

A possible *Pararcus diepenbroeki* vertebra from the Vossenveld Formation (Triassic, Anisian), Winterswijk, the Netherlands

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Abstract

An isolated, completely ossified vertebra tentatively ascribed to the non-cyamodontid placodont *Pararcus diepenbroeki* is described from the Anisian Vossenveld Formation in Winterswijk, the Netherlands, and compared to other material from the same locality. This fossil is the first completely ossified vertebra of the taxon and most likely originates from an adult specimen. It was recovered c. 16 m deeper in the stratigraphy than previously described material of the species, which is thus far known only from Winterswijk. Based on the slanting angle of the transverse process, the vertebra is interpreted to originate from the dorsal region. Besides the overall agreements in morphology that warrant a tentative identification as *Pararcus diepenbroeki*, the newly described vertebra deviates from other known *Pararcus* vertebrae in the presence of a longer, well-ossified neural spine and a strongly constricted, less pachyostotic and ovaloid vertebral centrum. General agreement in morphology with previously described vertebrae suggests this novel condition indicates a different anatomical position and perhaps a varied ossification pattern.

Keywords: Anisian, Muschelkalk, Winterswijk, *Pararcus diepenbroeki*, placodonts, vertebra

Introduction

The Winterswijkse Steengroeve near the Dutch town of Winterswijk is a quarry complex comprising four limestone quarries, one of which remains in active use. This quarry complex exposes approximately 40 m of intertidal and shallow marine strata of the Vossenveld Formation, which corresponds to an interval of the Lower Muschelkalk Member in the Muschelkalk Formation (Upper Germanic Trias Group; Van Adrichem Boogaert & Kouwe, 1993–1997). These deposits are early to middle Anisian in age and correlate with the Wellenkalk facies (Hagdorn & Simon, 2010), although absolute dates are so far lacking. Muschelkalk deposits were formed during flooding of the European continent in the Middle Triassic under the influence of basinal subsidence in the aftermath of the Pangean break-up. The area of present-day Winterswijk was positioned towards the north-western margin of the Germanic Basin, which covered most of present-day Central and Eastern Europe (Hagdorn et al., 1999).

The overall transgressive sequence exposed at the Winterswijkse Steengroeve includes a variety of depositional facies that are preserved as a stack of laminated, argillaceous or bioturbated mudstones with several marlstone and dolomitised packstone beds (Oosterink, 1986). The tetrapod assemblage of this succession includes skeletal material of (marine) sauropterygians and trackways from terrestrial vertebrates (e.g. Oosterink et al., 2003). Oosterink (1986) provided an initial stratigraphic scheme, including a numbering of distinguishable sedimentary units. Layer 14 (after Oosterink, 1986) is approximately 2–7 cm thick and probably represents a tempestitic condensation horizon that originated on the shoreline as landwash or in the subtidal zone through the process of winnowing. Elements from Layer 14, as in Layer 9, generally display traces of abrasion as a consequence of transport by water, indicating the material was introduced post-mortum (Klein et al., 2015). A surface area of approximately 10 m² of Layer 14, which is typically covered by a thin layer of unconsolidated mud in outcrop, was

systematically excavated in August 2014. Among the finds was a comparatively large vertebra exhibiting a distinct morphology that suggests attribution to *Pararcus diepenbroeki*. This placodont taxon was recently described on material originating higher in the quarry (Layer 36; Klein & Scheyer, 2014), for which it thus far represents an endemic species. The specimen presented here is housed in the collection of Naturalis Biodiversity Center in Leiden, the Netherlands (inv. no. RGM.791811); it is described and compared to the holotype of *Pararcus diepenbroeki* (Klein & Scheyer, 2014). In addition, the significance of novel morphological characters and of its occurrence in the Layer 14 assemblage are discussed.

Institutional abbreviations

CHW – Private collection H. Winkelhorst, Aalten, the Netherlands; RGM – (former) Rijksmuseum van Geologie en Mineralogie, now Naturalis Biodiversity Center in Leiden, the Netherlands; TWE – Museum TwentseWelle, Enschede, the Netherlands; StIPB – Steinmann-Institute, Division of Paleontology, University of Bonn, Bonn, Germany.

