



Anarosaurus heterodontus CHW 189.
Collection Herman Winkelhorst. Photo: Jelle Heijne

The taphonomy of the Anisian of Winterswijk

– insights into a unique environment

U vindt een samenvatting aan het eind van de tekst.

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Abstract | The Triassic rocks of the Winterswijkse Steengroeve offer a unique window into the history of our planet. Preserved are mainly the remains of Sauropterygia, fish and invertebrates in various grades of completeness. The environment of these marine animals such as *Nothosaurus* was a special place where life was able to thrive despite difficult circumstances. Their skeletons can provide valuable information that can be unraveled through taphonomy, literally the laws of the grave. We notice, when looking through the many private and public collections, that the Winterswijk fossils show very diverse patterns ranging from isolated bones to almost complete skeletons. But what causes these variations, and what does this mean for the interpretation of the depositional environment? Here, we will discuss these patterns and support the existing taphonomical analysis by adding sedimentological evidence. This research on the skeletons from Winterswijk



shows that the animals lived in shallow water and washed ashore on the carbonate mud flats after their death. There, the skeletons fell apart due to the water movements. The better-preserved skeletons must have been protected from these processes by natural depressions in the sediment, or were overgrown by the present microbial mats. Sedimentology, the structure of the rock itself, provides more evidence for this environment. Petrological thin sections confirmed this interpretation of the depositional environment. The biolaminates, or ‘bindstones’ were capable of trapping vertebrate remains that were deposited by higher-energy events characterized by slightly coarser sediment. Furthermore, the larger grain size in layer 14 than in layer 9 shows an increase of energy in the environment.

Winterswijk, a unique window into the Anisian

As is already shown throughout this volume, the Muschelkalk deposits from Winterswijk provide a unique window into the Anisian of the Western Germanic Basin. This distinction is not only represented by the large number of endemic species (Klein & Albers, 2009; Neenan *et al.*, 2013; Klein & Scheyer, 2014; Klein *et al.*, 2016; Maxwell *et al.*, 2016), but also by the rapid alternation of marine and terrestrial environments. In the petrified remains of the shallow mudflat environment of Winterswijk, many skeletons of marine reptiles were found. This high number of articulated and associated remains is another unique aspect of the Winterswijk fossil locality as it is unrivaled within the entire Germanic Basin. In order to understand the depositional environment, important clues can be found in the skeletons of the organisms that inhabited it. From taphonomical studies, the fossilization process can be understood, which in its turn provides clues on the life and death of these marine animals.

The Winterswijk locality, situated near the western margin of the Rhenish Massif, consisted of a shallow marine environment subjected to large variation in water depth. During periods of relative lowstand, the very shallow and even emerged conditions resulted in mudcracks and terrestrial trackways throughout the section (Faber, 1958; Dülfer & Klein, 2006; Marchetti *et al.*,; and During *et al.*, this volume) The presence of marine reptiles, although almost exclusively taxa specialized for shallow-water habitats, along with marine invertebrates and fish confirms that the marine influence was probably dominant. Hagdorn and Simon (2010) attribute the laminated limestones and dolomites to an algal origin. This occurrence of algal laminates is of importance as Orr *et al.*, (2016) discuss the ability of microbial mats to stick cadavers to the substrate and thereby protect them from disarticulation. It is inferred that these mechanisms contributed to the preservation of the Winterswijk vertebrate fossils (Heijne *et al.*, 2019).

