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The Muhi Quarry: A Fossil-Lagerstätte from the Mid-Cretaceous (Albian-Cenomanian) of Hidalgo, Central México

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1. Introduction

The German word *lagerstätten* (singular, *lagerstätte*) describes sedimentary deposits with an important concentration of fossil material in a variable state of preservation. According to Seilacher (1970), there are two types of *lagerstätte*: Concentration deposits (*Konzentrat-lagerstätte*) and conservation deposits (*Konservat-lagerstätte*). Concentration deposits are originated by sedimentological and biological processes that promote the accumulation of a high density of fossil remains, particularly hard parts such as shells and bones. Conservation deposits are distinguished by uncommon depositional conditions (for example, rapid burial, anoxia, and/or hypersalinity) that favor exceptional preservation of an organism (Seilacher, 1970; Seilacher et al., 1985). Conservation deposits have received more consideration in the literature and in several instances are regarded as "snapshots" of a particular moment in the history of life (Benton & Harper, 2009; Nudds & Selden, 2008). Although concentration deposits are not mainly distinguished by a high-quality preservation of organic remains, its fossil richness provides information suitable to elaborate paleobiological inferences about an ancient community.

A few Mexican marine Cretaceous deposits are distinguished by important concentrations of fossil remains, usually in a high state of preservation. The localities which have been considered as *Fossil-lagerstätten* in México include: Vallecillo quarry, Nuevo León (northern México) of early Turonian age (Blanco-Piñón et al. 2002); Múzquiz quarries, Coahuila (northern México) of late Turonian-early Coniacian age (Stinnesbeck et al., 2005); Xilitla quarries, San Luis Potosí (central México) of Turonian age (Blanco-Piñón et al., 2006); and Tlayúa quarry, Puebla (central México) of Albian age (Alvarado-Ortega et al., 2007). A sedimentary deposit with comparable characteristics was discovered about 13 years ago in northwestern sector of the state of Hidalgo, central México; the locality is formally known as Muhi Quarry. Paleontological work carried out in the site since its discovery, has allowed recovering an important sample of fossil remains, which represents a diverse marine community of mid-Cretaceous age. Because of the importance of the site, we discuss taphonomic evidence to consider the Muhi Quarry as a *Fossil-lagerstätte*.

2. Historical review

The Muhi Quarry is geographically located at 20°49'21.5" N and 99°15'38.3" W, set in northwestern sector of the state of Hidalgo, central México (Figure 1). The quarry has been worked for more than 30 years for flagstone by the Yánez family inhabitants of the San Pedro town in Zimapán. Before the first visit by personal of the University of Hidalgo in 1998, Sergio and Ignacio Yánez did not understand the presence of fish in the stones. Once they were instructed about the importance of the discovery, they started paying attention on the specimens during the exploitation. Previously they used to sell them together with the slabs for building. At the same time, kids living around the place became hard collectors (Figure 2). The first specimen formally recovered from the quarry corresponds to a beautifully preserved pachyrhizodontid head. Since that moment, more than 2,200 specimens have been collected including invertebrates and fish.

The real diversity of the quarry is still unknown since new taxa are discovered every year. Although the fauna is not completely described because of the newness of the discovery, it is remarkable the presence of new species and new records for America, including the shrimp *Aeger hidalguensis* (Feldman et al., 2007), which only Cretaceous sister species *Aeger libanensis* Roger, 1946, comes from the Cenomanian of Lebanon (Feldman et al., 2007); and the fishes *Ichthyotringa mexicana* Fielitz & González-Rodríguez, 2008, which sister species were also found in the Cenomanian Lebanese localities of Namoura, Hakel and Hajula; undescribed halecoid fishes previously known from some localities of Western Tethys; agonids earlier found in Cenozoic localities of Europe (González-Rodríguez & Schultze, 2010); and tetraodontiforms (González-Rodríguez et al., 2011).

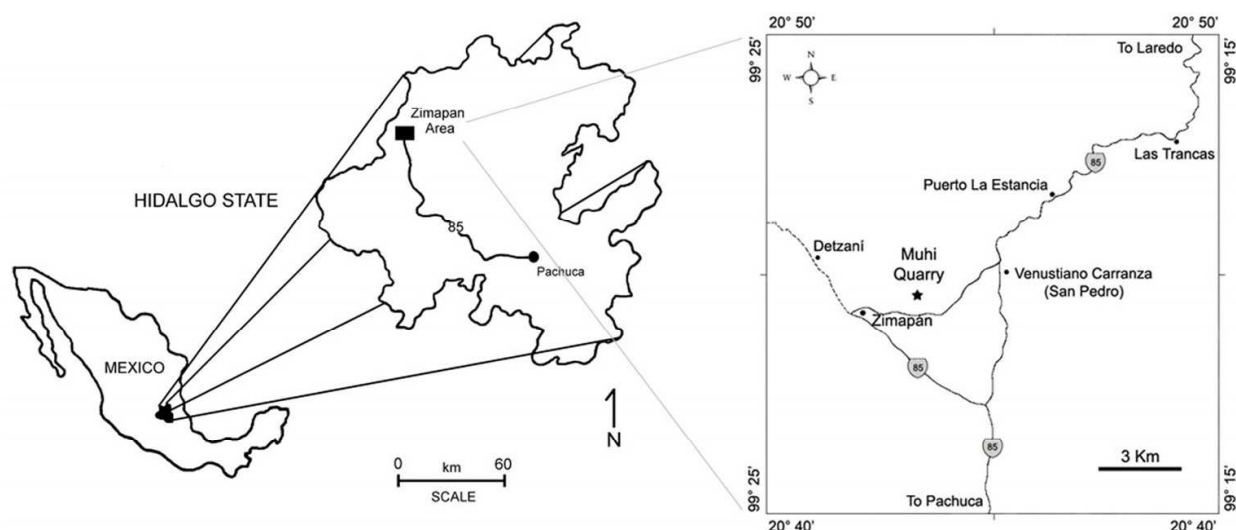


Fig. 1. Index map showing the location of the Muhi Quarry at the Zimapán Area, northwestern sector of Hidalgo, central México.

