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

John Cawley [a,*], Jens Lehmann [b], Frank Wiese [c], Jürgen Kriwet [a]

[a] University of Vienna, Geozentrum, Department of Palaeontology, Althanstr. 14, 1090 Vienna, Austria
[b] University of Bremen, Faculty of Geosciences, Geosciences Collection, Klagenfurter Str. 4, 28359 Bremen, Germany
[c] Georg-August-Universität Göttingen, Department of Geobiology, Geoscience Centre, Goldschmidtstr. 3, 37073 Göttingen, Germany

ABSTRACT

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 homoplastic 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 *Anomoeodus subclavatus* in the Campanian of Sweden.

© 2020 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

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 Fossillagerstätte of the late Campanian Baumberge Formation. However, there is a second Upper Cretaceous Fossillagerstätte 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 *Berycopsis*, *Cimolichthys*, Clupeiformes indet., *Enchodus*, *Hoplopteryx*, ?*Osmeroides*,

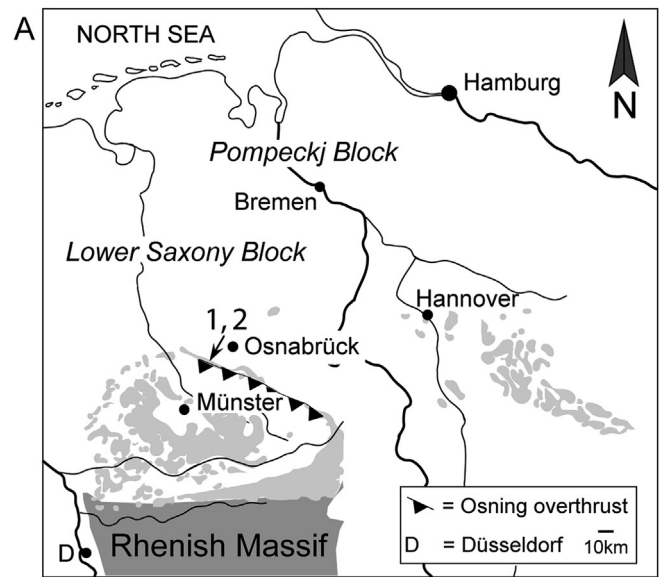Pynodontiformes indet., *Pycnodus*, Teleostei indet., and *Xiphactinus* (Wittler, 1995; Wittler and Roth, 2003, 2004). Moreover, the Hesseltal Formation provided also three specimens of a yet undescribed, new form of pycnodontiform fish from the lower Turonian *Mytiloides hattini* inoceramid zone of 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; Martín-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., Trabucho-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 its 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;

Localities at Lengerich 1*: Dyckerhoff, active quarry 2*: Galgenknapp, protection reserve
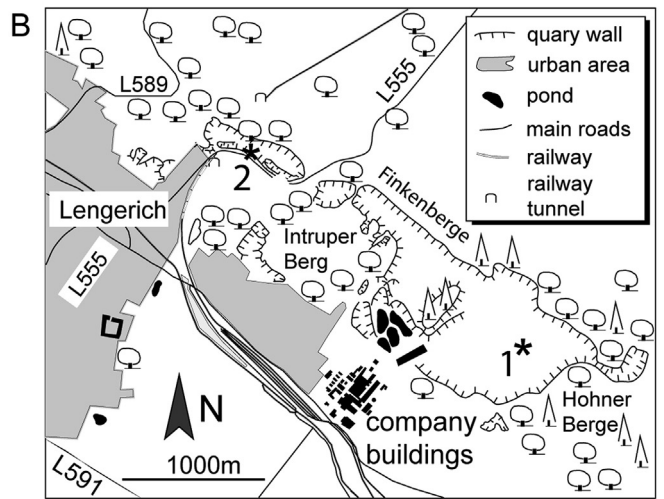
Fig. 1. Map showing the localities within Lengerich where the specimens of *Njoerdichthys dyckerhoffi* gen. et sp. nov. were collected. A, map of Northern Germany with Late Cretaceous outcrop and indicating the position of Lengerich, tectonic units in italics. B, map of Lengerich showing the two fossil quarries where *Njoerdichthys* gen. nov. was collected.

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
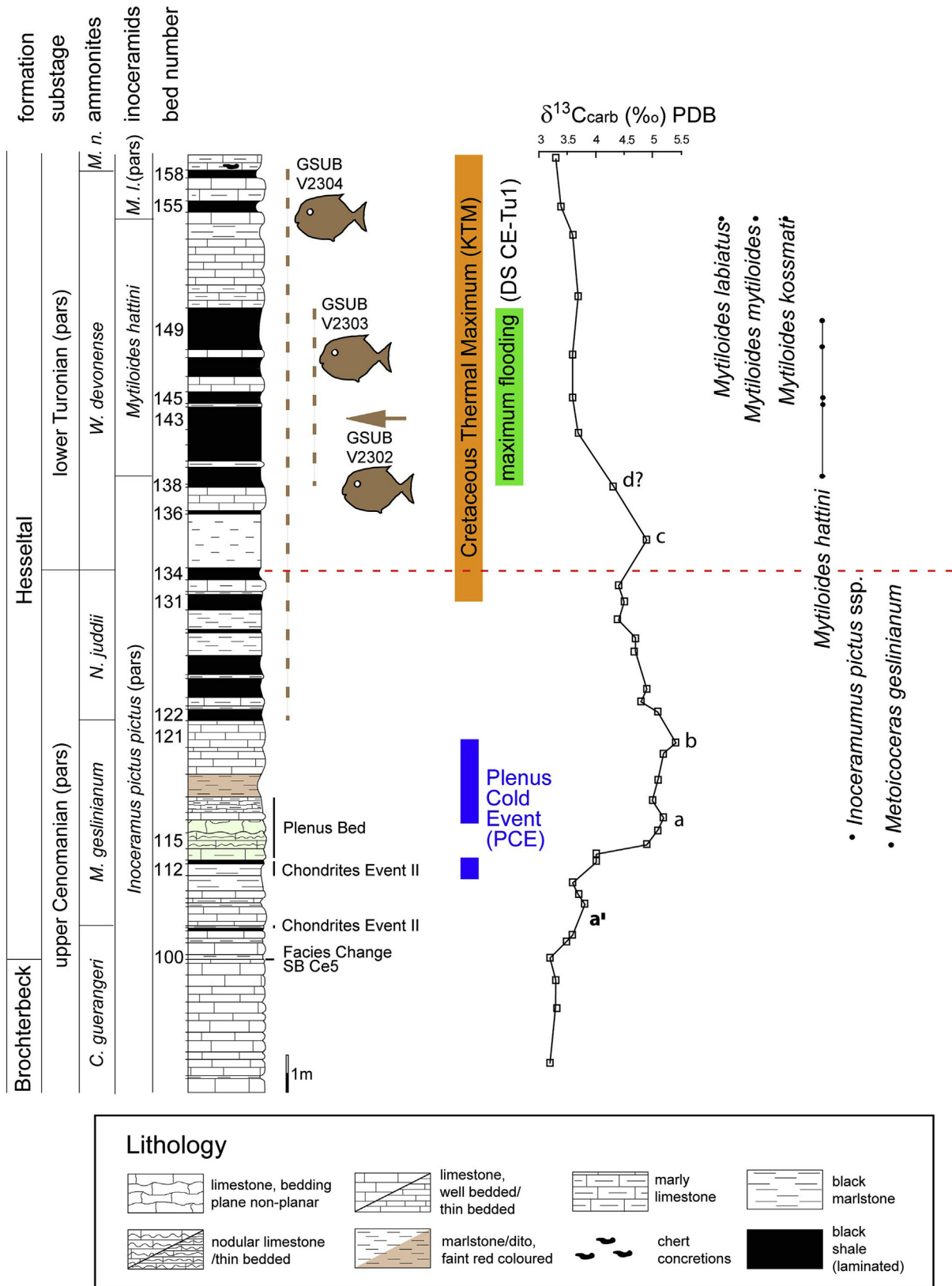
Fig. 2. Measured section of the Lengerich localities with litho- and bio-stratigraphic subdivision, ammonite and inoceramid record, mfs and $\delta^{13}C$ curve after Lehmann (1999) where specimens of *Njoerdichthys dyckerhoffi* gen. et sp. nov. were collected. The measured section is based on the active Hohne working quarry of the Dyckerhoff AG (number 1 in Fig. 1). Ammonites zones: *C. guerangeri = Calycoceras guerangeri*, *M. geslinianum = Metoicoceras geslinianum*, *N. juddii = Neocardioceras juddii*, *W. devonense = Watinoceras 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 $\delta^{13}C$ curves, ammonite and inoceramid zonations were plotted against the $\delta^{13}C$ 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'Brian 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-termed but severe cooling pulse interrupted progressive warming in the late Cenomanian *Metoicoceras geslinianum* ammonite Zone (Jefferies, 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 $\delta^{13}C$ curve, the Plenus Cold Event is positioned between subordinate isotope marker 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 MZ8 microscope. They were subsequently either placed in oil emulsion or dusted with NH_4Cl 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 Schultze (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** Nursall, 1996a

Genus *Njoerdichthys* gen. nov.
Type species: *Njoerdichthys dyckerhoffi* 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 "ιχθύος", "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 tooth rows; 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 *Polazzodus* 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), *Acrorhinichthys* Taverne and Capasso, 2015a (very angular dorsally), *Iemanja* Wenz, 1989 (elongated snout), *Flagellipinna* Cawley and Kriwet, 2019 (rhomboid);

- no postparietal brush-like extension: *Akromystax* Poyato-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: *Acrorhinichthys* (five), *Akromystax* (four), *Flagellipinna* (two), *Gladiopycnodus* (none), *Macromesodon* Blake, 1905 (four), *Pankowskichthys* Taverne and Capasso, 2014a, 2014b (two), *Paranursallia* (two), *Polazzodus* (two), *Sylvienodus* (two), *Turbomesodon* Poyato-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), *Polazzodus* (one), *Nursallia tethysensis* Capasso et al., 2009 (one);
- three dentalosplenial teeth: *Acrorhinichthys* (five), *Apomesodon gibbosus* Wagner, 1851 (four), *Akromystax* (four), *Nursallia tethysensis* (two), *Turbomesodon* (two), *Tricerichthys* Taverne and Capasso, 2015b (one);
- three vomerine tooth rows: *Polazzodus* (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), *Iemanja* (reniform), *Piranhamesodon* Kölbl-Ebert et al., 2018 (exterior cutting teeth and medial limpet-shaped cones);
- three prearticular tooth rows: *Coccodus* (two), *Stenamara* Poyato-Ariza and Wenz, 2000 (two), *Damergouia* Vullo et al., 2017 (two), *Gyrodus* Agassiz, 1833 (four), *Brembodus* Tintori, 1981 (five), *Polygyrodus* 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), *Polazzodus* (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), *Iemanja* (anterior and posterior);
- maxillary bone with reniform outline: *Sylvienodus* and *Polazzodus* ("ax-shaped")
- no parietal (pa) or dermosupraoccipital (dso) spines: *Pankowskichthys* (nuchal = dso + pa), *Monocerichthys* (nuchal), *Joinvillichthys* (nuchal), *Rostropycnodus* (nuchal);
- curved, short parietal: *Nursallia* Blot, 1987 (curved, very broad), *Gibbodon* Tintori, 1981 (rectangular, long), *Hayolperichthys* 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), *Pycnodus* 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).

