Paleobiology and taphonomy of fishes from the Late Cretaceous marine ecosystems of northeastern Mexico

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Chapter 1

Abstract

The platy limestone deposit of Vallecillo in the northeastern Mexican state of Nuevo León is well known for its exceptionally well preserved faunal assemblage of vertebrate in addition to invertebrate fossils of Late Cretaceous (Latest Cenomanian-middle Turonian) age. Large marine reptiles are associated with cartilaginous as well as sarcopterygian and actinopterygian fishes that populated an open marine environment, at least 300 km away from the nearest coast. The most common fishes in the Vallecillo platy limestone member are the halecomorph needle fish *Rhynchodercetis yovanovitchi*, the teleost *Tselfatia formosa*, the pycnodont *Nursallia gutturosum* and the pachyrhizodont fish *Goulmimichthys roberti*.

Goulmimichthys roberti is a fusiform taxon that resembles modern tunas or mackerels. The fish reached a maximum length of 650 mm and is interpreted as a sustainable high-speed swimmer that formed schools in the pelagic. 177 individuals from Vallecillo were reviewed including 11 specimens from deposits near Múzquiz in Coahuila, about 400 km to the north of Vallecillo. These latter deposits reflect significantly more shallow and more near-shore environments extending the stratigraphical and environmental range of the taxon previously known from the Cenomanian to Santonian. *Goulmimichthys roberti* may thus have migrated between shallow environments and the pelagic.

Taphonomic analyses point to articulated and complete specimens in both deposits, Vallecillo and Múzquiz, excluding a phase of carcass transportation. Different embedding positions suggest that the sea bottom of the northern (Múzquiz) deposits must have been more soften.

Specimens from Vallecillo are majorly preserved with open mouth and spread-out fins which is interpreted as a result of respiratory stress associated with anoxic sea bottom conditions. The oxygen-deficient bottom also excluded scavengers and favored preservation. Specimens from Múzquiz were rapidly phosphatized preserving additional details, and corpses were covered in a soft mud sediment that prevented the carcass to turnover into a lateral position as seen in Vallecillo.

During the revision of *G. roberti*, the first Cretaceous isopod was revealed on a specimen from Vallecillo. The isopod is directly attached to the skull of the fish host and

slightly twisted exposing the right body side. The isopod is nearly complete with most of the appendages allowing for an assignation to a new species of Cymothoidae named *Mothocya vallecillae*. A parasitic lifestyle is based on hook-like distal articles on all appendages (dactyli) as well as the position on the host, close to the gills. Modern *Mothocya* populate the branchial cavity of the host and feed on tissue, blood and mucus. A scavenging mode of life appears unlikely for *M. vallecillae* due to the anoxic bottom conditions reported from Vallecillo and the preservation of host and parasite which exclude the interference of scavengers.

Mothocya vallecillae is of special interest because of the direct association to *G. roberti* which belongs to an pelagic ecosystem. Parasitic isopods directly attached to the fish host are presently only reported from Solnhofen in Germany.

The teleost *Tselfatia formosa* is a frequent member of the Vallecillo fish assemblage. The fish resembles modern fan fishes and is characterized by extraordinary long dorsal and anal fins, pseudo fulcra on the main rays of the unpaired fins, and small pectorals above the ventral column. A review of 149 specimens revealed two different body shape types which are interpreted as sexual shape dimorphism excluding ontogenetic variation. Deeply keeled specimens are interpreted as females that are twice as long as high compared to torpedo-shaped males which are three times longer than wide.

The teleost is frequently articulated and complete and the unpaired fins are retracted behind modified scales which allow for comparison to extant fan fishes (e.g. *Pteraclis* and *Pterycombus*). A membrane between the fin rays is concluded due to fin preservation and arrangement. Taphonomic analyses suggest that *Tselfatia formosa* inhabited deeper water environments similar to recent fan fishes.

Chapter 2

Introduction

Vallecillo is located 100 km north of Monterrey, the capital city of the northeastern Mexican state of Nuevo León (Figure 1). Shallow quarries to the south of the village yield yellow to light grey platy marly limestones that are extracted for commercial purposes, e.g. floor tiles and flagstones (Figure 2 A and B). The limestone layers are each only a few centimeters thin, flat, and finely layered, even showing millimetrical lamination, thus qualifying for an assignation as *plattenkalk*. The sediment splits parallel to the lamination, frequently exposing a slab and counter slab preservation of fossils (Figure 2 C). At Vallecillo, the extraction and preparation of the limestone slabs is entirely manual and an exceedingly exhausting work. Quarrymen use large bars and a hammer to break each slab out of a block and to split it into smaller pieces (Figure 2 B).

The importance of the quarry and its fossils was first recognized 1995 by a private collector from Monterrey. He called the attention of the paleontologist W. Stinnesbeck, who initiated the first scientific investigations together with Dr. López Oliva (Blanco-Piñón et al. 2001, 2002, Blanco-Piñón 2003; Ifrim 2006, Giersch 2014). Fossils are scientifically investigated since that time and dated to the Cenomanian-Turonian (93 Ma) using planctic foraminifers and invertebrates (Ifrim 2006).

The research on the fishes from Vallecillo was first conducted by Blanco-Piñón (et al. 2001 2002; 2003), who provided an initial overview of the fishes in his dissertation and initial species descriptions e.g. *Vallecillichthys multivertebratum*, *Rhynchodercetis regio* or *Robertichthys riograndesis* (Blanco-Piñón and Cavin 2003; Blanco-Piñón and Alvarado-Ortega 2006; 2007; Blanco-Piñón et al. 2007; 2008). Giersch (2014) revised many of the osteological descriptions in his thesis and introduced careful preparation of the specimens prior to description, arguing that a lack of fossil preparation leads to inappropriate descriptions. His work includes specimens not only from Vallecillo but also from the northern deposits of Múzquiz: la Mula, Carranza, Los Temporales, El Rosario and Tanque Nuevo. These deposits reflect a shallow shelf ramp during the early late Cretaceous that differs from the coeval pelagic Vallecillo environment. In the dissertation presented here, only few fossils from Múzquiz were examined and come from San Carlos, Piedritas, El Pilote, Carranza and Los Temporales (Figure 1).

Rather, the present work is primarily based on material from Vallecillo. This Konservat-Lagerstätte has become increasingly interesting because fossils are excavated on a continuous basis as work in the quarries is ongoing. During the past decade the best and most complete of these fossils have been collected by a collector from Monterrey, Ing. Mauricio Fernandez Garza, with the idea to make this invaluable material accessible to the public. A public museum is presently built in the center of Monterrey which is exclusively dedicated to the paleontological wealth of the Vallecillo fossil deposit and will be opened in autumn 2023. The collection of Ing. Fernandez Garza, consisting of >1000 Vallecillo specimens, has been available for investigation for the author of this thesis, but the majority of these specimens remains undescribed.

The taphonomic work presented here is the first one that has been conducted on Vallecillo fishes. It provides a first palaeobiological reconstruction of the lifestyle of the pachyrhizodont *Goulmimichthys roberti* as well as the teleost *Tselfatia formosa* and a first taphonomic description of their preservation using the largest amount of data yet available. In addition, the first isopod *Mothocya vallecillae* from Vallecillo is described.



Figure 1: Location of the platy limestone deposit of Vallecillo and the northern deposits of Múzquiz in Mexico.



Figure 2: The Vallecillo outcrop (A). Slabs are extracted using iron bars and a hammer (B) and split into a slab and couterslab (C).

2.1 Depositional environment of Vallecillo

There are numerous Plattenkalk localities known, such as Solnhofen in Germany, Haqel, Hjoula, en Nammoura and Sahel in Lebanon, the Santana and Crato Formation in Brazil and Las Hoyas and El Montsec in Spain (Selden and Nudds 2012). Most of the platy limestone localities were deposited in a shallow marine setting similar to the famous Solnhofen locality. Solnhofen represents a shallow lagoon community with hyper saline bottom water, but in contrast to Solnhofen, the platy limestone from Vallecillo was formed in the open ocean. The deposit is located in north-eastern Mexico and comprises yellow to light grey platy limestones of Late Cenomanian-middle Turonian age (Late Cretaceous) that are finely laminated and assigned to the Agua Nueva Formation. This 7 m thick limestone-marl alteration known as the Vallecillo member was deposited in the outer shelf environment of the ancient Gulf of Mexico (Ifrim, 2006).

These limestones were formed at the end and during the oceanic anoxic event 2 (OAE2), which is a global anoxic event that occurred during the early Late Cretaceous (Uppermost Cenoman), because of extreme greenhouse conditions. High atmospheric CO_2 concentrations, high ocean spreading rates and submarine vulcanism initiated climate change and extreme temperature fluctuations that reached 36 to 42 C° in the ocean (Snow and Duncan 2005; Bice et al. 2006). Such conditions caused problems with thermohaline convections leading to ice free poles, an interruption of carbonate deposition and to substantially embedding of organic rich matter that is today preserved as black shale (Ifrim 2006; Ifrim et al. 2011b). These black shales form the basis of the Vallecillo Member and, in the aftermath of this global event, the Vallecillo Plattenkalk Member that

contains numerous fossils. Stagnation of the ocean circulation and low O_2 dissolubility was caused by these extreme water temperatures. The marine ecosystem suffered from a breakdown of the carbon factory and the extinction of deep-dwelling foraminifers which are important for the food chain in the ecosystem. The faunal turnover is documented by a decrease in foraminiferal diversity and small-sized individuals reaching early maturity. An increase of the low-oxygen tolerant species *Heterohelix* has been documented from the Cenomanian-Turonian boundary and reflects the expansion of the oxygen minimum zone (Keller und Pardo 2004). Ammonoids and inoceramid bivalves were also affected during the latest Cenomanian and show a major extinction event (Ifrim and Stinnesbeck 2007, 2008, Ifrim et al. 2011b, Ifrim 2015). Despite the fact that inoceramids inhabited anoxic environments their planktotrophic larvae suffered from these anoxic conditions, as their oxygen-dependent larvae had to cross the extended oxygen minimum zone to reach the seafloor for further development (Ifrim 2006; Ifrim et al. 2011b).

A slow recovery of carbonate producing organisms is identified in the early and middle Turonian. Ammonoids become more abundant but not very diverse (Ifrim 2006). Benthic inoceramids remain rare during the early Turonian until a flood of *Mytiloides* sp. occured which is probably initiated trough larval transportation by currents (Ifrim 2006).

Larger vertebrates and fishes were less affected by the OAE2 event, but suffered from the low O_2 content in the water, food web disturbances and fluctuating water temperatures. Because the Vallecillo sea floor was hostile, due to the stagnant anoxic water conditions, life persisted in the oxygenated parts of the water column. Inoceramid bivalves are the only animals that persisted under the anoxic conditions. These benthic organisms were probably supported by chemosymbiothic bacteria, which tolerate anoxic and dysoxic environments (Ifrim et al. 2011b). The preservation of marine animals as fossils was favored by the extreme conditions at the anoxic sea floor. Currents are nearly absent and benthic organisms are limited to inoceramids. Scavengers are totally excluded. Carcasses were embedded in an oxygen-free setting and are therefore nearly complete and articulated preserved. Bones are recrystallized to calcite but soft tissue is also obtained. Vertebrate bodies are usually compressed and show a slab and counter slab preservation which is typical for Vallecillo.

2.2 The Cretaceous fish radiation

The mid Cretaceous was marked by significant climatic turbulences and greenhouse conditions which were triggered by a rise in oceanic crust production and oceanic volcanism (Cavin et al. 2007). Two climatic phases can be distinguished from the Albian to Santonian (Giersch 2014) (Figure 3). The first phase extends from Albian, Cenomanian to Lower Turonian and is characterized by a drastic sea level rise and falling sea surface temperatures. Sea surface temperature reaches a maximum of 36 to even 42 C° at the Cenomanian-Turonian boundary (Bice et al. 2006; Forster et al. 2007b; O'Brien et al.

2017). In the second phase from the Cenomanian-Turonian boundary to the Santonian, the fluctuating sea level finally reaches a stable and low level while temperatures remain high.

The opening of the Atlantic ocean as well as the expansion of the Western Interior Seaway during the Albian to Turonian age, allowed for species migration between the central Tethys and the Gulf of Mexico (Cavin 2008). Giersch (2014) documented several vicariant (Aptian-Santonian) events which are documented by fossil findings from e.g. the Haq localities in Lebanon, Santana in Brazil, Komen in Slovenia, Agoult in Morocco, the English Chalk, and Mexican localities. For instance, *Neoproscinetes*, *Vinctifer* and *Notelops* previously reported from the Santana Group in Brazil are also present in the Albian Tlayúa locality in the Mexican state of Puebla. For the Cenomanian, *Dixonanogmius*, known to exist in the Múzquiz localities of northern Coahuila is now documented from the English Chalk and Slovenia (Komen), and *Scombroclupea*, well known from Tethyan sites in Morocco, Lebanon, Croatia and Slovenia is reported from the La Mula locality in northern Múzquiz (Giersch et al. 2011). For the Turonian, numerous species from Vallecillo (e.g. *Tselfatia*, *Goulmimichthys*, *Heckelichthys*) show either identical or closely related species in Morocco, Germany, Itlay, Lebanon and Slovenia and must have crossed the still narrow Atlantic ocean.

According to Cavin et al. (2007) the diversity of ichthyodectiform, elopomorph, tselfatiiform, clupeomorph, pachyrhizodont, protobramoid and aulopiform fish show a positive correlation with high sea temperatures during global greenhouse intervals (OAEs) of the Aptian to Santonian, with a peak at the end-Cenomanian OAE2, but there is no direct evidence yet for this interpretation from Mexican localities.

In Mexico the maximum of fish diversification is seen in the Albian instead of the Cenomanian. Diversity is highest in the Albian Tlayúa locality in Puebla, and from there the number of species seems to slowly decrease (Figure 3). Several species known from Tlayúa got extinct but were replaced by new ones documented in Vallecillo, which turn out to be long-lived in the second climatic phase (Turonian to Santonian) (Giersch 2014).

This may be an artifact, due to insufficient paleontological knowledge of other Mexican sites and species descriptions (Giersch, 2014). During this work, for example, *Goulmimichthys roberti*, a yet undescribed pachycormid, a fragment of *Dixonanogmius*, *Rhynchodercetis yovanovitchi*, *Vallecillichthys multivertebratum*, and a coelacanth were identified from the Cenomanian San Carlos locality (Stinnesbeck et al. 2020). More research will certainly add new species to the fossil record.

In the Mexican localities the number of basal bony fishes (Osteichthyes) including the Teleosteomorpha, decreases from Albian to Coniacian, while Teleost diversity increases. Diversification of teleosts, which by far represents the dominant fish group today, initiated during the late Jurassic and accelerated during the Late Cretaceous, likely favored by high ocean water temperatures (Cavin et al. 2007). Basal Acanthomorph fish assigned to the Euteleostei, are recorded from the Albian-Cenomanian boundary onwards (Cavin et al.

2007; Giersch 2014).

The exact reasons behind the Cretaceous fish radiation are not fully understood, but in addition to climatic changes, other factors likely played a role, e.g. genome duplication (Santini et al. 2009).

For the diversity in pycnodont fish during the Cenomanian-Turonian boundary for example, a positive correlation to sea level and sea surface temperature is detected (Cawley et al. 2021). The rise in oceanic crust production is here assumed to contribute to the diversity which led to an increase in area to be colonized by reefs (Cavin et al. 2007). Apart from that it is assumed that high temperatures favor high productivity rates while shortening the generation time, food supply, growth rate and the mutability in fish (Rohde 1992). Environmental changes favoring species diversification as the opening of the Atlantic ocean, also leading to fish migration, or the availability of new resources are therefore not excluded.

After the Cretaceous/Paleogene extinction however, Acanthomorph fish probably occupied a wide variety of biomes and replaced neopterygian lineages (Cawley et al. 2021). Further investigations in Vallecillo could help to understand this process.

