Njoerdichthys dyckerhoffi gen. et sp. nov. (Pycnodontiformes, lower Turonian) northward migration caused by the Cretaceous Thermal Maximum

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A B S T R A C T

A new pycnodont taxon, Njoerdichthys dyckerhoffi gen. et sp. nov., from the Turonian of the Lower Saxony Basin of Germany is described and its systematic positions is established based on phylogenetic analyses of three specimens using slightly altered data matrices. All analyses display some differences to previous analyses but show very similar results to each other apart from the interpretation of the position of several taxa such as, e.g., Palaeobalistum. The new pycnodontiform specimens from northwestern Germany are unambiguously identified as a derived member of Pycnodontidae with close relationships to Abdobalistum and Nursallia? goedeli because of the unique combination of characters. One of the three specimens represents a juvenile form. Its morphological characters are limited, but it shares some characters with Njoerdichthys dyckerhoffi gen. et sp. nov. and is consequently allocated to the new taxon. The systematic placement of the new taxon, Njoerdichthys gen. nov., within Pycnodontidae is surprising since it does not display the one autapomorphic character (postparietal brush-like extension for muscle attachment) previously proposed to define this clade, but rather displays a combination of derived and homoplasic characters indicating that the definition of supra-generic taxa needs to be re-evaluated in the future by including more and new taxa. The distribution of pycnodontiform fishes in the Cretaceous appears to concur with changes in global climatic conditions, where high upper-ocean temperatures and high sea levels allow these fishes to migrate into higher latitudes as evidenced by the occurrence of the new taxon and Anomoedodus subclavatus in the Campanian of Sweden.

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1. Introduction

Fossil bony fishes and their remains are known since the 19th century from uppermost Cretaceous deposits of northern and western Germany (Roemer, 1841, 1854; von der Marck, 1885; Siegfried, 1954). This is mainly based on the Fossil Lagerstätte of the late Campanian Baumberge Formation. However, there is a second Upper Cretaceous Fossil Lagerstätte containing well-preserved fish in the Cenomanian–Turonian boundary interval. This succession of basinal, blackish laminated marlstones (“black shales”) belongs to the Hesseltal Formation (Hiss et al., 2007a, 2007b), which occurs in Westphalia and Lower Saxony (northern Germany). Although its academic exploitation did start only a couple of decades ago, it produced a large number of new insights into the occurrence and taxonomy of Cretaceous aquatic vertebrates (Kriwet and Gloy, 1995; Maisch and Lehmann, 2000; Diedrich, 2001, 2012, 2014; Müller, 2008; Stumpf et al., 2019). Apart from these extraordinary Fossil Lagerstätten, significant fish finds in the basinal facies of the Late Cretaceous are rare (e.g. von der Marck, 1860, 1862; Lehmann et al., 1997). Literature data (see above) in combination with cursory records from the lower–middle Turonian proximal greensand facies limiting the northern rim of the Rhenish Massif (see sedimentological data, e.g., in Dölling et al., 2018; Berensmeier et al., 2018) provide insights into the terminal Cenomanian to middle Turonian faunal composition of bony fishes of the north German parts of the Central European Cretaceous shelf seas, including the actinopterygians Berycopsus, Cimolichthys, Clupeiformes indet., Enchodus, Hoplopteryx, Osmeroides,
Pycnodontiformes indet., *Pycnodus*, Teleostei indet., and *Xiphactinus* (Wittler, 1995; Wittler and Roth, 2003, 2004). Moreover, the Hesseltal Formation provided also three specimens of a yet undescribed, new form of pycnodontiform fish from the lower Turonian *Mytiloides hattini* inoceramid zone of the Lengerich sections (Westphalia), which are very rare in this latitude, except for few cranial and postcranial skeletal remains from the English Chalk and isolated teeth and dentitions from the late Cenomanian and late Turonian of Lower Saxony (Woodward, 1909; Kriwet, 2002; Licht and Kogan, 2011; Vullo et al. 2018). Of particular interest is the timing of occurrence as it falls into the early Turonian Cretaceous Thermal Maximum (KTM) as indicated in Huber et al. (2018). Being classical representatives of Tethyan subtropical warm waters (Kriwet, 2001a, b; Martin-Abad and Poyato-Ariza, 2013), the occurrence of completely preserved pycnodontiform fish in different growth stages in the Boreal Realm suggests rather the presence of a population instead of random vagrants as seen in extant coral fish associations (e.g., Welsh et al., 2013). This raises the question of its palaeobiogeographic significance and that of the fish assemblages in general (see discussion in Maisch and Lehmann, 2000). The scope of our paper, therefore, is to (1) describe the new species and to assess its systematic position within Pycnodontiformes and (2) discuss the palaeobiogeographic affinities of the Cenomanian/Turonian bony fish fauna based on the new pycnodontiform fish record and a literature review in the context of available palaeoclimatic trends in the late Cenomanian/middle Turonian time interval.

1.1. Geological framework

The Hesseltal Formation (Hiss et al., 2007a) is exposed in several quarries in the northern part of the Münsterland Cretaceous Basin of Westphalia (Hesseltal, Lengerich, Halle/Westfalen: Kaplan, 1992, 2011; Hilbrecht and Dahmer, 1994; Lehmann, 1999; Richardt, 2010) and the Lower Saxony Cretaceous Basin (Wunstorf, Höver, Sack Syncline; Lower Saxony: e.g., Keller, 1982; Hilbrecht and Dahmer, 1994; Voigt et al., 2008; Fig. 1). It consists of grey to white, rarely reddish limestones, alternating with dark grey to black, laminated C$_{org}$-bearing marlstones with C$_{org}$ contents hardly exceeding 3% (e.g., Trabuco-Alexandre et al., 2010; Hetzel et al., 2011; Blumenberg & Wiese, 2012). Lithologically a bit incorrect, these laminated marls are referred to as “black shales”, which are famous for their well-preserved invertebrates (inoceramids: Hilbrecht and Dahmer, 1991; ammonites: Wippich, 2005; Hauschke et al., 2011; Klug et al., 2012; Kennedy and Kaplan, 2019; crustaceans: Neumann and Jagt, 2003; Hauschke et al., 2011; Schöllmann and Hauschke, 2012). Even more fascinating is the rich vertebrate assemblage (Zawischa, 1982; Kriwet and Gloy, 1995; Maisch and Lehmann, 2000; Müller, 2008; Diedrich, 2012, 2013, 2014; Smith et al., 2019; Stumpf et al., 2019).

