

Article

Diversity Patterns of Late Jurassic Chondrichthyans: New Insights from a Historically Collected Hybodontiform Tooth Assemblage from Poland

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Abstract: Here, we provide a detailed taxonomic reassessment of a historically collected chondrichthyan dental assemblage from the lower Kimmeridgian of Czarnogłowy in north-western Poland and discuss its significance for better understanding hybodontiform diversity patterns prior to their post-Jurassic decline in fully marine environments. In spite of its low taxonomic diversity, consisting of four large-toothed taxa (viz., *Strophodus udulfensis*, *Asteracanthus ornatissimus*, *Planohybodus* sp. and cf. *Meristodonoides* sp.), this assemblage is remarkable in that there are only very few Mesozoic hybodontiform assemblages with more large-toothed genera or even species. Comparisons with other European Late Jurassic hybodontiform-bearing localities demonstrate fairly homogenous distribution patterns characterized by large-bodied epipelagic forms of high dispersal ability. This is in stark contrast to post-Jurassic hybodontiform associations, which are dominated by smaller species that were predominantly bound to marginal marine and continental waters, suggesting a major reorganization of chondrichthyan communities during the Early Cretaceous.

Keywords: Chondrichthyes; Hybodontiformes; diversity; biogeography; Kimmeridgian; Late Jurassic; Poland



Citation: Stumpf, S.; Meng, S.; Kriwet, J. Diversity Patterns of Late Jurassic Chondrichthyans: New Insights from a Historically Collected Hybodontiform Tooth Assemblage from Poland. *Diversity* **2022**, *14*, 85. <https://doi.org/10.3390/d14020085>

Academic Editors: Michael Wink and Eric Buffetaut

Received: 23 November 2021

Accepted: 23 January 2022

Published: 26 January 2022

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1. Introduction

The Late Jurassic marks a critical time interval in the history of life leading to dramatic episodes of global environmental perturbation at the Jurassic/Cretaceous (J/K) boundary [1], which seemingly affected vertebrate communities in both the terrestrial and marine realms (e.g., [2–7]). Among marine vertebrates, hybodontiform shark-like chondrichthyans, which form a supposed sister group to the elasmobranch crown encompassing modern sharks, skates and rays (=Neoselachii *sensu* [8]), witnessed a diversity decline in marine ecosystems from the Early Cretaceous onwards, before they predominately occurred in marginal marine and continental environments, where they flourished and diversified until they finally vanished at the end of the Cretaceous (e.g., [9–15]). However, the controlling factors driving the diversity dynamics of post-Jurassic hybodontiforms remain unresolved.

Hybodontiforms, whose fossil record is dominated by isolated dental remains (see [16] for overview), have been recorded from various European Late Jurassic localities so far (e.g., [17–31]), with rather rare occurrences from Asia [32–35], Africa [36,37] and South America [38–40]. However, even after more than two centuries of extensive research, our knowledge of Late Jurassic hybodontiforms is still insufficient, such that their diversity and distribution patterns remain ambiguous and poorly understood.

The intention of this study is (1) to provide a detailed taxonomic reassessment of a historically collected hybodontiform dental assemblage from the lower Kimmeridgian of Czarnogłowy in north-western Poland and (2) to discuss its significance in terms of

ecology and biogeography for better understanding Mesozoic chondrichthyan life prior to the major environmental perturbations at the J/K boundary.

2. Materials and Methods

2.1. Fossil Material in This Study

Although numerous Late Jurassic marine vertebrate-bearing localities have been reported from Poland since the 19th century (e.g., [19,41–48]), chondrichthyan remains are rare, originating from a few localities so far [19,41,42,49,50].

The fossil chondrichthyan material that forms the focus of the present study is housed at the Institute of Geography and Geology, University of Greifswald, Germany, where it is catalogued under the repository numbers GG 303/1 to 303/94. The fossil material comprises isolated hybodontiform teeth that were originally collected during the first half of the 20th century from the now abandoned open-pit limestone quarry of Czarnogłowy (called Zarnglaff in the pre-1945 literature) in north-western Poland (Figure 1). Although first mentioned in 1784 by Brüggemann [51], it was not until the beginning of the 20th century that commercial mining started in Czarnogłowy. Mining activities continued until the 1970s, since when the Czarnogłowy quarry has been dormant and largely inaccessible due to flooding.

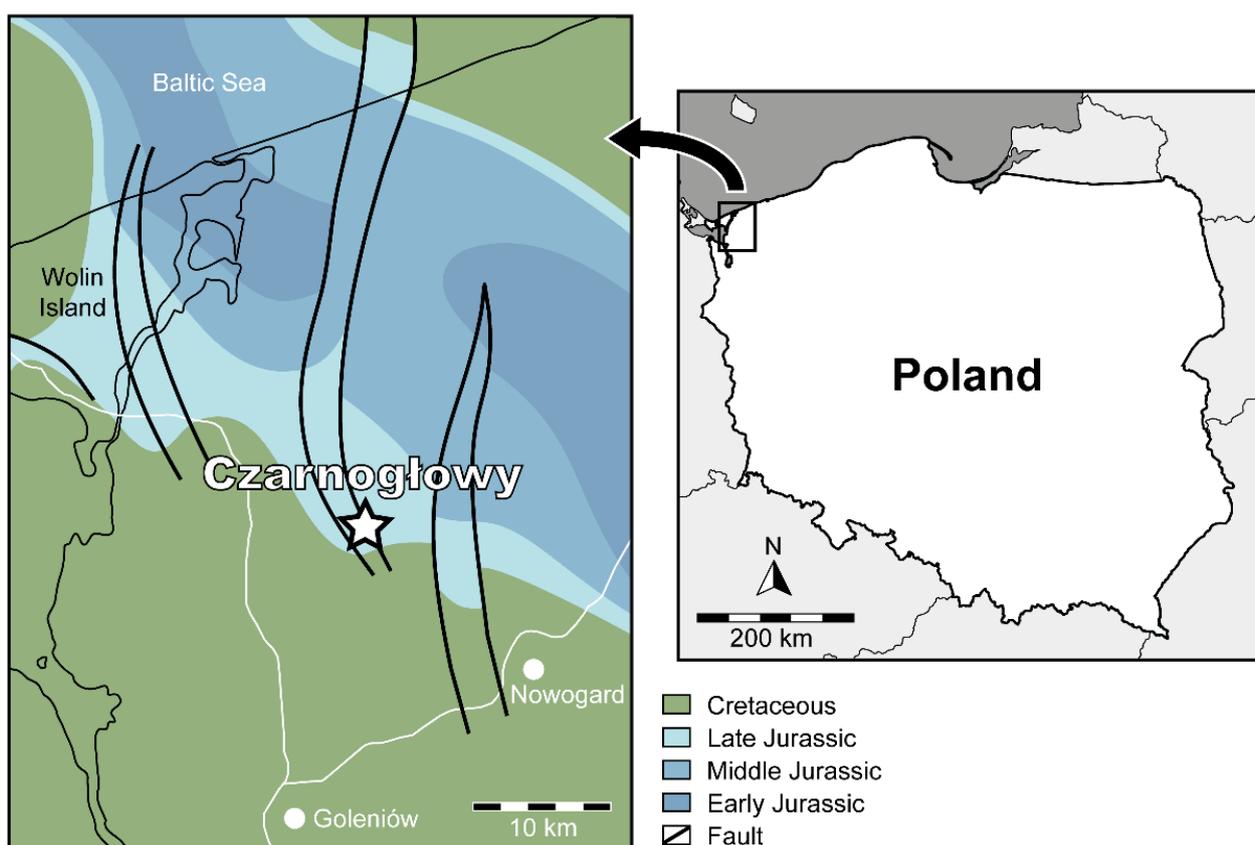


Figure 1. Location maps (geological map without Cenozoic cover; modified from [52]).