Njoerdichthys 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, Galgenknapp 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 Hesseltal 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 *Njoerdichthys* 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, GSUB V2302 (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 postcloacal 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.
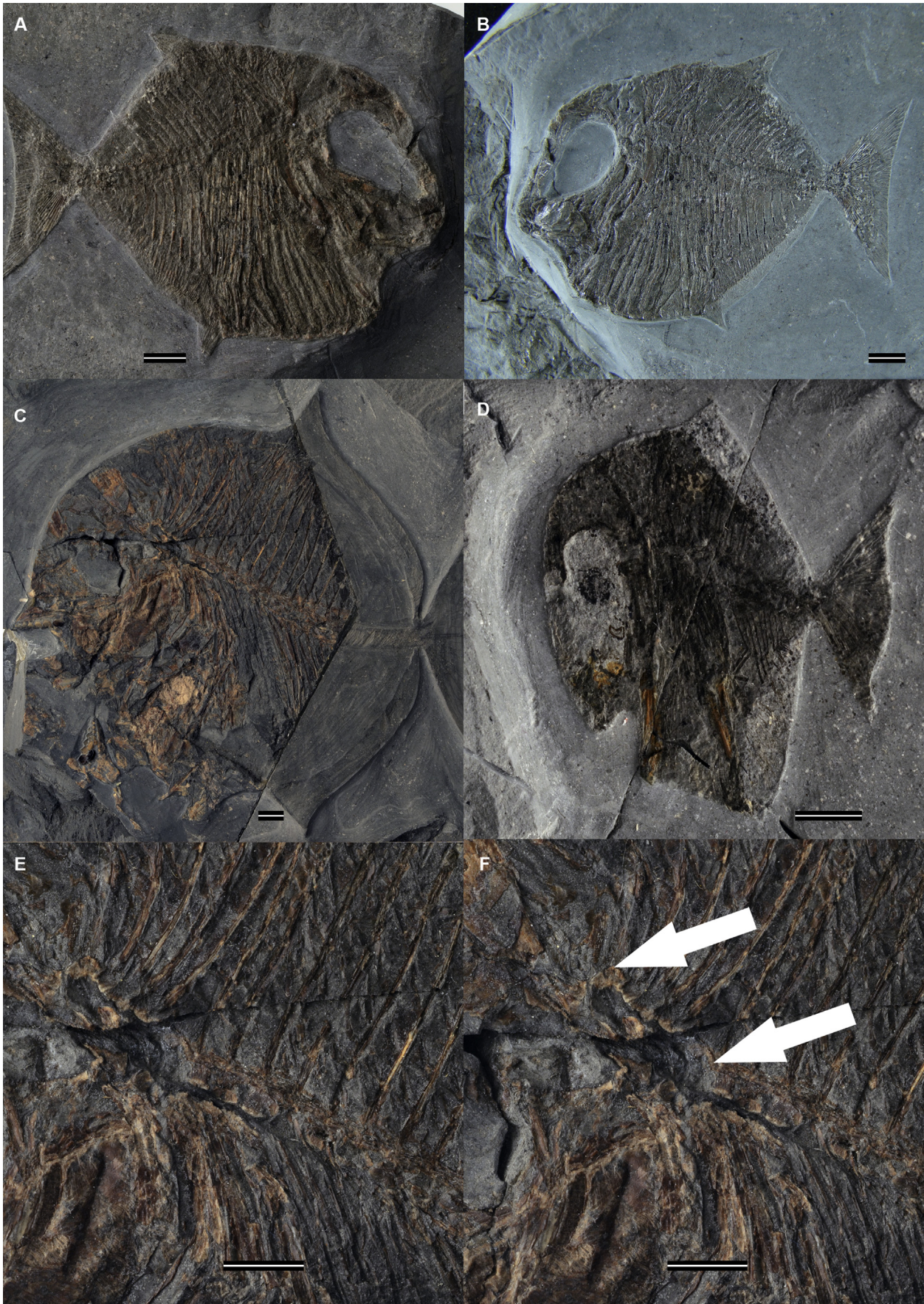
Fig. 4. Skull roof and jaw apparatus of *Njoerdichthys dyckerhoffi* gen. et sp. nov., GSUB V2302. Abbreviations: ang, angular; art, articular; dps, dermopterosphenotic; dso, dermo-supraoccipital; mx, maxilla; pa, parietal; pp, postparietal; prart, prearticular. Scale bar = 5 mm.

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 posterodorsal region of the dermatocranium 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 dermatocranium 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

Fig. 3. Specimens of *Njoerdichthys dyckerhoffi* gen. et sp. nov., under study. A, Holotype specimen GSUB V2302a. B, Holotype specimen counterpart GSUB V2302b. C, GSUB V2304. D, GSUB V2303, juvenile specimen. E, Synarcual located behind the cranium of *Njoerdichthys dyckerhoffi* gen. et sp. nov., GSUB V2304. F, Close up of GSUB V2304 where the synarcual is more clearly seen and is indicated by the large arrows. Scale bar = 5 mm.

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

Fig. 5. Opercular apparatus and pectoral girdle of *Njoerdichthys dyckerhoffi* gen. et sp. nov., specimen GSUB V2302. Abbreviations: cl, cleithrum; dhyo, dermohyomandibula; op, opercular; pop, preopercular; scl, supracleithrum. Scale bar = 5 mm.
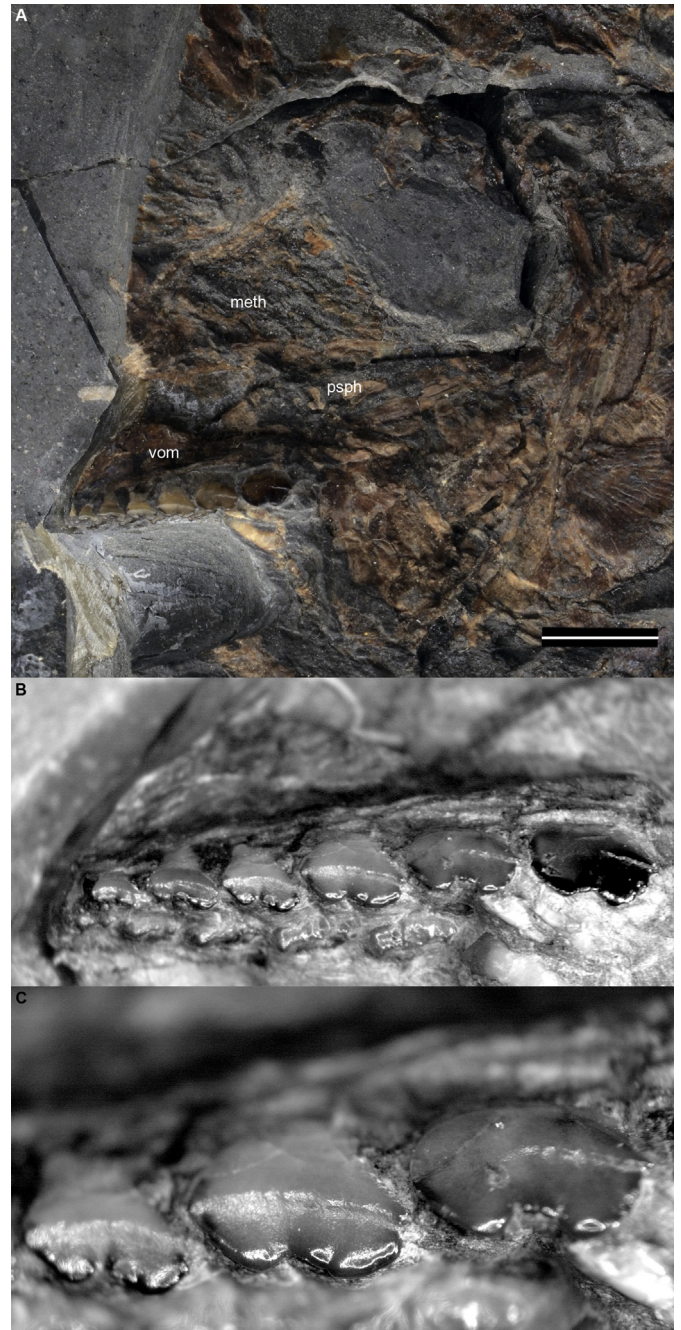

Fig. 6. *Njoerdichthys dyckerhoffi* gen. et sp. nov., specimen GSUB V2304. A, Associated upper jaw and hypertrophied mesethmoid. B, Close up of vomer. C, Close up of posterior lateral teeth of vomer showing the bicuspid apex characteristic of this taxon. Abbreviations: meth, mesethmoid; psph, parasphenoid; vom, vomer. Scale bar = 5 mm.

(Fig. 4). 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 bicuspid 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 arranged apices, which is surrounded by a very narrow groove with serrated margins. The indent of the two crest cusps is slightly incised.

The lower jaws are conspicuously short and consist of paired pre-articular, angular, and articular bones, as well as dentalosplenials (Figs. 8 and 9). The prearticulars are the most massive lower jaw elements and exhibit a well-developed and club-shaped lateral coronoid process, which is the site of insertion of the mandibular musculature (Fig. 8). Both prearticulars are slightly disarticulated in GSUB V2302b and exhibit a long and straight symphysis, where both prearticulars where sutured medially during life. The preservation and surface structure of the symphysis indicate that the prearticulars where not tightly fixed but some mobility probably was present. The teeth of the prearticulars are morphologically similar to those of the vomer. Lateral teeth also have a shallow, antero-posteriorly directed apical indent that is laterally confined by a crest with accentuate and posteriorly displaced apices. Median teeth are more oval in outline with a central bicuspid-multicuspid apex that is accompanied by a narrow rim with wrinkled margin. The long-axes of the lateral and median teeth are arranged perpendicular to the long-axis of the prearticular. Medial teeth are significantly smaller, have antero-posteriorly arranged long-axes

Fig. 7. Premaxilla of *Njoerdichthys dyckerhoffi* gen. et sp. nov., specimen GSUB V2302b. Abbreviation: pmx, premaxilla. Scale bar = 5 mm.

and display the same morphology and ornamentation as the central teeth. The prearticular teeth, particularly those of the most posterior lateral row are very similar in morphology to that seen in *Nursallia 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).

Visceral skeleton: Elements of the visceral skeleton are very poorly preserved and most bones are not identifiable. According to the available information, the hyomandibula is elongated and oriented obliquely with respect to the braincase. Generally, it is tightly fixed to the medial surface of the overlying preoperculum supporting the latter in pycnodonts. As far as can be established, the upper part of the hyomandibula is exposed above the preoperculum (Fig. 5). More information is, unfortunately not available. Branchial teeth as observed in several other pycnodonts (for review see Kriwet, 1999 and Poyato-Ariza and Wenz, 2002) are not preserved.

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 narrow 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 procurrent rays, about 25 principal fin rays, and several (seven?) ventral

Fig. 8. Lower jaw of *Njoerdichthys dyckerhoffi* gen. et sp. nov., specimen GSUB V2304. A, Lower jaw. B, Posterior lateral prearticular teeth showing the serrated margins and concave occlusal surface. C, Posterior median teeth with the characteristic raised bicuspid-multicuspid apex. Abbreviations; ang?, angular?; art?, articular?; prart, prearticular. Scale bar = 5 mm.

procurrent 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 hypochordal 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
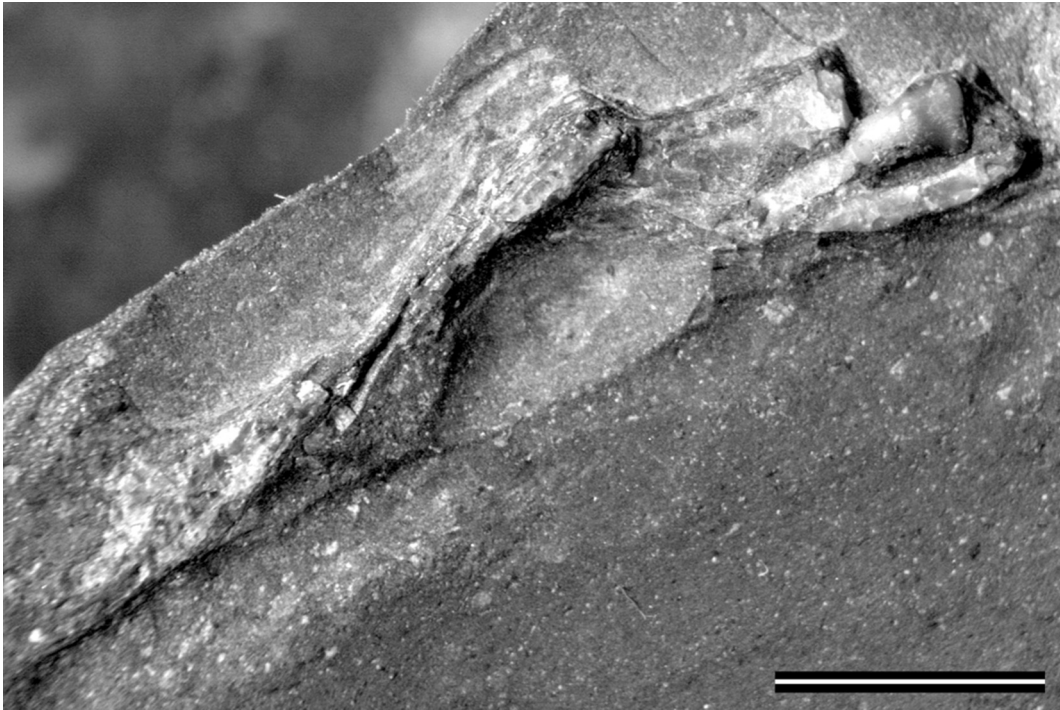
Fig. 9. Dentalosplenial of *Njoerdichthys dyckerhoffi* gen. et sp. nov., specimen GSUB V2304. Scale bar = 5 mm.

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.

Fig. 10. Axial skeleton showing the hyper-complex contact between adjacent arco-centra of *Njoerdichthys dyckerhoffi* gen. et sp. nov., specimen GSUB V2304. Scale bar = 5 mm.

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.
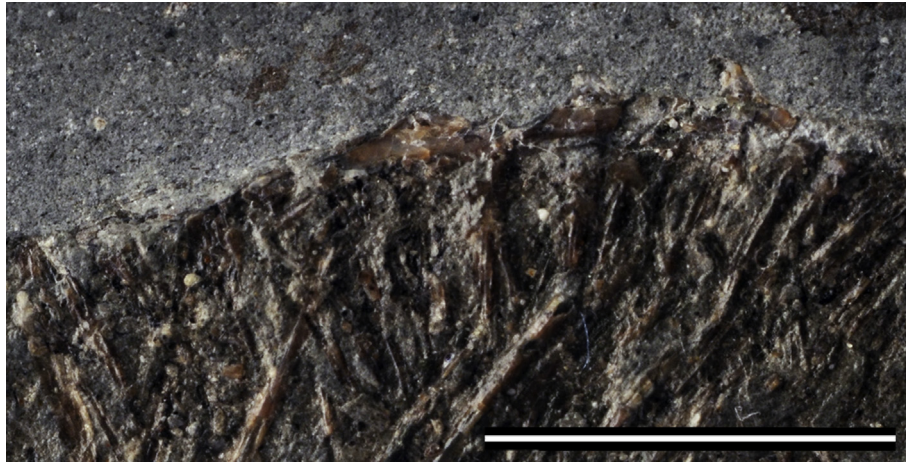
Fig. 11. Dorsal ridge scales of *Njoerdichthys dyckerhoffi* gen. et sp. nov., specimen GSUB V2302b. Scale bar = 5 mm.