Systematic paleontology

Sauropterygia (Owen, 1860)

Placodontia (Cope, 1871)

Genus *Pararcus* (Klein & Scheyer, 2014)

Type species *Pararcus diepenbroeki* (Klein & Scheyer, 2014)

Relevant part of original diagnosis: A large non-cyamodontoid placodont with ventrolateral expansion of neural arches of the posterior presacral and sacral vertebrae; these neural arches unfused (paired) and without a neural spine; vertebral centra deeply amphicoelous and notochordal; centra swollen and pachyostotic but only weakly constricted, with the lateral edges of the centra extending mostly parallel to each other (Klein & Scheyer, 2014).

Type locality: Winterswijkse Steengroeve, Winterswijk, The Netherlands.

Type horizon: Layer 36 (after Oosterink, 1986), Vossenveld Formation, Lower Muschelkalk (early Anisian, early Middle Triassic).

Description of the new material

RGM.791811 (Fig. 1) consists of an isolated vertebra recovered from Layer 14. A (possibly associated) small bone fragment is present in close proximity to the vertebra. The taphonomic history, possibly including factors such as post-mortem abrasion, agitation, trampling and/or weathering, has resulted in isolation of the vertebra and caused substantial damage to the



Fig. 1. RGM.791811 in posterior view. Note the dorsoventral elongation of the vertebral centrum, the narrow neural canal, and the elongated neural spine. The right margins of the vertebral centrum and right ventrolateral expansion are damaged, the right postzygapophysis is missing. Scale bar is 10 mm.

dextral side of the neural arch. The adjacent bone fragment, smaller than a rice grain, has been abraded beyond recognition and is not further considered here. The dextral side of both vertebral centrum and neural arch suffered some additional damage during excavation. Preparation has revealed the vertebra mainly in posterior view, but also allows for partial assessment of the morphology of ventral, dorsal and left lateral aspects. All sutures within the neural arch and between the neural arch and the centrum remained completely ossified and have not dissociated. The vertebra measures almost 91 mm in total (dorsoventral) height. The original total width, reconstructed through assumption of bilateral symmetry, would have been c. 84 mm (see Table 1 for all measurements).

The preserved dorsal expansion of the neural arch consists of a neural spine and the left postzygapophysis. The inferior articular processes and the bowl-shaped, posteriorly trending

Table 1. Measurements of RGM.791811 (in mm).

Dimension	Measurement
<i>Vertebra</i>	
Total height	90.5
Total width	84.2
<i>Vertebral centrum</i>	
Maximum height	35.0
Maximum width	32.6*
Constricted height	26.8
Dorsoventral height	24.4
<i>Neural arch</i>	
Width neural spine	14.0
Anteroposterior length	8.2
Length dorsal expansion	36.5
Width dorsal expansion	30.9*
Length neural arch	17.7
Maximum width neural arch	5.8
Minimum width neural arch	3.0
Length ventrolateral expansion	31.4
Width ventrolateral expansion	37.8
Length dorsolateral margin of ventrolateral expansion	34.3
Length costal articular facet	8.3
Width costal articular facet	6.2
Maximum depth costal articular facet	2.9
Angle ventrolateral expansion	25° to the horizontal

*Reconstructed through assumption of bilateral symmetry.

ridge that originally connected the postzygapophyses are incomplete. The right postzygapophysis is absent. The postzygapophysis carries a nearly horizontal terminal articular facet that is directed posterolaterally and provided articulation with the prezygapophysis of the succeeding vertebra. The neural canal is significantly constricted at half its height, which grants the neural canal an hourglass shape in posterior view. The margins of the neural canal flare out posterolaterally. The ventrolateral expansion is fan-shaped and slightly concave. It projects ventrolaterally at an angle of c. 25° with respect to the horizontal. The tip of the ventrolateral expansion accommodates the costal articular facet, which is a shallow but pronounced rugose concavity.

Unlike all vertebrae described by Klein & Scheyer (2014), RGM.791811 displays completely ossified, barely distinguishable sutures. The neural canal slightly enters the dorsal margin of the main posterior vertebral articular facet. The pedicles reach down laterally to approximately one-third of the height of the vertebral centrum. As the anterior main articular facet is clearly concave, and the left lateral margin of the posterior articular facet, although superficially damaged, appears somewhat con-

vex (see Fig. 2), the vertebral centrum is either procoelous or amphicoelous. The centrum is dorsoventrally elongated. The terminal portions, which accommodate the main articular facets anteriorly and posteriorly, form the broadest parts of the vertebral centrum, but constitute anteroposteriorly narrow ridges in ventral view. The middle portion of the vertebral centrum is exceptionally constricted laterally (see Fig. 2 and Table 1). As sauropterygian alpha taxonomy is predominantly founded on cranial characters (summarised in Rieppel, 2000), isolated vertebrae generally only have limited diagnostic value. However, several distinct characters of the vertebral morphology of *Pararcus diepenbroeki* are clearly present in RGM.791811, which supports identification as such.