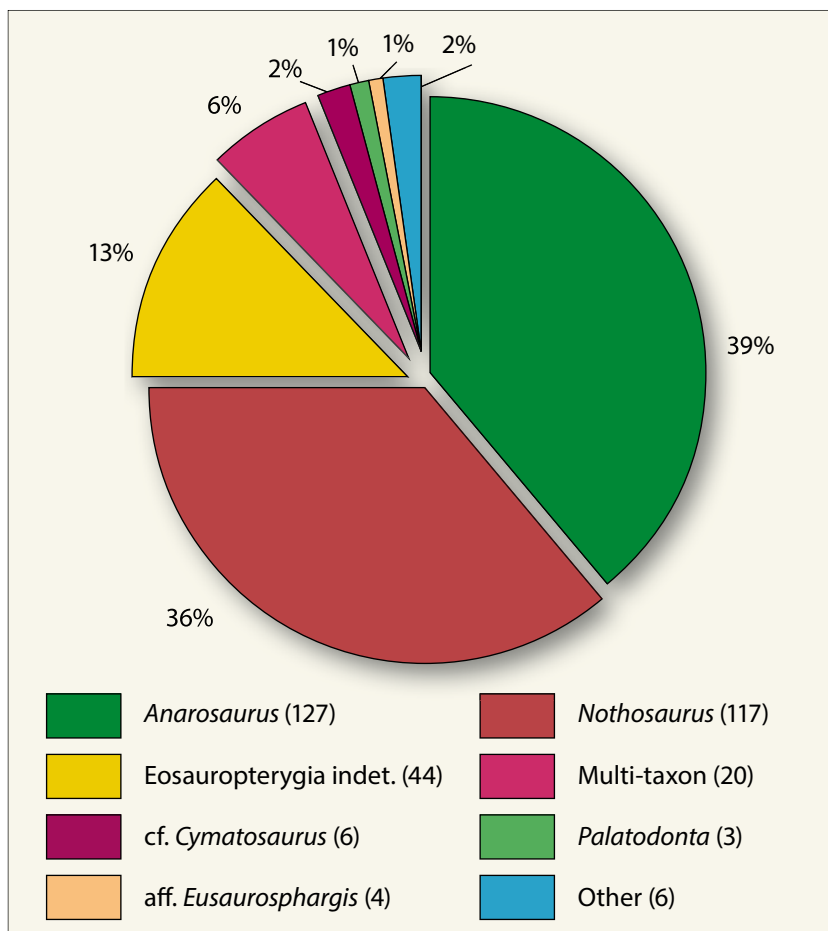


FIGURE 1. | Faunal assemblage of the 327 studied reptile remains by Heijne *et al.* (2019). Note the large abundance of the two genera *Anarosaurus* and *Nothosaurus* and the fact that the reptile fauna almost exclusively consists of *Sauropterygia* (Modified after Heijne *et al.*, 2019).

To assess the taphonomy of the Winterswijk Muschelkalk strata, a large dataset was collected by Heijne *et al.* (2019), comprising over 300 specimens from both private and public collections. The study was focused solely on the marine reptiles, mostly *Sauropterygia*. The faunal assemblage of Winterswijk, as recorded from this dataset, is presented in Figure 1. Of most specimens, excluding the unprepared slabs and isolated skulls, an outline drawing was created using the software ‘Inkscape’ (Fig. 2). Further drawings are included in the Appendix (www.geologienederland.nl > Grondboor & Hamer > Staringia 16). This was done in order to achieve an overview of the most striking disarticulation patterns shown in the assemblage. The specimens were examined extensively, and all patterns were discussed. The skeletons were tested for the ‘stick ‘n’ peel’ criteria stated by Orr *et al.* (2016). ‘Stick ‘n’ peel’ describes the process of organic material being trapped by microbial mats and subsequent peeling of elements by current activity.

To support the model presented by Heijne *et al.* (2019), petrographic thin sections and as polished sections were made of layer 9 and 14 (after



