# New insight into the distribution and palaeobiology of the pycnodont fish *Gyrodus*

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The pycnodont fish *Gyrodus* is reported for the first time from the Lower Cretaceous of Germany based on two lower jaw elements from the Hauterivian and Barremian. The stratigraphic and geographic distribution of *Gyrodus* is summarized. *Gyrodus* ranges from the Middle Jurassic to the Early Cretaceous making it one of the longest living pycnodonts. Unambiguous Late Cretaceous records of *Gyrodus* are still missing. *Gyrodus* displays its widest distribution and greatest taxonomic diversity in the Late Jurassic. The distribution of *Gyrodus* implies not only near-coastal mode of life but also a pelagic lifestyle conversely to most other pycnodonts. External body features and function of the unpaired fins support this interpretation.

Key words: Neopterygii, Pycnodontiformes, Gyrodus, Cretaceous, palaeobiogeography, Germany.

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## Introduction

Pycnodontiform fishes are a morphologically and ecologically distinctive group of neopterygians, and they are one of the most common neopterygian fish groups of many conservation Lagerstätten of Mesozoic age worldwide (e.g., plattenkalks of South Germany and Lebanon). The oldest figure of an articulated pycnodont fish (*Gyrodus* from southern Germany) dates back to the 18th century (Knorr 1755: pl. 22).

The evolutionary history of pycnodont fishes encompasses a period of about 175 million years from the Late Triassic to the Eocene (e.g., Tintori 1981; Blot 1987) with most pycnodonts being small to medium-sized fishes with a standard body length of about 25 cm or less. Only a few taxa with a standard body length of more than 50 cm are known. Pycnodonts are *inter alia* characterized by a highly developed and specialized heterodont crushing dentition, which is the most common part to become fossilized. Consequently, dental characteristics have been main characters in pycnodont identification for the last 150 years.

The genus *Gyrodus* is a characteristic faunal element of Late Jurassic marine environments and includes the largest known pycnodont (*G. circularis*, Upper Jurassic of southern Germany). The genus was previously supposed to be restricted to the Jurassic period only (Kriwet 2001a). The intention of this paper is (1) to report the first unambiguous findings of dental remains of *Gyrodus* from Lower Cretaceous outcrops of Germany, (2) to summarize the stratigraphic and biogeographic distribution of *Gyrodus*, and (3) to briefly assess the mode of life of *Gyrodus*.

*Institutional abbreviations.*—BMNH, The Natural History Museum, London, UK; BSP, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany;

NLH, Niedersächsisches Landesmuseum Hanover, Germany; JME, Jura Museum, Naturwissenschaftliche Sammlungen Eichstätt, Germany (JME SOS, specimens from the Solnhofen quarries); MB.f., Museum für Naturkunde, Berlin, Germany.

## Localities and material

The material that forms the focus of this study comes from two localities in NW Germany (Fig. 1A). The complete lower jaw element was recovered from lower Barremian clay deposits of the clay pit "Gott", which is located about 20 km SE of Hanover (TK 25 Sarstedt 3725; R 3560400 H 5814675) (Fig. 1B). The second fragmentary specimen comes from Hauterivian sediments of the clay pit "Engelbostel". This site is about 9 km NW of Hanover (TK 25 Garbsen 3523; R 3545000 H 5814675) (Fig. 1B). The stratigraphic ages are based on ammonite and belemnite zones (Mutterlose 1997, 1998). Both specimens are stored in the collections of the Niedersächsisches Landesmuseum Hanover under numbers NLH 102.971 and NLH 102.972, respectively. Material used for comparison comprises articulated and disarticulated material of Gyrodus hexagonus (de Blainville, 1818) (e.g., BMNH P.3774, MB.f. 1340) from the upper Kimmeridgian and lower Tithonian of southern Germany, G. circularis Agassiz, 1844 (e.g., BSP-AS I 507, holotype, JME SOS 3130) from the Tithonian of southern Germany, and several dozen isolated dentitions housed in the Natural History Museum, London and the Museum of Natural History, Berlin from different Upper Jurassic deposits. In addition, dentitions of pycnodonts with similar morphologies (e.g., Mesturus, Proscinetes, Coelodus-group, etc.) housed in the same collections were studied. The specimens were examined using a Wild M3Z binocular microscope. Digital images were obtained using digital macro-photography and a scan-



Fig. 1. General sketch map of Germany (**A**) with position of the clay pits "Gott" and "Engelbostel" (**B**) that yielded the dental remains described herein. Abbreviations: E, clay pit "Engelbostel"; G, clay pit "Gott"; H, Hanover.

ning electron microscope. Specimens shown in Figs. 2D, G, and H were coated with  $NH_4Cl$  prior to photography.