Belonging to the Mid-Polish Swell, which represents a NW–SE trending inverted anticlinal structure, the Late Jurassic sedimentary succession once accessible in the Czarnogłowy quarry ranges stratigraphically from the late Oxfordian to the early Tithonian, with a thickness of about 50 m [53–56]. According to Schmidt [53] and Richter [54], the hybodontiform material described herein originally derived from a two-to-three-meters-thick sequence of sandy, oolitic marlstone with occasional layers of wood remains. This interval, which is indicative of a warm, wave-agitated shallow-marine depositional environment, has also

yielded fragmentary remains of actinopterygians and marine reptiles (e.g., [44,49,53,54]) and is dated to the early Kimmeridgian based on ammonite evidence [55,56].

The historically collected hybodontiform assemblage presented herein was described in an unpublished thesis by Hoffmann [49], but the taxonomic identification by this author (see also [57] for brief summary) is challenged by recent advances in hybodontiform taxonomy. In addition, Hoffmann [49] also described rare dental remains of modern sharks retrieved from boulders collected around the abandoned Czarnogłowy quarry. However, while adding to the known taxonomic diversity of fossil chondrichthyans from Czarnogłowy, the precise stratigraphic position of this material within the Late Jurassic sedimentary succession once accessible in the Czarnogłowy quarry remains unknown.

2.2. Methods

All photographs presented in the text were obtained using a Nikon D5300 DSLR camera equipped with an AF-S DX Micro NIKKOR 40 mm f/2.8G lens. All photographs were rendered utilizing Adobe Photoshop CC 2021 and the accompanying figures were created using Adobe Illustrator CC 2021.

Descriptive tooth terminology used in this study largely follows that of Cappetta [16], whereas higher systematic relationships correspond to those of Maisey [58] and Rees and Underwood [59], although we acknowledge that currently available phylogenetic hypotheses for hybodontiforms are unsatisfactory [30,31].

3. Results

3.1. Systematic Palaeontology

Chondrichthyes Huxley, 1880 [60]

Elasmobranchii Bonaparte, 1838 [61]

Hybodontiformes Maisey, 1975 [62]

Hybodontidae Owen, 1846 [63]

Hybodontinae Owen, 1846 [63]

Planohybodus Rees and Underwood, 2008 [59]

Type species: *Planohybodus peterboroughensis* Rees and Underwood, 2008 [59]

Planohybodus sp.

Figure 2a–l.

3.1.1. Material

Sixteen incomplete teeth (GG303/1–16).

3.1.2. Description

The teeth are represented by partially preserved crowns forming a high and rather wide, somewhat labio-lingually flattened main cusp with well-developed cutting edges and a flattened labial crown face. The cusps have an oval cross-section (Figure 2g) and are slightly inclined distally and straight to somewhat sigmoid in mesio-distal view (Figure 2b,e). Partially preserved lateral cusplets are present in two teeth (Figure 2h–l), indicating that the main cusp was flanked by at least one pair of small lateral cusplets. The ornamentation consists of moderately well-developed vertical folds covering the lower parts of the labial (Figure 2a,d,h,k) and lingual crown faces, plus short, isolated folds occurring on the higher parts of the crown (Figure 2c,f,j,l).

