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Callovian (Middle Jurassic) hybodonts from Dzhidasai (Fergana Valley), western Kyrgyzstan

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Zusammenfassung

Taxa der Chondrichthyes sind nicht nur ein wesentlicher Bestandteil heutiger Ozeane, sondern waren dies auch für den größten Teils des Phanerozoikums, über 450 Millionen Jahren lang. Während dieses langen Zeitraums sind mehrere ihrer Familien ausgestorben, wie jene Gruppe, die im Mittelpunkt dieser Arbeit steht, die Hybodontiformes. Eine Gruppe, welche im Allgemeinen als Schwestergruppe der modernen Haie und Rochen bekannt ist. Hybodonten tauchten erstmals im späten Devon auf und überlebten das Massenaussterben an der Perm-Trias-Grenze. Während der Trias und dem frühen Jura waren sie in vielfältigen, aquatischen Lebensräumen dominant. Ab dem späten Jura und im Laufe der Kreidezeit verschwanden sie jedoch zunehmend aus offenen Meeren, möglicherweise aufgrund des zunehmenden Drucks durch moderne Haie, und starben schließlich in der späten Kreidezeit aus. In dieser Studie wurde fossiles Hybodonten-Material, in Form von isolierten Zähnen, aus der westkirgisischen Fundstelle Dzhidasai systematisch analysiert. Mehrere Spezies, darunter *Hylaeobatis verzillini* comb. nov.*, Lissodus verzillini* comb. nov.*, Lonchidion sp., Parvodus balabansaiensis* comb. nov.*,* und *Jiaodontus* cf. *montaltissimus* wurden anhand des fossilen Materials identifiziert und neu bewertet. Die identifizierten Taxa zeigen weite zeitliche Verbreitungen, von der Frühen Trias bis zur Späten Kreide, sowie räumliche Verbreitungen über Europa, Asien und Teile Nordamerikas hinweg, was ihre ökologische Anpassungsfähigkeit und paläobiogeographische Bedeutung während des Mesozoikums unterstreicht. Diese Taxa wurden dann zur Neubewertung der paläogeographischen Interpretation des Gebiets, während des mittleren Jura, herangezogen, wobei die Interpretation als marginale marine, Lagune oder brackisches Flussdelta unterstützt wurde. Besonders auffällig ist zudem der außergewöhnlich hohe Erhaltungsgrad der Zahnwurzeln, was Gegenargumente in Bezug auf die Idee von Wurzelresorption in Hybodonten aufwirft und alternative Interpretationen nahelegt, etwa ein besonders günstiges Ablagerungsmilieu.

Abstract

Chondrichthyans have played a significant role in marine ecosystems, not only in contemporary oceans but also throughout most of the Phanerozoic, for approximately 450 million years Over this incredibly long period of time, multiple of their families have gone extinct, like the group of interest of this thesis, the Hybodontiformes. They are generally known as the sister group to modern sharks and rays. Hybodonts first emerged during the Late Devonian and survived the Great Dying of the Permian-Triassic boundary. They were dominant members throughout most aquatic environments during the Triassic and Early Jurassic. However, starting in the Late Jurassic and throughout the Cretaceous, they increasingly disappeared from open marine environments, possibly due to increased pressure from their elasmobranch competitors. Finally, they disappeared during the Late Cretaceous, even before the fateful and famous end of the dinosaurs. In this study, hybodont fossil material, in form of isolated teeth, from the western Kyrgyzstan Dzhidasai locality was systematically analyzed. Several species, including *Hylaeobatis verzillini* comb. nov.*, Lissodus verzillini* comb. nov.*, Lonchidion sp., Parvodus balabansaiensis* comb. nov.*,* and *Jiaodontus* cf*. montaltissimus* were identified, described and reappraised, based on this material. These identified taxa exhibit broad temporal ranges from the Early Triassic to the Late Cretaceous and spatial distributions that span across Europe, Asia, and parts of North America, underscoring their ecological versatility and broad paleobiogeographic significance during the Mesozoic. The identified hybodonts were furthermore applied to reassess the Middle Jurassic paleoenvironmental interpretation of the area, fully supporting a marginal marine, lagoonal to brackish delta setting of the locality. Notably, an exceptional degree of root preservation was observed among the teeth, prompting counter arguments to the idea of root resorption in hybodonts and alternative interpretations, such as an exceptional type of depositional environment.

Keywords

Chondrichthyes; Hybodontiformes; Teeth; Crown-Root ratio; Morphology; Paleoenvironment; Spatial & Temporal distribution

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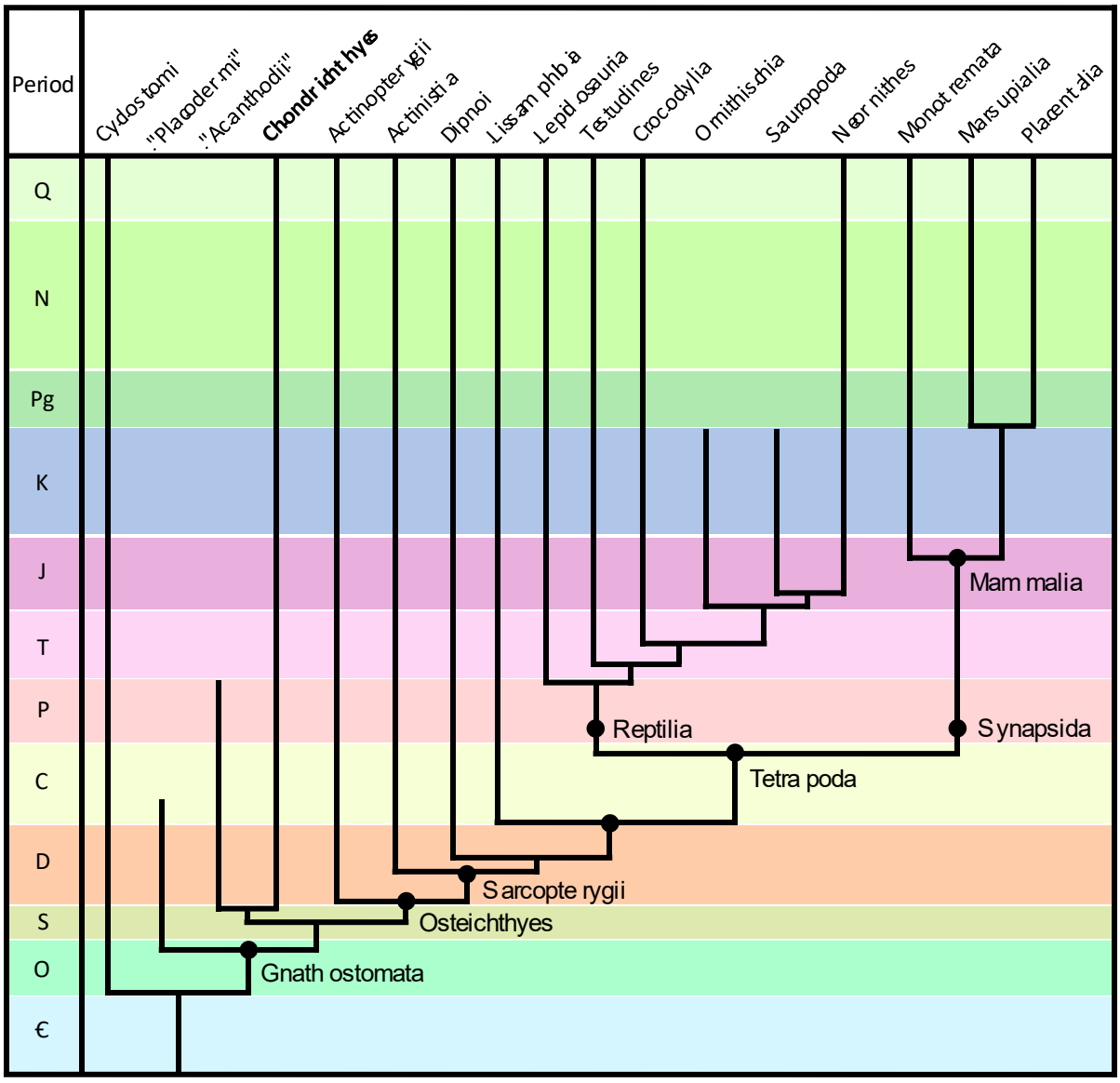
1. Introduction

Prior to the focus points of this study, which will be discussed in chapter 2, a short and wider introduction into the evolutionary history and phylogeny of the class Chondrichthyes will be given. Afterwards the order Hybodontiformes will be introduced in a general sense and lastly the focus will shift to the location itself, the hybodontiform taxa within and other aims of this thesis, such as the spatial and temporal distribution of these identified taxa, and a short excursion into the topic of root preservation in hybodonts.

1.1. Chondrichthyan Evolutionary History and Phylogeny

The class Chondrichthyes is, based on its fossil record, a very old one among vertebrates (Fig, 1a), with the first evidence of their occurrence, being denticle scale remains (Fig. 1b), extending well back to the Ordovician, roughly 450 Ma (Fig. 1) (Andreev et al. 2015, 2016; Boisvert et al. 2019; Brazeau & Friedman 2015; Maisey 2012; Nelson et al. 2016; Klimley 2013).

A



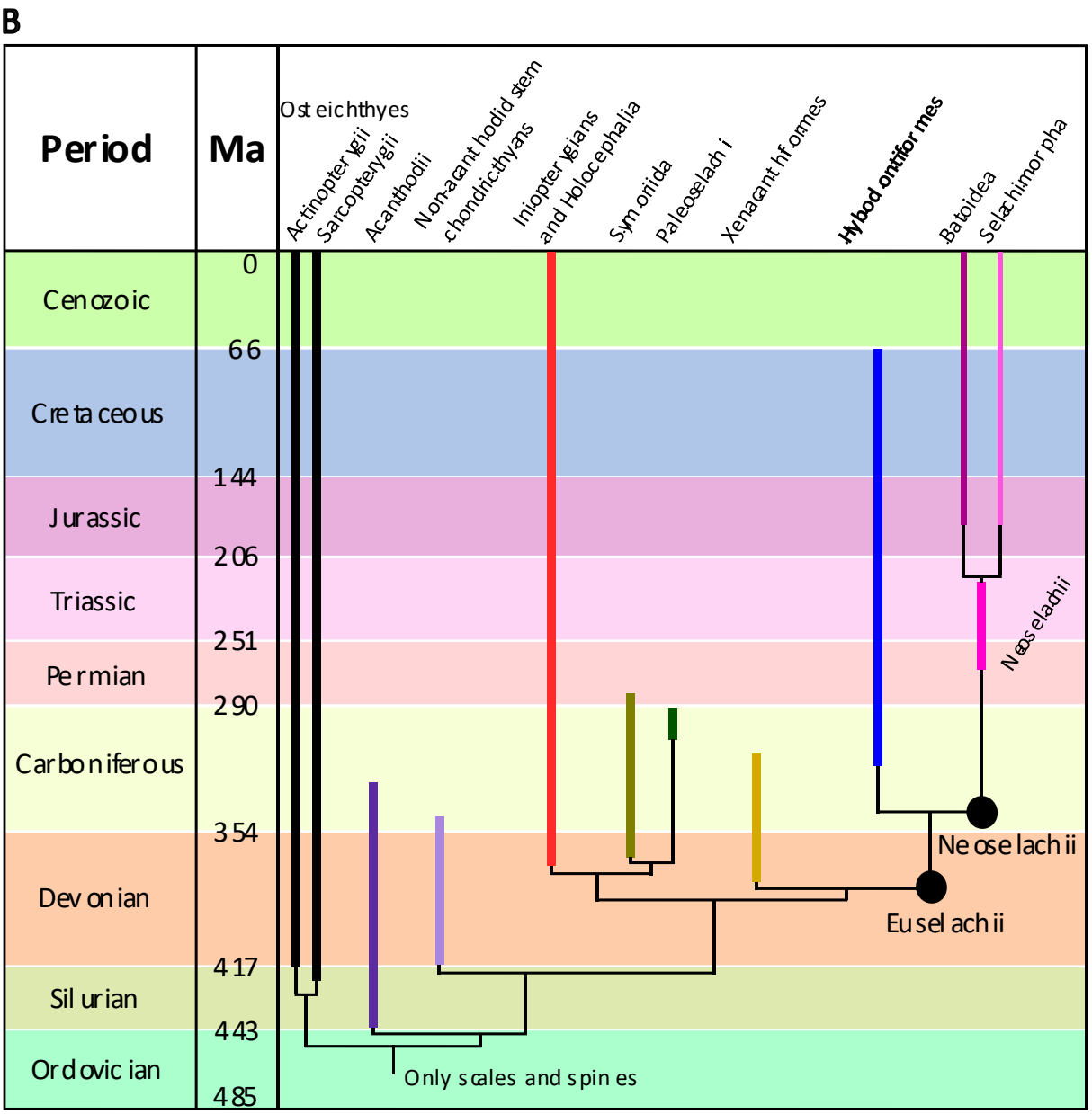


Figure 1. Phylogenetic hypotheses.
A: Simplified phylogeny of vertebrate groups (modified after Slobodian et al. 2021).
B: Simplified phylogeny of chondrichthyans (modified after Boisvert et al. (2019). The cladogram depicts the approximate time of first appearance (body fossils) and extinctions.
Coloured patches: Temporal ranges of fossils.
Comment: Scales and spines of chondrichthyans (and "acanthodians") are known since the Ordovician.

While denticles were already present in the fossil record by the Ordovician, the earliest teeth are only known from the Devonian onwards, most likely as a derivative of dermal denticles, concentrated in the jaw area (Klimley 2013). These earliest teeth, connected to the jaw by connective tissue, had a simple, continuous and open pulp cavity. This pulp cavity was surrounded by dentine, which in turn itself was covered by a hard layer of enameloid, that constitutes the tooth's surface (Klimley 2013). They were shaped cladodont, or multicusped, with one primary cusp at the centre and multiple, smaller branching cusps to either side of the primary one (Fig. 2) (Klimley 2013).

The sheer duration of the continued existence of chondrichthyans on this planet, navigating through changing environments and at least four mass extinction events, of course begs the question what made them so successful from an evolutionary point in the first place? The answer to that question lies in a complex interplay of multiple adaptations, which gave this group an evolutionary edge over their competitors at that time, such as Placoderms and Acanthodians for example (Klimley 2013).

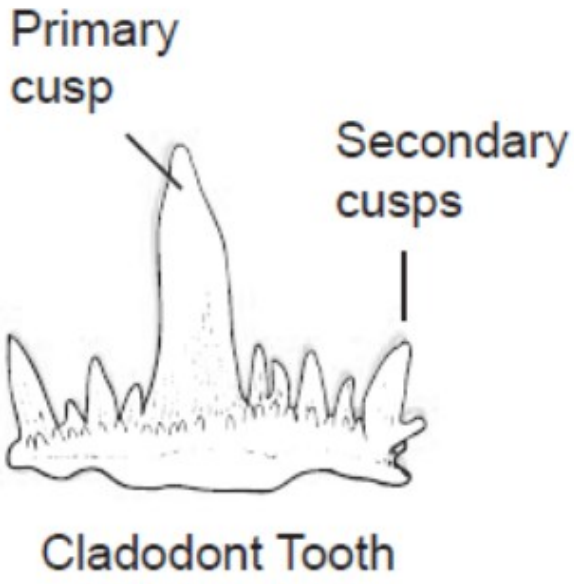


Figure 2. Schematic depiction of a cladodont tooth (after Kimley (2013).

These adaptations include, among other things, their unique skeletal structure made of soft and flexile cartilage with a hardened superficial apatite layer (Applegate 1967; Grogan & Lund 2004b; Klimley 2013). Their multiple rows of teeth with permanent tooth replacement are another one of their important adaptations (Boisvert et al. 2019), even though there is some evidence that tooth replacement rates in these ancient sharks were slower than in modern sharks (Maisey 1996). Lastly the ability of many of these ancient species to reproduce through internal fertilization, which is supported by the presence of claspers in the males of many species and could have provided an advantage over the larvae of egg laying species of other groups (Boisvert et al. 2019; Klimley 2013).

These are just a few important examples of adaptations which allowed chondrichthyans to take over the role of dominant predators as early as the Devonian (Klimley 2013) and make them one of the most enduring groups among fishes, and vertebrates as whole. A fact made evident by their continued survival since these ancient times of the Palaeozoic, as well as through their multiple re-diversifications after devastating extinction events such as the three events during the Devonian (Boisvert et al. 2019) and the famous Great Dying at the end of the Permian (Fig. 3b) (Klimley 2013).

Palaeozoic chondrichthyan diversity really jump started during the Devonian (Schnetz et al. 2024). The two main reasons for this great radiation of chondrichthyans during that period were most likely, on one hand, the increased extinction rates of other groups present during that time, which affected agnathans, acanthodians and placoderms, due to widespread loss of marine plant life (Benton 2005; Klimley 2013) and, on the other hand, incisive movements in the Earth's crust (Grogan & Lund 2004b; Klimley 2013) due to the coalescence of Pangaea during the end of the Devonian (Klimley 2013). This, in turn, resulted in an expansion of continental shelf areas. This expansion then promoted chondrichthyan radiations by providing extensive shallow-marine habitats with elevated ecological productivity. These environments furthermore increased niche heterogeneity, facilitated broader biogeographic connectivity,

and supported more complex trophic structures, all of which contributed to the evolutionary success and diversification of chondrichthyans during this period (Kriwet & Klug, 2008).

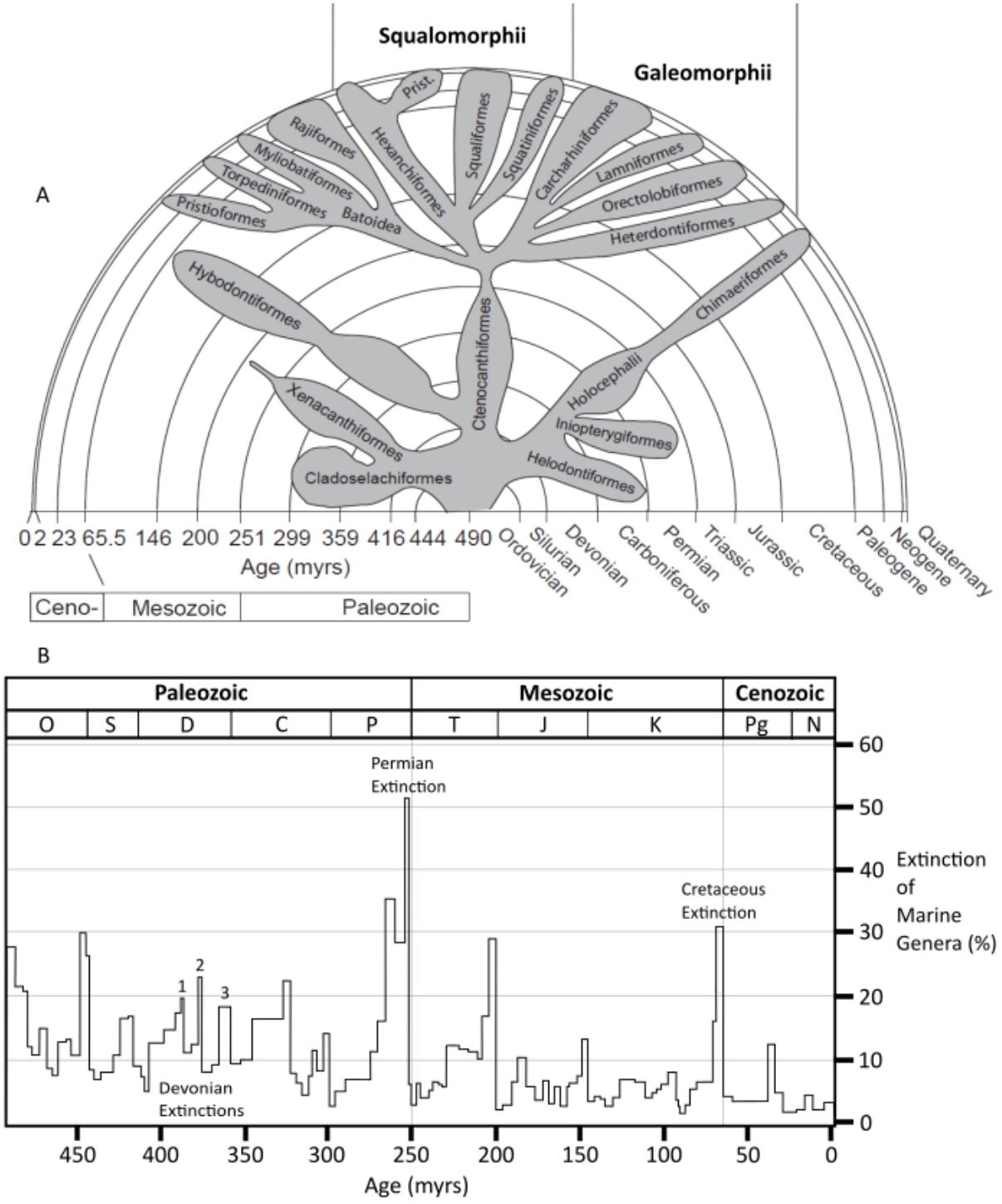


Figure 3. Modified after Kimley (2013).
(A) Approximate diversity of cartilaginous fishes over the Phanerozoic. The width of each branch is proportional to the diversity and abundance of a particular group at that time in geological history.
(B) Relative extinction rates of marine genera over geological time.

