Instytut Paleobiologii Polskiej Akademii Nauk

LATE CRETACEOUS AND EARLY PALEOGENE NAUTILIDS FROM POLAND, WESTERN UKRAINE, AND DENMARK

Łodziki późnej kredy i wczesnego paleogenu Polski, zachodniej Ukrainy oraz Danii

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Oświadczenie / Declaration

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Late Cretaceous and early Paleogene nautilids from Poland, western Ukraine, and Denmark

Summary

The research goal of this thesis is to present a palaeontological study of Late Cretaceous (Campanian–Maastrichtian) and early Paleogene (Danian) nautilid cephalopods from Poland, western Ukraine, and Denmark in the context of the end-Cretaceous mass extinction (for general background see **Introduction**; for the most important results see **Results of the thesis**).

The core of the dissertation consists of three chapters. In first two chapters, the results of detailed research on Polish and Danish specimens of *Epicymatoceras vaelsense*, the most enigmatic Late Cretaceous nautilid in Europe, are presented. These results significantly add to our understanding of the morphology, shell structure, taxonomic position, and stratigraphical range of this atypical nautilid. Moreover, they demonstrate the considerable potential of moulds (steinkerns) for studies of nautilid fossils. The third chapter presents the first comprehensive taxonomic study of nautilid faunas from the Upper Cretaceous–lower Paleogene of Poland and western Ukraine. These results form a basis for reconstructing regional nautilid turnover pattern in comparison with other European faunas. The chapters of this dissertation are summarised below.

Chapter I focuses on the taphonomy and ornamentation of the Late Cretaceous ribbed nautilid *Epicymatoceras vaelsense*, and seeks to understand the systematic position of this species and, more broadly, other ribbed nautilids. The study is based on material from the upper Campanian and lower Maastrichtian of Poland, which represents the first record of the genus *Epicymatoceras* from the Upper Cretaceous of Poland. In this context, the total stratigraphical and geographical range of *E. vaelsense* is also discussed.

The core of this chapter consists of a detailed description and interpretation of the shell ornamentation preserved on exceptionally well preserved external and internal moulds of this nautilid. Furthermore, the taphonomic pathways leading to the formation of the identified taphomorphs (that is preservational variants of a single taxon) are reconstructed, allowing for their interpretation with respect to the original shell structure.

The species *Epicymatoceras vaelsense*, the type species of the genus *Epicymatoceras*, is distinguished from all other post-Triassic nautilids by its strongly compressed, evolute

conch with a subquadrate whorl section (Goolaerts and Frank 2014). The genus Epicymatoceras was assigned to the family Cymatoceratidae on the basis of its distinctive transverse ribbing (Kummel 1964). However, this family is regarded by many workers as an artificial "litter bin" for ribbed offshoots of smooth nautilid lineages. Based on a study of ornamental morphogenesis in Cymatoceras (the type genus of the Cymatoceratidae), Chirat and Bucher (2006) demonstrated that the external shell ornament in Nautilus pseudelegans (the type species of Cymatoceras) does not represent true ribs, but rather is composed of overlapping tile-shaped lamellae of the outer prismatic layer. Based on this observation, Chirat and Bucher (2006) proposed that this character may be regarded as a new diagnostic feature of the cymatoceratid clade. Nevertheless, given the absence of adequate data, these authors could not determine if Epicymatoceras matched their new definition of the clade. The Polish material indicates that the external ribbing of E. vaelsense was originally composed of overlapping tile-shaped lamellae of the outer prismatic layer, therefore firmly supporting the placement of this taxon within Cymatoceratidae sensu Chirat and Bucher (2006). In a comparable vein, similar examinations of other ribbed nautilids in the studied material clarifies their taxonomic position (see Chapter III).

In addition, the Polish specimens of *Epicymatoceras vaelsense* provide new data on embryonic shell diameter in the genus *Epicymatocers*. The embryonic conch was recognised in the studied material on the basis of the reticulate ornament and the nepionic constriction observed in some specimens. Embryonic conch diameter in *E. vaelsense* is estimated to have been around 30 mm, near the maximum range of hatching size recorded for both Cretaceous and post-Cretaceous nautilids. This observation adds to our understanding of nautilid hatching size in the K–Pg boundary interval (compare Wani *et al.* 2011).

Chapter II presents a description and interpretation of new *Epicymatoceras vaelsense* specimens from the Maastrichtian of Denmark, which constitue the first Danish records of this species. The material assigned to *E. vaelsense* consists of three specimens from Jutland – one from the lower/upper Maastrichtian boundary interval, and two from the uppermost Maastrichtian chalk exposed at the "Dania" quarry. Given the European stratigraphic range of *E. vaelsense* (presented in Chapter I), the uppermost Maastrichtian specimens are interpreted as the youngest known records of *Epicymatoceras*, indicating that the genus extended into the latest Cretaceous. Furthermore, the Danish material allows for the recognition of the apertural margin of *Epicymatoceras* for the first time. The embryonic shell of *E. vaelsense* was also identified based on a well-defined nepionic constriction discernible on a specimen from "Dania". The embryonic shell of Danish *E. vaelsense* specimen (approximately 30 mm in

size), together with the previously reported embryonic shell diameters for Polish *Epicymatoceras* specimens (Chapter I) confirm that the diameter of the *Epicymatoceras* embryonic shell is close to the maximum observed among the Cretaceous to Recent nautilids.

Chapter III is the most comprehensive part of this thesis. It provides the first monographic study of nautilid faunas from the Upper Cretaceous–lower Paleogene of Poland and western Ukraine and documents regional nautilid turnover patterns across the K–Pg boundary. The fossiliferous Upper Cretaceous (Campanian–Maastrichtian) to lower Paleogene (Danian) epicontinental deposits of Poland and western Ukraine are a remarkable venue for such a study. In particular, regional Maastrichtian strata yield abundant and relatively well-preserved nautilid fossils, which permit an assessment of nautilid taxonomic composition and abundance prior to the end-Cretaceous biotic crisis.

The studied material includes 656 nautilid specimens from 64 sections, ranging from the middle Campanian to the Danian in Poland and from the upper Campanian to the lower upper Maastrichtian in western Ukraine. The geological setting, detailed characteristics, and updated stratigraphical position of the nautilid-bearing sections are presented as a background for understanding the nautilid succession. The most abundant Polish material is from the famous quarries at Piotrawin (upper Campanian) and Nasiłów (upper Maastrichtian) in the Middle Vistula River section, and from the Wola Piasecka quarry (upper Maastrichtian) near Lublin (for general setting, see Walaszczyk *et al.* 2016; Machalski *et al.* 2022). In western Ukraine, the most important collections are from the historical lower Maastrichtian section once exposed at Nahoryany near Lviv (Machalski and Malchyk 2016).

Representatives of three families, conventionally distinguished within the superfamily Nautilaceae of the order Nautilida, have been identified in the studied material: Nautilidae, Cymatoceratidae, and Hercoglossidae. The Late Cretaceous faunas from Poland and western Ukraine encompass 14 species: *Eutrephoceras ahltenense, Eutrephoceras? aquisgranense, Eutrephoceras darupense, Eutrephoceras dekayi, Eutrephoceras depressum, Eutrephoceras quadrilineatum, Eutrephoceras vastum, Cymatoceras intrasiphonatum, Cymatoceras loricatum, "Cymatoceras" patens, Epicymatoceras vaelsense, Angulithes westphalicus, Cimomia? galiciana, and Cimomia heberti. Additionally, these faunas contain several forms left here in open nomenclature: Eutrephoceras sp. A, Eutrephoceras sp. B, Eutrephoceras sp. C, Eutrephoceras spp., "Cymatoceras" sp. nova, Cymatoceratidae? indet., Epicymatoceras sp., Angulithes cf. neubergicus, Angulithes sp. nova, Cimomia sp. A, and Cimomia sp. B. Only two early Paleogene taxa have been identified from Poland: Eutrephoceras dekayi and Nautilidae indet. gen. et sp. nova?. The most abundant nautilid fauna, dominated by the genus* *Eutrephoceras* and the endemic (to Poland) species *Cymatoceras intrasiphonatum*, comes from the upper Maastrichtian sections in the Middle Vistula River section of Poland.

Inferences on the original shell structure of some ribbed taxa (*Cymatoceras intrasiphonatum* and *C. loricatum*) clarify their systematic position based on the lines of evidence employed for *Epicymatocers vaelsense* (see Chapter I), which is a considerable advance in our understanding the systematic position of these taxa. Taxa that do not match the new understanding of the family Cymatoceratidae (cf. Chirat and Bucher 2006) are provisionally referred to as "*Cymatoceras*" awaiting further studies. Among these ribbed nautilids, the common upper Maastrichtian species *Cymatoceras intrasiphonatum* is thoroughly described and illustrated for the first time (the original short description by Łopuski 1912 was supported by rather poor illustrations). Another important taxonomic result of this study is the inclusion of the Danian species *Eutrephoceras bellerophon* into synonimy of the Maastrichtian *E. dekayi*. Their proposed conspecifity has consequences for understanding nautilid turnover across the K–Pg boundary, as demonstrated below.

The Late Cretaceous and early Paleogene nautilid faunas of Poland and western Ukraine are compared with selected European faunas, including those from Denmark (Stevns Klint, Faxe), Sweden (Limhamn), northern Germany (Kroonsmoor, Isle of Rügen), as well as the Netherlands and Belgium (the historical type Maastrichtian area), and France (Vigny). Except for the Danian fauna of Denmark and Sweden, these faunas are generally much less abundant and diverse than the Poland and western Ukraine faunas.

With the exception of the ubiquitous *E. dekayi* and the extremely rare *Cimomia heberti* (the latter known from a single record from the lowermost Danian of Maastricht area), all European Late Cretaceous nautilid species identified during this study, including the ribbed forms conventionally assigned to the Cymatoceratidae, did not cross the K–Pg boundary. As such, despite the profound regional palaeogeographic and facies changes near the boundary, the nautilid diversity patterns reflect a genuine extinction related to the global end-Cretaceous crisis.

Precise reconstruction of Cretaceous nautilid extinction patterns is hampered by deficiences in the fossil record. In Poland, these are mostly related to hiatal gaps at the top of the Maastrichtian, such as in the Middle Vistula River section (see Machalski *et al.* 2022). A few nautilid specimens have been collected from an exeptionally complete section at Lechówka near Chełm (see Machalski *et al.* 2016), consisting of individual *E.? aquisgranense* and *Cymatoceras intrasiphonatum* specimens recovered just beneath the K–Pg boundary clay. A single specimen of *E.? aquisgranense* is also recorded from a slightly less complete

uppermost Maastrichtian section at Mełgiew near Lublin, which yields abundant ammonites and other fossils (Machalski *et al.* 2022 and references quoted therein). As observed in Chapter II, *Epicymatoceras vaelsense* is present in the uppermost Maastrichtian of Denmark. Collectively, these rare records suggest that at least a portion of the European Cretaceous nautilid fauna survived until the end of the Cretaceous.

Taxonomic revision of the studied material indicates that *Eutrephoceras dekayi* survived the K–Pg boundary. This is the most widespread species in the studied material, and is known from the Maastrichtian of North America, Europe, and Asia and from the Danian of Europe and Asia (the latter records under the name *E. bellerophon*). Its continuation into the Danian is consistent with the hypothesis that broadly distributed taxa are better suited to survive mass extinctions than those with limited geographical ranges (Jablonski 2008; Landman *et al.* 2014).

Furthermore, this study provides some insight on the environmental distributions of nautilids by assessing the facies in which nautilid fossils are preserved. During the Late Cretaceous (Campanian–Maastrichtian), nautilids were most common and diverse in opoka facies (see Jurkowska and Świerczewska-Gładysz 2022 for definition of opoka), as demonstrated by numerous records from the opoka-dominated Middle Vistula River section and Roztocze Hills. Conversely, nautilids were less common and diverse in white chalk facies, as demonstrated by rather uncommon records from eastern Poland (Chełm), Denmark, and northern Germany. Importantly, opoka was typically laid down in more proximal, shallower environments than chalk (Walaszczyk and Remin 2015; Machalski and Malchyk 2019).

Early Danian nautilid faunas are notably specimen- and species-poor across Europe, including the terrestrially-influenced gaize facies of the so-called Siwak exposed in the Middle Vistula River section. They became more abundant only in the middle Danian coral reefs of Denmark, southern Sweden and France. Alongside *E. dekayi*, large-shelled nautilids with complex sutures like *Hercoglossa danica* appear in these environments, reflecting external migrations.

The Supplementary Material for Chapter III, which consists of three appendices, is located on the CD attached to the printed version of this thesis. This includes:

Appendix 1. Material studied from Poland and western Ukraine.Appendix 2. Comparative material from Denmark and Germany.Appendix 3. Dataset for biometrics of *Eutrephoceras dekayi*.

References (see Introduction, pp. 19–22)

Łodziki późnej kredy i wczesnego paleogenu Polski, zachodniej Ukrainy oraz Danii

Streszczenie

Celem rozprawy doktorskiej niniejszej jest przedstawienie wyników paleontologicznego opracowania późnokredowych (kampan, mastrycht) oraz wczesnopaleogeńskich (dan) łodzików z Polski, zachodniej Ukrainy oraz Danii w kontekście masowego wymierania na granicy kredy i paleogenu (ogólne tło podjętej tematyki zostało zarysowane w Introduction; zaś najważniejsze wyniki przedstawiono w Results of the thesis).

Zasadniczą część dysertacji stanowią trzy rozdziały. W pierwszych dwóch rozdziałach rozprawy przedstawione zostały wyniki szczegółowych badań polskich i duńskich okazów gatunku *Epicymatoceras vaelsense*, najbardziej zagadkowego późnokredowego łodzika w Europie. Wyniki te znacząco poszerzają zakres naszej wiedzy na temat morfologii, pierwotnej struktury muszli, pozycji taksonomicznej oraz zakresu stratygraficznego tego nietypowego łodzika. Ponadto, wskazują one na znaczny potencjał okazów zachowanych w postaci ośródek w badaniach skamieniałości łodzików. Trzeci rozdział rozprawy przedstawia wyniki pierwszego kompleksowego opracowania taksonomii faun łodzików z górnej kredy i wczesnego paleogenu Polski i zachodniej Ukrainy. Wyniki te stanowią podstawę do rekonstrukcji regionalnego obrazu następstwa łodzików w porównaniu z faunami z innych części Europy. Rozdziały rozprawy zostały omówione poniżej.

Rozdział I skupia się na tafonomii i ornamentacji użebrowanego łodzika *Epicymatoceras vaelsense* z późnej kredy, w celu ustalenia pozycji systematycznej tego taksonu, a także innych łodzików o użebrowanej muszli. Badania te zostały oparte na materiale z górnego kampanu i dolnego mastrychtu Polski, który stanowi pierwszą dokumentację występowania rodzaju *Epicymatoceras* w Polsce. W tym kontekście omówiony został także całkowity zakres stratygraficzny i geograficzny *E. vaelsense*.

Główną część rozdziału stanowi szczegółowy opis i interpretacja ornamentacji muszli rozpoznawalnej na wyjątkowo dobrze zachowanych ośródkach zewnętrznych i wewnętrznych tego łodzika. Ponadto, zrekonstruowane zostały procesy tafonomiczne prowadzące do powstania zidentyfikowanych w pracy tafomorfów (czyli różnych stanów zachowania skamieniałości danego organizmu), co umożliwia ich interpretację w kontekście rozważań na temat pierwotnej struktury muszli.

Gatunek Epicymatoceras vaelsense, gatunek typowy rodzaju Epicymatoceras, różni się od wszystkich innych po-triasowych łodzików swoją silnie spłaszczoną, ewolutną muszlą o subkwadratowym przekroju muszli (Goolaerts i Frank 2014). Rodzaj Epicymatoceras został zaliczony do rodziny Cymatoceratidae na podstawie charakterystycznego użebrowania (Kummel 1964). Jednak obecnie wielu badaczy uważa tę rodzinę za sztuczny "kosz dla śmieci" dla użebrowych przedstawicieli różnych odgałęzień linii ewolucyjnych łodzików o gładkich skorupach. Na podstawie badań dotyczących morfogenezy urzeźbienia muszli Cymatoceras (rodzaj typowy dla Cymatoceratidae), Chirat i Bucher (2006) wykazali, że "użebrowanie" muszli Nautilus pseudelegans (gatunek typowy dla Cymatoceras) nie reprezentuje prawdziwych żeber, lecz składa się z zachodzących na siebie dachówkowatych lamelek zewnętrznej warstwy pryzmatycznej muszli. Na tej podstawie Chirat i Bucher (2006) zaproponowali, że ta cecha muszli może być uznana za diagnostyczną dla cymatoceratidów. Niemniej jednak, z powodu braku odpowiednich danych, autorzy ci nie byli w stanie określić, czy Epicymatoceras odpowiada nowej definicji tego kladu. Zbadany w niniejsze rozprawie materiał z Polski wskazuje, że użebrowanie E. vaelsense pierwotnie składało się z zachodzących na siebie dachówkowatych blaszek zewnętrznej warstwy pryzmatycznej, co jednoznacznie potwierdza przynależność tego taksonu do rodziny Cymatoceratidae w rozumieniu Chirata i Buchera (2006). Analogiczne badania przeprowadzone na innych przedstawicielach użebrowych łodzików pozwoliły na wyjaśnienie ich pozycji systematycznej (zob. Rozdział III).

Okazy *Epicymatoceras vaelsense* z Polski dostarczają ponadto nowych danych na temat rozmiarów muszli embrionalnej rodzaju *Epicymatoceras*. Muszla ta została rozpoznana w badanym materiale na podstawie siateczkowatej ornamentacji oraz przewężenia nepionicznego zaobserwowanego na niektórych okazach. Średnica muszli embrionalnej *E. vaelsense* wynosi około 30 mm, co stanowi wartość bliską maksymalnym rozmiarom muszli embrionalnej odnotowanym u łodzików kredowych i późniejszych. Ta obserwacja powiększa zakres naszej wiedzy na temat wielkości muszli embrionalnej łodzików po obu stronach granicy K–Pg (por. Wani i in. 2011).

Rozdział II zawiera opis i interpretację nowych okazów *Epicymatoceras vaelsense* z mastrychtu, które stanowią pierwszą dokumentację występowania gatunku w Danii. Materiał zaliczony do *E. vaelsense* składa się z trzech okazów pochodzących z Jutlandii. Jeden z nich pochodzi z pogranicza dolnego i górnego mastrychtu, zaś dwa pozostałe z utworów

najwyższego mastrychtu odsłaniających się w kamieniołomie "Dania". Biorąc pod uwagę znany zakres stratygraficzny *E. vaelsense* w Europie (przedstawiony w Rozdziale I), okazy z kamieniołomu "Dania" zostały uznane za najmłodsze znane okazy rodzaju *Epicymatoceras*. Sugerują one, że rodzaj ten przetrwał do samego końca okresu kredowego. Ponadto, duński materiał pozwala po raz pierwszy rozpoznać kształt ujścia muszli *Epicymatoceras*. Na jednym z okazów z "Danii" została również zidentyfikowana muszla embrionalna, rozpoznawalna na podstawie obecności wyraźnego przewężenia nepionicznego Średnica muszli embrionalnej duńskiego okazu *E. vaelsense* wynosi w przybliżeniu 30 mm, co w połączeniu z danymi na temat polskich okazów (Rozdział I) potwierdza, że *E. vaelsense* miał jedną z największych muszli embrionalnych spośród łodzików znanych od kredy do dzisiaj.

Rozdział III stanowi najbardziej obszerną część rozprawy. Jest to pierwsze monograficzne studium faun łodzikowych z utworów górnej kredy i dolnego paleogenu Polski oraz zachodniej Ukrainy, stanowiąc dokumentację regionalnego następstwa tych głowonogów na szeroko rozumianym pograniczu kredy i paleogenu. Bogate w skamieniałości epikontynentalne utwory górnej kredy (kampan–mastrycht) i dolnego paleogenu (dan) Polski i zachodniej Ukrainy stanowią znakomity obszar do przeprowadzenia takich badań. Zwłaszcza utwory mastrychckie dostarczają obfitych i stosunkowo dobrze zachowanych skamieniałości łodzików, co pozwala na ocenę składu taksonomicznego i liczebności łodzików przed kryzysem biotycznym na granicy kredy i paleogenu.

Badany materiał obejmuje 656 okazów łodzików z 64 stanowisk, obejmujących przedział od środkowego kampanu do danu w Polsce oraz od górnego kampanu do dolnej części górnego mastrychtu w zachodniej Ukrainie. W pracy przedstawiono ogólny kontekst geologiczny, szczegółową charakterystykę oraz zaktualizowaną pozycję stratygraficzną profili, z których pochodzą badane łodziki, co pomaga lepiej zrozumieć ich następstwo czasowe. Najbogatsze materiały z Polski pochodzą ze słynnych kamieniołomów w Piotrawinie (górny kampan), Nasiłowie (górny mastrycht) w profilu środkowej Wisły oraz Woli Piaseckiej (górny mastrycht) w pobliżu Lublina (regionalne tło geologiczne tych odsłonięć opisali Walaszczyk i in. 2016 oraz Machalski i in. 2022). W zachodniej Ukrainie najważniejsze zbiory pochodzą z historycznego profilu dolnego mastrychtu w Nagórzanach koło Lwowa (Machalski i Malchyk 2016).

W badanych materiale zidentyfikowano przedstawicieli trzech rodzin konwencjonalnie wyróżnianych w obrębie nadrodziny Nautilaceae w rzędzie Nautilida: Nautilidae, Cymatoceratidae oraz Hercoglossidae. Późnokredowe fauny z Polski i zachodniej Ukrainy obejmują 14 gatunków: *Eutrephoceras ahltenense, Eutrephoceras? aquisgranense*,

Eutrephoceras darupense, Eutrephoceras dekayi, Eutrephoceras depressum, Eutrephoceras quadrilineatum, Eutrephoceras vastum, Cymatoceras intrasiphonatum, Cymatoceras loricatum, "Cymatoceras" patens, Epicymatoceras vaelsense, Angulithes westphalicus, Cimomia? galiciana, a także Cimomia heberti. Ponadto zbadane fauny zawierają szereg form pozostawionych w otwartej nomenklaturze: Eutrephoceras sp. A, Eutrephoceras sp. B, Eutrephoceras sp. C, Eutrephoceras spp., "Cymatoceras" sp. nova, Cymatoceratidae? indet., Epicymatoceras sp., Angulithes cf. neubergicus, Angulithes sp. nova, Cimomia sp. A oraz Cimomia sp. B. Tylko dwa wczesnopaleogeńskie taksony zostały zidentyfikowane z Polski: Eutrephoceras dekayi oraz Nautilidae indet. gen. et sp. nova?. Najliczniejsza fauna łodzików, zdominowana przez rodzaj Eutrephoceras oraz endemiczny dla Polski gatunek Cymatoceras intrasiphonatum, pochodzi z klasycznych odsłonięć górnego mastrychtu w profilu środkowej Wisły.

Wnioski wypracowane na podstawie badań analogicznych do tych omówionych dla *Epicymatoceras vaelsense* (zob. Rozdział I) pozwoliły na ustalenie pierwotnej budowy muszli niektórych użebrowanych łodzików w badanym materiale (*Cymatoceras intrasiphonatum* i *C. loricatum*), a w konsekwencji na wyjaśnienie ich pozycji systematycznej. Natomiast taksony, które nie odpowiadają nowemu pojmowaniu rodziny Cymatoceratidae (por. Chirat i Bucher 2006), zostały tymczasowo sklasyfikowane jako "*Cymatoceras*" do czasu przeprowadzenia dalszych badań. Wśród użebrowych łodzików, pospolity gatunek *Cymatoceras intrasiphonatum* z górnego mastrychtu został po raz pierwszy dokładnie opisany i zilustrowany (oryginalny krótki opis Łopuskiego z 1912 roku był opatrzony słabymi ilustracjami). Innym ważnym rezultatem przeprowadzonej analizy taksonomicznej jest włączenie dańskiego gatunku *Eutrephoceras bellerophon* do synonimiki mastrychkiego gatunku *E. dekayi*. Ich konspecyficzność ma znaczenie dla zrozumienia wymierania łodzików na granicy K–Pg, co zostanie przedstawione poniżej.

Fauny łodzików z późnej kredy i wczesnego paleogenu Polski i zachodniej Ukrainy porównano z wybranymi faunami europejskimi, w tym z Danii (Stevns Klint, Faxe), Szwecji (Limhamn), północnych Niemiec (Kroonsmoor, Wyspa Rugia), a także Holandii i Belgii (historyczny obszar typowy piętra mastrychckiego) oraz Francji (Vigny). Poza dańską fauną z Danii i Szwecji, fauny łodzików są zazwyczaj dużo mniej liczne i mniej zróżnicowane niż te z Polski i zachodniej Ukrainy.

Z wyjątkiem powszechnie występującego *Eutrephoceras dekayi* oraz skrajnie rzadkiego łodzika *Cimomia heberti* (znanego z pojedynczego okazu z najniższego danu okolic Maastricht), żaden z europejskich gatunków późnokredowych łodzików

zidentyfikowanych w niniejszej pracy, nie przeszedł granicy K–Pg. Dotyczy to wszystkich form o użebrowanej muszli, tradycyjnie zaliczanych do Cymatoceratidae. Na tej podstawie można wyciągnąć wniosek, że pomimo znacznych regionalnych zmian paleogeograficznych oraz facjalnych na przełomie kredy i paleogenu, zaobserowane zmiany w składzie taksonomicznym oraz liczebności faun łodzików odzwierciedlają rzeczywiste wymieranie związane z globalnym kryzysem pod koniec kredy.

Precyzyjne odtworzenie wzorca wymierania kredowych łodzików jest utrudnione przez luki w zapisie kopalnym. W Polsce głównym problemem jest powszechne występowanie luki stratygraficznej w stropie mastrychtu, na przykład w profilu środkowej Wisły (zob. Machalski i in. 2022). Tuż poniżej iłu granicznego K–Pg w wyjątkowo kompletnym profilu w Lechówce koło Chełma (zob. Machalski i in. 2016) znaleziono pojedyncze okazy *E.? aquisgranense* i *Cymatoceras intrasiphonatum*. Pojedynczy okaz *E.? aquisgranense* został również znaleziony w nieco mniej kompletnym profilu najwyższego mastrychtu w Mełgwi koło Lublina, gdzie występują liczne amonity i inne skamieniałości (patrz Machalski i in. 2022 oraz cytowane tam prace pierwszego autora). Inny gatunek, *Epicymatoceras vaelsense*, został stwierdzony w najwyższym mastrychcie Danii (Rozdział II). Te rzadkie znaleziska sugerują, że przynajmniej część europejskiej fauny łodzików przetrwała do samego końca kredy.

Rewizja taksonomiczna badanego materiału wskazuje, że gatunek *Eutrephoceras dekayi* przetrwał granicę K–Pg. Jest to najpowszechniejszy gatunek w badanym materiale, znany z mastrychtu Ameryki Północnej, Europy i Azji oraz z danu Europy i Azji (w tych ostatnich przypadkach pod nazwą *E. bellerophon*). Jego kontynuacja do danu jest zgodna z hipotezą, że szeroko rozprzestrzenione taksony mają większe szanse na przetrwanie masowych wymierań niż te o ograniczonym zasięgu geograficznym (Jablonski 2008; Landman i in. 2014).

Przeprowadzone badania dostarczyły ponadto danych na temat rozprzestrzenienia łodzików w różnych środowiskach, co dokonano na podstawie analizy facji, w których zachowały się ich skamieniałości. W późnej kredzie (kampan-mastrycht) łodziki były najliczniejsze i najbardziej różnorodne w facjach opoki (definicja opoki została podana przez Jurkowską i Świerczewską-Gładysz 2022). Potwierdzają to liczne znaleziska z opok odsłoniętych w profilu środkowej Wisły oraz na Roztoczu. Z drugiej strony, łodziki były mniej liczne i zróżnicowane w facjach kredy piszącej, czego dowodzą niezbyt liczne znaleziska z obszaru wschodniej Polski (Chełm), Danii oraz północnych Niemiec. Warto

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dodać, że opoka zazwyczaj osadzała się w płytkich, bardziej proksymalnych środowiskach niż kreda pisząca (Walaszczyk i Remin 2015; Machalski i Malchyk 2019).

Fauny łodzików wczesnego danu są bardzo ubogie pod względem liczby okazów i gatunków w całej Europie, w tym w pozostającej pod silnym wpływem lądu facji gez tzw. Siwaka, która odsłania się w profilu Wisły. Większa liczba łodzików pojawiła się dopiero w środkowym danie, w rafach koralowych Danii, południowej Szwecji i Francji. Oprócz *E. dekayi*, w tych środowiskach pojawiły się łodziki o dużych muszlach i skomplikowanych liniach przegrodowych, takie jak *Hercoglossa danica*, które musiały przybyć tu z innych części świata.

Materiał uzupełniający do Rozdziału III, który składa się z trzech aneksów, jest zawarty na CD dołączonym do papierowej wersji rozprawy. Pliki te obejmują:

Aneks 1. Materiał badany z Polski i zachodniej Ukrainy.

Aneks 2. Materiał porównawczy z Danii i Niemiec.

Aneks 3. Zbiór danych do analiz biometrycznych Eutrephoceras dekayi.

Literatura (patrz Introduction, str. 19–22)

Introduction

A dramatic mass extinction took place at the end of the Cretaceous (66 Ma), driven by the Chixculub impact and/or Deccan flood volcanism (see Schulte *et al.* 2010; Keller *et al.* 2020). This global biotic crisis irreversibly restructured the taxonomic composition of Earth's biosphere, as exemplified by the turnover from dinosaurs to mammals, and the complete extirpation of rudist reefs. As during other mass extinctions, entire branches were than trimmed from the tree of life, while often closely-related clades were spared (D'Hondt 2005).

The differential survival of related clades during the Cretaceous–Paleogene (K–Pg) crisis has been of long-standing interest, in particular for understanding drivers of extinction selectivity during large-scale environmental perturbances. For cephalopods (class Cephalopoda), the extinction of ammonites has ranked among the most intriguing aspects of the K–Pg mass extinction, especially when contrasted with the survival of the similarly external-shelled nautilids (Landman *et al.* 2014). Nautilids – that is, members of the order Nautilida – form the only extant clade within the subclass Nautiloidea (Kummel 1964; Dzik 1984). Two nautilid genera, *Nautilus* and *Allonautilus*, thrive along coral reef slopes in the southwest Pacific Ocean and the southeast Indian Ocean (Ward 1987; Ward *et al.* 2016).

In contrast to the complex shell structures of ammonites, the nautilids have maintained a relatively simple, coiled shell morphology throughout their evolutionary history. These differences in shell morphology between ammonites and nautilids, combined with proposed differences in their reproductive strategies, metabolic rates, and/or geographic distribution, may have contributed to the distinct evolutionary trajectories of these two groups during the end-Cretaceous crisis (Landman *et al.* 2014; Tajika *et al.* 2023). Hypotheses linking the extinction resilience of particular cephalopod groups with their geographical range (Landman *et al.* 2014) or hatching size (Wani *et al.* 2011) are of particular interest in this context.

The issue of extinction-selectivity also extends to the proposed, poorly-understood extirpation of all ribbed nautilids at the K–Pg boundary (Ward *et al.* 2016). Ribbed nautilds have been traditionally assigned to the family Cymatoceratidae (Kummel 1964). Despite recent attempts to define this family based on shell structure criteria (Chirat and Bucher 2006), the lack of agreement on its validity increases the interpretive chaos regarding the extinction of ribbed nautilids.

These, and other unresolved problems in our understanding of nautilid turnover across the end-Cretaceous mass extinction, call for integrated studies at local, regional, and global scales. However, in contrast to the ammonites, nautilids have not been thoroughly studied in the boundary interval, as they are generally rare in most end-Cretaceous and lower Paleogene successions (Stilwell and Grebneff 1996; Landman *et al.* 2014). Moreover, considerations about nautilid turnover patterns across the K–Pg boundary are hampered by the scarcity of recent taxonomic studies and the often imprecise location of specimens relative to the boundary. Additionally, no prior work has explicitly focused on identifying those nautilid species which managed to survive the K–Pg boundary event and subsequently gave rise to post-Cretaceous lineages.

The Upper Cretaceous to lower Paleogene sections of Europe yield nautilid faunas that are potentially important for understanding nautilid extinction and survival patterns across the K-Pg boundary (Goolaerts 2018). In particular, Campanian-Danian shallow-marine, epicontinental deposits of Poland and western Ukraine provide a remarkable opportunity to study regional nautilid turnover across the K-Pg boundary, as they yield abundant nautilid fossils (for a preliminary report, see Malchyk 2018). These fossils are typically preserved as moulds (steinkerns) left after dissolution of originally aragonitic shells of these cephalopods (Janiszewska et al. 2017). This, at first sight rather discouraging state of preservation may be a contributing factor to our limited knowledge of their taxonomy, evolutionary history, and palaeoecology. Prior to this dissertation, Polish nautilids have only been sparingly studied (Łopuski 1912; Kongiel and Matwiejówna 1937; Machalski et al. 2016). The situation is even worse in western Ukraine, where mid-19th century monographs (Kner 1848; Favre 1869) remain the main references for Cretaceous nautilid palaeontology. The current thesis aims to fill these gaps by providing a thorough palaeontological study of Late Cretaceous and Early Paleogene nautilids from Poland, western Ukraine, and Denmark in the context of the end-Cretaceous mass extinction.

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Chapter I

Shell ornament, systematic position and hatching size of *Epicymatoceras vaelsense* (Nautilida): New insights based on specimens in mould preservation from the Upper Cretaceous of Poland¹

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Abstract

The fossil record of Nautilida in carbonate facies is skewed towards moulds (steinkerns) in various states of preservation, which complicates assessment of the original shell ornament of many taxa. As a remarkable exception, moulds of *Epicymatoceras vaelsense* from upper Campanian and lower Maastrichtian (Upper Cretaceous) siliceous limestones (opoka) in Poland retain details of the original shell ornament, allowing conclusions on the original structure of the shell wall, systematic position and hatching size of this nautilid to be drawn. Both external and internal moulds are present in the material studied, which are referred to as taphomorph 1 and 2, respectively. Based on morphology and inferred taphonomy, it is proposed that the external ribbing of *E. vaelsense* was originally composed of overapping, tile-shaped lamellae of the outer prismatic layer, a character recently suggested to be a synapomorphy for the cymatoceratid clade. The diameter of the embryonic conch of *E. vaelsense* is estimated to have been around 30 mm, which is near the maximum range of hatching size recorded for Cretaceous and younger nautilids. On the basis of the inferred shell structure of *E. vaelsense*, it is speculated that living individuals of this nautilid were covered

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by a dense periostracal cover similar to that of Recent *Allonautilus scrobiculatus*. This study demonstrates that nautilid moulds may provide a better source of palaeontological data than conventionally accepted.

Keywords:

Cephalopoda, Taphonomy, Fossilisation, Campanian, Maastrichtian, Central Europe

Introduction

Preservation of original shell material in extinct representatives of the order Nautilida de Blainville, 1825 is not common. As a result of diagenetic dissolution of aragonite, many fossil nautilids are known solely from mould (steinkern) preservation. In particular, this holds true for nautilids preserved in the carbonate facies (white chalk, limestone) that is widespread in the European Upper Cretaceous (Shimansky 1975; Wilmsen and Esser 2004; Jagt 2012; Frank *et al.* 2013; Wilmsen 2016; Malchyk 2016). Different types of mould preservation (taphomorphs *sensu* Crampton 2004; Wilmsen 2016) may bias morphological analysis of specimens which, in turn, hinders their proper systematic and phylogenetic assessment. This is particularly true for ribbed nautilids, which occurred in many Late Cretaceous marine ecosystems in Europe (Wiedmann 1960; Shimansky 1975; Wilmsen 2000; Wilmsen and Esser 2004; Jagt 2012; Wilmsen 2016; Malchyk 2016).

The taxonomic status of ribbed nautilids has been debated for a long time. Spath (1927) erected the family Cymatoceratidae, with *Cymatoceras* Hyatt, 1883 as type genus, to accommodate all known "ribbed" post-Triassic Nautilida, a view supported by Kummel (1956, 1964). In contrast, the validity of grouping all post-Triassic ribbed genera into a single family has been questioned by others, e.g., Wiedmann (1960), Shimansky (1975), and Wilmsen and Yazykova (2003). In particular, Tintant and Kabamba (1983) and Tintant (1989, 1993) have argued that ribs could have appeared in unrelated nautilid lineages as a result of adaptation to life in high-energy environments. This explains why Tintant (1993) considered the family Cymatoceratidae to be a kind of "litter bin" for ribbed ffshoots of smooth nautilid lineages. Chirat and Bucher (2006) also challenged the monophyly of the Cymatoceratidae and proposed that only taxa with an external ornament composed of overlapping lamellae of the prismatic layer should be assigned to the cymatoceratid clade.

The size of the embryonic shells is an important character in nautiloid evolution (Dzik and Korn 1992). This is especially important within the context of the debate on the contrasting fates of ammonites and nautilids during the Cretaceous–Paleogene mass extinction (Wani *et al.* 2011; Goolaerts *et al.* 2014; Landman *et al.* 2014, 2015). It is possible to estimate the size of the embryonic conch on the basis of the position of the nepionic constriction which marks the hatching point on the innermost whorl (Landman *et al.* 1983; Wani *et al.* 2011) and the presence of reticulate ornament characteristic of embryonic nautilid shells (Arnold *et al.* 1987).

For obvious reasons, previous studies on morphogenesis of ribs and its systematic implications as well as on size embryonic conch in fossil nautilids concentrated on specimens with preserved shells. In the present paper, remarkably well-preserved moulds of Epicymatoceras vaelsense (Binkhorst van den Binkhorst, 1861), the type species of the genus Epicymatoceras Kummel, 1956, are described from upper Upper Cretaceous siliceous limestones (so-called opoka) in Poland. For post-Triassic standards, this is an atypical nautilid that is characterised by a strongly compressed, relatively evolute conch with a subquadrate whorl section and flattened or slightly concave venter (Kummel 1956; Jagt et al. 1998; Goolaerts and Frank 2014). Epicymatoceras was assigned to the family Cymatoceratidae by Kummel (1964), but Chirat and Bucher (2006, p. 62) were not able to confirm whether or not it matched their new definition of the cymatoceratid clade, proposed on the basis of shell structure. In addition, data on the size of the embryonic conch have not yet been published for this taxon. For these reasons, the present paper focusses on details of the ornament that is preserved on moulds of E. vaelsense, presents a taphonomic analysis of these and, finally, draws conclusions on the systematic position and hatching size of this nautilid. Speculations are also presented on the nature of the periostracum of E. vaelsense, on the basis of comparisons with Recent Allonautilus scrobiculatus (Lightfoot, 1786). In order to avoid potential pitfalls in interpretation, the term "ribs" is used here in its widest possible meaning to denote all types of transverse, commarginal ornament of the shell, with the exception of growth lines.

Preliminary results of the present study were outlined in Malchyk *et al.* (2016). Specimens studied are housed in the collections of the Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland (abbreviated ZPAL).

Provenance of material

Four specimens of *Epicymatoceras vaelsense* from the upper Upper Cretaceous of Poland were available for the present study. One of these, ZPAL N.III/68, originates from upper Campanian strata at Strzeżów (Nida Trough), while ZPAL N.III/69–71 are from lower Maastrichtian deposits that crop out at Dziurków (Middle Vistula River section) (Text-fig. 1A).

Strzeżów

This is a disused quarry in the village of Strzeżów, north of Miechow (= locality Strzeżów I of Jurkowska 2016, fig. 3). Exposed are about 7 m of sandy opoka (i.e., limestone with abundant sponge spicules and an admixture of detrital quartz) with marly intercalations (Jurkowska and Uchman 2013; Jurkowska, 2016). These strata are rich in inoceramid and pectinid bivalves, belemnites, gastropods, echinoids and sponges (Świerczewska-Gładysz and Jurkowska 2013). In terms of inoceramid zonation, the Strzeżów section represents the upper Campanian "Inoceramus" inkermanensis and "I." costaecus zones (Jurkowska 2016). A specimen of the ammonite Pachydiscus (Pachydiscus) perfidus de Grossouvre, 1894, is available from approximately the same level at Strzeżów. This taxon is restricted to the upper Campanian Nostoceras hyatti Zone in the Middle Vistula River section (Błaszkiewicz 1980; Machalski 2012a), which encompasses the "Inoceramus" altus and "I." inkermanensis inoceramid zones (Walaszczyk 2004). In summary, ZPAL N.III/68 originates either (and more probably) from the upper part of the "Inoceramus" inkermanensis Zone or from the lower part of the overlying "I." costaecus Zone. In terms of the Belemnitella-based subdivision, this is the interval from the uppermost Belemnitella minor I Zone to the lower part of the Belemnitella minor II Zone of Remin (2015). For the stratigraphical position of the Strzeżów section, reference is made to Text-fig. 1B.

Dziurków

This is an active quarry at the eastern end of the village of Dziurków, near Solec (Middle Vistula River Section) at which a succession of opoka, c. 12 m in thickness, is exposed (Walaszczyk 2012, fig. 1). The section yields abundant sponges (Świerczewska-Gładysz 2006), belemnites (Remin 2012), inoceramids (Walaszczyk 2004), non-inoceramid bivalves, gastropods, nautilids and ammonites (Machalski 2012a). It was assigned to the lower part of the lower Maastrichtian *Endocostea typica* inoceramid Zone by Walaszczyk (2004). In terms

of the Belemnella-based zonation, this stratigraphical interval belongs to the upper part of the Belemnella obtusa Zone (sensu Remin 2012; see also Walaszczyk et al. 2016). The precise provenance within the section is known only for one specimen of E. vaelsense (ZPAL N.III/69). It comes from the lower part of the section, in co-occurrence with a specimen of Pachydiscus (Pachydiscus) neubergicus (von Hauer, 1858) (Machalski 2012a). The latter taxon is one of the markers used to define the GSSP for the base of Maastrichtian Stage at Tercis les Bains, France (Machalski 2012a and references therein). Another biostratigraphically important ammonite taxon from Dziurków is Hoploscaphites quadrispinosus (Geinitz, 1850), which ranges from the bottom of the "Inoceramus" costaecus to the middle of the Endocostaea typica zone in terms of inoceramid biostratigraphy (Machalski 2012b; Machalski and Malchyk 2016, fig. 4). The stratigraphical position of the section at Dziurków is shown in Text-fig. 1B.

Stratigraphical range of *Epicymatoceras vaelsense*

Prior to the present study, *Epicymatoceras vaelsense* was recorded from the southeast Netherlands, northeast Belgium (Binkhorst van den Binkhorst 1861; Jagt *et al.* 1998; Jagt 2012; Goolaerts and Frank 2014) and northwest Germany (Schlüter 1876; Holzapfel 1877). The original figures of Binkhorst van den Binkhhorst and Schlüter are reproduced here in Text-fig. 2A–E.

The type material of *E. vaelsense* is from the lower Maastrichtian in the Vaals area, province of Limburg, the Netherlands (Binkhorst van den Binkhorst 1861). However, the exact stratigraphical provenance of these specimens is unknown. Jagt *et al.* (1998) and Jagt (2012) provided more detailed data on the stratigraphical and geographical distribution of *E. vaelsense* in the southeast Netherlands, northeast Belgium and the Aachen area (Germany). On the basis of their data, the species is known from the localities Altembroeck, Maastricht (ENCI-HeidelbergCement Group quarry), Aachen (Schneeberg), Kosberg, Malensbosch, Nieuwe Weg-Zeven Wegen and Vijlenerbosch. In lithostratigraphical terms, this corresponds to the lower/middle Vijlen Member (intervals 0–4; Gulpen Formation) that is of late early to early late Maastrichtian age. To date, it is not known from intervals 5 and 6 of this member, of early late Maastrichtian age (Keutgen *et al.* 2010; Walaszczyk *et al.* 2010).

Schlüter (1876) described two specimens from the "Mucronaten-Kreide", one from Vaels (Vaals) near Aachen and the other from Lüneburg, northern Germany. The latter locality is also referred to as Zeltberg (Schulz 1979). In Schlüter's time only lower

Maastrichtian strata of the *Belemnella obtusa* Zone (*sensu* Schulz 1979) were exposed at this locality (Birgit Niebuhr, pers. comm. to MM 2016).



Text-fig. 1. Location of the sections that have yielded the specimens of *Epicymatoceras vaelsense* studied herein (A) and their position in the stratigraphical scheme for the Campanian and Maastrichtian stages in Poland (B). Abbreviation: *Blt. - Belemnitella*.

Schönfeld (1985) recorded *Epicymatoceras vaelsense* from upper Santonian strata (upper part of *Marsupites/granulata* Zone) in Westphalia (northwest Germany), but, for the time being, this record is regarded to be doubtful and in need of reinvestigation.

Single specimen (GM 2017.2) of *Epicymatoceras vaelsense* labelled Frejlev?, therefore coming probably from the lower/upper Maastrichtian interval of Jutland, northern Denmark, and two specimens (GM 2017.1 and 2017.3) of *E. vaelsense* from the topmost Maastrichtian chalk exposed at the quarry "Dania" (Jutland), are housed in the collections of the Geological Museum, Copenhagen (personal observations by OM and MM, these specimens will be described in a separate note).

On the basis of these data, the specimen of *E. vaelsense* from the upper Campanian of Strzeżów is considered to be the oldest unequivocal record of this genus known to date. The specimens from the quarry "Dania", although still unpublished, should be regarded as the youngest records, indicating that *Epicymatoceras* ranged into the latest Maastrichtian, possibly even to the K–Pg boundary.