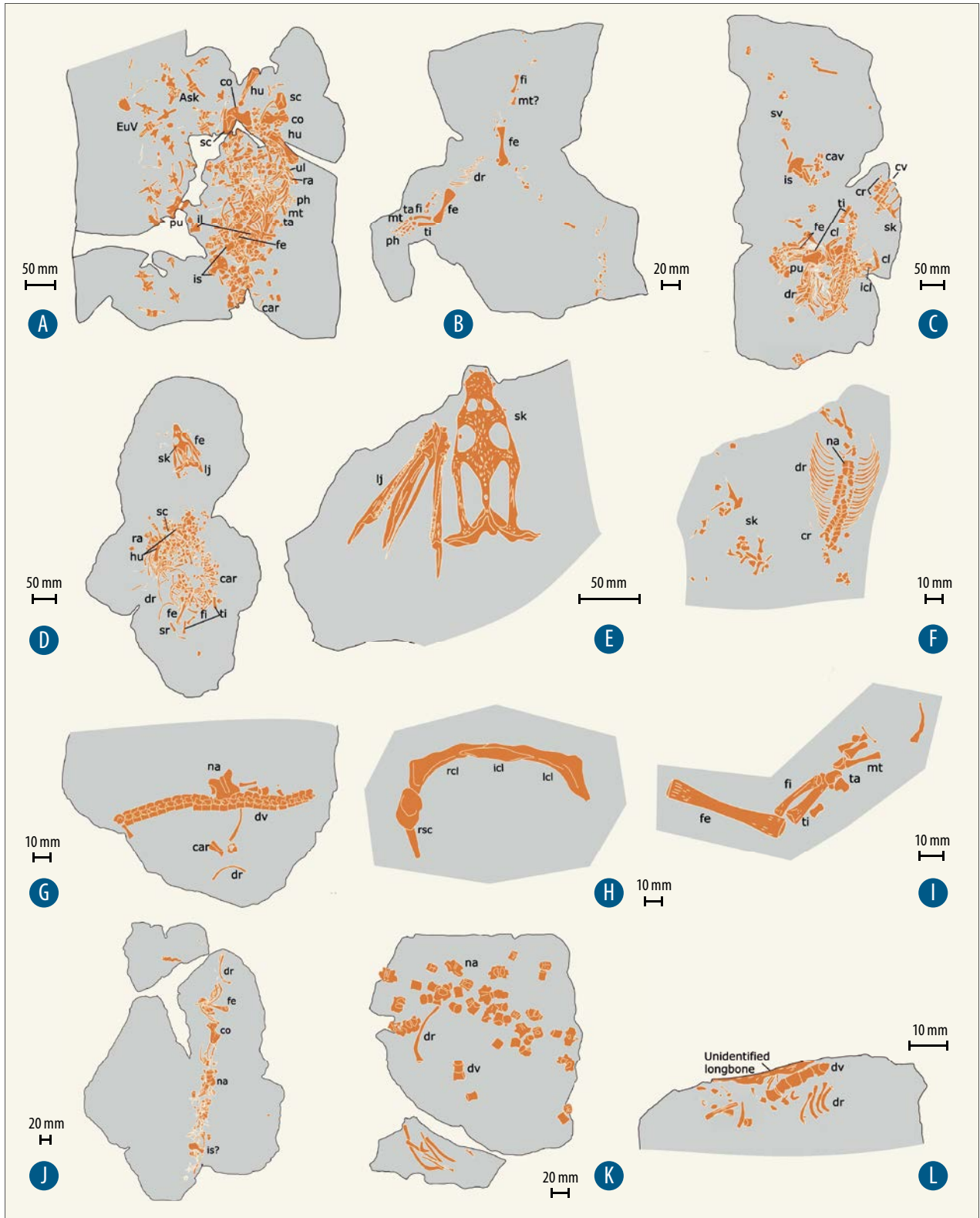


FIGURE 2. | The twelve recurring patterns in the Winterswijk fossils illustrated with A, multi-taxon assemblage NMNHL RGM 449487. B, Multi-individual assemblage CHW 241. C, Articulated partial Nothosaurus skeleton JLW 102 (StIPB R-647). D, Disarticulated Nothosaurus skeleton TWE 480000473. E, Skull and displaced lower jaw of Nothosaurus TWE 480000474. F, Skeleton with disarticulated skull of Anarosaurus CHW 345. G, Articulated vertebral column of Anarosaurus CHW 344. H, Articulated pectoral girdle of Nothosaurus TWE 480000416. I, Isolated hind limb of Eosauropterygia indet. JLW 129. J, Elongated spread remains of Nothosaurus CHK 1. K, Clustered vertebrae and ribs of Nothosaurus CBW 6. L, Trapping of bones in TWE 480000588. Abbreviations- Ask: Anarosaurus skull roof, car: caudal rib, cav: caudal vertebra, cl: clavicle, co: coracoid, cr: cervical rib, cv: cervical vertebra, dr: dorsal rib, dv: dorsal vertebra, Euv: aff. Eusaurosphargis vertebra, fe: femur, fi: fibula, hu: humerus, icl: interclavicle, il: ilium, is: ischium, lcl: left clavicle, lj: lower jaws, mt: metatarsals, na: neural arch, ph: phalanges, pu: pubis, ra: radius, rsc: right scapula, sc: scapula, sk: skull, sr: sacral rib, sv: sacral vertebra, ta: tarsals, ti: tibia, ul: ulna (Modified after Heijne et al., 2019).



Oosterink, 1986) to better understand the sedimentology. The sectioned bone-bearing rocks from layer 9 were taken from the collection of the Institute of Geosciences, Bonn, Germany.

Patterns in the Winterswijk fossil assemblage

Within the dataset of Heijne *et al.* (2019), a total of twelve recurring disarticulation patterns were recognized. A further, thirteenth pattern is the occurrence of isolated bones. It is the most common in Winterswijk and comprises about 80% of the vertebrate finds. The other patterns, already described extensively by Heijne *et al.* (2019), show a diverse array of disarticulation styles. Here, these results are summarized. Figure 2 shows the twelve patterns observed in Winterswijk with an illustration of a representative specimen for each pattern. Of these, the isolated limbs are the most common after the isolated bones. The rarest finds are indeed the articulated and relatively complete skeletons that resisted most of the disarticulation processes.