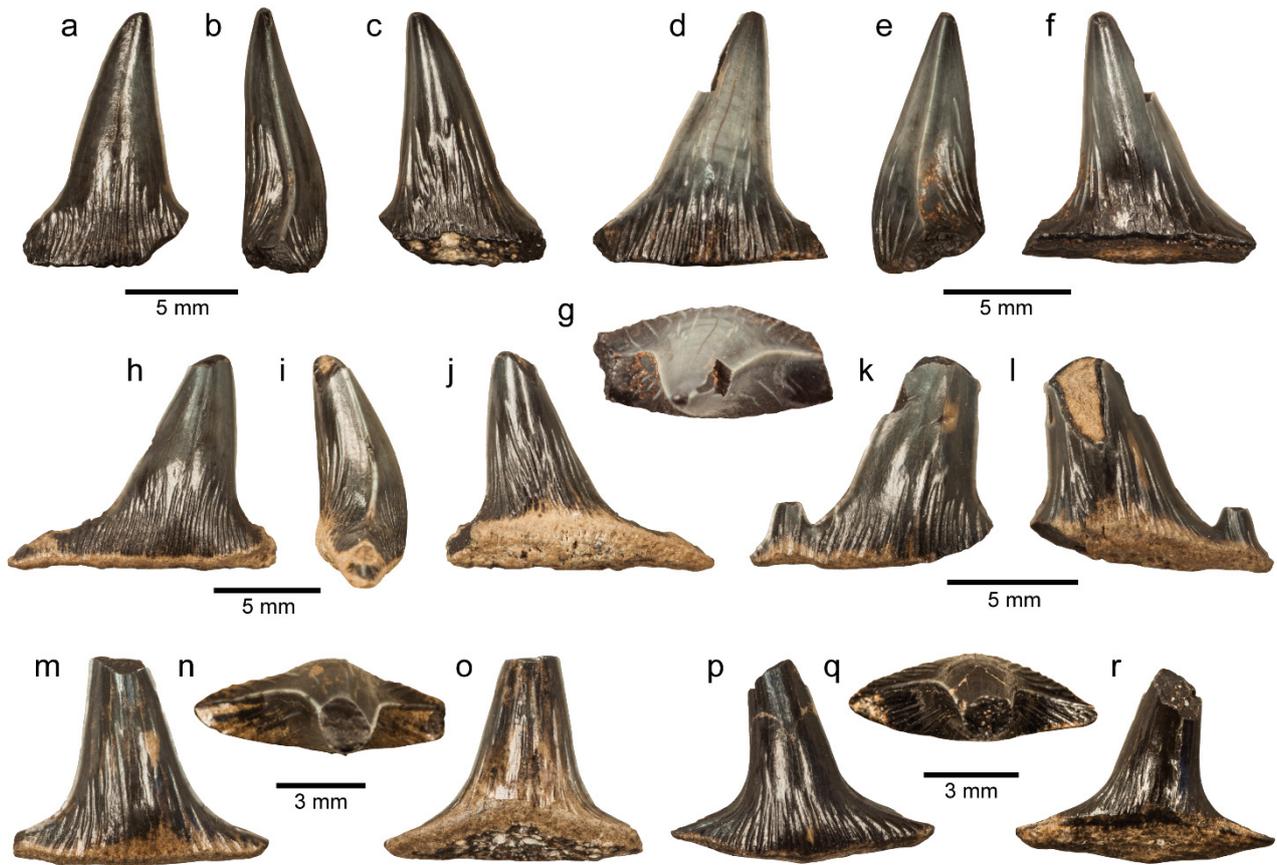


Figure 2. Historically collected hybodontiform teeth from the lower Kimmeridgian of Czarnogłowy, Poland. (a–l) *Planohybodus* sp., GG 303/1 in (a) labial, (b) mesial and (c) lingual view; GG 303/2 in (d) labial, (e) distal, (f) lingual and (g) apical view; GG GG303/3 in (h) labial, (i) mesial and (j) lingual aspect; GG 303/4 in (k) labial and (l) lingual view. (m–r) cf. *Meristodonoides* sp., GG 303/17 in (m) labial, (n) apical and (o) lingual aspect; GG 303/18 in (p) labial, (q) occlusal and (r) lingual view.

3.1.3. Remarks

The above-described teeth (plus those referred to below as cf. *Meristodonoides* sp.) were tentatively assigned by Hoffmann [49] to *Hybodus* sp. 1 and *Hybodus* sp. 2, respectively. Although generally accepted to form a highly polyphyletic assemblage encompassing numerous unrelated species characterized by very similar tooth morphologies (e.g., [30,59,64–66]), the taxonomic content of *Hybodus* Agassiz, 1837 [67] has become better understood in recent decades, which has led to the recognition of new genera such as *Planohybodus* Rees and Underwood, 2008 [59], *Secarodus* Rees and Underwood, 2008 [59], *Meristodonoides* Underwood and Cumbaa, 2010 [68] and *Crassodus* Maisch and Matzke, 2016 [66], as well as *Durnonovariaodus* Stumpf et al., 2021 [31]. All these taxa are readily distinguished from each other by unique combinations of dental characters. The high and rather wide, labiolingually compressed tooth crown morphology displayed by the above-described teeth from Czarnogłowy and the presence of a flattened labial crown face, combined with the oval cross-section of the principal cusp, plus the presence of well-developed cutting edges and simple, non-bifurcating folds covering the lower parts of the crown, are dental features that are consistent with those found in teeth attributed to *Planohybodus*. This hybodontiform has a fossil record ranging from the Middle Jurassic to the Early Cretaceous [29,59,69–71], with the potentially youngest fossil records of *Planohybodus* being represented by a few fragmentary teeth from the Santonian of the USA [72], but more complete material is needed to unambiguously confirm the presence of *Planohybodus* in the Late Cretaceous.

Planohybodus falls into three currently accepted species, comprising *P. peterboroughensis* [59] from the Callovian–Oxfordian of England, *P. grossiconus* (Agassiz, 1843) [67]

from the Bathonian of England, Scotland and France [18,59,69] and *P. ensis* (Woodward, 1916) [73] from the Berriasian–Barremian of England and Spain [59,70,73–76]. While the type species of *Planohybodus*, *P. peterboroughensis*, is known from both dental and skeletal material, the remaining two species are known from isolated teeth only. The species *P. marki* Pinheiro et al., 2013 [77], which has been proposed based on a few fragmentary tooth crowns recovered from the pre-Aptian Early Cretaceous of Brazil, is here regarded as *nomen dubium* due to the incomplete nature and the absence of any dental features unambiguously supporting its inclusion in the genus *Planohybodus*. In addition, rare fragmentary teeth from the Berriasian of Bornholm, Denmark, may constitute a yet undescribed species of *Planohybodus* [59,78], but more complete material is needed to verify this.

Planohybodus apparently was a common and widely distributed constituent of Late Jurassic marine ecosystems, as inferred from abundant fossil occurrences reported from Europe [26,29,31,79,80]. In addition, Alvarado-Ortega et al. [40] described a partially preserved tooth attributed to *Planohybodus* sp. from Kimmeridgian–Tithonian deposits in Mexico, whose generic affinities are here considered dubious due to its incomplete and fragmentary condition. The teeth from Czarnogłowy cannot be assigned to any currently accepted species of *Planohybodus*, particularly because dental features for use in distinction between *P. peterboroughensis*, *P. grossiconus* and *P. ensis* mainly relate to differences in main cusp proportions and the number of lateral cusplets, which makes species identification of incomplete tooth crowns difficult. Therefore, the Czarnogłowy teeth are here simply left in open nomenclature as *Planohybodus* sp.

cf. *Meristodonoides* sp.

Figure 2m–r.

3.1.4. Material

Two partially preserved teeth (GG303/17,18).

3.1.5. Description

The teeth are represented by two incomplete, labio-lingually compressed crowns displaying a slender, slightly distally inclined main cusp with a round cross-section (Figure 2n,q) and moderately well-developed cutting edges. The main cusp displays a mesial and a distal heel at its base. Lateral cusplets are not preserved. The ornamentation is restricted to the lower parts of the labial and lingual crown faces and consists of moderately simple, non-bifurcating vertical folds (Figure 2m,o,p,r).

3.1.6. Remarks

Although poorly preserved, the overall morphology displayed by the above-described teeth indicates close morphological resemblance to *Meristodonoides*, which was originally recognised in the Cretaceous of the USA [68] to include *M. rajkovichi* (Case, 2001) [81] from the Cenomanian of Minnesota, *M. butleri* (Thurmond, 1971) [82] from the Aptian or Albian of Texas, *M. montanensis* (Case, 1978) [83] from the Campanian of Montana and Wyoming and *M. novojerseyensis* (Case and Cappetta, 2004) [84] from the Maastrichtian of New Jersey, as well as *M. multiplicatus* Cicimurri et al., 2014 [85] from the Santonian–Campanian of Mississippi. The oldest fossil record that can be assigned to *Meristodonoides* dates back to the Late Jurassic and is represented by a yet undescribed species known from a single partial skeleton from the lower Tithonian of England [26]. In addition, incomplete teeth reminiscent of *Meristodonoides* were reported from the Kimmeridgian of England [25] and Switzerland [29]. However, the Polish material presented here cannot unambiguously be assigned to *Meristodonoides* due to its incomplete and fragmentary nature, which consequently led us to assign the above-described teeth from Czarnogłowy to cf. *Meristodonoides* sp.

Asteracanthus Agassiz, 1837 [67]

Type species: *Asteracanthus ornatissimus* Agassiz, 1837 [67]

Asteracanthus ornatissimus Agassiz, 1837 [67]
Figure 3.

