Wierzbowski, 1978) of the Częstochowa Sponge Limestone Fm. in the Szczyty Basin developed in front of the elevated blocks with bioherm complexes from south and east. These bedded limestones are the subject of the present study and have been seen in several small quarries, mostly abandoned now, along the Warta River valley. This indicates that the tectonic activity of the two superimposed fault directions very strongly influenced the character of the Late Jurassic sedimentation in the study area forming an intricate facies pattern (Fig. 1).

The study area between Raciszyn and Lisowice is dominated by the occurrence of well-bedded sponge limestones including smaller-sized microbial-siliceous sponge bioherms which are, however, only locally developed. The character of the ammonite faunas commonly found in the Upper Jurassic deposits in the area of study indicates an open marine environment – both towards the south and the south-west, as shown additionally by the occurrence of Mediterranean to north-western Subboreal faunas, but also towards the north-east as marked by the occurrence of Boreal faunas (Wierzbowski, 1978, 2017; Matyja, Wierzbowski, 1997, 2000). These observations strongly help understanding of the Late Jurassic palaeogeography of the Fore-Sudetic Monocline which is actually mostly devoid of Upper Jurassic deposits. According to Matyja and Wierzbowski (1995; see also Valečka, 2019) all these areas were originally covered by Late Jurassic deposits, including the deep-water sponge megafacies, especially during the Oxfordian and Early Kimmeridgian. The development of a branch of the active rift system possibly stretching in the south-western part of the Polish Basin between Wrocław and Poznań with a high heat flow has been proposed for the Permian and the Triassic, but also later, up to the end of the Jurassic, before these areas were elevated and eroded forming the Fore-Sudetic Monocline (Karnkowski, 1999; Karnkowski *et al.*, 2023). This palaeogeographic to palaeotectonic pattern corresponds well to the preservation of the deep-water Late Jurassic facies in the west, but it is also in agreement with several other kinds of evidence which have been recognized, such as *e.g.*, the activity of hydrothermal fluids during the Jurassic (*e.g.*, Oszczepalski *et al.*, 2018) as well as the formation diagenetic clay minerals from pore fluids and the observation of the remains of gaseous and liquid hydrocarbons present at that time (*e.g.*, Maliszewska, Kuberska, 2009) as discovered in the Permian deposits of the Fore-Sudetic Monocline.

Materials and methodology. Ammonites occur fairly commonly in the studied succession. The sections considered here refer to nowadays abandoned quarries (see *e.g.*, Matyja, Wierzbowski, 1997, fig. 2; see also Fig. 1): Pj113, Pj114, Pj125, Pj126, Pj145, Pj146, between Lisowice and Raciszyn, which yielded abundant ammonites in the past, especially from the Hauffianum Subzone. The collection of ammonites studied here consists of over 100 specimens determined to the genus level (and additionally in a large part to the species level) and is composed of common representatives of four families: Oppeliidae, Perisphinctidae, Ataxioceratidae, and Aulacostephanidae, besides locally encountered Cardioceratidae, and rare Aspidoceratidae. Although many specimens have already been described and illustrated (Wierzbowski, 1978, 2022; Matyja, Wierzbowski, 1997, 2000; Wierzbowski *et al.*, 2010), some are new and have not

