FIGURE 1. | *Skull of* Cymatosaurus fridericianus *Fritsch, 1894, the type species of the genus with a skull length of ~200 mm (Lower Muschelkalk, Zementwerk Halle-Nietleben, Sachsen-Anhalt, Germany) (collection of IGWH).*

Ancestors to the plesiosaurs?

On Triassic Pistosauroidea and the potential presence of cymatosaurs in Winterswijk

U vindt een samenvatting aan het eind van de tekst.

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Abstract | This contribution aims to give a taxonomical, morphological, and paleobiological overview of the knowledge of the interesting group of cymatosaurids. These are usually outnumbered by their Triassic kin: nothosaurs and pachypleurosaurs. However, the genus *Cymatosaurus* was among the first sauropterygians (both stratigraphically and historically) that were described. Cymatosaurids fall in the direct phylogenetic lineage towards the famous plesiosaurs that ruled the seas until the end of the Cretaceous, long after all other sauropterygians went extinct. Cymatosaurids equipped their descendants with important prerequisites for this lifestyle, such as increased growth rates (i.e. faster metabolism). This enabled pistosaurs and later the plesiosaurs to inhabit open seas and thus to survive the environmental changes at the end of the Triassic. Nevertheless, cymatosaurids remain the least known of all Triassic Sauropterygia.

Systematic Paleontology

SAUROPTERYGIA Owen, 1860
EUSAUROPTERYGIA Tschanz, 1989
PISTOSAUROIDEA Baur, 1887-90
CYMATOSAURIA Huene, 1944
CYMATOSAURIDAE Huene, 1944

Phylogeny and Stratigraphical and Paleobiogeographical Occurrences

The following summary is largely based on the works of Rieppel (1995, 1997, 2000).

Cymatosauridae falls inside the clade Pistosauroidea alongside the Pistosauria and the Plesiosauria. The exact pistosauroid tree reads (*Corosaurus* (*Cymatosaurus ((Augustasaurus, Pistosaurus) (Bobosaurus*, (crowngroup Sauropterygia, including plesiosaurs)))) (Rieppel, 2000). Cymatosauridae consists of two genera: *Corosaurus* from the Olenekian (Lower Triassic) Alcova Limestone Member of the Chugwater Formation (Wyoming, USA) and *Cymatosaurus* from the upper Olenekian to middle Anisian (Lower to Middle Triassic) of various Upper Buntsandstein to Lower and maybe Middle Muschelkalk localities from the Germanic Basin.

For obvious reasons, this article will focus on *Cymatosaurus* and other basal pistosauroid remains from the Germanic Basin. *Cymatosaurus* is a very important taxon because it is considered to represent a Triassic stem group closely related to the Plesiosauria (Huene, 1944; Rieppel, 1997, 2000). *Cymatosaurus* is thus far only known from rare finds of isolated, complete or fragmentary, skulls. Its alpha (i.e. species) taxonomy is therefore solely based on skull morphology. Currently, five species are recognized as valid taxa.

Cymatosaurus latifrons Gürich, 1884, with a skull length of 150-175 mm, is known from the Upper Buntsandstein of Krapkowice and from the Lower Muschelkalk of Gogolin (Poland). *C. fridericianus* Fritsch, 1894, the type species of the genus with a skull length of 200 mm, was found in the Lower Muschelkalk of Halle-Nietleben (Sachsen-Anhalt, Germany) (Fig. 1). *C. minor* Rieppel & Werneburg, 1998 was a rather small species described from the Lower Muschelkalk of the Ilm valley (Thuringia, Germany) with a skull length of only 85.8 mm. Recently, *C. erikae* Maisch, 2014 was erected based on a three-dimensionally preserved skull that is anteriorly incomplete. It was found in the Upper Buntsandstein near Jenzig Mountain close to Wogau (Thuringia, Germany) and its reconstructed skull length was estimated to be around 200 mm. Maisch (2014) resurrected *C. gracilis* Schrammen,1899, which was considered synonymous with *C. latifrons* by Rieppel (2000).

