Netherlands Journal of Geosciences — Geologie en Mijnbouw | 84 – 3 | 213 - 220 | 2005

Remains of *Clidastes* Cope, 1868, an unexpected mosasaur in the upper Campanian of NW Germany

M.W. Caldwell* **& C.G. Diedrich**

University of Alberta, Department of Earth and Atmospheric Sciences, and Department of Biological Sciences, Edmonton, Alberta, Canada T6G 2E9.

* Corresponding author. Email: mw.caldwell@ualberta.ca

Manuscript received: December 2004; accepted: January 2005

Abstract

The mosasaurine *Clidastes* sp. is recognised from cranial and post-cranial remains collected at four localities in NW Germany. Cranial material was found in pelagic turbiditic marls which crop out near the village of Beckum, while post-cranial skeletal elements were collected from sandy limestones exposed near the villages of Schöppingen, Coesfeld and Billerbeck. In stratigraphic order, the units producing these specimens of *Clidastes* are the Coesfeld, Baumberge and Beckum formations of late Campanian (Late Cretaceous) age. The cranial material comprises the anterior part of a skull and a single isolated tooth, while post-cranial bones comprise a few isolated vertebrae and a partial skeleton including forelimb bones and an articulated vertebral column. *Clidastes* is known to date from the western North Sea Basin (England), southern Sweden, as well as from North America (Western Interior Seaway and Gulf Coast).

Keywords: *Clidastes*, mosasaurs, Münsterland, Germany, upper Campanian, palaeogeography

Introduction

Until the studies of Lindgren (1998), Diedrich & Mulder (2004) and Lindgren & Siverson (2004), the mosasaurine *Clidastes* (i.e., *C. liodontus* Merriam, 1894 and *C. propython* Cope, 1869) had never been identified outside of North America. *Clidastes liodontus* is the stratigraphically older taxon, occurring in sediments ranging in age from early Coniacian to Santonian; it is replaced by *C. propython* by the end of the Santonian or the beginning of the early Campanian. By mid-Campanian time, *C. propython* is no longer recognised among mosasaur taxa in North America.

The most intriguing mention of *Clidastes* outside of North America is the late Campanian record by Diedrich & Mulder (2004). Lindgren & Siverson's (2004) report places 'clidastine' mosasaurs in Europe already in the early Campanian, as based on their identification of isolated teeth. Those authors also noted that the Swedish record provided a minimum age for the transoceanic distribution of North American *Clidastes*, previously held to be endemic. Furthermore, they argued that both in North America and Europe, 'clidastines' disappeared at the end of the early Campanian (Russell, 1967). However, Diedrich & Mulder's (2004) material is far more compelling as it includes a well-preserved snout, and presents a definite late Campanian record of 'clidastines' outside of North America.

According to Russell (1967) and Bell (1997), 'clidastines' are basal mosasaurine mosasaurs. The latter author also concluded that 'clidastines' did not constitute a monophyletic assemblage, but rather a series of successive and thus successional basal mosasaurines forming a Hennigian comb at the base of the Mosasaurinae. *Clidastes liodontus* was the most basal mosasaurine in Bell's (1997) hypothesis, with *C. propython* in a sister group position to Globidensini and Plotosaurini. Bell (1997) also identified as terminal taxa, two other species, the not yet formally described *'Clidastes moorevillensis'* (see Shannnon, 1975) and an undescribed new species; neither of these will be discussed further in the present study. The origin of the name *Clidastes* comes from Cope (1868) where he named

the genotype species, *Clidastes iguanavus*, from a single vertebral element that is now considered to be the isolated vertebra of an indeterminate *Mosasaurus* (Kiernan, 1992); the genotype specimen is now a very complete skull and skeleton of *Clidastes propython* collected from the Selma Formation of Alabama (Academy of Natural Sciences Philadelphia, ANSP 10193).

Here, we present an overview of the localities which yielded mosasaur material contained in collections of the Geologisch-Paläontologisches Institut der Westfälischen Wilhelms-Universität Münster (GPIM), and discuss the sedimentology and stratigraphy of strata exposed there. We shall briefly re-characterise specimens available, comparing them to both *Clidastes* and *Mosasaurus*. Comparison with the latter genus is of value as species assigned to that taxon appear to 'take over' from *Clidastes* during the mid-Campanian (Russell, 1967, 1970; Bell, 1997). In addition, we shall explore the question whether the 'clidastines' of the Münsterland Basin enjoyed a temporary refugium of some sort (although this is not likely), or whether they could represent a 'grade' of evolution between *Clidastes* and *Mosasaurus*. Evidence in support of either hypothesis is marginal, but some morphological features shown by Münsterland *Clidastes* are suggestive of the latter possibility. We shall also discuss the conclusions on 'clidastine' extinctions as drawn by Lindgren & Siverson (2004) in the light of Diedrich & Mulder's (2004) identification of *Clidastes* sp. from the study area and in consideration of additional 'clidastine' material presented below.