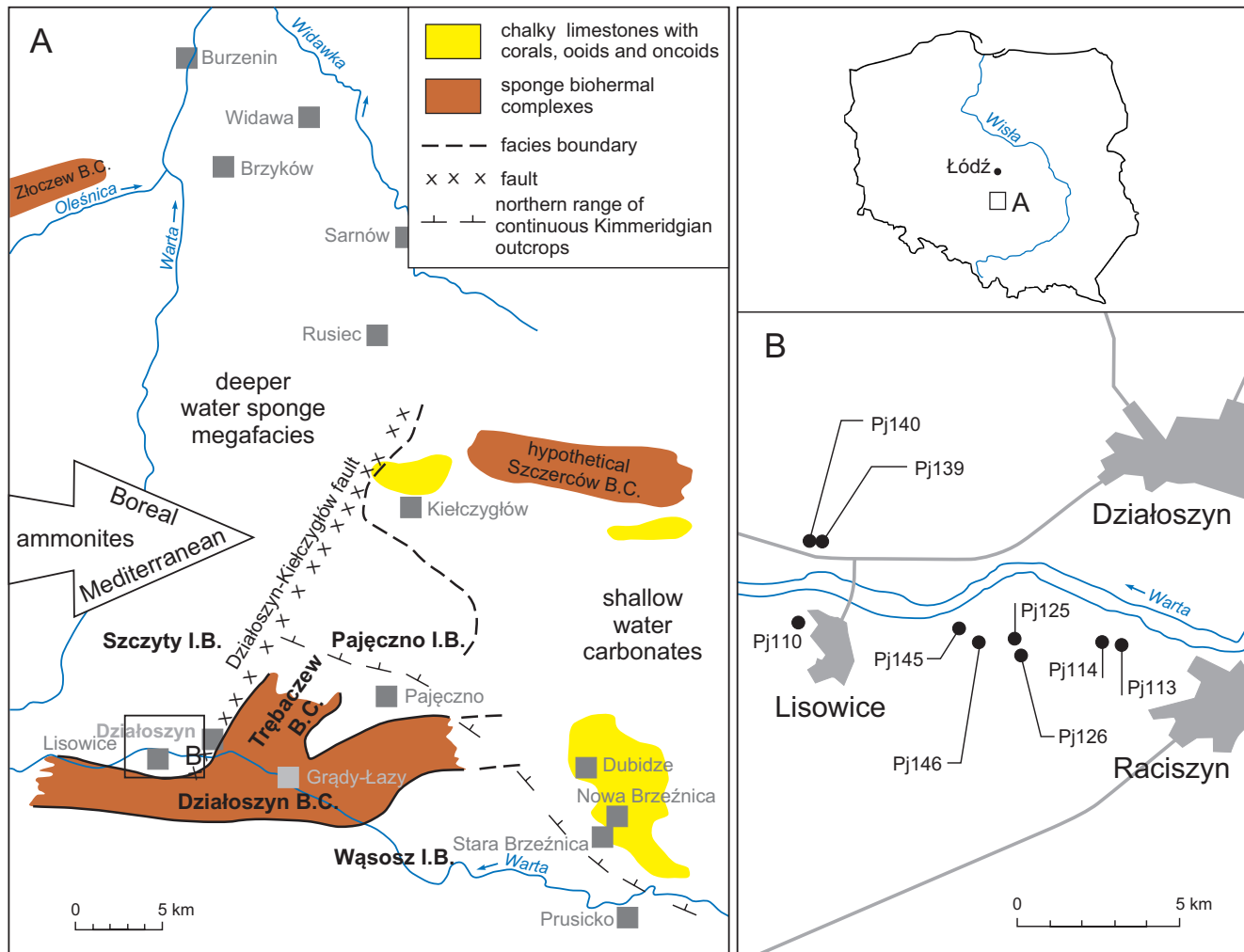


Fig. 1A. Geological map of the of the Wieluń Upland and adjoining areas (after Wierzbowski, 2017, somewhat modified) showing the Late Jurassic shallow-water carbonates and deeper-water deposits of the sponge megafacies including biohermal complexes (B.C.) to interbiohermal basins (I.B.).
B. Location of the quarries discussed in the study

been presented so far. The ammonites were often referred precisely to particular beds, but sometimes to main informal lithostratigraphic units – groups of beds of the succession only. These data enabled the recognition of general changes in the occurrence of particular groups of ammonites within the whole stratigraphic interval of the Hauffianum Subzone (Fig. 2, see also below).

The specimens are housed in the S.J. Thugutt Geological Museum, Faculty of Geology, University of Warsaw (MWGUW collections nos: A/10; A/33; A/50; A/108).

The dimorphism of ammonites, if it is strongly marked in the shell morphology, is expressed morphotaxonomically both at the generic and species levels. This refers especially to the commonly recognized forms of the families Ataxioceratidae, Aulacostephanidae and Oppeliidae whose taxo-

nomic interpretation accepted herein is especially close to those presented by Atrops (1982) in relation to Ataxioceratidae, by Wierzbowski (2022) in relation to Aulacostephanidae, and by Wierzbowski *et al.* (2010) in relation to Oppeliidae. Such is also the interpretation of micro- and macroconchs in Aspidoceratidae because of their marked morphological difference. On the other hand, the taxonomic interpretation of Perisphinctidae follows that of Meléndez *et al.* (2009) in relation to Passendorferiinae who recognized both morphs as easily comparable within a single biospecies. Such an approach, although purely descriptive is “fully conscious”, because it makes easier the study of evolutionary transformations in the lineages, especially those constrained by heterochrony, which are closely related to changes in environmental conditions.

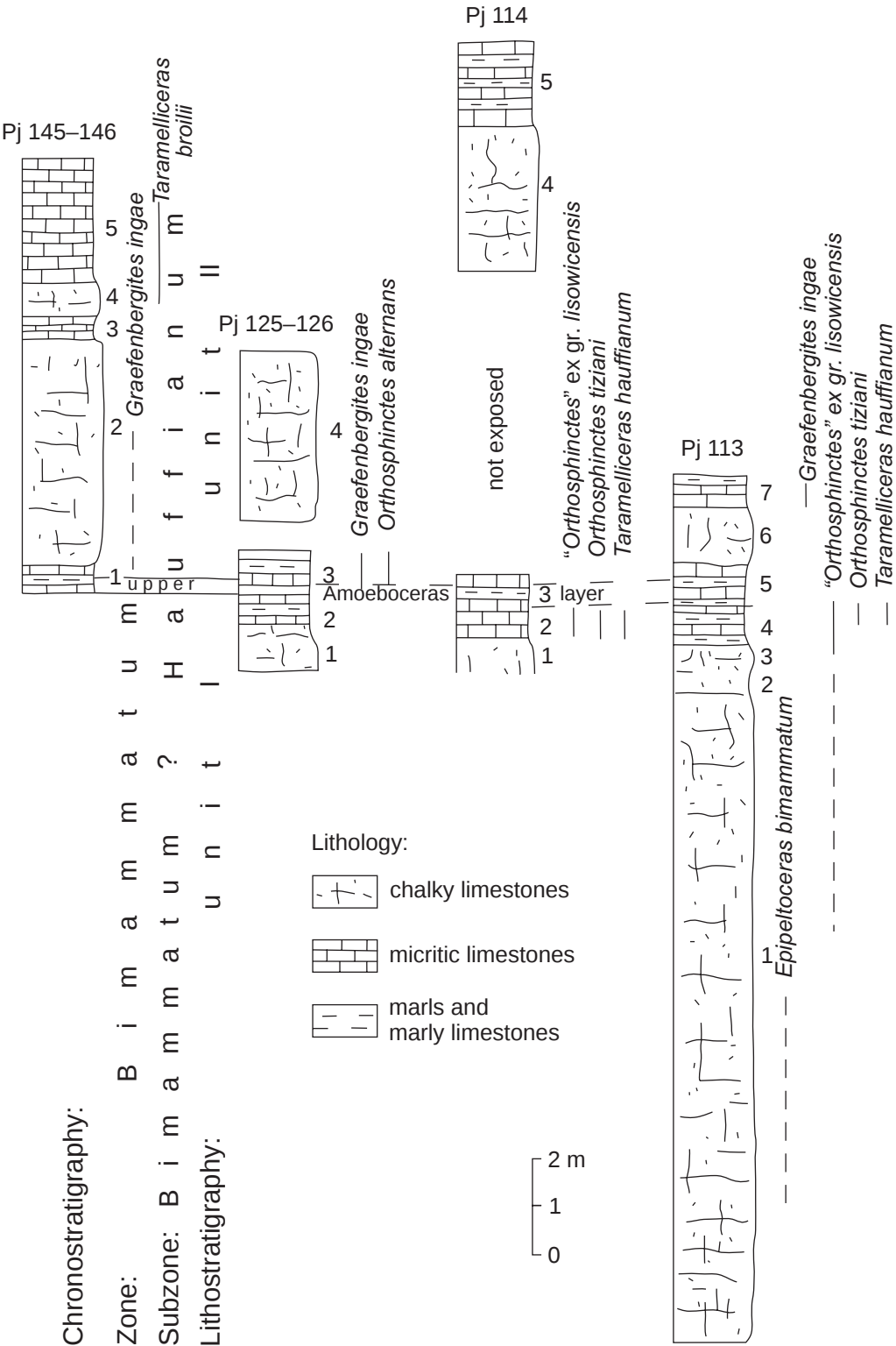


Fig. 2. Lithostratigraphic and chronostratigraphic correlation of deposits of the upper Bimammatum Zone (uppermost Bimammatum to Hauffianum subzones) of the lowermost Kimmeridgian in the Wieluń Upland