3. Lithostratigraphy, sedimentary environment, and age

The Muhi Quarry is a calcareous rock sequence belonging to the La Negra Facies of the El Doctor Formation, consisting of micritic limestones, bedded and/or nodular cherts, and laminae of barely consolidated mixture of siliciclastic clay and calcium carbonate. The

sedimentary sequence shows a lithological variability indicative of an outer sea shelf setting, which received temporal pulses of pelagic waters, and occasionally influx of near-shore waters maybe during storms (Bravo-Cuevas et al., 2009). The age of the Muhi Quarry hinges on its stratigraphic relationships with other Mexican Mesozoic rock units and on the fish fauna that it bears; the deposit is considered of mid-Cretaceous (Albian-Cenomanian) age (Bravo-Cuevas et al., 2009; González-Rodríguez & Bravo-Cuevas, 2005).



Fig. 2. The Muhi Quarry at Zimapán Area, northwestern sector of Hidalgo, central México. A. Panoramic view of the quarry; B. Exploitation of the quarry for flagstone and gravel; C. The Yánez brothers, workers of the quarry; D. Prospecting and collecting of fossil material by kids of the Zimapán area.

4. Material and methods

In order to characterize the fossil assemblage of the Muhi Quarry, we used taphonomic indicators. The fossil assemblage was classified considering life habitat and state of preservation of the record, including autochthonous, parautochthonous or allochthonous concentrations; a mixed assemblage is referred to autochthonous-parautochthonous, parautochthonous-allochthonous, or autochthonous-allochthonous (after Kidwell et al., 1986). In addition, we considered the “time averaging” involved in its formation (Kidwell & Bosence, 1991).

The taphonomic features evaluated comprise: (1) Anatomical completeness, (2) disarticulation, and (3) fragmentation. The deformation of the axial skeleton and closure/openness of jaws were evaluated in fishes. Anatomical completeness (1) refers to the percentage of bones

preserved in an individual specimen (Brett & Baird, 1986). We considered three states, as follows: complete (100% of skeletal elements present); partially complete (at least 50% of skeletal elements present); and incomplete (less than 50% of skeletal elements present). Disarticulation (2) was evaluated in crinoids, echinoids, crustaceans, and fishes. This feature refers to the number of hard parts scattered and/or displaced from their original anatomical position (Hill, 1979). Degree of disarticulation was measured as: slightly disarticulated (less than 25% of skeletal elements scattered and/or displaced); moderately disarticulated (25%-50% of skeletal elements scattered and/or displaced); and highly disarticulated (more than 50% of skeletal elements scattered and/or displaced). Thus, articulated specimens mean that all hard parts are in their original anatomical position. Fragmentation (3) refers to the breaking of the skeletal elements, caused by scavengers, predators and/or physical factors (for example, transport produced by currents or wind) (Benton & Harper, 2009; Speyer & Brett, 1988). Three states were recognized: low fragmentation (0-30% of skeletal elements broken), medium fragmentation (30%-70% of skeletal elements broken), and high fragmentation (70-100% of skeletal elements broken) (Brett & Baird, 1986).

According to Bienkowska (2004), deformation of fish axial skeleton includes: vertebral series straight, slightly arched, arched, or S-shaped; this condition is related to a post-mortem effect. Moreover, openness/closure of jaw was used as a relative indicator of level-oxygenation.

5. Fossil concentration of the Muhi Quarry

The fossil concentration of the Muhi Quarry represents a polytypic association defined by an accumulation of invertebrates, vertebrates, and trace fossils. The sample consists of about 2,200 specimens in a variable state of preservation. Invertebrates include ammonites, crustaceans, echinoids, and crinoids. Vertebrate groups comprise cartilaginous fishes and bony fish; remains belonging to an unidentified reptile are also present. Class-level distribution of this record is shown in Figure 3. There are numerous coprolites, probably produced by some fossil groups, such as fish, crustaceans, and/or cephalopods.

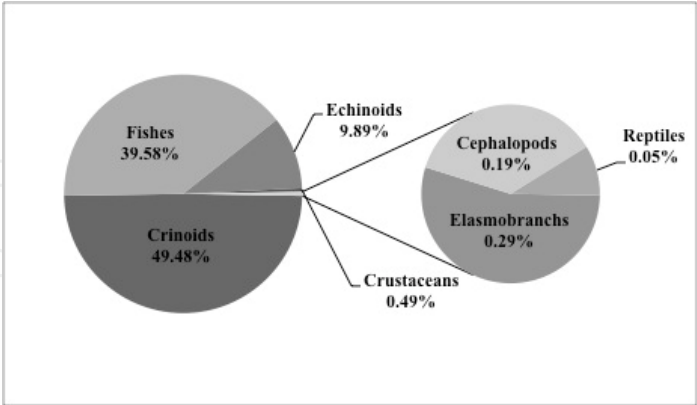


Fig. 3. Class-level distribution of fossil concentration in the Muhi Quarry, mid-Cretaceous (Albian-Cenomanian) of Hidalgo state, central México.

Crinoids are the most abundant group, including about 1,000 un-stalked forms of the Order Comatulida, which are comparable to the Upper Jurassic to Lower Cretaceous genus *Saccocoma* (Turek et al., 1989). Numerous disarticulated echinoid spines (about 200 specimens) are present. Crustaceans and ammonites are less abundant in comparison with other

invertebrates of the quarry. Crustaceans include specimens belonging to Aegeridae and Palinuridae families (Feldmann et al., 2007), consisting of about 10 specimens. Ammonites include five poorly preserved specimens tentatively assigned to ?*Mortoniceras* sp. (Bravo-Cuevas et al., 2009; González-Rodríguez & Bravo-Cuevas, 2005).

