Zum Häutungsverhalten einiger Trilobiten aus den Rupbach-Schiefern (spätes Oberemsium bis frühes Eifelium; Rhenoherzynikum)

[Engl.: Molting-habits of some Rupbach-valley Trilobites (Upper Emsian/Lower Eifelian; Rhenohercynian Zone)]

MIRCO ALBERTI

Some molting-habits and related taphonomic implications of the trilobites *Aulacopleura (Paraaulacopleura)* n. sp., *Cyphaspides* n. sp., *Chotecops sollei* Struve, 1984 and *Kettneraspis* sp. from the "Gutenacker" quarry such as *Diademaproetus* n. sp., *Rhenocynproetus* n. sp., *Cyphaspis* spp., *Harpes* sp., *Acastoides* n. sp., *Destombesina* n. sp., *Barrandeops* n. sp., *Kettneraspis seiberti* Basse, 2004, *Leonaspis kleini* Basse, 2004 and *Koneprusia* spp. from the "Heckelmanns Mühle" fossil site are described. Both sites are situated in the Rupbach-valley in the south-eastern part of the Rhenish Slate Mountains, known for its numerous transitional Lower/Middle Devonian faunas. The variety of supposed molt procedures was high both extra- and intraspecifically. Infaunal molting occurred in some cases and may explain the occurrence of moult ensembles inside of some debris flows (lahars). Infaunal molting can be recognized by typical molting configurations as according to previous work and/or the "accordion-effect", introduced herein. The function of specific anterior pleural spines, developed in some Odontopleuridae is interpreted as an auxiliary means for exuviation. An "anchor molt strategy" is considered possible and described for species with anchor-shaped cephala, especially *Diademaproetus*. In the "Heckelmanns Mühle"-fauna molting rather followed individual rhythms whereas in "Gutenacker" clustered molt remains are indicative of synchronized molting events. The latter site was apparently frequented especially for exuviation by some species.

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Introduction

The Rupbach-valley is a tributary of the Lahn-river in the south-eastern Rhenish Slate Mountains ("Rheinisches Schiefergebirge"), Germany. The rocks that outcrop here are of Lower to Middle Devonian age and known for their rich fossil fauna. Named by REQUADT & WEDDIGE (1978), the Rupbach Shales (Rupbach-Schiefer) record the transition of the shallow-marine "rhenish" facies to the "Hercynian" offshore facies at the southern margin of the paleocontinent Laurussia. Late Rupbach Shales can be seen as a local equivalent of the common Wissenbach Slates (Wissenbacher Schiefer) and like these were formerly subject to mining for roofing material. This brought to light a peculiar fossil fauna which caused pioneer scientists like KAYSER (1884) or MAURER (1876) to establish the name "Orthocerasschiefer" (=Orthoceras shales) for what is now called Rupbach Shales. Recent work has focused on the rich trilobite faunas found in some Rupbach shales. The two most famous locations „Gutenacker“ and „Heckelmanns Mühle“ alone have yielded about three dozens of different trilobite species representing a broad range of typical known forms of that time. These trilobite faunas are specified in ALBERTI (2013), BASSE (2002, 2003, 2006), BASSE & HEIDELBERGER (2002), BASSE & MÜLLER (1998, 2004, 2011), FLICK & STRUVE (1982) and FLICK et al. (2006). The trilobites are regularly found articulated. In addition to the complete specimens numerous disarticulated remains were discovered, documenting various stages of disintegration; several of them obviously represent exuviae. This material is used to examine the molting of some Rupbach-valley trilobites with the aim to document particular molting-habits to gather some more information about the former environments.

Moulting

Trilobites, like all arthropods, molted to accommodate their growth. RICHTER (1937) already realized a potential of the shed integuments to be fossilized in a specific way. HENNINGSMOEN (1975) furthermore suggested that exuviae had a better chance of being preserved than trilobite-bodies because they would have been less attractive to scavengers. He also gave distinctive criteria to recognize exuviae and like MCNAMARA & RUDKIN (1984) noticed the necessary fact that there had to be different modes of exuviation because of the great morphological variety developed in trilobites. Studies e.g. by BUDIL & BRUTHANSOVÁ (2005), BUSCH & SWARTZ (1985) or SPEYER (1985) even brought to light different types of molting within single species. Different molt procedures resulted in various configurations of the shed parts which SPEYER (1985) termed molt ensembles. Outside influences very likely played a role for the choice of the molt strategy. RUSTÁN et al. (2011) pointed out that these influences could lead to infaunal molting in some circumstances.

Geological Setting

The examined material comes from the „Gutenacker“-quarry, named after the nearby village of Gutenacker as well as from „Heckelmanns Mühle“-quarry, which is situated near a mill called Heckelmanns Mühle in the valley which is located south of the village of Steinsberg. Both quarries are situated in the lower part of the Rupbach-valley, a tributary of the Lahn-river in the west of Limburg an der Lahn. Geographically the Rupbach-region belongs to the Taunus mountain-range, in the south-eastern part of the Rhenish Slate Mountains. Geologically the area belongs to the Lahn-Syncline which is the south-eastern part of the SW-NE-striking Hessian Synclinorium which also comprises the Hörre-zone and the Dill-Syncline in the north east. The Lahn-Syncline can be delineated stratigraphically from the rest of the Rhenish Slate Mountains by the insertion of Middle Devonian deposits and on the whole comprises a depositional history extending into the Mississippian. The distinction is based on a specific facies change around the Lower/Middle Devonian boundary. As part of the Rhenohercynian Zone the region was situated on the shelf on the southern margin of the continent Laurussia. Until the upper Lower Devonian the conditions here were shallow marine with a typical “rhenish” facies, characterized by a rather coarse siliciclastic sedimentation sourced from the nearby continent. After the late Lower Devonian (uppermost Emsian) the coastline shifted to the north. This resulted in a change from a shallow water facies to the deep marine “hercynian” facies, which is characterized by an increasingly calcareous, finely clastic sedimentation. This transgression was caused by epirogenetic crustal movements which also resulted in different volcanic phases. The first keratophyric and later basic volcanic rocks can be found widespread as tuffites, submarine effusives or coarse-grained intrusives (BENDER et al., 1993). Several of these volcanic structures became the foundations which enabled the formation of reefs in the Middle to late Upper Devonian. The Lahn-Syncline is cropping out in the “rhenish” Lower Devonian basement at its south-western end comprising several partial synclines. The lower Rupbach-valley transects from these the northernmost Balduinstein-Syncline and the southernlying Wasenbach-Syncline whose fillings with sediments and volcanic rocks stratigraphically reach into the Upper Devonian (FLICK & STRUVE 1982).

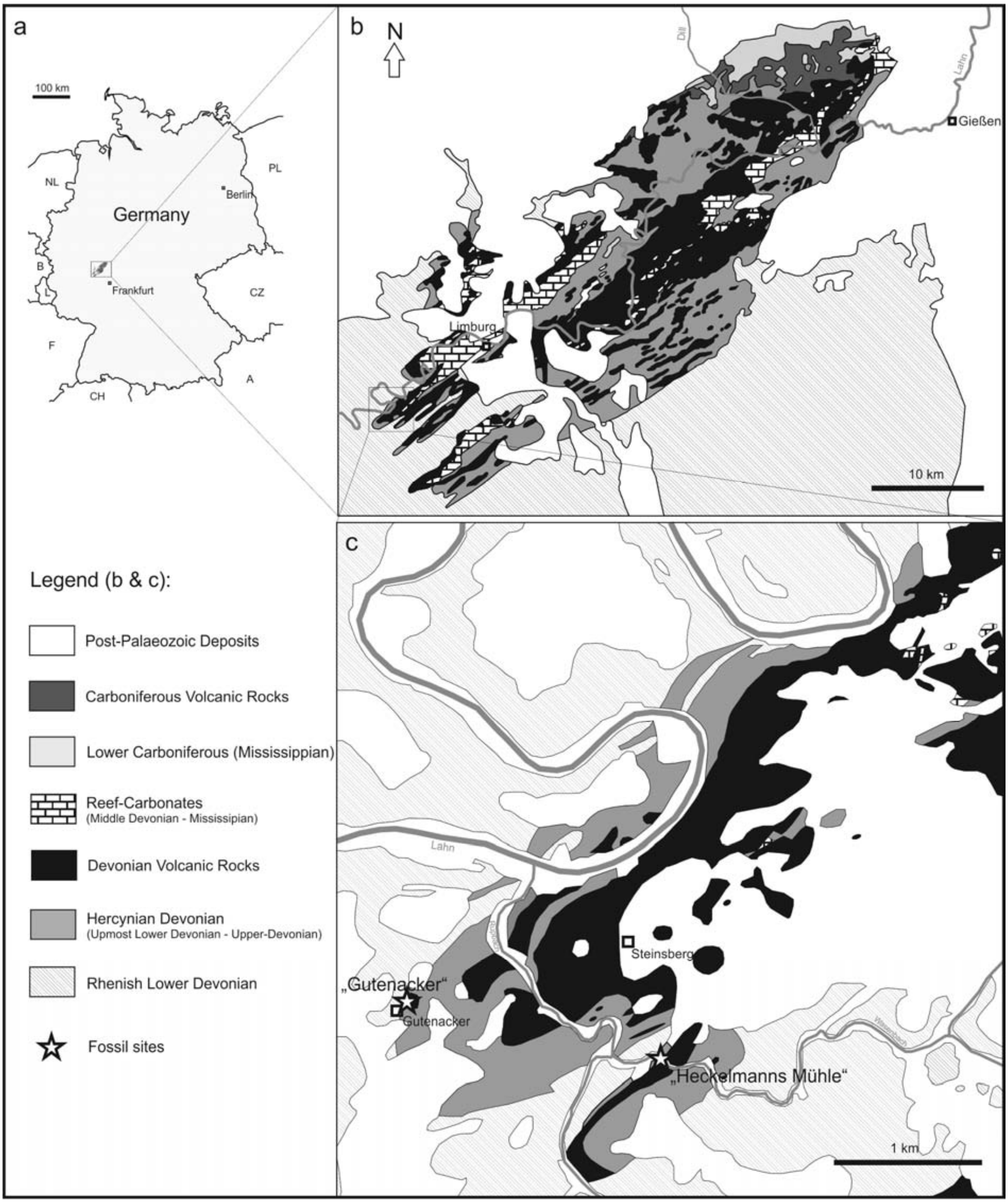

Figure 1: Geological Setting. a) – Geographical localization of the Lahn-syncline in Germany. b) - Geology of the Lahn-Syncline (simplified after Flick, 2010); the north-eastern lying Hörre-zone is not depicted. c) – Geology of the southwestern Lahn-Syncline / Rupbach-region (simplified after Requadt, 1990) showing the situation of the mentioned fossil-sites.

Defining for the geology of the Rupbach-valley are the Rupbach Shales. The Rupbach-valley is the type-locality of the Rupbach-Shales (Requadt, 2008). The age of these more or less foliated, calcareous clay stones was defined by Requadt & Weddige (1978) as ranging from the late Upper Emsian to the Lower Givetian based on conodonts. An overview of the macro-fauna of the Rupbach-shales is given to some extend with fossil-list 10 in Requadt (1990). Petrologically the change from "rhenish" to "hercynian" facies was achieved within the Rupbach shales petrologically seen until the end of the Lower Devonian, whereas the gradual change in biofacies was accomplished in the lower Middle Devonian.

Characteristic of the early Rupbach Shales is a temporal coexistence of both facies in small spaces. Argillaceous shales with a distinctly pelagic fauna (synonymous with the term „Orthocerasschiefer“) are found in close spatial proximity to predominantly neritic faunas. This indicates a distinctive relief of the hercynian depositional basin divided by deep-sea basins and deep-sea ridges. SCHRAUT (1999) assumed that the surface of the ridges was again divided by smaller-scaled ridges and troughs (Fig. 2). As a result of tectonical processes during the Variscan orogeny the south-western Lahn-Syncline was segregated into several special folds and tectonic wedges having a principal north-western tendency. Both locations are situated in the so-called Lahntaler Schuppe (Requadt, 2008) [engl. = Lahn-valley wedge] at the north-western margin of the Lahn-Syncline.

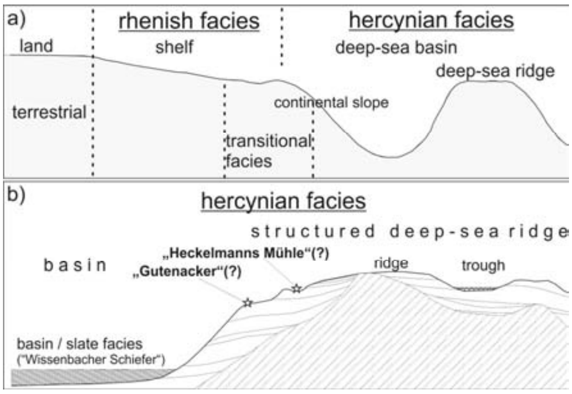

Figure 2: a) – Sketch showing the differentiated facies (altered, after SCHRAUT, 1999). b) – Scheme of the Hercynian environment (based on SCHRAUT, 1999) with probable situations of the described locations.

“Gutenacker”-locality

The „Gutenacker“-fossil site corresponds to fossil site SCH 11 in REQUADT (1990) and is specified in FLICK & STRUVE (1984). The site is located in an old quarry in the east of the village Gutenacker. The quarry was formerly run for the exploitation of a keratophyre-sill which resulted from alkalitrachytic melts that had intruded into Rupbach Shales during the volcanic Givet-Adorf-phase (FLICK & NESBOR, 1988). These bluish-grey, beige when weathered, mudstones were subjected to a contact metamorphic modification during the intrusion of the melts. Where there was no contact metamotphic effect (e.g. vitrifaction or hardening) the Rupbach Shales were mildly foliated parallel to their bedding. The shales underlying the sill contain a rich fossil record dominated by pelagic-hemipelagic elements such as nautiloids and goniatites. Along with these a trilobite fauna existed which appears to be rather neritic. FLICK & STRUVE (1984) deduced a possible waterdepth at or below 50 meters for this depositional environment. The distinct pelagic-hemipelagic faunal impact here most possibly indicates a position at the outer rim of a deep-sea ridge (Fig. 2 b). This is also supported by the occurrence of *Struveaspis* sp., which is a typical inhabitant of the Wissenbach slates (Wissenbacher Schiefer). The age of the deposits was defined by FLICK & STRUVE (1984) as earliest Eifelian. An already Eifelian age was corroborated through the occurrence of the goniatite *Pinacites jugleri* here (SCHUBERT, 1996).

“Heckelmanns Mühle”-locality

Another name sometimes used for the location „Heckelmanns Mühle“ is „Steinsberg“ after the nearby village of Steinsberg. It is a collective name for several fossil bearing outcrops on both sides of a steeply dipping alkalibasaltic sill (diabase) which concordantly intruded Rupbach shales during the volcanic Givet-Adorf-phase (FLICK & NESBOR, 1988). The fossil bearing country rocks were exposed when the diabase was exploited in a quarry. The author hitherto distinguishes eleven fossil sites assigned to the Rupbach Shales (Fig. 3), which are not always similar to the sites described by FLICK et al. (2006). The sites 2, 3 and 5 (here) are consistent with fossil sites “7”, “8” and “12” in FLICK et al. (2006). The fossil sites 4 and 6-10 were first exploited after the year 2006 and were not known to FLICK et al. (2006). Different from FLICK et al. (2006) and REQUADT (1990) the sites 6-10 proved the existence of Rupbach-Shales underlying the diabase-sill in the south-western part of the quarry. REQUADT (1990) barely mentioned any macro-fauna in the Rupbach-Shales of "Heckelmanns Mühle" (except those of one site, called SCH 9 in fossil-list 10). Fossil sites 9 and 10 are distinctive mud flow-horizons. Site 8 is a layer comprising a lot of alleged crinoid roots. Site 7 represents a broad area between sites 6 and 8 comprising several layers which were not subdivided for this work due to conditions of exposure. Some of the layers apparently derived from mud flows. Proper statements on the origin of the highly foliated Rupbach-Shales cropping out in fossil site 6 cannot be made so far. The deposits exposed by fossil sites 1-11 extend (ascertained) from the Lower Devonian late Upper Emsian to the Middle Devonian Middle Eifelian, with the Lower/Middle Devonian boundary situated above the south-eastern dipping sill. According to REQUADT (1990) the Rupbach Shales range until the Givetian in this quarry. The foliation of the medium to dark grey, beige or white when weathered silty mudstones varies from undiscernible near the sill to roof slate-like in some younger sections above the diabase. The foliation is more or less oblique to the bedding. Especially the Lower Devonian sequences contain several intercalary beds indicated as mudflow deposits. Their small lateral distributions imply that the depositional environment must have been structured by a certain relief. Around the Lower/Middle Devonian boundary there are found some lumachelle-like deposits which following FLICK et al. (2006) might be explained in the context of distal tempestites, whose products rained out in the depositional environment which itself assumedly was situated below storm wave base. FLICK et al. (2006) characterized several of the above mentioned mudflows as lahars and also mentioned the occurrence of rhyolitic ashes in the Middle Devonian sequences derived from subaerial volcanism.

