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Source: Acta Palaeontologica Polonica, 59(4) : 887-902

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2012.0147

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A new placodont sauropterygian from the Middle Triassic of the Netherlands

NICOLE KLEIN and TORSTEN M. SCHEYER



Klein, N. and Scheyer, T.M. 2014. A new placodont sauropterygian from the Middle Triassic of the Netherlands. *Acta Palaeontologica Polonica* 59 (4): 887–902.

A new genus and species of a non-cyamodontoid placodont is described on the basis of an incomplete and disarticulated skeleton from Winterswijk, the Netherlands, dated as early Anisian (Lower Muschelkalk). The new taxon is unique in a ventrolateral expansion of the neural arches of the posterior presacral and sacral vertebrae, in which the transverse process is incorporated. It has a round, plate-like pubis and ischium, and the only preserved long bone indicates elongated limbs. The holotype, which is relatively large (>1.35 m) for a basal sauropterygian, has still un-fused halves of neural arches and no distinct neural spine developed yet. The new taxon is assigned to non-cyamodontoid placodonts based on its round girdle elements, the morphology of dorsal-, sacral-, and caudal ribs, the straight medial and mediolateral elements of gastral ribs, and the presence of un-sutured armour plates. In spite of the large size of the holotype, there is evidence that the animal was not yet fully grown, based on the paired neural arches, and general poor ossification of the bones. The un-fused halves of neural arches are interpreted as skeletal paedomorphosis, which is typical for vertebrates with a secondary marine life style. The sacral region seems to be highly flexible.

Key words: Sauropterygia, Placodontia, non-cyamodontoid placodonts, neural arches, paedomorphosis, locomotion/swimming style, Triassic, Muschelkalk, Netherlands.

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Received 20 December 2012, accepted 11 April 2013, available online 12 April 2013.

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Introduction

Triassic Sauropterygia is a very diverse and successful group of marine reptiles, which appeared by the end of the Early Triassic (Olenekian) in the Panthalassa Sea (Li 2006). At the beginning of the Middle Triassic, Sauropterygia were distributed in high numbers along the western (i.e., Germanic Basin, Alpine Triassic) and eastern Tethys (China) (e.g., Rieppel 2000a; Li 2006). They can be divided into two major groups, Placodontia and Eosauropterygia. The latter includes Pachypleurosauria, Nothosauroidea, and Pistosauroidea, which also incorporates the Plesiosauria (Rieppel 2000a). Nothosaurs and pachypleurosaurs became extinct in the Ladinian, placodonts persisted until the Rhaetian (Rieppel 1999, 2000a, b), and Plesiosauria are the only sauropterygians that thrived until the end of the Cretaceous.

Several new Triassic sauropterygian taxa have been described recently, especially from the eastern Tethyan province, mainly from Guizhou and Yunnan Province, China (Li 2000; Li and Rieppel 2002; Jiang et al. 2008a, b; Zhao et al. 2008). Besides new placodont, pachypleurosaur, and nothosaur taxa, three basal eosauropterygian taxa have been described from the Middle Triassic of China, which show a combination of pachypleurosaur and nothosaur characters (Jiang et al. 2008a; Shang et al. 2011; Cheng et al. 2012). The sauropterygian fauna from western Tethys was described mainly in the 19th and 20th century (summarized in Rieppel 2000a). With few exceptions (Nosotti and Rieppel 2002; Buffetaut and Novak 2008) only the Middle Triassic (early Anisian) locality of Winterswijk, the Netherlands, has produced additional diagnostic material and new taxa from the Germanic Basin in the last decade (Klein and Albers 2009; Klein 2009, 2012; Neenan et al. 2013). The current paper reports a new placodont taxon from this locality.

Placodontia can be divided into an un-armoured placodontoid grade and the heavily armoured monophyletic Cyamodontoidea (Rieppel 2000a; Neenan et al. 2013). The placodontoid grade contains three taxa: *Paraplacodus broilii* Peyer, 1931 and two species of *Placodus* (*P. gigas* Agassiz,

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1833, and *P. inexpectatus* Jiang, Motani, Hao, Rieppel, Sun, and Schmitz, 2008). Cyamodontoidea are more diverse, currently with at least nine genera (e.g., Rieppel 2000a, 2001; Zhao et al. 2008). Both groups are known from the western and eastern Tethys but are less abundant in the latter (e.g., Hagdorn and Rieppel 1999; Li 2000; Rieppel 2000a; Li and Rieppel 2002; Jiang et al. 2008b; Zhao et al. 2008; Neenan et al. 2013). Placodonts have a unique morphology, with a massive and akinetic skull with a reduced but specialized dentition, enabling a durophagous diet (Scheyer et al. 2012). Cyamodontoidea show numerous armour plates fused into one or two dorsal, and in some cases, also a ventral armour shield (Rieppel 2002; Scheyer 2007, 2010). *Paraplacodus*, on the other hand, lacked any kind of armour plates and *Placodus* only shows a single row along its vertebral column (Rieppel 2000a, b; Jiang et al. 2008b). The postcranial skeleton of many cyamodontoids is only incompletely known due to the armour cover, whereas that of *Paraplacodus* and *Placodus* is well known (Drevermann 1933; Rieppel 1995, 2000a, b, 2002; Jiang et al. 2008b).

The new placodont comes from the Winterswijk locality, from layer 36, which is several metres above the main productive bone bed of layer 9 (Oosterink 1986). Layer 36 still belongs to the Vossenveld Formation, which correlates with the Wellenkalk facies (Hagdorn and Simon 2010) and is early Anisian in age. Limestone of layer 36 indicates a shallow marine environment with rare evidence of bioturbation and turbulence. The limestone is micritic, not laminated, and much harder, indicating deeper water when compared to layer 4 or layer 9 of the same quarry (Oosterink 1986; Klein 2010, 2012; Oosterink et al. in press). Winterswijk is unique when compared to the numerous localities of the Germanic Basin because it produces not only a large number of isolated bones of marine reptiles, but also articulated and associated skeletons (Oosterink et al. 2003, in press). The pachypleurosaur *Anarosaurus heterodontus* is known from several skeletons and skulls, representing different size classes (Rieppel and Lin 1995; Klein 2009, 2012). *N. marchicus* is known from a number of complete skulls (Albers 2011) and several incomplete skeletons (NK unpublished data). *N. winkelhorsti* is only known from a complete skull (Klein and Albers 2009). Recently a disarticulated but fairly complete postcranial skeleton of a basal pistosauroid was described (Klein 2010; Sander et al. 2013). Placodonts are mainly known from fragmentary material (Oosterink et al. 2003; Albers 2005) but also from one complete skull (Neenan et al. 2013).

Institutional abbreviations.—MHI, Muschelkalkmuseum Hagdorn, Ingelfingen, Germany; StIPB, Steinmann-Institute, Paleontology, University of Bonn, Bonn, Germany; TWE, Museum TwentseWelle, Enschede, the Netherlands.

Other abbreviations.—arp, armour plates; c, centrum; co, coracoid; cr, caudal rib; cv, caudal vertebra; cvc, centrum of caudal vertebra; dr, dorsal rib; g, gastral rib; h, haemapophysis; is, ischium; llb, lower limb bone; mt, metatarsal; na, neural arch; nacv, neural arch of caudal vertebra; ph, phalanx; prez, prezygapophysis; poz, postzygapophysis; pu, pubis; ta, tarsal; uib, unidentified bone; un, ungual.

Systematic palaeontology

Sauropterygia Owen, 1860

Placodontia Cope, 1871

Genus *Pararcus* nov.

Type species: *Pararcus diepenbroeki* sp. nov., by monotypy; see below.

Etymology: From Latin *par*, pair and *arcus*, arch.

Pararcus diepenbroeki sp. nov.

Figs. 1–7.

Etymology: In honour of Gerben Diepenbroek, a dedicated collector of Winterswijk fossils, who found and donated this specimen.

Holotype: TWE 480000454, vertebrae and ribs from the posterior trunk and sacral region, two ischia, one pubis, hind limb bones, caudal vertebrae and ribs, gastral ribs, and armour plates (for list of bones see SOM 1 in Supplementary Online Material available at http://app.pan.pl/SOM/app59-Klein_Scheyer_SOM.pdf).

Type locality: Winterswijk quarry, Winterswijk, the Netherlands.

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

Referred material.—Cast of an isolated fused neural arch (StIPB CHW302) from layer 36 or one layer above.

Diagnosis.—A large non-cyamodontoid placodont with ventrolateral expansion of neural arches of the posterior presacral and sacral vertebrae; these neural arches un-fused (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; plate-like pubis with a distinct obturator foramen; plate-like ischium with a distinct concave anterior margin; dorsally flattened limb bone with one end distinctly broader and much more massive than the other, the broader articulation facet being roughly oval, whereas the other articulation facet is much narrower but still thick with a round-triangular shape, one straight (?preaxial) margin, and a slightly curved (?postaxial) margin towards the broader end; absence of angled lateral gastral elements; ventral process of the haemapophyses neither pointed nor expanded; four different types of un-fused armour plates varying in size and shape.

Description of the holotype

TWE 480000454 is a three-dimensionally preserved, incomplete, and disarticulated skeleton of a large animal, whose bones are distributed over several slabs that are partially connected to each other (Figs. 1, 2; SOM 1).

