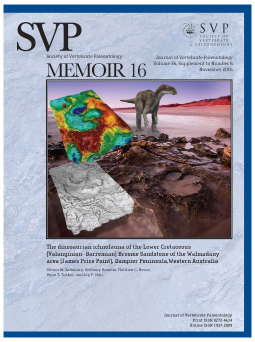

Journal of Vertebrate Paleontology

ISSN: 0272-4634 (Print) 1937-2809 (Online) Journal homepage: http://www.tandfonline.com/loi/ujvp20

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To cite this article: Federico L. Agnolin, Octávio Mateus, Jesper Milàn, Marco Marzola, Oliver Wings, Jan Schulz Adolfssen & Lars B. Clemmensen (2018): Ceratodus tunuensis, sp. nov., a new lungfish (Sarcopterygii, Dipnoi) from the Upper Triassic of central East Greenland, Journal of Vertebrate Paleontology

To link to this article: https://doi.org/10.1080/02724634.2018.1439834

Journal of Vertebrate Paleontology e1439834 (6 pages)
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DOI: 10.1080/02724634.2018.1439834

ARTICLE

CERATODUS TUNUENSIS, SP. NOV., A NEW LUNGFISH (SARCOPTERYGII, DIPNOI) FROM THE UPPER TRIASSIC OF CENTRAL EAST GREENLAND

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ABSTRACT—The fossil record of post-Paleozoic lungfishes in Greenland is currently restricted to a few brief reports of isolated and undetermined tooth plates coming from the uppermost Fleming Fjord Formation (late Norian) in Jameson Land, central East Greenland. Here, we describe *Ceratodus tunuensis*, sp. nov., a new dipnoan from a thin bed of calcareous lake mudstone from the Ørsted Dal Member of the Fleming Fjord Formation. The *Ceratodus* fossil record indicates that during the Late Triassic, this genus was restricted to the middle latitudes of the Northern Hemisphere. This record matches previous paleobiogeographical analyses and indicates that terrestrial biota during the Late Triassic was strongly influenced by paleolatitude.

Citation for this article: Agnolin, F. L., O. Mateus, J. Milàn, M. Marzola, O. Wings, J. Schulz Adolfssen, and L. B. Clemmensen. 2018. *Ceratodus tunuensis*, sp. nov., a new lungfish (Sarcopterygii, Dipnoi) from the Upper Triassic of central East Greenland. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2018.1439834.

INTRODUCTION

Lungfishes have a very long evolutionary history. The oldest fossil record of Dipnoi is Devonian (see Long, 2011), but finds become notably abundant in post-Paleozoic deposits (Martin, 1982; Schultze, 2004). Living forms are represented by three genera in South America, Africa, and Australia (Nelson et al., 2016).

Fossil lungfish tooth plates are only relatively common in Upper Triassic rocks from Europe (Schultze, 2004). Apart from that, European dipnoans still have a patchy fossil record. Several genera of dipnoans have been described from the Upper Devonian of East Greenland (Lehman, 1959; Bendix-Almgreen, 1976), but so far the only post-Paleozoic reports of dipnoans have been restricted to brief mentions of isolated tooth plates coming from the uppermost Fleming Fjord Formation (late Norian) in Jameson Land (Jenkins et al., 1994; Clemmensen et al., 1998, 2016).

Here, we describe tooth plates and jaw bones belonging to *Ceratodus tunuensis*, sp. nov., a new lungfish taxon from the uppermost Fleming Fjord Formation. As the first post-Paleozoic record of fossil lungfishes from Greenland, these specimens add valuable information on the genus *Ceratodus*.

Institutional Abbreviation—NHMD, Natural History Museum of Denmark, Copenhagen, Denmark.

MATERIALS AND METHODS

Geological Setting

During the Triassic, what is now East Greenland was located at the northern rim of the Pangaean supercontinent at about 40°N and bounded to the north by the Boreal Sea (Nøttvedt et al., 2008; Clemmensen et al., 2016). Triassic sediments are well exposed in the Jameson Land Basin, located in central East Greenland at about 71°N in the present-day land areas of Jameson Land and Scoresby Land (Fig. 1).