Articulated trilobite remains which were primarily important for the current studies were mainly found within the Lower Devonian deposits of the "Heckelmanns Mühle"-locality. These deposits are furthermore characterized by a particularly high diversity of species and forms. Some layers alone yielded 14 of more than two dozens of taxa known from „Heckelmanns Mühle“ so far. Some mudflow deposits appeared to be particularly rich in individuals. The overall character of the fauna appears to be rather neritic. Compared with SCHRAUT (1999) the environment probably was well-lit and situated in a water depth between 30 to 50 meters; however it was shallower than the "Gutenacker"-environment. Pelagic-hemipelagic faunal elements occurred occasionally. Appropriate environments were located on or at the deep-sea ridges. With regard to the presence of mudflows the environment most probably was situated in a trough, which presumably was located at the rim of a ridge as shown in Figure 2 b. The occurrence of mud flows might also explain the high specific diversity of trilobites which does not seem to decline in the succeeding autochtonous deposits. By taking the example of the Lower Emsian *Limoptera*-porphyroid KIRNBAUER & WENNDORF (1995) proved on this that incidents like mud flows could "vaccinate" ecotopes with extraneous faunal elements having a permanent impact under certain circumstances.

„The mud flow-problem“

The abundance of complete trilobites in „Heckelmanns Mühle“ is explained by a rapid deposition. FLICK et al. (2004) therefore attributed mud flows (lahars) which supposedly derived from an area in the South. Corresponding indications are actually found in some deposits. These decimeter-thick mud flow-beds can clearly be distinguished from turbidites, normally deposited by rather sparse suspension currents, in absence of an internal gradation. More indications are found in other special sedimentary features such as a chaotic orientation of the embedded fossils (Fig. 4). Such deposits obviously originate from rather dense mass flows. Surprising in this context is the presence of trilobite remains in respective layers, which represent more or less complete molt ensembles following SPEYER (1985). This occasionally gave rise to doubts about the mud flow-nature of the sediments as it ought to be assumed, that molt ensembles should be rummaged herein. Even if it is assumed that sedimentary blocks might have been transported within the mud flows, this must have resulted in more dismembered molt ensembles. Furthermore, fossils typically show a certain orientation within such sedimentary blocks which is not the case here. As a comparison all crinoids whose alleged roots are found in a distinct layer immediately underlying (cut by) one of the mud flows, are mostly disarticulated and drifted apart; but the present exuviae obviously seem barely disturbed as if they were shed in situ. Of particular significance in this context might be the observations of RUSTÁN et al. (2011) that trilobites occasionally were able to molt infaunal. Some cases are shown below which suggest that infaunal molting did actually occur within the current fauna.

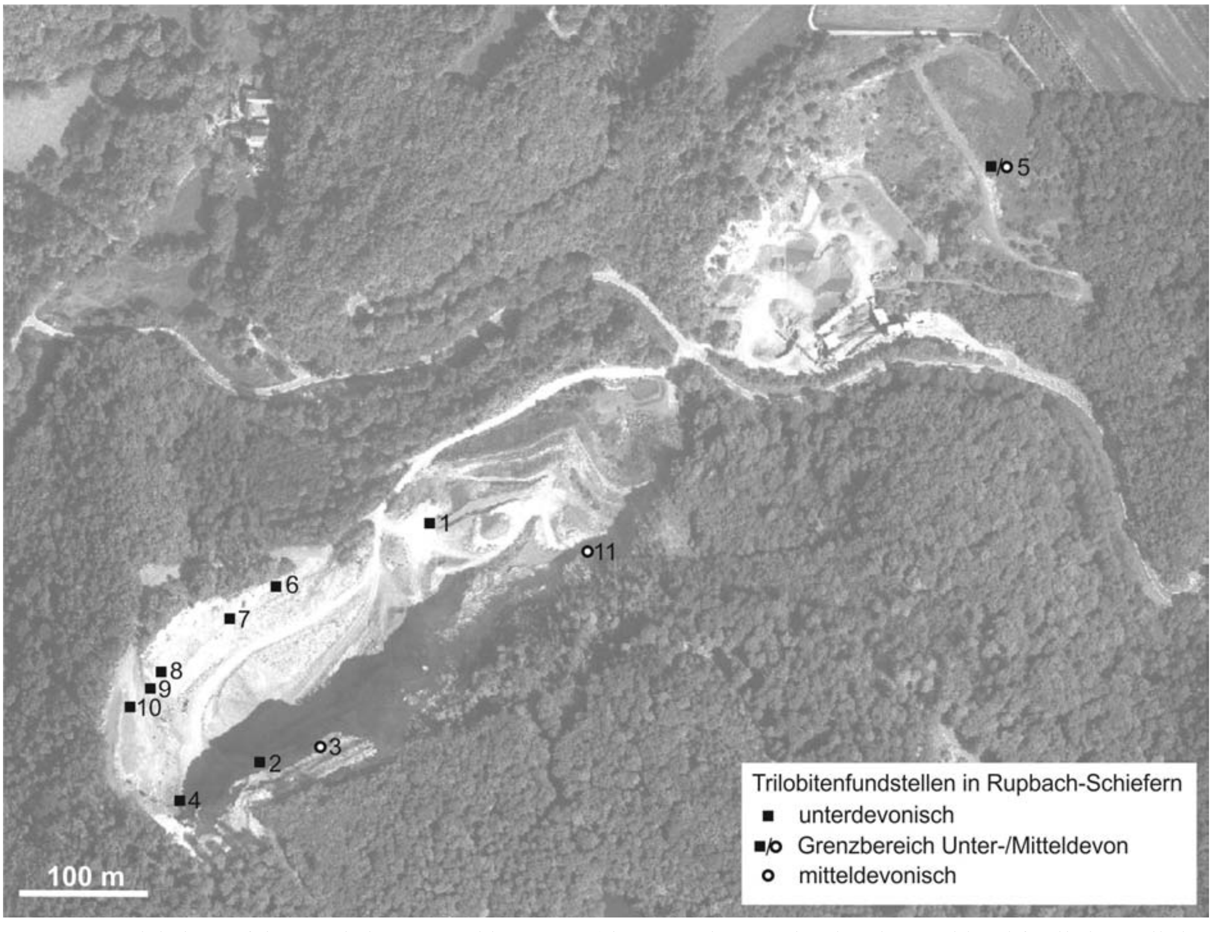

Figure 3: Aerial photo of the "Heckelmanns-Mühle"-quarry (shot around 2010) showing the considered fossil-sites. All sites are assigned to the Rupbach-Shales and prove the existence of Rupbach-Shales underlying the diabase-sill in the south-western part of the quarry different from FLICK et al. (2006) and REQUADT (1990). Due to progressive mining the sites 1-4 are not existent anymore. Site 5 is dumped with soil.

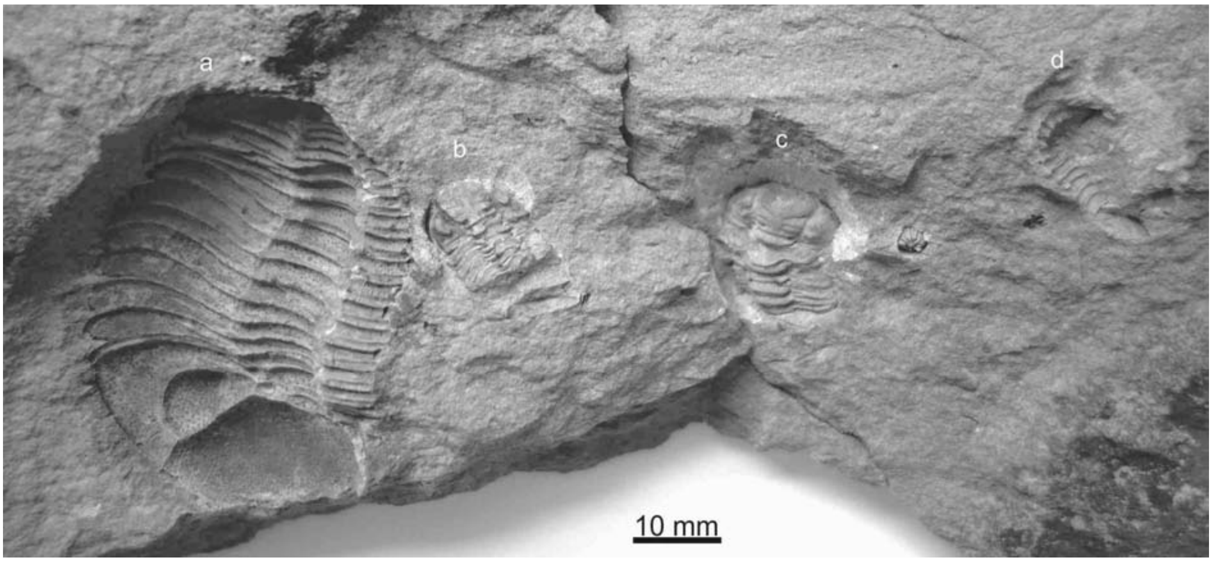

Figure 4: Sample out of a mud flow-deposit from „Heckelmanns Mühle“-locality containing one inverted *Barrandeops* sp. (a) and three *Acastoides* sp. (b)-(d). The disarticulated specimen (c) might be an exuvia. Specimen (d) is lying on its side.

Material

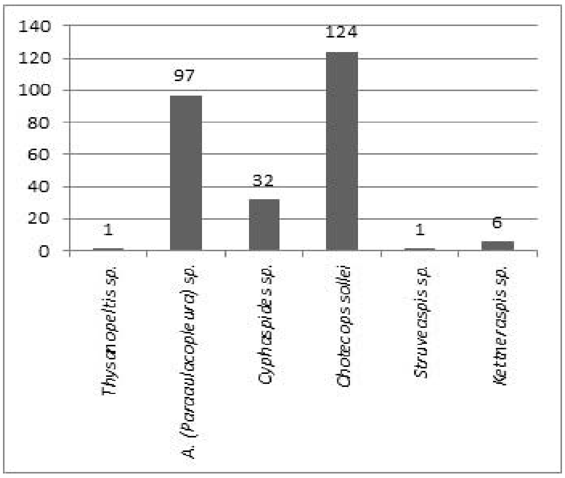

Figure 5: Frequency histogram concerning the considered specimens from the „Gutenacker“-fossil site.

For current research 261 trilobite-fossils from „Gutenacker“-locality were examined. From the Lower Devonian parts of the “Heckelmanns Mühle”-locality alone more than 4100 trilobite-fossils were considered not including countless specimens from the lumachelle-like deposits at the Lower-/Middle Devonian boundary which were cropping out in the northern part of the quarry and out of the slaty Middle Devonian deposits. This comprises material from isolated armour parts through to complete trilobite exoskeletons such as a number of exuviae which were normally recognized as molt ensembles. The fossils were collected during the last twenty-five years. Due to the local conditions a zoned sampling could be done at best rudimentarily. A specification of the original orientation (upright or upside down) in most cases is not possible anymore. Unless noted otherwise (SMF = Forschungsinstitut Senckenberg; PWL = Naturhistorisches Museum Mainz / Landessammlung für Naturkunde Rheinland-Pfalz.) all specimens are located in the authors collection.

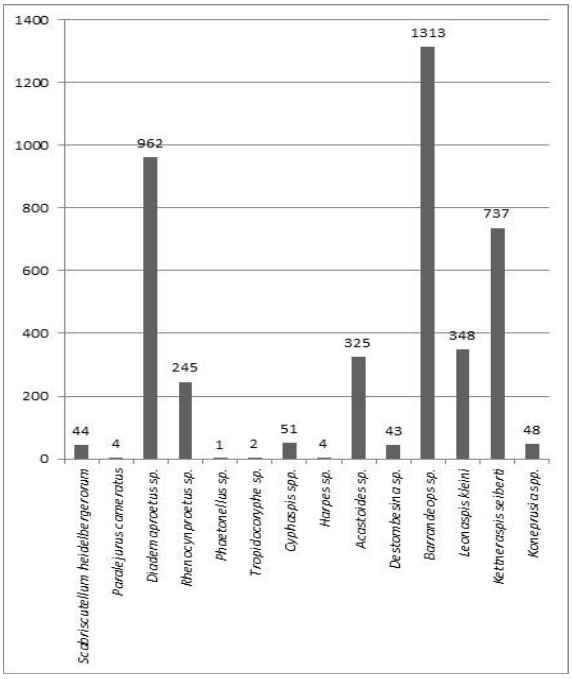

Figure 6: Frequency histogram concerning the considered trilobites deriving from the Lower Devonian sections of the „Heckelmanns Mühle“-fossil site.

Extensive work on both trilobite faunas is currently done by BASSE & MÜLLER [in prep.]. Unfortunately the results from this had not been published until the completion of this paper. Knowing about the upcoming publication of BASSE & MÜLLER [in prep.] the trilobites, still labelled here by the help of open nomenclature, are expected to be identified as follows: *Aulacopleura (Paraaulacopleura)* n. sp. G = *Aulacopleura (Paraaulacopleura) lemkei, Cyphaspides* n. sp. G = *Cyphaspides albertii*, *Diademaproetus* n. sp. L = *Diademaproetus habenichti*, *Rhenocynproetus* n. sp. L = *Rhenocynproetus vanvierseni*, *Acastoides* n. sp. L = *Acastoides poschmanni*, Destombesina n. sp. L = *Destombesina schumacherorum*, *Barrandeops* n. sp. L = *Barrandeops (Lahnops) steinmeyeri*, *Koneprusia* spp. = *Koneprusia martini*. Currently these names are just nomina nuda.

„Gutenacker“-trilobites

The location „Gutenacker“ so far yielded fossils of the trilobites *Thysanopeltis sp.*, *Aulacopleura (Paraaulacopleura)* n. sp. G, *Cyphaspides* n. sp. G, *Chotecops sollei* Struve, 1984, *Struveaspis* sp. and *Kettneraspis* sp. More or less complete or articulated specimens were determined as moult remains nearly without exception. As far as the material allowed specific observations the results are described below.

Aulacopleura (Paraaulacopleura) n. sp. G

In *Aulacopleura (Paraaulacopleura)* n. sp. G two basic molt patterns can be observed which may be combined. The facial sutures were opened regularly. At least one or often both librigenae were separated. This resulted in typical „axial shield“ configurations (HENNINGSMOEN, 1975), comprising of thoracopygons and attached cranidia. In addition joints between thoracic segments were sometimes opened for exuviation. Configurations with the thorax separated in two or more parts are found frequently. No specific segments were preferred in this. Sometimes the pygidium was shed separately. Such decompositions were conceivably caused by back-bending contractions of the thorax with more or less struggling movements (to be compared with the molt scheme of *Rhenocynproetus*, shown in Figure 17). Depending on whether the integument could be shed easily or not, these shedding-movements appear to have been less intense (Fig. 7 f-i). Quite often clustered assemblages were found comprising several molt remains of specimens of nearly the same size. An accumulation by floating can be excluded in some cases when perfectly intact molt ensembles are assembled (Fig. 7 g). This suggests that molting was a synchronized event for at least specific groups or else all individuals of *Aulacopleura (Paraaulacopleura)* n. sp. G in the environment.