Mosasaur records from Germany

Well-preserved and easily identifiable mosasaurs are not at all common in the marine Cretaceous (Campanian) deposits of NW Germany. From the Münsterland, previous authors have rather cautiously identified some specimens as *Leiodon* sp., and added quite some indeterminate mosasaur remains (Von der Marck, 1892; Sachs, 2000). The recent study of a mosasaur snout from the upper Campanian (Diedrich & Mulder, 2004) has resulted in its assignment to *Clidastes*.

The four localities which have produced mosasaur remains are situated near Beckum (Beckumer Berge, SE Münsterland), in Baumberge near Schöppingen (NW) and at Coesfeld and Billerbeck in the central Münster Basin (Fig. 1). The Münster Basin is characterised in the south by greensands deposited in coastal environments during the Albian-Turonian, while in the basin centre and northwesterly portions are found sandy carbonate to carbonate rocks deposited in more open-water, pelagic environments during the Cenomanian-Maastrichtian (Arnold, 1964; Hiss, 1995).

In numerous quarries near Beckum, upper Campanian marls and carbonates are being excavated for cement production; one of these outcrops, the Phoenix quarry, has produced a well-preserved mosasaur snout, comprising the premaxilla and fragments of the right and left maxillae. This specimen was mentioned by Giers (1958), and has recently been identified as *Clidastes* by Diedrich & Mulder (2004). The strata near Beckum are turbiditic marls of Late Campanian age (Giers, 1958;

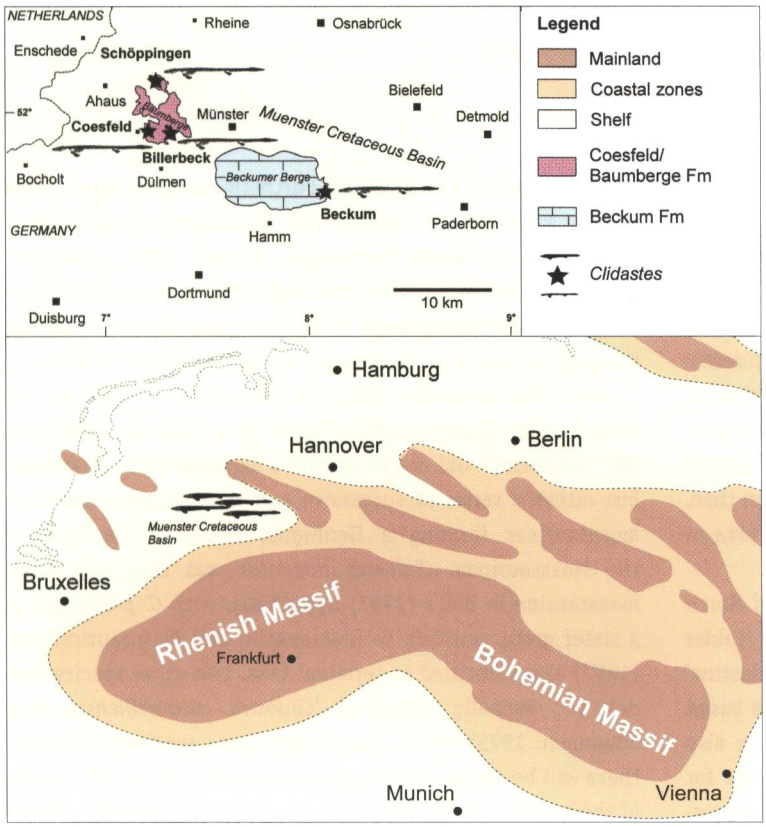

Fig. 1. The four Clidastes *sites near Beckum, Billerbeck, Schöppingen and Coesfeld in NW Germany; darkened zones indicate outcrops of the upper Campanian Beckum, Coesfeld and Baumberge formations (redrawn after Hiss (1995), Campanian palaeogeography after Ziegler (1990)).*

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Arnold, 1964). The Beckum Formation comprises lower to mid-upper Campanian pelagic facies, exposed at quarries there (Fig. 1), of 10 - 25 metres of cyclic carbonate flysch sequences, turbidites and submarine slumps with ichnofabrics typical of allochthonous sediments of the carbonate ramp facies (Häntzschel, 1964; Riegraf, 1995; Wolf, 1995). These carbonate types are distributed only in the eastern part of the Münster Basin during the late Campanian. The exact provenance of the snout tip was noted to be the so-called 'Kiebitzbank', an orbulinarite at the top of the Nünningsbank Member (middle upper Campanian; see Giers, 1958).