Comparison

The vertebrae of Placodontia are characterised by high and narrow neural canals, elongated transverse processes, and deeply amphicoelous and notochordal centra (Rieppel, 2000: 12). Besides the zygapophyses, an accessory intervertebral articulation (hyposphene-hypantrum) is present below the pre- and postzygapophyses and distinctly developed in the dorsal region (Rieppel, 2000). The posterior presacral and sacral vertebrae of the *Pararcus diepenbroeki* holotype TWE 480000454 carry a ventrolateral expansion on the paired, unfused neural arches with an incompletely developed neural spine (Klein & Scheyer, 2014: 892). The vertebral centra are deeply amphicoelous, notochordal, pachyostotic and weakly constricted (Klein & Scheyer, 2014: 888). Overall dimensions of individual elements in the presumed subadult TWE 480000454 generally agree with those of *Placodus gigas* (Klein & Scheyer, 2014). Notable agreements with *Blezingeria* also exist (Klein & Scheyer, 2014), which has similar (albeit generally longer, well-developed) neural spines and amphicoelous vertebral centra (Fraas, 1896; Huene, 1951).

A second individual of *P. diepenbroeki* is represented by fused neural arch StIPB CHW302 that is disassociated from its vertebral centrum and carries a short neural spine (Klein & Scheyer, 2014). StIPB CHW302 is slightly larger than the neural arches in TWE 480000454, and the ventrolateral expansions project at an angle that is nearly 40° less than those described for the (posterior presacral and sacral) vertebrae in the holotype. These differences in size, degree of fusion, and the condition of the dorsoventral expansions and neural spine are believed to relate to ontogeny and the more anterior anatomical position of StIPB CHW302 in the vertebral column (Klein & Scheyer, 2014).

Although overall morphology identifies RGM.791811 as *Pararcus diepenbroeki*, this specimen morphologically differs in other key aspects (Fig. 3). The vertebral centra in TWE 480000454 display a relatively simple cylindrical and robust morphology whereas the centrum in RGM.791811 is markedly elongated dorsoventrally (e.g. as in the thalattosaur

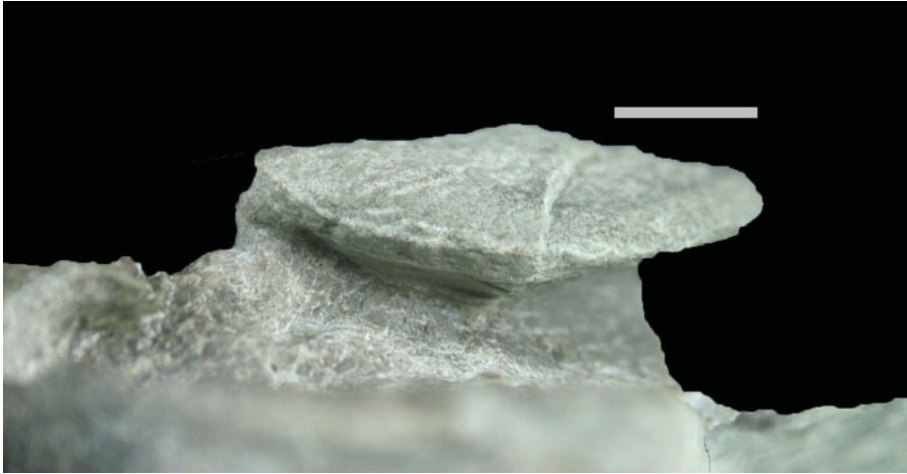


Fig. 2. Vertebral centrum of RGM.791811 in right lateral view, ventral is to the right. The short vertebral centrum is laterally constricted in the middle. The centrum terminates posteriorly in an expanded portion (conceivably accentuated by postdepositional compression) that accommodates the main articular facet, which appears slightly convex, possibly as a result of abrasion or distortion. Scale bar is 10 mm.