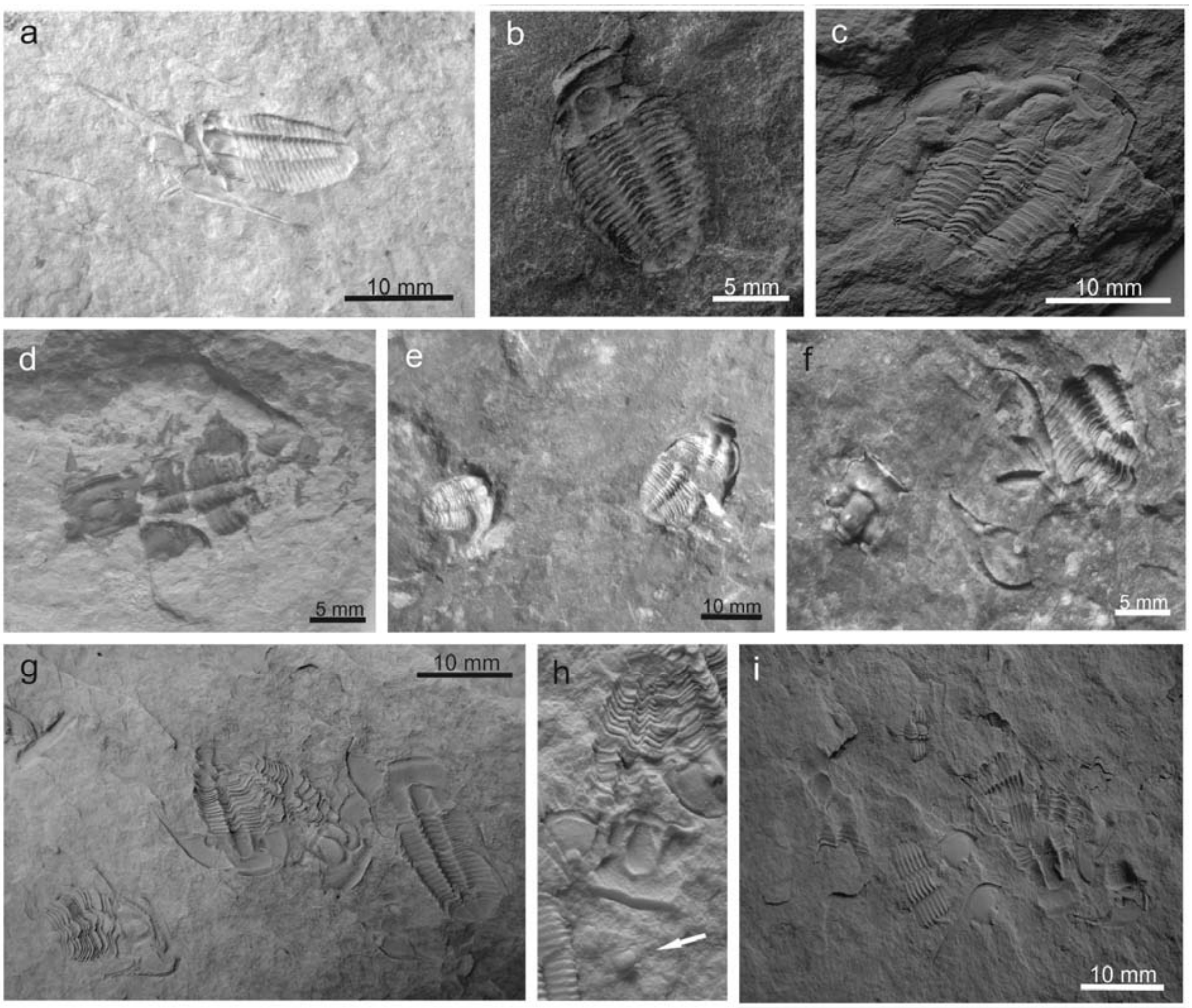

Figure 7: Molt remains of *Aulacopleura (Paraaulacopleura)* sp. from „Gutenacker". a) – Undisturbed „axial shield"-configuration with related librigenae. b) - Isolated „axial shield". c),d),e) – Molt ensembles with dissected thorax. f) – The scattered situation of this specimens molt elements might indicate rather vigorous shedding-movements. g) - Clustered assemblage of four complete molt ensembles. h) – Dissected „axial shield" within the group shown in g). In front of it the specimen had shed its hypostome (arrow). Moreover this exuvia was discarded upside down, which might have been the result of certain shedding-movements. i) – Clustered molt elements of three specimens.

***Cyphaspides* n. sp. G**

Molt ensembles of *Cyphaspides* n. sp. G are generally configured rather constantly. The joints between thoracic segments were obviously functional for exuviation. As a result the thorax of exuviae is frequently dissected into several parts. The facial sutures remained fused as these were non-functional for exuviation. Even isolated and possibly far drifted cephala are always found complete. Different from the salterian mode the cephalon was not tilted forward. The cephala were rather bent backwards (Fig. 10 c), which formed ecdysial openings at the front through which the trilobites could leave their integuments (Fig. 8). Apart from a slight twist the molt elements of dissected exuviae are always found retaining their original orientation.

The molting configurations of *Cyphaspides* n. sp. G suggest a molt procedure similar to that of *A. (Paraaulacopleura)* n. sp. G, which came along with back-bending, struggling contractions of the thorax (Fig. 8). However the shedding-movements seem to have been less intense compared to some *A. (Paraaulacopleura)* as the molt elements of *Cyphaspides* are found barely dispersed. Several clustered assemblages of molt ensembles give rise to the assumption that moltings were synchronized events for *Cyphaspides*, too.

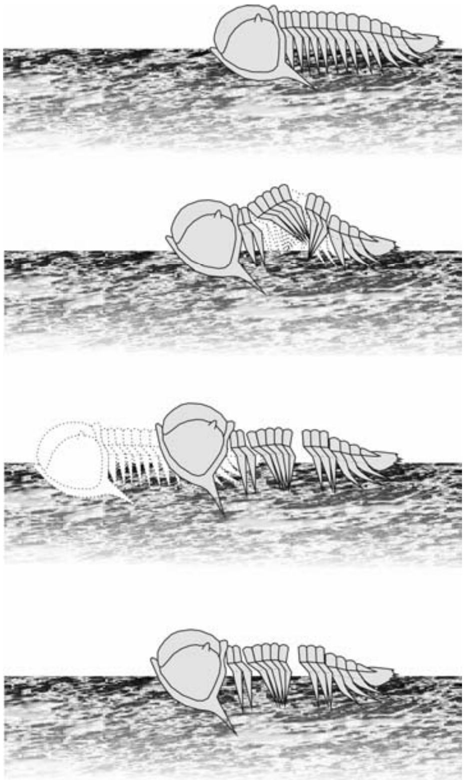

Figure 8: Sketch showing the probable molt procedure of *Cyphaspides* n. sp. G. Presumably, the integument was shed by back-bending and/or struggling thoracic movements. It is assumed that the genal spines were stuck into the ground to subsequently shed the cephalon in a backward movement. The backward-bending of the cephalon formed an ecdysial gape at the front through which the trilobite could leave its integument.

There is a noticeable dominance of specifically sized specimens (Fig. 9).

The habitat seemed to have been preferred by individuals of that certain size for some reason. As such specimens derive from different layers this must have been the case regularly. From the monospecific size distribution can also be deduced that the „Gutenacker“-environment obviously was not the permanent habitat of *C. albertii*, but was especially frequented for molting.

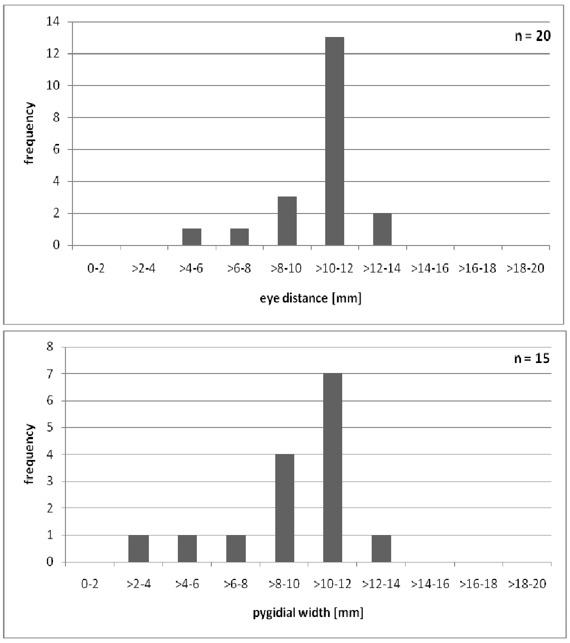

Figure 9: Frequency histogram for eye-distances (above) and pygidial-widths (below) measured in *Cyphaspides* sp. from „Gutenacker“ (2 mm class intervals). The markedly dominating class comprises trilobites of about 25 mm in length.

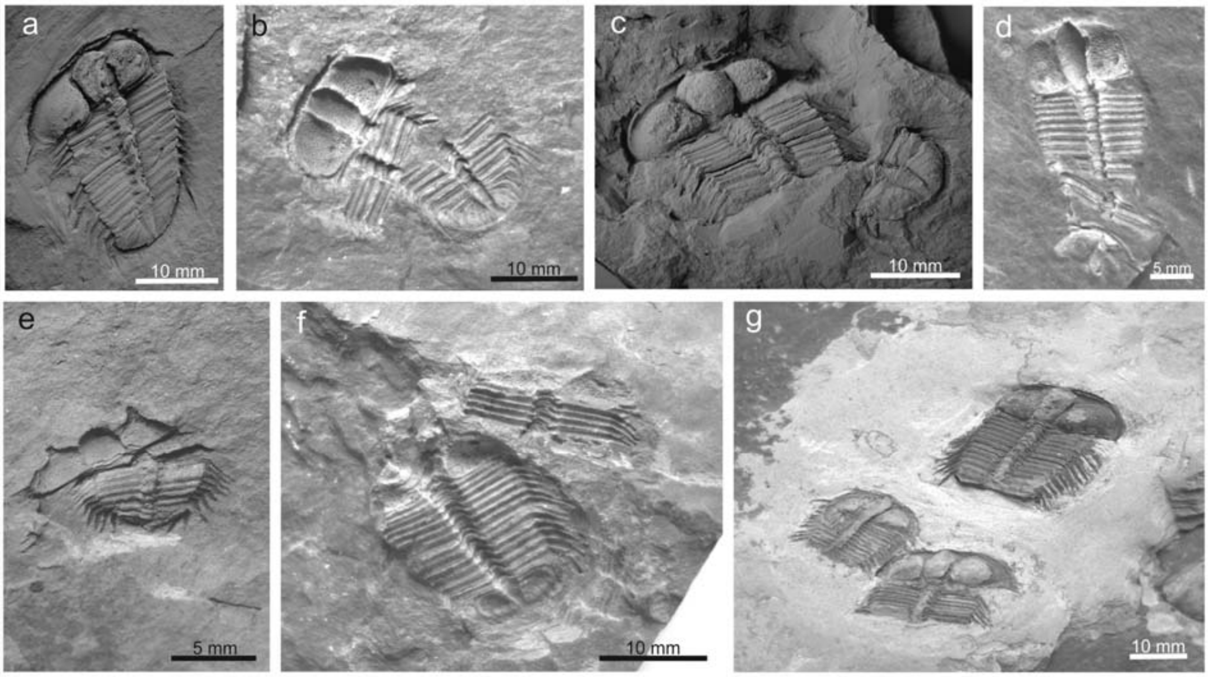

Figure 10: Exuviae of *Cyphaspides* sp. from „Gutenacker". a)-d) – Specimens with typically dissected thorax [b) is situated in PWL]. The mode of dissection suggests a molt procedure with back-bending and/or struggling thoracic movements. Specimen c) shows a typical backward curvature of the cephalon which formed the ecdysial gape at the front. It is assumed that therefore the genal spines were stuck into the ground. e) – Very small specimen with its cephalon untypically flipped forward. f), g) – Small groups of exuviae of up to three specimens. Note that the cephalic shields in g) are curved upward.

Chotecops sollei Struve, 1984

The relatively abundant remains of *Chotecops sollei* in the "Gutenacker"-quarry sometimes occurred in mass assemblages. FLICK & STRUVE (1984) noticed that these cases do not result from catastrophic events but are molt remains which were shed in their actual molting-place or were assembled there by drifting. Among these two chief configurations can be distinguished. Firstly there are molt ensembles comprising outstretched thoracopygons and separated cephala which in the following text, regardless of the molt elements´ orientation to one another, are labelled as „salteroid"-types. Such configurations resulted from molt procedures similar to the salterian mode in that way that the cephala most likely were separated from the outstreched thoracopygons in a "Body-upright Procedure" (SPEYER, 1985). Actual Salter´s configurations have not been found in *C. sollei* so far.

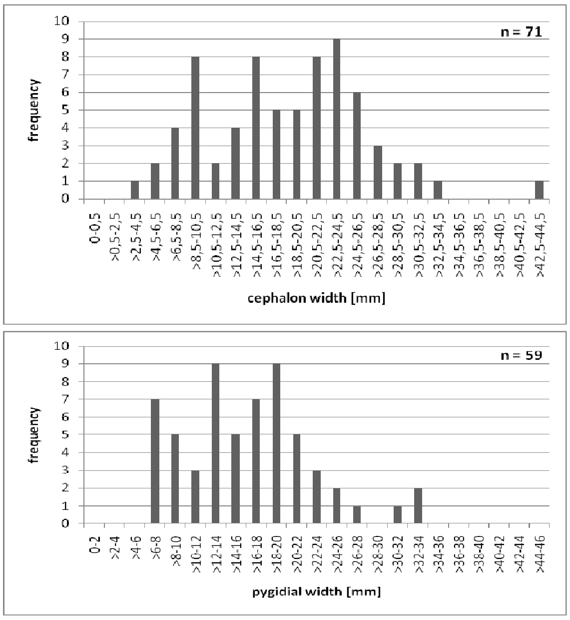

Figure 11: above) – Frequency histogram for cephalon width measurements of *Chotecops sollei* from „Gutenacker" (2 mm class intervals). The histogram exhibits several peaks most probably representing different instars. Referring to the statistical studies of BUSCH & SWARTZ (1985) at least seven instar stages can be determined. The occurrence of six instars is proved for the "Gutenacker"-site. below) – The above distribution is principally approved by the according frequency histogram for pygidial width measurements (2 mm class intervals).

Secondly molt elements have been found which possibly resulted from „Body Inversion Molt Procedures“ (SPEYER, 1985). Corresponding configurations with typically recurved thoracopygons predominantly comprise clustered assemblages and major clusters (Fig. 13 g,h). “Salteroid”-type configurations are rather found isolated as single remains. The reason for this phenomenon is speculative. Probably the „Body Inversion Molt Procedure“ was a rather critical process when considering the possibility of predatory attacks because the trilobite had to reveal its less armored ventral side. That is why this procedure might predominantly have been practiced in the protective entourage of other individuals. Basically, the molt clusters provide evidence of synchronized molting events in *Chotecops sollei*. It remains unclear if the isolated, mostly „salteroid“-type exuviations even happened temporally segregated from the before mentioned events or that they were only practiced within spatial segregation. The gregarious molting events seemingly involved trilobites of all ages. The molt remains in some assemblages include all sizes (Fig. 13 h). However such accumulations might be induced by floating in some cases. Other clusters are comprised of markedly similarly sized specimens (Fig. 13 g). At least during exuviation *C. sollei* probably liked to cluster in groups of individuals of the same age, although this habit was apparently not as highly developed as for example in *Cyphaspides* n. sp. G. In the latter species, groups of the same age obviously frequented different habitats for molting.