While fossil evidence of older taxa exists, it is assumed that chondrichthyans did not become common in the ancient world's oceans until the Middle Devonian at around 380 Ma. One of these first chondrichthyan taxa, which were presumably common in these ancient oceans was the genus *Cladoselache* (Fig. 4), which is known from complete skeletons (Boisvert et al. 2019; Miller et al. 2003; Klimley 2013). Newer studies suggest a close relationship of *Cladoselache* to the chondrichthyan order Symmoriiformes and with it a closer relationship to Holocephali (Coates et al. 2017).

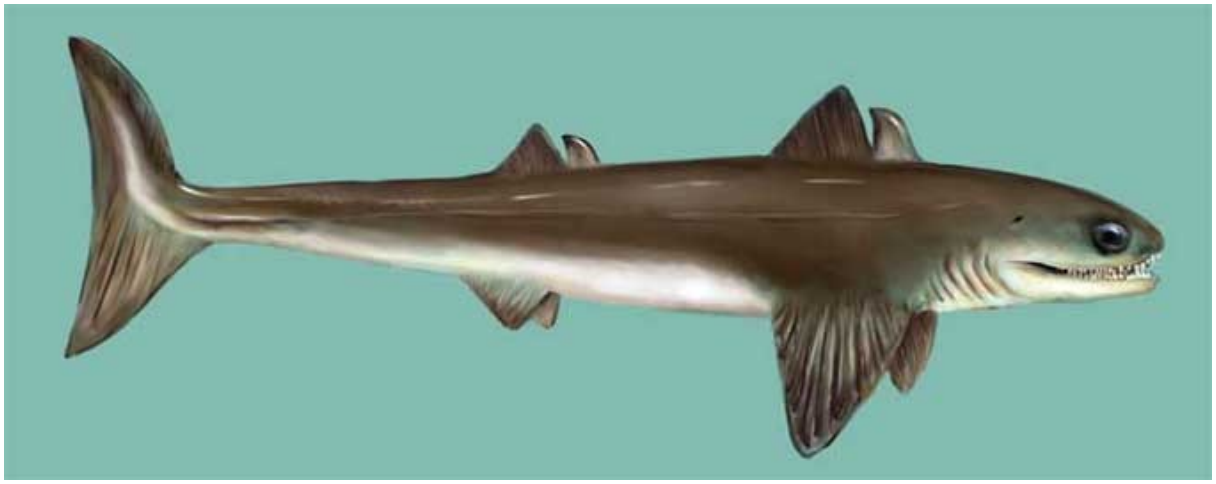


Figure 4. Artistic depiction of *Cladoselache*, one of the first common chondrichthyans, which is known from complete skeletons.

By the end of the Devonian the Cladoselachiformes had diversified further, with the appearance of members of Symmoridae (Fig. 1) and Eugeneodontidae. Another group, the Xenacanthiformes (Fig. 1; Fig. 3a), appeared a little earlier in the Devonian as well (Carroll 1988; Nelson et al. 2016; Klimley 2013). In contrast to other Palaeozoic sharks, the latter is especially noteworthy for its ability to live in freshwater environments (Klimley 1987; 2013).

Also common during the end of the Devonian were two other groups of Palaeozoic sharks, the Hybodontiformes and the Ctenacanthiformes (Fig. 3a) (Klimley 2013). The former group will get a more in depth look in chapter 1.2. and members of the latter are among the earliest well-known euselachians. However, they are not considered direct ancestors of modern sharks but rather represent a stem-group lineage within early elasmobranch evolution, basal to hybodonts and neoselachians (Fig. 3a) (Coates et al. 2017, 2018; Frey et al. 2019; Ginter et al. 2010). Common during that period were the holocephalans as well, to which modern chimaeras belong, however only a few of them survived the end-Permian mass extinction (Fig. 3a) (Klimley 2013).

But the holocephalans were of course not the only group that suffered significant losses during the biggest of all mass extinction events in Earth's history (Fig. 3a/3b). Most plesiomorphic sharks disappeared alongside many holocephalans at the boundary between the Palaeozoic and Mesozoic during which 50-75% of all families were lost in the oceans, with a considerable time lapse until recovery started, which translates to around 80-90% of species going extinct (Benton 2003; Klimley 2013). More recent figures are tending more towards 80%

than 90% though (Stanley 2016). The survivors of this cataclysmic event were probably migratory species and/or feeding generalists, like the hybodont *Hybodus* (Klimley 2013).

1.2. Hybodontiformes

The hybodontiforms, the primary focus of this study, first appeared during the Famennian of the Late Devonian (Hairapetian & Ginter 2009). They became then increasingly common throughout the subsequent Carboniferous and Permian periods (Klimley 2013). Even though the group only barely managed to survive the "Great Dying" of the end-Permian mass extinction event, they quickly re-diversified again during the following Mesozoic. This is especially well shown by examples from China, where hybodontiform sharks are common components of pre- as well as post-PTME (Permian-Triassic mass extinction) chondrichthyan faunas, both in marine and freshwater environments (Wen et al. 2022). The example of the Luoping Biota in particular shows how an increase in durophagous predators, as many hybodonts are, not only made the food web more complex in the area but also emphasized the recovery of marine ecosystems after the end-Permian mass extinction (Wen et al. 2023).

The Hybodontiformes experienced their peak in diversity throughout the Triassic and Early Jurassic, where they held the position as dominant predators in the marine environments off the coasts of Europe and North America firmly in their grasps (Klimley 2013). Their success and abundance continued throughout the Mesozoic, until their decline during the Late Jurassic and Cretaceous, possibly due to increased competition by their phylogenetic sister group, the neoselachians or modern sharks (Benton 2005; Boisvert et al. 2019). This possible competition drove them out of open marine habitats, into coastal and freshwater environments and ultimately ended in the extinction of the group during the Late Cretaceous, even before the famous extinction event at the end of the Cretaceous, which wiped out all non-avian dinosaurs as well (Benton 2005; Klimley 2013).

It is assumed, that the majority of hybodonts likely were comparatively rather sluggish swimmers, capable of only short bursts of speed, perhaps one of the features that led to them being outcompeted by modern sharks (Klimley 2013). Their paired pectoral fins were used to stabilize them in the water column, while the dorsal and anal fins prevented yaw, like the swords of sailboats (Klimley 2013).

1.2.1. Anatomical features

In general hybodont jaws predominantly show a hyostylic suspension, which means that the jaws are suspended primarily from the skull via the hyomandibula and lack a direct palate-cranial support, i.e. their upper jaw is not fused or tightly braced to the chondrocranium for example, just attached by ligaments via two points on either side of the chondrocranium (Fig. 5) (Carroll 1988; Klimley 2013; Lane & Maisey 2012). This style of articulation is like that of extant groups, such as Heterodontiformes, Lamniformes and Carcharhiniformes (Boisvert et al. 2019).

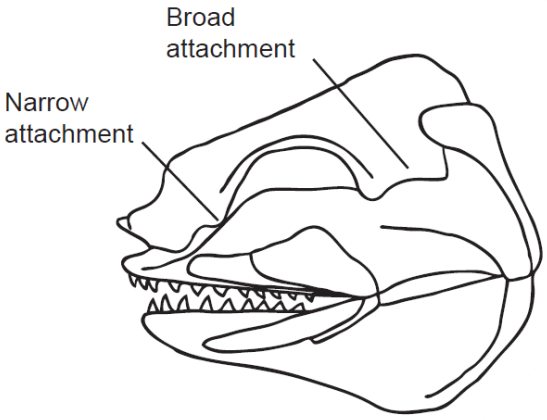


Figure 5. Illustration of hybodont jaw attachment at the example of *Hybodus*. After Klimley (2013).

This lack of cranio-palatal articulation sets hybodonts apart from more basal sharks, which retained an amphistylic type of jaw suspension, in which the palatoquadrate is attached directly to the chondrocranium, not just via ligaments, additionally to the hyomandibular support (Lane & Maisey 2012).

The jaws in hybodontiforms also usually display non-fused symphyseal joints in both mandible and palatoquadrate, for which *Tribodus limae* shows clear evidence for example, but which is also present in other hybodont genera, such as *Asteracanthus* and *Lonchidion* (Lane & Maisey 2012).

Hybodont jaws furthermore show an intact hyoid arch, which provides skeletal support, as well as the possible presence of internal jaw structures, such as trabecular cartilage in force-bearing jaw regions (Lane & Maisey 2012). This is especially noteworthy in durophagous forms, as this type of arrangement afforded flexibility and shock absorption (Lane & Maisey 2012).

Another main characteristic of hybodonts is the precedence of their two dorsal fins by robust and prominent finspines. These finspines are generally elongated, with a gentle, posterior curve (Maisey 1978). The ornamentation of these finspines varies between species and is a topic that would far exceed the scope of this brief introduction into Hybodontiformes. However, generally the ornamentations can be divided into two main types (Maisey 1982; Stumpf et al. 2021): Fin spines having longitudinal ribs and fin spines boasting multiple tubercles, arranged in rows.

In modern sharks finspines are only present in members of Heterodontiformes and some squaliforms (Compagno 1984; Nelson et al. 2016). The main differences between the finspines of these two groups and the ones possessed by hybodontiforms are that hybodontiform finspines are comparatively generally larger, more robust and have more ornamentation (Compagno 1984; Maisey 1982).

Additionally, male hybodontiform specimens possess either a single or double pair of cephalic spines in the supratemporal region of the head on the skull (Maisey 1982; Stumpf et al. 2021). Currently there is no evidence that these cephalic spines also appear in females, as all specimens that lack claspers also lack cephalic spines (Maisey 1982). Furthermore, it remains speculative if cephalic spines were present in juvenile individuals or were only developed with advancing maturity (Maisey 1982).

Cephalic spines consist of a large, curved basal plate, which is convex antero-posteriorly, and a prominently recurved crown covered in a thin cap of enameloid. At the tip most of these spines possess a single retrorse barb (Maisey 1982).

The lateral and posterior basal plate lobes are separated by a lateral indentation, while the mesial and posterior lobes are separated by a mesial indentation. As the spines are usually asymmetrical, as well as present on both sides of the head, it becomes necessary to distinguish between their mesial and lateral sides (Maisey 1982).

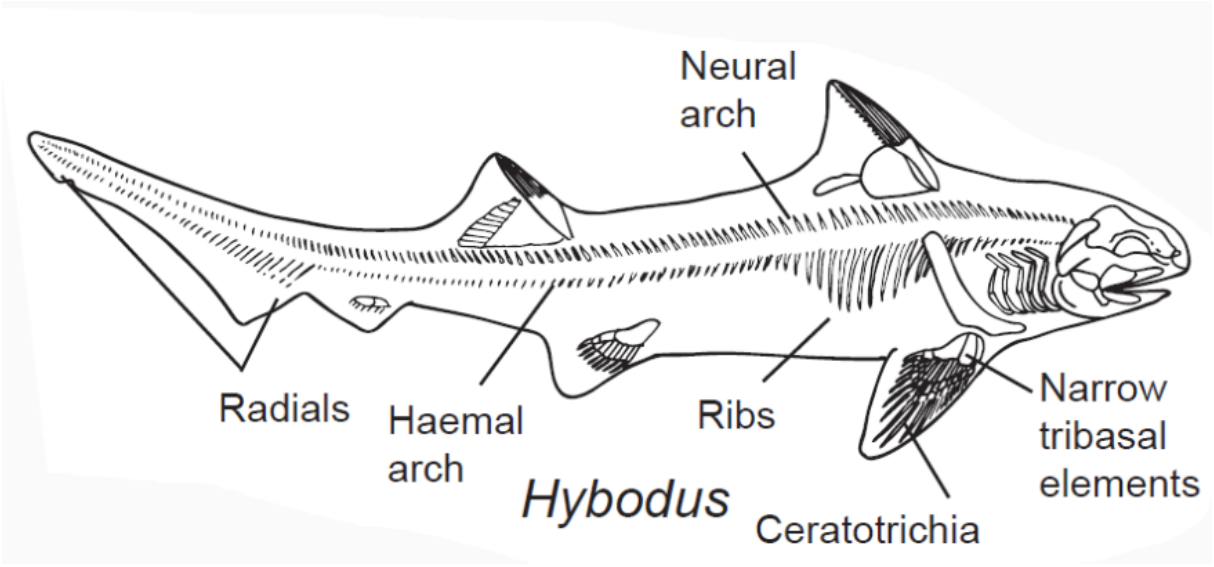


Figure 6. Simplified skeletal anatomy of hybodonts at the example of *Hybodus* (modified after Klimley (2013).

Other significant anatomical aspects of hybodontiforms include a better support of the pectoral fins, due to their shoulder bones (the scapulocoracoids), on both flanks of the sharks, being ventrally connected by a cartilaginous plate in their pelvic regions (Klimley 2013). Their pectoral fins were also able to more easily rotate to a wider range of angles, while adjusting the vertical position in the water column, due to the three elements attached to the shoulder bone at the base of the fin being more elongated and narrower than their counterparts in ctenacanthids (Fig. 6; Klimley 2013). The distal portions of the fins were supported by flexible ceratotrichia (Fig. 6), while the stiffer cartilaginous radial elements extended only proximally. This structural arrangement allowed the fins to be more flexible and manoeuvrable compared to a fin supported solely by cartilage (Grogan & Lund 2004a; Klimley 2013). These ceratotrichia can be described as very flexible, fin rays made of a collagenous protein (Moss 1977). This increased flexibility allowed the muscles within the fin to curve them from either the front to the back or from the base to the tip, which enabled the hybodont sharks to more efficiently steer themselves while swimming (Grogan & Lund 2004a; Klimley 2013). While hybodontiform

pectoral fins are made more flexible through ceratotrichia, they are still more robust and proximally reinforced when compared to the pectoral fins of modern sharks. Apart from hybodonts, and chondrichthyans in general, these ceratotrichia are known from a variety of other gnathostome groups as well, including for example arthrodiran placoderms (Ferrón et al. 2017) and possibly also some acanthodians (Burrow et al. 2020). Hybodonts possess a larger and longer basal skeletal element, the basipterygium, which supports the fin radials. Elasmobranchs on the other hand possess pectoral fins that are even more widely supported just by flexible ceratotrichia extending distally from a smaller basal cartilage, allowing greater manoeuvrability. This contrast suggests that hybodonts relied on stiffer, stronger fins for locomotion (Hoffmann et al., 2020). The pelvic fin comparison is very similar to the pectoral fins, as in elasmobranchs the pelvic fin radials articulate primarily with a comparatively small basipterygium. In contrast, in hybodontiform sharks, most pelvic fin radials articulate directly with a relatively larger and elongated basipterygium, indicating a more robust proximal skeletal framework for the pelvic fins as well (Pears et al. 2022).

The caudal fin of hybodontiform sharks also surpasses the ones possessed by ctenacanthids in both function and efficiency. The radials of their caudal fins extended outward from the base to the tip of the fin and showed a form longer at the base and shorter at the tip (Fig. 6) (Carroll 1988; Klimley 2013). Here the radials also do not actually extend all the way to the outer margin of the fin but are again distally substituted partway by extraordinarily flexible ceratotrichia, like in their pectoral fins (Klimley 2013). This number of radial elements increases the caudal fin flexibility greatly, which is further enhanced and supported by the accompanying musculature, that helps stabilize and control the overall shape of the fin during movement (Klimley 2013). During this movement, from side to side, the more flexible lower lobe trails a little behind the stiffer upper lobe, which results in a more efficient forward thrust. These two lobes of the caudal fins are not equal in size, with the upper lobe being much larger than the lower one, a style of caudal fin usually named “heterocercal” (Fig. 6) (Klimley 2013).

Dorsally to the notochord lie neural arches (Fig. 6) which serve several critical functions related to protection of the spinal cord, structural support and integrity of the vertebral column, as well as attachments for muscles and ligaments, flexibility and movement of the vertebral column and nerve signal transmission (Klimley 2013). Like the dorsal neural arches, ventrally to the notochord lie haemal arches (Fig. 6) which offer protection for the important arteries and veins below the notochord and extend into well-developed ribs throughout the midsection of the body (Klimley 2013).

Hybodontiform sharks are also distinguished from both earlier chondrichthyans and modern elasmobranchs by their vertebral morphology. Unlike Elasmobranchii, which possess heavily mineralized, prismatic calcified vertebral centra providing structural rigidity and efficient load bearing during swimming (Applegate, 1967; Dean & Summers, 2006), hybodonts retained weakly calcified centra throughout their evolutionary history (Maisey, 1982, 1983, 2005).

1.2.2. Teeth and dermal denticles

Hybodontiform sharks show a wide range of tooth morphologies, useful for a variety of tasks ranging from crushing hard-shelled invertebrates to gripping soft bodied prey animals. A more detailed description of the types of tooth morphologies, present in the Dzhidasai locality specimens, which form the focus of this thesis, follows in Chapter 5.

However, a major distinction between hybodontiforms and modern sharks lies in the presence of specialized enlarged foramina in the tooth root, through which nerve fibres and blood vessels are directed into the tooth crown. The majority of Mesozoic hybodont teeth lack these specialized foramina, while they are generally present in the teeth of modern sharks (Maisey 1982; Patterson 1966).

As is common in chondrichthyans, the body of most Mesozoic hybodonts also was covered in a dense layer of coarse dermal denticles (Maisey 1982). Hybodontiform dermal denticles were most likely generally monodontode, which means that each denticle is comprised of just a singular element and does not grow by apposition or addition of subsequent layers, for which *Tribodus limae* offers the clearest evidence (Maisey & Denton 2016). This pattern, as well as the continuous shedding and replacing of these monodontode denticles, mirrors that of modern sharks and rays (Maisey & Denton 2016). *Tribodus limae* further highlights that, in contrast to modern elasmobranchs two-size squamation patterns are present at least in some hybodont taxa, with larger thorn-like denticles interspersed with much smaller "cock's-comb" denticles (Maisey & Denton 2016). In *Tribodus limae,* these two classes are spatially interspersed, with small denticles often overlying or filling gaps between larger ones (Maisey & Denton 2016). So, it is possible that this type of complex size differentiation and patterned squamation may represent a derived condition within the group of hybodontiforms (Maisey & Denton 2016).

The dermal denticles of hybodont sharks furthermore come in a plethora of morphotypes, which often possess high pointed cusps, that point either in an apical or distal direction (Maisey 1982; Reif 1978). There are numerous ridges running down from the cusp towards the broader base of the scales. The base itself is either flat or slightly convex or concave, with an only weakly developed neck (Maisey 1982; Reif 1978).

The scales can also show a complex histology. The orthodentine, which is a form of dentine composed of straight tubes, of the crown comes in a thick layer below the enameloid cap (Maisey 1982; Reif 1978). The orthodentine of the base, and lower parts of the crown, on the other hand can grade into osteodentine, which is a type of dentine that more closely resembles bone (Maisey 1982; Reif 1978). Lastly the basal plate itself is rather thin and consists of acellular bone with several basal canals (Maisey 1982; Reif 1978).

A few of the denticle characters may represent hybodontiform synapomorphies, like the high-pointed cusps, conical shape of the crown with ridges and the absence of a prominent neck (Maisey 1982; Reif 1978). Contrary to these, other characteristics are more widespread among chondrichthyans, like the presence of a basal plate, as well as basal and neck canals (Maisey 1982; Reif 1978).

1.2.3. Tooth histology and enameloid microstructure

The enameloid layer of hybodont teeth that covers the tooth crown is usually comparatively rather thin and composed of only a single layer of randomly oriented fluorapatite crystallites, known as Single Crystallite Enameloid (SCE) (Fig. 7), which generally lacks microstructural differentiation, similar to Palaeozoic cladodont teeth (Enault et al. 2013; Hoffman et al. 2016; Maisey 1982; 1989; Reif 1973).