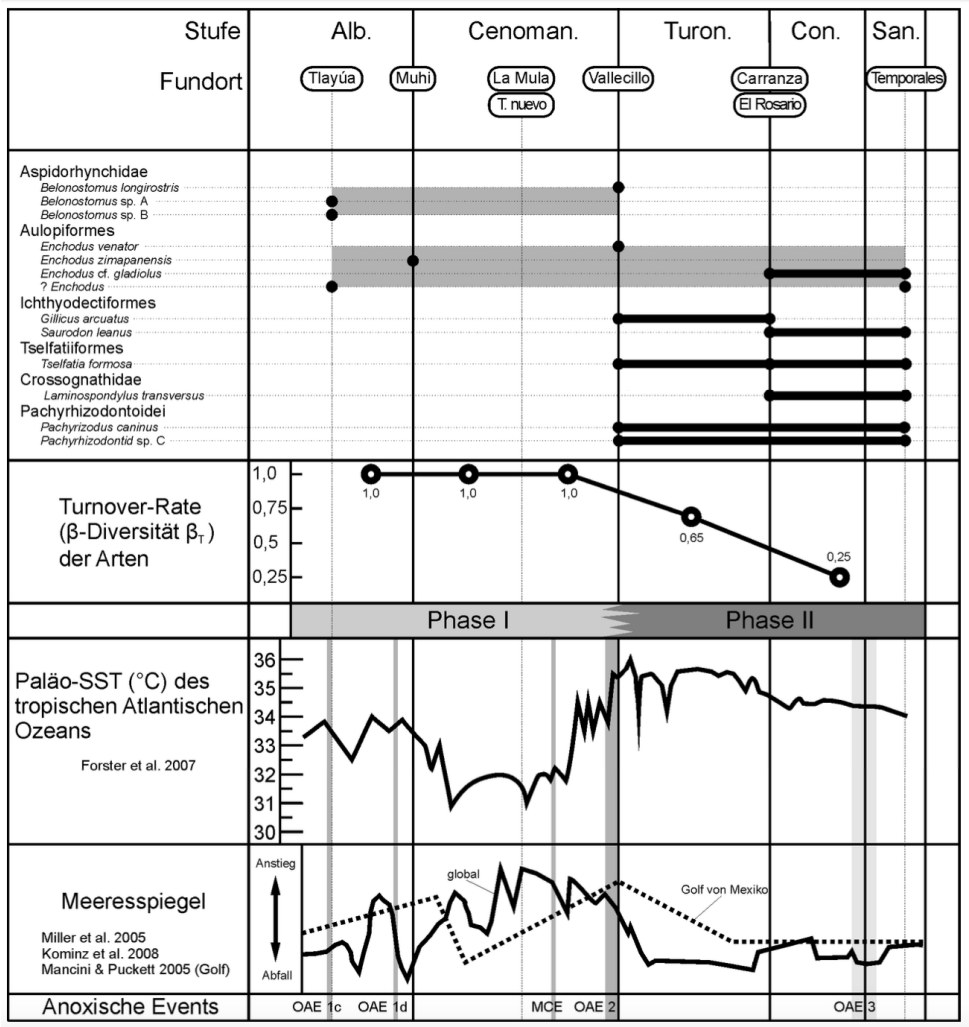

Figure 3: Sea level and temperature fluctuations during the Cretaceous correllated to species diversity seen in mexican localities. (Illustration taken from Giersch 2014).

2.3 The marine fauna from Vallecillo

During the early Turonian, Vallecillo was located about 300 to 400 km off the coast in an outer shelf environment with water depths of about 200 m (Ifrim et al. 2011a, 2011b). Climatic conditions where subtropical and surface water temperature may easily reached 36°C. (Sea surface temperature for the Cretaceous is estimated by planktonic foraminifera ($\delta^{18}O$) and fossil Thaumarchaeota (TEX_{86}) (Bice et al. 2006; Forster et al. 2007a; O'Brien et al. 2017). The Vallecillo area formed part of the western Gulf of Mexico and was connected to the Western Interior Seaway (WIS) to the North and the Tethys to the East, favoring species variety and migration (Figure 4). The assemblage is therefore a mixture of endemic species, along with taxa known from the WIS and the Tethys. Fast moving and torpedo-shaped Actinopterygian and cartilaginous predators are frequently preserved together with reptilians and invertebrates. Sarcopterygians are represented by a yet undescribed member of Latimeriidae, but Actinopterigians clearly dominate the assemblage. Euteleostei reach 3%, while Teleosts make up to 75% of the assemblage and basal Osteichthyes including Teleosteomorph fish reach 22% of the fauna (% in relation to species number) (Giersch 2014). The most abundant fish species are *Rhynchodercetis yovanovitchi*, *Nursallia gutturosum* and *Tselfatia formosa* (Ifrim 2006; Ifrim et al. 2005; Ifrim and Stinnesbeck 2007; Giersch 2014; unpublished Master's thesis: Stinnesbeck, 2017; Stinnesbeck et al. 2019), but *Goulmimichthys roberti* is also an abundant component of the assemblage (Stinnesbeck et al. 2020).

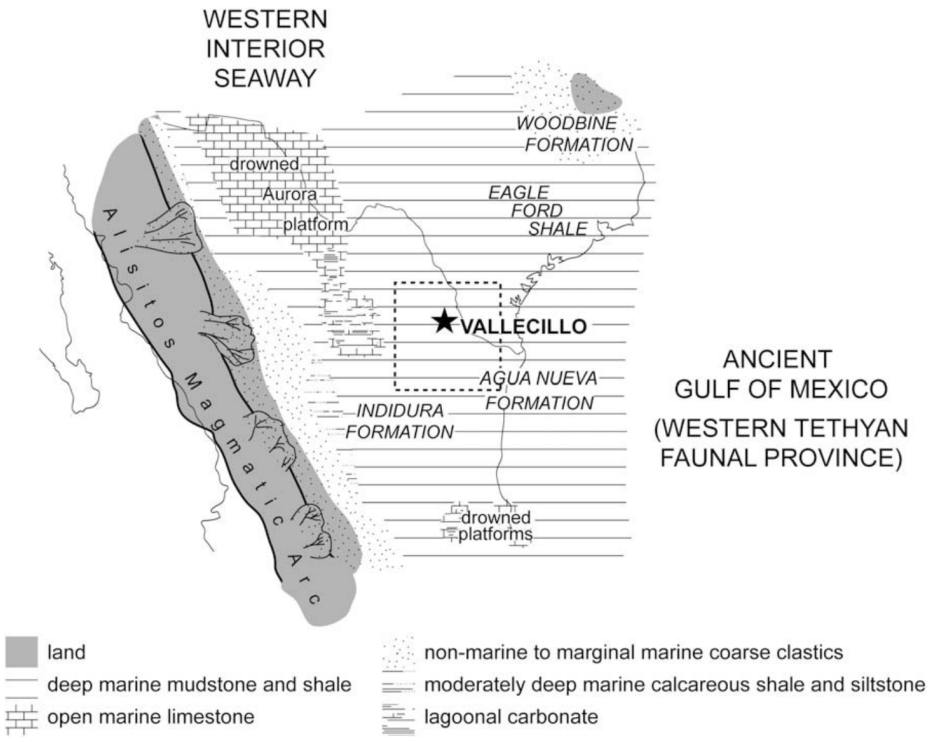

Figure 4: Geographic map of Vallecillo during the Cenomanian-Turonian. (Illustration taken from Ifrim and Stinnesbeck 2008).

2.3.1 Cartilaginous taxa

Cartilaginous taxa comprise a filter feeding shark (*Aquilolamna milarcae*), duro-phagous sharks (*Ptychodus*), mackerel sharks (*Cretoxyrhina*) and skates (Batomorphi) (Vullo et al. 2021) (Figure 5 A-D). With the exception of *A. milarcae* none of the sharks or rays have been scientifically described. The holotype of *Aquilolamna milarcae* is a 1660 mm long individual of specialized planktivorous sharks that are characterized by extremely long and slender pectoral fins. *Aquilolamna milarcae* is special because it shows that wing-like fins have evolved independently in two distantly related clades of filter-feeding elasmobranchs, long before modern manta and devil rays (Vullo et al. 2021). An underwater flight by slow flapping movements of the pectoral fins is assumed.

Ptychodus is the most frequent shark of the assemblage. *Ptychodus* is a cosmopolitan shark mainly documented by isolated teeth and known from the Aptian to Campanian (Jambura and Kriwet 2020). Species are differentiated by their dental morphology and probably fed on hard shelled organisms such as ammonoids or inoceramids. Specimens from Vallecillo are present as juveniles and adults and range from 2200 to 5750 mm length. Individuals show soft tissue preservation and are nearly complete with preserved vertebrae and a skin shadow preservation (Figure 5 B).



Figure 5: Sharks from Vallecillo comprise a filter feeding taxon named *Aquilolamna milarcae* (A), sharks with crushing teeth such as *Ptychodus* (B) and lamniform sharks asigned to *Cretoxyrhina* (C). Skates are very rare but also present (D). Scale bars 100 mm.

2.3.2 Sarcopterygians

Sarcopterygians are present by a member of Latimeriidae (Figure 6). The material ranges from 170 to 380 mm total length but a reconstruction of Giersch (2014) revealed a standard length of at least 600 mm. Different ontogenetic stages are present leading to the assumption that adults coexisted with juveniles in the pelagic. This life style is similar to modern *Latimeria* providing fossil evidence for the migration from shallow marine habitats to deeper areas of the ocean. According to Giersch (2014) the undescribed coelacanth owns features that justify the erection of a new genus and species, but also presents features seen in recent *Latimeria,* meaning that the Vallecillo coelacanth could be the nearest fossil ancestor. Some of these features are a urohyal similar to *Latimeria*, a convex ventral margin of the pterygoid as only known from *Latimeria*, a basibranchial dentition composed of several elements as in *Diplurus*, *Axelrodichthys* and *Latimeria*, ossified ribs in the caudal region of the abdominal spine as in *Macropomoides*, a high number of fin rays of the second dorsalis as well as analis, and paired fins in comparison to all other fossil coelacanths. The taxon is therefore closely related to *Latimeria* (Giersch 2014). The verification and description of the taxon is still pending.

Specimens documented here are either disarticulated and incomplete or articulated and nearly complete. Intermediary stages are nearly absent. With one exception all articulated individuals are laterally embedded. Both preservational stages could be tentatively explained by the deep water environment: Most carcasses were rapidly buried because the animal died beyond the buoyancy line and remained well-articulated and complete. Disarticulated specimens probably represent surface-dwelling individuals which suffered from post-mortem transportation and buoyancy. The taphonomy was never described for the coelacanth of Vallecillo and further research is needed.

A single individual from the Cenomanian San Carlos locality near Múzquiz is exceptionally well preserved with rhombic scales covering the body. The individual is 415 mm long and is thus the largest articulated specimen documented from the area. The individual from San Carlos is yet undescribed.



Figure 6: Coelacanth from Vallecillo. Scale bar 50 mm.

2.3.3 Actinopterygians

There are numerous actinopterygians from Vallecillo needing documentation. Holosteans as well as Teleost species are documented, but teleosts clearly dominate the assemblage. The following orders are presently identified: Pachycormiformes, Pycnodontiformes, Aspidorhynchiformes, Ichthyodectiformes, Protobramoidei, Tselfatiiformes, Pachyrhizodontoidei, Aulopiformes, Acantomorph fish and ancestral relatives to modern Xiphioidea (Carangiformes). 12 species from Vallecillo are presently described to species level, but the number of species is certainly higher. An overview is presented here.

2.3.3.1 Pachycormiformes

Pachycormiformes are marine fish ranging from the Middle Jurassic to the Late Cretaceous (Friedman et al. 2010). Vertebral components are usually not ossified, pectoral fins are scythe-shaped and the axial skeleton is largely cartilaginous (Figure 7). The clade comprises pelagic predators as well as toothless suspension feeders. Five suspension feeding genera are known: *Asthenocormus*, *Leedsichthys* and *Martillichthys* (all Jurassic in age) and the Cretaceous *Bonnerichthys* and *Rhinconichthys* (Dobson et al. 2019). *Leedsichthys*, the largest bony fish ever recorded, reached approx. 9000 mm length. The Cretaceous (Coniacian-Maastrichtian) *Bonnerichthys* known from the Western Interior Seaway may have reached 5000 mm (Friedman et al. 2010). *Rhinconichthys* is a Cenomanian-Turonian taxon of up to 2000 to 2700 mm length which bears enlarged gill rankers (Schumacher et al. 2016) but only the skull has been described to date. Pachycormid specimens from Vallecillo reach up to 1160 mm length and thus appear quite small in comparison to *Rhinconichthys*. It is unknown whether larger individuals existed in Vallecillo, whether only juveniles are present, or whether the Vallecillo species was small-sized. The length of *Asthenocormus* was estimated to reach 1320 mm but the referred specimen is a juvenile (Schumacher et al. 2016). A small individual was documented from Vallecillo (600 mm) and one disarticulated specimen is known to the author from an unknown location. Specimens from Vallecillo lack teeth which suggests a filter-feeding mode of life.



Figure 7: Undescribed pachycormid fish from Vallecillo. Scale bar 100 mm.

2.3.3.2 Pycnodontiformes

Pycnodonts are durophagous fishes, present from the Late Triassic (Norian) to the Eocene, with a notable diversification in the Jurassic and Cretaceous (Poyato-Ariza and Wenz 2002). At Vallecillo, probably two species are present: *Nursallia gutturosum* and a small undescribed pycnodont fish only represented by a single fossil specimen.

Nursallia gutturosum is characterized by a deep and laterally compressed body as well as a durophagous dentition to crush hard-shelled prey (Stinnesbeck et al. 2019) (Figure 8). *Nursallia gutturosum* was previously documented from the Lower Cenomanian of Morocco (Poyato-Ariza and Wenz 2002). Most pycnodontid taxa are documented from coastal complex areas (e.g. Solnhofen) (Nursall 1996; Delsate and Kriwet 2004), but a size range distribution of *N. gutturosum* from Vallecillo indicates that the taxon spent significant life time in the pelagic. Vallecillo specimens may have crushed ammonoid shells or they had an opportunistic feeding style but gut contents have not been documented, despite >90 specimens analyzed for this review (Stinnesbeck et al. 2019 and new material). Other pycnodont fish fed on invertebrate bivalves, echinoderms, snails or small actinopterygians (Kriwet 2001). It is therefore assumed that pycnodonts were omnivorous feeders but also highly specialized predators on generic or even specific level (Kriwet 2001; Kriwet 2005). Indigestible shell fragments were probably regurgitated as known from recent actinopterygians (Kriwet 2001; Kriwet 2005). Sexual dimorphism is documented for *N. gutturosum* by two types of dorsal fin length, with specimens with a long dorsal fin interpreted as males (Stinnesbeck et al. 2019). Individuals from Vallecillo reached up to 610 mm length and probably formed schools in the pelagic as no shelter existed.

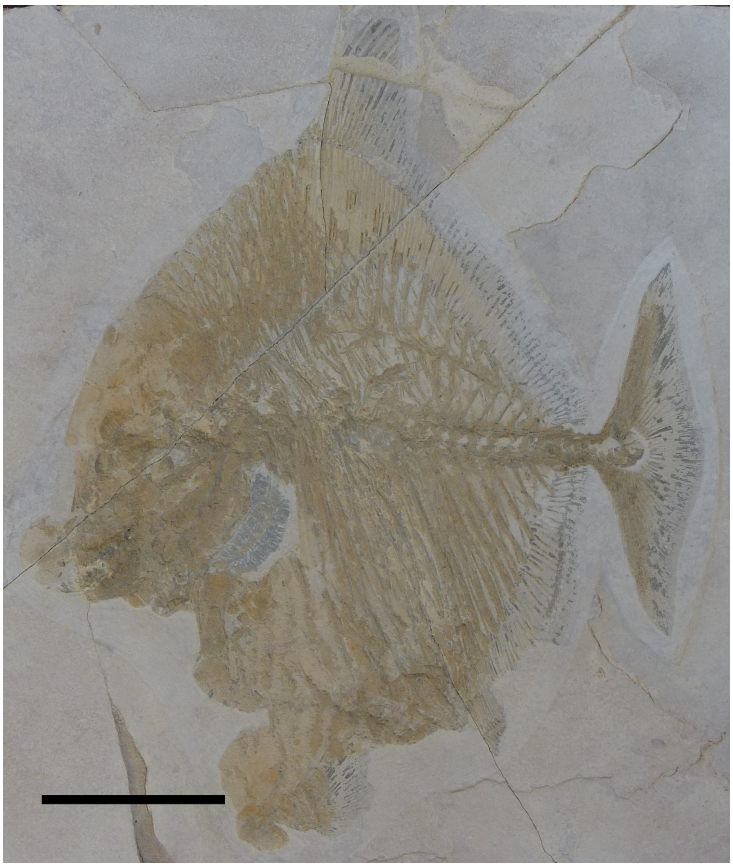

Figure 8: *Nursallia gutturosum* from Vallecillo. Scale bar 100 mm.