Results

Epicymatoceras taphomorphs

The shell wall of extant nautilids is composed of three principal layers, listed here from outermost to innermost: 1) conchiolin periostracum, usually extremely thin, but thicker in *Nautilus belauensis* Saunders, 1981 and thickest in *Allonautilus scrobiculatus* Lightfoot, 1786, 2) an aragonite layer composed of prismatic crystals (referred to as the outer prismatic layer), and 3) a layer of nacreous aragonite interbedded with sheets of conchiolin (Ward 1987). The nacreous layer is bounded on the inner surface by a thin prismatic layer, referred to as the inner prismatic layer (Gregoire 1987). The latter becomes progressively embedded in nacre during shell growth (Gregoire 1987) and is here not considered further. A major structural discontinuity marks the boundary between the prismatic and nacreous layers (Ward 1987, fig. 1.15).

It is parsimonious to assume that the original shell wall of *Epicymatoceras* was also composed of three principal layers. Generally, the organic periostracum will not be preserved in the fossil record, and aragonitic layers in the shells of *Epicymatoceras* have also disappeared in the present material, having been dissolved during diagenesis. This resulted in the mouldic preservational type that is characteristic of fossils of taxa with originally aragonitic shells in the Upper Cretaceous opoka facies in Poland (e.g., Abdel-Gawad 1986). Both external and internal moulds are present in material studied, here referred to as taphomorph 1 and 2, respectively. The term "taphomorph" refers to preservational variants of a fossil; for more details, reference is made to Crampton (2004) and Wilmsen (2016). The surface of external moulds illustrates details of the outer shell surface, and that of simple internal moulds preserves the ornament of the inner shell surface. Whenever both (or more) original surfaces are recorded on the surface of a single internal mould, these are referred to as composite internal moulds (McAlester 1962; Crampton 2004; Wilmsen 2016). The preservational variants of *Epicymatoceras* from Poland are described and analysed below.



Text-fig. 2. Original figures of *Epicymatoceras vaelsense* from the Upper Cretaceous of northwest Europe. A–C – type specimen of *Nautilus vaelsensis* Binkhorst van den Binkhorst, 1861 (his pl. 5, fig. 2a–c) from the upper lower Maastrichtian of southern Limburg, the Netherlands, in (A) lateral, (B) apertural and (C) ventral views. D–E - Nautilus vaelsensis of Schlüter (1876) (his pl. 51, fig. 3) from the lower Maastrichtian of Lüneburg, northern Germany, in (D) lateral and (E) ventral views.

Taphomorph 1

Three external moulds of *Epicymatoceras vaelsense* (ZPAL N.III/69–71, all preserved in negative relief) from the lower Maastrichtian opoka at Dziurków are assigned to taphomorph 1 (Text-figs 3A, 4, 5A).

ZPAL N.III/69 (Text-fig. 3A) comprises portions of phragmocone and body chamber. No positive counterpart of this specimen is available. The maximum preserved diameter is c. 93 mm. Strong transverse ribbing is the most prominent feature of this specimen. Ribs are ribbon like, up to 4 mm wide, and separated by very nar- row grooves (<1 mm). Ribs bifurcate and trifurcate at mid-flank. The rib boundaries are irregular. In one place, the middle portion of a rib is broken off (arrowed in Text-fig. 3A), revealing the underlying part of another rib. Taking into account the fact that ZPAL N.III/69 represents the external shell surface as seen "from the inside", the observed pattern is interpreted here to reflect a series of lamellae, analogous to imbricated roof tiles, with each lamella ("tile") arising from beneath the preceding one and growing in an apertural direction.

The embryonic conch of ZPAL N.III/69 is well delimited from the post-embryonic portion of the shell by the nepionic constriction, visible as a prominent ridge on the innermost whorl of the mould (arrowed in Text-figs 3A, 5A). It shows a fine reticulate pattern that is formed by the intersection of transverse growth lines and longitudinal lirae, the latter being much stronger and distinct than the former. Such ornament is typical of nautilid embryonic shells (Landman *et al.* 1983; Arnold *et al.* 1987; Ward 1987). The diameter of the exposed part of the embryonic conch is c. 15 mm. Its total diameter has to be estimated because the embryonic conch was partially covered by the successive whorl. Assuming that in *Epicymatoceras vaelsense* every next whorl covered the previous one by about 50 percent of its height (Text-fig. 2A, D), the original diameter of the embryonic conch in ZPAL N.III/69 may be estimated to have been about 30 mm.

ZPAL N.III/70 (Text-fig. 4A–C) is much less complete than the preceding specimen and comprises portions of the outer flank, ventrolateral shoulder and venter. The specimen is obliquely distorted due to compaction, and 101 mm long in the largest preserved dimension. ZPAL N.III/70 is highly informative as far as our interpretation of the original shell structure of *E. vaelsense* is concerned. The ornament of this specimen is composed of a series of limestone "lamellae" with concave adapertural margins at the venter (Text-fig. 4A–C). In cross section, these "lamellae" are relatively thick along their adapical margins and thin out towards the aperture, being separated from each other by voids (Text-fig. 4A). In lateral view (Text-fig. 4B), the "lamellae" are morphologically identical to the ribbon- like imprints of ribs present on the flank in specimen ZPAL N.III/69 (compare Text-figs 3A and 4B). In ZPAL N.III/70, the "lamellae" are additionally adorned with fine transverse lines, possibly growth increments, a feature not seen in ZPAL N.III/69.



Text-fig. 3. Specimens of *Epicymatoceras vaelsense* from the Upper Cretaceous of Poland. A – incomplete external mould, ZPAL N.III/69 (taphomorph 1) from the lower Maastrichtian at Dziurkoów; a spot where a rib has broken off is arrowed in order to draw attention to the surface of another, underlying rib; another arrow in the umbilical region of the specimen marks the position of nepionic constriction. B – internal mould, ZPAL N.III/68 (taphomorph 2) from the upper Campanian at Strzeżów.

In an attempt to assess ZPAL N.III/70 in terms of its original shell structure, the specimen has to be imagined in reverse view, i.e., positive elements must be considered to have been originally negative and vice versa. In this way, the limestone "lamellae" observed on the mould are considered here to have been original voids in the shell wall. In contrast, the present voids and cavities on the surface of the specimen are regarded to have been spaces previously occupied by true lamellae of the original shell material. The resulting reconstruction of the shell ornament of this specimen is illustrated in Text-fig. 6A. This interpretation is strongly influenced by the data presented by Chirat and Bucher (2006), who described the shell structure of *Cymatoceras varusensis* (d'Orbigny, 1850) from the "Neocomian" of France, and *C. sakalavum* Collignon, 1949, from the Albian of Magadascar. If this analogy between our moulds and the shell-based specimens is correct, the original shell of *E. vaelsense* was composed of a rather thin outer prismatic layer, developed as a series of adaperturally projected and overlapping tile-shaped lamellae, and of an underlying layer, possibly much thicker, that was composed of nacre (compare Text-fig. 6A herein and Chirat and Bucher 2006, fig. 2).



Text-fig. 4. Details of shell ornament as preserved in specimen ZPAL N.III/70 from Dziurkow, in different views and magnifications (A–C) to show overlapping siliceous limestone (opoka) "lamellae" which correspond to cavities between successive tile-shaped lamellae of the prismatic layer in the original shell.



Text-fig. 5. Casts of embryonic shells of *Epicymatoceras vaelsense* with fine reticulate pattern, characteristic of nautilid embryonic shells. Arrowed in A is the boundary between embryonic and post-embryonic portions of the shell (marked by a ridge corresponding to the nepionic constriction). A – specimen ZPAL N.III/69 from Dziurków. B – specimen ZPAL N.III/68 from Strzeżów.

Specimen ZPAL N. III/71 (not illustrated) is poorly preserved, heavily crushed and partially covered by a rusty limonitic crust. It represents part of the phragmocone and measures c. 81 mm in diameter. The ornament is partially effaced but does show the same general pattern as other specimens assigned here to taphomorph 1. Neither size nor ornament of the embryonic shell can be deter- mined in this specimen.

Taphomorph 2

A single specimen, ZPAL N.III/68 (Text-figs 3B and 5B), from the upper Campanian opoka of Strzeżów elongs here. It is an internal mould preserved in positive relief, obliquely distorted as a result of compaction. The specimen measures c. 110 mm in diameter, and comprises the phragmocone and part of the body chamber (Text-fig. 3B). Wide, open umbilicus comprises about 23% of shell diameter. The umbilical shoulder is broad and rounded, except for the youngest preserved part of the specimen where it is sharp and overhangs the umbilicus, most probably due to oblique distortion of the mould. Flanks are flat, the ventrolateral shoulder angular and the venter flat. The suture line is weakly sinuous and shows a shallow lateral lobe and a shallow saddle across the venter.

The radial ornament of ZPAL N.III/68 consists of sigmoidal narrow ribs (up to 1 mm wide), which are separated by much wider interspaces (Text-fig. 3B). Thus, this is the reverse of the situation seen in taphomorph 1, in which ribs are wide and rib interspaces narrow. At first, such differences might be regarded as taxonomically important, warranting separation at the specific level of the present specimen from the others in collection studied. However, they are considered as merely reflecting preservational differences of a single species. The strongest rib flexure is across the venter and on the ventrolateral shoulder (Text-fig. 3B). They are most accentuated on the early part of the phragmocone and on the ventrolateral shoulder; their effacement on the flanks of the body chamber probably is a preservational artifact.

The nepionic constriction is not discernible in ZPAL N.III/68. However, its innermost whorl reveals reticulate pattern dominated by spiral lirae which gradually fades away adaperturally (Text-fig. 5B). In view of the fact that in some nautilids the reticulate pattern may either disappear before the nepionic constriction or slightly persist past it (Arnold *et al.* 1987; Landman *et al.* 2017; Marcela Cichowolski, pers. comm.), its extent cannot be used as a precise measure of the embryonic conch diameter in ZPAL N.III/68. One may suppose, however, that it was comparable in size to that in ZPAL N.III/ 69.

Discussion

Although rather limited in number of specimens, the present collection of moulds of *Epicymatoceras vae*lsense, does allow some important conclusions to be drawn. These concern firstly the original shell structure of this nautilid and taphonomic pathways that led to the formation of moulds; secondly, the systematic po- sition of *Epicymatoceras*; thirdly, structural and functional analogies with Recent *Allonautilus scrobiculatus*, and lastly, the hatching size of *E. vaelsense* within the context of embryonic shell variation that has previously been documented for other nautilids.

Shell structure and taphonomic pathways

By analogy with shell-preserved cymatoceratids described by Chirat and Bucher (2006), it has been suggested above that the aragonitic shell of Epicymatoceras vaelsense consisted of an outer prismatic layer that was developed as a series of imbricated, adaperturally projected lamellae, and of an underlying layer, possibly thicker and composed of nacre (Text-fig. 6A). This structure of the shell wall in Epicymatoceras was imprinted on the moulds in two different ways and resulted in two distinctive taphomorphs (Text-fig. 6B). In taphomorph 1, the surface of the external moulds reflects e as a negative relief e the imbricated structure of the external surface of the original shell (i.e., upper block in Text-fig. 6B). In taphomorph 2, the ribbed surface of the internal mould is more difficult to interpret. If this were a simple internal mould, it would reflect the inner surface of the original shell wall. However, if it were a composite internal mould, it reflects additionally the "intermediate" original interface between the prismatic and nacreous layers, superimposed on the former. It is impossible to draw any firm conclusions in this respect. In general, ornament of the internal mould studied consists merely of narrow ribs that are much weaker than the prominent ribbon-like ribs preserved on the sur- faces of specimens assigned to taphomorph 1 (compare relevant portions of Text-fig. 6B). This matches observations made by Chirat and Bucher (2006, p. 59), who noted that the external lamellate ornament of the outer prismatic layer of shellpreserved cymatoceratids was reflected merely as narrow and weakly imprinted ribs on the corresponding internal moulds, "being levelled off by a thick nacreous layer".



Text-fig. 6. Original ornament and its preservation in *Epicymatoceras vaelsense*. A – reconstructed cross section of the shell to show the succession of overlapping radial tile-shaped lamellae of the prismatic layer and adaperturally open cavities between them. B – details of ornament visible on the surface of external (upper block) and internal (lower block) moulds. Abbreviations: pl – outer prismatic layer, ncl – nacreous layer, 1 – lamellae, c – cavities, cm – moulds reflecting the shape of the original cavities, vl – voids left after dissolution of lamellae.

Four stages in the formation of moulds of *Epicymatoceras* (Text-fig. 7A–D) may be recognised on the basis of morphological and taphonomic features:

Stage A. Burial of shells of dead nautilids on the sea floor, possibly after a necroplanktonic stage; rapid decomposition of the periostracum and infilling of cavities between lamellate extensions of the prismatic layer with soft sediment.

Stage B. Dissolution of nautilid shells, most probably in a taphonomically active zone just below the sediment-water interface; this likely occurred in the early stages of diagenesis, when the sediment was not fully lithified yet but firm enough to preserve voids that were produced by dissolution of shell layers.

Stage C. Compaction of sediment and voids; full transformation (lithification) of sediment into the present-day siliceous limestone (opoka), resulting in a relatively precise preservation of details of ornament.

Stage D. Splitting a piece of opoka with embedded specimen of *Epicymatoceras*, yielding two preservational classes of specimens which retain details of shell ornament in different aspects, depending on whether they are part or counterpart (taphomorphs 1 and 2, respectively).


Text-fig. 7. Reconstruction of the taphonomic history of *Epicymatoceras vaelsense* to show the origin of the different preservation types of specimens studied. A – burial stage, with aragonitic shell still preserved, B – stage of aragonite dissolution, C – compaction stage, D – "collecting stage" with different taphomorphs originating as part and counterpart of the same specimen after splitting the rock matrix; indicated are details of ornament visible on the external (taphomorph 1) and internal moulds (taphomorph 2). Abbreviations: pl – outer prismatic layer, ncl – nacreous layer, cm – sediment infillings (in A) and moulds (in B–D) of the original voids or cavities in the prismatic layer, v – void left after dissolution of shell material.

Systematic position

The genus *Epicymatoceras* was established by Kummel (1956) and placed in the family Cymatoceratidae, on the basis of its pronounced ribbing (Kummel, 1964). As noted earlier, Wiedmann (1960) and many subsequent authors (Shimansky 1975; Tintant and Kabamba 1983; Tintant 1989, 1993; Wilmsen 2000; Wilmsen and Yazykova, 2003) questioned the validity of grouping all ornamented genera into a single family, the Cymatoceratidae.

Shimansky (1975) placed *Epicymatoceras* in the family Nautilidae de Blainville, 1825, whereas Dzik (1984) considered the genus to be a taxon of uncertain taxonomic position.

A recent study of the morphogenesis of ornament in *Cymatoceras* Hyatt, 1883, the type genus of the family Cymatoceratidae, has demonstrated that the ribs of *Nautilus pseudelegans* d'Orbigny, 1840, which is the type species of *Cymatoceras*, actually represent overlapping, tile-shaped lamellae of the outer prismatic layer (Chirat and Bucher 2006). Based on this observation, those authors suggested that this character might be considered a synapomorphy of the emended cymatoceratid clade. As pointed out by Chirat and Bucher (2006), many other nautilid taxa that had traditionally been assigned to the Cymatoceratidae on the basis of their ribbing actually reveal different styles of external ornament, which may include "normal" ribs, fasciculate growth lines as well as divaricate imbrication (Chirat and Bucher 2006).

In view of the lack of adequate literature data, Chirat and Bucher (2006, p. 62) could not to confirm whether or not *Epicymatoceras* matched their revised definition of the clade, based on the presence of imbricated shell extensions. The present observations suggest that *Epicymatoceras vaelsense* was indeed characterised by this imbricate pattern of lamellae on the outer shell surface. As such, it does correspond to the new definition of the Cymatoceratidae by Chirat and Bucher (2006). In other words, the genus *Epicymatoceras* may be regarded as a "true" cymatoceratid (*sensu* Chirat and Bucher 2006).

The same style of ribbing was noted on moulds of *Cymatoceras loricatum* (Schlüter, 1876) from the lower Maastrichtian white chalk ("Schreibkreide") of Kronsmoor, northern Germany, by Wilmsen and Esser (2004). In places, it can also be seen on material of *Epicymatoceras monstrum* from the upper Maastrichtian of Mangyshlak, Kazakhstan (Shimansky 1975, pp. 31, 122, Text-fig. 7; pl. 27, fig. 3). Thus, these two taxa appear to meet the criteria for the new definition of a cymatoceratid clade (*sensu* Chirat and Bucher 2006).

Speculations on periostracum

In the interpretation presented here, the external surface of the prismatic layer in *E. vaelsense* was composed of adaperturally projected and overlapping, tile-shaped lamellae, separated by voids, or cavities (Text-fig. 6A). According to Ward (1987, p. 20), a possible function of outer shell ornament in shells of Recent nautilids may be to serve as attachment for the periostracum. It is therefore speculated here that the empty spaces in the prismatic layer of *E. vaelsense* served as anchorage zones for the periostracum. Chirat and Bucher (2006, p. 60) discussed this possibility for other cymatoceratids but did not obtain any firm conclusions.

Those authors quoted papers by Ward (1987) and Ward and Saunders (1997) in which the structure of the periostracum in Recent *Nautilus* Linnaeus, 1758 and *Allonautilus* Ward and Saunders, 1997 had been described. In *Nautilus macromphalus* Sowerby, 1848 and *N. pompilius* Linnaeus, 1758, the periostracum consists of a very thin continuous sheet of organic material (between 1 and 5 mm thick), resting on top of the outer prismatic layer. In *N. belauensis*, the periostracum is much thicker (about 1 mm), but has a similar structure. In *Allonautilus scrobiculatus*, however, the periostracum is utterly different in structure and appearance (Ward 1987, Ward and Saunders 1997). It is thick and dense, being developed as a series of long sheets (up to 10 mm in length) that extend outwards at low angles from the shell wall and split into numerous thin irregular layers from thicker basal "leaves" emerging from between successive in- crements of the outer prismatic layer. This is best seen in fig. 1.18 in Ward (1987), which presents SEM images of the contact zone between the periostracum and prismatic layer in *Allonautilus scrobiculatus*.

It is speculated here that the inferred shell structure in *E. vaelsense* (Text-fig. 6A) was homologous to that described in *A. scrobiculatus*, although the latter is observable only at a microscopic scale, while the former can be seen with the naked eye. If this difference is merely a matter of size, the Late Cretaceous nautilid *Epicymatoceras vaelsense* must have been covered *in vivo* by a particularly dense and prominent periostracal "fur". Its functional role remains mysterious; Ward (1987) noted that in *A. scrobiculatus* it might have served as a protective cover against epibionts and/or predators. He also mentioned the deleterious effect of a dense periostracal cover for shell streamlining in that modern species. Paradoxically, the aragonitic shell of *E. vaelsense* was markedly streamlined in comparison with that of its coeval cymatoceratid allies. For the time being, this apparently contradictory co-presence of a streamlined shell shape and an "anti-streamlined" periostracal crust cannot be explained. Ideally, specimens in shell preservation might offer more clues.

Hatching size

Impressions of the embryonic conch as preserved in specimens of *Epicymatoceras vaelsense* permit some conclusions on hatching size of this nautilid to be drawn. The embryonic conch is discernible in specimen ZPAL N.III/69. The diameter of the embryonic conch in this specimen may be estimated at 30 mm; embryonic conch of another specimen ZPAL N.III/68 was probably of comparable size (see above).

Present observations allow a comparison of hatching sizes of *Epicymatoceras* and of other Cretaceous and post-Cretaceous (Paleogene and Recent) nautilids (Landman *et al.* 1983;

Matsumoto *et al.* 1984; Arnold *et al.* 1987; Landman 1988; Saunders *et al.* 1996; Cichowolski 2003; Cichowolski *et al.* 2005; Wani and Ayyasami 2009; Wani *et al.* 2011; Landman *et al.* 2017). Previously recorded ranges of hatching diameter (i.e., diameter of hatchlings), summarised in Table 1 and Text-fig. 8, are 9–32 mm for the family Nautilidae, 15–32 mm for the Cymatoceratidae and 20–22 mm for the Hercoglossidae (Note: family names follow the conventional subdivision of the Nautilida by Kummel 1956, 1964). Data on *Epicymatoceras* presented here suggest that the hatching size in this genus falls within the largest of known ranges (see Table 1, Text-fig. 8).

Several authors have discussed differences in number of eggs and hatching sizes between nautilids and ammonites, in the context of the Cretaceous–Paleogene (K–Pg) extinction event (Landman *et al.* 1983; Landman 1984; Ward 1987; Gallagher 1991; de Baets *et al.* 2012; Landman *et al.* 2014, 2015). All have suggested that nautilids produced a few large eggs and embryos, while ammonite reproduction involved hundreds or thousands of much smaller embryos (<1 to maximum 2.6 mm in diameter) (Landman *et al.* 1983; Ward 1987; Landman 1988; Landman *et al.* 1996; Laptikhovsky *et al.* 2013). It is commonly assumed that this reflected fundamental differences in the mode of life of newly hatched individuals, which are thought to have been nektobenthic in nautilids and planktonic in ammonites. For this reason, it was often suggested that differences in number, size and mode of life between nautilid and ammonite hatchlings determined the different fates of these groups across the K–Pg boundary, with ammonites driven to extinction as a result of the collapse of the planktonic ecosystem (albeit with some delay, as some groups did range into the earliest Paleogene; Machalski and Heinberg 2005; Landman *et al.* 2014, 2015).

Table 1. Data on hatching diameter of Cretaceous and post-Cretaceous nautilids, based on literature and the present study. See Text-fig. 8 for graphical presentation of the results.

Family	Species	Age	Geographic location	Number of measurements	Hatching diameter (mm)		No in Text-	Reference
					Range	Average	fig. 8	
Nautilidae	Nautilus belauensis	Recent	Pacific	2	30.4-31.8	31.1	1	Arnold et al. 1987
	Nautilus macromphalus	Recent	Pacific	4	25.4-27.4	26.2	2	Arnold et al. 1987
	Nautilus pompilius	Recent	Indo-Pacific	91	22.6-27.4	26.1	3	Arnold et al. 1987
	Allonautilus scrobiculatus	Recent	Pacific	4	24.5-26.0	25.6	4	Arnold et al. 1987
	Nautilus praepompilius	Paleogene (late Eocene)	Kazakhstan	1	c.23	c.23	5	Saunders et al. 1996
	Eutrephoceras clementinum	middle Turonian	India	60	?	20	6	Wani and Ayyasami 2009
	Eutrephoceras cf. dekayi	Campanian or Maastrichtian	USA	1	14.2	14.2	7	Landman 1988
	· ·	late Maastrichtian	USA	1	10	10	8	Landman et al. 2017
	Eutrephoceras dekayi	Campanian–Maastrichtian	USA	4	9.2-10.4	9.6	9	Landman et al. 1983
	· ·	early Maastrichtian	USA	11	12.6-16.2	14	10	Landman et al. 2017
	Eutrephoceras dekayi?	late Campanian	USA	1	10.7	10.7	11	Landman et al. 2017
	Eutrephoceras nebrascensis	late Campanian	USA	2	10.1-10.6	10.3	12	Landman et al. 2017
	Eutrephoceras sp.	early Campanian	Antarctic Peninsula	1	28.2	28.2	13	Cichowolski et al. 2005
	Eutrephoceras subplicatum	early Campanian–late Maastrichtian	Antarctic Peninsula	?	?	<i>c</i> .32	14	Cichowolski et al. 2005
Cymatoceratidae	Anglonautilus japonicus	early Cenomanian	Japan	?	?	c.15	15	Matsumoto et al. 1984
	Cymatoceras perstriatum	Valanginian–Barremian	Argentina	?	?	<i>c</i> .32	16	Cichowolski 2003
	Cymatoceras patagonicum	Turonian	Argentina	?	?	c.30	17	Cichowolski 2003
	Epicymatoceras vaelsense	late Campanian–early Maastrichtian	Poland	1	<i>c</i> .30	<i>c</i> .30	18	this study
Hercoglossidae	Hercoglossa forbesianus	late Albian–earliest Cenomanian	India	1	22.2	22.2	19	Wani <i>et al.</i> 2011
	Cimomia angustus	late Albian–earliest Cenomanian	India	1	20.4	20.4	20	Wani <i>et al</i> . 2011



Text-fig. 8. Hatching diameter in Cretaceous (K), Paleogene (Pg) and Recent (Rec.) nautilids based on references in Table 1. Each circle with number corresponds to average diameter of the embryonic conch as recorded in quoted references.

The large hatching size in *Epicymatoceras vaelsense* documented herein is in concert with previous data for other Cretaceous nautilids. However, it should be noted that this trait did not protect *Epicymatoceras* from extirpation just prior, or at, the Cretaceous–Paleogene boundary. The stratigraphically youngest specimens of this genus recorded to date are from the topmost Maastrichtian chalk at the quarry "Dania" in northern Denmark (see above).

Conclusions

A small collection of moulds of the nautilid *Epicymatoceras vaelsense* from upper Campanian and lower Maastrichtian (Upper Cretaceous) siliceous limestones (opoka) in Poland is described and illustrated in the present paper. The moulds retain details of the original shell ornament, allowing conclusions on the original structure of the shell wall, the systematic position, and the hatching size of this nautilid to be drawn.

In the material studied, two preservational variants, referred to as taphomorph 1 and 2, are distinguished being represented by external and internal moulds, respectively. Based on morphology and inferred taphonomy of specimens in hand, it is concluded that the external ribbing of *E. vaelsense* was originally composed of overlapping tile-shaped lamellae

of the outer prismatic layer, a character recently suggested to be diagnostic of the cymatoceratid clade. Additionally, it is speculated that living specimens of *E. vaelsense* had a dense cover of periostracum that was similar to, or even more prominent than, the periostracal "fur" seen on the surface of extant *Allonautilus scrobiculatus*.

The diameter of the embryonic conch in *E. vaelsense* may be estimated to have been around 30 mm, which is near the maximum range of hatching size recorded for Cretaceous and post-Cretaceous nautilids.

In summary, the present paper demonstrates that nautilid fossils in mould (steinkern) preservation may be a better source of palaeontologic information than is conventionally expected, provided they are carefully interpreted in terms of morphology and taphonomic history.

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Chapter II

First record of *Epicymatoceras vaelsense* (Nautilida) from the Maastrichtian white chalk of northern Denmark²

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Abstract

The atypical Late Cretaceous nautilid *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1861) is described and illustrated on the basis of three specimens from the Maastrichtian white chalk of Denmark. One of these is probably from the lower/upper Maastrichtian boundary interval at Frejlev, while the other two originate from the uppermost Maastrichtian chalk as exposed in the Dania quarry; both localities are in Jylland, northern Denmark. These are first reports of *E. vaelsense* from Denmark; the species has previously been recorded from the uppermost Campanian and lower Maastrichtian of the Netherlands, Belgium, northern Germany and Poland. The presence of *E. vaelsense* in the topmost Maastrichtian white chalk in the Dania quarry is considered the youngest record of *Epicymatoceras* known to date, suggesting the persistence of the genus until the end of the Cretaceous. The diameter of the embryonic conch of the Dania quarry, confirming earlier observations that the species possessed one of the largest embryonic conchs amongst Late Cretaceous nautilids.

Keywords:

Upper Cretaceous, Cephalopoda, *Epicymatoceras*, Denmark, embryonic conch, K-Pg mass extinction

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Introduction

Fossil nautilids are uncommon in Maastrichtian and Danian deposits of Denmark. In addition, they are still rather poorly presented in the literature (e.g., Ravn 1902; Rosenkrantz 1944, 1960; Gravesen 2001). The following species have been described from the Maastrichtian and Danian of Denmark: Eutrephoceras darupense (Schlüter, 1876), E. bellerophon (Lundgren, 1867), ?Cymatoceras patens (Kner, 1848) [reffered as "Cymatoceras" patens in Chapter III], Hercoglossa danica (von Schlotheim, 1820) and Danathuroidea fricator (Beck, 1835). Of these, E. darupense has been recorded from the lower/upper Maastrichtian interval at Frejlev (Jylland), ?C. patens from the same interval and locality as well as from the lower Maastrichtian of Møns Klint, south-eastern Denmark, while E. bellerophon, H. danica, and D. fricator are on record from the middle Danian at Faxe and the upper Danian at Saltholm, both in Sjælland, eastern Denmark (Ravn 1902). Rosenkrantz (1944) reported on the presence of Eutrephoceras and Hercoglossa in the Maastrichtian chalk of Stevns Klint, south-eastern Sjælland. In addition, several specimens assigned to Eutrephoceras, Cimomia(?), Cymatoceras or "Nautilus" (?) have been recorded from Maastrichtian strata exposed at Møns Klint, Gedser Odde in south- eastern Denmark and in Jylland, northern Denmark (Gravesen and Jakobsen 2013), see Text-fig. 1A.

The aim of the present note is to describe and illustrate the first records of the nautilid *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1861) from the Maastrichtian white chalk of Denmark. This material, three specimens in total, comes from two Maastrichtian sites in Jylland, northern Denmark (Text-fig. 1B). The specimens studied are stored in the collections of the Natural History Museum of Denmark, Copenhagen (registration numbers MGUH 33073, 33074 and 33075); they were briefly mentioned by Malchyk *et al.* (2017, p. 3). These new specimens contribute to a better understanding of regional and global patterns of nautilid turnover during the Late Cretaceous and early Paleogene interval, which is significant in the context of the ongoing debate on the nature of the Cretaceous–Paleogene (K–Pg) mass extinction (e.g., Goolaerts *et al.* 2014; Landman *et al.* 2014; Goolaerts 2018; Malchyk 2018).

Stratigraphy and localities

Traditionally, the upper Campanian to Maastrichtian chalk in Denmark has been subdivided into ten microbrachiopod zones (Surlyk 1970, 1984). These were correlated with the conventional European belemnite zonal scheme, according to which the base of the Maastrichtian was defined by the first occurrence (FO) of *Belemnella lanceolata* (e.g., Birkelund 1957; Schulz and Schmid 1983; Christensen 1996, 1997). However, in recent years, the definition of the Campanian–Maastrichtian boundary has changed. The Global Stratotype Section and Point (GSSP) for the base of the Maastrichtian Stage is placed at the 115.2 m level at Tercis near Dax, south-west France (Odin 2001; Odin and Lamaurelle 2001). According to the Tercis definition, the base of the Maastrichtian Stage is significantly higher than the level of the FO of *Belemnella lanceolata* (e.g., Walaszczyk 2004; Remin 2012; see also Machalski 2012). Therefore, the Campanian–Maastrichtian boundary as defined at Tercis is placed in Denmark within the *Rugia spinosa–Terebratulina subtilis* Zone of Surlyk (1970, 1984) (Text-fig. 1C).

The precise geographical provenance of one of the specimens studied (MGUH 33074) is unknown. However, as stated on the original label, it is most likely from Frejlev, northern Denmark (Text-fig. 1B). The Frejlev section spans the lower–upper Maastrichtian interval boundary, the *Rugia tenuicostata–Meonia semiglobularis* Zone to the *Meonia semiglobularis–Ruegenella humboldtii* Zone of Surlyk (1984) (Text-fig. 1C). In terms of belemnite zonation, this stratigraphic interval belongs to the lower part of the *Belemnitella junior* Zone and the upper part of the *Belemnella fastigata* Zone (Schulz 1979; Schulz and Schmid 1983). Therefore, MGUH 33074 is probably from eitherthe uppermost lower Maastrichtian *Ru. tenuicostata–Me. semiglobularis* Zone, or from the lowermost upper Maastrichtian *Me. semiglobularis–Rue. humboldtii* Zone.

Specimens MGUH 33073 and MGUH 33075 are from the Dania limestone quarry. This is an abandoned chalk pit, currently overgrown by vegetation (S.L. Jakobsen, personal communication 2018), situated on the south side of Mariager Fjord (Text-fig. 1A). A Maastrichtian–Danian boundary succession of carbonate deposits, c. 30 m thick, was formerly available at this quarry (Håkansson and Hansen 1979). The Maastrichtian part of the Dania quarry succession corresponds to the *Argyrotheca stevensis–Magas chitoniformis* brachiopod Zone (Text-fig. 1C), which is the equivalent of the *Belemnella kazimiroviensis* Zone (Schulz 1979; Schulz and Schmid 1983; Surlyk 1984; Birkelund 1993) and can be correlated with the *Palynodinium grallator* dinoflagellate Zone of Hansen (1977). It should also be noted that the Maastrichtian part of the Dania succession yielded the topmost Maastrichtian zonal coccolith species *Micula prinsii* (Håkansson and Hansen 1979). The precise position of both nautilid specimens within the Dania section is unknown. However, they are safely assigned a latest Maastrichtian age, based on the data presented above. Specimen MGUH 33073 was collected by Mogens Steentoft Nielsen at the beginning of the 21st century and subsequently transferred

to the collections of the Natural History Museum of Denmark (Copenhagen), having been declared Danekræ (catalogue number 886, see http://www.danicafossils.dk/).



Text-fig. 1. A – Map of Denmark with localities mentioned in the text. B – Location of the two sections that yielded the nautilid *Epicymatoceras vaelsense* in northern Denmark. C – Stratigraphy of upper Campanian and Maastrichtian strata in north-western Europe. Sources: 1) Birkelund (1957); 2) Surlyk (1984); 3) Surlyk (1970). Abbreviations: *A.: Argyrotheca; Gi.: Gisilina; M.: Magas; Me.: Meonia; Rue.: Ruegenella; Ru.: Rugia; Te.: Terebratulina; Tri.: Trigonosemus.* Chronostratigraphy modified according to the new definition of the base of the Maastrichtian Stage and subsequent correlations (Odin 2001; Odin and Lamaurelle 2001; Walaszczyk 2004; Remin 2012).

Systematic Paleontology

Order Nautilida Agassiz, 1847 Superfamily Nautilaceae de Blainville, 1825 Family Cymatoceratidae *sensu* Chirat and Bucher, 2006 Genus *Epicymatoceras* Kummel, 1956

TYPE SPECIES: Nautilus vaelsensis Binkhorst van den Binkhorst, 1861. P. 15, pl. 5, fig. 2.

DIAGNOSIS: "Widely evolute, greatly compressed; whorl section subquadrate, nearly twice as high as wide; ventral shoulders angular, venter narrow and flattened; flanks only slighty inflated; umbilical shoulders broadly arched; suture with shallow ventral lobe and shallow lateral lobe; position of sipchuncle unknown; surface bearing fine sinous ribs that curve backward toward ventral shoulders and form slight sinus on venter" (Kummel 1964, p. K454).

Epicymatoceras vaelsense (Binkhorst van den Binkhorst, 1861)

(Text-fig. 2A–C)

1861. Nautilus vaelsensis, Nobis.; Binkhorst van den Binkhorst, p. 15, pl. 5, fig. 2a-c.

1876. Nautilus vaelsensis Binkhorst van den Binkhorst; Schlüter, p. 177, pl. 51, fig. 3.

1887. Nautilus vaelsensis Binkhorst van den Binkhorst; Holzapfel, p. 68, pl. 4, fig. 4.

1956. Epicymatoceras vaelsense (Binkhorst van den Binkhorst, 1861); Kummel, p. 439.

2012. Epicymatoceras vaelsense (Binkhorst van den Binkhorst, 1861); Jagt, p. 141, pl.30, figs G–H.

MATERIAL: Three specimens in mould preservation (MGUH 33073, 33074 and 33075). Specimen MGUH 33074 probably originates from the lower/upper Maastrichtian boundary at Frejlev. Specimens MGUH 33073 and 33075 come from the topmost Maastrichtian succession in the Dania limestone quarry.

DESCRIPTION: Specimen MGUH 33073 (Text-fig. 2A) from the Dania quarry is an internal mould comprising the larger part of the phragmocone, measuring ap- proximately 73 mm in maximum preserved diameter. The whorl section is compressed and subquadrate. Coiling is relatively evolute. The umbilicus is wide, c. 25 per cent of the diameter, with steeply inclined

umbilical wall and broadly rounded umbilical shoulder. The flanks are flat. The ventrolateral shoulder of this specimen is angular in the early part of conch and seems to be more rounded in the latest stage, as preserved. The venter is generally flat; however, it seems to be slightly convex on the outermost part of the last preserved whorl of the phragmocone. The position of the siphuncle is uncertain. The ornamentation of MGUH 33073 consists of coarse radial ribs, up to 3 mm in maximum width and separated by narrow and deep grooves (> 1 mm). Ribs arise at the umbilical seam, broadening across the flank with a sigmoidal curve and suddenly curving backwards at the ventrolateral shoulder, forming a narrow ventral sinus. They are poorly expressed and almost effaced on the higher flank and the early stages of the phragmocone, but are stronger and more convex at mid-flank and ventrolateral shoulder on the later part of the phragmocone.

A nepionic constriction delimiting pre- and post- hatchling stages is well recognised as a narrow depression on the innermost whorl (Text-fig. 2A). The embryonic conch is characterised by a poorly expressed reticulate pattern dominated by longitudinal lirae and measures about 15 mm in visible diameter. Based on the assumption that in the early whorl stages in *Epicymatoceras* the height of every next whorl is half covered by the next one (see Malchyk *et al.* 2017), the total embryonic diameter is estimated to have been approximately 30 mm, thus matching the hatching diameter reported for specimens of *E. vaelsense* from the Upper Cretaceous of Poland.

MGUH 33074 (Fig. 2B) from Frejlev(?) is probably the most complete specimen of *E. vaelsense* ever to have been recorded. It is an internal mould of the phragmocone and a large portion of the body chamber, extending to the aperture with a maximum preserved conch diameter of c. 128 mm. A partially preserved apertural margin is recognised on the right side of the specimen studied as a slightly curved outline (Fig. 2C). Unfortunately, the shape of the hyponomic and ocular sinuses could not be determined due to the fragmentary preservation of the specimen. One may note that the ribs tend to become weaker and less pronounced in the adapertural part of the shell, when compared to the main body of the individual (Fig. 2C). Conch shape is relatively evolute, gradually becoming more evolute towards the later whorl stages. The whorl section is compressed with generally flattened flanks. The umbilicus is large and comprises about 27 per cent of the diameter, the umbilical wall is inclined and the umbilical shoulder is broadly rounded. The ventrolateral shoulder is angular, the venter is flat. The surface of MGUH 33074 is ornamented by very prominent ribbing. Ribs are about 1 mm in width at the umbilicus and become up to 4–5 mm wide towards the aperture, showing some bifurcation at mid-flank. Ribs are strongly expressed on the phragmocone and become less

conspicuous on the adapertural part of the body chamber. The embryonic conch is not visible in this particular specimen.



Text-fig. 2. The cymatoceratid *Epicymatoceras vaelsense* from the Maastrichtian of northern Denmark (Jylland). A – Specimen MGUH 33073 from the Dania quarry. The arrow indicates the nepionic constriction between embryonic and post-embryonic parts of the shell. B and C – Specimen MGUH 33074, probably from Frejlev. B: Left view. C: Right view of a partially broken body chamber displaying the apertural margin (arrow).

MGUH 33075 from Dania is a fragmentary internal mould consisting of three fragments, not illustrated here. The largest piece comprises a portion of the umbilicus and flank and measures about 50 mm in length. One of the other remaining fragments is preserved as an external impression, probably of part of the lower and middle flank, and another one is the internal mould of a portion of the lower flank.

COMPARISON: *Epicymatoceras* Kummel, 1956 is an atypical Late Cretaceous nautilid genus that belongs to the family Cymatoceratidae Spath, 1927 (*sensu* Chirat and Bucher 2006; for a detailed discussion of the systematic position of *Epicymatoceras*, see Malchyk *et al.* 2017). Its relatively evolute conch colling and prominent radial ribbing of the shell surface

makes it easily recognisable (e.g., Kummel 1956; Goolaerts and Frank 2014; Malchyk *et al.* 2017). At present, it comprises only two species, namely *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1861) and *E. monstrum* Shimansky, 1975. The former has been recorded from the Netherlands, Belgium, Germany and Poland in Europe, with a stratigraphic range from the upper Campanian to the lower Maastrichtian (Binkhorst van den Binkhorst 1861; Schlüter 1876; Holzapfel 1887; Jagt *et al.* 1998; Jagt 2012; Goolaerts and Frank 2014; Malchyk *et al.* 2017). In the original description of Binkhorst van den Binkhorst (1861, p. 15), *Nautilus vaelsensis* is diagnosed as follows: "*Testâ compressâ, discoïdali, striis numerosis, proximantibus, arcualis, ornatâ. Aperturâ subquadrilaterâ. Septis paululúm arcuatis*". The second species, *E. monstrum*, is known exclusively from the upper Maastrichtian of Mangyshlak, Kazakhstan (Shimansky 1975).

The morphological features of the present material allow it to be identified as *Epicymatoceras vaelsense*. However, the Danish specimens differ from the type material of *E*. *vaelsense* from the lower Maastichtian of Vaals, province of Limburg, the Netherlands (Binkhorst van den Binkhorst 1861, pl. 5, fig. 2a–c), in having a slightly more convex venter and more strongly impressed ribbing. The specimens studied here are most closely similar to conspecific material from the upper Campanian and lower Maastrichtian of Poland (Malchyk *et al.* 2017, fig. 3A–B), but the Danish specimens show more rounded ventrolateral shoulders. These differences are most probably the result of intraspecific variability of *E. vaelsense*.

Epicymatoceras monstrum, as described and figured by Shimansky (1975, p. 122, pl. 27, fig. 3), from the upper Maastrichtian of Mangyshlak is a generally similar form; however, it differs from the Danish specimens in having a much wider umbilicus (U \sim 30 per cent), more rounded umbilical and ventrolateral shoulders and more convex venter.

OCCURRENCE: *Epicymatoceras vaelsense* is known from the upper Campanian to Maastrichtian of Belgium and the Netherlands (Binkhorst van den Binkhorst 1861; Jagt *et al.* 1998; Jagt 2012; Goolaerts and Frank 2014), Germany (Schlüter 1876; Holzapfel 1887), Poland (Malchyk *et al.* 2017) and Denmark (this work).

Discussion and conclusion

The first record of the genus *Epicymatoceras* from the Upper Cretaceous white chalk deposits of northern Denmark (Jylland) is presented. The Danish occurrences include three specimens of *Epicymatoceras vaelsense*, one from the lower/upper Maastrichtian boundary interval, the other two from the top of the Maastrichtian. Previous data on the stratigraphic range of *E. vaelsense* across Europe extended from the upper Campanian to the lower Maastrichtian (see above). On the basis of these data, the specimens described from the Dania quarry represent the youngest known records of *Epicymatoceras* to date, indicating that the genus extended into the latest Maastrichtian. Nevertheless, despite the persistence of *Epicymatoceras* until the end of the Cretaceous, all ribbed Cretaceous nautilids within the family Cymatoceratidae became extinct prior to, or at, the Cretaceous–Paleogene boundary (e.g., Ward *et al.* 2016b; Malchyk *et al.* 2017).

It is possible to recognise the adapertural margin of *Epicymatoceras* for the first time; it was observed as a slightly curved outline on the preserved portion of the body chamber in specimen MGUH 33074, probably from Frejlev.

The cast of the embryonic conch of *Epicymatoceras vaelsense* is observable in specimen MGUH 33073 from the Dania quarry; its diameter is estimated to have been c. 30 mm. These new data on *E. vaelsense* from Denmark and the previously recorded hatchling diameter of *Epicymatoceras* from the upper Campanian from Poland confirm that the hatching size in this genus is near the maximum known range recorded for Cretaceous, Cenozoic and Recent nautilids (Landman *et al.* 1983; Matsumoto *et al.* 1984; Arnold *et al.* 1987; Landman 1988; Saunders *et al.* 1996; Cichowolski 2003; Cichowolski *et al.* 2005; Wani and Ayyasami 2009; Wani *et al.* 2011; Malchyk *et al.* 2017; Landman *et al.* 2018).