## Systematic description

*Remarks.*—Pycnodonts have been recognized as a taxonomic unit since the description of Agassiz (1833–44). However, their relationships have been considered controversial since the beginning of the last century. Phylogenetic analyses using defined synapomorphic character states of pycnodonts have only been employed recently (Nursall 1996a; Kriwet 2001a; Poyato-Ariza and Wenz 2002). The results of these analyses, of which only the two most recent ones employed

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rigorous cladistic techniques, differ in several details. However, as the Ph.D. thesis of Kriwet (2001a) is not published yet, we follow the systematics proposed by Poyato-Ariza and Wenz (2002). *Gyrodus* is recognized as one of the most basal members of Pycnodontiformes and is placed in its own family Gyrodontidae (Poyato-Ariza and Wenz 2002).

Class Osteichthyes Huxley, 1880 Subclass Actinopterygii Cope, 1887 Division Halecostomi Regan, 1923 *sensu* Patterson (1973)

Order Pycnodontiformes Berg, 1937

Family Gyrodontidae Berg, 1940

Genus Gyrodus Agassiz, 1833

*Type species: Stromateus hexagonus* de Blainville, 1818 from the lower Tithonian of the "Solnhofener Plattenkalke", Bavaria, Germany.

### Gyrodus sp.

Description.-Specimen NLH 102.971 is an almost complete right prearticular with dentition. Only the tip of the rather massive prearticular bone and parts of the coronoid process are missing. The symphyseal area is rather deep and antero-posteriorly elongated (Fig. 2A<sub>1</sub>, A<sub>2</sub>). The base of the lateral coronoid process is broad. The dentition consists of crushing teeth. The tritorial teeth are arranged in four longitudinal rows without intercalating teeth between them. The principal row comprises transversely elongated and obliquely placed teeth (Fig.  $2A_1$ ). The main teeth are much broader than any of those positioned in medial or lateral rows. In occlusal view, they expose an oval outline with a transverse coronal indent surrounded by a well-marked and crimped wall. The medial edge of the teeth is tapering forming a low and blunt, displaced apex. A second, marginal wall delimiting a shallow, outer groove and following the outer tooth margin is usually developed. Anteriorly, the groove is deepest. Teeth of the medial tooth row are much smaller and restricted to the anterior half of the dentition (Fig. 2A<sub>1</sub>). Although more rounded, they display the same occlusal morphology as the principal teeth. However, a low and medially displaced apex on the wall is only developed in the posteriormost teeth. The main row is flanked laterally by two tooth rows. Teeth of the first lateral row are much smaller and more rounded. They are arranged with their long axes parallel to the labial margin. The central indent is very shallow and inconspicuous; thus, the walls meet and form a very blunt apex accompanied laterally by an indent. Teeth of the second lateral row are almost as large as the principal teeth and display generally the same morphology. The long axes of these teeth are arranged perpendicular to the labial margin. The lateral apex is well developed but blunt. A very small and displaced central tubercle is present in the apical furrow of most teeth. The posterior part of the outer rim is absent in several teeth.

The second specimen (NLH 102.972) is a fragmentary prearticular dentition and consists of three teeth of the outermost and two smaller teeth of the first lateral row (Fig. 2B). The teeth exhibit the same sculpture as those of the complete speci-