The thickness of the Triassic succession in East Greenland varies between 1.0 and 1.7 km (Nøttvedt et al., 2008). At the beginning of the Triassic, the Jameson Land Basin is interpreted as a marine bay (Boreal Sea), which gradually underwent regression and continental emergence up through the

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Early Triassic (Clemmensen, 1980a, 1980b; Nøttvedt et al., 2008). These overlying sediments are continental and comprise alluvial fan, river, aeolian dune, saline lake, and freshwater lake deposits (Clemmensen, 1980a; Clemmensen et al., 1998). The prominent freshwater lake deposits from the uppermost part of the Triassic succession (the Fleming Fjord Formation) are particularly well exposed in cliff sides facing the Carlsberg Fjord (Fig. 2). The Fleming Fjord Formation is of Norian–early Rhaetian age, and the fossil-bearing layer in the Carlsberg Ford beds has a likely age of about 208 Ma (see Clemmensen et al., 1998).

The new finds of fossil lungfish remains are from a thin (0.1–0.5 m thick) calcareous mudstone bed in the Carlsberg Fjord beds of the Ørsted Dal Member from the uppermost part of the Fleming Fjord Formation (Jenkins et al., 1994; Clemmensen et al., 1998, 2016). The calcareous mudstone bed formed in an ephemeral to semiperennial lake. The lungfish remains are associated with numerous freshwater bivalves, undetermined amphibian remains, and fragments of testudinatans.

Eight specimens were collected during the GeoCenter Møns Klint Dinosaur Expeditions in 2012 and 2016 and are deposited in the NHMD under institutional numbers 115910 to 115917.

Terminology

In the present article, we follow the terminology of Churcher et al. (2006; see also Churcher and De Iuliis, 2001) for the tooth plates, and that of Martin (1981) for jaw-bone structures. Distinction between upper and lower tooth plates follows the criteria detailed by Martin (1980, 1981). The angle between the medial and lingual margins of the tooth plate is termed 'inner angle' following Vorobyeva and Minikh (1968). Histological terminology follows Kemp (2001). Measurements were taken as in Apesteguía et al. (2007).

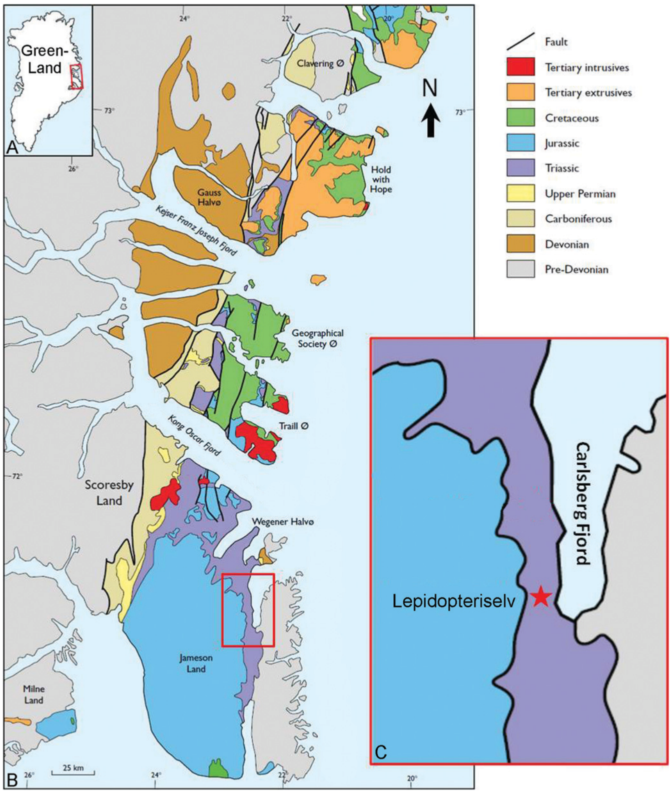

FIGURE 1. Location map of the East Greenland showing the Mesozoic deposits in the Jameson Land Basin. **A**, small insert showing Greenland, with East Greenland indicated by the box. **B**, geological map of East Greenland, with the Carlsberg Fjord locality indicated by the box. **C**, close-up of the eastern part of the basin near Carlsberg Fjord and the locality with Upper Triassic rocks at Lepidopteriselv. Modified from Stemmerik et al. (1997).