The base of the Hesseltal Formation represents a significant 3rd order sequence boundary, SB (SB Ce 5 of Wilmsen, 2003 and Richardt and Wilmsen, 2012; SB Ce 6 of Robaszynski et al., 1998). It is commonly referred to as the “Facies Change” or “sub plenus erosion surface” (Fig. 2), which can be safely correlated between northern Germany, England and France (Ernst et al., 1984; Owen, 1996; Robaszynski et al., 1998; Fig. 2). The Facies Change marks likewise the onset of the terminal Cenomanian/early Turonian Oceanic Anoxic Event 2 (OAE 2) with its positive stable carbon isotope ($\delta^{13}$C) excursion (OAE2-CIE) and the subordinate isotope marker a$-d$, well documented from northern Germany and the working area (e.g., Lehmann, 1999; Voigt et al., 2007, 2008). It has been recorded from a large number of sections and boreholes and provide an excellent tool for an interbasinal correlation of the Cenomanian/Turonian transition interval (e.g. Paul et al., 1999; Tsikos et al., 2004; Jarvis et al., 2006, 2011; Voigt et al., 2007, 2008). Furthermore, the good interbasinal correlation enables a calibration of biostratigraphic frameworks (e.g. ammonites, inoceramids, planktonic foraminifera: Gale et al., 2005).

The Cenomanian/Turonian successions of Lengerich ranges from the upper Cenomanian well into the upper Turonian, exposing the Brochterbeck, Hesseltal and Lengerich formations (Kaplan, 1992; Hilbrecht and Dahmer, 1994; Lehmann, 1999; Kaplan and Wiese, 2000; Wiese and Kaplan, 2001, 2004; Hiss et al., 2007b). The entire Hesseltal Formation has a thickness of c. 18 m, and in our Fig. 2, only the lower part is presented, exhibiting two black shale belts (beds 122—134, beds 136—149). The $\delta^{13}$C curve of Lehmann (1999; for methods and sampling procedure see therein) shows an expanded OAE2-CIE, and the subordinate isotope marker a$-d$ can be recognized (Fig. 2). Based on biostratigraphic data given in...
Fig. 2. Measured section of the Lengerich localities with litho- and bio-stratigraphic subdivision, ammonite and inoceramid record, mfs and δ13C curve after Lehmann (1999) where specimens of Njoerdichthys dyckerhoferi gen. et sp. nov. were collected. The measured section is based on the active Hohne working quarry of the Dyckerhoff AG (number 1 in Fig. 1). Ammonites zones: C. guerangeri = Calycoceras guerangeri, M. geslinianum = Metoicoceras geslinianum, N. juddii = Neocardiores juddii, W. devonense = Wattinoceras devonense, M. n. = Mammites nodosoides, M. l. = Mytiloides labiatus inoceramid zone. PCE after Jenkyns et al. (2017), position of KTM after Huber et al. (2018). Nomenclature of phases of stable isotope curve adapted from the Halle section, Voigt et al. (2007).
Gale et al. (2005) and Voigt et al. (2007, 2008) in conjunction with the therein given δ¹³C curves, ammonite and inoceramid zonations were plotted against the δ¹³C curve and applied to the log of the Lengerich section (comp. Fig. 2). This correlation identifies the base of the Turonian in bed 135. As a bed-by-bed correlation between the Halle DIMAC quarry and Lengerich is possible (pers. comm. U. Kaplan), the second black shale belt (136–149) is the interval comprising the Watinoceras Bed in Voigt et al. (2007) and Smith et al. (2019) (Watinoceras Event of Kennedy and Kaplan, 2019), located above subordinate isotope marker d (Fig. 2). This interval marks likewise the early Turonian maximum flooding of DS Ce-Tu 1 in Smith et al. (2019).

In addition, a progressive palaeotemperature increase characterizes the Cenomanian/Turonian transition interval (see compilation in O’Brien et al. 2017) and the early Turonian KTM (Huber et al., 2018), the position of which is intrapolated against the Lengerich section (Fig. 2). A short-terminated but severe cooling pulse interrupted progressive warming in the late Cenomanian Metolecoceras geslinium ammonite Zone (Jefferys, 1962; Plenus Cold Event of Gale and Christensen, 1996) with a drop of palaeowater temperatures from ca. 22 to 14 °C (Zheng et al., 2013, see, e.g., O’Connor et al., 2019 for more details). On the δ¹³C curve, the Plenus Cold Event is positioned between subordinate isotope markers A and B (e.g. Jenkyns et al., 2017), which corresponds approximately the interval from the upper part of the Plenus Bed to Bed 121 (Fig. 2).

1.2. Provenance of the material

The section in Fig. 2 is based on fieldwork from two closely located sections, the Hohne working quarry of the Dyckerhoff AG and the abandoned Galgenknapp quarry. The Hohne working quarry of the Dyckerhoff AG (locality 1) is located west of the city of Lengerich. Specimens GSUB V2303 and GSUB V2304 were recovered from a rock dump in the central part of the quarry in 1995. Judging from the find location, GSUB V2303 comes most likely from the main black shale bundle (beds 138 to 149, lower Turonian Watinoceras devonense Zone; Watinoceras Event, Fig. 2). Conversely, it is not possible to establish the exact provenance of specimen GSUB V2304 other than that it comes from somewhere between beds 122 and 158 (terminal Cenomanian Neocardioceras juddii to basal lower Turonian Mammites nodosoides ammonite zone; Fig. 2).

The abandoned Galgenknapp quarry (Fig. 1) is one of the former Dyckerhoff AG quarries and is now a nature protection area. Specimen GSUB V2302/1 and 2 was collected in situ from a bedding plane about 25 cm below the top of bed 143 on the southern slope of the Galgenknapp quarry in 1995 (Fig. 2). This bed belongs to the main black shale belt of the Cenomanian–Turonian transition in Westphalia and belongs to the Watinoceras devonense ammonite zone (earliest Turonian). Nevertheless, although two of the specimens cannot precisely be located within the stratigraphic succession at Lengerich, all material comes from beds, which unequivocally represent the post-Plenus warming phase and the KTM (Fig. 2). This makes these specimens important for providing new insights into the palaeobiogeographic distribution of pycnodontiform fishes in the context of global climatic changes.

2. Material and methods

The material comprises three more or less complete skeletons of a pycnodontiform fish (Fig. 3). Specimen GSUB V2302/1 and 2 consists of part and counterpart displaying most of the characters used to establish its systematic position and define it as a new taxon. Specimen GSUB V2303 represents a juvenile individual with soft-parts being preserved. The third and biggest specimen GSUB V2304 lacks the posterior part of the body and the caudal fin. All specimens were collected and prepared by private collector Udo Resch (Eichstätt), who became famous for his skills in preparing fossils (Hoffmann et al., 2020) and for important fossil finds of crustaceans and insects from the Upper Jurassic Solnhofen limestone in southern Germany that were exclusively collected by him and named after him and his parents (Schweigert, 2010; Winkler, 2017; Nagler et al., 2017; Bechly, 2019). The material for this paper is deposited in the Geosciences Collection of the University of Bremen, Germany (GSUB).