Late Campanian sandy limestones found in the southern Baumberge have been quarried for at least two centuries as building stones. In 1852 - 1853, a partial skeleton was discovered at one of the quarries near Schöppingen, exactly which one has never been documented.

The isolated tooth and vertebrae from the Coesfeld-Billerbeck area were surface collected and have no data on exact horizon and stratigraphic unit either. In these more westerly parts of the Münster Basin, the fossil-rich Coesfeld and Baumberge formations crop out at the Coesfeld, Billerbeck and Schöppingen mosasaur sites situated in the Baumberge hills (Fig. 1). Here the facies are composed of sandy limestones (Hiss, 1995), which have produced many invertebrate fossils and a small number of partially disarticulated mosasaur post-cranial elements. At all Baumberge localities strata are assignable to the *Hoplitoplacenticeras dolbergense* ammonite zone and the *Belemnitella mucronata* belemnite zone. These biozones indicate a late Campanian age for all of these units (see Riegraf, 1995) at Beckumer Berge and Baumberge.

Systematic palaeontology

Family Mosasauridae
Subfamily Mosasaurinae
Genus *Clidastes* Cope, 1868

Clidastes *sp.; Fig. 2A - C*

Locality and horizon – from the vicinity of Beckum (Beckumerberge; see Fig. 1); Beckum Formation.

Material – GPIM A.3D-3, a skull fragment comprising the anterior part of the premaxilla with articulated fragments of the left and right maxilla; a number of attached and incipient replacement teeth are present (Fig. 2A - C).

Description – While this specimen was recently well described by Diedrich & Mulder (2004), we re-characterise it here by comparison to other clidastine taxa and specimens. The anterior portion of the premaxilla is well preserved but includes only a short section of the premaxillary bar. In outline, beginning at the tip of the well-developed predental rostrum, and ending at the ventral margins of the contact with the maxillae, the premaxillary describes an equilateral triangle (Fig. 2A - C); a similar morphology is seen in the figured specimen of *Clidastes liodontus* (Fig. 2D - F), FHSM VP 13909 which is also recognised as the earliest known specimen of *C. liodontus* (Everhart et al., 1997). In contrast, the premaxillary tip in *C. propython* is obtuse, in other words, nearly conical with the lateral faces of the premaxilla being much longer than the width at the contact with the maxillae (Fig. 2G - I). Both these species, as well as the present specimen, possess a distinct and very well-developed predental rostrum; in all 'clidastines' this rostrum is the equivalent of at least one tooth pit diameter in length (Fig. 2A, D, G). In GPIM A.3D-3, the sutures between the premaxilla and maxillae are acutely angled towards the midline of the snout, thus creating a waisted or strongly constricted morphology to the premaxillary bar (Fig. 2C); the same morphology is seen in *C. liodontus* (Fig. 2D). In contrast, the sutural contact between the premaxilla and maxillae in *C. propython* is much more sloping and obtuse; the premaxillary bar becomes thinner over a much greater distance moving posteriorly along the snout. In ventral view, both GPIM A.3D-3 (Fig. 2A) and *Clidastes liodontus* (Fig. 2G) have acutely angled tooth rows that diverge sharply from the midline. In contrast, that of *Clidastes propython* is obtusely angled and near-parallel to the midline of the snout. In short, the snouts of GPIM A.3D-3 and of *Clidastes liodontus* are much broader and more robust, particularly at the premaxillary-maxillary suture, than that of *Clidastes propython*. The latter is a much more narrow-snouted animal.

In lateral view, there are no major differences between GPIM A.3D-3 (Fig. 2B) and *Clidastes liodontus* (Fig. 2E) or *C. propython* (Fig. 2H). Rather, all three show a similar profile, except for the sutural trace in GPIM A.3D-3 which is slightly steeper than in either of the other two. In lateral view, it is also clear that the teeth of GPIM A.3D-3 are not procumbent, but rather are straight and directed ventrally, as in *C. liodontus* and *C. propython*.

cf. Clidastes *sp.*

Locality – Billerbeck (Fig. 1).

Material – GPIM A.3D-4 (Fig. 3A, B), a single tooth lacking enamel.

