A new Meckel’s cartilage from the Devonian Hangenberg black shale in Morocco and its position in chondrichthyan jaw morphospace (#76196)

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A new Meckel's cartilage from the Devonian Hangenberg black shale in Morocco and its position in chondrichthyan jaw morphospace

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Fossil chondrichthyan remains are mostly known from their teeth, scales or fin spines only, whereas their cartilaginous endoskeletons require exceptional preservational conditions to become fossilized. While most cartilaginous remains of Famennian (Late Devonian) chondrichthyans were found in older layers of the eastern Anti-Atlas, such fossils were unknown from the Hangenberg black shale (HBS) and only a few chondrichthyan teeth had been found therein previously. Here, we describe a Meckel's cartilage from the Hangenberg black shale in Morocco, which is the first fossil cartilage from these strata. Since no teeth or other skeletal elements have been found in articulation, we used elliptical Fourier (EFA), principal component (PCA), and hierarchical cluster (HCA) analyses to morphologically compare it with 41 chondrichthyan taxa of different size and age and to evaluate its possible systematic affiliation. PCA and HCA position the new specimen closest to some acanthodian and elasmobranch jaws. Accordingly, a holocephalan origin was excluded. The jaw shape as well as the presence of a polygonal pattern, typical for tessellated calcified cartilage, suggest a ctenacanth origin and we assigned the new HBS Meckel's cartilage to the order Ctenacanthiformes with reservations.

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Abstract

Fossil chondrichthyan remains are mostly known from their teeth, scales or fin spines only, whereas their cartilaginous endoskeletons require exceptional preservational conditions to become fossilized. While most cartilaginous remains of Famennian (Late Devonian) chondrichthyans were found in older layers of the eastern Anti-Atlas, such fossils were unknown from the Hangenberg black shale (HBS) and only a few chondrichthyan teeth had been found therein previously. Here, we describe a Meckel's cartilage from the Hangenberg black shale in Morocco, which is the first fossil cartilage from these strata. Since no teeth or other skeletal elements have been found in articulation, we used elliptical Fourier (EFA), principal component (PCA), and hierarchical cluster (HCA) analyses to morphologically compare it with 41 chondrichthyan taxa of different size and age and to evaluate its possible systematic affiliation. PCA and HCA position the new specimen closest to some acanthodian and

elasmobranch jaws. Accordingly, a holocephalan origin was excluded. The jaw shape as well as the presence of a polygonal pattern, typical for tessellated calcified cartilage, suggest a ctenacanth origin and we assigned the new HBS Meckel's cartilage to the order Ctenacanthiformes with reservations.

Introduction

Fossil chondrichthyans (sharks, rays and chimaeroids) are mainly known from the Devonian onward (Brazeau & Friedman 2015). Exceptional, putative chondrichthyan, as well as acanthodian finds date back to the Silurian (Burrow & Rudkin 2014; Andreev et al. 2016). Only teeth, scales and fin spines of chondrichthyans (whole group, including acanthodians) are strongly mineralized while chondrichthyan endoskeletons are predominantly made of unmineralized cartilage that is only rarely preserved (Seidel et al. 2020).

Despite the difficulties of preservation, chondrichthyan skeletons are frequently found in the middle and late Famennian strata in the Tafilalt and Maïder regions of southern Morocco and constitute important contributions to the understanding of early vertebrates (Ginter et al. 2002; Derycke et al. 2008; Frey et al. 2018; Frey et al. 2020). However, in the late Famennian Hangenberg black shale layers of Morocco, nearly no vertebrate remains have been collected or described so far. The only known contributions to the vertebrate fossil record that are known from these strata are a few chondrichthyan teeth, which are not described but only mentioned in the literature (Klug et al 2016; Frey et al. 2018) as well as some chondrichthyan ichnofossils from layers just above the Hangenberg black shale (basal Hangenberg Sandstone; Klug et al 2021). Here, we

describe a lower jaw found in the Anti-Atlas that represents the first reported cartilaginous remain from the Moroccan Hangenberg black shale.

Outcrops of sediments that were laid down in the time around the end-Devonian Hangenberg crisis can be found at many localities of the Tafilalt and Maïder regions of the Anti-Atlas (Kaiser et al. 2011, 2015; Klug et al. 2021). The Hangenberg crisis was a global mass extinction event at the Devonian/ Carboniferous boundary (Caplan & Bustin 1999; Kaiser et al. 2011), which reflects one of the six largest mass extinction events in earth's history. The Hangenberg crisis followed the Kellwasser event at the Frasnian/ Famennian boundary and affected vertebrate groups to an extent that is comparable to the Big Five mass extinctions (McGhee 1996; McGhee et al 2012, 2013). Therefore, it is seen as a bottleneck in vertebrate evolution and the recovery of formerly diverse vertebrate groups (such as some agnathans, sarcopterygians and placoderms) after the event was minimal (Sallan and Coates 2010; Frey et al. 2018). Indeed, the Hangenberg crisis was more severe than formerly thought and caused a larger diversity loss ~~on~~ genus level than the Kellwasser event (Sallan & Coates 2010). The Hangenberg black shale marks the main extinction phase of the event and was laid down during a supposed global transgression linked with widespread anoxia, likely caused by eutrophication that led to global extinctions of numerous invertebrate groups (Algeo & Scheckler 1998; Sallan & Coates 2010; Kaiser et al 2011, 2015). While invertebrate remains are quite common in the Hangenberg black shale (Schmidt, 1924; Marynowski et al. 2012; Klug et al. 2016; Zhang et al. 2019), it lacks vertebrate remains, which makes the new Meckel's cartilage a particularly important fossil.

The cartilaginous endoskeletons of chondrichthyans are covered by a thin layer of calcified cartilage (Kemp & Westrin 1979; Dean & Summers 2006, Seidel et al. 2016, 2020; Maisey et al. 2020). This thin layer typically shows a distinct polygonal pattern, which is caused by the presence of tesserae, namely the tessellated calcified cartilage (Seide et al. 2016, 2020, 2021; Maisey et al. 2020). Such cartilage is characteristic for modern as well as Devonian crown chondrichthyans (elasmobranchs and holocephalans, Long et al. 2015; Maisey 2020) while these polygonal structures tend to be less distinct in acanthodians (stem chondrichthyans), where only subtessellated calcified cartilage or globular calcified cartilage is reported (Dean & Summers 2006; Brazeau & Friedman 2014; Brazeau 2020; Maisey et al. 2020). Globular calcified cartilage builds the inner layer of tessellated calcified cartilage and can build the entire hard tissue. If globular calcified cartilage is present on the surface a granular pattern is to expect (Burrow et al. 2015; Maisey et al. 2020). Subtessellated calcified cartilage shows fissures along the surface which result in an unorganized pattern. Tessellated calcified cartilage with an outer prismatic layer, in contrast, is well organized and a polygonal pattern is distinct (Maisey et al. 2020; Seidel et al. 2020).