The specimens were prepared mechanically with the help of a Wild M2B microscope. They were subsequently either placed in oil emulsion or dusted with NH₄Cl prior to photography. The nomenclature used by many authors for describing dermal skull bones in actinopterygians follows the traditional (‘orthodox’) terminology for mammals and is not based on homology criteria. The difficulties in establishing homology and the great variability of dermal elements in the heads of actinopterygian fishes (see, for instance, Gregory, 1933) led to the publication of different names for the same bone and that are rather unintelligible (see also Schultze and Arsenault, 1985). Therefore, the terminology for the dermal head skeleton used in this study follows that of Jollie (1962) and Schultze (1993). The terminology for the caudal skeleton follows Arratia and Schultz (1992) as well as Schultze and Arratia (1986). The terminology for the squamation follows Poyato-Ariza and Wenz (2002, 2005). The phylogenetic relationships of the German pycnodont were explored using cladistic principles. The analysis in this study was conducted using Winclada software of Nixon (1999–2002) on a PC. Characters are mainly those of Poyato-Ariza and Wenz (2002, 2005), but all characters were scrutinized and are unweighted and unordered here.

2.1. Systematic palaeontology

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Cope, 1887
Series Neopterygii Regan, 1923
Order Pycnodontiformes Berg, 1937
Family Pycnodontidae Naurall, 1996a
Genus Njoerdichthys gen. nov.
Type species: Njoerdichthys dyckerhofti sp. nov.

Included species. Only the type-species is currently assigned to this genus.

Derivatio nominis. Named after the Germanic god “Njörd”, who navigates water and wind in German mythology, and from the Greek substantive “ichthyos” — fish.

Diagnosis. Pycnodontid fish with the following combination of characters: small to medium sized; trapezoid body outline; head profile oblique; parietal process absent; three dentalosplenial and two premaxillary chisel-shaped grasping teeth; three vomerine and prearticular teeth with serrated margin and a bicuspid-multicuspid apex; predorsal length/standard length 70%; dorsal and anal fins low and falcate; dorsal fin with 40 axonosts; dorsal ridge scales in close contact with each other and subtriangular with central apex; anal fin with 44 axonosts; ventral ridge scales with a single, blunt slightly posteriorly inclined spine; two postanal ridge scales; peltate squamation pattern; non-mosaic cloacal scale pattern without bifid scale; no post-anal notch; differentiated caudal pedicle; caudal fin low with concave trailing edge.

Taxonomic comparison. The new taxon can be readily differentiated from other pycnodontiform fishes by the following characters:

- Body form: Rhinopycnodus Taverne and Capasso, 2013a (elongated skull), Sylvienodus Poyato-Ariza, 2013 and Polazazzodus Poyato-Ariza, 2010 (ovoid), Joinvillichthys Taverne and Capasso,
2014a, 2014b (dorso-ventrally flattened, very elongated skull = rostrum), Coccodus Pictet, 1850 ( fusiform), Gladiopycnodus Taverne and Capasso, 2013b ( fusiform, elongated snout), Rostropycnodus Taverne and Capasso, 2013b ( very elongated snout), Acrorinchithys Taverne and Capasso, 2015a ( very angular dorsally), lemanna Wenz, 1989 ( elongated snout), Flagellipinna Cawley and Kriwet, 2019 ( rhomboid);

• no postparietal brush-like extension: Akromystax Poyo-Ariza and Wenz, 2005 (yes), Sylvienodus (yes), Rhinopycnodus (yes);
• no temporal opening: Akromystax (yes), Paranursallia Taverne et al., 2015 (yes)
• three chisel-shaped dentalosplenial teeth: Acrorinchithys (five), Akromystax (four), Flagellipinna (two), Gladiopycnodus (none), Macromesodon Blake, 1905 (four), Pankowskichthys Taverne and Capasso, 2014a, 2014b (two), Paranursallia (two), Polazodus (two), Sylvienodus (two), Tubemosophys Poyo-Ariza and Wenz, 2004 (two);
• two premaxillary teeth: Akromystax (eight), Sylvienodus (one), Rhinopycnodus (one), Pankowskichthys (none), Gladiopycnodus (none), Monocerichthys Taverne and Capasso, 2013b (none), Rostropycnodus (none), Polazodus (one), Nursallia tethysensis Capasso et al., 2006 (one);
• three dentalosplenial teeth: Acrorinchithys (five), Apomesodon gibbosus Wagner, 1851 (four), Akromystax (four), Nursallia tethysensis (two), Tubemosophys (two), Tricerichthys Taverne and Capasso, 2015b (one);
• three vomerine tooth rows: Polazodus (five), Coelodus Heckel, 1854 (five), Nursallia tethysensis (five);
• oval vomerine and prearticular tooth morphology with median ridge and serrated edges: Nursallia Blot, 1987 (circular/subcircular), Nursallia tethysensis (circular/subcircular with serrated edges and no median ridge), Coccodus (triangular), lemanna (reniform), Piranhamesodon Köhl-Ebert et al., 2018 (exterior cutting teeth and medial limpet-shaped cones);
• three prearticular tooth rows: Coccodus (two), Stenamara Poyo-Ariza and Wenz, 2000 (two), Damergouia Vullo et al., 2017 (two), Gyrodus Agassiz, 1833 (four), Brembudos Tintori, 1981 (five), Polgyrodus White, 1927 (five), Serrasalmimus Vullo et al., 2017 (one);
• no dermal cheek cover: Gyrodus (small bony scales covering cheeks) and Mesturidae Nursall, 1996b (irregular polygonal scales covering cheeks)
• peltate squamation pattern: Sylvienodus (clathrate), Joinvillichthys (imbricate), Pankowskichthys (imbricate), Gladiopycnodus (imbricate), Monocerichthys (imbricate), Polazodus (clathrate), Palaeobalistum orbiculatum de Blainville, 1818 (imbricate sensu stricto Nursall, 1996a, 1996b), Nursallia (peltate and scales extended also to the caudal region), Coccodus (no scales);
• anterior sagittal flanges of neural and haemal spines: Arduafrons Frickhinger, 1991 (no flanges), Gladiopycnodontidae Taverne and Capasso, 2013b (no flanges), Gyrodus (anterior and posterior), lemanna (anterior and posterior);
• maxillary bone with reniform outline: Sylvienodus and Polazodus (“ax-shaped”)
• no paurial (pa) or dermosupraoccipital (dso) spines: Pankowskichthys (nuchal = dso + pa), Monocerichthys (nuchal), Joinvillichthys (nuchal), Rostropycnodus (nuchal);
• curved, short paurial: Nursallia Blot, 1987 (curved, very broad), Gibbodon Tintori, 1981 (rectangular, long), Hayopercichthys Taverne and Capasso, 2015b (rectangular, long), Gyrodus (curved, long), Ducrotayichthys Taverne and Capasso, 2015b (short, broad);
• dorsal ridge scales: Monocerichthys, Pankowskichthys and Rostropycnodus (none);
• caudal fin with concave distal border: Nursallia (vertical), Gyrodus (forked), Mesturus (convex distal border), Pyncodus Agassiz, 1833 (double emarginated), Gebrayelichthys Nursall and Capasso, 2004 (narrow);
• no small spines on margin of dermosupraoccipital without small spines on margin: Piranhamesodon (spiny margin), Nursallia tethysensis (spiny margin).