Slab TWE 480000454-A shows a single ischium (Figs. 1, 5M); slab TWE 480000454-B contains a pubis, the second ischium, one incomplete large centrum, ten isolated circular round centra, and three isolated halves of neural arches from

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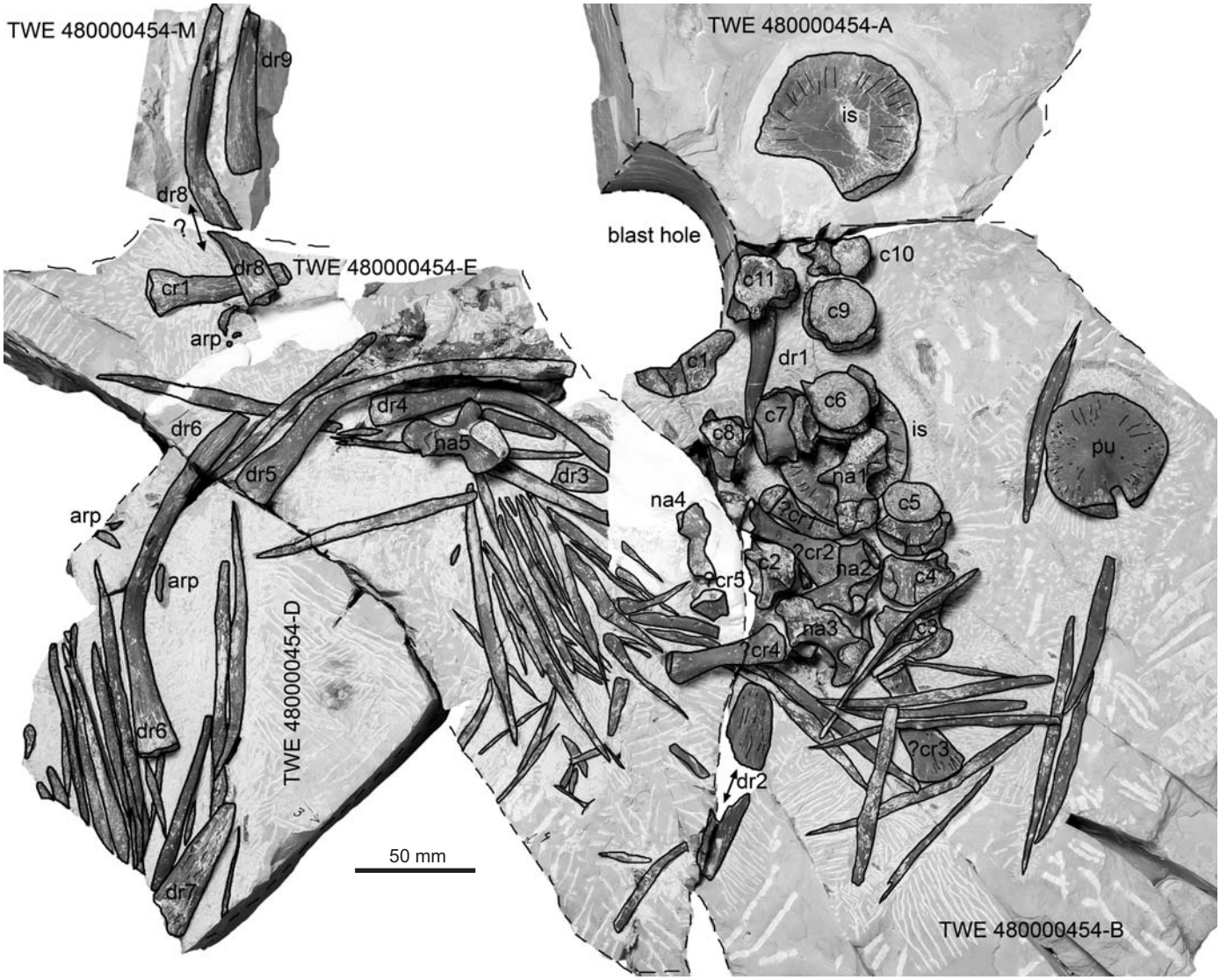


Fig. 1. Outline and overview of the connected slabs TWE 480000454-A, -B, -D, -E, and -M of *Pararcus diepenbroeki* gen. et sp. nov. from the Vossenveld Formation, Lower Muschelkalk, Winterswijk, the Netherlands. TWE 480000454-A shows a single plate-like girdle bone (is). TWE 480000454-B contains disarticulated vertebrae from the posterior presacral and sacral region (c1–11, na1–3), fragments of dorsal ribs (dr1, dr2), elements of gastral ribs (un-labelled), the second ischium (is), the round, plate-like pubis (pu), and three bones, most likely representing sacral- or caudal ribs (?cr1–3). TWE 480000454-D, -E, and -M mainly contain dorsal ribs (dr3–9) and elements of gastral ribs as well as two more isolated halves of neural arches (na4, na5), and a caudal rib (cr1).

the posterior trunk region, complete and incomplete dorsal ribs, two possible sacral or caudal ribs, and 15 fragments of gastral rib elements (Figs. 1, 3); slab TWE 480000454-D contains fragments of dorsal ribs, 15 fragments of gastral rib elements, and two small armour plates (Figs. 1, 5A); slab TWE 480000454-E contains two isolated halves of neural arches from the posterior trunk region, complete and incomplete dorsal ribs, two possible sacral or caudal ribs, and around 35 fragments of gastral rib elements (Figs. 1, 6D); slab TWE 480000454-G contains ten centra of caudal vertebrae, one isolated half of a neural arch from a caudal vertebra, one element of a gastral rib, three haemapophyses, a fragment of a possible lower limb bone, two metatarsals, three flat round tarsals, four phalanges, as well as numerous armour plates (Figs. 2C, D, 6C); slab TWE 480000454-H contains a single, yet unidentified limb bone (Fig. 5L); slab TWE 480000454-J contains one half of a neural arch of the posterior trunk region, two dorsal rib fragments, two sacral or caudal ribs, and two large and several tiny armour plates (Fig. 2B); slab TWE 480000454-K contains two halves of a disarticulated neural arch of the posterior trunk region, a distally striated end of a dorsal rib, three caudal ribs, the proximal part of a caudal rib, a possible sacral or caudal rib, two elements of gastral ribs, one ungual, 21 larger armour plates as well as numerous tiny armour plates, and one unidentified bone (Figs. 2A, 4A–C); slab TWE 480000454-M contains two distally incomplete dorsal ribs (Fig. 1).

TWE 480000454-A is connected with TWE 480000454-B

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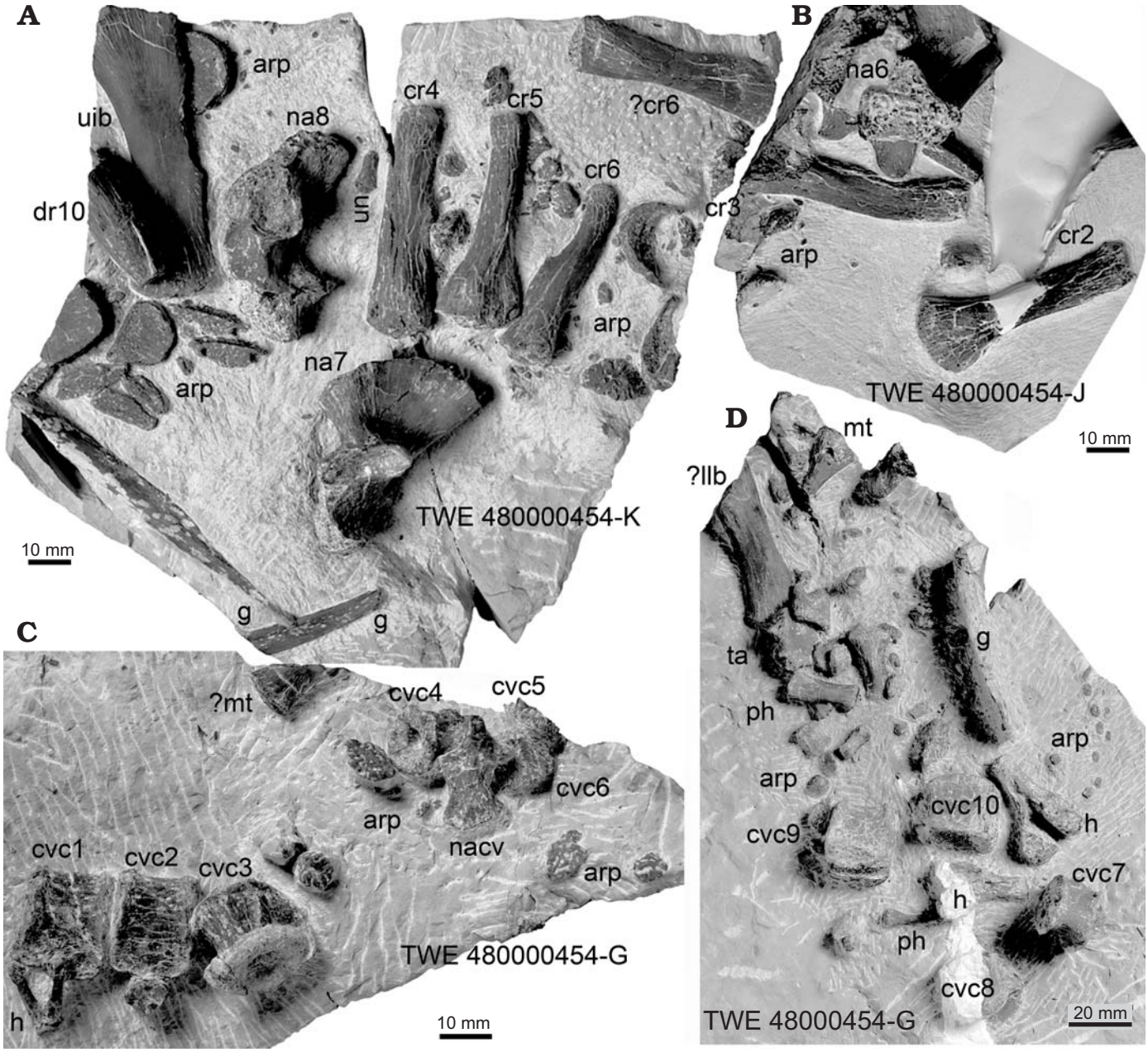


Fig. 2. Overview of slabs of *Pararcus diepenbroeki* gen. et sp. nov. from the Vossenveld Formation, Lower Muschelkalk, Winterswijk, the Netherlands. **A**. TWE 480000454-K contains a disarticulated neural arch (na7, na8), caudal ribs (cr4–6), an ungual (un), a possible caudal rib (?cr6), gastral rib fragments, and plate-like, curved, as well as keeled, shield-like armour plates. TWE 480000454-K is connected with TWE 480000454-J by a caudal rib (cr3). **B**. TWE 480000454-J contains another caudal rib (cr2), half of a neural arch (na6), fragments of dorsal ribs, and armour plates. **C**, **D**. Details of slab TWE 480000454-G which contains remains of caudal vertebrae centra (cvc1–10, nacv), haemapophyses, parts of a gastral rib (g), several bones of zeug- and autopodium (?llb, mt, ta, ph), and armour plates (arp).

by a centrum (cv10; Fig. 1). TWE 480000454-B is connected to TWE 480000454-E by a sacral or caudal rib (?cr3; Fig. 1). TWE 480000454-E is connected to TWE 480000454-D by a dorsal rib and an incomplete gastral rib (dr6; Fig. 1). TWE 480000454-K and TWE 480000454-J are connected by a caudal rib (cr3; Fig. 2). TWE 480000454-E and TWE 480000454-M are connected by a dorsal rib (dr8; Fig. 1). Note that the numbers given for some bones do not refer to their anatomical position but will help to identify the bones in the figures.