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.

Fig. 12. Cloacal region of *Njoerdichthys dyckerhoffi* gen. et sp. nov., specimen GSUB V2302. Abbreviations: amcs, anterior modified cloacal scales; pmcs, posterior modified cloacal scales. Scale bar = 5 mm.

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.
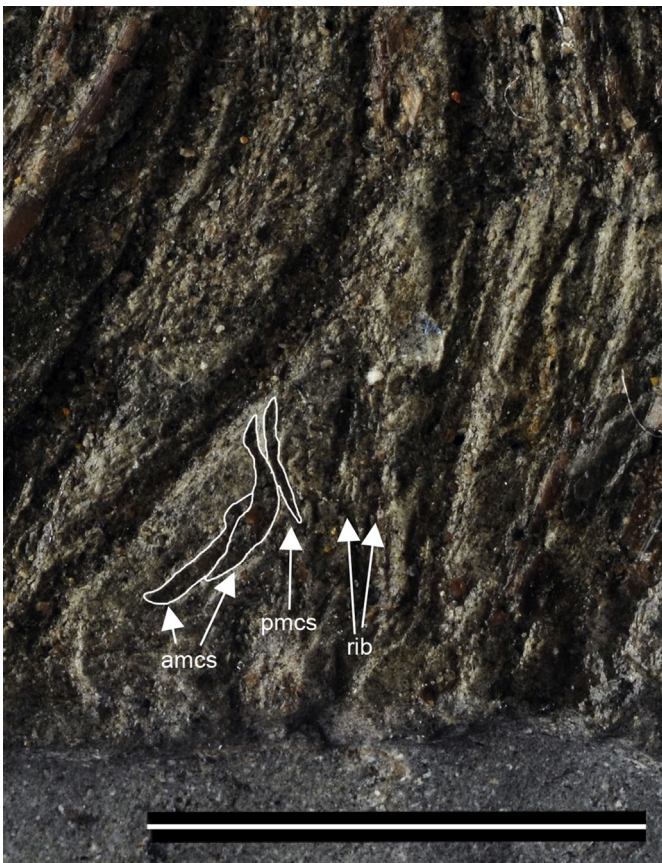
Paramesturus Taverne, 1981 is the most basal pycnodontiform. The rather basal position of *P. orbiculatum* in this analysis is, conversely, quite surprising. The bootstrap values are generally low with most clades collapsing. Best supported are only two clades. The first one is node V (*P. gutturosa* 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] abdominal region plus part of the caudal region) and one apomorphy (Character 8. Morphology of parietal bones: [3] curved and very broad) Node X containsthe two *Njoerdichthys* specimens with

a bootstrap value of 83 and are supported by four homoplasies (Character 40. Groove on vomerine and prearticular teeth: [1] present; 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 also excluded 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 Proscinetinae 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 vertebrae: [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; Character 87. Branchial teeth: [1] absent). Node Z (*P. gutturosa* + *N. veronae*) with a bootstrap support of 81 is supported by 11 homoplasies (Character 2. Relative position of dorsal apex: [2] in the point of insertion of the dorsal fin; Character 7. Caudal pedicle: [0] differentiated; Character 8. Morphology of parietal bones: [3] curved and
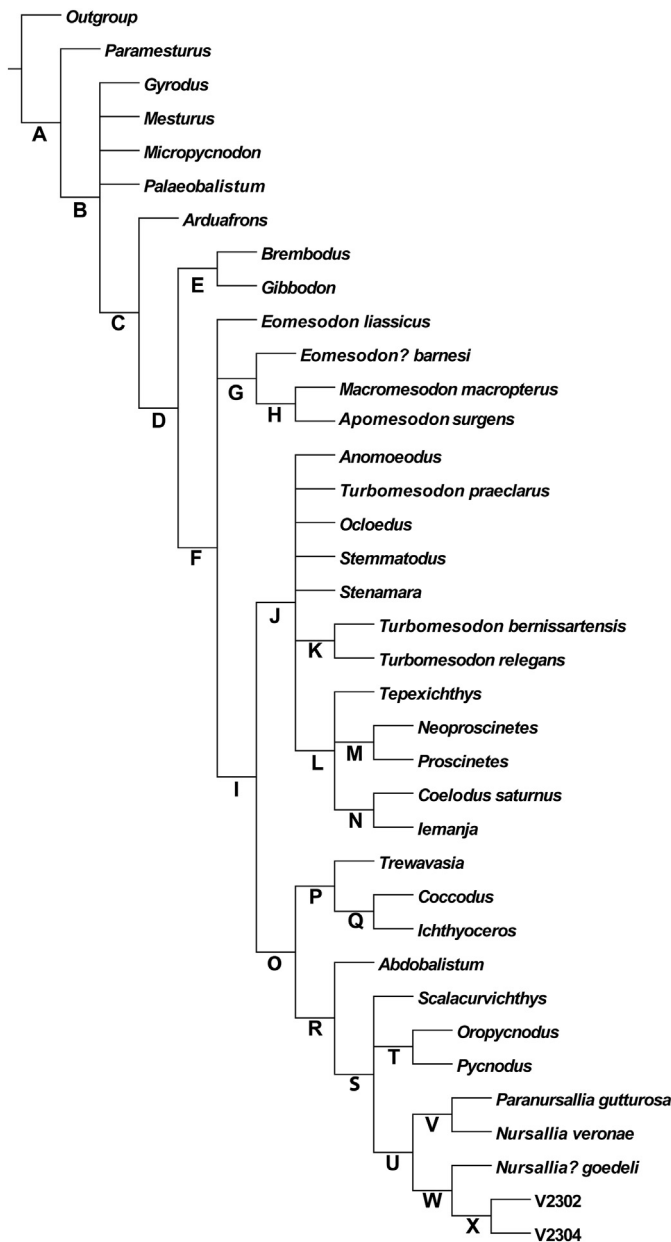

Fig. 13. Strict consensus tree depicting the systematic position of *Njoerdichthys dyckerhoffi* gen. et sp. nov. based on the data matrix by Cawley and Kriwet (2018) where all characters are unordered and uninformative characters excluded.
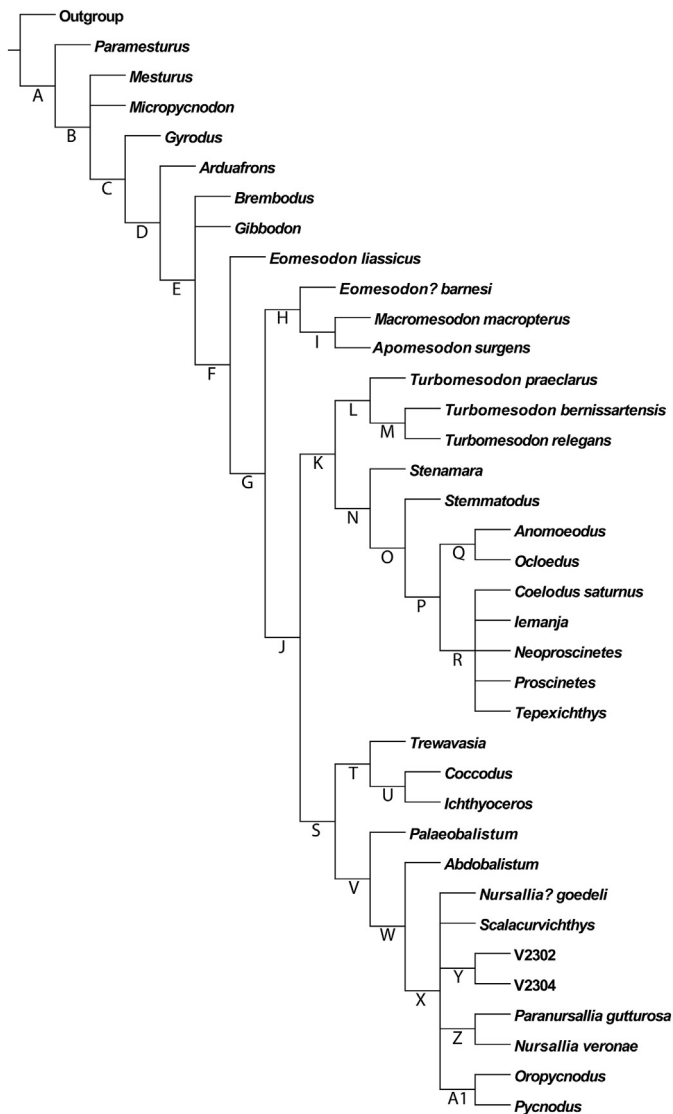
Fig. 14. Strict consensus tree depicting the systematic position of *Njoerdichthys dyckerhoffi* gen. et sp. nov. with branchial teeth characters included and characters regarding number of teeth on oprearticular and vomer excluded.

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: [1] absent). Oropycnodus and Pycnodus (Node A1) with a bootstrap support of 54 are supported by nine homoplasies (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 epichordal elements of caudal endoskeleton: [1] six to eight; Character 57. Number of caudal principal fin rays: [0] 20–25; Character 58. Morphology of caudal fin: [5] double emarginated; Character 77. Arrangement of

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 epichordal elements of caudal endoskeleton: [1] six to eight, Character 60. Ossification of scales: [3] incomplete in all scales, Character 70. Number of differentiated dorsal ridge scales: [4] seven to nine; **Node O:** Character 11. (Post) Parietal process: [0] absent, Character 50. Position of dorsal fin (predorsal length/standard length): [2] 50%–59%, Character 55. Number of anal axonosts: [5] nine or less, Character 60. Ossification of scales: [0] complete in all scales; **Node Y:** Character 29. Number of vomerine tooth rows: [1] three, Character 38. Groove on vomerine and prearticular teeth: [1] present, Character 43. Number of autogenous anterior neural spines: [4] six or less, Character 69. Scutellum-like contour scales: [2] present, ventral only, Character 71. Arrangement of dorsal ridge scales: [1] point contact; **Node E1:** Character 25. Morphology of premaxillary and dentary teeth: [2] robust, barely incisiform, Character 28. Morphology of vomerine teeth: [1] circular to subcircular contour, Character 41. Neural and haemal adjacent arcocentra: [3] hyper-complex contact, 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 55. Number of anal axonosts: [4] 50 or more, Character 58. Morphology of caudal fin: [6] vertical, Character 61. Distribution of scales: [2] abdominal region plus part of the caudal region. The apomorphies supporting each node are: **Node D1:** Character 69. Scutellum-like contour scales: [1] present, dorsal only; **Node O:** Character 28. Morphology of vomerine teeth: [4] triangular contour, Character 70. Number of differentiated dorsal ridge scales: [5] one or two, Character 76. Number of ventral keel scales: [5] two or three; **Node E1:** Character 8. Morphology of parietal bones: [3] curved and very broad.

All three analyses display some differences to the analysis of Poyato-Ariza and Wenz (2002) but show very similar results to each other apart from the interpretation of the position of several taxa (e.g. *Palaeobalistum*). The derived position of *Njoerdichthys* gen. nov. within Pycnodontidae with close relationships to *N.? goedeli* is supported by Analyses 1 and 3, but not by analysis 2. Our analyses here also exemplify well the differences in interpreting characters
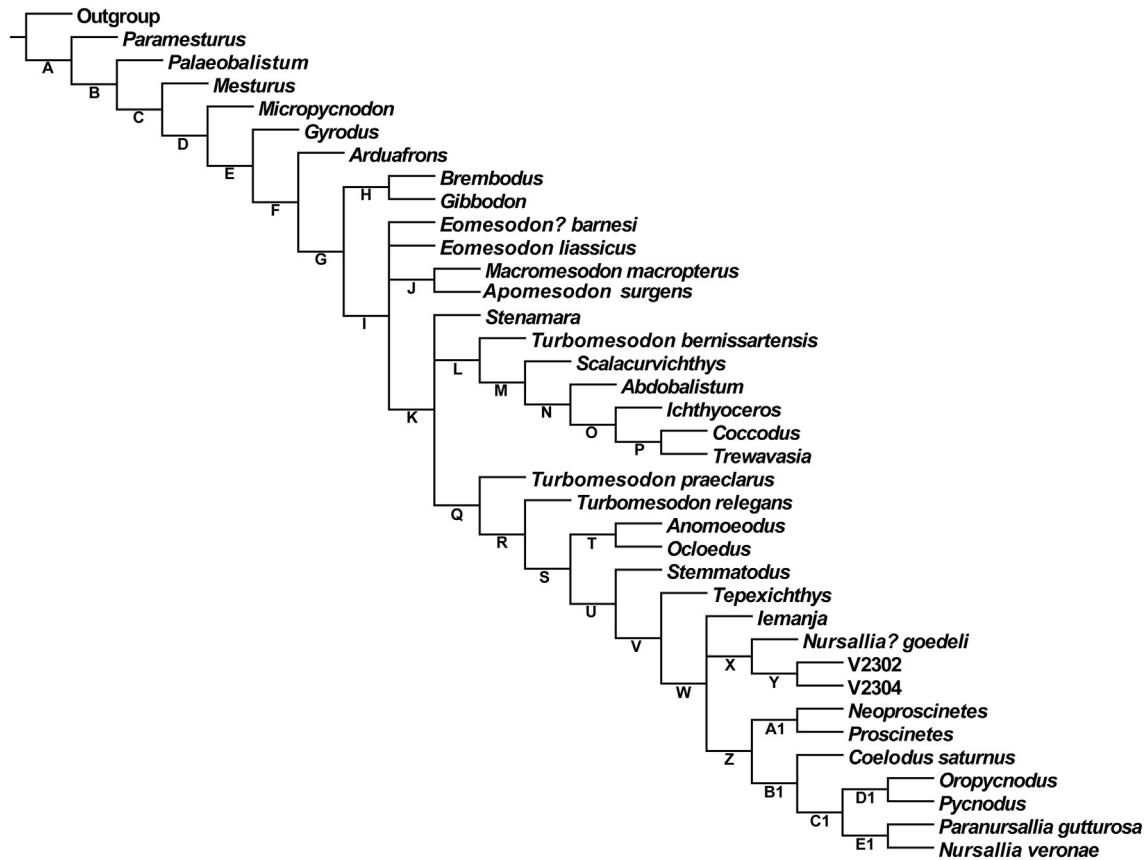
Fig. 15. Strict consensus tree depicting the systematic position of *Njoerdichthys dyckerhoffi* gen. et sp. nov. where all uninformative characters, branchial teeth characters and characters regarding number of teeth on prearticular and vomer excluded.