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Chapter III

Late Cretaceous and early Paleogene nautilid faunas from Poland and western Ukraine and their significance for understanding the nautilid turnover across the K–Pg boundary³

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Abstract

The Upper Cretaceous (Campanian-Maastrichtian) to lower Paleogene (Danian) epicontinental deposits of Poland and western Ukraine provide a remarkable opportunity to study nautilid turnover across the Cretaceous-Paleogene (K-Pg) boundary. In particular, regional Maastrichtian deposits yield abundant and relatively well-preserved nautilid fossils, permitting an assessment of nautilid taxonomic composition and diversity prior to the end-Cretaceous biotic crisis. In this monograph, 656 specimens belonging to the conventionally defined families Nautilidae, Cymatoceratidae, and Hercoglossidae - are described from 64 sections exposing middle Campanian to Danian deposits in Poland and upper Campanian to lower upper Maastrichtian deposits in western Ukraine. The material comprises 14 Late Cretaceous species: Eutrephoceras ahltenense, *Eutrephoceras?* aquisgranense, Eutrephoceras darupense, Eutrephoceras dekayi, Eutrephoceras depressum, Eutrephoceras quadrilineatum, Eutrephoceras vastum, Cymatoceras intrasiphonatum, Cymatoceras loricatum, "Cymatoceras" patens, Epicymatoceras vaelsense, Angulithes westphalicus, Cimomia? galiciana, and Cimomia heberti. Additionally, the Late Cretaceous faunas contain several forms left here in open nomenclature: Eutrephoceras sp. A, Eutrephoceras sp. B, Eutrephoceras sp. C, Eutrephoceras spp., "Cymatoceras." sp. nova, Cymatoceratidae? indet., Epicymatoceras sp., Angulithes cf. neubergicus, Angulithes sp. nova, Cimomia sp. A, and Cimomia sp. B. Only two early Paleogene species are reported: E. dekayi and Nautilidae indet. gen. et sp. nova?. The most abundant nautilid fauna, dominated by Eutrephoceras and the endemic Cymatoceras intrasiphonatum, are from the classic upper Maastrichtian outcrops

³ Original contribution.

in the Middle Vistula River section of Poland. The Late Cretaceous and early Paleogene nautilid faunas of Poland and Ukraine are compared with much less abundant and diverse nautilid faunas from other regions in Europe. With the exception of the ubiquitous Eutrephoceras dekayi and a solitary Cimomia heberti specimen, all of the characteristic European Late Cretaceous nautilid species, including the ribbed forms conventionally assigned to the Cymatoceratidae, did not cross the K-Pg boundary. As such, despite the profound regional palaeogeographic and facies changes near the boundary, the nautilid fossil record reflects a genuine extinction related to the end-Cretaceous crisis. However, detailed interpretation of Cretaceous nautilid extinction patterns is hampered by uppermost Maastrichtian stratigraphic gaps (hiatuses) in sections with abundant nautild fossils. In Poland, single Eutrephoceras? aquisgranense and Cymatoceras intrasiphonatum specimens recovered just below the K-Pg boundary clay in exceptionally complete Lechówka section and a single individual of *E*.? *aquisgranense* from a slightly less complete section at Melgiew suggest that at least a portion of the Cretaceous nautilid fauna survived until the end of the Cretaceous. To these, uppermost Maastrichtian records of Epicymatoceras vaelsense from Denmark must be added. Importantly, Eutrephoceras dekayi is the most widespread species in the studied material, as it is known from North America, Europe, and Asia. Its survival into the Danian is consistent with the hypothesis that broadly distributed taxa are better suited to survive mass extinctions than those with limited geographical ranges. Early Danian nautilid faunas are species- and specimen-poor, as exemplified by the fauna from the Middle Vistula River section. Instead, Paleogene nautlids are first found in abundance in the middle Danian reefs of Denmark and France. Large taxa with complicated suture lines, such as the cosmopolitan Hercoglossa danica, are prominent in these reefal faunas.

Key words:

Campanian, Maastrichtian, Danian, Cephalopoda, Nautiloidea, Nautilida, Nautilaceae, Taxonomy, Mass extinction.

Introduction

The Cretaceous–Palaeogene (K–Pg) mass extinction was driven by the Chixculub impact and/or Deccan flood volcanism (see Alvarez *et al.* 1980; Schulte *et al.* 2010; Keller *et al.* 2020). It irreversibly restructured the taxonomic and cladistic composition of global biota, as exemplified by the turnover from dinosaurs to mammals, and the complete extirpation of rudist reefs. As during other mass extinctions, entire branches were selectively trimmed from the tree of life (D'Hondt 2005). The differential survival of related clades during the K–Pg biotic crisis has been of long-standing scientific interest, in particular for understanding drivers of extinction selectivity during large-scale environmental crises (e.g., Jeffery and Smith 1998 for sea urchins, Field *et al.* 2018 for birds).

For cephalopods, the extinction of ammonites has ranked among the more intriguing aspects of the K-Pg mass extinction, given the survival of the similarly external-shelled nautilids (Landman et al. 2014; Tajika et al. 2023; Ward et al. 2016a). The distinct evolutionary trajectories of ammonites and nautilids during the end-Cretaceous environmental crisis have been linked to different reproductive strategies, metabolic rates, and/or geographic ranges (Landman 1988; Landman et al. 2014; Tajika et al. 2023). As for the latter factor, Landman et al. (2014) compiled a database of all occurrences of ammonites and the nautilid genus Eutrephoceras in the last 0.5 Myr of the Maastrichtian, including those representatives that appear to have briefly survived into the Danian. Their study demonstrated that most end-Maastrichtian ammonite genera were geographically restricted, possibly rendering them comparatively vulnerable to extinction. The geographic distribution of the (briefly) surviving Danian ammonite fauna was significantly greater than that of other genera, implying that broadly distributed genera were more extinction-resilient. The broad geographic distribution of the Jurassic-Miocene nautilid genus Eutrephoceras during the late Maastrichtian was similar to the most widely distributed ammonites, which suggests that wide geographical range reduced extinction vulnerability, at least across the K-Pg boundary. The issue of extinction-selectivity also extends to the proposed, poorly-understood extirpation of all ribbed nautilids at the K-Pg boundary (Ward et al. 2016a: fig. 19). Importantly, no prior work has explicitly focused on identifying those nautilid species which managed to survive the K-Pg boundary event and subsequently gave rise to post-Cretaceous lineages.

Any attempts to solve these problems should be based on nautilid records across the K–Pg interval, integrated at local, regional, and global scales. However, in contrast to the ammonites (e.g., Ward 1983, 1990, 1996; Kennedy 1989; Machalski 2013; Landman *et al.*

2014; Goolaerts *et al.* 2014; Witts *et al.* 2021), nautilids have not been thoroughly studied in the boundary interval, and are generally rare in most end-Cretaceous and lower Paleogene successions (Stilwell and Grebneff 1996; Landman *et al.* 2014; Ward *et al.* 2016a).

As aptly observed by Goolaerts (2018), the Campanian–Danian deposits of Europe yield nautilid faunas that are potentially important for understanding nautilid extinction and survival patterns across the K–Pg boundary. In particular, the Campanian–Danian shallowmarine, epicontinental deposits of Poland and western Ukraine provide a remarkable opportunity to study a regional record of nautilid turnover across the K–Pg boundary. The Maastrichtian succession, in particular, yields abundant and relatively well-preserved nautilid faunas prior to the end-Cretaceous crisis. While these faunas are exclusively represented by mould (steinkern) preserved specimens, they remain a valuable source of palaeobiological information (Machalski and Malchyk 2016; Malchyk *et al.* 2017; Malchyk 2018). Given their abundance, these faunas would certainly contribute to a better understanding of nautilid evolution across the K–Pg boundary, especially when compared with coeval, albeit much less abundant and diversified, faunas from elsewhere – in particular, from the classic localities in northern Denmark (including Stevns Klint and Faxe), Sweden (Limhamn), and northern Germany (Kronsmoor and the Isle of Rügen).

In view of the above, the present work seeks to provide the first monographic study of nautilid faunas from the Upper Cretaceous – lower Paleogene of Poland and western Ukraine and document their regional turnover patterns, particularly in the context of the K–Pg mass extinction. All nautilid taxa recognised in the Campanian, Maastrichtian, and Danian deposits of Poland and western Ukraine are described and compared to nautilid records from elsewhere.

Previous work

Only a few works dealt with Polish nautilid faunas prior to Malchyk *et al.* (2017), and Malchyk (2018). Łopuski (1912) described several taxa from the Maastrichtian of the Lublin Upland, and Kongiel and Matwiejówna (1937) briefly described some Maastrichtian and Danian nautilids from the Middle Vistula River section. Some Late Cretaceous nautilids from Poland were discussed by Dzik (1984) in his overview of the phylogeny of the subclass Nautiloidea Agassiz (1847). The literature is even more sparse for western Ukraine – especially in the vicinity of Lviv, from which Late Cretaceous nautilids were described only in the classic mid-19th century monographs of Alth (1850), Kner (1848), and Favre (1869).

The reader is referred to Machalski and Malchyk (2016) for a historical overview and stratigraphical reassesment of these classic western Ukrainian Campanian and Maastrichtian successions, although no upper upper Maastrichtian and Danian deposits are present in that area. The most important contributions about coeval nautilid faunas from other parts of central Europe are those by Ravn (1902), Rosenkrantz (1944, 1960), and Malchyk and Machalski (2018) for Denmark; Moberg (1885) and Lundgren (1867) for southern Sweden; Reich and Frenzel (2002) and Wilmsen and Esser (2004) for northern Germany (Isle of Rügen and Kroonsmoor, respectively).

Recent advances in the Upper Cretaceous stratigraphy of Poland and western Ukraine (e.g., Walaszczyk 2004; Dubicka and Peryt 2012; Remin 2012; Machalski 2012b; Machalski and Malchyk 2016; Walaszczyk *et al.* 2016; Jurkowska 2016) form a framework for stratigraphically constraining the identified nautiloid species. Furthermore, extensive work on the facies development and palaeogeography of Polish and western Ukrainian nautilid-bearing deposits form a robust background for inferences about nautilid habitat (e.g., Jurkowska *et al.* 2019; Machalski and Malchyk 2019; Machalski *et al.* 2022). References to the stratigraphy and facies of other nautilid-bearing localities mentioned in text are provided, where relevant for comparative purpuses.

Geological setting

The present study focuses on nautilid collections from the Upper Cretaceous (middle Campanian and Maastrichtian) and lower Paleogene (Danian) successions of Poland and western Ukraine (Text-fig. 1A). To simplify, the study area can be subdivided into four regions (Text-fig. 1B, C): (1) the Miechów Upland, (2) the Middle Vistula River section (together with the adjacent area east of the Vistula River), (3) the Lublin Upland, and (4) the Roztocze Hills. The vast majority of the studied material was collected from Campanian and Maastrichtian strata, although a few specimens are from the Polish Danian.

Structurally, the study area lies in the southeastern Szczecin-Miechów and Kościerzyna-Puławy synclinoria. These units border the Mid-Polish Anticlinorium (Swell) from the southwest and northeast, respectively (e.g., Żelaźniewicz *et al.* 2011). The Mid-Polish Anticlinorium formed through inversion of the Mid-Polish Trough, which constituted the easternmost part of the Epicontinental Central European Basin System (Krzywiec 2006; Voigt *et al.* 2008; Żelaźniewicz *et al.* 2011; Krzywiec *et al.* 2018; Remin *et al.* 2022a, b).

Palaeogeographically, the study area is located in the eastern portion of the epiplatform Boreal sea, which during the Late Cretaceous extended from Denmark through Germany to southeastern Poland and Ukraine (Remin *et al.* 2022a, b). At this time, an emerged landmass likely existed in the southern Mid-Polish Trough (Text-fig. 2A, B), which is usually referred to as the Dobrogea-Łysogóry Land (Samsonowicz 1925; Walaszczyk and Remin 2015; Remin *et al.* 2022a, b) or the Krukienic Island (Pasternak *et al.* 1968, 1987; Walaszczyk 1992; Dubicka and Peryt 2014; Machalski and Malchyk 2019). Its existence has been inferred from facies relationships within marine deposits that were deposited in roughly parallel belts relative to the hypothetical shoreline (Text-fig. 2A, B). Sandstones, sandy gaizes and opokas were deposited nearshore in the shallowest environments, opokas and limestones with no significant quartz admixture were located further offshore, and white chalk was deposited in the most distal, deeper offshore settings (Text-fig. 2C; Walaszczyk and Remin 2015; Machalski and Malchyk 2019; Remin *et al.* 2022a, b).


Text-fig. 1. A – Study area in Poland and western Ukraine, with nautilid-bearing localities marked. B – Localities in the Miechów Upland, Lublin Upland and Roztocze regions. C – Localities in the Middle Vistula River section (MVRs) and west of the Vistula River.



Text-fig. 2. A – Palaeogeographic map of the studied area during the Late Cretaceous (Campanian and Maastrichtian), with approximate position of opoka and chalk facies (modified after Jurkowska *et al.* 2019, fig. 1); UKR – Ukrainian. B – General facies patterns around the proposed Krukienic Island. During the early late Maastrichtian (the "*junior* Transgression" of German authors), the chalk facies reached further westward than presented in this figure. C – Proposed relationships between main facies types, including opoka and chalk, along a proximal-to-distal transect from Krukienic Island (line C in Fig. 2B; modified after Machalski and Malchyk 2019, fig. 3).

The most common regional lithology is opoka (see Jurkowska and Świerczewska-Gładysz 2022 for definition). The origin of this carbonate-siliceous rock is linked to the mass occurrence of siliceous sponges, mainly non-lithistid Demospongiae, the spicules of which were the primary source of biogenic silica. Some opoka intervals are rich in fossils (e.g., Abdel-Gawad 1986), including abundant nautilids; in contrast, white chalks yield less diversified nautilid fauna (Text-fig. 2C).

With regards to macrofaunal biostratigraphy (see Text-fig. 3), the first comprehensive study of the Cretaceous–Danian succession of the Middle Vistula River section – the main reference section for the study area – was by Pożaryski (1938). Based on macrofaunal associations, Pożaryski (1938) introduced a series of local levels along the Vistula River designated by Latin letters (Text-fig. 3). These informal units were used by Gaździcka (1978), Peryt (1980), and subsequent authors. In a benchmark contribution, Błaszkiewicz (1980) described the Campanian and Maastrichtian ammonite succession of the Middle Vistula River section and discussed the associated stratigraphy. Subsequently, Walaszczyk (2004) established a new inoceramid-based subdivision of Campanian and lower Maastrichtian strata in the Middle Vistula River section.

The placement of the Campanian–Maastrichtian boundary in this monograph deserves further explaination, as it has changed significantly since Błaszkiewicz (1980). The latter author placed the base of the Maastrichtian at the first occurrence (FO) of the belemnite *Belemnella lanceolata*, in accordance with the western European schemes of Jeletzky (1951) and Birkelund (1957). However, subsequent inoceramid (Walaszczyk *et al.* 2002, 2016; Walaszczyk 2004), belemnite (Remin 2012, 2015) and ammonite (Machalski 2012a,b) studies have substantially revised the Campanian–Maastrichtian boundary level. At present, it is based on correlations with the Global Stratotype Section and Point (GSSP) for the base of the Maastrichtian Stage, which is formally defined at the 115.2 m level of the quarry section at Tercis les Bains, Landes, southwest France (Odin 2001; Odin and Lamaurelle 2001). These data indicate that the base of the Maastrichtian Stage is significantly higher than the FO of *Belemnella lanceolata* (e.g., Walaszczyk *et al.* 2002, 2016; Walaszczyk 2004; Remin 2012; Machalski 2012a,b). Therefore, several traditionally "Maastrichtian" sections are now placed in the upper Campanian. The reader is referred to Walaszczyk *et al.* (2016) for an updated summary of regional stratigraphy.

A summary of the macrofaunal biostratigraphy of Campanian and Maastrichtian nautilid-bearing deposits in Poland and Ukraine, with stratigraphic ranges of key sections indicated, is presented in Text-fig. 3; the Danian stratigraphy is briefly discussed below. All nautild-bearing sections are listed in alphabetic order and described in the next chapter.



Text-fig. 3. Regional stratigraphic scheme of the Campanian and Maastrichtian, with ranges of key nautilidbearing sections. Chronostratigraphy following Tercis-based and traditional Boreal definitions of the base of the Maastrichtian Stage (Odin 2001).

Middle Vistula River section

The vast majority of studied nautilid material originates from the Middle Vistula River section. Structurally, this composite section belongs to the Puławy segment of the Kościerzyna-Puławy Synclinorium. The Middle Vistula River section comprises a series of natural and artificial outcrops of Albian to Danian deposits, located along the banks of – or, in some cases, at some distance from – the Vistula River (e.g., Pożaryski 1938; Błaszkiewicz 1980; Peryt 1980; Dubicka and Peryt 2012; Walaszczyk 2004, 2012; Walaszczyk *et al.* 2016). The river exposes successively younger strata towards the north, due to the homoclinal structure of the Puławy segment.

The middle Campanian–lower Maastrichtion strata outcrop in a series of relatively good exposures between Sulejów and Kłudzie on the western bank of the Vistula River, and between Wałowice and Kamień on the eastern bank (see Text-fig. 1C). This interval is represented by marls, opokas, and marly opokas (Pożaryski 1938; Błaszkiewicz 1980; Abdel-Gawad 1986; Dubicka and Peryt 2012), referred by Walaszczyk (2004) to five informal lithostratigraphic units – namely, the Dorotka, Pawłowice, Potrawin, Solec, and Dziurków opokas. The most abundant nautilid material is from the Piotrawin and Dziurków quarries (Text-fig. 1C).

The "mid-Maastrichtian" marly chalk facies is poorly exposed along the banks of the Vistula River (Dubicka and Peryt 2011, 2012), and no nautilid fossils are available for study from this interval. Excellent outcrops re-appear near Kazimierz Dolny (Text-fig. 1C), where the Maastrichtian–Danian boundary interval is also accesible (e.g., Kongiel 1935; Pożaryska 1952; Hansen *et al.* 1989; Machalski 1998; Machalski *et al.* 2022). Upper Maastrichtian strata are represented by the Kazimierz Opoka, a c. 50 m thick opoka unit with marly and limestone intercalations (e.g., Błaszkiewicz 1980; Abdel-Gawad 1986; Machalski 1998, 2005a). A distinct shallowing within the Kazimierz Opoka has been inferred based on taphonomic and palaeoecological constraints (Machalski and Malchyk 2019).

The Danian is represented by the Siwak, with a thin glauconitic sandstone bed at the base traditionally referred to as the Greensand. The Maastrichtian–Danian boundary (that is, the K–Pg boundary) in the Middle Vistula River section is placed at the top of the Kazimierz Opoka (Machalski 1998; Machalski and Jagt 2018; Machalski *et al.* 2022; for opposing views, see Remin *et al.* 2021). The Siwak proper is c. 50 m thick and consists of glauconitic gaizes with limestone intercalations. This unit belongs to the lower, but not lowermost, Danian (Hansen *et al.* 1989; Machalski 1998; Żarski *et al.* 1998; Machalski *et al.* 2022). The Siwak represents a shallower, more nearshore environment than the underlying Cretaceous

deposits, based on faunal palaeoecology and a significant quartz contribution (see discussion in Machalski *et al.* 2022).

The most abundant late Maastrichtian nautilid material from the Middle Vistula River section come from Bochotnica, Kazimierz Dolny (the Town Quarry), and Nasiłów (Text-fig. 1C), while a limited number of Danian specimens are from the Siwak.

Miechów Upland

The Upper Cretaceous deposits of the Miechów Upland belong to the southeastern Szczecin– Miechów Synclinorium, traditionally referred to as the Miechów Synclinorium (Żeleźniewicz *et al.* 2011), and range from Albian to Maastrichtian (Rutkowski 1965; Marcinowski 1974; Walaszczyk 1992; Jurkowska 2016). They unconformably overlay Jurassic substrate, and are covered in their central and southern parts by Miocene deposits of the Carpathian Foredeep (Pożaryski 1977; Jurkowska 2016). Nautilid material from the Miechów Upland is rather sparse and originates from five outcrops (Text-fig. 1B) that expose middle Campanian–lower Maastrichtian opokas with marly intercalations (Jurkowska 2016; see Jurkowska *et al.* 2019 for lithofacies).

Lublin Upland and Roztocze

A large number of studied nautilid specimens are from Campanian and Maastrichtian strata exposed in the central and eastern Lublin Upland and the Roztocze Hills (Text-fig. 1B). The Lublin Upland localities are primarily concentrated south and east of Lublin, ranging to Chełm near the Polish-Ukrainian border (Text-fig. 1B). Most outcrops expose upper Maastrichtian opokas that are similar in facies development to the Kazimierz Opoka in the Middle Vistula River section (see overview in Machalski *et al.* 2022). The white chalk facies is only accessible in a large chalk pit at Chełm (Dubicka and Peryt 2011; Machalski *et al.* 2021; Machalski and Bitner 2024). In a few places, the Maastrichtian–Danian boundary and some Danian deposits are preserved, for instance at Mełgiew west of Lublin (Machalski 2005a,b) and Lechówka near Chełm; notably, Lechówka is the only place in Poland where the K–Pg boundary clay has been documented (Racki *et al.* 2011; Machalski *et al.* 2016, 2022). Wola Piasecka, Klimusin, Chełm, and Rejowiec (Text-fig. 1B) are the richest exposures with respect to nautilid fossils in the Lublin Upland.

The Roztocze region (Text-fig. 1B) is a range of hills, 185 km long and up to 28 km wide, which extends from Kraśnik in Poland to Lviv in western Ukraine (Buraczyński 1997). It is structually positioned along the southwestern margin of the Kościerzyna–Puławy

Synclinorium, bordering the Carpathian Foredeep to the northeast. Campanian and lower Maastrichtian strata of the Roztocze Hills are mainly represented by opokas and gaizes with an admixture of detrital quartz. These clearly shallow-water deposits yield locally rich macrofossil assemblages and terrestrial flora (Kin 2010; Halamski 2013; Machalski and Malchyk 2016; Remin 2018). In particular, Hrebenne (Text-fig. 1B) captures a particularly rich nautilid fauna.

In the Roztocze Hils of western Ukraine, Campanian and Maastrichtian strata are known from several classic locations: for instance, at Potelych near Rava Ruska, Nahoryany south of Lviv, and in Lviv itself (Text-fig. 1B; Machalski and Malchyk 2016). Traditionally, these deposits were considered Maastrichtian and subdivided into two belemnite zones: the lower Maastrichtian Belemnella lanceolata and the upper Maastrichtian Belemnitella junior Zones (Pasternak 1959, Pasternak et al. 1968, 1987; Havrylyshyn et al. 1991). However, following the redefinition of the Campanian-Maastrichtian boundary, the Potelych succession, from where a unique land flora was described by Nowak (1907a,b) and Halmski (2013), is now considered to fall within the upper Campanian inoceramid "Inoceramus" costaecus Zone (Machalski and Malchyk 2016). In turn, the Nahoryany section belongs to the lower Maastrichtian inoceramid Endocostea typica and Trochoceramus radiosus Zones, while the Lviv marls correspond to the lower upper Maastrichtian inoceramid Spyridoceramus tegulatus Zone (Machalski and Malchyk 2016). An alternative inoceramid biostratigraphy was presented in Walaszczyk et al. (2016), and is followed here (Text-fig. 3). In terms of available nautilid specimens, the Nahoryany locality (Text-fig. 1B; see Machalski 2024 for overview) stands out in the Ukrainian Roztocze Hills.

Nautilid-bearing localities in Poland and western Ukraine

Aleksandrów (lower Maastrichtian)

Several rural quarries once existed in Aleksandrów, a village located west of the Middle River Vistula section (Text-fig. 1C; see geological map of Pożaryski (1948) for detailed location). According to Pożaryski (1948), the Aleksandrów section was represented by opoka assigned to local horizon v, as defined in the Middle Vistula River section (Pożaryski 1938). This corresponds to the lower Maastrichtian in the present subdivision (Text-fig. 3).

Material studied: One specimen of Eutrephoceras ahltenense (MUZ PIG 12.II.1071).

Antoniów (upper Campanian)

A series of small rural quarries once existed northeast of Antoniów, in the "Góry Wielkie" forest, west of the Middle Vistula River section (Text-fig. 1C; see geological map of Pożaryski (1948) for detailed location). According to Pożaryski (1948), the quarries exposed gaizes with cherts and limestone intercalations assigned to local horizon *t*. Pożaryski (1948) reported large pachydiscid ammonites and echinoids (*Echinocorys*) from this locality. In the current subdivision (Text-fig. 3), the Antoniów section lies within the upper Campanian. <u>Material studied</u>: Two specimens of *Eutrephoceras ahltenense* (MUZ PIG 12.II.1045 and 1076).

Basonia (middle Campanian)

A village on the right bank of the Vistula River, Middle Vistula River section (Text-fig. 1C). A few, currently inaccessible opoka outcrops are marked in this area by Pożaryski (1938, fig. 2), and Błaszkiewicz (1980, fig. 1). Pożaryski (1938) assigned the sections exposed at Basonia (his Bassonia) to local horizon *o*. In terms of biostratigraphy, the Basonia sections correspond to the ammonite *Bostrychoceras polyplocum* Zone (Text-fig. 3). <u>Material studied</u>: One specimen of *Eutrephoceras* spp. (MZ VIII Mc-669).

Bliżów (lower Maastrichtian)

A small, abandoned quarry located on a hill in the eastern part of the village of Bliżów, Roztocze (Text-fig. 1B). The section exposes ca. 10 meters of opoka with abundant fauna, dominated by sponges, bivalves, and cephalopods (Kin 2010, 2011). According to Kin (2010, 2011), the section represents the upper inoceramid *Endocostea typica* Zone and the lowermost inoceramid *Trochoceramus radiosus* Zone (Text-fig. 3; see also Walaszczyk *et al.* 2016).

Material studied: Two specimens of Eutrephoceras dekayi (ZPAL N.III/18 and 243).

Bochotnica (upper upper Maastrichtian and Danian)

This site, located on the right bank of the Vistula River, contains the best known localities at the northern end of the Middle Vistula River section (Text-fig. 1C). A succession of upper upper Maastrichtian and Danian strata is exposed in several quarries in Bochotnica (Pożaryski 1938, Kongiel 1935, Kongiel and Matwiejówna 1937, Putzer 1942, Pożaryska 1952, Błaszkiewicz 1980, Peryt 1980, Abdel-Gawad 1986, Machalski and Walaszczyk 1987, Machalski 1998, Machalski and Jagt 2018, Machalski *et al.* 2022). All of these quarries have

been abandoned, and today are largely inaccessible due to heavy vegetative overgrowth. A small quarry in the eastern part of the village, behind the old water mill, provides a wellexposed Cretaceous-Paleogene (K-Pg) section (Machalski and Jagt 2018, Machalski et al. 2022). The base of this section consists of a few metres of opoka, representing the upper Kazmierz Opoka (Machalski 1996), and is terminated by a hard limestone with a burrowed top (Machalski 1998, Machalski et al. 2022). The opoka corresponds to the upper part of local horizon x and horizon y of Pożaryski (1938). Biostratigraphically, it corresponds to the belemnite Belemnella kazimiroviensis, inoceramid Tenuipteria argentea, and ammonite Hoploscaphites constrictus crassus Zones (Text-fig. 3). The opoka is overlain by a thin layer of marly glauconitic sandstone with phosphatic nodules (the Greensand), passing gradually upwards into the Siwak gaizes, which are usually a few metres thick (Machalski and Jagt 2018, figs. 1, 2). Fossils are abundant in the opoka and largely consist of sponges, bivalves, gastropods, and cephalopods (Abdel-Gawad 1986, Machalski 2005a, b, Świerczewska-Gładysz 2006). The Greensand also contains abundant fossils (Machalski 1998, Machalski and Jagt 2018), but no nautilids have been recorded from this unit. Fossils are rare and rather inconspicuous in the Siwak, and are mainly represented by minute gastropods, bivalves, and echinoids (Krach 1981, Machalski 1986, Machalski and Jagt 2018).

<u>Material studied</u>: In total, 16 upper Maastrichtian specimens (MWGUW 003598; MZ VIII Mc-247, 573, 574/a and b, 585, 586/1, 4, and 6, 589/1–2, 593, 606 and 639; ZPAL N.III/128, 326), identified as *Eutrephoceras ahltenense*, *E.? aquisgranense*, *E. dekayi*, *E. vastum*, and *Cymatoceras intrasiphonatum*. Two Danian specimens of *Eutrephoceras dekayi* (MZ VIII Mc-247, ZPAL N.III/246).

Chełm (lower upper Maastrichtian)

A large working cement plant chalk pit (CEMEX Polska) is located east of Chełm (Text-fig. 1C). The section was studied by Dubicka and Peryt (2011), Machalski *et al.* (2021), and recently by Machalski and Bitner (2024). It exposes a marly chalk succession, c. 40 m. thick, which is presently quarried in four levels (V to II; the uppermost level I no longer exists). Chalk from the lower levels (V and IV) is dark and contains abundant pyrite. In contrast, chalk from levels III and II is brighter, largely devoid of pyrite, and appears to be transitional to opoka, which is typical for higher portions of the regional succession (Dubicka and Peryt 2011). In terms of biostratigraphy (Text-fig. 3), the chalk corresponds to the lower upper Maastrichtian belemnite *Belemnitella junior* Zone. The whole section was previously assigned to the ammonite *Hoploscaphites constrictus lvivensis* Zone (Machalski 2012a, b;

Dubicka and Peryt 2011) based on the occurrence of the eponymous scaphitid subspecies (Machalski 2005b). However, subsequent *in situ* collecting proved that level III – and by implication, level II – are better assigned to the higher ammonite *Hoploscaphites constrictus crassus* Zone, as they yield morphologically transitional specimens between the two subspecies (Machalski *et al.* 2021; see Text-fig. 3). The chalk preserves relatively common bivalves, ammonites, and irregular echinoids assigned to *Echinocorys* (see Machalski 2005a, Dubicka and Peryt 2011).

<u>Material studied</u>: In total, 23 nautilid specimens (ZPAL N.III/258–268, 276–277, 279–285, 353, 355 and 370), identified as *Eutrephoceras? aquisgranense*, *E. dekayi*, *E. depressum*, *Eutrephoceras* spp., and *Cymatoceras intrasiphonatum*. Some specimens come from loose heaps of chalk material and therefore are not precisely located within the section; other specimens are localized within individual quarry levels.

Ciszyca Górna (middle Campanian)

The name Ciszyca Górna refers to two temporarily active quarries in Ciszyca Górna, on the left bank of the Vistula River, Middle Vistula River section (Text-fig. 1C; see Walaszczyk 2004 for detailed locations). These two quarries expose 8 and 10 metres of opoka, respectively (Walaszczyk 2004), and are well-known for their rich fossil assemblages, dominated by sponges, bivalves, gastropods, and cephalopods, the latter including the heteromorph ammonite *Didymoceras* (Błaszkiewicz 1980). This is local horizon r of Pożaryski (1938) and the upper Dorotka Opoka of Walaszczyk (2004). The opoka exposed at Ciszyca Górna represents the middle ammonite *Didymoceras donezianum* Zone (Błaszkiewicz 1980) and the inoceramid "*Inoceramus*" tenuiliniatus Zone (Text-fig. 3; Walaszczyk 2004; Walaszczyk *et al.* 2016).

Material studied: Six specimens of *Eutrephoceras* spp. (MZ VIII Mc-382/3–5, 384/1, 396 and 407/3).

Ciszyca Kolonia (middle Campanian)

A small village south of Ciszyca Górna (Text-fig. 1C). Small exposures of opoka occur there, representing the lower part of local horizon *p* of Pożaryski (1938), and the lower Dorotka Opoka of Walaszczyk (2004). Biostratigraphically (Text-fig. 3), this is the lower ammonite *Didymoceras donezianum* Zone (Błaszkiewicz 1980) and the lower inoceramid "*Inoceramus*" *tenuillineatus* Zone (Walaszczyk 2004, Walaszczyk *et al.* 2016).

Material studied: One specimen of Eutrephoceras ahltenense (MZ VIII Mc-711).

Dorotka (middle Campanian)

A small, abandoned quarry, ca. 50 m north of the main road in Dorotka, on the left bank of the Vistula River, Middle Vistula River secion (Text-fig. 1C). A succession of thickbedded opoka is exposed at the quarry (Walaszczyk 2004). This is local horizon *o* of Pożaryski (1938) and the Dorotka Opoka of Walaszczyk (2004). The section yields relatively abundant sponges, bivalves, and cephalopods. It belongs to the inoceramid *Cataceramus subcompresus* Zone (Walaszczyk 2004, Walaszczyk *et al.* 2016) and the upper ammonite *Bostrychoceras polyplocum* Zone (Text-fig. 3, Błaszkiewicz 1980).

<u>Material studied</u>: Four specimens (MZ VIII Mc-313, 422, 688; MUZ PIG 12.II.1069), identified as *Eutrephoceras* spp. and "*Cymatoceras*" patens.

Dziurków (lower lower Maastrichtian)

An active quarry on the eastern end of the village of Dziurków near Solec, Middle Vistula River section (Text-fig. 1C). It exposes a ca. 12 m thick succession of opoka, with abundant fauna dominated by sponges, bivalves, and cephalopods (Walaszczyk 2004, Świerczewska-Gładysz 2006, Remin 2012, Machalski 2012a, Malchyk *et al.* 2017). Several beds are replete with fragmented baculitid specimens. The opoka belongs to the Dziurków Opoka (Walaszczyk 2004). According to Walaszczyk (2004), the section represents the lower inoceramid *Endocostea typica* Zone, which corresponds to the upper belemnite *Belemnella obtusa* Zone *sensu* Remin (2012). This is the ammonite *Pachydiscus neubergicus* Zone of Machalski (2012b).

Material studied: In total, 24 nautilid specimens (MZ VIII Mc-448, 487/1–2; ZPAL N.III/51– 57, 96–71, 131, 257, 339–344, 351–352, 376) identified as *Eutrephoceras ahltenense*, *E.? aquisgranense*, *E. darupense*, *E. dekayi*, *E. quadrilineatum*, *E. vastum*, *Eutrephoceras* spp., "Cymatoceras" patens, Epicymatoceras vaelsense, and Cimomia? galiciana.

Gozdawa (upper Campanian)

Several rural quarries once existed between the villages of Gozdawa and Ludwików, west of the Middle Vistula River section (Text-fig. 1C; see geological map of Pożaryski (1948) for detailed locations). These sections exposed gaizes with cherts assigned by Pożaryski (1948) to the highest portion of local horizon *t*. Biostratigraphically, this lies in the upper ammonite *Nostoceras hyatti* (= N. *pożaryski*) Zone and the lower belemnite *Belemnella*

lanceolata Zone *sensu* Błaszkiewicz (1980); that is, it is assigned to the upper Campanian in the present subdivision (Text-fig. 3).

Material studied: One specimen of *Epicymatoceras vaelsense* (MUZ PIG 12.II.1082).

Góra Puławska (Danian)

A village on the left bank of the Vistula River, directly opposite of Puławy, Middle Vistula River section (Text-fig. 1C). A large quarry existed here, the remnants of which are still discernible on the escarpment on the right side of the route to Janowiec. The locality was mentioned by Kongiel (1935, fig. 1), Kongiel and Matwiejewówna (1937), Kongiel (1949), and Krach (1981). Pożaryska (1952) and Pożaryska and Pożaryski (1951) provided detailed descriptions of the section. The quarry exposed a 15 m thick gaize succession with limestone intercalations, representing the upper Siwak. It is placed in the Danian, based on macrofaunal and lithological similarities to the stratigraphically better-resolved Siwak exposures in Nasiłów and Bochotnica (Hansen *et al.* 1989, Machalski *et al.* 2022). In addition to the quarry, small isolated Siwak outcrops were once available in Góra Puławska, including deep ravines descending towards and on the banks of the Vistula River (Kongiel 1949).

<u>Material studied</u>: Two specimens of *Eutrephoceras dekayi* (MZ VIII Mc 249/2 and 569), the first from an outcrop on the river bank, the second probably from the quarry itself.

Hrebenne (lower Maastrichtian)

In this study, Hrebenne refers to a temporary outcrop that was accessible during the construction of a new border terminal on the Polish side of the Polish-Ukrainian border near Hrebenne, Roztocze (Text-fig. 1B, see Kin 2010, fig. 1C for detailed locality sketch). It consisted of a ca. 11 m thick marly opoka succession, and yielded abundant macrofauna, dominated by sponges, bivalves, and cephalopods (Kin 2010, Machalski 2010). The Hrebenne section corresponds to the inoceramid *Trochoceramus radiosus* Zone (Text-fig. 3; Kin 2010, see also Walaszczyk *et al.* 2016).

<u>Material studied</u>: In total, 64 nautilid specimens (ZPAL N.III/1, 2, 6–13, 72–117, 130, 157, 158, 211–214, 356) identified as *Eutrephoceras ahltenense*, *E. dekayi*, *E. depressum*, *E. vastum*, *Eutrephoceras* spp., *Cymatoceras loricatum*, "C". *patens*, and *Cimomia heberti*.

Janowiec (upper upper Maastrichtian)

Several disused, heavily overgrown opoka quarries along the left escarpment of the Vistula River near the village of Janowiec, Middle Vistula River section (Text-fig. 1C). The

massive yellow opoka is ca. 12 metres thick and may be correlated to the lower part of the Town Quarry succession in Kazimierz Dolny (Abdel-Gawad 1986). This is the lower part of local horizon *x* of Pożaryski (1938), and the lower Kazimierz Opoka (Machalski 1996). Biostratigraphically (Text-fig. 3), the section corresponds to the belemnite *Belemnella kazimiroviensis* Zone, the inoceramid *Tenuipteria argentea* Zone (Walaszczyk *et al.* 2016) and the ammonite *Hoploscaphites constrictus crassus* Zone (Błaszkiewicz 1980; Machalski 2012b). Fossils are rare and mainly consist of sponges (Pożaryska and Pożaryski 1951; Świeczewska-Gładysz 2006).

<u>Material studied</u>: Four nautilid specimens (MZ VIII MC-628, 631; MWGUW 003601 and 003604), identified as *Eutrephoceras vastum* and *Cymatoceras intrasiphonatum*.

Janów (upper upper Maastrichtian and Danian)

A local road leading up the hill in Janów, north of the road to Chełm, reveals a succession referred to as the Janów locality (Text-fig. 1B). The succession was briefly described by Popiel (1977) and consists of marly opoka overlain by a thin glauconitite layer, passing upwards into Siwak-equivalent deposits (Machalski, personal communication). Based on regional comparisons, the opoka from Janów is assigned to the belemnite *Belemnella kazimiroviensis* and ammonite *Hoploscaphites constrictus crassus* Zones (Text-fig. 3), and overlying deposits to the Danian.

Material studied: One specimen of Cymatoceras intrasiphonatum (ZPAL N.III/38).

Jawor Solecki (upper Campanian or lowermost Maastrichtian)

Several small rural quarries once existed in the village of Jawor Solecki, west of the Middle Vistula River section (Text-fig. 1C; see geological map in Pożaryski (1948) for detailed location of these quarries). The quarries exposed soft sandy glauconitic opoka assigned to local horizon *u* (Pożaryski 1948). No updated biostratigraphy is available for these outcrops. However, specimens of a giant scaphitid ammonite *Hoploscaphites quadrispinosus* (Geinitz, 1850) *sensu* Machalski (2012b) have been found in this locality (Machalski, personal communication; collected by I. Walaszczyk). The range of this ammonite (Machalski and Malchyk 2016, fig. 4) corresponds to the belemnite *Belemnella lanceolata* Zone of Błaszkiewicz (1980), which is mostly upper Campanian, but ranges into the lowermost Maastrichtian in current subdivisions (Text-fig. 3).

Material studied: One specimen of Epicymatoceras vaelsense (MUZ PIG 12.II.1079).

Józefów (middle Campanian)

A series of opoka outcrops that existed along the left bank of the Vistula River near Józefów, Middle Vistula River section (Text-fig. 1C). These outcrops (mentioned by Pożaryski 1938 and Błaszkiewicz 1980, fig. 1) are largely inaccessible at present. Pożaryski (1938) assigned the Józefów opoka to local horizon *r*. According to Błaszkiewicz (1980), this is the ammonite *Didymoceras donezianum* Zone (Text-fig. 3).

Material studied: Three specimens of "Cymatoceras" patens (MUZ PIG 12.II.1086/1-3).

Kamienny Dół (upper upper Maastrichtian and Danian)

An old, overgrown quarry in a ravine in the northern portion of Kazimierz Dolny, Middle Vistula River section (Text-fig. 1C). Kamienny Dół is best known for a spectacular partial skeleton of *Thoracosaurus*, a Danian marine crocodile (Żarski *et al.* 1998). Nearly six metres of opoka outcrop here, representing the upper Kazimierz Opoka in the upper upper Maastrichtian (Machalski 1996; Text-fig. 3).

Material studied: One specimen of Eutrephoceras dekayi (ZPAL N.III/132).

Kamień South and North (upper Campanian)

Kamień refers to a series of opoka outcrops which once existed in the village of Kamień, although they are presently destroyed (Text-fig. 1C; see Pożaryski 1938, fig. 2, Błaszkiewicz 1980, fig. 1, Walaszczyk 2004, figs. 1 and 2, Machalski 2012a, fig. 1). Pożaryski (1938) assigned all of these strata to local horizon *u*. Walaszczyk (2004, fig. 1) drew a boundary between his Piotrawin Opoka and Solec Opoka in the middle of Kamień. Machalski (2012a) collected fossils from two temporary exposures at Kamień, referred to as Kamień South and Kamień North (Text-fig. 1C). He assigned the uppermost Piotrawin Opoka exposed at Kamień South to the inoceramid *Trochoceramus costaecus* Zone (Text-fig. 3). Correspondingly, Machalski (2012a, Text-fig. 2) assigned the Kamień North section to the lowermost Dziurków Opoka in the lithostratigraphic subdivision of Walaszczyk (2004), and to the inoceramid "*Inoceramus*" *redbirdensis* Zone (Text-fig. 3) in the corresponding inoceramid scheme. Opoka exposures in both sites yield sponge, bivalve, and gastropod remains, as well as rare cephalopods and echinoids.

<u>Material studied</u>: In total, 13 specimens from Kamień. Four specimens (MZ VIII Mc-494, 495, and 497; MUZ PIG 12.II.1065), identified as *Eutrephoceras vastum* and "*Cymatoceras*" *patens*, are labelled "Kamień" in museum collections, and may have been collected from either Kamień North or Kamień South. Nine specimens (ZPAL N.III/127, 171–176, 215 and

218), identified as *Eutrephoceras darupense*, *Eutrephoceras* spp., *Cymatoceras* cf. *loricatum*, "C." *patens*, and "C." sp. nova, are from Kamień South.

Kazimierz Dolny (upper upper Maastrichtian)

A huge, abandoned opoka quarry (the so-called Town Quarry) is situated in the southern outskirts of Kazimierz Dolny, on the left bank of the Vistula River, Middle Vistula River section (Text-fig. 1C). The quarry section exposes ca. 30 m of opoka with marly and hard limestone intercalations (Pożaryski 1938, Pożaryska and Pożaryski 1951, Pożaryska 1952, Abdel-Gawad 1986, fig. 8), corresponding to local horizon *x* (Pożaryski 1938) and the lower Kazimierz Opoka (Machalski 1996). In terms of biostratigraphy (Text-fig. 3), the Town Quarry section corresponds to the belemnite *Belemnella kazimiroviensis* Zone, inoceramid *Tenuipteria argentea* Zone (Walaszczyk *et al.* 2016) and ammonite *Hoploscaphites constrictus crassus* Zone (Błaszkiewicz 1980, Machalski 2012b). Fossils are not as common as in the higher opoka levels exposed at Nasiłów and Bochotnica. The fossil assemblage is dominated by sponges, bivalves, gastropods, and cephalopods (e.g., Krach 1931, Błaszkiewicz 1980, Abdel-Gawad 1986, Machalski 2005a, Świerczewska-Gładysz 2006). Terrestrial flora remains – conifer twigs – also occur in these deposits (Halamski 2013).

<u>Material studied</u>: In total, 63 specimens (MKD/MP-2, 4, 63/1–2, 1056, 1058–1059, 1095, 1146–1147; MUZ PIG 13.II.479, 481–482; MWGUW 002167, 002360, 002370, 003600; MZ VIII Mc-528, 529/1–2, 533, 539, 542, 545, 546, 547/1–2, 550/2, 551; ZPAL N.III/118–119, 133, 146–155, 160–165, 208–209, 249, 269, 271, 311, 314, 316, 320, 357–360, 365–366, 368), identified as *Eutrephoceras ahltenense*, *E.? aquisgranense*, *E. dekayi*, *E. quardilineatum*, *E. vastum*, *Eutrephoceras* spp., *Cymatoceras intrasiphonatum*, *Angulithes* cf. *neubergicus*, and *Cimomia heberti*.

Klimusin (upper upper Maastrichtian)

An abandoned quarry on a hill at the southern end of the village of Klimusin, southeast of Lublin (Text-fig. 1B; Machalski 2005a, fig. 1B). The quarry exposes an opoka succession, c. 7 m thick, that contains abundant fauna dominated by sponges, gastropods, bivalves, and cephalopods (Machalski 2005b). The overall facies and macrofaunal characterisics are similar to the upper Kazimierz Opoka exposed at Nasiłów and Bochotnica in the Middle Vistula River section (Abdel-Gawad 1986, see also Machalski and Malchyk 2019). Biostratigraphically (Text-fig. 3), this succession is assigned to the belemnite *Belemnella kazimiroviensis* Zone, the inoceramid *Tenuipteria argentea* Zone (Walaszczyk *et al.* 2016)

and the ammonite *Hoploscaphites constrictus crassus* Zone (Błaszkiewicz 1980, Machalski 2012b).

<u>Material studied</u>: In total, 14 specimens (ZPAL N.III/169, ZPAL N.III/28–37) identified as *Eutrephoceras dekayi* and *Cymatoceras intrasiphonatum*.

Kłudzie (upper Campanian and lower Maastrichtian)

Kłudzie (Text-fig. 1C) refers to two opoka exposures on the right bank of the Vistula River near the village of Kłudzie, Middle Vistula River section. These outcrops are designated Kłudzie South and Kłudzie North by Walaszczyk (2004, fig. 1) and Machalski (2012a, fig. 1). At Kłudzie South, the opoka succession is c. 18 m thick; at Kłudzie North, it is 9 m thick (Walaszczyk 2004). A distinctive level called the "Boundary Marl" occurs in both localities, marking the boundary between the Solec Opoka and the Dziurków Opoka (Walaszczyk 2004, fig. 3) The whole Kłudzie succession belongs to local horizon v of Pożaryski (1938). The combined section exposed at Kłudzie South and Kłudzie North spans the upper Campanian inoceramid "*Inoceramus*" *redbirdensis* Zone and lower Maastrichtian inoceramid *Endocostea typica* Zone, with the "Boundary Marl" marking the Campanian– Maastrichtian boundary (Text-fig.3, Walaszczyk 2004). In terms of belemnite stratigraphy, the Kłudzie succession belongs to the belemnite *Belemnella inflata* and *B. vistulensis* Zones (Remin 2012, see also Walaszczyk *et al.* 2016).

