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# Nautilid beaks: unsuspected disparity and palaeoecological interpretation

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Nautiluses are key to understanding the evolution of cephalopods, as they are their only outer-shelled modern representatives. Their chitinous beaks possess a calcified tip on the upper beak called a rhyncholite. These rhyncholites are found abundantly in the fossil record from Middle Triassic onwards and are described as being morphologically stable. Because of their feeding function, they likely carry information related to their diet and environment. Yet, the morphological variability of these fossils was poorly investigated. Here, we characterized the morphology of rhyncholites through time, together with morphologically similar fossils from the Jurassic and Cretaceous, the rhynchoteuthis. We digitized 254 specimens using X-ray microtomography (μCT) and performed a shape analysis using 3D geometric morphometrics. The morphological continuum observed between rhyncholites and rhynchoteuthis leads us to consider them as close relatives of nautilids, if not part of this group. The highest rhyncholites morphological disparity is observed after their apparition in Triassic. Triassic rhyncholites are morphologically closer to modern ones, probably sharing their opportunistic carnivorous diet and able to feed on hard items. This ability might have been advantageous during the Marine Mesozoic Revolution. During this arms race period, competition might have favoured the emergence of new forms like rhynchoteuthis, and the exploration of new niches as seen in Cretaceous morphologies indicating a possible diet shift toward softer prey items. Altogether, rhyncholites and rhynchoteuthis testify of a nautilids evolutionary history richer than what can be deduced from the shells only and carry important information that could improve reconstructions of past food-webs. Nautilus, □ *rhyncholites, rhynchoteuthis, 3D morphometrics, Marine Mesozoic Revolution*

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Nautiluses, as the only modern representatives of phragmocone-bearing cephalopods, are key taxa to better understand the biology and evolution of recent and extinct cephalopods. Mostly known in the fossil record through their shells, the Nautilida likely diverged in the Devonian (Teichert & Matsumoto 2010, Kröger *et al.* 2011, King & Evans 2019, Pohle *et al.* 2022, Huang *et al.* 2022). After surviving major extinction events, and despite witnessing the appearance of coleoids and other marine forms, Nautilida have persisted until the present day. *Nautilus* and *Allonautilus* are currently the sole survivors of the once extremely diverse group of externally shelled cephalopods. This long and rich evolutionary history makes them key taxa to better understand the evolution, biology, and ecology of extinct nautilids as well as cephalopods more generally.

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Modern nautiluses are opportunistic predators and scavengers and eat their prey using a parrot-like beak capable of gripping and crushing hard food items such as crustaceans (Saunders & Ward 2010). This beak is made of chitinous lower and upper jaws (Fig. 1). Among living cephalopods, nautilus are the only forms to possess calcified tips, called rhyncholite on the upper jaw (Fig. 1), and conchorynch on the lower jaw. Due to their robustness and arrow-like shape, rhyncholites fossilize well, and isolated specimens are found abundantly in the fossil record from the Middle Triassic to the present day (Teichert 1964; Tajika *et al.* 2023; Fig. 2). Because of the superficial stasis observed in the shell over time that led to the 'living fossil' reputation of nautilus (Ward 1984) – they have remained almost unchanged over time – the relevance of their beaks for understanding their biology and ecology has been overlooked. As soft tissues are poorly preserved in the fossil record (e.g. Klug *et al.* 2021), major gaps exist in our understanding of the role of nautilids in ancient food webs. However, through their feeding function, beaks carry critical information related to diet and environmental pressures which cannot be inferred from shells alone.

Few studies to date have tried to link rhyncholites shape and function (Gasiorowski 1973; Saunders *et al.* 1978; Tanabe *et al.* 1980; Klug 2001). The most recent study by Klug (2001) compared rhyncholites of the Triassic *Germanonautilus* to those of modern nautilus. As the morphology of these rhyncholites are similar, Klug (2001) suggested a conservation of feeding function and diet from the Triassic to the present day with animals being opportunistic predators and scavengers. This has reinforced the idea of Nautilida showing morphological stasis through time. However, quantitative data are lacking to support this hypothesis, as well as studies on intermediate time periods.

Over their long evolutionary history, Nautilida survived major environmental and ecological changes. One of these major events that began shortly after the appearance of the first rhyncholites in the Triassic is the Marine Mesozoic Revolution (MMR; Vermeij 1987;

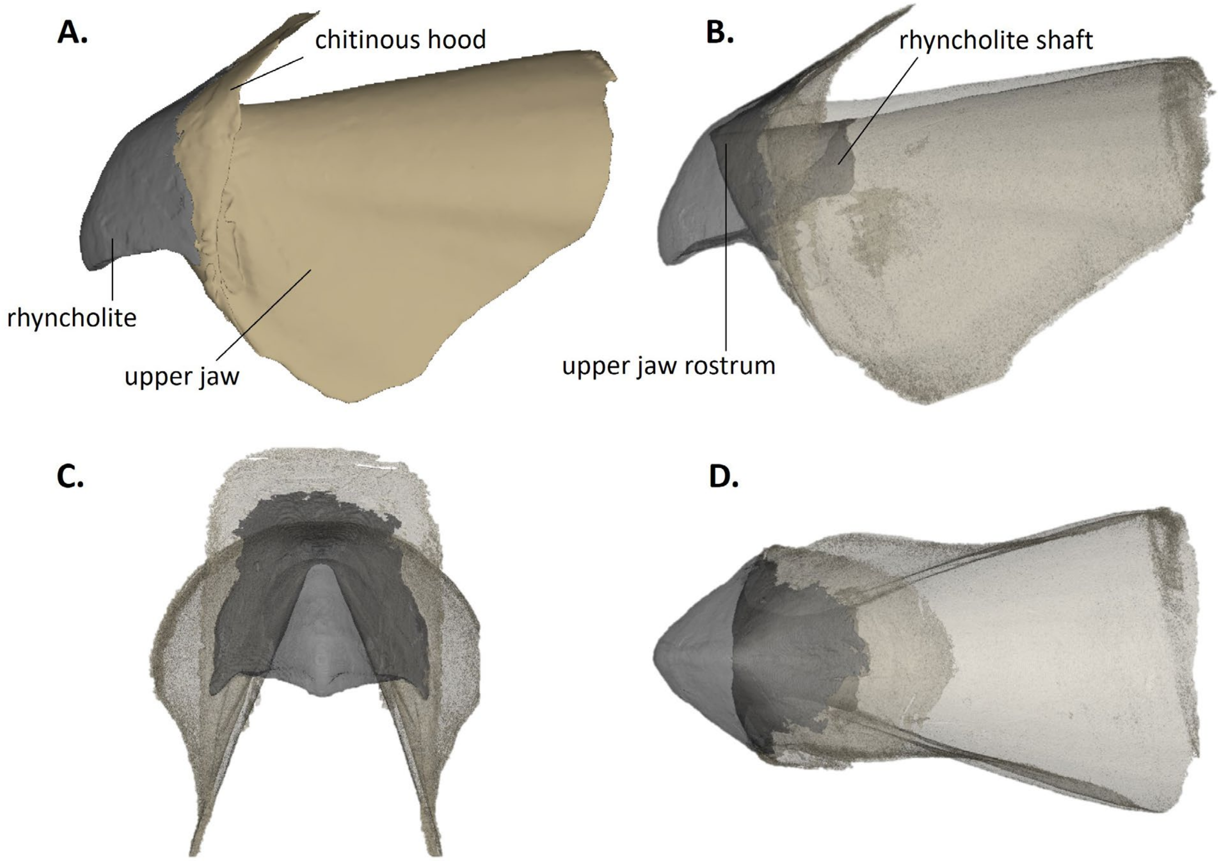

*Fig. 1.* 3D reconstruction of modern nautilus upper beak in three conventional views. A, 3D reconstruction of rhyncholites (grey) and upper jaw (brown) in lateral view. B–D, same reconstruction with transparency to illustrate rhyncholites insertion and connection with the upper jaw, in lateral view (B), frontal view (C), and dorsal view (D). Note the thinning of the rhyncholites in A and B, which forms a thin covering over the hood. Illustrated specimen: *Nautilus macromphalus* (AMNH_IZC 00249968).

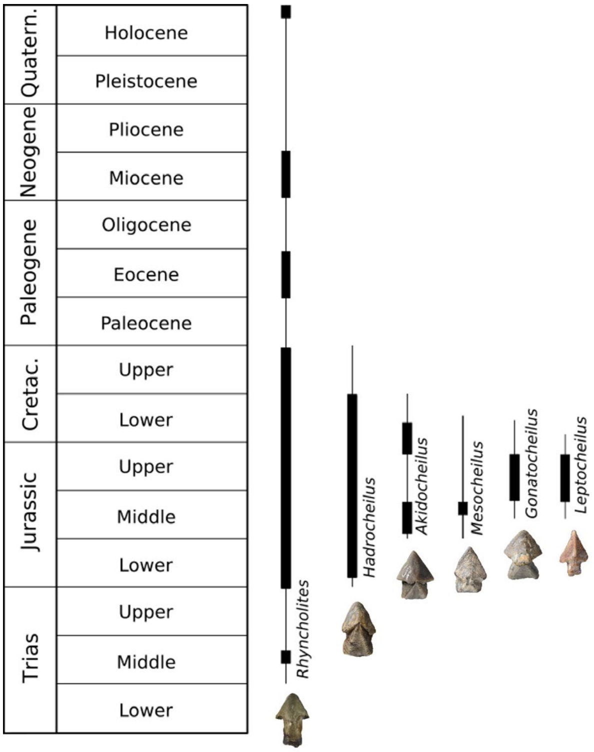

*Fig. 2.* Stratigraphical range of rhyncholites and rhynchoteuthis genera. Thick line corresponds to periods of higher abundance and thin line is the stratigraphic extension documented in the fossil record.