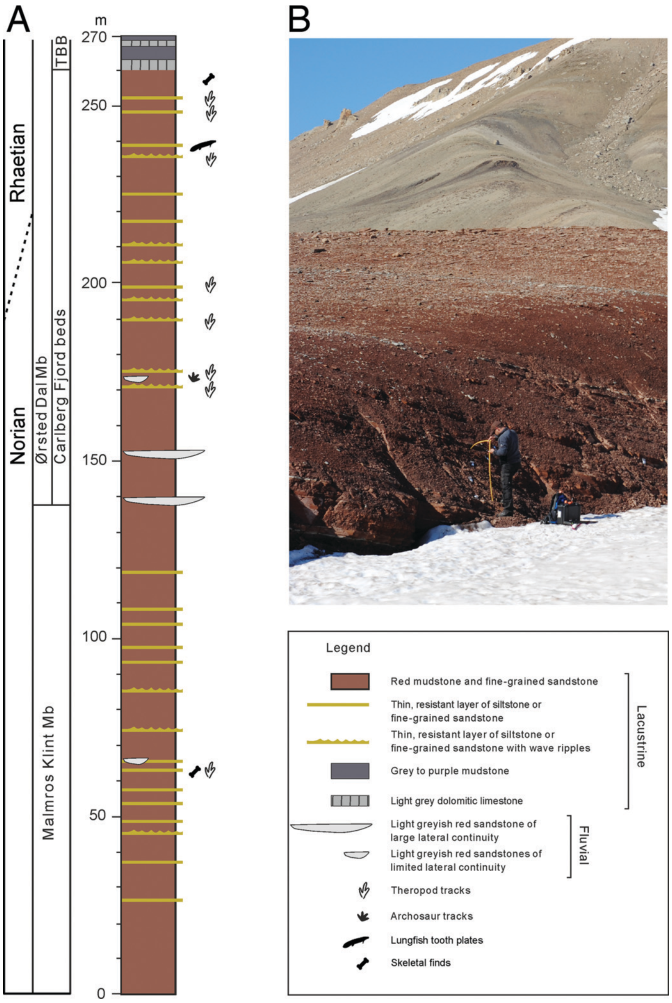

FIGURE 2. **A**, stratigraphic scheme of the Triassic succession exposed at Carlsberg Fjord. **B**, field photo showing the reddish-brown bedded lacustrine sediments of the Ørsted Dal Member.

SYSTEMATIC PALEONTOLOGY

DIPNOI Müller, 1845
CERATODONTIDAE Gill, 1873
CERATODUS Agassiz, 1838
CERATODUS TUNUENSIS, sp. nov.
(Figs. 3–5)

Holotype—NHMD 11590, a right upper tooth plate lacking the labial half of the first ridge (Fig. 3A).

Referred Material—NHMD 11911, an upper left tooth plate with incomplete mesial margin and first ridge (Fig. 3B); NHMD 115912, an upper left tooth plate (Fig. 3C); NHMD 115913, a fragmentary left lower tooth plate (Fig. 3D); NHMD 115914, an incomplete left lower tooth plate (Fig. 4A); NHMD 115915, an incomplete left lower tooth plate (Fig. 4B); NHMD 115916, an incomplete left lower tooth plate (Fig. 4C); NHMD 115917, a right nearly complete jaw