The enameloid ultrastructure, which is the finer organization of enameloid when compared to the enameloid microstructure, of neoselachian taxa is distinctive when compared to the SCE of hybodonts, as they possess an outer shiny layer (Shiny Layered Enameloid SLE) (Fig. 7), which is underlain by a parallel-fibered layer (Parallel Bundled Enameloid PBE) (Fig. 7), and a tangled layer after that (Tangled Bundled Enameloid TBE) (Fig. 7) (Enault et al. 2013; Maisey 1982; Reif 1973).

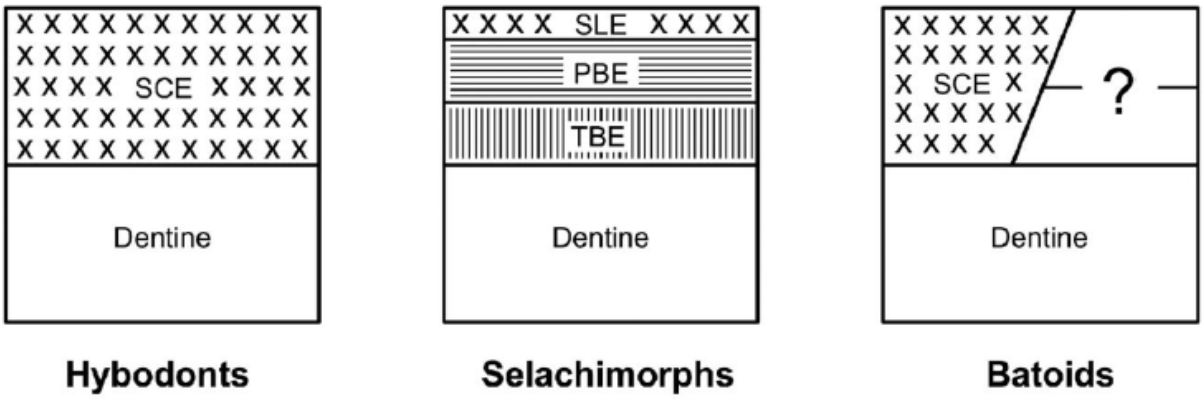


Figure 7. Schematic organization of the enameloid layers in hybodonts, selachimorphs and batoids (after Enault et al. (2013).
Abbreviations:
SCE – Single Crystallite Enameloid;
TBE – Tangled Bundled Enameloid;
PBE – Parallel Bundled Enameloid;
SLE – Shiny Layered Enameloid.

1.2.4. Reproductive strategies

When considering only oviparous taxa of modern sharks, there are none that are capable of reproducing in freshwater environments, as all modern elasmobranchs adapted to stay permanently in freshwater are viviparous. In contrast, it is very possible that, at least some, oviparous hybodont taxa were able to reproduce in freshwater environments (Cuny & Chanthasit 2023), which would indicate a major difference concerning the reproductive strategies of modern elasmobranchs and hybodonts (Cuny & Chanthasit 2023).

Oviparity seems to be the common type of reproduction among hybodontiform sharks, given the evidence of multiple egg capsule findings. This is also consistent with the notion that oviparity appears to be a more common adaptation in taxa with smaller body size (Cuny & Chanthasit 2023; Fischer et al. 2010; Krüger et al. 2021; Musick & Ellis 2005). This capacity to lay eggs in freshwater environments might therefore have represented a major advantage in the process of migrating and surviving in freshwater environments due to the increased

competitive pressure by neoselachians in marine environments (Cuny & Chanthasit 2023; Rees & Underwood 2008).

Like juvenile sharks today, which often live in the shallow, brackish water among mangrove roots, as those offer apt protection for the young sharks, ancient hybodontiforms could have pursued very similar strategies (Fischer et al. 2010; Krüger et al. 2021). Even though mangroves as such were not present during the Jurassic, aquatic horsetails, such as *Neocalamites* or *Equisetites*, would certainly have been able to provide a similar environment to the hybodonts of that time, while also providing an ideal substrate for them to attach their egg capsules to, when considering the stems of the aquatic horsetails (Fischer et al. 2010; Krüger et al. 2021). The current consensus is that hybodontiform sharks produced the egg case morphogenus known as *Palaeoxyris*, as they not only span the geological range of *Palaeoxyris*, but the palaeoenvironments in which all these egg capsules have been found, being freshwater fluvial or deltaic conditions, are also a perfect match for hybodontiform sharks (Cuny & Chanthasit 2023; Krüger et al. 2021).

1.2.5. Mesozoic hybodontiform evolution and diversity

The Mesozoic marks a period of great change in the history of hybodontiforms, as Mesozoic members represent the terminal members of their group, which already boasted a lengthy Palaeozoic evolutionary history (Maisey 1982).

Hybodontiform sharks were the dominant selachian group in both marine, as well as non-marine environments during the Triassic and Early Jurassic (Klug et al. 2010; Rees & Underwood 2002; 2005; 2008; Stumpf et al. 2021). A situation that was changing by the Late Jurassic, as during that time hybodontiforms were already reduced to just a minor component in open marine environments, largely being replaced by better adapted neoselachians (Rees & Underwood 2005; 2008; Stumpf et al. 2021).

Contrary to that, they managed to keep a high diversity throughout restricted marine and lagoonal settings, as well as fluvial to delta environments, which continued throughout the Cretaceous until their extinction in the Late Cretaceous (Maisey 2012; Rees & Underwood 2008).

Dominant hybodont genera throughout the Mesozoic include genera such as *Hybodus*, *Acrodus*, *Lonchidion* and *Lissodus* (Maisey 1982).

2. Goals of the present study

This thesis has multiple goals it aims to achieve with the applied methods and materials used, both of which will be outlined in detail in chapter 4.

These goals include:

Presenting a detailed description of the hybodontiform taxa present in the Dzhidasai locality of the western Kyrgyz Balabansai Formation via concise systematics and morphological descriptions of the fossil material and setting these identified hybodontiforms in a spatial and temporal framework, comparing Dzhidasai to other localities from which these taxa are already known from.

Combining the resulting taxa of the systematic palaeontology with the current paleoenvironmental interpretation of the Dzhidasai locality, based on the work of Averianov et al. (2005, 2008).

Analysing the exceptional root preservation of the Dzhidasai teeth, especially in the context of the interpretations made by Böttcher (2024).

3. Geological and stratigraphical setting

The fossil material that forms the focus of this study was recovered from the Middle Jurassic sediments of the Balabansai Formation (=Balabansai Svita) (Fig. 8 & Fig. 9), which is part of three Middle Jurassic Formations present in the northern part of the Fergana Valley in western Kyrgyzstan. Together with the coal bearing and commercially mined Tashkumyr Svita and the Igrysai Svita, which is mostly comprised of brown and greenish sandstones (Averianov et al. 2005).

The Balabansai Formation ranges from the Late Bathonian to the Callovian and is exposed West of the city of Tashkumyr (or Tashkömür) (Fig. 9a). Its greyish and reddish beds have already yielded some important fossils of terrestrial and aquatic vertebrates from this, thus far, poorly studied part of Central Asia and it is represented by a sequence of multifaceted sand-, silt- and claystone, complimented by rarer appearances of gravels and marls, with a thickness of up to 250 metres (Fig. 8) (Averianov et al. 2005, 2008; Martin & Averianov 2010).

However, even though it yielded abundant isolated remains, only little attention has been paid to the chondrichthyan fossil material until now. The only available account being Nessov & Kaznyshkin (1988). Rees & Underwood (2005) however, also cannot be understated in its importance for taxonomic considerations.

Figure 8. The Balabansai Svita and its multiple kinds of deposits.

The Balabansai Formation was deposited during increasingly arid conditions in a fluviatile to possibly marginal marine, lagoonal or delta setting (Averianov et al. 2005, 2008). While the other two formations can be classified as terrestrial deposits, accumulated in a humid climate, which contain Early Jurassic (Tashkumyr) and Middle Jurassic (Igrysai) flora (Averianov et al. 2005). This increase in aridity of the Central Asian climate, which is noticeable in the deposits of the Balabansai Svita, had its origin during the Callovian stage, which provides only further evidence for the Callovian age of this stratigraphic unit (Averianov et al. 2005). This Jurassic

succession is then superimposed by a broad section of Cretaceous red bed, with a layer of conglomerates of Cretaceous age at their base (Averianov et al. 2005).

3.1. The Dzhidasai locality – FBX-23

The material analysed in this thesis, consisting of 4.747 hybodontiform teeth (Table 1), originates from the Dzhidasai locality, designated FBX-23, which is one of multiple fossil bearing localities of the Balabansai Svita and falls directly into a lens of Middle Jurassic age (Fig. 9b) (Averianov et al. 2005, 2008).

Locality FBX-23 is situated approximately 5 km South-West of the city of Tashkumyr, which represents the only excavated locality West of the city, on the right bank of the Naryn River (Averianov et al. 2005, 2008; Martin & Averianov 2010), with the coordinates N41°19’34.0’’, E72°06’43.7’’, according to Martin & Averianov (2010). It is confined to the upper, red coloured part of the Balabansai Svita and situated approximately nine metres below the formation’s upper boundary. (Averianov et al. 2005, 2008; Martin & Averianov 2010).

Between the years 2001 and 2003 a total of around one metric ton of matrix was screenwashed at this locality, comprising thousands of hybodontiform teeth and dermal denticles (Martin & Averianov 2010). Thus, the Balabansai Formation, despite having not produced any articulated skeletons, is one of the most important and productive hybodontiform-bearing formations of Middle Jurassic age worldwide.

All the sites of the Balabansai Svita (Fig.9b), which have been used for microvertebrate collections, were formed by disastrous mud flows that transported vertebrate remains from continental nearshore shallow areas to the basin (Averianov et al. 2005), which is the reason why the Balabansai microvertebrate remains are mainly concentrated in lenses of varying sizes, with a width of up to around 10 metres in the case of FBX-23 (Averianov et al. 2005). The deposits between these lenses on the other hand usually lack vertebrate remains of any kind (Averianov et al. 2005).

Also noteworthy is that already completed examinations of the microvertebrates from different parts of the formation has, so far, not revealed any noteworthy distinctions of the faunal compositions between the Balabansai Svitas lower and upper segments (Averianov et al. 2005).

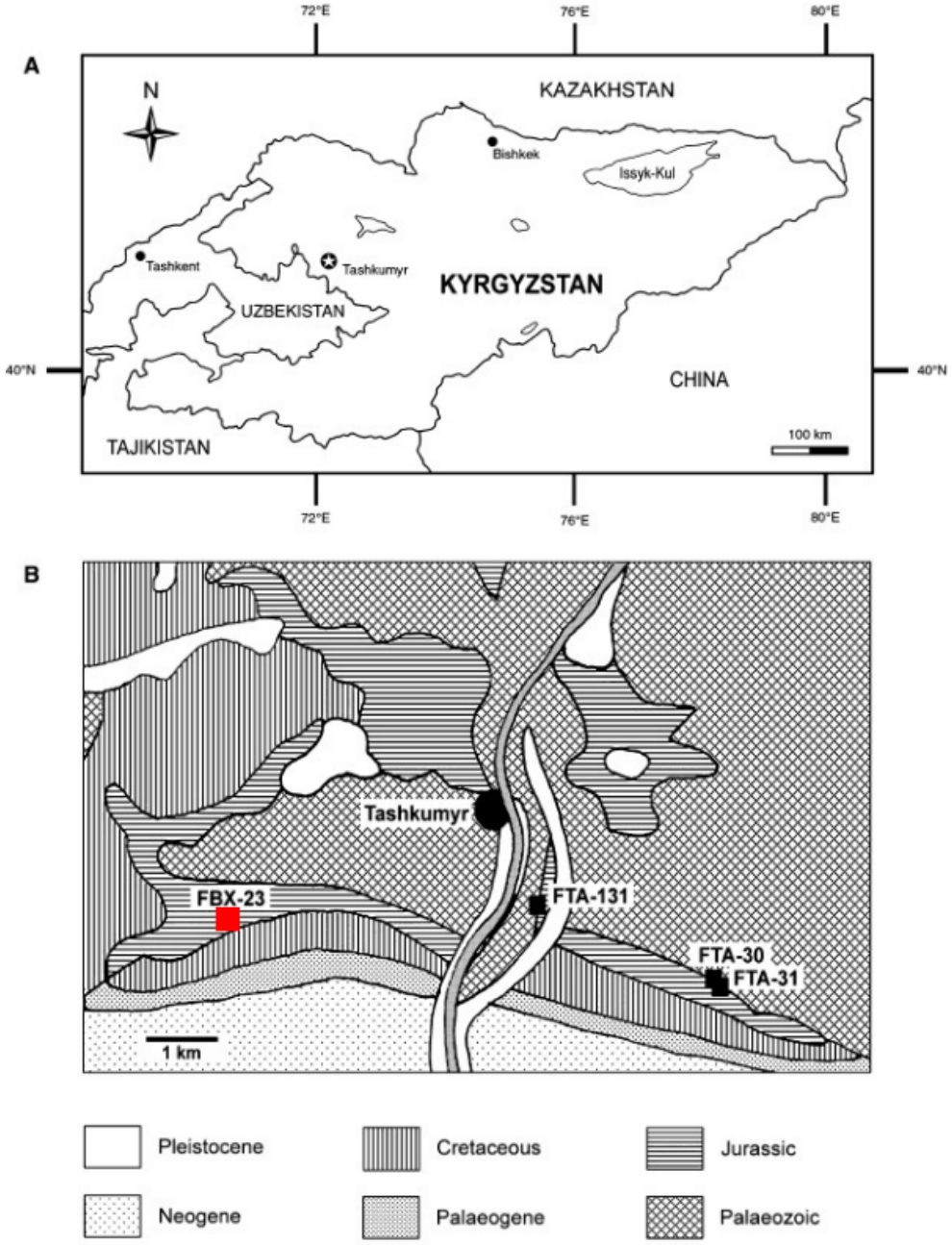


Figure 9.
(A) Simplified, geographical map of the wider region of Kyrgyzstan.
(B) Geological map of the area around Tashkumyr city, showing the position of the main fossil localities of the Balabansai Formation, including the Callovian locality FBX-23 (marked in red), where the fossil material for this thesis has its origin (modified after Averianov et al. 2005).

4. Materials and Methods

The fossil material analyzed in this study, consists of 4.747 complete as well as fragmentary hybodontiform teeth (Fig. 10). For a more in-depth view of the taxa/tooth ratio see Table 2-3.

All teeth that were recovered from the Dzhidasai locality are very small, with none of them exceeding 5 mm in both mesiodistal width and apicobasal height. However, despite this minute size their state of preservation is largely exceptional, with a great number of specimens being almost completely preserved, with only very little damage, concerning both the crowns and roots. However, while the state of preservation of most roots is largely exceptional, all these roots are still attached to their corresponding crowns and no isolated tooth roots were identified in the analyzed fossil material.

Traces of abrasion and wear, due to prolonged use, are more common, however there are still numerous specimens that beautifully depict the different kinds of ornamentations present on the teeth of the different taxa (Fig. 13-18).

The fossil material, designated as FBX-23, is currently kept at the Department of Paleontology of the University of Vienna, Austria, but will eventually be deposited at the Zoological Institute of the Russian Academy of Sciences in St. Petersburg, Russia.

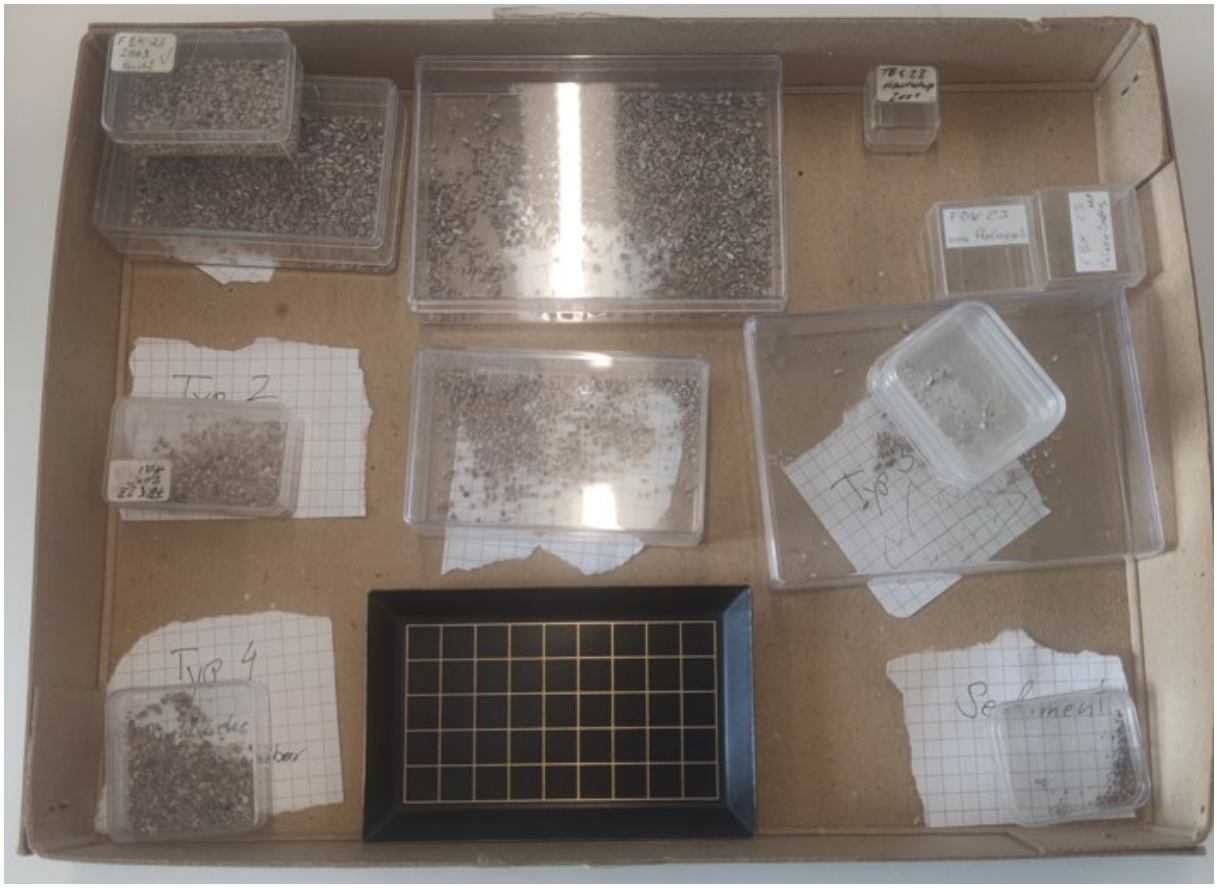


Figure 10. Fossil material analyzed in this study from the Dzhidasai locality. Hybodontiform teeth sorted according to rough morphotypes.

The methods of this study focus mainly on microscopy, light microscopy as well as scanning electron microscopy (SEM), due to the small size of the fossil material.

The first method employed was light microscopy via a LEICA MZ12 model microscope and a LEICA CLS150 light machine, present in the Department of Paleontology of the University of Vienna. This equipment was used to separate the fossil material, with tweezers, small brushes and a picking needle, and roughly sort the teeth into three main morphotypes (Fig. 11):

1. Teeth with a broad and flat crown.
2. Teeth with one prominent, central cusp and no lateral cusplets.
3. Teeth with a main cusp and multiple, lateral cusplets.

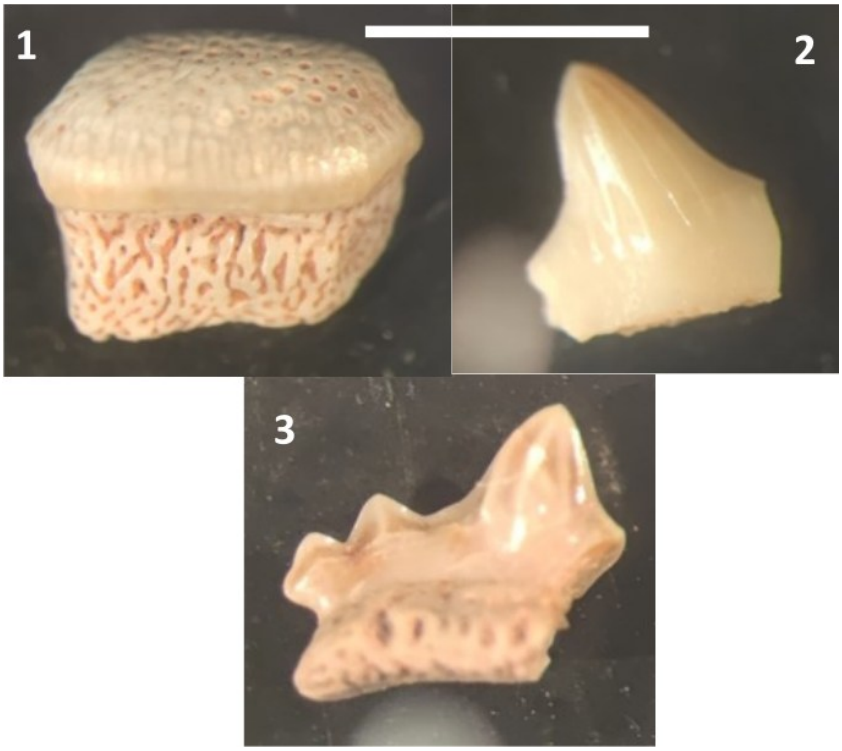


Figure 11. Examples of the three main tooth morphotypes as seen under a light microscope. Scale bar equals 1 mm.

