FIGURE 1. | *Placodontiform morphotypes that have been found in Winterswijk.* Palatodonta bleekeri *(A) is the closest relative of the placodonts, and had small sharp teeth for eating soft prey. The placodonts* Placodus gigas *(B) and* Cyamodus hildegardis *(C) had large crushing teeth for eating hard-shelled prey. Note the heavy armour in* Cyamodus. *Reconstructions by Jaime Chirinos.*

The importance of Winterswijk for understanding placodontiform evolution

U vindt een samenvatting aan het eind van de tekst.

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Abstract **| Placodontiformes are basal, semi-aquatic sauropterygians that mostly preyed upon hard-shelled organisms and often had substantial dermal armour. While their fossil remains are rare, they can be found in Triassic sediments throughout Europe, the Middle East and southern China, often in the form of their unusually large, tablet-shaped teeth. Winterswijk, however, boasts one of the most important fossil records for placodontiforms in the world, with two unique genera that are not currently known from anywhere else: *Palatodonta bleekeri* and *Pararcus diepenbroeki*. Other than these, more widespread genera are probably also represented in the form of *Placodus* sp. and *Cyamodus* sp.**

What are placodonts?

Firstly, it is important to establish the difference between Placodontiformes and Placodontia (the latter also being called placodonts). Placodontiformes is the term we use that includes Placodontia and their closest relative, *Palatodonta* (Neenan *et al.*, 2013). They are a group of sauropterygians that inhabited shallow, aquatic environments during the Middle and Late Triassic of modern-day Europe, the Middle East and southern China (once the margins of the Tethys Ocean) (Neenan *et al.*, 2015) (Fig. 1). Placodontia is a relatively diverse group, with at least 13 genera and, amongst other things, are character-

ised by massive, rounded teeth associated with a diet consisting of hard-shelled prey such as bivalves (known as durophagy) (Crofts *et al*., 2017; Neenan *et al*., 2014). Importantly, these teeth are not only located on the usual jaw bones that one might expect, but also on the palatine bone of the palate (the roof of the mouth). This gave placodonts a unique form of 'tooth battery' that allowed them to pulverise hard-shelled prey with ease. That being said, not all placodonts were durophagous. The enigmatic *Henodus* (and potentially its sister-taxon, *Parahenodus*), secondarily lost this condition in favour of what has been interpreted as baleen-like structures (similar to the condition seen in modern-day mysticete whales), indicative of a potential filter-feeding role (e.g. de Miguel Chaves *et al*., 2018).

Placodonts can traditionally be divided into placodontoids, the marine iguana-like group with no or very little armour (Rieppel, 2000a), and Cyamodontoidea, the turtle-like, heavily-armoured group (Rieppel, 2002; Scheyer, 2010) (Fig. 1). Both of these 'morphotypes' can be found at Winterswijk. However, placodontiforms from this locality are relatively rare compared to other sauropterygians, such as pachypleurosaurs and nothosaurs (Oosterink *et al*., 2003). Nevertheless, Winterswijk boasts two unique genera, *Palatodonta* and *Pararcus*, as well as examples of the widely-distributed *Placodus* and *Cyamodus*, species of which can be found in both Europe and China (Jiang *et al*., 2008; Rieppel, 1995; Wang *et al*., 2019). This makes Winterswijk one of the most important localities for our understanding of placodontiform evolution.

FIGURE 2. | *The holotype specimen of* Palatodonta bleekeri, *TW480000470. CT scanning revealed a specialized row of teeth on the palate, which helped to identify it as a close relative of Placodontia (Neenan* et al., *2013). Photograph by Georg Oleschinski, University of Bonn.*