Kelley *et al.* 2003; Buatois *et al.* 2016; Antell & Saupe, 2021). This 'arms race' led to an exceptional evolutionary radiation both in predators, who developed better tools to eat harder foods (durophagy), and in their prey, who strengthened their defences (Bardhan & Chattopadhyay, 2003; Harper 2003). Although cephalopods are always mentioned as components of this ecological revolution (e.g. Mc Roberts 2011; Tackett & Bottjer 2012) the identity of these cephalopods is not well documented. Molecular clock analyses on extant taxa indicate a significant diversification of coleoids during the MMR, which may have been linked to the appearance of novel feeding strategies (Tanner *et al.* 2017). Yet, the part played by nautilids in the MMR has never been investigated, as their shell allows only limited palaeocological interpretation. While the shells that evolved during the Mesozoic and Early Cenozoic exhibit high morphological disparity, rhyncholites have been suggested to show little disparity over time (Gasiorowski 1973; Teichert & Matsumoto 2010; Tintant & Kabamba 1985).

Another group of fossils, which are present from the Jurassic to the Cretaceous (Figs 2, 3) are called rhynchoteuthis (from *Rhynchoteuthis* d'Orbigny 1847). They exhibit an overall morphology that is similar to that of rhyncholites except for a slight difference in the posterior part called the shaft (Figs 3, 4). These structures have been interpreted by Gasiorowski (1973) as adaptations to specialized diets in response to the colonisation of deeper waters. Because they have never been found *in situ*, the attribution of these arrow shaped structures is debated (see details in material and methods). Because their overall morphology is so similar to rhyncholites, we investigate these forms along with rhyncholites.

The aim of this study is to explore the disparity of rhyncholites through time. Here, we quantitatively characterize the morphology of rhyncholites and rhynchoteuthis from the Triassic to present day using 3D geometric morphometric approaches (Zelditch *et al.* 2012). This method allows to consider the complete shape variability of the object and to detect subtle morphological variations (Zelditch *et al.* 2012). We test the idea that Nautilida diversified their feeding habits during the MMR in response to the appearance of novel niches and explore the similarity between rhyncholites and rhynchoteutis.

## Material and methods

### Nomenclature and parataxonomy

*In situ* rhyncholites are rare in the fossil record. A few specimens have been found associated with a shell, eliminating any doubt regarding their affinity to Nautilida (Foord 1891; Dietl & Schweigert 1999; Klug *et al.* 2021). Beyond these few occurrences, a variety of arrow shaped structures similar to rhyncholites have been found isolated in sediments. Their affinity to any Nautilida genus is impossible to establish with certainty. A parataxonomical system is thus used for their classification. To date, many genera and species have been described, without reaching a consensus (Till 1906, 1907; Shimansky 1947, 1949; Houša 1969; Teichert 1964; Geyssant 1970; Teichert & Spinosa 1971; Geyssant & Geyer 1972; Gasiorowski 1973; Kostak *et al.* 2010; Pacaud 2010; Weaver *et al.* 2012). In this study, we use the taxonomy proposed by Gasiorowski (1973) based on the work of Till (1907, 1908). Their taxonomic characters are the best defined and, therefore, the most reproducible. The term *Rhyncholites* (Faure-Biguet 1819) is used for morphologies similar to that of modern nautilus and are known in the fossil record from the Middle Triassic onwards. To avoid any confusion, in this study, we use the unitalicized term 'rhyncholites' to refer to the calcified tip of the beak of Nautilida *sensu lato* (fossil and modern), and the italicized term '*Rhyncholites*' to refer to the fossil genus. Rhynchoteuthis refers to

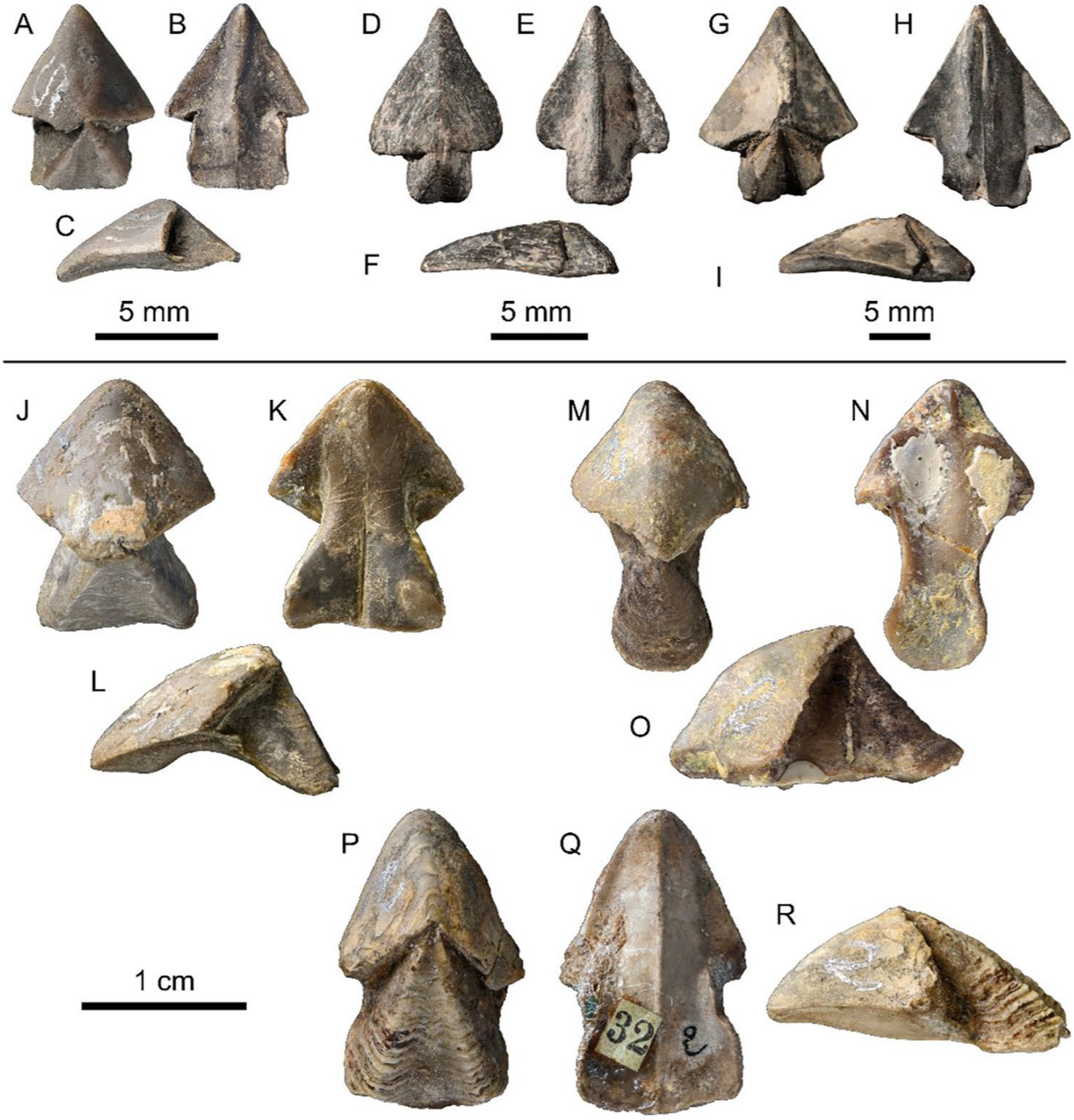

*Fig. 3.* Illustration of *Rhyncholites* and rhynchoteuthis genera. A–C, *Akidocheilus* (Coll. OSUG n° UJF-ID.16030). D–F, *Leptocheilus* (Coll. UB n° UBGD.294217). G–I, *Mesocheilus* (Coll. UB n° UBGD.294196). J–L, *Gonatocheilus* (Coll. SU n° SU.PAL.2017.0.24.73.0). M–O, *Rhyncholites*, (Coll. SU n° SU.PAL.2022.0.52.2). P– R, *Hadrocheilus* (Coll. OSUG, n° UJF-ID.11835). Scale bar A – I: 5mm; J – R: 10 mm. Pictures L. Cazes/O. Bethoux/I. Rouget.

fossils similar to *Rhyncholites* but with a tripartite shaft (Fig. 3). This group occurs only from the Early Jurassic to the Late Cretaceous (Fig. 2) and is, according to Gasiorowski (1973), divided into five genera: *Hadrocheilus, Akidocheilus, Mesocheilus, Leptocheilus* and *Gonatocheilus* (Fig. 3). Following Gasiorowski's recommendations, our study is conducted at the genus level, as the different species of *Rhyncholites* and rhynchoteuthis appear to be questionable.

As no rhynchoteuthis have been found *in situ*, the debate on their taxonomic affinity continues. If their affinity to belemnites or other coleoids is set aside (Shimansky 1949; Clarke 1986; Klug *et al.* 2005; Tanabe *et al.* 2015 a, b), three candidates remain: the ammonites, the nautilids, or a group of unknown cephalopods. The hypothesis that rhynchoteuthis are parts of ammonite beaks has been extensively argued by Riegraf & Schmitt-Riegraf (1995) based on their co-occurrence