The “Gutenacker”-locality generally has yielded a broad range of sizes of *C. sollei*. Six of at least seven „instars“ have been recorded so far (Fig. 11). Even though unambiguous corpses of *Chotecops sollei* are hardly known from „Gutenacker“ (SCHUBERT (1996) figured the only one completely articulated specimen known to the author.) the broad age range suggests that this place was regularly inhabited by this species.

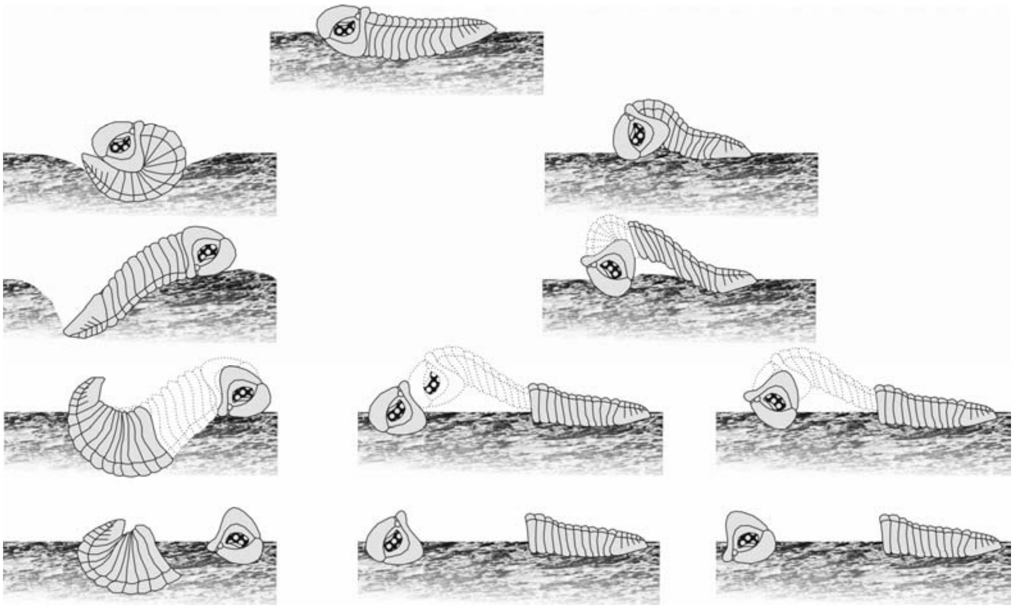

Figure 12: The molt ensembles of *Chotecops* occurring at „Gutenacker“-site can be explained with the scheme after SPEYER (1985). The sequence at the left shows a „Body Inversion Molt Procedure“. The sequences at the right show „Body-upright Molt Procedures“ resulting in “salteroid”-type ensembles. Actual Salter´s configurations resulted from the far right sequence.

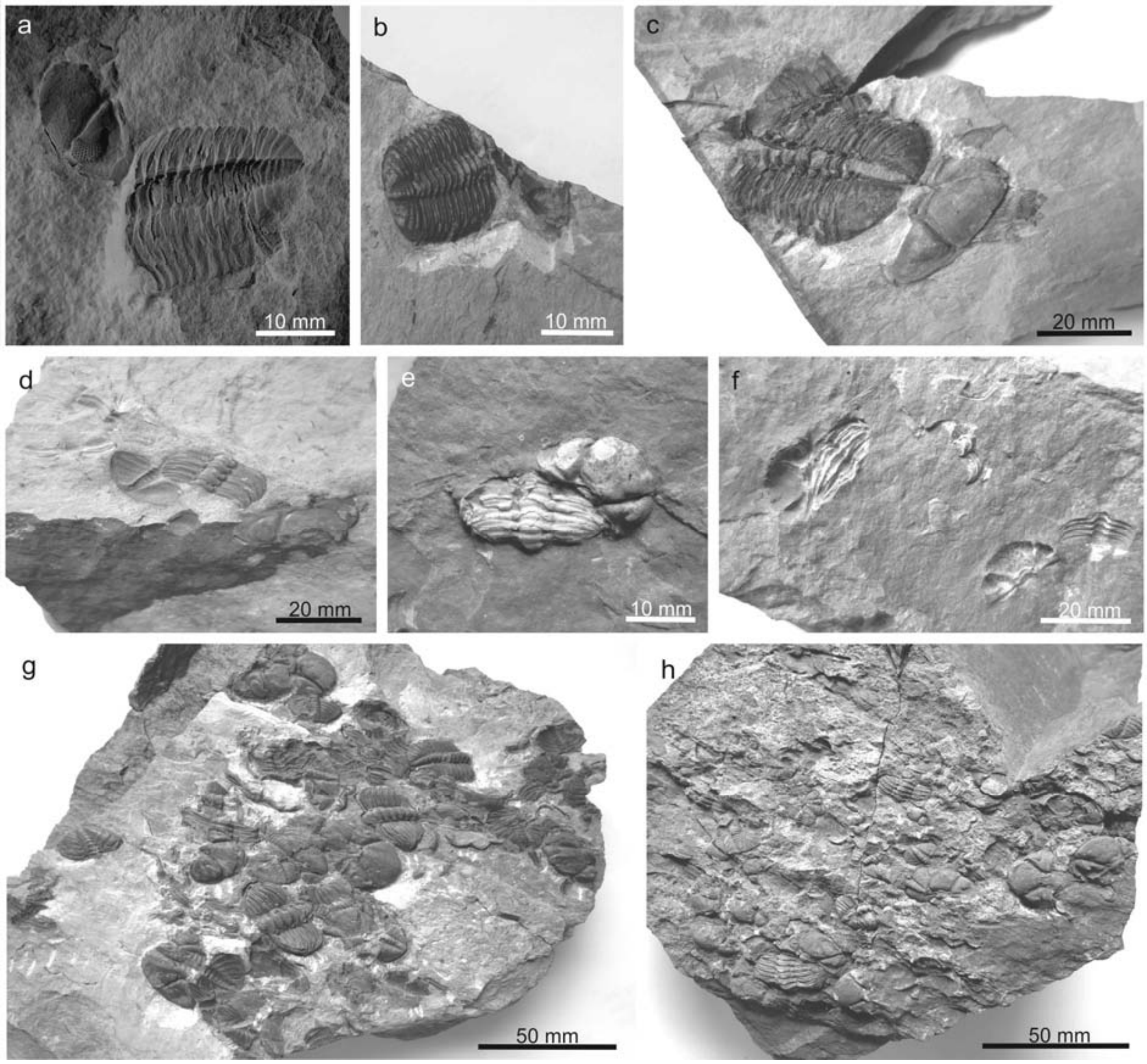

Figure 13: Molt remains of *Chotecops sollei* Struve, 1984 from „Gutenacker“. a),b),c) – „Salteroid“ molt ensembles comprising an outstreched thoracopygon and the shed cephalon. In b) the cephalon is upside-down. In c) the cephalon is lying behind the thoracopygon. d) – slightly disarticulated exuvia. e) – Molt ensemble comprising a cephalon plus recurved thoracopygon. f) – Remains of two specimens. One molt ensemble similar to e) at the left and a second widely decomposed specimen. The hypostome of one specimen is lying in between. g) – Molt cluster comprising cephala, pygidia and more or less recurved trunks of equally sized specimens. h) – Accumulation of molt remains showing rather wide ranges of degrees and individual sizes. This accumulation might have been influenced by floating.

***Kettneraspis* sp. G**

Only one articulated specimen of *Kettneraspis* sp. G is known from the „Gutenacker“-locality (Fig. 14). This specimen is not an exuvia with certainty. But its remarkable up curved posture is very similar to some molt configurations found in the morphologically comparable *Kettneraspis seiberti* Basse, 2004 from “Heckelmanns-Mühle” which are described in Figure 28. In the local *Kettneraspis* as in *K. seiberti* there is a denticulation developed along the anterior margins of the librigenae which might have had a similar auxiliary effect on the molt procedures. So far it remains unclear if *Kettneraspis* sp. G was also equipped with pronounced anterior pleural spines like *K. seiberti*.

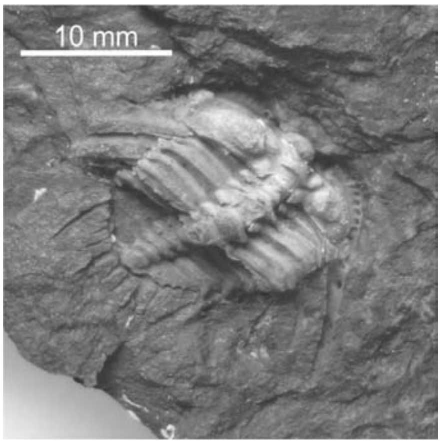

Figure 14: The upward curved posture of this *Kettneraspis* sp. from „Gutenacker“ is similar to molt configurations found in *Kettneraspis seiberti* Basse, 2004 from the „Heckelmanns-Mühle“-fossil site which are explained in Figure 29.

Of *Thysanopeltis* sp. and *Struveaspis* sp. the “Gutenacker”-fossil site only yielded isolated armor-parts so far which were not usable for the current topic.

„Heckelmanns-Mühle“-trilobites

From the „Heckelmanns Mühle“-locality more than two dozens of trilobite species are known altogether. In addition to the Lower Devonian species listed in Figure 6 this number also comprises the trilobites *Thysanopeltis* sp., *Macroblepharum pmuelleri* Basse, 2002, *Sculptoproetus*? sp., *Tafilaltaspis* sp., *Xiphogonium* sp., *Aulacopleura (Paraaulacopleura)* sp., *Cyphaspides* sp., *Psychopyge psyche* Basse, 2003, *Radiaspis* sp. and *Perunaspis* sp. sourced from the whole sequence (Lower and Middle Devonian). Should the existence of further species mentioned in FLICK et al. (2006) be substantiated, more than forty species could be encountered. The trilobites were quite often found complete or as more or less articulated remains from which several were identified as exuviae. This allowed further examinations on the molting of the following trilobites.

Diademaproetus n. sp. L

Exuviae of *Diademaproetus* n. sp. L can frequently be identified by a dissection of one or both librigenae. However typical „axial shield“ configurations are not known. Quite often exuviae can also be recognized by a separation of the pygidium. Thus obviously primarily functional for exuviation obviously were the facial sutures as well as the joint between thorax and pygidium. The conjunction of the joints between the thoracic segments seemed to have been rather rigid.

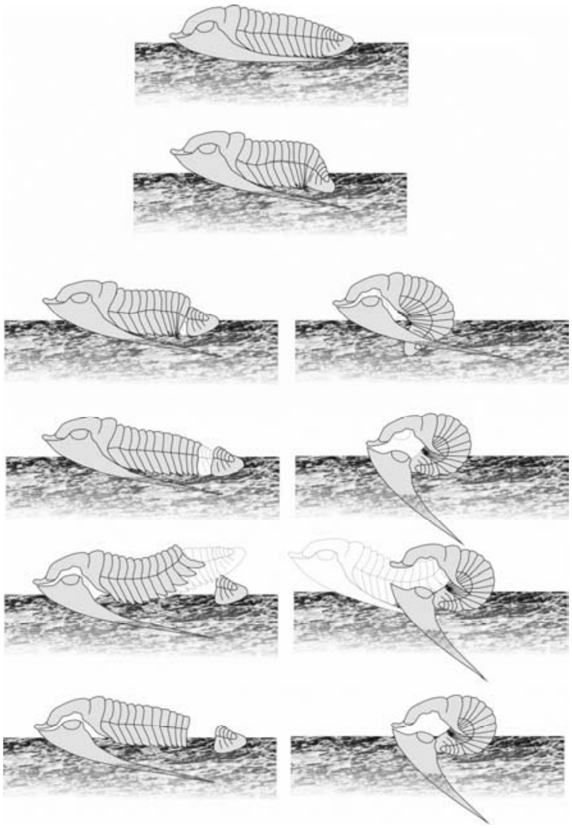

Figure 15: Schematic depiction of two possible molt strategies of *Diademaproetus* n. sp. L. Both strategies have in common that the genal spines were dug into the ground like an anchor. This allowed the trilobite to shed the cephalic part by stemming against the anchored cephalon with a backward movement (= „anchor molt strategy“). The backward movement was sometimes caused by curling the thorax like in the right sequence. The animal withdrew its integument through an opening that formed through opening of the facial sutures. Quite a few molt ensembles give rise to the speculation that the integument could also have been withdrawn in a completely backward pointed movement like shown in the left sequence.

Characteristic of *Diademaproetus* are its long and robust genal spines which makes the cephalon appear like an anchor. Several molt ensembles suggest that the genal spines actually had an anchor-like function within the molt procedure. Thus a so-called „anchor molt strategy" is supposed (Fig. 15) for the molting of *Diademaproetus*. Therefore the genal spines were dug into the ground like an anchor which provided enough drag to shed the cephalon by stemming against the fixed integument with a backward movement. In doing this the facial sutures occasionally opened and the librigenae were twisted sideward as can be recognized in Figures 16 a-f. This hinge-like twisting supposedly happened when the long genal spines were pulled out with a backwards movement. Of course the animals had to be sufficiently elastic for this purpose; what normally can be supposed for their soft stage ("Butter-stadium"). In some cases the backward movement obviously was provoked by a recurving of the thorax; such examples are shown in Figures 16 a,b. When the facial sutures were opened the animal supposedly emerged out of its integument forwards through the resulting opening (see right sequence in Figure 15). Less clear is the molt procedure which might have evoked molt ensembles with isolated pygidia. The portion of such configurations (~ 50 %) is considerable. Contrary to the statement of HENNINGSMOEN (1975), that perhaps all exuviating trilobites emerged forwards out of their old exoskeleton, in these cases the animals might have shed their integument in a completely backward directed motion as it is shown in the scheme shown in Figure 15 (left sequence).