<u>Material studied</u>: Three specimens labelled "Kłudzie" (MUZ VIII Mc-489/1–2 and 490) identified as *Eutrephoceras vastum* and *Eutrephoceras* spp. It is not known whether these specimens are from the upper Campanian or the lower Maastrichtian.

Krasnobród (upper Campanian)

A large abandoned quarry northeast of the town of Krasnobród, Roztocze (Text-fig. 1B, see Niechwedowicz 2018, fig. 1E for detailed location). The quarry exposes a ca. 15 m thick opoka succession, with thin marly intercalations. Remin (personal communication in Halamski 2013) assigned the Krasnobród succession to the belemnite *Belemnella lanceolata* Zone, corresponding to the inoceramid "*Inoceramus*" costaecus Zone (Text-fig. 3). Subbsequently, Remin (2018) suggested a slightly higher biostratigraphic position, placing this section at the transition from the belemnite *Belemnella inflata* to the *Belemnella vistulensis* Zones (*sensu* Remin 2012; see also Niechwedowicz 2018, fig. 2). These belemnite zones correlate with the upper inoceramid "*Inoceramus*" costaecus Zone and the inoceramid

(Walaszczyk 2004, Walaszczyk *et al.* 2016). The inoceramid "*Inoceramus*" costaecus Zone seems to be better documented (Text-fig. 3), given the presence of "*I*." costaecus and *Hoploscaphites quadrispinosus* (sensu Machalski and Malchyk 2016) from the quarry in the Museum Sanktuarium Maryjne at Krasnobród (Machalski, personal communication). Additionally, the Krasnobród section shares a similar regional (Roztocze) peak in land flora abundance with the Potelych section, Ukraine (Halamski 2013), which also represents the inoceramid "*I*." costaecus Zone (Machalski and Malchyk 2016). The quarry yields numerous invertebrate remains, including sponges, bivalves, gastropods, and cephalopods (e.g., Kin 2010, Janiszewska *et al.* 2018).

<u>Material studied</u>: Four specimens (ZPAL N.III/219, 224, and 322–323), identified as *Eutrephoceras dekayi*, *E. vastum*, and "*Cymatoceras*" patens.

Krępa Górna (upper Campanian or lower Maastrichtian)

A single opoka outcrop marked by Pożaryski (1948) north of the village of Krępa Górna, west of the Middle Vistula River section (see Text-fig. 1; map in Pożaryski 1948 for detailed location). No updated stratigraphy of this section is available today. This may represent either the upper Campanian or lower Maastrichtian in current subdivisions, based on extrapolation of geological relationships from the Middle Vistula River section (Walaszczyk 2004).

Material studied: One specimen of Eutrephoceras vastum (MUZ PIG 12.II.1081).

Lechówka (uppermost Maastrichtian and Danian)

A small abandoned quarry situated near the village of Lechówka, west of Chełm, eastern Lublin Upland (Text-fig. 1B). The outcrop was described by Popiel (1977), Racki *et al.* (2011), Machalski *et al.* (2016), Machalski *et al.* (2019), and Machalski *et al.* (2022). It is exceptional amongst Polish Cretaceous-Paleogene boundary sections in that it provides a complete boundary succession, including the basal Danian boundary clay (Racki *et al.* 2011, Machalski *et al.* 2016; Text-fig. 3). The stratigraphy is described in detail by Racki *et al.* (2011) and Machalski *et al.* (2016). The Maastrichtian portion of the succession consists of c. 4 m of opoka and marls. According to Machalski *et al.* (2016), deposits up to a level of 120 cm below the boundary clay correspond to the ammonite *Hoploscaphites constrictus crassus* Zone of Machalski (2012b). The uppermost Maastrichtian, ranging up to the K–Pg boundary clay, is assigned on dinoflagellate evidence to the highest Maastrichtian ammonite *H.*

constrictus johnjagti Zone, although the index taxon of this zone has not yet been identified (Machalski *et al.* 2016).

<u>Material studied</u>: Two uppermost Maastrichtrian specimens, ZPAL N.III/270, identified as *Eutrephoceras? aquisgranense*, and ZPAL N.III/272, identified as *Cymatoceras intrasiphonatum* (erroneously numbered ZPAL N. 3/59 and N. 3/61, respectively, in Machalski *et al.* 2016). *E.? aquisgranense* originates from a level 30 cm below the boundary clay, and *Cymatoceras intrasiphonatum* from a level 60 cm below the boundary clay (see Machalski *et al.* 2016). These are the youngest precisely localised Cretaceous nautilids in Poland.

Lopoczno (upper Campanian)

A c. 8 m thick succession of opoka exposed along a c. 500 m long natural outcrop along the high, steep escarpment of the Vistula River, directly below the village of Łopoczno, Middle Vistula River section (Text-fig. 1C). Today, the exposure is inaccessible due to intense erosion of the escarpment. Pożaryski (1938) assigned the Łopoczno succession to local horizon *s*. According to Walaszczyk (2004), the Łopoczno section represents the upper Pawłowice Opoka and the upper part of the upper Campanian inoceramid *Sphaeroceramus pertenuiformis* Zone (Text-fig. 3).

Material studied: Two specimens of Eutrephoceras spp. (MZ VIII Mc-360 and 665).

Lviv (lower upper Maastrichtian)

A number of marly chalk outcrops, traditionally referred to as the "Lviv Opoka" or "Lviv Marls", existed within and around Lviv (Text-fig. 1B) during the 19th and early 20th centuries (Łomnicki 1897; Kner 1848; Favre 1869; Rogala 1911; Syniewska 1923; Machalski and Malchyk 2016). They yielded sparse fossils, including sponges, bivalves, ammonites, brachiopods, and echinoids (Łomnicki 1897; Kner 1848; Favre 1869; Rogala 1911; Syniewska 1923; Pasternak *et al.* 1968). Based on the latter work, the Lviv section represents the conventional lower upper Maastrichtian belemnite *Belemnitella junior* Zone (Text-fig. 3). With regards to scaphitid ammonites, museum collections contain rare specimens of *Hoploscaphites constrictus crassus* and more common specimens of *H. constrictus lvivensis* and *H. tenuistriatus* (Machalski 2005b). These data suggest that the chalk outcrops in Lviv broadly corresponded to the chalk succession exposed in Chełm (Text-fig. 3). However, it cannot be excluded that the Lviv succession may have ranged slightly lower than the Chełm

successuion, based on the presence in Lviv of a typical mid-Maastrichtian scaphitid, *H. tenuistriatus*, that is absent in Chełm (Machalski *et al.* 2021).

<u>Material studied</u>: Three specimens (DPM NANU PZ-K-N1765, N1767 and NHMW 1862/0005/0020), representing *Eutrephoceras ahltenense* and *Cimomia*? *galiciana*.

Marianów (upper Campanian or lower Maastrichtian)

Several small outcrops existed north of the village of Marianów, west of the Middle Vistula River section (Text-fig. 1C; see map in Pożaryski (1948) for detailed locations). According to Pożaryski (1948), the Marianów quarries exposed sandy glauconitic gaize with numerous fauna, which he assigned to local horizon *u*. In the current biostratigraphy, this is either upper Campanian or lower Maastrichtian (Text-fig. 3).

<u>Material studied</u>: Four specimens (MUZ PIG 12.II.1052/1–3 and 1077) identified as *Eutrephoceras darupense, Eutrephoceras spp., "Cymatoceras" patens, and Epicymatoceras vaelsense.*

Maruszów (upper Campanian)

A series of small rural quarries existed southwest of the village of Maruszów, west of the Middle Vistula River section (Text-fig. 1C; see map in Pożaryski (1948) for location). According to Pożaryski (1948), these quarries exposed sandy glauconitic opoka with abundant fauna, assigned to local horizon t in the Middle Vistula River section. According to Błaszkiewicz (1980, fig. 1), the section at Maruszów represents the ammonite *Nostoceras pozaryski* (= *N. hyatti*) Zone (Text-fig. 3). A fragmentary mosasaur skull has been recovered in the Maruszów area (Sulimski 1968; Machalski *et al.* 2003).

Material studied: Two specimens of "Cymatoceras" patens (MUZ PIG 12.II.1073 and 1087).

Melgiew (uppermost Maastrichtian and Danian)

The Cretaceous–Paleogene succession exposed in a quarry at the top of a hill near the village of Mełgiew, east of Lublin (Text-fig. 1), was first described by Pożaryski (1956). Subsequently, Machalski (2005a) excavated a deep trench near the former quarry, from which macrofauna and microfauna were studied by Machalski (2005a) and Dubicka and Peryt (2012), respectively. The trench section encompassed over 1 m of marly opoka, capped by a hard limestone bed with rare burrows at the top, and ca. 1.7 m of overlying gaize with Siwak-type limestone intercalations (Machalski 2005a, fig. 2B). Recent excavations exposed an additional opoka interval below the interval described by Machalski (2005a). The opoka

exposed at Mełgiew differs from the typical varieties in Nasiłów, Bochotnica, and Kazimierz Dolny in the Middle Vistula River section, in that it is very friable and easily disintegrates after atmospheric exposure (Machalski *et al.* 2022).This locality is one of the most important K–Pg sites in extra-Carpathian Poland. Based on abundant scaphitid fauna, Machalski (2005a, b; 2012b) identified the highest Maastrichtian ammonite scaphitid *Hoploscaphites constrictus johnjagti* Zone (Text-fig. 3; Machalski 2012b, fig. 1, see also Dubicka and Peryt 2012, fig. 2, Walaszczyk *et al.* 2016, fig. 3). The overlying gaizes are placed in the Danian (Machalski 2005a, Machalski *et al.* 2022). Besides ammonites, the opoka contains relatively abundant small bivalves, gastropods, scaphopods, and brachiopods (Machalski 2005a).

Material studied: One specimen of Eutrephoceras? aquisgranense (ZPAL N.III/278).

Mętów (upper upper Maastrichtian and Danian)

This locality, situated in the village of Mętów near Lublin, was described by Pożaryski (1956) (under the name Mentów) and Machalski (2005a, fig. 1), who excavated a trench close to the site of the (currently inaccessible) quarry described by Pożaryski. The K–Pg boundary interval was exposed in this trench, consisting of 1.5 m of opoka with burrowed hard limestone at the top, overlain by a c. 0.5 m thick bed of highly glauconitic marl. The K–Pg interval at Mętów does not differ in facies development from Wola Piasecka (Text-fig. 3). The index taxon of the ammonite *Hoploscaphites constrictus crassus* Zone occurs in the opoka, and the overlying glauconite-rich deposit is Danian (Machalski 2005a). Material studied: One specimen of *Cymatoceras intrasiphonatum* (ZPAL N.III/39).

Nahoryany (lower Maastrichtian)

During the 19th century, two quarries exposing sandy limestones and marls ("the Nahoryany Opoka") existed near the village of Nahoryany (Nagórzany in older Polish literature), south of Lviv in western Ukraine (Text-fig. 1B). No traces of these quarries can be discerned in the present landcape. The Nahoryany quarries were famous across Europe due to their rich fossil content, including large ammonites, nauitilds, bivalves, and gastropods (e.g., Kronenthal 1843, Kner 1848, 1852, Kennedy and Summesberger 1987, Pasternak *et al.* 1987, Bakayeva 2011). According to Christensen (1987), the Nahoryany section yielded the belemnite *Belemnella (Pachybelemnella) inflata*, which is known from the belemnite *Belemnella lanceolata* and *B. pseudobtusa* Zones *sensu* Schulz (1979) in the Kronsmoor section, northern Germany. In the inoceramid zonation of Walaszczyk *et al.* (2002) and Walaszczyk *et al.* (2016), the section corresponds to the upper inoceramid *Endocostea typica*

inoceramid Zone and the lower inoceramid *Trochoceramus radiosus* Zone. Machalski and Malchyk (2016) suggested that the lower inoceramid *Endocostea typica* Zone was present as well (see Text-fig. 3).

<u>Material studied</u>: In total, 59 specimens (DPM NANU PZ-K-N65, N321, N339, N487/1–2, N489/1–2, N491/1–9, N493/1–2, N494, N1252, N1774, N1775/1–2, N1776, N1777, N1786/1–6, N1781/1–3, N1788/1–2, N1789/1–2; GBA 1869/006/006, 1869/006/0005/001–003, 1869/006/0005/001; NHMW 1843/0046/0004, 1848/0002/0009; 1848/0002/0014, 1862/0005/0012, 1862/0005/0014, 1865/0010/0542, 2004z0117/0001, 2018/0327/0001, 2018/0327/0001; Ukk 87, 88/a–c, 89(a)–(b), 90), identified as *Eutrephoceras ahltenense, E. dekayi, E. quadrilineatum, E. vastum, Eutrephoceras* sp. A, *Eutrephoceras* sp. C, *Eutrephoceras* sp., "*Cymatoceras*" patens, Angulithes westphalicus, Cimomia heberti, and Cimomia? galiciana.

Nasiłów (upper upper Maastrichtian and Danian)

This is the best known K-Pg boundary locality near Kazimierz Dolny, Middle Vistula River section (Text-fig. 1C). This section, which exposed in a large abandoned quarry, has been thoroughly described (e.g., Pożaryski 1938, Putzer 1942, Pożaryska 1952, Błaszkiewicz 1980, Peryt 1980, Abdel-Gawad 1986, Machalski and Walaszczyk 1987, Hansen et al. 1989, Machalski 1998, Świerczewska-Gładysz and Olszewska-Nejbert 2006, Remin et al. 2021; Machalski et al. 2022). It exposes ca. 12 metres of opoka, corresponding to the upper part of horizon x and horizon y of Pożaryski (1938) and to the upper Kazimierz Opoka (Machalski 1996). At the top of the opoka succession, there is a hard limestone layer riddled with burrows (Machalski 1998, Machalski et al. 2022), which is overlain by a thin bed of phosphatebearing marly glauconitic sandstone (the Greensand). The latter unit gradually transitions into a c. 15 m thick succession of gaizes with limestone intercalations, assigned to the Siwak. Biostratigraphically (Text-fig. 3), the Kazimierz Opoka exposed at Nasiłów belongs to the belemnite Belemnella kazimiroviensis Zone, the inoceramid Tenuipteria argentea Zone of Walaszczyk et al. (2016), and the ammonite Hoploscaphites constrictus crassus Zone of Błaszkiewicz (1980) and Machalski (2012b). The ammonite Menuites terminus Zone has also been documented, based on rare specimens of this pachydiscid ammonite (Machalski and Jagt 1998; Machalski 2005a). Based on dinoflagellates, Hansen et al. (1989) placed the Siwak at Nasiłów in the lower, but not lowermost, Danian. Machalski and Jagt (2018) tentatively suggested a middle and/or late Danian age of the Siwak based on echinoids. Fossils are very common in the opoka, and include ammonites, gastropods, bivalves, brachiopods, corals, and

sponges (Abdel-Gawad 1986, Machalski 2005a, b, Świerczewska-Gładysz 2006, Machalski *et al.* 2022). Nautilids are abundant, occasionally forming "nests" composed of many individuals of *Cymatoceras intrasiphonatum* (Machalski and Malchyk 2019; ZPAL N.III/179(1)–204(1) and ZPAL N.III/327(3)–336(3)). The Greensand is replete with Maastrichtian and Danian fossils (Machalski 1998), including scallop and oyster shells, phosphatised sponges (Świerczewska-Gładysz and Olszewska-Nejbert 2006), and belemnite rostra (Keutgen *et al.* 2017).

<u>Material studied</u>: In total, 117 upper Maastrichtian specimens (MKD/MP 10, 24, 32–33, 41, 42, 64–68, 72–73, 180, 239, 279, 347, 910; MGWGUW 009624; MZ VIII Mc-557/1, 3, 559/1–2, 545, 554, 560–563, 565, 607, 651, 653, 694, 696; ZPAL N.III/120–126, 129, 134–145, 156, 166, 177–204, 206, 210, 216, 217, 222–223, 225, 231, 248, 313, 315, 317–319, 321, 324, 327–336, 349, 361–364, 367) identified as *Eutrephoceras ahltensense*, *E. dekayi*, *E. quadrilineatum*, *E. vastum*, *Eutrephoceras* spp., *Cymatoceras intrasiphonatum*, *Cimomia heberti* and *Cimomia* sp. A. Three Danian specimens represented a single individual of *Eutrephoceras dekayi* (ZPAL N.III/324) and two specimens of Nautilidae indet. gen. et sp. nov.? (ZPAL N.III/220–221).

Niegosławice (lower Maastrichtian)

The opoka succession exposed near the village of Niegosławice, southeast of Miechów, Miechów Upland (Text-fig. 1B) lies within the lower Maastrichtian inoceramid *Endocostea typica* Zone (A. Jurkowska, personal communication).

<u>Material studied</u>: Two specimens (MUZ PIG 28 and 48) identified as *Eutrephoceras dekayi* from the archival collection of A. Mazurek.

Olbrachcice (upper Campanian)

An outcrop near the village of Olbrachcice, Miechów Upland (Text-fig. 1B), was mentioned by Pożaryski (1966), who assigned the section to local horizon *u* as defined in the Middle Vistula River section (Pożaryski 1938). A few metres of marly, poorly fossiliferous limestone are exposed at Olbrachcice. A "*Inoceramus*" costaecous specimen from Olbrachcice was identified by I. Walaszczyk (personal communication), which places the section in the epynomous upper Campanian inoceramid "*Inoceramus*" costaecous Zone (Text-fig. 3).

Material studied: One specimen of Eutrephoceras spp. (ZPAL N.III/20).

Okale (upper Maastrichtian)

The village of Okale is located southeast of Kazimierz Dolny, Middle Vistula River section (Text-fig. 1C). Currently, there are no exposures in this area, which exposed the lowermost part of local horizon x in the geological map of Pożaryski (1938, fig. 2). On the map of Błaszkiewicz (1980, fig. 1), Okale falls into the ammonite *Hoploscaphites constrictus crassus* Zone (Text-fig. 3). This part of the succession represents the lowermost Kazimierz Opoka (Machalski 1996), located beneath the Town Quarry section. To the south of Okale, marly outcrops represent local horizon w (Pożaryski 1938), equivalent to the upper part of the conventional lower upper Maastrichtian belemnite *Belemnitella junior* Zone of Błaszkiewicz (1980) (Text-fig. 3).

<u>Material studied</u>: Six specimens (MZ VIII Mc-512, 514/1–3, 515 and 516) identified as *Eutrephoceras vastum* and *Cymatoceras intrasiphonatum*. Four specimens are labeled as "Okale - quarry/Maastrichtian – horizon *x*". The label of specimen MZ VIII Mc-516 describes its provenance as "Okale – Dobre".

Opole Lubelskie (upper Maastrichtian)

A temporary roadside exposure of marly chalk in the western outskirts of Opole Lubelskie yielded some fossils. By lithological correlation with the Middle Vistula River section, these strata most probably represent the lower upper Maastrichtian – that is, the conventional belemnite *Belemnitella junior* Zone (compare, e.g., Błaszkiewicz 1980, Dubicka and Peryt 2011).

<u>Material studied</u>: Two specimens (ZPAL N.III/246 and ZPAL N.III/247) identified as *Eutrephoceras*? *aquisgranense* and *E. dekayi*.

Parchatka (Danian)

A village between Puławy and Kazimierz Dolny, on the right bank of the Vistula River, Middle Vistula River section (Text-fig. 1C). The locality was mentioned by Kongiel (1935, fig. 1), Kongiel and Matwiejewówna (1937), Pożaryska (1952), Kongiel (1949), Krach (1981), Machalski (1988), and Machalski *et al.* (2022). Small natural exposures are accessible in ravines perpendicular to the Vistula River valley, and expose a succession of glauconitic marly gaizes of the middle Siwak (Pożaryska and Pożaryski 1951, Machalski 1988). The Siwak at Parchatka is assigned to the Danian, based on analogy with better constrained sections at Nasiłów and Bochotnica (Machalski *et al.* 2022). Fossils are locally common at

Parchatka, including oyster shells and echinoid tests (Machalski 1998, Machalski and Jagt 2018).

<u>Material studied</u>: Six specimens of *Eutrephoceras dekayi* (MZ VIII Mc 246, 248; ZPAL N.III/245, 325, 374 and 375) and one specimen of Nautilidae indet. gen. et sp. nova?.

Pełczyska (lower Maastrichtian)

A natural outcrop at the village of Pełczyska, east of Miechów, Miechów Upland (Text-fig. 1B), exposes a marly opoka succession containing sponges, bivalves, and inoceramids. According to Jurkowska (2016), these strata represent the lower Maastrichtian inoceramid *Endocostea typica* Zone (Text-fig. 3).

<u>Material studied</u>: One specimen of *Cimomia? galiciana* (ZPAL N.III/346; ex. Jurkowska's collection).

Piotrawin (upper Campanian)

A large abandoned quarry, situated on the high river escarpment south of the village of Piotrawin on the eastern bank of the Vistula River, Middle Vistula River section (Text-fig. 1C; see Walaszczyk *et al.* 2004, fig. 1 for detailed location). However, the quarry is located closer to the village of Kaliszany, and it is referred to as the Kaliszany site in older literature (Łopuski 1911, 1912). This represents the key upper Campanian locality in the Middle Vistula River (Pożaryski 1938, Błaszkiewicz 1980, Walaszczyk 2004, Machalski 2012a, Niechwedowicz 2018). The quarry exposes c. 30 m of opoka, accessible along three exploitation levels. This is local horizon *t* of Pożaryski (1938) and the Piotrawin Opoka *sensu* Walaszczyk (2004). The section contains abundant fauna dominated by sponges, bivalves, gastropods, cephalopods, and echinoids (Walaszczyk 2004; Świerczewska-Gładysz 2006; Remin 2015). The Piotrawin section corresponds to the upper Campanian inoceramid "*Inoceramus*" altus and "*I*." inkermanensis Zones (Walaszczyk 2004, Walaszczyk *et al.* 2016), the ammonite Nostoceras pozaryskii (= N. hyatti) Zone of Błaszkiewicz (1980), and the belemnite Belemnitella minor I Zone sensu Remin (2015) (Text-fig. 3).

<u>Material studied</u>: In total, 77 nautilid specimens (MKD/MP 70–71, 74–77, 172–173, 178, 181–182, 212, 220, 322, 345–346, 349, 358, 360, 368, 638, 641, 919; MUZ PIG 12.II.1046, 1056, 1061/1–7, 1080, 1084, 1088; VIII Mc-262/3, 436, 438, 440/1–2, 441/1–2, 443, 446, 450, 456–458, 462/1–3, 472/1–3, 656; ZPAL N.III/45, 47–48, 159, 177, 178, 207, 232–242, 309, 350; MZ VIII Mc-472/1–3, 436, 438, 440/1–2, 441/1–2, 442/1–2, 443, 446, 450, 457, 458, 462/1–3, 656; MKD/MP 70–71, 74–77, 172–173, 178, 181–182, 212, 219–220, 322,

345–346, 349, 358, 360, 368, 636, 641, 919; MUZ PIG 12.II.1046, 1056, 1064) identified as *Eutrephoceras ahltenense*, *E. dekayi*, *E. quardilineatum*, *E. vastum*, *Eutrephoceras* spp., "*Cymatoceras*" patens, *C. loricatum*, *Epicymatoceras* sp., *Angulithes westphalicus*, *Cimomia*? galiciana.

Piotrowice (upper upper Maastrichtian)

A village south of Lublin (Text-fig. 1B). According to Jagt and Kin (2010), a temporary outcrop at this village exposed an opoka succession belonging to the belemnite *Belemnella kazimiroviensis* and ammonite *Hoploscaphites constrictus* Zones (Text-fig. 3). <u>Material studied</u>: One specimen of *Cymatoceras intrasiphonatum* (ZPAL N.III/ 310).

Potelych (upper Campanian)

A large, abandoned quarry situated northwest of the village of Potelych, near the town of Rava-Ruska, western Ukraine, not far from the Polish-Ukrainian border (Text-fig. 1B). It exposes a ca. 8 m thick succession of sandy limestones and marls, with relatively common sponges, bivalves, gastropods, and cephalopods (e.g., Nowak 1907a, b, Pasternak *et al.* 1987, Halamski 2013, Machalski and Malchyk, 2016, Janiszewska *et al.* 2018). A rich assemblage of floral remains was recovered from a ravine that was once situated in an area presently occupied by quarry excavations (Nowak 1907a, b; Pasternak *et al.* 1987; Halamski 2013). In terms of biostratigraphy (Text-fig. 3), the succession corresponds to the upper Campanian inoceramid "*Inoceramus*" *costaecus* Zone of Walaszczyk (2004), which was recognized based on the presence of the index taxon (Machalski and Malchyk 2016).

<u>Material studied</u>: Six specimens (ZPAL N.III/41–44, 49, 50), identified as *Eutrephoceras dakayi*, *Eutrephoceras* spp., "*Cymatoceras*" *patens*, *Angulithes* sp. nova, and *Cimomia* sp. B

Prawiedniki (upper upper Maastrichtian and Danian)

The village of Prawiedniki is located south of Lublin (Text-fig. 1B). In the present context, this name refers to a temporary trench dug during construction of a local route, where displaced opoka, glauconitic gaize, and Siwak-type gaize were sampled for macrofauna (Machalski 2005a, fig. 1B). He reported that the opoka at Prawiedniki contained fauna typical for the upper Maastrichtian belemnite *Belemnella kazimiroviensis* and ammonite *Hoploscaphites constrictus crassus* Zones (Text-fig. 3).

Material studied: One specimen of Cimomia heberti (ZPAL N.III/40).

Przedmieście (lower Maastrichtian)

A large, abandoned quarry in the eastern part of the village of Przedmieście, west of Solec, Middle Vistula River section (Text-fig. 1, see Walaszczyk (2004), fig. 1 for detailed location). A c. 10 m thick opoka succession is exposed there (Walaszczyk 2004), which corresponds to the Dziurków Opoka. In terms of biostratigraphy (Text-fig. 3), the Przedmieście section belongs to the inoceramid *Endocostea typica* Zone of Walaszczyk (2004).

<u>Material studied</u>: Two specimens (MUZ PIG 12.II.1047 and MUZ PIG 12.II.1085) identified as *Cymatoceras loricatum* and "*Cymatoceras*" *patens*. According to the original label, MUZ PIG 12.II.1047 originates from Przedmieście Dalsze, whereas MUZ PIG 12.II.1085 is from Przedmieście Bliższe. Localities under these names are marked in Pożaryski (1938, fig. 1), but their relationship to the present quarry is not clear.

Raj (upper Campanian)

An abandoned quarry in a ravine, south of the village of Raj, on the left bank of the Vistula River, Middle Vistula River section (Text-fig. 1C; see Walaszczyk (2004), fig. 1 for detailed location). The section exposes c. 7 metres of opoka, representing local horizon *t* of Pożaryski (1938) and the upper Piotrawin Opoka of Walaszczyk (2004). According to Walaszczyk (2004), the section belongs to the upper Campanian inoceramid "*Inoceramus*" *inkermanensis* Zone (Text-fig. 3). The opoka exposed at Raj yields abundant fossils, including sponges, bivalves, gastropods, and cephalopods (Walaszczyk 2004, Świerczewska-Gładysz 2006, Machalski 2012a, Remin 2012).

Material studied: Four specimens of *Eutrephoceras* spp. (MZ VIII Mc-433/1 and 3–4, and ZPAL N.III/46).

Raj North (uppermost Campanian)

An abandoned quarry southeast of Solec, on the left bank of the Vistula River, Middle Vistula River section (Text-fig. 1C; see Walaszczyk (2004), fig. 1 for detailed location). A 9 m thick succession of brittle, marly opoka is exposed in this quarry (Walaszczyk 2004, Machalski 2012a), corresponding to the Solec Opoka of Walaszczyk (2004). The succession corresponds to the upper inoceramid "*Inoceramus*" *costaecus* and lower inoceramid "*I.*" *redbirdensis* Zones of Walaszczyk (2004) (Text-fig. 3).

<u>Material studied:</u> Two specimens (ZPAL N.III/230 and ZPAL N.III/244), identified as *Eutrephoceras vastum* and "*Cymatoceras*" *patens*.

Rejowiec (upper upper Maastrichtian)

A large, abandoned, partially flooded cement plant quarry near Chełm, in the eastern Lublin Upland (Text-fig. 1C). The section is composed of 30 m of marls and opokas, which were exploited along four levels. Dubicka and Peryt (2012, fig. 2) placed the quarry section in an interval between the Kazimierz (Town Quarry) and Nasiłów Quarry sections, based on foraminiferal assemblages. However, the inaccessible interval between these two sections is only a few metres thick (Machalski, personal communication). As such, it is improbable that the section at Rejowiec is precisely equivalent to such a thin interval in the Middle Vistula River section (Machalski, personal communication). Machalski (2005b) recorded the upper upper Maastrichtian index taxa of the belemnite *Belemnella kazimiroviensis*, inoceramid *Tenuipteria argentea* and ammonite *Hoploscaphites constrictus crassus* Zones throughout the Rejowiec section (Text-fig. 3). The fauna at Rejowiec is dominated by sponges, bivalves, gastropods, and cephalopods.

<u>Material studied</u>: In total, 11 nautilid specimens (ZPAL N.III/3–5, 14–16, 27, 222, 226–227, and 373), identified as *Eutrephoceras*? *aquisgranense*, *E. depressum*, *Eutrephoceras* spp., and *Cymatoceras intrasiphonatum*.

Rybitwy (middle and/or upper Campanian)

A historical opoka outcrop south of Józefów on the right bank of the Vistula River, Middle Vistula River section (Text-fig. 1C). According to Błaszkiewicz (1980, fig. 1), the opoka exposed at Rybitwy represents the ammonite *Didymoceras donezianum* Zone, spanning the middle – upper Campanian boundary (Text-fig. 3).

Material studied: Six specimens of *Eutrephoceras* spp. (MZ VIII Mc-349, 351/1–2, 352, 352/1–2).

Rzeżuśnia (middle Campanian)

An active quarry at the eastern end of the village of Rzeżuśnia, southwest of Miechów, Miechów Upland (Text-fig. 1B). The quarry exposes about 18 m of opoka with cherts and marly intercalations (Jagt *et al.* 2004, Świerczewska-Gładysz and Jurkowska 2013, Jurkowska and Uchman 2013). The Rzeżuśnia section corresponds to the middle Campanian inoceramid *"Inoceramus" azerbaydjanensis* and *"I." vorhelmensis* Zones (Jagt *et al.* 2004; Jurkowska 2016), which correspond to the ammonite *Neancyloceras phaleratum* Zone of Błaszkiewicz (1980) (Text-fig. 3). The most common fossils at Rzeżusnia are sponges, bivalves, gastropods, cephalopods, and echinoids (Jagt *et al.* 2004, Świerczewska-Gładysz and Jurkowska 2013, Jurkowska 2016).

Material studied: One specimen of Eutrephoceras spp. (ZPAL N.III/345).

Sadkowice (upper Campanian)

There are two abandoned quarries in the village of Sadkowice on the left bank of the Vistula River, Middle Vistula River section (Text-fig. 1C; see Walaszczyk (2004), fig. 1 for detailed location). The quarries are referred to as Sadkowice North and Sadkowice Quarry by Walaszczyk (2004) and respectively expose 7 and 10 metres of opoka. According to Walaszczyk (2004), these sections are assigned to the Piotrawin Opoka, partially overlap, and belong to the upper Campanian inoceramid "*Inoceramus*" *inkermanensis* Zone (Text-fig. 3). <u>Material studied</u>: Three specimens (MUZ PIG 12.II.1055, 1067 and 1071), identified as *Eutrephoceras ahltenense, E. vastum*, and "*Cymatoceras*" *patens*. Specimens MUZ PIG 12.II.1055 and 1097 are labelled "Sadkowice, N, Solec", which probably means that they were collected from the Sadkowice North section of Walaszczyk (2004). Specimen MUZ PIG 12.II.1071 is labelled as "Sadkowice, W, Solec" and possibly comes from the outcrop referred to as Sadkowice Quarry by Walaszczyk (2004).

Solec (upper Campanian)

An outcrop on a hill slope in the western part of the town of Solec, Middle Vistula River section (Text-fig. 1C; see Walaszczyk 2004, fig. 1 for detailed location). The outcrop exposes c. 14 metres of opoka, belonging to the Solec Opoka (Walaszczyk 2004). The succession belongs to the transitional zone between the inoceramid "*Inoceramus*" costaecus and "*I*." redbirdensis Zones (Text-fig. 3; Walaszczyk 2004). Fossils are relatively rare in this outcrop (Walaszczyk 2004, Machalski 2012a).

Material studied: Nine specimens (MUZ PIG 12.II.1060, 1063, 1066/1–2; MZ VIII Mc/475, 482, 699, 700), identified as *Eutrephoceras dekayi*, *E. vastum*, *Eutrephoceras* spp., and "*Cymatoceras*" patens.

Stoki (upper Campanian)

A series of small, rural quarries once existed in the village of Stoki, west of the Middle Vistula River section (Text-fig. 1C). According to Pożaryski (1948), the quarries at Stoki exposed sandy glauconitic gaizes with hard limestone intercalations yielding relatively numerous fauna. Pożaryski (1948) assigned these deposits to local horizon t, which can be

correlated with the upper ammonite *Nostoceras pożaryski* (= *N. hyatti*) and lower belemnite *Belemnella lanceolata* Zones of Błaszkiewicz (1980) (Text-fig. 3).

<u>Material studied</u>: Two specimens of *Eutrephoceras darupense* (MUZ PIG 12.II.1057 and 1068).

Stryjno (upper Maatrichtian)

The village of Stryjno, southeast of Lublin (Text-fig. 1B), lies in an area where opokas of the upper Maastrichtian belemnite *Belemnella kazimiroviensis* Zone are exposed. No further data on this historical outcrop are available.

Material studied: Two specimens of Cymatoceras intrasiphonatum (MZ VIII Mc-673/2-3).

Strzeżów (upper Campanian)

An inactive quarry in the village of Strzeżów, north of Miechów, Miechów Upland (= locality Strzeżów I of Jurkowska (2016), fig. 3; see also Text-fig. 1B). The quarry section exposes a ca. 7 m thick succession of sandy opoka with marly intercalations (Jurkowska and Uchman 2013, Jurkowska 2016). Biostratigraphically, this section represents the inoceramid "*Inoceramus*" *inkermanensis* and "*I*." *costaecus* Zones (Jurkowska 2016), which correspond to the uppermost belemnite Belemnitella minor I Zone and the lower belemnite *Belemnitella minor* II Zone of Remin (2015). The Strzeżów section yields abundant sponges, bivalves, gastropods, cephalopods, and echinoids (Świerczewska-Gładysz and Jurkowska 2013; Malchyk et al. 2017).

<u>Material studied</u>: Three specimens (ZPAL N.III/68, 338 and 347) identified as *Eutrephoceras dekayi*, "*Cymatoceras*" *patens*, and *Epicymatoceras* vaelsense.

Sulejów (middle Campanian)

Several opoka outcrops existed near the village of Sulejów on the left bank of the Vistula River, Middle Vistula River section (Text-fig. 1C; see Pożaryski 1938, fig. 2, Błaszkiewicz 1980, fig. 1). According to Błaszkiewicz (1980, fig. 1), the opoka from Sulejów represents the ammonite *Neancyloceras phaleratum* Zone (Text-fig. 3). Material studied: One specimen of *Eutrephoceras* spp. (MZ VIII Mc-676).

Wałowice (middle Campanian)

Several opoka outcrops once existed near the village of Wałowice on the right bank of the Vistula River, Middle Vistula River section (Text-fig. 1C; see also Pożaryski 1938, fig. 2

and Błaszkiewicz 1980, fig. 1). According to Błaszkiewicz (1980), the section corresponds to ammonite *Neancyloceras phaleratum* Zone.

Material studied: One specimen of Eutrephoceras spp. (MZ VIII Mc-289).

Wałowice-Kolonia (middle Campanian)

This name refers to a temporary opoka outcrop near the village of Wałowice-Kolonia, on the right bank of the Vistula River, Middle Vistula River section (Text-fig. 1C). According to Błaszkiewicz (1980, fig. 1), Wałowice-Kolonia lies in an area where deposits of the ammonite *Neancyloceras phaleratum* Zone are exposed (Text-fig. 3). <u>Material studied</u>: One specimen of *Cymatoceras loricatum* (ZPAL N.III/17).

Wierzchoniów (upper upper Maastrichtian and Danian)

A village east of Bochotnica, Middle Vistula River section (Text-fig. 1C). The locality was mentioned by Kongiel (1935, fig. 1) and Kongiel and Matwiejewówna (1937). Today, there are no outcrops in this area, but based on descriptions by these authors, the section was identical to the nearby Bochotnica section. Therefore, opoka-lithology upper Maastrichtian fossils labelled Wierzchoniów in museum collections are from the upper Kazimierz Opoka, from the interval corresponding to the belemnite *Belemnella kazimiroviensis*, inoceramid *Tenuipteria argentea*, and ammonite *Hoploscaphites constrictus crassus* Zones (Text-fig. 3). <u>Material studied</u>: Three upper Maastrichtian specimens in opoka preservation (MZ VIII Mc-568, 666, 666/1), indentified as *Eutrephoceras vastum* and *Cymatoceras intrasiphonatum*.

Wola Piasecka (upper upper Maastrichtian and Danian)

A large, recently abandoned quarry east of Lublin, near Piaski (Text-fig. 1B). The quarry exposes an opoka succession, up to 10 m thick, that is terminated by a hard limestone layer with abundant burrows (Machalski *et al.* 2022). The opoka is overlain by Danian glauconitic gaizes that pass upwards into poorly exposed marls. Based on lithological and faunal data, these deposits are interpreted as equivalents of the Greensand and Siwak in the Middle Vistula River section (Machalski *et al.* 2022). According to Machalski *et al.* (2022), the opoka yields index fossils of the belemnite *Belemnella kazimiroviensis*, inoceramid *Tenuipteria argentea* and ammonite *Hoploscaphites constrictus crassus* Zones (Text-fig. 3). Abundant fossils occasionally occur in concentrations, including a remarkable "nest" of *Cymatoceras intrasiphonatum* (Machalski and Malchyk 2019, fig. 2B; specimen ZPAL N.III/288(2)–308(2)).

Material studied: In total, 43 specimens (ZPAL N.III/151, 205, 228, 229, 250–256, 273–275, 286–308, 312, 337, 354, 369, 371–372), identified as *Eutrephoceras ahltenense*, *E. dekayi*, *Eutrephoceras* spp., and *Cymatoceras intrasiphonatum*.

Wojszyn (upper upper Maastrichtian and Danian)

The remnants of an old quarry are still visible on the left bank of the Vistula River near Wojszyn, south of Nasiłów, Middle Vistula River section (Text-fig. 1C). According to Pożaryski (1938), the Wojszyn section exposed the same K–Pg succession as the Nasiłów and Bochotnica sections, including several metres of opoka (upper part of local horizon x and local horizon y). Therefore, these strata represent the upper Kazimierz Opoka (Machalski 1996), and the biostratigraphic assignment of the opoka from Wojszyn is identical to that exposed in Nasiłów and Bochotnica (Text-fig. 3).

Material studied: One specimen of Eutrephoceras vastum (MZ VIII Mc-608).

Wólka Maziarska (lower Maastrichtian)

A series of small peasant quarries existed in the village of Wólka Maziarska (currently part of Wólka Gonciarska), west of the Middle Vistula River section (Text-fig. 1C, see map in Pożaryski 1948 for detailed location). According to Pożaryski (1948), the quarries at Wólka Maziarska exposed calcareous gaizes assigned to local horizon *u* (see Text-fig. 3). The gaizes contained numerous fauna, but no updated review is available for this locality, except for a specimen of *Hoploscaphites constrictus anterior* Błaszkiewicz, 1980 (reported by Błaszkiewicz 1980), which suggests an upper lower Maastrichtian age (M. Machalski, personal communication).

<u>Material studied</u>: Five specimens (MUZ PIG 12.II.1051, 1053, 1058, 1062 and 1075), identified as *Eutrephoceras ahltenense*, *E. dekayi*, and *Eutrephoceras* spp.

Wyględów (upper Campanian or lower Maastrichtian)

A series of small rural quarries existed in the village of Wyględów, west of the Middle Vistula River section (Text-fig. 1C; see map in Pożaryski (1948) for detailed location). According to Pożaryski (1948), the Wyględów quarries exposed sandy opoka with hard limestone intercalations, representing local horizon *u*. No biostratigraphic data of these deposits are available, but they might represent either the upper Campanian or lower Maastrichtian in current schemes (Text-fig. 3).

<u>Material studied</u>: Three specimens (MUZ PIG 12.II.1049–1050 and 1083) identified as *Eutrephoceras ahltenense, Eutrephoceras* sp. B, and Cymatoceratidae? ident.

Wylągi (upper upper Maastrichtian and Danian)

A village east of Kazimierz Dolny in the Middle Vistula River section (Text-fig. 1C). At present, there are no outcrops in the area, but according to Pożaryski (1938), the outcrop at Wylągi exposed a K–Pg succession similar to Nasiłów and Bochotnica. Therefore, opokalithology fossils labelled "Wylągi" in museum collections come for the upper part of the upper upper Maastrichtian Kazimierz Opoka, from the interval corresponding to the belemnite *Belemnella kazimiroviensis*, inoceramid *Tenuipteria argentea*, and ammonite *Hoploscaphites constrictus crassus* Zones (Text-fig. 3).

<u>Material studied</u>: Four upper Maastrichtian specimens in opoka preservation (MZ VIII Mc-667–668, 310/1 and 610/2), identified as *Eutrephoceras vastum* and *Cymatoceras intrasiphonatum*.

Material and methods

Institutional abbreviations

ANSP, the Academy Natural Sciences of Drexel University; GSA, GeoSphere Austria, Bundesanstalt für Geologie, Geophysik, Klimatologie und Meteorologie (Federal Institute for Geology, Geophysics, Climatology and Meteorology, formerly Geologische Bundesanstalt (GBA), Vienna, Austria; GM-B, Goldfuss Museum, University of Bonn, Germany; GM-K, Geologisk Museum, Københavns Universitet (Geological Museum, University of Copenhagen, Denmark); GZG, Geowissenschaftliches Zentrum der Universität Göttingen (Geoscience Center, Faculty of Geoscience and Geography, University of Göttingen, coll. Manfred Kutscher), Göttingen, Germany; IPM, MNHN, Laboratoire de Paléontologie, Museum National d'Histoire Naturelle de Paris (Laboratory of Palaeontology, France National Museum of Natural History), Paris; KM, Kreidemuseum Rügen (Chalk Museum Rügen, coll. Manfred Kutscher), Sagard, Germany; LO, Geologiska institutionen, Lunds Universitet (the Department of Geology, Lund University), Sweden; MKD/MP, Muzeum Przyrodnicze, Oddział Muzeum Nadwiślańskiego (Natural History branch of the Vistula Museum), Kazimierz Dolny, Poland; MUZ PIG, Muzeum Geologiczne Państwowego Instytutu Geologicznego–Państwowego Instytutu Badawczego (Geological Museum, Polish Geological Institute–National Research Institute), Warsaw, Poland; **MWGUW**, Muzeum Geologiczne im. Stanisława Józefa Thugutta, Wydział Geologii Uniwersytetu Warszawskiego (Stanisław Józef Thugutt Geological Museum, Faculty of Geology, University of Warsaw), Poland; **MZ**, Muzeum Ziemi – Polska Akademia Nauk (Museum of the Earth – Polish Academy of Sciences) Warsaw, Poland; **NHMW**, Naturhistorisches Museum Wien (Museum of Natural History Vienna), Austria; **OESM**, Geomuseum Faxe, Østsjællands Museum (Geomuseum Faxe, Museum of Eastern Zealand), Faxe, Denmark; **PZ-K**, **SMNH**, Derzhavnyi pryrodoznavchyi Muzei Natsionalnoi Akademii Nauk Ukrainy (State Museum of Natural History, National Academy of Sciences of Ukraine), Lviv, Ukraine; **UkK**, Senckenberg Naturhistorische Sammlungen Dresden Museum für Mineralogie und Geologie (Senckenberg Natural History Collections of Dresden), Germany; **ZPAL**, Instytut Paleobiologii im. R. Kozłowskiego Polskiej Akademii Nauk (Institute of Paleobiology, Polish Academy of Sciences), Warsaw, Poland.

Material

The studied nautilid material consists of 656 specimens from 64 sites in Poland and western Ukraine (Text-fig. 1A–C). The majority of the Polish material is stored in the Institute of Paleobiology, Polish Academy of Science (PAN) in Warsaw, and primarily consists of specimens gathered by Prof. Marcin Machalski. Additional material is located in the Natural History Museum in Kazimierz Dolny; the Geological Museum, Polish Geological Institute–National Research Institute; the Stanisław Józef Thugutt Geological Museum, Faculty of Geology, University of Warsaw; and the Museum of the Earth, PAN, Warsaw. The western Ukrainian specimens are located in the State Museum of Natural History, National Academy of Sciences of Ukraine (Lviv); the Federal Institute for Geology, Geophysics, Climatology and Meteorology (Vienna); the Museum of Natural History, Vienna; and the Senckenberg Natural History Collections of Dresden.