Palatodonta bleekeri: the tiny placodont ancestor

Palatodonta was found in Layer 9 of the Vossenveld Formation by Mr Remco Bleeker, and was described in 2013 (Neenan *et al*., 2013). The fossil consists of a skull of a juvenile animal, preserved in right lateral view (Fig. 2). Though tiny in size, with a length of only 2 cm, *Palatodonta* revolutionised our understanding of not only placodont evolution, but of sauropterygian evolution as a whole. Indeed, *Palatodonta* even helped to answer a question that palaeontologists have been asking for over a century: how did the unique dentition of placodonts originate? Until the discovery of *Palatodonta*, it was unclear whether the ancestors of placodonts were durophagous, thus necessitating the palatal dentition which evolved later; or if the palatal dentition evolved first for another purpose and then became adapted for durophagy by Placodontia. We now know that the latter alternative was the case. *Palatodonta* had a full row of pointed teeth on its palatine bone, as well as narrow pointed or peg-like teeth in the rest of the jaws (Fig. 1A). This means that it was not durophagous, and probably ate softer prey such as fish, squid, worms and possibly soft-shelled molluscs. It is only later in placodontiform evolution that this unusual dental morphology became adapted for durophagy, with the once pointed teeth becoming much larger, more rounded and flatter, as well as reduced in number.

Palatodonta also hints that placodonts, and perhaps even Sauropterygia as a whole, may well have originated in what is now Western Europe. This has put Winterswijk on the map as a key location for our understanding of sauropterygian evolution and palaeobiogeography.

Pararcus diepenbroeki: the placodont that lost its head

Not long after *Palatodonta* was introduced to the world, *Pararcus* was

Figure 3. | Pararcus diepenbroeki *holotype TWE 480000454 Klein & Scheyer (2014). Image courtesy of Nicole Klein.*

described in 2014 by Klein & Scheyer (2014). The holotype specimen (TWE 480000454) was discovered by Mr Gerben Diepenbroek in Layer 36 of the Vossenveld Formation which is several metres above the more fossiliferous Layer 9. This placodont is unusual in that it was classified as a new genus despite the fact that there is no preserved head, which is the most diagnostic part of the skeleton. This is because numerous parts of the postcranium are actually well-preserved and display clear characteristics that identify *Pararcus* as a previously unknown placodontoid placodont (Fig. 3).

Figure 4. | Pararcus diepenbroeki *specimen RGM.791811 in posterior view (modified after During* et al.*, 2017). The right margins of the vertebral centrum and right ventrolateral expansion are damaged, the right postzygapophysis is missing.*

Interestingly, despite the relatively large size of the holotype (~2 m, approximately the same size as *Placodus gigas*), this animal was clearly sub-adult. The neural arches of the vertebrae are unfused, indicating that the animal was still growing. This would potentially make *Pararcus* the largest placodont known when fully grown. Later, During *et al.* (2017) described a vertebra ascribed to *Pararcus* that was fully ossified, indicating that it came from an adult individual (Fig. 4). Unfortunately, however, despite identifying the vertebra as being from the dorsal region, it was not any larger than the vertebrae recovered from the holotype, so could not be used to reconstruct the size of an adult *Pararcus*.

Placodus sp. and *Cyamodus* sp.: the first placodonts found in Winterswijk

Palatodonta and *Pararcus* may be the placodontiform 'celebrities' of Winterswijk, but the first taxa found at this locality were the much more common and geographically widespread *Placodus* and *Cyamodus* (Fig. 5). Both of these genera are well-known from European Muschelkalk and Alpine facies (i.e. *P. gigas, C. hildegardis, C. kuhnschnyderi, C. muensteri, C. rostratus*; Rieppel, 2000b), but can also be found on the opposite side of the Tethys in what is modern-day south China (*P. inexpectatus*: Jiang *et al.* (2008); and *C. orientalis*: Wang *et al.* (2019)).