2.3.3.3 Aspidorhynchiformes

Aspidorhynchid fish have a nearly cosmopolitan distribution ranging from the Middle Jurassic to the Late Cretaceous (Bogan et al. 2011). Four genera (*Aspidorhynchus*, *Belonostomus*, *Vinctifer* and *Richmondichthys*) are documented (Bogan et al. 2011), but only *Belonostomus* is present in Vallecillo. *Belonostomus longirostris* is a long, sinuous fish with an elongated snout bearing two different series of teeth. The body is covered with robust ganoid scales giving the taxon a characteristical appearance (Figure 9). Ontogenetic variation appears in the dentition of the premaxilla and is described by Giersch (2014). Specimens documented here range from 350 mm to 1150 mm length. Information about the taphonomy is given in the section of unpublished results.

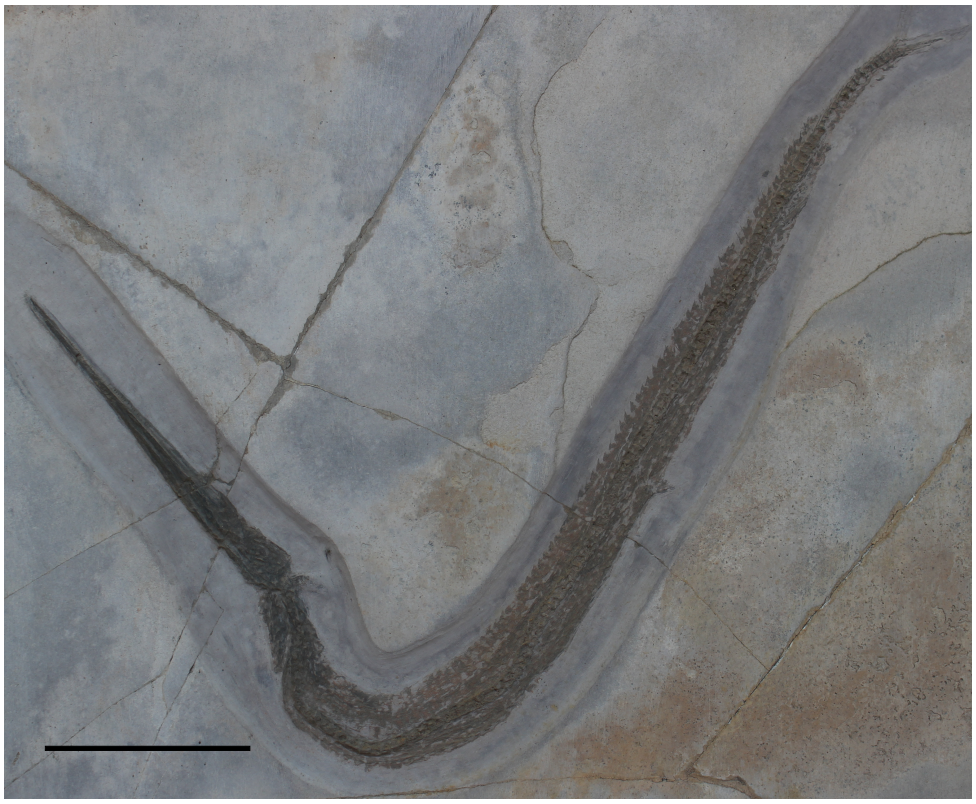

Figure 9: *Belonostomus longirostris* from Vallecillo. Scale bar 100 mm.

2.3.3.4 Ichthyodectiformes

Ichthyodectiforms ranged from the Middle Jurassic to the Late Cretaceous and had an almost worldwide distribution (Taverne 2008; Cavin et al. 2012). Most members are elongated fusiform predators and open-water sustained swimmers ranging from a few centimeters to almost six meters length (Taverne 2008). The protruded lower jaw led to the nickname "bull-dog fish". In Vallecillo three species are present: *Gillicus arcuatus*, *Vallecillichthys multivertebratum* and *Heckelichthys* n. sp.

Gillicus is documented from the Lower Maastrichtian of Japan (Taverne 2008), the Early Campanian of Alabama and the Albian-Turonian of Colorado, while in Mexico it has only been documented from the Turonian of Los Pilotes quarry near Múzquiz Coahuila (Alvarado-Ortega and Porras-Múzquiz 2009). The taxon is characterized by sabre-shaped maxilla which is almost straight in *Vallecillichthys* (Cavin et al. 2012) (Figure 10 A). Minute teeth and gill rankers seen in *Gillicus arcuatus* from Vallecillo may suggest a planktivorous feeding habit (Giersch 2014). A standard length of 1500 to 2000 mm is given by Giersch (2014). The biggest individual documented here is 1420 mm in length.

Vallecillichthys multivertebratum is a large and fusiform predator reaching 1770 mm length (personal obs.) (Figure 10 B). The fish shows an extremely superior mouth and preferentially hunted fish schools from beneath. Giersch (2014) noted that the upper jaw can be swiveled upwards and that the lower jaw could actively expand allowing the animal to swallow several fish at the same time. This is also seen in gut contents. The schooling

fish *Rhynchodercetis* is frequently preserved and interpreted as surface dweller. Other fish observed as gut content are *Tselfatia formosa* and *Nursallia gutturosum* (Giersch 2014 and pers. observation). The prey was drawn into the mouth by swimming movements and not through negative pressure induced by mouth opening. The main propulsion was generated by the caudal fin and the posterior part of the trunk. Undulation was only possible on the caudal part of the body (Giersch 2014). There is more information regarding the taphonomy in the section of unpublished results.

Heckelichthys is known from the Upper Cenomanian of Slovenia, Morocco and Mexico and the Lower Turonian of Croatia (Taverne 2008). The body is elongated and the caudal fin shows an asymmetrical-homocercal appearance (Figure 10 C). Giersch (2014) compared the material from Vallecillo with *H. vexillifer* (Slovenia) and *H. microdon* (Croatia), formerly described as *Chirocentrites* (Taverne 1986). The author found unique features to justify the erection of a new species. A standard length of 252 mm is given for *Heckelichthys preopercularis* from the Albian-Cenomanian Muhi quarry, whereas a standard length of 210 mm is presented by Giersch (2014) for *Heckelichthys* sp. from Vallecillo (Baños-Rodríguez et al. 2020). Specimens documented here reach up to 1120 mm length.

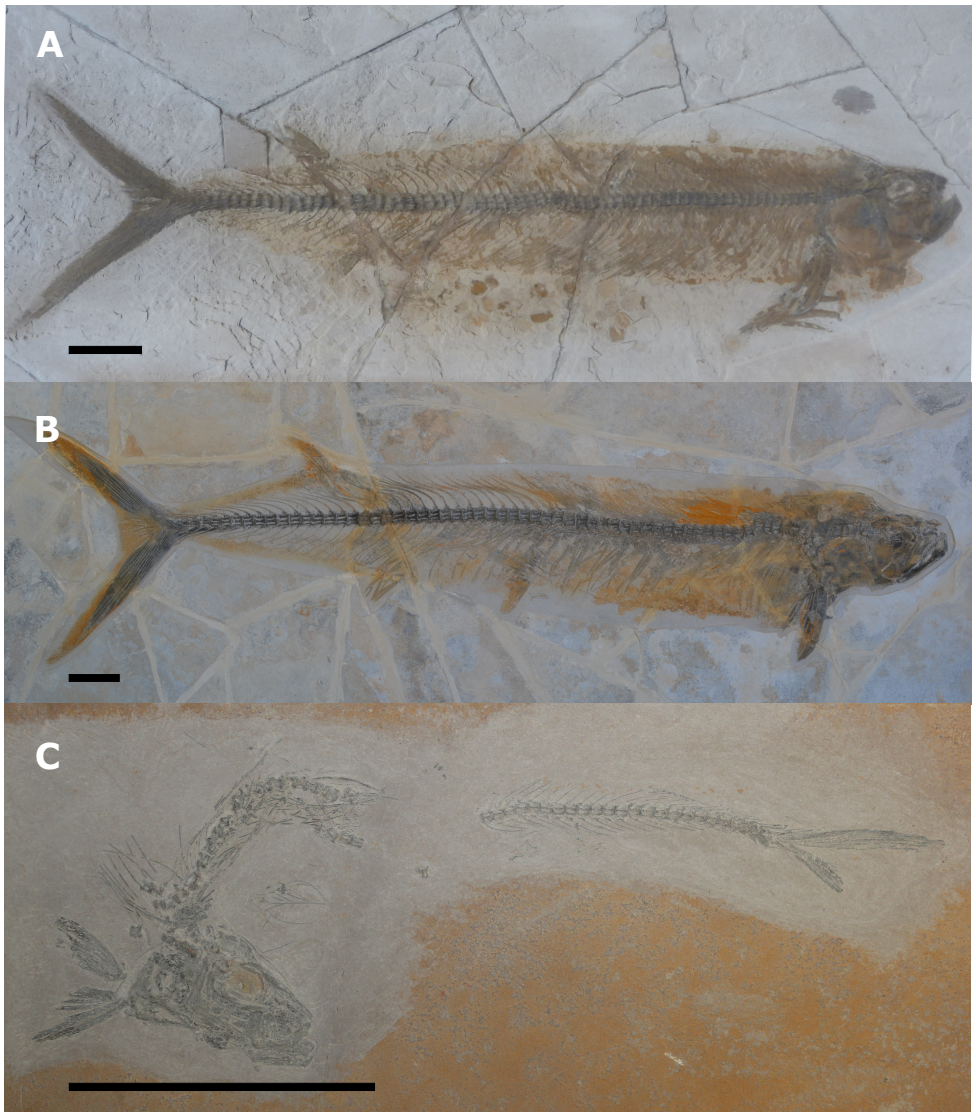

Figure 10: Ichthyodectiform fish from Vallecillo: *Gillicus arcuarus* (A), *Vallecillichthys multivertebratum* (B) and *Heckelichthys sp.* (C). Scale bars 100 mm.

2.3.3.5 Protobramoidei

Araripichthys sp. is the only documented bramoid fish from Vallecillo (Figure 11). The taxon is deep bodied, laterally compressed and lacks pelvic fins (Maisey and Moody 2001). For a long time the fish has only been known from the Albian Santana Formation of Brazil (*A. castilhoi*), the Aptian of Venezuela (*A. axelrodi*) and the Turonian of Morocco (*A. corythophorus*) (Cavin 1997; Maisey and Moody 2001; Blanco-Piñón and Cavin 2003). Species from Venezuela and Morocco were deposited in a shallow epicontinental sea, whereas the Brazilian species is recorded from a restricted interior basin. This shallow environment differs from that of *Araripichthys* from Vallecillo, which lived in an open marine environment. A standard length of 250 to 300 mm is given by Maisey and Moody (2001). Specimens documented here range from 100 to 530 mm.



Figure 11: Undescribed *Araripichthys* specimen from Vallecillo. Scale bar 100 mm.

2.3.3.6 Tselfatiiformes

Tselfatiiform fishes had a wide distribution during the Cretaceous and possess unusually long dorsal and anal fins, a forked caudal fin, small pectoral fins and a large abdominal cavity surrounded by long ribs. Teeth are small, pointed and often curved like a hook (Maisch and Lehmann 2000; Gayet 2012). Ifrim (2006) therefore proposed that *Tselfatia formosa* feeds on small prey and pelagic squids but this is not confirmed, as gut contents are preserved as compact mass without the identification of skeletal compartments (Stinnesbeck et al. 2023). Tselfatiiform fish from Mexico are represented by *Bananogmius*, *Dixonanogmius* and *Tselfatia*.

The teleost *Tselfatia formosa* is the only representative of the family known from Vallecillo. The taxon has also been reported from Morocco, Italy, Croatia, Germany and Mexico (Sorbini 1976; Bardack and Teller-Marshall 1980; Maisch and Lehmann 2000; Blanco-Piñón 2003). *Tselfatia formosa* was originally described by Arambourg (1943, 1954) and characterized by extraordinary long dorsal and anal fins which resemble those of recent fan fishes (Figure 12). Similar to, e.g. *Pteraclis*, the dorsal and anal fins are retracted behind modified scales that slightly expand the body outline. Specimens from Vallecillo are large, reaching up to 750 mm length, and display sexual shape dimorphism with two different body shape types (Stinnesbeck et al. 2023- work documented here). Trilliant-shaped individuals are twice as long as wide (2:1 body ratio), with a notable

rhombic shape. The deepest point of the ventral body is between the pelvic and anal fins. Torpedo-shaped individuals are three times longer than wide (3:1) and less curved. A trilliant-shaped body with a broader abdominal cavity is interpreted as female, needing a broader belly for reproduction. Torpedo-shaped individuals are interpreted as males needing adaptations for male to male competition. It is assumed that *T. formosa* inhabited deeper water and practiced a lifestyle similar to modern fan fishes (Stinnesbeck et al. 2023- work documented here).



Figure 12: *Tselfatia formosa* from Vallecillo. Scale bar 100 mm.

2.3.3.7 Pachyrhizodontoidei

Pachyrhizodont fishes are known since the Jurassic and show a cosmopolitan distribution during the Cretaceous (Gayet et al. 2012). These fearsome predators are frequent in Vallecillo and reached over 1m length. Their stream lined bodies are well-adapted to the pelagic and their forked tails enable rapid propulsion. At least five different species are present: *Pachyrhizodus caninus*, *Tingitanichthys heterodon*, *Goulmimichthys roberti* and two unidentified species (Morphotypes A and B).

Pachyrhizodus caninus is an alpha-predator in Vallecillo that populated the Western Interior Seaway and in the Mesozoic Gulf of Mexico. *Pachyrhizodus caninus* is known from

the Coniacian-Santonian Niobara Chalk of Kansas but the disarticulated early Turonian specimen described by Giersch et al. (2010) from Vallecillo is the oldest record of the species (Figure 13 A). The fish reached 1600 to 2000 mm length in the WIS, equivalent to the size of the Vallecillo individual which was estimated to 2000 mm length (Giersch et al. 2010; Giersch 2014). There are several unidentified pachyrhizodonts in Vallecillo that are similar to *P. caninus*.

Goulmimichthys roberti is a torpedo-shaped high speed swimmer that comprises 9% of the Vallecillo fish assemblage (Ifrim 2006) (Figure 13 B). The fish was originally described from this locality by Blanco-Piñón (2003) and Blanco and Cavin (2003). According to Giersch (2014), *G. roberti* shows some characteristics of the genus *Rhacolepis*. These include teeth of equal size on maxilla and premaxilla, narrow hypurals, a fused infraorbital with the same outline as seen in *Rhacolepis* and caudal spurns on exoccipitale and pteroticum. The pachyrhizodont is therefore more similar to *Rhacolepis* than to *Goulmimichthys* but has enough features to differentiate from both. A detailed verification of these traits is still pending. The genus *Rhacolepis* is known from the Santana Formation of Brazil (Lower Cretaceous) and the Albian Tlayúa locality (González-Rodríguez et al., 2013b; González-Rodríguez et al., 2016). *Goulmimichthys* is documented from the Turonian of Colombia (*G. gasparinii*) and Morocco (*G. arambourgi*) (Cavin, 1995; Cavin, 2001; Páramo-Fonseca, 2001; Blanco-Piñón, 2003; Alvarado-Ortega et al., 2006; González-Rodríguez et al., 2016). *Goulmimichthys roberti* from Vallecillo ranges from 100 to 650 mm length and preyed on small fish. A taphonomic analysis and a case of paleo-parasitism are presented here (Stinnesbeck et al. 2020; Stinnesbeck et al. 2021).

Tingitanichthys heterodon is another fusiform pachyrhizodont with a long dorsal fin running over the spine (Figure 13 C). According to Giersch (2014) the fish reached 300 mm total length but specimens documented here show a maximum length of 430 mm. The taxon was described by Arambourg (1954) and later revised by Taverne (1996) using individuals from Djebel Tselfat in Morocco (Giersch 2014). Individuals from Vallecillo show that the taxon dispersed across the Atlantic into the western Tethys.

At least two unidentified pachyrhizodont species are present in Vallecillo and here documented as Morphotype A and Morphotype B. Morphotype A shows extraordinary long pectoral fins and a dorsal fin that runs over the entire spine, similar to *T. heterodon* (Figure 13 D). The skull resembles *Motlayoichthys sergioi* from the Albian-Cenomanian Muhi quarry in Mexico (Arratia et al. 2018) but verification is still pending. Morphotype A is represented by juvenile and adult individuals. Morphotype B possesses small dorsal and pectoral fins and is solely represented by large-sized individuals interpreted as adults (Figure 13 E). The caudal fin shows a crescent shape.