Additional specimens were collected during original fieldwork in the Lublin area and the Middle Vistula River section from 2016–2019 (Text-fig. 1B). Furthermore, several specimens were kindly donated by late prof. Andrzej Radwański, Agata Jurkowska, Maciej Duda, Ireneusz Walaszczyk and Zbigniew Remin.

Some of the specimens studied here were previously described and/or illustrated by following authors: Kner (1848): NHMW 2004z0117/0001; Geinitz (1849): Ukk 87, 90; Favre (1869): GSA 1869/006/006, 1869/006/0005/001, 1869/006/0005/002); Kongiel and

Matwiejewówna (1937): MZ VIII Mc-246–247; Wilmsen and Esser (2004): NHMW 2004z0117/0001; Frank (2014): NHMW 2004z0117/0001; Machalski *et al.* (2016): ZPAL N.III/269–273 (under catalogue number ZPAL N.3/58–61); Malchyk *et al.* (2017): ZPAL N.III/68–71; Janiszewska *et al.* (2018): ZPAL N.III/125, 159, 219 and 244; Machalski and Malchyk (2019): ZPAL N.III/288(2)–308(2). A summary of examined specimens is provided in Appendix 1.

Comparative studies were conducted on material from central Europe (see Appendix 2), including nautilid cephalopods from the Campanian–Maastrichtian and Danian deposits of northern Germany, northern Denmark, and southern Sweden in the Senckenberg Natural History Collections of Dresden, Germany; the Natural History Museum of Denmark, Geological Museum, Copenhagen; the Geomuseum Faxe, Denmark; the Department of Geology, Lund University, Sweden, and the private collections of Manfred Kutscher, Sassnitz, Rügen, Germany which bear the prefix GZG.STRG (Geoscience Center, Göttingen), with some specimens housed at Chalk Museum Rügen, Germany.

The studied material is mostly represented by complete or fragmentary moulds (steinkerns) left after dissolution of the originally aragonitic nautilid shells. These may represent three distinctive taphomorphs as defined by Crampton (2004): (1) external moulds, (2) simple internal moulds, and (3) composite internal moulds. These various preservation states resulted from different taphonomic pathways, reflecting differences in the timing of shell dissolution and/or variable extents of sediment compaction and lithification, among other possible drivers. In some cases, taphomorph analysis enabled identification of delicate details of the original shell structure and sculpture, as exemplified by selected specimens of the nautilid *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1861) from the upper Campanian and lower Maastrichtian of Poland (Malchyk *et al.* 2017). The reader is referred to McAlester (1962), Crampton (2004), and Wilmsen (2016a,b) for more detailed considerations on molluscan shell preservation.

Only a few studied specimens (e.g., ZPAL N.III/244 and ZPAL N.III/219 from Krasnobród, Poland) partially retain original aragonitic shell material. For more details, the reader is referred to Janiszewska *et al.* (2018).

Methods

The taxonomic approach adopted here is based on a populational definition of species (Dzik 1984, 1990; Machalski 2005a,b), using simple biometrics applied to the studied material where an assessment of morphological variation is possible. However, this approach is challenging for the majority of the studied specimens due to their poor preservation.

The nautilid conch consists of the septate phragmocone and the living chamber, which usually occupies approximately half of the last whorl (Text-fig. 4). The terminology of nautilid conch features is based on Teichert (1964) and summarized in Text-fig. 4. Measurements of maximum conch diameter (D_{max}), whorl breadth (Wb), whorl height (Wh), and umbilical diameter (U) were obtained with a Vernier Calliper, and are given in millimeters and as percentages of maximum conch diameter (in brackets; Text-fig. 4; see relevant tables throughout the text).



Text-fig. 4. Important morphological terms and biometric parameters used for systematic fossil nautilid classification (modified after Wilmsen and Esser 2004), A – Lateral view of the conch; B – Septum in frontal view.

Date were analyzed using PAST (Hammer *et al.* 2001) to compare shell proportions – specifically, Wb/Wh and Wb/Wh to D_{max} ratios across selected specimens of *Eutrephoceras dekayi* (Morton, 1834), and Wb/Wh, Wb/ D_{max} , and U/ D_{max} ratios across selected specimens of *Cymatoceras intrasiphonatum* (Łopuski, 1912).

Photographic documentation of the studied specimens was mostly conducted by Grażyna Dziewińska and Marian Dziewiński (Institute of Paleobiology, PAS), and by the author during visits to other institutions. Specimens were photographed with a digital camera (Nikon D5 with Nikkro Macro 55 lens, and Canon SX160 IS with 28–448 mm F3.5–5.9 zoom lens), in some cases after coating with ammonium chloride (NH₄Cl).

Reconstructions of adult shells of selected nautilid taxa are inspired by Dzik (1984) and based on actual specimens with two comments: 1) the restorations are often intuitively retrodeformed for specimens deformed by compaction, 2) as the apertures of the studied specimens are rarely intact, they are reconstructed based on the course of growth lines and comarginal ribs close to the aperture. Reconstructions were performed by Bogusław Waksmundzki (University of Warsaw), with detailed guidance from the author. All plates and Text-figures were processed using CorelDraw 2017 and Affinity Photo 2.

Supraspecific systematics

Since the nautiloid classification of Flower and Kummel (1950), there has been considerable development in our understanding of post-Triassic nautiloid phylogeny, morphology, and systematics (e.g., Wiedmann 1960; Kummel 1964; Shimansky 1957, 1975; Dzik 1984; Tintant and Kabamba 1983; Matsumoto *et al.* 1984; Tintant 1989; Engeser 1999; Mutvei 2015). However, there are still considerable controversies surrounding family and generic classifications, driven by significantly different approaches in various systematic schemes (King and Evans 2019). While Kummel (1964, *Treatise*) proposed a subdivision of post-Triassic nautilids – that is, the superfamily Nautilaceae Blainville, 1825 – into six families (Table 1), other authors have vigorously opposed splitting the Nautilaceae (see Wilmsen 2000; Wilmsen and Yazykova 2003; Wilmsen and Esser 2004 for review).

The classification problem is best epitomized by the "ribbed" nautilids, which have traditionally been classified as a separate family, Cymatoceratidae Spath, 1927 (e.g., Kummel 1956, 1964; Matsumoto *et al.* 1984). However, Wiedmann (1960) and many subsequent authors (e.g., Shimansky 1975; Tintant and Kabamba 1983; Tintant 1989, 1993; Wilmsen 2000, Wilmsen and Yazykova 2003) have questioned the grouping of all ribbed post-Triasic nautiloid genera into the Cymatoceratidae, regarding it as a polyphyletic "waste-basket" for ribbed nautiloids. In a recent study, Chirat and Bucher (2006) concluded that the transverse ridges ("ribs") on various nautilids conventionally assigned to the Cymatoceratidae actually represent genetically unrelated radial ornamental features that may not be homologous across genera, supporting doubts about the monophyly of the Cymatoceratidae. These authors argued that the ribbing of the genus *Cymatoceras* Hyatt, 1883 – specifically in *Nautilus pseudelegans*
d'Orbigny, 1840, the type species of the genus *Cymatoceras* – does not consist of the classic comarginal ribs, but actually represents a system composed of overlapping radial tile-shaped lamellae of the outer prismatic shell layer. Chirat and Bucher (2006) suggested that the ornament design observed on *N. pseudoelegans* could be considered a synapomorphy of the emended cymatoceratid clade, enabling a differentiation between "false" and "true" cymatoceratids. This approach has been adopted by Malchyk *et al.* (2017), and in this monograph where specimen preservation is suitable. However, in most cases the studied fossils are not sufficient for any sensible re-consideration of their generic and suprageneric position. As such, a traditional approach to supraspecific nautilid systematics is followed here (Kummel 1964; see Table 1).

Table 1. Systematic placement of nautilids (order Nautilida) within nautiloids (Subclass Nautiloidea) and nautilid subdivision proposed by Kummel (1964). Families represented in studied material are marked in bold.

Subclass	Order	Superfamily	Family
			Tainoceratidae Hyatt, 1883
			Rutoceratidae Hyatt, 1884
		Tainocerataceae Hyatt,	Tetragonoceratidae Flower, 1945
		1883	Rhiphaeoceratidae Ruzhentsev and Shimansky,
			1954
			Koninckioceratidae Hyatt in Zittel, 1990
			Trigonoceratidae Hyatt, 1884
		Trigon correte coos Uriett	Centroceratidae Hyatt in Zittel, 1990
			Grypoceratidae Hyatt in Zittel, 1990
		1884	Permoceratidae Miller and Collinson, 1953
			Syringonautilidae Mojsisovics, 1902
		Aipoceratidae Hyatt, 1883	
Nauthoidea Agassiz,	Nautifida Agassiz,	Aipocerataceae Hyatt,	Solenochilidae Hyatt, 1893
1047	1047	188	Scyphoceratidae Ruzhentsev and Shimansky,
			1954
			Clydonautilidae Hyatt in Zittel, 1900
		Clydonautilaceae Hyatt	Liroceratidae Miller and Youngquist, 1949
		in Zittel, 1900	Ephippioceratidae Miller and Youngquist, 1949
			Iberionautilidae Popov, 1951
			Nautilidae Blainville, 1825
			Pseudonautilidae Shimansky and Erlanger, 1955
		Nautilaceae Blainville,	Paracenoceratidae Spath, 1927
		1825	Cymatoceratidae Spath, 1927
			Hercoglossidae Spath, 1927
			Aturiidae Chapman, 1857

Systematic Paleontology

Order Nautilida Agassiz, 1847 Superfamily Nautilaceae de Blainville, 1825 Family Nautilidae Blainville, 1825 Genus *Eutrephoceras* Hyatt, 1894

TYPE SPECIES: *Nautilus dekayi* Morton, 1834 (p. 291, pl. 8, fig. 4) by original designation of Hyatt (1894: p. 555).

DIAGNOSIS: "Nautiliconic, generally subglobular; whorl section reniform, broadly rounded ventrally and laterally; aperture marked ventrally by broad shallow rounded hyponomic sinus; umbilicus small to occluded; surface smooth; suture only slightly sinuous; annular lobe may be present; siphuncle small, variable in position" (Kummel 1964, p. K449).

Eutrephoceras ahltenense (Schlüter, 1876) (Pls 1–3; Text-fig. 5)

- 1876. Nautilus ahltenensis sp. n.; Schlüter, p. 176, pl. 49, figs 1-3.
- 1889. Nautilus restrictus n. sp.; Griepenkerl, p. 98, pl. 10, figs 1, 2; pl. 11, fig. 1.
- 1912. Nautilus ahltenensis Schlüter; Łopuski, p. 187.
- 1956. Eutrephoceras ahltenensis (Schlüter, 1876); Kummel, p. 380.
- 1956. Eutrephoceras restrictus (Griepenkerl, 1889); Kummel, p. 383.
- 1960. *Eutrephoceras ahltenensis* (Schlüter, 1876); Wiedmann, p. 166, pl. 20, figs I, J; pl. 21, fig. C (lower).
- pars 2013. *Eutrephoceras* cf. *ahltenense*; Wilmsen, Säbele and Schneider, pl. 2, figs 2, 3 only.

?2013 Eutrephoceras ahltenense; Wilmsen, Säbele and Schneider, pl. 2, figs 4, 5.

TYPE: The specimen figured by Schlüter (1876) on his pl. 49, figs 1–3 from "Mucronaten-Kreide", Ahlten, Hannover (i.e., upper upper Campanian, ammonite *Neancyloceras bipunctatum*/ echinoid *Galerites roemeri* Zone = belemnite *Belemnitella langei* Zone; see Niebuhr 2004) is designated as lectotype herein. MATERIAL: 40 specimens: one from Aleksandrów (MUZ PIG 12.II.1071); two from Antoniów (MUZ PIG 12.II.1045, 12.II.1076); one from Bochotnica (MWGUW 003598); one from Ciszyca Kolonia (VIII Mc-711); one from Dziurków (ZPAL N.III/54); one from Hrebenne (ZPAL N.III/12); three from Kazimierz Dolny (MWGUW 002167, 003600; ZPAL N.III/316); one from Lviv (PZ-K-1765); 11 from Nahoryany (PZ-K-491/2–3, 1252, 1786/2–5, 1788/2; 1789/1–2; NHMW 1862/0005/0014); five from Nasiłów (ZPAL N.III/140–141, 156, 210 and 362); six from Piotrawin (ZPAL N.III/178; MKD/MP-75, 220, 346, 358, 919); one from Sadkowice (MUZ PIG 12.II.1072); two from Wola Piasecka (ZPAL N.III/253; 312); three from Wólka Maziarska (MUZ PIG 12.II.1051, 1053 and 1075) and one from Wyględów (MUZ PIG 12.II.1049).



Text-fig. 5. Reconstruction of the adult shell of *Eutrephoceras ahltenense* (Schlüter, 1876), mostly based on specimen ZPAL N.III/156, upper Maastrichtian, Nasiłów, Poland (Pl. 3, Fig. 1a–d), and specimens figured by Schlüter (1876, pl. 49, figs 1–3) from the upper upper Campanian, Ahlten, Hannover, northern Germany; A – lateral, B – apertural, C, D – ventral views, E – septum in frontal view; weak ocular and strong hyponomic sinuses are arrowed in A and D, respectively.

DESCRIPTION: All specimens are preserved as simple or composite internal moulds ranging from incomplete phragmocones to phragmocones with large portions of the body chamber, up to 205 mm in estimated diameter (specimen MWGUW 003600). The largest individuals attain over 18 cm in maximum preserved diameter (Table 2).

In the present species (Text-fig. 5), the conch is involute, moderately depressed (Wb/Wh ratios of 0.8 to 1.5), with a small, deep umbilicus, comprising ca. 8% of the maximum preserved diameter. The umbilical wall is moderately steep. The umbilical shoulder is broaudly rounded. The whorl section is semirectangular in early stages, and becomes subquadrate with ontogeny. The flanks are generally flat. The venter is broad and sligtly flattened. The ventrolateral shoulders are broadly rounded. The conch surface is generally smooth, although rarely displays poorly visible growth lines. The suture line shows a shallow lobe on the lateral and venteral sides (see Text-fig. 5). The siphuncle position is ventral, slightly below the middle of septum.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
PZ-K-491/2	86	71 (83)	_	_	10 (12)
PZ-K-491/3	68	_	48 (71)	-	8 (12)
PZ-K-1252	~100	~97 (97)	_	_	~11 (11)
PZ-K-1765	~57	_	_	_	~8 (14)
PZ-K-1786/2	71	63 (89)	51 (72)	1.23	-
PZ-K-N1786/3	87	65 (75)	64 (73)	1.01	6(7)
PZ-K-1786/4	63	~52.5 (83)	34 (54)	~1.55	4 (6)
PZ-K-1786/5	82	56 (68)	70 (80)	0.8	6(7)
PZ-K-1788/2	137	71 (52)	81 (59)	0.88	8 (6)
PZ-K-1789/1	_	81	~73	1.11	7 (6)
PZ-K-1789/2	101	90 (79)	79 (78)	1.01	4 (4)
MKD/MP-75	184	110 (60)	108 (59)	1.01	_
NHMW 1862/0005/0014	93	56.5 (60)	58.5 (63)	0.96	_
MUZ PIG 12.II.1045	~144	—	~67.7 (47)	_	_
MUZ PIG 12.II.1076	~98.5	_	~51.6 (52)	_	_
MWGUW 003600	~205	100 (49)	110 (54)	0.91	16 (17)
ZPAL N.III/156	~103	~77 (75)	~74 (72)	1.04	_

Table 2. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Eutrephoceras ahltenense* (Schlüter, 1876).

DISCUSSION: According to Wiedmann (1960), *Eutrephoceras ahltenense* has a characteristic subquadrate whorl section that easily distinguishes it from related taxa.

However, juvenile forms can be confused with the co-occurring eutrephoceratid E. *quadrilineatum*, which shares the semirectangular shape of the whorl section. Nevertheless, adult forms of E. *ahltenense* are characterized by a clearly subquadrate shape of the whorl section, a flattened venter, and a more sinuous suture line. In contrast, in late ontogenetic stages E. *quadrilineatum* has a rather sub-rectangular whorl section shape, a broadly rounded venter with no flattening, and a straight suture line.

The specimens described as *Nautilus restrictus* by Griepenkerl (1889, p. 98, pl. 10, figs 1–2; pl. 11, fig. 1) from the "Mucronaten-Schichten" of Ahlten mainly differ from Schlüter's type material (1876, p. 176, pl. 49, figs 1–3) in the more dorsal position of their siphuncle. However, the difference in siphuncle position may result from ontogenetic changes in conch morphology or alternatively could simply reflect intraspecific variation (cf. Wani and Ayyasami 2009). The reader is also referred to a similar discussion on *E. dekayi* (see below). Therefore, following Wiedmann (1960), *E. restrictus* is synonimized herein with *E. ahltenense*.

OCCURRENCE: Upper Campanian of Germany (Schlüter 1876; Griepenkerl 1889; Wilmsen, Säbele and Schneider 2013) and Campanian–Maastrichtian of Poland (Łopuski 1912; this study).

Eutrephoceras? aquisgranense (Holzapfel, 1887) (Pls 4, 5; Text-figs. 6, 7)

- 1887. Nautilus aquisgranensis n. sp.; Holzapfel, p. 67, pl. 4, figs 1, 2.
- 1912. Nautilus aquisgranensis Holzapfel; Łopuski, p.189, pl. 1, fig. 7.
- 1975. Eutrephoceras donbassicum sp. nov.; Shimansky, p. 68, pl. 8, fig. 2.
- 2016. ?*Eutrephoceras aquisgranensis* (Holzapfel, 1887); Machalski, Vellekoop, Dubicka and Peryt, figs 4a-d.

TYPE: Holzapfel (1887, p. 68) mentioned six specimens from the "Aachener Kreide" (= Vaals Formation, lower Campanian, see Jagt 1989), which are syntypes of the species. Two of the originals, illustrated by Holzapfel (1887; pl. 4, figs 1–2) from the "Grünsand" of Aachen and Vaals, are designated herein as lectotype and paralectotype, respectively.

MATERIAL: 16 specimens: one from Bochotnica (ZPAL N.III/128); two from Chełm (ZPAL N.III/260, 263); two from Dziurków (ZPAL N.III/51, 53); six from Kazimierz Dolny (VIII Mc-547/2, ZPAL N.III/164, 269, 311, 358 and 360); one from Lechówka (ZPAL N.III/270); one from Mełgiew (ZPAL N.III/278); one from Opole Lubelskie (ZPAL N.III/247); and two from Rejowiec (ZPAL N.III/227, 373).



Text-fig. 6. Reconstruction of the adult shell of *Eutrephoceras? aquisgranense* (Schlüter, 1876), based mostly on specimens ZPAL N.III/227, upper Maastrichtian, Rejowiec (Pl. 5, Fig. 5; Text-fig. 7B) and ZPAL N.III/247, Opole Lubelskie, Poland (Pl. 5, Fig. 1); A – lateral, B – apertural, C, D – ventral views; hyponomic sinus is arrowed in D.

DESCRIPTION: The species is represented by incomplete composite internal moulds, mostly obliquely or ventro-dorsally flattened as a result of *post mortem* compaction (except for Pl. 4, Fig. 1a–d). The largest available individuals attain ca. 6 cm in maximum preserved diameter (Table 3).

The present species (Text-fig. 6) is characterized by a slightly depressed (Wb/Wh ratios of ~0.7), involute conch with a semi-circular whorl section. The flanks are slightly flattened, converging towards the broadly rounded venter. The umbilicus appear to be small in early ontogenetic stages (e.g., specimen VIII Mc-547/2, Pl. 4, Fig. 1a–d), and occludes with conch growth. The suture line is moderately sinuous with a shallow lateral lobe (Text-fig. 6). The conch surface is covered with very fine, closely spaced, longitudinal striae visible throughout all ontogenetic stages (Text-fig. 7). The striae are about 1 mm in width; the distance between two adjacent striae is usually >1 mm (e.g., specimen ZPAL N.III/51, see Pl. 5, Fig. 3). The siphuncle position cannot be discerned in any studied specimens.



Text-fig. 7. Fine ornamentation of *Eutrephoceras? aquisgranense* (Schlüter, 1876), upper Maastrichtian. A – ZPAL N.III/260, Chełm, Poland. B – ZPAL N.III/227, Rejowiec, Poland.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
VIII Mc-547/2	28	14 (50)	20 (71)	0.7	2.5 (1)
ZPAL N.III/164	~24	-	_	-	occluded
ZPAL N.III/227	~ 65	39 (60)	26 (40)	1.5	occluded
ZPAL N.III/247	~ 45	~33 (73)	_	_	occluded
ZPAL N.III/263	~ 20	-	_	-	occluded
ZPAL N.III/269	~31 in length	-	_	-	occluded
ZPAL NIII/311	~90	~42 (47)	~52 (58)	0.81	occluded
ZPAL N.III/358	~42	~35 (83)	~21 (50)	~1.6	occluded
ZPAL N.III/360	59 in length	47	_	-	occluded
ZPAL N.III/373	~21	~15 (71)	~11 (52)	~1.4	occluded

Table 3. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Eutrephoceras?* aquisgranense (Holzapfel, 1887).

DISCUSSION: The species is characterized by an involute, globose conch ornamented with fine longitudinal striate, which according to Holzapfel (1887) is one of the most significant diagnostic characters of the species. *E. donbassicum* Shimansky, 1975 from the Maastrichtian of Ambrosievka, Donbas, eastern Ukraine has a similar striate conch ornamentation (see Shimansky 1975, p. 69, pl. 8, fig. 2b) and may be a junior synonym of this species. As observed by Machalski *et al.* (2016, p. 212), this ornamentation style is not typical for the genus *Eutrephoceras*, but is rather associated with the Triassic/Jurassic *Cenoceras* Hyatt, 1883. As such, this species is tentatively assigned to *Eutrephoceras* with a query. However, true *Cenoceras* have ovate trapezoidal whorl sections and suture lines that are utterly different from the present material (compare Kummel 1956; Dzik 1984).

OCCURRENCE: Lower Campanian of Aachem, western Germany (Holzapfel 1887), upper Maastrichtian of Poland (Łopuski 1912 and this study), Campanian–Maastrichtian of the Donbas, eastern Ukraine, and Maastrichtian/?Danian of Crimea, southern Ukraine (Shimansky 1975).

Eutrephoceras darupense (Schlüter, 1876) (Pl. 6, Fig. 1a-c, ?Fig. 2a-d)

1876. Nautilus darupensis n. sp.; Schlüter, p. 176, pl. 49, figs 4,5.1876. Nautilus cf. neubergicus Redtenbacher, 1873; Schlüter, p. 174, pl. 48, figs 3–5.

- 1956. Eutrephoceras darupensis (Schlüter, 1876); Kummel, p. 381.
- 1960. *Eutrephoceras darupense* (Schlüter, 1876); Wiedmann, p. 157, pl. 21, figs C–D; pl. 23, figs F, P; Text-fig. 2.
- 1999. Eutrephoceras darupense (Schlüter, 1876); Wittler, Roth and Legant, p. 37, Text-figs 47a-b, 48.
- 2000. *Eutrephoceras darupense* (Schlüter, 1876); Wilmsen, pl. 2, figs 5a-b; pl. 4, figs 4a-b, 5a-b; pl. 5, figs 11, 24-25.
- ?2010. Eutrephoceras aff. darupense (Schlüter, 1876); Kin, p. 55, fig. 30A-L.
- 2013. Eutrephoceras darupense (Schlüter, 1876); Wilmsen, Säbele and Schneider, pl. 3, figs 2–4.

TYPE: The holotype and syntype are specimens GM-B 98a (GM-B-46) and GM-B 98b (GM-B-47) from the "Mucronaten-Kreide" (lower upper Campanian, *Belemnitella mucronata* Zone) of Westphalia, northwestern Germany (Frank 2014).

MATERIAL: Six specimens: one from Dziurków (VIII Mc-448, Pl. 6, Fig.1a–c); one from Marianów (MUZ PIG 12.II.1052/2); one from Piotrawin (MKD/MP-181); and two from Stoki (MUZ PIG 12.II.1057, 1068). Additionally, a specimen from Kamień South (ZPAL N.III/215, Pl. 6, Fig. 2a–d) is tentatively assigned here.

DESCRIPTION: The species is represented by more-or-less deformed, simple and composite internal moulds of phragmocones with retained portions of the body chambers. The largest individuals attain over 7 cm in maximum preserved diameter (Table 4).

The species is characterized by a highly involute, somewhat depressed conch with an occluded umbilicus. The whorl section is sub-rectangular with Wb/Wh ratios of ca. 1.06, and the maximum Wb is on the lower flanks. The flanks are weakly convex, gradually passing into broadly rounded ventrolateral shoulders and venter. The conch surface is smooth. The suture line is moderately sinuous, with a small saddle near the umbilical shoulder followed by shallow lateral and ventral lobes. The siphuncle position changes from ventro-central to ventral.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
MUZ PIG 12.II.10.52/2	~35.5	25.24 (0.71)	26 (73)	0.9	occluded
MUZ PIG 12.II.1057	~53	~33.1 (62)	~31 (58)	1.06	occluded
MUZ PIG 12.II.1068	_	10.3	7.4	1.39	occluded
VIII Mc-448	76	54 (71)	50 (66)	1.08	-
ZPAL N.III/215	45.5	~28 (61)	~30 (66)	0.9	occluded

Table 4. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Eutrephoceras darupense* (Schlüter, 1876).

DISCUSSION: The present material corresponds well in whorl section, suture shape, and the closed umbilicus to *Eutrephoceras darupense* (e.g., Schlüter 1876, Wilmsen 2000). Despite its general similarity to *E. darupense*, a specimen from Kamień, Middle Vistula River section (ZPAL N.III/215), has a centrally positioned siphuncle (see Pl. 6, Fig. 2a–d) and is assigned here with some degree of reservation.

E. aff. *darupense* of Kin (2010) from the lower Maastrichtian of Hrebenne, Poland resembles the present species in general conch shape, but differs in having a less sinusous suture and a dorsally positioned siphuncle. For further discussion on *E. darupense* synonomy and comparisons with other *Eutrephoceras* species, the reader is referred to Wiedmann (1960) and Wilmsen (2000).

OCCURRENCE: Coniacian–Campanian of northern Germany, Upper Cretaceous of England and France, Turonian–Campanian of Spain (e.g., Wiedmann 1960, Wilmsen 2000), and upper Campanian–lower Maastrichtian of Poland (this study).

> Eutrephoceras dekayi (Morton, 1834) (Pls 7–9; Text-figs 8–14)

1834. Nautilus dekayi, Morton, p. 33, pl. 8, fig. 4.

1867. Nautilus bellerophon (M.U.H.); Lundgren, p. 14, fig. 1.

pars 1869. *Nautilus dekayi* Morton; Favre, p. 7, pl. 3, fig. 2, only [non fig. 1 =*Eutrephoceras* sp. A].

- pars 1874. *Nautilus dekayi* Morton; Geinitz, p. 183, pl. 32, fig. 3 only [non fig. 4 =*Eutrephoceras depressum* Binkhorst van den Binkhorst, 1861; non fig. 5 =*Eutrephoceras vastum*? Kner, 1848].
- 1885. Nautilus bellerophon Lundgren; Moberg, p. 9, pl. 1, figs 3-6.
- pars 1889. *Nautilus dekayi* Morton; Griepenkerl, p. 97, pl. 10, fig. 3 only [non fig. 4 =*Eutrephoceras depressum* Binkhorst van den Binkhorst, 1861].
- 1902. Nautilus bellerophon (Lundgren); Ravn, p. 236, pl.4, figs 1-2.
- 1912. Nautilus dekayi Morton; Łopuski, p. 187.
- 1935. Nautilus sp.; Kongiel, p. 46.
- 1937. Nautilus dekayi Morton; Kongiel and Matwiejewówna, p. 4, pl. 1, figs 12-13.
- 1937. Nautilus bellerophon Lundgren; Kongiel and Matwiejewówna, p. 4, pl. 2, figs 1-2.
- 1957. Eutrephoceras bellerophon (Lundgren); Mutvei, Text-fig 18, pl.15, figs 4-6.
- 1959. Eutrephoceras bellerophon (Lundgren); Shimansky, p. 173, pl. 1, figs 3-4.
- pars 1960. *Eutrephoceras depressum* (Binkhorst van Binkhorst, 1861); Wiedmann, p. 154 (see for synonymy).
- 1962. Eutrephoceras dekayi (Morton); Shimansky, pl. 42, fig. 2.
- 1975. *Eutrephoceras bellerophon* (Lundgren); Shimansky, p.73, pl. 8, fig. 6; pl. 9, fig. 1.
- pars 1977. *Eutrephoceras hebertinum* (d'Orbigny, 1850); Bignot and Geyssant, p. 12, pl. 1, figs 7-11only [non pl. 1., fig. 5,6 which is indeterminate]
- 2007. Eutrephoceras dekayi (Morton, 1834); Landman, Johnson, Garb, Edwards and Kyte, p. 55, fig. 23 (with synonymy).
- ?2013. Eutrephoceras aff. bellerophon; Jagt, Bakel, Gremers, Deckers, Dortangs et al., p. 207, fig. 14A–B.
- 2018. *Eutrephoceras dekayi* (Morton, 1834); Landman, Grier, Cochran, Grier, Petersen, and Towbin, fig. 3; fig. 10; fig. 14. pl. 67, figs 1–9.

TYPE: The holotype of *Eutrephoceras dekayi* is the original of *Nautilus dekayi* Morton (1834, p. 291, pl. 8, fig. 4) from the Maastrichtian of New Jersey, USA, by subsequent designation of Whitfield (1892, p. 243, pl. 37, figs. 2–3). For a detailed discussion of the holotype, see Landman *et al.* (2004, 2018).

MATERIAL: 60 specimens: two from Bliżów (ZPAL N.III/18 and 243); two from Bochotnica (VIII Mc-247; ZPAL N.III/326); one from Chełm (ZPAL N.III/266); three from Dziurków (ZPAL N.III/257, 342 and 344); two from Góra Puławska (VIII Mc-249 and 569); 11 from Hrebenne (ZPAL N.III/7, 80, 83–84, 92, 95–96, 99, 101, 110 and 115); one from Kamienny Dół (ZPAL N.III/132); 11 from Kazimierz Dolny (MUZ PIG 13.II.482; ZPAL N.III/146, 148, 152–155, 161, 163, 249 and 357); one from Klimusin (ZPAL N.III/169); one from Krasnobód (ZPAL N.III/323); four from Nahoryany (GBA 1869/006/0005/001, 003; Ukk 89a–b); two from Nasiłów (MKD/MP-910; ZPAL N.III/324); two from Niegosłowice (MUZ PIG 28 and 48); one from Opole Lubelskie (ZPAL N.III/246); five from Parchatka (VIII Mc-246, 248; ZPAL N.III/245, 325 and 374); six from Piotrawin (MKD/MP-70–71, 172; MUZ PIG 12.II.1056; ZPAL N.III/234 and 241); one from Potelych (ZPAL N.III/438); one from Wola Piasecka (ZPAL N.III/255); and one from Wólka Maziarska (MUZ PIG 12.II.1062).

COMPARATIVE MATERIAL: The type specimen (LO 175 T) of *Nautilus bellerophon*, originally described by Lundgren (1867, p. 14, fig. 1) from the middle Danian of Limhamn, southern Sweden; two specimens (LO 709 and 710 T) from the same horizon and locality; the original material of Moberg (1885, p. 9, pl. 1, figs 5–6) from the same location; 241 specimens from the same horizon at Faxe, eastern Denmark (GM-K and OESM collections comprising 76 and 38 specimens, respectively).

DESCRIPTION: All specimens are preserved as simple and composite internal moulds (the latter with clearly discernible growth lines; see Text-fig. 9), which range from complete to septate specimens (phragmocones) or their fragments. Some specimens are more-or-less ventro-dorsally flattened due to compaction. The largest available individuals attain over 8 cm in maximum preserved diameter (Table 5), with the maximum preserved diameter of a complete adult individual ca. 98 mm (ZPAL N.III/148 from Kazimierz Dolny; see Pl. 7, Fig. 2a–c).

The present species (Text-fig. 8) is characterised by an involute, relatively globose conch with a depressed whorl cross-section (Wb/Wh ratios range from 1.11 to 1.5). The umbilicus is very small in the early stages (12–13% of maximum preserved diameter), and occludes with ontogeny. The umbilical wall are slightly convex, and the umbilical shoulders are well-rounded. The flanks and venter are rounded. The suture line is slightly sinuous and shows a weak lateral lobe (see Text-fig. 8; Pl. 8, Fig. 2a–c). The conch surface is either

generally smooth or covered with fine growth lines, which can be discerned on particularly well-preserved composite moulds (e.g., MUZ PIG 13.II.482 and ZPAL N.III/249 from Kazimierz Dolny; for the latter, see Text-fig. 9). The growth lines follow the shape of the hyponomic sinus on the ventral side and ocular sinuses on the flanks (see Text-fig. 9). The siphuncle has a sub-central position, and is relatively small and circular.



Text-fig. 8. Reconstruction of the adult shell of *Eutrephoceras dekayi* (Morton, 1834), based mostly on ZPAL N.III/148 (Pl. 7, Fig. 2a–c), 155 (Pl. 7, Fig. 1a–c) and 249 (Text-fig. 9), all from the upper Maastrichtian, Kazimierz Dolny, Poland. A – lateral, B – apertural, C, D – ventral views, E – septum in frontal view; ocular and hyponomic sinuses are arrowed in A and D, respectively.

DISCUSSION: Two species, *dekayi* and *bellerophon*, have been designated for North American and European Late Cretaceous (Campanian–Maastrichtian) and early Paleogene (Danian) globose representatives of the genus *Eutrephoceras* which are similar in general conch proportion, suture shape, and siphuncle position.

The oldest available name is *Nautilus dekayi* Morton, 1834, a species introduced on the basis of a specimen from the "marls of Monmouth and Burlington counties, New Jersey" and designated by Hyatt (1894) as the type species of the genus *Eutrephoceras*. According to

Landman *et al.* (2004), the holotype of *E. dekayi* (specimen ANSP 1984, reproduced here in Text-fig. 10) originates from the upper Navesink Formation (probably from the lower Maastrichtian), Monmouth County, New Jersey, USA (see also Landman *et al.* 2018).

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
GBA 1869/006/0005/001	_	39.16	28.5	1.37	occluded
GBA 1869/006/0005/003	_	34.5	24.7	1.39	—
MKD/MP-70	~54	~53.5 (99)	_	-	~3 (5)
MKD/MP-71	~66	36 (55)	42 (64)	0.85	occluded
MKD/MP-172	~65	~48 (74)	_	—	occluded
MKD/MP-910	33.5	31 (93)	21 (63)	1.47	occluded
VIII Mc-246	37.5	22 (59)	20 (53)	1.1	occluded
VIII Mc-247	49	31.5 (64)	26.5	1.18	occluded
VIII Mc-248	_	~29	~25.5	~1.13	—
VIII Mc-249/2	25	14 (56)	14.1 (56.4)	0.99	occluded
Ukk 89a	~40	—	_	—	—
Ukk 89b	_	29.3	23.3	1.25	occluded
ZPAL N.III/7	_	52	39	—	_
ZPAL N.III/80	_	34	42	1.24	_
ZPAL N.III/99	_	36	45	1.25	_
ZPAL N.III/101	_	59	66	1.2	_
ZPAL N.III/110	_	34	51	1.5	_
ZPAL N.III/115	_	31	40	1.3	_
ZPAL N.III/148	~80	56 (70)	66 (82)	1.2	occluded
ZPAL N.III/154	_	29	46	1.58	_
ZPAL N.III/155	~65	45 (69)	59 (91)	1.3	occluded
ZPAL N.III/249	57	36 (63)	48 (84)	1.33	occluded
ZPAL N.III/257	—	23	31	1.35	_
ZPA1 N.III/344	_	22	33	1.5	—

Table. 5. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Eutrephoceras dekayi* (Morton, 1834).

Eutrephoceras dekayi (Morton, 1834) is traditionally considered to be an exclusively Cretaceous species fairly common in the upper Campanian to Maastrichtian of North America (e.g., Whitfield 1892; Miller 1847; Meek 1876; Kummel 1956; Miller and Garner 1962; Landman *et al.* 2007, 2018) and the Maastrichtian of Europe (e.g., Łopuski 1912, Kongiel and Matwiejewówna 1937). It is important to note that Favre (1869), Geinitz (1874) and Griepenkerl (1889) erroneously described several European forms – such as *E. depressum* (Binkhorst van den Binkhorst, 1861) and *E. vastum* (Kner, 1848) from the Maastrichtian of Ukraine and Germany, respectively – under the name *Nautilus dekayi* (see, e.g., Meek 1876,

Wiedmann 1960, also discussion below). *E. dekayi* is characterized by a sub-globose conch shape, involute coiling, a reneiform whorl cross-section, a slightly sinuous suture, and a subdorsal siphuncle position.



Text-fig. 9. Well preserved composite internal mould of *Eutrephoceras dekayi* (Morton, 1834), with clearly discernible massive growth lines following the hyponomic sinus on the venter (arrowed in D); ZPAL N.III/249, upper Maastrichtian, Kazimierz Dolny, Poland. Note the presence of epizoan serpulids in A and B, and two triangular, healed (non-fatal), unsuccesful predation marks (bites, probably from a fish or coleoid cephalopod onto the living nautilid) arrowed in C. Black spots in C and D are manganese coatings on the mould surface.



Text-fig. 10. Holotype of *Nautilus dekayi* Morton, 1834, specimen ANSP 19484, Maastrichtian, New Jersey, USA. A – apertural, B – ventral, C – lateral views.

Another species, *N. bellerophon* Lundgren, 1867, was proposed for nautilid material from the middle Danian reefal limestone at Limhamn (in older literature, Annetorp), southern Sweden. In the original description of Lundgren (1867, p. 14), *N. bellerophon* is diagnosed as: "*N. nucleo, globuloso, inflato, laevigato; loculamento ultimo maximo; aperture lata, parte ventrali dilatata, septis perpaullum arcuatis; umbilico parvo*". The type specimen of *E. bellerophon* (LO 175 T) is the original of *N. bellerophon* Lundgren (1867, fig. 1), illustrated here in Text-fig. 11. The name *E. bellerophon* (Lundgren, 1867) has been applied by Shimansky (1975) to Maastrichtian and Danian specimens from the former Soviet Union.

While the possible conspecifity between these nominal taxa – for instance, between *Nautilus dekayi* and *N. bellerophon* – has been briefly discussed by previous authors (e.g., Wanner 1902; Wiedmann 1960), the nature of their taxonomic relationships has remained unresolved. Examination of the original *Eutrephoceras bellerophon* material described by Lundgren (1867) and Moberg (1885) (see Text-fig. 11) and numerous specimens of this species from the Danian Faxe Formation, Denmark (Text-fig. 12), and comparisons with published North American *E. dekayi* and European *E. hebertinum* material, suggests that the taxonomic separation of these species is unfounded. [Morphometric and geographic data of the comparative *E. dekayi* material used in this work are provided in Appendix 3 as Tables S1 and S2.] No significant differences can be identified between these materials, although comparison is often difficult due to differential preservation. This is supported by the biometric data presented in Text-fig. 13 and Text-fig. 14, which demonstrate an overlap in the variation of Wb/Wh and Wb/Wh to D ratios between *E. dekayi* (Wb/Wh = 1.54 in the holotype) and *E. bellerophon* (Wb/Wh = 1.43 in the holotype). In addition, the siphuncle

position in *E. dekayi* and *E. bellerophon* changes in the same way, with an ontogenetic transition from dorsum to center. As such, *E. bellerophon* is conspecific to North American and European *E. dekayi*, which is the older, valid name for this taxon in accordance with the International Commission on Zoological Nomenclature (ICZN) code (1999).



Text-fig. 11. Holotype of *Nautilus bellerophon* Lundgren, 1867. A-C – specimen LO 175 T, Danian, Faxe Formation, Limhamn, southern Sweden in lateral (A), ventral (B) and apertural (C) views. D, E – Reproduction of the original figure of Lundgren (1876, fig. 1).



Text-fig. 12. Various *Eutrephoceras dekayi* Morton (1834) specimens from the middle Danian limestone at Faxe, eastern Denmark. A, B – OESM-8142 in lateral (A) and ventral (B) views respectively; C-E – OESM-6542 in lateral (C-D) and ventral (E) views; F, G – LO 710 T (original of Moberg, 1885: pl.1, fig. 6a) in lateral (F) and apertural (G) views; H, I –GM-K 1991.3302 in lateral (H) and ventral (I) views; J-L – GM-K 1991.3260 in lateral (J), apertural (K) and ventral (L) views.



Text-fig. 13. Plot of whorl breadth (Wb) to whorl-height (Wb) ratio in Eutrephoceras dekayi (Morton, 1834).

As mentioned above, *E. dekayi* has been confused with some European forms, especially by Favre (1869), Geinitz (1874), and Griepenkerl (1889). In particular, specimens from the lower Maastrichtian of Nahoryany (western Ukraine), illustrated by Favre (1869; pl. 3, fig. 1a–c and fig. 3) as *Nautilus dekayi*, were referred by Wiedmann (1960) to *Cymatoceras* n. sp. and *Eutrephoceras vastum*, respectively. After a detalied examination of Favre's type material, housed in the GeoSphere Austria (Vienna), specimen GBA 1869/006/0005/002 (Favre 1869, pl. 3, fig. 1a–c) is presently reassigned to *Eutrephoceras* sp. A (Pl. 14, Fig. 1a–d). Furthermore, the specimen illustrated by Favre (1869) in his pl. 3, fig. 2 appears to match *E. dekayi perlatum*, one of three varieties proposed by Miller and Garner (1962) for *Eutrephoceras* specimens from the U.S. Western Interior, Gulf Coastal Plain, and Atlantic Coastal Plain. However, Landman *et al.* (2004, p. 47) hesitated to use the varietal names, stating: "*It is possible that the range of variation exhibited by these three varieties is characteristic of a single population*".



Text-fig. 14. Plot of whorl breadth to whorl-height ratio (Wb/Wh) versus conch diameter (D) in *Eutrephoceras dekayi* (Morton, 1834).

Other specimens from Nahoryany, identified by Geinitz (1874; pl. 32, figs 4–5) as *N*. *dekayi*, correspond to *Eutrephoceras depressum* and *E. vastum*?, respectively. Specimens recorded as *N. dekayi* by Griepenkerl (1889, pl. 10, fig. 4), from the lower upper Campanian belemnite *Belemnitella mucronata* Zone of Königslutter, northwestern Germany, correspond to *E. vastum*.

In their study of the nautilids from the "Calcaire Pisolithique" of Vigny (middle Danian, Paris Basin), Bignot and Geyssant (1997) proposed that their Eutrephoceras hebertinum (d'Orbigny, 1850) is conspecific to, and has priority over, Eutrephoceras bellerophon (Lundgren, 1867). However, Pacaud (2018) illustrated syntypes of the Nautilus hebertinus d'Orbigny, 1850 from the Danian of Montainville (Yvelines) in his fig. 192, A–C and referred them to Cimomia hebertina (d'Orbigny, 1850), based on the shape of the suture line. To increase the confusion, the specimens from Vigny illustrated by Bignot and Geyssant (1997, pl. 1, figs 7-11), although fragmentary, match better the characteristics of the genus Eutrephoceras than that of Cimomia and more specifically that of *E. dekayi* as understood here. In contrast, the specimen from Montereau illustrated by Bignot and Geyssant (1997, pl.1, fig. 5– 6) as the holotype of *E. hebertinum* is poorly preserved and indeterminable. Further complication stems from the fact that the specimens described by d'Orbigny from Montereau are claimed Maastrichtian, not Danian in age by Pacaud (2018). The specimen

identified as *Eutrephoceras* aff. *bellerophon* from the lower Danian of the Maastrichtian type area (Jagt *et al.* 2013) seems to represent *E. dekayi* as understood here, although its fragmentary preservation precludes firm identification.

OCCURRENCE: As understood here, *E. dekayi* is mainly known from the upper Campanian– Maastrichtian of the USA (e.g., Morton 1834; Whitfield 1892; Miller and Garner 1962; Landman *et al.* 2004, 2007, 2018); the Maastrichtian of Poland (Łopuski 1912; Kongiel and Matwiejewówna 1937; this study), Ukraine (Favre 1869; Geinitz 1874; this study) and the ?upper Campanian of north Africa (Wanner 1902). As *E. bellerophon*, this species has been identified from the Danian of Poland (Kongiel and Matwiejewówna 1937; this study), Denmark (Ravn 1902, Rosenkrantz 1960), Sweden (Johnstrup 1866, Lundgren 1867, Moberg 1885), France (see above), probably the Netherlands (see above), f (Russia (Shimansky 1975), Kazakhstan, and the Caucasus (Shimansky 1975).

The material described here is from the Maastrichtian–Danian of the Middle Vistula River section, the lower Maastrichtian of Roztocze, and the lower Maastrichtian of Nahoriany, western Ukraine.

Eutrephoceras depressum (Binkhorst van den Binkhorst, 1861) (Pl. 10)

1861. *Nautilus depressus*, Nobis; Binkhorst van den Binkhorst, p. 12, pl. 5b, fig. 1a–b. 1874. *Nautilus dekavi*, Morton 1834; Geinitz, pl. 32, fig. 4a–b.