Njoerichtys dyckerhoffi sp. nov.

Holotype. GSUB V2302 (Fig. 3A and B), part and counterpart of completely articulated, holomorphic specimen displaying characters of the cranial and postcranial skeleton, Paratypes are GSUB V2304 (Fig. 3C), which is the largest specimen and preserves the cranial and postcranial skeleton anterior to the medial fins, and a juvenile specimen represented by GSUB V2303 (Fig. 3D).

Diagnosis. As for genus by monotype.

Derivatio nominis. The species name is based on its occurrence in the Hohne working quarry of the Dyckerhoff AG company.

Type locality and stratum. Holotype came from bed 143 of the former Dyckerhoff AG quarry, Galgenknappp quarry. Paratype specimens were discovered in the Hohne working quarry of the Dyckerhoff AG, located west of Lengerich, Germany. Both localities form part of the Hessetal Formation. All specimens found in laminated marlstones (“black shales”).

Age. The holotype comes from the lower Turonian Mytiloides hattini inoceramid or Watinoceras devonense ammonite zone, respectively, as does paratype GSUB V2303. Paratype GSUB V2304 could also have been derived from the terminal Cenomanian Neocardioceras juddii ammonite Zone (Fig. 2).

Description.

General morphology. The three specimens assigned to Njoerichtys n. gen. differ in size and superficially also in the head profile (Fig. 3). However, the skull of specimen GSUB V2304 is disarticulated and the material was mechanically prepared so that the skull profile seems to be artificially rounded. Both specimens, GSUBV2302 (holotype) and GSUB V2304 agree in the orientation of the mouth gape, in the number of scale rows and autogenous neural spines, the morphology and number of dentalosplenial teeth, the morphology of vomerine and prearticular teeth, the number of vomerine and prearticular and tooth rows, morphology of arcocentra (as far as can be ascertained), and arrangement and morphology of sagittal flanges. Unfortunately, the ridge scales, which might also be a reliable character for specific identification, have been lost during preparation of GSUB V2304. The holotype GSUB V2302 is rather small with a standard length of only 4.2 cm, a head length measured from the tip of the snout to the posterior border of the cranium of 1.9 cm and a body height of 3.3 cm. The profile of the head is oblique. The outline of the body is trapezoid and the head length/body height ratio is 58%. There is no distinct dorsal prominence but a weakly developed dorsal apex, which corresponds to the anterior-most point of dorsal fin insertion. A distinct ventral apex is absent. The ventral margin of the body is almost horizontal and straight before the anal fin as seen in the holotype (GSUB V2302a, Fig 3a). The body tapers posteriorly to the caudal insertion points of the dorsal and anal fins, where the caudal peduncle begins, which is rather broad and distinct. A post-cloacal notch as found in several other pycnodontids is not present. The second specimen, GSUB V2304, is comparably larger but lacks the posterior portion of the body and all unpaired and pelvic fins. The antero-ventral part is disarticulated and the lower jaw elements have lost their connection with the skull. The dermal skull roof is lacking so that some endocranial elements are discernible. The head length/body height ratio is 58%. The rounded profile of the head is obviously a preparatory artefact.
Cranium: Both the dermato- and endocranium of *Njoerdichthys dyckerhoffi* sp. nov. are poorly preserved or disarticulated so that it is impossible to identify all elements unambiguously (Fig. 4). The ornamentation of the preserved dermal skull elements consists of reticulated ridges and subordinate small pits. The parietals (=frontals in the traditional nomenclature) are short and strongly arched above the orbits. The postparietals (=parietals in the traditional nomenclature) also are short and roughly triangular in outline. The median dermosupraoccipital sutures anteriorly the parietals and laterally the postparietals. The relationships of the postparietals and parietals to the dermopterotic-dermosphenotics complex, which forms the postero-dorsal margin of the orbit, are ambiguous because the latter elements are preserved only as very small bony fragments or imprints in the matrix.

The postparietal region is foreshortened but only fragments of the bony elements are preserved. A small bone in the postero-dorsal region of the dermocranium probably represents the dermosupraoccipital (Fig. 4). This bone is median, unpaired and slightly rectangular in outline. A brush-like, postparietal process (“post-parietal peniculus”) is absent and a temporal opening in the lateral wall of the dermocranium seems not to have been developed as indicated by the remaining bony fragments.

In all pycnodontiforms, the braincase is roofed dorsally by the rather large, median supraotic bone in the otico-occipital region, which consists of a slightly expanded base and a large ascending plate, which ends just beneath the dermal skull covering. The supraotic is a chondral bone that is found in only a few extinct neopterygians fishes, but which differs in pycnodont fishes in its general morphology (Maisey, 1999). It is very difficult to identify in the new taxon, but remains can be seen in GSUB V2302, where the overlying dermal elements are lacking. However, any details are obscured by preservation. Due to the poor state of preservation, other identifiable endocranial elements of the braincase also are difficult to identify. However, the paired exoccipitals, which are fused to some anterior dorsal neural arch elements to form a bony block (synarcual of Nursall and Maisey, 1991), can be seen in GSUB V2304 (Fig. 3E and F). This bony block surrounds the neural canal and might be a protecting element for the notochord during cranial elevation (Kriwet, 2005).

The opercular apparatus consists of operculum and preoperculum (Fig. 5). Sub- and interoperculum are absent as they are in all pycnodontiform fishes. The operculum is small and narrow, and situated at the dorso-posterior edge of the preoperculum (Fig. 5). The preoperculum is very elongated with a narrow dorsal and a
slightly expanded ventral portion. Both the operculum and pre-operculum are heavily damaged in all specimens and prevent further description or identification of sensory canals. The cheeks are not covered by any dermal elements as far as can be determined. There is only a single tubular infraorbital preserved in specimen GSUB V2302b and imprints of some more; the rest has been most likely lost post mortem. Unfortunately, it is not possible to ascertain their correct number or their ornamentation.

The long and slightly downward inflected parasphenoid is only partly preserved in GSUB V2304 but lacking in the holotype (Fig. 6). It is not possible to decide whether there is a fenestra in the complex ventral keel of the parasphenoid, which represents a synapomorphy of Pycnodontidae sensu Nursall (1996a).

The snout is supported by the anterior portion of the unpaired mesethmoid bone (Fig. 6), which is normally T-shaped in cross-section in pycnodontiforms. The plate-like posterior portion of the mesethmoid that generally envelops the anterior crest of the parasphenoid and the dorsal crest of the vomer in pycnodonts is lacking in the holotype and is only partially preserved in the paratype GSUB V2304.