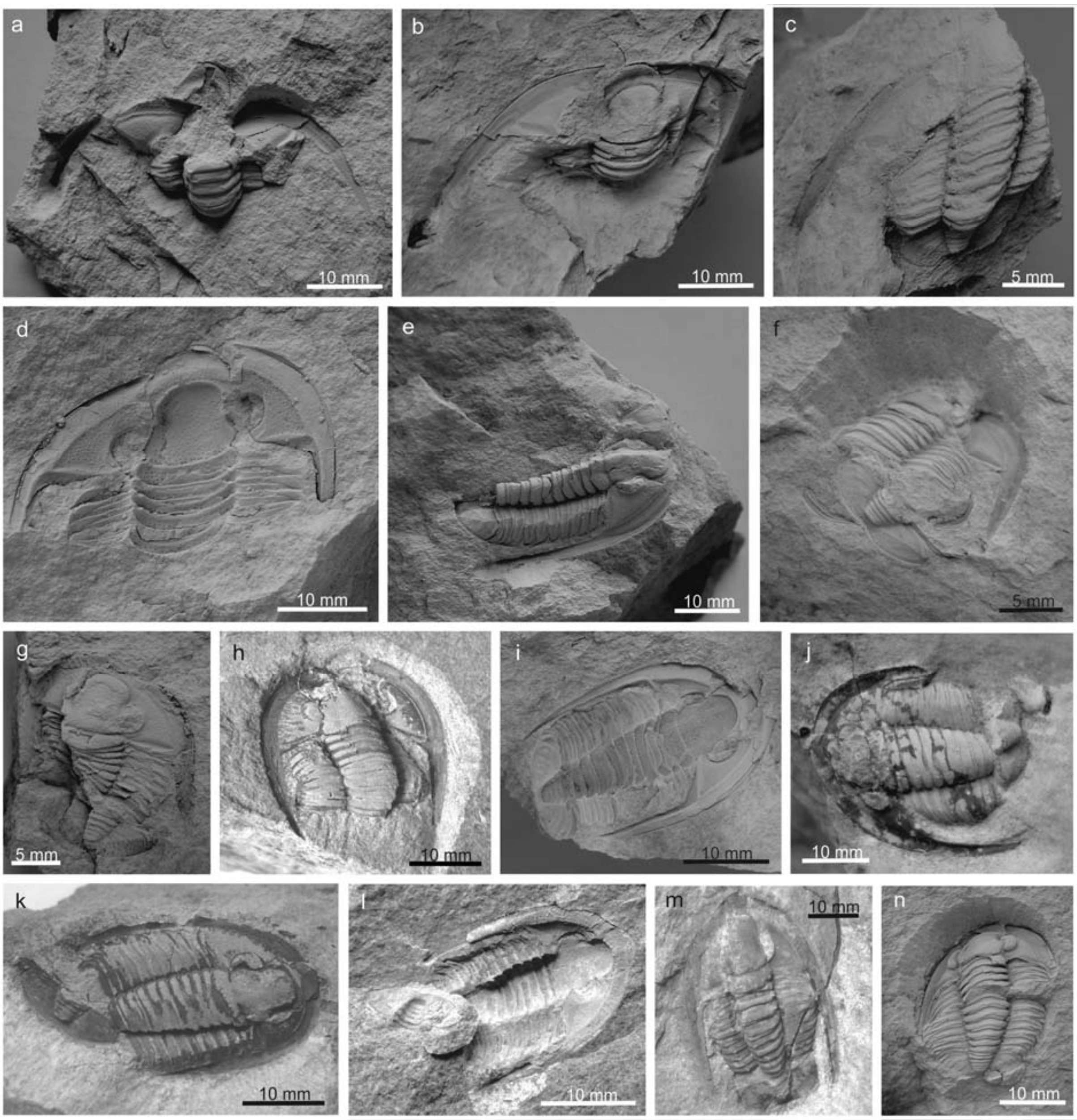

Figure 16: Exuviae of *Diademaproetus* sp. from „Heckelmanns Mühle“. a),b),c) – Recurved specimens with free cheeks twisted sidewise. d) – Anterior part of an integument with librigenae detached and slightly twisted sidewise. e) – Outstretched specimen with left librigena rotated sidewise. f),g),h),i) – Specimens with partially detached librigenae and segregated pygidia (pygidium is missing in h). j),k),l),m) – Outstretched specimens with separated pygidia. n) – One of only a few specimens showing an opening of a thoracic joint.

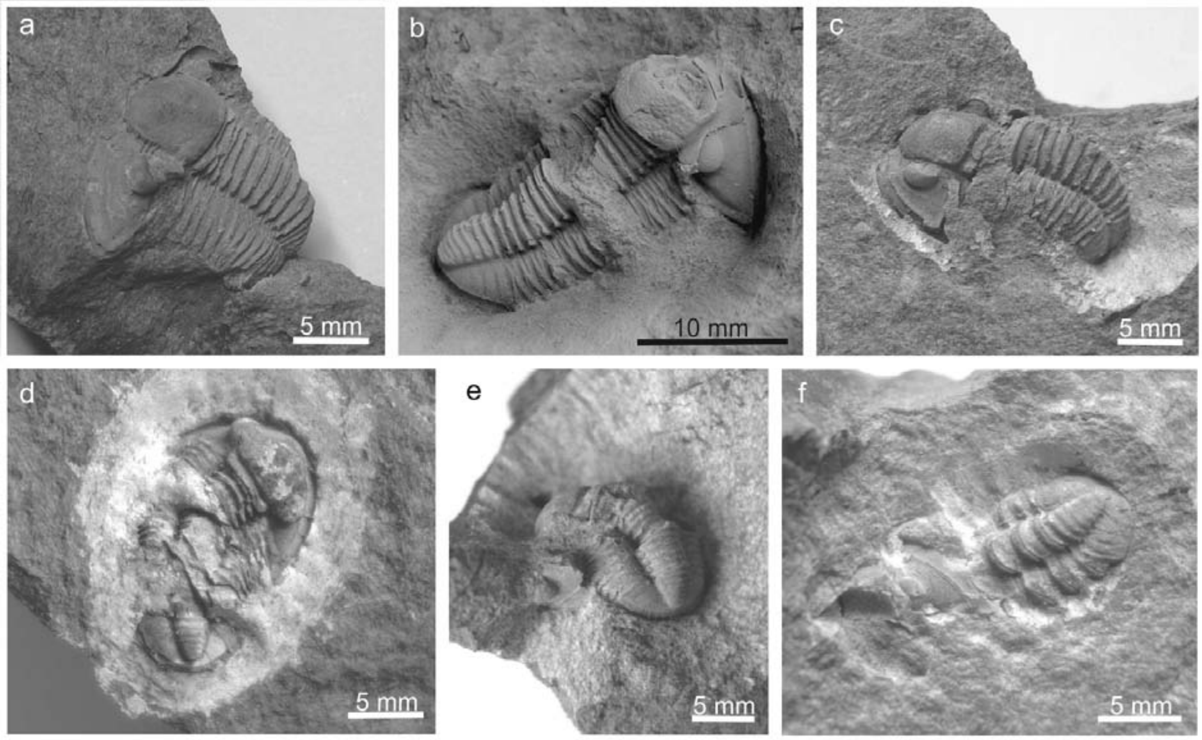

Figure 17: Exuviae of *Rhenocynproetus* sp. from „Heckelmanns Mühle. a)-e) Typical configurations potentially derived from more or less vigorous back-bending and/or struggling thoracic movements (see Figure 18). In a),b),c) and e) the facial sutures are opened, too. f) – Specimen with stretched posterior part. This „accordion-effect“ might have resulted from an infaunal molt procedure.

Rhenocynproetus n. sp. L

Exuviae of *Rhenocynproetus* n. sp. L frequently occur with a dissected thorax and/or a detached pygidium. Such configurations most probably can be traced back to thoracic contractions during the molt procedure which might have involved back-bending movements as shown in Figure 18 with back-bending movements. This procedure resulted in a shedding of variously sized thoracic parts, the pygidium, or a combination of both. The intensity of the ecdysial movements can be deduced from the way the molt elements are dispersed. In the course of such activities the facial sutures also opened frequently through detaching the librigenae. By this an ecdysial opening was formed through which the animal emerged forward out of its old integument. The short genal spines might have dug into the ground to facilitate this.

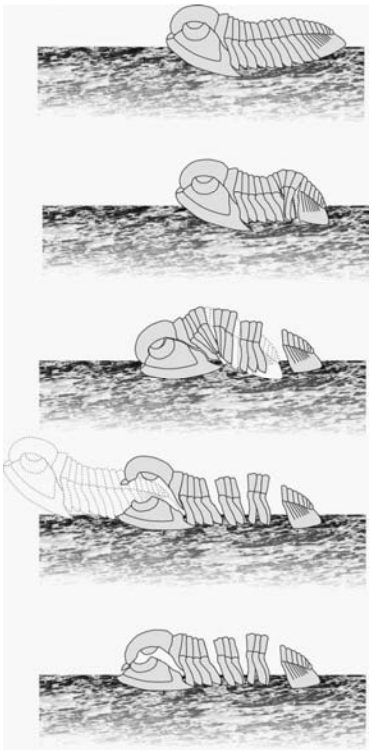

Figure 18: Sketch showing the supposed regular moult procedure of *Rhenocynproetus* n. sp. L from the configuration of most moult ensembles can be concluded that ecdysis within this species regularly happened with intense thoracic contractions. Thereby the facial sutures opened frequently.

As almost all known molt ensembles appear to have derived from a molt procedure as shown in Figure 18 this seems to have been the regular mode of molting in *Rhenocynproetus* n. sp. L. An exception is the specimen shown in Figure 17 f. The posterior part of this molt ensemble shows features of an "accordion effect" (Fig. 23). The pygidium such as the (at least) four posterior thoracic segments were shed beginning from the rear end and were embedded in situ. This kind of elongation needs a frictional drag which could only have been provided by a surrounding dense medium, namely the sediment. Also the upright position of the individually isolated thoracic segments needs to be explained with the supporting effect of the surrounding sediment. Without such a support the isolated segments very probably would have fallen over. Thus the present configuration indicates a molt procedure that happened infaunal or at least partly within the ground. At this it remains unclear if this infaunal molting was practiced on purpose or if it was a forced reaction to an accidental burial caused by a mud flow. Actually the fossil derives from a supposed mud flow-deposit. The find at least shows that *Rhenocynproetus* n. sp. L was capable of infaunal molting.

***Cyphaspis* spp.**

Trilobites of the genus *Cyphaspis* appear in „Heckelmanns Mühle" with several species which were not distinguished for the present study. Corresponding exuviae are indicative of openings between thoracic joints, openings of facial sutures, or a combination of both. The configurations of complete molt ensembles suggest molt procedures very similar to those supposed for *Rhenocynproetus* (Fig. 18). A low extent of dispersion of the molt elements implies minor intense ecdysial movements. From *Cyphaspis* sp. L small clustered assemblages of exuviae are known (Fig. 19 d).

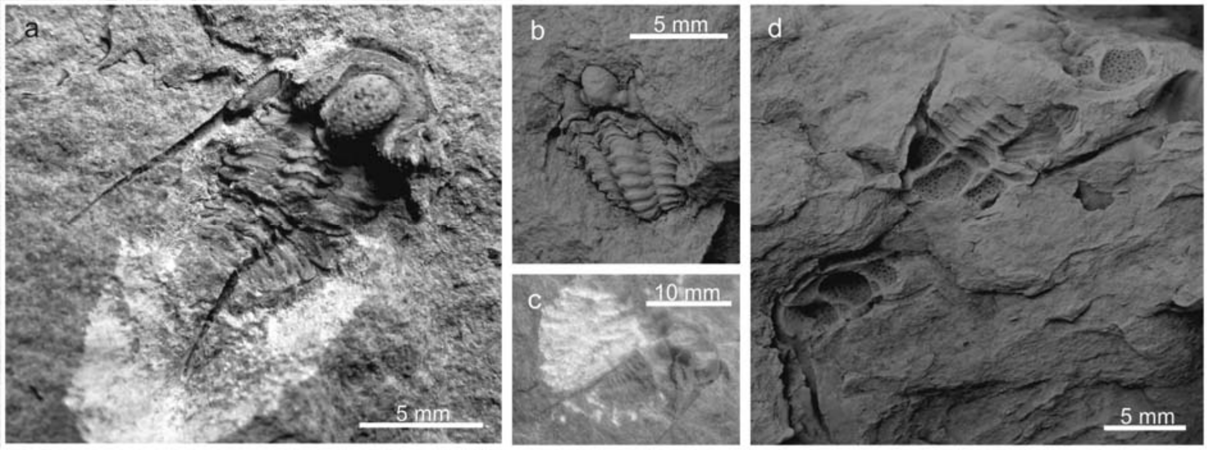

Figure 19: Molt remains of *Cyphaspis* spp. The specific decomposition of the integuments can be explained by thoracic contractions during ecdysis. In specimens a) and c) the free cheeks are detached. d) – shows the clustered remains of three *Cyphaspis* sp. L. At least the central specimen is identified as an exuvia.

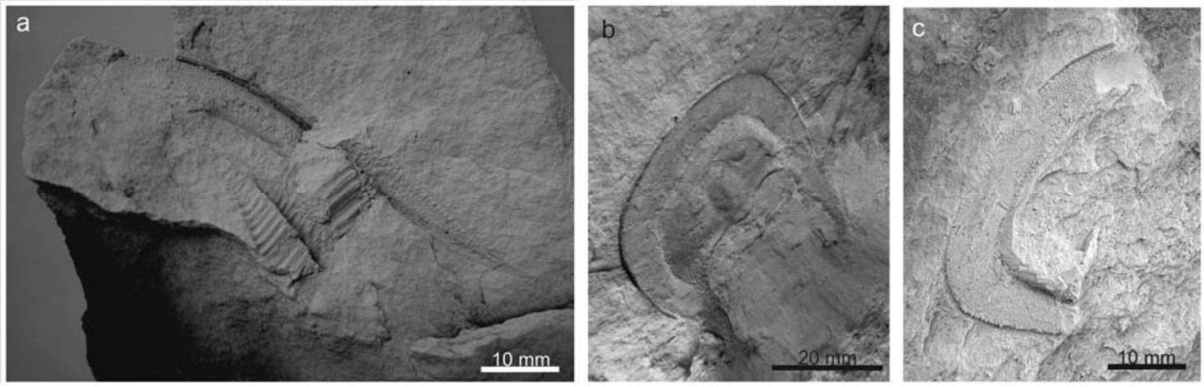

Figure 20: *Harpes* sp. from „Heckelmanns Mühle“. a) – Fragmentary molt ensemble. The partially preserved upper lamella is obviously lying unjointed on the horseshoe shaped lower lamella. The thorax is curled backward and was apparently detached from the cephalon. b),c) – Isolated cephalon, comprised of b) – upper lamella (negative imprint) and c) – lower lamella (recognizable by the presence of the lower external rim). Even if a detachment of both lamellae cannot be recognized, as it might be expected after the Harpes mode of molting, this might still be a molt element.

Harpes sp.

The specific “Harpes mode of molting” (HENNINGSMOEN, 1975) was first described by RICHTER (1920). In this peculiar procedure the cephalon is split into two parts (= upper and lower lamella) by opening a suture along the entire cephalic margin, called the „marginal-interlamellar suture“. The horseshoe-shaped lower lamella and the upper lamella, representing the main part of the cephalic shield, had to be opened to split the exoskeletal pillars within the fringe. Otherwise these connective pillars between upper and lower lamella would have obstructed a shedding of the cephalic integument. Different from HENNINGSMOEN (1975) who supposed an opening of an exuvial gape to the front, it is supposed here that the cephalon was shed by a backward movement through a rear-facing opening which was formed by lifting up the upper lamella to the front (Fig. 22).

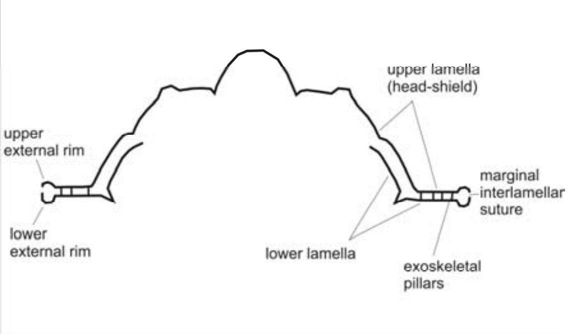

Figure 21: Schematic cross section through a *Harpes*-cephalon (based on MOORE, 1959).

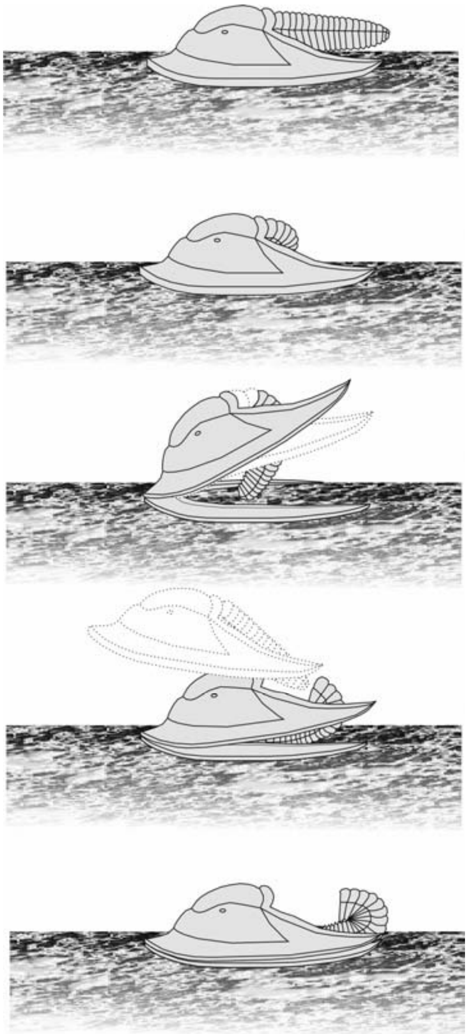

Figure 22: Sketch showing the supposed molt procedure of *Harpes* sp.

