

A new dipnoan species *Janvierpaucidentes tuulingi* gen. et sp. nov. from the Pragian (Early Devonian) of Mimerdalen, Svalbard (Norway), with an unusual dentition

Una nueva especie de dipnoo *Janvierpaucidentes tuulingi* gen. et sp. nov. del Praguense (Devónico Inferior) de Mimerdalen, Svalbard (Noruega), con una dentición inusual

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Abstract: A new dipnoan lower jaw from the Wood Bay Formation (Pragian) of Svalbard (Norway), preserves a partial dentary and partial toothplates referred to the new species *Janvierpaucidentes tuulingi* gen. et sp. nov. The more complete toothplate is elongate with three short rows of teeth but is damaged medially. A large number of dipnoans are known from the Early Devonian, showing a range of dentitions. Other tooth-plated dipnoans from this time period include *Diabolepis speratus*, *Speonesydron iani*, *Tarachomyx oepiki*, *Tarachomyx multicostatus*, *Ichnomyx kurnae* and *Ichnomyx karatajae*, and two unnamed toothplates from Vietnam. In *Melanognathus canadensis*, rows of teeth are located along the prearticular, which is otherwise covered in a shagreen of denticles; this denticle-dominated dentition also characterized *Uranolophus wyomingensis*. The dentition of *Janvierpaucidentes tuulingi* differs from these toothplate morphologies and is highly unusual in having the more rostral and caudal tooth rows nearly paralleling the jaw margin, with a maximum angle between the tooth rows approaching 180 degrees. In this character, *Janvierpaucidentes tuulingi* is more comparable to taxa such as *Xylognathus macrustenus* from the Carboniferous, increasing the already high disparity of lungfish dental morphology in the Devonian.

Resumen: Una nueva mandíbula inferior perteneciente a un dipnoo de la Formación Wood Bay (Praguense) de Svalbard (Noruega) se compone de partes de los huesos dentarios y de varias placas dentales referidas a la nueva especie *Janvierpaucidentes tuulingi* gen. et sp. nov. La placa dental más completa que se conserva es alargada y se compone de tres filas cortas de dientes, pero se encuentra dañada medialmente. Numerosos dipnoos del Devónico temprano muestran una gran variedad de denticiones. Otros dipnoos caracterizados por placas denticuladas de este período incluyen a *Diabolepis speratus*, *Speonesydron iani*, *Tarachomyx oepiki*, *Tarachomyx multicostatus*, *Ichnomyx kurnae* e *Ichnomyx karatajae*, y dos placas dentales pertenecientes a dipnoos indeterminados de Vietnam. En *Melanognathus canadensis*, las filas de dientes se disponen en el hueso prearticular, asociadas a un conjunto de numerosos denticulos; este tipo de dentición dominada por denticulos también es característica de *Uranolophus wyomingensis*. No obstante, la dentición de *Janvierpaucidentes tuulingi* difiere de estas morfologías de las placas dentales en que las filas de dientes más rostrales y caudales son casi paralelas al margen de la mandíbula, con un ángulo máximo entre las filas de dientes que ronda los 180 grados. La morfología dental de *Janvierpaucidentes tuulingi* se asemeja a la de taxones como *Xylognathus macrustenus* del Carbonífero, contribuyendo así a aumentar la ya de por sí alta disparidad morfológica de la dentición conocida en los dipnoos del Devónico.

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INTRODUCTION

Lungfish (Dipnomorpha; Sarcopterygii) first evolved in the Early Devonian (Lochkovian–Emsian, 419–393 My), and are characterized by a modified upper and lower jaw dentition, associated with the pterygoid and prearticular bones, respectively. Also possessing this modified dentition is *Youngolepis praecursor* Chang & Yu, 1981, sister taxon to the Dipnoi, recently described

as having a tooth-plated dipnoan-like dentition in the upper jaw (Cui *et al.*, 2022). Early Devonian taxa retaining this tooth-plated dentition include the basal taxon *Diabolepis speratus* Chang & Yu, 1984 (Smith & Chang, 1990), along with *Tarachomyx oepiki* Barwick, Campbell & Mark-Kurik, 1997 and *Tarachomyx multicostatus* Qiao & Zhu, 2008, all having a large number

of tooth rows on the plate. Unnamed toothplates from Vietnam also have this morphology (Tong-Dzuy & Janvier, 1994; Mondéjar-Fernández *et al.*, 2020).

Other tooth-plated forms are *Ichnomyrax kurnai* Long, Campbell & Barwick, 1994, *Ichnomyrax karatajae* Reisz, Krupina & Smith, 2004, *Jessenia concentrica* Otto & Bardenheuer, 1996 and *Speonesydrium iani* Campbell & Barwick, 1984, one difference in these species being the reduction of the number of tooth rows on the plate. Typically, in all these taxa, there is a size gradation of teeth from smaller medially and larger (newer teeth added) laterally. Tooth rows are initiated medially, and as the teeth become larger, the rows expand laterally, and the toothplate increases in size. In *Ichnomyrax* and

Speonesydrium, a rounded 'heel cushion' is present medially (Campbell & Barwick, 1984; Long *et al.*, 1994; Reisz *et al.*, 2004), while in *Jessenia* the toothplate is resorbed medially and replaced with denticles (Otto & Bardenheuer, 1996). Other dentition types in the Early Devonian include that in *Uranolophus wyomingensis* Denison, 1968, with denticles covering the pterygoid and prearticular and a 'tooth ridge' along the lateral margin of these. In *Melanognathus canadensis* Jarvik, 1967, rows of individual teeth line the lateral margin of the denticulated prearticular and palate (Schultze, 2001). Finally, multiple taxa possess a 'dipnorhynchid dentition', dominated by thickened, smoother plates of dentine, such as *Dipnorhynchus* Jaekel, 1927, *Cath-*