Axial skeleton

Vertebral centra.—Most of the largest preserved centrum (c1) was destroyed by a blast hole (Fig. 1). The fragment is visible in ventral view and interpreted as belonging to the anterior presacral region and is further identified as a cervical vertebra because it carries a parapophysis (Figs. 1, 3). The surface of c1 is sculptured by grooves and striations. The same slab contains ten isolated and mainly complete vertebral centra (c2–11), which are preserved in different

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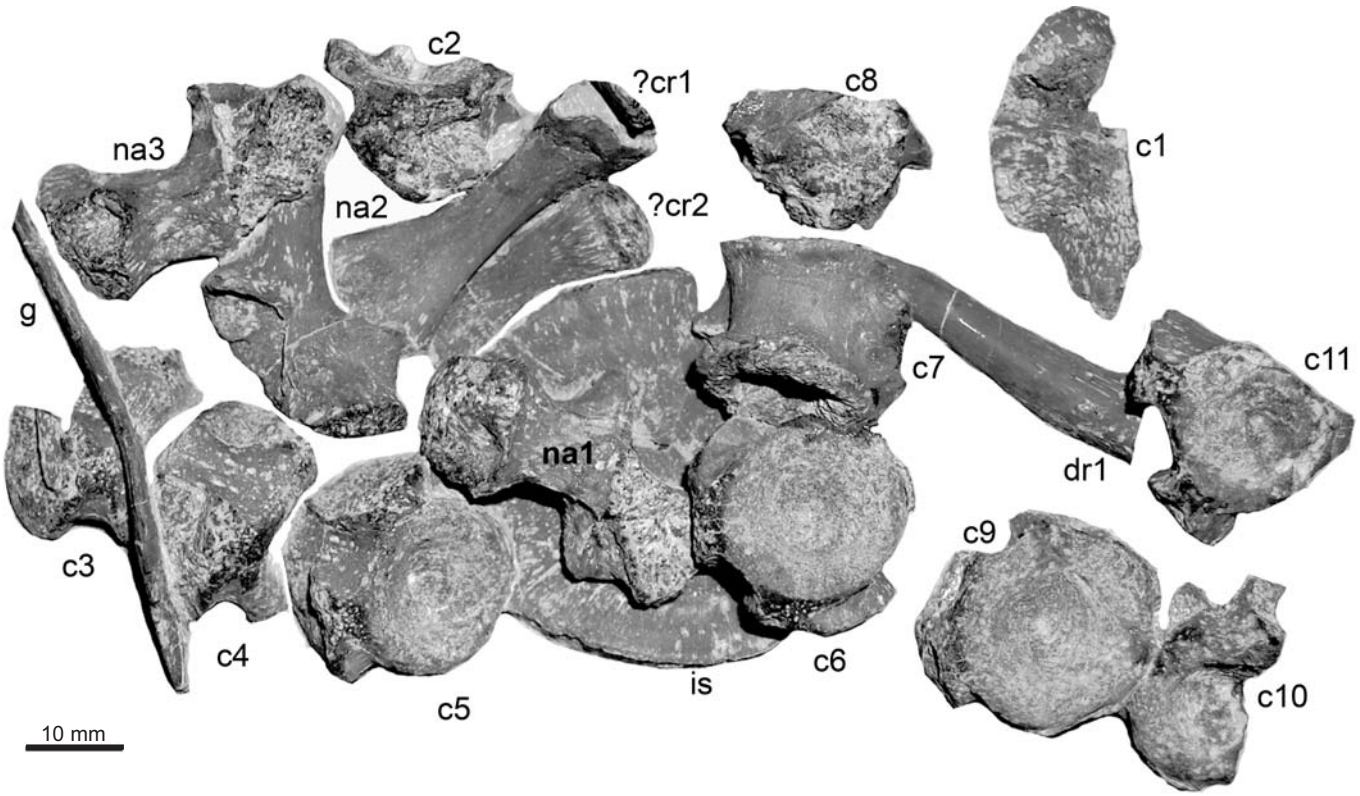


Fig. 3. Part of slab TWE 480000454-B of *Pararcus diepenbroeki* gen. et sp. nov. from the Vossenveld Formation, Lower Muschelkalk, Winterswijk, the Netherlands, showing presacral and sacral vertebrae, which had been disarticulated into centra (c1–11) and isolated halves of un-fused neural arches (na1–3). In the background of c6, c7, and na1 lies the plate-like ischium (is).

views (Figs. 1, 3). All share a nearly circular round shape, are deeply amphicoelous, and carry a broad and deep rectangular neural canal, which is defined by large oval and rugose articulation facets (pedicels) (Fig. 3). The articulation facets are clearly pronounced and extend laterally in c6–9 as far down as to the middle of the centrum (Fig. 3). These large articulation facets identify c6–9 as centra of presacral-, sacral-, and/or proximal caudal vertebrae, which in some Eosauropterygia have an extended articulation facet (Klein 2012; Sander et al. 2013). In the other centra, the pedicels did not reach as far down but still occupy the upper third of the centrum. The larger sizes of c10–11 indicate these as presacral vertebrae. C2–5 are interpreted as caudal vertebrae due to their decreasing size. The centra are all swollen and pachyostotic but are constricted around the middle, resulting in pronounced and distinctly thick anterior and posterior margins (Fig. 3).

Nine complete and one incomplete centrum of caudal vertebrae are preserved (cvc1–10; Fig. 2C, D). The much smaller centra are laterally compressed, the neural canal is small, and the centra do not carry pedicels. Their size decreases gradually, whereas their length increases (SOM 1). One of those caudal centra shows a short facet for a haemapophysis (cvc7; Fig. 2D). The dorsal surfaces of the centrum do not show butterfly-shaped or cruciform facets, typical of Eosauropterygia, but rather the simple rectangular facets typical of placodonts (Rieppel 2000a, b).

Neural arches.—Whereas disarticulation during fossilization of centra and neural arches is typical for adult Sauropterygia, it is remarkable that all preserved neural arches of specimen TWE 480000454 have fallen apart into two halves. The halves are not broken but clearly separated along their midline suture, which is also indicated by their symmetrical shape (Fig. 4). Consequently, in spite of its large size, the neural arch was still paired, and sutures were not fully ossified during the life of this individual. Altogether, nine halves of neural arches (na1–8, nacv) are distributed over several slabs (Figs. 1–4). Eight halves (na1–8) are of a similar size (SOM 1) and morphology, but nacv is much smaller and has a different morphology (Fig. 4).

To better understand the morphology and symmetry of these un-fused halves of neural arches, one right half (na7 from slab -K) was fully prepared out of the sediment (Figs. 2A, 4A, B). It was then compared against its counterpart (na8) to get an idea how a complete neural arch looked and where the centrum was sutured (Fig. 4C$_2$). This revealed that the halves of the neural arches originally had a posteriorly directed anatomical position on the centrum, shown by the position of the pedicels, and of the pre- and postzygapophyses. Measured clockwise on the medial side, in the anatomically correct position, the prezygapophysis has an angle of around 270°, indicating that it lies nearly horizontal, but the postzygapophyses have an angle of around 50°, resulting in a steep slanting position.

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Besides being paired, the morphology of the neural arches is unique (Fig. 4). The ventrolateral region, in which the transverse process is incorporated, is largely expanded (Fig. 4). The dorsal part makes only ¼ of the ventral width. In anterior view, it has a dorsally protruded, spherical and rugose articulation facet, which tapers distinctly ventrally towards the prezygapophysis (Fig. 4A, B). This dorsal part forms the basis of the incompletely developed neural spine (Romer 1956). The still to develop neural spine is very well separated by a distinct margin. The large oval prezygapophysis is situated in the middle of the neural arch and forms a shallow bowl. The prezygapophyseal facet in na7 measures 20 mm in length and 10 mm in width, which makes it rather large. At its posterior end, the prezygapophysis has a circular depression. The mediodorsal articulation facet forms a straight margin in anterior view with the counterpart of the neural arch (Fig. 4A_1, B_1). The ventral region of the medial margin is deeply concave, contributing to the neural canal. The ventral region of the neural arch half is fan-shaped and has a convex margin in anterior view (Fig. 4A_1, B_1). The straight medial part of the ventral margin is composed of the articulation facet to the pedicels of the centrum. The lateral margin is straight except for its dorsal region, which is overturned laterally. The ventral region of the lateral margin represents the articulation facet to the corresponding rib (arrows in Fig. 4C, D). In anterior view, the postzygapophysis is visible as a short spike located between the overturned dorsal end and the prezygapophysis. The anterior surface carries grooves dorsally (above the prezygapophysis) and a radially running striation ventrally (below the prezygapophysis).

In posterior view (Fig. 4A_2, B_2), the dorsal part is constricted and ends in the short postzygapophysis (length: 11.5 mm, width: 8 mm), which has an overturned posterior margin and a convex dorsal surface. The ridge, which proceeded laterally to the top of the postzygapophysis, continues ventromedially into a bowl-shaped protrusion carrying two deep, round grooves before it reaches the medial articulation facet. Below the medial articulation facet, the medial margin is deeply concave, contributing to the neural canal. Medioventrally, it carries the extensive articulation facet to the centrum. Only half of that articulation facet is visible in posterior view. It is a pronounced, deeply concave rugose surface, leaving the medial margin in posterior view much shorter than in its anterior view. The articulation facet has a deep, round groove dorsally. Its ventral part is fan-shaped but the aforementioned articulation surface reaches into it. Lateral to the articulation facet of the centrum, the ventral region has a distinct, nearly round depression, making the ventral margin very thin here. Then it thickens again towards the lateral margin, where the articulation facet to the corresponding rib is located (arrows in Fig. 4C, D).