Based on this rough, first categorization teeth with especially high potential for a meaningful gain of information were chosen for further analysis under an electron microscope. Subsequently, the chosen teeth were fastened to aluminum stubs via adhesive pads, and the samples were gold coated with a SC 500 Sputter Coater. Lastly the SEM analyses were carried out with a JSM-6400 Scanning Microscope (Fig. 12). Both machines used are located at the Department of Paleontology of the University of Vienna.

The SEM images generated then aided, together with already existing literature, in the completion of morphological descriptions of the teeth and subsequent identification of the taxa present in the Dzhidasai locality.

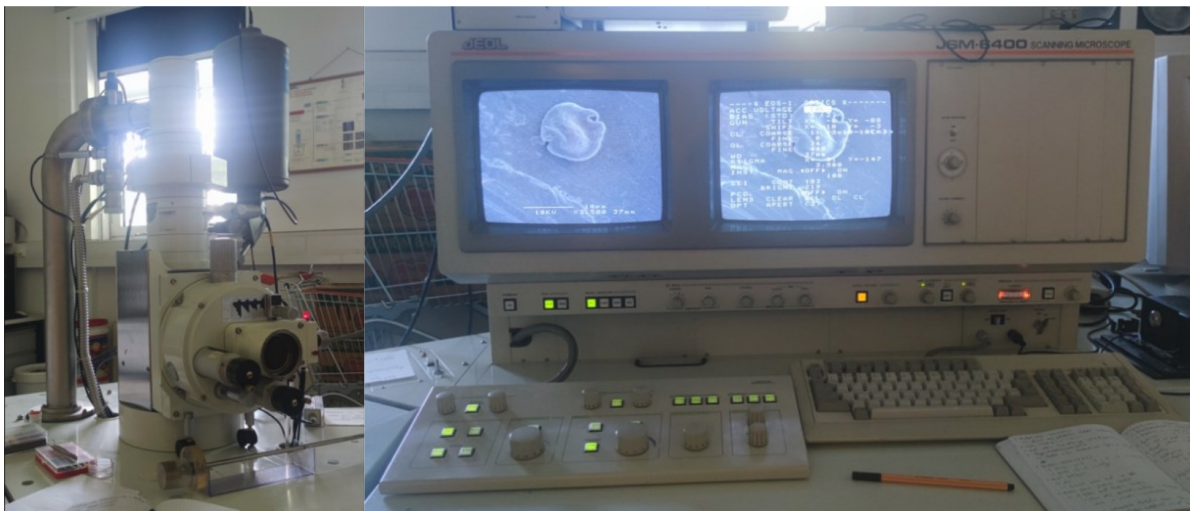


Figure 12. Electron Microscope (JSM-6400 Scanning Microscope) used and its associated monitors.

5. Systematics & Spatiotemporal Implications of the Dzhidasai hybodont taxa

The following chapter provides an extensive overview of the systematic paleontology, a thorough morphological description of the hybodontiform taxa identified within the Kyrgyz locality described above via their recovered and prepared teeth. Key characteristics of the morphological descriptions include the overall tooth size and crown shape, the root shape and structure and the surface features of the teeth, including the presence of ridges, cusps, cusplets and other additional ornamental structures. This chapter will also set the identified taxa in a spatiotemporal framework, comparing the Dzhidasai locality to other localities these taxa are already known from.

The systematic scheme here adopts that proposed by Rees and Underwood (2002) in a simplified form. The term "cusp" is used for the central main apex of the crown, and the term "cusplets" for the mesial and distal smaller apices accompanying the main apex. The morphological terminology is based on Duffin (1985) and Rees and Underwood (2002).

Class **Chondrichthyes** Huxley, 1880
Subclass **Elasmobranchii** Bonaparte, 1838
Order **Hybodontiformes** Patterson, 1966
Family **Lonchidiidae** Herman, 1977
Genus ***Hylaeobatis*** Woodward, 1916
Type species ***Hylaeobatis problematica*** Woodward, 1916 from the Early Cretaceous of Sussex, England
***Hylaeobatis verzilini* comb. nov.** Nessov & Kaznyshkin, 1988

Referred material: A total of 2.566 complete and fractured teeth (Table 2) from the Balabansai Formation, Dzhidasai locality (FBX-23), Fergana Valley, western Kyrgyzstan (Fig. 9a). Four of which (FBX-23_10, FBX-23_16, FBX-23_29 & FBX-23_30) are illustrated in Fig. 13.

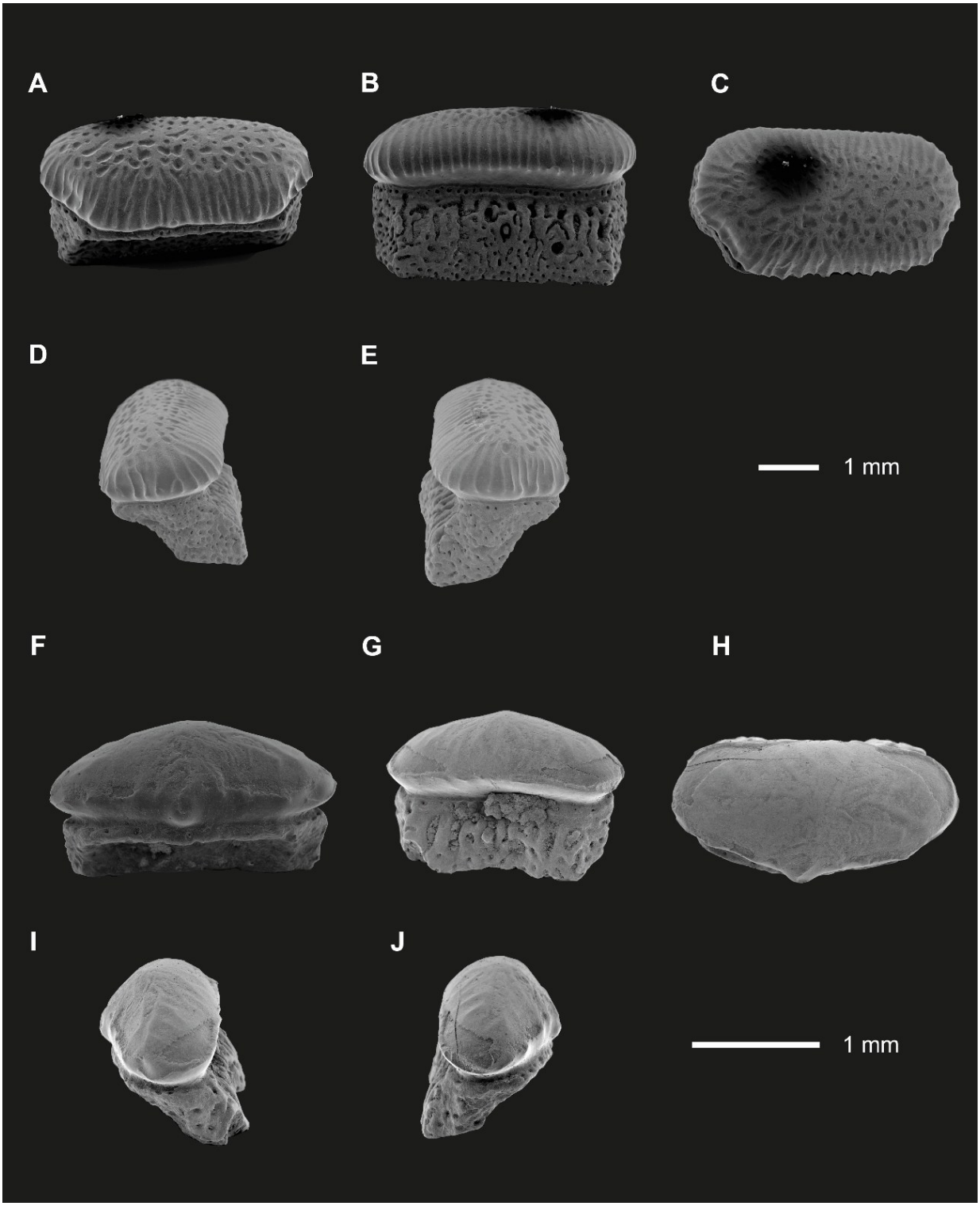
Description: *Hylaeobatis* teeth found in this location are relatively big, when compared to the teeth of other taxa present in this sample, as will be made clear over the course of this chapter. They vary in size, ranging from around 2 mm to just over 4.5 mm in mesiodistal width and from around 1 mm to 3 mm in apicobasal height.

The crown may show a very shallow rise in the centre, which could be interpretated as a very flat central cusp, though most of the time it is almost completely flat, with only a very slight convexity. Furthermore, it has a very regular, oval to a slight, subtriangular shape with no lateral cusplets and only a small labial peg, if at all, is present.

The occlusal surface is strongly ornamented with rounded grooves, which get elongated on the sides of the crown, where they are also separated by vertical ridges. However, in many specimens these ornamentations are strongly abraded. The vertical ridges reach to around

the lower third to the lower fourth of the crown. There they stop at a subtle, horizontal suture line, below which the crown surface is smooth and shows no ornamentation.

The roots are high and anaulacorhize, exhibiting a plethora of foramina and in a variety of shapes and sizes. On the labial side the root shows a shallow depression right below the crown-root junction.



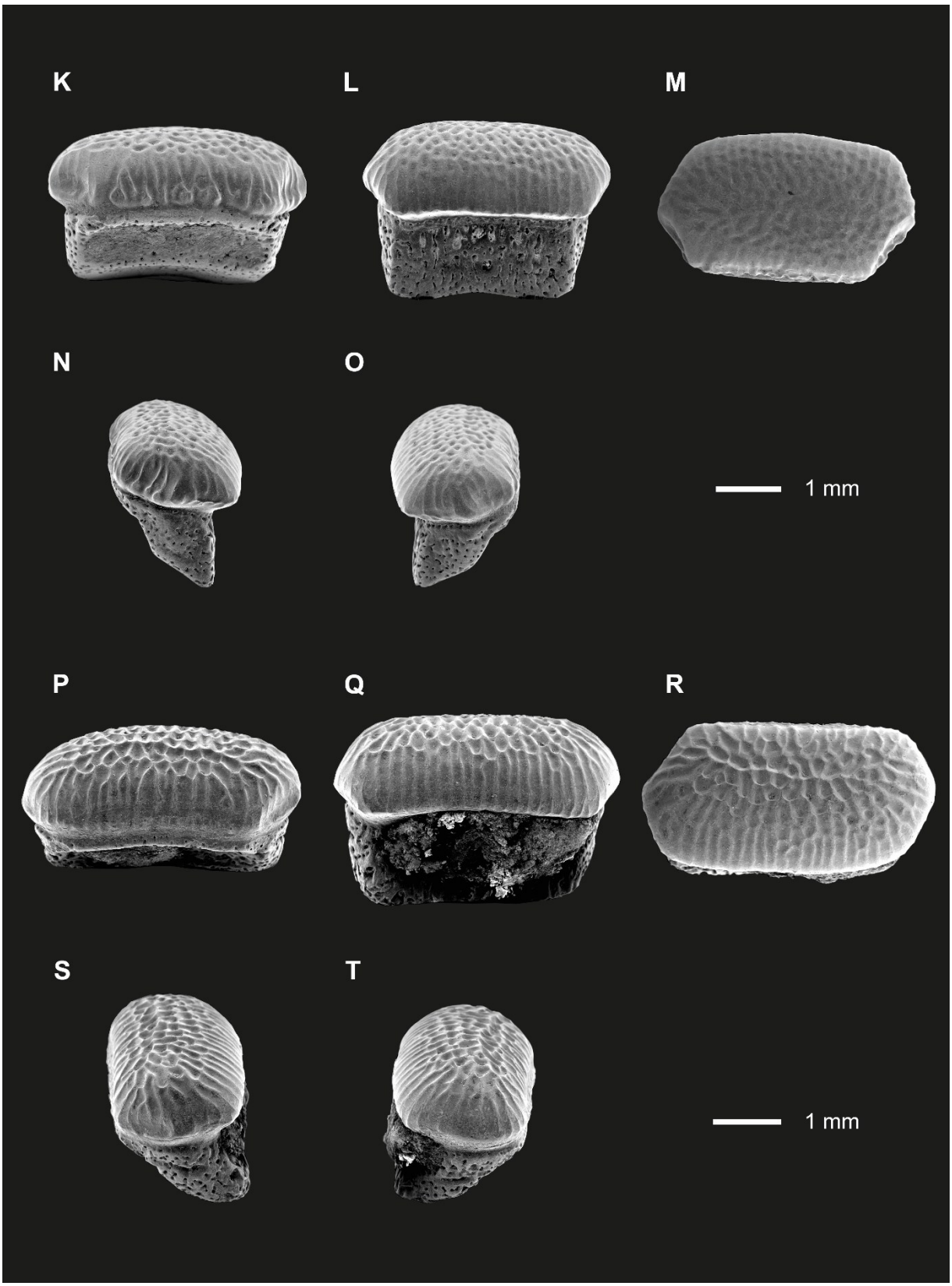


Figure 13. *Hylaeobatis verzilini* comb. nov. from the Callovian, Dzhidasai locality, Balabansai Formation, Fergana Valley, western Kyrgyzstan.
a-e: Posterolateral tooth (FBX-23_10) in labial (a), lingual (b), occlusal (c) & lateral (d & e) views.
f-j: Posterolateral tooth (FBX-23_16) in labial (f), lingual (g), occlusal (h) & lateral (i & j) views.
k-o: Posterolateral tooth (FBX-23_29) in labial (k), lingual (l), occlusal (m) & lateral (n & o) views.
p-t: Posterolateral tooth (FBX-23_30) in labial (p), lingual (q), occlusal (r) & lateral (s & t) views.

Remarks: The teeth of *Hylaeobatis* with their flattened crowns are a crushing-type dentition, used primarily to crack the hard shells of invertebrate prey animals. Teeth of this type are usually situated laterally in the back of the jaws for maximal efficiency. Furthermore, it suggests the teeth were positioned in a pavement-like arrangement (Woodward 1916). The pores permeating the roots are most likely the remnants of nerve canals or blood vessels.

The overall morphology of the teeth described above is very similar to the general shape of posterior teeth of *Hylaeobatis problematica* (Woodward 1916). They are, however, significantly smaller, as teeth assigned to *Hylaeobatis problematica* can measure up to 15 mm in mesiodistal width and 7 mm in apicobasal height (Duffin & Sweetman 2011). Furthermore, the teeth described here possess a suture-like line cutting off ornamentation on the sides of the crown and especially well visible on the lingual crown face, which is not present in specimens of *Hylaeobatis problematica*.

Teeth of this morphology found in the Balabansai Svita were described by Nessov & Kaznyshkin 1988 and assigned to the genus *Palaeobates* by establishing the species *Palaeobates verzilini*. However, Rees & Underwood 2005 argued that the fossil material actually falls into two groups, belonging to the genera *Hylaeobatis* and *Lissodus* respectively. The present study agrees with this reassessment and subsequent assignment of the teeth described above and illustrated in Fig. 13 to the genus of *Hylaeobatis*. Furthermore, it therefore suggests the transfer of the present species to *Hylaeobatis*, as *Hylaeobatis verzilini* comb. nov. , based on the significant size difference and other diagnostic features outlined above. As such, the present locality also represents the oldest known record of *Hylaeobatis* (Rees & Underwood 2005).

Fossil evidence for the genus *Hylaeobatis*, including teeth and cephalic spines, has so far been found in formations from the Early Cretaceous, such as the Wealden formations in England (Rees & Underwood 2002; Woodward 1916).

However, as already mentioned above, the teeth assigned to *Palaeobates* (Nessov & Kaznyshkin 1988) were reassigned by Rees & Underwood (2005) to the genera *Hylaeobatis* and *Lissodus* respectively, a reassessment this study completely agrees with as well. While this reassignment had no effect on the effective, temporal and only very little effect on the spatial distribution of *Lissodus*, as will be made clear below, the same cannot be said for *Hylaeobatis*. Since the genus is, as mentioned above, otherwise only known from Cretaceous deposits. As such, due to the reassignment by Rees & Underwood 2005 and the results of the present study the temporal range of the genus *Hylaeobatis* extends as far back as the Middle Jurassic (Fig. 14).

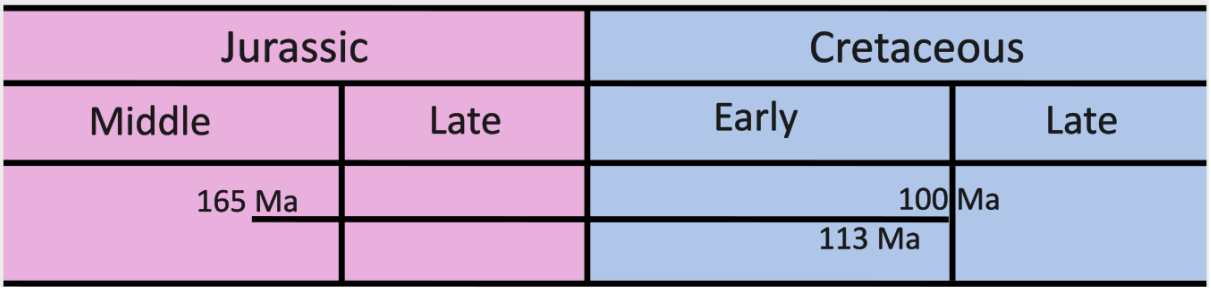


Figure 14. Temporal range of the hybodont genus *Hylaeobatis*.

In terms of its spatial distribution the genus *Hylaeobatis* is primarily known from multiple English localities, especially the Isle of Wight (Fig. 15) (Dineley & Metcalf 1999; Sweetman 2011; Woodward 1916), but also from the USA, more precisely Central Texas (Fig. 15) (Winkler et al. 1989, 1990).

Other than that, the only known occurrence of *Hylaeobatis* in Asia, so far, is in fact the Balabansai Svita of Kyrgyzstan (Fig. 15) described also in this study (Nessov & Kaznyshkin 1988; Rees & Underwood 2005) This makes it quite possible that between the Middle Jurassic and the Early Cretaceous *Hylaeobatis* vanished in wide parts of its initial distribution range, specifically in Asia, indicating the need for further research in that direction.

Figure 15. Spatial distribution of *Hylaeobatis*.

Genus ***Lissodus*** Brough, 1935

Type species ***Hybodus africanus*** Broom, 1909 from the Scythian (Early Triassic) of Bekker's Kraal, South Africa.