Fig. 2. Dental remains of *Gyrodus* spp. **A**. Right prearticular dentition of *Gyrodus* sp. (NLH 102.971) from the lower Barremian of clay pit "Gott"; occlusal (A<sub>1</sub>), mesial (A<sub>2</sub>), and lateral (A<sub>3</sub>) views. **B**. Fragmentary prearticular dentition of *Gyrodus* sp. (NLH 102.972) from the Hauterivian of clay pit "Engelbostel"; occlusal view. **C**. Articulated prearticulars of *Gyrodus hexagonus* (de Blainville, 1818) (MB.f. 1345) from the Kimmeridgian of Solnhofen, Bavaria; occlusal view. **D**. Posterior principle prearticular teeth of *Gyrodus hexagonus* (de Blainville, 1818) (MB.f. 1345) from the Kimmeridgian of Solnhofen, Bavaria; occlusal view. **E**. Latero-posterior prearticular tooth of *Gyrodus hexagonus* (de Blainville, 1818) (MB.f. 1367) from the Kimmeridgian of Solnhofen, Bavaria; occlusal view. **F**. Left prearticular of *Gyrodus circularis* Agassiz, 1844 (JM SOS 3130) from the Kimmeridgian of Wintershof, Bavaria; occlusal view. **G**. Unidentified pycnodont vomer (aff. *Gyrodus*? sp.) (MB.f. 7133) from the Hauterivian, Lower Cretaceous, of Langenberg near Oker, northern Germany; occlusal view. **H**. Left prearticular of an unidentified pycnodont (aff. *Gyrodus*? sp.) (MB.f. 7233) from an Lower Cretaceous erratic of the Baltic Sea; occlusal view. Scale bars 5 mm.

Discussion.—The combination of four longitudinal prearticular tooth rows without intercalating teeth with generally two crenulated apical rings, a tubercle in the apical indent in at least some teeth, and a medial or lateral apex on the inner wall are considered characteristic for Gyrodus dentitions (Thies 1985; Kriwet 2000). The two specimens from the Lower Cretaceous of northern Germany display these characters and are accordingly assigned to Gyrodus. Gyrodus is one of the most commonly cited pycnodont genera in the Late Jurassic, with about 32 described species (e.g., Wagner 1851; Woodward 1895; Lambers 1991). Most of these species, however, may not be valid. Only two species: Gyrodus hexagonus (de Blainville, 1818) and G. circularis Agassiz, 1833 were based on more than isolated remains including articulated skeletons from the Late Jurassic (Kimmeridgian and Tithonian) of the Solnhofen and Nusplingen plattenkalks of southern Germany.

A second genus, *Polygyrodus* White, 1927 may be related to *Gyrodus* (Kriwet, 2001a). The only species, *P. cretaceus* (Agassiz, 1844) from the Turonian–Campanian of England, Switzerland, and Germany (Roemer 1841; Woodward 1895; White 1927), is known from isolated dentitions and its assignment to Gyrodontidae might be disputable, because this assumption is based on similarities in dental structures. Teeth of *Polygyrodus* differ in the arrangement and occlusal sculpture (compare Woodward 1909: pl. 35: 5, 6). The most notable differences to teeth of *Gyrodus* are the elevated and obtusely acuminate crown with a coarsely wrinkled and irregular apex, and a single, very narrow groove that is generally restricted to one side of the crown. In addition, the teeth are very irregularly arranged so that distinct tooth rows are difficult to identify.

A comparison with all described species of Gyrodus is difficult, because most of the species are based on isolated and fragmentary dental remains and the prearticular dentition in many specimens is not known. Therefore, we compared the dentitions mainly with those of G. hexagonus (Fig. 2C-E) and G. circularis (Fig. 2F), which are the only two Gyrodus species established for articulated skeletal remains. Species based on isolated dental remains and assigned to Gyrodus were also considered. The two Early Cretaceous specimens described herein resemble G. hexagonus in tooth morphology and sculpture (Fig. 2C-E), especially in the presence of an occlusal indent with a central tubercle in several teeth that is surrounded by a crimped wall with an additional anterior one (Fig. 2E). The occlusal prearticular tooth surfaces of G. circularis are, conversely, more strongly sculptured than those of G. hexagonus and the specimens presented here when unworn with a less developed central indent and a more wrinkled wall surrounding it (Fig. 2F). In addition, the posterior main teeth lack the central apical indent; instead, they expose a broad and blunt, irregularly wrinkled and folded apex (compare also Kriwet 2000: fig. 6). Continuous wear results in constant loss of the crimped walls and the lateral blunt apex, and may render identifications difficult (Fig. 2B). Despite the differences to some *Gyrodus* species (e.g., *G. cricularis*) and similarities to others (e.g., *G. hexagonus*), an assignment to any *Gyrodus* species of the specimens described here is impossible without more complete material. Consequently, we leave both specimens in open nomenclature. Minor morphological differences between both specimens may fall within the intraspecific variation of tooth ornamentation or may be the result of wear. However, because of the different stratigraphic occurrences both specimens may belong to different species.