In medial view (Fig. 4A_3, B_3), the medial articulation facet (max. length: 15 mm, height: 20 mm, or 23.5 mm if the protruded dorsal part is included) of the neural arches' counterpart covers the entire dorsal half. It is broad, angled, and tapers slightly ventrally, resulting in a roughly balloon-like shape. Finally, it meets the sharp ridge that continues posteriorly into the protrusion that leads to the upper margin of the postzygapophysis and anteriorly into the anterior margin of the shallow depression, which is formed by the prezygapophysis. The region below the zygapophyses is concave and is constricted in anteroposterior view, forming the upper half of the neural canal. The base of the upper part of the neural canal ends in the margin of the articulation facet connecting the centrum to the neural arch. This margin is also sharply protruded and runs parallel to the upper margin, which connects both zygapophyses. In medial view, the ventral part largely consists of the articulation facet to the centrum (length: 18 mm, height: ~20.5 mm). This facet is dorsally broad but tapers distinctly ventrally, and also resembles the form of an oval balloon (Fig. 4A_3, B_3). The left part of the ventral articulation facet to the centrum is positioned anteriorly, but the right part is positioned more posteriorly.

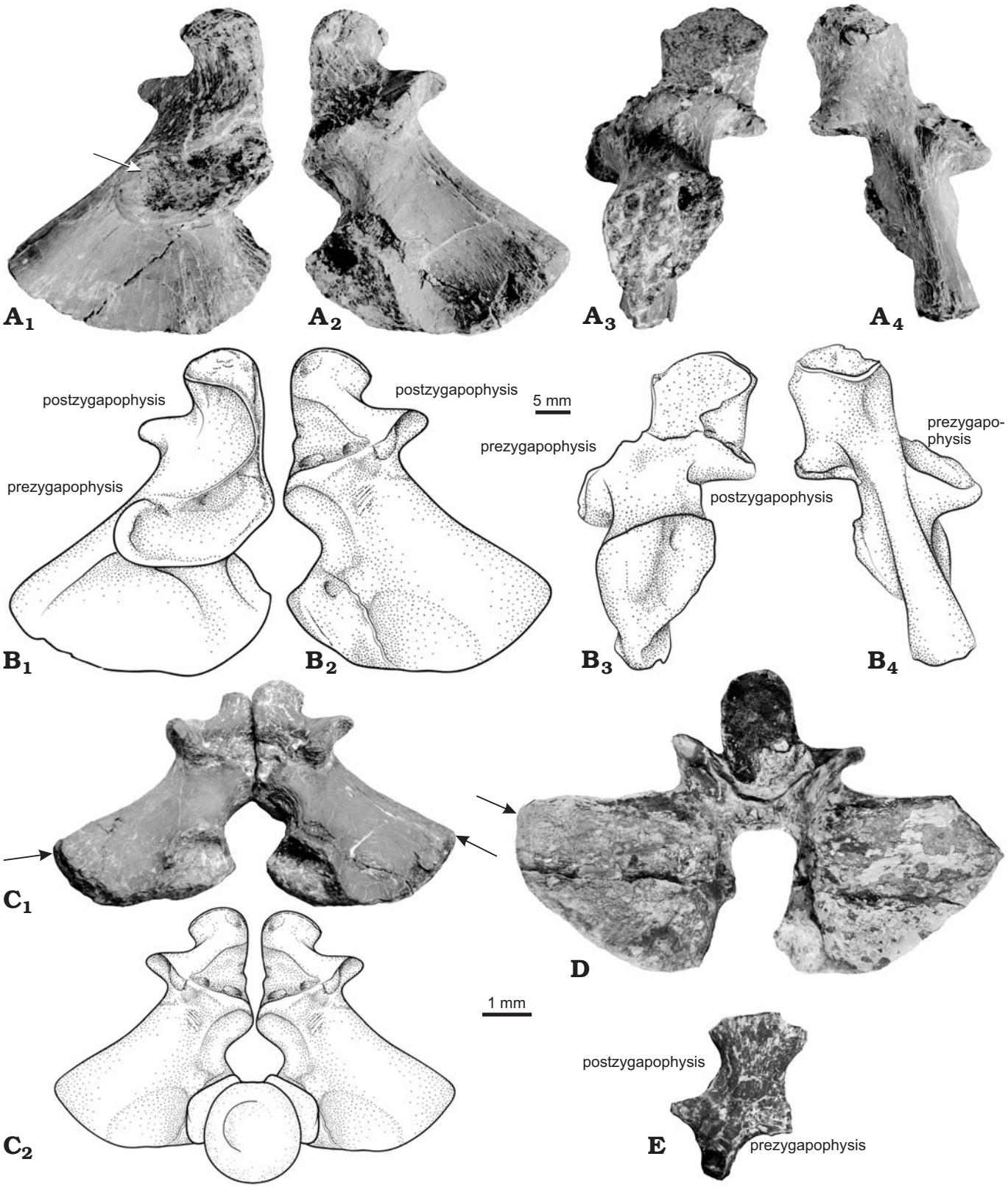
In lateral view (Fig. 4A_4, B_4), the broadest part of the neural arch is formed by the dorsal articulation facet. The top of the postzygapophysis can be observed on the left side, below the overturned lateral margin, and on the right side, the prezygapophysis is visible. The facet of the prezygapophysis starts at the same height as the postzygapophysis medially, but it reaches lower to the middle of the neural arch. In lateral view, the prezygapophysis dips down and opens ventrally (Fig. 4A_4, B_4). From the middle region downwards, the element is short and nearly rectangular. The entire ventral margin is medially broad (= articulation facet to the centrum), but laterally much thinner. A hyposphene-hypantrum articulation is present but is poorly ossified and incomplete (Fig. 4). Na1–8 share the fan-shaped ventrolateral expansion where the ribs must have articulated, pointing ventrally.

The neural arches are interpreted as belonging to the last presacral, sacral and/or the first caudal vertebrae. The similar size and morphology, and position close to each other, suggests that na2 and na3 as well as na7 and na8 once had formed complete neural arches. From what is visible, na1, na4, na5, and na6 share the same morphology but undoubtedly cannot be linked together. Because of sacralisation of the last presacral vertebra (Drevermann 1933; Rieppel 1995) and the incomplete nature of the specimen, the exact number of sacral vertebrae cannot be determined.

Another isolated half of a neural arch (nacv), which is visible in lateral view (Fig. 4E), measures only half the length of the previously described neural arches (SOM 1). Its dorsal

Fig. 4. Paired (un-fused) neural arches of specimen TWE 480000454 (A–C, E, F) and the cast of the fused neural arch StIPB CHW302 (D) of *Pararcus diepenbroeki* gen. et sp. nov. from the Vossenveld Formation, Lower Muschelkalk, Winterswijk, the Netherlands. **A**. Photographs (**A**) and drawings (**B**) of the isolated half of the disarticulated neural arch (na7 from slab TWE 480000454-K) in anterior (A_1, B_1), posterior (A_2, B_2), medial (A_3, B_3), and lateral (A_4) views. Note the symmetrical shape, the huge prezygapophysis, the incorporation of the transverse processes, and the expanded fan-shaped ventral part. The arrow marks the ventrolateral articulation facet to the corresponding rib. Note the knobby round and rugose structure of the dorsal articulation facet, which forms the basis of the yet only incompletely developed neural spine. The suture to the counterpart of the neural arches half (visible in medial view) and the →

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pedicels of the corresponding centrum (visible in medial and posterior view) are also strongly rugose. **C**. The two isolated halves of an un-fused neural arch (na7, na8, slab TWE 480000545-K) have been re-assembled in posterior view in this image. Ventrally, the articulation facet to the corresponding centrum is well visible. The postzygapophyses are clearly steeply angled (arrows mark the articulation facet to the ribs). Photograph (C_1), drawing of an reconstructed complete vertebrae (C_2). **D**. Fused neural arch, which also shows the ventrolateral expansion, resulting here in a horizontal articulation facet to the corresponding rib (arrow). **E**. Neural arch of caudal vertebra from slab TWE 480000454-G, which represents half of an un-fused neural arch of a caudal vertebra. The different morphology when compared to the halves of the neural arches of the posterior presacral and sacral vertebrae (B, D) is discussed in the text.

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region is rectangular and broad, representing a short neural spine; the middle region is slightly constricted; and the region carrying the pre- and postzygapophyses is broadest. It did not show a ventrolateral expansion, but this might be related to the lateral view in which it is preserved. The prezygapophysis is broad and massive; the lower postzygapophysis is pointed and smaller. Both lay nearly horizontal when brought into the correct anatomical position (Fig. 4C). The transverse process is short but distinct and has an oval articulation facet for a rib (Fig. 4C$_1$, D, arrows). Contrary to na1–8, navc has a short but clear neural spine. The small size, presence of a transverse process with a rib articulation facet, and its association with centra of caudal vertebrae indicate that nacv belonged to a caudal vertebra. The nacv shows no evidence that it carried armour plates, such as rugosities on its neural spine.

Dorsal ribs.—Several dorsal ribs are preserved of which five are largely complete (dr1, dr4–6, dr8; Figs. 1, 5A). The proximal heads of the ribs are moderately striated and swollen but complete pachyostosis of the ribs is not apparent. The ribs are slightly curved in their anterior third. The middle part of the ribs has a smooth surface, and in dorsal view, a very thin dorsal ridge, more tactile than visible. The striated distal part is slightly swollen again (e.g., dr5, dr6) but by far not as broad as the proximal end (Fig. 5A). It is not clear if those ribs are complete or if the distal part has disarticulated due to poor ossification, as is the case in a pachypleurosaur (Klein 2012). Dr1 is shorter and more slender, and its surface is completely smooth when compared to the other dorsal ribs. Its distal end is hollow, possibly indicating that the distal part of that rib is missing. Dr1 seems to originate from a different part of the trunk region when compared to the other ribs. Dr2 is only distally preserved and also differs from the other ribs because it is very broad, dorsally convex and ventrally flat (Fig. 1).