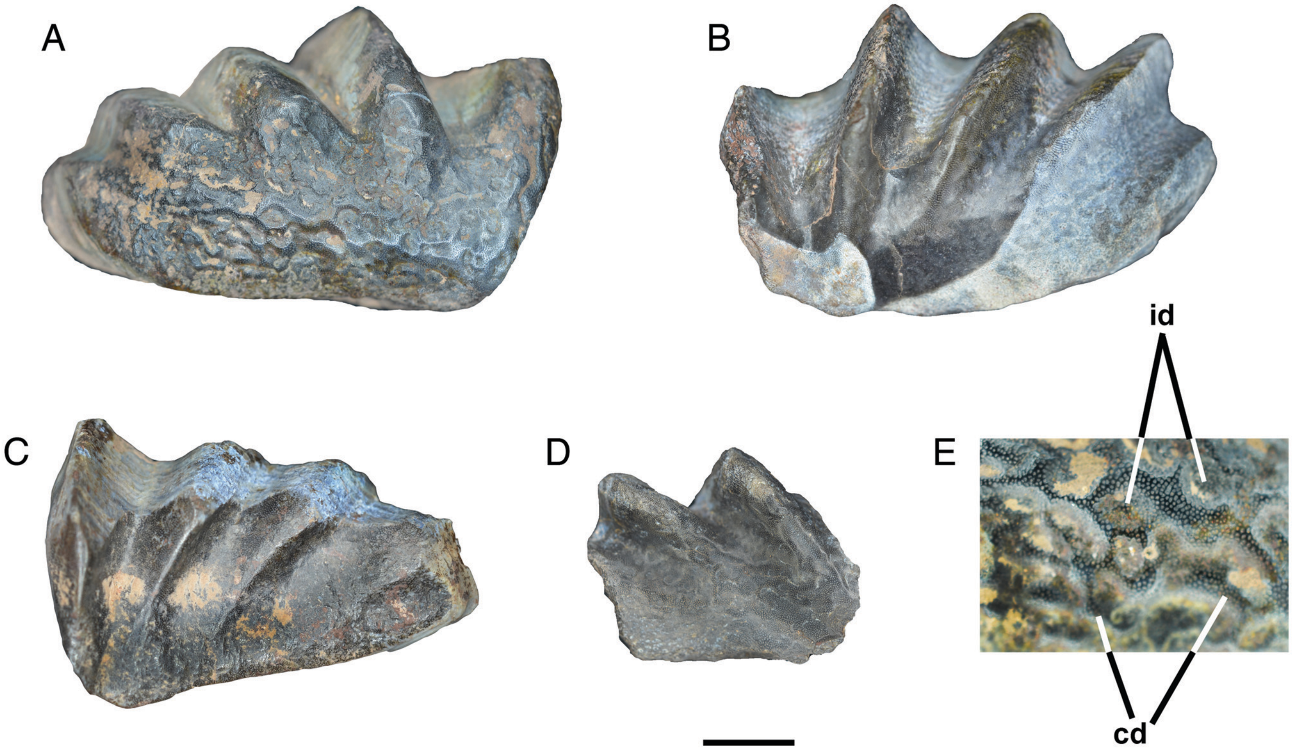

FIGURE 3. *Ceratodus tunuensis*, sp. nov., holotype and referred material. **A**, **E**, holotype NHMD 115910, a right upper tooth plate (**A**), with details of the tooth plate occlusal surface (**E**); **B**, NHMD 115911, an upper left tooth plate; **C**, NHMD 115912, an upper left tooth plate; **D**, NHMD 115913, fragmentary left lower tooth plate. **Abbreviations**: **cd**, circumdenteonal dentine; **id**, interdenteonal dentine. Scale bar equals 1 cm.