**Jaw apparatus and dentition:** The jaw apparatus displays the general pycnodontiform pattern. Teeth-bearing elements are the unpaired vomer in the roof of the mouth, and the paired premaxillae, dentalosplenials, and prearticulars (Figs. 4 and 6). The maxillae are edentulous in pycnodontiforms and only a left, reniform maxilla is preserved in specimen GSUB V2302b partially covering the prearticular and coronoid process on the lower jaw.
The premaxillae are incompletely conserved in part and counterpart of the holotype. Most of the ascending premaxillary process is broken off, but it seems to have been rather long, covering major parts of the snout-covering mesethmoid. The tooth-bearing portion carries two elongated, incisiform grasping teeth (Fig. 7).

The vomer is partially visible in the holo- and paratype, where it bears three rows of distinctive teeth (Fig. 6). Lateral vomerine teeth have a sub-oval to rounded outline with antero-posteriorly directed long axes, a shallow median indent and a laterally displaced bicuspoid or slightly serrated crest. The two cusps of the crest are arranged antero-posteriorly. Laterally, the crest is accompanied by a faint, cingulum-like structure, which is wrinkled or weakly crenulated. Teeth of the principal row are also oval to suboval in outline with a central somewhat more blunt crest with two low antero-posteriorly directed apical indent that is laterally constricted. Teeth of the prearticulars are morphologically similar to those of the vomer. Lateral teeth also have a shallow, bicuspoid-multicuspid apex present on the smaller medial teeth (Fig. 8C) is not observed on N. tethysensis (Capasso et al., 2009). However, the central bicuspid-multicuspid apex present on the smaller medial teeth (Fig. 8C) is not observed on N. tethysensis (Capasso et al., 2009; fig. 6). This dental character, along with other characters (see “Taxonomic comparison”) clearly differentiate this taxa from N. tethysensis. The angular and articular form the posterior and postero-ventral part of the mandibular arch, but the suture between angular and articular is obscured (Fig. 8). The ornamentation of the lower jaw elements consists of slightly radiating ridges.

The left distorted dentalosplenial, which is preserved posterior to the left prearticular in GSUB V2304, is caudally elongated and simple without divergent branches (Fig. 9). It bears three chisel-shaped, grasping teeth. This is confirmed by the impression of the left dentalosplenial in the holotype (GSUB V2302a).

Girdles and paired fins: The pectoral and pelvic girdles are rather incomplete. The cleithrum exhibits the typical morphology for pycnodonts with a large, sub-rectangular, dagger-shaped, and rostrally curved ventral portion becoming narrower towards the supracleithrum (Fig. 5). The supracleithrum is splint-like but its connection to the posttemporal region of the skull is not preserved. The ornamentation consists of radiating ridges and grooves. The life position and morphology of the pectoral fin, which consists of at least ten rays, is very difficult to establish. The pelvic girdle and fins are not preserved.

Axial skeleton: There are about 18–19 vertebral elements, excluding those forming part of the caudal endoskeleton. Each arcocentrum is in contact with its anterior and posterior neighbours. The nature of the contact between arcocentra is ambiguous in the holotype, but there seem to be several interdigitating zygapophyses (Fig. 10). This observation is confirmed by observations in GSUB V2304. The haemal and neural arcocentra are expanded laterally to surround the notochord completely, especially in the postabdominal trunk. The neural and haemal spines are long and thin and bear anterior sagittal flanges, which, when well-preserved, are quite long, reaching far to the distal ends of the spines. The six anterior-most neural spines are separated from the neural arches (Fig. 5). The presence of autogenous spines is an exceptional condition of pycnodonts and their development is probably related to cranial kinesis (Nursall, 1996a).

Unpaired fins: The dorsal and anal fins are low, elongated and falcate with the dorsal fin being about 15% shorter than the anal fin (Fig. 3). The predorsal length/standard length ratio is 72% and the preanal length/standard length is 63% in the holotype. It is very difficult to establish the correct number of dorsal and anal pterygiophores, but there are about 40 dorsal and 44 anal elements supporting the fins. Two to three pterygiophores of the dorsal and anal fins are associated with one neural and haemal spine respectively. The caudal fin is poorly preserved as are the other fins. It is homocercal, rather small, with a concave trailing edge (Fig. 3).

The caudal exoskeleton consists of at least six dorsal procurent rays, about 25 principal fin rays, and several (seven?) ventral

![Fig. 7. Premaxilla of Njoerdichthys dyckerhoffi gen. et sp. nov., specimen GSUB V2302b. Abbreviation: pmx, premaxilla. Scale bar = 5 mm.](image-url)
procurent rays. The fin rays are segmented in a step-like fashion and distally branched. The ventral fin lobe has about as many rays as the dorsal one, but there is no distinct diastema dividing the caudal fin in an upper and lower lobe.

Uroneurals, epurals, and basal or fringing fulcra associated with the unpaired fins are absent, a general condition in pycnodontiforms.

Caudal endoskeleton: The caudal peduncle is short but distinct. Ossified vertebral centra are absent in the caudal endoskeleton, as in all pycnodontiforms. The identification and homology of hypochondral elements in pycnodontiforms is quite difficult (see Lambers, 1991, and Poyato-Ariza and Wenz, 2002, for discussion). The number of elements supporting the caudal fin rays is low, certainly not exceeding six. The endoskeleton, unfortunately, is too poorly preserved for a detailed analysis. Urodermals are not preserved in the specimens described here.

Squamation: The scale covering and ridge scales of *Njoerdichthys* gen. nov. are poorly preserved. The squamation corresponds to Nursall’s (1996a) peltate pattern, in which scales are restricted to the body in front of the dorsal and anal fin with complete ossified scales being limited to the antero-ventral trunk, whereas scale bars continue antero-dorsally. This character combination matches characters 75 [2] “ossification complete in ventral scales, incomplete in dorsal scales” and 76[3] “scales only in abdominal region” of Poyato-Ariza and Wenz (2002). There are eight dorso-ventral...
scale rows with the dorsal scales being reduced to thickened scale bars. The post-abdominal body is devoid of scales. It is not possible to identify the form of the scales. The ventral scales display a reticulated ornamentation.

The number of dorsal and ventral ridge scales is difficult to establish due to the poor preservation of the contours of the specimens. There are at least seven dorsal ridge scales, probably ten to 12 ventral, and two postanal scutes. All ridge scales are in close contact with each other. The dorsal ridge scales are subtriangular with a central, blunt, and low elevation (Fig. 11). The ventral ridge scales are very narrow, almost scutellum-like with a single, rather blunt and posteriorly directed spine in the ones preceding the cloacal notch. Other spines are absent.

**Cloaca:** The cloaca is characterized by modified scales in most pycnodontiforms with the exception of Mesturidae and bear systematic significant features (Nursall, 1996a; Poyato-Ariza and Wenz, 2002). The cloacal scale pattern of *Njoerdichthys* gen. nov. corresponds to the non-mosaic type without bifid scales sensu Poyato-Ariza and Wenz (2002: fig. 41). The anal notch is bordered anteriorly by at least two elongated, modified scales whereas the posterior border is marked by fragments of some (probably two) modified posterior scales and a rib (Fig. 12).