Description – This tooth is approximately 35 mm in height. In occlusal view it presents an oval outline. There are two distinct carinae, one mesial, one distal, as preserved by the dentine portion of the tooth. However, because the enamel is missing, it is not possible to determine what features the carinae might have possessed, i.e., serrated or not.

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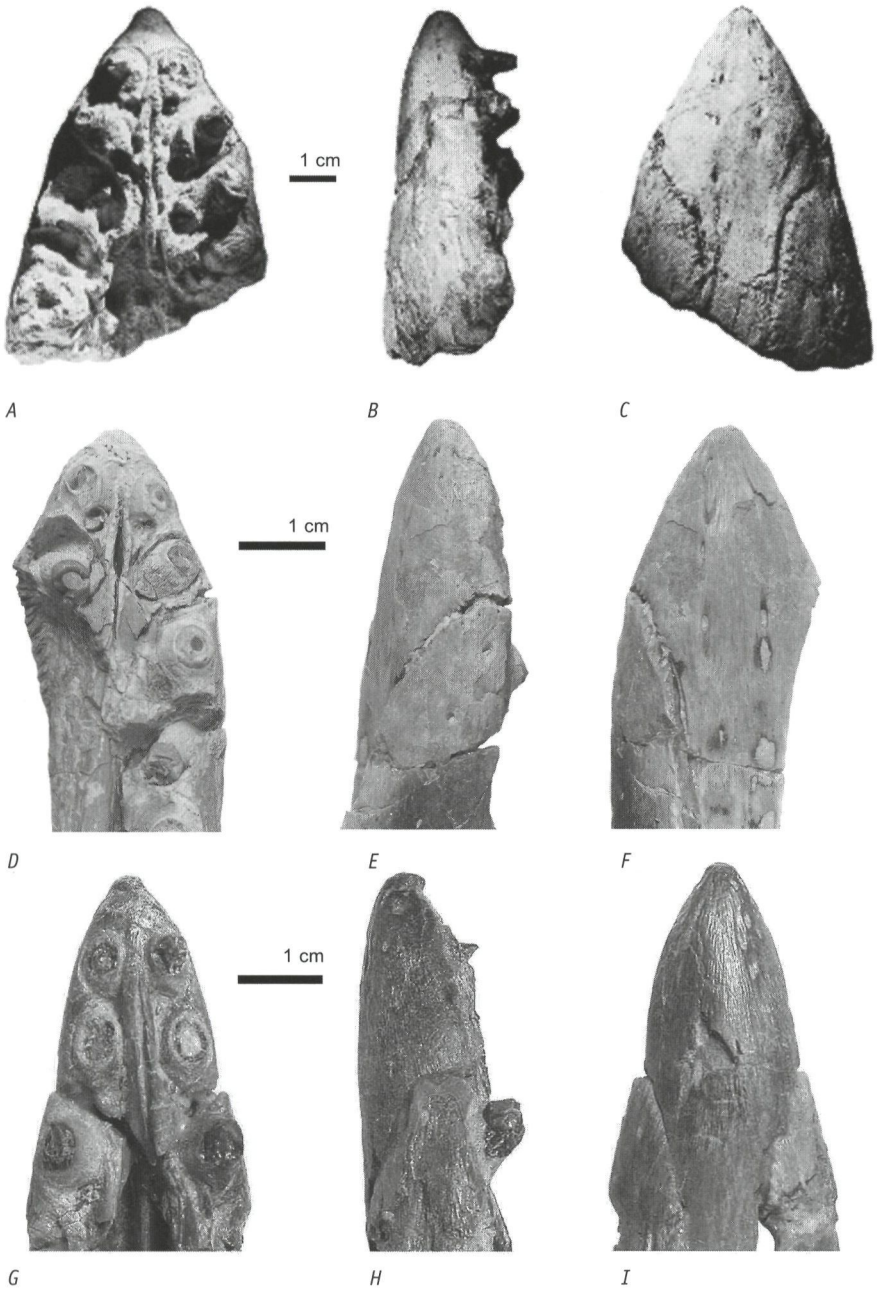

Fig. 2. Comparison of snout tips of Clidastes *sp. (A - C) from the upper Campanian of NW Germany (GPIM A.3D-3),* C. liodontus *(D - F) from the Coniacian of Kansas (FHSM VP 13909), and* C. propython *(G - I) from the Santonian of Kansas (unnumbered specimen).*

Locality – From Schöppingen near Steinfurt, Coesfeld Formation (Fig. 1).