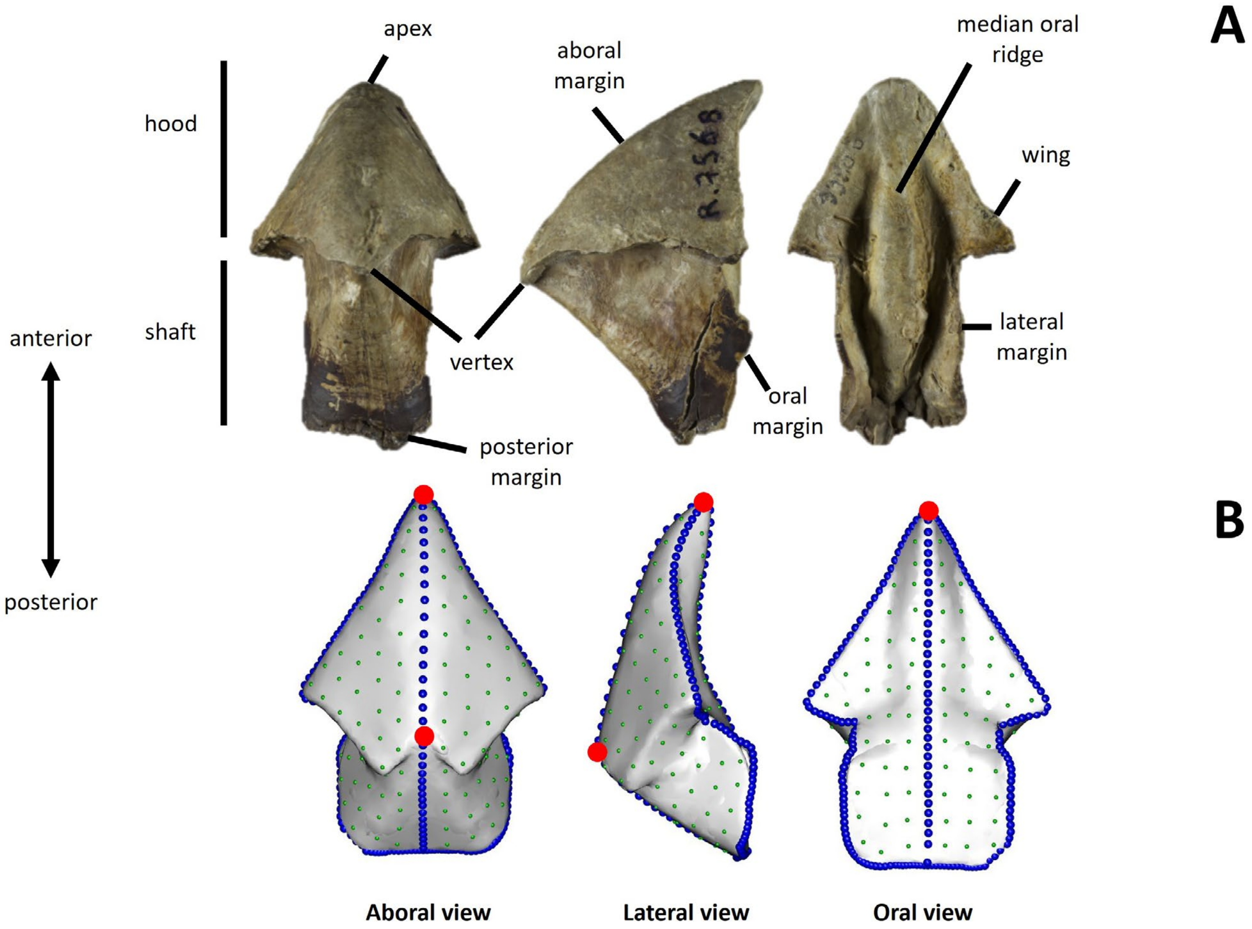

*Fig. 4.* A, anatomy of the rhyncholites illustrated by *Rhyncholites gigantea*. B, landmarks sampling for geometric morphometric analysis. Anatomical landmarks in red, sliding curve semi-landmarks in blue, sliding surface semi-landmarks in green. The illustrated specimen is the theoretical mean shape of the dataset.

with some neoammonoid taxa, as well as the discovery of ammonite jaws with calcareous tips on both upper and lower jaws (Tanabe *et al.* 1980; Lehman *et al.* 1980; Kanie 1982). These jaws, called rhynchaptychus-type jaws (Lehman *et al.* 1980; Tanabe *et al.* 2015a), have been described in Phylloceratina (*Hypophylloceras*: Tanabe *et al.* 2015a; *Phyllopachyceras*: Tanabe & Landman 2002; Tanabe *et al.* 2013) and Lytoceratina (*Tetragonites*, *Gaudryceras*, *Aanagaudryceras*: Tanabe *et al.* 1980, 2012; Lehmann *et al.* 1980; Kanie 1982; Tanabe and Landman 2002; Tanabe *et al.* 2015a). However, these rhynchaptychus-type jaws only occur in the Cretaceous (Tanabe *et al.* 2015a) and to date none are known from the Jurassic.

The upper jaw of Lytoceratina described by Tanabe *et al.* (1980, fig. 2A–C) and Kanie (1982, pl. 39, figs 3, 5a–c, pl. 40, fig. 1a, b) was later recognized as a misidentified lower jaw (Tanabe & Landman 2002; Nemoto & Tanabe 2008; Tanabe *et al.* 2015a). Therefore, the upper jaw of Lytoceratina is still unknown. Moreover, the calcified tip of the upper jaw in the Phylloceratina appears to consist of a thin layer of calcite, more similar to the conchorhynch calcite covering than to the massive tip of rhynchoteuthis or *Rhyncholites*. Therefore, we consider that there is insufficient evidence to assert that rhynchoteuthis were parts of ammonite beaks, and that instead we argue that their affinity is unknown, but probably related to Nautilida due to the close morphological resemblance and lack of evidence for affinity to any other group. The study of these structures along with rhyncholites is useful to better understand the evolution of these groups.

## Specimens

The dataset comprises 254 specimens including 241 fossils of *Rhyncholites* and rhynchoteuthis, and 13 modern rhyncholites, most of them coming from museum collections (see details in Supplementary Table 1). Fossil samples come from 38 French localities and one in southern India. As stratigraphical levels are inconsistently described in collections, we decided to study the variability of forms at the scale of geological periods, which are known with certainty for all specimens. This allows us to analyse a larger number of samples than if we had chosen the stage. This is appropriate for an exploration of the 3D morphological variability of *Rhyncholites* and rhynchoteuthis.

Sampling details by genus and period are given in Table 1. In total, the dataset is composed of 12 Triassic specimens, 113 Jurassic specimens, 99 Cretaceous specimens, and 17 Palaeogene specimens. Late Jurassic and Early Cretaceous specimens are especially well represented in this dataset. Although appearing imbalanced, this reflects what is known in the fossil record in terms of temporal distribution, number of genera, and morphological disparity (Fig. 2; Till 1906; Gasiorowski 1973). The modern nautilus dataset is composed of 2 *Allonautilus scrobiculatus*, 5 *Nautilus pompilius* and 6 *Nautilus macromphalus*.

*Table 1.* Genera and age distribution of the specimens used in this study.

| Genera | Sampling by genus | Period | Sampling by Period |
|---|---|---|---|
| *Akidocheilus* | 56 | Jurassic | 6 |
| | | Cretaceous | 50 |
| *Gonatocheilus* | 99 | Jurassic | 86 |
| | | Cretaceous | 13 |
| *Hadrocheilus* | 27 | Jurassic | 1 |
| | | Cretaceous | 26 |
| *Leptocheilus* | 15 | Jurassic | 15 |
| *Mesocheilus* | 2 | Jurassic | 2 |
| rhyncholites | 55 | Triassic | 12 |
| | | Jurassic | 3 |
| | | Cretaceous | 10 |
| | | Palaeogene | 17 |
| | | Modern | 13 |

*Fossil specimens.*- 45 from Sorbonne Université (Paris); 41 from the Université de Bourgogne; 11 from the Réserve Géologique des Alpes de Haute Provence (Aix en Provence); 49 from the Musée national d'histoire naturelle – Luxembourg; 10 from a private collection (Gilles Bailly); 58 from the Observatoire des Sciences de l'Univers de Grenoble; 25 from the Muséum national d'Histoire naturelle (Paris); 2 from Delhi University, Geology Department (Delhi).

*Modern specimens.*- 4 *Nautilus macromphalus* from the American Museum of Natural History (New-York); 9 specimens from the Muséum national d'Histoire naturelle (Paris) (2 *Allonautilus scrobiculatus*, 2 *Nautilus macromphalus*, 5 *Nautilus pompilius*). The details of all specimens are given in Sup. Table 1. All specimens are considered adults based on their shell size.

## *Methods*

*Digitization.*- Specimens from the MNHN and the private collection were digitized by photogrammetry using a Canon g7 mark ii camera and the software Agisoft Metashape (version 1.4.0). All other specimens were digitized using an X-ray microtomograph (µCT) X-Tek HMX 160 µCT system (Nikon, X-Tek Systems Ltd.) at the University of Hull, Department of Engineering, Hull, UK, at a cubic voxel resolution between 2 and 3 µm. The surfaces were reconstructed in 3D using the Amira software (version 6.3.0). A comparison test on five specimens digitized both with photogrammetry and microtomography was conducted. There were no significant differences between the methods (PERMANOVA on symmetrized Procrustes coordinates, see statistics section below, p-value > 0.05), and, therefore, the two methods were considered comparable. In modern specimens, the thickness of the rhyncholites tapers sharply in its posterior part, becoming a thin calciferous covering, attached to the chitinous surface of the hood (Fig.1). In fossil specimens, this thin covering is not present because of systematic wear and tear during fossilization. The full extent of the missing parts in fossil specimens remains unknown, however. Therefore, to allow the morphological comparison between modern and fossil rhyncholites, a virtual erosion was performed on the modern specimens. We empirically removed 3 or 4 superficial layers of pixels on the surface (depending on the initial resolution), using the 'erode' function in the Materialize Mimics (v.21.0) software (Fig. 5).

*Geometric morphometrics.*– As only a few landmarks can be recognized on both rhyncholites and rhynchoteuthis, a traditional two-dimensional landmark-based approach does not adequately represent the objects shape. Therefore, to quantify the shape of the rhyncholites (modern and fossil) and rhynchoteuthis, we used a three-dimensional landmark-based approach (Fig. 4), following the method of Roscian *et al.* (2022). A set of anatomical landmarks, sliding curve, and surface semi-landmarks were used. Sliding semi-landmarks are transformed into geometrically homologous landmarks that can be used to compare shapes (Gunz *et al.* 2005). Semi-landmarks are allowed to slide along the predefined curves and surfaces while minimizing the bending energy (Gunz & Mitteroecker