3. Discussion

3.1. Systematic position of *Njoerdichthys* gen. nov

The interrelationships of pycnodontiform fishes previously were analysed by Nursall (1996a), Poyato-Ariza and Wenz (2002, 2005), Kriwet (2004, 2005) and Ebert (2020). Nursall’s (1996a) hypothesis is based on proposed synapomorphies but does not included a cladistic analysis sensu stricto. The analyses of Poyato-Ariza and Wenz (2002, 2005), on the contrary, employed cladistic principles and used a data matrix including 33 taxa and 105 characters, 34 of which were processed as ordered. Ordering of characters is, nonetheless, arguable because this introduces a priori hypotheses that have to be explained independently. Conversely, all steps from one character to another have the same length when characters are treated as unordered.
The focus of the phylogenetic analyses presented in this study is focusing on the systematic position of the new pycnodontiform from northwestern Germany. We do not intend to present a new comprehensive phylogenetic hypothesis of pycnodontiform interrelationships including all previously newly described taxa (compare 'Taxonomic comparison'). Nevertheless, the taxonomy of pycnodontiforms is generally addressed because of new information derived from this study.

The phylogenetic analyses presented in this study are based mainly on the data matrix by Poyato-Ariza and Wenz (2002, 2004) with the addition of Scalacurvichthys (Cawley and Kriwet, 2018). Characters were scrutinized and some characters were re-coded, especially for Nursallia goedeli Heckel, 1854 and Palaeobalistum orbiculatum de Blainville, 1818 based on specimens housed in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich and the Museum für Naturkunde Berlin (see Appendix A). The outgroup composition of Poyato-Ariza and Wenz (2002) was used to polarise characters. Conversely to Poyato-Ariza and Wenz (2002) all characters are treated as unordered (Fitch parsimony) and unweighted. Three cladistic analyses were performed to determine the position of the German pycnodontiform based on slightly modified data matrices, to establish characters for the diagnosis and whether there are significant differences if the data matrix is altered. The new data matrices were analysed with the WinClada software program, version 1.00.08, on a PC. The following settings were employed: heuristic search, multiple TBR + TBR algorithm that searches for trees using tree bisection-recombination method of branch swapping with 1000 replications, DELTRAN optimization that puts changes on the tree as late as possible and initial MaxTrees setting was 30,000. Bootstrap option with 1000 replications was used to calculate the support of nodes. Specimens GSUB V2302 and GSUB 2304 were added to the data matrix (see Appendix B for characters and states as applied to Njoerdichthys). Specimen GSUB V2303 did not yield enough data for reconstructing its systematic position within Pycnodontiformes employing cladistic principles.

The first analysis is based on the original data matrix by Cawley and Kriwet (2018) treating all characters as unordered and excluding all uninformative characters (17 characters). This resulted in 88 characters and 37 taxa, of which 36 belong to the ingroup (Appendix C). Fig. 13 corresponds to the strict consensus tree of 26 equally parsimonious trees (MPTs) at 590 evolutionary steps. The consistency index (CI) of the MPTs is 0.43, the retention index (RI) is 0.47. The strict consensus tree has a length of 624 evolutionary steps, the CI is 0.40 and the RI is 0.47. The arrangement is similar to that of Poyato-Ariza and Wenz (2002) although significant differences are present (Fig. 13). According to the present analysis, the clade Pycnodontiformes is supported by two homoplastic and five apomorphic characters (two of these, several dermal supraoccipitals and a long, superficial premaxillary process are autapomorphies of the order as outlined in Poyato-Ariza and Wenz, 2002). For characters supporting the other nodes see Appendix D.
**Paramesturus** Taverne, 1981 is the most basal pycnodontiform. The rather basal position of *P. orbiculatum* in this analysis is, conversely, quite surprising. The bootstrap values are generally low with most clades collapsing. Best supported are only two clades. The first one is node V (*P. gutturosa* and *N. veronae*) with bootstrap support of 73. This node is supported by six homoplasies (Character 7. Caudal pedicle: [0] differentiated; Character 25. Morphology of premaxillary and dentary teeth: [2] robust, barely incisiform; Character 28. Morphology of vomerine teeth: [1] circular to subcircular contour; Character 37. Number of teeth on main prearticular tooth row: [2] eight or nine; Character 39. Crenulations in vomerine and prearticular teeth: [0] absent; Character 63. Distribution of scales: [2] eight or nine; Character 67. Ornamentation: [1] ridges; Character 70. First dorsal ridge scale: [1] about same size than subsequent ridge scales; Character 71. Scutellum-like contour scales: [2] present, ventral only).

In the second analysis, an additional character concerning the presence of branchial teeth was included in the data matrix. Kriwet (1999) reviewed the dental structures in the pharyngeal chamber of pycnodontiforms and considered these structures to be homologous to similar structures in teleosts. He also assumed that branchial teeth are absent in plesiomorphic pycnodontiforms, an assumption not fully supported by Poyato-Ariza and Wenz (2002), because of the presence of branchial teeth-like structures in *Gyrodus* (e.g. Lambers, 1991: fig. 11). These structures, however, are more likely gill rakers as found in a wide variety of actinopterygians. Poyato-Ariza and Wenz (2002) did not consider branchial teeth in their analysis because of the great morphological variation found within pycnodontiforms. We agree that there is variation in morphology and probably arrangement that needs further examination (compare Kriwet, 1999), but we do not concur with the statement that it is not possible to code the absence and presence of these structures in pycnodontiforms. We, however, included characters 39 (number of teeth in principal vomerine tooth row) and 46 (number of teeth on main prearticular tooth row) from the data matrix because the replacement and growth of teeth still is not fully understood, and we regard this character as being ambiguous.

The resulting data matrix thus consists of 87 characters. Fig. 14 corresponds to the strict consensus tree of 24 equally parsimonious trees (MPTs) at 577 evolutionary steps. The consistency index (CI) of the MPTs is 0.43; the retention index (RI) is 0.53. The strict consensus tree has a length of 597 evolutionary steps, the CI is 0.41 and the RI is 0.50. The hypothesis about pycnodontiform interrelationships resulting from this analysis has many differences from analysis 1 due to low resolution (Fig. 14) such as a sub-family Prosconetiinae is not supported. The bootstrap values are also generally rather low for this analysis and only four nodes are supported by more than 50%.