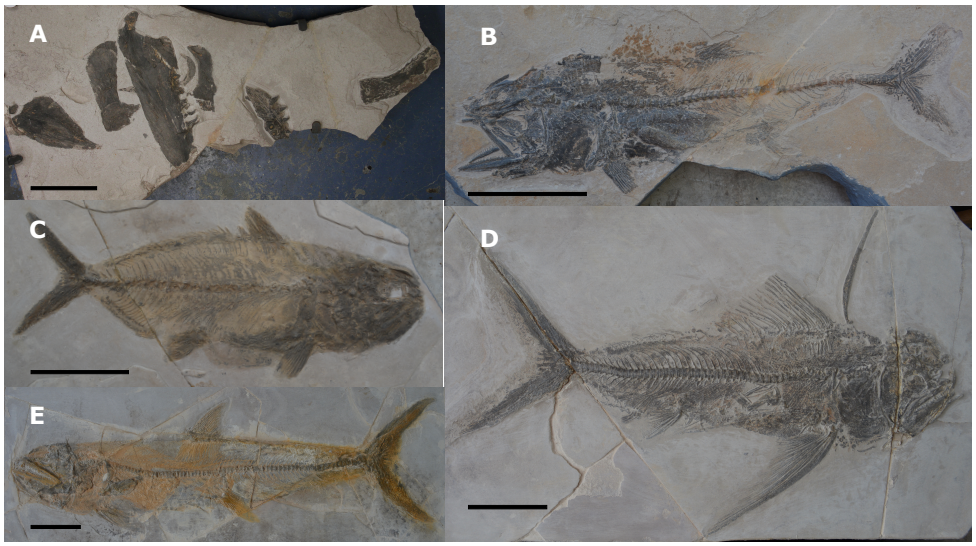

Figure 13: Pachyrhizodont fish from Vallecillo: *Pachyrhizodus caninus* (A), *Goulmimichthys roberti* (B), *Tingitanichthys heterodon* (C) and two unidentified pachyrhizodont species. Type A (D) with remarkable long pectoral fins and type B (E) with short pectoral and pelvic fins. Scale bars 100 mm.

2.3.3.8 Aulopiformes

Two species of Aulopiform fish are documented in Vallecillo, *Rhynchodercetis yovanovitchi* and *Enchodus venator*.

Rhynchodercetis yovanovitchi is the most abundant fish taxon in Vallecillo. An excavation by Ifrim (2006) revealed that *R. yovanovitchi* makes up to 79% of the assemblage. It is a slender fish of about 500 mm length which was similar in appearance to recent needlefish (Belonidae) and may also have hunted in schools near the water surface (Giersch 2014) (Figure 14 A). Specimens are frequently found as gut content of pachyrhizodont fish and in the Ichthyodectiform *Vallecillichthys multivertebratum*. The genus *Rhynchodercetis* was originally described by Arambourg (1943, 1954) from Morocco and is also known from England, Italy, Slovenia, Lebanon and Canada (Blanco-Piñón and Alvarado-Ortega 2006). The taxon from Vallecillo was first described as *R. regio* n. sp. by Blanco-Piñón and Alvarado-Ortega (2006) but a later revision by Giersch (2014) led to the conclusion that there are no sufficient osteological reasons to erect a new species.

Enchodus venator is also known as "saber-tooth herring" because of the long fangs in the upper and lower jaw. It is a slender and elongated predator (Figure 14 B). *Enchodus* has a cosmopolitan distribution ranging from the Cenomanian to the early Paleocene, but *E. venator* is restricted to the Cenomanian-Turonian transition and only documented from Morocco, Italy and Mexico (Cavin 1999; Fielitz and González-Rodríguez 2010; Giersch 2014). Gut contents show large fishes, as long as the predator itself, revealing an aggressive hunting behavior. Specimens documented here range from 40 mm to nearly 800 mm length.

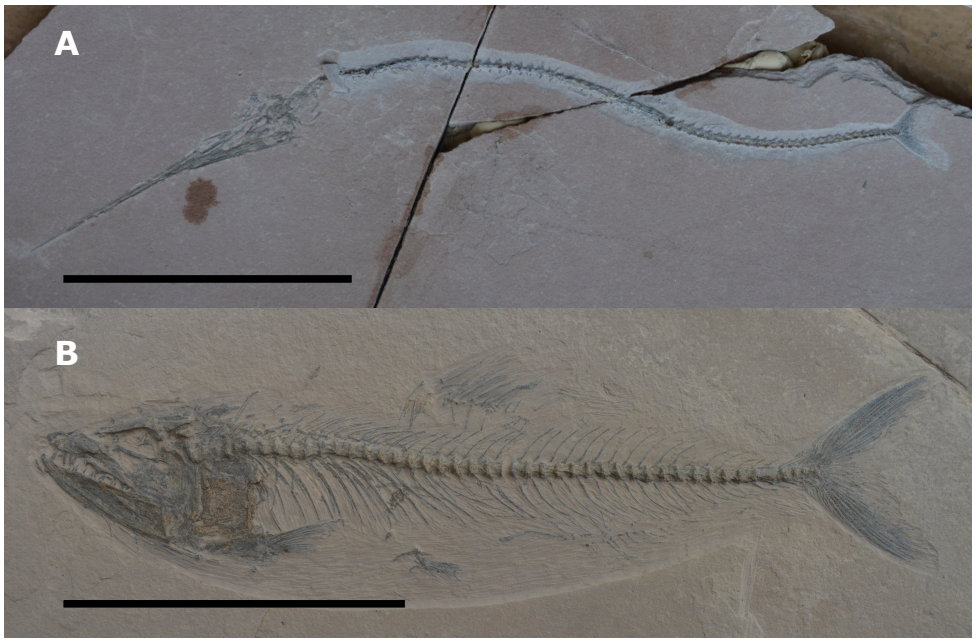

Figure 14: *Rhynchodercetis yovanovitchi* (A) and *Enchodus venator* (B) from Vallecillo. Scale bars 100 mm.

2.3.3.9 Acanthomorph fish

Acanthomorph fishes are known since the Cenomanian and show a worldwide distribution (González-Rodríguez and Fielitz 2008). The first record of this group in Mexico is documented by González-Rodríguez and Fielitz (2008) from the Albian-Cenomanian Muhi quarry in the state of Hidalgo. One adult and three juveniles of *Muhichthys cordobai* were reported. Further findings have been reported from the Muhi quarry and the Cenomanian El Chango quarry near Tuxtla Gutiérrez in Chiapas (Alvarado-Ortega and Than-Marchese 2012; González-Rodríguez et al. 2013a, 2016; Cantalice et al. 2021). In Vallecillo, several undetermined species are present and represented by juvenile and adult individuals, which leads to the assumption that individuals spend the entire life cycle in the pelagic (Figure 15 A). Some individuals from Vallecillo resemble *Muhichthys cordobai* from Muhi, but descriptions are still pending. Documented specimens range from 50,6 mm to 470 mm length (Figure 15 A and B).

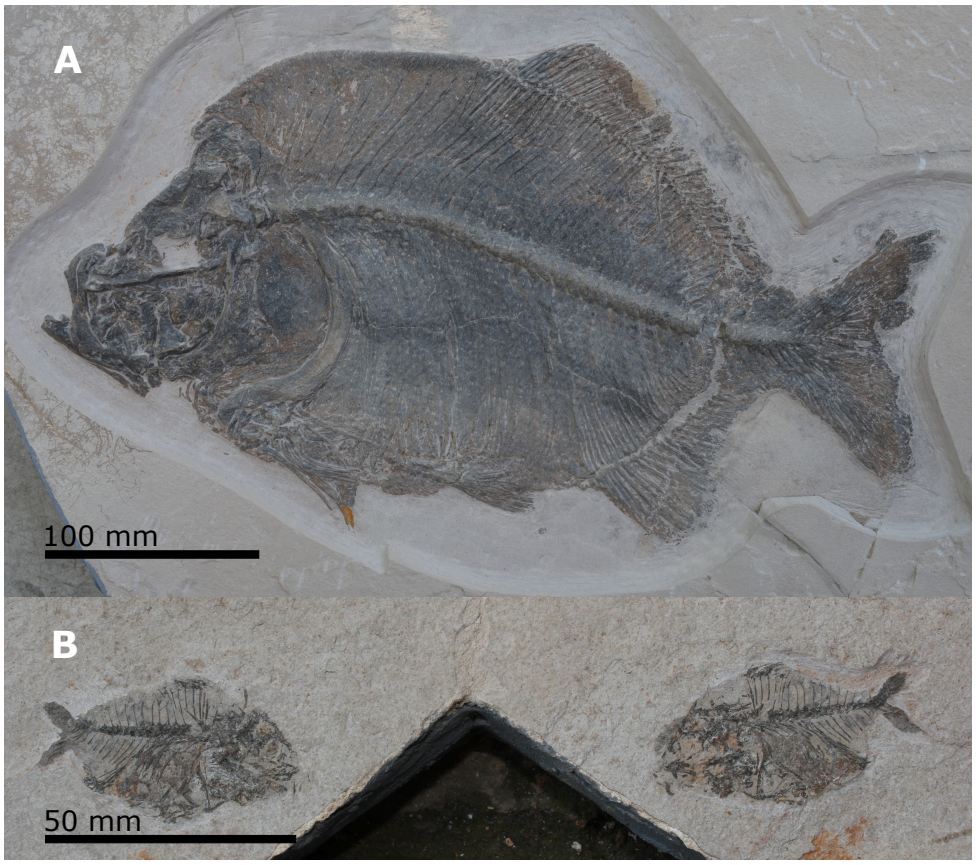

Figure 15: Undescribed acanthomorph fish from Vallecillo. The species presented here is present by juvenile and adult individuals (A). Scale bar 100 mm. Smaller specimens probably belong to a different species (B), compared to species illustrated in A. Scale bar 50 mm.

2.3.3.10 Undetermined Swordfish-like individuals – "*Protospyraena*" *stebbingi* (Woodward 1909) or Xiphioidea?

In the past years, several swordfish-like individuals have been discovered in Vallecillo which are difficult to interpret. Due to their long rostra and fusiform morphology they closely resemble modern Xiphioidei but this group is stratigraphically much younger.

Xiphioidei possess elongated premaxillares forming a rostrum, and villiform teeth that may be reduced and even lost during ontogeny (*Xiphias gladius*) (Otero 2019). Five groups are known (*Hemingwayidae*, *Plaeorhynchidae*, *Blochiidae*, *Xiphiidae* and *Istiophoridae*) but only the two latter clades have extant representatives. The group ranges from Paleocene to Holocene age. *Protosphyraena* on the other hand, is a swordfish-like predator of the Cretaceous which was assigned to Pachycormidae (Amalfitano et al. 2017). The genus is characterized by scythe-like pectoral fins, blade like teeth and an almost conical rostrum but its worldwide distribution is only based on highly fragmentary material. As a representative of Pachycormidae, ossification (skeleton ossification e.g. vertebrae) is incomplete, which evidently contrasts specimens from Vallecillo. According to Friedman et al. (2016) flat rostra from the Upper Cenomanian of the English Chalk, interpreted

by Woodward (1909) as *P. stebbingi*, are related to tselfatiiform fishes instead of Pachycormids (*Protosphyraena*). Amalfitano et al. (2019) later reported on two additional rostra of *"Protosphyraena" stebbingi* from the Upper Cretaceous (Upper Cenomanian and Lower Turonian) of Italy and tentatively placed them in the order of Tselfatiiformes. The Italian rostra are dorsoventrally flattened with rounded edges and tips and thus closely similar to rostra from Vallecillo and the one from the English Chalk. Amalfitano et al. (2019) state that the rostra differ from the genus *Protosphyraena* due to midline grooves and paired nutrient canals indicating two paired bones instead of one medial rostrodermethmoid forming the rostrum of *Protosphyraena* and other pachycormids. Therefore the fossil rostra from Italy and the English chalk are tentatively interpreted as *"Protosphyraena" stebbingi*. Dorsoventrally flattened rostra formed by paired premaxillae are indeed known from the Coniacian tselfatiiform fish *Martinichthys* (Taverne 2000b), but the latter does not resemble the findings from Vallecillo. One undescribed Xiphioid documented from the Cenomanian (Hgula) of Lebanon (Gayet et al. 2012) is also not quite comparable to the specimens from Vallecillo. The individual from Lebanon possesses a large dorsal fin that runs over the entire back, is small sized (320 mm) and the rostrum is thin, small and probably ovoid in cross-section. Individuals from Vallecillo appear to be toothless and the premaxillares are joined into a pointed rostrum substantially longer than the lower jaw (Figure 16 A). In contrast to the fossils from Italy and the English Chalk, in which only fragments of the rostra are preserved, there are nearly complete individuals in the Vallecillo assemblage allowing for a future interpretation of the rest of the body (Figure 16 B). Individuals documented here reach 2000 mm length. Swordfish-like specimens are here reported for the first time from Vallecillo, but similar rostra (~400 mm) are known to the author from the coeval Múzquiz Plattenkalk localities in Coahuila.

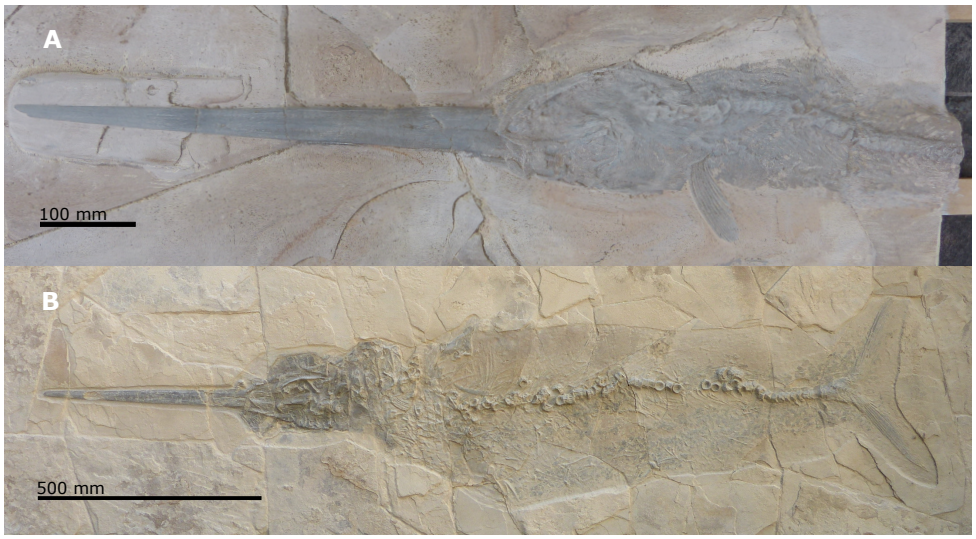

Figure 16: Undescribed swordfish-like individuals from Vallecillo tentatively assigned to *"Protosphyraena" stebbingi* (Woodward 1909). Close up of the skull showing the fused premaxillares forming the pointed rostrum (A) (scale bar 100 mm) and a complete specimen allowing the interpretation of the rest of the body (B) Scale bar 500 mm.

2.3.4 Reptiles

Marine reptiles are represented by undetermined marine turtles (17 C), plesiosaurs (e.g. *Mauriciosaurus fernandezi*), a tooth of a pliosaur (*Polyptychodon* sp.) and aigialosaurs (*Vallecillosaurus donrobertoi*) (Buchy et al. 2005; Buchy 2007; Smith and Buchy 2008; Frey et al. 2017) (Figure 17 A-C). Aigialosaurs from Vallecillo are present by complete adult and juvenile specimens which are well preserved (Figure 17 A) displaying gut content (e.g. *Rhynchodercetis*), soft tissue preservation and even a female with 4 embryos inside. Most of the material is still undescribed.

The aigialosaur *Vallecillosaurus donrobertoi* is thought to be one of the last common ancestors of Mosasauridae as well as modern varanoids and preserved with soft tissue (Smith and Buchy 2008) (Figure 17 B). The taxon shares a combination of skeletal characters combining aigialosaurs, mosasaurs, dolichosaurs and living varanoids. Smith and Buchy (2008) argue that aigialosaurs were originally considered as amphibious, capable for locomotion on land and in the water, but the presence of *V. donrobertoi* in an outer shelf environment leads to the assumption that animals crossed significant distances of the open sea. The authors claim that the taxon was well adapted to the pelagic. This interpretation is supported by the Vallecillo female with fully developed embryos, thus indicating that these marine reptilians were viviparous, without the necessity to return to beaches to lay their eggs.