- pars 1960. *Eutrephoceras depressum* (Binkhorst van Binkhorst, 1861), Wiedmann, p.154, pl. 17, fig. E; pl. 18, figs A–B (see for synonymy).
- 2012. *Eutrephoceras depressus* (Binkhorst van den Binkhorst, 1861); Jagt, p. 141, pl.29, figs A, C; pl. 30, figs C–E.

TYPE: The specimen illustrated by Binkhorst van den Binkhorst (1861; pl. 5b, fig. 1a–b) from the upper Maastrichtian, Kunrade (now Kunrade Formation), Limburg, the Netherlands (Jagt 2012).

MATERIAL: Ten specimens: five from Chełm (ZPAL N.III/262, 265, 279–281); one from Hrebenne (ZPAL N.III/10); one from Nahoryany (Ukk 87); one from Nasiłów (ZPAL N.III/138); and two from Rejowiec (ZPAL N.III/14, 16).

DESCRIPTION: The studied specimens are preserved as simple internal moulds, slightly obliquely distorted due to *post mortem* compaction. The largest available individuals attain over 5 cm in maximum preserved diameter (Table 6).

The conch of the present species is involute and globular, with a reniform whorl section (Wb to Wh ratio ranges of 1.3). The umbilicus is closed, and the umbilical shoulders are rounded. The most complete specimen, Ukk 87 from Nahoryany, has an estimated diameter of ca. 53 mm (Table 6). The flanks are convex. The venter and ventrolateral shoulders are widely rounded. The conch surface is smooth. The suture line is straight to slightly sinuous. The siphuncle has a ventral position.

Table 6. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Eutrephoceras depressum* (Binkhorst van den Binkhorst, 1861).

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
Ukk 87	53	44 (83)	35 (66)	1.25	occluded
ZPAL N.III/10	53.5	51 (95)	49 (91)	1.04	occluded
ZPAL N.III/14	35	~28 (80)	20 (57)	1.4	occluded

DISCUSSION: The present species is similar to the Early Cretaceous (Albian–Coniacian) *Eutrephoceras bouchardium* (d'Orbigny, 1840) in general conch shape, suture line, and closed umbilicus, but differs in having a clearly ventral siphuncle position. As described above, *E. dekayi* is distinguished from the present species in having a more depressed whorl section, a sub-central siphuncle position, and a more sinuous suture line. According to Wiedmann (1960), a specimen from Köpinge (Sweden), lower/middle upper Campanian (*=stobaei/basiplana* Zone to lower *minor/polyplocum* Zone of the northwestern German zonation; see fig. 9 in Christensen 1986) that was described by Moberg (1885, pl. 1, figs 3–4) as *Nautilus bellerophon* corresponds to *E. depressum*. However, an examination of Moberg's type material (1885) in the Department of Geology, Lund University (Sweden), showed that it is conspecific with *E. dekayi* as understood here (see discussion for *E. dekayi*).

OCCURRENCE: Maastrichtian of the Netherlands (Binkhorst van den Binkhorst 1861, Jagt 2012), Poland and Ukraine (this study).

Eutrephoceras quadrilineatum (Favre, 1869) (Pls 11, 12; Text-fig.15)

1869. Nautilus quadrilineatus; Favre, p. 10, pl. figs 4a-b.

1956. Eutrephoceras quadrilineatus (Favre, 1869); Kummel, p. 383.

1960. Eutrephoceras quadrilineatus (Favre, 1869); Wiedmann, p. 173, pl. 20, fig. L.

1975. Eutrephoceras ?quadrilineatus (Favre, 1869); Shimansky, p. 70, Text-fig. 20.

TYPE: Holotype is the original of Favre (1869; pl. 3, fig. 4) from the lower Maastrichtian of Nahoryany, western Ukraine.

MATERIAL: 17 specimens: one from Dziurków (ZPAL N.III/57); 5 from Nahoryany (PZ-K0339, 487/1, 491/6; GBA 1869/006/006; NHMW 1862/0005/0012); one from Kamień South (ZPAL N.III/176); one from Kaziemierz Dolny (ZPAL N.III/359); three from Nasiłów (MKD/MP-73, 347; ZPAL N.III/313); and five from Piotrawin (MUZ PIG 12.II.1084; VIII Mc-472/1–2, 656; ZPAL N.III/47 and 237).



Text-fig. 15. Reconstruction of the adult shell of *Eutrephoceras quadrilineatum* (Favre, 1836), based on specimen MZ VIII Mc-656, upper Campanian, Piotrawin, Poland (Pl. 12, Fig, 1a–b) and the specimen figured by Favre (1869, pl. 3, figs 4a–b), from the lower Maastrichtian, Nahoryany, western Ukraine. A – lateral, B – apertural and C, D – ventral views; the rather deep hyponomic sinus is arrowed in D.

DESCRIPTION: All studied specimens are preserved as internal moulds, which are usually incomplete. The largest individuals attain over 13 cm in maximum preserved diameter (Table 7).

The present species (Text-fig. 15) is characterized by an involute, somewhat compressed conch with a Wb/Wh ratio of ca. 0.98. The whorl section varies from sub-rectangular to trapezoidal in shape, with Wh slightly exceeding Wb. The flanks are slightly flattened. The ventrolateral shoulders and venter are broadly rounded. The small and deep umbilicus, comprising around 7% of the diameter, has a narrowly rounded umbilical wall that gradually transitions into the lower flanks. The conch surface is generally smooth, although sometimes ornamented with growth lines. The suture line is nearly straight with a very shallow lateral lobe (Text-fig. 15). The siphuncle position is uncertain.

Table 7.	Measurements	(in	mm;	in	brackets	%	of	$D_{max})$	of	the	studied	specimens	of	Eutrephoceras
quadriline	eatum (Favre, 18	36).												

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
PZ-K-339	117.5	75 (64)	66 (56)	1.14	_
PZ-K-487/1	142	79 (56)	90 (63)	0.88	_
PZ-K-491/6	29	-	22 (76)	_	2 (7)
GBA 1869/006/006	129.5	66 (51)	68.5 (53)	0.96	18 (14)
MKD/MP-73	97	54 (56)	42 (43)	1.28	_
MKD/MP-347	118.5	83 (70)	63 (53)	1.31	_
VIII Mc-472/1	74	33.5 (45)	43 (58)	0.77	_
VIII Mc-472/2	74	33.5 (45)	43 (58)	0.77	_
VIII Mc-656	155	73 (47)	94 (61)	0.77	_

DISCUSSION: According to Wiedmann (1960) and Shimansky (1975), *Eutrephoceras quadrilineatum* can be distinguished from other *Eutrephoceras* species by its trapezoidal whorl section. As mentioned above, *E. quadrilineatum* is similar to juvenile specimens of *E. ahltenense* (see discussion for *E. ahltenense*), but differs in its whorl-width index, a less sinuous suture line, and a smaller umbilicus.

OCCURRENCE: Upper Campanian–Maastrichtian of Poland and Western Ukraine (Favre, 1869; this study).

Eutrephoceras vastum (Kner, 1848) (Pl. 13, Pl. 15, Fig. 2a–b, Pl. 16, Fig. 1a–b; Text-fig. 16)

1848. Nautilus vastus m.; Kner, p. 6, pl. 1, fig. 1a-c.

1889. Nautilus dekayi Morton; Griepenkerl, pl. 10, fig. 4.

1956. Eutrephoceras vastus (Kner, 1850); Kummel, p. 343

1960. Eutrephoceras vastum (Kner, 1850); Wiedmann, p. 158, pl. 21, figs A-B.

1974. Nautilus dekayi Morton, 1834; Geinitz, pl. 32, fig. 4-5

1975. Eutrephoceras vastum (Kner, 1850); Shimansky, p. 72, Text-fig. 21.

TYPE: The lectotype is the specimen illustrated by Kner (1848; pl. 6, fig. 1a–c) from the lower Maastrichtian, Nahoryany, western Ukraine, as designated herein.

MATERIAL: 63 specimens: two from Bochotnica (VIII Mc-573, 574a); two from Dziurków (VIII Mc-487/1–2); 17 from Hrebenne (ZPAL N.III/8, 13, 72, 74, 77, 86–87, 90, 103, 105, 107, 109, 112, 114, 130, 213–214); one from Janowiec (VIII Mc-631); three from Kamień (VIII Mc-494–495, 497); four from Kazimierz Dolny (MUZ PIG 13.II.479, VIII Mc-539; ZPAL N.III/147, 368); two from Kłudzie (VIII Mc-489/1–2); one from Krasnobród (ZPAL N.III/219); one from Krępa Górna (MUZ PIG 12.II.1081); 12 from Nahoryany (PZ-K-65, 321, 1774, 1776–1777, 1787/1, 1788/1; GBA 2016/058; NHMW 2018/0327/0001–0002, 1848/0002/0009, 1848/0002/0014); six from Nasiłów (MKD/MP-32; MGWGUW 009624; VIII Mc-554, 563, 651, 696); one from Okale (VIII Mc-514/1); three from Piotrawin (VIII Mc-450, 457; ZPAL N.III/350); one from Raj North (ZPAL N.III/244); one from Sadkowice (MUZ PIG 12.II.1055); two from Solec (VIII Mc-699–700); two from Wierzchoniów (VIII Mc-666–666/1); one from Wojszyn (VIII Mc-608); and two from Wylagi (VIII Mc-667–668).



Text-fig. 16. Reconstruction of the adult shell of *Eutrephoceras vastum* (Kner, 1848), based mostly on the specimen NHMW 2018/0327/0002 (Pl. 13, Fig. 3a–b), lower Maastrichtian, Nahoryany, western Ukraine (Pl. 13, Fig. 3a–b), and on the type specimen figured by Kner (1848, pl. 1, fig. 1a–c), from the lower Maastrichtian, Nahoryany, western Ukraine; A – lateral, B – apertural, C, D – ventral views, E – septum in frontal view; hyponomic sinus arrowed in D.

DESCRIPTION: The studied specimens are represented by more-or-less deformed simple internal moulds, mostly phragmocones with portions of the body chamber preserved. Only one specimen, ZPAL N.III/219 from Krasnobród, retains some original aragonitic shell material. The largest available individuals are over 26 cm in maximum preserved diameter (Table 8).

The present species (Text-fig. 16) is characterized by a globular, involute, and highly depressed conch (Wb/Wh ratio of ca. 1.3) with an occluded umbilicus. The whorl section is semi-lunate, rapidly increasing in Wb and slowly increasing in Wh. In some specimens, the Wb exceeds the conch diameter (e.g., specimen ZPAL N.III/219 from Krasnobród). The flanks are convex and converge towards a broadly rounded venter without clearly defined ventrolateral shoulders. The suture line has a moderately deep saddle near the umbilical shoulder. The mould surface is generally smooth, sometimes ornamented with poorly visible growth lines. The siphuncle has a ventro-central or ventral position.

DISCUSSION: The present species is one of the most common nautilids in the studied material. It is characterized by a strongly inflated conch (Wb to maximum preserved diameter of ca. 0.8), a semi-lunate whorl section shape, and a ventro-central or ventral siphuncle position. According to Wiedmann (1960), *Eutrephoceras vastum* differs from *E. dekayi* (Morton, 1834) and *E. sphaericum* (Forbes, 1845) in the siphuncle position (sub-central in *dekayi* and *sphaericum*); from *E. indium* (d'Orbigny, 1850) and *E. darupense* (Schlüter, 1876) it differs in having a wider whorl breadth (Wiedmann 1960). Furthermore, the suture line in *E. vastum* has a characteristic deep saddle near the umbilical shoulder (see Text-fig. 16). *E. depressum* resembles the present species in general conch shape and siphuncle position, but differs in whorl section and suture shape (see above). *E. bouchardium* (d'Orbigny, 1840) is differentiated from the present species by its semi-circular whorl section and nearly straight suture.

OCCURRENCE: *Eutrephoceras vastum* is mainly known from the lower Maastrichtian of Nahoryany, western Ukraine (Kner 1848). It has also been reported from the Maastrichtian of the Donbas and Crimea, southeastern Ukraine, and Mangyshlak, Kazakhstan by Shimansky (1975). The described specimens are from the Campanian–Maastrichtian of the Middle Vistula River section, the lower Maastrichtian of Roztocze, and the lower Maastrichtian of Nahoryany, western Ukraine.

Table 8. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Eutrephoceras vastum* (Kner, 1848).

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
PZ-K-321	209	130.8 (63)	120 (57)	1.09	occluded
PZ-K-1774	165	149 (90)	11.15 (67)	12.96	occluded
PZ-K-1776	153	139.5 (91)	75 (49)	1.86	occluded
PZ-K-1777	141	125 (89)	~77 (55)	1.62	occluded
PZ-K-1787/1	92	79 (86)	66 (72)	1.19	occluded
PZ-K-1788/1	121	110 (91)	89 (73)	1.24	occluded
GBA 2016/058	~240	~137 (57)	_	-	occluded
MKD/MP-32	~262	~205 (78)	_	-	occluded
MUZ PIG 12.II.1055	_	~152.6	~111.5	~1.36	_
VIII Mc-450	45	41 (91)	24 (53)	1.7	occluded
VIII Mc-457	26	16 (61)	16 (61)	1	occluded
VIII Mc-487/1	~37.5	_	~23 (61)	-	occluded
VIII Mc-489/1	63	38 (60)	31 (49)	1.22	occluded
VIII Mc-489/2	37	21 (57)	19 (51)	1.1	occluded

VIII Mc-497	112	44 (39)	59 (53)	0.74	occluded
VIII Mc-514/1	~62.5	~38 (61)	-	—	occluded
VIII Mc-554	84	59 (70)	43 (53)	1.31	occluded
VIII Mc-563	~175	_	~105 (60)	_	occluded
VIII Mc-574a	63.5	45 (71)	39 (61)	1.15	occluded
VIII Mc-608	39	30 (77)	25 (64)	1.2	occluded
VIII Mc-666/1	19	18 (95)	10 (53)	1.8	occluded
NHMW 2018/0327/0001	~140.5	122.5 (87)	91 (65)	1.34	occluded
NHMW 2018/0327/0002	~120	~123	-	—	occluded
NHMW 1848/0002/0009	151.5	165.5	94	1.8	occluded
NHMW 1848/0002/0014	~67	~69	_	_	occluded
ZPAL N.III/8	_	74	50	1.48	occluded
ZPAL N.III/90	31	27 (87)	17 (55)	1.58	occluded
ZPAL N.III/213	230	140 (60)	155 (67)	0.9	occluded
ZPAL N.III/219	~115	126	110	1.15	occluded

Eutrephoceras sp. A (Pl. 14)

pars 1869. *Nautilus dekayi* Morton, 1834; Favre, p. 7, pl 3, figs 1a-c only. 1960. *Cymatoceras* n. sp.?; Wiedmann, pl. 17, fig. D

MATERIAL: Two specimens from Nahoryany (PZ-K-491/5 and GBA 1869/006/0005/002).

DESCRIPTION: Specimens PZ-K-491/5 and GBA 1869/006/0005/002 are small, simple internal moulds of incomplete phragmocones, measuring ca. 33 mm and 12.3 mm in maximum preserved diameter, respectively (Table 9).

In the present species, the conch is involute with a depressed and reniform whorl section (Wb/Wh ratio of ca. 1.4). The flanks are slightly rounded. The ventrolateral shoulders are rounded, and the venter is near flattened. The umbilicus is small, deep, and comprises ca. 6% of the maximum preserved diameter; the umbilical wall is steep and and the umbilical shoulder is rounded. The conch surface bears poorly visible, transverse fold-like ribs (Pl. 14, Figs 1a, 2a). The suture line is slightly sinuous with a small saddle near the umbilical shoulder and a shallow lateral lobe. The siphuncle position lies between the center and venter (see Pl. 14, Fig. 2a).

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
PZ-K-491/5	33	26 (79)	18 (55)	1.44	2 (6)
GBA 1869/006/0005/002	12.3	12.3 (1)	8.8 (71)	1.39	_

Table 9. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Eutrephoceras* sp. A.

DISCUSSION: According to the original definition of Hyatt (1894, p. 555), representatives of the genus *Eutrephoceras* have a generally smooth conch after the nepionic stage. Nevertheless, some eutrephoceratid species show ribs or fold-like undulations on the external conch surface – for example, *E. bouchardium* (d'Orbigny, 1840), *E. subplicatum* (Steinmann, 1895), and *E. antarcticum* (Cichowolski *et al.*, 2005) as a variable intra-specific character (e.g., Miller 1947; Cichowoski *et al.* 2005). The present species seems to belong to the "ribbed" eutrephoceratid group as well.

The general conch proportions, whorl section shape, small umbilicus, and suture line pattern allow this material to be assigned to *Eutrephoceras* Hyatt, 1894. One of the specimens studied here, GBA 1869/006/0005/002, was originally identified as *Nautilus dekayi* by Favre (1869, pl. 3, fig. 1a–c), and later referred by Wiedmann (1960) to *Cymatoceras* n. sp., likely due to the presence of fold-like ribs.

The Nahoryany material resembles *E. dekayi* (Morton, 1834) in general conch shape and suture line. However, *Eutrephoceras* sp. A is ornamented with transversal fold-like ribs, while the post embryonic-conch surface of *E. dekayi* is generally smooth (see above).

E. subplicatum and *E. antarcticum* specimens from the Campanian–Maastrichtian of the James Ross Basin, Antarctica were described by Cichowolski *et al.* (2005). They are similar in general conch shape and the presence of ribbed ornamentation in later growth stages, but differ in suture line shape (straighter in *E. subplicatum* and more sinuous in *E. antarcticum*) and siphuncle position (more ventral in both species). Moreover, *E. antarcticum* differs from the present species in that it possesses a slight ventral depression.

Eutrephoceras sp. B (Pl. 15, Fig. 1a–c)

MATERIAL: One specimen, MUZ PIG 12.II.1050, from Wyględów.

DESCRIPTION: Specimen MUZ PIG 12.II.1050 is an incomplete internal mould comprising the adult body chamber with the last several septa of the phragmocone, measuring ca. 163 mm in estimated diameter. Coiling appears to have been involute, with a depressed and semicircular whorl section (Wb/Wh ratio of \sim 1.21). The umbilicus is missing, but probably was originally small or closed. The flanks and ventrolateral shoulders are rounded. The venter is generally rounded, and the suture line is straight. The conch surface is smooth. The siphuncle position is uncertain.

DISCUSSION: According to the original label, specimen MUZ PIG 12.II.1050 was assigned to *Nautilus* sp., but characteristic features such as the general conch shape, the smooth surface, and the simple suture line indicate that it belongs to *Eutrephoceras* Hyatt, 1894.

At first glance, the present form is most similar to *Eutrephoceras sublaevigatum* (d'Orbigny, 1850) from the Turonian of the Elbtal Group, Saxony, Germany (Wilmsen 2016b, p. 61, Text-fig. 2b, pl. 1–3, 4a–b) in conch shape, whorl section, straight suture shape, and the small umbilicus. However, considering the poor preservation of the studied specimen and the considerable differences in stratigraphic position, the present specimen is left in open nomenclature as *Eutrephoceras* sp. B.

Eutrephoceras sp. A – which is a juvenile part of an individual – clearly differs from the present specimen in its reniform whorl section, more sinuous suture line, and the presence of transverse ornamentation.

OCCURRENCE: Upper Campanian/lower Maastrichtian, Wyględów, west of the Middle Vistula River section.

Eutrephoceras sp. C (Pl. 16, Fig. 2a–b)

MATERIAL: One specimen from Nahoryany (PZ-K-1786/1).

DESCRIPTION: Specimen PZ-K-1786/1 is an internal mould comprising the phragmocone and a small part of the body chamber, measuring approximately 105 mm in maximum preserved diameter (Table 10). The coiling is involute. The whorl section is slightly depressed and subquadrate. The umbilical shoulder is somewhat overlapping, and the umbilical wall is narrowly rounded. The umbilicus is closed. The flanks are generally flat. The ventrolateral shoulders and venter are rounded. The suture line is slightly sinuous, with a very shallow lateral lobe. The conch surface is smooth. The siphuncle position is unknown.

Table 10. Measurements (in mm; in brackets % of D_{max}) of the studied specimen of *Eutrephoceras* sp. C.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
PZ-K-1786/1	105	~64 (61)	69 (66)	~0.93	3.5 (3)

DISCUSSION: *Eutrephoceras* sp. C, like the previously described *Eutrephoceras* sp. A, originates from the lower Maastrichtian of Nahoryany. Nevertheless, there are distinct differences in the conch morphology of these forms, enabling their separation. In particular, *Eutrephoceras* sp. C displays a more compressed whorl section and a higher whorl expansion rate compared to *Eutrephoceras* sp. A. Furthermore, *Eutrephoceras* sp. C lacks ribs. *Eutrephoceras* sp. C differs from *Eutrephoceras* sp. B in having a less inflated and subquadrate whorl, as well as in its suture pattern.

OCCURRENCE: Lower Maastrichtian of Nahoryany, western Ukraine.

Eutrephoceras spp.

(not illustrated)

MATERIAL: 108 specimens: one from Basonia (VIII Mc-669); nine from Chełm (ZPAL N.III/258–259, 264, 267, 276–277, 282, 353, 355); six from Ciszyca Górna (VIII Mc-382/3– 5, 384, 396, 407/3); three from Dorotka (VIII Mc-313, 422, 688); three from Dziurków (ZPAL N.III/342–343, 376); 19 from Hrebenne (ZPAL N.III/76, 78–79, 88–89, 91, 97–98, 100, 102, 106, 108, 113, 116–117, 157–158, 211–212); two from Kamień South (ZPAL N.III/173–174); four from Kazimierz Dolny (VIII Mc-529/2, 545–546, 550/2); one from Kłudzie (VIII Mc-490); two from Łopoczno (VIII Mc-360 and 665); one from Marianów (MUZ PIG 12.II.1052/3); four from Nahoryany (PZ-K-491/7, 491/9, 493/1–2); three from Nasiłów (VIII Mc-557/2, 561; ZPAL N.III/143); one from Olbrachcice (ZPAL N.III/20); 25 from Piotrawin (MUZ PIG 12.II.1046, 1061/1–2, 1061/4–7, 1064; VIII Mc-438, 440/1–2, VIII Mc-441/1–2, 442/1–2, 443, 446, 456, 462/1–2, 262/3, 472/3; ZPAL N.III/235–236, 238); one from Potelych (ZPAL N.III/44); four from Raj (VIII Mc-349, 351/1–2, 352, 352/1– 352/2); one from Rzeżuśnia (ZPAL N.III/345); five from Solec (MUZ PIG 12.II.1060, 1063; VIII Mc-475, 482, 484); one from Sulejów (VIII Mc-676); one from Wałowice (VIII Mc-289bis); two from Wola Piasecka (ZPAL N.III/254, 256); one from Wólka Maziarska (MUZ PIG 12.II.1058).

DESCRIPTION AND DISCUSSION: All specimens are strongly deformed, poorly preserved internal moulds of various conch fragments which match the definition of *Eutrephoceras* Hyatt, 1894 with regards to their preserved morphology, but are indeterminate at the species level.

OCCURRENCE: Upper Campanian-Maastrichtian of Poland and western Ukraine.

Nautilidae indet. gen. et sp. nova? (Pls 17, 18; Text-fig. 17)

MATERIAL: Three specimens: two from Nasiłów (ZPAL N.III/220–221) and one from Parchatka (ZPAL N.III/375).



Text-fig. 17. Reconstrution of the adult shell of Nautilidae indet. gen. et sp. nova?; based on specimens ZPAL N.III/220 (Pl. 17, Fig. 1a–d) and 221 (Pl. 18, Fig. 1a–f), both from the Danian, Nasiłów, Poland. A – lateral, B – apertural, C, D – ventral views; ocular and hyponomic sinuses are arrowed in A and D, respectively.

DESCRIPTION: The present material consists of three simple internal moulds which retain white powdery remnants of the original shell. All specimens are laterally crushed, incomplete phragmocones with portions of the body chamber, with estimated diameter of the complete specimens ca. 240 mm (ZPAL N.III/240) and 174 mm (ZPAL N.III/375). The species attains over 24 cm in maximum preserved diameter (Table 11).

The original conch coiling of the present species (Text-fig. 17) appears to have been moderately evolute, with a strongly compressed and subtrapezoidal whorl section (Wb/Wh ratio of ca. 0.74). The flanks are flat and convergent towards the narrow, slightly convex venter. As judged from the curvature of the dorsal parts of the body chambers (Pl. 18, Fig. 1d, e), the umbilicus appears to be open and relatively wide (see Text-fig. 17). The umbilical shoulder is rectangular, and the umbilical wall is narrow and almost parallel to the coiling axis. The suture line shows a deep lateral lobe. The conch surface is generally smooth, with only poorly visible growth lines on lateral flanks (e.g., specimen ZPAL N.III/221). The siphuncle has a ventral position (Pl. 17, Fig. 1c).

Table 11. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of Nautilidae indet. gen. et sp. nova?.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
ZPAL N.III/220	240	55 (23)	100 (42)	0.55	_
ZPAL N.III/221	~ 171 in	_	_	_	_
	length				
ZPAL N.III/375	175	-	99 (56)	_	_

DISCUSSION: The present specimens were previously treated as *Teichertia similis* Shimansky, 1959 by Malchyk (2018), a species known from the Danian of Crimea, southern Ukraine and Kazakhstan (Shimansky 1959). However, additional examination of specimen ZPAL N.III/220 reveals that the siphuncle has a clearly ventral position, typical for the family Nautilidae Blainville, 1825, while in *T. similis* (Hercoglossidae Spath, 1927) the siphuncle is located closer to the dorsum. In addition, *T. similis* has a narrow umbilicus and a complex suture pattern, showing a narrow ventral saddle and wide lateral lobe.

In comparison with the other nautilid species described from Campanian–Danian deposits of Poland and western Ukraine, this material differs by having a strongly compressed and sub-trapezoidal whorl and a sinusoidal suture pattern, which renders the taxonomic assignment of this material uncertain.

OCCURRENCE: Danian, Middle Vistula River section, Poland.

Family Cymatoceratidae Spath, 1927

REMARKS: The family Cymatoceratidae was originally established by Spath (1927), with Cymatoceras Hyatt, 1884 as the type genus, to encompass all known "ribbed" post-Triassic nautilids. However, the validity of grouping all ornamented genera into a single family has been questioned by various authors who suggested that ribbing could have evolved independently in unrelated nautilid lineages (e.g., Tintant and Kabamba 1983; Tintant 1989, 1993). Recently, Chirat and Bucher (2006) proposed that only taxa with external ornamentation composed of overlapping tile-shaped lamellae of the outer prismatic layer should be assigned to the cymatoceratid clade. This ornamentation has been previously observed in the genera Cymatoceras Hyatt, 1884, Eucymatoceras Spath, 1927, Neocymatoceras Kobayashi, 1954, and Epicymatoceras Kummel, 1956 (Chirat and Bucher 2006; Malchyk et al. 2017). Many other nautilid taxa that were traditionally assigned to the Cymatoceratidae on account of their ribbing patterns have different external ornament styles, which may include "normal" ribs, fasciculate growth lines, and divaricate imbrication (Malchyk et al. 2017). The criterion proposed by Chirat and Bucher (2006) enables "true" cymatocerases to be distinguished from "false" cymatocerases. However, since the revision of nautilid taxonomy is beyond the scope of the present work, the generic name Cymatoceras is retained for these forms to be consistent with the classification scheme proposed in the Treatise on Invertebrate Paleontology (Kummel, 1964). The genus is put in brackets (as "Cymatoceras") for these species which may be safely identified as "false" cymatocerases based on inferences regarding their external ornament.

Genus Cymatoceras Hyatt, 1884

TYPE SPECIES: *Nautilus pseudoelegans* d'Orbigny, 1840 (p.70, pl. 8) by the original designation of Hyatt (1884, p. 301).

DIAGNOSIS: "Involute, generally subglobular with rounded whorl section but this feature variable; degree of involution varying from occluded to slightly evolute conch; suture only

slightly sinuous; position of siphuncle variable; surface with conspicuous ribs that cover whorl sides and venter" (Kummel 1964, p. K453).

Cymatoceras intrasiphonatum (Łopuski, 1912) (Pls 19–24; Text-figs 18–21)

1912. Nautilus patens Kner var. intrasiphonata mihi; Łopuski, p.185, pl. 1, figs 5-6.

- 1989. Cimomia intrasiphonata (Łopuski); Błaszkiewicz, p. 261, pl. 164, fig. 3
- 2016. ?*Cymatoceras intrasiphonatus* (Łopuski, 1912); Machalski, Vellekoop, Dubicka and Peryt, p. 212, figs 5a-b.

TYPE: The lectotype is the original of Łopuski (1912; pl. 1, figs 5–6) from the upper Maastrichtian, probably from Kazimierz Dolny, Poland.

MATERIAL: 215 specimens: 10 from Bochotnica (MZ VIII Mc-574/b, 585, 586/1, 586/4, 586/6, 589/1-2, 593, 606, 639); six from Chełm (ZPAL N.III/261, 268, 283-285, 370); three from Janowiec (MWGUW 003601, 003604; VIII Mc-628); one from Janów (ZPAL N.III/38); 32 from Kazimierz Dolny (MKD MP-2, 4, 63/1-2, 1056/P, 1058/P, 1059/P, 1095/P, 1146/P, 1147/P; MUZ PIG 13.II.481; MZ VIII Mc-528, 529/1, 533, 542, 547/1, 551; MWGUW 002360, 002370; ZPAL N.III/118-119, 133, 149-150, 165, 208-209, 271, 314, 316, 320, 365, 366); 13 from Klimusin (ZPAL N.III/28-37, 167-168 and 170); one from Lechówka (ZPAL N.III/272); one from Metów (ZPAL N.III/39); 93 from Nasiłów (MKD/MP-10, 24, 41-42, 64-68, 72, 180, 239, 279; VIII Mc-557/1, 557/3, 559/1-2, 560, 562, 565-566, 607, 653, 694; ZPAL N.III/120-126, 129, 134-135, 137, 139, 142, 144-45, 166, 179(1)-204(1), 206, 216-217, 223, 225, 231, 248, 315, 317–319, 321, 327(3)–336(3), 349, 361, 363–364 and 367); five from Okale (MZ VIII Mc-512, 514/2-514/3, 515-516); one from Piotrowice (ZPAL N.III/310); six from Rejowiec (ZPAL N.III/3-5, 27, 222 and 226); two from Stryjno (MZ VIII Mc-673/2-3); one from Wierzchoniów (MZ VIII Mc-568); 38 from Wola Piasecka (ZPAL N.III/151, 205, 228–229, 250–252, 273–275, 286, 288(2)–308(2), 337, 354, 369, 371– 372); and two from Wylagi (MZ VIII Mc-610/1-2).



Text-fig. 18. Reconstruction of the adult shell of *Cymatoceras intrasiphonatum* (Łopuski, 1912), based mostly on the specimens MKD MP 67 (Pl. 20, Fig. 2a–c), ZPAL N.III/120 (Pl. 24, Fig. 1a–d), ZPAL N.III/124 (Pl. 24, Fig. 2a–d), and ZPAL N.III/349 (Text-fig. 20), all from the upper Maastrichtian, Nasiłów, Poland. A – lateral, B – apertural, C, D – ventral views, E – septum in frontal view; ocular and hyponomic sinuses arrowed in A and D, respectively.

DESCRIPTION: The present material consists of simple and composite internal and external moulds in various states of preservation and completeness, ranging from septate parts of the shell (phragmocones) to more complete adult individuals with preserved parts of the body chamber. The largest available, almost complete individuals attain over 18 cm in maximum preserved diameter (Table 12).
In the present species (Text-fig. 18), the coiling is relatively evolute with a wide umbilicus, composing ca. 15% of the maximum preserved diameter. The umbilical wall and umbilical shoulder are narrowly rounded. Shell proportions vary among specimens, with no discernible differences between stratigraphically distinct "populations" in the Kazimierz Opoka (Text-fig. 19). There is variation in conch proportions between ontogenetic stages of the shell. At earlier growth stages, typically represented by phragmocones, the whorls are narrow with an angular ventrolateral shoulder and an occasionally nearly flat venter (Pl. 19, Fig. 2a; Pl. 20, Fig. 1a). At later growth stages, typically represented by specimens with preserved body chamber parts, the whorls become more inflated with a rounded ventrolateral shoulder (Pl. 24, Figs 1a-b, 2a-b). Shell ornamentation also changes with ontogeny. Earlier growth stages (usually phragmocones), show distinct sigmoidal narrow ribs with a deep sinus on the venter (Pl. 19, Figs 1a-d, Fig. 2a; Text-figs 20-21). The ribs are up to 1 mm wide and are separated by much wider interspaces. The ribbing pattern is only occasionally discernible on internal moulds (e.g., Pl. 19, Fig. 2a-c), but is clearly visible on a particularly wellpreserved composite internal mould of a phragmocone and its external mould counterpart (Text-fig. 20A-B). Another remarkable specimen, an internal composite mould of a phragmocone (Text-fig. 21A), reveals strong ornament in the attachment scar of a pycnodonteinae oyster, the left valve of which reveals details of the nautild ornamentation as preserved on the attachment scar (Text-fig. 21B-C). Both individuals indicate that the ornamentation of Cymatoceras intrasiphonatum was - at earlier growth stages - composed of overlapping tile-shaped "lamellae", similar to those previously observed in Epicymatoceras (Malchyk et al. 2017), and thus matching the new definition of the genus as proposed by Chirat and Bucher (2006). Although such observations are hindered by the often poor preservation of the studied moulds, it seems that the ribs gradually efface near the end of the phragmocone (at a diameter of approximately 10-12 cm) so the body chamber is covered by delicate growth lines only. The suture line shows a small, distinct saddle near the umbilical shoulder, a broad lateral lobe, and a wide ventral saddle. The siphuncle position is dorsal.



Text-fig. 19. Scatter plots showing relationships between maximum conch diameter (D) and umbilical diameter (U), whorl breadth (Wb) and whorl height (Wh), and maximum conch diameter (D) and whorl breadth (Wb) in selected specimens of *Cymatoceras intrasiphonatum* (Łopuski, 1912).



Text-fig. 20. Ornamentation of *Cymatoceras intrasiphonatum* (Łopuski, 1912), ZPAL N.III/349, upper Maastrichtian, Nasiłów, Poland. A – external mould in negative relief. B – composite internal mould of the same individual.

DISCUSSION: The species was originally diagnosed by Łopuski (1912) as a variety of *Nautilus patens* Kner, 1848 based on material from Kazimierz Dolny, Polanówka, and Chełm – that is, various upper Maastrichtian levels. The only specimen figured by Łopuski (1912, pl. 1, figs 5–6), which is designated as the lectotype herein, appears to be obliquely deformed by compaction, and seems to represent an incomplete phragmocone with strong ribbing (the poor quality of the illustration does not enable the author to discern suture lines).

Lopuski (1912) made particular reference to the material described and illustrated by Favre (1869) and Schlüter (1876) from the upper Campanian to lower Maastrichtian of western Ukraine and Germany, respectively. However, Lopuski's specimens are not conspecific with the stratigraphically lower "*Cymatoceras*" patens, and represent a younger, distinct species. More specifically, *Cymatoceras intrasiphonatum* differs from "*C*." patens in the clearly dorsal position of the siphuncle and the more sinuous suture line, showing a deep saddle near the umbilical shoulder (Lopuski 1912; Wilmsen and Esser 2004; Machalski *et al.* 2016). It should be noted that the "*Nautilus patens* Kner var. *intrasiphonata*" of Lopuski (1912) was assigned to *Cimomia* by Błaszkiewicz (1989). However, the presence of imbricated radial ribbing observed in the specimens illustrated in Text-figs 20–21 points to their assignement to the genus *Cymatoceras*, as defined by Chirat and Bucher (2006).



Text-fig. 21. Ornamentation of *Cymatoceras intrasiphonatum* (Łopuski, 1912), ZPAL N.III/369, upper Maastrichtian, Wola Piasecka, Poland, in different views and magnification. A – internal, partially composite mould with compactionally depressed area (marked), corresponding to the attachment surface of the oyster figured in B and C; note the distinctive ornamentation of the shell surface. B, C – external ornament structure imprinted as negative relief on the attachment scar of encrusting oyster *Pycnodonte (Gryphaea) vesicularis* (Lamarck, 1806).

Cymatoceras intrasiphonatum is the most common nautilid in the studied material. It occurs abundantly in Kazimierz Dolny and the Lublin area, occasionally forming storm-generated accumulations composed of partially imbricated and fragmented conchs ("nautilid nests"; see Machalski and Malchyk 2019). Two "nests" are known from Nasiłów (ZPAL N.III/179(1)–204(1) and ZPAL N.III/327(3)–336(3)) and one from Wola Piasecka (ZPAL N.III/288(2)–308(2)).

OCCURRENCE: Upper Maastrichtian of Poland (Łopuski 1912; Machalski *et al.* 2016; Malchyk, 2019; this study). There are no records of this species outside Poland; it appears endemic to the present-day area of Middle Vistula River section and Lublin Upland.

Wb (%) Wh (%) Specimen Wb/Wh U (%) Dmax MKD/MP-4 169 73 (43) 93 (55) 0.78 26 (15) MKD/MP-24 134 48 (36) 88 (66) 0.54 20(15) MKD/MP-41 ~149 _ ~23 (15) _ _ MKD/MP-42 140 42 (30) 80 (57) 0.52 19(14) 102.5 MKD/MP-63/2 ~168 69 (41) 0.67 20(12) (61) ~109 MKD/MP-64 ~216 126 (58) ~0.86 26.5 (12) (50) MKD/MP-65 ~98 (56) ~175 ~78 (45) 0.79 _ ~96.5 MKD/MP-66 ~182 ~62 (34) 0.64 35 (19) (53) MKD/MP-67 85 (54) 156 56 (36) 0.65 24 (15) MKD/MP-68 127.5 48 (38) 71 (56) 0.67 24 (19) 57 0.78 MKD/MP-180 23.5 (41) 30 (53) 14 (25) ~21.5 MKD/MP-1056 ~160 ~88 (55) _ _ (13) MWGUW 002360 133 55 (41) 71.5 (54) 0.76 18(14) MWGUW 003604 155 44 (28) 93 (60) 0.47 23.5 (15) VIII Mc-515 120 49 (41) 74 (62) 0.66 _ VIII Mc-551 121.5 40 (33) 54.5 (45) 15 (12) 0.73 VIII Mc-559/1 100.5 36.4 (36) 78 (78) 0.46 24 (24) VIII Mc-560 165 59 (36) 89 (54) 0.66 23 (14) VIII Mc-562 ~80 ~66 (82) — _ ~12(15) VIII Mc-566 156 50 (32) 78 (50) 0.64 24 (15) VIII Mc-568 ~153 _ ~82 (54) _ 21 (14) VIII Mc-593 117.5 40 (34) 65 (55) 0.61 18(15) VIII Mc-673/2 59 16 (27) 30 (51) 0.53 8 (13) ~ 19.8 VIII Mc-694 128 51 (40) 67 (52) 0.76 (15)ZPAL N.III/32 40 17 (43) 24 (60) 0.71 ~5 (10) ZPAL N.III/33 35 47 0.74 ____ — ~11 (17) ZPAL N.III/34 ~64 21 (33) 32 (50) 0.65 ZPAL N.III/35 121 37 (31) 65 (54) 0.57 24 (20) ZPAL N.III/37 42 4 (9) 14 (33) 25 (60) 0.56 ZPAL N.III/118 135 46 (34) 71 (53) 19(14) 0.65

Table 12. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Cymatoceras intrasiphonatum* (Łopuski, 1912).

ZPAL N.III/119	122	38 (31)	68 (56)	0.55	16 (13)
ZPAL N.III/120	149	55 (37)	72 (48)	0.76	23 (15)
ZPAL N.III/121	140	53 (38)	78 (56)	0.68	18 (13)
ZPAL N.III/122	160	~59 (37)	97 (61)	~0.96	21 (13)
ZPAL N.III/123	80	30 (38)	40 (50)	0.07	_
ZPAL N.III/124	185	78 (42)	94 (51)	0.83	23 (13)
ZPAL N.III/125	142	58 (41)	79 (55)	0.73	19 (13)
ZPAL N.III/126	~125	39 (31)	72 (58)	0.54	~19 (15)
ZPAL N.III/129	56	16 (29)	26 (46)	0.62	9 (16)
ZPAL N.III/134	_	60	68	0.88	_
ZPAL N.III/135	61	20 (33)	36 (59)	0.55	12 (20)
ZPAL N.III/137	54	17 (31)	29 (72)	0.59	9 (16)
ZPAL N.III/145	145	43 (30)	79 (54)	0.54	25 (17)
ZPAL N.III/149	41	15 (37)	22 (54)	0.68	_
ZPAL N.III/150	37	_	22 (59)	_	4 (11)
ZPAL N.III/151	_	69	73	0.95	_
ZPAL N.III/165	~46	_	~25 (54)	_	_
ZPAL N.III/166	~150	56 (37)	_	_	_
ZPAL N.III/167	_	44	80	0.55	_
ZPAL N.III/168	137	50 (36)	74 (54)	0.68	18 (13)
ZPAL N.III/182(1)	~160	~70 (44)	~80 (50)	0.87	~30 (19)
ZPAL N.III/183(1)	_	69	66	1.04	_
ZPAL N.III/206	_	76	120	0.63	_
ZPAL N.III/208	~175	_	~101 (58)	_	~20 (11)
ZPAL N.III/209	173	_	90 (52)	_	31 (18)
ZPAL N.III/216	~42	~19 (45)	_	_	_
ZPAL N.III/217	66	30 (45)	35 (53)	0.86	14 (21)
ZPAL N.III/222	181	_	104 (57)	_	_
ZPAL N.III/223	_	75	72	1.04	_
ZPAL N.III/225	150	61 (41)	76 (51)	0.8	23 (15)
ZPAL N.III/226	185	_	97 (52)	_	_
ZPAL N.III/229	160	68 (43)	86 (54)	0.79	_
ZPAL N.III/231	~92	~44 (48)	~54 (59)	0.81	_
ZPAL N.III/248	156 in length	78	88	0.88	_
ZPAL N.III/250	127	_	77 (61)	_	22 (17)
ZPAL N.III/271	132	~50 (38)	69 (52)	0.72	15 (11)
ZPAL N.III/272	107		55 (51)	_	13(12)
	107	_	55 (51)		15 (12)

ZPAL N.III/310	_	40	42	0.95	—
ZPAL N.III/314	~56	~28 (50)	~24 (43)		_
ZPAL N.III/315	57	_	29 (51)	_	10 (18)
ZPAL N.III/317	66	20 (30)	36 (55)	0.55	9 (14)
ZPAL N.III/318	147	59 (40)	68 (46)	0.87	18 (12)
ZPAL N.III/319	131	39 (30)	78 (5)	0.5	20 (15)
ZPAL N.III/320	187	~65 (35)	96 (51)	~0.68	29 (16)
ZPAL N.III/321	_	59	94	0.63	_
ZPAL N.III/327(3)	120	63 (53)	64 (53)	0.98	_
ZPAL N.III/361	35	14 (40)	21 (60)	0.66	~3 (8)
ZPAL N.III/363	119	49 (41)	64 (54)	77	_
ZPAL N.III/364	127	~72 (67)	74 (5)	0.97	14 (11)
ZPAL N.III/366	~165	_	~84 (51)	_	~27 (16)
7DAL NIHI/267	250 in	80	122	0.72	24
LFAL 1N.111/30/	length	07	122	0.75	<i>2</i> 4
ZPAL N.III/371	52	~15 (29)	26 (50)	~0.58	11 (21)

Cymatoceras loricatum (Schlüter, 1876) (Pl. 25)

- 1876. Nautilus loricatus sp. n; Schlüter, p. 180, pl. 51, figs 1–2.
- 1889. Nautilus loricatus Schlüter, 1876; Griepenkel, p. 398, pl. 9, figs 4-5.
- 1956. Cymatoceras loricatus (Schlüter, 1876); Kummel, p. 425.
- 1999. *Cymatoceras loricatus* (Schlüter, 1876); Wittler Roth and Legant, p. 44, Text-figs 51a-b, 54a-b.
- 2004. *Cymatoceras loricatum* (Schlüter, 1876); Wilmsen and Esser, p. 493, pl. 1, figs 1ab, 2.
- 2010. Cymatoceras loricatum (Schlüter, 1876); Kin, p. 54, fig. 29A-F.
- 2013. *Cymatoceras loricatum* (Schlüter, 1876); Wilmsen, Säbele and Schneider, p. 102, pl. 5, figs 1–6.

TYPE: The holotype is specimen GM-B 99 (GM-B-45) (Schlüter 1876; pl. 51, fig. 1–2) from the "Mucronaten-Kreide" (lower upper Campanian, belemnite *Belemnitella mucronate* Zone) at Haldem (Stemweder Berg), near Osnabrück, Germany (Frank, 2014).

MATERIAL: Seven specimens: one from Hrebenne (ZPAL N.III/73); four from Piotrawin (MKD/MP-182, 360, 638 and 641); one from Przedmieście Dalsze (MUZ PIG 12.II.1047); and one from Wałowice Kolonia (ZPAL N.III/17).

DESCRIPTION: The available material is represented by deformed internal and external moulds, representing phragmocones and body chamber fragments. The largest available individuals attain over 21 cm in maximum preserved diameter (Table 13).