Fishes are the second most abundant group, consisting of several complete specimens, and numerous skulls, fins, and vertebral series; the sample includes about 800 specimens in a variable state of preservation. The diversity recorded at the moment holds isolated shark teeth and vertebrae, two incomplete bodies of Rajiformes, and 15 Neopterygian families. Majority of the fish groups are under detailed taxonomic study, in addition to an unidentified reptile.

6. Taphonomy: A preliminary approach

6.1 Fishes

The fish assemblage mainly consists of incomplete skeletons highly disarticulated, whereas partially complete skeletons show a variable degree of disarticulation; a low frequency of complete articulated skeletons or slightly disarticulated is observed (Figure 4A). This

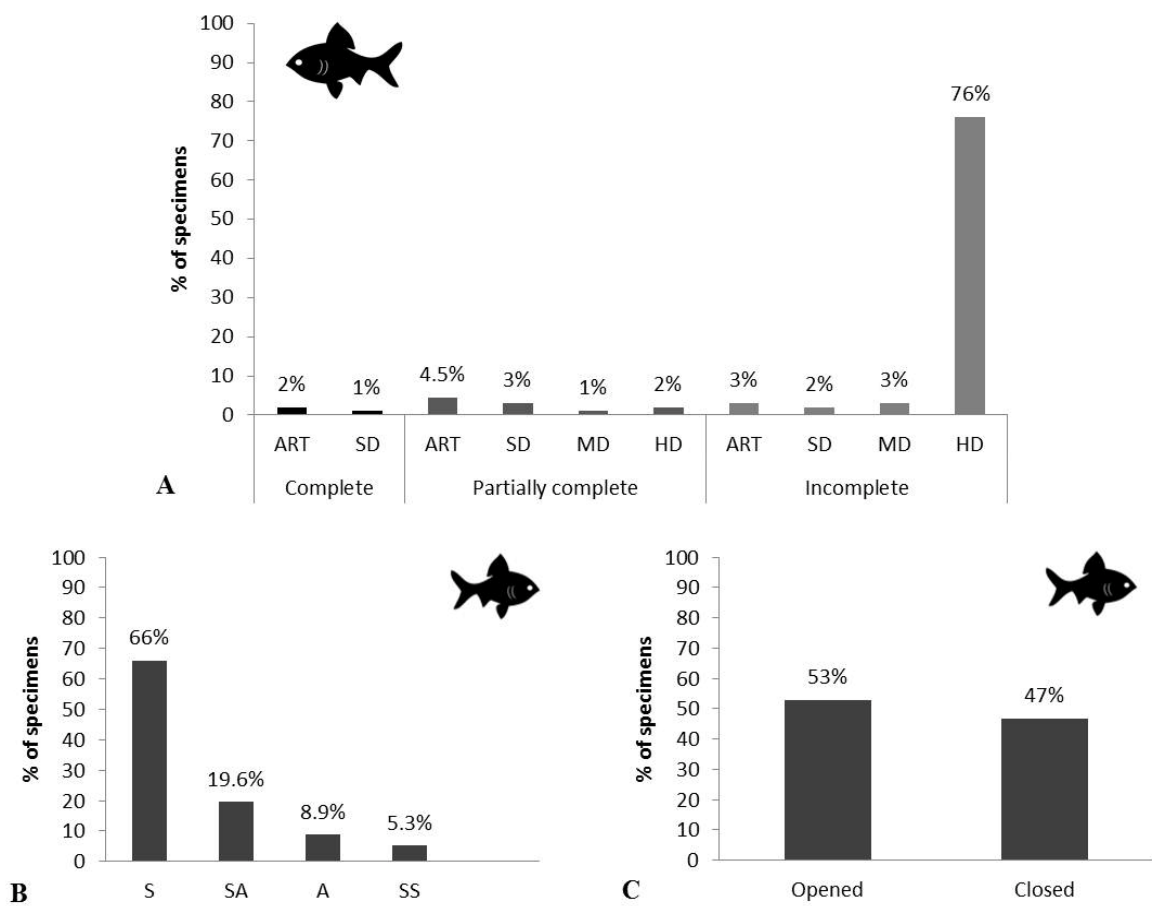


Fig. 4. Frequency distribution of taphonomic features evaluated in bony fish. A) Taphonomic grades of anatomical completeness and disarticulation. B) Deformations of axial skeleton. C) Specimens with jaws opened or closed. Abbreviations: ART= articulated, SD= slightly disarticulated, MD= moderately disarticulated, HD= highly disarticulated, S= straight, SA=slightly arched, A= arched, SS= S-shaped.

pattern points to a slight degree of anatomical completeness and a high state of disarticulation, which suggests that the majority of fish carcasses experienced a full flotation related to water warm conditions (Elder, 1985; Elder & Smith, 1988). In full floating conditions fishes commonly lose dermal skull bones and/or the skull is completely disarticulated from the body (Wilson 1980, 1988a, 1988b); fish thanatocenosis of the Muhi Quarry exhibits this pattern. Moreover, the low degree of anatomical completeness observed, implies a relatively high post-mortem transport, turbulence, decay, and/or bioturbation (McGrew, 1975).

Scavenging frequently occurs in high or sufficient oxygenated waters (Elder, 1985). In particular, the scavenging effect on fish bones produces a pattern of disarticulation that is distinguished by skeletal parts scattered in all directions and without orientation (Smith & Elder, 1985). This condition is rarely observed in the fish skeletons recovered from Muhi Quarry, thus suggesting low or none scavenging activity at the site of deposit, which in turn is indicative of low levels of water oxygenation (Smith & Elder, 1985).