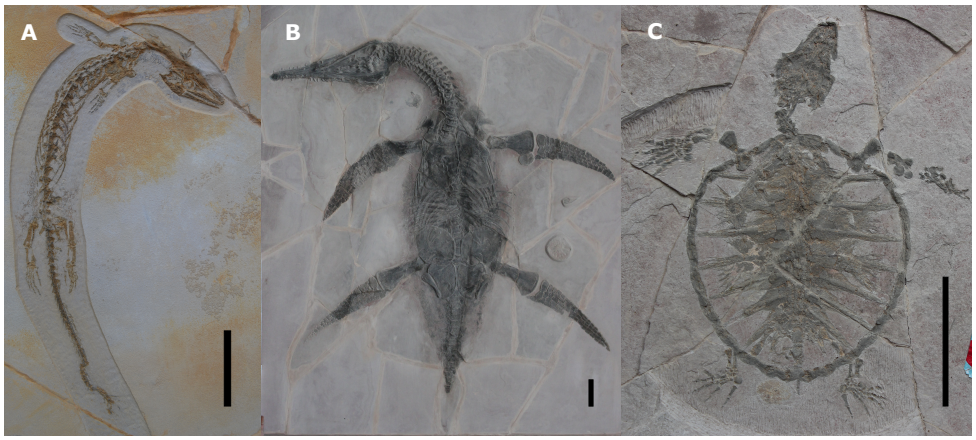

Figure 17: Marine reptilians from Vallecillo: A small aigialosaur (A), the plesiosaur *Mauriciosaurus fernandezi* (B) and an undescribed turtle (C). Scale bars 100 mm.

2.3.5 Invertebrates

Ammonoids, cirripeds, inoceramids and one parasitic isopod infesting the pachyrhizodont *Goulmimichthys roberti* represent the invertebrate fauna of Vallecillo (Ifrim and Stinnesbeck 2007, 2008, Ifrim et al. 2011a, Ifrim, 2013; Stinnesbeck et al. 2021) (Fig A-C). Ammonoids are represented by nine species which occasionally show epizoic cirripeds (*Stramentum*) on their shells (Ifrim 2006; Ifrim and Stinnesbeck 2007, Ifrim et al. 2011a; Ifrim 2013). *Stramentum puchellum* colonized the shells during the life time of the am-

monite forming several generations (Figure 18 A). They probably survived the ammonoids live and were buried alive (Ifrim et al. 2011a).

The isopod *Mothocya vallecillae* is the first parasite documented from Vallecillo. The holotype and only known specimen is directly attached to the skull of *Goulmimichthys roberti*, a common pachyrhizodont fish comprising 9% of the assemblage. The fish is a well-adapted high speed swimmer reaching a length of 450 mm. The isopod *M. vallecillae* measures 13 mm and is preserved in dorsal view on the 380 mm long individual (Figure 18 C). A scavenging lifestyle is excluded for the isopod due to the anoxic bottom conditions at the Vallecillo sea floor and the claw like dactyli of all pereopods affiliating the parasite to *Mothocya* (Stinnesbeck et al. 2021- work presented here). Extant *Mothocya* populate the branchial cavity, and exceptionally, the buccal cavity of fish hosts. Specimens feed on host blood and small pieces of muscle tissue. Their body is usually dorso-ventrally flattened to reduce water resistance and the danger of being removed by cleaner fish. The isopods are often twisted to one direction as a response to growth on the host (Smit et al. 2014; Nagler und Haug 2016). A similar lifestyle is suggested for *M. vallecillae*.

Inoceramid bivalves are the only benthic organisms that persisted at the Vallecillo sea floor (Figure 18 B). Five species are present reaching adult stages (Ifrim et al. 2011b). The size range conducted by Ifrim et al. (2011b) shows two maxima from 60 to 70 mm and 90 to 100 mm length, indicating a full growth and anoxic resistance. Chemoautotrophic bacteria probably allowed the inoceramids to live in these oxygen deficient bottom environments but their larvae had to drift up to oxygenated surface water and probably floated there prior to metamorphosis (Ifrim et al. 2011b).

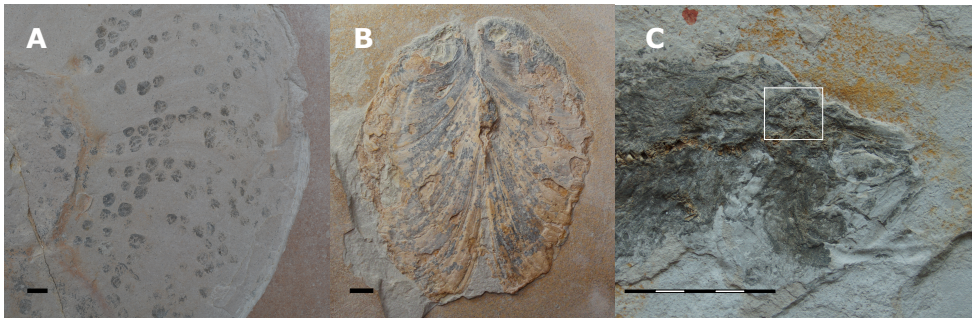

Figure 18: Invertebrates from Vallecillo: The ammonoid *Pseudaspidoceras flexuosum* with cirripeds on the shell (A), inoceramid bivalve (B) and the parasitic isopod *M. vallecillae* infesting *G. roberti* (C). Scale bars 10 mm in A and B. Scale bar 50 mm in C.

2.4 Taphonomy

Taphonomy is the study of fossil formation and thus a key aspect of paleontology. It deals with the processes taking place after the death of an organism and the forces a decaying body is exposed to. The preservation of invertebrate and vertebrate fossils from Vallecillo is described in detail.

Fossil preservation in Vallecillo

Ammonites from Vallecillo are laterally preserved but occasionally also in a vertical or oblique position (Ifrim 2006 and personal observation). The aragonitic shell of ammonites is always altered to calcite, but in smaller specimens (e.g. <100 mm) it is dissolved. The phosphatic sipho on the other hand, is frequently preserved. Larger and thicker shells pressed into the sediment may have been protected from dissolution (Ifrim 2006).

Inoceramid bivalves possess an inner aragonitic layer and an outer thick prismatic shell layer made of calcite. Inoceramids are preserved as closed valves that were pressed together, leading to pressure dissolution of the inner aragonitic layer while the prismatic layer remains preserved.

Cirriped crustaceans (*Stramentum*) are preserved as calcite.

Vertebrates are compressed to less than 15 mm thickness (Blanco-Piñón 2003; Ifrim 2006). Large fish skulls are preserved three-dimensionally but are also compressed. Bones are recrystallized as dark grey calcite while teeth are white preserving the original enamel. Gut content and coprolites are present as dark grey calcite. The majority of the vertebrate specimens are nearly complete and articulated. Carcasses were not transported and were rapidly embedded in a soft sediment. Nevertheless, this is species dependent. Ifrim (2006), for example, reported that 93% of the *Rhynchodercetis yovanovitchi* specimens are present as isolated skulls, body fragments or vertebrae. According to this observation, *R. yovanovitchi* must have been a surface dweller and disintegrated specimens suffered from post-mortem transportation.

The anoxic bottom zone must have been sufficiently extended to preserve fish and reptilian carcasses extending 1000 mm length, thereby preventing scavenging. Large carcasses of pachyrhizodont fish, sharks or aigialosaurs may have persisted on the sea floor and slowly decomposed there without being affected by bottom currents causing bone transportation (Figure 19 A). Even tiny body compartments remained in close distance to the main body and did not drift away. Isolated skulls or body parts are exceedingly rare and specimens are usually nearly complete while disarticulated. The rare presence of fossil Batoids suggests that oxygenated bottom conditions may occasionally have interrupted the prevailing oxygen-deficient to anoxic conditions of the Vallecillo sea bottom.

Currents are very rare and almost not existent, as only a single specimen of *N. gutturosum* and *T. formosa* (out of several hundred of specimens) is documented to be exposed to a current (pers. observation) (Figure 19 B). Bioturbation has never been documented

from Vallecillo. The sediment was occasionally soft enough to preserve ammonoids in an upright position and some few fish in a dorsal or ventral position. Nevertheless, the majority of the fish specimens is laterally embedded.

Coprolites are preserved but have not yet been described.

Gut content is frequently preserved in Vallecillo and allows the analysis of predator prey relationships (Figure 19 C). One specimen of *Enchodus venator* suffocated from swallowing another fish and *R. yovanovitchi* is the most abundant gut content in pachyrhizodont fish, *Vallecillichthys multivertebratum* and aigialosaurs.

Evidence of respiratory stress is indicated by open mouth and spread fins. Evidence for tetany is documented for *G. roberti* and *T. formosa* (Stinnesbeck et al. 2020-work presented here). Body arching is often associated with high salinity levels or dehydration; arching is documented in *G. roberti*, *V. multivertebratum* and *Belonostomus longirostris* (unpublished results).

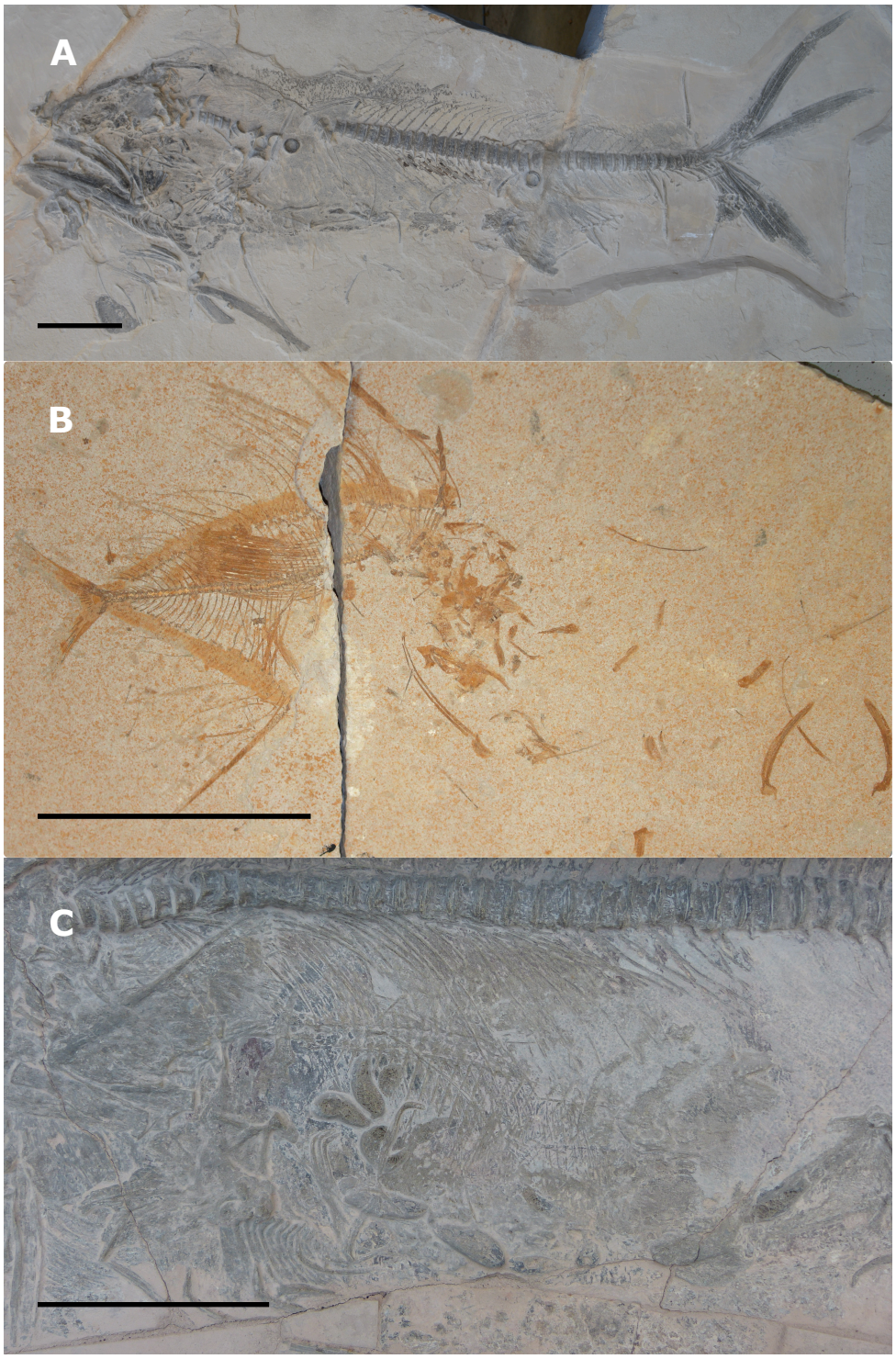

Figure 19: Preservation in Vallecillo. Large pachyrhizodont fish decayed on the sea floor without been transported. Disarticulated bones remain close to the main body (A). *Tselfatia formosa* showing bone dispersal by currents (B). Gut content of a large pachyrhizodont fish (C) with remains of *N. gutturosum* and *G. arcuatus* still distinguishable. Scale bars 100 mm.

2.5 Objectives

The principal objective of this work is an approximative description of the latest Cenomanian-middle Turonian Vallecillo plattenkalk, with emphasis on its environmental conditions and faunal assemblage. This important Gulf of Mexico locality provides a unique insight into a hitherto little known pelagic ecosystem of the Western Tethys during a time of extreme climatic conditions and geologic changes, i.e. the global Cenomanian-Turonian boundary mass extinction. The high preservational quality of the Vallecillo fossil assemblage offers a rare showcase to document both aut- and synecological aspects of the fauna, i.e. it enables a study of interactions between individual species with their environment as well as the interactions among two or more species, or a population, with their environment, e.g. predator prey interactions, animal biology and faunal dispersal. The locality even allows for a study of the abundance and distribution of the species, which in paleontology is rarely the case.

To exemplify this potential, the author selected the pachyrhizodont fish *Goulmimichthys roberti* and the teleost *Tselfatia formosa*. Both species are represented by abundant well preserved fossils and thereby offer a suitable amount of data.

Among others the author focused on the following questions: Was *G. roberti* permanently living in the Vallecillo region? Did this pachyrhizodont migrate, e.g. to more shallow environments in the Múzquiz region to the North? How is *G. roberti* preserved? No taphonomic and preservational studies were conducted previous to this analysis. For this purpose 177 individuals were documented and a size range conducted. Preservational stages were classified and the taphonomy of individuals from Vallecillo and northern Múzquiz deposits were compared.

During the work on *G. roberti* the first case of paleo-parasitism was documented for Vallecillo, leading to the second work presented here, the taxonomic description and autecological analysis of the isopod *Mothocya vallecillae*. Fossil parasites are extremely rare in the fossil record and this is the first case documented from a pelagic environment of the Cretaceous. Interestingly, the Vallecillo *Mothocya* was already similar in life-style to modern representatives, as concluded from morphological characters of the parasite and its location on the host skull.

The third analysis presented here presents a reconstruction of the biology and taphonomy of *Tselfatia formosa*. This abundant teleost from Vallecillo is also known from other Tethyan locations but its preservation and taphonomy has never been investigated in detail. A size range distribution is conducted here, based on 149 individuals and their preservation is documented. Results show that both juvenile and adult *T. formosa* are present in Vallecillo and that sexual dimorphism is present. The extraordinarily elongated dorsal and anal fins were probably retracted behind modified scales and were used for rapid acceleration and maneuvering as seen in extant fan fish of the Pacific.