A

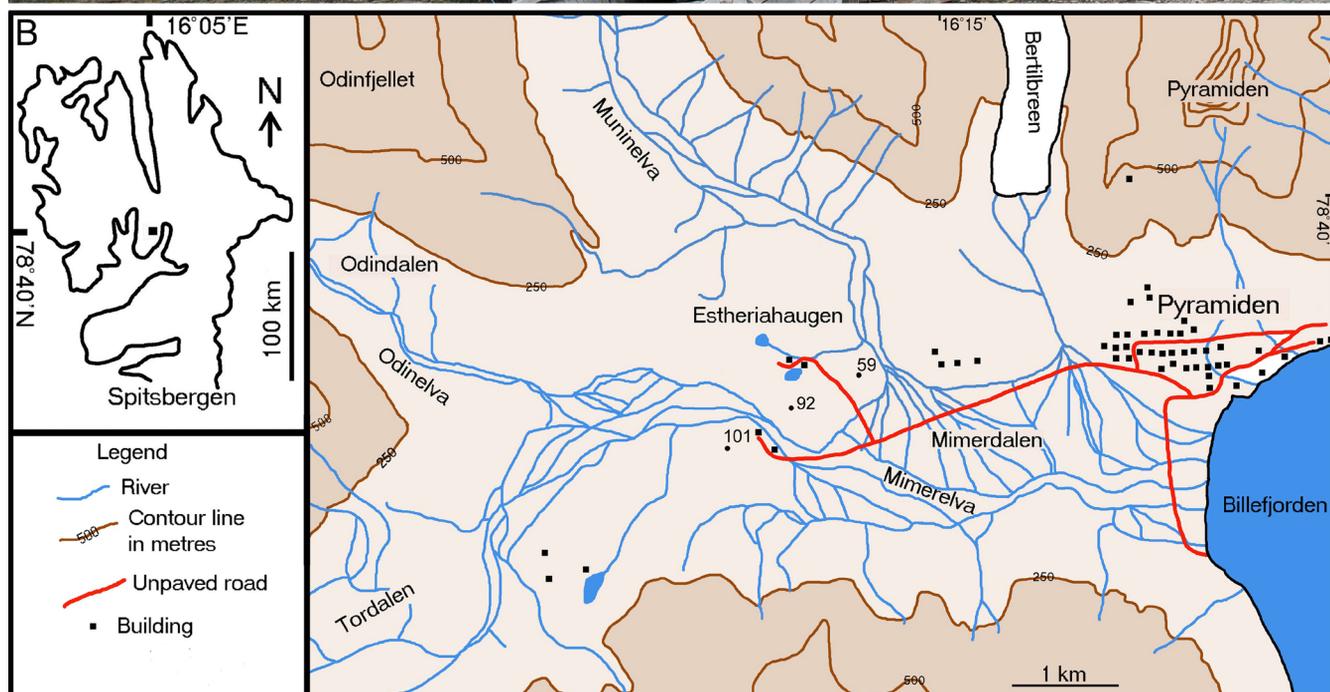


Figure 1. 'Tormi Hill'. **A**, Photograph of 'Tormi Hill' from Estheriahaugen with the mountain Yggdraskampen (highest point 585 m) in the background; **B**, locality map for 'Tormi Hill'. The 92-meters spot height indicates 'Tormi Hill'. Other spot heights are also metres above sea level.

Iorhynchus Campbell, Barwick & Senden, 2009, and *Sorbitorhynchus* Wang, Drapala, Barwick & Campbell, 1993 (Campbell & Barwick, 1982, 1985, 1999; Shitao *et al.*, 1993; Qiao & Zhu, 2015). The new lungfish dentary from Svalbard described below is clearly a tooth-plated form, but with differences with respect to other Devonian taxa and similarities to later taxa from the Carboniferous, like *Uronemus splendens* (Traquair, 1881) and more specifically *Xylognathus macrustenus* Smithson, Richards & Clack, 2016.

Possible Early Devonian dipnoans have only recently been described from Spitsbergen (Svalbard) by Clément *et al.* (2006) from southern Andrée Land. The material comprised disarticulated remains, with only an opercular bone of the skull being identifiable; the rest were too fragmentary to allow a new species to be erected. Clément *et al.* (2006) considered the deposits producing these lungfish remains to be either late Emsian or early Eifelian in age. The new dipnoan species described here, whilst found geographically not far away in Dickson Land (just to the southeast of Andrée Land), is older, being late Pragian in age, near the Pragian–Emsian boundary. The specimen described below is likely a different taxon from the material described by Clément *et al.* (2006), although further collecting of both is required. It thus represents the oldest known lungfish from Spitsbergen, also the oldest dipnoan from the Old Red Sandstone continent (Laurussia) and equal in age to the oldest Australian dipnoans (Gondwana; Tab. 1). It was previously thought that the dipnoans evolved in Gondwana, but that hypothesis can no longer be assumed.

FOSSIL LOCALITY

The locality where the new dipnoan was collected is on a conspicuous flat-topped hill (Fig. 1A) with alternating bands of red and grey rock (sedimentological details below). Topographical maps of Svalbard do not have a name for this hill, but it is indicated on these maps by a 92-metre spot height just south of Estheriahaugen (Fig. 1B). On the specimen labels from the site, we informally named the hill ‘Tormi Hill’ after Tormi Tuuling, a member of our 2016 party who suggested we should prospect the hill for fossils.

Geology and depositional environment of the ‘Tormi Hill’ area

The Lower Devonian deposits in the vicinity of ‘Tormi Hill’ consist of almost upright beds of variable thickness alternating between red mudstones and grey conglomerates (when fresh, but becoming redder with weathering). These conglomerates are more resistant to weathering and form the hilltops, clearly visible in satellite images (Fig. 2A). The red mudstones are generally the thicker units and represent flood plain deposits. They were certainly shallow water deposits at times, as numerous ripples are preserved on many

bedding planes (Fig. 2B). The thinner conglomerates are coarse-grained, with the larger clasts exhibiting a fair degree of rounding. This indicates a high-energy environment, representing channel deposits. They are variable in thickness and nature, even a short distance along strike and there is much variability in sections with both unsorted massive conglomerates as well as thinner, sandier layers (Fig. 2C). Also, present are cross-beds (Fig. 2C), leaving little doubt as to their fluvial nature. This is all consistent with the conglomerates being laid down by braided streams. Most of the conglomerates contain fossil remains.

The most productive unit so far found, including where the new dipnoan was collected, is the final grey layer on the northwest slope of the ‘Tormi Hill’ (Fig. 2D). This unit is one of the thicker conglomerates on the hill at about 1 m thick (Fig. 2E). However, this unit varies considerably along strike both in thickness and composition. When fresh, the unit is extremely hard but becomes friable with weathering. The unit has very large numbers of osteostracan headshields within the coarse makeup (Fig. 2F). Also present in large numbers are partially articulated arthrodire remains and porolepiform head plates and scales. Rarer still are acanthodian spines, plant stems and the unique dipnoan specimen described below. It is unclear how far along strike this mass of fossil remains extends due to burial by overburden. The fossils are similar in size, indicating size sorting. One hypothesis is that they were deposited on a bend of the stream where the energy was lowered enough to allow the fossils to drop out of the water flow.