Material – GPIM A.3D-2 (Fig. 3C - N); associated post-cranial fragments including two scapular fragments (Fig. 3C - D), a complete metacarpal V (Fig. 3E), a single complete ulnare (Fig. 3F) (44 mm in width), a fragment each of metacarpal III (Fig. 3G) and metacarpal IV (Fig. 3H), distal fragments of three phalanges (Fig. 3I - K), two fragmentary vertebrae (Fig. 3L - M) as well as an articulated section of twelve dorsal vertebrae with well-preserved neural spines and fragmentary centra (Fig. 3N).

Description – The scapular fragments are too small and bear no distinctive structures allowing certain identification at even the generic level. However, because all this material was found in association, the scapular fragments are here referred to as cf. *Clidastes* along with the other non-diagnostic and fragmentary remains (i.e., fragments of metacarpal III, IV, phalangeal fragments, two fragmentary vertebrae and the articulated section of dorsal vertebrae). From this associated mass of elements and bone fragments, there are two identifiable pieces that also possess genus-level diagnostic characters supporting our assignment of this material to cf. *Clidastes*. These include the complete ulnare and metacarpal V. The ulnare (Figs 3F, 4A - C) is a five-sided irregular polygon. The regularity of each margin, i.e., the degree of ossification and the straightness of the sides, is developed in this manner only in *Clidastes* (Caldwell, 1996). Comparisons between *Clidastes liodontus* and *Mosasaurus conodon* clearly indicate, that while the carpus is highly ossified in both taxa, only in *C. liodontus* is the ulnare