The ranges of most important stratigraphically ammonites only are indicated in the studied sections of the quarries

DESCRIPTION OF THE LITHOLOGICAL SUCCESSION AND CHANGES IN ITS FAUNAL CONTENT

The deposits of the upper part of the Bimammatum Zone, corresponding mostly to the Hauffianum Subzone, consist of bedded to massive chalky limestones with an abundant benthic fauna (siliceous sponges, brachiopods, serpulids, bryozoans, bivalves) and intervening packets of thin-bedded micritic limestones of the mudstone type and marls with a generally poor benthic fauna; the succession attains about 20 meters in thickness in the area at Raciszyn–Lisowice (Matyja, Wierzbowski, 1997, text-fig. 2; 2006, fig. B1.17; see also Wierzbowski *et al.*, 2010). The whole succession is subdivided into informal units: two (I and II) in the Bimammatum Zone – Hauffianum Subzone, additionally, these are subdivided into beds/ bed sets as follows: unit I – beds 1–5 in Pj113, beds 1–3 in Pj114, beds 1–3 in Pj125, Pj126, and bed 1 in Pj145, Pj146 quarries; unit II – beds 6, 7 in Pj113, beds 4, 5 in Pj114, bed 4 in Pj125, Pj126, and beds 2–5 in Pj145, Pj146 quarries (Matyja, Wierzbowski, 1997; Fig. 2).

The lower lithological unit (I) of the uppermost Bimammatum Subzone to Hauffianum Subzone is represented by a prominent, about 15 meters thick, set of beds composed of bedded chalky limestones with cherts locally replaced by the massive limestones of small bioherms commonly containing sponge mummies and cyanobacteria crusts; these are followed by alternating thin-bedded micritic limestones and marls, about 2 m in thickness including the “upper Amoebocheras layer”. The deposits of unit II begin with well-bedded white, friable chalky limestones about 4 meters in thickness with dark cherts, and include the overlying micritic limestones with thin marly intercalations attaining about 5 meters in thickness (Matyja, Wierzbowski, 1997; see also Wierzbowski *et al.*, 2010).

Each lithology of the described deposits of the upper part of the Bimammatum Zone corresponding mostly to the Hauffianum Subzone contains a different ammonite assemblage. The larger-sized perisphinctids with especially common representatives of Ataxioceratidae and larger-sized oppeliids are typical of chalky limestones with abundant benthic fauna, whereas the thin-bedded micritic limestones with marly intercalations with poor benthic fauna yield mostly oppeliids, with especially common small-sized *Taramelliceras* (*Metahaploceras*) *litocerum* (Oppel) (M) – *Glochiceras* (*Coryceras*) *modestiforme* (Oppel) (m), associated with some larger *Taramelliceras* (*Taramelliceras*), like *T. broilii* (Wegele) (M) and *G. (Lingulaticeras)* (m). Additionally, in the thin-bedded micritic limestones and marls, placed in the lower part of the succession studied, there occur locally abundantly small-sized Boreal cardioceratids of

the genus *Plasmatites* defining the “upper Amoebocheras layer” (see Matyja, Wierzbowski, 1997, 2000). The base of the Planula Zone shows once more the appearance of a short-timed “invasion” of Boreal cardioceratid (*Plasmatites*) and Subboreal aulacostephanid (*Pictionia*) ammonites. These Boreal to Subboreal ammonites, in a similar way to those occurring in the “upper Amoebocheras level”, appeared possibly near the peak of the transgression which brought small-sized progenetic to dwarfed forms (Matyja, Wierzbowski, 2000) and which existed but temporarily, in the longer term being unable to colonize the area. On the other hand, some Passendorferiinae related to the genus *Graefenbergites* arrived also at that time, and these occur mostly at the transition from the micritic limestones and marls of unit I to the more massive chalky limestones of unit II.

The whole discussed limestone succession represents the Częstochowa Sponge Limestone Formation developed as fossiliferous, soft, friable “chalky limestones”. These deposits were attributed to the Miedzno Chalky Limestone Member founded already by Malinowska (1972) in some other parts of the Wieluń Upland, and emended by Wierzbowski (1978).

STRATIGRAPHIC AND PALAEOGEOGRAPHIC INTERPRETATION OF THE AMMONITE FAUNAS IN THE HAUFFIANUM SUBZONE

The base of this Submediterranean/Mediterranean subzone is interpreted as being marked by the occurrence of *Taramelliceras* (*T.*) *hauffianum* (Oppel) directly above *Epipeltoceras bimammatum* (Quenstedt) as recognized in the Raciszyn quarries east of Lisowice (Matyja, Wierzbowski, 1997, pl. 4: 11). The former species is recorded also in a middle part of the Subzone (e.g., Wierzbowski, 1978, pl. 1: 13, 14; see also Wierzbowski *et al.*, 2010, fig. 2). The upper boundary of the Hauffianum Subzone is placed directly below the first occurrence of *Subnebrodites matyjai* Wierzbowski et Główniak indicating the base of the Planula Zone in Pj139/140 quarry at Lisowice (Wierzbowski *et al.*, 2010; see also Matyja, Wierzbowski, 1997 where this species was originally interpreted as *S. minutum*). The common oppeliid ammonites of the Hauffianum Subzone include taxa such as *Taramelliceras* (*Taramelliceras*) *broilii* (Wegele) and *T. (Metahaploceras)* *litocerum* (Oppel) which appear already in a higher part of the Bimammatum Subzone and range upwards into the Planula Zone (Wierzbowski *et al.*, 2010). The local stratigraphic subdivision of the Hauffianum Subzone at Lisowice was based mostly on oppeliid ammonites (Matyja, Wierzbowski, 1997) and included the *litocerum* horizon (which contained the “upper Amoebocheras layer” at the

base) in the lower part of the Subzone, and the *broilii* horizon above.