## Stratigraphic and geographic distribution of *Gyrodus*

The oldest record of *Gyrodus* (*G. goweri*) comes from the Middle Oolites series of Scotland, which are Bajocian (Middle Jurassic) in age (Grey-Egerton 1869). Isolated teeth displaying the characteristic *Gyrodus* tooth morphology and sculpture (Grey-Egerton 1869: fig. 1) and a fragmentary trunk represent this species. However, the material is too fragmentary to allow any specific identification and therefore should be considered as *Gyrodus* sp. *Gyrodus* was also reported from the Bathonian (Great Oolite) of the Stonesfield Slate in England (Agassiz 1835), and Galton et al. (1980) indicated the presence of isolated teeth of *Gyrodus* in the middle Callovian of northern France but did not provide any figure or description.

Gyrodus had its greatest taxonomic diversity and geographic distribution in the Late Jurassic (Kriwet 2000, see above). Isolated and fragmentary remains are known from several localities in Great Britain, e.g., Corallian Group of Yorkshire, and Kimmeridgian Clay of Dorsetshire and Cambridgeshire (e.g., Woodward 1895). In Germany, completely articulated and well-preserved specimens occur in the famous Upper Jurassic lithographic limestones of Baden-Württemberg (Nusplingen; Heineke 1906: G. circularis) and Bavaria (Solnhofen area, Eichstätt, Kehlheim, Brunn; Lambers 1999: G. hexagonus and G. circularis). Additional isolated dentitions and teeth were reported from Oxfordian and Kimmeridgian strata in Lower Saxony, northern Germany (Fricke 1875, Mudroch and Thies 1996). The specimens from the lower Kimmeridgian limestones of Cerin in France identified as Gyrodus by Saint-Seine (1949) belong to more derived members of pychodonts (Wenz et al. 1993; Lambers 1999). Isolated dentitions from the Late Jurassic referred to Gyrodus are known from the upper Kimmeridgian of the Solothurn Turtle Limestone Member, Switzerland (Sulser and Meyer 1998), many Upper Jurassic marine deposits in France (e.g., Astre 1955; Cornuel 1880; Sauvage 1901, 1902), and from the Tithonian of Sicily (Gemmellaro 1868). Gyrodus also occurs in the Kimmeridgian of northeastern Spain (unpublished data).

The presence of *Gyrodus* in the Oxfordian of the western (Caribbean) part of the Tethys (Jagua Formation, Cuba; Gregory 1923; Kriwet 2001b) and along the western maritime coast of South America (Chile; Martill et al. 1998; Arratia and Schultze 1999; Kriwet 2000) indicates a westward migration in its early evolutionary history. Dunkle and

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Maldano-Koerdell (1953) described isolated remains including a well-preserved dentition from the Kimmeridgian of Mexico, the only document of *Gyrodus* in this area. In the Tithonian, *Gyrodus* extended its geographic range also eastwards, where it is known from the Tithonian of Siberia and Japan (Mantell 1844; Schaeffer and Patterson 1984).

Early Cretaceous records of *Gyrodus* are very rare and mostly questionable. Remains assigned to G. atherfieldensis White, 1927 and G. minor Agassiz, 1844 were reported from the Aptian Greensand and the Albian part of the Speeton Clay of England, respectively (Woodward 1895). G. ather*fieldensis* is characterised by smooth teeth, which may be the result of abrasion and hence the attribution of this specimen to Gyrodus remains arguable. Conversely, G. minor exhibits an ornamentation similar to that of other Gyrodus species. Pictet et al. (1858-60: pl. 8: 27-33) assigned isolated pycnodont teeth from the Valanginian of Switzerland to Gyrodus, and Cornuel (1877, 1883, 1886) described and figured jaw fragments with teeth of G. contiguidens from the Hauterivian and G. sculptus from the Neocomian of France. The teeth of all these records show a Gyrodus-like sculpture when unworn. A dental remain of G. ellipticus described by Eichwald (1868) from the Lower Cretaceous of Russia is more similar to teeth of Coelodus and Ocloedus respectively.

Fabre et al. (1982) indicated the presence of *Gyrodus* in the Berriasian (Lower Cretaceous) of southern France (Var Department) without description or figure and it remains unclear whether the specimen consists of isolated dental or articulated skeletal remains.