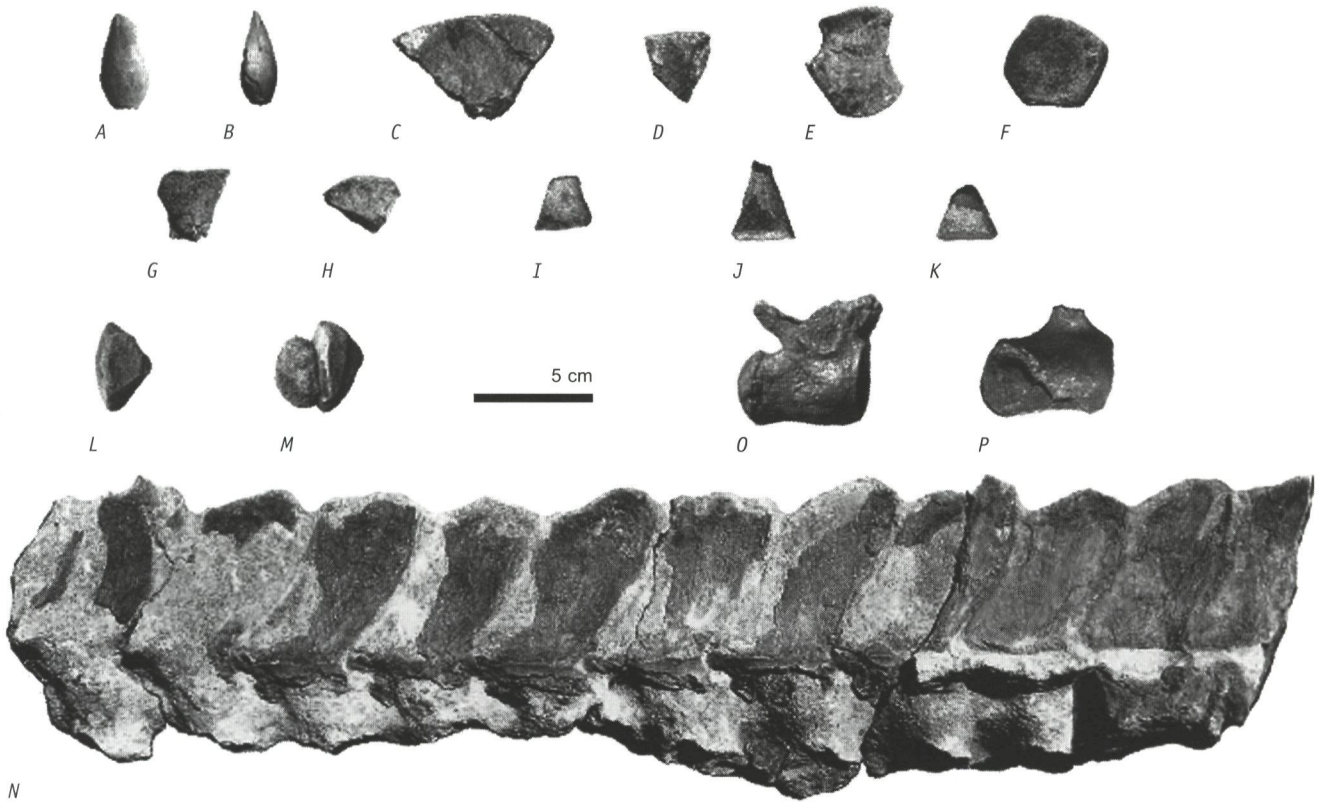

Fig. 3. Mosasaur remains from the upper Campanian of NW Germany, assigned here to cf. Clidastes *sp.; A - M – GPIM 3D-4, Isolated tooth, lacking enamel, labial and lateral aspect; GPIM A.3D-2; C, D – scapula fragments; E – radius; F – ulnar; G – metacarpus III; H – metacarpus IV; I - K – phalanx (half); L, M – vertebra centra fragments; N – articulated twelve dorsal vertebrae (proc. spinosi), lateral; O, P – GPIM A.3D-5, two disarticulated vertebrae.*

polygonal. In contrast, in *Mosasaurus* the element is subrounded. Metacarpal V is 50 mm in length and bears two distinct articular facets (proximal and distal tips). The proximal facet articulates with the ulnare while the more distal facet articulates with the first phalangeal element of the fifth digit. The distal portion of metacarpal V is extremely expanded so that is 1.5 times wider at this end of the element as compared to its proximal tip. The element resembles a bottom-heavy spool. Further support for the 'clidastine' nature of these manal elements is obtained by comparisons between metacarpal V of *Clidastes liodontus*, GPIM A.3D-2, and *Mosasaurus conodon* (Fig. 4a - c). Metacarpal V is an unusually shaped metacarpal in all mosasaurine mosasaurs. But in *Clidastes* it resembles the morphology of the radius (Fig. 4c). This is not the case in *Mosasaurus*, where metacarpal V is irregularly shaped (Fig. 4c) and does not at all resemble the radius. By comparison, metacarpal V in GPIM A.3D-2 (Fig. 4b) shows a radius-like outline as well as an outline which is similar, though admittedly more compressed, to the metacarpal V of *Clidastes liodontus*.

Locality – From near Coesfeld, Coesfeld Formation.

Material – GPIM A.3D-5 (Fig. 3O - P): two disarticulated vertebrae found in a single limestone block (original in H.W. Oosterink Collection, unregistered; casts at GPI Münster).

Description – Both vertebrae are approximately 58 mm in length; one is preserved in lateral view while the other shows the ventral surface. The condyle and cotyle of each centrum are very nearly round. Just anterior to the condyle of the first vertebra (Fig. 3O), the centrum is noticeably constricted in lateral view. This vertebra also preserves the left postzygapophysis, and both the right and left prezygapophyses are still attached to the lamina of the neural arch. The facets for the zygapophyses are all strongly inflected towards the midline; in other words, the articular faces of the zygaphophyses have lost their horizontal orientation. It is not possible at this point, due to limited preparation, to determine whether there are well-developed zygosphenes and zygantra on either of the two vertebrae, or not; the possession of well-developed accessory processes would strongly support our assignment to *Clidastes*. These two vertebrae are mid-trunk to posterior trunk in position (as determined by the size of the parazygapophyses (Fig. 3P)) and as such, if in possession of accessory articulations, clearly indicate *Clidastes* as this is the only mosasaurine mosasaur that bears zygosphenes and zygantra on the more posterior dorsal or trunk vertebrae.

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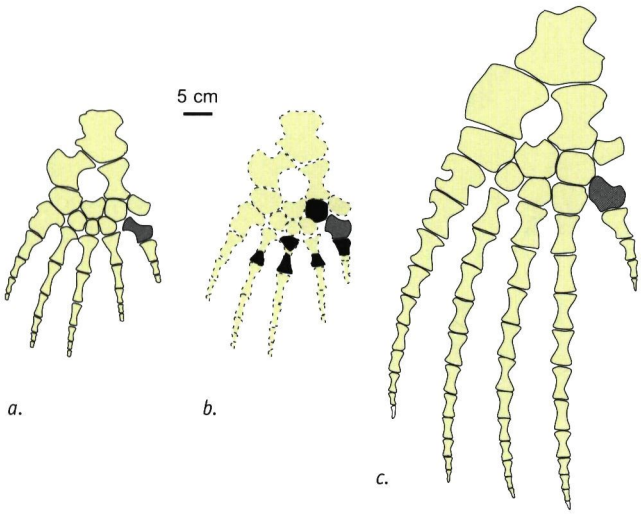