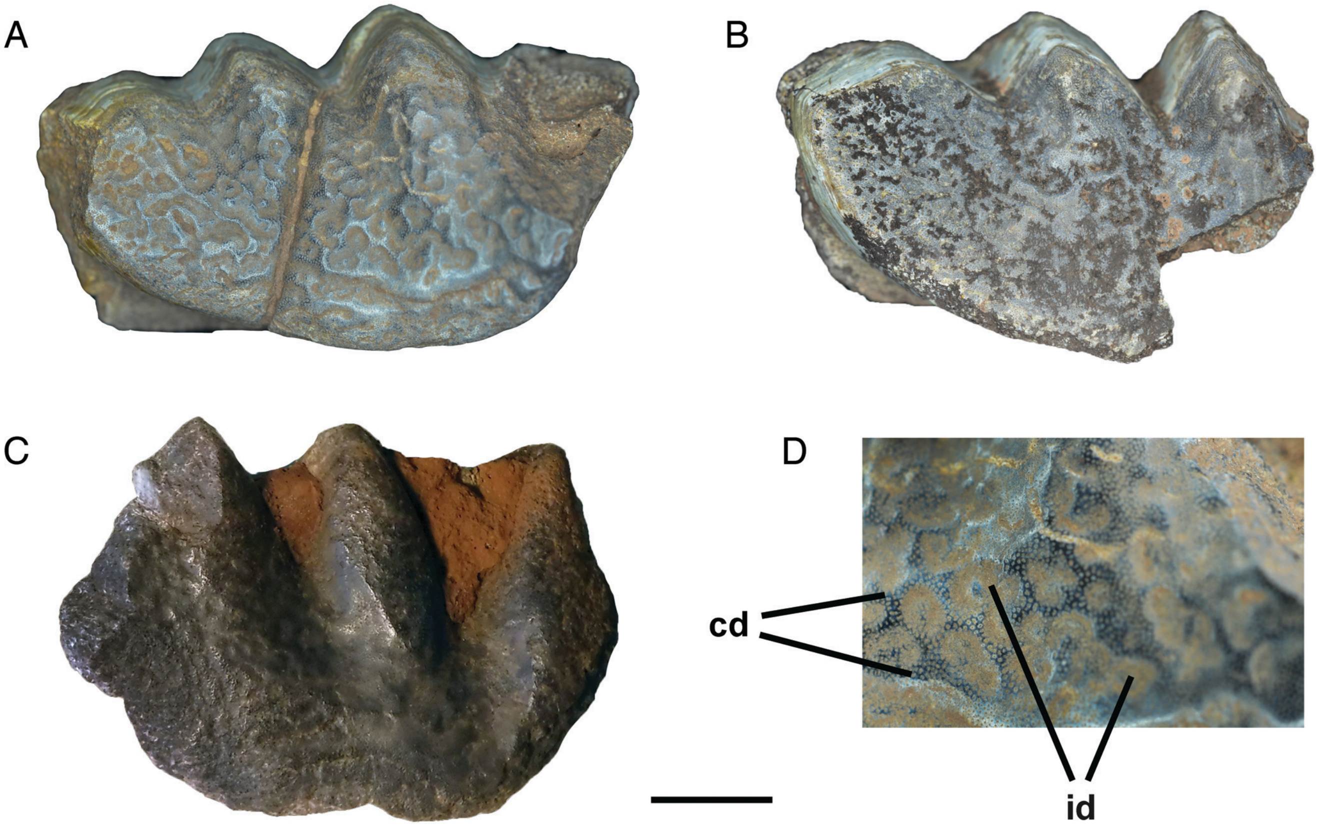

FIGURE 4. *Ceratodus tunuensis*, sp. nov., referred material. **A**, NHMD 115914, an incomplete left lower tooth plate; **B**, NHMD 115915, an incomplete left lower tooth plate; **C**, **D**, NHMD 115916, an incomplete left lower tooth plate (**C**), with details of tooth plate occlusal surface (**D**). **Abbreviations**: **cd**, circumdenteonal dentine; **id**, interdenteonal dentine. Scale bar equals 1 cm.

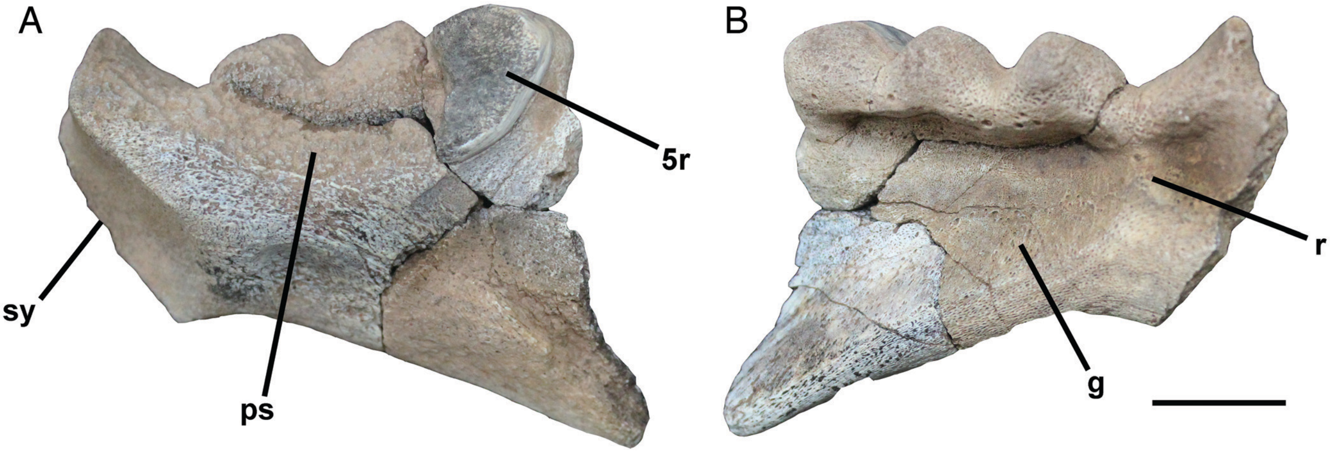

FIGURE 5. *Ceratodus tunuensis*, sp. nov., referred material, NHMD 115917, right lower jaw bone. **A**, lateral and **B**, medial views. **Abbreviations**: **g**, prearticular groove; **ps**, tooth plate scar; **r**, Ruge's ridge; **sy**, symphysis of jaw bone; **5r**, fifth ridge. Scale bar equals 2 cm.

bone including the last ridge of the corresponding tooth plate (Fig. 5).

