FIGURE 1. | *One of the major fossil quarries of the Anisian Guanling Formation in Luoping, South China.* *See text on page 150.*

The Vossenveld Formation and biotic recovery from the Permo-Triassic extinction

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U vindt een samenvatting aan het eind van de tekst.

Abstract | The Vossenveld Formation exposed in the Winterswijk quarry (eastern Netherlands) was formed along the western border of the Triassic Germanic Basin and preserves a diverse fauna in marginal marine environments. Discovered fossils include diverse marine reptiles, amphibians, fishes, various invertebrates, as well as trace fossils and plants. The Winterswijk paleofauna is the only well-documented marginal marine ecosystem recorded in the early part of the Triassic, providing us with a precious opportunity to understand ecosystem evolution after the Permo-Triassic mass extinction.

Permo-Triassic mass extinction (PTME) and Triassic times

The Triassic was a time of revolution, as circa 90 % of life forms went extinct across the Permo-Triassic boundary and the 'modern fauna' subsequently originated during this period. On land, the PTME marked the extinction of formerly dominant groups, including herbivorous pareiasaurs as well as carnivorous gorgonopsians (Benton, 2015), some 252 million years ago (Ma). The PTME also marks the early origin of stem groups of modern clades like salamanders, frogs, mammals, turtles, lizards, crocodilians, and dinosaurs – the group including birds (Benton, 2015). In the sea, it is traditionally posited that the Mesozoic Marine Revolution started in the Jurassic (Vermeij, 1977). However, the appearance of sea-living predatory gastropods, crustaceans and especially marine reptiles in the Triassic indicates that this revolution actually started not very long after the mass extinction event (Chen & Benton, 2012).