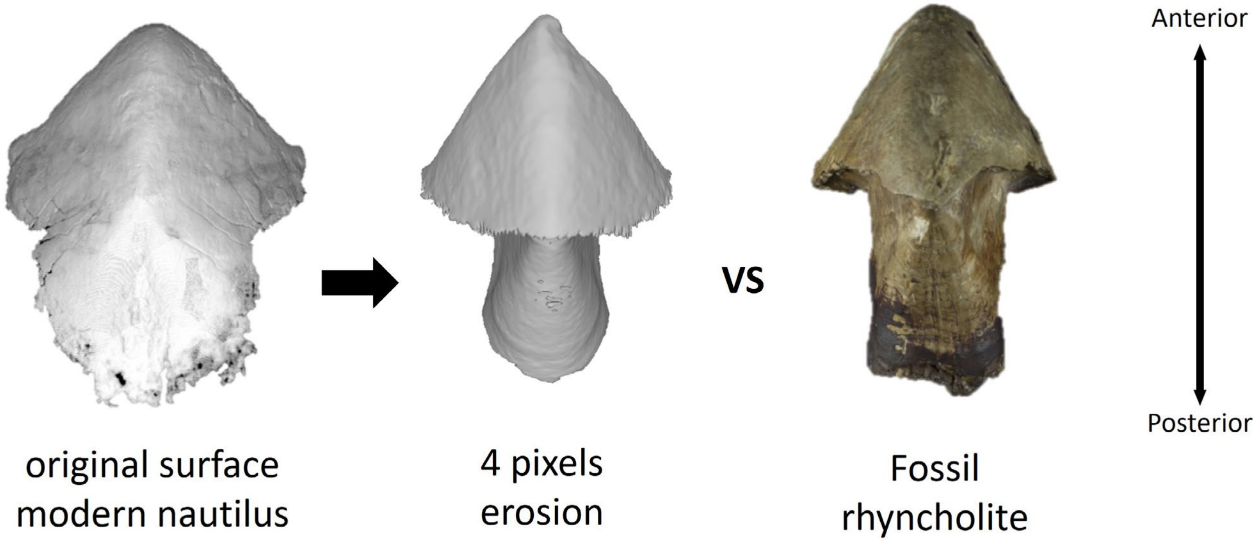

*Fig. 5.* Pixel erosion method. The illustrated modern specimen belongs to *Nautilus macromphalus* before digital erosion (left) ant after digital erosion (centre). For comparison purpose, a fossil specimen of *Rhyncholites gigantea* is included. All are in aboral view.

2013). Two anatomical landmarks were digitized at the apex and vertex of the rhyncholites. Three curves were placed between these anatomical landmarks: one from the apex to the vertex passing along the medial oral line composed of 52 sliding curve semi-landmarks, one from the vertex to the apex following the aboral ridge composed of 17 sliding curve semi-landmarks, and one forming a loop departing from the apex following the lateral and posterior edge of the rhyncholites composed of 161 sliding curve semi-landmarks. A template composed of 182 sliding surface semi-landmarks added to the previously described landmarks and curves semi-landmarks was digitized on a 'mean' specimen allowing to characterize the oral and aboral surfaces of the rhyncholites (Fig. 4).

Subsequent analyses were performed using the R software (v.4.2.2, R Core Team, 2020). Based on the anatomical landmarks, all the sliding surface semi-landmarks of the template were projected on each specimen and adjusted to their curves and surfaces to minimize the bending energy, using the R Morpho package (Schlager 2017). All measured individuals were subjected to a generalized full Procrustes superimposition using the Morpho package. This procedure allowed us to standardize the configurations of landmarks for position, scale, and orientation. To limit the bias caused by different preservation conditions between the left and right parts of the rhyncholites, the landmark configurations obtained after Procrustes superimposition were mirrored and the mean position for each pair of points was calculated using the Geomorph package (Adams *et al.* 2021). These new symmetrized coordinates were used as shape variables in the subsequent analyses. Rhyncholites size was estimated from centroid size, i.e., the square root of the sum of the squared distances from each landmark to the centroid of the landmark configuration. Virtual shapes along the axes of the Principal Components Analysis (PCA) were reconstructed using the Geomorph package by plotting a set of Procrustes shape variables in tangent space and displaying the shape of specimens at the ends of the range of variability along each principal component axis.

*Statistics.*- The symmetrized Procrustes coordinates were analysed using a Principal Component Analysis (PCA) on the variance-covariance matrix using the ade4 R package (Chessel *et al.* 2004). Shape differences between genera and ages were tested using a PERMANOVA (non-parametric multivariate analysis of variance based on 9999 permutations) and associated pairwise post-hoc tests, considering the first PC axes whose cumulative variance explains more than 95% of the total variance. Linear regressions between shape (represented by the PC axes) and centroid size were used to assess the effect of evolutionary allometry (Klingenberg 2016). To visualize the overall morphological proximity of the considered groups in the morphospace, neighbour joining trees based on shape were computed in R using scores on the set of significant PC axes. The R package dispRity (Guillerme 2018) was used to investigate morphological disparity between groups and through time, from the PCA scores using sum of variances (SOV) as our chosen metric. The datasets were subsampled for 1000 bootstrap replicates to generate confidence intervals. All supplementary material is available at https://doi.org/10.48579/PRO/SGEMAE.

# Results

## *Size*

There is a significant size difference between rhyncholites and rhynchoteuthis (Fig. 6; t-test, p-value < 0.001). Fossil specimens are, on average, larger than modern ones. Among the rhynchoteuthis, *Leptocheilus* are significantly smaller than other genera. *Hadrocheilus* are larger and more variable than other genera. Fossil rhyncholites are bigger than modern ones, and exhibit a greater variation, the most striking example being the 5-cm-long *Rhyncholites gigantea*. Among modern species, rhyncholites from *Nautilus macromphalus* are bigger than those from *Nautilus pompilius* and exhibit a larger size range (Fig. 6). The two rhyncholites of *Allonautilus scrobiculatus* are among the smallest rhyncholites of the modern specimens under study. There is no allometry as indicated by the absence of a correlation between PCA scores and centroid size, neither for the entire data set, nor for any genus taken separately (Supplementary Fig. 1).

## *Geometric morphometrics*

*Rhyncholites.*– In the literature, rhyncholites are considered as morphologically stable since the Middle Triassic (Saunders 1978; Ward 1984), 'with a high degree of overlap in the morphology of rhyncholites belonging to different extant species of *Nautilus*' (Saunders 1978). To study the morphological variability in modern and fossil rhyncholites, a PCA was performed. Out of the significant axis, only the first five explain more than 5% of the total variance and are discussed here (PC1 = 39.01%; PC2 = 14.94%; PC3 = 9.70%; PC4 = 6.73%; PC5 = 5.29%; cumulative variance = 75.67% of the total variance; Fig. 7, Supplementary Fig. 2). The main shape variation associated with these PCs is as follows

1. PC1 mainly reflects a size and shape gradient of the shaft (Fig. 7). At the most negative values, the shaft is long, about 1.5 times the length of the hood. It has a spatulate shape, wide and rounded in its posterior part, with a constriction in its anterior part, just before the junction with the hood. At the most positive values, the shaft is much shorter, barely as long as the hood. Its posterior edge is straighter, narrower, and widens anteriorly towards the junction with the hood.
2. PC2 is characterized by a greater deformation of the shaft and the hood (Fig. 7). Negative values are associated with a robust morphology, with a shaft that is slightly longer than the hood. In aboral view, the shaft is spatulate with a constriction in the anterior part. The hood is sub triangular, almost twice as wide as long, with a rounded apex forming an angle of about 90°. In lateral view, the oral margin

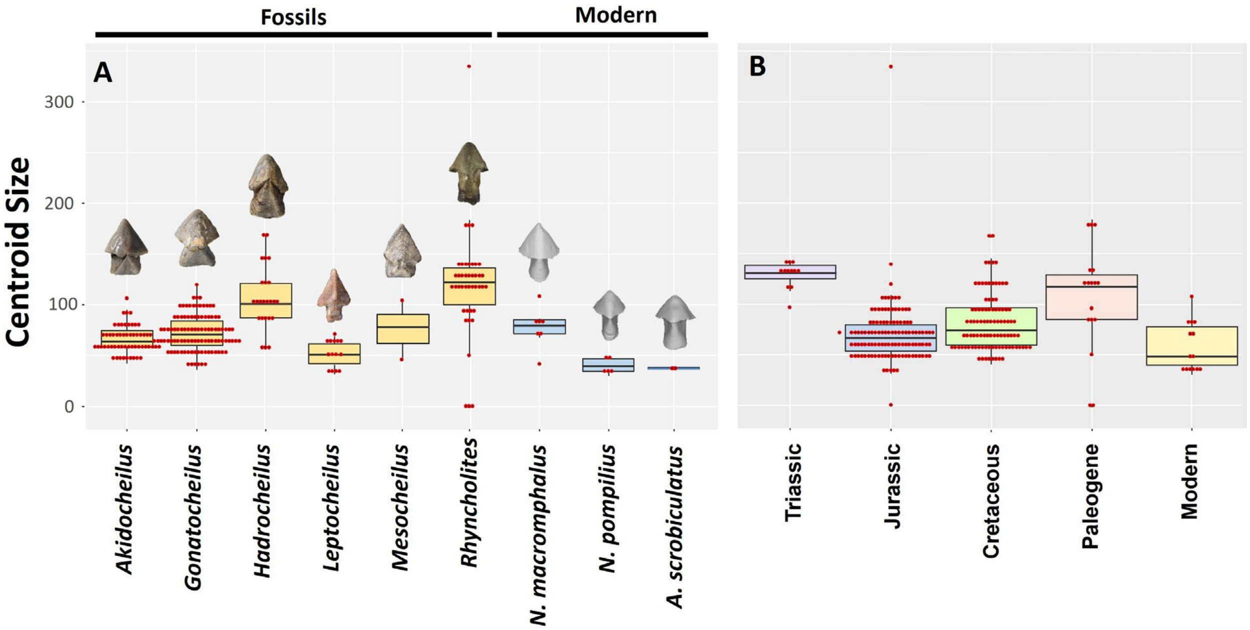

*Fig. 6.* Centroid size variations. A, between genera (for fossil specimens) and species (for modern specimens); yellow, fossil specimens; blue, modern specimens. B, between eras.