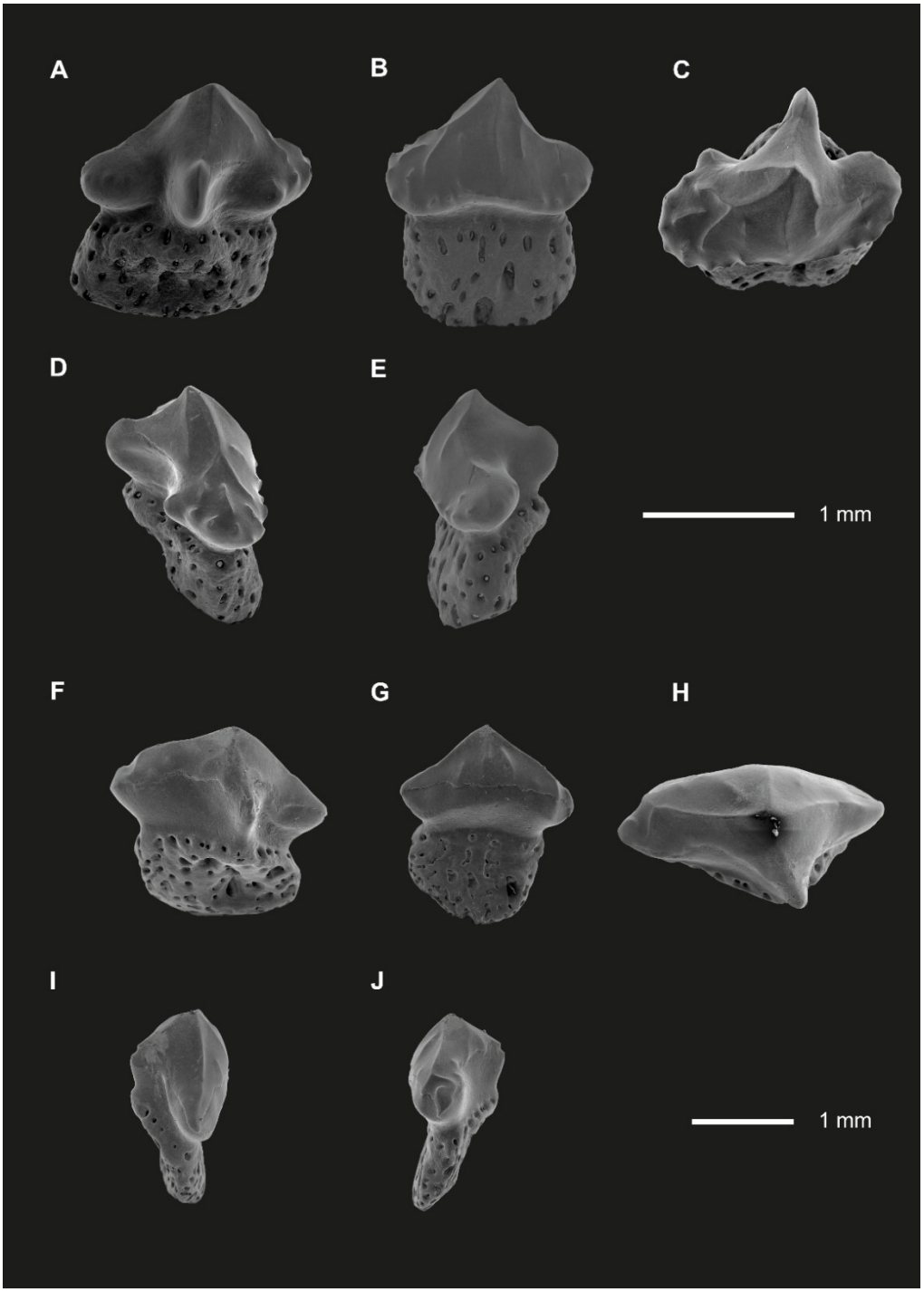
Lissodus verzilini **comb. nov.** Nessov & Kaznyshkin, 1988

Referred material: A total of 1.433 complete and fractured teeth (Table 2) from the Balabansai Formation, Dzhidasai locality (FBX-23), Fergana Valley, western Kyrgyzstan (Fig. 9a). Four of which (FBX-23_01, FBX-23_03, FBX-23_11 & FBX-23_23) are illustrated in Fig. 16.

Description: The teeth of *Lissodus* show a consistent size of around 1.5 mm to just over 2 mm in mesiodistal width and 1 mm to 2 mm in apicobasal height throughout the analysed sample. Despite the similar size, the crowns of *Lissodus* teeth of this locality show a considerable range of dental variation, where the teeth of the Dzhidasai locality can be grouped into two main morphotypes.

The first is characterized by a more prominent central cusp and a very broad base of the crown, where the sides reach over the width of the root in a wing-like manner (FBX-23_01, 02

& 03). These crowns show a triangular shape in lateral views. Contrary to that, the second morphology shows a more rounded crown with a less pronounced central cusp, however this central rise is still the highest point of the crown (FBX-23_04, 11 & 19). No additional upwards oriented cusplets are present in either of the morphotypes and both exhibit a prominent labial peg with a broad base. Ornamentation is present in both morphotypes. FBX-23_01 & 02 show ornamentation along the surface of the crown mainly in form of the occlusal crest as well as additional, mostly vertical, ridges. The teeth of the second morphotype show more extensive ornamentation on their broader occlusal surfaces, in the form of grooves and ridges as well as granulae. These granulae are present mainly on the labial side. Some show visible traces of abrasion as well. The roots are filled with mainly round shaped foramina and exhibit a depression on the labial side of the root, below the labial peg of the crown.



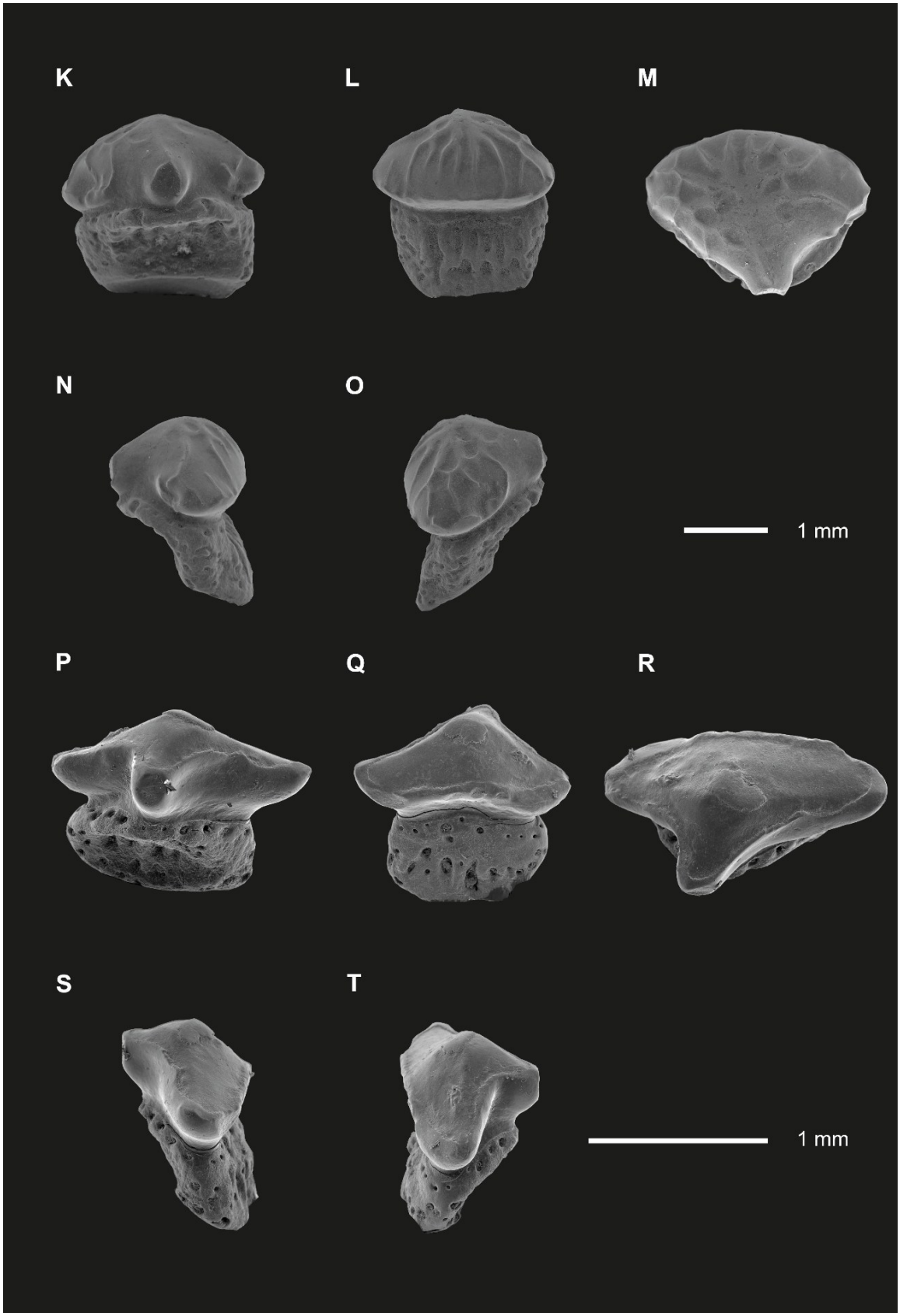


Figure 16. *Lissodus verzilini* comb. nov. from the Callovian, Dzhidasai locality, Balabansai Formation, Fergana Valley, western Kyrgyzstan.
a-e: Anterior tooth (FBX-23_01) in labial (a), lingual (b), occlusal (c) & lateral (d & e) views.
f-j: Anterior tooth (FBX-23_03) in labial (f), lingual (g), occlusal (h) & lateral (i & j) views.
k-o: Posterolateral tooth (FBX-23_11) in labial (k), lingual (l), occlusal (m) & lateral (n & o) views
p-t: Lateral tooth (FBX-23_23) in labial (p), lingual (q), occlusal (r) & lateral (s & t) views.

Remarks: Both morphotypes presumably mainly served the purpose of durophagous feeding by first grabbing and then crushing hard-shelled prey animals. The more pronounced cusps of morphotype one seem suited to grip and hold on to prey animals and as such were most likely positioned towards the front of the jaws (Rees & Underwood 2005). Morphotype two on the other hand exhibits even more of a crushing character to break open the hard-shelled prey. These teeth, therefore, had their position more laterally, towards the back of the jaws (Rees & Underwood 2005, 2008). *Lissodus* thus mainly exhibits a type of dentition of a durophagous feeder, whose main prey consisted of hard-shelled invertebrates. However, due to the cusps present in morphotype one it also was not impossible that they could also prey on a wider variety of different animals, including soft-bodied fishes for example, present in its environment (Rees & Underwood 2005, 2008). The pores permeating the roots are most likely the remnants of nerve canals or blood vessels (Rees & Underwood 2005).

Following the taxonomic review of Rees & Underwood (2002), *Lissodus* sensu stricto is characterized by low-crowned, labiolingually broad teeth with a single, centrally placed cusp and a relatively smooth or faintly ornamented crown surface As such, these teeth are distinguished from *Lonchidion* and *Parvodus* in the absence of pronounced lateral cusplets and finer ridges on the crown, and from *Hylaeobatis* in the generally different crown shape. (Duffin 2001; Rees & Underwood 2002). Based on the description provided above and the dental morphology reported by Nessov & Kaznyshkin (1988), the teeth, for which they established the species *Palaeobates verzilini*, exhibit the suite of characters that Rees & Underwood (2002) used to delimit *Lissodus* sensu stricto, mentioned above. Thus, the dental material originally described as *Palaeobates verzilini* Nessov & Kaznyshkin, 1988 is here recombined as *Lissodus verzilini* (Nessov & Kaznyshkin, 1988) comb. nov. as the teeth exhibit the diagnostic combination of a low, labiolingually broad crown with a single central cusp, subdued crown ornament, and a basal root plate bearing large nutritive foramina.

These teeth furthermore differ from already established species of *Lissodus*. The teeth of *Lissodus leiodus* (Woodward 1887) show a less pronounced and more rounded main cusp as well as an overall much larger size, growing up to around 11 mm in mesiodistal width (Rees & Underwood 2005). Teeth of *Lissodus leiopleurus* (Woodward 1889a) are, similarly to *L. leiodus* larger than the teeth described above, with a mesiodistal width of up to almost 9 mm. The ornamentation pattern of *L. leiopleurus* is also more pronounced and mainly characterized by coarse vertical folds and depending on the position in the jaws, lateral cusplets may also be present (Rees & Underwood 2005). The crowns of both *Lissodus africanus* (Broom 1909) as well as *Lissodus tumidoclavus* (Duffin et al. 2023), while similar in overall size, show a more elongated shape than the *Lissodus* specimens in this sample (compare Duffin et al. 2023). The teeth of *Lissodus hasleensis* (Rees 1998) are as well much bigger with a mesiodistal width of up to 9 mm and further show a much more triangular character in labial and lingual views, with both axial ends drooping down (Rees 1998). *Lissodus angulatus* (Stensiö 1921) is characterized by a high central cusp and ornamentation in form of fine vertical ridges. Teeth of *L. angulatus* are also much larger with a mesiodistal width of up to 7 mm (Duffin et al. 2023). *Lissodus cassangensis* (Teixiera 1956) possesses a sharper, higher central cusp, giving the teeth a more pyramidal shape, and a more pronounced and rounder labial peg (De Blanger

2005). *Lissodus minimus* (Agassiz 1839) shows a much more triangular crown shape in occlusal view, as well as much less pronounced labial pegs. Teeth of *L. minimus* may also grow slightly larger than the teeth of the here studied locality, with a mesiodistal width of up to 5 mm (Vida et al. 2025). The crown of *Lissodus cristatus* (Delsate & Duffin 1999) is more elongated as well as significantly more compactly built, with almost no central cusp visible and accessory cusplets may be present as well (Delsate & Duffin 1999; Yamagishi 2009). *Lissodus lepagei* (Duffin 1993) shows a more robust and labiolingually compressed crown morphology, with less pronounced ornamentation and a crenulated occlusal crest (Pla et al. 2013). *Lissodus nodosus* (Seilacher 1943) possesses a visibly lower crown than the morphologies described here, with the lateral-most portions of the crown bending slightly downwards (Pawlak et al. 2022). *Lissodus wardi* (Duffin 1985) teeth too are significantly bigger than the Kyrgyz specimens described here, with a medio-distal width of up to almost 8 mm. The crowns furthermore are more robust, with a low coronal profile and a very low central cusp (Duffin 2001). *Lissodus levis* (Woodward 1887), too is significantly larger, measuring up to 7 mm mesiodistally. This species, too, possesses additionally a considerably lower coronal profile than the teeth described above *(*Duffin *2001).*

The temporal range of *Lissodus* is to this date a hotly debated topic. Some studies suggest that fossils attributed to *Lissodus* span all the way from the latest Devonian (Famennian), over the great mass extinction event at the Permian-Triassic boundary, and even to the end of the Cretaceous (Maastrichtian), where hybodonts in general have gone extinct (Fig. 17). A timeframe spanning almost 300 million years (360 Ma to 66 Ma) (Fischer 2008). This would easily make it the hybodont taxon spanning the longest timeframe in general.

Other research on the other hand proposes a significantly more restricted range. Excluding the Paleozoic range of the genus and limit it from the Early Triassic to the end of the Early Cretaceous (Albian) (Fig. 17). Which constitutes a much more restricted timeframe spanning roughly 150 million years (252 Ma to 100 Ma) (Rees & Underwood 2002).

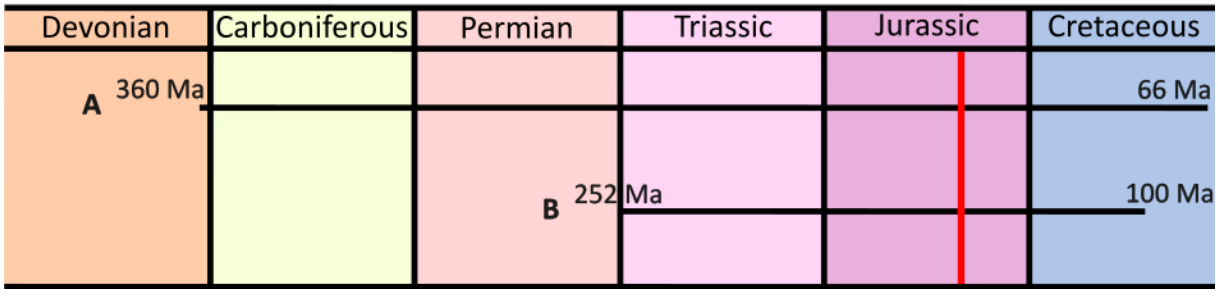


Figure 17. Temporal range of the hybodont genus *Lissodus*.
A: Extended range proposition
B: Restricted range proposition
Black: Known fossil range
Red: Temporal range of this study - Callovian

However, debating which of these two temporal ranges of *Lissodus* is more sensible would exceed the scope of this study, especially since the Callovian placement of the Dzhidasai

locality (Fig. 21) fits the remains described above nicely in the middle of both hypotheses regardless.

Lissodus exhibited a widespread spatial distribution, with fossil evidence spanning multiple continents, including Europe, North America, Africa, Australia and Asia.

Europe shows multiple instances of fossil sites containing *Lissodus* remains. Reported examples include Palaeozoic localities in Ireland from Lower Carboniferous deposits (Duncan 2004), but also Mesozoic deposits, such as the Atherfield Point Chale Clay Member in the Isle of Wight, England (Dineley & Metcalf 1999) and continental Europe with material discovered in the Höganäs Formation, Sweden (Fischer 2008). The genus is also known from the american Chinle Formation (Heckert et al. 2007). The noteworthy Karoo beds of South Africa have also produced *Lissodus* remains, extending the genus' spatial range into Africa as well (Duffin et al. 2023). It is even known from the Canning Basin, pushing the spatial distribution all the way to Australia too (Roelofs et al. 2016).

Asian localities where *Lissodus* has been known so far include for example the Indian Tiki Formation (Kurma & Sharma 2019), as well as the Japanese Taho Formation (Goto et al. 2010). Now the genus is also known from the Dzhidasai locality of Kyrgyzstan as well, further broadening the Asian distribution area of this hybodont genus.

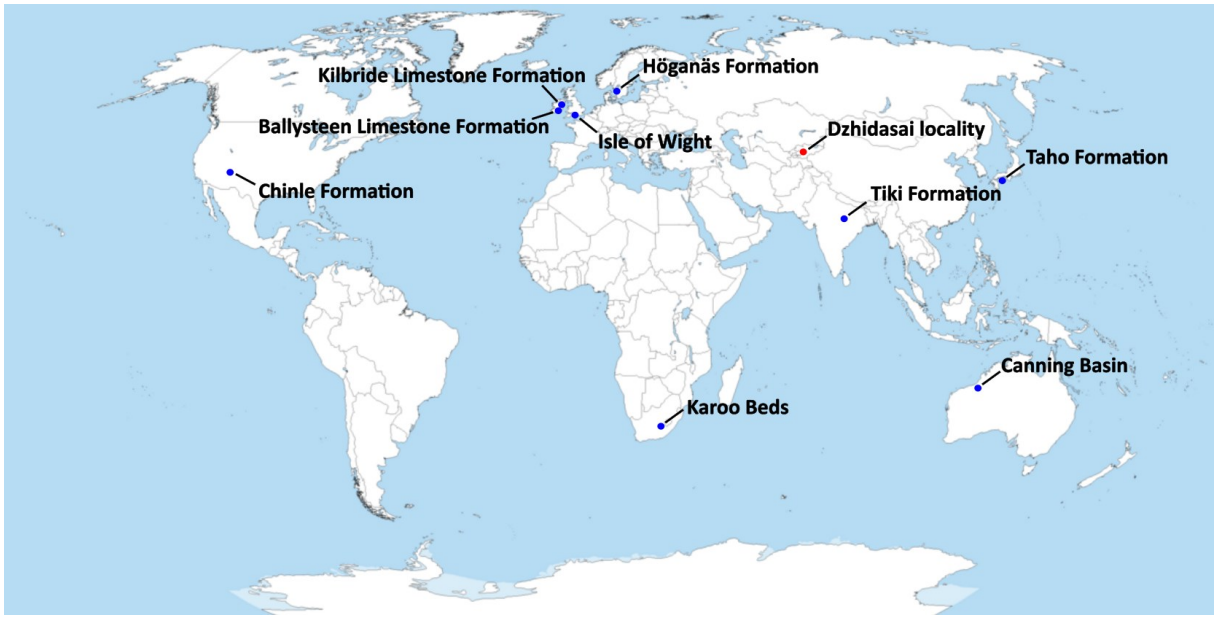


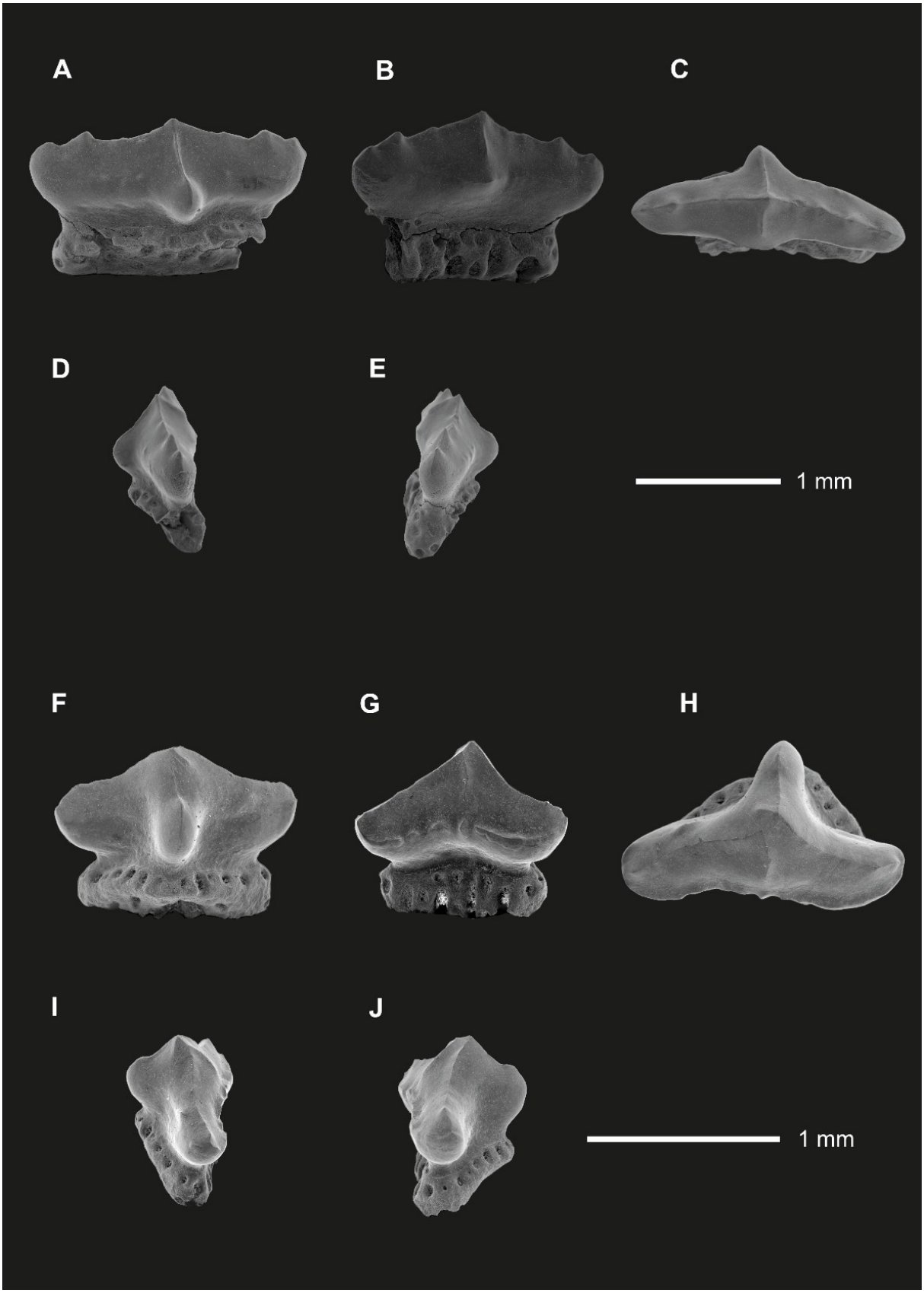
Figure 18. Spatial distribution of *Lissodus*.