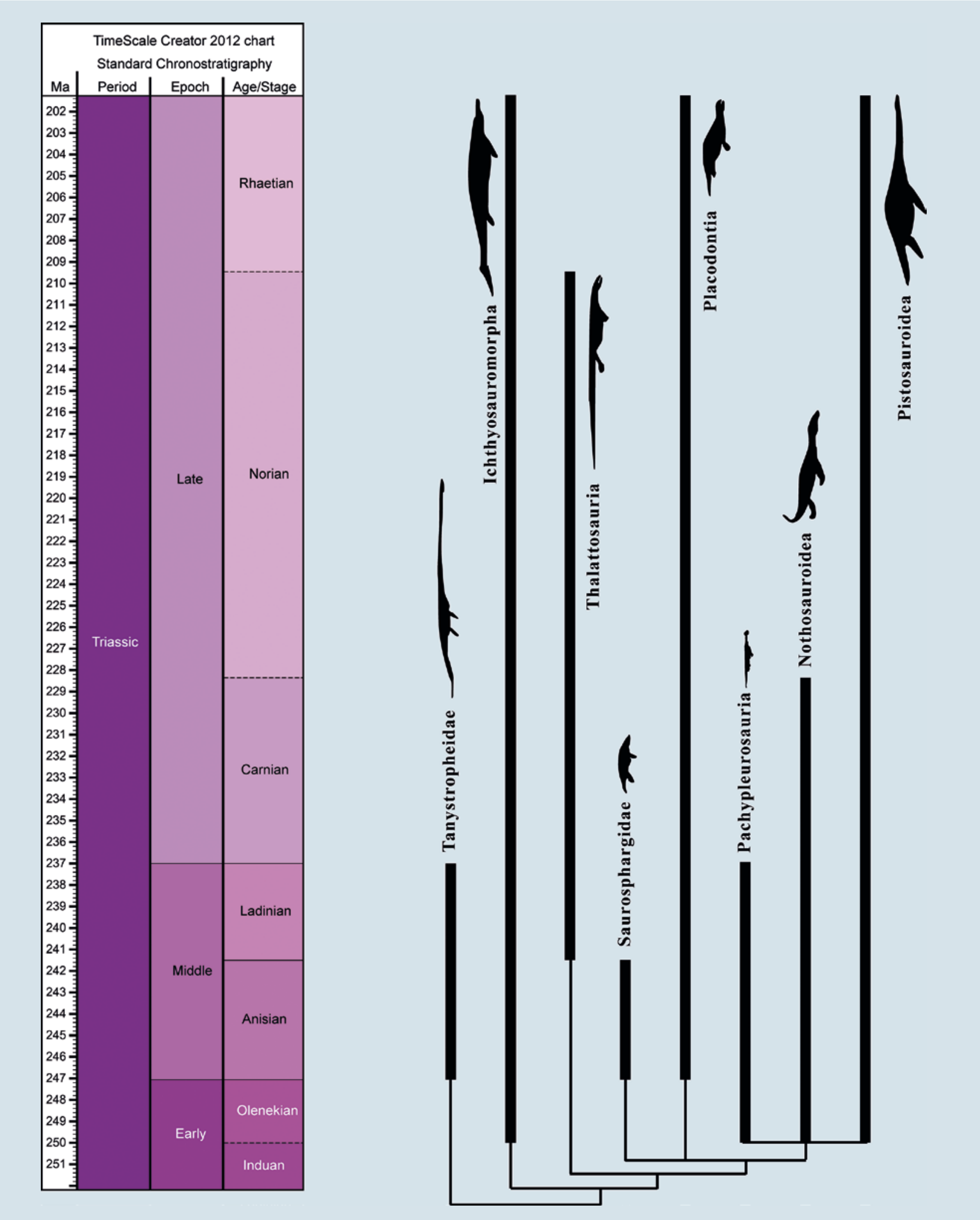

FIGURE 2. | *Stratigraphic distribution of major Triassic marine reptile clades.*

The origin of Triassic marine reptiles and its implication for biotic recovery

The timing and pattern of marine biotic recovery from the PTME is a controversial topic. Traditional views hold that this recovery was very slow and followed a step-wise pattern with low trophic-level groups recovering first (Chen & Benton, 2012). Contrary to this traditional opinion, extensive compilations of the predator record across the Permo-Triassic boundary show that recovery was rapid (Brayard *et al*., 2009; Stanley, 2009; Romano *et al*., 2016; Scheyer *et al*., 2014). Most recently, Song *et al*. (2018) used an updated database of global fossil occurrences to propose a top-down recovery from the PTME in which a reversed trophic pyramid in Early Triassic ecosystems was followed by a conventional pattern since the Middle Triassic. Song *et al*. (2018) furthermore suggested that taxonomic and ecological recoveries were decoupled, with taxonomic recovery having been achieved by the beginning of the Middle Triassic (earliest Anisian, ~247 Ma) while ecological recovery proceeded until the end of Triassic.

During the Early-Middle Triassic recovery stage, a diverse assemblage of reptiles rapidly invaded the marine realm and advanced into most predatory niches of the marine ecosystems during the remainder of the Triassic (Fig. 2). These include ichthyosauromorphs (Fröbisch *et al*., 2013; McGowan & Motani, 2003; Sander, 2000), sauropterygians (Rieppel, 2000; Liu *et al*., 2014), thalattosaurs (Müller, 2005), and the unusually long-necked tanystropheid protorosaurs (Liu *et al*., 2017). These clades represented the top predators of their times, analogous to marine mammals in today's oceans.

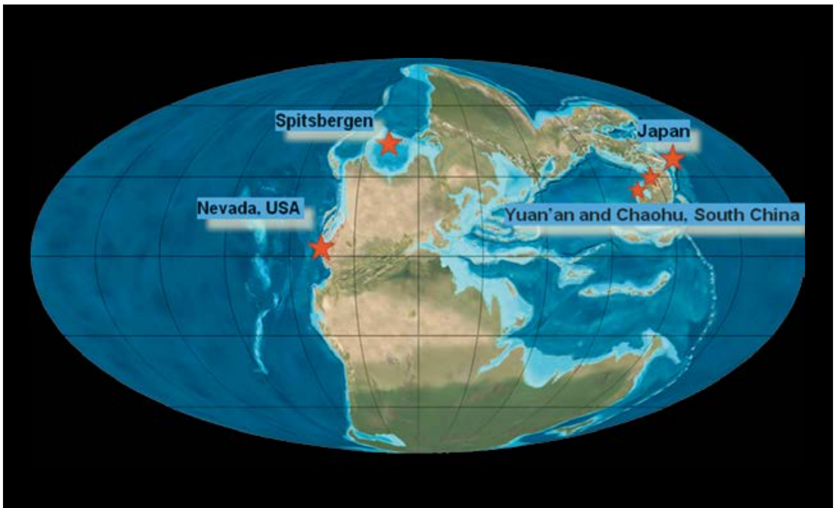

FIGURE 3. | *Palaeogeographic distribution of major Early Triassic Lagerstätten with well-preserved marine reptiles. The base map is from http://deeptimemaps.com/.*