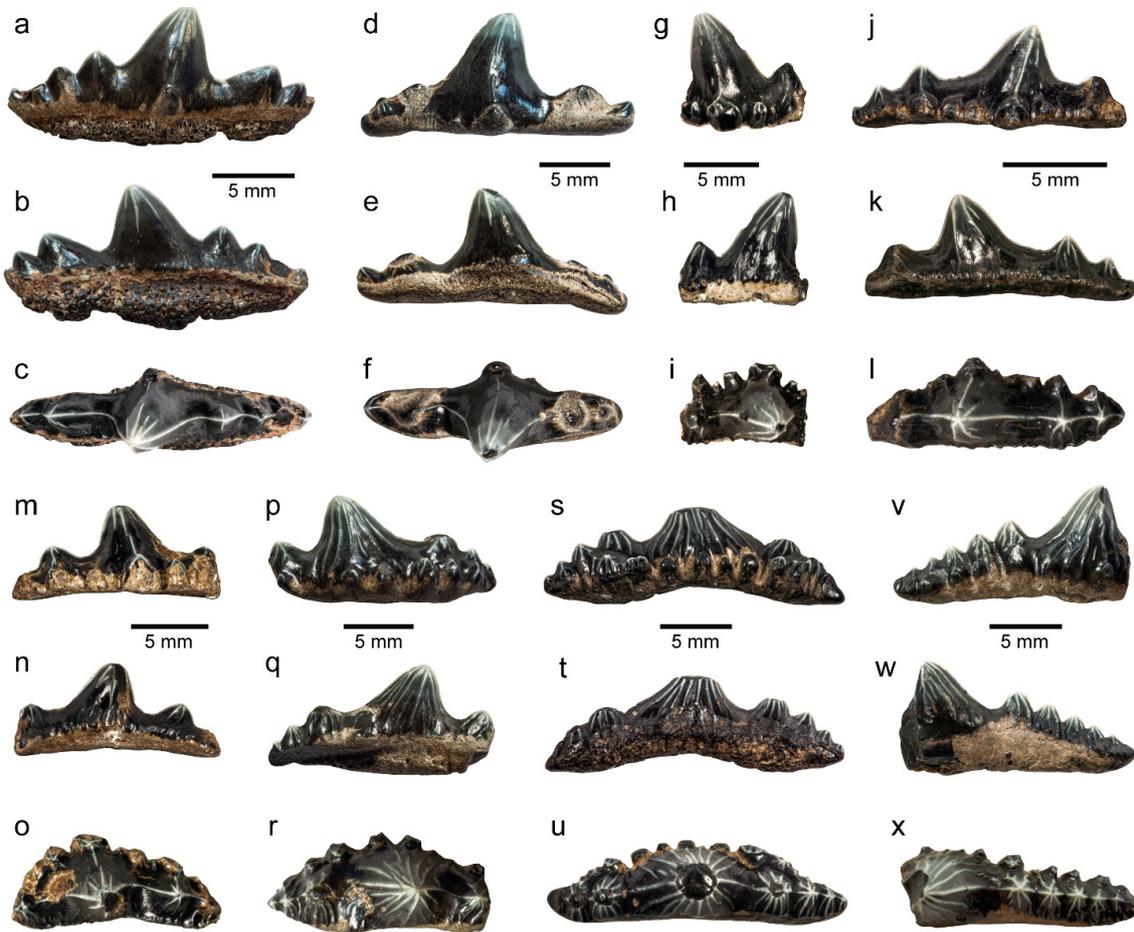


Figure 3. Historically collected hybodontiform teeth from the lower Kimmeridgian of Czarnogłowy, Poland. *Asteracanthus ornatissimus* Agassiz, 1837. GG 303/19 in (a) labial, (b) lingual and (c) apical view; GG 303/20 in (d) labial, (e) lingual and (f) apical view; GG 303/21 in (g) labial, (h) lingual and (i) apical aspect; GG 303/22 in (j) labial, (k) lingual and (l) apical view; GG 303/23 in (m) labial, (n) lingual and (o) apical view; GG 303/29 in (p) labial, (q) lingual and (r) apical view; GG 303/30 in (s) labial, (t) lingual and (u) apical aspect; GG 303/31 in (v) labial, (w) lingual and (x) apical view.

3.1.7. Material

Fifteen incomplete teeth (GG303/19–33).

3.1.8. Description

The teeth are characterized by fairly robust multicuspid crowns with a moderately high and robust, conical to somewhat pyramidal main cusp that is slightly distally inclined and flanked by three to five pairs of well-developed lateral cusplets, which diminish in size away from the main cusp. The cutting edges are moderately well-developed and continuous across the cusp and cusplets. The crowns are ornamented with moderate to strongly developed folds that descend from the main cusp and the lateral cusplets labially and lingually, with short, isolated folds occasionally occurring intercalated between them.

All teeth display a series of well-defined bulbous nodes aligned along the labial base of the crown, each one of them being ornamented with short, apically merging folds (Figure 3a,d,g,j,m,p,s,v). In addition, there is a series of very short vertical folds aligned along the lingual base of the crown (Figure 3b,h,k,n,q). The tooth root is present in a

single tooth only (Figure 3a–c). It is incomplete and has suffered from erosion, displaying numerous very small and irregularly arranged foramina.

The teeth can be further separated into two morphotypes. The first morphotype includes teeth that are relatively narrow labio-lingually with a more slender main cusp and reduced tooth crown ornamentation consisting of a few folds that cover the upper parts of the labial and lingual crown faces (Figure 3a–o). There may be a vertical fold on the labial crown face connecting the apex of the main cusp with the labial node at its base (Figure 3j), which is generally larger than the neighbouring ones (Figure 3a,d,g,j,m).

The second morphotype encompasses teeth that are more robust, with a stout, somewhat pyramidal main cusp and a more pronounced ornamentation comprising well-defined folds that descend from the main cusp and lateral cusplets down to the base of the tooth crown (Figure 3p–x). The folds covering the teeth of this morphotype may bifurcate basally (Figure 3r,u,x).

3.1.9. Remarks

The above-described teeth from Czarnogłowy were assigned by Hoffmann [49] to *Polyacrodus* sp. and *Hybodus obtusus*, respectively. While the genus *Polyacrodus* Jaekel, 1889 [86] is now considered a *nomen dubium* [59,87], the species *Hybodus obtusus* Agassiz, 1843 [67] was recently identified to represent a junior synonym of *Asteracanthus ornatissimus* [30].