Genus ***Lonchidion*** Estes, 1964

Type species ***Lonchidion selachos*** Estes, 1964 from the Maastrichtian (Late Cretaceous) Lance Formation of eastern Wyoming, U.S.A.

Lonchidion sp.

Referred material: A total of 114 complete and fractured teeth (Table 2) from the Balabansai Formation, Dzhidasai locality (FBX-23), Fergana Valley, western Kyrgyzstan (Fig. 9a). Four of which (FBX-23_07, FBX-23_17, FBX-23_21 & FBX-23_31) are illustrated in Fig. 19.



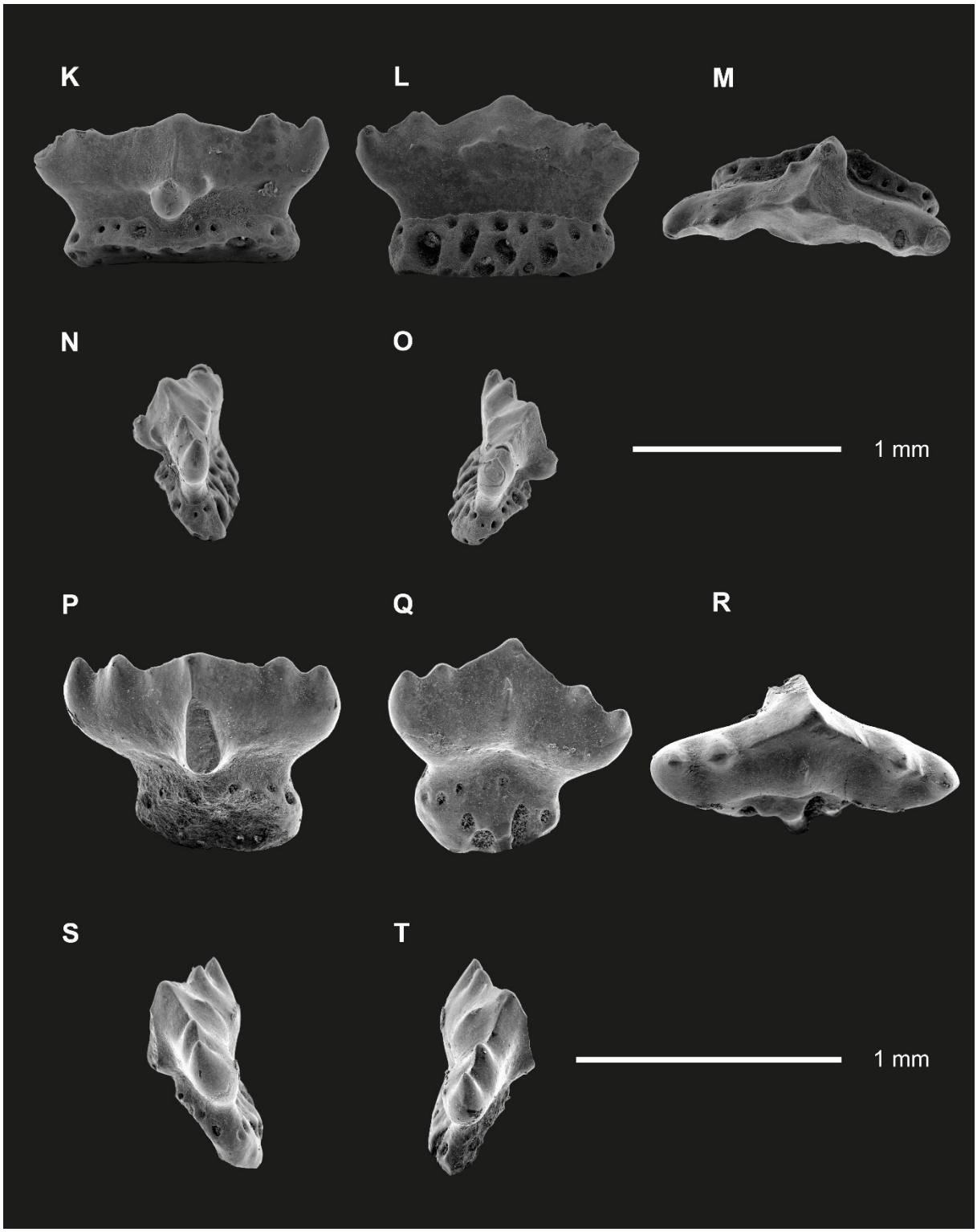


Figure 19. *Lonchidion sp.* from the Callovian, Dzhidasai locality, Balabansai Formation, Fergana Valley, western Kyrgyzstan.
a-e: Lateral tooth (FBX-23_07) in labial (a), lingual (b), occlusal (c) & lateral (d & e) views.
f-j: Anterolateral tooth (FBX-23_17) in labial (f), lingual (g), occlusal (h) & lateral (i & j) views.
k-o: Lateral tooth (FBX-23_18) in labial (k), lingual (l), occlusal (m) & lateral (n & o) views
p-t: Lateral tooth (FBX-23_31) in labial (p), lingual (q), occlusal (r) & lateral (s & t) views.

Description: The teeth of *Lonchidion* present in this sample show rather a consistent size. They are roughly 1 mm to a bit over 2 mm in mesiodistal width and about 1 mm to just under 1.5 mm in apicobasal height.

The crown is low in profile, mesodistally elongated and may be asymmetrical, with the highest point being a rather low central cusp. Up to two minute, lateral cusplets on either side may be present as well. The labial peg is well developed, with a broad base and finer tip, and surmounted by a weak vertical ridge that extends up to the apex of the main cusp. A weak vertical ridge may be present on the lingual crown face. The labial crown face may be ornamented with granulae. The crown is slightly incised above the sharply visible crown-root junction

Apart from the occlusal crest, which is weak to moderately well-developed and extends from the main cusp across all lateral cusplets, and a few vertical ridges, mainly on the occlusal surface of the labial peg, there is little to no ornamentation observable.

The low root is slender at the crown-root junction and broadens towards its base, with a noticeable offset in regard to the crown on the lingual side. It is perforated by numerous rounded foramina of varying sizes and a shallow depression on the labial side may be present as well.

Remarks: The serrated nature of the crown, as well as the sharp central cusp and presence of additional, lateral cusplets suggest these teeth were positioned laterally to anterolaterally in the jaws and served as cutting dentition used against soft tissue targets, mainly due to the serrated nature of the occlusal crests. Although, they presumably could have also served a gripping function secondarily.

Under the sharp crown-root junction runs a line of relatively small and circular pores, constituting the endings of nerve canals. Contrary to these relatively small pores visible towards the top of the root, the pores situated lower, towards the base of the roots get bigger and less circular in appearance, which are as well most likely remnants of nerve canals or blood vessels.

The teeth of this sample are assigned to the family Lonchidiidae and furthermore the genus *Lonchidion*. Primarily due to the taxa comprising this group being characterized by the presence of prominent protuberances on the labial sides of the cusps and a flat root possessing a single row of circular foramina along the upper, labial root face (Klug et al. 2010).

The recovered specimens of this locality also provide a very important improvement of the fossil record of *Lonchidion* during the Jurassic period, which so far has shown a distinctive lack of specimens (Rees & Underwood 2002). However, due to the combination of size, age and morphology of the teeth illustrated above, it is not possible to assign them more accurately than genus level in the scope of the present study.

The temporal range of the hybodont genus *Lonchidion* spans from the Middle Triassic (Ladinian) (Johns et al. 2014) to the Late Cretaceous (Maastrichtian) (Fig. 20) (Gates et al. 2019), making it one of the longest-surviving hybodont genera, spanning basically almost the entirety of the Mesozoic, surviving until the Hybodontiformes in general went extinct.

Which in turn makes the fossil material examined in the present study fit in quite nicely with the accepted temporal range of the *Lonchidion* genus (Fig. 20), similarly to *Lissodus*, as mentioned above.

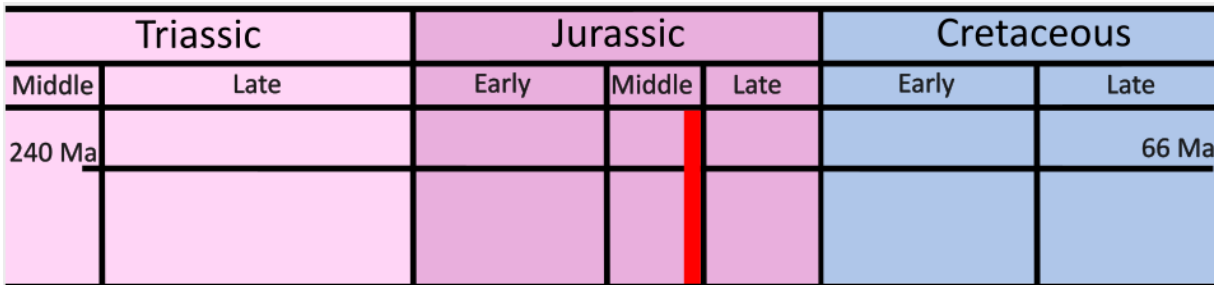


Figure 20. Temporal range of the hybodont genus *Lonchidion*.
Black: Known fossil record
Red: Temporal range of this study - Callovian

The hybodont genus *Lonchidion* is known from fossil sites across multiple continents, including North America, Europe, Africa and Asia, therefore exhibiting a very widespread geographic distribution.

These include multiple examples from the United States, including the famous, Maastrichtian Hell Creek formation of Montana (Wynd et al. 2020), the Triassic Dockum Group of Texas and New Mexico (Heckert et al. 2007) and the Late Cretaceous Lance Formation of Wyoming, from where the type species was described. (Fig. 21) (Estes 1964). From Europe this hybodont genus is known for instance, from Upper Triassic deposits of Spain (Fig. 21) (Manzanares et al. 2016). It is also present in North African deposits, with an example of the Moroccan, Late Cretaceous Kem Kem beds (Fig. 21) (Lasseron et al. 2020).

Apart from the Balabansai locality analysed in this study, *Lonchidion* has already been described from another Kyrgyz locality, specifically from the Triassic Lake deposits of the Madygen Formation (Fig. 21) (Fischer et al. 2011), with the Dzhidasai locality of this study further cementing the presence of this genus in Central Asia.

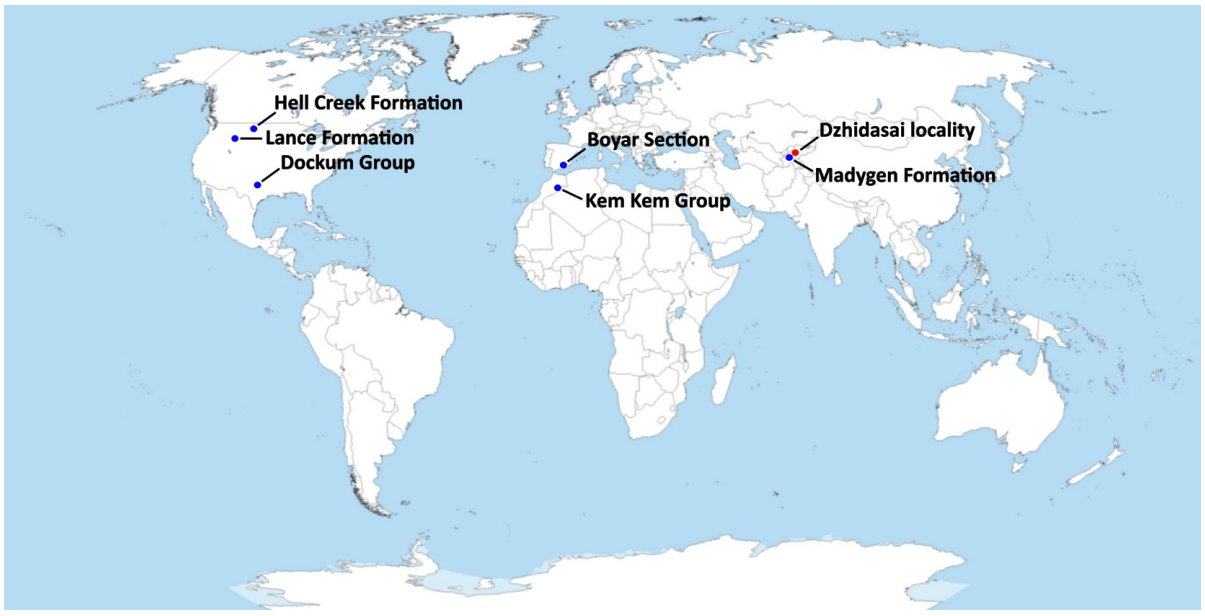


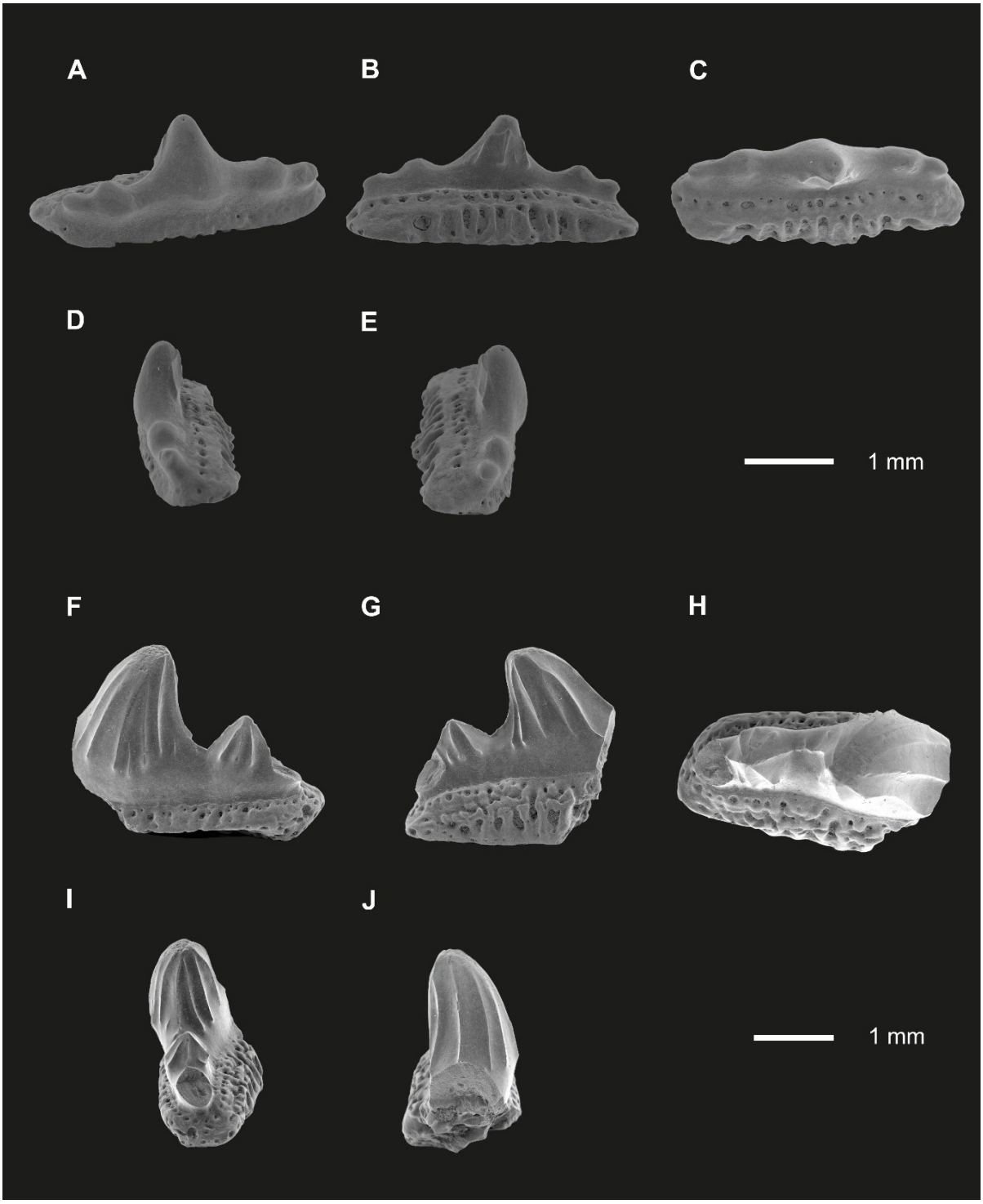
Figure 21. Spatial distribution of *Lonchidion*.

Genus ***Parvodus*** Rees & Underwood, 2002

Type species ***Lissodus rugianus*** Ansorge, 1990 from the Early Cretaceous of Rügen, northern Germany.

Parvodus balabansaiensis **comb. nov.** Nessov & Kaznyshkin, 1988

Referred material: A total of 507 complete as well as fractured teeth (Table 3) from the Balabansai Formation, Dzhidasai locality (FBX-23), Fergana Valley, western Kyrgyzstan (Fig. 9a). Four of which (FBX-23_06, FBX-23_13, FBX-23_15 & FBX-23_28) are illustrated in Fig. 22.