Among the cartilaginous remains, jaws are one of the most relevant anatomical structures from an evolutionary perspective. The evolution of jaws, the Meckel's cartilage, is seen as a key innovation of gnathostomes enabling the first gnathostomes to broaden their range of feeding strategies and prey upon a much greater diversity of animals (DeLaurier & Gerhart, 2018; Deakin et al. 2022). These innovations contributed greatly to the radiation of gnathostomes and possibly to the decline of agnathans (Brazeau & Friedman 2015; Hill et al. 2018). Nevertheless, only very few quantitative

studies about jaw shapes have been published. For example, Hill et al. (2018) quantified jaw shape in modern and in Palaeozoic fishes and demonstrated that jaw shape has a greater disparity in modern fish clades than during the early gnathostome radiation (Silurian and Devonian). This is mostly caused by the great morphological disparity among modern actinopterygians (Hill et al. 2018). Deakin et al. (2022) also mentioned an increasing disparity in jaw shape with ongoing evolution but the functional disparity of early vertebrate jaws to be highest very early in jaw evolution and optimized for a predatory function. Anderson et al. 2011 also deals with jaw disparity and the influence of environmental changes such as the Kellwasser event, which does not seem to affect jaw disparity very much.

The phylogenetic relations within the chondrichthyan total group are still a widely discussed topic (Hanke & Wilson 2006; Brazeau 2009; Davis et al. 2012; Burrow & Rudkin 2014; Brazeau & Friedman 2015; Brazeau & de Winter 2015; Giles et al 2015; Qiao et al. 2016) and acanthodians were just recently recognized as stem chondrichthyans (Zhu et al. 2013; Coates et al. 2017; Rücklin et al. 2021). Members of this group show characteristics of both principal lineages of living gnathostomes (chondrichthyans and osteichthyans), are covered with scales and are often referred to as “spiny sharks” because of the spines in front of their dorsal, anal and paired fins as evident in most taxa of this group (Miles 1970, 1973; Burrow & Rudkin 2014; Qiao et al. 2016). The relationship between jaw shape and phylogeny remains an elusive question since ecological factors likely influence jaw shape to a great degree as well.

Our main aim in this article is, 1) to give a detailed description of this novel find and 2) to determine its possible systematic affiliation. For the latter, we used geometric

morphometrics since the Meckel's cartilage was found ~~solitarily~~ with no further skeletal parts, teeth or scales associated and is therefore hard to assign to a specific taxon. We applied elliptical Fourier (EFA), principal component (PCA) and hierarchical cluster analyses (HCA) to the new small Meckel's cartilage and 41 more chondrichthyan and acanthodian lower jaws. By this action, a morphospace is created which is informative about the relationship between lower jaw shape and phylogeny.

Materials & Methods

The specimen PIMUZ A/I 5139 (Fig.1) was found in the Moroccan Anti-Atlas at the locality Madene El Mrakib (N30.73093°, W4.70749°). Permit for fossil collection and export were given by the Ministère de l'Energie, des Mines, de l'Eau et de l'Environnement, Rabat, Morocco. The specimen is stored at the Palaeontological Institute and Museum of Zurich (Switzerland). It was largely exposed, but covered parts were carefully prepared using a thin steel-needle. Photos of the specimen showing its shape, proportions and preservation (Fig. 1) were taken using a Nikon D2X. Colour and contrast were slightly adjusted in Adobe Photoshop (Adobe Inc. 2019). To show the structure of the fossil's surface in more detail, close-ups were taken with a Leica MZ16 F microscope (Fig. 1C, D, E) and gently adjusted in colour and contrast as well.

Morphometrics

Morphometric techniques together with multivariate and cluster analysis are standard methods to quantify morphology and evaluate groupings or affinities among taxa (Kaesler & Waters 1972; Younker & Ehrlich 1977; Ferrario et al. 1999; Daegling &

Jungers 2000). Here, we use morphometric analyses to compare the new isolated Meckel's cartilage to shapes of other lower jaws with known systematic affiliation and find the most similar shape, or group of shapes, to help determine the new Meckel's cartilage ~~origin~~ at least approximately. To carry out the analyses, outlines of 41 lower jaws representing the main stem and crown chondrichthyan orders were drawn based on photographs and illustrations from the literature (App. 1) using the vector-based software Affinity Designer (Affinity 2019). Sampling is constrained by the limited number of well-preserved fossils of Meckel's cartilages. The jaw shapes used in the analysis were chosen based on the quality of preservation and completeness of the Meckel's cartilage as could be seen in the publications. The sampled jaws belong to taxa from different periods and localities and cover a wide range of sizes (App. 2). This broad sampling range (regarding time, locality and size) was used to find general differences in shape between the different groups. All Meckel's cartilage outlines were digitized in TPS software (Rohlf, 2015). Elliptic Fourier Analysis (EFA) was then performed in the Momocs package (Bonhomme et al., 2014) in R (R Development Core Team, 2020) to statistically compare all sampled lower jaw shapes. A total number of 25 harmonics were considered, which gather nearly 99% of the cumulative harmonic power (seen as a measure of shape information) and reconstructs actual morphologies with high accuracy. We obtained a virtual morphospace by performing a principal component analysis (PCA, Fig. 2) on the preordination data to plot the main shape variations. To quantify the morphological similarity amongst the studied jaws, a Hierarchical Cluster Analysis (HCA) using the R package 'dendextend' (Galili et al. 2019) was conducted. Phylogenetic signal was assessed using the lambda and K statistic with 1,000 random

permutation in the R package ‘phytools’ (Revell 2012). Additionally, a Mantel test, correlating phenetic (morphological) and phylogenetic distances was performed in order to assess the degree of morphological convergence in our sample. These metrics are expected to show greater decoupling and, consequently, lower correlation where homoplasy occurs. We repeated the tests in a set of 1000 phylogenetic trees that accounted for phylogenetic and stratigraphic uncertainty. The tree topology is based on Klug et al. (ongoing research). Polytomies were randomly resolved 1000 times and each resulting tree was calibrated by randomizing the tip age of every species within the chronostratigraphic unit, at age or subperiod rank, where their first appearance occurs, using the R package ‘paleotree’.

Results

Systematic Palaeontology

Class Chondrichthyes Huxley, 1880

Subclass ? Elasmobranchii Bonaparte, 1838

Order ? Ctenacanthiformes Glikman, 1964

The Meckel’s cartilage with a total length of 18 mm and a height of up to 6 mm is nearly complete and preserved in lateral view (Fig. 1A). The posterior part is somewhat incomplete in the main plate and entirely missing in the counterpart (Fig. 1A, B, D). While most of the specimen is visibly different from the sediment due to its internal structure and colour, in the posterior part the Meckel’s cartilage limits are less clear and

the exact borders between fossil and sediment are difficult to determine. The specimen shows a bright grey to white colour and most of it is somewhat brighter than the sediment. In the main fossil plate and in the counterpart, a distinctive polygonal pattern of the calcified cartilage is visible mainly in the posterior part (Fig. $1E_{1,2}$) while in the middle to anterior part, the specimen is mineralized in a bright colour. The tessellation is not as geometric as in some modern species (Seidel et al. 2020,2021) but the polygons are distinct. In some areas, the borders of the polygonal tesserae are clearly distinguishable by white outlines that most likely represent the intertesseral fibres (Seidel et al. 2016). Even though the tesserae borders are distinct, the corners, as well as the borders in general are rounded and less distinct. Despite the blurriness, the pattern is very similar to the one that can be seen in the crown chondrichthyan *Tristychius arcuatus* (Brazeau & Friedman 2014, fig. 5C, D).