Lower Devonian history of fossil vertebrate research in Mimerdalen

Mimerdalen is located to the extreme east of Dickson Land (see Piepjohn & Dallmann (2014) for the topography and geology of the area), but most Lower Devonian research in this area has been conducted further west along Dickson Bay. Alfred Nathorst and his team were the first scientists to collect Devonian fossils in the Dickson Land in 1882 as part of a Swedish geological expedition (Nathorst, 1884). The vertebrate fossils Nathorst and his team collected were forwarded to E. Ray Lankester for description (Lankester, 1884). All the Early Devonian fossils Lankester (1884) described came from Dickson Bay. From Mimerdalen, Lankester (1884) only described Middle Devonian (Givetian) remains (see Newman *et al.* (2019) for discussion regarding the age of these deposits).

Later expeditions conducted research in the area, but it was Stensiö’s 1916 and 1917 expeditions that provided a wealth of information on the Devonian strata of Mimerdalen (Stensiö, 1918). From the Lower Devonian, he reported the heterostracan *Pteraspis nathorsti* (now known as *Doryaspis nathorsti* (Lankester, 1884)) and the sarcopterygian *Porolepis posnaniensis* (Kade, 1858) from red and green sandstones. He also noted



Figure 2. 'Tormi Hill' views. **A**, Satellite view of Mimerdalen with 'Tormi Hill' indicated by black arrow; **B**, shallow water ripple marks in a red mudstone; **C**, crossbedding in a sandstone channel deposit; **D**, general view of 'Tormi Hill' with the foreground grey sandstone layer being the most faunally productive; **E**, close-up view of the most fossil productive grey sandstone layer; **F**, visible osteostracan headshields (white arrow) on the surface of the most fossil productive grey sandstone layer.

from the 'arkosic' (the conglomerates mentioned above) rocks and sandstones on the southern side of Mimerdalen the presence of *D. nathorsti*, the arthrodire *Acanthaspis* sp. and a new species of acanthodian *Onchus mimer* (which was not formally described and so is considered a *nomen nudum*). Stensiö's *Acanthaspis* specimens were later used by Heintz (1929) to erect the species *Svalbardaspis stensioei* (now known as *Arc-*

tolepis stensioei (Heintz, 1929)). Stensiö (1918) also reported the presence of *Porolepis* sp. and *D. nathorsti* on the southern tip of Estheriahaugen, and 'Porolepis-horizons' in the valley between the mountains Odens and Torsfjellet. This indicates he was aware that 'Tormi Hill' contained Early Devonian fossils, although it seems he missed the osteostracan concentration. Stensiö (1918) considered the fauna above equivalent

to those collected from Dickson Bay, and so were the same aged strata.

Vogt (1941) also collected a large suite of fossils in his expeditions in 1925 and 1928. The English-Norwegian-Swedish expedition of 1939 only spent a day in Mimerdalen (Føyn & Heintz, 1943). However, these and later expeditions tended to concentrate on the structural geology and newer strata (e.g., Piepjohn & Dallmann, 2014; Berry & Marshall, 2015) rather than the Early Devonian fossils where attention was focused further north (e.g., Blicek *et al.*, 1987).

Age of the deposit

Dallmann *et al.* (2004) published a detailed map (1:50,000) of the Billefjorden area that included Mimerdalen. They considered the Lower Devonian strata as equivalent to the Wood Bay Formation found further north. They recognised two members in Mimerdalen, the Dicksonfjorden Member and the stratigraphically lower Austfjorden Member. They thought the Lower Devonian strata was quite thin, with the top of the Dicksonfjorden Member and the bottom of the Austfjorden Member bounded by unconformities. On their map, ‘Tormi Hill’ is located in the middle of the Dicksonfjorden Member. However, they do not give an indication of the age of these deposits other than to say the Wood Bay Formation was Lochkovian to Emsian in age.

Piepjohn and Dallmann (2014) go into more detail on the stratigraphy of Dickson Land, including Mimerdalen. They also summarise the history of research of the Devonian of Spitsbergen and the various divisions and names. Of importance to this article is the stratigraphy, particularly their stratigraphical column (Piepjohn & Dallmann, 2014, fig. 2). The Austfjorden Member was Pragian in age. They placed the Pragian–Emsian quite high up in the Dicksonfjorden Member, not far from its top represented by an unconformity. This would place ‘Tormi Hill’ around the Pragian–Emsian boundary. However, they do not state why they placed the Pragian–Emsian boundary where they did.

Pernègre and Blicek (2016) provided a stratigraphy based on assemblages of fossils in the Dicksonfjorden-Austfjorden area, which includes Mimerdalen. This stratigraphy was based mostly on the heterostracans, which are very rare at ‘Tormi Hill’. However, along with the heterostracans they included osteostracans to form stratigraphical assemblages (Pernègre & Blicek, 2016, fig. 4, tab. 2). Regarding the osteostracans, according to Pernègre and Blicek (2016), *Nectaspis areolata* Wängsjö, 1952 is found in assemblage 6 and *Nectaspis peltata* Wängsjö, 1952 in assemblage 8. As *N. peltata* has been collected from ‘Tormi Hill’ (Fig. 4), it indicates the strata belong to assemblage 8 of Pernègre and Blicek (2016). Assemblage 8 occupies the majority of the Dicksonfjorden Member, with only

a thin sequence consisting of assemblage 7 occupying the base (Pernègre & Blicek, 2016, fig. 4). Assemblage 7 is situated at the base of the Emsian according to Pernègre and Blicek (2016, fig. 6). However, they have a dotted line between the Austfjorden and Dicksonfjorden members. This indicates they are not sure exactly where the boundary of the two members is, or indeed the placement of the Pragian–Emsian boundary.

Clearly, previous authors have struggled with identifying the Pragian–Emsian boundary in Mimerdalen. However, recently (in 2016), Charles Wellman (University of Sheffield, UK) has extracted spores from the Lower Devonian hills in Mimerdalen, including ‘Tormi Hill’. The spore assemblage from ‘Tormi Hill’ is in the PE Zone (*polygonalis–emsiensis* Zone) of Richardson and McGregor (1986), which indicates a late Pragian age (Wellman, pers. comm., 2022). Therefore, we can say that the new dipnoan described below is from the late Pragian. This information also indicates that assemblage 8 of Pernègre and Blicek (2016) is late Pragian in age; therefore, all Early Devonian deposits in Mimerdalen are Pragian in age. Figure 3 summarises our understanding of the biostratigraphy.