The first pattern, illustrated in Figure 2A, is the occurrence of a multi-taxon assemblage where multiple taxa are embedded on one slab. It is commonly known as 'De Kist' (English: 'The chest'), with specimen number NMNHL RGM 449487. It contains the closely associated skeleton of a *cf. Cymatosaurus* and the scattered remains of *aff. Eusaurophargis*. An assemblage of multiple individuals bearing only one species is also presented. CHW 241 (Fig. 2B) shows the limbs of a larger *Anarosaurus* among very small vertebrae and ribs of another *Anarosaurus*. Heijne *et al.* (2019) dismiss the possibility of the smaller individual being an embryo. JLW 102 (Fig. 2C) is an example of a partially articulated *Nothosaurus* skeleton, which is mostly disarticulated except for the axial skeleton (i.e. the vertebrae and ribs). Another completely disarticulated skeleton of *Nothosaurus* is TWE 480000473 (Fig. 2D). It is almost complete and is spread over a small area. Articulated skulls (Fig. 2E) are common for both *Anarosaurus* and *Nothosaurus*. TWE 480000474 is one of the largest *Nothosaurus* skulls from Winterswijk, measuring about 15 cm. Disarticulated skulls are more common in *Anarosaurus*, as can be seen in CHW 345 (Fig. 2F). Articulated vertebral columns are often found in Winterswijk and can be preserved in isolation, as is the case in CHW 344 (Fig. 2G). TWE 480000416 (Fig. 2H) shows the isolated shoulder girdle of a *Nothosaurus*, a pattern which is seen several times in the assemblage. Isolated limbs, as seen in JLW 129 (Fig. 2I), are also very common. Over 40 of these limbs are identified, most of which belong to *Anarosaurus* or *Eosauropterygia* indet.

Figure 2J shows CHK 1, an elongate disarticulated skeleton, most likely of *Nothosaurus*. Not all completely disarticulated remains are deposited longitudinally, most bones form clusters as is seen in CBW 6 (Fig. 2K). These clusters can be concentrated around larger bones which might have sheltered the smaller remains from currents as, is seen in TWE 480000588 (Fig. 2L).

Sedimentological observations

It is very important to add sedimentological information when discussing taphonomy. If the environment is initially misunderstood, it can lead to a further misunderstanding of the taphonomy. A striking example is found in the Berlin Ichthyosaur State Park in Nevada, USA. Here, it was implied by Camp (1980) that the ichthyosaur carcass assemblage was the result of beaching, similar to modern whales. However, Hogler (1992) found that the sediments did not indicate a coastal environment, but rather a deep marine facies. This illustrates the importance of a sedimentological analysis to either confirm or reject an existing hypothesis. The analysis presented here is based on both a polished section and three thin sections, all containing bone material. Further sedimentological- and geochemical analyses of the Winterswijk section, although not specifically on the bone bearing horizons, is presented in During *et al.*, this volume page 167.



FIGURE 3. | Polished sedimentological section of a bone-bearing rock from layer 9 (after Oosterink, 1986). The piece (CJH 002) contains a humerus of eosauropterygian affinity, which is embedded isolated and at an angle to the sediment. The disturbance in the layering is caused by the occurrence of bioturbation.



Polished section, layer 9

For the polished section, a fossil that was uncovered in 2017 was used. The adjacent sediment was cut on all four sides and polished to show the sedimentary structures (Fig. 3). The 5 cm long sauropterygian humerus, derived from layer 9 of the section was found as an isolated bone within the layer. Apart from one neural arch, no other remains were discovered in the vicinity. The humerus is positioned at an angle of around 45° to the bedding plane, and is embedded in the coarser portion of the sediment. This coarser sediment, consisting mostly of sparite, is caused by bioturbation and clearly disrupts the laminations (Fig. 3).

Thin sections

Of two fossil-bearing layers, thin sections were made to show and investigate the bone-sediment interface, and to pinpoint the exact depositional environment during emplacement of the vertebrate remains. The analyzed thin sections are from layer 9 and 14, with the layer 9 samples being from the excavations by the University of Bonn, and the layer 14 sample from the private collection of the first author. Analysis of the thin sections was performed by the second author at the University of Bonn. Of the available thin sections, three were selected to be discussed in more detail, as most information and sedimentary structures were found in these sections. Two of these originate from layer 9 (13-194 and 382-2) and one from layer 14 (CJH 084). All sections are carbonates, and can be classified as biolaminites, or bindstones according to the modified Dunham classification (Embry & Klovan, 1971). We observed finely interlaminated, organically bound particles. The general depositional regime seems to be low-energy carbonate formation, while some laminae clearly show signs of higher-energy deposition evidenced by the sedimentary structures described below.