The ventral edge of the Meckel's cartilage is gently convexly curved. The ventral ridge is discernible in spite of the compaction especially in the middle to posterior part. It follows the shape of the outline of the jaw until about 2.5 mm distance from the posterior end when it bends upwards (Fig. 1A). The Meckel's cartilage becomes higher from posteriorly until just before the articulation. It displays one bulge at the thickened anterior end, which is about 4 mm long and might represent the symphysis. This bulge is followed by a shallow depression, which is 3.5 mm long and a shallow bulge of about 2.5 mm length. The preservation is insufficient to identify muscle attachments with confidence. We assume that the anterior 9 mm was the tooth-bearing part (dental sulcus) because the concave upper edge anterior to the articulation ends there and it appears like the dorsal side broadens from this point anteriorly. The next depression

extends over 7.5 mm and ends at the articulation. Although the specimen is flattened, the retroarticular flange (cf. Long et al. 2015) at the posterior end is still preserved as a knob. The articulation is positioned dorsally in the posterior end of the jaw but unfortunately the preservation does not allow to determine the exact shape of the articulation and it seems incomplete.

Morphometric Analyses

The PCA shows clear separation between the jaws of the two chondrichthyan clades Elasmobranchii and Holocephalii (Fig. 2). PC 1 (59% of variance) is mostly related to changes in jaw thickness with decreasing thickness from negative to positive scores. PC 2 (13% of variance) mainly reflects changes of the jaw curvature (from strongly convex to slightly concave), with a decrease in curvature from negative to positive scores (Fig. 2). PC 3 (6% of variance) mostly describe changes in the curvature of the anterior end of the jaw as well as changes of the roundness of the posteroventral edge of the jaw (Fig. 2). Holocephalan jaws occupy high PC1 scores of about 0.05 to 0.17 and positive PC2 scores and show relatively slender and only slightly curved morphologies. Elasmobranch jaws occupy a wider score range with PC1 scores between -0.8 to 0.08 and PC2 scores between 0.07 and 0.10 (Fig. 2). Most of them plot in the centre of the morphospace between PC1 scores of about -0.5 and 0.01 and PC2 scores around 0.0. Elasmobranch jaws show ~~a~~ greater shape variation than holocephalan jaws, from thick and bulky to relatively slender. Acanthodian jaws occupy PC1 scores from -0.11 to 0.10 and PC2 scores of -0.12 to 0.05 (Fig. 2) and overlap to a large extent with elasmobranch and holocephalan jaws. Acanthodian jaw shapes vary

from bulky and curved to slender and straight. The new specimen plots at -0.01/0.025 (PC1/PC2), which is close to the other sampled acanthodians and some elasmobranchs. The new specimen plots closest to the acanthodian taxa *Ischnacanthus sp. and Latviacanthus ventspilsensis.* Furthermore, some ctenacanths plot very close: *Dracopristis hoffmanorum, Ctenacanthus sp. Heslerodus divergens,* as well as another elasmobranch of the order Synechodontiformes*: Palidiplospinax occultidens* (Fig. 2). In the dendrogram derived from the HCA, the new Hangenberg black shale Meckel's cartilage plots closest to the acanthodian *Latviacanthus ventspilsensis*. The acanthodian *Ischnacanthus sp.* and the elasmobranch of *Heslerodus divergens* constitute sequential ~~outgroups~~ to those two (Fig. 3). Overall, there is not a clear grouping among the three classes (Fig. 3). However, at a lower clustering rank, a separation between holocephalans and elasmobranchs is supported while acanthodians plot together with either elasmobranchs or holocephalans (Fig. 3). We find a significant phylogenetic signal as measured by the metrics K (equal to 0.501 ± 0.071; *p*-value = 0.004 ± 0.004) and lambda (equal to 0.995 ± 0.123; *p*-value = 0.0001 ± 0.0001; Fig. 4), but no significant correlation in between phenetic and phylogenetic distances in the Mantel tests (R statistic = -0.045 ± 0.009; *p*-value = 0.632 ± 0.032, all data expressed in mean ± standard deviation, Fig. 5).

Discussion

Our methodological framework based on EFA, PCA and HCA allows for discriminating holocephalans from elasmobranchs as well as some clades of lower systematic rank, but discrimination of acanthodians as a whole from holocephalans and elasmobranchs is not evident (Figs. 2, 3). We detect a strong phylogenetic signal in our dataset (Fig. 4),

altogether suggesting that outline jaw shape by itself can be, to some extent, informative for systematic placement of disarticulated remains and add support to other evidence. However, it has to be kept in mind, that our morphometric analysis considers two-dimensional outline shape and, potentially, some relevant anatomical information to discriminate among other groups might not be captured. Further, the lack of correlation in Mantel tests (Fig. 5) entail the presence of homoplasy, which might hinder the interpretations of phylogenetic affinity from general morphology. Similarities in jaw shape can also result from adaptation. Jaw shape can, for example, be an adaption to a certain lifestyle as in durophagous sharks (Herbert & Motta 2018) or in general be connected to diet in combination with water depth (Motta & Huber 2012). Small variations in shape could also occur due to fossilisation, preparation and errors in redrawing the different outlines, but we do not expect this to have a major effect in our results as preliminary studies have supported that biological signal is still well preserved when minor taphonomical alterations exist (Angielczyk & Sheets 2007).

The inclusion of the new Hangenberg black shale jaw in the analysis revealed that it is most similar in shape to lower jaws of certain acanthodian (i.e., *Ischnacanthus sp.* and *Latviacanthus ventspilsensis*) as well as elasmobranchs (the ctenacanths *Dracopristis hoffmanorum*, *Ctenacanthus sp.*, and *Heslerodus divergens*; and the synechodontiform *Palidiplospinax occultidens*) (Figs. 2, 3). A holocephalan affinity is unlikely as all considered taxa from this group fall in a separate area of the morphospace. The Hangenberg black shale jaw sits slightly closer to acanthodian jaw shapes than to elasmobranch jaw shapes but whether it is of acanthodian or of elasmobranch origin is

difficult to ascertain solely from those analyses and further information is needed to determine its possible origin.

Besides the HBS Meckel's cartilage, the only vertebrate fossils known from the Hangenberg black shale are some poorly preserved chondrichthyan teeth (Klug et al. 2016), which are not determined but could be of symmoriiform origin (? *Stethacanthus*, Coates & Sequeira 2001, fig. 5 F-I). However, given the analyses a holocephalan origin seems unlikely. The exclusion of a holocephalan origin is further supported by the absence of a terminally positioned articulation which is typical for holocephalans (Coates et al. 2017, character matrix). Due to incomplete preservation of the articulation it cannot be compared in detail to other chondrichthyan lower jaws.

Among the few characters present in the new HBS Meckel's cartilage, some can help to further distinguish its most probable affinity. Thus, the jaw of the ctenacanth *Heslerodus divergens* (Hodnett et al. 2021) seems to share some features not directly captured by outline analysis, which are less distinct in both acanthodian jaws that plot close to the HBS jaw. The jaw of *Heslerodus divergens* has a relatively thin anterior to middle part comparable to the first 9 mm of the new jaw that we described as the probable tooth bearing part. Following this, in both jaw shapes, a ridge is present leading to a second depression that ends in the articulation. In the jaw of *Heslerodus divergens* this shape is more distinct than in the HBS jaw while both acanthodian jaws are dorsally straighter shaped (Fig. 6). Additionally, Hodnett et al. (2021) describes "*a well-developed ventral ridge on the lateral margin of the Meckel's cartilage, that extends over two thirds the length of the jaw*", as a synapomorphy of ctenacanths. A ventral ridge is one of the few features of the new Hangenberg black shale jaw, ~~that is well~~ recognizable (Fig. 1).