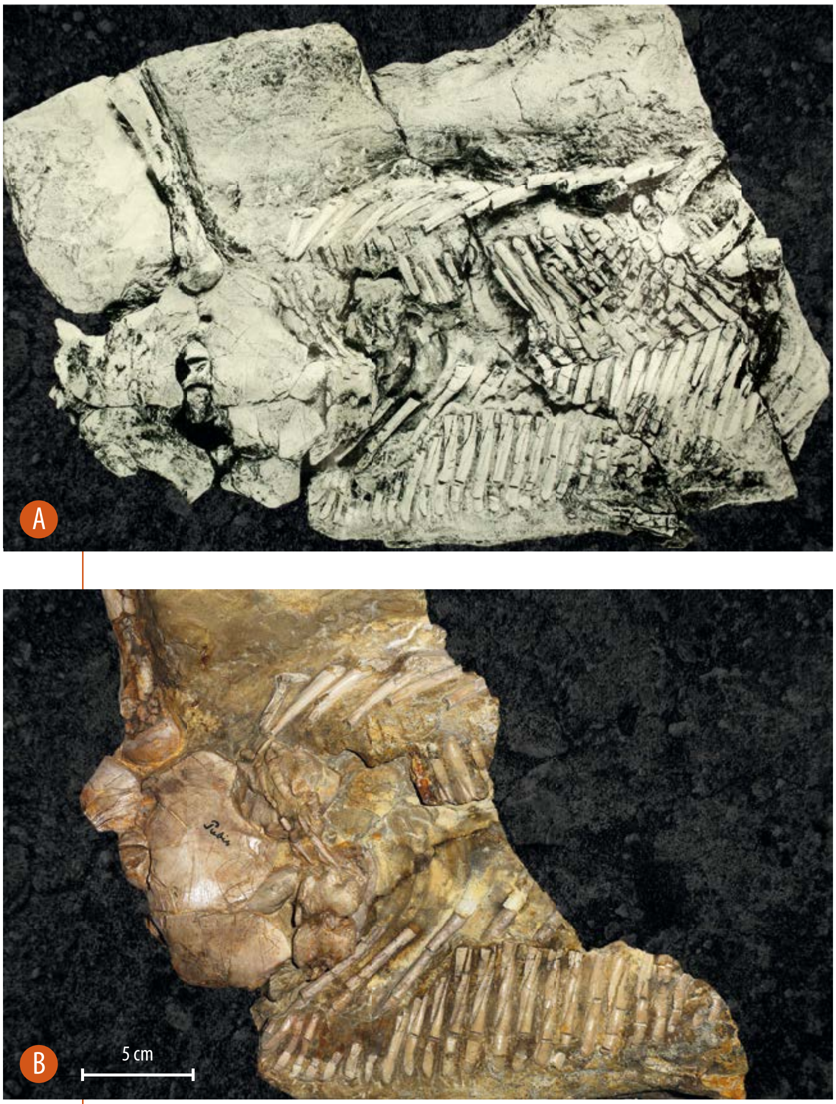

FIGURE 2. | *A: Original specimen of* 'Proneusticosaurus silesiacus' *(MG UWr. 4438s) from the Middle Triassic of Poland, photographed from the publication of Volz (1902). B: WWII surviving postcranial remains of* 'Proneusticosaurus silesiacus' *(MG UWr. 4438s). Note the now incomplete femur and pelvic girdle. (photo credits Dawid Surmik, University of Silesia).*

Cymatosaurus 'multidentatus' Huene, 1958 is only known from a very small, incomplete lower jaw (~15 mm) that originated from early Anisian sediments of the Lechtaler Alps (Austria). *Cymatosaurus 'erythreus'* from the Upper Buntsandstein of Rüdersdorf is only known from a skull fragment. According to Rieppel (2000), the latter fossils are both too fragmentary and thus insufficiently diagnostic for distinguishing between species. However, both specimens clearly show features that justify an assignment to *Cymatosaurus* (Rieppel, 1995). The lower jaw fragment is especially informative because it documents the expansion of the genus from the Germanic Basin (Poland and eastern Germany) into the Alpine Triassic by the early Anisian. In addition, there are indications for the occurrence of the genus in the Guanling Formation (Anisian) in Panxian, Guizhou, China. The formal presentation of a thus-far unpublished skull associated with the anterior trunk region of apparent cymatosaurian affinity from these deposits may immensely increase the paleogeographic range of *Cymatosaurus*.