The perisphinctid ammonites in the lower part of the Hauffianum Subzone show a remarkable occurrence of Passendorferiinae, attributed originally to the genus *Passendorferia* (see Matyja, Wierzbowski, 1997, p. 87, fig. 3), but interpreted herein as belonging to the genus *Graefenbergites*, and described as *G. ingae* sp. nov. (see palaeontological part of the study; see also Pls. 1–4). These are associated with some Ataxioceratidae – especially of the genus *Orthosphinctes*, including the microconch species *O. (O.) tiziani* (Oppel) (Matyja, Wierzbowski, 1997, pl. 6: 1) in a lower part of the Subzone, but also the macroconch *O. (Pseudorthosphinctes) alternans* Enay (see Wierzbowski, 1978, pl. 8; 3), the latter ranging possibly upwards from the Bimammatum Subzone. Additionally, the common macroconch species include the “*Orthosphinctes (Pseudorthosphinctes) lisowicensis* Wierzbowski group (see Wierzbowski, 1978, pl. 9: 1, 2, and additionally “*Pomerania helvetica*” in: pl. 4: 2; 5: 1; see also Matyja, Wierzbowski, 1997, p. 87, pl. 6: 3), and some other related forms, whose systematical status is, however, not clear, and which are recorded from the lower part of the Subzone. These forms show close phylogenetic relation to the discussed *Graefenbergites* species and represent possibly a new ataxioceratid lineage developed during the Hauffianum Subchron (see also below).

The stratigraphical interval of the Hauffianum Subzone can be interpreted also on the basis of Subboreal and Boreal ammonites in the standard Subboreal and Boreal zonations. The occurrence of the Boreal cardioceratid genus *Plasmatites*, represented by the abundant assemblage of *P. bauhini* (Oppel) – *P. praebauhini* (Salfeld) and *P. lineatum* (Quenstedt) in the “upper Amoebocheras layer” in the lower part of the Subzone (e.g., Matyja, Wierzbowski, 1997, pl. 5: 1–4; 2000), along with the occurrence of the same fauna directly above the boundary with the Planula Zone, indicates correlation of the Hauffianum Subzone with some parts of the Boreal Bauhini Zone. Similarly, the occurrence of *Pictonia densicostata* Buckman at the base of the Hauffianum Subzone (Matyja, Wierzbowski, 1997, pl. 5: 6–11), and additionally *P. normandiana* (Tornquist) directly above the top of the Subzone (see Wierzbowski, 2022, p. 70, pl. 5: 2; see also Matyja, Wierzbowski, 1997, pl. 5: 5 – originally described as “*Pictonia densicostata*”), indicate that the Hauffianum Subzone correlates with some parts of the NW European Baylei Zone, and that the boundary between the Densicostata Subzone and the Normandiana Subzone of the Baylei Zone runs possibly near the boundary between the Hauffianum Subzone and the Planula Zone. Also, the common occurrence of the NE Subboreal genus *Vineta*, including a form close to *V. jaekeli* Dohm, in the Hauffianum Subzone in the Wieluń Upland (Wierzbowski *et al.*, 2010, pl.

8: 2) indicates correlation with a part of the Jaekeli Zone (see also Wierzbowski *et al.*, 2023).

PHYLOGENETIC IMPORTANCE OF PASSENDORFERIINAE AMMONITES FROM THE HAUFFIANUM SUBZONE

The discussed ammonites of the subfamily Passendorferiinae were discovered in the lower part of the Hauffianum Subzone in three quarries (Pj113, Pj125, Pj145, actually abandoned) between Raciszyn and Lisowice on the left side of the Warta River valley. All these specimens come from a similar stratigraphic position – from the uppermost part of the micritic limestone – marly beds at the top of unit I, and the directly overlying chalky limestones of the lower part of unit II, close to “upper Amoebocheras layer” (see Fig. 2). They are represented both by macroconchs attaining up to about 250 mm diameter, and some smaller incomplete specimens ranging in size to about 120 mm diameter – almost surely representing microconchs. The whole assemblage is homogenic and belongs to the only one species – *Graefenbergites ingae* sp. nov. (Pls. 1–4).

The genus *Graefenbergites* was established in southern Germany in the stratigraphic interval of the Semimammatum Subzone (or horizon) of the Hypselum Zone of the uppermost Oxfordian in the northern Franconian Alb (Schairer, Schlamp, 2003). The recognized assemblage of species – *Graefenbergites idoceratoides* (Dorn) and *G. arancensis* (Meléndez) shows a wide distribution in this level in the Submediterranean areas of Europe (possibly occurring also in the topmost part of the Bifurcatus Zone), being known from Spain to central Poland (Meléndez, 1989; Wierzbowski, Matyja, 2014; Maisch, Matzke, 2018). Although recognized at that time in a narrow stratigraphic interval – the genus *Graefenbergites* has been treated always as having a large phylogenetic importance, and according to e.g., Meléndez *et al.* (2006, fig. 3) its occurrence strongly suggested a close phylogenetic relationship between Passendorferiinae and Ataxioceratinae. On the other hand, an opposite opinion was expressed by other authors (Enay, Howarth, 2019, p. 51) according to whom: “*Graefenbergites* appears to be intermediate between Passendorferiinae and Ataxioceratinae (...), (but it) does not prove they are phylogenetically related”. Thus, the discovery of the new *Graefenbergites* fauna at a younger level, in the lowermost Kimmeridgian deposits, as presented herein, is of marked importance for phylogenetic considerations.