Majority of fish specimens do not show axial skeleton deformation, but some exhibit an arched or S-shaped body (Figure 4B). The bending of the vertebral column is explained as a natural post-mortem effect (Bienkowska, 2004; Jerzmanska, 1960); but, a straight condition of the vertebral column suggests a slow rate of decay which is delayed in conditions of high salt concentrations (Hecht, 1933) and /or low levels of water oxygenation (Schäfer, 1972). Based on these evidences, it is possible that changes in the salinity and oxygenation of the mass water produced the post-mortem effect pattern observed in the Muhi Quarry fishes.

Proportion of fish specimens with an opened and closed jaw is almost equal (Figure 4C, Figure 5H-G). Openness of the jaws indicates sudden death of the fish caused by asphyxiation, poisoning, heat shock or choking up of the gills produced by suspended particles in the water (Ciobanu, 1977, as cited in Bienkowska, 2004; Elder & Smith, 1988; Wilson, 1988b). This suggests that the cause of death of the Muhi Quarry fishes was diverse; it is probable that differential causes of death were related to environmental fluctuations of salinity and oxygenation at the site of deposit.

6.2 Crinoids

Several strata of the Muhi Quarry are covered by comatulids (Figure 6A); its anatomical completeness varies from complete to partially complete individuals, and the majority of the specimens are articulated (Figure 7, Figure 6B-D). Complete disarticulation of recent comatulids occurs relatively fast after a few days, unless they are rapidly buried or removed from the normal cycle of post-mortem disintegration (Blyth Cain, 1968; Liddell, 1975; Meyer, 1971). It is remarkable that majority of the comatulids have their arms coiled, indicating dehydration caused by hypersaline waters (Seilacher et al., 1985). Hence, we propose a sudden death promoted by hypersaline waters, accompanied by a rapid burial in the Muhi Quarry comatulids; but it is also probable that a low-level of oxygenation additionally promoted their death.

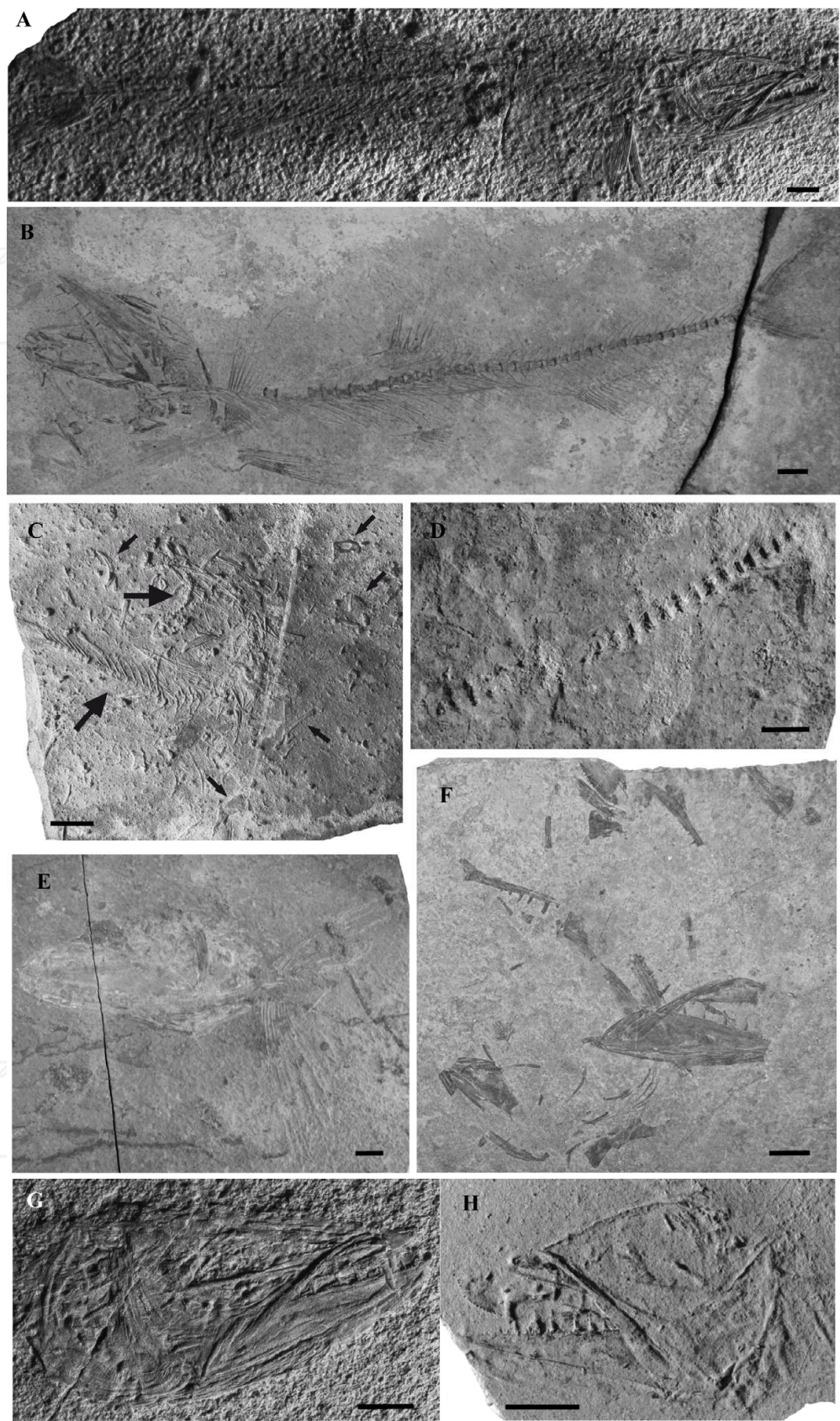


Fig. 5. States of preservation in enchodontids, most abundant fish group from the Muhi Quarry (except D). (A-B) Well-preserved specimens. A) UAHMP-1059, complete and

articulated individual with vertebral series straight. B) UAHMP-608, complete and slightly disarticulated individual with the head rotated upwards. (C-F) Moderate to poorly preserved specimens. C) UAHMP-3166, slab showing a partially complete enchodontid specimen (lower large arrow) with the head bones disarticulated (small arrows), which can be attributed to scavenging activity; a juvenile indeterminate specimen is also preserved in the same slab (upper large arrow). D) UAHMP-2968, isolated vertebral series of unidentified specimen. E) UAHMP-2202, skull slightly disarticulated. F) UAHMP-2203, skull bones highly disarticulated. (G-H) Openness/Closure of jaws. G) UAHMP-2170, specimen with jaws closed. H) UAHMP-784, specimen with jaws opened. Scale bars equal 1 cm.