(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.
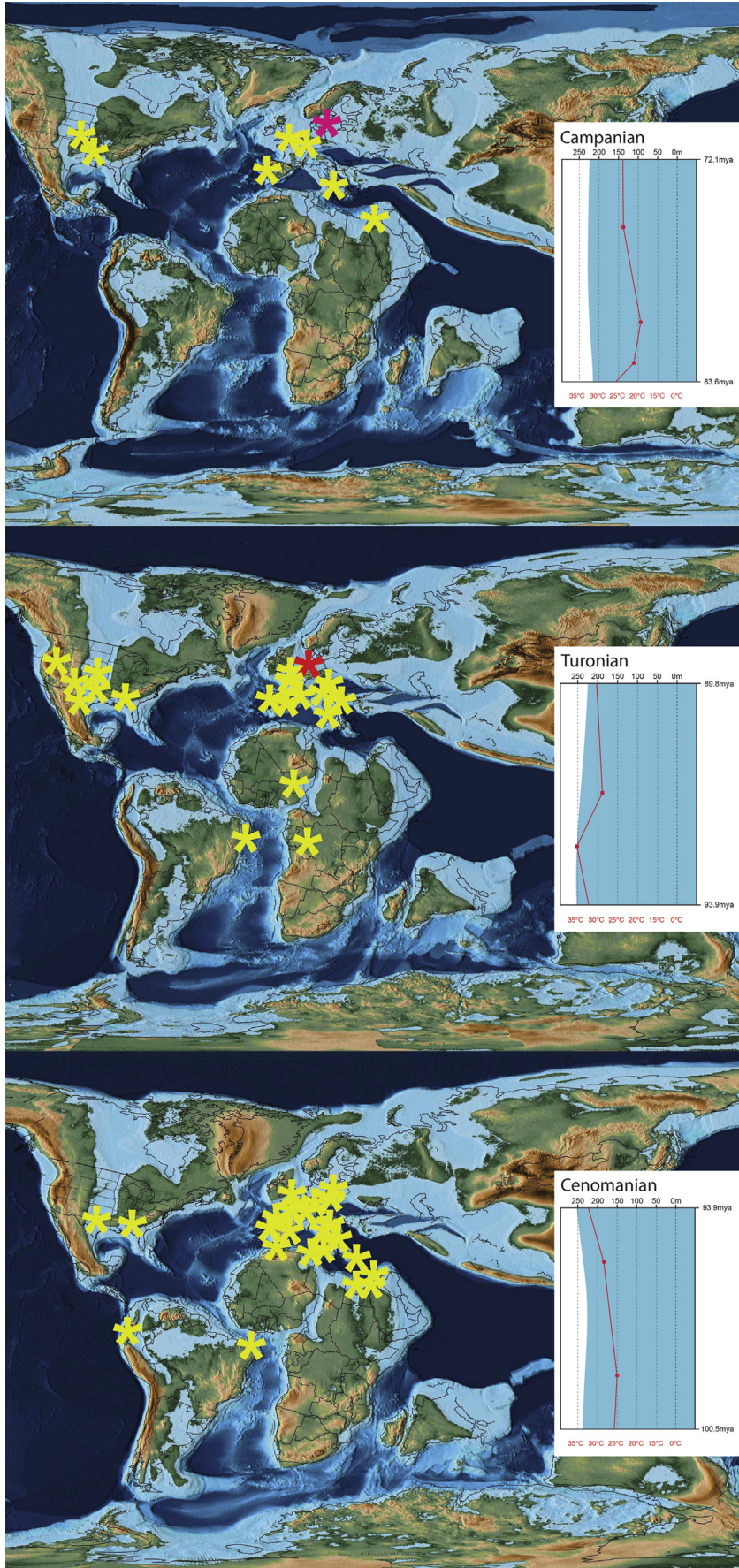
The character combination of *Njoerdichthys* gen. nov. places the new taxon unambiguously into the crown group of Pycnodontidae. Poyato-Ariza and Wenz (2002) identified a single autapomorphic character of Pycnodontidae, the presence of a postparietal brush- or peniculus-like process. The new taxon from 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*, *Flagellipinna*, *Coccodus*, *Paracoccodus*, *Coruscihthys*, *Libanopycnodus*, *Sigmapycnodus*, *Haqelpycnodus*, *Hensodon*, *Ichthyoceros*, *Nursallia*, *Palaeobalistum*, and *Trewavasia*; 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 (*Anomoeodus pauciseriale, Anomoeodus willetti*; Woodward, 1893, 1895, 1909; Kriwet, 2002).
- Nardó (Campanian−Maastrichtian) in Italy (*Pseudopycnodus nardoensis*; Taverne, 1997).

- Cinto Euganeo (Cenomanian−Turonian) of northern Italy (*Paranursallia* sp.; Sorbini, 1976).
- Messina (Cenomanian) in Sicily (*P. gutturosa*; Leonardi, 1966).
- Vallecillo (Turonian) in Mexico (*Nursallia* sp., *Nursallia* aff. *tethysensis*, *Paranursallia gutturosa*; Blanco-Piñón et al., 2002; Alvarado-Ortega et al., 2019; Stinnesbeck et al., 2019).
- Polazzo (Santonian) in northern Italy (*Polazzodus*; Poyato-Ariza, 2010).
- Komen and Slovenia (Cenomanian−Turonian) (*Coelodus*, *Nursallia,* cf. *Polazzodus*; Heckel, 1854; Gorjanovic-Kramberger, 1895, 1902; Križnar, 2014).
- Dongargaon (Maastrichtian) in India ("*Pycnodus*" *lametae*; Woodward, 1908; Mohabey and Udhoji, 1996).
- Niobrara formation, Kansas (Coniacian−Turonian) in the U.S.A (*Micropycnodon*; Hibbard and Griffham, 1941, 1945; Dunkle and Hibbard, 1946; Nursall, 1999; Cronin and Shimada, 2019).

Early Cretaceous pycnodonts known from articulated skeletons are *Neoproscinetes* Figueiredo and Silva Santos, 1987 (Brazil), *Iemanja* (Brazil), *Ocloedus* (Spain), *Stemmatodus* (Italy), *Costapycnodus* (Italy), *Stenamara* (Spain), and *Tepexichthys* Applegate, 1992 (Mexico). Since their first recorded occurrence in the Late Triassic (Tintori, 1981; Poyato-Ariza and Martín-Abad, 2013), pycnodontiforms have always been present with high species diversities in the Western Tethys region. It is this stable environment with favourable climatic conditions that supports the overall dispersal pattern within basal pycnodonts (Cavin, 2008). For most of the Mesozoic and Early Cenozoic, the general distribution of land masses and associated marine platforms were contributing factors to the increasing diversity of pycnodonts in the Western Tethys. This hypothesis is further supported by the inferred dispersal patterns of basal pycnodonts (Cavin, 2008). A look at the phylogenetic relationships of pycnodont taxa to each other consistently supports a move from the Tethys to other regions (Martín-Abad and Poyato-Ariza, 2013). Any such changes in distribution only ever involved individual taxa, no dispersal event seemingly was the result of vicariance or radiation events including major groups. Overall, the biogeographical history of pycnodonts is explained as a series of expansion-contraction patterns, where certain taxa occasionally moved away from the Tethys to colonise new areas. Any disappearance from these localities is assumed to have represented a slowly progressive affair. When the Tethys finally closed during the Early Cenozoic, the extinction of pycnodonts soon followed, probably showcasing the importance of the Tethys as a centre of expansion and contraction for the group. The Cretaceous seemingly was one of the most significant periods in the evolutionary history of pycnodonts as a large diversity and disparity of forms evolved in this time period, and they had a wide distribution range all over Earth (see Appendix E for palaeobiogeography of Cretaceous pycnodonts). It is during this time that distinctive distribution patterns can be observed with certain areas being reliable centres of diversity and new localities being colonised by pycnodonts as environmental conditions changed. In the earliest stage of the Cretaceous, the Berriasian, pycnodonts are restricted to England, France, Germany, Portugal and Spain (Woodward, 1918; Peybernes and Oertli, 1972; Brenner, 1976; Kemper, 1976; Gomez-Pallerola, 1982). During the Early Cretaceous, they spread further east into Europe with Austria being the furthest eastward occurrence of their

European distribution recorded thus far (Pictet et al., 1858−1860; de Beaumont and Masson, 1979). The earliest Cretaceous South American records are *Gyrodus huiliches* Gouiric-Cavalli et al., 2019 and *Tranawuen agrioensis* Gouiric-Cavalli et al., 2019; both taxa from Argentina (Valanginian−Hauterivian). The Aptian going into the Albian stage has pycnodonts being recorded in Brazil such as *Neoproscinetes* and *Iemanja* (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 (Marramá 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* Wilmsen, 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 (Löscher, 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 Coniacian and continuing in the Santonian, their range is reduced to just southern Europe and southern regions of North America (Heckel, 1854; Everhart, 2007; Poyato-Ariza, 2010; Cronin and Shimada, 2019). The Campanian sees a further northward expansion of pycnodontiforms as *Anomoeodus subclavatus* is recorded in Kristianstad Basin, Sweden (Davis, 1890; Siverson, 1992). Within the Kristianstad Basin, it is located in the *Belemnellocamax balsvikensis* belemnite biozone (lowermost upper Campanian) of the Åsen assemblage (Christensten, 1975; Bazzi et al., 2015). While there is a general trend of climatic cooling during

---

Fig. 16. Distribution maps of pycnodont fishes through three stages of the Late Cretaceous with sea surface temperature that was present at the time. *Njoerdichthys dyckerhoffi* gen. et sp. nov. represented by a red star. The other most northerly occurring pycnodont present during the Campanian, *Anomoeodus subclavatus* is indicated by a pink star. Palaeomaps taken from Scotese (2014). Sea surface temperature curve modified from Martin et al. (2014) which was established using a combination of oxygen isotope composition of fish teeth from various localities relating to the Western Tethys and previous studies (Kolodny and Raab, 1988; Kolodny and Luz, 1991; Lécuyer et al. 1993, 2003; Pucéat et al., 2003, 2007; Billon-Bruyat et al. 2005; Héran, 2006; Bernard et al. 2010; Dera et al. 2011). The seawater temperatures were computed by Martin et al. (2014) using the phospate-water temperature scale (Lécuyer et al., 2013).

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 (Surlyk and Christensen, 1974; Surlyk and Sørensen, 2010; Sørensen et al., 2013) is recorded at Kristanstad 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 (Surlyk and Christensen, 1974; Sørensen and Surlyk, 2008; Surlyk 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, 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., 2006), formiciine ants (Archibald et al., 2011) and staphylinid beetles (Brunke et al., 2017). Among bony fishes, expansion of a clade's geographic range into higher latitudes during higher temperatures can be seen in Esocidae (Newbrey et al., 2008a), characiforms (Otero et al., 2008; Newbrey et al., 2008b, 2009), and Amiidae and Lepisosteidae (Eberle et al., 2014). The fossil record of freshwater teleosts during the Cenozoic reveals that tropical lineages were present in higher latitudes during periods of high temperatures and were absent from such regions when temperatures decreased (Lavoué, 2019).

4. Conclusion

Njoerdichthys 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 Nursalliinae, but this subfamily was shown to be paraphyletic and future phylogenetic work will test the validity of this subfamily more rigorously. The second finding is that *Njoerdichthys 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 Mesozoic. This, in combination with general Cretaceous pycnodontiform occurrence patterns and along with the discovery of *Anomoeodus subclavatus* in the Kristanstad 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.