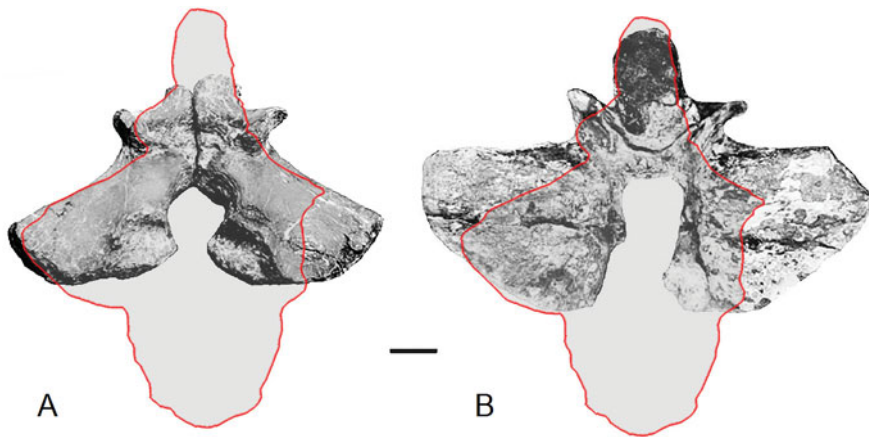


Fig. 3. *Pararcus diepenbroeki* vertebrae in posterior view modified from Klein & Scheyer (2014). The contour of RGM.791811 (shaded and outlined in red) is projected on the referred specimens to illustrate the relative size and morphology of RGM.791811. Scale bar is 10 mm. A. Na7+8 from TWE 480000454. B. StIPB CHW302.

Anshunsaurus huangguoshuensis; Liu & Rieppel, 2005), resulting in an ovaloid posterior articular facet. *Blezingeria* is only known from vertebrae, of which centra with both more cylindrical as well as with more ovaloid geometries have been described (Fraas, 1896; Huene, 1951). The morphology of the ventrolateral expansions on the corresponding neural arches does not correspond to that observed in RGM.791811 or in material previously assigned to *Pararcus diepenbroeki* (Klein & Scheyer, 2014). The vertebral centrum of RGM.791811 exhibits a strong lateral constriction in ventral view to a degree thus far unseen in Placodontia, and is more slender than the pachyostotic vertebral centra of the *Pararcus diepenbroeki* holotype, or such taxa as *Blezingeria* and *Anshunsaurus huangguoshuensis*. The non-ossified sutures that formed the connection with the pedicles in the centra of the sacral vertebrae in TWE 480000454 extend laterally to the middle of the centrum. The flared ventrolateral expansions of RGM.791811 are oriented dorsoventrally rather than the more posterodorsal-anteroventral tilt described for the neural arch halves in TWE 480000454.

The neural arch halves na7 and na8 in TWE 480000454 are assigned to a single vertebra from the sacral region. StIPB CHW302 was assigned to an unspecified but more anterior position within the vertebral column. The relative angle at which the ventrolateral expansions are set in RGM.791811 with respect to StIPB CHW302 and the neural arches in TWE 480000454 suggests that RGM.791811 occupied a position between those of StIPB CHW302 and na7 and na8. The robust neural arch StIPB CHW302 is interpreted to represent a cervical or anterior dorsal vertebra (see also Klein & Scheyer, 2014), with the relatively large surface area of the ventrolateral expansions possibly relating to the attachment of the large cervical musculature associated with durophagy (Scheyer et al., 2012). Anterior dorsal vertebrae generally carry the longest neural spines (Romer, 1956; p. 226). This is, however, not the case for *Placodus gigas*, where neural spine height increases posteriorly into the sacral domain (Drevermann, 1933). Such a condition may explain the relatively reduced neural spine in StIPB CHW302. Based on the inferred cervical to more anterior dorsal position of StIPB CHW302

and the posteriormost dorsal to sacral or first caudal positions of the neural arch halves in TWE 480000454, RGM.791811 is concluded to be a middle or posterior dorsal vertebra. The holotype is lacking all ossified sutures. StIPB CHW302 represents a fused neural arch, but was dissociated from the vertebral centrum. Specimen RGM.791811 is a fully ossified and articulated vertebra, which indicates that it belonged to a skeletally mature individual.