Dental remains of supposed *Gyrodus* species recovered from the lower Hauterivian in the western Harz Mountains (Langenberg near Oker, northern Germany) and from a Lower Cretaceous erratic of the Baltic Sea in the collections of the Museum für Naturkunde, Berlin (Fig. 2E, F) represent a quite different, probably new pycnodont taxon. Characters distinguishing this Baltic Sea pycnodont from *Gyrodus* include more prearticular tooth rows, very small teeth in the tooth rows accompanying the central row of the vomer, and globular tooth crowns without apical indent, which are partly surrounded by a narrow rim with smooth margins.

Although the fossil record of Late Cretaceous bony fishes is quite good (e.g., Cavin 2001) the knowledge of Late Cretaceous pychodont fishes is surprisingly limited and restricted to questionable records of isolated teeth and jaw fragments. Articulated skeletal remains are known only from few pycnodonts, e.g., Anomoeodus muensteri from the Cenomanian-Turonian of Bohemia (Fritsch 1878). White (1927) described an imperfect vomer probably from the Terebratulina-zone (Turonian?) of England as Gyrodus benetti. The morphology of teeth and the size and arrangement of teeth in the first lateral tooth rows, which accompany the central tooth row and which are restricted to the posterior part of the dentition, are uncharacteristic for Gyrodus. Another pychodont remain from the Cenomanian of France was named Gyrodus carentonensis by Coquand (1860). This species is characterised by a well-developed, bulbous and wrinkled margin surrounding an apical indent that lacks any central apex. The morphology of the teeth is close to that of teeth of *Gyrodus* but differs slightly, so that Sauvage (1879) erected the genus *Cosmodus* for this species and also assigned *Pycnodus sculptus* Agassiz, 1844 and *Pycnodus imitator* Cornuel, 1877 from the Lower Cretaceous of northern France, and *Cosmodus grandis* Sauvage, 1879 from the Cenomanian of northern France to this genus. These species, however, are more likely to belong to a species-group with teeth similar to species generally assigned to *Coelodus* (e.g., Woodward 1895).

## Mode of life

Most remains of Gyrodus occur in shallow marine, nearcoastal deposits (Kriwet 2001b), although pycnodonts from freshwater deposits are known (Longbottom 1988; Poyato-Ariza et al. 1998). It can be assumed that Gyrodus showed a lifestyle similar to other marine pychodonts (Kriwet 2001a, b), which is interpreted to be comparable to modern coral fishes (Kriwet 2001c). Most pychodonts superficially resemble recent coral fishes in their most often deep, rounded, and laterally compressed body (except for Coccodus spp.), their generally prognathous snout, the deep skull profile, and their elongated anal and dorsal fins. The elongated dorsal and anal fins in combination with a generally high caudal fin in most pycnodonts provide propulsive forces and increased stability, manoeuvrability, and locomotion in a subdivided environment such as reefs or lagoons (Nursall 1996b). The outer form of the caudal fin varies among pycnodonts. A fan-shaped caudal fin is present in Apomesodon, Eomesodon, Macromesodon, and Stemmatodus; it is cleaver-shaped in Brembodus, Coccodus, Ichthyoceras, and "Palaeobalistum" orbiculatum. Proscinetes has a concave trailing edge, whereas Coelodus and *Pycnodus* are characterized by an undulating trailing edge with central concavity. Nursallia finally has a vertical trailing edge. For figures of caudal fins see Poyato-Ariza and Wenz (2002: figs. 24–32 and 35, 36). The function of the caudal fin in most pychodonts is to intensify lateral undulations, which is sufficient for slow swimming, where high powers or great speed are not necessary (Lund 1967). Consequently, the morphology of the unpaired fins points to a balistiform propulsion technique in most of these taxa, the dorsal and anal fins undulating more or less simultaneously (Nursall 1996b). This indicates that most pychodonts were undeniably slow swimming but highly manoeuvrable. In addition, the absence of ossified vertebral centra, the presence of anterior autogenous neural spines, and reduced squamation in most pychodonts are not designed to rapidly generate anteriorly directed forces. As a consequence, it can be assumed that most pychodonts had certainly a rather poor fast-start performance.