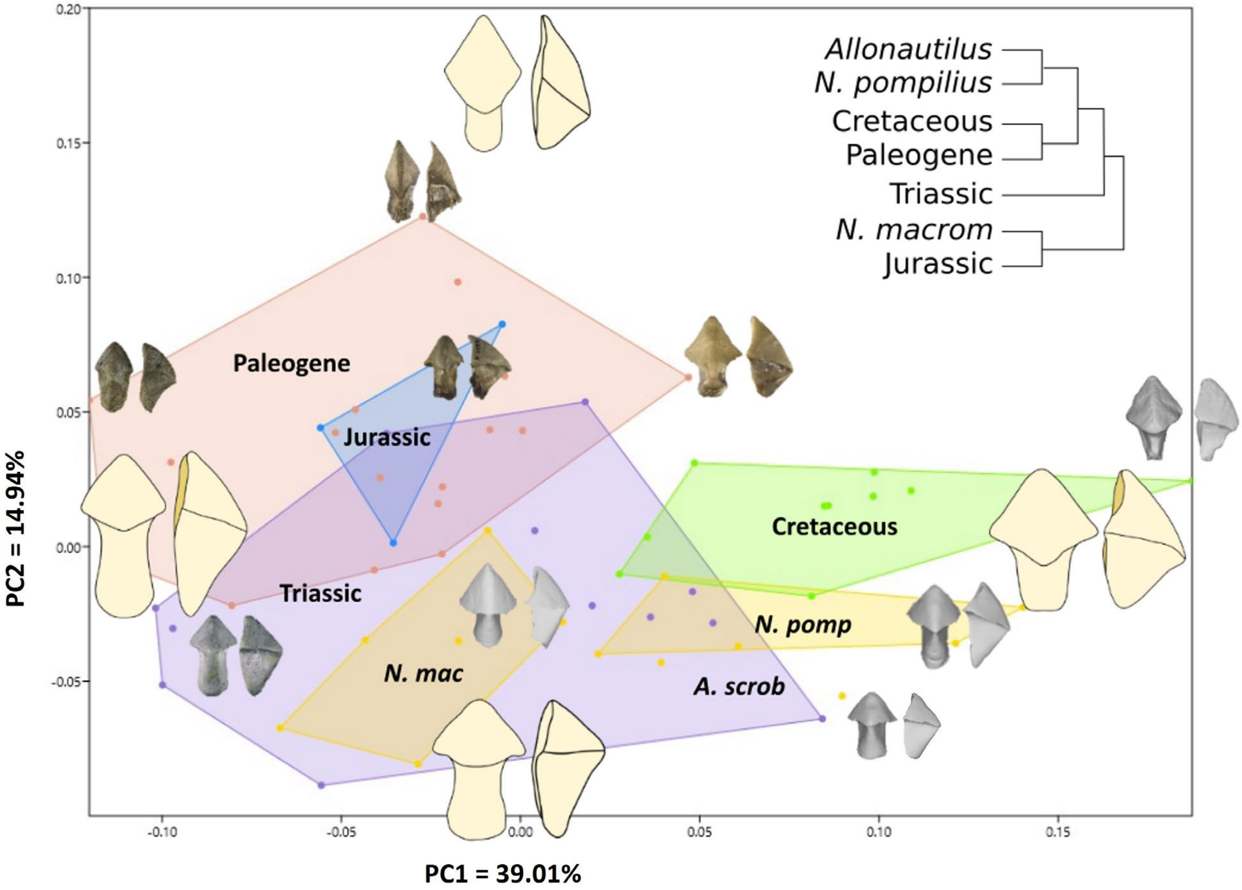

*Fig. 7.* Rhyncholites shape differentiation between periods. The first two principal axes of the PCA on the symmetrized Procrustes coordinates based on rhyncholites only are displayed. The theoretical shape at the extremity of each axis is illustrated in beige. Pictures of some specimens were added for illustration. A morphological proximity tree realized by Neighbour joining on the first four axes of the PCA is displayed.

is slightly rounded and convex. Positive values are associated with a more slender morphology with a very short shaft. The lateral margins are parallel, and the posterior margin is rounded in aboral view. The hood has a rhomboid shape with a long posterior part and a very sharp apex, with an angle of about 70°. In lateral view, the aboral margin of the hood has a curved slope. The anterior part of the oral margin is straight except for a slight depression just before the apex which gives the rhyncholites a slight 'claw-like' appearance.

3. PC3 mainly corresponds to different stages of preservation of the lateral sides of the hood and the posterior margin of the shaft (Supplementary Fig. 2). These areas are very thin and usually erode in fossil material. This preservation variability is uniformly spread across all species and time periods and is, therefore, considered as intra-group variability.
4. PC4 is mainly driven by a few extreme Triassic shapes with a short and rounded shaft, displaying in lateral view a very high profile and a strongly convex oral margin (Supplementary Fig. 2). PC5 tends to differentiate specimens with a large shaft, high profile, and concave oral margin from to specimens with an hourglass shaped shaft displaying a marked constriction and a larger posterior part in dorsal view, and a lower and flatter profile (Supplementary Fig. 2).

Modern forms are included in the morphological variability of the fossil forms. The fossil forms are spread over a large part of the morphospace, especially positive values of PC2, while the modern forms are all grouped at negative values (Fig. 7).

The first PC axis is mainly driven by the shape differences between Cretaceous and some modern species (*N. pompilius, A. scrobiculatus)*, and the rest of the dataset (Fig. 7). PC2 reflects the morphological shift between the Palaeogene and Jurassic specimens, and the rest of the dataset (Fig. 7). PC4 tends to reflect period order through time, with the Triassic/Jurassic group standing out from other periods (Supplementary Fig. 2). No group discrimination is visible on PC 3 and 5 which represent shape variability common to all groups (Supplementary Fig. 2).

The modern species, *Nautilus macromphalus, N. pompilius*, and *Allonautilus scrobiculatus* (to a lesser extent as the sample is composed of only two specimens) are well separated, showing different shapes between species (Fig. 7, Supplementary Fig. 2). Rhyncholites from *N. macromphalus* differ from those from other species along PC1. *Allonautilus scrobiculatus* rhyncholites are more similar to those of *N. pompilius* than *N. macromphalus,* as shown on the neighbour joining tree, yet they differ along PC2.

*Rhynchoteuthis.*- To study the morphological variability of rhyncholites and rhynchoteuthis together, a second PCA was performed on the total dataset after new Procrustes superposition. Out of the significant axis, only the first five explained more than 5% of the total variance and are discussed here (PC1 = 38.53%; PC2 18.99%; PC3 = 9.64%; PC4 = 6.87%; cumulative variance = 74.03% of the total variance; Fig. 8; Sup. Fig. 3). On all axes, fossil *Rhyncholites* occupies a broader area of the morphospace than initially expected compared to rhynchoteuthis, supporting the significant morphological variability described earlier. Based on the two first axes, significant morphological differences are found between rhyncholites and rhynchoteuthis, but a morphological continuum exists between the two groups (Fig. 8). No discrimination between groups can be made on PC3 and PC4 (Supplementary Fig. 3).

A broad range of variation is observed among the genera *Hadrocheilus*, *Gonatocheilus,* and *Akidocheilus,* while *Leptocheilus* show a much lower variability, comparable to that found in *Rhyncholites*. The three best recognized genera, *Gonatocheilus, Hadrocheilus,* and *Leptocheilus*, are relatively well separated in the morphospace while *Akidocheilus* and *Mesocheilus* overlap with several other species, with the small

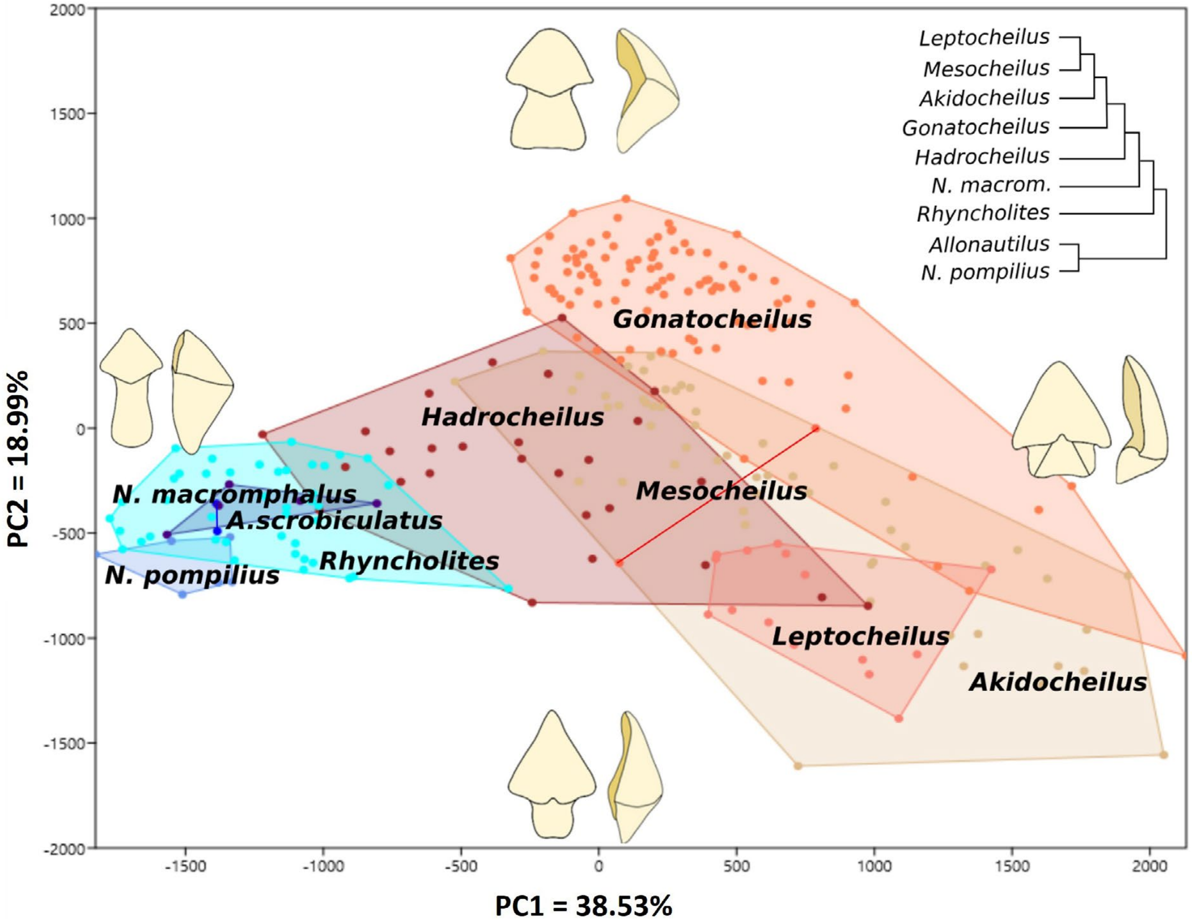

*Fig. 8.* Rhyncholites (blue) and rhynchoteuthis (orange) shape differentiation between genera and species. The first two principal axes of the PCA on the symmetrized Procrustes coordinates are displayed. The theoretical shape at the extremity of each axis is illustrated in beige. A morphological proximity tree realized by Neighbour joining on the first four axes of the PCA is displayed.

sample size of *Mesocheilus* preventing further interpretation for this group. This observation is consistent with their description as intermediate forms (Till 1906; Gasiorowski 1973).