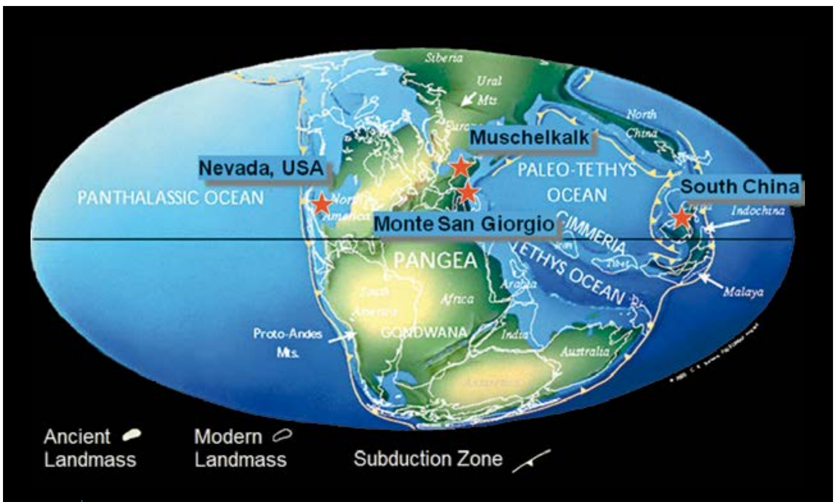

FIGURE 4. | *Palaeogeographic distribution of major Anisian Lagerstätten with well-preserved marine reptiles. The base map is from http://scotese.com/.*

The morphologically most diverse of these clades is the Sauropterygia (placodonts, pachypleurosaurs, nothosaurs, pistosaurs, and probably saurosphargids). However, with the exception of the pistosaurs, sauropterygians remained restricted to their presumable location of origin, the Tethys Ocean and connecting marginal basins (Rieppel, 2000). This also applied to the marine tanystropheid protorosaurs (Liu *et al*., 2017). Ichthyosaurs, on the other hand, had rapidly spread around the globe by the end of the Early Triassic, and their region of origin remains unknown (Sander, 2000; McGowan & Motani, 2003). Thalattosaurs appeared relatively late, at the end of the Anisian, in the western Tethys, but had spread over the northern hemisphere by the Late Triassic (Müller, 2005).

Early-Middle Triassic marine fossil Lagerstätten

In modern marine environments, top predators play a key role in stabilizing ecosystems (Casini *et al*., 2012; Steneck, 2012). Therefore, the study of fossil Lagerstätten preserving marine reptiles is crucial for the reconstruction of the biotic recovery from the PTME (Chen & Benton, 2012; Benton *et al*., 2013). Fossil Lagerstätten that preserve nearly complete ecosystems provide us with almost unbiased snapshots of the diversification history of life.

Previous research has shown that documentation of the diversification history of Mesozoic marine reptiles, especially forms from shallow environments, is susceptible to taphonomic bias and other geological factors such as sea level change (Benson *et al*., 2010, 2011; Kelley *et al*., 2014). Most Triassic marine reptiles are usually interpreted as adapted to shallow marine habitats (McGowan & Motani, 2003; Motani *et al*., 2013; Müller, 2005; Rieppel, 2000). Therefore, the focused study of well-preserved fossil Lagerstätten preserving Triassic marine reptiles can help to avoid biases caused by diverse geological factors (e.g., Sahney & Benton, 2008). Although the exact recovery rate remains debated, most workers agree that ocean chemistry and ecosystems had become stabilized by Anisian times. A comparison of fossil communities between Anisian faunas and those of the Early Triassic enables testing of different hypotheses regarding the timing and pattern of biotic recovery.