The present species is characterized by an involute, moderately compressed conch with a wide, broadly rounded venter. The flanks are slightly convex. The ventrolateral shoulders seem to be broadly rounded. The umbilicus is very narrow, with rounded umbilical walls and shoulders. The suture line is weakly sinuous and shows a small saddle near the umbilical shoulder, a shallow lateral lobe, and a ventral saddle. The ornamentation preserved on specimen ZPAL N.III/73 (not figured) appears only at the last stage of the phragmocone and consists of poorly expressed, almost effaced ribs. In contrast, the conch surface of specimen ZPAL N.III/17 is covered by broad, flat ribs showing a wide sinus on the venter. These ribs are up to 8 mm in width and separated by narrow grooves that are ca. 1 mm wide (Pl. 25, Fig. 1). The siphuncle position is uncertain.

Table 13. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Cymatoceras loricatum* (Schlüter, 1876).

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
MKD/MP-182	~141	64 (45)	89.5 (63)	0.71	occluded
MKD/MP-360	~155	_	_	-	~6 (4)
MKD/MP-638	215	_	~131 (61)	_	~30 (14)

DISCUSSION: The assignment of these specimens to *Cymatocera loricatum* is based on the set of morphological features and conch parameters described by prior workers (Schlüter 1876; Wilmsen and Esser 2004; Kin 2010). Schlüter (1876) established his species *Nautilus loricatus* based on a single specimen, preserved as a composite internal mould, from the upper Campanian of northwestern Germany. According to Schlüter (1876), *N. loricatus* is characterized by a very narrow or closed umbilicus, a slightly compressed whorl cross-section, a weakly sinuous suture line, a ventral siphuncle position, and characteristic ornamentation described as "imbricated armour-plate-like bands" ("*Mann kann bei derselben nich in gewohnlichen Sinne von Rippen and Furchen reden, da sie den übereinandergelegten*

Schienen eines Panzers ähnlich ist"; Schlüter 1876, p. 180). A similar imbricated ribbing pattern, resembling imbricated roofing tiles, was described by Wilmsen and Esser (2004), based on well-preserved material from the lower Maastrichtian of Kronsmoor, northern Germany. These ornamental features match the new definition of the cymatoceratid clade proposed by Chirat and Bucher (2006).

OCCURRENCE: Uppermost lower Campanian to lower Maastrichtian of Germany (Schlüter 1976: Wittler *et al.* 1999; Wilmsen and Esser 2004), and lower Maastrichtian of Poland (Kin 2010). The described material is from the middle Campanian at Wałowice Kolonia, Middle Vistula River section, Poland, and the lower Maastrichtian at Hrebenne, Roztocze, Poland.

"*Cymatoceras*" *patens* (Kner, 1848) (Pls 26, 27, Pl. 32, Fig. 1a–b; Text-figs 22, 23)

- 1848. Nautilus patens Kner, p. 7, pl. 1, fig. 2-2a.
- 1869. Nautilus interstriatus, v. Strombeck; Favre, p. 3, pl.1, figs 3-5.
- 1869. Nautilus patens Kner; Favre, p.5, pl. 2, fig. 1.
- 1876. Nautilus patens, Kner; Schlüter, p. 178, pl. 50, fig. 1-5.
- 1902. Nautilus patens Kner; Ravn, p.241.
- 1956. Cymatoceras patens (Kner, 1850); Kummel, p. 426.
- 1975. *Cymatoceras patens* (Kner, 1850); Shimansky, p. 111, Text-fig. 23a-b [reproduction of the type of Kner, 1848]
- 2002. Cymatoceras patens (Kner, 1847); Reich and Frenzel, p. 144.
- 2004. *Cymatoceras patens* (Kner, 1848); Wilmsen and Esser, p. 493, pl. 1, fig. 3; pl. 2, figs 1a–c, 2a–b; pl. 3, figs 1a–b, 2a–b, 3–4, 5a–b, 6–7; pl. 4, figs 1a–c, 2–3, 4a–b (with full synonymy).
- 2010. Cymatoceras patens (Kner, 1848); Kin, p. 55, fig. 29g-n.
- 2012. Cymatoceras patens (Kner, 1848); Jagt, p. 140, Text-fig. 82a-b.
- 2013. Cymatoceras patens; Wilmsen, Säbele and Schneider, pl. 4, fig. 1.
- 2021. Cymatoceras patens (Kner, 1848); Jagt, fig. 4a-b.

TYPE: The holotype is specimen NHMW 2004z0117/0001 from Nahoryany (lower Maastrichtian) (Text-fig. 24).

MATERIAL: 61 specimens: one from Dorotka (MUZ PIG.12.II.1069); five from Dziurków (ZPAL N.III/52, 55, 56, 131, 352); 11 from Hrebenne (ZPAL N.III/1–2, 75, 81–82, 85, 93–94, 104, 111, 356); three from Józefów (MUZ PIG 12.II.1086/1–3); two from Kamień (MUZ PIG 12.II.1065; ZPAL N.III/218); three from Kamień South (ZPAL N.III/171–172, 175); two from Krasnobród (ZPAL N.III/224, 322); one from Marianów (MUZ PIG 12.II.1052/1); two from Maruszów (MUZ PIG 12.II.1073 and 1087); five from Nahoryany (PZ-K-489/1–2, 494, 1775/2; NHMW 2004z0117/0001, type specimen of *N. patens*); 19 from Piotrawin (MKD/MP-74, 76–77, 173, 178, 212, 322, 345, 349, 368; MUZ PIG 12.II.1061/3, 1080; VIII Mc-436, 458; ZPAL N.III/159, 232–233, 240, 242); two from Potelych (ZPAL N.III/49–50); one from Przedmieście Bliższe (MUZ PIG 12.II.1085); one from Raj North (ZPAL N.III/230); one from Sadkowice (MUZ PIG 12.II.1067); and one from Strzeżów (ZPAL N.III/347).

DESCRIPTION: The species is represented by specimens with simple and composite internal moulds, which are mostly incomplete phragmocones or phragmocones with parts of the body chamber preserved. Only two specimens, ZPAL N.III/224 and 322 from Krasnobród, retain recrystallized aragonitic shell material. The largest available individuals attain over 16 cm in maximum preserved diameter (Table 15).

The present species (Text-fig. 23) is characterized by a compressed Wb/Wh ratio of 0.63 to 1.14 and a relatively evolute conch with a wide and deep umbilicus, comprising ca. 11% of the preserved diameter. The umbilical wall is steeply inclined and the umbilical shoulder narrowly rounded. The whorl cross-section is semi-ovoid, with the greatest breadth on the lower flank. The flanks are slightly convex. The ventrolateral shoulders and venter are broadly rounded. Original shell material is partially preserved on specimens ZPAL N.III/224 and 322 from Krasnobród. Their shell is around 1.8 mm in thickness, completely recrystallized, and composed of coarse calcite crystals (see Janiszewska *et al.* 2018 for detailed microstructual analysis of ZPAL N.III/224). The outer shell surface is covered by commarginal "ribs", ca. 1 mm in width, which are separated by wide interspaces covered with intervening fine lirae (see Pl. 26; Text-fig. 23). The ribs arise at the umbilical margin, forming a broad and adorally convex curve on the flank and a narrow sinus on the venter (Pl. 27, Fig. 3). The suture line is weakly sinuous and shows a weak saddle on the umbilical shoulder, a shallow lateral lobe, and a broad ventral saddle. The siphuncle has a subventral position.



Text-fig. 22. Reconstruction of the adult shell of "*Cymatoceras*" *patens* (Kner, 1848), based on the specimens ZPAL N.III/322, upper Campanian, Krasnobród, Poland (Pl. 26, Fig. 1a–c), NHMW 2004z0117/0001, lower Maastrichtian, Nahoryany, western Ukraine (Text-fig. 23), and the specimens of Wilmsen and Esser (2004, pl. 2, figs 1–2, pl. 3., figs 1–7) from the upper Campanian – lower Maastrichtian, Kronsmoor, northern Germany. A – lateral, B – apertural, C, D – ventral views, E – septum in frontal view, F – external ornament; hyponomic sinus is arrowed in D.

Table	15. Measurements	(in mm; in	n brackets	% of	D _{max})	of the	studied	specimens	of	"Cymatoceras"	patens
(Kner,	1848).										

J 1						
Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)	
PZ-K-65						-
PZ-K-489/1	117	53 (45)	69 (59)	0.77	8 (6)	
PZ-K-494	110	66 (60	58 (53)	1.14	16 (15)	
PZ-K-1775/2	~105	-	~61 (59)	_	_	
MKD/MP-74	117.5	52 (44)	81 (69)	0.64	9 (7)	
MKD/MP-173	153	~86 (56)	-	_	16 (10)	
MKD/MP-178	160	62 (39)	97 (61)	0.63	6 (3)	
MKD/MP-349	~161	~99 (61)	_	—	~11 (7)	

*holotype

MKD/MP-368	215	_	~131 (61)	_	~30 (14)
*NHMW 2004z0117/0001	~115.5	~49 (43)	~66 (57)	~0.74	~15 (13)
ZPAL N.III/49	121	—	66 (55)	_	27 (22)
ZPAL N.III/50	124	-	69 (77)	-	24 (19)
ZPAL N.III/56	~49	~28 (57)	~29 (60)	0.96	_
ZPAL N.III/104	87	-	53 (61)	-	18 (21)
ZPAL N.III/111	_	~54	54	~1	_
ZPAL N.III/175	_	33	49	0.67	_
ZPAL N.III/224	135	66 (48)	~93 (68)	~0.97	_
ZPAL N.III/230	_	60	73	0.82	_
ZPAL N.III/322	151	61 (40)	90 (60)	0.67	_
ZPAL N.III/352	76	~33 (43)	44 (58)	~0.75	-

DISCUSSION: Careful examination of original shell material partially preserved on specimens ZPAL N.III/224 and 322 from Krasnobród, and additional material from the Maastrichtian of Kronsmoor, northern Germany (specimen Shk 734, the original of Wilmsen and Esser (2004, pl. 3, fig. 5)), shows that the ornamentation of this species consists of commarginal "ribs" on the outer shell, while the external ornament of *Cymatoceras pseudelegans* (d'Orbigny, 1840), the type species of the genus *Cymatoceras* Hyatt, 1884, is composed of overlapping, tile-shaped lamellae on the outer prismatic layer (Chirat and Bucher 2006).

Considering that *patens* exhibits a distinct external ornamentation style that does not align with the new definition of the genus *Cymatoceras* and the family Cymatoceratidae proposed by Chirat and Bucher (2006), it is here referred to as "*Cymatoceras*" *patens*. It appears to belong to a different, likely new genus, which should be examined in future studies. *Nautilus interstriatus*, v. Strombeck, 1863 shares the same ornamentation pattern and shell proportions and therefore is treated as conspecific with the present species (see illustrations of *N. interstriatus* from Nahoryany in Favre 1869, pl. 1, figs 3–5).



Text-fig. 23. Holotype of *Nautilus patens* Kner, 1848. A – Specimen NHMW 2004z0117/0001, lower Maastrichtian, Nahoryany, Western Ukraine. B – Reproduction of the original figure of Kner (1848, Pl. 1, fig. 2). C – Suture line of the holotype.

OCCURRENCE: Upper Campanian to lower Maastrichtian of northern Germany (Schlüter 1876; Wolanski 1932; Reich and Frenzel 2002; Wilmsen and Esser 2004; Wilmsen, Säbele and Schneider 2013), the lower Maastrichtian of the Netherlands (Jagt 2012), Denmark (Ravn 1902), and the upper Campanian–lower Maastrichtian of Poland (Błaszkiewicz 1980; Wilmsen and Esser 2004; Kin 2010; this study) and western Ukraine (Kner 1848; this study).

"*Cymatoceras*" sp. nova (Pl. 28)

Compare:

1876. Nautilus loricatus Schlüter, p. 180, pl. 51, figs 1-2.

- 1991. *Cymatoceras loricatus* (Schlüter, 1876); Wittler, Roth and Legant, p. 44, Text-figs 51a-b, 54a-b.
- 2004. Cymatoceras loricatum (Schlüter, 1876); Wilmsen and Esser, p. 493, pl. 1, figs 1a-b, 2.

?2013. Cymatoceras cf. patens; Wilmsen, Säbele and Schneider, pl. 4, fig. 3.

MATERIAL: One specimen, ZPAL N.III/127, from Kamień South.

DESCRIPTION: ZPAL N.III/127 is an external mould of the phragmocone and a large portion of the body chamber, measuring about 185 mm in maximum preserved diameter (Pl. 26; Table 14). The coiling is involute. The whorl cross-section appears to be originally compressed with slightly convex flanks, gradually transitioning into broadly rounded ventrolateral shoulders. The venter is rounded. The small, relatively deep umbilicus, comprising around 4% of the diameter, has a broadly rounded umbilical wall. The conch surface of ZPAL N.III/127 displays sigmoidal narrow ribs of up to 1 mm width, which are separated by much wider interspaces (Pl. 26, Fig. 1). The ribs arise at the umbilical seam, transit smoothly across flanks with a broad saddle, and curve backwards at the ventrolateral shoulders, forming a shallow sinus. The suture line and the siphuncle position are not visible.

Table 14. Measurements (in mm; in brackets % of D_{max}) of the studied specimen of "Cymatoceras" sp. nova.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
ZPAL N.III/127	~185	_	~95 (51)	_	8 (4)

DISCUSSION: At first glance, the present species is similar to *Cymatoceras loricatum* Schlüter (1876) in general conch shape, its compressed whorl cross-section, and its small umbilicus; however, these species differ in their respective ornamentation patterns. In particular, *C. loricatum* has broad ribs up to 8 mm width, separated by very narrow grooves, whereas specimen ZPAL N.III/127 reveals fine, densely spaced ribs. The author is not aware of any similar Late Cretaceous nautilid forms, suggesting that the specimen from Kamień represents a new species closely related to *loricatum*. This proposed new species will be formally defined and described in a future publication. As described above, the outer surface of ZPAL N.III/127 consists of fine, closely spaced transversal ribs that do not match the revised definition of the cymatoceratid clade proposed by Chirat and Bucher (2006). Therefore, the specimen has been tentatively referred to "*Cymatoceras*".

OCCURRENCE: "*Cymatoceras*" sp. nova is known only from the upper Campanian of the Middle Vistula River section, Poland.

Cymatoceratidae? indet. (not illustrated)

MATERIAL: one specimen from Wyględów (MUZ PIG 12.II.1083).

DESCRIPTION AND DISCUSSION: Specimen MUZ PIG 12.II.1083 is a fragment of internal mould comprising a portion of the outer flank, and is ca. 60 mm long. The surface is ornamented by poorly expressed, almost effaced ribs. In comparison to other cymatoceratids from the study area, the ribs are rounded and seem to increase in thickness with conch diameter. Considering the fragmentary preservation of MUZ PIG 12.II.1083, its assignment to the family Cymatoceratidae is uncertain.

OCCURRENCE: Upper Campanian or lower Maastrichtian of Wyględów, Middle Vistula River section, Poland.

Genus Epicymatoceras Kummel, 1956

TYPE SPECIES: *Nautilus vaelsensis* Binkhorst van den Binkhorst, 1861 (p. 15, pl. 5, fig. 2) by the original designation of Kummel (1956, p. 439); Late Cretaceous (Maastrichtian), Vaals, the Netherlands.

DIAGNOSIS: "Widely evolute, greatly compressed; whorl section subquadrate, nearly twice as high as wide; ventral shoulders angular, venter narrow and flattened; flanks only slightly inflated; umbilical shoulders broadly arched; suture with shallow ventral lobe and shallow lateral lobe; position of siphuncle unknown; surface bearing fine sinuous ribs that curve backward toward ventral shoulders and form slight sinus on venter" (Kummel, 1956, p. K454).

> *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1861) (Pl. 29, Figs 1–3; Text-fig. 24)

1861. *Nautilus vaelsensis*, Nobis.; Binkhorst van den Binkhorst, p. 15, pl. 5, fig. 2a–c.
1876. *Nautilus vaelsensis* Binkhorst van den Binkhorst; Schlüter, p. 177, pl. 51, fig. 3.
1887. *Nautilus vaelsensis* Binkhorst van den Binkhorst; Holzapfel, p. 68, pl. 4, fig. 4.

- 1956. *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1861); Kummel, p. 439.
- 2012. Epicymatoceras vaelsense (Binkhorst van den Binkhorst, 1861); Jagt, p. 141, pl.30, figs G-H.
- 2017. *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1862); Malchyk, Machalski, Waksmundzki and Duda, p. 5, fig. 3A–B.
- 2018 Epicymatoceras vaelsense (Binkhorst van den Binkhorst, 1862); Malchyk and Machalski, p. 231, fig. 2a-c.

TYPE: The holotype is the original of Binkhorst van den Binkhorst (1862; pl. 5, fig. 2a–c) from the upper lower Maastrichtian of southern Limburg, the Netherlands.

MATERIAL: Eight specimens: four from Dziurków (ZPAL N.III/69–71, 339); one from Jawor Solecki (MUZ PIG 12.II.1079); one from Gozdawa (MUZ PIG 12.II.1082); one from Marianów (MUZ PIG 12.II.1077), and one from Strzeżów (ZPAL N.III/68).

DESCRIPTION: The best-preserved material, with distinctive traces of the ornamentation and the embryonal shell, was described by Malchyk *et al.* (2017, figs 3–5). The largest studied individuals attain over 11 cm in maximum preserved diameter (Table 16).

The material illustrated here (Pl. 29, Figs 1–3) comprises badly crushed or fragmentary specimens with characteristic ornamentation. Generally, the present species (Text-fig. 24) is a relatively evolute nautilid with a subquadrate, strongly compressed whorl cross-section, with a Wb/Wh ratio of c. 0.48. The wide umbilicus, which averages 23% of maximum preserved conch diameter (i.e., specimen ZPAL N.III/68; fig 3B in Malchyk *et al.* 2017), has a steeply inclined umbilical wall and a broadly rounded umbilical shoulder. The flanks and venter are flat. The ventrolateral shoulders are angular. The external mould surface (taphomorph 1 *sensu* Malchyk *et al.* 2017, fig. 6B) retains strongly imbricated transverse ornamentation, which consist of a series of "lamellae" separated by voids or cavities (e.g., MUZ PIG 12.II.1077 and ZPAL N.III/339 from this study, and ZPAL N.III/69–71 from Malchyk *et al.* 2017), whereas the ornamentation of the internal moulds (taphomorph 2 *sensu* Malchyk *et al.* 2017), fig. 6B) consists of sigmoidal narrow ribs up to 1 mm wide, which are separated by much wider interspaces (e.g., specimen ZPAL N.III/68 in Malchyk *et al.* 2017). The suture line is weakly sinuous and shows a shallow lateral lobe and a shallow saddle across the venter (ZPAL N.III/68; see fig. 3B in Malchyk *et al.* 2017). The siphuncle position

is uncertain. The embryonic conch has an estimated total diameter of c. 30 mm. It is delineated from the post-embryonic portion of the shell by the nepionic constriction, visible as a prominent ridge on the innermost whorl of specimen ZPAL N.III/69 (Malchyk *et al.* 2017).



Text-fig. 24. Reconstruction of the adult shell of *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1861), based mostly on the specimens ZPAL N.III/68, upper Campanian, Strzeżów (Malchyk *et al.* 2017, fig. 3B) and ZPAL N.III/69, lower Maastrichtian, Dziurków, Poland (Malchyk *et al.* 2017, fig. 3A). A – lateral, B – apertural, C, D – ventral views; hyponomic sinus is arrowed in D.

Table 16. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1861).

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
ZPAL N.III/68	~110	~24 (21)	~50 (45)	0.48	~25 (23)
ZPAL N.III/69	~93	_	51 (54)	-	~25 (26)
ZPAL N.III/71	81	_	-	_	30 (37)

DISCUSSION: The reader is referred to Malchyk *et al.* (2017) and Malchyk and Machalski (2018) for a thorough discussion of this species, as the specimens described here do not contribute any novel information due to their poor state of preservation. The characteristic ornamentation – composed of overlapping, tile shaped lamellae – firmly places the genus within the family Cymatoceratidae as redefined by Bucher and Chirat (2006).

OCCURRENCE: Upper Campanian to Maastrichtian of Belgium and the Netherlands (Binkhorst van den Binkhorst 1861, Jagt *et al.* 1998, Jagt 2012, Goolaerts and Frank 2014),

Germany (Schlüter 1876, Holzapfel 1887), Poland (Malchyk et al. 2017), and Denmark (Malchyk and Machalski 2018).

Epicymatoceras sp. (Pl. 29, Fig. 4)

MATERIAL: One incomplete internal mould from Piotrawin (specimen ZPAL N.III/309).

DESCRIPTION: ZPAL N.III/309 is a portion of the internal mould of the body chamber, ca. 108 mm long, with a partly preserved apertural margin that forms a broad shallow rounded hyponomic sinus, ca. 2 mm deep. The specimen shows a subquadrate and slightly depressed whorl cross-section, with a Wb/Wh ratio of ~1.35. The flanks are generally flat, but seem to become slightly convex towards the aperture. The ventrolateral shoulders are lightly angular; the venter is flat. The ornament consists of sigmoidal transverse ribs, forming a shallow sinus on the venter. The ribs are c. 1–2 mm in width and are separated by wider interspaces (>1 mm). They are coarser and more expressed near the apertural margin than on the venter and flanks.

DISCUSSION: The subquadrate, compressed whorl cross-section, flattened venter and flanks, and characteristic radial ribbing allow this specimen to be assigned to *Epicymatoceras*. However, it is left in open nomenclature, as it differs from other forms referred to this genus in having a much wider venter, a less compressed whorl cross-section (in the present specimen Wb/Wh is 1.35, while in *Epicymatoceras vaelsense* (Binkhorst van den Binkhorst, 1861) and *Epicymatoceras monstrum* Shimansky, 1975 Wb/Wh is 0.48 and 0.7–0.9, respectively), and more flattened flanks.

OCCURRENCE: Upper Campanian of Piotrawin, Middle Vistula River section, central Poland.

Family Hercoglossidae Spath, 1927 Genus *Angulithes* de Montfort, 1808

TYPE SPECIES: Angulithes triangularis de Montfort, 1808 (p. 7).

DIAGNOSIS: "Conch very involute, generally compressed, whorls sides slightly convex, strongly convergent, venter narrowly rounded to angular. Suture moderately sinuous with a narrowly rounded ventral saddle, a broad lateral lobe, a narrow, rounded saddle. And small lobe on the umbilical shoulder. Siphuncle small and located near the dorsum" (Kummel, 1956, p. 454).

Angulithes cf. neubergicus Redtenbacher, 1873

(Pl. 30)

Compare:

- 1858. Nautilus sowerbianus (d'Orbigny, 1840); Hauer, p. 14, pl. 1, figs 1-2.
- 1873. Nautilus neubergicus nov. sp.; Redtenbacher, p. 97, pl. 22, fig. 4.
- 2012. Angulithes (Angulithes) neubergicus (Redtenbacher, 1873); Summesberger and Zorn, pl. 7, figs. 1a–d; pl. 8, figs. 1a–d.

TYPE: The syntypes, by subsequent designation of Summesberger and Zorn (2012), are specimens GBA 1873/001/0005/01 and 1873/001/0005/02 from the Maastrichtian Gosau Group of Krampen, Neuberg (Styria, Austria). GBA 1873/001/0005/01 is the original of Redtenbacher (1873: pl. 22, fig. 4).

MATERIAL: One specimen, ZPAL N.III/160, from Kazimierz Dolny.

DESCRIPTION: ZPAL N.III/160 is a slightly deformed internal mould of the phragmocone and a portion of the body chamber, measuring ca. 108 mm in maximum preserved diameter (Table 17). It is a relative compressed involute nautilid (Wb/Wh ratio of ca. 1.22) with an ovoidal whorl section. The umbilicus is small, shallow, and comprises ca. 9% of the conch diameter. The umbilical wall is inclined and the umbilical shoulders are somewhat rounded, with a gradual transition into the lower flank. The outer flanks are generally flat, converging to a narrowly rounded venter. The suture line is slightly sinuous, with a small saddle near the umbilical shoulder and a shallow lateral lobe. The siphuncle position is uncertain.

Table 17. Measurements (in mm; in brackets % of Dmax) of the studied specimen of *Angulithes* cf. *neubergicus* Redtenbacher, 1873.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
ZPAL N.III/160	108	~75 (69)	~61 (56)	~1.22	10 (9)

DISCUSSION: *Nautilus neubergicus* was originally erected by Redtenbacher (1873, pp. 97– 98) based on two specimens from the lower Maastrichtian of Neuberg (Styria, Austria), one of which was previously referred to *Nautilus sowerbianus* by Hauer (1858). His species was synonymized with *Angulithes* (*Angulithes*) *fleuriausianus* (d'Orbigny, 1840) by Wiedmann (1960). While Redtenbacher's material indeed shows some similarity with *A. fleuriausianus*, the latter species has a more angular venter and distinctly convergent flanks, leading to a characteristic triangular whorl section shape. Furthermore, *A. fleuriausianus* is a typical Cenomanian species known from England, France, Spain, Germany, Austria, Tunisia, Israel, India, and New Mexico (after Wilmsen 2000). According to Summesberger *et al.* 2017, *A. neubergicus* differs from the co-occurring nautilid *Cimomia gosavica* (Redtenbacher, 1873) in having a slenderer conch shape and a more fastigiate venter. *Cimomia? galiciana* (Alth, 1850) from the lower Maastrichtian of Poland and Ukraine (see below) is fairly similar, but has a different suture line and a closed umbilicus.

Specimen ZPAL N.III/160, from the upper Maastrichtian of Kazimierz Dolny (Poland), resembles the type material of *Angulithes neubergicus* from the lower Maastrichtian of Austria (Redtenbacher 1873; Summesberger and Zorn 2012) in general conch shape and suture line, but differs in having a less compressed whorl section and a more rounded venter outline. Therefore, ZPAL N.III/160 is kept in open nomenclature.

OCCURRENCE: Angulithes cf. neubergicus is from the Upper Maastrichtian of Poland.

Angulithes westphalicus (Schlüter, 1872) (Pl. 31, Pl. 32, Fig. 2a-b)

- 1872. Nautilus westphalicus n. sp.; Schlüter, p. 13.
- 1876. Nautilus westphalicus (Schlüter, 1872); Schlüter, p. 175, pl. 47, figs 1–2.
- 1956. Angulithes westphalicus (Schlüter, 1872); Kummel, p. 457, Text-fig. 33/I.
- pars 1960. Angulithes (Angulithes) fleuriausianus (d'Orbigny, 1840); Wiedmann, pl. 19, fig. A, only.
- 1999. Deltoidonautilus westphalicus (Schlüter, 1872); Wittler, Roth and Legant p. 37, Text-figs 51a-b, 52.
- 2000. Angulithes westphalicus (Schlüter, 1872); Wilmsen, p. 37, pl. 3, fig. 1a-b; pl. 5, figs 6.
- ?2001. Angulithes cf. westphalicus (Schlüter, 1872); Fözy, pp. 34–36, pl. 5.

2010. Angulithes westphalicus (Schlüter, 1872); Frank, p. 490, fig. 3A-I.

2017. *Angulithes westphalicus* (Schlüter, 1872); Summesberger *et al.*, p. 10, pl. 1, figs 1–3, pl. 2, figs 1–3, pl. 3, figs 4–5, pl. 4, figs 1–3.

TYPE: The lectotype, by subsequent designation of Frank (2010), is specimen GM-B 97, the original of Schlüter (1876, p. 175, pl. 47, figs 1–2) from the lower Campanian at Dülmen (Westphalia, Germany), housed in the Goldfuss Museum, University of Bonn, Germany.

MATERIAL: 13 specimens: ten from Nahoryany (PZ-K-487/2, 491/1, 491/4, 491/8, 1786/6; NHMW 1843/0046/0004; Ukk 88a–88c and 90); and three from Piotrawin (ZPAL N.III/45, 48 and 239).

DESCRIPTION: The present species is represented by specimens with internal mould preservation, which are mostly more-or-less complete phragmocones. The largest available individuals attain over 8 cm in maximum preserved diameter (Table 18).

The present species has an involute, compressed conch with a triangular whorl. The umbilicus varies from small to closed, with a vertical umbilical wall and rounded umbilical shoulder. The flanks are convex, converging towards a narrowly rounded venter. The venter is rounded in the early stages of ontogeny and becomes rather sub-angular in outline with conch growth. The conch surface is smooth. The suture line shows a small saddle near the umbilical shoulder, following a shallow lateral lobe and a shallow ventral saddle. The siphuncle position is unknown.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
PZ-K-487/2	67	34 (51)	37 (55)	0.92	occluded
PZ-K-491/1	60	47 (78)	41 (68)	1.15	occluded
PZ-K-491/4	40	25 (63)	24 (60)	1.04	occluded
Ukk 88a	30	16 (53)	20 (66)	0.8	occluded
Ukk 90	~83	_	~53.8 (65)	_	occluded

Table 18. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Angulithes westphalicus* (Schlüter, 1872).

DISCUSSION: For a detailed discussion of the species, the reader is referred to Frank (2010). The described specimens from Nahoryany and Piotrawin are closely similar in general conch shape and suture to *Angulithes westphalicus* from the upper Campanian of northern Cantabria,

Spain, as described by Wilmsen (2000). Specimen Ukk 90 from Nahoryany – illustrated and designated as *Nautilus laevigatus* d'Orbigny by Geinitz (1849, pl. 3, figs 2a–b) – corresponds to *A. westphalicus*, not *A. fleuriausianus* (d'Orbigny, 1840) as suggested by Wiedmann (1960; see also Wilmsen 2016b).

OCCURRENCE: Upper Santonian (Wittler *et al.* 1999) to upper Campanian of Germany (Schlüter 1876), Spain (Wilmsen 2000), ?Hungary (Fözy 2001), Poland and western Ukraine (this study).

Angulithes sp. nova (Pl. 33, Fig. 1a–b, Text-fig. 25)

MATERIAL: One specimen, ZPAL N.III/42, from Potelych.

DESCRIPTION: ZPAL N.III/42 is an obliquely deformed internal mould, ca. 88 mm in maximum preserved diameter, comprising a partial phragmocone and a large portion of the body chamber with some degree of shell preservation (Table 19).

In the present species (Text-fig. 25), the coiling appears to have been involute with a slightly compressed, ovoidal whorl section. The umbilicus is narrow, with an overhanging umbilical wall. The umbilical shoulders are narrowly rounded. The flanks seem to be weakly convex, with maximum whorl width at the mid-flanks. The venter is rounded, with a keel-like ridge at its middle on the body chamber, which gradually increases in width towards the aperture; the ventrolateral shoulders are broadly rounded. The conch surface is covered by coarse, asymmetric, and somewhat flattened transversal undulations (see Text-fig. 25). The suture line shows a shallow lateral lobe. The siphuncle position is uncertain.



Text-fig. 25. Reconstruction of the adult shell of *Angulithes* sp. nov based on ZPAL N.III/42, upper Campanian, Potelych, western Ukraine (Pl. 33, Fig. 1a–b). A – lateral, B – apertural, C, D – ventral views, hyponomic sinus is arrowed in D.

Table 19. Measurements (in mm; in brackets % of D_{max}) of the studied specimen of Angulithes sp. nova.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
ZPAL N.III/42	~88	~45 (51)	~35 (40)	~ 1.28	?occluded

DISCUSSION: The assignment of this slightly deformed specimen to *Angulithes* is based on the shape of its suture and whorl section, and the presence of a remarkable ventral keel on its body chamber. Although radial ornamentation is not common in *Angulithes*, some authors have recognized coarse ribbing in representatives of this genus. For example, *A. vascogoticus* (Wiedmann 1960) from the late Campanian of Spain shows fold-like undulations at the venter and flanks, like those of *Anglonautilus* Spath, 1927 (for further discussion, see Wilmsen 2000). The Potelych material is distinctive in having a triangular whorl section and a distinct suture shape. *Angulithes galea* (Fritsch *in* Fritsch and Schlönbach 1872) from the late Turonian of Czech Republic (Frank 2010) also bears ribs, but differs from *Angulithes* sp. nova in having a depressed, obtusely sagittate whorl section and a distinct suture line.

OCCURRENCE: Upper Campanian of Potelych, western Ukraine.

Genus Cimomia Conrad, 1866

TYPE SPECIES: *Nautilus burtini* Galeotti, 1837 from the Eocene of Belgium, by original designation of Conrad (1866, p. 102).

DIAGNOSIS: "Subglobular to subdiscoidal, nautiliconic; whorls broadly rounded laterally and ventrally; umbilicus small, umbilical shoulders low, broaudly rounded; surface smooth exept for growth lines; suture with broad, shallow, rounded ventral saddle, broad, shallow lateral lobe, narrow and higher rounded lateral saddle near umbilical shoulder, and broad, rounded lobe on umbilical wall; siphuncle small, variable in position, but never marginal" (Kummel, 1964, p. K456).

> *Cimomia? galiciana* (Alth, 1850) (Pl. 33, Fig. 2a–c; Pl. 34, Fig. 2; Pl. 35, Fig. 3; Text-fig 26)

- 1850. Nautilus galicianus m.; Alth, p. 203, pl. 10, fig. 26a-b.
- 1869. *Nautilus galicianus* (Alth, 1850); Favre, p. 6, pl. 2, fig. 2. [re-illustration of the type of Alth, 1850].
- 1956. Pseudocenoceras galicianus (Alth, 1850); Kummel, p. 385.
- ?1912. Nautilus galicianus Favre (?); Łopuski, p. 188.
- 1960. Angulithes (Cimomia) galicianus (Alth, 1850); Wiedmann, p. 178, pl. 22, fig. G.
- 1975. Cimomia ?galicianus (Alth, 1849); Shimansky, p. 135, Text-fig. 26.

TYPES: The holotype is the original of Alth, 1850 (pl. 10, fig. 26) from the "Kreidemergel von Lemberg" (lower upper Maastrichtian in current meaning).

MATERIAL: 10 specimens: two from Dziurków (ZPAL N.III/340 and 351); two from Lviv (PZ-K-1767; NHMW 1862/0005/0020); two from Nahoryany (PZ-K-1775/1; NHMW 1865/0010/0542); one from Pełczyska (ZPAL N.III/346); and three from Piotrawin (MUZ PIG 12.II.1088; ZPAL N.III/177 and 207).

DESCRIPTION: The material is presented by internal moulds of phragmocones or phragmocones with the body chamber, which are more-or-less deformed due to *post portem* compaction. The largest available individual of the species is over 10 cm in maximum preserved diameter (Table 20).

Specimens range from 42 mm to 192 mm in estimated diameter. The conch is involute, discoidal, and strongly compressed, with an ovoidal whorl section that increases rapidly in height (Wb/Wh ratio ~ 0.63); the greatest width is at the middle flank. The

umbilicus is very narrow and almost closed with a rounded umbilical wall, which smoothly passes into the lower flank. The flanks are flat and converge towards the narrowly rounded and slightly convex venter, without distinct ventrolateral shoulders. The conch surface is generally smooth. However, specimen NHMW 1865/0010/0542 from Nahoryany shows coarse transversal fold-like undulations throughout ontogeny (see Pl. 34, Fig. 2), which was previously unknown in this species. The suture line shows a small saddle at the umbilical shoulder, a deep lateral lobe, and a shallow saddle near the ventrolateral shoulder. The siphuncle position is unknown.



Text-fig. 26. Reconstruction of the adult shell of *Cimomia*? *galiciana* (Alth, 1850) based on specimen NHMW 1862/005/0020 (Pl. 34, Fig. 2) and the specimen figured by Favre (1869, pl. 2, fig. 2 [re-illustration of the type of Alth, 1850]), both from the lower upper Maastrichtian, Lviv, western Ukraine; A – lateral, B – apertural, C, D – ventral views; hyponomic sinus is arrowed in D.

Table 20. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Cimomia? galiciana* (Alth, 1850).

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
PZ-K-1767	~57	-	-	-	~6 (11)
PZ-K-1775/1	102	~49 (48)	~78 (76)	~0.63	8 (10)
NHMW 1862/0005/0020	~76.5	_	~49.5 (65)	_	occluded
ZPAL N.III/207	~192	_	~117 (61)	_	occluded

DISCUSSION: The species is characterized by a discoidal, strongly compressed conch with an ovoidal whorl section (holotype: $Wb/D_{max} - 0.58$; Wiedmann 1960), that easily distinguishes it from other representatives of *Cimomia* Conrad, 1866.

In the original description of Alth (1850, p. 203), *Nautilus galicianus* is designated as a smooth nautilid that is most closely related to *N. fleuriausianus* d'Orbigny, 1840 and *N. sowerbianus* d'Orbigny, 1840, but differs from both in having a smaller conch, a smaller umbilicus size, and a flattened conch shape. Upon re-examination of Alth's type material, Favre (1869) noted that the external surface of the *N. galicianus* holotype specimens consists of rounded, muted, and evenly spaced ribs, which are clearly visible on the flanks. Both specimen NHMW 1865/0010/0542 from Nahoryany and the holotype of *N. galicianus* (Favre 1869, pl. 2, fig. 2) shows a similar transversal fold-like undulation on conch surface, which is atypical for the genus *Cimomia*. Consequently, the present species is tentatively assigned to *Cimomia* with a query.

Kummel (1956) assigned the present species to *Pseudocenoceras* Spath, 1927, but it clearly differs from representatives of *Pseudocenoceras* in having a very narrow umbilicus and the ovoidal whorl section shape.

Cimomia? galiciana shows a close affinity with *C. gosavica* (see discussion in Wiedmann 1960). Both species have a very narrow, almost closed umbilicus, and a strongly compressed and ovoidal whorl section. However, the holotype of *Nautilus gosavicus* from the Santonian Gosau Group of Neffgraben, Rußbach, Salzburg (Austria) – as figured by Redtenbacher (1873; pl. 22, figs 22a–b) and refigured by Summesberger *et al.* (2017; pl. 6, figs. 2a–d) – seems to have a more inflated conch and a straighter suture line that lacks a saddle on the umbilical shoulder.

OCCURRENCE: Upper Campanian to Maastrichtian of Poland and western Ukraine (Alth 1850; Favre 1869; Łopuski 1912 and this study).

Cimomia heberti (Binkhorst van den Binkhorst, 1861) (Pl. 34, Fig. 1a–b; Pl. 35, Fig. 2a–d; Text-fig. 27)

- 1861. *Nautilus heberti*, Nobis; Binkhorst van den Binkhorst, 1862, p. 13, pl. 5, fig. 1a–b.
- 1960. Angulithes (Cimomia) heberti (van Binkhorst, 1861); Wiedmann, p. 23, pl. 22, fig. N.

2012. Cimomia heberti (Binkhorst van den Binkhorst, 1861); Jagt, p. 139, Text-figs 76-78.

pars 2012. Cimomia sp. 1; Jagt, p. 140, Text-fig. 80, pl. 29, figs B, D-F (only).

TYPE: The species was originally introduced as *Nautilus heberti* by Binkhorst van den Binkhorst (1861) based on several specimens from Kunrade (i.e., upper Maastrichtian, Kunrade Limestone facies of the Maastricht Formation, see Jagt and Jagt-Yazykova 2012), which were probably combined by Binkhorst van den Binkhorst (1861; pl. 5, fig. 1a–b) into his original figure. The reader is referred to Jagt (2012) for discussion on the type specimen of the species, which is beyond the scope of the present work.

MATERIAL: Eight specimens: three from Hrebenne (ZPAL N.III/6, 9, 11); two from Nahoryany (PZ-K-1787/2–1787/3); one from Kazimierz Dolny (ZPAL N.III/162); one from Nasiłów (MKD/MP-33); and one from Prawiedniki (ZPAL N.III/40).

DESCRIPTION: The described material is represented by internal moulds, which consist of incomplete phragmocones and phragmocones with large portions of the body chamber. The maximum preserved diameter of the most complete adult specimen (MKD/MP-33 from Nasiłów, not illustrated here) is ca. 237 mm (Table 21).

The present species (Text-fig. 27) has an involute, globular, and depressed conch with a sub-triangular whorl section (Wb/Wh ratio ~1.25). The maximum whorl breadth is at the umbilical margin, from where the convex flanks converge towards the venter. The venter is rounded without distinct ventrolateral shoulders. The umbilicus is occluded. The conch surface is smooth. The suture line is nearly straight, with a shallow saddle near the umbilical shoulder. The siphuncle position is not visible.

Table 21. Measurements (in mm; in brackets % of D_{max}) of the studied specimens of *Cimomia heberti* (Binkhorst van den Binkhorst, 1861).

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
PZ-K-1787/2	75	61 (81)	46 (61)	1.33	5 (6)
PZ-K-1787/3	145	99 (68)	64 (44)	1.55	10 (7)
MKD/MP-33	237	116 (49)	145 (61)	0.8	_
ZPAL N.III/40	58	~42 (72)	32 (55)	~1.3	_
ZPAL N.III/162	55	_	40 (72)	_	occluded

DISCUSSION: The species *Nautilus heberti* was originally described by Binkhorst van den Binkhorst (1861) based on material from Kunrade. In view of the as yet unresolved confusion surrounding the actual type of the species (see Jagt 2012), the present identifications are based on comparison with the illustration by Binkhorst van den Binkhorst (1861: pl. 5, figs. 1a–b). The material described herein matches this illustration in general conch shape and proportion and suture line shape.



Text-fig. 27. Reconstruction of the adult shell of *Cimomia heberti* (Binkhorst van den Binkhorst, 1861), based on specimen ZPAL N.III/40 upper Maastrichtian, Prawiedniki, Poland (Pl. 34, Fig. 1a–b), and the specimen figured by Binkhorst van den Binkhorst (1861, pl. 5, fig. 1a–b), from the upper Maastrichtian, Kunrade, the Netherlands. A – lateral, B – apertural, C, D – ventral views, E – septum in frontal view; hyponomic sinus is arrowed in D.

OCCURRENCE: *Cimomia heberti* is known from the upper Maastrichtian of the Netherlands (Binkhorst van den Binkhorst 1861; Jagt 2012). A single specimen has been reported from the unit IVf-7 of the Meerssen Member of the Maastricht Formation as exposed in the Ankerpoorts-Curfs quarry, the Netherlands, which is currently interpreted as lowermost Danian (Jagt 2012, p. 139, Text-fig. 76). The specimens described herein are from the Maastrichtian of Poland and the lower Maastrichtian of western Ukraine (Nahoryany).

Cimomia sp. A (Pl. 35, Fig.1a–d)

MATERIAL: One specimen from Nasiłów (ZPAL N.III/136).

DESCRIPTION: ZPAL N.III/136 is preserved as an internal mould of the phragmocone and a large portion of the body chamber, ca. 82 in estimated diameter (Table 22).

The present species is represented by an involute, compressed shell with an ovoid whorl section, which rapidly increases in breadth (Wb/Wh ratio ca. of 0.76). The flanks are slightly convex and smoothly coverage without developing a ventrolateral shoulder into the rounded venter, showing a weak depression near the body chamber (Pl. 35, Fig. 1b). The suture line is almost straight. The siphuncle position is unknown.

Table 22. Measurements (in mm; in brackets % of D) of the studied specimen of Cimomia sp.

Specimen	D _{max}	Wb (%)	Wh (%)	Wb/Wh	U (%)
ZPAL N.III/136	82	42 (51)	55 (67)	0.76	occluded

DISCUSSION: The described specimen shows close similarities with *Cimomia gosavica* Redtenbacher (1873) from the upper Santonian of Gosau, Austria, as described by Summesberger *et al.* (2017), in having a compressed and highly ovoidal whorl section, but differs in its suture pattern. Furthermore, C. *gosavica* is a stratigraphically distinct species that ranges within the Santonian of Austria (e.g., Summesberger *et al.* 2017). The present material differs from *C.? galiciana* in having a more inflated conch and a distinct suture shape. *C. heberti* is a similar form, but has a clearly depressed conch and a more triangular whorl section.

OCCURRENCE: upper Maastrichtian, Nasiłów, Poland.

Cimomia sp. B

(not illustrated)

MATERIAL: One specimen from Potelych (ZPAL N.III/43).

DESCRIPTION AND DISCUSSION: ZPAL N.III/43 is an obliquely distorted internal mould of an incomplete phragmocone fragment. Due to its poor preservation, the specimen cannot be identified at the species level. However, its morphological features, including an involute, depressed conch and probably an originally sub-ovoidal whorl section, suggest that it can be referred to the genus *Cimomia*.

OCCURRENCE: Upper Campanian of Potelych, western Ukraine.

A summary of nautilid faunas from Poland and western Ukraine

Abundant nautilid faunas, representing the conventionally distinguished families Nautilidae (Blainville, 1825), Cymatoceratidae (Spath, 1927), and Hercoglossidae (Spath, 1927), have been recorded from the study area. In total, 26 nautilid taxa were identified, encompassing both firm species-level identifications and forms left in open nomenclature (see Text-fig. 28). For full species lists from particular localities, the reader is referred to the *Nautild-bearing localities in Poland and Ukraine* section.

Collectively, the Late Cretaceous faunas encompass 14 species: Eutrephoceras ahltenense, Eutrephoceras? aquisgranense, Eutrephoceras darupense, Eutrephoceras dekayi, depressum, Eutrephoceras quadrilineatum. Eutrephoceras Eutrephoceras vastum. *Cymatoceras* intrasiphonatum, *Cymatoceras* loricatum, "Cymatoceras" patens, Epicymatoceras vaelsense, Angulithes westphalicus, Cimomia? galiciana, and Cimomia heberti. Additionally, the Cretaceous faunas contain several forms left here in open nomenclature: Eutrephoceras sp. A, Eutrephoceras sp. B, Eutrephoceras sp. C, Eutrephoceras spp., "Cymatoceras." sp. nova, Cymatoceratidae? indet., Epicymatoceras sp., Angulithes cf. neubergicus, Angulithes sp. nova, Cimomia sp. A, and Cimomia sp. B. Only two early Paleogene taxa have been identified from Poland: Eutrephoceras dekayi and Nautilidae indet. gen. et sp. nova?.