Series	Stage	Formation	Member	Fauna
Lower Devonian	Pragian	Wood Bay	Dicksonfjorden	Assemblage 8 <i>Arctolepis decipiens</i> <i>Nectaspis peltata</i>
				Assemblage 7 <i>Arctaspis maxima</i> <i>Dicksonosteus</i> sp. <i>Parameteoraspis lanternaria</i>
			Austfjorden	Assemblage 6 <i>Dicksonosteus arcticus</i> <i>Heintzosteus brevis</i> <i>Lehmanosteus hyperboreus</i> <i>Nectaspis areolata</i> <i>Hildenaspis</i> sp.

Figure 3. Biostratigraphical column (not to scale) showing the faunal distribution of the vertebrate fauna. Fossil assemblages from Pernègre and Blicek (2016).

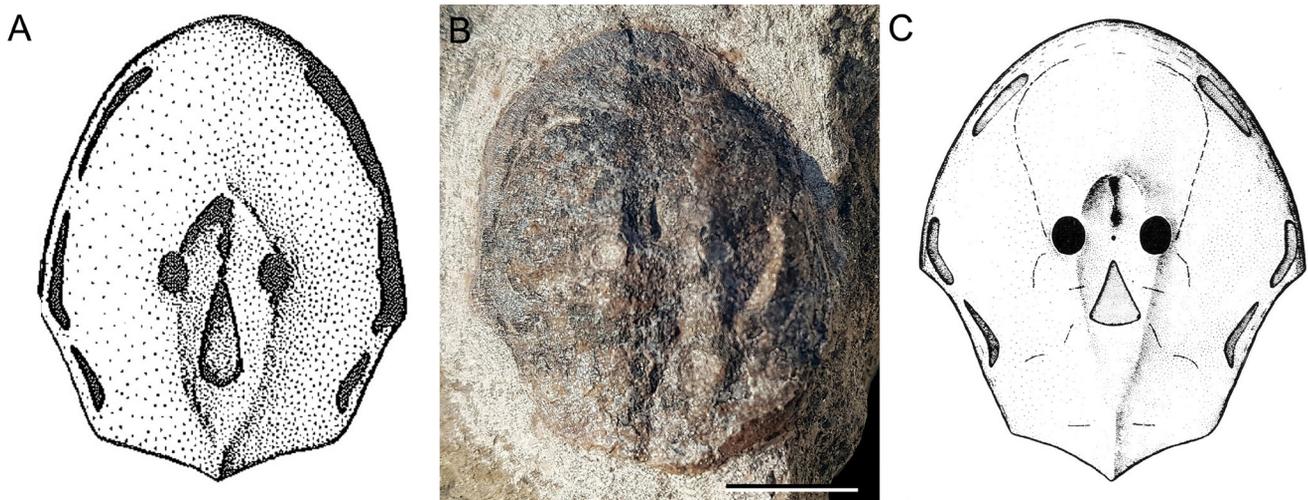


Figure 4. The osteostracan genus *Nectaspis*. **A**, Reconstruction of *Nectaspis peltata* (Janvier, 1981, fig. 35); **B**, PMO 249.467, a *N. peltata* specimen from ‘Tormi Hill’; **C**, reconstruction of *Nectaspis areolata* (Janvier, 1981, fig. 36); scale bar = 10 mm.

MATERIALS AND METHODS

PMO 249.466 is preserved in three dimensions, representing a partial lower jaw missing most of the left ramus of the dentary and the jaw articulation on the right ramus. Lack of sensory canals externally suggests that the submandibular bone series is absent from this right ramus. Only a small portion of the left toothplate is present; that on the right is better-preserved but still damaged and incomplete medially.

The specimen was photographed (Leica EOS) and CT-scanned (Core Research Labs, Natural History Museum, Nikon Metrology XT H 225 ST), the latter with the following parameters: voltage = 180kv; current = 105 uA; filter = 1.0 mm Tin; number of projections = 6207; exposure = 708 seconds; voxel size = 0.01500168 mm. Investigation of individual X-ray μ -CT-slices was performed in Avizo 3D, while segmentation and reconstruction of 3D models were made using Mimics Materialise and Geomagic Wrap.

Institutional abbreviations. PMO, Palaeontological collections of the Natural History Museum at the University of Oslo.

SYSTEMATIC PALAEOLOGY

DIPNOMORPHA Ahlberg, 1991

Order DIPNOI Müller, 1845

Genus *Janvierpaucidentes* nov. gen.

Type-species. *Janvierpaucidentes tuulingi* n. sp.

Diagnosis. As for species.

Janvierpaucidentes tuulingi n. sp.

Figures 5, 6, Supplementary Information Figure 1, File 2

Holotype and only specimen. PMO 249.466, Natural History Museum, University of Oslo.

Etymology. *Janvierpaucidentes* in honour of Philippe Janvier, for his lifetime’s research on fossil fishes includ-

ing lungfish, and for his work on the Early Devonian of Svalbard, particularly on the ostracoderms; *pauci*, Latin for ‘few’ and *dentes*, Latin for ‘teeth’, referring to the reduced number of tooth rows present; *tuulingi* for Tormi Tuuling who first noted the potential of ‘Tormi Hill’ and suggested investigating the site.

Type locality and horizon. ‘Tormi Hill’ (Lat. 78° 39’ 3” N Long. 16° 11’ 45” E), 3 km NE of the abandoned Russian mining town of Pyramiden, Spitsbergen, Svalbard. In the lower part of the Dicksonfjorden Member of the Wood Bay Formation (late Pragian).

Diagnosis. A tooth-plated lungfish with a prearticular (lower jaw) tooth plate bearing three tooth rows with a similar number of teeth on each row; large maximum angle of approximately 180 degrees between the tooth rows, with the rostral (row 1) and caudal (row 3) being aligned with the jaw margin. It differs from other Early Devonian tooth-plated lungfish: from *Diabolepis* and *Tarachomyx* in having fewer tooth rows; from *Ichnomylax* and the unnamed toothplate from Vietnam (Mondéjar-Fernández et al., 2020) in lacking denticles between the tooth rows; from all of these in having an elongate toothplate and large maximum angle between the tooth rows, the rostral and caudal being aligned with the jaw margin. Similar to the Carboniferous taxon *Xylognathus macrustenus* in these latter characters; differing from *X. macrustenus* in having only one tooth row between the rostral and caudal most tooth rows, and this middle tooth row being similar in length to the former two rows.