The new species *Graefenbergites ingae* shows, in a similar manner to the older species of this genus, the characteristic development of ornamentation consisting of prorsiradiate

biplicate and single ribs with strong constrictions and parabola on the strongly evolute inner whorls, and numerous secondary ribs on the outer whorls, where trifurcate and even polygyrate rib subdivision occurs. Whereas the primary ribs are weakly prorsiradiate, the secondary ribs show commonly an even stronger prorsiradiate course. Such development of ornamentation on the inner whorls, and the flattened whorl sides, reveal a similarity to some Passendorferiinae, especially to the genus *Sequeirosia* Meléndez (see Meléndez, 1989; Meléndez, D'Arpa, 2002). In fact, the late representatives of that genus known from the Bifurcatus Zone, from Spain to central Poland (cf. Meléndez *et al.*, 2009, fig. 3) such as: “*S. n. sp. A*” in: Meléndez (1989, p. 190–191, pl. 16: 1) and “*Perisphinctes* sp. ex gr. *tenuis* Enay” in: Brochwicz-Lewiński (1973, pl. 22: 1a, b), reveal inner whorls very similar to those of *Graefenbergites*. This may suggest the origin of *Graefenbergites* in the continuation of the discussed Passendorferiinae lineage, the representatives of which occur in the Submediterranean areas as opportunistic invaders during short-time transgressive impulses.

A very specific development of ornamentation on the markedly less evolute outer whorls of *Graefenbergites*, is composed of more distant primary ribs showing trifurcate or polygyrate rib division. In the studied specimens of *G. ingae* nov. sp. from the Hauffianum Subzone of the lowermost Kimmeridgian, this type of ornamentation is observed at smaller diameters in the microconchs, already at about 80 mm diameter, but at markedly larger diameters in the macroconchs (at about 145–175 mm), and its appearance corresponds to the beginning of the body-chamber (Fig. 3; Pls. 1–4). This difference resulted possibly from changes in the offset time between the micro- and macroconchs, the former being possibly the earlier growing forms. The ornamentation is composed of prorsiradiate primaries, and numerous fairly long and thin secondary ribs, with an acute, very low angle of furcation, showing a marked forward swing of the secondary ribs, which is seen also on the ventral side. At larger diameters in macroconchs the secondary ribbing tends to disappear. Such a type of ribbing although generally characteristic of the family Ataxioceratinae, differs, however from typical representatives of the genus *Orthosphinctes* (as corresponding mostly to the *Orthosphinctes tiziani* group) which show more rectiradiate ribbing, shorter secondaries, and more evolute coiling.

Meléndez *et al.* (2006, p. 216) stated that there existed: “a sharp morphological gap between true representatives of the upper Oxfordian (Hypsulum to Hauffianum zones) (actually: uppermost Oxfordian and lowermost Kimmeridgian – comment added herein) *Orthosphinctes* of the *O. tiziani* (Oppel) group, and the earliest Kimmeridgian representatives of this line set around the group of “*Orthosphinctes polygyratus* (Reinecke)”, and these authors suggested even

the reactivation of the older genus name *Planites* de Haan for the latter.

A marked similarity of ornamentation to the discussed outer whorls of *Graefenbergites* is shown in numerous specimens of Ataxioceratinae traditionally attributed in the past to the genus *Orthosphinctes*, coming from the Hauffianum Subzone (and partly also the underlying Bimammatum Subzone) in the Wieluń Upland. These include: “*Orthosphinctes*” *lisowicensis* Wierzbowski (see Wierzbowski, 1978, pl. 9: 1, 2; Matyja, Wierzbowski, 1997, pl. 6: 3), the specimens of which differ from typical representatives of the ge-

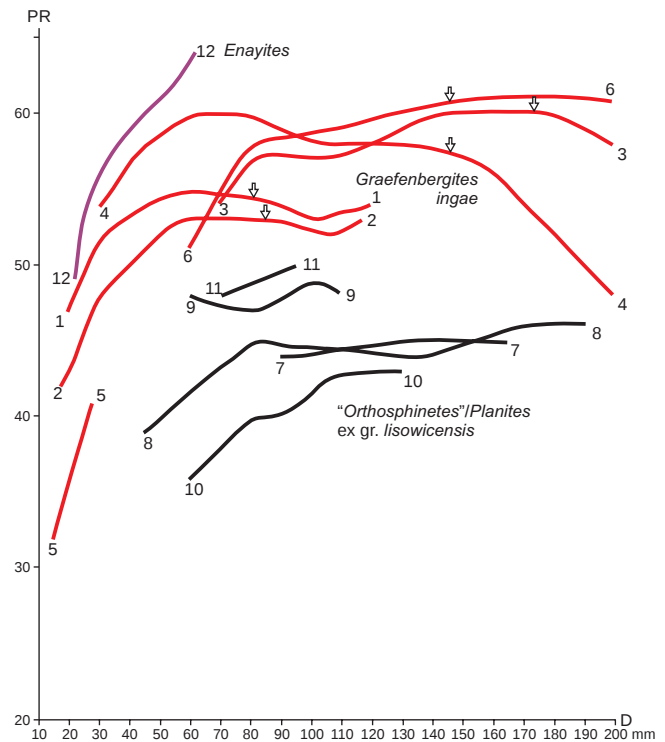


Fig. 3. Rib curves for ammonites of *Graefenbergites ingae* sp. nov. (the change of ornamentation corresponding to the beginning of the body-chamber is arrowed), and selected specimens of “*Orthosphinctes*” *lisowicensis* group; for comparison rib curve of the discussed Passendorferiinae microconch is given

Red: *Graefenbergites ingae* sp. nov.: 1 – holotype, microconch (Pl. 1: 1); 2 – paratype, microconch (Pl. 1: 2); 3 – paratype, macroconch (Pl. 2: 2); 4 – paratype, macroconch (Pl. 3: 3); 5 – inner whorls (Pl. 4: 2); 6 – macroconch (Pl. 4: 1). Black: “*Orthosphinctes*” *lisowicensis* Wierzbowski group: 7 – paratype, macroconch, quarry Pj113, bed 4 (“*Orthosphinctes*” *lisowicensis* in: Wierzbowski, 1978, pl. 9: 2); 8 – macroconch, quarry Pj113, bed 1 (“*Pomerania helvetica*” in: Wierzbowski, 1978, pl. 5: 1); 9 – macroconch, quarry Pj113, bed 1 (“*Pomerania helvetica*” in: Wierzbowski, 1978, pl. 4: 2); 10 – ? microconch, quarry Pj113, bed 2 (“*Orthosphinctes*” *lisowicensis* in: Matyja, Wierzbowski, 1997, pl. 6: 3); 11 – microconch, quarry Pj113 (“*Orthosphinctes*” aff. *polygyratus* in: Wierzbowski, 1978, pl. 8: 2). Violet: Passendorferiinae (microconch of the *Enayites*-type): 12 – quarries at Grądy-Lazy (Pl. 4: 3)