Node I (*Macromesodon macropterus* (Agassiz, 1834) + *Apomesodon surgens* (Poyato-Ariza and Wenz, 2002)) with a bootstrap support of 51 is supported by six homoplasies (Character 5. Mouth gape: [1] inclined; Character 39. Number of vertebræ: [0] 35 or more; Character 53. Morphology of the dorsal and anal fins: [4] rounded anteriorly; Character 56. Urodermals: [1] a series of three or more; Character 70. Number of differentiated dorsal ridge scales: [1] 18 or more; Character 87. Branchial teeth: [0] present). The *Njoerdichthys* specimens GSUB V2302 and GSUB V2304 which make up Node Y have the highest bootstrap support (96) and are supported by 12 homoplasies (Character 2. Relative position of dorsal apex: [2] in the point of insertion of the dorsal fin; Character 11. (Post) Parietal process: [0] absent; Character 28. Morphology of vomerine teeth: [3] reniform contour; Character 29. Number of vomerine tooth rows: [1] three; Character 32. Number of dentary teeth: [3] three; Character 36. Coronoid process: [2] high, club-shaped; Character 38. Groove on vomerine and prearticular teeth: [1] present; Character 60. Ossification of scales: [2] complete in ventral scales, incomplete in dorsal scales; Character 65. Ornamentation: [1] ridges; Character 68. First dorsal ridge scale: [1] about same size than subsequent ridge scales; Character 69. Scutellum-like contour scales: [2] present, ventral only).

![Fig. 13. Strict consensus tree depicting the systematic position of *Njoerdichthys dyckeri* gen. et sp. nov. based on the data matrix by Cawley and Kriwet (2018) where all characters are unordered and uninformative characters excluded.](image-url)
very broad; Character 25. Morphology of premaxillary and dentary teeth: [2] robust, barely incisiform; Character 37. Crenulations in vomerine and prearticular teeth: [0] absent; Character 44. Relative length of last neural spine not supporting precurrent caudal fin rays: [3] vestigial; Character 47. Number of hypochordal elements of caudal endoskeleton: [3] six to eight; Character 50. Position of dorsal fin (predorsal length/standard length): [2] 50%–59%; Character 58. Morphology of caudal fin: [6] vertical; Character 61. Distribution of scales: [2] abdominal region plus part of the caudal region; Character 87. Branchial teeth: [0] complete in ventral keel scales: [1] point contact; Character 79. Distribution of spines on ventral keel scales: [2] posterior region (at most two thirds) of the midline and 1 apomorphy (Character 69. Scutellum-like contour scales: [1] present, dorsal only).

This result shows that branchial teeth alone are not an informative character to be included in a phylogenetic analysis of pycnodont fishes. Additional characters exploring the range of morphologies in branchial teeth may be what is needed to produce higher resolution in future phylogenies.

Resolution gets better when all uninformative characters, the characters on the number of teeth in the main vomerine and prearticular tooth rows and the character concerning the branchial teeth are excluded from the original data matrix (Analysis 3). Fig. 15 corresponds to the strict consensus tree of 8 equally parsimonious trees (MPTs) at 568 evolutionary steps. The consistency index (CI) of the MPTs is 0.43; the retention index (RI) is 0.53. The strict consensus tree has a length of 568 evolutionary steps, the CI is 0.43 and the RI is 0.53. The arrangement of taxa is more similar to that of Analysis 1 but with important differences (Fig. 15). The bootstrap values for most clades are smaller than 50% as in both previous analyses. Exceptions include Node D1 (Oropycnodus + Pycnodus: 50), Node O (Coccodus + Ichthyoceros Gayet, 1984: 54), Node Y (Njoerdichthys; 91) and Node E1 (P. gutturosa + N. veronae: 76).

The homoplasies supporting each node are: **Node D1:** Character 10. Dermocranial fenestra: [1] present, Character 14. Endocranium posteriorly exposed: [1] yes, Character 19. Preopercular and hyomandibular: [4] preopercular of similar size to expanded superficial ornamented portion of hyomandibular; Character 41. Neural and haemal adjacent arcocentra: [2] complex contact, Character 45. Number of hypochordal elements of caudal endoskeleton: [1] six to eight, Character 50. Oscification of scales: [3] incomplete in all scales, Character 57. Number of differentiated dorsal ridge scales: [4] seven to nine, Character 60. Ossi-
(e.g., ordered versus unordered). The rather low indices in our analyses easily can be enhanced by, e.g., character ordering. This, however, introduces assumption a priori before these characters are adequately analysed.

The character combination of *Njoerdichthys* gen. nov. places the new taxon unambiguously into the crown group of Pycnodontidae. Poyato-Ariza and Wenz (2002) identified a single autapomorphic character of Pycnodontidae, the presence of a postparietal brush- or peniculus-like process. The new taxon from northwestern Germany differs in the absence of such a structure from all pycnodontids. No specimens display any remains of a brush-like process behind the occipital region. We nevertheless found several homoplastic and apomorphic characters supporting this clade (see Figs. 13–15, Appendix D) and other pycnodontids such as *N. tethysensis*, *Paranursallia spinosa* and *P. gutturosa* also lack this structure (Capasso et al., 2009; Taverne et al., 2015) which suggest this feature being secondarily lost.

Several new pycnodontiform fish taxa were described since the work of Poyato-Ariza and Wenz (2002) (e.g., Kriwet, 2004; Poyato-Ariza and Wenz, 2005; Poyato-Ariza, 2013; Taverne and Capasso, 2013a, b, 2014a, b, 2015a, b, 2018a, b; Taverne et al., 2015, 2019; Cawley and Kriwet, 2019). These taxa were not included in the phylogenetic analysis here, because we did not intend to alter the original taxon composition too much but to establish the position of *Njoerdichthys* gen. nov. for which the additional taxa were unessential. Important differences between *Njoerdichthys* gen. nov. and these taxa are provided in the ‘Taxonomic comparison’ section above.

3.2. Palaeogeographic distribution of Cretaceous pycnodontiforms

Articulated skeletal remains of Late Cretaceous pycnodontiforms are comparably rare and occur mostly in Conservation Lagerstätten. Famous localities, where complete or disarticulated pycnodontiform skeletons were recovered, are:

- Laveiras (Cenomanian) in Portugal (*Sylvienodus*; Poyato-Ariza, 2013).
- Jebel Tselfat (Cenomanian–Turonian) (*Paranursallia gutturosa*; Arambourg, 1954; Khalloufi et al. 2010) and the Agoult Lagerstätte (Cenomanian–Turonian) (*Pycnodontidae sensu Nursall, 1996a; Murray et al. 2013) in Morroco.
- Haqel and Hajula (upper Cenomanian) and Namoura (middle Cenomanian) in Lebanon (*Gebrayelichthyidae, Gladiopycnodontidae, Rhinopycnodus, Acrorhinichthys, Flagellipinnia, Cocodus, Paracocodus, Coruscithys, Libanopycnodus, Sigma-pycnodus, Haqelpycnodus, Hensodon, Ichthyoceros, Nursallia, Palaeobalistum, and Trevawasia*; Pictet, 1850; Davis, 1887; White and Moy-Thomas, 1941; Gayet, 1984; Forey et al., 2003; Kriwet, 2004; Nursall and Capasso, 2004, 2008; Capasso et al., 2009; Taverne and Capasso, 2013a, b, 2014a, b, 2015a, b, 2018a, b).
- Sussex (Cenomanian–Campanian) in southern England (*Anomoeadus pauciseriale, Anomoeadus willeti*; Woodward, 1893, 1895, 1909; Kriwet, 2002).
- Nardò (Campanian–Maastrichtian) in Italy (*Pseudopycnodus nardoensis*; Taverne, 1997).
Europe with Austria being the furthest eastward occurrence of their occurrence from these localities relating to the Western Tethys and previous studies (Kolodny and Raab, 1988; Kolodny and Luz, 1991; Lécu,

