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)