Important marine fossil Lagerstätten dating to the Spathian substage of the late Early Triassic are known from Nevada, Spitsbergen, Japan, and the Yuan'an and Chaohu localities of South China (Fig. 3). The Nevada (Kelley *et al.*, 2016) and Spitsbergen (Hurum *et al.*, 2018) localities are characterized by moderately deep shelf deposits. Japanese (Nakajima *et al.*, 2014) and Chaohu (Li *et al.*, 2007) localities are characterized by deep water deposits that likely formed on the continental slope. All these deposits preserve mainly ichthyosaurs that appear to have adopted a pelagic life-style early on, including the development of live birth (Motani *et al.*, 2014). Yuan'an is located in a shallow intraplatform basin and preserves an endemic group possibly related to ichthyosaurs, the hupehsuchians (Cheng *et al.*, 2019).

The Anisian Lagerstätten containing well-preserved marine reptiles (Fig. 4) include the Fossil Hill Member of Nevada, the Besano Formation of Monte San Giorgio (Switzerland and Italy), and the Guanling Formation of SW China (Panxian and Luoping faunas). The Fossil Hill Member is characterized by moderately deep shelf deposits and associated deep-water fauna overwhelmingly dominated by ichthyosaurs, including large-bodied to giant forms (Fröbisch *et al.*, 2013). Both the Besano Formation (Rieppel, 2019) and the SW China faunas (Benton *et al.*, 2013; Fig. 1) are

FIGURE 1. | *One of the major fossil quarries of the Anisian Guanling Formation in Luoping, South China.*

located in typical intraplatform basins with occasional connections to the open sea. These localities all preserve a highly diverse fauna of marine reptiles, including multiple representatives of major marine reptile lineages (Fig. 5). Thalattosaurs are thus far unknown from the Anisian of SW China. However, they are encountered in the Besano Formation, which accounts for their earliest conclusive occurrence in the fossil record. In addition, the Besano and Guanling formations preserve a highly diverse and abundant fish fauna, indicating normal marine conditions (López-Arbarello *et al.*, 2016; Benton *et al.*, 2013).

Although not a Lagerstätte in the strict sense, the Anisian to middle Ladinian (247-241 Ma) Muschelkalk deposits of the Germanic Basin also represent a classical and important source of information on Triassic marine reptile evolution, having produced the historically earliest of such finds. The first placodonts, nothosaurs, pistosaurs, and tanystropheids, mainly consisting of isolated skulls and postcranial bones, were described from German outcrops of the Muschelkalk in the 19th century (Meyer, 1854; Rieppel, 2000). More complete skeletons became later known from the Besano Formation (Rieppel, 2019) and the SW Chinese Lagerstätten (Benton *et al.*, 2013). Ichthyosaurs, however, are extremely rare finds (Sander, 1997). Muschelkalk deposits are not only found in Germany, but also in neighboring Switzerland, France, Poland, and The Netherlands.

The Vossenveld Formation fauna in Winterswijk

Following a brief review of the faunas from the early part of the Triassic all over the world, it becomes clear that our understanding of Triassic marine ecosystems is restricted to the normal marine habitats of the Triassic seas. This is why the Vossenveld Formation of western Germany and The Netherlands as a marginal marine deposit, and its best outcrop, the Winterswijk quarry, play an unique role in our understanding of early part of the Triassic life. The Vossenveld Formation is middle Anisian in age and, as such, represents an interval of the Lower Muschelkalk lithostratigraphy. It was deposited on carbonate tidal flats in a dry, subtropical setting, and preserves a uniquely large number of partial and partially articulated marine reptile skeletons, outnumbering such finds from the remainder of the Muschelkalk by an order of magnitude (Heijne *et al.*, 2019).