Description. *Janvierpaucidentes tuulingi* is known from a partial lower jaw, preserving a small part of the left ramus and more of the right ramus, although the region of the jaw articulation is missing, as are the ventral parts of the ramus. There is a space between the two rami (cr, Fig. 5A, 5C, 5E), but this is more likely to be a crack than a symphysis. Small, irregular denticles are present along the antero-ventral margin of the dentary (de, Fig. 5A, 5B). On the right lower jaw ramus, a labial pit is visible anterolaterally (l.pit, Fig. 5A, 5B, 5E, 5F),

but more posteriorly, the right toothplate has shifted laterally across the dentary, *post mortem*. Some parts of the Meckelian cavity may be present (**Mk.c**, Fig. 5A, 5B), although the lateral margins of this cavity cannot be fully determined because the dentary is damaged here. Laterally, the right ramus includes what appears to be two separate bones below the dentary (Fig. 5C, 5D, black question marks) which might be the sub-

mandibulars, but the irregular nature of the ‘margins’ of these bones suggests that these are instead cracks in the dentary bone. The margin below this region is also damaged. Another argument against these being submandibular bones is that an anteroposteriorly directed mandibular canal, which runs across the submandibular bones in other lungfish taxa, is absent. It should be noted that the more dorsal oral canal also cannot

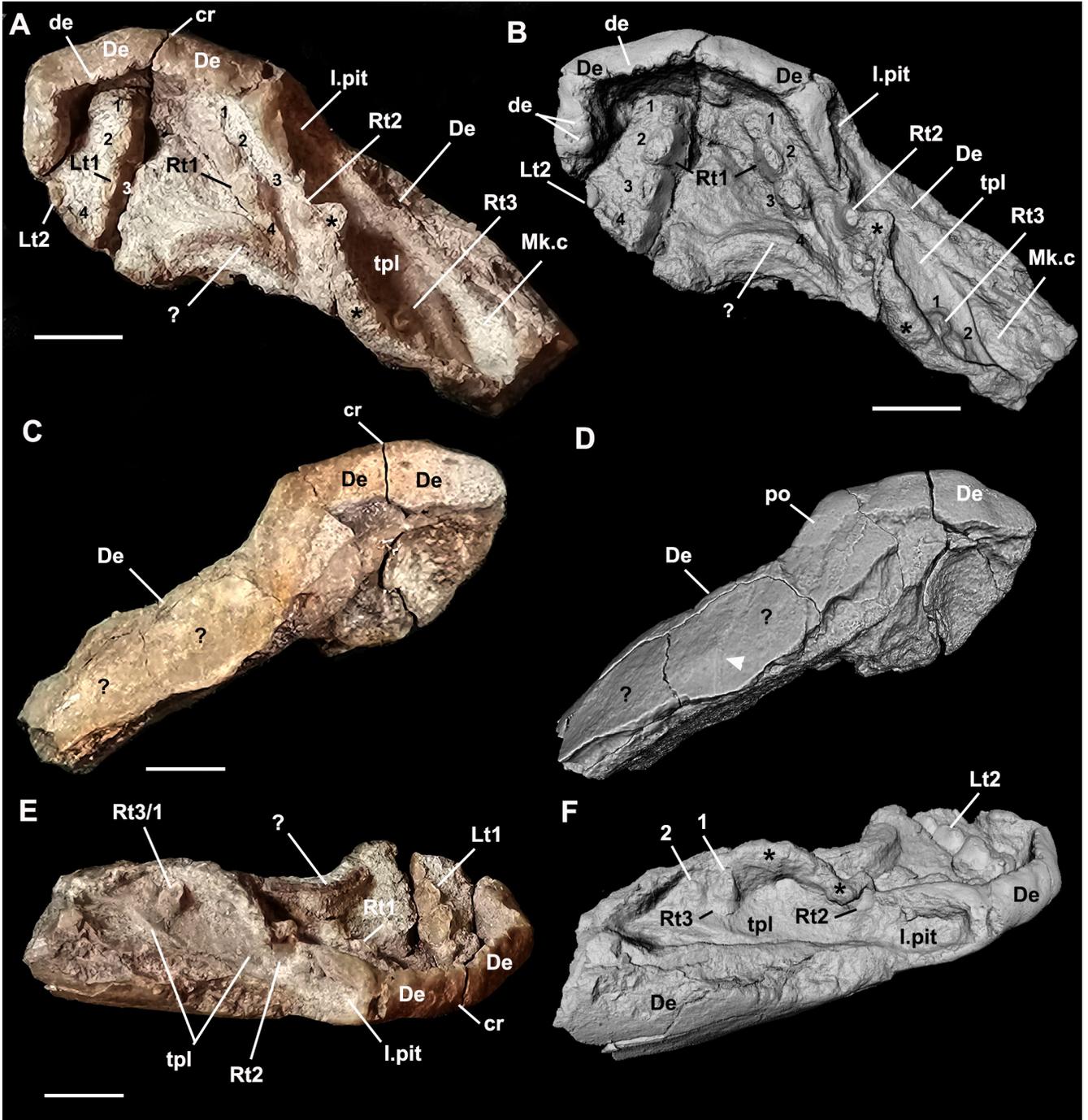


Figure 5. *Janvierpaucidentes tuulingi*, PMO 249.466, lower part of the Dicksonfjorden Member of the Wood Bay Formation (late Pragian), Svalbard. **A, C, E**, Macrophotos; **B, D, F**, segmented X-ray μ -CT scans; **A, B**, dorsal view of the dentary and prearticular toothplates, black asterisk indicates rock partially covering tooth rows 2 and 3; **C, D**, ventral view of the dentary, including faint pores (**po**), black question marks indicate two bones which may be submandibular bones given their position, although boundaries between these bones are more likely to represent cracks, white arrowhead indicates groove along the jaw ramus; 1–4, tooth number, ‘1’ represents the latest tooth to be added; **cr**, crack; **De**, dentary; **de**, denticle; **L**, left; **I.pit**, labial pit; **Mk.c**, Meckelian cavity; **po**, pores; **R**, right; **t**, tooth row; **tpl**, toothplate; scale bar = 10 mm.