nus *Orthosphinctes* in their less evolute coiling, markedly prorsiradiate ribs, and longer secondaries showing a characteristic forward sweep at the ventral side (but note that some forms attributed in the past to this species e.g., by Wierzbowski *et al.*, 2010, pl. 10: 6, shows more rectiradiate ribbing and are possibly closer to the true *Orthosphinctes*). Closely related is also “*Pomerania helvetica* (Geyer)” (see Wierzbowski, 1978, pl. 4: 1, 2; pl. 5: 1), which differs in being somewhat more involute, and somewhat more densely ribbed, representing possibly but a variant of “*O.*” *lisowicensis* (Matyja, Wierzbowski, 1997, p. 87). All these Ataxioceratinae specimens from the Hauffianum Subzone (and possibly the upper part of the Bimammatum Subzone) of the Wieluń Upland are macroconchs, having possibly their microconchiate counterparts in much smaller, fully grown forms similar to the “*Orthosphinctes* (*Orthosphinctes*) aff. *polygyratus* (Reinecke)” of Wierzbowski (1978, pl. 8: 2). It is worth noting that in the same beds of the Hauffianum Subzone were recorded forms corresponding well to the genus *Orthosphinctes* – both microconchs, such as *Orthosphinctes* (*Orthosphinctes*) *tiziani* (Oppel) (see Matyja, Wierzbowski, 1997, pl. 6: 1) and macroconchs such as *Orthosphinctes* (*Pseudorthosphinctes*) *alternans* Enay (see Wierzbowski, 1978, pl. 8: 3).

These observations clearly suggest the existence of two distinct groups of Ataxioceratinae in the studied deposits of the Hauffianum Subzone corresponding to two separate phylogenetic lineages: (1) that representing the continuation of the *Orthosphinctes* lineage, and marking possibly its decline at this level, corresponding to the “true *O. tiziani* (Oppel) group” (Meléndez *et al.*, 2006, p. 216), and (2) a newly emerged lineage corresponding to the *Planites* group possibly evolved from the discussed Passendorferiinae ammonites of the genus *Graefenbergites*, as shown by the similarity in development of their outer whorls.

The suggested close phylogenetic relationship between the discussed Passendorferiinae ammonites (*Graefenbergites ingae* sp. nov.) and the newly formed Ataxioceratinae (“*Orthosphinctes*”/*Planites lisowicensis* group) needs, however, additional comments. The detailed comparison of the stratigraphic ranges of the two assemblages of ammonites in the lower part of the Hauffianum Subzone in the Wieluń Upland (Fig. 2) shows that the well-developed assemblage of “*O.*” *lisowicensis* generally precedes (or but slightly overlaps) the appearance of *G. ingae* sp. nov. This indicates that the environmental requirements of the two forms were partly different. It is worth noting, moreover, that both the forms are practically unknown in the Mediterranean areas. It may be additionally suggested that the known stratigraphic ranges of the discussed ammonite assemblages in the Wieluń Upland represent but fragments of their original succession in other areas of the Submediterranean Province.

It seems probable that the full evolutionary development of the discussed ammonites included at its base the hypothetical initial Mediterranean Passendorferiinae from the Bimammatum Chron. Their occurrence in any areas of the Submediterranean Province began the process of heterochronic changes which affected the ornamentation of the shells of the ammonites. The process resulted in the appearance of a new type of ribbing composed of triplicate and polygyrate ribs on the final part of the body-chamber. This heterochronic process corresponding possibly to hypermorphism was associated with later offset time of Passendorferiinae ammonites because of their appearance in the new environment. The following developments, probably in peripheral areas with different environmental conditions, led to the formation of new forms of Ataxioceratinae – possibly as an effect of another process of heterochrony – acceleration in growth rate – which successively limited the earlier stages of passendorferiid ornamentation. According to this interpretation the process of development of the discussed new forms of Ataxioceratinae corresponded to a parapatric model of speciation. The large specimens of *Graefenbergites ingae* recognized at the top of the succession studied represent forms closer, however, to the ancestral populations, the appearance of which in the area of study corresponded to the maximum range of transgression.

Some help in recognition of the hypothetical forerunner of the discussed lineage is a passendorferiid ammonite of the Hauffianum Subzone, found together with other ammonites, such as *Taramelliceras* cf. *hauffianum* (Oppel), *T. cf. costatum* (Quenstedt), in small abandoned quarries at Grądy-Łazy, east of Działoszyń. It comes from well-bedded chalky limestones possibly corresponding to lithological unit I, and thus from stratigraphically older deposits than those which yielded the discussed *Graefenbergites ingae* sp. nov. This passendorferiid ammonite (Pl. 4: 3) is covered with dense biplicate and subordinately also single ribs; such a type of ribbing continues up to the end of the last whorl preserved, and it is similar to that of the inner whorl of *Graefenbergites ingae* sp. nov. The corresponding rib-curve (see Fig. 3) shows a marked increase in the number of ribs per whorl along with the growing diameter of the specimen, but in its final course deviates vertically from the typical rib-curves of *Graefenbergites ingae* sp. nov. This specimen, although without its final aperture preserved, is possibly a microconch, and it can be easily accommodated in a widely treated microconch assemblage of the *Enayites* type – treated as a microconch group of early Passendorferiinae. The distinctive features of the specimen discussed are its very dense ribbing and the prorsiradiate course of the secondary ribs. The overall affinities of this specimen are certainly with typical Mediterranean forms of Passendorferiinae: it bears quite a close resemblance to the form described as “*Passen-*

dorferia (Enayites) aff. *gygii* Brochwicz-Lewiński & Różak” by Cecca and Savary (2007) from the Rosso-Ammonitico of Monte Inici, north-western Sicily, the stratigraphic position of which corresponds possibly also to the Hauffianum Subzone.