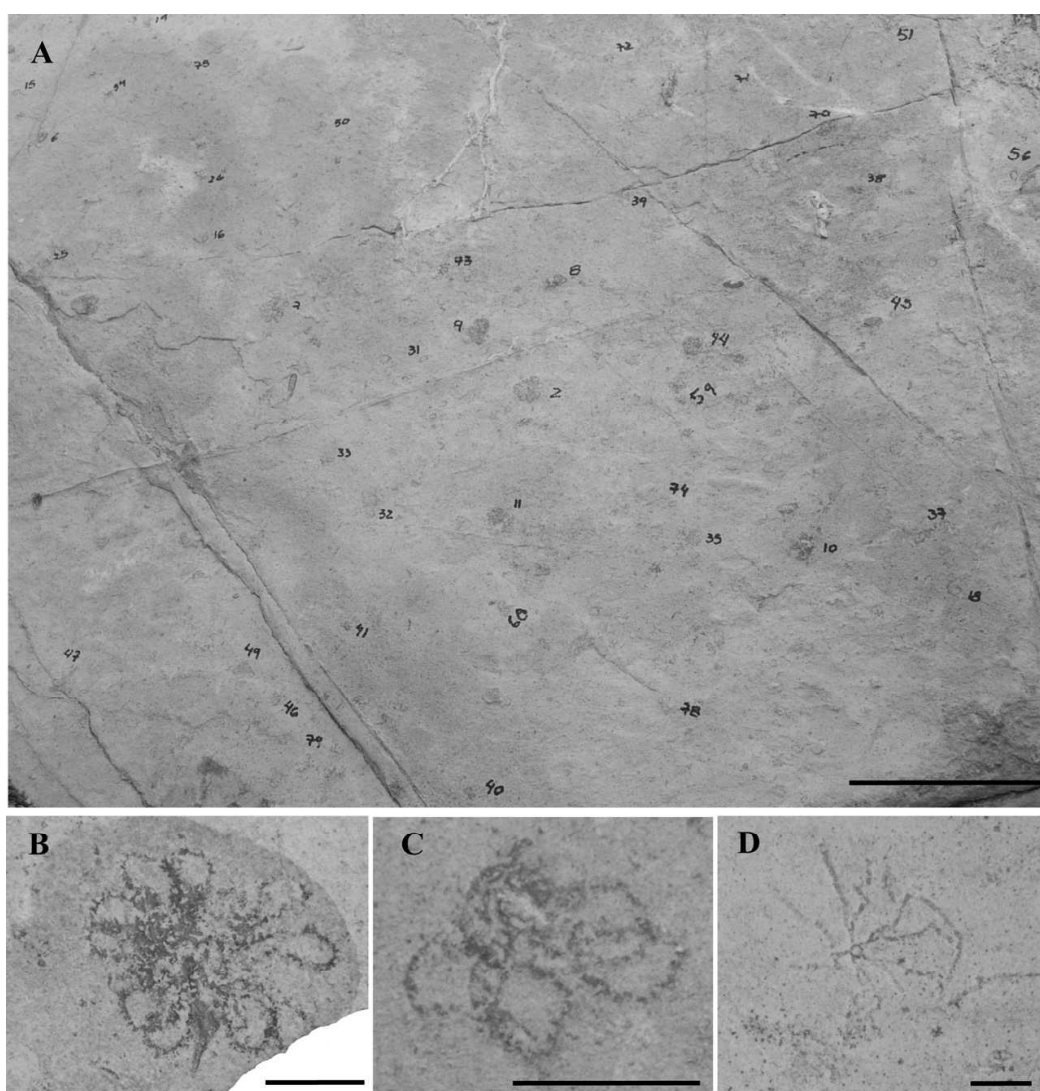


Fig. 6. States of preservation in the comatulids of the Muhi Quarry. A) Complete stratum covered by comatulids in a fine state of preservation (Scale bar equals 5 cm). (B-D) Well-preserved specimens. B) UAHMP-2892, complete and articulated individual. C) UAHMP-3099, partially complete and articulated individual. D) UAHMP-3685, incomplete and slightly disarticulated individual. Scale bars in B-D equal 1 cm