References

Synoptische Übersicht der fossilen Ganoiden. In: Agassiz, L. (Ed.), Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde 1.

Agassiz, L. (Ed.), 1834. Feuilleton additionnel aux recherches sur les poissons fossiles. Addition à la préface, vol. I. Petitpierre, Neuchàtel et Soleure, Petitpierre.

Agassiz, L. (Ed.), 1833—1844. Recherches sur les poissons fossiles. Neuchiitel et Soleure, Petitpierre.

Alvarado-Ortega, J., Severiano, K.M.C., Barrientos-Lara, J.I., Díaz-Cruz, J.A., Than-Marchese, B.A., 2019. The Huehuetla quarry, a Turonian deposit of marine vertebrates in the Sierra Norte of Puebla, central Mexico. Palaeontologia Electronica 22, 1—20.

Applegate, S.P., 1992. A new genus and species of Pycnodont from the Cretaceous (Albian) of Central Mexico, Tepexi de Rodríguez, Puebla. Revista del Instituto de Geología, Universidad Nacional Autónoma de México 10, 164—178.

Arambourg, C. (Ed.), 1952. Les vertébrés fossiles des gisements de Phosphates (Maroc -Algérie - Tunisie). Notes Memoires du Service géologique du Maroc, Paris.

Arambourg, C., 1954. Les poissons Crétacés du Jebel Tselfat (Maroc). Notes et Mémoires du Service Géologique du Maroc 118, 1—187.

Archibald, S.B., Johnson, K.R., Mathewes, R.W., Greenwood, D.R., 2011. Intercontinental dispersal of giant thermophilic ants across the Arctic during Early Eocene hyperthermals. Proceedings of the Royal Society B: Biological Sciences 278, 3679—3686.

Arratia, G., Schultze, H.P., 1992. Reevaluation of the caudal skeleton of certain actinopterygian fishes: III. Salmonidae. Homologization of caudal skeletal structures. Journal of Morphology 214, 187—249.

Bazzi, M., Einarsson, E., Kear, B.P., 2015. Late Cretaceous (Campanian) actinopterygian fishes from the Kristanstad Basin of southern Sweden. Geological Society, London, Special Publications 434, 277—292.

de Beaumont, G., Masson, H., 1979. Une mâchoire de poisson pycnodonte (*Microdon* sp.) dans l'Urgonien de la nappe de Morcles. Bulletin de la Société Vaudoise des Sciences Naturelles 74, 251—257.

Bechly, G., 2019. New fossil Odonata from the Upper Jurassic of Bavaria with a new fossil calibration point for Zygoptera. Palaeoentomology 2, 618—632.

Berensmeier, M., Dölling, B., Frijia, G., Wilmsen, M., 2018. Facies analysis of proximal Upper Cretaceous deposits from the southwestern Münsterland Cretaceous Basin (northwest Germany). Cretaceous Research 87, 241—260.

Berg, L.S., 1937. A classification of fish-like vertebrates. Bulletin de l'Académie des Sciences de l'URSS, Classe des Sciences Mathématiques et Naturelles 4, 1277—1280.

Bernard, A., Bernard, A., Lécuyer, C., Vincent, P., Amiot, R., Bardet, N., Buffetaut, E., Cuny, G., Fourel, F., Martineau, F., Mazin, J.M., Prieur, A., 2010. Regulation of body temperature by some Mesozoic marine reptiles. Science 328, 1379—1382.

Billon-Bruyat, J.P., Lécuyer, C., Martineau, F., Mazin, J.M., 2005. Oxygen isotope compositions of Late Jurassic vertebrate remains from lithographic limestones of western Europe: implications for the ecology of fish, turtles, and crocodilians. Palaeogeography, Palaeoclimatology, Palaeoecology 216, 359—375.

Blake, J.F., 1905. A monograph of the fauna of the Cornbrash. Palaeontographical Society 32, 33.

Blanco-Piñón, A., Frey, E., Stinnesbeck, W., López Oliva, J.G., 2002. Late Cretaceous (Turonian) fish assemblage from Vallecillo, northeastern Mexico. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 225, 39—54.

de Blainville, H.D., 1818. Nouveau dictionnaire d'histoire naturelle. Poissons fossiles, Delerville, Paris.

Blumenberg, M., Wiese, F., 2012. Imbalanced nutrients as triggers for black shale formation in a shallow shelf setting during the OAE 2 (Wunstorf, Germ.). Biogeosciences 9, 4139—4153.

Brenner, P., 1976. Ostracoden und Charophyten des spanischen Wealden (Systematik, Okologie, Stratigraphie, Palaogeographie). Palaeontographica Americana 152, 113–201.

Blot, J., 1987. Studi e Ricerche sui Giacimenti Terziari di Bolca V. L'ordre des Pycnodontiformes. Museo civico di storia Naturale, Verona.

Breitkreuz, H., Diedrich, R., Metzdorf, R., 1991. Fossilfunde aus der Schwarz-Bunten Wechselfolge (Ober-Cenoman bis Unter-Turon) des Ostwestfalendammes bei Bielefeld. Berichte des Naturwissenschaftlichen Vereins von Bielefeld und Umgegend 32, 37–48.

Brito, P.M., Yabumoto, Y., 2011. An updated review of the fish faunas from the Crato and Santana formations in Brazil, a close relationship to the Tethys fauna. Bulletin Kitakyushu Museum of Natural History, Serie A 9, 107–136.

Brunke, A.J., Chatzimanolis, S., Metscher, B.D., Wolf-Schwenninger, K., Solodovnikov, A., 2017. Dispersal of thermophilic beetles across the intercontinental Arctic forest belt during the early Eocene. Scientific Reports 7, 12972.

Capasso, L.L., Abi Saad, P., Taverne, L., 2009. Nursallia tethysensis sp. nov., a new pycnodont fish (Neopterygii;† Halecostomi) from the Cenomanian of Lebanon. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 79, 117–136.

Cappetta, H., 1972. Les poissons Crétacés et Tertiaires du Bassin des Iullemmeden (Republique du Niger). Palaeovertebrata 5, 179–251.

Cavin, L., 2008. Palaeobiogeography of Cretaceous bony fishes (Actinistia, Dipnoi and Actinopterygii). In: Cavin, L., Longbottom, A., Richter, M. (Eds.), Fishes and the break-up of Pangea. Geological Society, London, Special Publications 295, pp. 165–183.

Cawley, J.J., Kriwet, J., 2018. A new pycnodont fish, Scalacurvichthys naishi gen. et sp. nov., from the Late Cretaceous of Israel. Journal of Systematic Palaeontology 16, 659–673.

Cawley, J.J., Kriwet, J., 2019. A new genus and species of pycnodontid fish Flagellipinna rhomboides, gen. et sp. nov. (Neopterygii, Pycnodontiformes), from the Upper Cretaceous (Cenomanian) of Lebanon, with notes on juvenile form and ecology. Journal of Vertebrate Paleontology 39, e1614012.

Christensen, W.K., 1975. Upper Cretaceous belemnites from the Kristianstad area in Scania. Fossils and Strata 7, 1–69.

Cione, A.L., 1977. Algunas consideraciones sobre Pycnodontiformes [Pisces, Holostei] procedentes de la Formación Yacoraite, Cretácico Tardío de la Provincia de Salta, Argentina. Ameghiniana 14, 315–316.

Cope, E.D., 1887. Zittel's Manual of palaeontology. The American Naturalist 21, 1014–1019.

Cronin, T.J., Shimada, K., 2019. New Anatomical Information on the Late Cretaceous Bony Fish, Micropycnodon kansasensis (Actinopterygii: Pycnodontiformes), from the Niobrara Chalk of Western Kansas, USA. Transactions of the Kansas Academy of Science 122, 19–28.

Dartevelle, E., Casier, E., 1949. Les poissons fossiles du Bas-congo et de regions voisines. Deuxieme Partie. Annales du Musée du Congo Belge, Série A 2, 201–256.

Davis, J.W., 1887. The fossil fishes of the Chalk of Mount Lebanon, in Syria. The Scientific Transactions of the Royal Dublin Society 3, 457–636.

Davis, J.W., 1890. On the fossil fish of the Cretaceous formations of Scandinavia. The scientific transactions of the Royal Dublin Society, Series 2 4, 363–434.

Dera, G., Brigaud, B., Monna, F., Laffont, R., Pucéat, E., Deconinck, J.F., Pellenard, P., Joachimski, M.M., Durlet, C., 2011. Climatic ups and downs in a disturbed Jurassic world. Geology 39, 215–218.

Diedrich, C., 2001. Die Großammoniten-Kolktaphozönosen des Puzosia-'Event I (Ober-Cenoman) von Halle/Westf. (NW-Deutschland). Münstersche Forschungen zur Geologie und Paläontologie 90, 1–208.

Diedrich, C., 2012. Stomach and gastrointestinal tract contents in Late Cenomanian (Upper Cretaceous) teleosts from Black Shales of Germany and analysis of fish mortality and food chains in the upwelling influenced pre-North Sea Basin of Europe. New Mexico Museum of Natural History and Science 57, 241–254.

Diedrich, C.G., 2013. Facies related phylostratigraphy of the benthic neoselachian Ptychodus from the Late Cretaceous (Cenomanian/Turonian) of the Pre-North Sea Basin of Europe. Cretaceous Research 41, 17–30.

Diedrich, C., 2014. Skeleton of the fossil shark Isurus denticulatus from the Turonian (Late Cretaceous) of Germany — Ecological Coevolution with Prey of Mackerel Sharks. Paleontology Journal 1–20.

Dölling, B., Dölling, M., Hiss, M., Berensmeier, M., Püttmann, T., 2018. Upper Cretaceous shallow-marine deposits of the southwestern Münsterland (northwest Germany) influenced by synsedimentary tectonics. Cretaceous Research 87, 261–276.

Dunkle, D.H., Hibbard, C.W., 1946. Some comments upon the structure of a pycnodontid fish from the Upper Cretaceous of Kansas. University of Kansas Science Bulletin 31, pp. 161–181.

Eberle, J.J., Gottfried, M.D., Hutchison, J.H., Brochu, C.A., 2014. First record of Eocene bony fishes and crocodyliforms from Canada's western Arctic. PloS One 9, e96079.

Ebert, M., 2020. A new genus of Pycnodontidae (Actinopterygii) from the Upper Jurassic of France and Germany, included in a phylogeny of Pycnodontiformes. Zoological Journal of the Linnean Society 188, 434–454.

Ernst, G., Wood, C.J., Hilbrecht, H., 1984. The Cenomanian–Turonian boundary problem in NW-Germany with comments on the north-south correlation to the Regensburg Area. Bulletin of the Geological Society of Denmark 33, 103–113.

Everhart, M.J., 2007. Remains of a pycnodont fish (Actinopterygii: Pycnodontiformes) in a coprolite; An uppermost record of Micropycnodon kansasensis in the Smoky Hill Chalk, western Kansas. Transactions of the Kansas Academy of Science 110, 35–44.

Figueiredo, F.J., Silva Santos, R., 1987. Considerações taxinômicas dos picnodontidos da Formaçaõ Gramame (camada de Fostato), Pe. Anais X congreso brasileiro de Paleontologia, Rio de Janeiro, pp. 25–31.

Forey, P.L., Yi, L., Patterson, C., Davies, C.E., 2003. Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. Journal of Systematic Palaeontology 1, 227.

Frickhinger, K.A., 1991. Fossilien-Atlas Fische. Mergus Verlag, Melle.

Gale, A.S., Christensen, W.K., 1996. Occurrence of the belemnite Actinocamax plenus in the Cenomanian of SE France and its significance. Bulletin of the Geological Society of Denmark 43, 68–77.

Gale, A.S., Kennedy, W.J., Voigt, S., Walaszczyk, I., 2005. Stratigraphy of the Upper Cenomanian–Lower Turonian chalk succession at Eastbourne, Sussex, UK—ammonites, inoceramid bivalves and stable carbon isotopes. Cretaceous Research 26, 460–487.

Gayet, M., 1984. Ichthyoceras spinosus nov. gen., nov. sp., du Cénomanien inférieur de Hakel (Liban) et ses affinités avec le genre Trewavasia (Pisces, Pycnodontiformes, Coccodontidae). Bulletin du Museum National d'Histoire Naturelle 6, 287–307.

Gomez Pallerola, J.E., 1982. Nuevas aportaciones a la ictiofauna y a la flora del Neocomiense del Montsech de Rubies (Lérida). Boletin Geologico Y Minero 93, 199–213.

Gorjanovic-Kramberger, K., 1895. De Piscibus fossilibus Comeni, Mrzleci, Lesinae et M. Libanonis et appendix de piscibus oligocaenicis ad Tüffer, Sagor et Trifail. Djela Jugoslavenske Akademije Znanosti i Umjetnosti 16, 1–68.

Gorjanovic-Kramberger, K., 1902. Palaeo-Ichthyologiai adalékok. A Magyar Kir. Földtani intézet évkönyve 14, 1–20.

Gouiric-Cavalli, S., Remírez, M., Kriwet, J., 2019. New pycnodontiform fishes (Actinopterygii, Neopterygii) from the Early Cretaceous of the Argentinian Patagonia. Cretaceous Research 94, 45–58.