\[C_{19}/C_{15}\]

of Neoproscinetes and lemanja (Brito and Yabumoto, 2011). This was also a time of high species numbers of pycnodonts being recorded in North America with Kansas being the most northerly occurrence recorded for the group so far (Lane, 1944). The Late Cretaceous, beginning with the Cenomanian, witnesses further expansion eastwards for the pycnodonts as they appear in high diversity and disparity in Lebanon, displaying their highest disparity in their evolutionary history (Marrama et al., 2016; Cawley and Kriwet, 2019). They also migrated further south, where pycnodonts occurred in what now is Croatia, Tunisia, Egypt, Ecuador and Brazil (Agassiz, 1833–1844; Weiler, 1935; Leonardi, 1966; Kriwet, 2001a, c; Machado and Brito, 2006; Taverne et al., 2015). This is by far the widest range in the distribution of pycnodonts during the Cretaceous. Their ranges shrink slightly progressing into the Turonian with no representatives in Asia, but their numbers in Europe being still strong.

The most interesting change that can be seen is that Njoerdichthys gen. nov. from Lengerich is, so far, the most northerly record of pycnodontiforms recorded in the Cretaceous. This northward expansion can be convincingly explained to be triggered by peak surface water temperature in the course of the KTM (Fig. 2, Fig. 16; Huber et al., 2018) at a very high sea level with wide, interconnected shelf areas (maximum flooding of DS Ce-Tu 1 sensu Wilsen, 2003).

However, because the occurrence of articulated Njoerdichthys gen. nov. is restricted to black shale horizons at Lengerich, it could be argued that this reflects rather a taphonomic window instead of a preference to warm water conditions. However, teeth or jawbones of pycnodontid fish are fairly massive and resistant and have a high potential of being preserved in marl- or limestone - the sedimentary rocks forming a large part of the succession. As an example serves the occurrence of the massive teeth of the durophagous Neoselachian Ptychodus. Only a single articulated specimen was recorded from black shales of the Hesseltal Formation (Müller, 2008), but its isolated teeth can often be found in Cenomanian–Turonian strata throughout northern Germany (Löschker, 1910; Kemper, 1976; Kruckow, 1979; Breitkreuz et al., 1991; Wittler and Roth, 2003, 2004; Müller, 2008; Diedrich, 2013). This is not the case in Njoerdichthys gen. nov. One of us (JL) sieved many hundred microfossil samples from Lengerich and adjacent areas, also from intervals without black shales, but not a single pycnodontid tooth was encountered.

Going into the Cenomanian and continuing in the Santonian, their range is reduced to just southern Europe and southern regions of North America (Heck, 1854; Everhart, 2007; Poyato-Arzia, 2010; Cronin and Shimada, 2019). The Campanian sees a further northward expansion of pycnodontiforms as Anomoedus subclavatus is recorded in Kristianstad Basin, Sweden (Davis, 1890; Siverson, 1992). Within the Kristianstad Basin, it is located in the Belemnlocamax balsvikensis belemnite biobzone (lowermost upper Campanian) of the Åsen assemblage (Christensen, 1975; Bazzi et al., 2015). While there is a general trend of climatic cooling during

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the Campanian—Maastrichtian, a small rise in sea temperature can be observed in lower mid palaeolatitudes during the early late Campanian (see fig. 8 in O’Brien et al., 2017) and a warm temperate to subtropical climate (Surløy and Christensen, 1974; Surløy and Sørensen, 2010; Sørensen et al., 2013) is recorded at Kristianstad Basin. Additionally, the shallow marine deposits of the Kristianstad Basin indicate a coastal environment with a diverse assemblage of marine macroinvertebrates such as bryozoans, brachiopods, bivalves and echinoids (Surløy and Christensen, 1974; Sørensen and Surløy, 2008; Surløy and Sørensen, 2010; Sørensen et al., 2012); suitable habitat and prey for a pycnodontiform fish. In the Maastrichtian, the range of pycnodonts expands further south from Europe to cover South America (Argentina) and especially Africa (Morocco, Niger, DRC) (Dartevelle and Casier, 1949; Arambourg, 1954. Les poissons Crétacés du Jebel Tselfat (Maroc). Notes et Mémoires du Service Géologique du Maroc, 10, 164–322; Arambourg, 1952; Wenz, 1969; Cappetta, 1972; Cione, 1977; Vullo et al., 2017). Pycnodontiforms are a lineage whose distribution appears to concur with changes in global temperatures where occurrences in high latitudes correlate with high temperatures at that time in Earth’s history. This is a pattern that can also be seen in crocodyliforms and their ancestors (Markwick, 1998; Mannion et al., 2015), non-marine turtles (Nicholson et al., 2015, 2016), birds (Mayr, 2009; Stidham and Eberle, 2016), primates (Smith et al., 2015), freshwater teleosts during the Cenozoic reveals that tropical lineages are present in higher latitudes during the early Turonian when temperatures worldwide were at their highest during the Mesozoic. This, in combination with general Cretaceous pycnodontiform occurrence patterns and along with the discovery of Anomoeodus subclavatus in the Kristianstad Basin of Sweden during the early late Campanian, when temperatures were increasing again is additional evidence that pycnodont fishes expand their ranges into higher latitudes when the climate becomes warmer and that climate has played an important role in their distribution through time. This suggests that climatic conditions might have been major drivers for pycnodontiform distribution patterns.

4. Conclusion

Njerjerdithys dyckerhoffi gen. et sp. nov. is significant for two reasons: First, despite lacking a postparietal process, it is still found to be a member of the Pycnodontidae, particularly Nursallinae, but this subfamily was shown to be paralyptic and future phylogenetic work will test the validity of this subfamily more rigorously. The second finding is that Njerjerdithys dyckerhoffi gen. et sp. nov. was found to exist in marine environments at high latitudes during the early Turonian when temperatures worldwide were at their highest during the Cretaceous. This, in combination with general Cretaceous pycnodontiform occurrence patterns and along with the recovery of Anomoeodus subclavatus in the Kristianstad Basin of Sweden during the early late Campanian, when temperatures were increasing again is additional evidence that pycnodont fishes expand their ranges into higher latitudes when the climate becomes warmer and that climate has played an important role in their distribution through time. This suggests that climatic conditions might have been major drivers for pycnodontiform distribution patterns.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2020.104590.