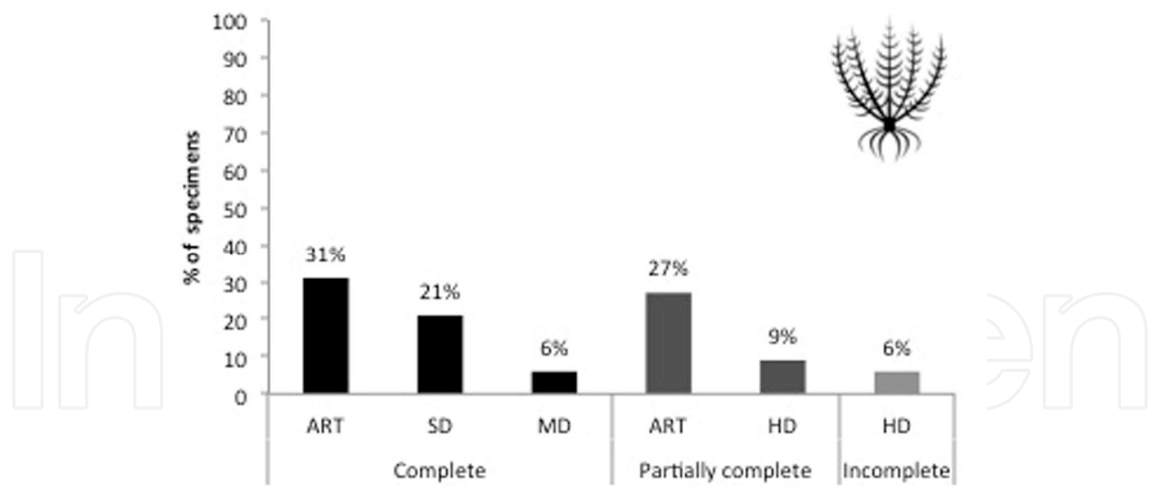


Fig. 7. Frequency distribution of taphonomic features evaluated in crinoids, including anatomical completeness and disarticulation. Abbreviations are as in Figure 4.

6.3 Other invertebrates

Crustaceans belonging to Aegeridae are well preserved (Figure 8A-B); majority of the specimens are complete or partially complete individuals, a small proportion are disarticulated and/or broken (Figure 9). The presence of non-fragmented fragile skeletal elements (such as the lightly sclerotized exoskeleton of crustaceans) is indicative of a low-energy environment (Brett & Baird, 1986). It has been shown that scavengers, bacteriological decay, and infaunal bioturbation rapidly destroyed fresh carcasses of decapods; therefore, they occasionally persist more than one to two weeks, whereas in a setting without any physical disturbance, disintegration occurs after one week (Plotnick, 1986). Hence, the presence of well-preserved crustaceans in the Muhi Quarry suggests a rapid burial, and non-physical damage of their carcasses. Only one specimen belonging to *Palinurus* is poorly preserved; a similar condition also is observed in ammonites referable to *?Mortoniceras* sp. (Figure 8C-D).

On the other hand, echinoids are represented by numerous isolated spines (Figure 8E-F). This is a common condition in fossil echinoids preservation, due to spines are separated from the body almost immediately after their death; implying post-mortem transport. Echinoid spines are heavy enough for avoiding individual or collective transport over long distances; thus, they are usually found near or at the original habitat of the individual (Schäfer, 1972).

6.4 General taphonomic consideration

The preliminary taphonomic evaluation performed in the macrofossils of the Muhi Quarry, suggests that fluctuations of oxygenation-level and salinity occurred at the site of deposit, related to temporal lowering of dissolved oxygen and to a salinity increment in the mass water. Based on the depositional environment proposed by Bravo-Cuevas et al. (2009), it is probably that these stagnant conditions were controlled by alternated influx of neritic waters and open oceanic waters, further occasionally influx of coastal waters. Additional detailed taphonomic and geochemical studies will lead to precise and corroborate this contention.

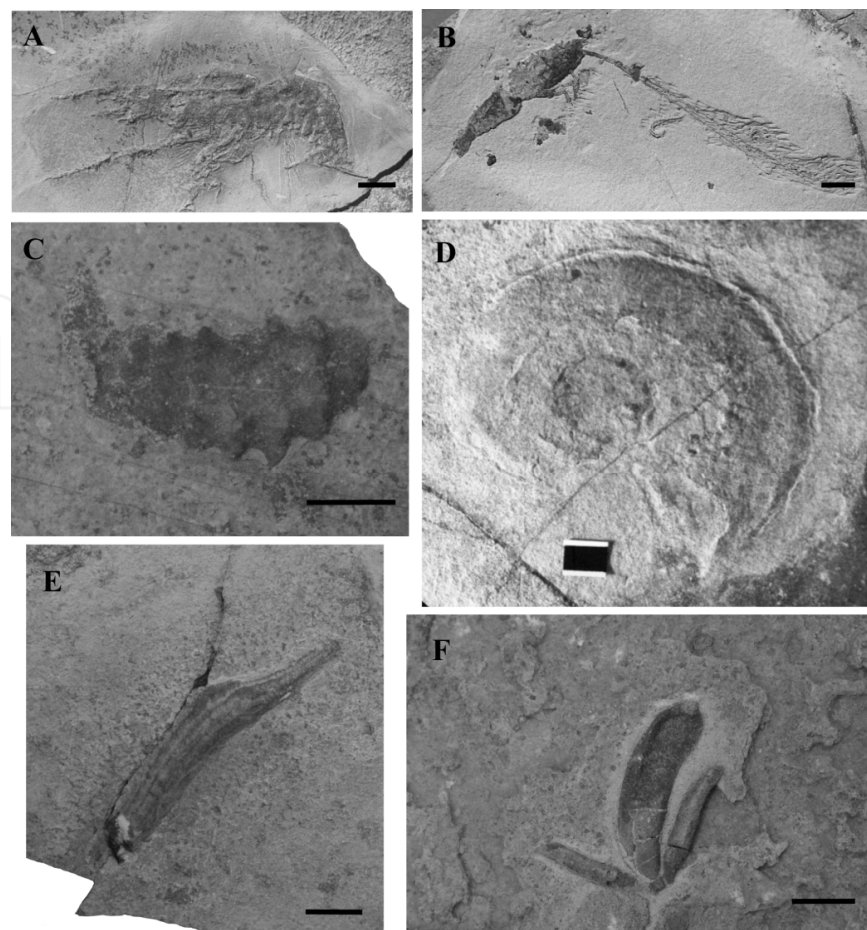


Fig. 8. States of preservation in other groups of invertebrates from the Muhi Quarry. (A-B) Aegeridae well preserved specimens. A) UAHMP-711, complete and articulated individual. B) UAHMP-824, complete and slightly disarticulated individual. (C-D) Ammonoid specimens poorly preserved. C) UAHMP-1465, isolated fragment of shell. D) UAHMP-2032, mold of an ammonite referable to *?Mortoniceras* sp. (E) UAHMP-702, isolated and partially articulated and (F) UAHMP-741, partially articulated spines of echinoids. Scale bars equal 1 cm.