Layer 14 (CJH 084)

CJH 084 was collected from the surface of layer 14 and the slab contains a high number of mm-sized fragmentary bones. This accumulation of bone fragments continued laterally for at least several square meters (Personal observation J.H.). The thin section (Fig. 4) was cut through a bone fragment to show the sediment directly

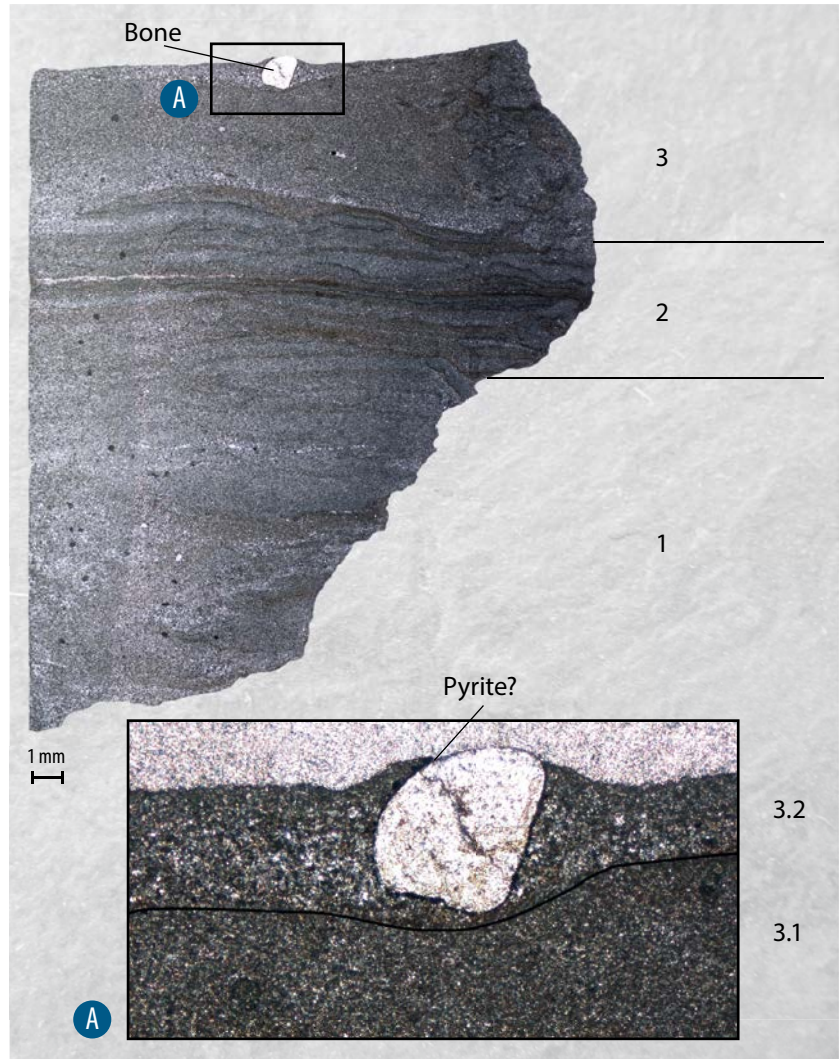


FIGURE 4. | Thin section of CJH 084 from layer 14 showing three units with- A: close up of the embedded bone.

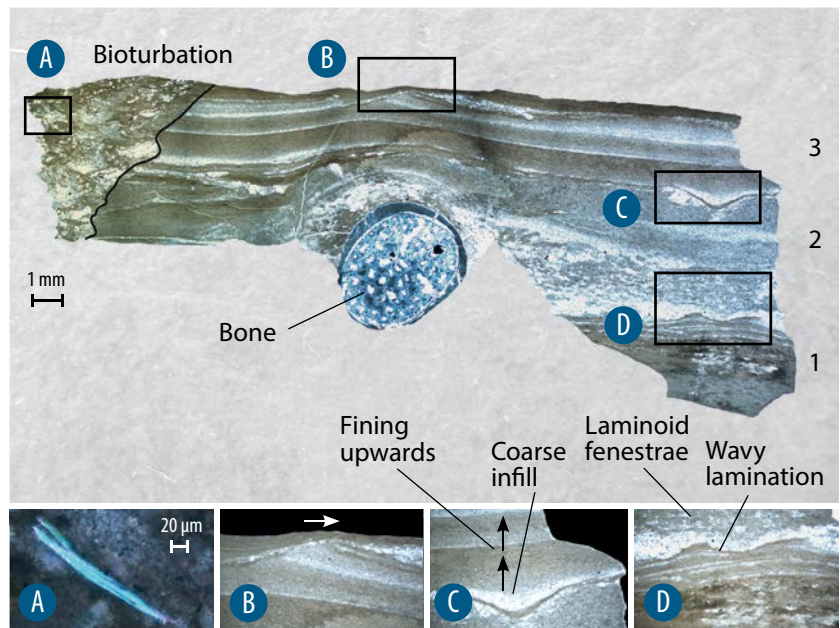


FIGURE 5. | Thin section of 382-2 from layer 9 showing three units with A, small microfossil B, planar cross-lamination C, graded bedding and infilling of a trough D, wavy lamination.