Ischnacnathus sp. shows a ventral ridge as well but when comparing the HBS jaw ventral ridge to the other two, the one of *Heslerodus divergens* is a lot more similar (Fig.6).

In addition, a distinct polygonal structure is visible on the surface of the jaw (Fig. 1C). This pattern is characteristic for tessellated calcified cartilage, which is widely accepted as a synapomorphy of ~~modern~~ and extinct crown chondrichthyans (Brazeau & Friedman 2014; Long, et al. 2015; Seidel et al. 2016, 2021; Maisey et al. 2020). Tessellated calcified cartilage is made of an inner layer of globular calcified cartilage and an outer layer of prismatic calcified cartilage (Maisey et al 2020). Only the outer prismatic layer shows the typical polygonal pattern while the globular calcified cartilage shows a granular surface (see for example the acanthodian *Climatius reticulatus* in Burrow et al. 2015, fig. 1, I).

Fossils of the acanthodian group (stem chondrichthyans) mostly do not show a polygonal pattern, since no prismatic outer layer is present but only globular calcified cartilage (Maisey et al. 2020). However, Maisey et al. (2020) describes the presence of subtessellated calcified cartilage in some acanthodians, while actual tessellated calcified cartilage (showing the outer prismatic layer) is apparently absent (Brazeau & Friedman 2014). Acanthodians like *Climatius (Burrow et al. 2015)*, *Ischnacanthus* (Burrow et al. 2018) or *Cheiracanthus* (den Blaauwen 2019) are mentioned to show this subtessellated calcified cartilage. When looking at *Climatius,* it appears granular and no actual polygons are visible on the surface as mentioned above (Burrow et al. 2015, fig. 1, I). In *Ischnacanthus* (Burrow et al. 2018), a subtessellated calcified cartilage is described using histology; we cannot compare the HBS specimen to that. In

Cheiracanthus (den Blaauwen 2019), the surface appears *"globular or randomly tessellated"*. To sum this up, acanthodian fossils, or stem chondrichthyans, show a rather globular or irregular pattern (Burrow et al 2015 fig. 1, I; Long et al. 2015, fig. 9, A), which differs a lot from the regular polygonal pattern in crown chondrichthyans.
A polygonal pattern is evident in the new specimen but the borders of the single tesserae are slightly blurred taphonomically, which might have been caused by dissolution of the unmineralized collagen between the tiles (intertesseral fibre; Seidel et al 2016). However, the pattern is distinct and regular, making an elasmobranch origin more likely than an acanthodian origin. In fact, it is as regular as the polygonal pattern in the crown chondrichthyan *Tristychius arcuatus* (Brazeau & Friedman 2014).
Based on the results from morphometric analyses and the presence of both a ventral ridge on the lateral margin and tessellated calcified cartilage with a regular polygonal pattern, we assign the new Meckel's cartilage to the order Ctenacanthiformes with some reservations (Fig. 7). To some degree, this classification remains tentative and a bigger sample size could help to test the hypothesis. Further fossil finds as well as a better understanding of the early development of tessellated calcified cartilage in early fishes could help to classify the new jaw in more detail. However, this study presents an important fossil find, filling a gap in the fossil record and provides crucial information about the difficulties of determining the systematic affiliation of isolated cartilaginous fossil remains.

Conclusions

The newly described Meckel's cartilage is the first known fossil cartilage remain from the Hangenberg black shale from the Moroccan Anti-Atlas. It is 18 mm in length, ventrally convexly curved and shows a biconcave dorsal edge. PCA and HCA reveal a strong similarity in shape with certain acanthodians and elasmobranchs and a

phylogenetic signal is detected in our dataset. We conclude~~,~~ that jaw shape can be informative about the systematic placement of disarticulated skeletal elements but further information is needed since homoplasy is ~~suggested.~~ The structure of the tessellated calcified cartilage was used as a character for classification. It shows a distinct polygonal pattern which is characteristic for crown chondrichthyans. Furthermore, its general shape as well as the shape of the ventral ridge were compared to two of the jaws that were classified as the most similar by PCA and HCA analyses. This comparison suggests a ctenacanth affiliation. Considering ~~all~~ mentioned evidence~~s~~, we assigned the new lower jaw to the order Ctenacanthiformes, tentatively.

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Figure 1

Meckel's cartilage outlines and close ups

Meckel’s cartilage of a ctenacanth chondrichthyan from the Hangenberg black shale, Madene El Mrakib; PIMUZ A/I 5139. A, lateral view; B_1, traced outline and ventral ridge; B_2, counterpart with outline; C, Close up of the anterior area; D, close up of the posterior area; $E_{1,2}$, Close-up photos of the cartilage showing the polygonal pattern. Abbreviations: sym - symphysis, ma - muscle attachment area, vr - ventral ridge, re.fl - retroarticular flange. Scale bar for A, $B_{1,2}$ equals 5 mm. Scale bar for C, D, $E_{1,2}$ equals 1 mm. Arrow indicates Anterior (A) and Posterior (P).