Sacral and/or caudal ribs.—Six sacral or caudal ribs are identified (cr1–6). The ribs are all of similar length (SOM 1) and distally (but not proximally) broadened (Fig. 5B–G). Cr2 and cr6 are more straight and symmetrical when compared to the others (Fig. 5C, G). Cr4 is most likely the first caudal rib by its shortness and contrasting morphology (Fig. 5E). The ribs all show similar uneven/rough surfaces, which are covered by thin sediment-filled cracks.

Six additional bones (?cr1–6, Figs. 1, 2, 5H–K) possibly also represent sacral or caudal ribs, but they differ in morphology and size from those previously described (SOM 1). However, sacral and caudal ribs are variable in shape in Sauropterygia (e.g., Drevermann 1933: figs. 62–67). They all share a slightly to moderately constricted shaft with expanded articulation facets at both ends, in contrast to ribs (cr1–6). One end is thick and almost round, whereas the other is more flat but both are of similar width, except for ?cr3, in which one end is distinctly broader and more flat than the other end (Fig. 5K). In ?cr2, ?cr3, and ?cr5 both articulation surfaces are turned toward each other. Rib ?cr2, which has distinct proximal and distal articulation facets (Fig. 5H), is very similar to a sacral rib of *Placodus* figured by Drevermann (1933: fig. 66).

Haemapophyses.—Together with the caudal vertebrae, three disarticulated haemapophyses are preserved (Fig. 2C, D). Two of them show two massive knobby, round articulation facets with a rugose surface and a short straight rod-like ventral process, which is neither pointed nor expanded (Fig. 2D). Another haemapophysis appears less pachyostotic and has less massive articulation facets (Fig. 2C).

Gastral ribs.—Numerous fragments (>55) of disarticulated gastral ribs are distributed over the slabs (Fig. 1). These seem to have formed a dense ventral rib cage (Fig. 6D). Each gastral rib was composed of several elements, which is evident because of bi-furcated, pointed articulation facets in some elements (Fig. 5N, arrow). However, the exact number of elements forming one complete gastral rib remains unclear because of disarticulation. The specimen contains mainly straight or minimally curved medial and mediolateral elements (Figs. 1, 5N, 6D), but not a single, sharply angled lateral element, although these are characteristic of *Paraplacodus broilii*, *Placodus gigas*, and *P. inexpectatus* (e.g., Drevermann 1933: figs. 6, 7; Rieppel 2000b: 17; Jiang et al. 2008). The length and broadness of the fragments varies but all are dorsoventrally flattened, large, and swollen (pachyostotic) in their midshaft region.

Appendicular skeleton

Pubis.—The pubis is a plate-like round bone, anteroposteriorly slightly longer than lateromedially wide (Figs. 1, 5N; SOM 1). It carries a deep open rectangular obturator foramen (4.2 mm × 8 mm), which was most likely located posterolaterally as is typical for most Sauropterygia (NK personal observations, but see *Psephoderma* in Pinna and Nosotti 1989). The anterolateral, posterolateral, and posterior margins are straight, when compared to the highly convex medial half of the pubis. The anterolateral articulation facet to the ilium is much thicker (15 mm) and more massive when compared to the thin posterolateral articulation facet to the ischium and its entire medial part (7.7 mm). The lateral articulation surface is very rugose. The pubis carries a radial sculpture and its margins are frayed.

Ischium.—The right and left plate-like ischia is preserved, although one is largely covered by two centra and half of a neural arch (Figs. 1, 2A, 3, 5M). The very flat bone is principally round with a concave anterior margin and a convex posterior margin. The medial margin is straight, being the medioventral symphysis to its counterpart. The lateral margin is convex with a thick, oval, and rugose articular joint. In ventrodorsal view, this section of the margin is straight. The lateral and medial edges of the concave margin are both pronounced, with the medial edge being somewhat longer. The ischium shows a radial sculpturing and its margins are frayed. The lateral half of the element is thicker than the medial half.

Autopodium.—Several disarticulated bones of a foot are preserved (Fig. 2D). Two metatarsals (mt) can be identified: a distal end (Fig. 2C) and a proximal end with a thick triangular head, most likely from mtI or mtV (Fig. 2D). The astragalus and calcaneum are both preserved (Fig. 5O). The astragalus,

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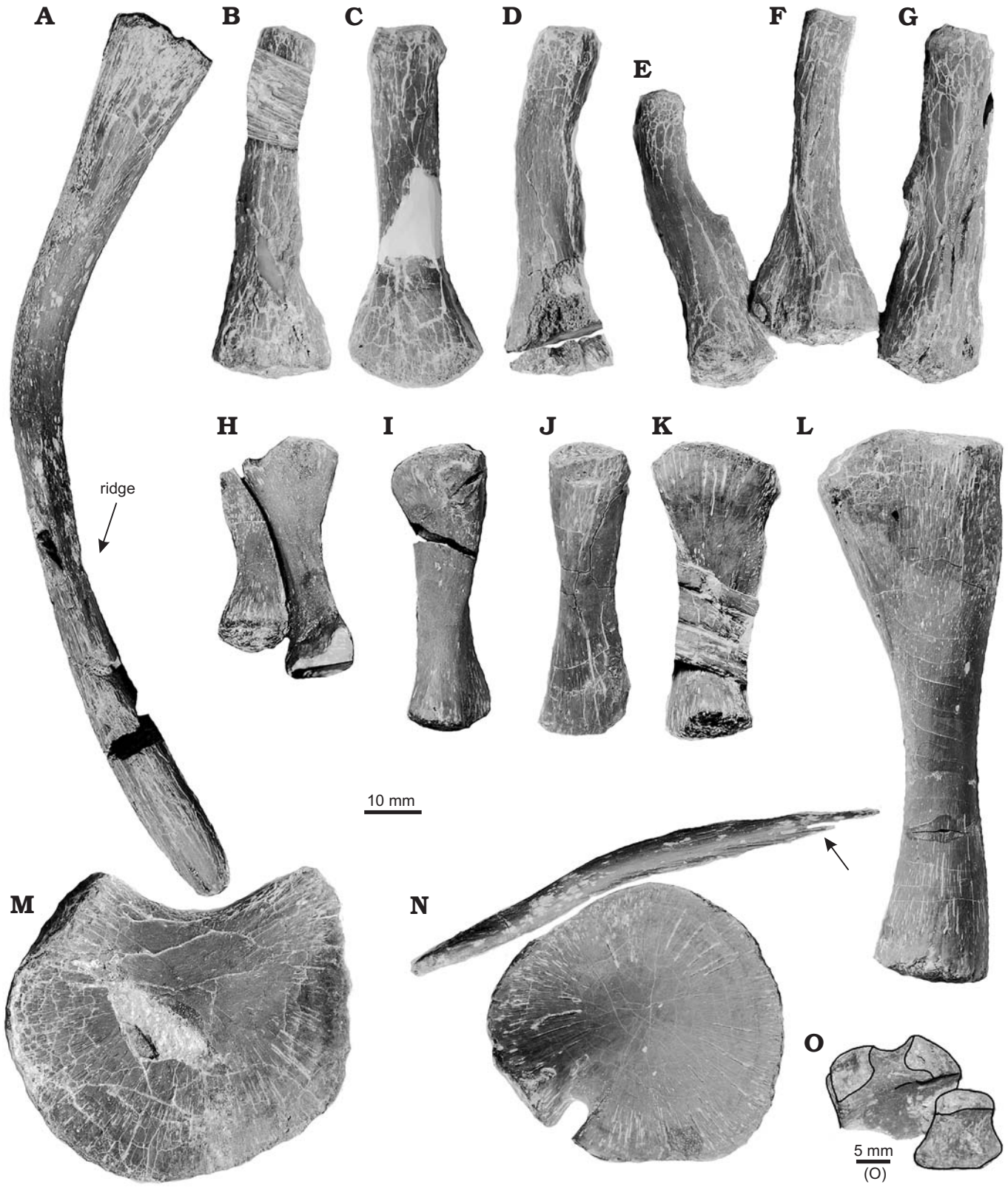


Fig. 5. Ribs, appendicular and girdle bones of specimen TWE 480000454 of *Pararcus diepenbroeki* gen. et sp. nov. from the Vossenveld Formation, Lower Muschelkalk, Winterswijk, the Netherlands. **A**. Dorsal rib (dr6) from slab TWE 480000454-D and -E (mirrored). Note the distinctly swollen and striated proximal end, the slight curvature in the anterior half of the process, and the slightly swollen and again striated distal end of the rib. **B**–**K**. Sacral and/or caudal ribs from slabs TWE480000454-B, E, J, K, which show a very diverse morphology. **L**. Unidentified limb bone from slab TWE 480000454-H. **M**. Ischium with concave anterior margin from slab TWE480000454-B. **N**. Plate-like pubis and medial element of a gastral rib with a furcate articulation facet from slab TWE480000454-A. **O**. Astragalus and calcaneum from slab TWE480000454-G.

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which dips down into the sediment and is therefore only incompletely visible, exhibits two bulged, knob-like articulation facets that are connected by a concave narrow bridge, resulting in a proximal concavity. This area has a distinct ridge. The rest of the bone seems to be round and plate-like. The calcaneum has one articulation facet at its smaller end, which is convex and has a pronounced ridge. The rest of the bone then broadens and is roughly trapezoid. The tarsals are followed by two relatively long phalanges, which are constricted but not hour-glass-shaped, and two much shorter and stout phalanges (Fig. 2D). Another long but very slender phalanx lies a short distance apart and presumably represents a phalanx from the first finger. Associated with the autopodial elements are tiny armour plates (Figs. 2C, D, 6C).