Gregory, W.K., 1933. Fish skulls. A study of the evolution of natural mechanisms. Transactions of the American Philosophical Society 23, 75–481.

Hauschke, N., Schöllmann, L., Keupp, H., 2011. Oriented attachment of a stalked cirripede on an orthoconic heteromorph ammonite implications for the swimming position of the latter. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 262, 199–212.

Heckel, J., 1854. Über den Bau und die Eintheilung der Pycnodonten, nebst kurzer Beschreibung einiger neuer Arten derselben. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse 12, 433–464.

Héran, M.A., 2006. Mammifères et Climat: Reconstitutions Paléoclimatiques d'Europe Occidentale sur la base des Faunes Fossiles (Unpubl. PhD thesis). Université Claude Bernard Lyon 1, 349.

Hetzel, A., März, C., Vogt, C., Brumsack, H.-J., 2011. Geochemical environment of Cenomanian–Turonian black shale deposition at Wunstorf (northern Germany). Cretaceous Research 32 (4), 480–494.

Hibbard, C.W., Graffham, A., 1941. A new pycnodont fish from the Upper Cretaceous of Rooks County, Kansas. University of Kansas Quarterly Bulletin 27, pp. 71–77.

Hibbard, C.W., Graffham, A., 1945. Micropycnodon, a new name for Pycnomicrodon Hibbard and Graffham not Hay. Transactions of the Kansas Academy of Science 47, 404.

Hilbrecht, H., Dahmer, D.D., 1991. Inoceramen aus den Schwarzschiefern des basalen Unter-Turon (Oberkreide) von Helgoland und Misburg. Geologisches Jahrbuch 120, 245–269.

Hilbrecht, H., Dahmer, D.D., 1994. Sediment dynamics during the Cenomanian–Turonian (Cretaceous) Oceanic Anoxic Event in northwestern Germany. Facies 30, 63–84.

Hiss, M., Kaplan, U., Wiese, F., 2007a. Hesseltal-Formation. In: Niebuhr, B., Hiss, M., Kaplan, U., Tröger, K.A., Voigt, S., Voigt, T., Wiese, F., Wilmsen, M. (Eds.), Lithostratigraphie der norddeutschen Oberkreide. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften 55. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 37–38.

Hiss, M., Kaplan, U., Wiese, F., 2007b. Lengerich-Formation. In: Niebuhr, B., Hiss, M., Kaplan, U., Tröger, K.-A., Voigt, S., Wiese, F., Wilmsen, M. (Eds.), Lithostratigraphie der norddeutschen Oberkreide. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften 55. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 41–42.

Hoffmann, R., Bestwick, J., Berndt, G., Berndt, R., Fuchs, D., Klug, C., 2020. Pterosaurs ate soft-bodied cephalopods (Coleoidea). Scientific Reports 10 (1), 1230.

Huber, B.T., MacLeod, K.G., Watkins, D.K., Coffin, M.F., 2018. The rise and fall of the Cretaceous Hot Greenhouse climate. Global and Planetary Change 167, 1–23.

Huxley, T.H., 1880. On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proceedings of the Zoological Society of London 43, 649–662.

Jarvis, I., Gale, A.S., Jenkyns, H.C., Pearce, M.A., 2006. Secular variation in Late Cretaceous carbon isotopes: a new δ13C carbonate reference curve for the Cenomanian–Campanian (99.6–70.6 Ma). Geological Magazine 143, 561–608.

Jarvis, I., Lignum, J.S., Gröcke, D.R., Jenkyns, H.C., Pearce, M.A., 2011. Black shale deposition, atmospheric CO2 drawdown, and cooling during the Cenomanian-Turonian Oceanic Anoxic Event. Paleoceanography 26, 1–17.

Jefferies, R.P.S., 1962. The palaeoecology of the Actinocamax plenus subzone (lowest Turonian) in the Anglo-Paris Basin. Palaeontology 4, 609–647.

Jenkyns, H.C., Dickson, A.J., Ruhl, M., van den Boorn, S.H.J.M., 2017. Basalt-seawater interaction, the Plenus Cold Event, enhanced weathering and geochemical

change: deconstructing Oceanic Anoxic Event 2 (Cenomanian–Turonian, Late Cretaceous). Sedimentology 64 (1), 16–43.

Jollie, M. (Ed.), 1962. Chordate morphology. Reinhold Publishing Corporation, New York.

Kaplan, U., 1992. Die Oberkreide-Aufschlüsse im Raum Lengerich/Westfalen. Geologie und Palaontologie in Westfalen 21, 7–37.

Kaplan, U., 2011. Turonium und Unterconiacium (Oberkreide) im Steinbruch DIMAC bei Halle (Westfalen), Teutoburger Wald (Östliches Münsterländer Kreidebecken). Geologie und Palaontologie in Westfalen 81, 75–105.

Kaplan, U., Wiese, F., 2000. 90 Millionen Jahre zurück - die Steinbrüche in Lengerich. Kalk. Natur und Landschaft 1, 31–69.

Keller, S., 1982. Die Oberkreide der Sack-Mulde bei Alfeld (Cenoman - Unter-Coniac). Lithologie, Biostratigraphie Inoceramen. Geologisches Jahrbuch 64, 3–171.

Kemper, E., 1976. Geologischer Führer durch die Grafschaft Bentheim und die angrenzenden Gebiete, mit einem Abriß der emsländischen Unterkreide. Verlag Heimatverein der Grafschaft Bentheim, Nordhorn.

Kennedy, W.J., Kaplan, U., 2019. Ammoniten aus dem Turonium des Münsterländer Kreidebeckens. Das Munster 92, 3–223.

Khalloufi, B., Ouarhache, D., Lelièvre, H., 2010. New paleontological and geological data about Jbel Tselfat (Late Cretaceous of Morocco). Historical Biology 22, 57–70.

Klug, C., Riegraf, W., Lehmann, J., 2012. Soft–part preservation in heteromorph ammonites from the Cenomanian–Turonian Boundary Event (OAE 2) in north–west Germany. Palaeontology 55, 1307–1331.

Kölbl-Ebert, M., Ebert, M., Bellwood, D.R., Schulbert, C., 2018. A piranha-like pycnodontiform fish from the Late Jurassic. Current Biology 28, 3516–3521.

Kolodny, Y., Luz, B., 1991. Oxygen isotopes in phosphates of fossil fish; Devonian to Recent. In: Taylor, H.P., O'Neil, J.R., Kaplan, I.R. (Eds.), Stable Isotope Geochemistry: a Tribute to Samuel Epstein. Geochemical Society, University Park, pp. 105–119.

Kolodny, Y., Raab, M., 1988. Oxygen isotopes in phosphatic fish remains from Israel: Paleothermometry of tropical Cretaceous and Tertiary shelf waters. Palaeogeography, Palaeoclimatology, Palaeoecology 64, 59–67.

Kriwet, J., 1999. Pycnodont fishes (Neopterygii,† Pycnodontiformes) from the Lower Cretaceous of Uña (E-Spain) with comments on branchial teeth in pycnodontid fishes. In: Arratia, G., Schultze, H.P. (Eds.), Mesozoic Fishes 2 - Systematics and the Fossil Record. Verlag Dr. Friedrich Pfeil, Munich, pp. 215–238.

Kriwet, J., 2001a. Palaeobiogeography of pycnodontiform fishes (Actinopterygii, Neopterygii). Seminario de Paleontología de Zaragoza 5, 121–130.

Kriwet, J., 2001b. Feeding mechanisms and ecology of pycnodont fishes (Neopterygii, †Pycnodontiformes). Mitteilungen aus dem Museum für Naturkunde zu Berlin, Geowissenschaftliche Reihe 4, 139–165.

Kriwet, J., 2001c. A comprehensive study of pycnodont fishes (Neopterygii, Pycnodontiformes): morphology, taxonomy, functional morphology, phylogeny, and palaeobiogeography (unpublished PhD thesis). Humboldt-University, Berlin, pp. 1–582.

Kriwet, J., 2002. *Anomoeodus pauciseriale*, a new pycnodont fish (Neopterygii, Pycnodontiformes) from the White Chalk Formation (Upper Cretaceous) of Sussex, South England. Paläontologische Zeitschrift 76, 117–123.

Kriwet, J., 2004. A new pycnodont fish genus (Neopterygii: Pycnodontiformes) from the Cenomanian (Upper Cretaceous) of Mount Lebanon. Journal of Vertebrate Paleontology 24, 525–532.

Kriwet, J., 2005. A comprehensive study of the skull and dentition of pycnodont fishes. Zitteliana 45, 135–188.

Kriwet, J., Gloy, U., 1995. Zwei mesopelagische Raubfische (Actinopterygii: Euteleostei) aus dem Unterturon der Kronsberg-Mulde bei Hannover/Misburg (NW-Deutschland). Berliner geowissenschaftliche Abhandlungen E 16, 335–355.

Križnar, M., 2014. Ostanki zob piknodontnih rib (Actinopterygii, Pycnodontidae) iz krednih plasti Mrzleka pri Solkanu (Slovenija). RMZ Materials and Geoenvironment 61, 183–189.

Kruckow, T., 1979. Wirbeltier-Zähne aus dem Muschelkalk und der Kreide von Helgoland. Abhandlungen des naturwissenschaftlichen Vereins in Bremen 39, 55–76.

Lambers, P.H., 1991. The Upper Jurassic actinopterygian fish *Gyrodus dichactinus* Winkler, 1862 (*Gyrodus hexagonus* [Blainville, 1818]) from Solnhofen, Bavaria and anatomy of the *Gyrodus* Agassiz. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 94, 489–544.

Lane, H.H., 1944. A Survey of the Fossil Vertebrates of Kansas: Part I: The Fishes. Transactions of the Kansas Academy of Science 47 (1903), 129–176.

Lavoué, S., 2019. Origins of Afrotropical freshwater fishes. Zoological Journal of the Linnean Society zlz039. https://doi.org/10.1093/zoolinnean/zlz039.

Lécuyer, C., Grandjean, P., O'Neil, J.R., Cappetta, H., Martineau, F., 1993. Thermal excursions in the ocean at the Cretaceous-Tertiary boundary(northern Morocco): δ^{18}O record of phosphatic fish debris. Palaeogeography, Palaeoclimatology, Palaeoecology 105, 235–243.

Lécuyer, C., Picard, S., Garcia, J.P., Sheppard, S.M., Grandjean, P., Dromart, G., 2003. Thermal evolution of Tethyan surface waters during the Middle-Late Jurassic: Evidence from δ^{18}O values of marine fish teeth. Paleoceanography 18, 1076–1091.

Lécuyer, C., Amiot, R., Touzeau, A., Trotter, J., 2013. Calibration of the phosphate δ^{18}O thermometer with carbonate–water oxygen isotope fractionation equations. Chemical Geology 347, 217–226.

Lehmann, J., 1999. Integrated stratigraphy and palaeoenvironment of the Cenomanian–Lower Turonian (Upper Cretaceous) of northern Westphalia, North Germany. Facies 40, 25–70.

Lehmann, J., Maisch, M.W., Resch, U., 1997. Coelacanthiformes (Sarcopterygii, Actinistia) from the Cenomanian of NW Germany. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 206, 53–65.

Leonardi, A., 1966. L'ittiofauna cenomaniana di Floreste Messina. Palaeontographica italica 60, 33–67.

Licht, M., Kogan, I., 2011. Late Cretaceous pycnodont fishes (Actinopterygii, Neopterygii) from Saxony (Eastern Germany). Freiberger Forschungshefte C 540, 79–90.

Löscher, W., 1910. Die Westfälischen Galeritenschichten mit besonderer Berücksichtigung ihrer Seeigelfauna. Inaugural-Dissertation zur Erlangung der Doktorwürde. Unpubl. PhD thesis. E. Sch weizerbart'sch e Verlagsbuchhandlung Nägele & Dr. Sproesser, Stuttgart, 313 pp.

Machado, L.P.C., Brito, P.M., 2006. The new genus *Potiguara* (Actinopterygii: Pycnodontiformes) from the Upper Cretaceous of Northeast Brazil. Journal of Vertebrate Paleontology 26, 1–6.

Maisch, M.W., Lehmann, J., 2000. *Tselfatia formosa* ARAMBOURG, 1943 (Teleostei) from the Upper Cretaceous of Lower Saxony (Northern Germany). Neues Jahrbuch für Geologie und Paläontologie - Monatshefte 2000 499–512.

Maisey, J.G., 1999. The supraotic bone in neopterygian fishes (Osteichthyes, Actinopterygii). American Museum Novitates 3267, 1–52.

Mannion, P.D., Benson, R.B., Carrano, M.T., Tennant, J.P., Judd, J., Butler, R.J., 2015. Climate constrains the evolutionary history and biodiversity of crocodylians. Nature Communications 6, 8438.

Marramá, G., Villier, B., Dalla Vecchia, F.M., Carnevale, G., 2016. A new species of *Gladiopycnodus* (Coccodontoidea, Pycnodontomorpha) from the Cretaceous of Lebanon provides new insights about the morphological diversification of pycnodont fishes through time. Cretaceous Research 61, 34–43.

Martin, J.E., Amiot, R., Lécuyer, C., Benton, M.J., 2014. Sea surface temperature contributes to marine crocodylomorph evolution. Nature Communications 5, 1–7.