Presumably the uplift of the upper lamella was evoked by an erection of the recurved thorax. The cephalon was eventually shed with a backward movement caused by a further recurving of the thorax. At that point the neck joint or joints within the thorax occasionally opened through which the animal could leave its exuvia. The opened cephalon tended to close again after exuviation, likely as an effect of a resilient hinge-like joint at the front. In this respect the frequently found isolated cephala, comprised of associated upper and lower lamella, (Fig. 20 b,c) might well be molt remains.

***Acastoides* n. sp. L**

In the course of the exuviation of *Acastoides* n. sp. L the neck joint or joints between thorax and pygidium were preferably opened. The dissection of the latter seemed to have dominated in terms of numbers. As the facial sutures were non-functional the cephala were always dissected as a whole; but not in Salter´s mode. Other configurations, comprising the molt elements cephalon and thoracopygon or cephalothorax and pygidium supposedly represent regular, epibenthic molt procedures. Other configurations of *Acastoides* n. sp. L have been found which seem to be the results of endobenthic molt procedures. The pattern of such configurations is basically similar to the molt pattern which RUSTÁN et al. (2011) described for infaunal moltings of *Paciphacops (Paciphacops) argentinus* (Thomas, 1906) from the Upper Silurian of Argentina: A mostly articulated thoracopygon, exhibiting a gentle dorsal curvature of its anterior portion and a dorsal upward curve of the cephalon (Fig. 24 f,g). Taken by itself, this is not an unambiguous evidence of a corresponding infaunal molting; particularly since there is no clear separation of the cephalon. A dorsal bending might as well be symptomatic for a carcass. Decisive here is the fact that the anterior thoracic segments are segregated (Fig. 24 f). These segments obviously were shed one after the other, beginning from the rear (in that case the middle thorax). This produced a concertina-like arrangement of the exuvia. The isolated thoracic segments were slightly tilted forward by the drag but did not fall over.

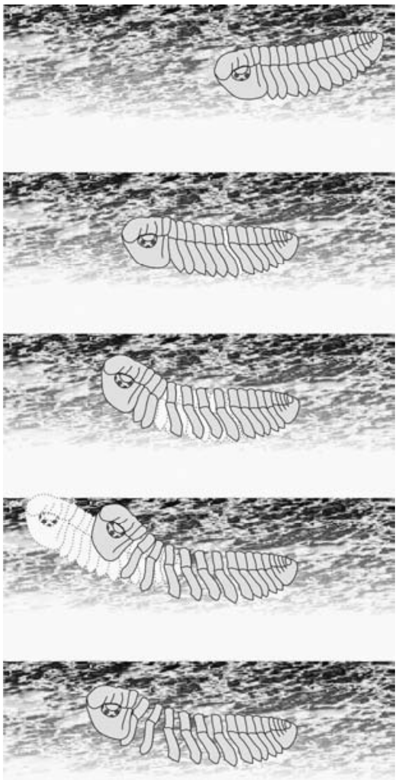

Figure 23: Scheme of an infaunal molt procedure of *Acastoides* n. sp. L. The molt elements were shed and fixed by the help of the frictional and supporting properties of the surrounding sediment. If the segments were separated within the forward movement bit by bit and starting from the rear, an accordion-like stretched molt ensemble remained (= “accordion-effect”).

Such a pattern can be explained with a supporting effect of the surrounding sediment, which is why the “accordion effect” (accordion = alternative term for the musical instrument concertina) is classified by the author as evidencing infaunal molting. The shedding of each molt element happened by means of friction within the surrounding sediment. At this the rather stable joints amid the thoracic segments could open in addition to the predominantly functional gapes between cephalon and thorax (neck joint) or thorax and pygidium. The infaunal molt configuration shown in Figure 24 f does not originate from a distinct mud flow deposit. That is why it is supposed here that infaunal molting might have been practiced regularly by *Acastoides* n. sp. L. What actually determined the animals´ choice of molting strategy remains unclear. According to ALBERTI (2015) the trilobites of the “Heckelmanns Mühle”-habitat had to be aware of predatory attacks.

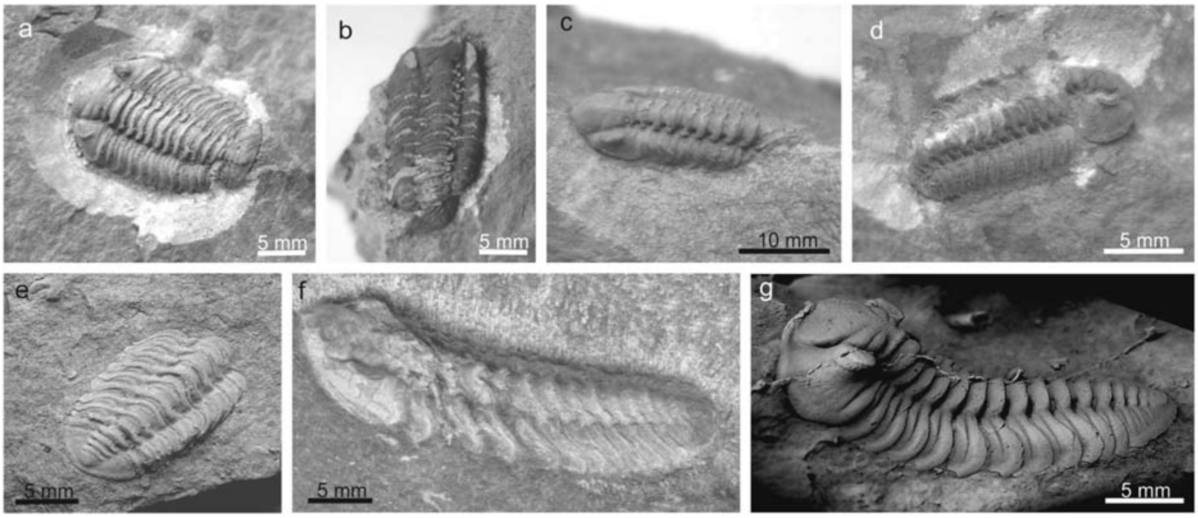

Figure 24: *Acastoides* sp. from „Heckelmanns Mühle“. a),b) – Molt ensembles with seperated pygidia. c) – Specimen with missing posterior thoracal segments and pygidium. d) – Exuvia with detached cephalon. e) – An isolated thoracopygon as a typical remnant of a procedure similar to d). f) – Molt ensemble resulting from an infaunal molting. This is indicated by the stretched thorax that retained most of its principal shape („accordion-effect“) such as a dorsal curvature of the anterior thoracic portion including the cephalon, similar to the pattern described in RUSTÁN et al. (2011). g) – Specimen (silicone-cast [SMF 88190-89] and photograph made by Peter Müller) showing a notable dorsal curvature of the anterior thorax and cephalon. Even if no “accordion-effect” can be noticed this specimen might be an exuvia resulting from an infaunal molt procedure.

Destombesina n. sp. L

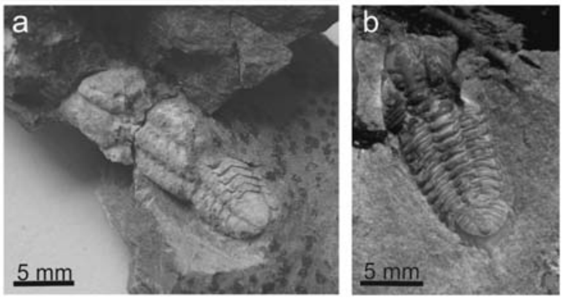

Figure 25: Two exuviae of *Destombesina* sp. from „Heckelmanns Mühle“. Both specimens show a separation of the thorax after the first thoracic segment. The cephalon and attached first segment are slightly laterally tilted. In a) an additional joint amid the central thorax is opened. In b) additionally the joint between thorax and pygidium is opened.

Within the scope of this work there were only two fossils of *Destombesina* n. sp. L examined which were unambiguously determined as molt remains (Fig. 25). Based on these specimens it is suggested that the joints between the thoracic segments seem to have been mostly functional in the course of exuviation. Because of the small number of objects it could not be assessed in how far the opening of the joint after the first thoracic segment, recognizable in both specimens, was a consistent mechanism or whether this is a mere accidental feature. Obviously further joints between other thoracic segments or between thorax and pygidium were occasionally opened. The facial sutures had no apparent function for exuviation. The molt ensembles of *Destombesina* n. sp. L basically resemble such configurations deriving from regular epibenthic molt procedures of *Acastoides* n. sp. L (Fig. 24 a-d).

Barrandeops n. sp. L

Among the molt ensembles of *Barrandeops* sp. from „Heckelmanns Mühle“ at least three fundamental types can be made out. These are firstly molt ensembles of the „salteroid“ type, secondly molt ensembles with dissected thorax and in the third place configurations resulting from infaunal molt procedures.

The numerically dominating “salteroid” molt ensembles are principally comprised of the molt elements cephalon and thoracopygon. Therefore the neck joint between cephalon and thorax did function as exuvial gape. As a typical representative of the Phacopinae *Barrandeops* had no functional facial sutures. There appears to be a broad variety in the orientation of the cephala relative to their corresponding thoracopygons; up until cases of cephala located at the rear of the thoracopygons. Actual Salter´s configurations were rarely found in „Heckelmanns Mühle". The procedures which resulted in the current configurations were probably consistent with the ecdysial strategies in phacopid trilobites after SPEYER (1985) as shown simplified in Figure 12. Configurations resulting from eventual „Body Inversion Molt Procedures" were not found in „Heckelmanns Mühle". A recurved thorax characteristic of such configurations could only be observed at best rudimentarily in a few cases (Fig. 26 b and d). Occasional positioning of the thoracopygon behind the cephalon (situation of the cephalon at the rear of the pygidium; see Figures 26 h,i,j) supposedly happened with the forward motion of the animal if the thoracic integument had not yet detached completely at that point.

The second type of molting found in *Barrandeops* n. sp. L from „Heckelmanns Mühle" is rather unusual for any phacopid. Within these procedures the otherwise rather stable joints between thoracic segments were opened so that the thorax was dissected into several parts (Fig. 26 k-n). Corresponding configurations are similar to those of some of the above mentioned Proetida, like *Rhenocynproetus*, *Cyphaspides* or *Cyphaspis*, whose supposed molt procedures are explained in Figures 8 or 18. That is, with more or less intense back-bending and/or wriggling thoracic movements; while SPEYER (1985) stated that salterian exuviations probably proceeded gradually, without erratic body movements. It might be speculated that the current dissected molt ensembles were stress-induced. That is to say when molt procedures which were already in progress, had to be accomplished hastened because of disturbing impacts (e.g. storms or mud flows) by means of erratic body movements.

It remains unclear to what extend the third type of exuviation was performed due to special situations such as a burial within a mud flow, or whether infaunal molting was part of the regular behavioral repertoire of *Barrandeops* n. sp. L. The specimen shown in Figure 26 o at least represents evidence of infaunal molting as according to RUSTÁN et al. (2011). This is demonstrated by the perfectly articulated thoracopygon which exhibits a gentle dorsal curvature and the isolated cephalon which is pushed up and gently bent backward immediately in front of the thorax.

Several, otherwise perfectly articulated specimens are lacking a pygidium or posterior thoracic portion. Such remains cannot be identified as exuviae without further verification as their features might as well correspond to predatory impacts. The specimen shown in Figure 26 p, however, reveals a pattern that cannot be readily attributed to a predatory attack but more likely represents an exuvia which is suggested by its concertina-like stretching of the posterior thoracic portion. Unusual in this context is the lacking of the pygidium which over a corresponding procedure should have been pulled off in situ within the sediment. Is it perhaps conceivable that this animal emerged its integument, partly stuck within a mud flow, moving rearward? This again would contradict the statement of HENNINGSMOEN (1975) that perhaps all exuviating trilobites emerged forward out of their old exoskeleton. Beside (possibly) *Cyphaspis* sp. L *Barrandeops* n. sp. L is the only species known from „Heckelmanns Mühle" whose molt ensembles occurred in clustered assemblages (Fig. 26 j). These small assemblages of similarly sized individuals are indicative of synchronized molt events in (at least specific groups of) *Barrandeops* n. sp. L.

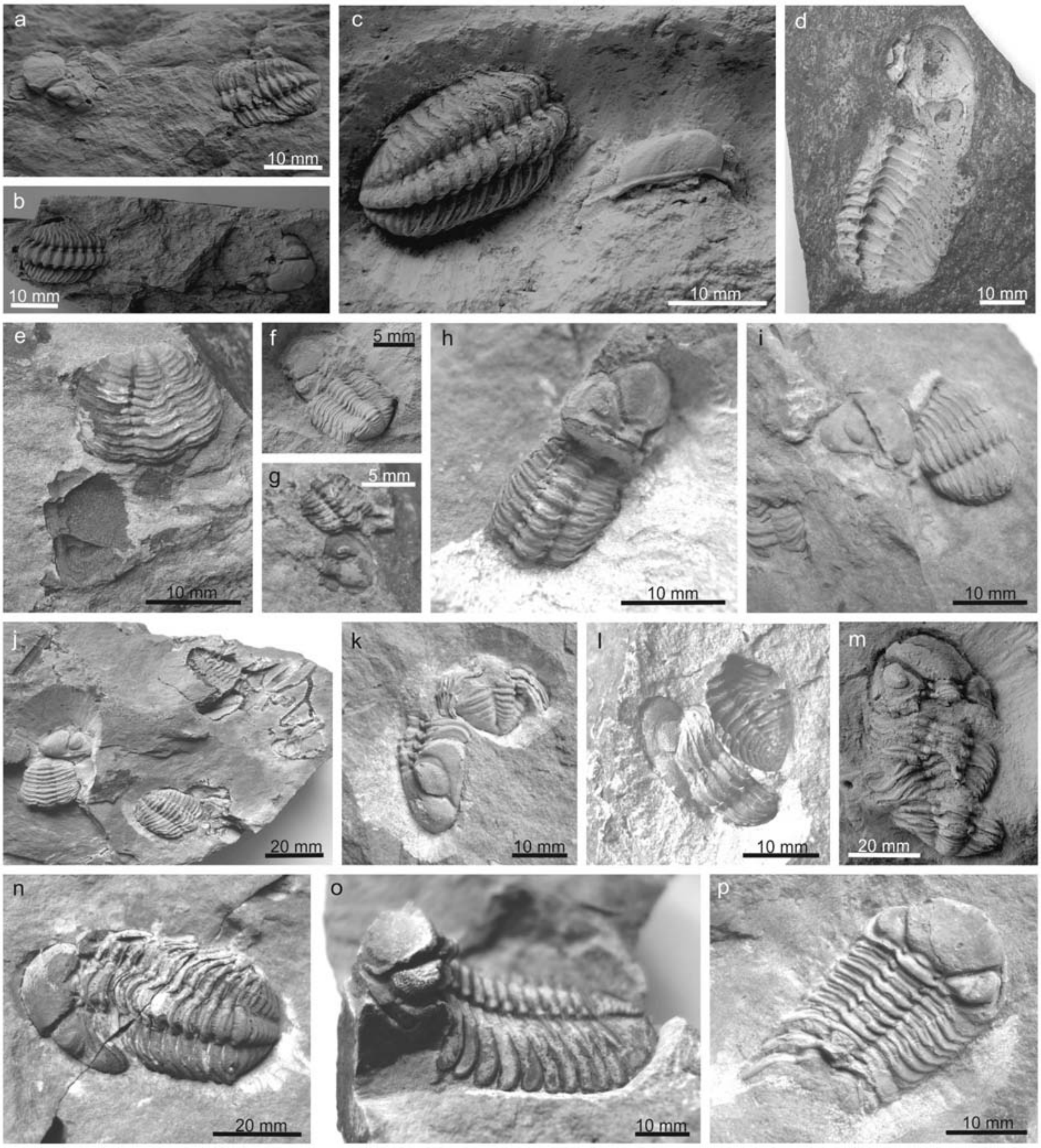

Figure 26: Molt remains of *Barrandeops* sp. from „Heckelmanns Mühle“. a)-j) „Salteroid“-type molt ensembles comprising cephala and thoracopygons. In a)-g) the cephalon was shed in front of the thoracopygon. Only in c) and e) the cephalon was tilted. In h) and i) the cephalon is located behind the thoracopygon. j) – Accumulated moult remains of three individuals. In the left ensemble the cephalon was placed down behind the thoracopygon. The right ensemble, comprising cephalon shed in front of the thoracopygon, as a whole was laid upside down. k),l),m),n) – Molt ensembles with dissected thoraxes. o) – Typical infaunal molt configuration after Rustán et al. (2011); a perfectly articulated, dorsally bent thoracopygon with the cephalon separated and pushed up slightly, dorsally tilted in front of the first thoracic segment. p) – Specimen lacking its pygidium; the dissected posterior thoracic segments are stretched.