The genus *Asteracanthus* was originally described by Agassiz [67] from the Late Jurassic of Europe on the basis of isolated dorsal fin spines ornamented with stellate tubercles to include the species *A. ornatissimus*, *A. acutus*, *A. minor* and *A. semisulcatus*. Since that time, additional species have been attributed to *Asteracanthus* based on isolated tuberculate dorsal fin spines (e.g., [17,21,88–90]). Later, following the discovery of associated dental and skeletal material from the Callovian of England, the genus *Strophodus* Agassiz, 1838 [67] became a junior synonym of *Asteracanthus* [18,91]. This taxonomic scheme has generally been accepted until very recently, when the first articulated skeleton with tuberculate fin spines was described from the lower Tithonian of southern Germany by Stumpf et al. [30]. This unique, exceptionally well-preserved female specimen, which was referred to the type species of *Asteracanthus*, *A. ornatissimus*, possesses multicuspid grasping teeth consistent with referral to those traditionally assigned to *Hybodus obtusus* and thus provided strong evidence that *Asteracanthus* and *Strophodus* may in fact represent two distinct, valid genera that are readily distinguished from each other by very different dental morphologies [30]. *Strophodus* is characterized by prominent, uniquely shaped crushing teeth [92], whereas the teeth of *Asteracanthus* [30] are rather more similar to those of *Hybodus* [64,93] and *Egertonodus* Maisey, 1987 [64,94] than to those of other hybodontiforms, suggesting closer phylogenetic relationships. Nevertheless, the systematic position of both *Asteracanthus* and *Strophodus* within Hybodontiformes still remains dubious and unresolved due to the lack of any reliable phylogenetic framework [30,31]. Likewise, much uncertainty still surrounds the taxonomic content of *Asteracanthus*, particularly given the absence of any fossil material suitable for inferring possible morphological characters for use in species differentiation. This led Stumpf et al. [30] to tentatively re-define the genus *Asteracanthus* as monotypic to include the type species, *A. ornatissimus*, whose stratigraphic range, as now understood, is Bathonian to Valanginian.

Late Jurassic fossil remains of *A. ornatissimus* are known from several European localities, in particular from those that were formed under fully marine conditions (e.g., [17–20,25,26,95–98]), suggesting that this species might have predominantly been bound to open marine environments. The dentition of the recently described skeleton from the lower Tithonian of southern Germany indicates that the general dental morphology displayed by female individuals of *A. ornatissimus* does not vary between the upper and lower jaw [30]. This suggests that the herein reported teeth from Czarnogłowy, which can actually be separated into two morphotypes, may pertain to different species of *Asteracanthus*. On the other hand, the presence of two very similar tooth morphotypes co-occurring in the same strata could possibly also be related to intra- rather than interspecific variation, such

as gynandric and/or ontogenetic heterodonty, which cannot be determined more closely based on the current data available. However, the lower Kimmeridge Clay Formation of England yielded a yet undescribed specimen of *Asteracanthus*, which is represented by an articulated skull including teeth, cephalic spines and a partial dorsal fin spine [26], whose detailed description may aid a better understanding of the taxonomic content of this enigmatic Mesozoic hybodontiform shark-like chondrichthyan. In consequence, we recommend assigning the above-described teeth from Czarnogłowy to *A. ornatissimus* until their specific identity can unambiguously be determined.

Acrodontinae Casier, 1959 [99] *sensu* Maisey, 1989 [58]

Genus *Strophodus* Agassiz, 1838 [67]

Type species: *Strophodus longidens* Agassiz, 1838 [67]

Strophodus udulfensis (Leuzinger et al., 2017) [29]

Figures 4 and 5.

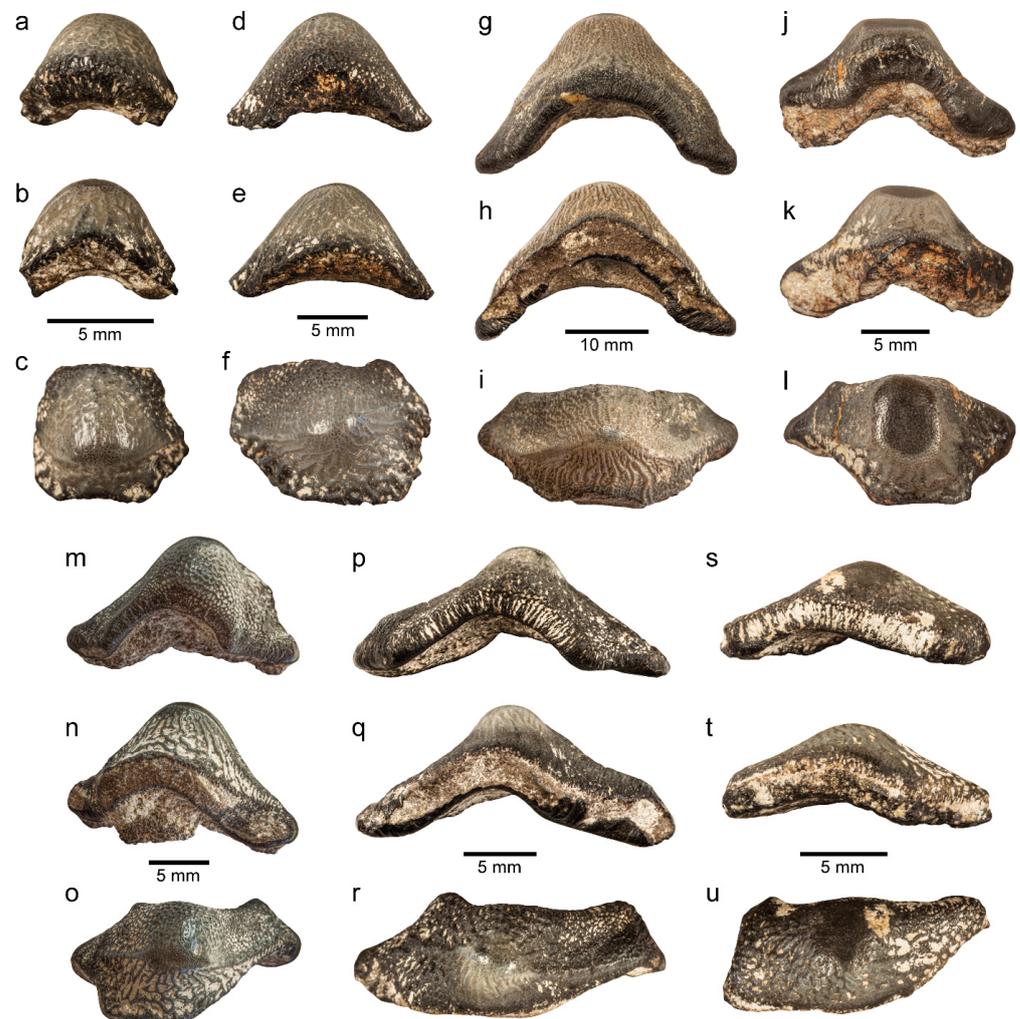


Figure 4. Historically collected hybodontiform teeth from the lower Kimmeridgian of Czarnogłowy, Poland. *Strophodus udulfensis* (Leuzinger et al., 2017). (a–f) Symphyseal teeth; GG 303/34 in (a) labial, (b) lingual and (c) apical view; GG 303/35 in (d) labial, (e) lingual and (f) apical view. (g–i) First anterior tooth; GG 303/36 in (g) labial, (h) lingual and (i) apical aspect. (j–u) Second anterior teeth; GG 303/37 in (j) labial, (k) lingual and (l) apical view; GG 303/38 in (m) labial, (n) lingual and (o) apical view; (p–u) second lateral teeth; GG 303/39 in (p) labial, (q) lingual and (r) apical view; GG 303/40 in (s) labial, (t) lingual and (u) apical aspect.