Type Locality—The specimens were collected during the 1990s American-Danish expeditions as well as later by the expeditions conducted by the Geocenter Møns Klint Dinosaur Expeditions to Lepidopteriselv at the eastern margin of the Jameson Land Basin (71°15.791′N, 22°32.614′W and 71°15.629′N, 22°32.737′W).

Type Horizon—Thin calcareous mudstone layer in the late Norian Carlsberg Fjord beds of the Ørsted Dal Member in the Fleming Fjord Formation (Fig. 2).

Etymology—The specific name *tunuensis* is from 'Tunu,' the Inuit word for East Greenland.

Diagnosis—Robust dipnoan diagnosable on the basis of the following combination of characters (autapomorphies marked by an asterisk*): (1) five ridges on upper tooth plates and four ridges on lower tooth plates; (2) relatively short crests that are separated by wide and shallow inter-ridge furrows; (3) upper tooth plates with well-developed mesiointernal angle; (4) lower tooth plates with lingual margin uniformly convex*; (5) upper tooth plates with straight to slightly concave lingual margin; (6) first ridge of upper tooth plates subequal in size to other ridges; and (7) occlusal surface of the tooth plates with wide and deep occlusal pits that are randomly distributed along most of the tooth plate.

DESCRIPTION

The new species is represented by jaw bones and both upper and lower tooth plates. The specimens are considered as belonging to the same species based on similar size and shape, similar robustness, and coincidence in most features, including presence of irregular occlusal pits along the crushing surface (Table 1). Based on the relative stages of wear defined by Martin (1980), none of the plates belong to juvenile or senile individuals.

Upper Tooth Plates

The upper tooth plates are relatively robust and high-crowned. They are roughly subtriangular in contour, being mesiodistally elongate. The ridges are relatively short and robust, with a flat and wide occlusal surface. The ridges are separated by wide and shallow inter-ridge furrows. The inner angle is about 95° in upper tooth plates. The occlusal surface of the plates is very wide and broad, and slightly concave. The whole occlusal surface shows abundant, wide, and irregular occlusal pits that result in a roughly reticulate pattern. Interdenteonal and circumdenteonal dentine are not arranged in an ordered pattern. The plate surface is covered by randomly situated punctuations corresponding to pulp canals (Bemis and Northcutt, 1992) of dentine. There is no trace of hypermineralized dentine free of denteons or petrodentine (Kemp, 2001). The upper tooth plates have five acute ridges, showing low and wide crests along each ridge. The ridges converge at the mesiointernal angle and do not originate anteriorly as in several neoceratodontids (sensu Kemp, 1997). The ridges are relatively straight, and the first ridge is only slightly posteriorly curved and has a nearly straight mesiobuccal margin. The fifth ridge is robust and is not twinned. Ridge size is as follows: 1 > 2 > 4 > 3 > 5. The mesiointernal angle is pronounced, being represented by a relatively well-developed bump. It is located at the level of the second ridge. Denticulations cannot be observed in the buccal margin of the crests. Inter-ridge furrows are relatively shallow and wide, with a rounded lingual end. The first furrow is as deep and wide as the other furrows. The mesiobucal margin of the plate is convex and lacks any sign of contact with the opposite tooth plate.

Lower Tooth Plates

The lower tooth plates have four robust ridges, showing low crests along at the buccal half of each ridge. The inner angle is about 100° in lower tooth plates. The ridges converge at the mesiointernal angle of the plate. The first ridge is not preserved in any specimen. However, the scar left on the jaw bones indicates that this ridge was large, robust, and with a uniformly convex mesiobuccal margin. The fourth ridge is robust and is not twinned. Ridge size is as follows: 1 > 4 > 2 > 3. A mesiointernal keel is absent. The mesial and lingual margins form a continuous convex margin. Denticulations are not observed in the buccal margin of the crests. Inter-ridge furrows are relatively shallow and wide, with a narrow lingual end. The first furrow is subequal in size and shape to the remaining furrows.