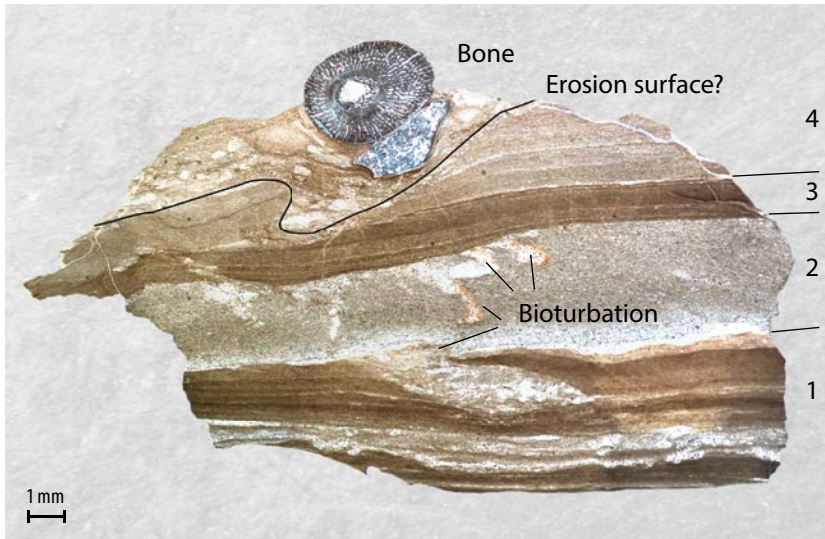


FIGURE 6. | Thin section of 13-194 from layer 9 showing four units characterized by laminated sediment and bioturbation.

adjacent to the bone, and thus the depositional environment at the time of embedding. Although the section seems to be quite homogeneous, three units could be distinguished. The grains in this section are classified as microsparite and are about 10–20 μm in size. The grain size does not vary greatly throughout the section, especially in unit 1, except for some slight variation in the second unit and the top of the third unit (indicated by a 2 and a 3 respectively). Some discolorations can be seen on the irregular side of the slab, but this was most likely caused by chemical changes as a result of weathering. A close-up of the bone shows that unit 3 can be subdivided into 3.1 and 3.2. The lower unit 3.1 is finer than the overlying unit 3.2 containing the bone fragment. However, towards the top of unit 3.2, the grain size decreases again where the sediment covers the bone. The contact between 3.1 and 3.2 shows an irregular surface, which could have been caused by erosion. In this thin section, no clear evidence for bioturbation is seen. However, at the bottom of the slab, located near the lowest point of the thin section, a *Rhizocorallium* burrow could be identified macroscopically. Furthermore, it should be noted that opaque grains with a similar size as the carbonate grains are surrounding the bone fragment. These mineral grains appear black as polarized light does not pass through them, a property of metallic minerals. For Winterswijk, pyrite would be one of the most logical explanations, as this is a common mineral in the quarry.

Layer 9 (382-2)

This section is slightly thicker than the previous one as it was cut for analysis of the bone, which requires a different thickness. As a result, the color is darker in some areas, and the grains are harder to identify. Three units could be distinguished (Fig. 5), which contain several sedimentological structures, labelled 'A' through 'D'.

The first unit is formed by micrite which shows some variation in grain size and wavy lamination near the top (Fig. 5D). Although the contact is irregular, no erosion seems to have taken place since the wavy lamination is preserved. The second unit, containing the bone, is coarser and shows a higher content of dark elongated grains which could be similar to the ones attached to the bone in CJH084. However, these grains have a different shape, and are slightly red. Within the unit, laminoid fenestrae can be seen (Fig. 5D). The brighter spots indicate spaces that were filled with air or gas from decaying organic matter which were cemented later during diagenesis. The top of the second unit is irregular due to the covering of the bone, leaving a small bulge, and a small trough on the right side of the section (Fig. 5C). The trough was filled with coarser grains before the deposition of unit 3 started. Unit 3 shows the best examples of normal grading in the sample (Fig. 5C). It shows three to four laminated cycles of fining upwards carbonate grains (microsparite to micrite). Near the top of

this unit, planar cross-lamination can be seen (Fig. 5B), this is strikingly situated directly above the bulge created by the bone. The flow direction of the current is indicated by the arrow in Figure 5B. The leftmost side of the section shows a large mm-scale bioturbation in which a microfossil could be identified (Fig. 5A). This microfossil, which consists of a single carbonate crystal, is 200 μm long and could be a sponge spicule.

Layer 9 (13-194)

Similar to section 382-2, the original purpose of this section was to study the bone histology. Here, four units could be identified (Fig. 6).