Figure 5. Historically collected hybodontiform teeth from the lower Kimmeridgian of Czarnogłowy, Poland. *Strophodus udulfensis* (Leuzinger et al., 2017). (a–i) First lateral teeth; GG 303/41 in (a) labial, (b) lingual and (c) apical view; GG 303/42 in (d) labial, (e) lingual and (f) apical view; GG 303/43 in (g) labial, (h) lingual and (i) apical aspect. (j–r) Second lateral teeth; GG 303/44 in (j) labial, (k) lingual and (l) apical view; GG 303/45 in (m) labial, (n) lingual and (o) apical view; GG 303/46 in (p) labial, (q) lingual and (r) apical view.

3.1.10. Material

A total of 61 incomplete teeth (GG303/34–94).

3.1.11. Description

The teeth are massive and display a relatively high degree of heterodonty. Morphologically, the teeth can be roughly separated into those coming from tooth files of symphyseal (Figure 4a–f), anterior (Figure 4g–u) and lateral positions (Figure 5). Posterior teeth are absent in the fossil assemblage from Czarnogłowy. The root is missing in most teeth or is just partially preserved. In addition, the occlusal crown face may be somewhat damaged due to wear.

Symphyseal teeth are short mesio-distally and strongly domed, displaying a subrectangular outline in occlusal view (Figure 4c,f). There is a weak transverse crest extending across the occlusal face of the crown. The crown exhibits a complex ornamentation pattern consisting of frequently branching folds on the lingual half of the crown (Figure 4b,e) and reticulate folds on the labial half, which gives it a rough, more or less regularly pitted surface texture (Figure 4a,d).

The teeth of the first anterior file (Figure 4g–i) are relatively wide mesio-distally, symmetrical and strongly arched. The domed area is wide mesio-distally and smoothly rounded in labio-lingual aspect (Figure 4g,h). There is a moderately well-developed transverse crest that runs across the crown (Figure 4i). The ornamentation covering the occlusal surface of the crown comprises anastomosing folds on the lingual half (Figure 4h) and reticulate folds on the labial half (Figure 4g).

The anterior teeth of the second file (Figure 4j–u) are expanded mesio-distally and moderately arched and asymmetrical, the mesial extremity being slightly more elongated and tapered in occlusal view than the distal one (Figure 4l,o,r,u). The crown exhibits a weak transverse crest, which may be absent in smaller teeth (Figure 4u). Similar to symphyseal and first anterior teeth, the crown is ornamented by branching folds covering the lingual half (Figure 4k,n,q,t) and is reticulated on the labial half (Figure 4j,m,p,s).

The lateral teeth of the first file (Figure 5a–i) are wide mesio-distally and only slightly domed. They possess either a somewhat lenticular (Figure 5c,f) or parallelogram-shaped (Figure 5i) outline in occlusal view and lack a transverse crest. While in those teeth with a lenticular outline the domed area is positioned at about the centre of the crown, the parallelogram-shaped teeth are gently domed mesially. The tooth crown ornamentation displays a reticulate pattern (Figure 5c,f), which may turn into fine branching folds (Figure 5i).

The lateral teeth of the second file (Figure 5j–r) are larger and broader labio-lingually, exhibiting a subrectangular outline in occlusal aspect (Figure 5l,o,r). They are slightly domed mesially and lack a transverse crest. The tooth crown is entirely reticulated.

3.1.12. Remarks

The prominent crushing type teeth from Czarnogłowy were initially assigned to *Asteracanthus ornatissimus* by Hoffmann [49] following the long accepted taxonomic scheme of Woodward [18,89]. However, since this taxonomic concept has been challenged [30], these teeth are here assigned to *Strophodus*, which was apparently one of the most common and widely distributed Mesozoic hybodontiforms, given that fossil occurrences attributable to *Strophodus* have so far been reported almost worldwide from Middle Triassic to Early Cretaceous strata (e.g., [30,71,92,100–105]). *Strophodus*, as currently understood, encompasses at least 13 species, 11 of which have been named to date. These comprise (in stratigraphic order):

1. *S. cf. reticulatus* Agassiz, 1838 [67] from the Middle Triassic of Switzerland [100].
2. *S. smithwoodwardi* (Peyer, 1946) [106] from the Toarcian of Switzerland.
3. *S. dunaii* (Szabó and Főzy, 2020) [92] from the Aalenian of Hungary.
4. *S. tenuis* Agassiz, 1838 [67] from Aalenian–Bathonian strata of Germany and England [59].
5. *S. longidens* Agassiz, 1838 [67], which represents the type species originating from the Bathonian of France.
6. *S. magnus* Agassiz, 1838 [67] from the Bathonian of England, France and India [59,71,107].
7. *S. indicus* Sharma and Singh, 2021 [71] from the Bathonian of India.
8. *S. jaisalmerensis* Kumar et al., 2021 [108] from the Bathonian of India.
9. *S. medius* Owen, 1869 [109] from the Bathonian–Callovian of France, England and India [59,71].
10. *S. reticulatus* Agassiz, 1838 [67], which is probably the temporally and spatially most widespread species being reported from the Bathonian–Tithonian of England, France, Switzerland, Germany and Hungary [26,30,59,92,106,110].
11. *S. subreticulatus* Agassiz, 1838 [67] from the Kimmeridgian of Switzerland.
12. *S. udulfensis* (Leuzinger et al., 2017) [29] from the Kimmeridgian of Switzerland and possibly England.
13. *Strophodus* sp. from the Tithonian of Germany [111].

Morphological characters for use in species identification mainly focus on dental traits due to the lack of suitable skeletal material. There are just a few species that are known by articulated or at least partially articulated dentitions, such as *Strophodus medius*, *S. reticulatus*

and *S. magnus* [59,92,107]. These species share very similar dentition patterns consisting of up to six tooth files on each side of the jaws, which can be further separated into two files of relatively high, strongly arched anterior teeth, two files of enlarged lateral teeth and one or two files of small posterior teeth. In addition, a single file of symphyseal teeth occurs, restricted to the lower jaw [111], a condition shared with other hybodontiforms such as *Egertonodus* and *Asteracanthus* [30,75,94].