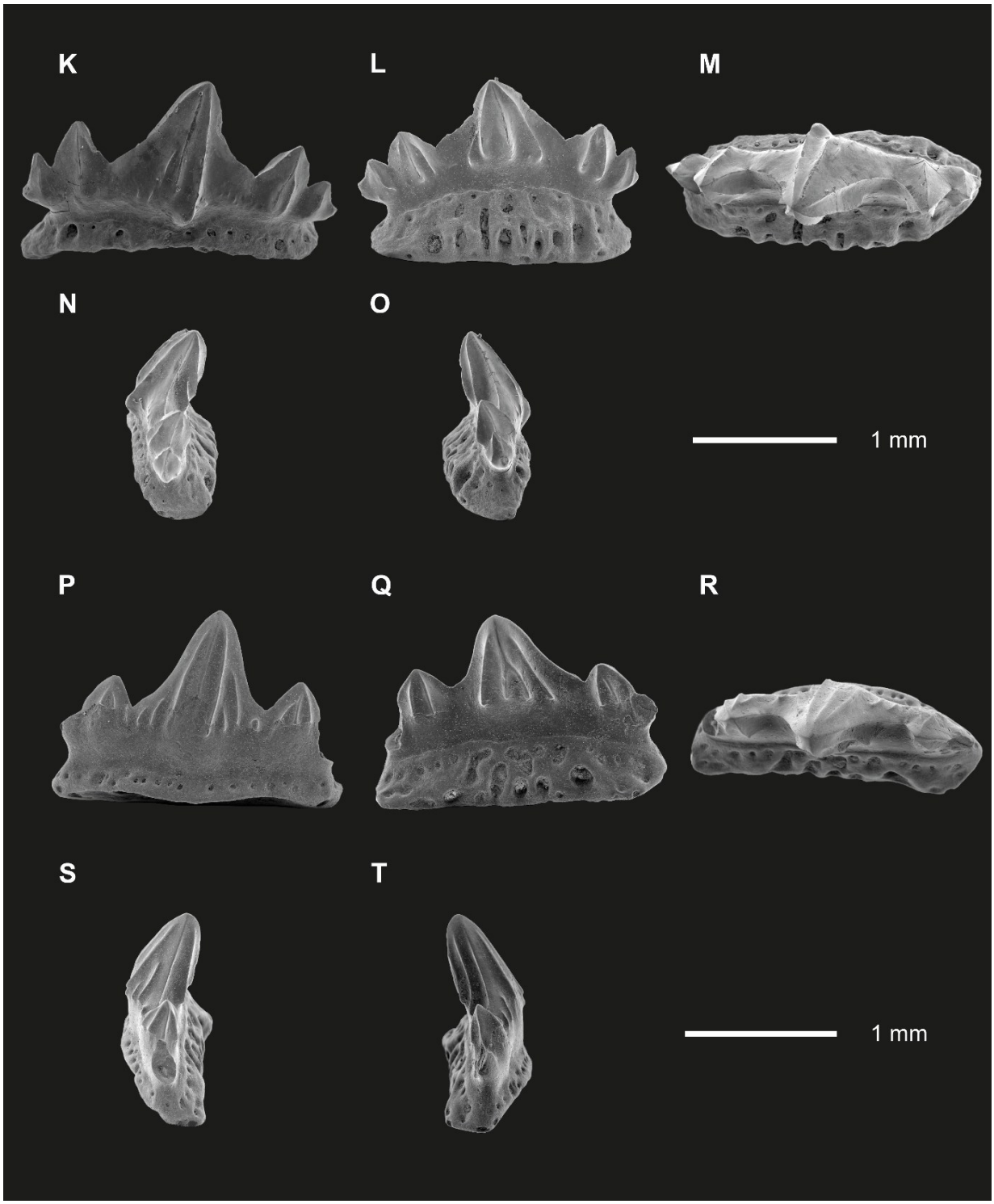


Figure 22. *Parvodus balabansaiensis* comb. nov. from the Callovian, Dzhidasai locality, Balabansai Formation, Fergana Valley, western Kyrgyzstan.

a-e: Lateral tooth (FBX-23_06) in labial (a), lingual (b), occlusal (c) & lateral (d & e) views.

f-j: Anterolateral tooth (FBX-23_13) in labial (f), lingual (g), occlusal (h) & lateral (i & j) views.

k-o: Lateral tooth (FBX-23_15) in labial (k), lingual (l), occlusal (m) & lateral (n & o) views.

p-t: Lateral tooth (FBX-23_28) in labial (p), lingual (q), occlusal (r) & lateral (s & t) views.

Description: The *Parvodus* teeth are, similarly to the *Hylaeobatis* specimens, comparatively big in the Dzhidasai assemblage. They possess a mesiodistal width in the range of around 2 mm to 3 mm and an apicobasal height of around 1 mm to 3 mm.

The crown, showing a gracile character, is composed of a high central cusp and up to two smaller, lateral cusplets on either side of the central main cusp. A labial peg, if present at all, is minute and thin. In the case of FBX-23_06 the entire crown is bent towards the lingual side of the tooth.

There is little ornamentation. Apart from the occlusal crest, which connects the central cusp to the lateral cusplets, vertical ridges along the labial and lingual surfaces are present.

The root is shallow and slender, though it broadens towards its base. It is perforated by a plethora of foramina, with a line of smaller and more rounded pores running directly beneath the crown-root junction.

Remarks: Due to the nature of the pronounced and sharpened cusps of the teeth it can be assumed that the teeth served primarily a gripping and cutting purpose and thus were most likely positioned anterolaterally to laterally in the jaws.

The pores permeating the roots are most likely the remnants of nerve canals or blood vessels.

Teeth of very similar morphology were also described by Nessov & Kaznyshkin (1988), for which they proposed the new species *Polyacrodus balabansaiensis* (Nessov & Kaznyshkin 1988). However, Rees & Underwood (2005) proposed that this species, as well as the second *Polyacrodus* species established by Nessov & Kaznyshkin (1988) – *Polyacrodus prodigialis* – are better referred to the genus of *Hybodus*. They further suggested that some teeth assigned to *Polyacrodus balabansaiensis*, by Nessov & Kaznyshkin (1988), more likely belong to a species of *Parvodus* (Rees & Underwood 2005). A notion that was continued by Wen et al. (2022), who also transferred this initial *Polyacrodus* species to the genus *Parvodus* (Wen et al. 2022). This study as well agrees to propose to assign these teeth recovered from the Dzhidasai locality (Fig. 16), which Nessov & Kaznyshkin (1988) referred to as *Polyacrodus balabansaiensis*, to the genus *Parvodus*, as they generally show morphology consistent with the initial description of *Parvodus* teeth (Rees & Underwood 2002). In terms of the general gracile character of the crown, the morphology of the main cusp and lateral cusplets, as well as the presence of a labial peg (Rees & Underwood 2002).

When compared to other described *Parvodus* species, *Parvodus balabansaiensis* comb. nov. can be distinguished by its combination of a relatively high, mesiodistally elongated crown, subdued ornamentation, and broad root bearing multiple small foramina. Specifically, teeth of *Parvodus curvidens* (Duffin & Thies 1997) are mainly distinguished by their curved character in occlusal view (Rees & Underwood, 2002). *Parvodus pattersoni* (Duffin 1985) mainly differs in having more numerous, lateral cusplets that extend further distally, whereas *P. balabansaiensis* comb. nov. displays fewer, but higher lateral cusplets and a smoother labial face (Rees & Underwood, 2002; Wills et al. 2019). *Parvodus rugianus* (Ansorge 1990) is characterized by being more heavily built and having more ornamentation than the teeth of other *Parvodus* species (Rees & Underwood, 2002). *Parvodus celsucuspus* (Rees et al. 2013)

can be distinguished as well, as it exhibits a very high, upright central cusp with continuous vertical ridging across much of the crown surface. The crown itself also shows a bent character with the axial ends drooping down when compared to the centre, and there may be more than two lateral cusplets present in *P. celsucuspus* (Rees et al. 2013). *Parvodus ominechonensis* (Breeden et al. 2024) teeth are more gracile, with a comparatively narrower, recurved main cusp and more vertical ridges as ornamentation on this main cusp. More lateral cusplets may also be present and the root is comparatively more lingually concave than in *P. balabansaiensis* comb. nov. (Breeden et al., 2024). Finally, *Parvodus huizodus* (Wen et al. 2022) differs in possessing a lower, more lingually concave crown with less ornamentation and a shorter root, but with potentially bigger foramina.

Based on these comparisons this study therefore suggests the transfer of this species initially assigned to *Polyacrodus* to *Parvodus* as *Parvodus balabansaiensis* comb. nov..

Initially fossil evidence indicated that species attributed to *Parvodus* existed from the Middle Jurassic (Bathonian stage) to the Early Cretaceous (Valanginian stage), approximately 168 to 137 million years ago (Penn & Sweetman 2023; Rees & Underwood 2002; Rees et al. 2013; Sweetman et al. 2014).

However, a more recent discovery, *Parvodus huizodus*, has been reported from the Early Triassic of China, suggesting that the genus's temporal range may extend back to approximately 252 million years ago (Fig. 23). (Wen et al. 2022). Increasing the temporal range of the genus from just roughly 31 million years all the way to 115 million years.

The Callovian fossil material analyses here does fit nicely into the proposed temporal range of the genus as well, even before this revision.

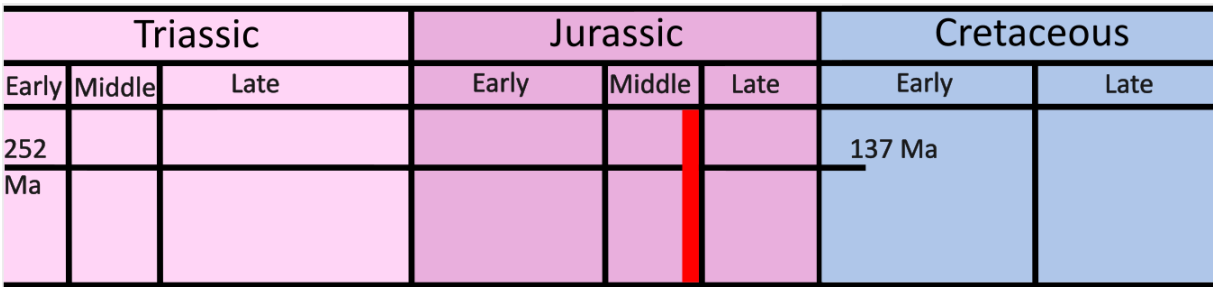


Figure 23. Temporal range of the hybodont genus *Parvodus*.
Black: Known fossil record
Red: Temporal range of this study - Callovian

Parvodus, similarly to *Lissodus* and *Lonchidion*, exhibits a wide geographical distribution, with fossil findings from the continents of Europe, North America and Asia.

European localities in which this genus is present include for example the Bathonian of England and Scotland (Rees & Underwood 2002), as well as from Berriasian-Valanginian boundary deposits of England (Fig. 24) (Rees & Underwood 2002). From Germany *Parvodus* remains are also known, specifically from the Kimmeridigan and the Berriasian-Valanginian boundary (Fig. 24) (Rees & Underwood 2002). Concerning Berriasian-Valanginian boundary deposits, *Parvodus* material is also known from those of Denmark and Sweden (Fig. 24) (Rees

& Underwood 2002). This hybodont genus is furthermore also known from Lower Cretaceous Cloverly Formation of the United States (Fig. 24) (Oreska et al. 2013).

Regarding examples of Asian distribution, so far *Parvodus* has been known from Lower Triassic Deposits of the Yunnan Province of China (Fig. 24) (Wen et al. 2022), and this study now broadens this distribution ranges for this genus further westwards into Asia as well.

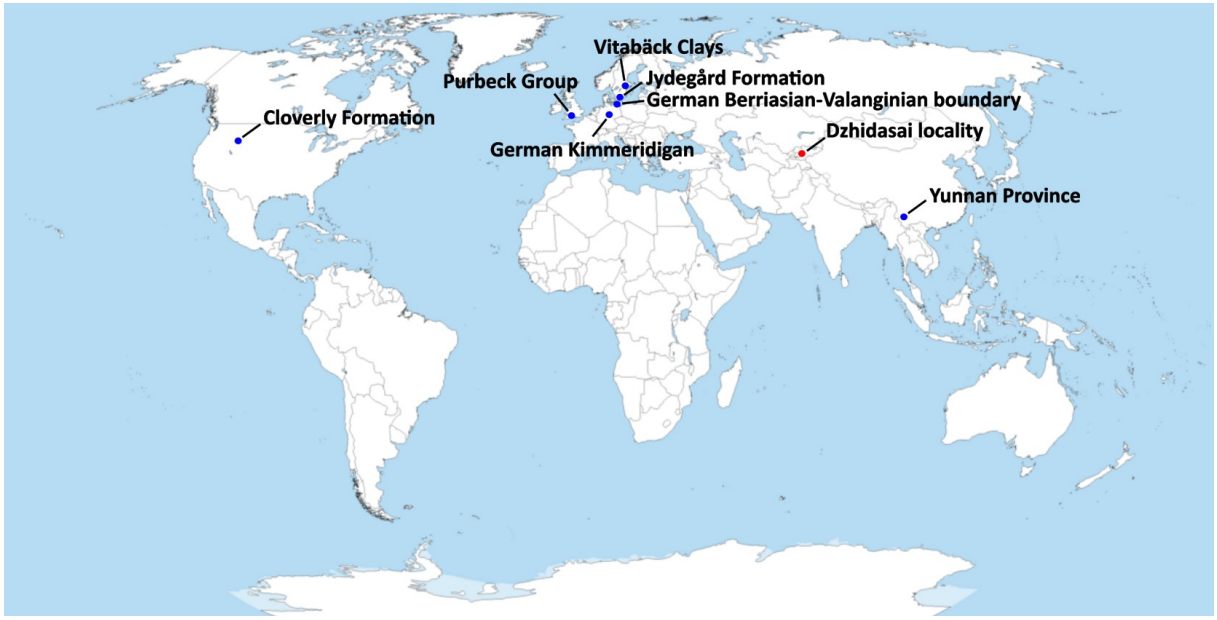


Figure 24. Spatial distribution of *Parvodus*.

Genus ***Jiaodontus*** Klug et al., 2010
Type species ***Jiaodontus montaltissimus*** Klug et al., 2010 from the Oxfordian (Late Jurassic) of NW China
Jiaodontus* cf. *montaltissimus Klug et al., 2010

Referred material: A total of 22 complete and fractured teeth (Table 3) from the Balabansai Formation, Dzhidasai locality (= FBX-23), Fergana Valley, western Kyrgyzstan (Fig. 9a). One of which (FBX-23_21) is illustrated in Fig. 25.

Description: The teeth of *Jiaodontus* cf. *montaltissimus* are minute, only measuring up to approximately 1 mm in mesiodistal width and 0.5 mm in apicobasal height. In labial and lingual views, the crown is characteristically low and often slightly asymmetrical, with a subdued central cusp flanked on either side by up to two diminutive lateral cusplets that decrease in size distally. The crown exhibits a gently arched profile, with the lateral edges curving downwards, imparting a faintly bent appearance to the entire crown. In occlusal view, the teeth exhibit a slight mesiodistal elongation. A continuous, weak to moderately developed occlusal crest extends from the main cusp across the lateral cusplets, forming a serrated cutting edge. The labial peg is well developed and positioned below the central cusp, supporting a delicate, vertical ridge that continues toward the apex of the main cusp. A

corresponding but weaker vertical ridge may also be present on the lingual crown face. Fine granular ornamentation may be present on the labial surface of the crown, especially near the base, just above the crown-root junction. The crown–root junction is distinctly incised and sharply demarcated, forming a belt-like transition between crown and root.

The root itself is comparatively low and slender but broadens towards its base and is perforated by numerous, small and round foramina on both its labial and lingual surfaces. Right under the sharp crown-root junction runs a line of relatively small and particularly circular pores. Contrary to that, the pores situated lower, towards the base of the roots, get a bit bigger, but still comparatively small, and less circular in appearance. A shallow labial depression occurs directly beneath the labial peg, while a subtle labial protuberance overlies this labial root depression directly under the crown base.

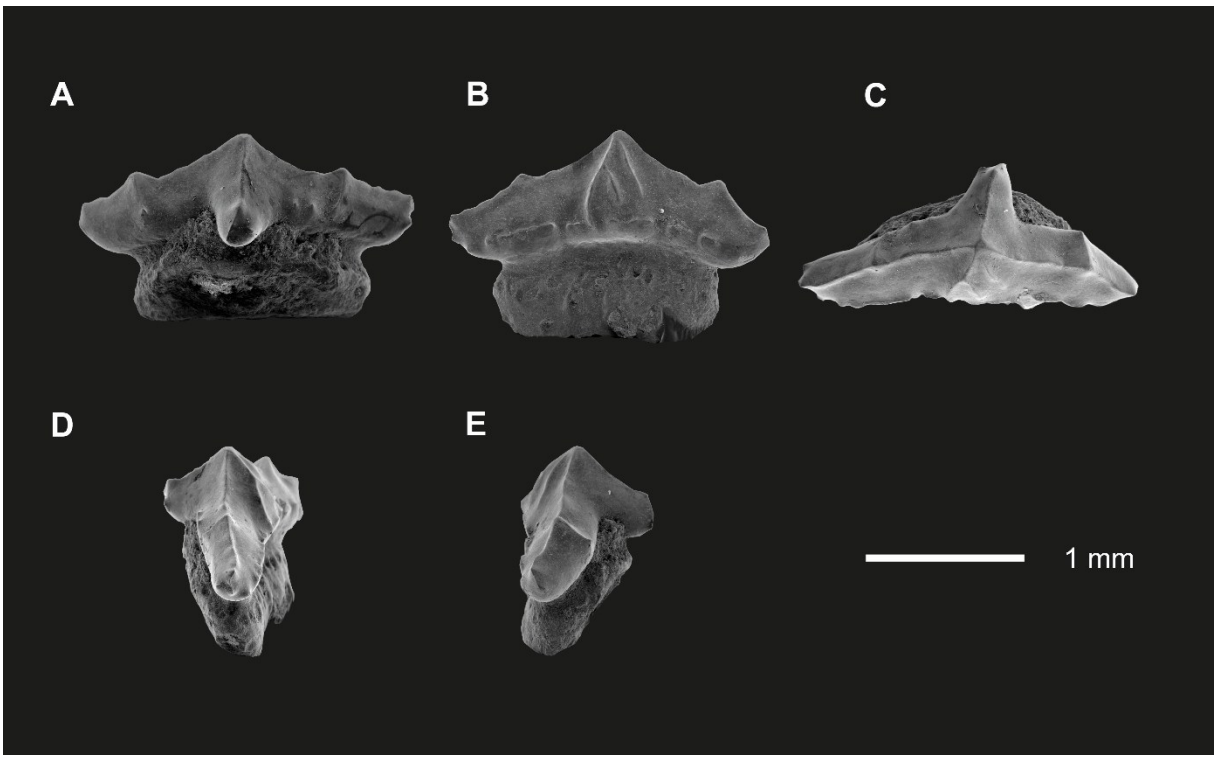


Figure 25. *Jiaodontus* cf. *montaltissimus* from the Callovian, Dzhidasai locality, Balabansai Formation, Fergana Valley, western Kyrgyzstan.
a-e: Lateral tooth (FBX-23_21) in labial (a), lingual (b), occlusal (c) & lateral (d & e) views.

Remarks: The teeth present in this sample were most likely positioned laterally towards the front of the jaws and are primarily a cutting-type dentition, due to the serrated nature of the occlusal crests, although they presumably could have also served a gripping function secondarily. The foramina littering the root most likely constituted the endings of nerve canals and blood vessels, used to supply and connect the teeth.

The teeth of this sample are assigned to the family Lonchidiidae, furthermore they belong most likely to the genus *Jiaodontus* and the species *Jiaodontus montaltissimus*. Mainly on the grounds of their smaller size when compared to the teeth of *Lonchidion* described above and the generally bent aesthetic of their crown, with the lateral cusplets dropping off when compared to the central main cusp. Their well-demarcated cusp and cusplets, which form a serrated cutting edge, their sparse ornamentation, which is only present in the form of vertical

ridges, apart from the occlusal crest forming a serrated cutting edge (Klug et al. 2010) and the overall smaller size of the foramina perforating the root, especially when compared to the teeth of *Lonchidion* described above.

Jiaodontus thrived during the Late Jurassic period, specifically the Oxfordian to Kimmeridgian stages, approximately 163 to 152 million years ago (Klug et al. 2010).

Additionally, teeth attributed to *Jiaodontus* have been recovered from the Phu Kradung Formation of northeastern Thailand, which dates to the Late Jurassic to Early Cretaceous periods. This suggests that the genus may have persisted into the Early Cretaceous, extending its temporal range slightly beyond the Late Jurassic (Fig. 26) (Cuny et al. 2014).

Now, with the presence of *Jiaodontus* remains in the fossil material of the Dzhidasai locality, this study slightly extends the temporal range of this genus from the Late Jurassic into the Middle Jurassic.

Figure 26. Temporal range of the hybodont genus *Jiaodontus*.
Black: Known fossil record.
Red: Extended temporal range into the Middle Jurassic based on this study

So far, both described species of *Jiaodontus* have been known from the Late Jurassic (Oxfordian age) deposits of the Qigu Formation in the southern Junggar Basin, Xinjiang Uyghur Autonomous Region, northwestern China (Fig. 27). Specifically, fossils have been unearthed at the Liuhuanggou locality, situated approximately 40 km southwest of the city of Ürümqi (Klug et al. 2010). *Jiaodontus* remains are also known from the Phu Kradung Formation of northeastern Thailand (Fig. 27) (Cuny et al. 2014).

However, now its distribution during the Middle Jurassic is widened even further westwards with this Kyrgyz locality, indicating that over the course from the Middle it the Late Jurassic its spatial distribution shrank towards just the more Eastern parts of its initial distribution area (Cuny et al. 2014; Klug et al. 2010).

Figure 27. Spatial distribution of *Jiaodontus*.

Hybodontiformes fam. gen. et sp. indet.