According to current knowledge, the genus *Cymatosaurus* is stratigraphically restricted to the late Olenekian – middle Anisian (Upper Buntsandstein, Lower – ?Middle Muschelkalk).
The skulls of the different species can be differentiated by the topology of particular sutures and by minor differences in dentition (summarized in Rieppel, 2000; Maisch, 2014). A future revision of these skulls and referred material involving novel research methods, such as micro-CT visualisation, is required. Studies into the braincase, dentition and tooth replacement, as well as careful consideration of intraspecific variability, should reveal whether all these species indeed represent valid taxa. High intraspecific variability was already documented for nothosaurs (Albers, 2011; Klein *et al*., 2015a) and is likely also present in *Cymatosaurus*, which would reduce the number of species.

Morphology

Skull – The overall shape of the skull of *Cymatosaurus* is similar to that of *Nothosaurus*. They share the elongated premaxillary rostrum with the constricted snout, the elongated postorbital skull with elongated upper temporal fenestra, and the strongly constricted parietal region (Fig. 1). Although the upper temporal fenestrae of *Cymatosaurus* are distinctly larger than the orbitae (i.e. eye sockets), they are not as elongated as in nothosaurs. The postorbital arch of *Cymatosaurus* is as narrow as in some nothosaurs but the jugal bone is larger than in nothosaurs. Most striking are the reduced and universally separated nasals, a feature *Cymatosaurus* shares with pistosaurs. *Cymatosaurus* does not have scleral ossicles (Rieppel, 2002).

The palate of *Cymatosaurus* is derived (when compared to other diapsids) because it features reduced interpterygoid vacuities and is completely closed. This condition is shared with nothosaurs, pachypleurosaurs and placodonts, but not with plesiosaurs (Maisch, 2014). The occiput is nevertheless open (Maisch, 2014: 222), which is a rather plesiomorphic feature. Plesiosaurs, however, also exhibit an open occiput that is interpreted to result from neoteny (O'Keefe, 2006). Nothosauroids, on the other hand, have a plate-like closed occiput, which is a very derived condition. According to Maisch (2014), these two important – derived vs. plesiomorphic – characters of the *Cymatosaurus* skull question its phylogenetic position as a potential stem-group plesiosaur. Maisch (2014) argued that, in the case of a cymatosaurian ancestry to the pistosaurian, and therefore plesiosaurian, lineages, the plesiosaur skull must have experienced several crucial reversals. Such profound regressive evolution of features would be unparalleled in vertebrate evolution. However, this consideration needs to be investigated in more detail with support of micro-CT data and with consideration of additional material before it can be confirmed or rejected. Whether one agrees with the ideas of Maisch (2014) or not, morphological details clearly have a profound impact on the reconstruction of phylogenetic relationships.

The lower jaw of *Cymatosaurus* is only incompletely known but seems to include a fortified short symphysis (Rieppel, 2000), which again differentiates it from *Nothosaurus*. *Cymatosaurus* has a heterodont dentition that involves enlarged and strongly procumbent premaxillary teeth and two maxillary fangs located immediately in front of the orbit (Rieppel, 2002). The maxillary tooth row is shorter than in *Nothosaurus*. Rieppel (2002) considered muscle reconstructions and osteological features to infer a stronger bite capacity for *Cymatosaurus* than for nothosaurs. However, the pincer-like jaws of *Cymatosaurus* suggest rapid, laterally directed bites similar to those reconstructed for *Nothosaurus* (Rieppel, 2002). Both nothosaurs and cymatosaurs most likely captured fish as well as sufficiently small reptiles and swallowed them whole. Despite of their similar feeding strategies, Rieppel (2002) suggested that these taxa experienced a significant degree of habitat partitioning because they rarely overlap in time and environment.