However, *Gyrodus* and *Proscinetes* show a slightly different body design. Their caudal fin is separated from the anal and dorsal fins by a distinctive caudal peduncle. In *Gyrodus*, the caudal fin is deeply forked conversely to other more typical pycnodonts (Fig. 3). Additionally, the dorsal and anal fins are falcate and low. The aspect ratio (AR) is higher than six (Nursall 1996b), which is well within the range of typical



Fig. 3. Late Jurassic pycnodonts to exemplify the body form and arrangement of unpaired fins. **A**. *Gyrodus hexagonus* (de Blainville, 1818) (JME SOS 3163) from the Tithonian of Eichstätt, southern Germany. **B**. *Apomesodon gibbosus* (Wagner, 1851) (JME SOS 3572a) from the Tithonian of Eichstätt, southern Germany. Scale bars 5 cm.

thunniform swimmers like recent mackerel sharks or tunas (AR 4.5 to 7.2; Sambilay 1990; Sfakiotakis et al. 1999). Thus, although its body was high and laterally flattened like in other pycnodonts and modern fishes with carangiform swimming mode (AR 1 to 2), the swimming mode of *Gyrodus* was probably more efficient than in those fishes. As mainly the caudal

fin effected progression, higher maximal speeds were achieved, as well. Starting performance also might have been better in *Gyrodus* because of the complete squamation indicating better body stability than in pycnodonts with reduced squamation (e.g., *Proscinetes*, *Eomesodon*, and *Pycnodus*). This indicates that *Gyrodus*, and probably *Proscinetes*, were not

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only living in structured, near-coastal habitats where they found most of their food, but also had a pelagic lifestyle enabling *Gyrodus* to cross deeper sea basins what was crucial for its wide distribution. This interpretation is supported by the spatial distribution pattern of *Gyrodus* especially in the Late Jurassic (Kriwet 2001b; this paper).

### Conclusions

More than 600 nominal pycnodont species have been described so far, of which only 76 species are known by more than isolated dental remains. Consequently, to understand patterns of pycnodont biodiversity and biogeography these dental remains have to be taken into account. However, one should keep in mind that dental remains alone cannot serve to resolve in-group phylogenies of pycnodonts (Poyato-Ariza 2003).

Biogeographic analyses based on all published records of pycnodonts by Kriwet (2001b) show that the spatial and temporal distribution of pycnodonts is consistent with current palaeobiogeographic reconstructions. Pycnodont distribution was rather patchy in the Late Triassic and Early to Middle Jurassic (Tintori 1981; Kriwet 2001b; Delsate and Kriwet 2004). Further distribution is correlated to the arrangement of continents and intracontinental constellations of water corridors and physical barriers. Gyrodus was, according to the current knowledge, the first pychodont to spread into the developing marine corridors with the continuous break up of the Pangean continent reaching the Caribbean part of the Tethys and the Pacific coast of South America as early as the Oxfordian (Kriwet 2000). Pycnodonts are very diverse in the Late Jurassic and Gyrodus is one of the most abundant pychodonts of this period. Pycnodonts subsequently followed the coastlines of South America and Africa and intruded continental influenced basins (e.g., Brazil, Niger) with the beginning of the break up of the South Atlantic Ocean in the Early Cretaceous (Maisey 2000). However, pycnodont records are very limited in Gondwana during the Early Cretaceous and Gyrodus has not been reported from this area so far. Early Cretaceous records of Gyrodus are still very scarce and most are in need of revision to establish the taxonomic diversity of this pycnodont for this time. The two specimens from the Barremian and Hauterivian presented in this study (NLH 102.971 and NLH 102.972) undoubtedly belong to Gyrodus and are the stratigraphic youngest records of Gyrodus from Germany. Unquestionable Late Cretaceous records of Gyrodus are still missing and most if not all specimens assigned to this genus may belong to other pycnodontiform groups. Consequently, the stratigraphic range of Gyrodus from the Middle Jurassic to the Early Cretaceous makes it one of the longest living pychodont taxa. The youngest record is G. minor Agassiz, 1844 from the Aptian and middle Albian of England. The almost complete absence of Gyrodus in Gondwana and the restricted distribution during the Early Cretaceous represents most probably a collecting bias when compared to the higher number of localities explored in Europe. The supposed pelagic mode of life of Gyrodus is supported by distribution pattern and external body morphology.

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