Martin-Abad, H., Poyato-Ariza, F.J., 2013. Historical patterns of distribution in pycnodontiform and amiiform fishes in the context of moving plates. Geologica Belgica 16, 217–226.

von der Marck, W., 1860. Ein prachtvoll erhaltener Kehlflosser aus dem westfälischen 'Pläner mit eingelagertem Grünsand'. Correspondenzblatt des Naturhistorischen Vereines der Preußischen Rheinlande und Westphalens 1860, 47.

von der Marck, W., 1862. Über *Elopopsis ziegleri*, einen neuen Fisch aus dem Pläner von Wessum. Correspondenzblatt des Naturhistorischen Vereins der Preußischen Rheinlande und Westphalens 1862, 70.

von der Marck, W., 1885. Fische der Oberen Kreide Westfalen. Palaeontographica 31, 32–33.

Markwick, P.J., 1998. Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. Palaeogeography, Palaeoclimatology, Palaeoecology 137, 205–271.

Mayr, G. (Ed.), 2009. Paleogene fossil birds. Springer-Verlag, Berlin.

Mohabey, D.M., Udhoji, S.G., 1996. *Pycnodus lametae* (Pycnodontidae), a holostean fish from freshwater Upper Cretaceous Lameta Formation of Maharashtra. Journal of the Geological Society of India 47, 593–598.

Müller, A., 2008. Ein artikulierter Fund von *Ptychodus* aus dem Obercenoman von Westfalen. Geologie und Palaontologie in Westfalen 70, 55–63.

Murray, A.M., Wilson, M.V.H., Gibb, S., Chatterton, B.D.E., 2013. Additions to the Late Cretaceous (Cenomanian/Turonian) actinopterygian fauna from the Agoult locality, Akrabou Formation, Morocco, and comments on the palaeoenvironment. In: Arratia, G., Schultze, H.P., Wilson, M.V.H. (Eds.), Mesozoic fishes 5 - Global Diversity and Evolution. Verlag Dr. Friedrich Pfeil, Munich, pp. 525–548.

Nagler, C., Haug, J.T., Glenner, H., Buckeridge, J., 2017. *Litholepas klausreschi* gen. et sp. nov., a new neolepadine barnacle (Cirripedia, Thoracica) on a sponge from the Upper Jurassic lithographic limestones of southern Germany. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 284, 29–42.

Neumann, C., Jagt, J.W.M., 2003. A ?carcineretid crab from Lower Turonian (Cretaceous) black shales of Misburg, Hannover area (Germany). Contributions to Zoology 72, 161–163.

Newbrey, M.G., Wilson, M.V.H., Ashworth, A.C., 2008a. Climate change and evolution of growth in Late Cretaceous to recent North American Esociformes. In: Arratia, G., Schultze, H.-P., Wilson, M.V.H. (Eds.), Mesozoic Fishes 4 – Systematics, Homology, and Character Definition. Verlag Dr. Friedrich Pfeil, Munich, pp. 311–350.

Newbrey, M., Murray, A.M., Wilson, M.V.H., Brinkman, D., Newman, A., 2008b. Paleolatitudinal response of Characiformes (Teleostei: Ostariophysi) to Cenozoic climate change. Journal of Vertebrate Paleontology 28, 121A.

Newbrey, M.G., Murray, A.M., Wilson, M.V.H., Brinkman, D.B., Neuman, A.G., 2009. Seventy-five-million-year-old tropical tetra-like fish from Canada tracks Cretaceous global warming. Proceedings of the Royal Society B: Biological Sciences 276, 3829–3833.

Nicholson, D.B., Holroyd, P.A., Benson, R.B.J., Barrett, P.M., 2015. Climate-mediated diversification of turtles in the Cretaceous. Nature Communications 6, 7848.

Nicholson, D.B., Holroyd, P.A., Valdes, P., Barrett, P.M., 2016. Latitudinal diversity gradients in Mesozoic non-marine turtles. Royal Society Open Science 3, 160581.

Nixon, K.C., 1999–2002. WinClada. Ver. 1.00.08. Ithaca, NY: Published by the author.

Nursall, J.R., 1996a. The phylogeny of pycnodont fishes. In: Arratia, G., Viohl, G. (Eds.), Mesozoic Fishes: Systematics and Paleoecology. Verlag Dr. Friedrich Pfeil, Munich, pp. 125–152.

Nursall, J.R., 1996b. Distribution and ecology of pycnodont fishes. In: Arratia, G., Viohl, G. (Eds.), Mesozoic Fishes: Systematics and Paleoecology. Verlag Dr. Friedrich Pfeil, Munich, pp. 115–124.

Nursall, J.R., 1999. The family Mesturidae and the skull of pycnodont fishes. In: Arratia, G., Schultze, H.P. (Eds.), Mesozoic Fishes 2: Systematic and Fossil Record. Verlag Dr. Friedrich Pfeil, Munich, pp. 158–188.

Nursall, J.R., Capasso, L., 2004. Gebrayelichthys (novum), an extraordinary genus of neopterygian fishes from the Cenomanian of Lebanon. In: Arratia, G., Tintori, A. (Eds.), Mesozoic fishes, 3: Systematics, Paleoenvironments and Biodiversity. Verlag Dr. Friedrich Pfeil, Munich, pp. 317–340.

Nursall, J.R., Capasso, L., 2008. Additional specimens from Lebanon reveal more of the structure of the pycnodont fish Trewavasia carinata (Davis, 1887). In: Arratia, G., Schulze, H.-P., Wilson, M.V.H. (Eds.), Mesozoic fishes 4: Homology and Phylogeny. Verlag Dr. Friedrich Pfeil, Munich, pp. 143–166.

Nursall, J.R., Maisey, J.G., 1991. Neoproscinetes Figueiredo and Silva Santos 1987. In: Maisey, J. (Ed.), Santana Fossils: an Illustrated Atlas. T. F. H. publications, Inc., New Jersey, pp. 125–137.

O'Brien, C.L., Robinson, S.A., Pancost, R.D., Sinninghe Damsté, J.S., Schouten, S., Lunt, D.J., Alsenz, H., Bornemann, A., Bottini, C., Brassell, S.C., Farnsworth, A., Forster, A., Huber, B.T., Inglis, G.N., Jenkyns, H.C., Linnert, C., Littler, K., Markwick, P., McAnena, A., Mutterlose, J., Naafs, B.D.A., Püttmann, W., Sluijs, A., van Helmond, N.A.G.M., Vellekoop, J., Wagner, T., Wrobel, N.E., 2017. Cretaceous sea-surface temperature evolution: Constraints from TEX86 and planktonic foraminiferal oxygen isotopes. Earth-Science Reviews 172, 224–247.

O'Connor, L.K., Robinson, S.A., Naafs, B.D.A., Jenkyns, H.C., Henson, S., Clarke, M., Pancost, R.D., 2019. Late Cretaceous temperature evolution of the southern high latitudes: A TEX86 perspective. Paleoceanography and Paleoclimatology 34, 436–454.

Otero, O., Valentin, X., Garcia, G., 2008. Cretaceous characiform fishes (Teleostei: Ostariophysi) from Northern Tethys: description of new material from the Maastrichtian of Provence (Southern France) and palaeobiogeographical implications. Geological Society, London, Special Publications 295, 155–164.

Owen, D., 1996. Interbasinal correlation of the Cenomanian stage; testing the lateral continuity of sequence boundaries. Geological Society, London, Special Publications 104, 269–293.

Paul, C.R.C., Lamolda, M.A., Mitchell, S.F., Vaziri, M.R., Gorostidi, A., Marshall, J.D., 1999. The Cenomanian–Turonian boundary at Eastbourne (Sussex, UK): a proposed European reference section. Palaeogeography, Palaeoclimatology, Palaeoecology 150, 83–121.

Peybernes, B., Oertli, H., 1972. La série de passage du Jurassique au Crétacé dans le Bassin sud-pyrénéen (Espagne). Comptes Rendus de l'Académie des Sciences 274, 3348–3351.

Pictet, F.-J. (Ed.), 1850. Description de quelques poissons fossiles du Mont Liban. Jules-Guillaume Fick, Genève.

Pictet, F.-J., Campiche, G., Tribolet, G., de (Eds.), 1858–1860. Description des fossiles du terrain Crétacé des environs de Sainte-Croix. J. Kessmann and H. Georg, Genève.

Poyato-Ariza, F.J., 2010. Polazzodus, gen. nov., a new pycnodont fish from the Late Cretaceous of northeastern Italy. Journal of Vertebrate Paleontology 30, 650–664.

Poyato-Ariza, F.J., 2013. Sylvienodus, a new replacement genus for the Cretaceous pycnodontiform fish "Pycnodus" laveirensis. Comptes Rendus Palevol 12, 91–100.

Poyato-Ariza, F.J., Martín-Abad, H., 2013. History of two lineages: comparative analysis of the fossil record in Amiiformes and Pycnodontiformes (Osteichthyes, Actinopterygii). Revista Espanola de Paleontologia 28, 79–90.

Poyato-Ariza, F.J., Wenz, S., 2000. A new pycnodontiform fish from the Early Cretaceous of Las Hoyas (Cuenca, Spain). Bulletin de la Societe Geologique de France 171, 251–258.

Poyato-Ariza, F.J., Wenz, S., 2002. A new insight into pycnodontiform fishes. Geodiversitas 24, 139–248.

Poyato-Ariza, F.J., Wenz, S., 2004. The new pycnodontid fish genus Turbomesodon, and a revision of Macromesodon based on new material from the Lower Cretaceous of Las Hoyas, Cuenca, Spain. In: Arratia, G., Tintori, A. (Eds.), Mesozoic Fishes 3: Systematics, Paleoenvironments and Biodiversity. Verlag Dr. Friedrich Pfeil, Munich, pp. 341–378.

Poyato-Ariza, F.J., Wenz, S., 2005. Akromystax tilmachiton gen. et sp. nov., a new pycnodontid fish from the Lebanese Late Cretaceous of Haqel and En Nammoura. Journal of Vertebrate Paleontology 25, 27–45.

Pucéat, E., Lécuyer, C., Sheppard, S.M., Dromart, G., Reboulet, S., Grandjean, P., 2003. Thermal evolution of Cretaceous Tethyan marine waters inferred from oxygen isotope composition of fish tooth enamels. Paleoceanography 18, 1029.

Pucéat, E., Lécuyer, C., Donnadieu, Y., Naveau, P., Cappetta, H., Ramstein, G., Huber, B.T., Kriwet, J., 2007. Fish tooth $\delta^{18}O$ revising Late Cretaceous meridional upper ocean water temperature gradients. Geology 35, 107–110.

Regan, C.T., 1923. The skeleton of Lepidosteus, with remarks on the origin and evolution of the lower neopterygian fishes. Proceedings of the Zoological Society of London 1923 445–461.

Richardt, N., 2010. Das Cenoman im Teutoburger Wald bei Halle/Westfalen: Eine integrierte stratigraphisch-sedimentologische, mikrofazielle und geophysikalische Analyse. Geologie und Palaontologie in Westfalen 78, 5–60.

Richardt, N., Wilmsen, M., 2012. Lower Upper Cretaceous standard section of the southern Münsterland (NW Germany)—carbon stable-isotopes and sequence stratigraphy. Newsletters on Stratigraphy 45, 1–24.

Robaszynski, F., Gale, A., Juignet, P., Amédro, F., Hardenbol, J., 1998. Sequence stratigraphy in the Cretaceous of the Anglo-Paris Basin, exemplified by the Cenomanian stage. In: de Graciansky, P.-C., Hardenbol, J., Jaquin, T., Vail, P.R. (Eds.), Mesozoic and Cenozoic Sequence Stratigraphy of European Basins. Society of Sedimentary Geology, Tulsa, pp. 363–385.

Roemer, F.A., 1841. Die Versteinerungen des Norddeutschen Kreidegebirges. Hahn'sche Hofbuchhandlung, Hannover.

Roemer, F.A., 1854. Die Kreidebildungen Westphalens. Verhandlungen des Naturwissenschaftlichen Vereins der preussischen Rheinlande und Westphalens 11, 29–180.

Schweigert, G., 2010. New genera and species of "thalassinideans" (Crustacea: Decapoda: Axiidea, Gebiidea) from the Upper Jurassic of Eichstätt and Brunn (S Germany). Archaeopteryx 27, 21–30.

Scotese, C.R., 2014. Atlas of Late Cretaceous Maps, PALEOMAP Atlas for ArcGIS. In: The Cretaceous, Maps 16 – 22, Mollweide Projection, vol. 2. PALEOMAP Project, Evanston.

Schöllmann, L., Hauschke, N., 2012. Fossilerhaltung und Taphonomie von Stramentum (Stramentum) pulchellum (Sowerby, 1843) (Crustacea: Stramentidae) aus dem Unterturon des Teutoburger Waldes (Nordrhein-Westfalen, Deutschland). Geologie und Palaontologie in Westfalen 84, 55–77.

Schultze, H.P., 1993. The head skeleton of fishes. In: Hanken, J., Hall, B.K. (Eds.), The skull, vol. 2. The University of Chicago Press, Chicago, pp. 189–254.