Although ammonites of the genus *Graefenbergites* have not been recognized in the coeval succession of the Hauffianum Subzone in southern Germany, it has yielded an assemblage of “*Orthosphinctes*”-like forms, occurring in a very similar stratigraphic position to that of the “*Orthosphinctes*” *lisowicensis* group from the Wieluń Upland. These ammonites attributed to the “*Orthosphinctes* ex gr. *tizianiformis*” group occur in a narrow stratigraphic “*tizianiformis*” horizon directly below the *bauhini* horizon, which is characterized by the common occurrence of cardioceratids of the *Plasmatites* (= “*Amoeboceras*”) *bauhini* group (Schweigert, Callomon, 1997; see also Jantschke, Schweigert, 2023), being well comparable to the “upper *Amoeboceras* layer” in the Wieluń Upland. The systematic position of the ammonites compared to “*Orthosphinctes*” *tizianiformis* Choffat in southern Germany is, however, doubtful, because originally this species was described from much older deposits belonging to the Middle Oxfordian of Portugal (Meléndez *et al.*, 2006). It is highly probable that the ammonites referred to as “*Orthosphinctes* ex gr. *tizianiformis*” from southern Germany are very close to the ammonites of the “*Orthosphinctes*” *lisowicensis* group discussed herein, which could result from the similar chronostratigraphic position of deposits bearing the “*Orthosphinctes*” ammonites in central Poland, and southern Germany, giving them character of a biostratigraphic horizon of over-regional character. These deposits in southern Germany – especially in the area of the Swabian Alb – belong to the uppermost part of the Impressamergel Formation – the succession of marls with intercalations of limestones, especially in its upper part, which ranges stratigraphically up to the Hauffianum Subzone of the Bimammatum Zone, and is covered by the well-bedded limestones of the Wohlgeschichtete-Kalke Formation representing the Planula Zone (*e.g.*, Schmid *et al.*, 2005). The uppermost part of the Impressamergel Fm., yielded abundant ammonites, and shows some features of condensation, especially at the top of the formation, corresponding also to the boundary of the now abandoned stratigraphic units: the Malm α and the Malm β (*e.g.*, Koerner, 1963; Schweigert, Callomon, 1997). These observations and comparison with the sections of the Wieluń Upland discussed here suggest that the succession of deposits in southern Germany is, however, incomplete. There is there a considerable period of non-deposition corresponding to the uppermost part of the Hauffianum Subzone, and the lowermost part of the Planula Zone. This period is generally of transgressive character and yields Passendorferiinae ammonites in the Wieluń Upland.

FINAL COMMENTS

The systematic classification of ammonites based on their phylogeny forms the foundation for biostratigraphic and palaeogeographic analysis of the entire Upper Jurassic. Submediterranean ammonite families of Mediterranean origin, such as Ataxioceratidae, Perisphinctidae, Oppeliidae and Aspidoceratidae, are especially important for the stratigraphy of the Upper Oxfordian and lowermost Kimmeridgian. However, the understanding of their phylogeny is not always complete and is at times subject to conflicting interpretations.

The most important group for the stratigraphy of the Upper Oxfordian to Lower Kimmeridgian is undoubtedly the Ataxioceratidae family, which according to Enay and Howarth (2019, p.112) remains “one of the most difficult to classify”. The lowest appearing member of the family is the genus *Orthosphinctes* which occurs as early as the top of the Bifurcatus Zone of the Upper Oxfordian and ranges at least into the Bimammatum Zone of the lowermost Kimmeridgian. However, the phylogenetic relations between this genus and younger members of the subfamily Ataxioceratinae are still subject to diverse interpretations. Although these younger forms, which appeared somewhere between the upper Bimammatum (Hauffianum) and lower Planula zones, are commonly classified as belonging also to the genus *Orthosphinctes* (see *e.g.*, Enay, Howarth, 2019), they are seen by some researchers as being more appropriately compared with the “overlooked” genus *Planites* (see Meléndez *et al.*, 2006, 2009).

The phylogeny of all these ammonites of the subfamily Ataxioceratinae also raises questions about their origin – whether they derive from Perisphinctinae (*e.g.*, Enay, Howarth, 2019) or from Passendorferiinae (*e.g.*, Meléndez *et al.*, 2009). It is also possible that both interpretations may be valid. The succession of deposits exposed in the Wieluń Upland yielded continuation, in the Hauffianum Subzone of the lowermost Kimmeridgian, of the Mediterranean passendorferiid ammonites of the genus *Graefenbergites*, previously known in Submediterranean Europe (and Poland) at the base of the Hypselum Zone (Semimammatum Subzone/horizon) of the uppermost Oxfordian (*e.g.*, Schairer, Schlamp, 2003; Wierzbowski, Matyja, 2014). These ammonites may be interpreted as forerunners of new evolutionary lineages, including the aforementioned “*Planites*”, but also the earlier appearing *Praeataxioceras* which seems to be related to younger *Ardesia*. Still another problem refers to the origin of younger Ataxioceratinae ammonites like *Progeronia*, *Crussoliceras* and *Garniersphinctes*, whose sudden appearance at the boundary between the Hypselocyclum and Divisum zones in the up-

permost Lower Kimmeridgian has been recently the subject of discussion (Wierzbowski, 2024; Schweigert *et al.*, 2025), and whose relation to older members of the subfamily has not become fully clarified.

PALAEONTOLOGICAL DESCRIPTIONS

The following abbreviations are used herein in the description of ammonites: D – diameter of specimen in mm; Wh – whorl height as a percentage of D; Ud – umbilical diameter as a percentage of D; PR – number of primary ribs per whorl, SR/PR – secondary/primary rib ratio counted on 5 primary ribs at given diameter.

Family Perisphinctidae Steinmann, 1890

Subfamily Passendorferiinae Meléndez, 1989

Genus *Graefenbergites* Schairer et Schlampp, 2003

The inner whorls, characterized by the low-oval whorl section and covered with simple and biplicate ribs of the Passendorferiinae type, contrast strongly with the outer whorls which show a high-oval whorl section and are covered with biplicate to polygyrate ribs with markedly projected long secondaries of the Ataxioceratinae type. The genus as originally established (Schairer, Schlampp, 2003) included the two species widely distributed in the Semimammatum Subzone (or horizon) of the lowermost Hypselum Zone (but possibly appearing already at the top of the Grossouvrei Subzone of the Bifurcatus Zone) of the Upper Oxfordian in Submediterranean Europe: *G. idoceratoides* (Dorn) and *G. arancensis* (Meléndez) (see *e.g.*, Wierzbowski, Matyja, 2014; Maisch, Matzke, 2018). The herein newly described species *Graefenbergites ingae* sp. nov. from the lower part of the Hauffianum Subzone of the Bimammatum Zone indicates the continuation of this ammonite lineage into the lowermost Kimmeridgian.