The overall morphology displayed by the teeth from Czarnogłowy is closest to that of *Strophodus udulfensis* from the Kimmeridgian of Switzerland [29]. In addition, teeth of this species may also occur in the Kimmeridgian of England [26,29]. Differences between the above-described teeth from Czarnogłowy and those of *S. udulfensis* include slightly divergent ornamentation patterns in the teeth of the first lateral file, in particular in those exhibiting a lenticular outline, which are entirely reticulated in the Czarnogłowy teeth, unlike in *S. udulfensis*, in which these teeth show a more complex ornamentation pattern mainly consisting of frequently branching folds. However, since such minor differences in tooth crown ornamentation do not necessarily mirror heterospecificity, mainly because it could also possibly be explained by gynandric heterodonty, the above-described teeth are here assigned to *S. udulfensis*, thus extending the geographical range of this species to the marginal marine ecosystems south of Fennoscandia.

The teeth from Czarnogłowy vary in size (see, e.g., Figure 5a–f), which is indicative of different ontogenetic stages, suggesting that they originally derived from both subadult and adult individuals.

4. Discussion

4.1. Palaeoecology

The hybodontiform faunal assemblage from the lower Kimmeridgian of Czarnogłowy comprises at least four large-toothed taxa characterized by different dental features that hint at a wide variety of possible feeding ecologies. While the tooth morphologies displayed by *Planohybodus* sp. and cf. *Meristodonoides* sp. suggest an adaptation towards tearing prey [59], the more robust teeth of *Asteracanthus ornatissimus* form an effective grasping dentition suitable for processing a wide dietary spectrum [30]. This contrasts with *Strophodus udulfensis*, whose teeth form a prominent, well-developed durophagous crushing dentition [29,92].

Chondrichthyans recovered from the late Oxfordian to early Tithonian succession of Czarnogłowy, aside from the historically collected hybodontiform assemblage presented in this contribution, are known from very rare crown elasmobranch teeth of uncertain stratigraphic origin described by Hoffmann [49], comprising a total number of eight fragmentary teeth, four of which can be identified below the order level to include the squatiniform *Pseudorhina alifera* (Münster, 1842) [112], the heterodontiform *Paracestracion falcifer* Wagner, 1857 [113] and the carcharhiniform *Palaeoscyllium formosum* Wagner, 1857 [113]. All these taxa are typical components of European Late Jurassic chondrichthyan associations, indicating high dispersal abilities [114]. However, whether the apparent dominance of hybodontiforms reflects an ecological signal, or simply a collection bias focused on macroscopic rather than microscopic chondrichthyan remains, is unclear. Evidently, the hybodontiform *Strophodus udulfensis* is represented by dental material that refers to different ontogenetic stages, suggesting that the marginal marine environments south of Fennoscandia might have provided shelter that maximized growth rates and at the same time minimized the risk of predation. This is in good accordance with other reported occurrences of *S. udulfensis* [29], which together with stable isotope data [115] suggest that this species was a shallow-water-preferring taxon, which may have moved to low-salinity environments for reproduction.

4.2. Late Jurassic Hybodontiform Diversity and Distribution Patterns

The diversity dynamics of Mesozoic hybodontiforms are still poorly understood and have yet to be statistically established. This is mainly because most species are known from

isolated teeth and/or fin spines only, which commonly display morphological traits that are either ambiguous or broadly distributed among representatives of this enigmatic group of extinct shark-like chondrichthyans. Conversely, articulated or disarticulated skeletons, which provide important taxonomic but also ecomorphological information, remain rather scarce in the hybodontiform fossil record (e.g., [30,31,64,94,116–118]), particularly due to specific taphonomic constraints that hinder the preservation of their poorly mineralized cartilaginous endoskeletons. This discrepancy has led to different taxonomic and systematic schemes [16,58,87], pending further research effort. Nevertheless, it is evident that hybodontiforms constituted a major component of Mesozoic marine ecosystems, especially during the Jurassic, the time when they flourished and expanded into various ecological niches, occurring in fully to marginal marine and even continental depositional environments (e.g., [24–26,29,35,59,93,118,119]). The vast majority of reported Late Jurassic hybodontiform occurrences come from Europe, which have received considerable research attention since the 19th century (e.g., [18,20–31,91,97]). Conversely, records of non-European Late Jurassic hybodontiforms are rather rare, patchy and strongly biased towards continental environments [32–40]. Nevertheless, despite the heterogeneous availability of productive localities, some interesting points, at least on a more local scale, can be deduced from the here reported hybodontiform assemblage from the lower Kimmeridgian of Czarnogłowy.

During the Late Jurassic, wide areas of Europe were covered by a shallow epicontinental shelf sea that formed the southern part of a trans-Pangaeian seaway linking the low-palaeolatitudinal Tethys Ocean to the high-palaeolatitudinal Boreal Sea [120,121]. This allowed the migration of marine vertebrates, such as marine reptiles [46], which according to Tyborowski and Błazejowski [48] display a faunal provincialism that falls into a transitional palaeobiogeographic belt connecting the Tethyan and Boreal faunal provinces (in contrast, see [122]). Conversely, distribution patterns of European Late Jurassic crown elasmobranchs display fairly homogeneous faunal compositions, reflecting minor provincialism without boreal influences [114]. Similarly, quite homogeneous distribution patterns are indicated for large-bodied hybodontiforms such as *Planohybodus*, *Asteracanthus*, *Strophodus* and possibly *Meristodonoides*, as inferred from the herein reported fossil chondrichthyan assemblage from Czarnogłowy, which shows close affinities with other European Late Jurassic hybodontiform-bearing localities, in particular to those from England [25,26,30,31], France [20,79,80,98] and Switzerland [29] (Figure 6; note that there is also a historically described tooth that is consistent with *Asteracanthus* from the Oxfordian–Kimmeridgian of Inowrocław in central Poland [19]). On the other hand, small-bodied hybodontiforms such as the lonchidiid *Parvodus* Rees and Underwood, 2008 [123] appear to have been rare and predominantly bound to marginal marine environments with reduced or fluctuating salinities (e.g., [23,24,80]). This suggests that their apparently restricted facies distribution might have been due to biotic and/or abiotic constraints, although it might also reflect a collection bias since their small teeth are likely to have been overlooked in the past.

As common predators occupying higher trophic levels in a wide range of marine Late Jurassic ecosystems, large-bodied hybodontiforms such as *Planohybodus*, *Asteracanthus* and *Strophodus* might have had an impact on crown group elasmobranchs, which experienced a diversity stasis during the Late Jurassic before attaining a subsequent diversity increase during the Early Cretaceous [5,124,125]. Therefore, differences in habitat and/or prey preferences might have served as controlling factors reducing the apparent competition potential between Late Jurassic hybodontiforms and their more advanced chondrichthyan counterparts [29,115].