Discussion

In placodonts, the neurocentral suture remains visible throughout the vertebral column, although separation of the neural arch from the centrum during fossilisation is rare (Riepel, 1995). In the *Pararcus diepenbroeki* holotype, all neural arches remained unfused and separated from their vertebral centra. It should be noted, however, that one pair of the caudal neural arch halves in the holotype has preserved one small but reasonably well-developed neural spine. StIPB CHW302 and RGM.791811 both preserve fused neural halves and lack a pronounced external expression of the neural suture, even though the neural arch StIPB CHW302 did dissociate from the corresponding vertebral centrum. This leaves RGM.791811 as the only presently known completely fused vertebra of *Pararcus diepenbroeki*. The ossification sequence of the axial skeleton in tetrapods varies greatly among taxa (see also discussion in Klein & Scheyer, 2014). A more anterior anatomical position of the partially fused neural arch StIPB CHW302 with respect to the fully fused vertebra RGM.791811 and again partially fused, predominantly posterior presacral and sacral axial elements in TWE 480000454 lends supports to a more localised ossification pattern within the axial skeleton. The inferred morphological positions and associated ossification of the known *Pararcus diepenbroeki* vertebrae suggest an ossification pattern that initiated in the middle of the vertebral column and subsequently proceeded anteriorly and posteriorly, as described for archosaurs (Brochu, 1996). This interpretation has to be considered with caution, since overall adult body size may vary and the referred material originates from three different individuals. Ossification of the dorsal vertebrae is imperative for locomotion (Romer, 1956), which may have advanced bone ossification in dorsal vertebrae relative to other domains. In *Placodus gigas*, the dorsal and anteriormost sacral vertebrae themselves are practically immobile (Drevermann, 1933), which precludes paraxial movement but does not rule out a supportive function for limb- or tail-propelled locomotion. RGM.791811 does carry a well-developed neural spine whereas the slightly larger StIPB CHW302 does not. This may, however, be a product of their different anatomical positions, or represent an expression of either developmental plasticity or ontogenetic stage.

The overall dimensions of RGM.791811 are intermediate between those of the other two referred specimens, although

it is closer in size to the TWE 480000454 material than to StIPB CHW302. Only the description of additional material representing varying size classes can reveal whether the observed discrepancy between element size and degree of ossification is taxonomical, ontogenetical or a product of intraspecific allometry.

The diagnosis for *Pararcus diepenbroeki* specifies a morphological condition for the neural arches of the posterior presacral and sacral vertebrae (Klein & Scheyer, 2014). The vertebral centra, however, are considered typical for the entire axial skeleton, which are thereby generally stated to be 'deeply amphicoelous and notochordal; centra swollen and pachyostotic but only weakly constricted, with the lateral edges of the centra extending mostly parallel to each other' (Klein & Scheyer, 2014: 888). This condition, also included as character 72 in a phylogenetic exploration by Klein and Scheyer (2014), is now shown to be variable within the axial skeleton. The morphology of the vertebra described here suggests the referred condition is specific for vertebrae in or around the posterior presacral and sacral domain, as the vertebral centra in the dorsal domain do not exhibit extensive pachyostosis and are strongly constricted. We therefore propose to restrict the original diagnosis of the vertebral centra to the presacral and sacral domain.

The limited overlap in the distribution of placodont remains within the stratigraphy of the Vossenveld Formation at the Winterswijkse Steengroeve indicates that the presently recognised placodont taxa do not necessarily constitute sympatric elements of the same paleoecological system. The placodont assemblage from the stratigraphic interval around Layer 9 (the main fossiliferous bone bed in the quarry) thus far includes the basal placodont *Palatodonta bleekeri* (Neenan et al., 2013), which carried pointed and peg-like teeth, and a small 'Cyamodus-like' placodontoid (Albers, 2005) that already exhibited a bulbous, robust dentition. The enigmatic aff. *Eusaurosphargis*, likely a placodont or closely related form, is present at these levels as well (Sander et al., 2014; Klein & Sichelschmidt, 2014), and its characteristic vertebrae with elongated transverse processes have also been encountered in the Layer 14 assemblage (M. Doring & D. Voeten, personal observation). Other, and generally substantially larger placodont material representing *Placodus* sp. and *Pararcus diepenbroeki* had only been recovered approximately 16 m higher in the stratigraphy (Oosterink et al., 2003; Albers, 2005; Klein & Scheyer, 2014) than Layer 14. In this respect, the relative stratigraphic proximity of Layer 14, provenance for the described vertebra, to Layer 9 is noteworthy, as it constitutes the lowermost occurrence of a large placodont in the Vossenveld Formation thus far. A reliable temporal framework within the stratigraphy of the Vossenveld Formation has not been established yet. Whether the younger occurrence of the larger placodonts *Pararcus diepenbroeki* and *Placodus* sp. with respect to most other sauropterygians in Winterswijk results from a habitat preference of the generally associated deeper paleobathymetrical setting (Klein

& Scheyer, 2014), rate of establishment thereof (Kelley et al., 2014), evolutionary biozonation, or results from preservational bias remains inconclusive.

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