Unidentified limb bones.—Slab TWE 480000454-H consists of a single limb bone (Fig. 5L). It has one massive broad end. The other end is much narrower and, in comparison to the rest of the material, is under-proportioned. The midshaft is constricted, with one margin being straight whereas the other is slightly curved. The larger end, with its oval articulation surface is slightly convex and more flat (13.5 mm) when compared to the smaller end (16.5 mm), which has a round-triangular articulation facet that is indented/depressed. Both ends carry striations, but the articulation facets are less rugose than that of the vertebrae. The midshaft carries two foramina. The ventral side is flattened, whereas its dorsal side is slightly convex.

Associated with the autopodial bones is an incomplete bone, which most likely represents a lower limb bone (?llb; Fig. 2D). Its margins are straight and its distal end is narrower than the preserved middle region.

Armour plates.—Four different types of armour plates are preserved. First are large and plate-like (Figs. 2A, 6B), of which two are nearly rectangular and one, lying below the unidentified bone, is round. Second and most common, are elongated and shield-like armour plates, with a sharp keel running across the midline (Figs. 2A, 6B). A third type of armour plate is curved with hooks on both ends and is not keeled (Fig. 6A). In addition, there are many tiny simple oval to round armour plates (Fig. 6C). All armour plates are heavily sculptured by grooves. Their visceral sides are very rugose (Fig. 6A).

Unidentified bone.—On slab TWE 480000454-K lies a large regularly formed flat bone, which could not be identified (uib; Fig. 2A). The complete end of the bone is slightly convex and roughly striated. The visible mid-portion has very straight margins before it broadens toward the incomplete end, which shows a finer striation.

Description of referred material

StIPB CHW302 is a cast of a complete fused neural arch in posterior view, with a total width of 90 mm and a length of 56 mm (Fig. 4D). The original bone is housed in the private collection of H. Winkelhorst, Aalten, the Netherlands. StIPB CHW302 is larger than the neural arches of TWE 480000454 (SOM 1). It shares the ventrolateral expansion, which has incorporated the transverse process. Contrary to na1–8 of TWE 480000454, the lateral margin of the expanded region has shifted upwards to a dorsal position in StIPB CHW302. The lateral-most region has the articulation facet to the corresponding rib, which is horizontal (Fig. 4D, arrow); in na1–8 the articulation facet points ventrally. The neural canal is rectangular, very high, and broad. Pre- and postzygapophyses are not well preserved in StIPB CHW302, but seem to be smaller when compared to na1–8. Contrary to the neural arches of TWE 480000454, a neural spine has developed but remains short (Fig. 4D). Because StIPB CHW302 shows the same characteristic ventrolateral expansion of the neural arch, it is assumed that it belongs to the same new taxon as the isolated halves of neural arches of TWE 480000454. Differences in morphology and fusion can be related to a more anterior anatomical position of StIPB CHW302. Differences in the ossification sequence of neural arches are documented in the pachypleurosaur *A. heterodontus* (Klein 2012), but not in the pachypleurosaur *Neusticosaurus* spp. (Sander 1989).

Remarks

The preserved bones of TWE 480000454 were compared in the traditional way to *Placodus gigas* as it has well-known postcranial elements. There is no indication of heavy armour or a closed shell in TWE 480000454 as is characteristic for Cyamodontoidea. *Paraplacodus* did not have any armour plates (Rieppel 2000a, b) and differs in most morphological features from the new taxon. However, mainly to identify unknown elements of TWE 480000454, postcranial bones of *Paraplacodus*, Cyamodontoidea as well as of *Eusaurosphargis*, *Blezingeria*, and *Helveticosaurus* are also considered for comparison.

Vertebrae.—The neural arches of TWE 480000454 are interpreted as belonging to presacral, sacral, and/or first caudal vertebrae; a more detailed analysis is not possible. They are unique in the expanded ventral part and their un-fused status in large, but not fully-grown, individuals. Un-fused halves of neural arches are not known so far from any Sauropterygia. In *P. gigas*, the fused neural arch rarely separates from the centrum, and yet this is the condition in the new specimen, *Paraplacodus*, and Eosauropterygia (Rieppel 2000a, b).

Some eosauropterygians have an expanded ventral region of the sacral neural arches (Klein 2012; Sander et al. 2013) but this is never as extensive as it is in TWE 480000454. In cyamodontoids, the transverse processes of sacral ribs are elongated, curved and sometimes fused with their corresponding ribs (Rieppel 2000a). The vertebral centra of *Blezingeria* Fraas, 1896 are amphicoelous, concentrically round and additionally share with TWE 480000454 broad and massive articulation facets for the ribs. The ventral part of the neural arches is also broad and massive in *Blezingeria*, but the neural arches are always fused to each other and carry a long neural spine (Huene 1951). TWE 480000454 lacks the

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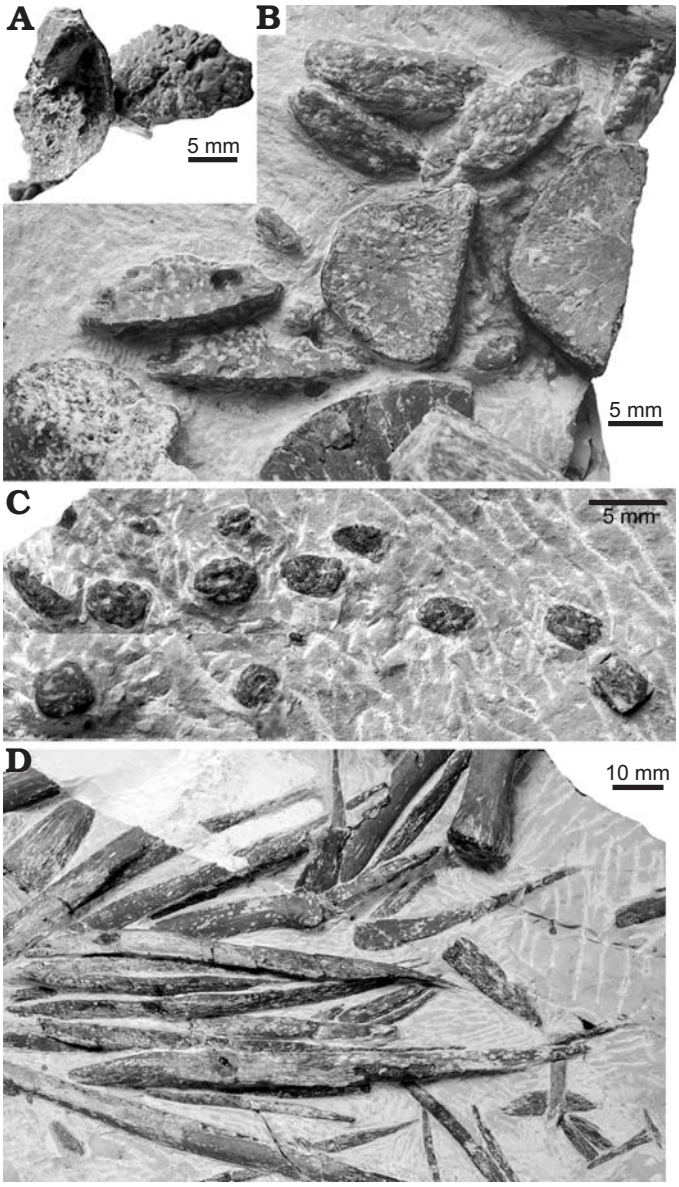


Fig. 6. Enlargement of armour plates and gastral elements of *Pararcus diepenbroeki* from the Vossenveld Formation, Lower Muschelkalk of Winterswijk, the Netherlands, from different slabs (see Figs. 1, 2). **A**. Curved armour plates with hooked ends, which are not keeled. **B**. Plate-like and shield-like keeled armour plates. **C**. Tiny small round-oval armour plates associated with autopodial bones. **D**. Enlargement of medial and mediolateral gastral rib elements.

characteristically elongated and distally expanded transverse processes of Saurosphargidae.

High neural spines are typical of most Sauropterygia, including *Placodus* and cyamodontoids (e.g., Rieppel 2000b and see references for newly described Chinese taxa). However, neural spines in TWE 480000454 are not yet developed and even in the fused neural arch of StIPB CHW302 the neural spine is very low.

Except for *Paraplacodus*, all placodonts share round, amphicoelous, and notochordral centra as does TWE 480000454. The size of the neural canals and the massiveness and extension of the pedicels is also similar in TWE 480000454 and *P. gigas* (Drevermann 1933: table 9). TWE 480000454 also shares similar sacral vertebrae with *P. gigas*, having the bowl-shaped broadened prezygapophyses. However, they stand nearly horizontal in TWE 480000454, but are inclined in *P. gigas* (Drevermann 1933: table 9). In contrast, the postzygapophyses in TWE 480000454 are more inclined than in *P. gigas*. The vertebrae of TWE 480000454 appear much more pachyostotic than those of *Placodus* (Drevermann 1933; Jiang et al. 2008b).

Ribs.—The dorsal ribs of TWE 480000454 resemble those of *Placodus* (Drevermann 1933: figs. 35–37; Jiang et al. 2008b) but seem to be somewhat more curved, which could be related to their anatomical position. Dr1 of TWE 480000454 resembles two ribs of *P. gigas* figured by Drevermann (1933: figs. 42, 43), which represent the rib of the last presacral vertebra. The ribs of TWE 480000454 differ distinctly from those of *Paraplacodus*, which are characterised by a very pronounced (uncinate) process (Rieppel 2000a: 645, fig. 5B).

Sacral and caudal ribs of TWE 480000454 are similar to *Placodus* (Drevermann 1933; Jiang et al. 2008b). Sacral ribs in Sauropterygia are variable (see e.g., Drevermann 1933: figs. 62–67; Rieppel 1994: figs. 20, 21; Jiang et al. 2008b), which makes a more accurate assignment of the sacral and caudal ribs of TWE 480000454 impossible. Also Dalla Vecchia (2006: 214) described how for a pistosaurid, the transition from "dorsals to sacrals and from sacrals to caudals" is gradual.

Drevermann (1933: fig. 97) described the haemapophyses of *P. gigas* as slender with a pointed process but clubbed thickened articular facets. The haemapophyses of TWE 480000454 are similar except for a straight and not pointed process and a more swollen (pachyostotic) appearance. *P. inexpectatus* and *Paraplacodus* share distally broadened and farther posteriorly bifurcated haemapophyses (Rieppel 2000a; Jiang et al. 2008b), which differs from the condition in TWE 480000454.