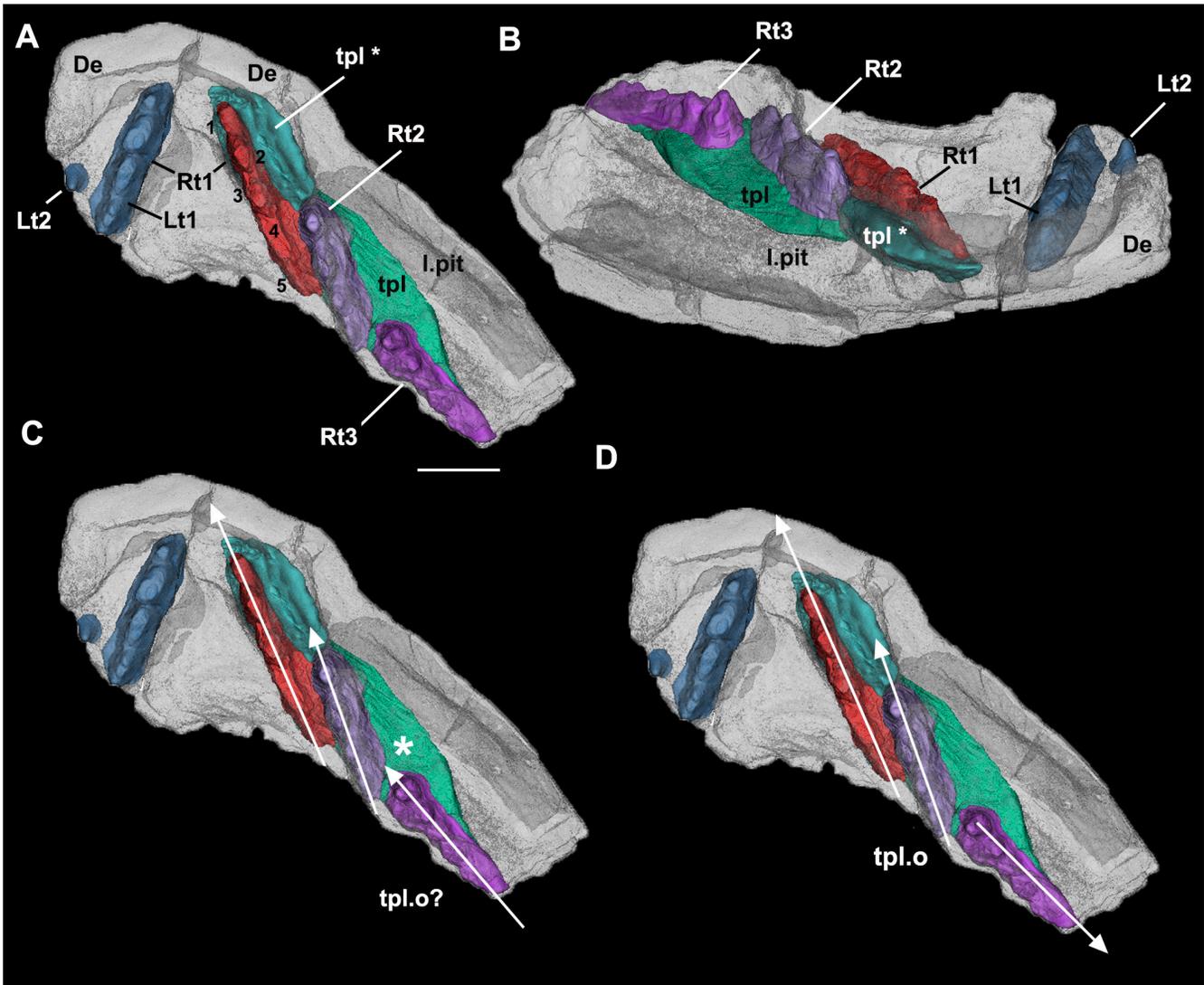


Figure 6. *Janvierpaucidentes tuulingi*, PMO 249.466, lower part of the Dicksonfjorden Member of the Wood Bay Formation (late Pragian), Svalbard. Segmented and reconstructed X-ray μ -CT scan of lower jaw, with toothplate and tooth rows presented in different colors. **A**, Dorsal view; **B**, anterior view; **C**, **D**, contrasting reconstruction hypotheses, dorsal view with arrows drawn through the tooth rows to indicate orientation, arrowheads show the position of the latest tooth to be added to the row. '?' indicates that with these parameters (particularly with respect to tooth row 3) the medial origin of the tooth rows is abnormally far posteriorly (**C**). In (**D**), the arrow is reversed for tooth row 3, positioning the tooth row origin closer to tooth row 1 and 2, and reconstructing a toothplate morphology similar to certain Carboniferous taxa; 1–5, tooth number, '1' represents the latest tooth to be added; **De**, dentary; **L**, left; **I.pit**, labial pit; **Mk.c**, Meckelian cavity; **R**, right; **t**, tooth row; **tpl**, toothplate; **tpl***, part of toothplate that has been folded *post mortem*; **tpl.o**, toothplate origin; scale bar = 10 mm.

be identified. There is an indication of a very shallow groove (Fig. 5D, white arrowhead), which in other lungfish is the location of the commissural canal connecting the oral and mandibular canals, located on a sub-mandibular bone. However, this identification seems unlikely given the absence of clear oral and mandibular canals.

The left toothplate is very damaged with only one partial tooth row and one tooth from a second row remaining (**Lt1**, **Lt2**, Fig. 5A, 5B, 5E, 5F). Four teeth can be identified in tooth row 1 (Fig. 5A, 1–4, 5B). The teeth themselves have been damaged, with the tips of teeth 2–4 having been removed, with potentially more damage to tooth 1 (Fig. 5A, 5B). Tooth 2 is large and broad-based, while tooth 3 and 4 are also large and appear

more medio-laterally compressed (particularly tooth 4). The surface of the toothplate itself cannot be seen (Fig. 5A).

The opposing toothplate is better preserved, although some parts are covered by rock (Fig. 5A, 5B). As part of the *post mortem* shifting of this toothplate, it appears that the lateral margin has been folded to some degree (Fig. 6A, **tpl***). Three separate rows of teeth can be identified, labelled **Rt1–Rt3** in Figure 5A, 5B. In tooth row 1, four teeth can be seen in the macrophoto of the lower jaw (Fig. 5A), with the fourth tooth being broken down to its base. A fifth tooth is present in the segmented X-ray μ -CT scan (Fig. 6A). As in toothrow 1 on the left toothplate, the teeth are damaged, with tooth cusps being lost in teeth 1–3. As on the left tooth-

plate, tooth 1 appears to have sustained more damage compared to teeth 2 and 3. These teeth are large and rounded, with no mediolateral compression of tooth 3, compared to its opposite on the left toothplate. By comparison, teeth 4 and 5 on the right toothplate appear strongly compressed, as occurs on tooth 4 on the left toothplate. The orientation of tooth row 1 matches that on the left toothplate, with these suggesting that the (unpreserved) origin of the toothplates will be more lateral than medial.