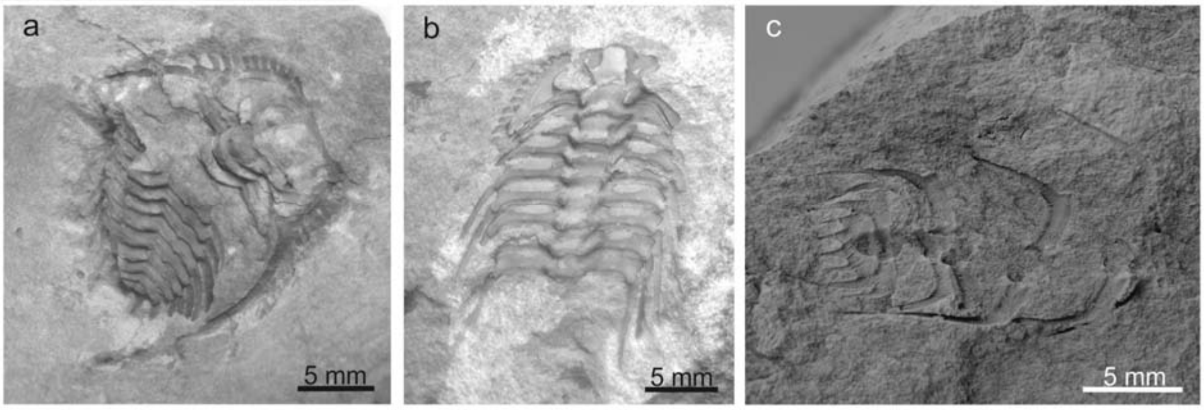

Figure 27: Molt ensembles of *Leonaspis kleini* Basse, 2004 from „Heckelmanns Mühle". a) – Exuvia with dissected thorax. b) – Cephalothorax lacking the right librigena such as the posterior thoracic portion. c) – Posterior portion. The separated thoracic segments and the pygidium were shed one by one in the trace of the forward moving trilobite. This might evidencet an „accordion effect".

Leonaspis kleini **Basse, 2004**

The few molt remains of *Leonaspis kleini* found so far hardly revealed any uniform molt pattern. Apparently the joints between the thoracic segments were predominantly functional for exuviation. Additionally, it appears that the facial sutures were occasionally opened (Fig. 27 b). In *L. kleini* no pronounced anterior pleural spines have been detected like in the comparably spiny taxa *Kettneraspis* or *Koneprusia*.

Kettneraspis seiberti **Basse, 2004**

Exuviation might have been an exceptionally challenging procedure for spiny species like *Kettneraspis seiberti*. It is conceivable that a comparably high drag had to be overcome to shed its long spiny molt elements. Because of the soft ground-conditions in the „Heckelmanns Mühle"-habitat there were hardly any possibilities to wedge the integument for that purpose. Thus the frictional drag within the sediment alone would have to be sustainable. In general this could be achieved by specific strategies like infaunal molting and the "anchor molt strategy" or on the other hand by means of specific anchoring elements. Remarkable in this context are ventrally directed structures ventrally on the lateral extremes of the pleurae (Fig. 28). HAAS (1968) described these antler-shaped extensions of the anterior pleural bands (= anterior pleural spines) in the congeneric *Kettneraspis leucothea* (Haas, 1968) but did not provide an explanation for their function. It is supposed here that the function of the anchor-like anterior pleural spines was actually to dig the exoskeleton into the ground in order to provide substantial support to the shedding of the integument. Whether such an anchoring might have been relevant for further habitual situations remains unclear.

Figure 28: This silicone-cast of the internal mould of a *Kettneraspis seiberti* Basse, 2004 from „Heckelmanns Mühle" (cast [SMF 88190-153] and photograph made by Peter Müller) superbly shows the ventrally directed, antler-shaped anterior pleural spines on the bottom side of the trilobite.

A similar function might be attributed to the denticals along the outside of the cephalic margins (librigenae). Among the molt ensembles of *Kettneraspis seiberti* basically two different configurations can be recognized. First, there are streched exuviae with a more or less dissected thorax. Normally affected by such dissections were the posterior thoracic portions which as a consequence frequently were stretched. Often one or sometimes both librigenae were separated. Presumably, such molt ensembles resulted from molt procedures as depicted in the left sequence shown in Figure 29. According to this the animals dug their exoskeleton into the ground using their anterior pleural spines to emerge from the so hitched integument with a forward movement once a gape had formed at the front by opening the facial sutures. The friction provided by the hitched anterior pleural spines obviously was big enough for some joints between the thoracic segments to open while the animals moved forward. Occasional stretching of dissected thoracic portions is explained by the resulting drag. The second type of molt ensembles are less commonly observed. These configurations are characterized by a remarkable upward curved posture of the thorax. Corresponding exuviae are frequently lacking their cranidium. In some cases the librigenae were separated too. Supposed molt procedures which resulted in such configurations are explained by the right sequence shown in Figure 29. According to this the animal buckled and dug its denticulated cephalon into the ground to push its contracted body forward against the cephalon. As such an opening of the facial sutures was forced through which the animal could leave its integument. It might be speculated that the latter molt procedure was especially exercised by animals whose opening of the facial sutures accidently caused difficulties.

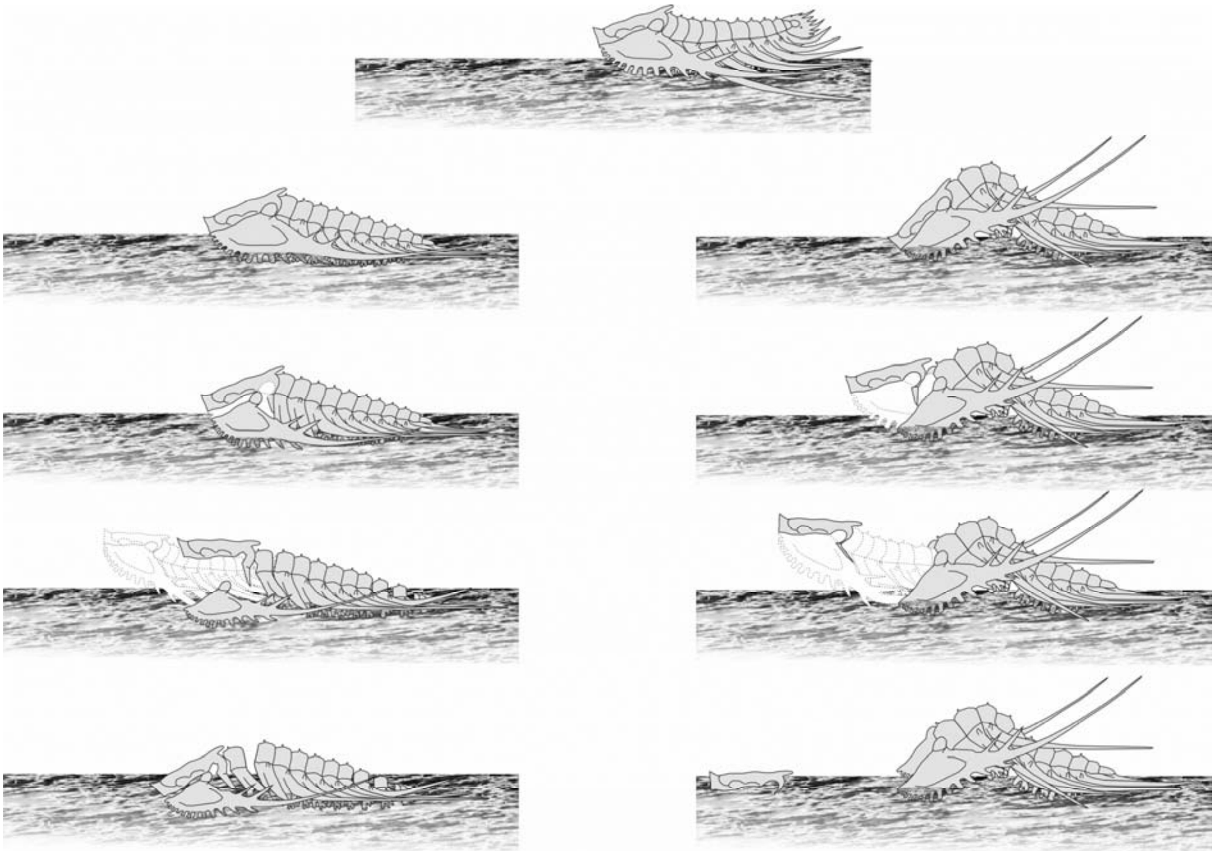

Figure 29: Sketch showing two supposed molt strategies of *Kettneraspis seiberti* Basse, 2004. In both cases it is assumed that the anterior pleural spines were used to dig the integument into the ground. The denticles along the cephalic margins (librigenae) did possibly function in a similar way. In molt procedures as depicted in the left sequence the animals simply stripped of their hitched integument by moving forward through an ecdysial gape formed between the facial sutures. In molt procedures shown in the right sequence the animal had to buckle and stem its body against the hitched cephalon (librigenae) in order for the facial sutures to open.

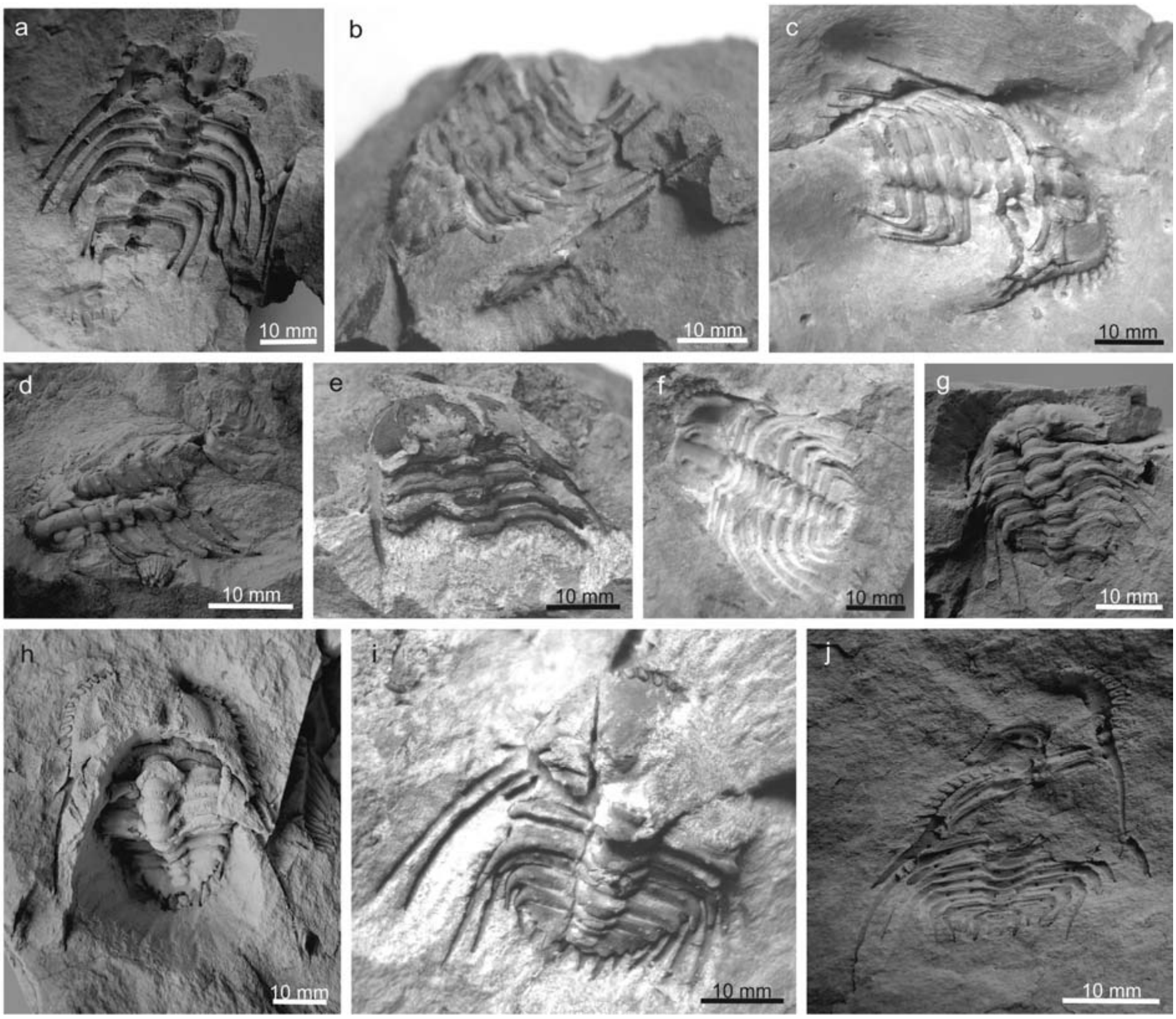

Figure 30: Molt remains of *Kettneraspis seiberti* Basse, 2004 from „Heckelmanns Mühle“. a),b) – Negative imprint (a) and internal mould (b) of a molt ensemble with separated pygidium and left librigena; posterior thoracic segments are dissected and stretched. c) – Specimen lacking the pygidium; the right librigena is separated; several thoracic joints are opened. d) – Specimen lacking its left librigena; pygidium and posterior thoracic segments are separated; several anterior thoracic joints are opened. e) – This specimen which is lacking its anterior part can be recognized as a molt remain by the opened facial sutures. f) – Exuvia lacking the left librigena. g) – Individual showing a separation and stretching of the posterior thoracic portion. h) – Specimen with buckled thorax; the cephalic portion is separated; the cranidium is lacking. i) – Buckled specimen lacking its right librigena and cranidium. The anterior thoracic segments seem to have been separated by the buckling movements. j) – Molt ensemble with dissected anterior thorax and separated cephalic elements.

Koneprusia spp.

The different known forms of *Koneprusia* found in „Heckelmanns Mühle“ were extremely spiny. Due to that reason molting in *Koneprusia* may be imagined as a difficult procedure. In this context it is striking that in *Koneprusia* very distinctive anterior pleural spines were developed which are analogous to the spiny species *Kettneraspis seiberti* (Fig. 31). It may be conceived that these peg-shaped anterior pleural spines which in turn came with hook-like spines did function like a hook and loop fastener when dug into the ground. Presumably, such anchoring supported the shedding of the very spiny integument. In several cases the ecdysial procedure obviously began with a dissection of the posterior armor-parts (Fig. 32 a,b). Other putative molt remains of *Koneprusia* reveal a bent posture similar to some molt ensembles found in *Kettneraspis* (Fig. 32 c,d).