7. Characterization and classification of the fossil assemblage

The fossil assemblage from the Muhi Quarry is mainly composed of nektonic animals, such as bony fish, sharks, crustaceans belonging to *Aeger* (Clarkson, 1998), and ammonites referable to *?Mortoniceras* sp. [this genus probably had a deep-nektonic mode of life (Reboulet et al., 2005)]; floating organisms like the comatulids are also present. It is reasonable to expect that several members of these groups may potentially live at or near the site of deposit; the occurrence of fishes in different ontogenetic stages (for example, enchodontids and berycoids) (Fielitz & González-Rodríguez, 2010; González-Rodríguez, & Fielitz, 2009) is consistent with this argument. Specimens from the Muhi Quarry show a variable degree of disarticulation, which is related to a differential movement of the specimen from its original source; nevertheless, it does not imply that they are out of its life habitat. Both considerations are related to a parautochthonous association (Kidwell et al., 1986; Martin, 1999). Additionally, it has been observed that carbonate sediments normally consist of the autochthonous or parautochthonous remains of organisms living at or near the site of the deposit (Maiklem, 1968).

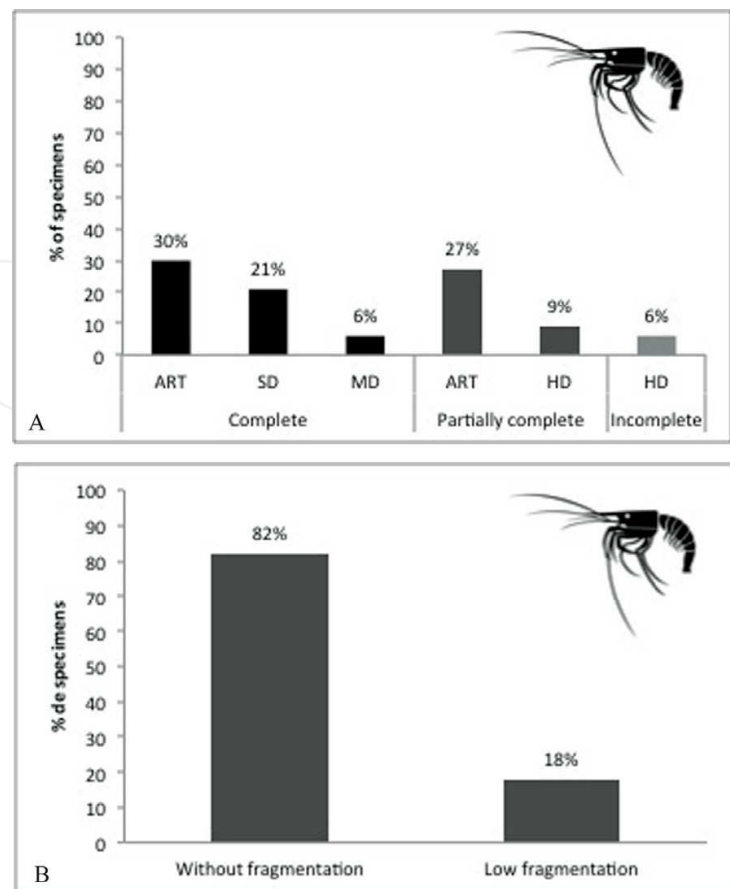


Fig. 9. Frequency distribution of taphonomic features evaluated in crustaceans. A) Taphonomic grades of anatomical completeness and disarticulation. B) Taphonomic grades of fragmentation. Abbreviations are as in Figure 4.

The record includes fossil material belonging to lepisosteids and to the spiny lobster *Palinurus*. Extant lepisosteid species are primarily freshwater fishes that occasionally swim into coastal marine or brackish environments, whereas fossil species are known from freshwater deposits or are thought to have been temporary immigrants from nearby freshwater tributaries (Grande, 2010). On the other hand, *Palinurus* is an epibenthic form typical of rocky, muddy and/or sandy bottoms (Alvarez et al., 1996). Considering the site of deposit that represents the Muhi Quarry, both groups occur in a foreign life habitat; furthermore, specimens referable to these taxa exhibit a low degree of preservation. Thus, they would be considered as allochthonous forms. Given this, the association of the Muhi Quarry is representative of a mixed assemblage, integrated mainly by parautochthonous forms and in a lesser degree by autochthonous forms, which is referred as a parautochthonous-allochthonous association (following Kidwell et al., 1986).

The fossil assemblage from the Muhi Quarry shows an effect of time-averaging. The presence of skeletal elements at the site of deposit with a differential durability (teeth, bones, and chitinous exoskeletons), which persist it at or near the sediment surface for variable periods of time, evidences an accumulation of specimens that not necessarily were alive at the same time (Flessa, 2008). Taphonomic evidence may also indicate time-averaging; particularly, specimens belonging to enchodontids, the most abundant group of fishes in the quarry, show a mixture of states of preservation, indicating some degree of time-averaging. By the same token,

variation in preservation among taxa is also indicative of time averaging; the co-occurrence of fish skeletons in a variable state of preservation, with delicate articulated chitinous exoskeletons belonging to crustaceans supports this argument. This variability in preservation within and among taxa leads to classified the fossil assemblage as a *within-habitat assemblage*, suggesting a time-averaging over time intervals ranging from years to thousand years (Flessa, 2008); specifically in marine fossil assemblages it would be expected at least centuries of extent of time-averaging (Kidwell & Bosence, 1991; Martin, 1999).