Postcranium - Thus far, no *Cymatosaurus* skull was found associated with diagnostic postcranial material. However, the second skull presented by Schrammen (1899) was found in association with gastral ribs. Volz (1902) described two incomplete postcranial skeletons from the Lower Muschelkalk of Poland (Gogolin, Zakrzów) and assigned both to the new genus *Proneusticosaurus*, but to different species (*P. madelungi*, and *P. silesiacus*) (Fig. 2). Only the posterior part of the holotype of *P. silesiacus* survived WWII. The specimen consisted of fragments of posterior dorsal ribs, parts of the gastral rib cage, two digits of the left manus, a number of posterior dorsal vertebrae, the complete right pubis and the ventral (medial) part of the left pubis, the proximal head of the right ischium, and the proximal part of the right femur. The morphologies of the dorsal vertebrae and the pubes of *'Proneusticosaurus'* clearly differ from those of *Nothosaurus* (Sues, 1987; Rieppel & Hagdorn, 1997). The distal ends of the lateral elements of the gastral ribs of *Proneusticosaurus* are broad and rounded, as in *Cymatosaurus* (Schrammen, 1899: plate 26) and do not taper as in *Nothosaurus* (Schröder, 1914).

No humerus was associated with *"Proneusticosaurus"*. Isolated sauropterygian humeri are common at localities of the Germanic Basin and usually diagnostic at sauropterygian group level (Rieppel, 1994; Bickelmann & Sander, 2008; Klein, 2010). This led Rieppel (1994) to refer a particular humeral morphotype to *Cymatosaurus* (Fig. 3), which was adopted by Klein (2010). A close relationship of this humeral morphotype with pistosauroids is corroborated by a very characteristic bone tissue type (Klein, 2010) that is very similar to the bone tissue type described for *Pistosaurus* (Krahl *et al*., 2013) and differs markedly from those of pachypleurosaurs, nothosaurs, and placodonts (Klein, 2010; Klein *et al*., 2015b, 2016). If correctly identified, the humerus of *Cymatosaurus*, which features a well-developed deltopectoral crest, epicondyles, and a distally notched ectepicondylar groove, is plesiomorphic when compared to the humerus of *Nothosaurus*.

cf. *Cymatosaurus* from Winterswijk

One of the most important discoveries in the Winterswijkse Steengroeve was made in 1999 by H. Winkelhorst. It consists of a large matrix block associated with several smaller slabs (NMNHL RGM 449487) that collectively presents a large amount of mixed reptile bones (Sander *et al*., 2014). The bone accumulation comprises a fairly complete skeleton lacking the skull, an associated skull fragment of

FIGURE 3. | *Comparison of Vossenveld humeral morphology of A) cf.* Cymatosaurus *(Wijk11-39), B)* Nothosaurus marchicus *(Wijk11-265), and C)* Anarosaurus heterodontus *(Wijk09-58) (all photos by Georg Oleschinski, IGPB).*

Anarosaurus, and several bones of the enigmatic *Eusaurosphargis* (see Scheyer *et al.,* in this volume). The accumulation was found between Layer 4 and Layer 9 (Oosterink, 1986) in the still active third quarry at Winterswijk. Former interpretations hypothesized that the skeleton belonged to a pachypleurosaur (Oosterink *et al*., 2003; Diedrich, 2013). However, based on humeral morphology (Rieppel, 1994, 1995), humeral histology (Klein, 2010), and general postcranial morphology (Sander *et al*., 2014; Klein *et al*., 2015a), the fairly complete skeleton on the main matrix block of NMNHL RGM 449487 was assigned to a basal pistosauroid, most likely cf. *Cymatosaurus* (Sander *et al*., 2014). In the same publication, a historical find from 1966, NMNHL RGM 445912, was also assigned to this taxon through its humeral morphology. Later, two incomplete skeletons from Winterswijk were assigned to cf. *Cymatosaurus* as well, again mainly based on humeral morphology (Klein *et al*., 2015a).

The morphology of the postcranial bones in these skeletons has been described and compared in detail (Sander *et al*., 2014; Klein *et al*., 2015a). Interestingly, the morphology of these skeletons differs in some aspects and beyond mere ontogenetic variation from that of *'Proneusticosaurus'*, although no humeri are known for that taxon (Volz, 1902). If the assignment of both taxa is proven to be correct, at least two different species of *Cymatosaurus* must have existed in the Anisian of Europe.