Figure 31: This lateral view of a *Koneprusia* n. sp. L from „Heckelmanns Mühle“ (silicone-cast [SMF 88190-127] and photograph made by Peter Müller) markedly demonstrates the ventrally directed, peg-shaped anterior pleural spines. These processes were probably stuck into the ground to support the trilobite in shedding its very spiny integument.

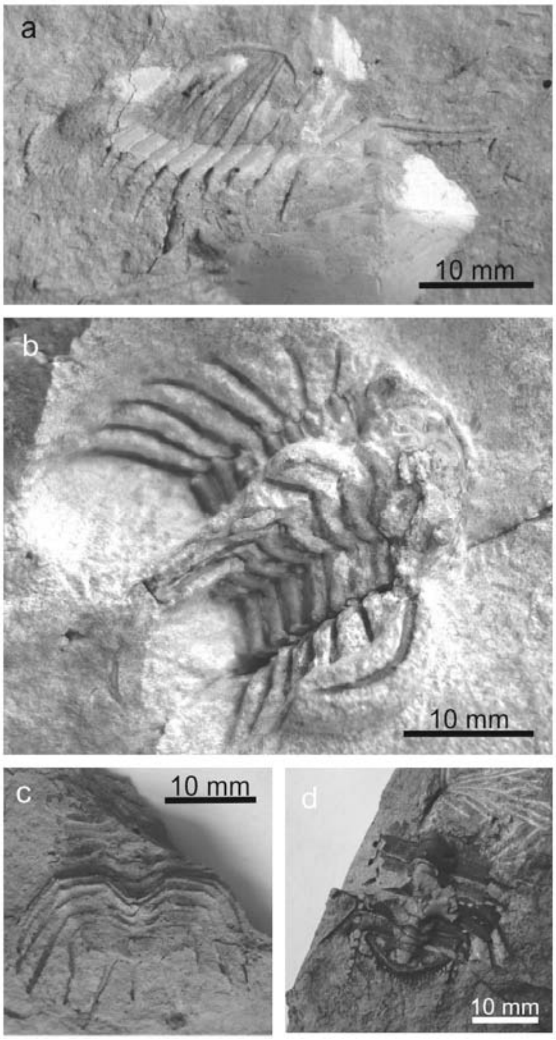

Figure 32: Probable molt remains of *Koneprusia* sp. from „Heckelmanns Mühle“. a) – Specimen with separated posterior segments. b) – Cephalothorax lacking the left librigena and the rest of the carapace after the seventh thoracic segment. c),d) – Fragmentary thoracopygons indicating a buckling of the thorax.

Conclusions / Discussion

The variety of molting-habits seems to have been little behind the diversity of the currently examined trilobite faunas. In view of the fact that the large variety of morphologies of the different examined taxa had to result in equally varying molt strategies, this observation by itself is not very surprising especially because recent arthropods also molt in different ways as a function of frame. More striking is the discovery, already made by authors like BUDIL & BRUTHANSOVÁ (2005), that different molt strategies also occurred intra-specifically. This might generally be explained by varying conditions in different environments; as for example rugged rock floors or reefs surely provided other opportunities for shedding than soft grounds. But the configurations differentiated here in each case originate from the very same habitats which were soft grounds. Presumably, a specific adaption to soft ground conditions were the distinctive anterior pleural spines developed in some Odontopleuridae. These were particularly pronounced in the endemic species *Kettneraspis seiberti* and *Koneprusia martini*. Corresponding processes are also known from taxa found in other areas, like *Dicranurus* from Morocco. All these taxa were extremely spiny. This resulted in a large internal surface compared to the animal´s size which must have produced a comparatively high friction while shedding. In order to shed the integument, this frictional force had to be transferred to the ground for which the anterior pleural spines probably had a major anchoring function. A similar function is assumed for the denticulation developed on the cephalic margins of some taxa, like *Kettneraspis* or *Leonaspis*. To support shedding by anchoring or digging the integument into the ground was a principle which was in evidence even more exemplary within the „anchor molt strategy“. The anchor-like cephala of *Diademaproetus* with their long genal spines were virtually predestinated for that purpose. Even comparably smaller genal spines, developed in *Rhenocynproetus* n. sp. L or *Cyphaspides* n. sp. G, might have been applied similarly in the course of exuviation. As such the backwards oriented genal spines could only have functioned in combination with a backward movement of the animal. Contrary to the statements of HENNINGSMOEN (1975) the author does not excludethe possibility that some molt procedures were accomplished through a completely backward oriented course of movement. Even some molt procedures of *Harpes* sp. presumably involved partly backward oriented movement sequences. In other molt strategies the shedding of the integument was obviously performed by means of more or less intense back-bent and/or struggling body-movements. Examples of this are found in *Aulacopleura (Paraaulacopleura)* n. sp. G, *Cyphaspides* n. sp. G, *Rhenocynproetus* n. sp. L, *Cyphaspis* spp. and *Barrandeops* n. sp. L but also in a specific variant in *Kettneraspis seiberti* and *Koneprusia* sp. As far as not conditioned physically (e.g. complicated detachment of the integument) different intraspecific molt strategies occurring within the same habitat supposedly can be traced back to external influences. These were eventual storm events, occasional mud flows or, as according to RUSTÁN et al. (2011), predatory influences which particularly manifested in infaunal moltings. The „accordion effect" is considered a result of infaunal molt procedures and is introduced here as a complementary feature to recognize infaunal molting in addition to the previously adduced „Rustán pattern". Configurations similar to the "Rustán pattern" have been recognized so far in *Barrandeops* n. sp. L and *Acastoides* n. sp. L; „accordion effects" have been observed in *Acastoides* n. sp. L, *Rhenocynproetus* n. sp. L such as probably in *Barrandeops* n. sp. L and *Leonaspis kleini*. Even within these species corresponding infaunal molt configurations apparently occurred exceptionally. On one hand this indicates that infaunal molting rather seemed to be a reaction on specific situations. On the other hand it is shown that these trilobites were basically able to molt infaunal and concretely were able to accomplish exuviation after occasionally having been buried by a mud flow. The question remains how these animals, which would have certainly been fragile after exuviation could have moved inside the sediment whereas other animals with their hardwearing exoskeleton and sturdy extremities obviously got stuck in there and died. BONINO & KIER (2010) denied that freshly exuviated trilobites were able to burrow. They even stated that animals during their soft stage were hardly able to move at all.

In one specific mud flow-deposit cropping out in „Heckelmanns Mühle" 4% of the trilobite fossils could be identified as molt remains. This number comprises specimens of *Diademaproetus*, *Rhenocynproetus*, *Cyphaspis*, *Harpes*, *Acastoides*, *Barrandeops* (*Lahnops)*, *Kettneraspis*, *Leonaspis* and *Koneprusia*. That is a remarkably high number of taxa considering that a mud flow was a temporally narrowly limited geological event. All the same the actual ecdysial procedure was a short phase within the comparably time-consuming process of molting; and according to present knowledge the procedure could hardly have been provoked arbitrarily. Assuming this is not an extraordinary case of a mud flow somehow coinciding with a synchronized collective molting event it must be accepted that molting within the fauna of „Heckelmanns Mühle" happened randomly. Because of temporarily individual molt intervals there seemingly were individuals in any stage of molting at any time. This was apparently the case for most of the local species; also shown by the fact that in deposits other than the mud flows molt ensembles are normally single finds. Evidences of gregarious molting events (regarding at least specific groups) have so far only been recognized in *Barrandeops* n. sp. L and *Cyphaspis* sp. L. Whereas in

„Gutenacker“ synchronized molting events seemed to have been the rule. Here corresponding moult accumulations have been recognized in all abundant species. There is some evidence that such molting events even concerned different species. Besides the usually monospecific comprised clusters there have been found molt remains of *Cyphaspides* and *Chotecops* together. At least for *Cyphaspides* n. sp. G there is evidence that the „Gutenacker“-habitat possibly was particularly frequented for molting.

To some degree the recent findings reveal a surprisingly complex image of the molting-habits of the examined trilobites. But still there are lot of open questions and some aspects remain no more than speculative. Thus it is to be hoped that coming research will reveal more details.

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References

ALBERTI, M. (2013): Farbenfrohe Trilobiten aus dem Taunus. *Fossilien, 30 (6)*; 330-338

ALBERTI, M. (2015): Angebissen und ausgespuckt? – Trilobit als Beuteopfer. *Fossilien, 32 (4)*; (in press)

BASSE, M. (2002): Eifel-Trilobiten. 1. Proetida.- Goldschneck-Verlag, Korb

BASSE, M. (2003): Eifel-Trilobiten. 2. Phacopida. 1. Cheiruriden, Acasten, Asteropygen. - Goldschneck-Verlag, Korb

BASSE, M. (2006): Eifel-Trilobiten. 4. Proetida (3), Phacopida (3). – Quelle & Meyer-Verlag, Wiebelsheim

BASSE, M. & HEIDELBERGER, D. (2002): Devonische Gastropoda und Trilobita aus der Lahnmulde (Rheinisches Schiefergebirge). – *Jahrbücher des Nassauischen Vereins für Naturkunde, 123*; 67-103

BASSE, M. & MÜLLER, P. (1998): Devon-Trilobiten aus dem Lahn-Dill-Gebiet. - *Fossilien 15 (1)*; 43-49

BASSE, M. & MÜLLER, P. (2004): Eifel-Trilobiten. 3. Corynexochida, Proetida (2), Harpetida, Phacopida (2), Lichida. - Quelle & Meyer-Verlag, Wiebelsheim

BASSE, M. & MÜLLER, P. (2011): *Psychopyge* aus dem Ober-Emsium der Lahn-Mulde. – *Jahrbücher des Nassauischen Vereins für Naturkunde, 132*; 41-59

BASSE, M. & MÜLLER, P. (2015): Trilobiten aus dem Rupbach-Schiefer der südwestlichen Lahnmulde, Taunus (mittleres Ober-Emsium bis frühes Eifelium, Rhenoherzynikum). (in press)

BENDER, P., HERBIG, H.-G., GURSKY, H.-J. & AMLER, M. R. W. (1993): Exkursionen A2 und B2: Beckensedimente im Oberdevon und Unterkarbon des östlichen Rheinischen Schiefergebirges – Fazies, Paläogeographie und Meeresspiegelschwankungen. – in: Amler, M. R. W. & Tietze, K.-W. [Hrsg.]: Sediment '93 – Exkursionsführer zu Exkursionen A1-3 und B1-3: 15-41, Marburg

BONINO, E. & KIER, C. (2010): The Back to the Past Museum Guide to Trilobites. – Back to the Past Museum, Puerto Morelos

BUDIL, P. & BRUTHANSOVÁ (2005): Moulting in Ordovician dalmanitoid and acastoid trilobites ot the Prague Basin. Preliminary observation. – *Geologica Acta, 3 (4)*; 373-383

BUSCH, R.M. & SWARTZ, F.M. (1985): Molting and description of a new homalonotid trilobite from Pennsylvania. – *Journal of Paleontology, 59 (5)*; 1062-1074

FLICK, H. (2010): Streifzüge durch die Erdgeschichte. Lahn-Dill-Gebiet: Riffe, Erze und edler Marmor. – Quelle & Meyer-Verlag, Wiebelsheim

FLICK, H., FLICK, U., MOE, A. & PRÖVE, A. (2004): Ein verdrückter „*Phacops*“ aff. *Major* aus dem Wasenbachtal, südwestliche Lahnmulde (Rheinisches Schiefergebirge). – *Mainzer geowissenschaftliche Mitteilungen, 32*; 77-94

FLICK, U., FLICK, H. & REQUADT, H. (2006): Die Trilobitenfauna des meta-alkalibasaltischen Lagerganges vom Wasenbachtal – Abbild unterschiedlicher mariner Lebensräume an der Wende Unter-/Mitteldevon in der südwestlichen Lahnmulde (Rheinisches Schiefergebirge). – *Mainzer geowissenschaftliche Mitteilungen, 34*; 21-48

FLICK, H. & NESBOR, H.D. (1988): Der Vulkanismus in der Lahnmulde. – *Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereins, N.F., 70*; 411-475

FLICK, H. & STRUVE, W. (1984): *Chotecops sollei* und *Chotecops ferdinandi* aus devonischen Schiefern des Rheinischen Schiefergebirges. – *Senckenbergiana lethaea, 63 (5/6)*; 473-495

HAAS, W. (1968): Trilobiten aus dem Silur und Devon von Bithynien (NW-Türkei). – *Palaeontographica, Abt. A 130 (1-6)*; 60-207

HENNINGSMOEN, G. (1975): Moulting in Trilobites. – *Fossils and Strata, 4*; 179-200

KAYSER, E. (1884): Die Orthocerasschiefer zwischen Balduinstein und Laurenburg an der Lahn. - *Jahrbuch der Preußischen Geologischen Landesanstalt (für 1883)*; 1-56.

KIRNBAUER, T. & WENNDORF, K.-W. (1995): Die Fauna der Porphyroide bei Singhofen im Westtaunus. – *Mainzer geowissenschaftliche Mitteilungen, 24*; 103-154

MAURER, F. (1876): Paläontologische Studien im Gebiet des rheinischen Devon. 3. Die Thonschiefer des Ruppbachthales bei Diez. - *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, 1876*; 808-848

MCNAMARA, K.J. & RUDKIN, D.M. (1984): Techniques of Trilobite Exuviation. – *Lethaia, 17*; 153-173

MOORE, R.C. (Ed.) (1959): Treatise on Invertebrate Paleontology (O) Arthropoda 1, Euarthropoda, Trilobitomorpha *Geological Society of America, University of Kansas Press*

REQUADT, H. (1990): Geologische Karte Rheinland-Pfalz 1:25.000, Erläuterungen, Blatt 5613 Schaumburg; 1-212

REQUADT, H. (1991): Fazies und Paläogeographie des Devons in der südwestlichen Lahnmulde (Rheinisches Schiefergebirge). – *Mainzer* *geowissenschaftliche Mitteilungen, 20*; 229-248

REQUADT, H. (2008): Südwestliche Lahnmulde (Rheinlad-Pfalz). – In: DEUTSCHE STRATIGRAPHISCHE KOMMISSION (Hrsg.): Stratigraphie von Deutschland VIII. Devon – *Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften, 52*; 204-220

REQUADT, H. & WEDDIGE, K. (1978): Lithostratigraphie und Conodontenfaunen der Wissenbacher Fazies und ihrer Äquivalente in der südwestlichen Lahnmulde (Rheinisches Schiefergebirge). – *Mainzer geowissenschaftliche Mitteilungen, 7*; 183-237

RICHTER, R. (1920): Beiträge zur Kenntnis devonischer Trilobiten. 3. Über die Organisation von *Harpes*, einem Sonderfall unter Crustaceen. – *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 37(8)*; 117-218

RICHTER, R. (1937): Vom Bau und Leben der Trilobiten, VIII. Die „SALTER´sche Einbettung“ als Folge und Kennzeichen des Häutungs-Vorgangs. – *Senckenbergiana 19 (5-6)*; 413-431

RUSTÁN, J.J.; BALSEIRO, D.; WAISFELD, B.; FOGLIA, R.D. & VACCARI, N.E. (2011): Infaunal molting in Trilobita and escalatory responses against predation. – *Geology, 39 (5), No. 5*; 495-498

SCHRAUT, G. (1999): Vom Fossilrest zur Rekonstruktion eines Lebensraums vor 390 Millionen Jahren. – *Spiegel der Forschung, 16 (2)*; 4-13

SPEYER, S.E. (1985): Moulting in phacopid trilobites. – *Transactions of the Royal Society of Edinburgh, 76*; 239-253

SCHUBERT, M. (1996): Die dysaerobe Biofazies der Wissenbacher Schiefer (Rheinisches Schiefergebirge, Harz, Devon). – *Göttinger Arbeiten zur Geologie und Paläontologie, 68*

THOMAS, I. (1906): Neue Beiträge zur Kenntnis der devonischen Fauna Argentiniens. – *Zeitschrift der Deutschen Geologischen Gesellschaft, 57*; 233-290