8. The Muhi Quarry: A *lagerstätte*

There exist various *Fossil-Lagerstätten* in México, characterized by diverse fauna of invertebrates and vertebrates, coming from different ages and several paleoenvironments: The Tlayúa quarry of Albian age is a locality frequently compared with Solnhofen because of the great diversity of fauna and the excellent state of preservation, including details of muscles, gills, digestive tracts, and stomach contents with fishes making up 70%–80% of the macrofossils deposited in a restricted basin with marine and freshwater influence (Alvarado-Ortega et al., 2007; Applegate et al., 2006); the El Chango and El Espinal quarries of Albian-Cenomanian age (Alvarado-Ortega et al., 2009) with plant remains, mollusks, crustaceans, insects and different fish taxa. Vega et al. (2006) suggested that these deposits were accumulated within a shallow lagoon or estuary with occasional freshwater influence; the Vallecillo quarry of early Turonian age (Blanco-Piñón et al., 2002) where the fauna consisting of invertebrates, sharks, neopterygians, and latimerioids was deposited on an open shelf, which is supported by the pelagic assemblage and the absence of submarine barriers in the region around Vallecillo, Nuevo León (Ifrim et al., 2005, 2010); the El Rosario quarries of late Turonian-early Coniacian age containing plant remains, invertebrates and vertebrates with anatomical details of soft tissues preserved and some specimens conserved in 3D, that were deposited in an open marine shelf environment, at least 100 km away from coast line (Stinnesbeck et al., 2005); and the Xilitla quarries of Turonian age containing invertebrates and fishes deposited in an open shelf environment with low energy influx (Blanco-Piñón et al., 2006). Although there are some similarities among supraspecific fish taxa within Muhi Quarry and other Late Cretaceous localities of México, at species level the Muhi fish are different, most of them representing new species. Moreover the paleoenvironment condition where the biota was deposited is dissimilar in most cases; although the proposed paleoenvironment for the Muhi quarry seems to be comparable to those of El Rosario and Xilitla quarries, the lithology, and paleobiota are quite different. We have not found inoceramids that are common in both localities and either plant remains.

The Muhi Quarry fauna has been previously compared with some Cenomanian fossil *lagerstätten* of the eastern Tethys such as Namoura, Hakel and Haula in Lebanon, Jebel Tselfat, Kem Kem beds and Daura in Morocco, Ein-Yabrud in Jerusalem, English Chalk in England, and Comen in Slovenia (Bravo-Cuevas et al., 2009; González-Rodríguez & Bravo-Cuevas, 2005), but there is a closer similarity with the lower Cenomanian fish fauna of Hakel and Haula in Lebanon which paleobiota also includes crustaceans and land plants. In these localities the fish beds consist of thin-bedded, siliceous limestone alternating irregularly with more massive limestone, nodules and lenses of impure chert occur occasionally throughout the beds (Patterson, 1967). The fish beds were deposited in small basins, 250 m across, which Hückel (1970) interpreted as sinkholes formed by tectonic activity on the contemporary seafloor, at the outer margin of the continental shelf (Forey et

al., 2003). The main difference among the Muhi Quarry and Hakel and Hajula quarries is the presence of land plants and terrestrial fauna in the Lebanese localities. This condition does not occur in the Mexican outcrop, suggesting that the Muhi fauna was deposited offshore.

9. Conclusion

The fossil concentration of Muhi Quarry represents a mixed assemblage integrated by a parautochthonous-allochthonous association; furthermore, it is evidenced that the fossil assemblage may be considered as a *within-habitat assemblage*. A preliminary taphonomic approach suggests that at site of deposit, occurred conditions of hypersalinity and/or low-level oxygenation, favoring an important accumulation of organic remains and its eventual differential preservation; further detailed taphonomic and geochemical studies will lead to precise and corroborate this argument. Nevertheless, stagnant conditions are commonly associated to the formation of a *Fossil-lagerstätte*. The Muhi Quarry is comparable in preservational and environmental conditions to other mid-Cretaceous Mexican quarries considered as *lagerstätten*, such as El Rosario and Xilitla, northern and central México, as well as to the Hakel and Hajula quarries of eastern Tethys, although the fish fauna seem to be endemic for the Atlantic Ocean and the Paleo- Caribbean province.

10. Acknowledgment

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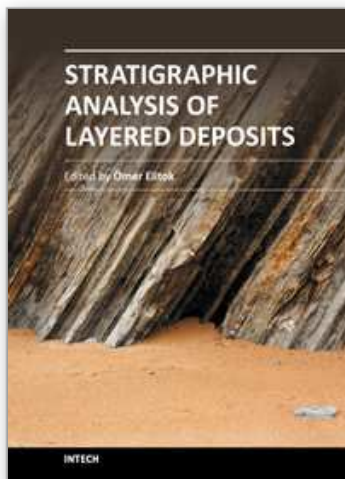
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Stratigraphy, a branch of geology, is the science of describing the vertical and lateral relationships of different rock formations formed through time to understand the earth history. These relationships may be based on lithologic properties (named lithostratigraphy), fossil content (labeled biostratigraphy), magnetic properties (called magnetostratigraphy), chemical features (named chemostratigraphy), reflection seismology (named seismic stratigraphy), age relations (called chronostratigraphy). Also, it refers to archaeological deposits called archaeological stratigraphy. Stratigraphy is built on the concept "the present is the key to the past" which was first outlined by James Hutton in the late 1700s and developed by Charles Lyell in the early 1800s. This book focuses particularly on application of geophysical methods in stratigraphic investigations and stratigraphic analysis of layered basin deposits from different geologic settings and present continental areas extending from Mexico region (north America) through Alpine belt including Italy, Greece, Iraq to Russia (northern Asia).

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