Referred material: A total of 105 mostly fractured teeth (Table 2) from the Balabansai Formation, Dzhidasai locality (FBX-23), Fergana Valley, western Kyrgyzstan (Fig. 9a). Two of which (FBX-23_34 & FBX-23_35) are illustrated in Fig. 28.

Description: The teeth of the indeterminable hybodont taxa present in this locality of the Balabansai Svita range in mesiodistal width from roughly 1.5 to 2.5. mm and show a consistent apicobasal height of around 2 mm.

They possess a high crown, which is composed of a singular, robust main cusp with a flared base. No lateral cusplets are present even in well-preserved specimen. No discernible labial peg is present to speak of, just a small broadening of the labial side of the crown body. Ornamentation is not present to moderately well developed. If present at all, the ornamentations show parallel ridges, primarily present on the labial side of the crown. These ridges may also be present on the lingual crown surface, but if so with fewer and lesser developed ridges. These ornamental ridges are usually only present in the upper three quarters of the crown, while the lower fourth shows a smooth surface with no ornamentation.

The root is moderately high, with a broad base and anaulacorhize, showing a plethora of differently sized pores. Right below the crown root junction these pores are comparatively small and show a highly rounded character, while lower on the root these pores show a bigger size and more oval character.

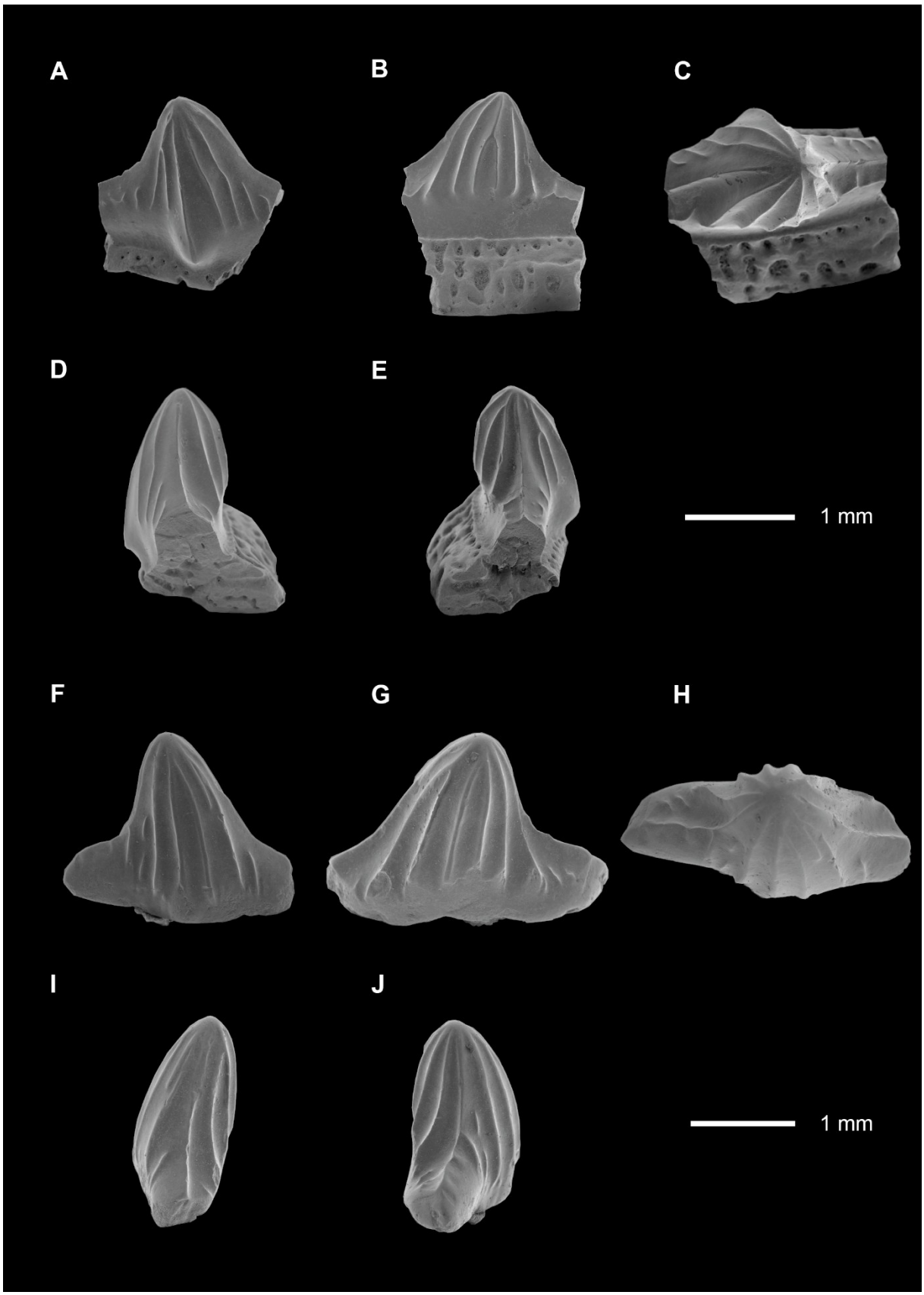


Figure 28. Hybodontiformes fam., *gen. et sp. indet.* from the Callovian, Dzhidasai locality, Balabansai Formation, Fergana Valley, western Kyrgyzstan.
a-e: Anterior tooth (FBX-23_33) in labial (a), lingual (b), occlusal (c) & lateral (d & e) views.
f-j: Anterior tooth (FBX-23_34) in labial (f), lingual (g), occlusal (h) & lateral (i & j) views.

Remarks: The sharp and robust singular cusp morphology of these teeth suggest a gripping kind dentition, used to bite and hold on to soft-bodied prey animals. It is likely that teeth of this design were positioned anterolaterally to right in the front of the animal's jaws.

The multitude of pores running through the root were most likely, as already mentioned above in the preceding parts of this chapter, constituting openings for blood vessels and nerve canals.

Due to their simplistic build and therefore following lack of distinguishing features, it is not possible, in the scope of this study, to identify these teeth on a more precise level than the order of Hybodontiformes.

6. Paleoenvironment of the Dzhidasai locality

The aim of this chapter is to connect the already established, Callovian paleoenvironmental interpretation of the area encompassing the Dzhidasai locality (FBX-23) of the Balabansai Svita, which was already briefly outlined in Chapter 4 above.

The current consensus regarding the Middle Jurassic paleoenvironment of this area is a marginal marine lagoon, a general representation of which is illustrated in Fig. 29, or an estuary/delta setting, due to the increasingly arid depositing conditions of the sediments of the Balabansai Formation (Averianov et al. 2005, 2008; Rees & Underwood 2005). This is especially noteworthy as the two adjacent formations, the Early Jurassic Tashkumyr and the Middle Jurassic Igrysai formations, show a much more terrestrial influence in their deposits, accumulated in a more humid climate (Averianov et al. 2005).

With this lagoonal to delta setting of the locality in mind, the thought may occur that chondrichthyan species are quite a rare sight in freshwater to marginal marine/brackish environments such as this. This is, of course, a notion that holds true for most modern ecosystems (Compagno et al. 2005). However, the situation is rather different when considering the above described hybodont assemblage.

6.1. Palaeogeographic and palaeoenvironmental implications of the Dzhidasai hybodont assemblage

All hybodont taxa of the Dzhidasai locality are, at least at genus level, known from similar aquatic environments, which will be briefly outlined below.

Hylaeobatis was initially described from the Wealden Group of the Isle of Wight in southern England, which is comprised of terrestrial, fluvial, lacustrine, floodplain and lagoonal strata (Sweetman 2011; Woodward 1916). These can be roughly divided into the fluvial deposits of the Wessex Formation and the lagoonal strata of the Vectis Formation (Sweetman 2011), therefore showing a high similarity to the present Balabansai Formation depositional environment.

The taxon *Lissodus* is known from restricted marine and lagoonal facies of east-central-south England and from the Bathonian of the Hebredian region of Scotland, which is mainly represented by freshwater and lagoonal environments as well (Rees & Underwood 2005, 2008).

Lonchidion has been found in freshwater as well as marine deposits in Europe, South Africa and North America, with a wide stratigraphic age range from the Early Triassic all the way to the Late Cretaceous (Cappetta 1987; Rees & Underwood 2002), with them being especially common in nonmarine settings of the Early Cretaceous (Rees & Underwood 2002). Even with *Lonchidion* showing a seemingly high tolerance for a wide range of salinities, these sharks were more common in non-marine environments, only occurring in fully marine setting during the Late Cretaceous (Rees & Underwood 2002). The Lance Formation of eastern Wyoming, where the *Lonchidion* type species *Lonchidion selachos* was firstly described, too, was deposited

along a shoreline in a subtropical climate (Clemens 1963; Elzanowski and Stidham 2011), showing a high degree of similarity to the conditions proposed for the Balabansai Svita.

Parvodus with its rich fossil record, also displays a preference for continental aquatic environments (Wen et al. 2022) and while these sharks occupied a wide range of different environmental settings, they seemingly never adapted to fully marine environments (Wen et al. 2022).

Jiaodontus as well is known, so far, only from freshwater environments, like meandering rivers, lakes and floodplains dominated by just these very same lakes (Cuny et al. 2014; Klug et al. 2010). The localities currently known as sources of *Jiaodontus* fossils, including the locality described in this thesis, are all situated in Asia, which suggests an endemic distribution of this genus (Cuny et al. 2014; Klug et al. 2010).

Figure 29. An artistic depiction of a Jurassic, lagoonal environment (after Stålenhag & Davour (2019).

7. Root preservation and destruction in Hybodontiformes

In most of the known localities, hybodontiform teeth are predominantly found in form of isolated cusps with their roots missing (Böttcher 2024). For most localities this ratio seems to be between 80-100% in favour of incomplete teeth without roots (Böttcher 2024). This loss in tooth roots seems to only occur in hybodont taxa and it is not the case in co-occurring xenacanthid or neoselachians teeth (Agassiz 1837; Böttcher 2024; Duffin 1982, 1998; Woodward 1889b).

Multiple different interpretations as to why that is the case have been proposed throughout the years. However, all of these have their fair share of problems as well (Böttcher 2024). Such hypotheses include the possibility that these rootless teeth could represent incompletely developed replacement teeth, where the crown is already mineralized, whereas the root still is un-mineralized, as is known in extant sharks (Böttcher 2024; Budker 1971; Moyer et al. 2015; Reif 1982). However, due to the oftentimes high grade of preservation, it is quite unlikely that rootless hybodont teeth are representing incompletely mineralized replacement teeth (Böttcher 2024). The chance that the tissue of the roots themselves might not have been mineralized is another idea, but this is contradicted by the fact that in skeletal finds the teeth almost always appear to be preserved with completely mineralized roots (Böttcher 2024; Witten et al. 2016). Also, a consideration is that the characteristic belt-like crown-root junction of hybodontiform teeth could be a weak point as well, though this connection should be strong enough to withstand the forces being applied upon it during prey capture and feeding (Birkenmajer & Jerzmańska 1979; Böttcher 2024; Kirkland et al. 2013; Koot et al. 2014; Seilacher 1943). Lastly it is also possible that the hybodontiform teeth found in various fossil deposits often lack their roots due to taphonomic processes (Böttcher 2024; Ginter et al. 2002; Johnson 1981; Reif 1971; Underwood & Rees 2002). Studies of earliest Cretaceous deposits for example indicate that root loss is caused by post-mortem decay, with teeth either missing roots entirely or having well-preserved ones when intact (Underwood & Rees 2002), as is the case for the teeth of the here analyzed Dzhidasai locality as well.

An alternative interpretation presented by Böttcher 2024 concerns a possible root resorption during tooth renewal in hybodonts, as it is known from bony fishes and tetrapods. Contradicting this idea is that tooth root resorption is unknown in all other extant, or extinct, sharks as teeth are shed but not resorbed since the teeth are not embedded in the jaw cartilage but anchored to the jaws by connective tissue. It is also unobserved in Mesozoic growing scales of the hybodontid type as well as the dermal skeleton in general (Böttcher 2024; Reif 1978, 1980a; Andreev et al. 2016). These scales were shed via the same principle as normally seen in shark teeth, by simply breaking down the anchoring fibres (Böttcher 2024; Reif 1980b).

Furthermore, root resorption in bony fish and tetrapods produces characteristic resorption pits, called “Howship’s lacunae” on the basal dentinal surfaces of the tooth crowns during resorption (Böttcher 2024; Everts et al. 2009). These pits were, however, not detected on the basal surface of hybodontiform crowns. This lack cannot be explained via taphonomic

or diagenetic processes either, especially since bony fish tooth crowns from the same layers did have this resorption sign preserved (Böttcher 2024). Against this Böttcher 2024 argues that in hybodontiforms tooth resorption was executed by, what are believed to be, a smaller, more primitive type of resorbing cells, which do not produce detectable lacunae during the resorbing process (Böttcher 2024; Domon et al. 1997; Witten & Huysseune 2009).

7.1. Exceptional root preservation in the Dzhidasai locality

The teeth from the locality analysed here differ substantially from the general trends described above as outlined by Böttcher 2024. The general root to no-root preservation ratio is 45 to 55%, for Dzhidasai hybodonts (Tables 1-3). The only taxa, in which ca. 90% lack their root are *Parvodus* and the unidentified hybodont (Table 3).

The objective of the following paragraphs is to discuss possible explanations and interpretations as to why the Dzhidasai locality shows such exceptional hybodont root preservation, either by themselves or in combinations. As the argument of root resorption during tooth replacement, made by Böttcher 2024, fails to adequately explain the extremely high proportion of not only intact, but essentially perfectly preserved hybodont roots.

Though, this locality also fails to provide any isolated hybodont roots, as preserved roots are only present in completely preserved teeth.

Table 1. Tooth count and root/no root ratio across all described hybodont taxa of the Dzhidasai locality.

With root	2.138 (45%)
Without root	2.609 (55%)
Sum of all teeth	4.747

Table 2. Tooth counts and root/no root ratio for the taxa *Hylaeobatis verzilini* comb. nov., *Lissodus verzilini* comb. nov. and *Lonchidion sp*.

Hylaeobatis verzilini		***Lissodus verzilini***		***Lonchidion sp.***	
1.078 (42%)	With root	915 (38%)	With root	44 (38%)	With root
1.488 (58%)	Without root	518 (62%)	Without root	70 (62%)	Without root
2.566	Sum	1.433	Sum	114	Sum

Table 3. Tooth counts and root/no root ratio for the taxa *Parvodus balabansaiensis* comb. nov., *Jiaodontus* cf. *montaltissimus* and Hybodontiformes fam., *gen.* et *sp.* indet.

Parvodus balabansaiensis		***Jiaodontus* cf. *montaltissimus***		**Hybodontiformes fam., *gen.* et *sp.* indet.**	
78 (15%)	With root	17 (77%)	With root	6 (6%)	With root
429 (85%)	Without root	5 (23%)	Without root	99 (94%)	Without root
507	Sum	22	Sum	105	Sum

The most likely explanation as to why the root preservation ratio of the Dzhidasai locality is extremely high (Table 1) lies in the environmental features of the depositional setting of this locality. A calm, low energy depositional setting would reduce the risk of the teeth taking physical damage, resulting in a higher preservation rate.

As already outlined in chapter 6 of this thesis, the most likely paleoenvironmental interpretation for this Kyrgyz locality is a lagoonal or estuary/delta setting (Averianov et al. 2005, 2008). This results in the surrounding sediments being more fine-grained, like the present claystone for example (Averianov et al. 2005, 2008). That would then lead to a more rapid burial and reduced physical damage to the teeth and their roots. A nearshore environment, like a lagoon for example, is furthermore usually characterized by a high influx of sediment, which could have quickly buried shed teeth, before their roots would have been lost. This would also be consistent with the locality as all excavation sites of the Balabansai Svita were formed by mud flows, which transported the remains from continental nearshore, shallow areas towards the basin (Averianov et al. 2005). Possible anoxic conditions, following such a rapid burial would prevent or at least reduce the breakdown and therefore enhance the preservation of these delicate structures by minimizing scavenger activity as well as enabling microbial delay.

Another possibility in context of a low energy environment would be the possible representation of the site as a lag deposit. A lag deposit is a sedimentary accumulation of coarse, relatively durable material, like teeth, that remain after the surrounding, finer sediment has been removed, most likely due to water currents in this case (Davis & Dalrymple 2012; Leopold et al. 2012). The remaining material could then show a higher proportion of complete teeth.

It is also possible that certain, chemical characteristics of the depositional environment may have supported a quick and stable mineralization of the teeth and their roots during the fossilization process, therefore increasing the rate of root preservation due to this enhanced stability. For example, the more carbonate and/or phosphate rich water and burial environment of a lagoonal environment could have supported and enhanced the mineralization process during fossilization. This is consistent with the disposition of the hybodont teeth excavated in this Kyrgyz locality, as they show a highly stable character and are quite resistant to mechanical stress, especially when considering their overall small size.

Other possible environmental factors could include a low scavenging rate in the depositional area or that, instead of a selective transport, there may have been minimal post-mortem transport in general, reducing the risk of mechanical destruction of the teeth, again playing into the interpretation of a low energy depositional environment.

In case of a high energy environment, like a bigger delta area for example, which, as established above is also a possible, though not quite as likely, paleoenvironmental interpretation of the area (Averianov et al. 2005, 2008), lighter, rootless crowns would have been transported faster and easier than fully preserved teeth with their roots intact, which may have resulted in the accumulation of fully intact teeth due to hydrodynamic sorting.

Of course, since over 50% of the analysed teeth of the Dzhidasai locality do in fact lack their roots (Table 1), it is likely that many of them did break over the course of the diagenetic processes, during their fossilization.

In contrast to Böttcher 2024 stating that the crown-root junction does not constitute a weak point of hybodont teeth and that a fracture pattern along this area is unknown from hybodonts, here it is observed that this junction apparently does indeed provide a weak point along which many crowns were separated from their roots. This is especially well observable in the teeth of *Hylaeobatis verzillini* comb. nov., as essentially all of the 1.488 crowns without roots attributed to this genus were severed from their roots along this crown-root junction. With most of the flat, isolated crowns being otherwise very well-preserved.

This is also consistent with the general morphology of hybodont crown-root junctions, as they essentially constrict the teeth in an almost belt-like manner and show no signs of being reinforced with a layer of enameloid (Fig. 15–18).

Lastly, it has been stated more than once, that complete hybodont teeth that retain their full root, supposedly primarily stem from dead individuals and do not constitute teeth shed throughout an animal's lifetime (Böttcher 2024; Rees & Underwood 2005). If that is indeed the case then this locality may constitute a hybodont-graveyard-like concentration deposit, where a great number of individuals lost their life over a very short period of time, due to some exceptional, most likely catastrophic, event in their environment.

8. Conclusion

Conclusively it can only be stated that the Callovian Dzhidasai locality of the Balabansai Svita in western Kyrgyzstan, indeed proves itself as a highly important fossil bearing site, especially in the context of hybodont research. The present study represents a significant step toward better understanding the taxonomic diversity and palaeoecological significance of hybodonts during the Middle Jurassic in Asia.

The detailed systematic analysis of the isolated teeth of the Callovian Dhhidasai locality allowed to identify and describe several species, i.e. *Hylaeobatis verzillini* comb. nov., *Lissodus verzillini* comb. nov., *Lonchidion sp.*, *Parvodus balabansaiensis* comb. nov., and *Jiaodontus* cf. *montaltissimus*, revealing a taxonomically low diverse hybodont assemblage adapted to marginal marine to brackish environments. These findings, as described in this study, not only expand the known geographic range of these genera but also emphasize the ecological versatility of hybodonts within transitional aquatic settings of the Middle Jurassic.

However, the results presented here also underscore how much remains to be explored, since research, as always, never stops. Figure 9b, for example, already shows there is still a significant amount of material from multiple other fossil-bearing sites of the Balabansai Svita site left to analyse, in terms of their taxonomic diversity and in a palaeogeographic context. The collected fossil material of these sites also vastly surpasses the here analysed 4.747 teeth (Table 1) of the Dzhidasai locality in terms of tooth quantity.

Future research should also integrate additional analytical approaches beyond classical morphology. Geochemical analyses for example could further contribute to paleoenvironmental reconstructions and elucidate potential euryhaline adaptations within the present hybodont taxa.

Moreover, the taxonomic revisions proposed here, such as the reassignment of *Palaeobates verzillini* to *Hylaeobatis* and *Lissodus* and *Polyacrodus balabansaiensis* to *Parvodus*, illustrate the importance of re-evaluating historical material using modern comparative frameworks. Extending such revisions across additional faunas could therefore significantly improve our understanding of hybodont systematics and their evolutionary trajectories leading up to their Cretaceous decline.

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