The gastral ribs of TWE 480000454 are similar to medial elements of *P. gigas* (see e.g., Drevermann 1933: figs. 47, 48, 53) but strongly curved lateral elements are not preserved in TWE 480000454. Cyamodontoids do not show an "indication of a strong angulation of the lateral elements" (Rieppel 2000a).

Appendicular bones.—The pubis of TWE 480000454 closely resembles that of *Hanosaurus hupehensis* (Rieppel 1998: figs. 1B, 5), except for a smaller articulation facet to the ischium in the latter. The cyamodontoid *Psephoderma* also has a round pubis with a clear obturator foramen (Pinna and Nosotti 1989). The pistosaurid *Bobosaurus* has a plate-like pubis with a deep semicular notch on its posterior margin, but it lacks an obturator foramen (Dalla Vecchia 2006). A similar pubis is described for *Corosaurus* but it has an obturator foramen (Storrs 1991: fig. 4). The round pubis of TWE 480000454 differs from the transverse-oval pubis of *Placodus* and *Paraplacodus*. The pubis of *Eusaurosphargis* is also transverse-oval (Nosotti and Rieppel 2003), while *Helveticosaurus* has a plate-like pubis with a distinct concave anterior margin. A pubis in the collection of the MHI (MHI 1113/20),

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which is assigned to *Blezingeria*, is identical to the pubis of TWE 480000454.

The morphology of the ischium of TWE 480000454 differs from any other described girdle element for Sauropterygia. The most distinct feature is its concave anterior margin. The ischium of *Placodus* has, although not as distinct as in *Paraplacodus*, *Cyamodus*, and Eosauropterygia, a roughly constricted lateral shaft-like region and a fan-shaped medial region. Its anterior margin is slightly concave and forms, together with the slightly concave posterior margin of the pubis, only a small (reduced) thyroid fenestra (Rieppel 2000a). The thyroid fenestra in TWE 480000454 was larger than that of *Placodus*. The ischium of the basal eosauropterygian *Wumengosaurus* largely resembles that of TWE 480000454 (Jiang et al. 2008a; Wu et al. 2011). The ischium of *Helveticosaurus* and *Eusaurosphargis* differs in all aspects from that of TWE 480000454 (Peyer 1955; Rieppel 1989; Nosotti and Rieppel 2003).

Limb bones.—TWE 480000454-H differs in shape and morphological details from any other limb bone of Sauropterygia (Rieppel 2000b). It is most likely a humerus or femur because of its large size in comparison to the other bones, but it could conceivably be an elongated lower limb bone. If the specimen is juvenile (see below), it is possible that certain adult characters have not yet developed. TWE 480000454-H does not represent an ulna or a radius, for proportional and morphological reasons. The placodonts ulna is a symmetrical element with broad distal and proximal ends (Rieppel 2000a; Jiang et al. 2008b). The curved radius is flat with a distinct rectangular proximal head and a similar sized straight distal end. The radius of *Largocephalosaurus* (Cheng et al. 2012) has a similar shape but differs in having a much shorter shaft region.

It is also not much like a placodont humerus, all of which are curved. The humerus of *Paraplacodus* (Rieppel 2000a) is proximally and distally broad and generally massive but distally more flat than proximally. It is distinctly curved (in *Paraplacodus* more than in any other placodont) with a concave postaxial margin and nearly straight preaxial margin. An ectepicondylar groove is present in placodonts but no entepicondylar foramen (Rieppel 1995). The humerus of *Cyamodus* is also curved (Rieppel 1995). The humerus of the cyamodontoid *Glyphoderma kangi* (Zhao et al. 2008: fig. 1) has a very distinct shape: it is proximally extremely narrow and slender, has a similar slender and narrow shaft region, but then expands greatly distally. Dorsally, the distal end has a triangular depression and an ectepicondylar groove is present.

It is also unlikely to be a femur because even young individuals have an internal trochanter. The tibia of *Paraplacodus* is much more slender, with a smaller proximal head, and a long and slender constricted midshaft (Rieppel 2000a: fig. 9A). The tibia of *Placodus* roughly resembles the morphology of Eosauropterygia, with a broad rectangular shape in dorsoventral view, resulting from nearly straight pre-and postaxial margins, and a long and slender, only slightly constricted midshaft. The proximal head is broader than the distal one, but proportions are different from TWE 480000454-H. The tibia of *Glyphoderma kangi* (Zhao et al. 2008: fig. 1) is much more curved proximally than TWE 480000454-H. One specimen of *Wumengosaurus* has a tibia that roughly matches TWE 480000454-H (Wu et al. 2011: fig. 5D), but this is uncertain because other *Wumengosaurus* tibiae show a different morphology (Jiang et al. 2008a; Wu et al. 2011; NK personal observations). Fibulae of Sauropterygia are generally less massive than TWE 480000454-H, and with nearly equally sized proximal and distal ends.

The bones of the autopodium of TWE 480000454 are similar to *Placodus* (Drevermann 1933; Jiang et al. 2008b). However, autopodial bones are in general not distinctive and seldom offer good characters for a diagnosis or comparison of taxa, especially when disarticulated.

Armour plates.—The preserved plate-like, curved and shield-like keeled armour plates of TWE 480000454 resemble the morphology and size of those of *P. gigas* (Drevermann 1933: figs. 17, 24–29). None of the armour elements shows a pillow-like, rhomboid or hexagonal outline, nor is there any suturing or fusion into larger armour elements. TWE 480000454 thus does not show any characteristics of heavy armour typical for Cyamodontoidea (even more in the pelvis region, see Scheyer 2010). The very tiny armour plates that are mainly preserved with the hind limb elements of TWE 480000454 (Fig. 6C) could be interpreted as pertaining to the limbs, similar to those found in turtles (Barrett et al. 2002).

Stratigraphic and geographic range.—*Pararcus diepenbroeki* gen. et sp. nov. is so far only known from the Vossenveld Formation, Lower Muschelkalk, Winterswijk, the Netherlands.

Concluding remarks

Taxonomic assignment.—In addition to Sauropterygia, several other marine reptiles were present in the Middle Triassic, including ichthyosaurs, thalattosaurs, and various neodiapsids that may be closely related to Sauropterygia. Some of these taxa show astonishing convergences with Sauropterygia, such as the Saurosphargidae (Li et al. 2011) and *Helveticosaurus* (Peyer 1955; Rieppel 1989). However, TWE 480000454 cannot belong to either of these because it lacks the characteristic elongated and distally expanded transverse processes of Saurosphargidae, and *Helveticosaurus* lacks armour plates.

Without a skull or a more complete skeleton, the assignment of TWE 480000454 to Sauropterygia is only tentative (but see phylogenetic analysis below). Based on its incomplete preservation, no sauropterygian synapomorphies could be identified. The assignment of TWE 480000454 to Placodontia is based on the following postcranial characters, as listed by Rieppel (2000b: 16): “[...] ventromedial gastral rib element straight; osteoderms present (not in *Paraplacodus*)”. Note that osteoderms are referred to as armour plates herein (sensu Scheyer 2007). The small armour plates and pachyostosis of TWE 480000454, and the absence of heavy

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armour, point to a closer relationship to non-cyamodontoid placodonts than to Cyamodontoidea.

TWE 480000454 shares with *Placodus* deeply amphicoelous and notochordal vertebral centra, pachyostosis of the vertebrae, the shape of the dorsal, sacral, and caudal ribs, at least three, maybe four sacral vertebrae (possible sacralization of the last presacral), and the size, number, and shape of some of the preserved armour plates (Fig. 6A, B). It differs from *Placodus* and all other taxa in several aspects. Autapomorphies of the new taxon are the morphology of the neural arches (i.e., ventrolateral expansion of neural arches, low neural spines) of the posterior presacral and sacral vertebrae, their un-fused nature in a large but not fully grown individual, the morphology of the zygopodial/zeugopodial bone (TWE 480000454-H; Fig. 5L), the plate-like round pubis and ischium, the absence of lateral gastral rib elements, and the straight ventral process of the haemapophyses.

All these characters justify the establishment of a new taxon, designated *Pararcus diepenbroeki* gen. et sp. nov.

Phylogenetic analysis.—TWE 480000454 was included in a newly compiled data matrix and phylogenetic analysis of diapsid reptiles with focus on Triassic Sauropterygia (Neenan et al. 2013; see SOM 2 for character coding; Fig. 7). From a total of 140 characters included in the character matrix, 25 could be coded for TWE 480000454, which equals 17.8%. The phylogenetic analysis contained 44 taxa and was performed using PAUP 4.0b10 for Microsoft Windows 95/NT (Swofford 2002) and PaupUP version 1.0.3.1 (Calendini and Martin 2005). Trees resulting from the analyses were built using Mesquite Version 2.75 (Maddison and Maddison 2011) and Adobe Photoshop Creative Suite. Analyses were performed using the heuristic search option (1000 replications; holding 100 trees per step; tree-bisection reconnection). All characters were equally weighted and treated as unordered. The strict consensus of the phylogenetic analysis (shortest tree = 573 steps; 9 most parsimonious trees; Consistency index = 0.33; Retention index = 0.656; Rescaled consistency index = 0.216) recorded *Pararcus diepenbroeki* gen. et sp. nov. in an unresolved polytomy with *Placodus* and cyamodontoids (Fig. 7), as was previously hypothesized from its morphology. Bremer support values of the analysis are also shown in Fig. 7. Deletion of critical (or wildcard) taxa such as Ichthyopterygia and Testudinata from the analysis caused changing topologies in other parts of the tree (identical to those mentioned in Neenan et al. 2013) but otherwise did not change the position of the new taxon within Placodontia. There are seven equivocal but unambigous autapomorphies (present under both, ACCTRAN and DELTRAN settings) separating *Pararcus diepenbroeki* gen. et sp. nov. from other members of Placodontia: character 72 (1 = vertebral centra with parallel lateral edges), character 77 (0 = cervical centra rounded ventrally), character 81 (0 = transverse processes of neural arches in dorsal region relatively short), character 88 (2 = number of sacral ribs four or more), character 93 (1 = the medial gastral rib element with two-pronged lateral process), character 109 (1 = limbs long and slender), and character 133 (1 = calcaneal tuber present). One equivocal but unambiguous synapomorphy is further shared by all members of Placodontia except *Paraplacodus*: character 70 (1 = vertebrae non-notochordal).