Fig. 4. Comparison of the forelimb elements of mosasaurine mosasaurs. a. Clidastes liodontus *(modified from Caldwell (1996)); the fifth metacarpal is grey for comparison purposes; b. Elements of the German cf.* Clidastes *indicated on forelimb of North American* Clidastes liodontus*; black and grey elements indicate limb fragments for CPIM A.3D-2; the grey element, identified as the fifth metacarpal is a diagnostic element for mosasaurines; c.* Mosasaurus conodon *SDSMT (modified from Caldwell (1996)); the fifth metacarpal is grey for comparison to that of* C. liodontus *and the German 'clidastine'.*

Discussion

We have taken the conservative position of not identifying GPIM A.3-D3 to species, but it could easily be argued in our opinion that this snout tip is assignable to *Clidastes* cf. *liodontus*. In this light, it is also possible to argue that one could dissect the snout characters to a level commensurate with diagnosis of a new species of late Campanian *Clidastes* from the Münster Basin. For example, the specific trace of the premaxillary-maxillary suture, could be used to justify specific differences from both *C. liodontus* and *C. propython*; in association with the unique, but mosasaurine, morphology of the fifth metacarpal, it would become a strong diagnosis. Again, however, we reiterate that we have taken the more conservative position, i.e., assignment to the genus only, in lieu of the recovery of more diagnositic material. This is a philosophical position intended to demonstrate the necessity to avoid cluttering the literature with form-taxa assignments. We encourage this sort of taxonomic conservatism as it is our opinion that some authors (e.g., Lindgren & Siverson, 2004) place too much confidence in form taxa, i.e., species-level identifications based on only tooth characters, that are then used to draw very broad and revisionist conclusions on palaeobiology and palaeoecology. Again, we caution against this form of overextension and overinterpretation of data. Further to our methodological and philosophical approach, we have taken the conservative position on identifying the Münster Basin fauna based on the probability that 'clidastine' phylogeny is more complex than currently reconstructed (see Bell, 1997). In other words, we consider it very likely that 'clidastines' were broadly distributed in Coniacian through Campanian seas around the globe, were far more diverse than is currently suspected, and that the supposed endemism of North American 'clidastines' (Gulf Coast and Interior Seaway), and their extinction at the end of the early Campanian (Lindgren & Siverson, 2004), is an artifact of taphonomy and collecting. For example, the report by Nicholls & Meckert (2002) of an unusual Pacific Coast Santonian-aged mosasaurine, *Kourisodon puntledgensis*, hints at the potential, but unknown diversity of this group of small mosasaurine mosasaurs. Those authors very clearly stated that with the exception of the teeth, the remainder of the skeleton of *Kourisodon* would have been easily assignable to *Clidastes*. This is intriguing for a number of phylogenetic and palaeobiogeographic reasons, and is also taxonomically problematic (which we shall not deal with here). Phylogenetically, it is important to note that *Kourisodon* would likely be placed within Bell's (1997) Hennigian comb representing the genus *Clidastes*; this of course means that it is a 'clidastine' if not a *Clidastes* sp. *Kourisodon* would be autapomorphic with respect to its tooth morphology, but little else. Based on Nicholls & Meckert's (2002) fig. 5, the premaxilla is morphologically more similar to *Clidastes liodontus* than to *C. propython*, and thus to GPIM A.3-D3. In terms of its temporal and spatial distribution, *Kourisodon* is a contemporary of *C. liodontus* and indicates an unsuspected Santonian record of a sister taxon living in a distinct biogeographic environment – the proto-Pacific Coast of North America. Additionally, we find it intriguing that Nicholls & Meckert (2002) assigned *Kourisodon* to Lingham-Soliar's (1995) 'Leidontini', and then compared this taxon to his re-characterisation of *Leiodon* based on the similarity of compressed teeth in both taxa. Historically, authors working on the Münster Basin mosasaurs had assigned the remains described here to *Leiodon*, in part because of an absence of more diagnostic materials, but also because the isolated teeth, when found, are ovate to