Conclusion

Placodontiforms were a fascinating group of nearshore sauropterygians with specialized diets and morphologies. While placodonts have been known since

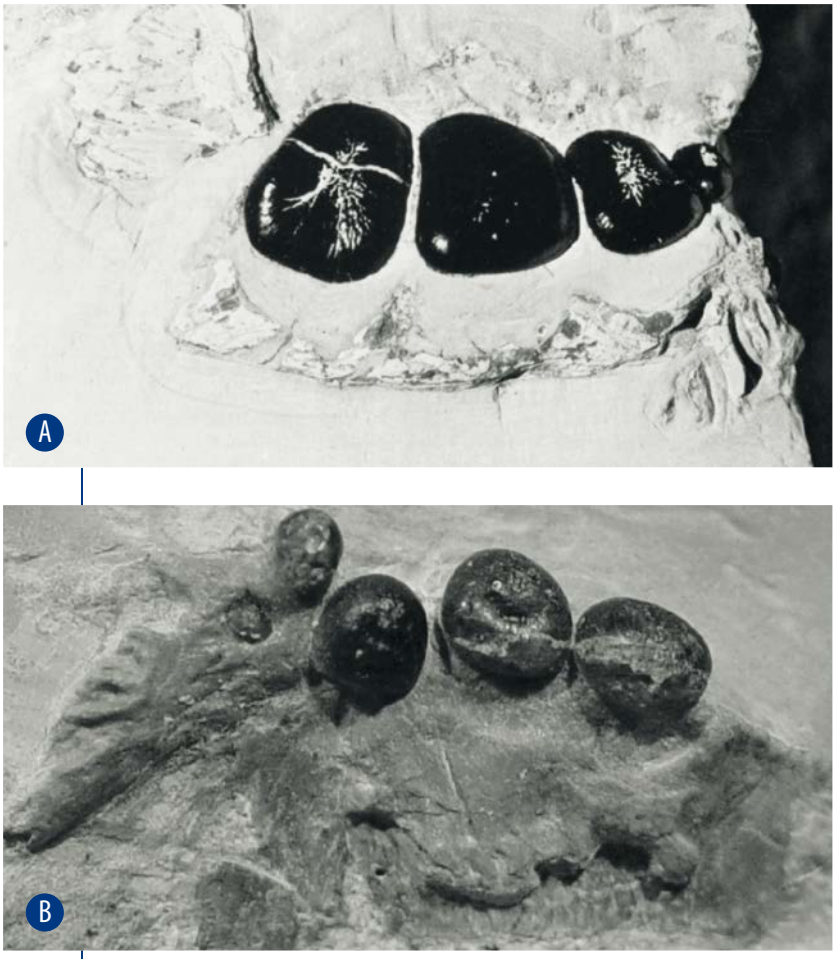

FIGURE 5. | *Jaw fragments containing teeth most likely from the widely-distributed placodonts* Placodus *sp. (A) and* Cyamodus *sp. (B), both of which have species found in Europe and southern China (images from Oosterink (1978) and Albers (2005)).*

the mid-nineteenth century, we did not truly understand the origins of their specialized dentition until *Palatodonta* was described from Winterswijk. When considering that Winterswijk is also home to another unique placodont, *Pararcus*, as well as the more common *Placodus* and *Cyamodus*, it is no wonder that it is now considered one of the most important placodontiform localities in the world. Time will only tell what other clues to placodont evolution Winterswijk holds.

Samenvatting

Placodontiformen zijn basale, semi-aquatische Sauropterygia. Hun dieet bestond voornamelijk uit schelpdieren, welke ze kraakten met de uitgebreide knobbeltanden over de hele boven- en onderzijde van hun mond. Hun fossielen zijn schaars, maar ze worden gevonden in sedimenten uit het Trias uit heel Europa, het Midden-Oosten en Zuid-China, vaak in de vorm van hun knobbeltanden. Winterswijk heeft een van de meest belangrijke fossielenbestanden van placodontiformen in de wereld, met twee unieke genera die nog nergens anders gevonden zijn: *Palatodonta bleekeri* en *Pararcus diepenbroeki*. Naast deze twee genera zijn andere wereldwijd verspreide genera waarschijnlijk ook aanwezig in de vorm van *Placodus* sp. en *Cyamodus* sp.

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