In the **middle Campanian**, the low diversity of the nautilid fauna at least partially reflects the sparsity of available specimens. Despite this limitation, four nautilid taxa were

documented from opoka facies in the Middle Vistula River section: *Eutrephoceras ahltenense* (Schlüter, 1876), *E.* spp., *Cymatoceras loricatum* (Schlüter, 1876), and "*C*." *patens* (Kner, 1848). In addition, *E.* spp., has been recorded from opoka in the Miechów Upland.

In the **upper Campanian**, a considerable increase in diversity was driven by (i) the appearance of numerous representatives of *Eutrephoceras* Hyatt, 1894, such as *Eutrephoceras ahltenense* (Schlüter, 1876), *Eutrephoceras dekayi* (Morton, 1834), *Eutrephoceras quadrilineatum* (Favre, 1869), and *Eutrephoceras vastum* (Kner, 1848), and (ii) new genera: *Epicymatoceras* Kummel, 1956, *Angulithes* de Montfort, 1808, and *Cimomia* Conrad, 1866. Of these, *Eutrephoceras* is the dominant genus throughout the upper Campanian–Maastrichtian succession. The richest nautilid fauna comes from opoka deposits in the Middle Vistula River section, which yield 15 forms dominated by *Eutrephoceras* spp. and "*Cymatoceras*" patens. Additionally, the Roztocze Hills section yields 6 taxa, and the Miechów Upland section yields 3 forms, including the earliest stratigraphic record of the genus *Epicymatoceras* (Malchyk *et al.* 2017).

In the **lower Maastrichtian**, nautilid faunal diversity rose to 18 taxa. The most abundant nautilid fauna comes from predominantly sandy opokas exposed in the Polish and western Ukrainian Roztocze Hills, which represent relatively shallow-water, nearshore environments (Text-fig. 2; Machalski and Malchyk 2019; Walaszczyk and Remin 2015; Remin *et al.* 2022a, b). The Roztocze Hills succession yields 13 forms, dominated by *E. ahltenense*, *E. dekayi*, and "*C.*" *patens*. The Middle Vistula River section also yields a diverse nautilid assemblage (11 taxa), which is dominated by "*C.*" *patens*. In turn, the Miechów Upland fauna yields only two species: *E. dekayi* and *Cimomia*? *galiciana* (Alth, 1850).

In the **upper Maastrichtian**, nautilid diversity decreases to 12 taxa. The lower upper Maastrichtian fauna occurs in relatively deep-water chalk facies (Walaszczyk and Remin 2015; Machalski and Malchyk 2019; Remin *et al.* 2022a, b; Machalski and Bitner 2024) documented from Chełm and historically in Lviv. These strata are relatively species- and specimen-poor. A more abundant and diverse nautilid fauna comes from the upper upper Maastrichtian opoka exposed in the Middle Vistula River section and in outcrops near Lublin. There are no upper upper Maastrichtian strata in western Ukraine. The Polish sections yield 11 taxa, with faunal composition dominated by *Cymatoceras intrasiphonatum* Łopuski, 1912. This species is the most common nautilid within the studied material, and is apparently endemic to Poland.



Text-fig. 28. Stratigraphic ranges of nautilid taxa in the Upper Cretaceous (middle Campanian–Maastrichtian) and lower Paleogene (Danian) of Poland and western Ukraine. The number of available specimens of each taxon is given in parentheses after its name.

Uppermost Maastrichtian strata are absent in the Middle Vistula River section and most Lublin Upland sections, as they were eroded during the early Danian (Machalski *et al.* 2022). Only two sites in the Lublin Upland preserve topmost Maastrichtian fossiliferous

deposits. The Lechówka locality yields individual specimens of *E.? aquisgranense* Holzapfel, 1887 and *Cymatoceras intrasiphonatum* found just beneath the K–Pg boundary clay (Machalski *et al.* 2016). Slightly less complete uppermost Maastrichtian strata at Mełgiew (Machalski *et al.* 2022) yield only a single *E.? aquisgranense* specimen; in contrast, ammonite fossils are notably abundant at Mełgiew (Machalski 2005a, b; Machalski *et al.* 2022). These finds suggest that at least a portion of the regional nautilid fauna survived until the end of the Cretaceous.

Lower Danian fauna show a drastic reduction in nautilid abundance and diversity relative to Upper Cretaceous records. Only two taxa, *Eutrephoceras dekayi* and Nautilidae indet. gen. et sp. nova, are known from the shallow-water sandy gaizes (Siwak) exposed in the Middle Vistula River section (Machalski *et al.* 2022)

In summary, regional Late Cretaceous nautilid diversity decreased towards the K–Pg boundary. With the notable exception of *E. dekayi*, these forms do not extend to the Danian. In combination with other nautilid records, this suggests that the Cretaceous nautilid fauna go extinct at and/or before the K–Pg boundary. To this end, records from Lechówka and Mełgiew suggest that at least some typical members of this fauna survived to the end-Cretaceous, placing some temporal constraints on their extinction (see Text-Fig. 28).

Comparison with other nautilid faunas

To better understand the studied Cretaceous–Paleogene nautilid succession, it is useful to compare it with coeval European nautilid faunas. To this end, important nautilid records are known from classic localities in Denmark (Frejlev, Møns Klint, Stevns Klint, and Faxe), Sweden (Limhamn), and northern Germany (Kronsmoor and the Isle of Rügen).

In Denmark and Sweden, nautilids have been reported from several Maastrichtian and Danian sections across Jutland (Jylland), Zealand (Sjælland), and southern Scania (Skåne). For a comprehensive overview of the general geological setting, the reader is referred to Surlyk (1997) and Surlyk and Håkansson (1999). Significant regional nautilid studies include Moberg (1885), Lundgren (1867), Ravn (1902), Rosenkrantz (1944, 1960), Malchyk and Machalski (2018), and Schnetler (2023). Nautilid-bearing strata include: 1) the lower Maastrichtian white chalk successions at the classic Møns Klint locality (Zealand; Jelby *et al.* 2014); 2) the lower/upper Maastrichtian white chalk succession at Frejlev (Jutland); 3) the upper Maastrichtian–lower Danian succession at Stevns Klint, Zealand, developed in chalk with bryozoan-mounds (see Surlyk *et al.* 2006; with detailed K–Pg stratigraphy in Machalski and Heinberg 2005); 4) upper Maastrichtian–lower Danian chalk successions in Jutland (Håkansson and Hansen 1979); and 5) Middle Danian sections with azooxanthellate coral mounds and bioclastic limestones at Faxe, Zealand (Bernecker and Weidlich 1990; Hvid *et al.* 2021) and Limhamn, Skania (Holland and Gabrielson, 1979).

In **northern Germany**, a crucial nautilid record is derived from the white chalk Boreal reference section for the Campanian–Maastrichtian boundary at Kroonsmoor (see Niebuhr *et al.* 2011 and Wilmsen *et al.* 2018 for stratigraphy, and Engelke *et al.* 2016, 2017 for invertebrate palaeoecology). Upper Campanian and lower Maastrichtian nautilids from Kroonsmoor were described by Wilmsen and Esser (2004). Another important northern German succession is the Isle of Rügen, where lower Maastrichtian white chalk outcrops both along the shoreline and inland (see Reich and Frenzel 2002 for facies and stratigraphy, and Nestler 1965 and Reich *et al.* 2018 for palaeoecology and environment). However, nautilids are rare and poorly preserved in this succession, and were only superficially discussed by Reich and Frenzel (2002).

Collectively, a critical evaluation of these nautilid records enabled the development of a composite nautilid succession from Denmark, Sweden, and northern Germany:

Upper Campanian: *Eutrephoceras* sp. and "*Cymatoceras*" *patens* (known only from Kroonsmoor; Wilmsen and Esser 2004).

Lower Maastrichtian: *Eutrephoceras ahltenense?*, *E. darupense**, *E. spp.* "*Cymatoceras*" patens, *Cymatoceras loricatum*, and *Epicymatocers vaelsense** (* – species from Frejlev in Jutland, Denmark that spans the lower–upper Maastrichtian boundary and are not precisely located, see Malchyk and Machalski 2018).

Upper Maastrichtian: *Eutrephoceras darupense**, *E.* sp., "*Cymatoceras*" *patens**, *Epicymatoceras vaelsense*, and *Hercoglossa*? sp. (* – see above; records referred to *E.* sp. and *Hercoglossa*? sp. are based on Rosenkrantz (1944), who listed these taxa from the uppermost Maastrichtian at Stevns Klint, Zealand, Denmark. Notably, Malchyk and Machalski (2018) recorded *E. vaelsense* from the uppermost Maastrichtian of Jutland).

Middle Danian: *Eutrephoceras dekayi*, *Hercoglossa danica*, *Danathuriodea fricator* Beck in Lyell, 1835, and *Cimomia* sp. (no lower Danian nautilids are known from the study area. However, the listed forms are abundant in the reefs of Faxe and Limhamn. In addition, *Hercoglossa scanica* Rosenkrantz (1970) was reported from Limhamn, but this species lacks a precise definition and is therefore considered doubtful at present).

An interesting nautilid fauna occurs in the Maastrichtian and lower Danian of the historical type area of the Maastrichtian Stage (southern Netherlands, northeastern

Belgium, with most outcrops located near Maastricht). The reader is referred to Jagt and Jagt-Yazykova (2012) for general stratigraphy, and to Schiøler *et al.* (1997) for associated sequence stratigraphy and paleoenvironmental interpretations. Vellekoop *et al.* (2019) focused on the palaeoecology of K–Pg interval and earliest Danian biota, while Jagt *et al.* (2023, 2024) provided the most recent stratigraphic and palaeontological synthesis of the Maastrichtian type area. The succession consists of shallow-, occasionally very shallow-water bioclastic carbonates (calcarenites and calcirudites) punctuated by several discontinuity surfaces. The lower portion of the Maastrichtian strata laterally passes eastwards into a distinctive indurated bioclastic unit referred to as the Kunrade Limestone (Jagt and Jagt-Yazykova 2012). Nautilids are rare near Maastricht, but are more abundant in the Kunrade facies. Sporadic finds were discussed by Binkhorst van den Binkhorst (1861), Jagt (2012), Jagt *et al.* (2013), and Goolaerts and Frank (2014).

A critical evaluation of these nautilid records enabled the synthesis of a generalized nautilid succession in the Maastrichtian type area:

Lower Maastrichtian: *Eutrephoceras depressum*, *E.* spp., "*Cymatoceras*" *patens*, and *Epicymatoceras vaelsense*.

Late Maastrichtian: *Eutrephoceras depressum. E. spp., Cimomia heberti, Cim. sp.* (for discussion of the taxonomic status of *Cim. heberti*, see the *Systematic Paleontology* section).

Lower Danian: *Eutrephoceras dekayi*?, *Cimomia heberti*, *Cimomia*? sp. (*E. dekayi* refers to *Eutrephoceras* aff. *bellerophon* of Jagt *et al.* 2013, with reference to the discussion in the *Systematic Paleontology* section. The *Cim. heberti* record refers to the specimen from the lowermost Danian unit IV-f-7 at the top of the Maastricht Formation, see Jagt 2012).

Another significant European nautild fauna stems from the **middle Danian of Vigny**, a classic section located 35 km northwest of Paris. This section consists of bioclastic limestones with zooxanthellate coralgal reefs (the so-called "*Calcaire Pisolithique*" or "Dano-Montian" in older works), which is currently dated to the middle Danian (see Bignot 1993 for stratigraphy, and Montenat *et al.* 2002 for sedimentology). The Vigny reefs (bioherms) developed in a much shallower environment than that ascribed to the coeval Faxe reefs (Bignot 1993). In Vigny, the middle Danian strata have yielded relatively abundant nautilids, but they are insufficiently documented with the notably exception of Bignot and Geyssant (1997). A critical evaluation of the Vigny fauna reveals the presence of two nautilid species: *Eutrephoceras dekayi* (Morton, 1834), which was previously identified by Bignot and

Geyssant (1977) as *Cimomia hebertina* (d'Orbigny, 1850) (see discussion in the *Systematic Paleontology* section), and *Hercoglossa danica* (v. Schlotheim, 1820). Additionally, *H. schoelleri* (Rosenkrantz, 1970) has been reported. However, this taxa is inadequately defined at present, and as such is considered doubtful.

Discussion

These extensive nautilid records illustrate a broader perspective on the Polish and western Ukrainian nautilid succession, with a particular focus on geographical, stratigraphical, and facies distributions, along with the the Maastrichtian–Danian boundary turnover (see Text-figs 29–31 and Table 22). It is important to note that the distribution patterns (Text-figs 29–30; Table 22) accurately reflect nautilid abundance and diversity only in those successions that have been extensively studied, resulting in rich nautilid collections. Such successions include the Middle Vistula River section, Poland (Campanian–Danian); the Faxe section, Denmark (Danian), and the Maastrichtian type area, the Netherlands (Maastrichtian–Danian succession). In particular, over 400 specimens have been reported from the Maastrichtian of the Middle Vistula River Section, and over 100 specimens from the Danian of Faxe. In contrast, the nautilid records from the Danian of the Maastrichtian type area (3 specimens, see Jagt 2012, Jagt *et al.* 2013) and the Middle Vistula River section (12 specimens) are very poor. However, as both areas have been extensively studied, it is reasonable to suggest that the number of reported nautilid fossils from these successions reflect original differences in the nautilid faunal composition and abundance.

Nautilid facies relationships

Like their modern representatives (Ward *et al.* 2016), Late Cretaceous and Danian nautilids were nektobenthic animals. As such, their facies distribution may reflect primary differences in environmental preference, rather than strictly reflecting preservational constraints (Table 22).
Table 22. Data on species-level nautilid taxa distribution in the Upper Cretaceous (Upper Campanian– Maastrichtian) and lower Paleogene (Danian) of Europe, based on this work and cited references. Abbreviations: RH – Roztocze Hills (Poland and western Ukraine); LU – Lublin Upland; MVRs – Middle Vistula River section; MU – Miechów Upland; NG – Northern Germany; DS – Denmark and Sweden; Mta – Maastrichtian type area; V – Vigny; mC – middle Campanian; uC – upper Campanian; IM – lower Maastrichtian; uM – upper Maastrichtian; ID – lower Danian; mD – middle Danian. The dominant facies is indicated for each region.

Taxon	RH opoka	LU opoka, chalk	MVRs opoka	MU opoka	NG chalk	DS chalk /reefs	Mta calcar- enites	V reefs
Eutrephoceras ahltenense	lM uM	-	mC, uC, lM, uM	-	uC	lM	-	-
Eutrephoceras? aquisgranense	-	uM	uM	-	-	-	-	-
Eutrephoceras darupense	-	uM	uC, lM	-	uC	lM, uM	-	-
Eutrephoceras dekayi	uC, lM	uM	uC, lM, uM, lD	uC,lM	-	mD	lD	mD
Eutrephoceras depressum	lM	uM	uM	-	-	-	lM, uM	-
Eutrephoceras quadrilineatum	lM	-	uC, lM, uM	-	-	-	-	-
Eutrephoceras vastum	lM	-	uC, lM, uM	-	-	-	-	-
Cymatoceras loricatum	lM	-	mC, uC, lM		uC, lM	-	-	-
Cymatoceras intrasiphonatum	-	uM	uM	-	-	-	-	-
"Cymatoceras" patens	uC, lM	-	mC, uC, lM	uC	uC, lM	lM	lM	-
Epicymatoceras vaelsense	-	-	uC, lM	uC	-	lM, uM	lM	-
Angulithes westphalicus	lM	-	uC	-	uC	-	-	-
Cimomia? galiciana	lM, uM	-	uC, lM	lM	-	-	-	-
Cimomia heberti	lM	uM	uM	-	-	-	uM, lD	-
Danathuroidea fricator	-	-	-	-	-	mD	-	-
Hercoglossa danica	-	-	-	-	-	mD	-	mD

In the late Campanian–Maastrichtian, nautilids are most abundant and diverse in the opoka facies, as exemplified by numerous records from the opoka-dominated Middle Vistula River section and the Roztocze Hills. In contrast, nautilids are less common and diverse in the white chalk facies, as demonstrated by sparse records from Denmark (e.g., Ravn 1902; Rosenkrantz 1944, 1960; Gravesen 2001; Malchyk and Machalski 2018) and northern Germany (Wilmsen and Esser 2004; present study). The reduced nautilid abundance and diversity in the white chalk facies may be attributable to several, non-mutually exclusive

factors. First, white chalk facies were generally deposited in deeper environments than opoka facies (Text-fig. 2; Walaszczyk and Remin 2015; Machalski and Malchyk 2019; Remin *et al.* 2022a, b). Additionally, preservational conditions were much more deleterious for aragonitic nautiloid shells during early diagenetic stages in the chalk, especially compared to opoka, which may have conceivably affected their preserved distribution pattern (Malchyk *et al.* 2017; Janiszewska *et al.* 2018). However, poor nautilid representation in the shallow-water calcarenites of the Maastrichtian type area may instead be related to unfavourable, highly energetic conditions, which were possibly not conducive to both nautilid life and preservation.

The facies associations of particular nautilid species are somewhat complex and defy ready generalization. Some ribbed nautilids (conventionally assigned to Cymatoceratidae), which have been suggested to be particularly well adapted to high-energetic shallow water environments (Tintant and Kamamba 1985; Wilmsen and Yazykova 2003), appear to be completely facies-independent. Specifically, the lower Maastrichtian "*Cymatoceras*" patens occurs across a variety of epicontinental facies, ranging from hemipelagic marl-limestone rhythmites to opoka, sandy opoka, and white chalk (Wilmsen and Esser 2004; this study). The geographical range of this species is also considerable, extending from the Netherlands to western Ukraine. However, the ribbed *Cymatoceras intrasiphonatum* is almost exclusively recorded from upper Maastrichtian opoka facies, and is geographically restricted to Poland. In contrast to these ribbed forms, smooth-shelled nautilids (genus *Eutrephoceras*) were widely distributed during the Upper Cretaceous–Paleogene in Europe, at least so far as facies and geographical range are concerned. Among Danian nautilids, the genera *Hercoglossa* and *Danathuroidea* seem to be restricted to reefal facies.

Maastrichtian-Danian boundary turnover

Within Poland and western Ukraine, almost all Late Cretaceous nautilid species, including the ribbed forms assigned to the Cymatoceratidae, did not cross the K–Pg boundary (Text-figs 28–30), with the sole exception of the ubiquitous *E. dekayi*. To some degree, this pattern could be ostensibly interpreted in terms of facies preferences, reflecting the fundamental restructuring of palaeogegraphic and facies relations across Europe (compare Text-figs 29 and 30). To this end, this restructuring resulted in the loss of chalk and opokadominated environments, which were replaced by bryzoan mounds and coral reefs in Denmark and France, and by the clastic-dominated shallow Siwak facies in Poland (Machalski *et al.* 2022). However, stratigraphical ranges of the studied taxa suggest that the

observed nautilid turnover largely resulted from a genuine mass extinction of nautilids during the end-Cretaceous environmental crisis. However, the precise species extinction pattern is difficult to assess. The most abundant and diverse late late Maastrichtian nautilid faunas stem from the Middle Vistula River section and the Lublin Upland, where the topmost Maastrichtian deposits are missing (Machalski *et al.* 2022). In the exceptionally complete Lechówka boundary section, single specimens of *E.? aquisgranense* and *Cymatoceras intrasiphonatum* occur just below the K–Pg boundary clay. The slightly less complete uppermost Maastrichtian section at Mełgiew yielded only a single individual of *E.? aquisgranense*, despite the presence of abundant ammonites and other fossils. In Denmark, specimens of *Epicymatoceras vaelsense* were recorded from topmost Maastrichtian. These records suggest that at least part of the European nautilid fauna survived just until the Cretaceous–Paleogene boundary.

Eutrephoceras dekayi successfully crossed the K–Pg boundary. This is the most widespread species in the studied material, and has been recorded from North America and Eurasia (see Text-fig. 31). Beyond Poland and western Ukraine, there is another nautilid survivor – that is, *Cimomia heberti* from the lowermost Danian in the Maastrichtian type area (see *Systematic Paleontology* section) – but only a single specimen has been recovered. The survival of *E. dekayi* into the Danian is consistent with the hypothesis that broadly distributed taxa are better suited to survive mass extinctions than those with limited geographical ranges (see Jablonski 2008; Landman *et al.* 2014, 2015) although admittedly *E. dekayi* did not survive into the Danian in North America (Text-fig. 31).

Early Danian nautilid faunas are very species- and specimen-poor, both in the Maastrichtian type area and in Poland (Text-fig. 30); nautilids only return to abundance in the middle Danian reefs of Denmark (Faxe and Linhamn) and France (Vigny; Text-fig. 30). In addition to ubiquitous *Eutrephoceras dekayi*, large-shelled specialised nautilids with complicated sutures, such as *Hercoglossa danica*, appear in these environments. These forms are probably relatively deep-water dwellers which migrated to Europe during the middle Danian eustatic highstand, analagous to the Eocene nautilid migrations documented by Dzik and Gaździcki (2001).



Text-fig. 29. Distribution of nautilid faunas during the late Maastrichtian, with palaeographic map after Jurkowska *et al.* (2019, fig. 1). Asterisks denote species from either the lower or upper Maastrichtian of Frejlev, Jutland. N = numbers of specimens, if available.



Text-fig. 30. Distribution of nautilid faunas during the Danian, with palaeographic map after Bernecker and Weidlich (2005, fig. 1). Abbreviations: L – lower Danian, M – middle Danian. N = numbers of specimens, if available.



Text-fig. 31. Geographical distribution of the nautilid *Eutrephoceras dekayi* (Morton, 1835) in the Late Campanian–Maastrichtian (A) and Danian (B). Palaeographic maps modified from Scotese (2014). A: 1 – Atlantic Coastal Plain: New Jersey, Delaware, Maryland, North Carolina, Georgia (USA); 2 – Western Interior Seaway: Missouri, Texas, New Mexico, Utah, Nebraska, South Dakota, Wyoming, Idaho, Montana (USA), Alberta (Canada); 3 – Gulf Coastal Plain: Arkansas, Tennessee, Alabama, Mississippi (USA); 4 – Maastricht (the Netherlands); 5 – Isle of Rügen (northeast Germany); 6 – Nida Trough, Middle Vistula River Section, Roztocze (central and eastern Poland); 7 – Nahoryany (western Ukraine); 8 – Saratov (Russia); 9 – Ayat River (Kazakhstan).

B: 1 – Limhamn (southern Sweden); 2 – Faxe, Zealand (eastern Denmark); 3 – Vigny (northern France); 4 –
Middle Vistula River Section (central Poland); 5 – Aksay, Mangyshlak region (northwestern Kazakhstan); 6 –
Nalchik, Caucasus (Russia).

Summary and conclusions

- 1. The Upper Cretaceous (Campanian–Maastrichtian) to lower Paleogene (Danian) epicontinental deposits of Poland and western Ukraine enable an examination of nautilid turnover across the Cretaceous–Paleogene (K–Pg) boundary.
- 2. In particular, the Maastrichtian deposits yield abundant, relatively well-preserved nautilid fossils, permitting an assessment of nautilid taxonomic composition and abundance prior to the end-Cretaceous crisis.
- 3. In total, 656 specimens representing 26 nautilid taxa belonging to the families Nautilidae, Cymatoceratidae, and Hercoglossidae are described from 64 sections, ranging from the middle Campanian to the Danian in Poland, and from the upper Campanian to the lower upper Maastrichtian in western Ukraine.
- 4. The identified material comprises 14 Late Cretaceous species Eutrephoceras ahltenense, Eutrephoceras? aquisgranense, Eutrephoceras darupense, Eutrephoceras dekayi, Eutrephoceras depressum, Eutrephoceras quadrilineatum, Eutrephoceras vastum, Cymatoceras intrasiphonatum, Cymatoceras loricatum, "Cymatoceras" patens, Epicymatoceras vaelsense, Angulithes westphalicus, Cimomia? galiciana, and Cimomia heberti. Additionally, these faunas contain several forms left in open nomenclature: Eutrephoceras sp. A, Eutrephoceras sp. B, Eutrephoceras sp. C, *Eutrephoceras* spp., "Cymatoceras." sp. nova, Cymatoceratidae? indet., Epicymatoceras sp., Angulithes cf. neubergicus, Angulithes sp. nova, Cimomia sp. A, and Cimomia sp. B. Only two early Paleogene taxa are recorded: E. dekayi and Nautilidae indet. gen. et sp. nova?.

- 5. The most abundant nautilid fauna, dominated by diverse *Eutrephoceras* and the endemic *Cymatoceras intrasiphonatum*, is from the classic upper Maastrichtian outcrops in the Middle Vistula River section of Poland.
- 6. The Late Cretaceous and early Paleogene nautilid faunas of Poland and Ukraine are compared with much less abundant and diverse nautilid faunas from other regions, including Denmark, northern Germany, and also the Netherlands, Belgium, and France.
- 7. With the exception of the ubiquitous *E. dekayi* and extremely rare *Cimomia heberti*, all identified European Late Cretaceous nautilid species, including the ribbed forms conventionally assigned to the Cymatoceratidae, did not cross the K–Pg boundary. Despite the profound regional paleogeographic and facies changes near the boundary, the observed palaeontological record reflects a genuine extinction related to the global end-Cretaceous crisis.
- However, a precise reconstruction of Cretaceous nautilid faunal extinction patterns is hampered by stratigraphic gaps, mostly linked to regional hiatuses at the top of the Maastrichtian.
- 9. Single E.? aquisgranense and Cymatoceras intrasiphonatum specimens recovered just beneath the K–Pg boundary clay at Lechówka, a single individual of E.? aquisgranense from slightly less complete section at Mełgiew, and specimens of Epicymatoceras vaelsense from topmost Maastrichtian of Denmark suggest that some proportion of the Cretaceous nautilid fauna survived until the end of the Cretaceous.
- 10. The species *Eutrephoceras dekayi* passed successfully the K–Pg boundary. Importantly, *E. dekayi* is the most widespread species in the studied material, and is known from North America, Europe, and Asia. Its survival into the Danian (from where it was usually reported as *E. bellerophon*) is consistent with the hypothesis that broadly distributed taxa are better suited to survive mass extinctions than those with limited geographical ranges.

11. Early Danian nautilid faunas are very species- and specimen-poor, as illustrated by the fauna from the Middle Vistula River section of Poland. Cenozoic nautilids only become abundant in the middle Danian reefs of Denmark and France. Large taxa with complicated suture lines, such as the cosmopolitan *Hercoglossa danica*, stand out in these reefal faunas; their appearance may be attributable to a migration-linked influx.

Supplementary material

Supplementary files for Chapter III are on the attached CD and include:Appendix 1. Material studied from Poland and western Ukraine.Appendix 2. Comparative material from Denmark and Germany.Appendix 3. Dataset for biometrics of *Eutrephoceras dekayi*.

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PLATES 1–35
1 – Eutrephoceras ahltenense (Schlüter, 1876), MUZ PIG 12.II.1045, upper Campanian, Antoniów.



1 – Eutrephoceras ahltenense (Schlüter, 1876), VIII Mc-711, middle Campanian, Ciszyca
 Kolonia. Casts of large chambers of a clionaid boring sponge are visible in Fig. 1d.



1-2 – *Eutrephoceras ahltenense* (Schlüter, 1876), 1 – ZPAL N.III/156, upper Maastrichtian, Nasiłów. 2 – ZPAL N.III/12, lower Maastrichtian, Hrebenne.



1-3 – *Eutrephoceras*? *aquisgranense* (Holzapfel, 1887), 1 – VIII Mc-547/2, upper Maastrichtian, Kazimierz Dolny; 2 – ZPAL N.III/263, upper Maastrichtian, Chełm; 3 – ZPAL N.III/270, upper Maastrichtian, Kazimierz Dolny.



1-6 – Eutrephoceras? aquisgranense (Holzapfel, 1887), 1 – ZPAL N.III/247, upper
Maastrichtian, Opole Lubelskie; 2 – ZPAL N.III/260, upper Maastrichtin, Chełm; 3 – ZPAL
N.III/51, lower Maastrichtian, Dziurków; 4 – ZPAL N.III/311, upper Maastrichtian,
Kazimierz Dolny; 5 – ZPAL N.III/227, upper Maastrichtian, Rejowiec; 6 – ZPAL N.III/269,
upper Maastrichtian, Kazimierz Dolny.



1-2 – Eutrephoceras darupense (Schlüter, 1876), 1 – VIII Mc-448, lower Maastrichtian,
 Dziurków; 2 – ?Eutrephoceras darupense (Schlüter, 1876), ZPAL N.III/215, upper
 Campanian, Kamień South.



 1-2 – Eutrephoceras dekayi (Morton, 1834), 1 – ZPAL N.III/155, upper Maastrichtian, Kazimierz Dolny; 2 – ZPAL N.III/148, upper Maastrichtian, Kazimierz Dolny.



1-3 – *Eutrephoceras dekayi* (Morton, 1834), 1 – VIII Mc-246, Danian, Parchatka; 2 – ZPAL N.III/245, Danian, Parchatka; 3 – VIII Mc-249/2, Danian, Góra Puławska.



1-3 – Eutrephoceras dekayi (Morton, 1834), 1 – ZPAL N.III/41, upper Campanian, Potelych;
 2 – ZPAL N.III/325, Danian, Parchatka; 3 – VIII Mc-248, Danian, Parchatka.



1 – *Eutrephoceras depressum* (Binkhorst van den Binkhorst, 1861), ZPAL N.III/10, lower Maastrichtian, Hrebenne.



1 – Eutrephoceras quadrilineatum (Favre, 1836), ZPAL N.III/ 57, lower Maastrichtian, Dziurków.



1 – Eutrephoceras quadrilineatum (Favre, 1836), VIII Mc-656, upper Campanian, Piotrawin.



1-4 – Eutrephoceras vastum (Kner, 1848), 1 – ZPAL N.III/368, upper Maastrichtian, Kazimierz Dolny; 2 – ZPAL N.III/214, lower Maastrichtian, Hrebenne; 3 – NHMW
2018/0327/0002, lower Maastrichtian, Nahoryany; 4 – ZPAL N.III/130, lower Maastrichtian, Hrebenne; casts of chambers of boring clionaid sponge are discernible in Fig 5.



1-2 – *Eutrephoceras* sp. A, 1 – GBA 1869/006/0005/002, lower Maastrichtian, Nahoryany; 2 – PZ-K-491/5, lower Maastrichtian, Nahoryany.



1 – *Eutrephoceras* sp. B; MUZ PIG 12.II.1050, upper Campanian or lower Maastrichtian, Wyględów; 2 – *Eutrephoceras vastum* (Kner, 1848), lower Maastrichtian, Nahoryany, PZ-K-65.



1 – *Eutrephoceras vastum* (Kner, 1848), PZ-K-321, lower Maastrichtian, Nahoryany; 2 – *Eutrephoceras* sp. C, PZ-K-1786/1, lower Maastrichtian, Nahoryany.



1 - Nautilidae indet. gen. et sp. nov.?, ZPAL N.III/220, Danian, Nasiłów.



1 - Nautilidae indet. gen. et sp. nov.?, ZPAL N.III/221, Danian, Nasiłów.


1-2 – Cymatoceras intrasiphonatum (Łopuski, 1912), upper Maastrichtian, Nasiłów. 1 – MKD/MP-180; 2 – MKD.MP-68.



1-2 – Cymatoceras intrasiphonatum (Łopuski, 1912), upper Maastrichtian, Nasiłów. 1 – MKD/MP-42; 2 – MKD/MP-67.



1-3 – Cymatoceras intrasiphonatum (Łopuski, 1912), upper Maastrichtian. 1 – MKD/MP-24,
 Nasiłów; 2 – MKD/MP-1058, Kazimierz Dolny; 3 – MKD/MP-4, Kazimierz Dolny. Casts of the chambers of clionaid boring sponges are visible on specimen figured in Fig. 1b, c.



1-2 – Cymatoceras intrasiphonatum (Łopuski, 1912), upper Maastrichtian, Nasiłów. 1 – ZPAL N.III/125; 2 – MKD/MP/64.



1-2 – Cymatoceras intrasiphonatum (Łopuski, 1912), upper Maastrichtian. 1 – ZPAL
N.III/145, Nasiłów; 2 – VIII Mc-568, Wierzchoniów. Chambers of boring clionaid sponges are preserved as imprints or internal casts in specimen in Fig. 1.



1-2 – *Cymatoceras intrasiphonatum* (Łopuski, 1912), upper Maastrichtian, Nasiłów. 1 – ZPAL N.III/120; 2 – ZPAL N.III/124.



1-3 – Cymatoceras loricatum (Schlüter, 1876), 1 – ZPAL N.III/17, middle Campanian,
 Wałowice-Kolonia; 2 – MUZ PIG 12.II.1047, lower Maastrichtian, Przedmieście; 3 – MKD/MP-638, upper Campanian, Piotrawin.



1 – "*Cymatoceras*" *patens* (Kner, 1848), ZPAL N.III/322, upper Campanian, Krasnobród. The specimen retains remnants of the shell, probably recrystallised into calcite.



1-3 – "*Cymatoceras*" *patens* (Kner, 1848), 1 – ZPAL N.III/352, lower Maastrichtian, Dziurków; 2 – ZPAL N.III/104, lower Maastrichtian, Hrebenne; 3 – ZPAL N.III/159, upper Campanian, Piotrawin.



1 – *Cymatoceras*? sp. nova (Schlüter, 1876), ZPAL N. III/127, upper Campanian, Kamień South.



1-3 – Epicymatoceras vaelsense (Binkhorst van den Binkhorst, 1862), 1 – MUZ PIG
12.II.1079, upper Campanian or lower Maastrichtian, Jawor Solecki; 2 – MUZ PIG
12.II.1082, upper Campanian, Gozdawa; 3 – MUZ PIG 12.II.1077, upper Campanian or
Lower Maastrichtian, Marianów; 4 – Epicymatoceras sp., ZPAL N.III/309, upper Campanian, Piotrawin.



1 – *Angulithes* cf. *neubergicus* Redtenbacher, 1873, ZPAL N.III/160, upper Maastrichtian, Kazimierz Dolny.



1 - Angulithes westphalicus (Schlüter, 1872), ZPAL N.III/45, upper Campanian, Piotrawin.



1 – "*Cymatoceras*" patens (Kner, 1848), ZPAL N.III/49, upper Campanian, Potelych; 2 – Angulithes westphalicus (Schlüter, 1872), UkK 90, lower Maastrichtian, Nahoryany.



1 – *Angulithes* sp. nov, ZPAL N.III/42, upper Campanian, Potelych. 2 – *Cimomia? galiciana* (Alth, 1850), PZ-K-1775/1, lower Maastrichtian, Nahoryany.



 3 – Cimomia heberti (Binkhorst van den Binkhorst, 1862); 1 – ZPAI N.III/40, upper Maastrichtian, Prawiedniki; 3 – ZPAL N.III/9, lower Maastrichtian, Hrebenne. 2 – Cimomia? galiciana (Alth, 1850), NHMW 1862/0005/0020, lower upper Maastrichtian, Lviv.



1 – Cimomia sp. A, ZPAL N.III/136, upper Maastrichtian, Nasiłów; 2 – Cimomia heberti
(Binkhorst van den Binkhorst, 1862), ZPAL N.III/162, upper Maastrichtian, Kazimierz Dolny.
3 – Cimomia? galiciana (Alth, 1850), ZPAL N.III/207, upper Campanian, Piotrawin.



Results of the thesis

- The thesis presents results of a palaeontological study of Late Cretaceous (Campanian and Maastrichtian) and early Paleogene (Danian) nautilids from Poland, western Ukraine, and Denmark in the context of the end-Cretaceous mass extinction.
- The results of detailed research on Polish and Danish specimens of *Epicymatoceras vaelsense*, the most enigmatic Late Cretaceous nautilid in Europe, are presented. These results significantly add to our understanding of the morphology, shell structure, taxonomic position, and stratigraphical range of this atypical nautilid.
- The taphonomic pathways leading to the formation of the identified taphomorphs of *E*. *vaelsense* are reconstructed, allowing for their interpretation with respect to the original shell structure.
- The Polish material indicates that the external ribbing of *E. vaelsense* was originally composed of overlapping tile-shaped lamellae of the outer prismatic layer, therefore firmly supporting the placement of this taxon within recently redefined family Cymatoceratidae.
- In addition, the Polish and Danish specimens of *E. vaelsense* provide new data on embryonic shell diameter in the genus *Epicymatocers*. Embryonic conch diameter in *E. vaelsense* is estimated to have been around 30 mm, near the maximum range of hatching size recorded for both Cretaceous and post-Cretaceous nautilids.
- The uppermost Maastrichtian specimens of *E. vaelsense* from Denmark are interpreted as the youngest known records of *Epicymatoceras*, indicating that the genus extended into the latest Cretaceous.
- The first monographic study of nautilid faunas from the Upper Cretaceous (Campanian and Maastrichtian) to lower Paleogene (Danian) of Poland and western Ukraine is provided and these faunas are compared to coeval faunas from selected regions of Europe, including Denmark, southern Sweden, northern Germany, the Netharlands and Belgium, and France.
- Representatives of three families representing the superfamily Nautilaceae of the order Nautilida, have been identified in the studied material: Nautilidae, Cymatoceratidae, and Hercoglossidae.
- The Late Cretaceous faunas from Poland and western Ukraine encompass 14 species: *Eutrephoceras ahltenense, Eutrephoceras? aquisgranense, Eutrephoceras darupense,*

Eutrephoceras dekayi, Eutrephoceras depressum, Eutrephoceras quadrilineatum, Eutrephoceras vastum, Cymatoceras intrasiphonatum, Cymatoceras loricatum, "Cymatoceras" patens, Epicymatoceras vaelsense, Angulithes westphalicus, Cimomia? galiciana, and Cimomia heberti.

- Additionally, these faunas contain several forms left here in open nomenclature: *Eutrephoceras* sp. A, *Eutrephoceras* sp. B, *Eutrephoceras* sp. C, *Eutrephoceras* spp., *"Cymatoceras"* sp. nova, Cymatoceratidae? indet., *Epicymatoceras* sp., *Angulithes* cf. *neubergicus*, *Angulithes* sp. nova, *Cimomia* sp. A, and *Cimomia* sp. B.
- Only two early Paleogene taxa have been identified from Poland: *Eutrephoceras dekayi* and Nautilidae indet. gen. et sp. nova?.
- The most abundant nautilid fauna, dominated by the genus *Eutrephoceras* and the endemic (to Poland) species *Cymatoceras intrasiphonatum*, comes from the upper Maastrichtian sections in the Middle Vistula River section of Poland.
- Inferences on the original shell structure of some ribbed taxa (*Cymatoceras intrasiphonatum* and *C. loricatum*) clarify their systematic position based on the lines of evidence first employed for *Epicymatocers vaelsense*, which is a considerable advance in our understanding of these taxa.
- Ribbed nautilids that do not match the new understanding of the family Cymatoceratidae are provisionally referred to as "*Cymatoceras*" awaiting further studies.
- Among the ribbed nautilids, the common upper Maastrichtian species *Cymatoceras intrasiphonatum* is thoroughly described and illustrated for the first time.
- Another important taxonomic result of this study is the inclusion of the Danian species *Eutrephoceras bellerophon* into synonimy of the Maastrichtian *E. dekayi*. Their proposed conspecifity has fundamental consequences for understanding nautilid turnover across the K–Pg boundary.
- With the exception of the ubiquitous *E. dekayi* and the extremely rare *Cimomia heberti*, all European Late Cretaceous nautilid species identified during this study, including the ribbed forms assigned to the Cymatoceratidae, did not cross the K–Pg boundary. As such, despite the profound regional palaeogeographic and facies changes near the boundary, the nautilid diversity patterns reflect a genuine extinction related to the global end-Cretaceous crisis.
- Precise reconstruction of Cretaceous nautilid extinction patterns is hampered by deficiences in the fossil record. In Poland, these are mostly related to hiatal gaps at the top of the Maastrichtian, such as in the Middle Vistula River section. A few nautilid specimens have been collected from an exeptionally complete section at Lechówka near Chełm, consisting of individual *E.? aquisgranense* and *Cymatoceras intrasiphonatum* specimens recovered just beneath the K–Pg boundary clay. A single specimen of *E.? aquisgranense* is also recorded from a slightly less complete uppermost Maastrichtian section at Mełgiew near Lublin. Together with the record of *Epicymatoceras vaelsense* from the uppermost Maastrichtian of Denmark, these records collectively suggest that at least a portion of the European Cretaceous nautilid fauna survived until the end of the Cretaceous.
- Results of the taxonomic revision of the studied material indicates that *Eutrephoceras dekayi* survived the K–Pg boundary. This is the most widespread species in the studied material, and is known from the Maastrichtian of North America, Europe, and Asia and from the Danian of Europe and Asia (the Danian records under the name *E. bellerophon*). Its continuation into the Danian is consistent with the hypothesis that broadly distributed taxa are better suited to survive mass extinctions than those with limited geographical ranges.
- During the Late Cretaceous (Campanian–Maastrichtian), nautilids were most common and diverse in opoka facies, as demonstrated by numerous records from the opoka-dominated Middle Vistula River section and Roztocze Hills. Conversely, nautilids were less common and diverse in white chalk facies, as demonstrated by rather uncommon records from eastern Poland, Denmark, and northern Germany.
- Early Danian nautilid faunas are notably specimen- and species-poor across Europe, including the terrestrially-influenced gaize facies of the so-called Siwak exposed in the Middle Vistula River section. They became more abundant only in the middle Danian coral reefs of Denmark, southern Sweden and France. Alongside *E. dekayi*, large-shelled nautilids with complex sutures like *Hercoglossa danica* appear in these environments, reflecting external migrations.



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OŚWIADCZENIE / DECLARATION

Rozprawa pod tytułem "Łodziki późnej kredy i wczesnego paleogenu Polski, zachodniej Ukrainy oraz Danii" składa się z trzech rozdziałów. Jestem jedyną autorką jednego z rozdziałów (III). Pozostałe dwa (I oraz II) są rozdziałami współautorskimi. Następne strony niniejszego oświadczenia zawierają szczegóły dotyczące mojego udziału w poszczególnych rozdziałach.

This dissertation entitled "Late Cretaceous and early Paleogene nautilids from Poland, western Ukraine and Denmark" consists of three separate chapters. I am the sole author of one chapter (III). The remaining two chapters (I and II) are co-authored. The following pages of declaration include details regarding my contribution to particular chapters.



Oksana Malchyk

Rozdział I / Chapter I

Shell ornament, systematic position and hatching size of *Epicymatoceras vaelsense* (Nautilida): New insights based on specimens in mould preservation from the Upper Cretaceous of Poland

Rozdział I powstał we współpracy z Marcinem Machalskim (Instytut Paleobiologii Polskiej Akademii Nauk), Bogusławem Waksmundzkim (Wydział Geologii Uniwersytetu Warszawskiego) oraz Maciejem Dudą (GEOKRAK sp. z. o. o., Kraków, Polska).

Badania zaplanował M. Machalski na podstawie zebranego przez siebie materiału. M. Duda dostarczył dodatkowy materiał badawczy. Rekonstrukcje na figurach 6 oraz 7 wykonał we współpracy ze mną B. Waksmundzki. Mój udział polegał na przeprowadzeniu analizy morfologicznej badanego materiału oraz interpretacji wyników i przygotowaniu manuskryptu (wszystkie te zadania były wykonane wspólnie z M. Machalskim). Również przygotowałam figury 1–5 oraz 8.

Chapter I was co-authored with Marcin Machalski (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland), Bogusław Waksmundzki (Faculty of Geology, University of Warsaw) and Maciej Duda (GEOKRAK sp. z. o. o., Kraków, Poland).

The study was conceived and designed by Marcin Machalski on the basis of the material collected by himself. M. Duda provided additional material. The reconstructions on figures 6 and 8 were prepared in cooperation with me by B. Waksmundzki. I contributed to morphological analysis of material studied, interpretation of the results and writing the manuscript (together with M. Machalski). I also prepared figures 1–5 and 8.

Oświadczam, że mój wkład w przygotowaniu rozdziału wynosi około 60 %. I declare that my contribution to the chapter is approximately 60 %.

Podpis współautorów / signature of the co-authors:







Maciej Duda

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Rozdział II / Chapter II

First record of *Epicymatoceras vaelsense* (Nautilida) from the Maastrichtian white chalk of northern Denmark

Rozdział II powstał we współpracy z Marcinem Machalskim (Instytut Paleobiologii Polskiej Akademii Nauk).

Opisałam materiał badawczy, napisałam większość tekstu pracy oraz przygotowałam wszystkie figury. M. Machalski zaplanował badania, dostarczył materiał badawczy oraz przeprowadził korektę ostatecznej wersji pracy.

Chapter II was co-authored with Marcin Machalski (Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland).

I described material, wrote most of the manuscript, and prepared all figures. M. Machalski conceived and designed the study, provided material, and proofread the final version of the manuscript.

Oświadczam, że mój wkład w przygotowaniu rozdziału wynosi około 75 %. I declare that my contribution to the chapter is approximately 75 %.

Podpis współautora / signature of the co-author:

Marcin Machalski