However, this interpretation is contradicted by the striking lack of *Cymatosaurus* skull material from Winterswijk. Although circa 10 skulls of *Nothosaurus* and around 25 skulls of the pachypleurosaur *Anarosaurus* are known from the Vossenveld Formation (Heijne *et al*., 2019), no skull of a cymatosaur or any other basal pistosauroid has been found in Winterswijk thus far. As mentioned earlier, other localities have yielded only skulls but no postcrania. Thus, certain doubts on the assignment of these skeletons from Winterswijk to basal pistosauroids persist. Nevertheless, due to the differences in bone histology, we can unequivocally exclude that the Winterswijk skeletons belong to a nothosaur. The possibility that they, as initially suggested by others, belong to a large pachypleurosaur still remains. *Anarosaurus* (Klein, 2009, 2012) is a very common member of the marine reptile fauna in Winterswijk and differs from all other European pachypleurosaurs in many aspects (Sues & Caroll, 1985; Sander, 1989; Rieppel, 1989). Besides morphological differences, *Anarosaurus* also differs from other pachypleurosaurs through its particular bone tissue type, which is similar to that of cf. *Cymatosaurus* (Klein, 2010; Klein & Griebeler, 2018). It is conceivable that *Anarosaurus* represents an earlier ontogenetic stage of cf. *Cymatosaurus* because there is no size overlap between their representative materials. However, there are many morphological differences between *Anarosaurus* (Klein, 2012) and the skeletons assigned to basal pistosauroid from Winterswijk (Sander *et al*., 2014; Klein *et al*., 2015a), which cannot be sufficiently explained by ontogenetic, sexual, or intraspecific variation alone. In addition, bone histology and mathematical modelled growth curves indicate advanced ontogenetic stages for at least some individuals of *Anarosaurus* (Klein & Griebeler, 2018).

In conclusion, finding a cymatosaurid skull in Winterswijk is crucial for several reasons. Firstly, it would unequivocally document the presence of this clade in the shallow marine environment along the western edge of the Germanic Basin. Secondly, it would further expand the stratigraphical distribution of the taxon to the middle Anisian. Thirdly, the unequivocal assignment of the above-mentioned skeletons to the cymatosaurid lineage will, in turn, help in future assignments of isolated bones from throughout the Anisian to specific taxa. Finally, it would corroborate the presence of advanced bone histology (relating to increased growth rates) at the very origins of the cymatosaurid clade.

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Abbreviations

IGWH, Institut für Geowissenschaften, Martin-Luther-Universität, Halle/Saale, Germany;
MGUWR, Institute of Geological Sciences, University of Wrocław, Poland;
NMNHL, National Museum of Natural History (NCB Naturalis), Leiden, The Netherlands.

Samenvatting

Deze bijdrage verschaft een taxonomisch, morfologisch, en paleobiologisch overzicht van de huidige kennis over de interessante groep der cymatosauriërs. Deze in zee levende reptielen waren beduidend minder talrijk dan hun naaste verwanten onder de Triassische Sauropterygia: de nothosauriërs en de pachypleurosauriërs. Desalniettemin was *Cymatosaurus* één van de eerste Sauropterygia (zowel stratigrafisch als historisch) die werd beschreven. Cymatosauriërs waren voorouders van de beroemde plesiosauriërs die de zeeën zouden domineren tot het einde van het Krijt, lang nadat alle andere Sauropterygia waren uitgestorven. Cymatosauriërs bezaten specifieke eigenschappen, zoals hogere groeisnelheden, die hun afstammelingen belangrijke voordelen boden voor deze levensstijl. Dit zorgde ervoor dat de pistosauriërs, en later ook de plesiosauriërs, de open zeeën konden bevolken en hiermee de wereldwijde klimatologische veranderingen aan het einde van het Trias overleefden. Desondanks blijven cymatosauriërs de minst bekende vertegenwoordigers van de Triassische Sauropterygia.

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