The prearticular bone is massive, wide, and robust, being notably anteroposteriorly shortened. It expands transversely in its posterior part. The tooth plate is fully attached to the bone. Due to the long symphyseal process of the prearticular, the tooth plates are separated from each other. The articular surface of the symphysis is decorated by upright minute grooves and ridges. The symphysis is notably dorsoventrally low and buccolingually extended, forming a linear-type symphysis as defined by Kemp

TABLE 1. Measurements (in mm) of selected specimens of *Ceratodus tunuensis*, sp. nov.

Dimension	NHMD 11590	NHMD 11911	NHMD 115912	NHMD 115914
Total length of the tooth plate	65.2	75	59	54
Total length of first ridge	—	—	37	—
Total length of second ridge	35	33	34	36
Total length of third ridge	33	32	33	34
Total length of fourth ridge	34	—	54	—
Total length of fifth ridge	20	—	—	—
Length of lingual margin	52	—	—	—

(1998). The orientation of the symphysis indicates a relatively wide jaw arcade. There is a deep and wide prearticular groove on the medial surface of the bone. The groove is double, being subdivided subvertically by a relatively shallow Ruge's ridge. It is located at the level of the first inter-ridge furrow.

DISCUSSION

Post-Paleozoic dipnoans bear prominent masticatory structures known as tooth plates. Due to their high fossilization potential, tooth plates are usually the only known elements of Mesozoic and Tertiary fossil dipnoans (Martin, 1982; Cavin et al., 2007; Skrzycki, 2015). In most cases, isolated tooth plates show enough features to allow determination at the species level and even might help to infer phylogenetic relationships (see also Cione and Gouiric-Cavalli, 2012; Skrzycki, 2015; Fanti et al., 2016).

Having relatively robust and thick crushing upper tooth plates with five or fewer ridges lacking tubercles, a convex lingual margin, and prearticular bone with a Ruge's ridge distinguishes *C. tunuensis* from all known pre-Triassic dipnoans (Martin, 1982, 1984; Apesteguía et al., 2007). Among ceratodontiforms, presence of five or fewer ridges on upper tooth plates is a feature exclusively shared by species of Ceratodontidae or Ptychoceratodontidae (Martin, 1982, 1984; Cavin et al., 2007).

The plates here described are referred to *Ceratodus* on the basis of robust and short ridges having a broad crushing occlusal surface with rounded contours (Martin, 1984; Schultze, 1991; Kemp, 1993; Cavin et al., 2007). This contrasts with the more elongate and acute ridges that are typical of ptychoceratodontids (sensu Martin, 1982; see also Skrzycki, 2015). Further, in contrast to ptychoceratodontids, including the well-known species *P. roemeri* and *P. serratus*, the occlusal pits in *C. tunuensis* are abundant over all of the occlusal surface and are not restricted to the inter-ridge furrows (Skrzycki, 2015).

Since the 19th century, isolated tooth plates mostly have been referred to the genus *Ceratodus*. However, these plates belong to a large number of genera, as demonstrated by Martin (1980, 1981, 1982, 1984; see also Martin et al., 1981). Analyses of abundant tooth plates by Martin (1980, 1982) resulted in the recognition of only two valid Triassic species referable to *Ceratodus* (*C. latissimus* and *C. kaupi*). Kemp (1993) described a third valid species, *C. diutinus*, from the Cretaceous of Australia. Although some authors have employed *Ceratodus* as a 'form genus' (e.g., Kirkland, 1988), as demonstrated by Kemp (1993, 1998), these taxa are not particularly similar to *C. latissimus* Agassiz, 1838, the type species of the genus (see also Pardo et al., 2010; Frederickson and Cifelli, 2016).

Taking into consideration the detailed analysis of ontogenetic and intraspecific variation of dipnoan tooth plates carried out by Skrzycki (2015), we noted some features that distinguish *C. tunuensis*, sp. nov., from other species of the genus *Ceratodus*.

Ceratodus tunuensis, sp. nov., differs from *C. kaupi* and *C. diutinus* by the different occlusal contour of upper tooth plates. In the latter two species, the profile of the tooth plates is very broad and relatively mesiodistally short, with a very deep lingual keel, a combination of traits absent in *C. tunuensis*, sp. nov.