The first PC sorts rhynchoteuthis towards positive values and rhyncholites toward negative values, with little overlap between the two groups (Fig. 8). Positive values on this PC1 are associated with morphologies possessing a short and large shaft, twice as wide as tall. The central part of the posterior margin presents a depression between the two lateral crests (characteristic of rhynchoteuthis). The hood is triangular and isosceles in aboral view, about twice as long as the shaft with a slightly rounded apex displaying an angle close to 60°. In lateral view, the rhyncholites is moderately high. The generally straight oral margin with a central depression creates a slightly arched overall shape in lateral view. The anterior part of the oral surface has a slight protuberance. The aboral margin is curved.

The negative values of PC1 are associated with narrow morphologies presenting a long shaft, twice as long as the hood (Fig. 8). In aboral view, the shaft is twice as long as wide, with a slight widening in its posterior part resulting in a spatulate morphology. The hood has a rhomboid shape and is slightly wider than long. The apex has an angle of about 80°, with a fairly sharp point. In lateral view, the rhyncholites is quite high. The oral margin is convex with a marked curvature of the posterior part. The oral surface is visible in its anterior part at the level of the hood, protruding from the wings. The aboral margin of the hood and the shaft are straight.

The second PC rather distinguishes the differences between the different genera of rhynchoteuthis (Fig. 8). *Leptocheilus* is found at the most negative values, *Gonatocheilus* at the most positive values, and *Hadrocheilus* in between, with very little overlap between these three genera. *Mesocheilus* and *Akidocheilus* both intersect with these three genera, placing them as morphological intermediaries.

The forms located at the most negative values of PC2 present a short and narrow shaft in aboral view, about as long as wide (Fig. 8). The triangular hood is about twice as long and wide as the shaft. Its apex forms a sharp angle of about 70°. In lateral view, the oral surface is visible and presents a convex bump at the level of the vertex, followed in the anterior third of the margin by a concave depression, creating a hook-like appearance in lateral view. The rhyncholite is moderately high and the shaft has a steep slope in this view.

Specimens at the most positive values of PC2 present a long shaft in aboral view, widen in the posterior part, tighten, and pinch in the anterior part, creating an overall cuneate shape (Fig. 8). The shaft is as long as it is wide in its posterior extremity. The rhomboid hood is as long and as wide as the shaft. Its apex is rounded and has an angle of about 70°. In lateral view, the rhyncholite is high. The oral surface is widely visible in its anterior part. The first anterior quarter presents a bump, followed in its posterior part by a deep depression, ending approximately at the level of the vertex. The aboral margin is quite rounded, presenting a soft and regular curvature on the hood, which plunges abruptly on the shaft. The posterior end of the shaft is slightly upturned dorsally.

The specimens of *Gonatocheilus* and *Akidocheilus* at the most negative values on the two axes of PCA have all been preserved with the wings of the hood more complete (broken more posteriorly than the others), with sediment between the wing and shaft. Their grouping in this area of the morphospace is therefore mostly due to their better preservation than the other specimens.

## *Variation through time*

The temporal distribution of rhyncholites in this morphospace shows different areas associated with certain time periods (Figs 7, 8, Supplementary Figs 2, 3). The Triassic forms occupy a central position in the morphospace. *Nautilus macromphalus* are included in the area of the morphospace occupied by Triassic specimens. The Jurassic forms occupy higher PC2 values, and their area partly overlaps the one for the Triassic forms. The Cretaceous forms are completely shifted towards higher PC1 values, slightly overlapping the space of the Triassic forms.

Rhyncholites of *Nautilus pompilius* are positioned close to those of Cretaceous forms on the neighbour joining tree, and in the morphospace are only slightly shifted towards negative PC2 values (Fig. 7). Specimens from the Palaeogene completely overlap the morphospace of the Jurassic forms and slightly overlap the morphospace of the Triassic forms but shifted towards higher values of PC2.

In rhynchoteuthis, Jurassic and Cretaceous forms occupy roughly the same area of the morphospace (Supplementary Fig. 4). Some specimens of *Hadrocheilus* from the Cretaceous seem to exhibit higher PC1 values than Jurassic specimens. More Cretaceous specimens are required to exclude a sampling bias in the observed pattern.

## *Disparity*

Disparity is higher in fossil specimens than in modern ones (Fig. 9; Tables 2, 3). The small sample size for *Allonautilus* and *Mesocheilus* prevents any

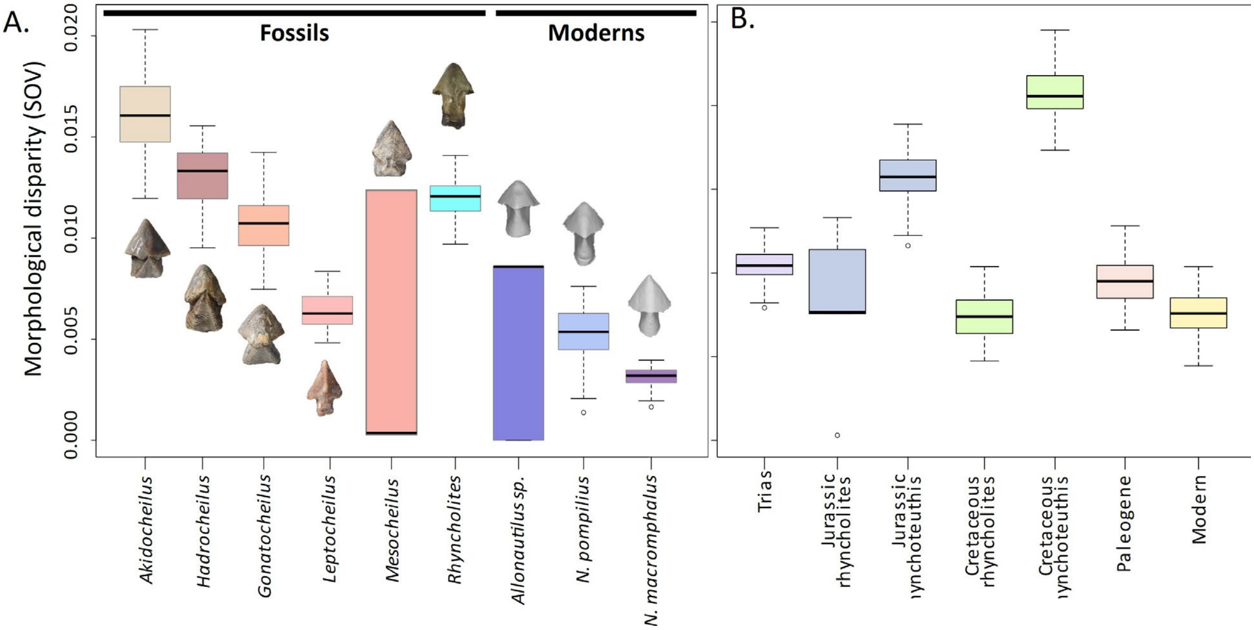

*Fig. 9.* Rhyncholites and rhynchoteuthis morphological disparity. A, between genera and species. B, through time. SOV: Sum of variance.

*Table 2.* Morphological disparity of each group. n = sampling per group. obs = observed disparity (not bootstrapped). bs.median = median bootstrapped disparity. 2.5%, 25%, 75% and 97.5% = confidence intervals. Modern species are in bold.

| group | n | obs | bs.median | 2.5% | 25% | 75% | 97.5% |
|---|---|---|---|---|---|---|---|
| *Akidocheilus* | 56 | 0.017 | 0.016 | 0.013 | 0.015 | 0.018 | 0.019 |
| *Gonatocheilus* | 99 | 0.010 | 0.010 | 0.008 | 0.010 | 0.011 | 0.013 |
| *Hadrocheilus* | 27 | 0.014 | 0.013 | 0.011 | 0.012 | 0.014 | 0.017 |
| *Leptocheilus* | 15 | 0.007 | 0.006 | 0.005 | 0.006 | 0.007 | 0.008 |
| *Mesocheilus* | 2 | 0.013 | 0.000 | 0.000 | 0.000 | 0.013 | 0.013 |
| Fossil *Rhyncholites* | 42 | 0.012 | 0.012 | 0.010 | 0.011 | 0.013 | 0.014 |
| ***A. scrobiculatus*** | 2 | 0.009 | 0.009 | 0.000 | 0.000 | 0.009 | 0.009 |
| ***N. macromphalus*** | 6 | 0.004 | 0.003 | 0.002 | 0.003 | 0.003 | 0.004 |
| ***N. pompilius*** | 5 | 0.006 | 0.005 | 0.002 | 0.005 | 0.006 | 0.007 |

*Table 3.* Morphological disparity through time. n = sampling per group. obs = observed disparity (not bootstrapped). bs.median = median bootstrapped disparity. 2.5%, 25%, 75% and 97.5% = confidence intervals.

| group | n | obs | bs.median | 2.5% | 25% | 75% | 97.5% |
|---|---|---|---|---|---|---|---|
| Triassic *Rhyncholites* | 12 | 0.011 | 0.011 | 0.007 | 0.010 | 0.011 | 0.012 |
| Jurassic *Rhyncholites* | 3 | 0.013 | 0.008 | 0.000 | 0.008 | 0.011 | 0.013 |
| Jurassic rhynchoteuthis | 110 | 0.016 | 0.016 | 0.013 | 0.015 | 0.017 | 0.019 |
| Cretaceous *Rhyncholites* | 10 | 0.008 | 0.007 | 0.004 | 0.006 | 0.008 | 0.010 |
| Cretaceous rhynchoteuthis | 89 | 0.021 | 0.021 | 0.018 | 0.020 | 0.022 | 0.024 |
| Palaeogene *Rhyncholites* | 17 | 0.010 | 0.010 | 0.007 | 0.009 | 0.011 | 0.012 |
| Modern *Rhyncholites* | 13 | 0.008 | 0.008 | 0.005 | 0.007 | 0.009 | 0.010 |

meaningful disparity analysis for these genera. The lowest disparity is observed in *N. macromphalus* indicating stable morphology for this species. Disparity is slightly higher in *N. pompilius*, yet still lower than any of the fossil genera. In general, rhynchoteuthis show a high disparity compared to rhyncholites. However, if the genera are considered separately, fossil rhyncholites have a high disparity compared to *Leptocheilus* and *Gonatocheilus* and is quite close to that of *Hadorcheilus*. Rhynchoteuthis presents a broad morphological disparity as soon as they appear in the Jurassic, and this disparity increases across the Cretaceous (Tables 2, 3, Figs 7, 9). In rhyncholites, the maximum disparity is observed just after their appearance in the Triassic, and then decreases during the Jurassic and Cretaceous. Because of the small sample size, Jurassic rhyncholites disparity as calculated here has to be interpreted carefully. The Palaeogene shows a small increase in disparity, before returning in modern specimens to levels similar to Cretaceous ones.