Tooth rows 2 and 3 are partially covered by rock, but in the rendered X-ray μ -CT scan, tooth row 2 has four teeth, and row 3 also appears to have four, but those in the rest of the tooth row are challenging to segment completely (Fig. 6A). Several of the teeth are broken and worn, making a determination of size difficult. Nevertheless, it appears that in toothrow 2, teeth 1 and 2 are the largest (Fig. 6A, 6B), while the other two teeth are smaller and possibly medio-laterally compressed. With respect to toothrow 3, macrophotos show the presence of a large tooth, with the cusp broken (Fig. 5E, **Rt3/1**). In the accompanying segmented CT-scan, a smaller tooth is present next to this tooth and is identified as tooth 2 (Fig. 5F, 2). However, it seems from this segmented scan that tooth 2 is worn. Both visible teeth are associated with the toothplate in the region (Fig. 5E, 5F, **tpl**). If the condition of tooth 2 is repeated in the remaining teeth in the row, this would explain why they are more difficult to segment, and appear smaller.

With respect to the orientation of the tooth rows, tooth rows 1 and 2 appear to be more parallel to one another, although the folding of the toothplate mentioned above may have affected the orientation of tooth row 1 to some degree. Tooth row 3 appears to be oriented more parallel to the right jaw ramus (Fig. 6A).

The toothplate on the right jaw ramus is best seen where it has shifted across the dentary (Fig. 5A, 5B, 5E, 5F), being broad, with a curved margin. More anteriorly and medially, the toothplate is hidden under rock, but examination of individual CT-scan slices indicates that a single toothplate is present (see Supplementary Information). In Supplementary Information Figure 1, the teeth and toothplate from a single CT-scan slice were highlighted in red, with the position of this slice indicated on the reconstructed right toothplate. Thus, in Supplementary Information Figure 1A, the slice runs between toothrow 1, tooth 3 to toothrow 2, tooth 1 (black arrowhead). The separation indicated by the white arrowhead is a crack through tooth 1; otherwise these are continuous. More posteriorly, in Supplementary Information Figure 1B, the region highlighted on the slice in red is seen, in the 3D reconstruction on the left, to cross tooth row 2, tooth 2 and onto the tooth plate near tooth row 3, tooth 1 (red arrowhead). The continuity of these areas in the slices supports the idea of the presence of a single toothplate underlying the three tooth rows, as does the full segmentation of this region in Figure 6A.

DISCUSSION

Currently, a large number of Early Devonian Dipnoi species are recognised (Tab. 1), with one of the earliest occurrences being the tooth-plated *Diabolepis speratus* from China (Lochkovian). The denticulated species *Uranolophus wyomingensis* from Wyoming is late Pragian to early Emsian in age, with other Pragian species belonging to tooth-plated taxa. These include *Speonesydrion iani*, *Ichnomyx kurnai*, *Janvierpaucidentes tuulingi* and also unnamed specimens from Vietnam (Tong-Dzuy & Janvier, 1994; Mondéjar-Fernández *et al.*, 2020). Schultze (2001) considered *Speonesydrion* to be a synonym of *Dipnorhynchus*, but Campbell and Barwick (2007) rejected this hypothesis. Another late Pragian species, *Westollrhynchus lehmanni*, occurs in Germany, although Campbell *et al.* (2009) expressed doubts about the validity of the genus, suggesting it should remain in *Dipnorhynchus* until better specimens are found. In Australia, further speciation seems to have occurred in a narrow time window in the Pragian (Campbell *et al.*, 2009, fig. 1), with dentine-plated taxa appearing, including multiple species of *Dipnorhynchus* (Tab. 1) as well as *Cathlorhynchus trismodipterus* and *C. zengi*. Emsian occurrences include *Tarachomyx oepiki* (Severnaya Zemlya) and *T. multicostatus* (Yunnan, China, both species tooth-plated), *Jessenia concentrica* (Germany, tooth-plated), *Melanognathus canadensis* (Canada, denticulated form with teeth along the prearticular) and *Sorbitorhynchus deleaskitus* (Guangxi, China, dentine-plated). Finally, *Ichnomyx karatajæ* (Siberia, tooth-plated) is just recorded as Early Devonian. These observations demonstrate the disparity of dental morphologies when the dipnoans first evolved. New investigations of the related dipnomorph *Youngolepis* have found that part of the dentition falls into the tooth-plated morphology, supporting previous suggestions that this is primitive for the Dipnoi (Cui *et al.*, 2022). Ahlberg *et al.* (2006) outlined how modulating different odontogenic (dentine-related) processes of addition and resorption in the lungfish dentition could produce the different Early Devonian dentitions: tooth-plated (tooth addition), dentine-plated (dentine deposition as sheets rather than teeth), and denticulated (dentine resorption).

The lower jaw of *Janvierpaucidentes tuulingi* preserves part of a right toothplate that is incomplete medially, shifted laterally and possibly distorted rostrally near toothrow 1; loss of the medial part of the plate means that the origins of the tooth rows are missing. As preserved, three short tooth rows are present and are more rostro-caudally oriented and overlapping to some degree, especially rows 1 and 2, resulting in a more elongate toothplate. This orientation, particularly the overlapping tooth rows differs somewhat from the typical Early Devonian tooth-plated dentition, where the tooth rows originate medially and expand laterally as new, larger teeth are added to the toothplate margins as the toothplate grows.

Table 1. List of Early Devonian lungfish (Dipnoi) taxa.

Early Devonian dipnoans		
Dipnoan species	Reference	Age
<i>Diabolepis speratus</i> Chang & Yu, 1984	Chang & Yu (1984)	late Gedinnian to early Siegenian (Lochkovian)
<i>Uranolophus wyomingensis</i> Denison, 1968	Denison (1968)	late Pragian to early Emsian
<i>Dipnorhynchus kiandrensis</i> Campbell & Barwick, 1982	Campbell & Barwick (1982)	lower Emsian or possibly upper Pragian
<i>Dipnorhynchus suessmilchi</i> (Etheridge, 1906)		lower Emsian or possibly upper Pragian
<i>Dipnorhynchus kurikae</i> Campbell & Barwick, 1985	Campbell & Barwick (1985)	lower Emsian or possibly upper Pragian
<i>Dipnorhynchus cathlesae</i> Campbell & Barwick, 1999	Campbell & Barwick (1999)	late Emsian
<i>Cathlorhynchus trismodipterus</i> Campbell, Barwick & Senden, 2009	Campbell <i>et al.</i> (2009)	Emsian (Currajong Limestone Member)
<i>Cathlorhynchus zengi</i> Qiao & Zhu, 2015	Qiao & Zhu (2015)	early Emsian
<i>Ichnomyx karatajae</i> Reisz, Krupina & Smith, 2004	Reisz, Krupina & Smith (2004)	Early Devonian
<i>Ichnomyx kumai</i> Long, Campbell & Barwick, 1994	Long, Campbell & Barwick (1994)	late Pragian
<i>Westollrhynchus lehmanni</i> (Westoll, 1949)	Schultze (2001)	Pragian
<i>Jessenia concentrica</i> Otto & Bardenheuer, 1996	Otto & Bardenheuer (1996)	lower Emsian
<i>Melanognathus canadensis</i> Jarvik, 1967	Schultze (2001)	Emsian
<i>Sorbitorhynchus deleaskitus</i> Wang, Drapala, Barwick & Campbell, 1993	Shitao <i>et al.</i> (1993)	late Emsian
<i>Speonesydrion iani</i> Campbell & Barwick, 1984	Campbell & Barwick (1984)	late Pragian
<i>Tarachomyx oepiki</i> Barwick, Campbell & Mark-Kurik, 1997	Barwick <i>et al.</i> (1997)	Emsian
<i>Tarachomyx multicostatus</i> Qiao & Zhu, 2008	Qiao & Zhu (2008)	late Emsian
<i>Erikia jarviki</i> Chang & Wang, 1995	Chang & Wang (1995)	early Emsian
Material from Spitsbergen	Clément <i>et al.</i> (2006)	late Emsian–early Eifelian
Toothplate from Vietnam	Mondéjar-Fernández <i>et al.</i> (2020)	Lochkovian–Pragian
Lungfish material from Vietnam Tong-Dzuy & Janvier (1987)	Tong-Dzuy & Janvier (1987)	Pragian