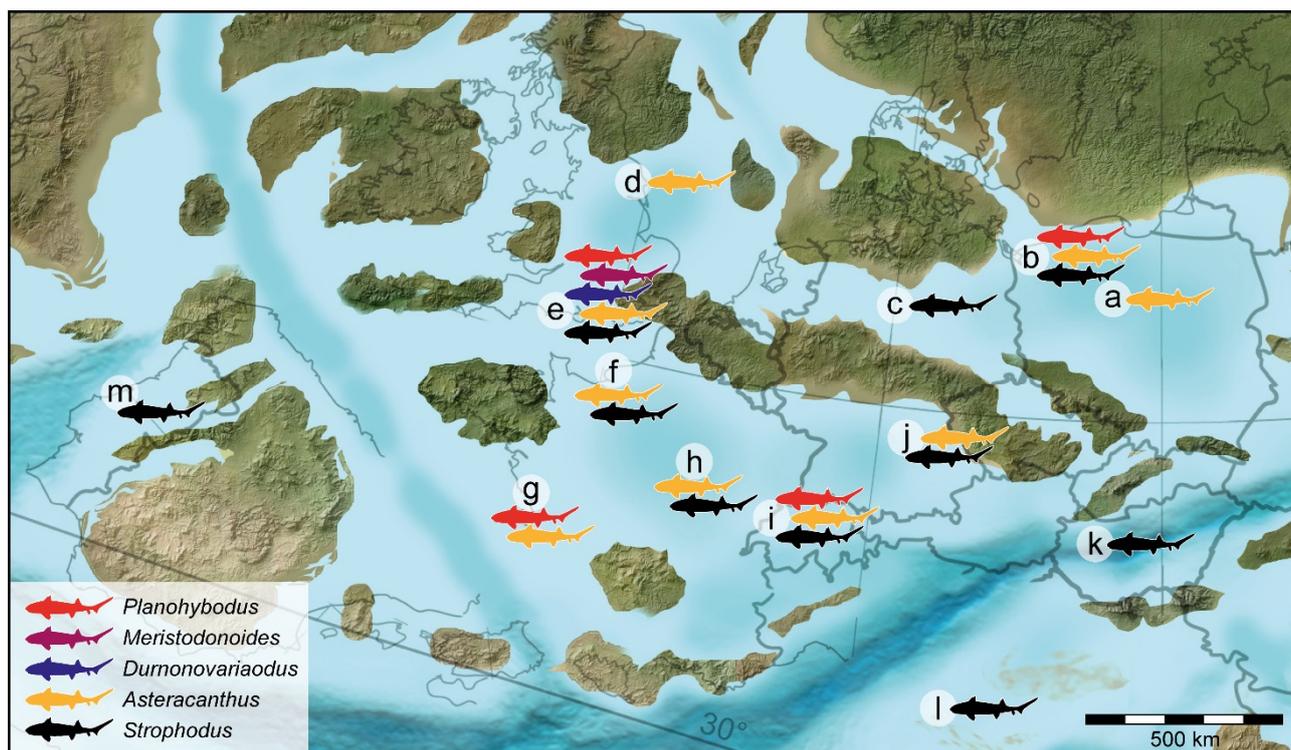


Figure 6. Rough reconstruction of Europe during the Late Jurassic depicting reported occurrences of large-toothed hybodontiform genera (taxa that cannot confidently be identified at genus level are excluded). (a) Oxfordian–Kimmeridgian of central Poland [19]; (b) Kimmeridgian of north-western Poland (this study); (c) Kimmeridgian of northern Germany [17]; (d) Oxfordian of northern England [97]; (e) Oxfordian–Tithonian of southern England [25,26,30,31]; (f) Kimmeridgian of north-western France [20]; (g) Tithonian of western France [20,79,80]; (h) Oxfordian of central France [98]; (i) Kimmeridgian of Switzerland [29]; (j) Kimmeridgian of southern Germany [28,30,111]; (k) Tithonian of Hungary [92]; (l) Kimmeridgian–Tithonian of Italy [105]; (m) Kimmeridgian of Portugal [21,22]. Palaeogeographic map © 2011 Colorado Plateau Geosystems Inc., Scottsdale, AZ, USA.

The genera *Planohybodus*, *Asteracanthus* and *Strophodus* were common and widespread during the Jurassic, especially during the Middle and Late Jurassic, the time when they reached their highest species diversity [30,59,92]. By the Early Cretaceous, their species diversity dropped significantly, resulting in a fossil record dominated by small-toothed forms, which predominantly occur in marginal marine depositional environments with reduced or fluctuating salinities (e.g., [70,74–76,126]). Potential causes driving the post-Jurassic diversity decline in fully marine hybodontiforms may include biotic constraints such as increasing risk of niche overlap with rapidly diversifying crown group elasmobranchs [5,118], probably accompanied by disruptions in the availability of preferred food resources (see [79,127]) caused by the environmental perturbations at the J/K boundary [1].

5. Conclusions

The present study, in which we reassessed a historically collected hybodontiform dental assemblage from the lower Kimmeridgian of Czarnogłowy initially described by Hoffmann [49], contributes to our knowledge of Mesozoic marine vertebrate life, providing promising clues for better understanding Late Jurassic chondrichthyan diversity and distribution patterns.

The taxonomic composition consisting of *Asteracanthus ornatissimus*, *Strophodus udulfensis* and *Planohybodus* sp., as well as cf. *Meristodonoides* sp., which is remarkable in that there are only a very few Mesozoic hybodontiform assemblages with more large-toothed genera or even species [31,59,118], demonstrates close faunal affinities to other European Late

Jurassic hybodontiform-bearing localities, indicating biogeographically homogenous distribution patterns characterized by large-bodied epipelagic forms of intermediate trophic position that were able to cross larger marine areas. This parallels patterns of biogeographic homogeneity displayed by crown elasmobranchs, which rapidly diversified from the Early Cretaceous onwards to become the most dominant chondrichthyan group. By contrast, post-Jurassic hybodontiform communities are dominated by small-bodied taxa that are largely confined to marginal marine environments with reduced salinities, indicating a major reorganization of chondrichthyan communities during the Early Cretaceous. This suggests that the dispersal abilities of post-Jurassic hybodontiforms were probably limited by both abiotic stress and biotic constraints, such as an increasing risk of competition from rapidly radiating crown elasmobranchs.

Author Contributions: Conceptualization, S.S., S.M. and J.K.; methodology, S.S.; validation, S.S.; formal analysis, S.S.; investigation, S.S.; data curation, S.S.; visualization, S.S.; writing—original draft preparation, S.S., S.M. and J.K.; writing—review and editing, S.S., S.M. and J.K. All authors have read and agreed to the published version of the manuscript.

Funding: Open Access Funding by the University of Vienna.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: All specimens in this study are housed at the Institute of Geography and Geology, University of Greifswald, Germany.

Acknowledgments: We thank Charlie Underwood (Birkbeck, University of London) and Gilles Cuny (Université Claude Bernard Lyon 1) for valuable discussions and support. Ron Blakey (Colorado Plateau Geosystems Inc.) is thanked for permission to use his palaeogeographic map. The authors are grateful to four anonymous reviewers, whose comments improved the quality of the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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