Unit 1 is laminated and shows a layer which is normally graded from microsparite to micrite, followed by a sparitic layer, which is then again followed by a graded layer. The uppermost layer of unit 1 shows a large disturbance caused by bioturbation. The following unit does not show much internal variation but is much coarser than unit 1. The contact between these units is irregular, which might be caused by erosion. Between the carbonate grains, many elongate dark minerals can be identified as well. Furthermore, the top of this layer shows bioturbation, albeit at a smaller scale. Above unit 2, a thinly laminated unit of fine-grained normally graded micrite is seen (unit 3) that is followed by the coarser, and more homogeneous unit 4. As the layers of unit 4 cannot be traced throughout the section, an erosion line was drawn. This 'erosion' can be caused by bioturbation followed by the deposition of the bone, or soft-sediment deformation. The disrupted area shows some clasts of larger grain size, within a very chaotic matrix. Below the leftmost process of the smaller bone, similar grains as seen in CJH 084 (Fig. 4) are found. In both sections from layer 9, the grain size is generally smaller than in layer 14 and is dominated by micrite, although microspartic and sparitic horizons are present. Furthermore, the layers show a larger variation of grain sizes which can be seen in the recurring normal-graded laminae.

Discussion

The patterns seen in the dataset (Fig. 2) show that the carcasses were subject to different conditions, depending on



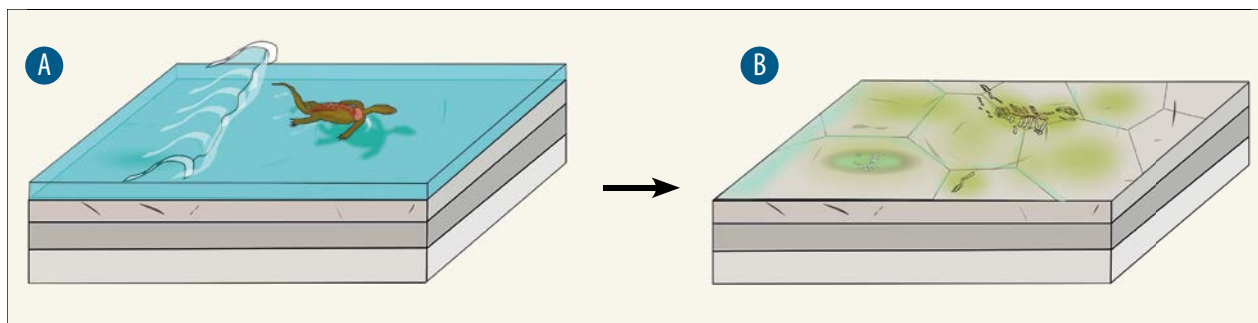


FIGURE 7. | Interpretation of the initial deposition of skeletons in the Winterswijk environment. These conditions can be found in layers 4 and 6, and are shifted laterally away from Winterswijk in layer 9 which resulted from a rise in sea level.

the duration of the floating phase, and the protection from the weak currents. Generally, the differential preservation of some specimens is attributed to ‘stick ‘n’ peel’ processes by Heijne *et al.* (2019). Furthermore, it should be noted that the soft sediment also played a role in the preservation of the carcasses. The effects of a ‘soupy’ substrate are discussed by Martill (1993) as an explanation for the variations in articulation in the ichthyosaurs of the Posidonienschiefer Fm. Although a true soupy substrate is not expected in Winterswijk, the soft sediment, combined with the high abundance of biofilms, would have contributed to the preservation of the skeletons. The sediment was not anoxic, as can be derived from the occurrence of bioturbation and the complete lack of soft-tissue preservation in these layers. However, the proposed high salinity (e.g. During *et al.*, this volume page 167; Maxwell *et al.*, 2016) caused a depauperate invertebrate fauna and an incomplete recycling of skeletal elements. In the fossil content, it can be seen that the facies changes from the lower layers 4 and 6 to the higher layers 9 and 14. The depositional environment changes as well. Figure 7 shows a reconstruction of the coastal, often subaerial conditions, seen in layer 4 and 6. The carcasses deposited onto the carbonate mudflats did not have a long phase in which currents displace the bones. Throughout the sampled section, the current- and wave activity was at its weakest here. The other layers represent a lateral shift to slightly deeper water conditions, but are interpreted to have formed in a similar environment.