Graefenbergites ingae sp. nov.

(Pls. 1–3; Pl. 4: 1, 2; Fig. 3)

1978. *Pomerania* cf. *girardoti* (Enay); Wierzbowski, p. 324, pl. 6: 1, text-fig. 5

1997. *Passendorferia* sp. indet.; Matyja, Wierzbowski, p. 87

Material. Six specimens including the holotype (MWGUW A/10/426 Pl. 1: 1) and the three paratypes (MWGUW A/10/379; MWGUW A/10/423, and MWGUW A/10 427: Pls. 1–3).

Type area and locality. Wieluń Upland, quarries between Raciszyn and Lisowice (Pj113, Pj125 and Pj145; see Matyja, Wierzbowski, 1997, fig. 2; Fig. 1).

Type horizon. Lowermost Kimmeridgian: lower part of the Hauffianum Subzone of the Bimammatum Zone; close to and directly above the “upper *Amoeboceras* layer” of the *litoceram* horizon (see Matyja, Wierzbowski, 1997, 2000, 2006; Fig. 2).

Derivation of the name. After name of my dog friend.

Diagnosis. Inner whorls strongly evolute with low-oval whorl section and single and biplicate ribs, outer whorls less evolute with high-oval whorl section and numerous prorsiradiate ribs showing fairly low biplicate to polygyrate subdivision.

Description. The material includes five medium-sized to large specimens attaining from about 115 mm to 260 mm in diameter, and one smaller-sized specimen about 45 mm in diameter representing the inner whorls – all of them coming from a narrow stratigraphical horizon directly above the upper *Amoeboceras* layer, in several neighbouring quarries situated between Raciszyn and Lisowice in the Wieluń Upland.

The inner whorls have dense prorsiradiate ribbing consisting of dominant bifurcate and rare single ribs with some parabolic ribs and deep prorsiradiate constrictions. This type of ribbing continuous up to about 70–80 mm diameter in microconchs, and up to about 145 to 175 mm diameter in macroconchs, and it is replaced thereafter by triplicate to polygyrate ribbing on the outer whorl (SR/PR = 2.6 to 3.6). The primary ribs are prorsiradiate, whereas the elongated closely-spaced secondaries appear at about 2/3 of the whorl height and cross the ventral side with some forward sweep. The number of primary ribs per whorl markedly increases up to 50–100 mm diameter (D) and it becomes stable or slightly decreases at larger diameters (Fig. 3). The last part of the shell can retain a few blunt, rounded ribs, whereas the secondary ribs almost completely disappear. The evolute character of the outer whorl of larger specimens is well seen (at D = 115–230 mm, Wh = 26–28, Ud = 50–54), although the inner whorls show more evolute coiling. The whorl section of the outer whorl is markedly higher than that of the inner whorls. Deep constrictions bordered in front by a single rib are commonly seen throughout all stages of development.

Three largest specimens (Pls. 2, 3; Pl. 4: 1) collected attaining 200–260 mm in diameter show preserved the peristome of the macroconch type. Two other smaller specimens (Pl. 1: 1, 2) which are almost surely microconchs, 115–120 mm in diameter, show some modification of ribbing at the end of the last whorl, close to the strong constriction, suggesting they are also fully grown: the secondary ribs cross the venter with some accentuation of their strength and with a marked forward sweep, and additionally some increase in rib density is observed – which is well seen in the holotype. They reveal a similar type of ornamentation as the

macroconchs, composed of triplicate and polygyrate ribs on the last whorl, but appearing at smaller diameters, and differing mostly in final size.

Discussion. The new species is similar to *G. idocera-toides* in its type of coiling and character of ornamentation. It differs, however, in its generally denser ribbing, and in attaining larger final sizes.

The species probably marks a stage in an evolutionary process that led from Mediterranean Passendorferiinae to the new branch of Submediterranean Ataxioceratinae, and it especially well fulfills the requirements of the forerunner of the younger *Orthosphinctes*-like group of the Planula to Planynota zonal assemblages of the lowermost Kimmeridgian, possibly corresponding to the genus “*Planites*” (see also the chapter on evolutionary development herein; see also *e.g.*, Meléndez *et al.*, 2006).

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Plates

PLATE 1

Graefenbergites ingae sp. nov.

- Fig. 1. Holotype, microconch, quarry Pj145, bed 1b; specimen MWGUW A/10/426
Fig. 2. Paratype, microconch, quarry Pj113, beds 5–7; MWGUW A/10/423



Andrzej Wierzbowski – New Passendorferiinae ammonites from the upper Bimammatum Zone (Hauffianum Subzone), lowermost Kimmeridgian of the Wieluń Upland, central Poland, and their biostratigraphic and phylogenetic importance

PLATE 2

Graefenbergites ingae sp. nov.

- Fig. 1. Paratype, macroconch, quarry Pj113, bed 7; MWGUW A/10/379 (*"Pomerania* cf. *girardoti*" in: Wierzbowski, 1978, pl. 6: 1)



Andrzej Wierzbowski – New Passendorferiinae ammonites from the upper Bimammatum Zone (Hauffianum Subzone), lowermost Kimmeridgian of the Wieluń Upland, central Poland, and their biostratigraphic and phylogenetic importance

PLATE 3

Graefenbergites ingae sp. nov.

Fig. 1. Paratype, macroconch, quarry Pj125/126, bed 3; MWGUW A/10/427



Andrzej Wierzbowski – New Passendorferiinae ammonites from the upper Bimammatum Zone (Hauffianum Subzone), lowermost Kimmeridgian of the Wieluń Upland, central Poland, and their biostratigraphic and phylogenetic importance

PLATE 4

Graefenbergites ingae sp. nov.

- Fig. 1. Macroconch, quarry Pj145, bed 2; MWGUW A/10/413
- Fig. 2. Inner whorls, quarry Pj125, beds 3c, d; MWGUW A/10/428
- Fig. 3. Passendorferiinae (microconch of the *Enayites*-type): Grądy–Łazy; MWGUW A/10/429



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