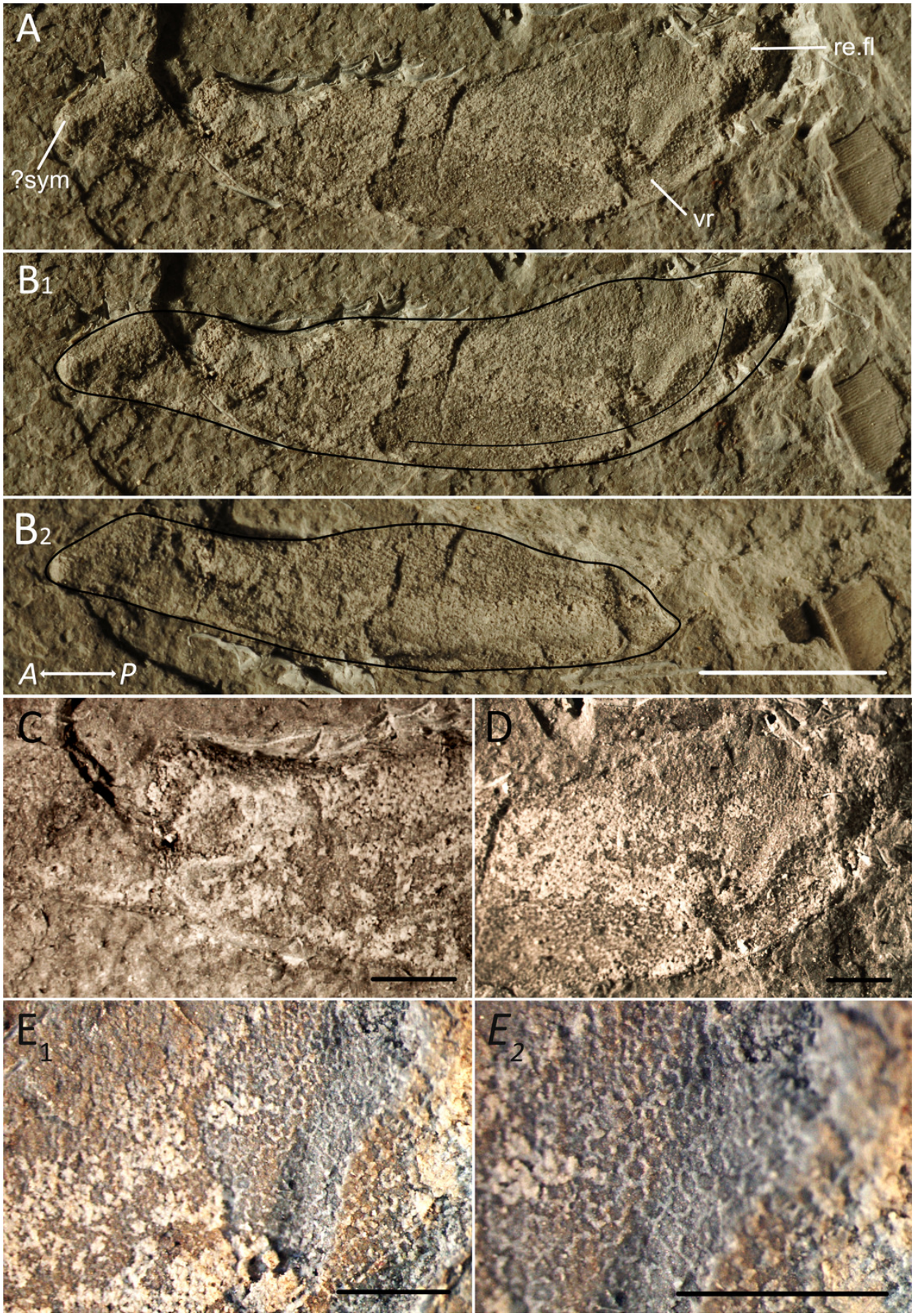

A
re.fl
?sym
vr
B1
B2
A
P
C
D
E1
E2

Figure 2

PCA and morphospace with all sampled lower jaws

Principal Component Analysis of some fossil and ~~modern~~ chondrichthyan lower jaws. Orange colours: acanthodians; purple colours: holocephalan; blue colours: elasmobranchs. The new lower jaw from the Hangenberg black shale is represented by a black dot and grey colours represent lower jaws of unknown class and order. A jaw morphospace is represented in the background showing the shape variation. The new Hangenberg black shale jaw plots close to jaws of acanthodians as well as elasmobranchs. Lv: Latviacanthus ventspilsensis, Is: Ischnacanthus sp., Po: Palidiplospinax occultidens, Dh: Dracopristis hoffmanorum, Ct: Ctenacanthus sp. Hd: Heslerodus divergens.

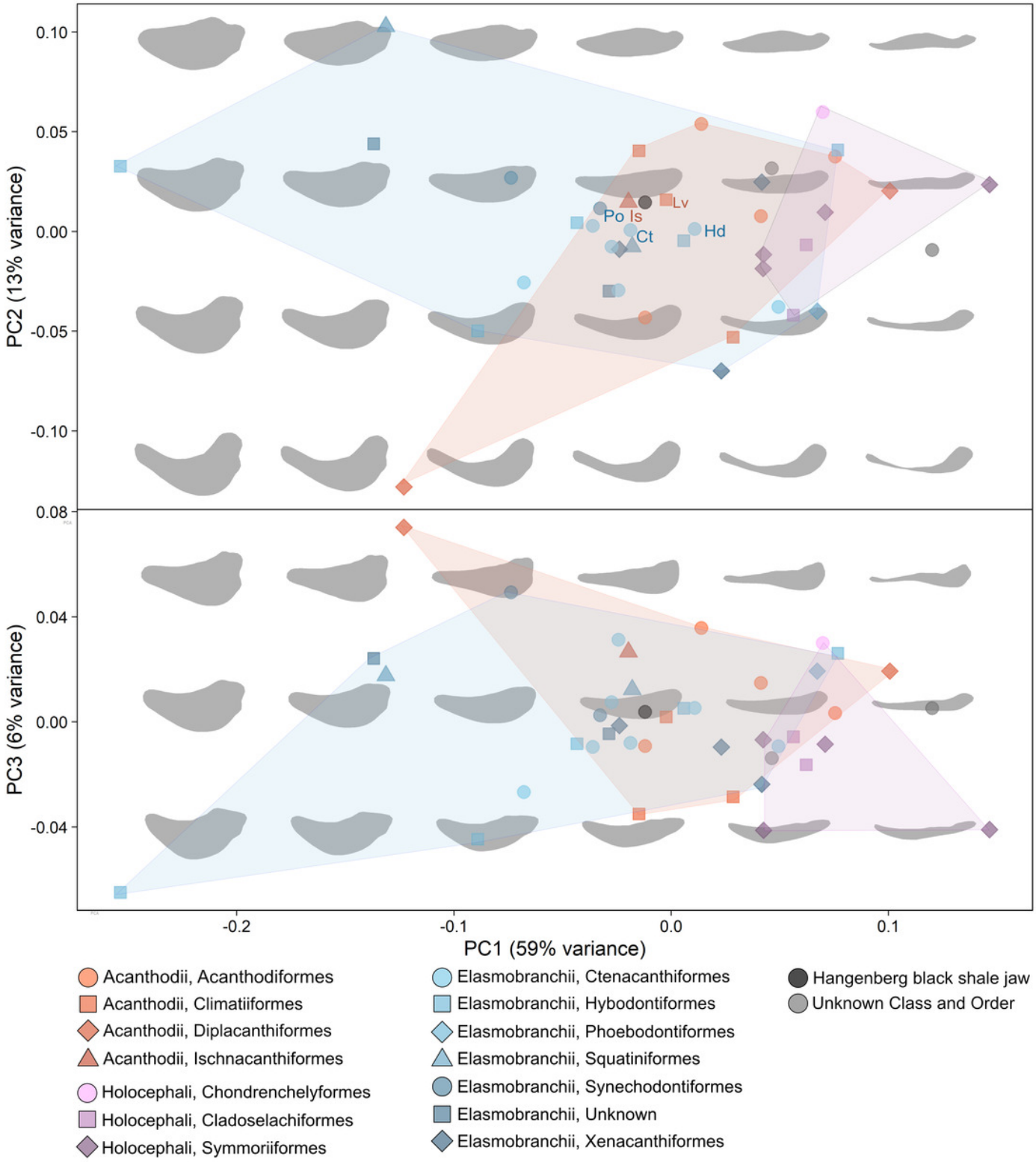

0.10
0.05
0.00
-0.05
-0.10
PC2 (13% variance)
Po
Is
Lv
Ct
Hd
0.08
0.04
0.00
-0.04
PC3 (6% variance)
-0.2
-0.1
0.0
0.1
PC1 (59% variance)
Acanthodii, Acanthodiformes
Acanthodii, Climatiiformes
Acanthodii, Diplacanthiformes
Acanthodii, Ischnacanthiformes
Holocephali, Chondrenchelyformes
Holocephali, Cladoselachiformes
Holocephali, Symmoriiformes
Elasmobranchii, Ctenacanthiformes
Elasmobranchii, Hybodontiformes
Elasmobranchii, Phoebodontiformes
Elasmobranchii, Squatiniformes
Elasmobranchii, Synechodontiformes
Elasmobranchii, Unknown
Elasmobranchii, Xenacanthiformes
Hangenberg black shale jaw
Unknown Class and Order

Figure 3

Dendrogram showing morphological distances of the sampled lower jaws

Dendrogram showing morphological distances regarding the first principal components from the PCA. Orange colours: acanthodians; purple colours: holocephalan; blue colours: elasmobranchs. The elasmobranchs plot mainly on the top, while holocephalan jaws plot mainly at the bottom. Acanthodian jaws are scattered over the whole dendrogram. The lower jaw from the Hangenberg black shale is closest to some acanthodian jaws such as that of Ischnacanthus sp.