Schultze, H.P., Arratia, G., 1986. Reevaluation of the caudal skeleton of actinopterygian fishes: I. Lepisosteus and Amia. Journal of Morphology 190, 215–241.

Schultze, H.P., Arsenault, M., 1985. The panderichthyid fish Elpistostege: a close relative of tetrapods. Palaeontology 28, 293–309.

Siegfried, P., 1954. Die Fisch-Fauna des westfälischen Ober-Senons. Palaeontographica Americana 106, 1–36.

Siverson, M., 1992. Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. Palaeontology 35, 519–554.

Smith, T., Rose, K.D., Gingerich, P.D., 2006. Rapid Asia–Europe–North America geographic dispersal of earliest Eocene primate Teilhardina during the Paleocene–Eocene thermal maximum. Proceedings of the National Academy of Sciences of the United States of America 103, 11223–11227.

Smith, K.T., Schwermann, A., Wilmsen, M., 2019. The oldest articulated mosasaurian remains (earliest Turonian) from Germany. Geologie und Palaontologie in Westfalen 91, 3–23.

Sorbini, L., 1976. L'ittiofauna Cretacea di Cinto Euganeo (Padova-Nord Italia). Bollettino del Museo Civico di Storia Naturale di Verona 3, pp. 479–567.

Sørensen, A.M., Surlyk, F., 2008. A brachiopod boring (Podichnus) in a Late Cretaceous oyster from a mangrove-like environment, Skåne, Sweden. Lethaia 41, 295–298.

Sørensen, A.M., Surlyk, F., Jagt, J.W.M., 2012. Adaptive morphologies and guild structure in a high-diversity bivalve fauna from an early Campanian rocky shore, Ivö Klack (Sweden). Cretaceous Research 33, 21–41.

Sørensen, A.M., Surlyk, F., Lindgren, J., 2013. Food resources and habitat selection of a diverse vertebrate fauna from the upper lower Campanian of the Kristianstad Basin, southern Sweden. Cretaceous Research 42, 85–92.

Stidham, T.A., Eberle, J.J., 2016. The palaeobiology of high latitude birds from the Early Eocene greenhouse of Ellesmere Island, Arctic Canada. Scientific Reports 6, 20912.

Stinnesbeck, E.S., Rust, J., Herder, F., 2019. Paleobiology and taphonomy of the pycnodont fish Nursallia gutturosum, based on material from the Latest-Cenomanian–middle Turonian Vallecillo platy limestone, Mexico. PalZ 93, 659–668.

Stumpf, S., Scheer, U., Kriwet, J., 2019. A new genus and species of extinct ground shark,† Diprosopovenator hilperti, gen. et sp. nov. (Carcharhiniformes,† Pseudoscyliorhinidae, fam. nov.), from the Upper Cretaceous of Germany. Journal of Vertebrate Paleontology, e1593185.

Surlyk, F., Christensen, W.K., 1974. Epifaunal zonation on an Upper Cretaceous rocky coast. Geology 2, 529–534.

Surlyk, F., Sørensen, A.M., 2010. An early Campanian rocky shore at Ivö Klack, southern Sweden. Cretaceous Research 31, 567–576.

Taverne, L., 1981. Les Actinoptérygiens de L'Aptien inférieur (Töck) d'Helgoland. Mittelungen aus dem geologish-paläontologisches Institut 51, 43–82.

Taverne, L., 1997. Les poissons crétacés de Nardò. 5°. Pycnodus nardoensis sp. nov. et considérations sur l'ostéologie du genre Pycnodus (Actinopterygii, Halecostomi, Pycnodontiformes). Bollettino del Museo di Storia Naturale di Verona 21, 437–454.

Taverne, L., Capasso, L., 2013a. Osteology and relationships of *Rhinopycnodus gabriellae* gen. et sp. nov. (Pycnodontiformes) from the marine Late Cretaceous of Lebanon. European Journal of Taxonomy 67, 1−14.

Taverne, L., Capasso, L., 2013b. Gladiopycnodontidae, a new family of pycnodontiform fishes from the Late Cretaceous of Lebanon, with the description of three genera. European Journal of Taxonomy 57, 1−30.

Taverne, L., Capasso, L., 2014a. On the "*Coccodus*" *lindstroemi* species complex (Pycnodontiformes, Gladiopycnodontidae) from the marine Late Cretaceous of Lebanon, with the description of two new genera. European Journal of Taxonomy 1−27.

Taverne, L., Capasso, L., 2014b. Ostéologie et phylogénie des Coccodontidae, une famille remarquable de poissons Pycnodontiformes du Crétacé supérieur marin du Liban, avec la description de deux nouveaux genres. Palaeontos 25, 3−43.

Taverne, L., Capasso, L., 2015a. Osteology and relationships of *Acrorhinichthys poyatoi* gen. et sp. nov. (Pycnodontiformes) from the marine Late Cretaceous of Lebanon. European Journal of Taxonomy 116, 1−30.

Taverne, L., Capasso, L., 2015b. New data on the osteology and phylogeny of Gladiopycnodontidae (Pycnodontiformes), a tropical fossil fish family from the marine Upper Cretaceous of Lebanon, with the description of four genera. Geo-Eco-Trop 39, 217−246.

Taverne, L., Capasso, L., 2018a. Osteology and relationships of *Libanopycnodus wenzi* gen. et sp. nov. and *Sigmapycnodus giganteus* gen. et sp. nov. (Pycnodontiformes) from the Late Cretaceous of Lebanon. European Journal of Taxonomy 1−29.

Taverne, L., Capasso, L., 2018b. Osteology and phylogenetic relationships of *Haqelpycnodus picteti* gen. and sp. nov., a new pycnodont fish genus (Pycnodontidae) from the marine Late Cretaceous tropical sea of Lebanon. Geo-Eco-Trop 42, 117−132.

Taverne, L., Layeb, M., Layeb-Tounsi, Y., Gaudant, J., 2015. *Paranursallia spinosa* n. gen., n. sp., a new Upper Cretaceous pycnodontiform fish from the Eurafrican Mesogea. Geodiversitas 37, 215−228.

Taverne, L., Capasso, L., Del Re, M., 2019. The pycnodont fishes from the Lower Cretaceous of the Capo d'Orlando, near Castellammare di Stabia (Naples, Campania, southern Italy), with the description of the new genus *Costapycnodus*. Geo-Eco-Trop 43, 53−74.

Tintori, A., 1981. Two new Pycnodonts (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). Rivista Italiana di Paleontologia e Stratigrafia 86, 795−824.

Trabucho Alexandre, J., Tuenter, E., Henstra, G.A., Van der Zwaan, K.J., Van de Wal, R.S.W., Dijkstra, H.A., De Boer, P.L., 2010. The mid-Cretaceous North Atlantic nutrient trap: black shales and OAEs. Paleoceanography 25, PA4201. https://doi.org/10.1029/2010PA001925.

Tsikos, H., Jenkyns, H.C., Walsworth-Bell, B., Petrizzo, M.R., Forster, A., Kolonic, S., Erba, E., Premoli Silva, I., Baas, M., Wagner, T., Sinninghe Damsté, J.S., 2004. Carbon-isotope stratigraphy recorded by the Cenomanian−Turonian Oceanic Anoxic Event: correlation and implications based on three key-locations. Journal of the Geological Society of London 161, 711−719.

Voigt, S., Aurag, A., Leis, F., Kaplan, U., 2007. Late Cenomanian to Middle Turonian high-resolution carbon isotope stratigraphy: New data from the Münsterland Cretaceous Basin, Germany. Earth and Planetary Science Letters 253, 196−210.

Voigt, S., Erbacher, J., Mutterlose, J., Weiss, W., Westerhold, T., Wiese, F., Wilmsen, M., Wonik, T., 2008. The Cenomanian−Turonian of the Wunstorf section (North Germany): global stratigraphic reference section and new orbital time scale for Oceanic Anoxic Event 2. Newsletters on Stratigraphy 43, 65−89.

Vullo, R., Cavin, L., Khalloufi, B., Amaghzaz, M., Bardet, N., Jalil, N.E., Jourani, E., Khaldoune, F., Gheerbrant, E., 2017. A unique Cretaceous−Paleogene lineage of piranha-jawed pycnodont fishes. Scientific Reports 7, 6802.

Vullo, R., Archambeau, J.P., Bailly, G., Bénéfice, P., 2018. Reassessment of *Cosmodus* Sauvage, 1879, a poorly known genus of large pycnodont fish (Actinopterygii, Pycnodontiformes) from the Cenomanian (Upper Cretaceous) of Western Europe. Cretaceous Research 91, 217−228.

Wagner, A., 1851. Beiträge zur Kenntniss der in den lithographischen Schiefern abgelagerten urweltlichen Fische. Abhandlungen der Mathematisch-Physikalischen Classe der königlich bayerischen Akademie der Wissenchaften, München 6, 1−80.

Weiler, W., 1935. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II: Wirbeltiere der Baharîje-Stufe (unterstes Cenoman). 16. Neue Untersuchungen an den Fischresten. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, N. F. 32, 1−57.

Welsh, J.Q., Goatley, C.H.R., Bellwood, D.R., 2013. The ontogeny of homeranges: evidence from coral reef fishes. Proceedings of the Royal Society, B 280, 20132066.

Wenz, S., 1969. Note sur quelques poissons actinoptérygiens du Crétacé supérieur de Bolivie. Bulletin de la Societe Geologique de France 7, 434−438.

Wenz, S., 1989. *Iemanja palma* n. g., n. sp., Gyrodontidae nouveau (Pisces, Actinopterygii) du Crétacé inférieur de la Chapada do Araripe (NE du Brésil). Comptes Rendus de l'Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'univers, Sciences de la Terre 308, 975−980.

White, E.I., 1927. Two new species and a new genus of Cretaceous pycnodonts from the south of England. Annals and Magazine of Natural History, Series 9, 186−191.

White, E.I., Moy-Thomas, J.A., 1941. Notes on the nomenclature of fossil fishes. Part III: Homonyms M-Z. Annals and Magazine of Natural History ser. II 7, 395−400.

Wiese, F., Kaplan, U., 2001. The potential of the Lengerich section (Münster Basin, northern Germany) as a possible candidate Global boundary Stratotype Section and Point (GSSP) for the Middle/Upper Turonian boundary. Cretaceous Research 22, 549−563.

Wiese, F., Kaplan, U., 2004. Der Mittel-/Ober-Turon Grenzbereich im Raum Lengerich. Geologie und Paläontologie in Westfalen 62, 37−70.

Wilmsen, M., 2003. Sequence stratigraphy palaeoceanography of the Cenomanian Stage in northern Germany. Cretaceous Research 24, 525−568.

Winkler, N., 2017. Two new penaeid shrimps (Crustacea: Decapoda: Dendrobranchiata) from the Solnhofen lithographic limestones (Upper Jurassic, southern Germany). Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 283, 9−24.

Wippich, M.G.E., 2005. Ammonoideen-Kiefer (Mollusca, Cephalopoda) aus Schwarzschiefern des Cenoman/Turon−Grenzbereichs (Oberkreide) im nördlichen Westfalen. Geologie und Paläontologie in Westfalen 65, 77−93.

Wittler, F., 1995. Fische aus dem Turon des Dortmunder Stadtgebietes. Arbeitskreis Palaeontologie Hannover 23, 41−59.

Wittler, F., Roth, R., 2003. Fazies und Fauna der Oberkreidegesteine im Dortmunder Stadtgebiet. I: Temporäre Aufschlüsse im Turon und Unterconiac zwischen 1988 und 2001. Stratigraphie und Fossilführung. Dortmunder Beiträge zur Landeskunde, naturwissenschaftliche Mitteilungen 36, 247−340.

Wittler, F., Roth, R., 2004. Dortmund zur Zeit der Saurier. Begleitbuch zur Ausstellung im Dortmunder Museum für Naturkunde, 10. Juli-22. September 2004. Dortmunder Museum für Naturkunde, Dortmund.

Woodward, A.S., 1893. Some Cretaceous pycnodont fishes. Geological Magazine 10, 433−451.

Woodward, A.S., 1895. Catalogue of the fossil fishes in the British Museum (Natural History). Part III. Containing the actinopterygian Teleostomi of the order Chondrostei (concluded), Protospondyli, Aëtheospondyli, and Isospondyli (in part). British Museum [Natural History], London.

Woodward, A.S., 1908. On some fish-remains from the Lameta beds at Dangargaon, Central Provinces. Palaeontologia Indica 3, 1−6.

Woodward, A.S., 1909. The fossil fishes of the English Chalk. Part V. Monograph of the Palaeontographical Society 63, 153−184.

Woodward, A.S., 1918. The fossil fishes of the English Wealden and Purbeck Formations. Part 2. Monograph of the Palaeontographical Society 70, 49−104.

Zawischa, D., 1982. Saurierzähne aus Wunstorf. Arbeitskreis Palaontologie Hannover 10, 16−17.

Zheng, X.Y., Jenkyns, H.C., Gale, A.S., Ward, D.J., Henderson, G.M., 2013. Changing ocean circulation and hydrothermal inputs during Ocean Anoxic Event 2 (Cenomanian−Turonian): evidence from Nd-isotopes in the European shelf sea. Earth and Planetary Science Letters 375, 338−348.

Appendix A. Supplementary data

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