The presented thin sections and the polished section exhibit distinct petrographic differences. These

differences are helpful in assessing the depositional conditions of layers 9 and 14. While layer 9 shows finely laminated and graded micritic limestone, layer 14 consists of coarser microsparite, is less laminated and contains no grading. Grading is a sign of waning flows, i.e. decreasing flow velocity. The coarser grains are indicative of a higher energy level, which is already hypothesized by Heijne *et al.* (2019) based on the fossil content. Generally, the sections can be classified as biolaminates, which are indicative of supratidal to intertidal environments (e.g. Noffke *et al.*, 2001). The darkest, fine grained laminae might have been formed by cyanobacterial mats binding the sediment together. Either these biofilms trapped available calcite, or they actively precipitated the calcite to form these layers (e.g. Noffke *et al.*, 2001). The bones are generally found in the coarser layers, which might explain the bone accumulations in both layer 9 and 14. The bones were washed in by slightly stronger currents and were then covered again by fine sediment and cyanobacterial mats. Although these sections show no clear signs for subaerial conditions, the presence of laminoid fenestrae and bacterial mats indicates a supratidal to intertidal environment. Although pyrite is often associated with anoxic conditions, this can be dismissed as the bioturbation provides evidence that this was not a very hostile environment.

If the pyrite is indeed primary, and not formed during diagenesis, it could be derived from bacteria involved in the decomposition of the organic matter. The bioturbation shows that the sediment was soft after deposition, which could have contributed to the embedding and thus preservation of the specimens. The polished section of layer 9 shows the extent of the bioturbation, which covers more than half of the slab. The bone being situated at an angle to the lamination indicates once more that the sediment must have been soft at the time of deposition allowing the bone to either sink in or be displaced by burrowing organisms.

Conclusion and further study

Winterswijk fossils, especially the associated remains, will remain a topic of interest for many years, as the quarry yields new finds every time enthusiasts are allowed to enter. This study shows that the specimens truly are unique and exhibit many different preservations. The disarticulation of these skeletons is controlled by many factors, mostly the duration of a floating phase and the depth of embedding by either soft sediment or microbial covering. The environment, dominated by micritic biolaminates, is typical for very shallow water, supra- to intertidal conditions to be precise. Very limited wave action ensured the bones were not dispersed over a large area but remained in the vicinity of the carcass as it decayed and disarticulated in situ. The environment, which was described by Heijne *et al.* (2019), is supported by the sedimentological analysis. Further study of the sedimentological aspects of the Winterswijk section will prove essential in understanding the different depositional environments present in the entire outcrop. For this, thin sections of every bed should be prepared and analyzed. As shown in Figure 5B, flow direction can be observed in the section. However, the original orientation is not always documented. This will be very important in the future to place the locality into a broader context. If the flow direction of the currents can be uncovered, their effect on the



dispersal of the bones and skeletons can be studied as well. Furthermore, the orientation of the coastline could be derived from these currents which could possibly provide clues on the lateral distribution of the fossils.

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Samenvatting

Het Trias gesteente van de Winterswijkse Steengroeve biedt ons een unieke inzicht in de geschiedenis van onze aarde. De leefomgeving van mariene reptielen zoals *Nothosaurus* was een bijzondere plek waar het leven ondanks zware omstandigheden voet aan de grond wist te krijgen. Hier zijn voornamelijk de overblijfselen van Sauroptrygia, vissen en ongewervelde dieren bewaard gebleven in verschillende maten van conservering. Van deze mariene reptielen zijn in het heden slechts de skeletten overgebleven. Deze skeletten kunnen echter waardevolle informatie bevatten die aan de hand van de tafonomie, letterlijk de wetten van het graf, kan worden ontrafeld. Wanneer we door de vele particuliere en openbare collecties kijken, zien we dat de Winterswijk-fossielen zeer uiteenlopende patronen vertonen, variërend van geïsoleerde botten tot bijna complete skeletten. Maar wat veroorzaakt deze variaties, en wat betekent dit voor de interpretatie van het afzettingsmilieu? Hier zullen we deze patronen bespreken

en de bestaande tafonomische analyse onderbouwen door sedimentologisch bewijs toe te voegen. Dit onderzoek naar de skeletten uit Winterswijk laat zien dat de dieren in ondiep water leefden, en na hun dood op de kalkwadden aanspoelden. Hier vielen de skeletten gedeeltelijk uit elkaar door het komen en gaan van het water. De beter behouden skeletten waren beschermd tegen deze processen door natuurlijke depressies in het sediment, of werden door de aanwezige microbiële matten overgroeid. De sedimentologie, de opbouw van het gesteente zelf, levert meer bewijzen voor deze leefomgeving. Aan de hand van petrologische slijpplaatjes kon deze interpretatie van het afzettingsmilieu worden bevestigd. De biolaminieten of 'bindstones' waren in staat om de kadavers op te vangen die werden afgezet door een sterkere stroming, gekenmerkt door iets grover sediment. Verder toont de grotere korrelgrootte in laag 14 dan in laag 9 een toename van de energie in het afzettingsmilieu.

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