In this regard, the orientation and location of tooth row 3 is problematic, especially if the two teeth seen in Figure 5A, 5B, 5E, 5F, are considered to be the most recent teeth added to the tooth row and toothplate ('1, 2') as in the accepted model of new tooth addition (e.g., Smith & Johanson, 2011). More posteriorly, in the region of tooth row 3, the toothplate looks undamaged, being broad with a curved lateral margin. The most rostral tooth in tooth row 3 is located well medial to this margin (e.g., Fig. 5B). By comparison, in tooth rows 1 and 2, the most anterior tooth is positioned at the lateral margin, where it has been added as the newest during development (although these teeth are smaller compared others in the row, damage to the teeth in general makes it difficult to assess the true size of these lateral-most teeth). If the visible teeth in tooth row 3 (Fig. 5) are equivalent to the more recently added teeth in tooth rows 1 and 2, this would suggest that the teeth in tooth row 3 stopped being added to the toothplate, which continued to grow beyond these teeth. This would be contrary to what is known about lungfish toothplate development (e.g., Smith & Krupina, 2001; Ahlberg *et al.*, 2006). As well, identifying tooth 1 in tooth row 3 as the most recently added would make the point of toothplate origin very difficult to determine, as the orientation of the tooth row would place this origin far posteriorly (arrows through tooth rows with arrowheads indicating tooth addition, Fig. 6C, **tpl.o?**).

An alternative interpretation reverses the direction of the arrow for tooth row 3 so that the latest tooth to be added (direction of the arrow in Fig. 6C, **tpl.o**) is more posterior, making the origin of this tooth row closer to that of tooth rows 1 and 2. This also means that the part

of the toothplate lacking teeth near here (Fig. 6C) no longer requires an explanation.

The tooth row configuration shown in Figure 6D suggests that the more rostral and caudal tooth rows (**t1**, **t3**) are developing in opposite directions, creating an elongate toothplate, with an intermediate tooth row between these (**t2**). This morphology is reminiscent of the toothplates assigned to the UK Carboniferous lungfish *Xylognathus macrustenus* (Smithson *et al.*, 2016), where the maximum angle between the tooth rows on the prearticular plate was 165 degrees (180 degrees on the pterygoid toothplate). It was noted that on the pterygoid toothplate, the more posterior tooth row (4) of *Xylognathus* was aligned directly behind the most anterior (1), but that on the prearticular, the more posterior was slightly offset laterally (Smithson *et al.*, 2016, figs. 4B, 5). This appears to be similar to *Janvierpaucidentes tuulingi*, although in *J. tuulingi*, only one tooth row is present between the anterior and posterior row (rather than the two in *X. macrustenus*), with this row being more similar in length (*J. tuulingi*), rather than shorter (*X. macrustenus*). This is the first time this type of elongate toothplate morphology, with such a high maximum angle between the tooth rows, has been described in the Devonian, much less Early Devonian, lungfish taxa.

CONCLUSIONS

A new dipnoan species, *Janvierpaucidentes tuulingi*, is described from the Early Devonian (Pragian) of Svalbard. The Early Devonian is a period of high morphological disparity in lungfish dentitions, with that of *J. tuulingi* belonging to the tooth-plated variety. Never-

theless, *J. tuulingi* shows considerable differences with respect to other Devonian tooth-plated taxa, primarily concerning the large angle between anterior and posterior tooth rows, resulting in an elongate toothplate. This is reminiscent instead of later Carboniferous taxa and the first time an elongate toothplate evolves. Thus, the dentition of *J. tuulingi* adds to the overall already high disparity of Early Devonian lungfish. However, because of the incomplete nature of the specimen, including the medial margin of the toothplate, we caution that more fieldwork to recover additional specimens of *Janvierpaucidentes tuulingi* is needed.

Supplementary information. Figure S1 is available at the Spanish Journal of Palaeontology web-site (<https://sepaleontologia.es/spanish-journal-palaeontology/>) linked to the corresponding contribution. Scan raw data and 3D models are available at the online repository morphosource (<https://www.morphosource.org/projects/000521472?locale=en>). The new taxonomic name in this paper, and the nomenclatural acts it contains, has been registered in ZooBank, the online registration system for the ICZN: <https://zoobank.org/NomenclaturalActs/A8522E73-8CB8-49D1-83FB-C7E79814F192>

Figure S1. Supplemental information. *Janvierpaucidentes tuulingi*, PMO 249.466, lower part of the Dicksonfjorden Member of the Wood Bay Formation (late Pragian), Svalbard. CT-scans to illustrate segmented slices crossing tooth rows, Avizo. **A**, Left image of reconstructed lower jaw, red line indicates position of single slice shown in right image. Using the paint tool, this slice crosses both tooth rows 2 and 3 demonstrating that these belong to the same toothplate. White arrowhead indicates crack, rather than separation of tooth rows onto separate plates, as illustrated in B; **B**, left image of reconstructed lower jaw, red arrowhead indicates position of single slice shown A, black arrowhead shows position of slice in right image. White arrowhead indicates crack from (A) running through a tooth, rather than being a separation of toothplates. These slices demonstrate that the three tooth rows are situated on one toothplate; **1**, **2**, tooth number, '1' represents the latest tooth to be added; **l.pit**, labial pit; **tpl**, toothplate.

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