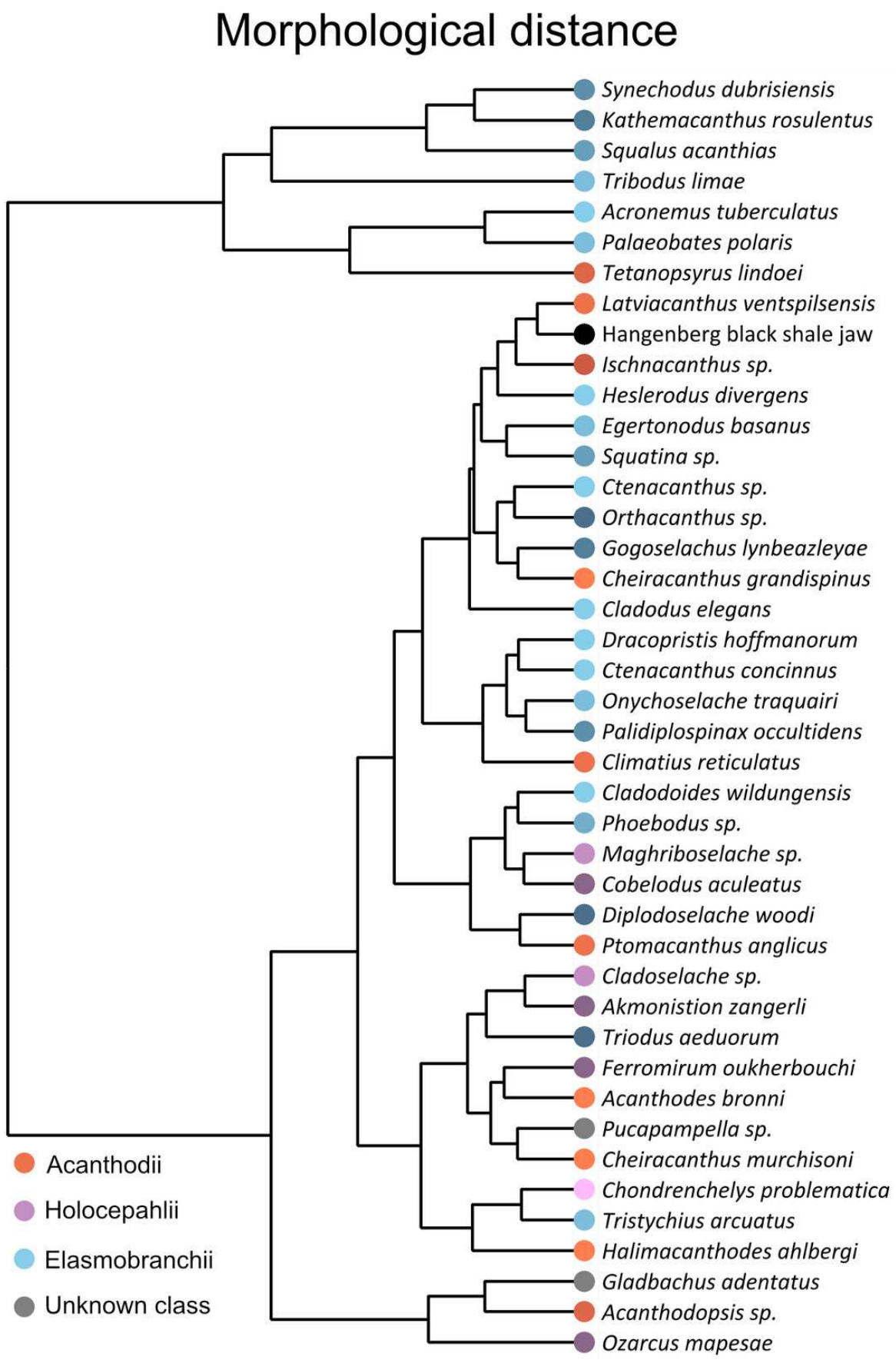

Morphological distance
Synechodus dubrisiensis
Kathemacanthus rosulentus
Squalus acanthias
Tribodus limae
Acronemus tuberculatus
Palaeobates polaris
Tetanopsyrus lindoei
Latviacanthus ventspilsensis
Hangenberg black shale jaw
Ischnacanthus sp.
Heslerodus divergens
Egertonodus basanus
Squatina sp.
Ctenacanthus sp.
Orthacanthus sp.
Gogoselachus lynbeazleyae
Cheiracanthus grandispinus
Cladodus elegans
Dracopristis hoffmanorum
Ctenacanthus concinnus
Onychoselache traquairi
Palidiplospinax occultidens
Climatius reticulatus
Cladodoides wildungensis
Phoebodus sp.
Maghriboselache sp.
Cobelodus aculeatus
Diplodoselache woodi
Ptomacanthus anglicus
Cladoselache sp.
Akmonistion zangerli
Triodus aeduorum
Ferromirum oukherbouchi
Acanthodes bronni
Pucapampella sp.
Cheiracanthus murchisoni
Chondrenchelys problematica
Tristychius arcuatus
Halimacanthodes ahlbergi
Gladbachus adentatus
Acanthodopsis sp.
Ozarcus mapesae
Acanthodii
Holocepahlii
Elasmobranchii
Unknown class

Figure 4

Phylogenetic signal metrics and tests of significance

Phylogenetic signal metrics and tests of significance performed in 1000 trees accounting for phylogenetic and stratigraphic uncertainty.