Chapter 3

Material and Methods

The fossils from Vallecillo were examined during two field trips to Mexico in 2017 and 2018. During this time the Ph.D. candidate was able to document about 500 fish specimens from Vallecillo and another 14 from the northern limestone deposits of Múzquiz, Coahuila. The material used in this dissertation comprises 166 individuals of the pachyrhizodont *Goulmimichthys roberti* from Vallecillo and 11 specimens from Múzquiz. One parasitic isopod infesting *G. roberti* from Vallecillo. 149 individuals of *Tselfatia formosa* were revised from Vallecillo as well as 3 specimens of *Dixonanogmius* from Múzquiz and a single specimen of *T. formosa* from Mesa las Tablas near Saltillo. Material from the northern Múzquiz deposits belong to the Cenomanian San Carlos deposit, the middle-Late Santonian Temporales deposit, the Turonian El Pilote quarry, the upper Turonian-lower Coniacian Carranza quarry and the Cenomanian-Turonian Piedritas locality. The material from Vallecillo is housed in the Colección Paleontológica de Coahuila in the Museo del Desierto (MUDE) at Saltillo and the collection of Ing. Mauricio Fernández Garza in Monterrey (M). The latter material of hundreds of fishes has been donated to a new paleontological museum in Monterrey that is exclusively dedicated to the Vallecillo fossil Lagerstätte. Until this museum opens, fossils are housed in the MUDE at Saltillo. Fossil material from Múzquiz is stored in the Museo de Paleontología de Múzquiz, Coahuila (MUZ).

Fossils were not collected randomly from the outcrop surface and the analyses are totally based on museum collections. Even though the Vallecillo quarries were repeatedly visited, no specific fieldwork was done. The total length and width of the individuals was measured using the instructions by Hastings et al. (2014). The horizontal distance from the anterior-most point of the skull to the tip of the longest caudal fin lobe was used. All photographs were taken by the Ph.D. candidate with a Nikon D5200 camera and figures were edited using the computer program Inkscape. Drawings were illustrated using the program Procreate.

Prof Dr. Jes Rust, PD Dr. Fabian Herder, Prof. Dr. J. Wolfgang Wägele and Prof. Dr. Wolfgang Stinnesbeck assisted in manuscript review and editing.

3.1 Taphonomy

The taphonomic analysis of *G. roberti* and *T. formosa* is based on osteological complete individuals, which may, however, been disarticulated. Specimens missing significant parts of the skeleton due to incomplete limestone slabs were not included in the taphonomic analysis.

Articulation and completeness is documented for *Goulmimichthys roberti* and *Tselfatia formosa*. Five taphonomic stages are identified in the field of articulation: articulated (at), slightly disarticulated (sld), partially disarticulated (pd), mostly disarticulated (md) and strongly disarticulated (sd). The bones of articulated specimens remain in their anatomical position. Slightly disarticulated specimens show the detachment of single fin rays or fins but the elements remain in close distance to the main body. In partially disarticulated individuals the skull, or the fins, are disarticulated while the rest of the body remained in original position. The original position of the bones is identifiable and detached components remain close to the main body. Mostly disarticulated specimens possess disarticulated body parts in close distance to the main body, but the former position of the bones is not easily identifiable. In strongly disarticulated individuals the original position of the bones is not identifiable. There are no detached parts that remained articulated. In *G. roberti* skeleton completeness is divided into four groups, instead of five: complete (c), nearly complete (nc), partially complete (pc) and incomplete (ic). Complete individuals lack only some few ribs or fin rays. Nearly complete individuals lack ribs or single fins but the body remains mostly complete. Partially complete specimens lost main body parts, e.g. the caudal fin or some vertebrae. Incomplete specimens lack more than 50% of the body, e.g. all fins and vertebrae. The detachment and absence of scales was not included into the analysis.

Fin preservation is classified into four groups in *G. roberti*: Preservation not visible (nv), disarticulated (d), fins spread and closed. Fins which do not allow the identification of "spread" or "closed", due to a slightly disarticulation of the fin rays, are marked as "preservation not visible". Disarticulated fins do not allow for further identification. Spread fins show a fan-like angle of 90°. In closed fins, rays are pressed together and no fin spreading is seen (Figure 22 A-B). Specimens with missing fins are marked as "not preserved". The preservation of the unpaired fins in *T. formosa* is documented in more detail. Four groups are here differentiated with a focus on fin spreading: disarticulated (d), not spread (ns), middle spread (ms) and fully spread (fs) (Figure 20 A-D). Retracted dorsal and anal fins remain parallel to the body and range between 0° to 20°. Middle spread fins show angle ranges of 21° to 40° and fully erected fins reach 90° (>41°). Specimen embedding, column preservation and bending of the body is only documented in detail for *G. roberti* from Vallecillo, as *T. formosa* shows no curvature of the body.

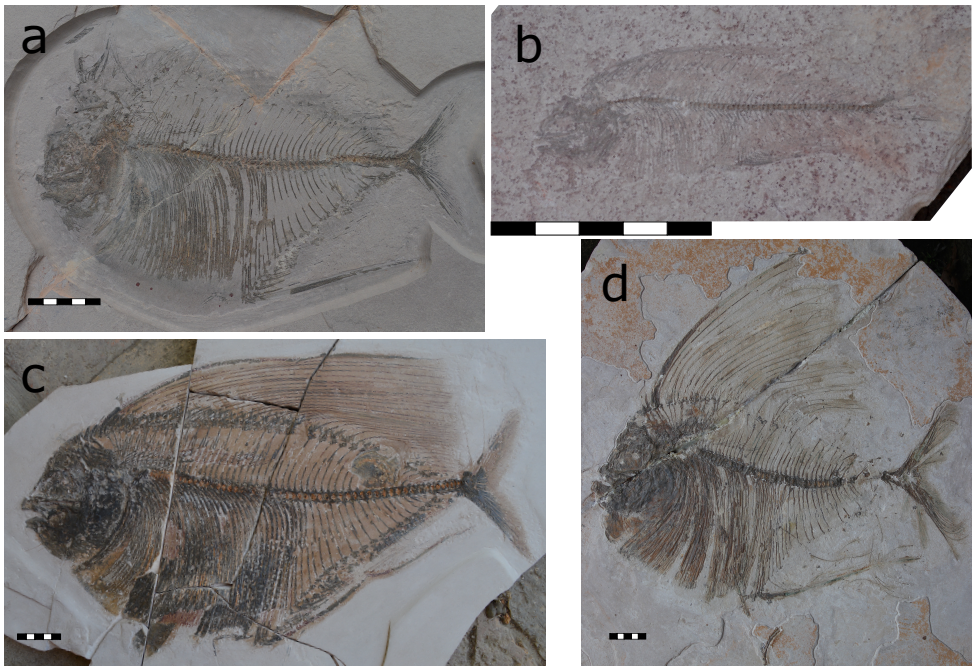

Figure 20: Preservation of the unpaired fins in *T. formosa*. Disarticulated dorsal fin (A), retracted fin (B), middle spread fin (C) and erected fin (D). Scale bars 50 mm.

The BENDING OF THE SPINAL COLUMN in *G. roberti* is classified into five stages: straight, bending in dorsal or ventral direction (aDV), laterally arched bending to the right or left (aRL), S-shape bending and disarticulation (d) (Figure 21 A-D). Breakage and disarticulation of the column, provoked by column bending (cbr), is documented separately. The embedding is solely documented in *G. roberti* because all *T. formosa* specimens are laterally preserved. Six embedding stages are differentiated for *G. roberti*: lateral embedding (L), dorsal (D), ventral (V), latero- dorsal (L-D), latero-ventral (L-V) and disarticulated. Individuals in lateral position exposing the dorsal or ventral body side show a latero-dorsally or latero-ventrally embedding.

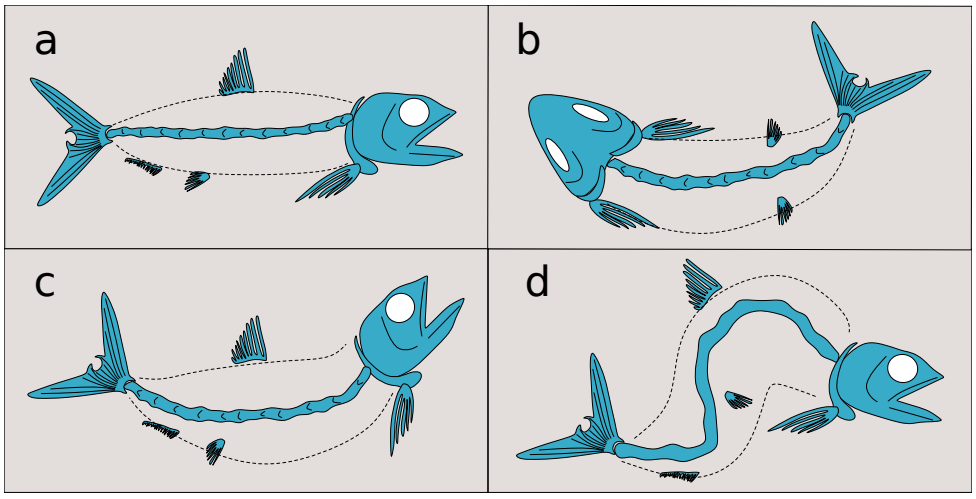

Figure 21: Bending of the spinal column documented in *G. roberti*. Straight embedding (A), lateral arched bending into the right or left (B), bending into ventral or dorsal direction and S-shape bending (D).

MOUTH OPENING is documented in both species. In *G. roberti* three stages are visible: closed (0°–10°) (cl), moderately open (11°–39°) (mo) and widely open (> 40°) (wo). In *T. formosa* three positions are detected: disarticulated (d), closed (c) and open (o) (Figure 22 C-E). Disarticulated skulls do not allow for a classification of the mouth opening and are therefore counted as disarticulated.

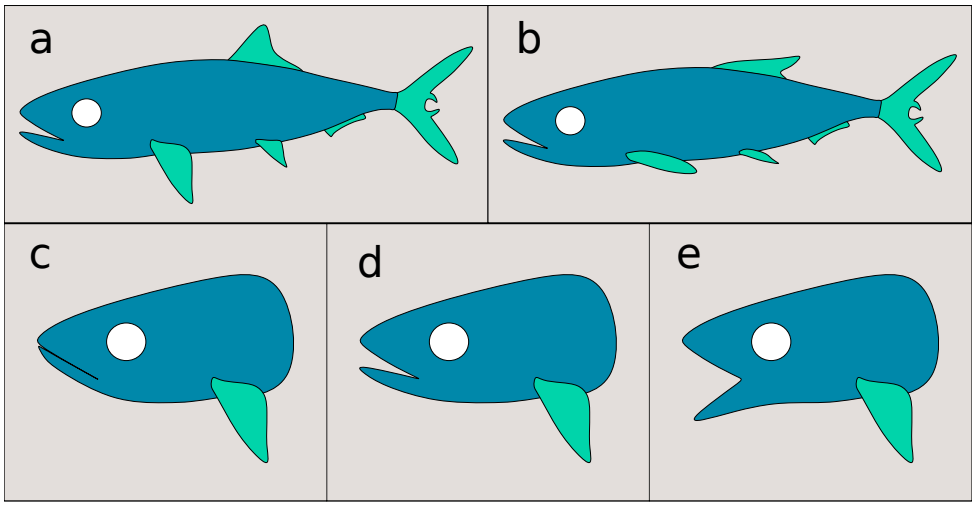

Figure 22: Fin and mouth positions seen in *G. roberti*. Spread fins (A) and fins with closed fin rays (B). Mouth closed (C), moderately open (D) and wide open (E).

In *T. formosa* two BODY SHAPE types are differentiated, while disarticulated and ambiguous specimens are also present. A rhombic (trilliant diamond cut) and a torpedo shape type are distinguished (Figure 23 A-F). Trilliant-shaped individuals are twice as long as wide, with a body length to width ratio of 2:1. Individuals are deeply keeled and less streamlined, with a rhombic shape. Torpedo-shaped specimens are three times longer than wide and thus present a length to width body ratio of 3:1. Specimens are more streamlined and dorsally less curved. A deeply keeled belly is absent or faintly marked. There are no other features that would justify the erection of two different *Tselfatia* species. Ambiguous individuals are not keeled enough to distinguish a rhombic-shape and not long enough to be interpreted as torpedo-shaped. Fragmentary specimens were not used for the body shape analysis.

A size range distribution is documented in *G. roberti* and *T. formosa*. Highly disarticulated and incomplete specimens were excluded from the size range analysis.

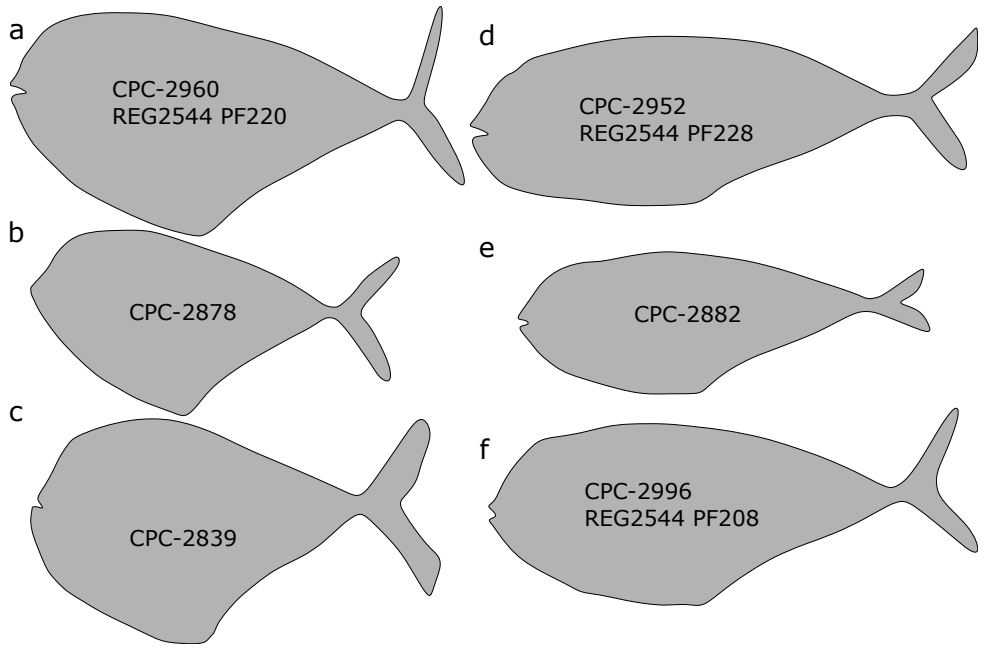

Figure 23: Body shape types detected in *T. formosa*. Trilliant-shaped individuals show a deeply keeled belly (A-C) in comparison to torpedo-shaped specimens (D-F). The collection numbers are placed inside each individual.

Chapter 4

Results

4.1 Publication 1 - Taphonomy and paleobiology of *Goulmimichthys roberti*

Stinnesbeck, E.S., Stinnesbeck, W., Herder, F. and Rust, J. 2020. **Taphonomy and paleobiology of the Late Cretaceous (Cenomanian-Turonian) pachyrhizodont *Goulmimichthys roberti* from Vallecillo and Múzquiz, northeastern Mexico**. Palaeogeography, Palaeoclimatology, Palaeoecology 543. doi.org/10.1016/j.palaeo.2020.109607.

177 individuals of the pachyrhizodont *Goulmimichthys roberti* were reviewed, comprising 166 from the middle Turonian Vallecillo deposit and 11 from the lesser known Cenomanian to Santonian localities of northern Coahuila in Múzquiz. The sites form a north-south trending transect of proximal to distal shelf conditions of the Paleo-Gulf of Mexico. Vallecillo thus represents a pelagic and open marine habitat whereas a shallow setting is visible for the northern localities. The pachyrhizodont *G. roberti* is documented in both ecological areas and therefore occupied a wider stratigraphic range and ecosystem as previously known.

Goulmimichthys roberti is a common member of the Vallecillo fish assemblage resembling modern scombrids. Fishes possess a fusiform body shape and a markedly forked caudal fin associated with sustained high-speed swimming. Specimens from Vallecillo range from 100 to 650 mm total length. A unimodal size distribution revealed a dominance of 250 to 450 mm long individuals (Figure 24). Specimens ranging from 100 to 250 mm are interpreted as juveniles and notably rare. Big individuals in a size range of 450 to 650 mm are interpreted as old and equally rare. Very small individuals beneath 100 mm length were not identified, probably due to preservational reasons. Vallecillo is therefore dominated by mature individuals spending their life in the pelagic realm. These results are consistent with a size range distribution of 7 specimens from Múzquiz (Figure 24). Múzquiz specimens range from 200 to 400 mm length, while very small or very

big individuals are absent. It is assumed that large and very small individuals did not populate the Vallecillo ocean. Results for Múzquiz must be taken with caution, because specimens were collected from different localities of distinct ages and do not represent a single population.