## Discussion

The general morphology of rhyncholites has been considered in the literature as remarkably stable since the Middle Triassic (Saunders 1978). As a result, the morphological variability of *Rhyncholites* has been poorly studied (Pacaud 2010, Tajika *et al.* 2023) reinforced by the outdated idea of evolutionary stasis in *Nautilus*, resulting in it being considered a 'living fossil' (Ward 1984). Post-Triassic nautilid shells do not present striking morphological variation but do display a few episodes of diversification, especially during the Jurassic and the Cenozoic when the shells show more diverse morphologies of cross-sections and new ornamentations (Tintant 1983; Teichert & Matsumoto 2010). Therefore, nautilids were considered an example of mosaic evolution, with few changes in the shape of their rhyncholites in contrast with abundant changes in the shape of their shell (Saunders 1978). The global morphological variability of rhyncholites has never been quantitatively investigated before and this oversight has prevented a full exploration of the evolution of nautilids. Here we quantified for the first time the 3D morphology of rhyncholites and rhynchoteuthis from the Triassic to current day. Our dataset is almost exclusively composed of French localities and reflects the local diversity through time. However, the fact that the two specimens from the Cretaceous of India analysed in this study are included within the range of variation of the French localities of the same time advocates for a weak geographical signal, but cannot by itself conclude on its absence. For this reason, our results are compared to previous work of Gasiorowski (1973) to discuss the observed patterns in a broader context.

The only study to explore morphological variation in fossil *Rhyncholites* and rhynchoteuthis and that attempted to link these data to environmental changes is a monograph by Gasiorowki (1973). This comprehensive article covers all the knowledge published on rhyncholites and rhynchoteuthis at the time of its publication (1973), at a worldwide scale and covering all time periods from the origin of the group to modern day. He found a correlation between morphology, which he interpreted in terms of function (crushing, cutting, and piercing), on the one hand, and depth, palaeogeographical distribution, and lifestyle (in swarms or solitary), on the other hand (Fig. 10). He concluded that there is an evolutionary trend from 'crushing' shapes (*Hadrocheilus* and *Rhyncholites*) to more specialized shapes: 'cutting' (*Gonatocheilus*) and 'piercing' (*Leptocheilus*). He considered *Mesocheilus* and *Akidocheilus* as transitional forms. The first morphology to appear in the Triassic are the 'crushing' shapes, found in the shallow waters of epicontinental seas linked to the Tethys, as isolated occurrences, indicating a solitary lifestyle. These morphologies are similar to modern shapes and are, therefore, considered to correspond to a generalist-like diet as in modern nautilus. 'Piercing' and 'cutting' morphologies are described as specialized shapes corresponding to a specialized diet. These morphologies, as well as transitional forms, appear later in the Middle Jurassic, and are found in deeper Tethyan waters, where they occur in clusters, suggesting a life in swarms. Gasiorowski (1973) also described niche partitioning in the water column, *Leptocheilus* living deeper in the water column than *Gonatocheilus*, and *Hadrocheilus* living in much shallower water (Fig. 10). These depth and morphological gradients are correlated to a size gradient, rhyncholites being smaller as the depth increases (Fig. 10). The hypothesis proposed by Gasiorowski (1973) is that as the water temperature increased in the Late Jurassic to Early Cretaceous, it allowed species to explore new ecological niches in deeper water. With an increase in water depth and pressure, the prey became smaller and softer, and the rhyncholites developed adaptations to these new resources. In the Cretaceous, the opposite transition is observed with successive extinction of the deeper-water species. Eventually, all rhynchoteuthis species disappeared and only rhyncholites survived until today (Fig. 2).

Our results allow us to shed further light on this scenario. We observe considerable variation in the shape of rhyncholites. In line with Gasiorowski's hypothesis, these different morphologies may reflect adaptations

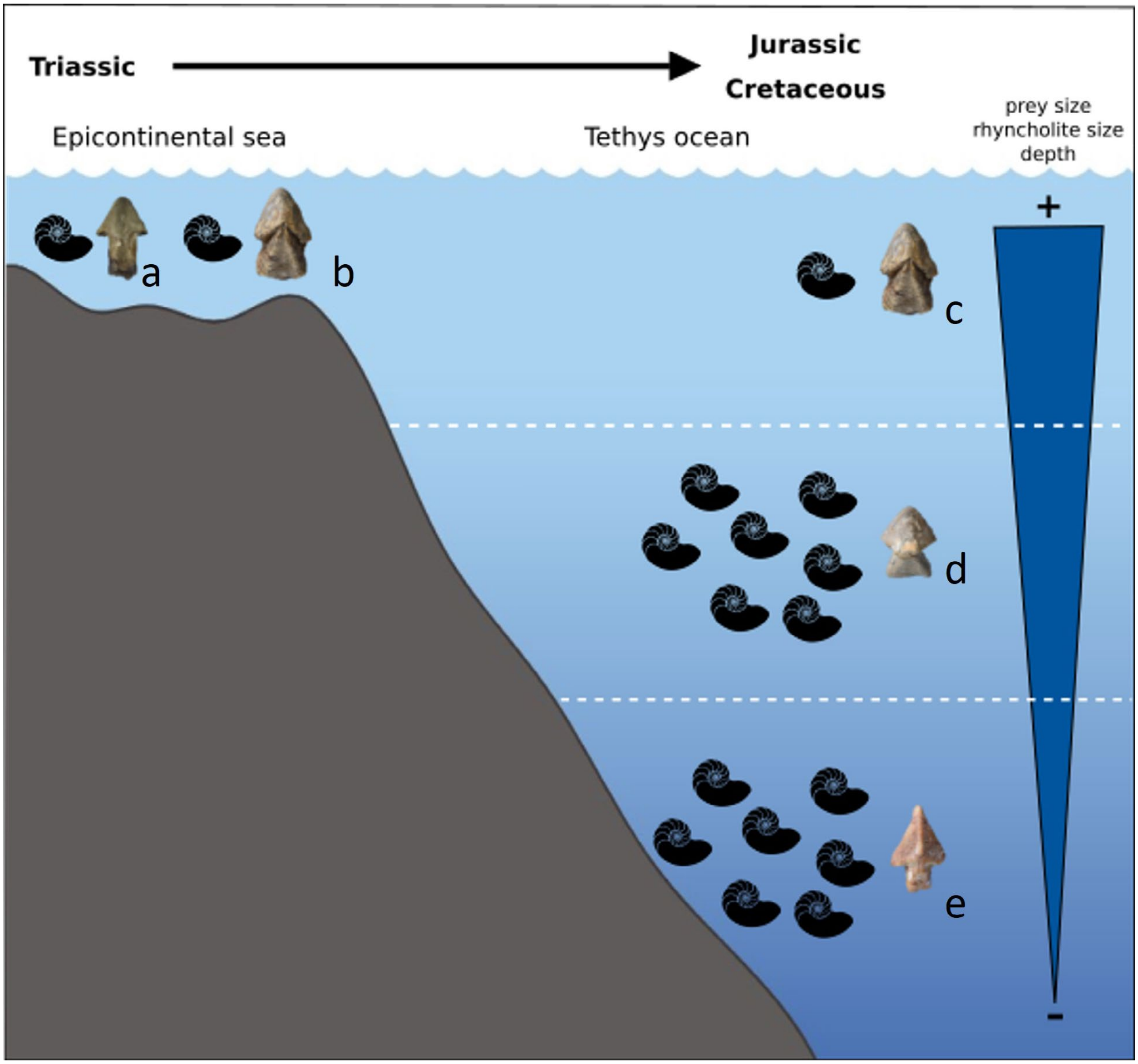

*Fig. 10.* Illustration of Gasiorowski's hypothesis of correlation between *Rhyncholites* and rhynchoteuthis morphology, depth distribution and lifestyle. The dark shell icons indicate the lifestyle (solitary organism *vs* swarm). *Rhyncholites:* (a). Rhynchotheutis: *Hadrocheilus* (b, c), *Gonatocheilus* (d), *Leptocheilus* (e).

to environmental changes and dietary shifts over time. The study of rhyncholites and rhynchoteuthis testify to a richer evolutionary history of nautilids than can be deduced from study of shells alone. The appearance of rhyncholites during the Triassic marked a turning point in nautilid evolution. Specimens from this period show a broad range of shape diversity, around a mean shape with a massive, rounded hood, and a large area of attachment to the chitinous jaw. This Triassic morphology is very similar to that of modern rhyncholites (especially those in *Nautilus macromphalus*). Modern nautiluses are considered opportunistic carnivores and have a durophagous diet, as they have been observed feeding on crustaceans, crabs, and lobsters, but also carrion (Ward & Wickstein 1980; Saunders & Ward 2010; Barord *et al.* 2021). Triassic nautilids probably showed a similar diet (Klug 2001). The appearance of rhyncholites in the Triassic would have enabled nautilids to handle and ingest a greater number of prey, cutting them with their anterior edge, tearing them with their apex, but especially crushing prey with hard shells. Nautilids were thus probably among the first cephalopods to exploit durophagy. The Triassic is the starting point of an intense arms race between hard-shelled prey and their predators, called the Marine Mesozoic Revolution (MMR; Vermeij 1987; Kelley *et al.* 2003; Buatois *et al.* 2016; Antell & Saupe 2021). Our data suggest that the nautilids were at the forefront of this revolution.