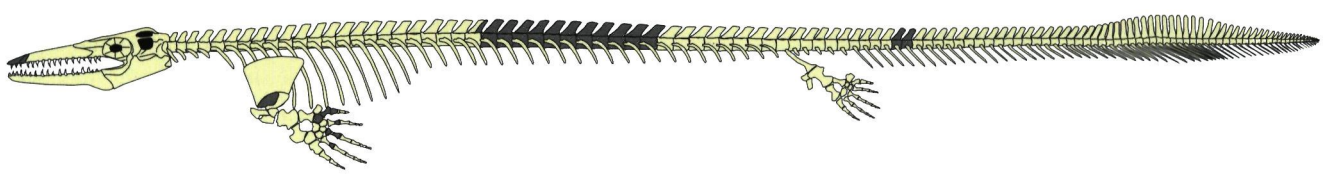

Fig. 5. Reconstruction of Clidastes liodontus *(redrawn from Williston, 1898) with marked areas (in grey) indicating the elements identified as* Clidastes *sp. and cf.* Clidastes *sp. and found in the Münster Basin.*

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compressed, similar to both *Kourisodon* and to the poorly diagnosed *Leiodon* (Sachs, 2000). In contrast to both Lingham-Soliar (1995) and Sachs (2000), we find no compelling data to indicate either the presence or validity of either *Leiodon* or *Mosasaurus* among the mosasaur remains from the Münster Basin. Our identifications support the assignment of all of the Münster Basin mosasaur remains to the mosasaurid genus *Clidastes* sp., or in more tentative cases, to cf. *Clidastes* sp. As noted by Russell (1967) and Bell (1997), *Clidastes* is characterised by a short, protruding rostrum that produces an acutely angled, V-shaped dorsal profile for the premaxilla; we find this character to be overwhelmingly well defined in GPIM A.3D-3 (Fig. 2C). Because of this synapomorphy for 'clidastine' mosasaurs, the snout tip from Beckum was referred to *Clidastes* by Diedrich & Mulder (2004), an identification we continue to support. This *Clidastes* identification contrasts sharply with that of Sachs (2000), who referred the specimen to *Leiodon*, and to Lingham-Soliar (1995), who assigned it to *Mosasaurus*. The post-cranial remains from Schöppingen were described as '*Mosasaurus camperi*' by Von der Marck (1858, 1892). Again, our study of those original material, and the additional post-cranial remains we figure and describe here, lends further support to our identification and assignment to cf. *Clidastes* sp. The post-cranial elements can be readily be compared to *C. liodontus* and show marked differences by comparison to *Mosasaurus* sp. (Figs 3C - P; 4A - C; 5). As such, it seems reasonable to postulate that the German 'clidastines', like those from the North American Western Interior Seaway and now the Pacific Coast, could well represent unknown temporal, spatial and phylogenetic diversity, and thus an additional new species. If new material provides additional corroborating evidence, then the phylogenetic placement of the Münster Basin 'clidastines' might well form a clade with *C. liodontus*, at least based on morphology of the premaxilla.

Conclusions

Mosasaurs are very poorly known from Upper Cretaceous marine deposits in Germany, and are mostly described from isolated teeth or bone fragments found in Turonian, Santonian, Campanian and Maastrichtian strata (Geinitz, 1849, 1872-75; Von Meyer, 1856; Von der Marck, 1858, 1892; Pompeckj, 1910; Darga, 1998). The mosasaur material re-characterised here was originally identified by Von der Marck (1858; 1892) as '*Mosasaurus camperi*'. Lingham-Soliar (1995) re-examined the material and identified it as '*Mosasaurus hoffmanni*', while Sachs (2000) suggested entirely new identifications for the material as '?*Plioplatecarpus*' and '?*Leiodon* sp.' As argued above, we have revised these original descriptions, added new information, and reassigned all of the Münster Basin mosasaurs to *Clidastes* sp. or cf. *Clidastes* sp. *Clidastes* has been recorded from the Upper Cretaceous (Turonian-Campanian) in England, although only very few of these old non-stratified records, such as a figured dentary fragment, are actually diagnostic (Milner, 1987). In Germany, the genus is now represented in the upper Campanian at four sites of the Münster Bay; these identifications and records extend the palaeobiogeographical range of *Clidastes* in the North Sea Basin of Europe. In association with Lindgren & Siverson's (2004) tooth identifications, the specimens described here confirm the trans-Atlantic distribution of the genus during the Late Cretaceous.

Acknowledgements

We thank Dr M. Bertling (Geologisch-Paläontologisches Museum of the Westfälischen Wilhelms-Universität Münster) for access to specimens in his care. We acknowledge the help of M. Everhart for permission to use his unpublished photographs of North American *Clidastes*. Finally we thank H.W. Oosterink for allowing the study, casting and publication of the two vertebrae found at Coesfeld. This material was thankfully prepared in the GPI Münster by M. Brinkmann, the snout tip was prepared by PaleoLogic.

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