The decay analysis of *G. roberti* revealed a frequently complete and articulated preservation in both locations, Vallecillo and Múzquiz. Carcass flotation is excluded and a rapid burial is assumed. All specimens from Vallecillo are laterally embedded (74.8%), in contrast to individuals from northern Múzquiz localities where 45.5% are embedded laterally. In Vallecillo 11.7% show a latero-dorsal and 9.8% a latero-ventral position. A fully ventral position is only seen in 1.2% of the specimens. A dorsal embedding is extremely rare (0.6%). 1.8% are disarticulated. The majority of the specimens is classified as slightly disarticulated (58.9%) and nearly complete (71.8%). A ventral and dorsal embedding is visible in Múzquiz and pointing to a different embedding type. Specimens from Múzquiz are laterally embedded (45.5%) but 18.2% are latero-dorsally and latero-ventrally embedded (both reach 18.2%). A dorsal preservation is seen in 9.1%. Ventral embedding is also seen in 9.1% of the specimens. Individuals from Múzquiz are slightly disarticulated (71.4%) and nearly complete (71.4%). These different embedding positions are explained by environmental conditions. Specimens from Múzquiz show a pit-like depression around their bodies reflecting a fine and muddy sediment. It is therefore likely that these fishes were instantly covered by the sediment after arriving on the sea bottom, without tumbling into a lateral position. In Vallecillo the sea bottom must have been more consolidated.

Goulmimichthys roberti from Vallecillo and northern Múzquiz localities is frequently embedded straight (>80%). A curvature of the body is nevertheless also identified in both localities. Body arching into a dorsal or ventral direction is observed in 6.7% of the Vallecillo specimens. Arching to the right or left, and an s-shape preservation are observed in 1.8% (Both categories reach 1.8%). 14.3% of the specimens from Múzquiz show column bending to the right or left.

The majority of specimens from Vallecillo display an open mouth (44.8%). A closed mouth is seen in 30.1% of the individuals. 17.2% are disarticulated preventing identification of the mouth opening, while in 8% identification was not possible e.g. due to a dorsal preservation. Múzquiz specimens are frequently preserved with a closed mouth (71.4%). An open mouth is visible in 14.3% of the individuals.

Fin preservation is documented for the dorsal, pectoral and pelvic fins. In specimens from Vallecillo, pectoral (60.1%) and pelvic fins (58.3%) are majorly spread. Dorsal fin spreading is identified in 32.5% of the specimens but in the majority of individuals the dorsal fin is not erected (41.1%). This is also seen in individuals from Múzquiz. Pectoral (42.9%) and pelvic fins (42.9%) are majorly spread but the dorsal fin is usually not preserved (42.9%) or closed (28.6%).

Recurring decay features were observed and led to the reconstruction of a decay pathway interpreted as successive decay stages. These include the detachment of fins, breakage

of the vertebral column and disintegration of the body into mainly articulated compartments. Four decay stages were differentiated: Stage 1 includes articulated and complete individuals and is documented in 28.2% of the individuals. In stage 2, decay is initiated with the detachment of the dorsal fin while the rest of the body remains complete and mostly articulated (38.7%). In stage 3, the vertebral column starts to disarticulate and a breakage of the column is observed behind the skull as well as at the height of the anal fin (12.9%). Skull disarticulation is not restricted to this stage. In the last stage, the body breaks up into compartments which remain majorly complete and articulated (8.6%). These parts remain in close distance to the main body. The detached body parts decompose independently after losing attachment leading to fully disarticulated individuals. Other decay features not restricted to these four stages comprise 11.7%.

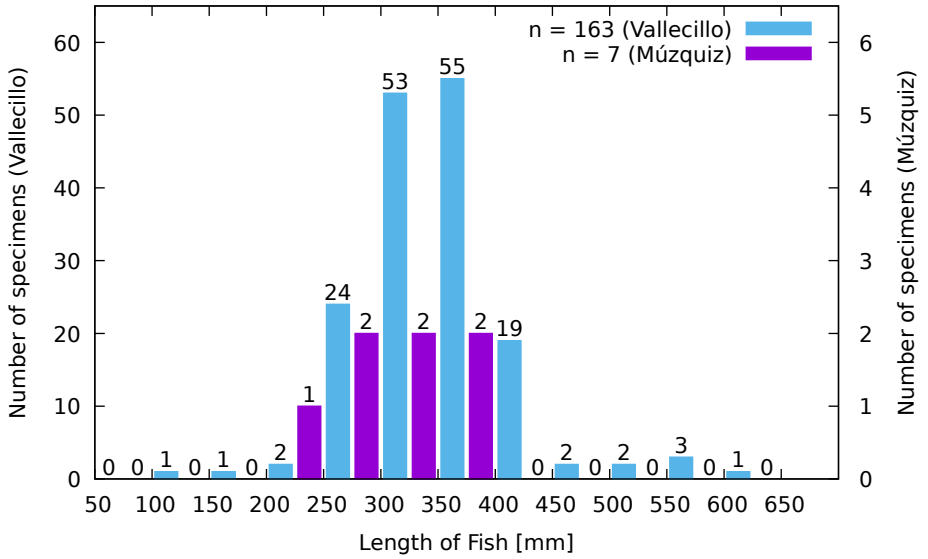

Figure 24: Size range distribution of *G. roberti* from Vallecillo and Múzquiz.

4.2 Publication 2 - A fish-parasitic isopod, *Mothocya vallecillae*

Stinnesbeck, E.S., Wägele, J.W., Herder, F., Rust, J. and Stinnesbeck W. 2021. **A fish-parasitic isopod (Cymothoidae) on the pachyrhizodont *Goulmimichthys roberti* from the lower Turonian (Upper Cretaceous) Vallecillo plattenkalk, NE Mexico**. Cretaceous Research, 129. doi.org/10.1016/j.cretres.2021.105019

The pachyrhizodont *Goulmimichthys roberti* is a common member of the Vallecillo fish assemblage reaching 100 to 650 mm total length (see above). The taxon resembles modern scombrids and is a well-adapted predator with a forked tail enabling rapid propulsion. A review of 166 individuals of *G. roberti* revealed the first Cretaceous isopod attached to this fish. *Mothocya vallecillae* is the first documented isopod from Vallecillo and the first isopod documented from the pelagic realm. *Mothocya vallecillae* is attached to a 380 mm long *G. roberti* individual at the dorso-lateral part of the skull, on the parietal bone. The isopod is oriented vertical to the host's longitudinal axis and 13 mm long as well as 5 mm wide. It is dorsally preserved with a slightly twisted posture exposing a part of the right body side.

Mothocya vallecillae is placed within Cymothoidae due of several features shared with external and buccal-inhabiting taxa. Some of these features are hooked dactyli on all appendages, small or absent eyes, pereonite tergites that are laterally narrower and pointed posteriorly, laterally rounded coxal plates that are visible in dorsal view (slender anteriorly), and lunate-shaped uropods (Figure 25 A and B). The position of the isopod on the fish skull supports a parasitic lifestyle because modern *Mothocya* populate the branchial cavity and sometimes the buccal cavity of the host. In contrast to the large numbers of scavengers attracted by the carcass of e.g. *Pachyrhizodus marathonensis* from the Santonian of Australia (Wilson et al. 2011), *G. roberti* is only infested by one individual. The hostile sea bottom conditions in Vallecillo favor the assumption that a scavenging lifestyle is less likely. As the host is articulated and complete it is assumed, that both individuals were rapidly buried. A rapid embedding under anoxic conditions reduces the time for decay and the possibility of the parasite to depart from the host. *Mothocya vallecillae* is therefore unique in several aspects. It is the first isopod from Vallecillo and in direct association to its vertebrate host. Besides that, it is associated with an open marine environment of about 200 m water depth. Carcass transportation is excluded due to the exceptional preservation of both, *G. roberti* and *M. vallecillae*.

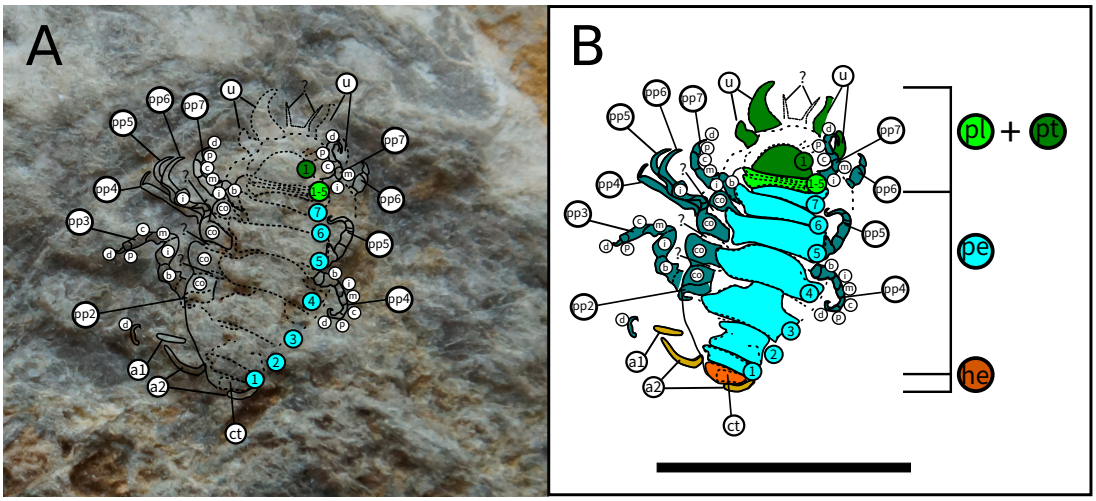

Figure 25: *Mothocya vallecillae* from Vallecillo. Abbreviations: a1, antennule; a2, antenna; b, basis; co, coxa; c, carpus; ct, cephalothorax; d, dactylus; h, head; i, ischium; m, merus; pp, pereopod; pl, pleon; p, propodus; pe, pereon; pt, pleotelson; pl, pleon; u, uropod.

4.3 Publication 3 - Taphonomy of *Tselfatia formosa*

Stinnesbeck, E.S., Herder, F., Rust, J. and Stinnesbeck, W. 2023. **Taphonomy of the teleost *Tselfatia formosa* Arambourg, 1943 from Vallecillo, NE Mexico**. PlosOne, 18(2). doi.org/10.1371/journal.pone.0280797.

A total of 149 individuals of the teleost *Tselfatia formosa* revealed two different body shape types interpreted as sexual shape dimorphism (SSD); a trilliant and a torpedo-shape type. Trilliant-shaped specimens are twice as long as wide, with a length to width body ratio of 2:1. The abdominal region is deeply keeled and creates the deepest point of the ventral body and a rhombic (trilliant diamond or diamond) shape. The curved back is anteriorly higher than the tail. 53.8% of the individuals are referred to as diamond-shaped. Torpedo-shaped individuals are three times longer than wide and thus present a length to width body ratio of 3:1. The deeply keeled belly is either absent or faintly marked, thus creating a more streamlined shape. The highest point of the dorsal body side is reached at the middle of the curved back. 23.1% of the individuals are classified as torpedo-shaped. There are no osteological differences or traits that justify the erection of two different *Tselfatia* species. In addition to torpedo and trilliant-shaped individuals, ambiguous specimens between the two types are identified. These individuals are not keeled enough to be included to trilliant diamond individuals nor are they interpreted as torpedo-shaped. 4.2% are referred to as ambiguous.

The size range distribution of *T. formosa* is based on 143 individuals and illustrates a unimodal size dispersion (Figure 26). Specimens range from 50 to 800 mm length, but Vallecillo is predominantly populated by individuals ranging from 400 to 650 mm length, interpreted as adults. Adult specimens between 400 to 600 mm are majorly trilliant-shaped and small individuals from 150 to 250 mm length torpedo-shaped. Ontogenetic variation is excluded as diamond and torpedo-shaped individuals are present in juvenile and adult stages. The different body shape types are therefore interpreted as Sexual Shape Dimorphism. Small individuals <50 mm are not documented, likely due to diagenetic destruction or a lack of preservation. Regarding the body shape types, small individuals are frequently torpedo-shaped and range from 150 to 250 mm length. Adult specimens ranging from 450 to 600 mm length are majorly trilliant-shaped whereas ambiguous specimens range from 500 to 600 mm length. Both body shape types are identified in juvenile and adult individuals.

Tselfatia formosa is laterally embedded and most specimens are nearly complete (55.0%) and nearly articulated (41.4%) preserved. These observations lead to the assumption that a transportation or flotation phase of the carcasses can be excluded. Fishes were rapidly buried, thus limiting the time of decay on the sea floor.

The dorsal fin of *T. formosa* from Vallecillo is frequently preserved in a middle spread position (36.2%). A full erection of the fin is seen in 28.2%. The anal fin of *T. formosa*

is mostly spread in middle position (43.0%) but a full erection is seen in 7.4% of the specimens. Therefore, the dorsal fin is more frequently erected than the anal fin which is often disarticulated (27.5%) preserved. Pectoral (51.0%) as well as pelvic fins (59.7%) are frequently not preserved and percentages of fin spreading are therefore not presented here.

Specimens are mostly embedded straight, without a fraction at the vertebral column (48.3%). This differs from *G. roberti* in which a curvature of the body is frequent and fractures of the vertebral column is often seen in the tail region.

The unpaired fins of *T. formosa* are retracted behind a groove which is formed by scales (lateral plates). These scales are preserved as skin shadow and slightly expand the body outline, as seen in extant fan fishes. The fins are bigger than previously documented and fin rays bend collectively into one direction, as if exposed to unidirectional currents.

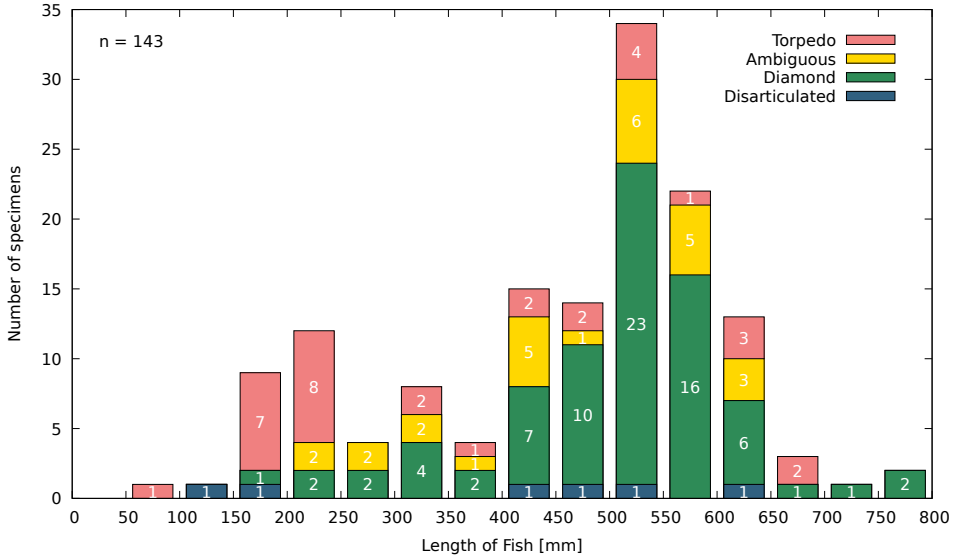

Figure 26: Size range distribution of *T. formosa* from Vallecillo.

Chapter 5

Discussion

Most Plattenkalk Lagerstätten reflect quiet water restricted coastal or lagoonal environments, e.g. Solnhofen (Germany) Namoura, Haqel and Hjoula (Lebanon), El Montsec and Las Hoyas in Spain, or Santana in Brazil (Forey et al. 2003; Selden and Nudds 2012). In this aspect, the Vallecillo Plattenkalk deposit is a notable exception as it clearly represents an open marine pelagic environment. The exceptionally well preserved fossil assemblage of Vallecillo thus opens a window not only into a hitherto little known paleogeographic region, the northwestern Paleo Gulf of Mexico, but it also allows us to understand a subtropical pelagic ecosystem of the late Cretaceous during and in the aftermath of a global ecological upheaval, i.e. OAE2. A period of extreme global oceanic and climatic conditions.

To date, most authors refer to the excellent preservation of Vallecillo fossils, whereas taphonomic studies of individual taxa are rare. Giersch (2014) described some taphonomic aspects of fishes from the northern La Mula outcrops and Ifrim (2006) covered the taphonomy of ammonoids from Vallecillo. A brief taphonomical description of the most abundant fish species (*Rhynchodercetis yovanovitchi*, *Nursallia gutturosum* and *Tselfatia formosa*) was also provided by the latter author. This line of investigation is followed here for important members of the Vallecillo Osteichthyes assemblage. A discussion for the published results obtained during this dissertation is presented.