On the other hand, the occlusal profile of the tooth plates of *C. tunuensis*, sp. nov., matches that of *C. latissimus* (Kemp, 1993). Further, in both *C. tunuensis*, sp. nov., and *C. latissimus*, the occlusal pits are abundant over all of the occlusal surface, and are not mainly restricted to inter-ridge furrows as in *C. kaupi* and *C. diutinus* (Kemp, 1993). In spite of such similarities, *C. tunuensis*, sp. nov., differs from *C. latissimus* in several important details. In *C. tunuensis*, sp. nov., the first ridge is short and robust, contrasting with the elongate condition exhibited by *C. latissimus* (Miall, 1878). In *C. tunuensis*, sp. nov., the upper tooth plate shows a pronounced mesiointernal angle, whereas in *C. latissimus* such an angle is absent (Kemp, 1993). Further, in *C. tunuensis*, sp. nov., lower tooth plates show a uniformly convex lingual margin, lacking any sign of the mesiointernal keel present in *C. latissimus* (Kemp, 1993).

The available information suggests that *C. tunuensis*, sp. nov., is a new lungfish species that belongs to the genus *Ceratodus* sensu stricto.

Paleoecological and Paleobiogeographical Implications

Ceratodus tunuensis, sp. nov., was found in rocks of the uppermost Fleming Fjord Formation, which is exclusively lacustrine-fluvial in origin (Clemmensen et al., 1998) and lacks any sign of marine influence. Cavin et al. (2007; see also Fernández et al., 1973; Kirkland, 1988) proposed that most, if not all, post-Paleozoic dipnoans were adapted to freshwater habitats (contra Schultze, 1991), a fact supported by the depositional origins of most known post-Triassic fossils.

The presence of *Ceratodus tunuensis*, sp. nov., in the Late Triassic (late Norian) of East Greenland constitutes an important addition to the geographical distribution of the genus *Ceratodus*. Late Triassic specimens unambiguously referable to *Ceratodus* are restricted to the Northern Hemisphere (Martin, 1982), and no pre-Cretaceous record of this genus is known in the Southern Hemisphere (see Kemp, 1993, 1997). From younger deposits, in the Upper Cretaceous and lower Paleogene, species referable to *Ceratodus* have been reported from Australia and South America (Kemp, 1993; Agnolin, 2010).

Ezcurra (2010) proposed, on the basis of the record of tetrapods, that by the Late Triassic, the geographical distribution of fauna was strongly paleolatitudinally influenced, with several tetrapod lineages restricted to well-defined paleolatitudinal belts. On the basis of the currently known fossil record, it is possible to infer that by the Late Triassic, dipnoans of the genus *Ceratodus* were restricted to middle latitudes.

By the Cretaceous, species of the genus *Ceratodus* are totally absent from Europe (Schultze, 2004), suggesting local extinction of the genus. By the Late Cretaceous, the genus *Ceratodus* is found in the Southern Hemisphere, suggesting a very late arrival of these lungfishes to Australia, and then South America (see Agnolin, 2010).

ACKNOWLEDGMENTS

We are grateful for the generous support to the 2012 and 2016 expeditions from the following foundations: Dronning Margrethes og Prins Henriks Fond, Arbejdsmarkedets Feriefond, Oticon Fonden, Knud Højgaards Fond, Louis Petersens Legat, Det Obelske Familiefond, and Ernst og Vibeke Husmans Fond. POLOG provided professional expedition logistics and camp solutions. A. Lynge is thanked for help with the Inuit species name. N. Klein is thanked for help in the field. Special acknowledge to L. Cavin, an anonymous reviewer, and the editor Charles Underwood; their observations greatly improved the quality of present contribution. Finally, we thank N. Natorp, director of Geocenter Møns Klint, for organizing the expeditions.

M.M. is supported by the Fundação para a Ciência e a Tecnologia doctoral fellowship SFRH/BD/99580/2014 (Ministério da Ciência, Tecnologia e Ensino superior, Portugal). Field work in Greenland by L.B.C. was partly supported by the Carlsberg Foundation.

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Submitted November 9, 2017; revisions received December 8, 2017; accepted December 11, 2017.
Handling editor: Charlie Underwood.