Winterswijk is located on the western border of the Muschelkalk Basin. Up to now, fossils including marine reptiles, amphibians, fish, invertebrates, plants, and terrestrial reptile tracks have been collected from Winterswijk (Heijne *et al.*, 2019). Identifiable reptiles are all coastal or shallow-water forms, including abundant pachypleurosaurs (Klein, 2009, 2012; Rieppel and Lin, 1995; Heijne *et al.*, 2019), abundant nothosaurs (Albers, 2011; Klein & Albers, 2009; Klein *et al.*, 2015, 2016; Heijne *et al.*, 2019), placodonts (Albers, 2005; Klein & Scheyer, 2014; Neenan *et al.*, 2013; Oosterink, 1978), probable pistosaurs (Sander *et al.*, 2014), the bizarre saurosphargids (Sander *et al.*, 2014), and tanystropheid protorosaurs (Wild & Oosterink, 1984). Amphibians are represented by rare remains of Temnospondyli (Oosterink & Diepenbroek, 1990). Fish finds consists of Elasmobranchii (Oosterink & Poppe, 1979), Sarcopterygii (Lankamp & Winkelhorst, 1998), and Actinopterygii (Oosterink & Poppe, 1979, Maxwell *et al.*, 2016). Invertebrates include insect remains (van Eldijk *et al.*, 2017), crustaceans (Klompmaker & Fraaije, 2011), bivalves (Klompmaker & Fraaije, 2011), gastropods (Klompmaker & Fraaije, 2011), brachiopods (Klompmaker & Fraaije, 2011), horseshoe crabs (Klompmaker & Fraaije, 2011), and jelly fish (van Eldijk *et al.*, this volume). There is one exception in the faunal list that may indicate temporary open water conditions: ammonoids recovered from the upper part of the section (Klompmaker & Fraaije, 2011). Finally, terrestrial plant matter was occasionally washed into the Winterswijk region from nearby landmasses (Klompmaker & Fraaije, 2011).

Trace fossils are represented by invertebrate trace fossils (e.g., Oosterink, 1990; Schulp *et al.*, 2017) but also by spectacular and highly abundant terrestrial reptile trackways pertaining to the ichnogenera *Rhynchosauroides* and *Procolophonichnium* (Dülfer & Klein, 2006). Strikingly, although the conclusive affinity

Figure 5. | *Representative marine reptile taxa from the Anisian Guanling Formation in Luoping, South China (From Liu* et al.*,2014).*

(A) The ichthyosaur Phalarodon atavus *(LPV 30872);*
(B) the ichthyosaur Mixosaurus *cf.* panxianensis *(LPV 30986);*
(C) the sauropterygian cf. Atopodentatus *(LPV 30172);*
(D) the saurosphargid Sinosaurosphargis yunguiensis *(LPV uncatalogued);*
(E) the pachypleurosaur Diandongosaurus acutidentatus *(IVPP V 17761);*
(F) the pachypleurosaur Dianopachysaurus dingi *(LPV 31365);*
(G) the nothosaur Lariosaurus *sp. (LPV 301881);*
(H) the nothosaur Nothosaurus zhangi *(LPV 20167);*
(I) the archosaur *cf.* Qianosuchus *(LPV 31411);*
(J) the tanystropheid protorosaur Dinocephalosaurus *cf.* orientalis *(LPV 30174).*

Scale bar equals 1 cm in (F), 0,5 cm in (I), and 10 cm in all others.

of the trackway producers remains unclear, the marine reptiles known from body fossils were not the producers of these ichnogenera. Trackways representing the ichnogenera *Brachychirotherium* and *Coelurosaurichnus* were also encountered in the section but remain rare (Oosterink *et al*., 2003). All the trackways and most of the marine reptile remains originate from the lower part of the section that is dominated by mud-cracked algal laminates (Heijne *et al*., 2019).

In conclusion, the Vossenveld Formation Lagerstätte exposed in the Winterswijk quarry is a unique record of substantial importance. Detailed study of this fauna allows us to reconstruct the food web of an early Middle Triassic marginal marine community along the western margin of the Triassic Muschelkalk Sea. The Winterswijk fauna expands the spectrum of Triassic marine ecosystems and offers valuable opportunities towards detailed comparison of faunas from the different Triassic depositional environments that are required for clarifying the timing and pattern of biotic recovery from the PTME.

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Samenvatting

De Vossenveld Formatie, die in de Winterswijkse Steengroeve (oostelijk Nederland) aan de oppervlakte komt, werd gevormd langs de westelijke grens van het Triassische Germanische Bekken en conserveert een soortenrijke ondiep mariene fauna. In deze afzettingen werden fossielen van verscheidene mariene reptielen, amfibieën, vissen en invertebraten ontdekt, alsmede sporenfossielen en plantenresten. De paleofauna van Winterswijk vormt het enige goed gedocumenteerde ondiep mariene ecosysteem uit de eerste helft van het Trias, en verschaft ons een waardevol inzicht in de ontwikkeling van ecosystemen na de Permo-Triassische massa-extinctie.

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