Ontogenetic stage of specimen TWE 480000454.—The size of TWE 480000454 indicates a rather large individual with a similar trunk-vent length as Drevermann (1933) reconstructed for *P. gigas* (~135 mm), on the basis of similar dimensions of preserved bones. In spite of its large size, individual TWE 480000454 was not fully grown. Indications of its early ontogenetic stage are: the un-fused and still paired neural arches with only incompletely developed neural spines of posterior presacral- and/or sacral vertebrae, the frayed and incompletely ossified margins of girdle elements, and the simple morphology of the preserved limb bones (e.g., TWE 480000454-H). All articulation facets of the vertebral elements show rough and rugose surfaces. This all implies a high amount of cartilage between the bones (Holliday et al. 2010) and ongoing ossification of sutures, which is typical for young, not fully grown individuals.

Ossification pattern of vertebral column.—Rieppel (2000a) stated that variation in the timing of ossification can be extensive in extant reptiles and also in sauropterygians. In archosaurs, closure of the neurocentral suture happens from the caudal to cranial end during ontogeny (Rieppel 1993; Brochu 1996; Ikejiri 2010). In addition, Sánchez-Villagra et al. (2009) noted an anteroposterior ossification trend in dorsal vertebrae and neural spines of the turtle *Pelodiscus*, and Maisano (2001, 2002) found that fusion along the vertebral column happens in squamates at different ontogenetic stages. Thus, it is possible that in other regions along the vertebral column of TWE 480000454, the neural arches had already fused to each other and a neural spine had developed. This is evident from the isolated half of a neural arch from a tail vertebra (nacv), which already had a neural spine (Fig. 2C, 4E). Fusion of the neural arch in the referred specimen (StIPB CHW302) could indicate an older ontogenetic age, as suggested by its larger size. Alternatively, the anterior vertebral column, from which StIPB CHW302 most likely originates, may have ossified earlier than the posterior vertebral column.

Skeletal paedomorphosis.—The un-fused halves of neural arches of posterior presacral and sacral vertebrae are the most distinct feature of TWE 480000454. According to Romer (1956: 226), paired neural arches are an embryonic character: “Embryologically, the neural arches arise as paired structures; during development, however, they grow upward and medially to fuse above the spinal cord, to form a completed arch. ... Above the point of union of the two sides the conjoined elements extend upward in a median neural spine.” It is unlikely that TWE 480000454 is an embryo because it is large, but it could represent an early ontogenetic stage (see above).

Disarticulation of the centrum and neural arch during fossilization is common in Eosauropterygia and can also occur in non-cyamodontoid placodonts, although more rarely

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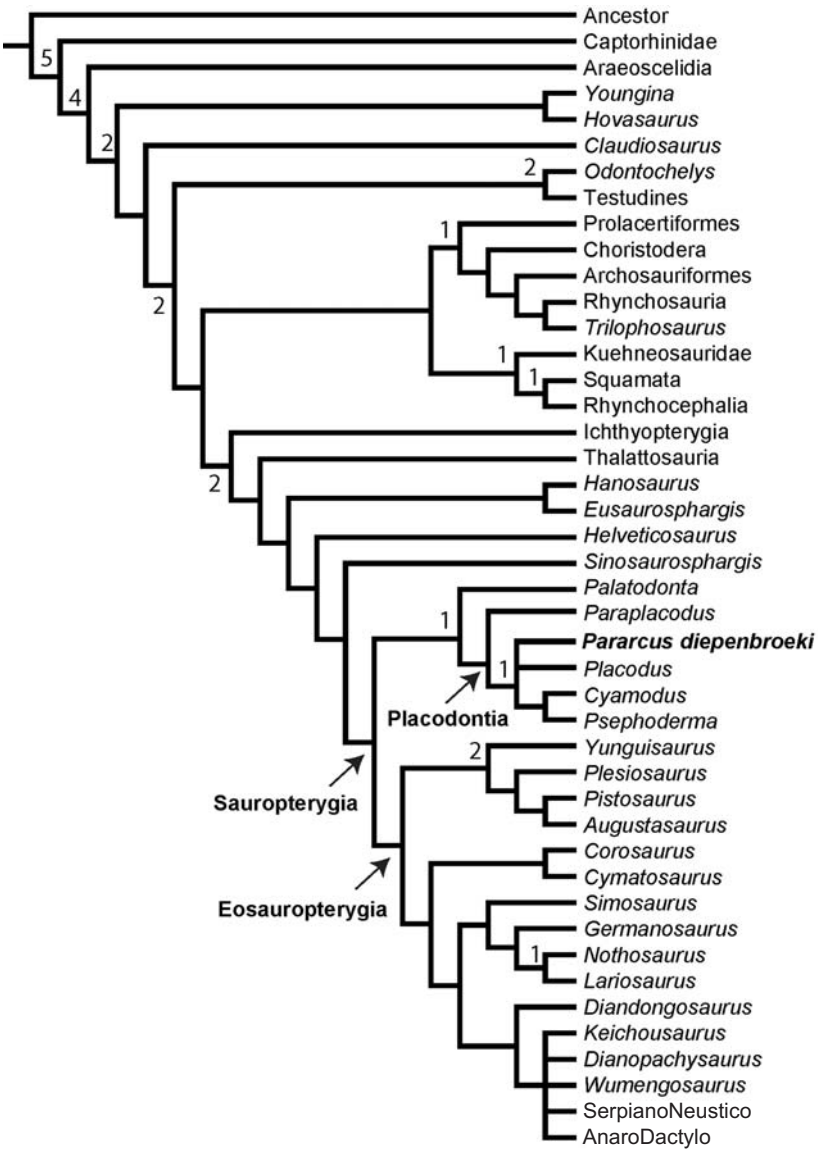


Fig. 7. Strict consensus tree of nine most parsimonious trees (minimum steps = 573) indicating the position of *Pararcus diepenbroeki* gen. et sp. nov. within Placodontia. For the analysis the character coding of the new taxon was added to the matrix of Neenan et al. (2013). Bremer support values are given above the nodes.

(Rieppel 2000a, b). This is because the neurocentral suture between centrum and neural arch is generally not well ossified in Sauropterygia. Thus, centra and neural arches, as well as sacral and caudal ribs, commonly remain separate in fully grown individuals. Paired neural arches, however, are not known for any sauropterygian and are also rare in other vertebrates. These rare exceptions include *Eusthenopteron* (Gregory et al. 1939), some lysorophian amphibians (Lepospondyli; Carroll 2000), and squamates, where the fusion happens in different ontogenetic stages, such as before or after skeletal maturity (Maisano 2001, 2002).

For the pachypleurosaur *Anarosaurus heterodontus*, incompletely fused halves of neural arches have been described for articulated specimens, representing early ontogenetic stages (size class I and II; Klein 2012). These neural arches have a furcate appearance in dorsal view and did not have a neural spine, only its base. However, an isolated/ disarticulated half of a neural arch has never been found.

Unfused halves of neural arches of the posterior presacral and sacral vertebrae are an autapomorphy of the new taxon seen in individuals that are not fully-grown and thus represent skeletal paedomorphosis. According to Rieppel (1989, 2000b), the skeleton of basally positioned Triassic Sauropterygia (stem-group sensu Rieppel 2000b) is subject to both skeletal paedomorphosis and pachyostosis. These trends are related to a secondarily marine lifestyle (Ricqlès 1975; Rieppel 1989). In Sauropterygia, skeletal paedomorphosis mainly affects the postcranial skeleton and includes absence of a calcified sternum, reduction of dorsal girdle elements and carpal and tarsal ossifications, absence of a hooked fifth metatarsal, and general reduction of epicondyles and apophyses on the long bones (Rieppel 1989, 2000b; limb simplification of Klein 2010, 2012). The aforementioned lack or incomplete fusion of the neurocentral suture and the lack of fusion of sacral ribs with their vertebrae can also be interpreted as skeletal paedomorphosis (Rieppel 2000b). Pachyostosis in marine reptiles is the hyper-development of bone to increase weight to achieve hydrostatic control of buoyancy and body trim (Houssaye 2009).

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Although the skeleton of TWE 480000454 is fairly incomplete, it shows both skeletal paedomorphosis in the vertebrae and ribs, and pachyostosis of the vertebrae. These features are not linked, but they contribute to a secondarily marine lifestyle, and this adaptation is much higher than probably in most other Triassic Sauropterygia. Additionally, the incomplete ossification of the posterior (sacral) vertebrae likely resulted in higher mobility in that body region, which is related to swimming style.

Acknowledgements

We are very thankful to Dennis Nieweg (TWE) for his warm reception and access to the Winterswijk fossils under his care. The members of the Muschelkalk Workgroup (Winterswijk, NL) as well as the Sibelco Europe MineralsPlus Winterswijk, to which the Winterswijksche Steen-en Kalkgroeve belongs and its manager Gerad ten Dolle, are acknowledged for their support during the joint excavations. We thank Herman Winkelhorst (NL) for permission to study and cast the specimen in his care, Olaf Dülfer and Natascha Makschinski (both StIPB) for preparation the specimens, Georg Oleschinski (StIPB) for the photographs, and Dorothea Kranz (StIPB) for the drawings. Many thanks to Martin Sander (StIPB) and Hans Hagdorn (MHI) for helpful discussions. Alexandra Houssaye (Muséum National d'Histoire Naturelle, Paris, France), Dorota Konietzko-Meier (StIPB), and Florian Witzmann (MfN) provided literature. Jessica Mitchell (StIPB) is acknowledged for linguistic improvement of the manuscript. We also would like to thank the reviewers Stefania Nosotti (MCSNM) and Thomas Stubbs (University Bristol, UK) for their helpful comments as well as the editor Mike Benton (University Bristol, UK) for further linguistic and editorial improvements. NK thanks the DFG (FOR533/N2) for funding. TMS acknowledges support by the SNF (grant no. 31003A 127053).

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