Triassic forms, being morphologically similar to modern ones, must have strongly contributed to the common impression of the morphological stasis of rhyncholites (Klug 2001). In the literature, *Rhyncholites* are considered slightly different in the Jurassic and Cretaceous with the appearance of the 'concavi' morphologies (with a concave oral margin in lateral view) in opposition to the 'convexi' morphologies (with a convex oral margin in lateral view) from the Triassic and Palaeogene (Gasiorowski 1973). It is possible that our data are insufficient to document this shift. However, Cretaceous specimens are occupying a new area of the morphospace characterized by reduced shafts and short pointy hoods. This global shaft size reduction could be related to a shift towards smaller prey. The shortening of the jaw attachment area may reflect a decrease in the pressure exerted on the beak and, therefore, a different function from that of Triassic species. This may correspond to a reduction in bite force associated with a transition to a softer diet.

In parallel, the rhynchoteuthis radiation through the Jurassic and Cretaceous presents a broad range of shape, and displays a faster morphological evolution compared to *Rhyncholites*. *Hadrocheilus* appears first, forming a morphological continuum with *Rhyncholites*. Except for their tripartite shaft, their overall morphology is very similar to *Rhyncholites,* and we can assume a similar opportunistic durophagous diet (Gasiorowski 1973; Klug 2001). As mentioned earlier, Gasiorowski (1973) explained that *Hadrocheilus,* and particularly the early and late representatives of the genus from the Early Jurassic and Late Cretaceous are found in the shallow epicontinental seas linked to Tethys and display a 'crushing' morphology. These observations are in accordance with the idea of a diet composed of crustaceans, bivalves, and other prey with shells, living on the sea floor.

During the Jurassic, rhynchoteuthis bearing organisms colonized new ecological niches characterized by deeper waters. This led to the appearance of *Gonatocheilus* living at intermediate depths, then *Leptocheilus* living in still deeper water (Gasiorowski 1973). The colonization of these new niches led to specialization of these organisms for prey living under high ambient pressure and whose size and thickness would therefore be reduced (Gasiorowski 1973). This is reflected in our study in terms of size, *Hadrocheilus* being the largest and *Leptocheilus* being the smallest form. On the other hand, this size gradient does not correspond to any shape gradient between these two genera. In *Leptocheilus*, we find a morphological shift similar to that in Cretaceous *Rhyncholites*, that is, towards forms with a very reduced shaft and an even thinner and more pointed hood, and the appearance of an arrow-shaped head. If we compare these morphologies to the rostrums of the beaks of modern coleoids, an elongation of this area together with a pointed tip are linked to a non-durophagous diet composed mostly of fish, as found in many species of squid (Kear 1994; Roscian *et al.* 2022). These morphologies allow the predator to cut flesh more easily and to handle food items much more precisely than short and robust morphologies such as observed in modern nautilus or octopus. Released selection for durophagy could have resulted in the reduction of the shaft, and therefore, of the jaw insertion area. This specialized diet is in line with what is known about the ecology of these forms, namely a migration to deeper waters in the Tethys.

In *Gonatocheilus*, we find a much more innovative morphology. The shaft is short but wide, indicating a strong attachment to the jaw. The hood is short but pointed, and the profile is arched, with a protruding bump present on the oral side of the tip. This kind of morphology does not occur anywhere else in modern or fossil cephalopods. It is, therefore, more complicated to explain the functional shift and associated diet. The combination of a robust morphology, large shaft, and short hood seems to indicate a diet at least partly durophagous. Living at depths intermediate between *Hadrocheilus* and *Leptocheilus*, it is, therefore, probable that its migration to this new ecological niche is associated with a change towards a more specialized diet. Since *Mesocheilus* and *Akidocheilus* are transitional morphologies between the three groups discussed above, it is likely that their diets also reflected this transition from a general to a more specialized and softer diet.

The 'arms race' characteristic of the Marine Mesozoic Revolution, therefore, probably played a major impact on cephalopod evolution. The fierce competition leading to the evolution of new morphological innovations must have favoured the emergence of rhynchoteuthis in Lower Jurassic. To escape increasing competition, these forms ventured into new ecological niches in deeper waters, leading to a dietary shift facilitated by shapes adapted to more specialized functions. Ammonites, some of which also developed a mineralized lower jaw in lower Jurassic, may have had an important role in the evolution of these trophic relationships. They could have been either nautilid competitors (Gasiorowski 1973) or their prey (Hoffman *et al.* 2021). The radiation of the much more agile coleoids must have increased the competitive pressure on the other cephalopods (Tanner *et al.* 2017). Rhynchoteuthis and 'Cretaceous type' *Rhyncholites* all disappeared at the end of the Mesozoic, perhaps related to adaptations for a specialized diet as well as a reduction in prey availability, as suspected of ammonites. The latter also disappeared at this time linked with the decline of several groups of plankton (Kruta *et al.* 2011). If ammonites were prey of rhynchoteuthis-bearers, their extinction might have contributed to the rhynchoteuthis extinction in the Cretaceous. Only broadly opportunistic morphologies capable of exploiting a large range of food resources persisted over time and crossed the Cretaceous-Palaeogene extinction event.

The diversity of *Rhyncholites* in the Palaeogene is a great surprise. The appearance of sharp shapes seems to attest to a new event of food specialization. The shaft shrinks slightly and the hood becomes long and sharp. The slenderer tip seems more fragile. It is hard to imagine that these forms were useful for durophagy. As with *Leptocheilus*, a comparison with modern coleoid rostrums suggests a transition towards a cutting function and softer diet. This tendency is stronger during the Eocene, but the evolutionary drivers of such a change are not known to date. It is from this time period that the origin of the modern *Nautilus* lineage dates back (Moore 1964; Teichert & Matsumoto 2010). Yet, surprisingly enough, the rhyncholites in the Palaeogene are very different from those of modern nautilus. On the other hand, there is a morphological similarity between Triassic and modern rhyncholites. This demonstrates the important role of studying the morphology of rhyncholites in helping to reconstruct the phylogeny of nautilids.

These results clearly highlight the high disparity in shaft shape and size, not only between the rhynchoteuthis and the rhyncholites, but also amongst the later. As mentioned above, because the shaft is the main insertion area on the chitinous beak, this variation probably impacted the degree of attachment between the two parts. It likely affected the upper beak morphology around the attachment area, with potential consequences on muscles insertions area and volume. As the upper beak shape of modern coleoids cephalopods is linked, to some extent, with habitat and trophic level (Roscian *et al.* 2022), understanding the connection between shaft and upper beak morphology could be informative for further functional studies.

To date only the shell and texture of the hood were considered as diagnostic characters in modern nautilus species (Saunders 2010). Here, the rhyncholites of *Nautilus pompilius* and *Allonautilus scrobiculatus* are similar in size. They are much smaller than those in *N. macromphalus,* which is not what one would have expected based on shell size. In addition, the three species exhibit different rhyncholites morphologies. The rhyncholites in *N. pompilius* and *A. scrobiculatus* are similar in shape and are clearly separated in rhyncholites morphospace from those in *N. macromphalus*. These morphological differences are not easily distinguished by the human eye, especially if only a small number of individuals are observed, but they are clearly visible in 3D morphological space. Therefore, morphological analysis of rhyncholites could be useful to elucidate current issues about nautilus taxonomy. The main shape difference between the group *N. pompilius* and *A. scrobiculatus,* on the one hand, and *N. macromphalus,* on the other hand, appear to be the size and shape of the shaft, which is longer and more spatulate in *N. macromphalus*, combined with a slightly sharper anterior point. Moreover, the morphological disparity observed in *N. pompilius* is higher than the one of *N. macromphalus*. *N. pompilius* is the species with the largest distribution and population size, the strongest polymorphism in shell, and recent studies evidenced a high genetic variation, with a strong geographic component affecting taxonomy (Vandepas *et al.* 2016*;* Wray *et al.* 2016; Combosch *et al.* 2017; Huang *et al.* 2022; Barord et *al.* 2023). Three new species of *Nautilus* recently described also show slight variation in shell morphology (Barord *et al.* 2023). These results have profoundly renewed the study of nautiluses and challenged their taxonomy (Tajika *et al.* 2021). In this context, comparing rhyncholites morphological variation with the molecular data between populations would be an incredible opportunity to reconsider the current taxonomy of the group as well as its evolution using rhyncholites.

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## Supplementary Information

**Supplementary material:** *(Accessible in repository* https://doi.org/10.48579/PRO/SGEMAE)

*Supplementary Fig. 1.* Relationship between size and shape. A, the first four principal axes of the PCA on the symmetrized Procrustes coordinates based on the entire dataset are displayed. Colour code represent the different genera. B, for each genus or species, the first principal axis of the PCA on the symmetrized Procrustes coordinates based on the entire dataset is displayed.

*Supplementary Fig. 2,* Rhyncholites shape differentiation between periods. PC 3, 4 and 5 of the PCA on the symmetrized Procrustes coordinates based on rhyncholites only are displayed. The theoretical shape at the extremity of each axis is illustrated in beige.

*Supplementary Fig. 3,* Rhyncholites (blue) and rhynchoteuthis (orange) shape differentiation between genera and species. The 3rd and 4th axes of the PCA on the symmetrized Procrustes coordinates are displayed. The theoretical shape at the extremity of each axis is illustrated in beige.

*Supplementary Fig. 4.* Rhynchoteuthis shape differentiation between periods. The first two principal axes of the PCA on the symmetrized Procrustes coordinates based on rhynchoteuthis only are displayed.

*Supplementary Table 1.* Full Dataset including: Specimen (name of CT scan), Collection, Genus, Species (as mentioned in collection), Locality, Era, Stage, Centroid size (Csize), and fives first PC axis (PC1-PC5). AMNH: American Museum of Natural History, New York. MNHN: Museum National d'Histoire Naturelle, Paris. OSUG: Observatoire des Sciences de l'Univers de Grenoble. RGHAP: Réserve Géologique des Alpes de Haute Provence. SU: Sorbone Université.

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