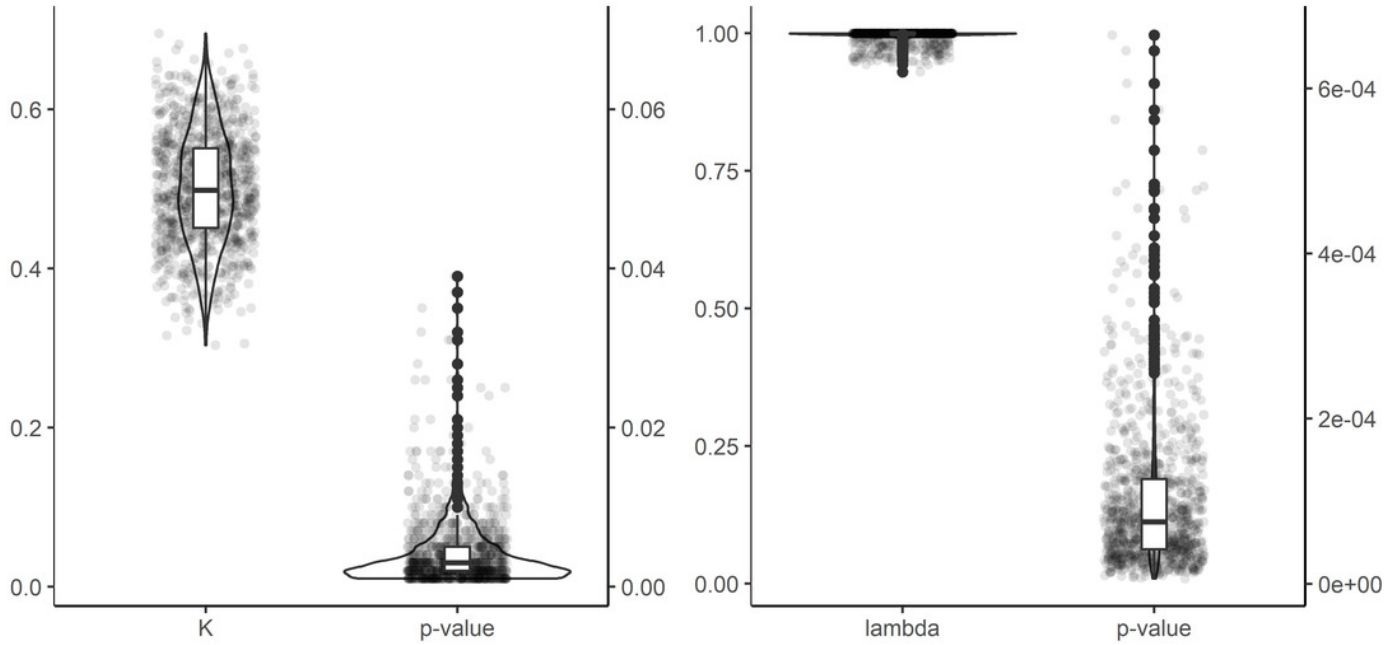


Figure 5

Mantel test results

Results of the Mantel test analysis performed in 1000 trees accounting for phylogenetic and stratigraphic uncertainty. R statistic values close to 1 or -1 support strong correlation, while values close to 0 support weak correlation

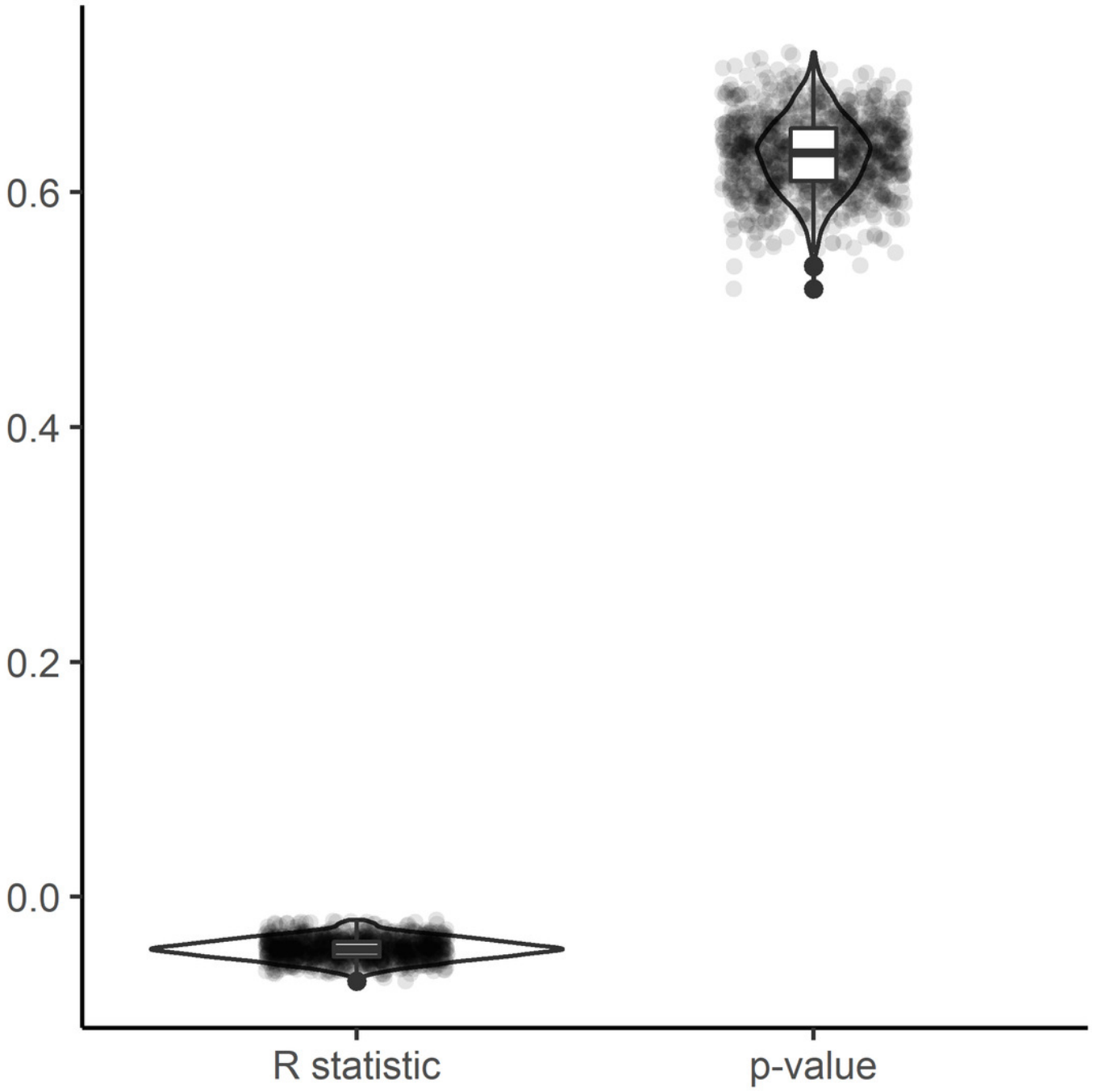

0.6
0.4
0.2
0.0
R statistic
p-value

Figure 6

visual jaw shape comparison

Direct comparison of the new HBS Meckel's cartilage (grey, top) with the two most similar jaw shapes of two different groups (pink, middle) and an overlay of both (pink and grey, bottom). A: the elasmobranch Heslerodus divergens. B: the acanthodian Ischnacanthus sp. Different characteristic points, that were not captured by the PCA directly, as well as the ventral ridge are compared and both shapes are shown in overlap with the HBS Meckel's cartilage.

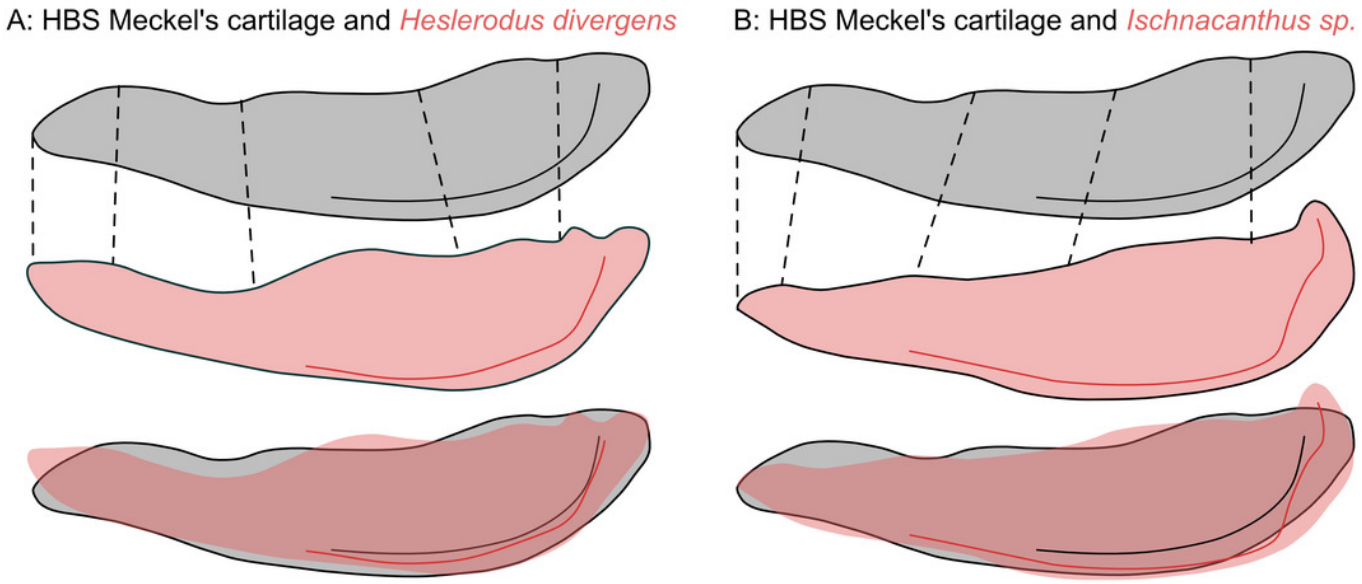
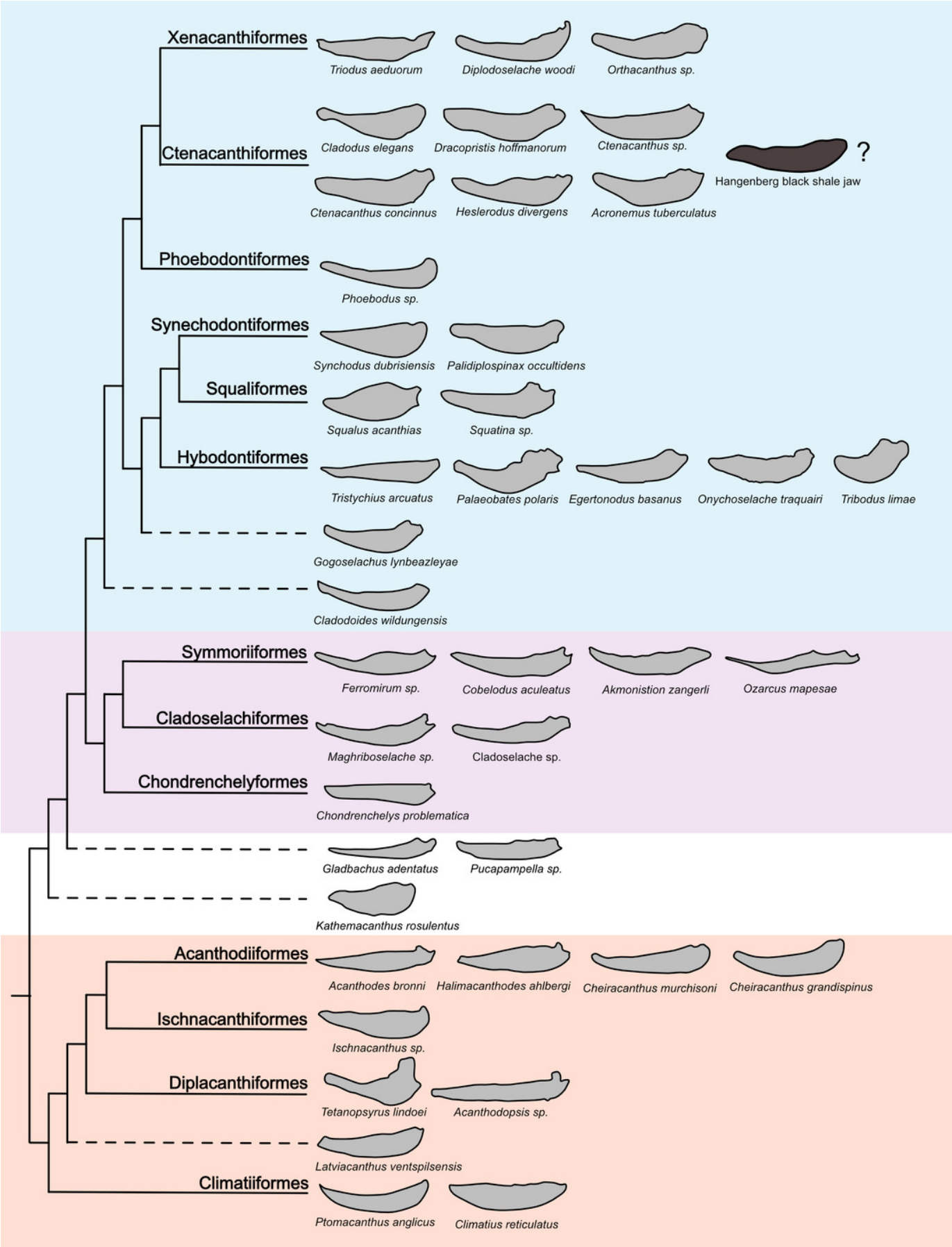


Figure 7

All sampled outlines in a phylogenetic tree showing the possible position of the new Meckel's cartilage

Simplified chondrichthyan phylogeny modified after Klug et al. (in prep.). The lower jaw from the Hangenberg black shale is figured together with the taxa used in the Fourier Analysis. The shapes of the lower jaws were redrawn from the literature (App. 1). The new HBS jaw is suggested to be of ctenacanthiform origin regarding the analyses and comparison of characters.


Xenacanthiformes
Triodus aeduorum
Diplodoselache woodi
Orthacanthus sp.
Ctenacanthiformes
Cladodus elegans
Dracopristis hoffmanorum
Ctenacanthus sp.
?
Hangenberg black shale jaw
Ctenacanthus concinnus
Heslerodus divergens
Acronemus tuberculatus
Phoebodontiformes
Phoebodus sp.
Synechodontiformes
Synchodus dubrisiensis
Palidiplospinax occultidens
Squaliformes
Squalus acanthias
Squatina sp.
Hybodontiformes
Tristychius arcuatus
Palaeobates polaris
Egertonodus basanus
Onychoselache traquairi
Tribodus limae
Gogoselachus lynbeazleyae
Cladodoides wildungensis
Symmoriiformes
Ferromirum sp.
Cobelodus aculeatus
Akmonistion zangerli
Ozarcus mapesae
Cladoselachiformes
Maghriboselache sp.
Cladoselache sp.
Chondrenchelyformes
Chondrenchelys problematica
Gladbachus adentatus
Pucapampella sp.
Kathemacanthus rosulentus
Acanthodiiformes
Acanthodes bronni
Halimacanthodes ahlbergi
Cheiracanthus murchisoni
Cheiracanthus grandispinus
Ischnacanthiformes
Ischnacanthus sp.
Diplacanthiformes
Tetanopsyrus lindoei
Acanthodopsis sp.
Latviacanthus ventspilsensis
Climatiiformes
Ptomacanthus anglicus
Climatius reticulatus