5.1 Publication 1 - Taphonomy and paleobiology of *Goulmimichthys roberti*

Stinnesbeck, E.S., Stinnesbeck, W., Herder, F. and Rust, J. 2020. **Taphonomy and paleobiology of the Late Cretaceous (Cenomanian-Turonian) pachyrhizodont *Goulmimichthys roberti* from Vallecillo and Múzquiz, northeastern Mexico**. Palaeogeography, Palaeoclimatology, Palaeoecology 543. doi.org/10.1016/j.palaeo.2020.109607.

Only the osteology of *Goulmimichthys roberti* has been described from Vallecillo prior to this dissertation (Blanco-Piñón 2003; Blanco-Piñón and Cavin 2003; Giersch 2014), with a maximum of only 7 fossil specimens available (e.g. Giersch 2014). Taphonomic studies similar to this work were not conducted. As many additional fossils were discovered in the past years, the present work is based on the largest amount of *G. roberti* individuals to date (177 specimens). Taphonomic analyses are here conducted for the first time and support the hypothesis of an anoxic Vallecillo sea floor. *Goulmimichthys roberti* from Vallecillo is frequently preserved with an open mouth and spread fins, characteristics which are associated with respiratory stress (Pan et al., 2015). These features documented here for the first time in the Vallecillo fish assemblage, have elsewhere been interpreted as solid evidence for abrupt mortality, suffocation or tetany (Bieńkowska-Wasiluk, 2010; Chellouche et al., 2012; Pan et al., 2019); they are here also interpreted as caused by a lack of oxygen on the sea floor. Fast swimming and healthy fishes could easily avoid the hostile bottom conditions but individuals already struggling with death may have ended up in these deep levels of the water column. The bodies of these individuals are predominantly "slightly disarticulated and nearly complete" preserved, which indicates that they have been out of reach for scavengers. This circumstances are here interpreted as a result of a toxic environment. The lethal anoxic bottom water zone must variously have extended into the water column as even large pachyrhizodont and ichthyodectid fish reaching well above 1m length are completely preserved and untouched by scavengers. Carcasses decayed on the sea floor without been transported. Bone dispersal caused by bottom currents is also absent in almost all specimens, thus indicating that quiet water and stagnant conditions must have prevailed near the sea floor for most of the time.

Specimens from Vallecillo are majorly laterally embedded and *in situ* decay occurred without a phase of transportation. In contrast to specimens from Múzquiz localities, individuals from Vallecillo remained on the sea floor for an extended period of time without being covered by soft lime sediment. This explains the different stages of decay which are yet unreported for Múzquiz (Figure 27 A-F).

In addition to its abundance in Vallecillo, *Goulmimichthys roberti* is here also documented from the Múzquiz localities of San Carlos, El Pilote, Carranza and Los Temporales. These outcrops in northern Coahuila are sparsely studied and scientifically almost unknown. Giersch (2014) documented 20 fishes from Carranza (Turonian-Coniacian) and the upper Santonian Temporales quarry, arguing that the low number of species is due to sparse sampling of the localities. The taphonomic study on *G. roberti* from Múzquiz presented here now shows that preservational differences exist between the Múzquiz localities and Vallecillo. Specimens from Múzquiz show a wider variety in embedding style and are frequently latero-ventrally as well as latero-dorsally embedded. Specimens are only "slightly disarticulated", thus showing a lower degree of disintegration (compared to Vallecillo). Different decay stages are therefore only seen in Vallecillo (Figure 27 A-F). Preservation is also better in Múzquiz. This is probably due to rapid embedding into

the fine lime mud sediment as evidenced by pit-like depressions around the individuals documented here. Specimens were instantly covered by the sediment and did not remain uncovered on the sea floor as in Vallecillo. In conclusion, the sediment of the Vallecillo sea floor must have been considerably more consolidated compared to Múzquiz.

A sudden mass mortality event is excluded for *G. roberti* from Vallecillo, based on the absence of fish concentrations in specific layers of the sediment sequence. The excellent preservation seen in Múzquiz is thus the result of rapid phosphatization of bones and soft tissue and rapid carcass coverage in the fine mud sediment, whereas specimens from Vallecillo are secondarily recrystallized to calcite and spent more time on the sediment surface, prior to embedding. They are generally less well preserved, making it difficult to differentiate small bones of e.g. the skull. Due to their different diagenetic history, they show a slab and counter-slab preservation when split.

The presence of *G. roberti* in five limestone deposits from Múzquiz extends the stratigraphic range of the taxon from the Cenomanian to the Santonian. In North America, this pachyrhizodont was previously known only from Vallecillo and therefore regarded as restricted to the Uppermost Cenomanian-middle Turonian (Blanco-Piñón and Cavin 2003; Giersch 2014). A wider stratigraphic range is thus known now, as well as a wider environmental range of the taxon from the pelagic to shallow shelf habitats. Limestones from El Pilote in northern Coahuila contain fishes, abundant crustaceans and a pterosaur wing but the assemblage is yet undescribed. The Carranza locality in that area is interpreted as an open marine shelf environment with about 50 m water depth (Ifrim et al. 2011a). Fishes, chelonioids and a fragment of the pterosaur *Muzquizopteryx coahuilensis* were documented from this site (pers. obs.). The middle to Late Santonian Los Temporales locality from the wider Múzquiz area contains fishes as well as raninid crustaceans documented by Vega et al. (2007). The presence of *Cenomanocarcinus vanstraeleni* suggests a water depth of <50 m and a benthonic community. Oxygenated bottom waters and a shallow shelf setting were concluded by the authors which is very different from the situation at Vallecillo. *Goulmimichthys roberti* therefore occupied a wider range of ecosystems and also had a wider stratigraphic range than previously known.

The unimodal size distribution of *G. roberti* from Vallecillo shows a peak of mature individuals between 250 to 450 mm length while juveniles remain undocumented. Large-sized adults probably migrated out of the pelagic but only future investigations in Múzquiz could clarify this hypothesis and provide further insight into the former life-style of this pachyrhizodont.

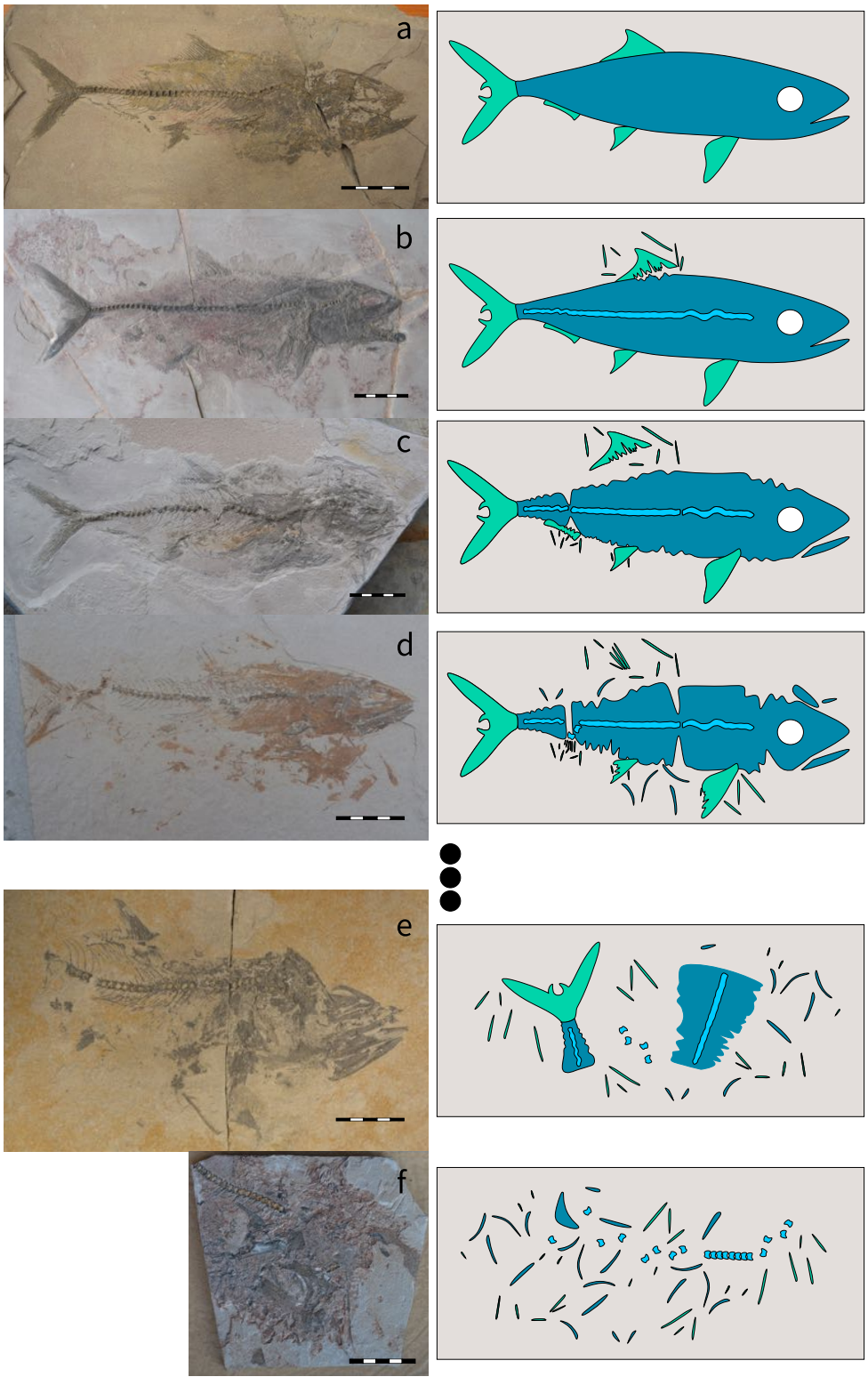

Figure 27: Decay stages of *G. roberti* from Vallecillo. Complete and articulated individual (A). Decay starts with the detachment of fins and a slight disarticulation of the vertebral column (B). Vertebral column breaks several times while compartments detach from the main body (C) Body breaks up into compartments but these remain majorly complete and articulated (D). Compartments decompose independently (E) leading to completely disarticulated and incomplete specimens (F). Scale bars 50 mm.

5.2 Publication 2 - A fish-parasitic isopod, *Mothocya vallecillae*

Stinnesbeck, E.S., Wägele, J.W., Herder, F., Rust, J. and Stinnesbeck W. 2021. **A fish-parasitic isopod (Cymothoidae) on the pachyrhizodont *Goulmimichthys roberti* from the lower Turonian (Upper Cretaceous) Vallecillo plattenkalk, NE Mexico**. Cretaceous Research, 129. doi.org/10.1016/j.cretres.2021.105019

Isopods are very rare in the fossil record but date back to the Carboniferous (Schram 1970). Specimens are often overlooked or destroyed by preparation. The majority is known from shallow lagoonal environments, e.g. one third of all fossil specimens is documented from the Jurassic Solnhofen Lagerstätte in Germany (Etter 2014) interpreted as lagoonal deposit. Specimens found in the Solnhofen deposit were probably washed into the lagoon from adjacent shallows. In Mexico, fossil isopods from the Cretaceous are documented from the upper Albian Tzu-tzu and el Espinal localities of Chiapas and the Valanginian-Hauterivian Barraca el Gavilán locality, as well as the Albian Tlayúa locality in Puebla (Wieder und Feldmann 1992, Feldmann et al. 1998; Vega et al. 2018; Vega et al. 2019). These individuals are documented by exuvia or body parts, without the presence of a vertebrate host. It is therefore not clearly known if these isopods were ectoparasites or scavengers. Some exuviae were clearly transported from the original habitat (e.g. *Natatolana poblana* and *Archaeoniscus* sp. from Puebla) (Feldmann et al. 1998; Vega et al. 2019). The new species described here as *Mothocya vallecillae* is quite unique as it is the first parasitic isopod from Vallecillo and directly associated with its host *G. roberti*. A direct association of parasite and host is extremely rare and has previously only been documented from Solnhofen by Nagler et al. (2016). The isopods from Solnhofen were directly attached to fish species (e.g. *Pholidophorus* sp., *Amblysemius belicianus*, *Caturus* sp., *Anaethalion angustus* and *Leptolepides sprattiformis*) and clearly represent a case of paleoparasitism (Nagler et al. 2016). Other isopods directly associated with fish are known from the Eocene Monte Postale site of the Bolca quarry in Italy known to represent a fore-reef or lagoon environment (Robin et al. 2019). Two electric rays were there associated with 23 isopods and interpreted as a case of selective scavenging, or micropredation.

In contrast to these reports, *M. vallecillae* is found in an open marine environment, populated by fast swimming pachyrhizodontids, ancient swordfish, large filter feeding-sharks as well as pachycormids (Vullo et al. 2021). The nearest coast was probably in 400 km distance with a water depth of about 200 m (Ifrim 2006; Ifrim et al. 2011b). A phase of transport is excluded due to articulation and completeness of both, host and parasite. *Goulmimichthys roberti* was rapidly embedded without a substantial time of disintegration at the sea floor and shows no signs of bone dispersal caused by scavengers. Currents are nearly absent in Vallecillo and anoxic bottom conditions favored fossil preservation. A

scavenging life-style of the isopod is therefore excluded.

A direct biological relationship is thus shown here between parasite and host. Isopods associated with a pachyrhizodont fish are only known from the Albian Toolebuc Formation of Australia, which was interpreted as a shallow marine environment (Wilson et al. 2011). 130 isopods were found in the carcass (opercular cavity) of the pachyrhizodont fish *Pachyrhizodus marathonensis* and were interpreted as scavengers. *Mothocya vallecillae* is thus the first parasitic isopod from Vallecillo, directly attached to its host found in a pelagic environment. Further research could clarify if the parasite predominantly lived in the pelagic or was transported on the host into this environment. A preference of *G. roberti* as main host is also not known as only one individual is documented.

5.3 Publication 3 - Taphonomy of *Tselfatia formosa*

Stinnesbeck, E.S., Herder, F., Rust, J. and Stinnesbeck, W. 2023. **Taphonomy of the teleost *Tselfatia formosa* Arambourg, 1943 from Vallecillo, NE Mexico**. PlosOne, 18(2). doi.org/10.1371/journal.pone.0280797.

Tselfatia formosa is known from the Upper Cenomanian of Morocco (Jebel Tselfat), the Upper Cenomanian of Italy (Cinto Eugeano), the Cenomanian-Turonian of Texas and Croatia, the Upper Cenomanian or Lower Turonian of Germany (Misburg) and the Cenomanian-Turonian of Mexico (Vallecillo) (Arambourg 1943, 1954; Sorbini 1976; Bardack and Teller-Marshall 1980; Maisch and Lehmann 2000; Blanco-Piñón 2003). Previous descriptions of the teleost are based only on a few specimens and their documentation is majorly focused on the osteology (Maisch and Lehmann 2000). Taverne (1975, 1983, 2000a) revised the Material from Italy (Sorbini 1976) and Morocco (Arambourg 1954) and emended earlier osteological descriptions as well as discussed the systematic position of the taxon. Maisch and Lehmann (2000) described a single specimen from the black shales of Lower Saxony. Blanco-Piñón et al. (2001; 2002; Blanco-Piñón 2003) were the first to describe *T. formosa* from Vallecillo. The authors recorded 5 specimens between 160 to 610 mm length. Ifrim (2006) presented a size range based on 56 specimens ranging from 80 to 780 mm length presenting an unimodal distribution with a peak at 480 to 580 mm length. Giersch (2014) revised and discussed the function and anatomy of the dorsal and anal fins and excluded the presence of a membrane between individual fin rays. He also documented the first color preservation on the scales and presented a size range distribution on the basis of 52 specimens. The size range presented by this author also shows an unimodal distribution with a dominance of individuals ranging from 350 to 450 mm length. Giersch (2014) therefore concluded that *T. formosa* spend its entire lifecycle in Vallecillo.

The size range presented here is by far the largest and based on 143 specimens. Specimens documented here extend the number of individuals and the documented size range

previously known. Individuals presented here range from 50 to 800 mm length. Results show that Vallecillo was majorly inhabited by adult individuals (>400 mm length) and that a high adult mortality existed, as already suggested by Giersch (2014). Migration of small specimens appears unlikely as small-sized individuals are preserved although not as frequent as seen in *N. gutturosum* from Vallecillo (Stinnesbeck et al. 2019).

Tselfatia formosa is not yet known from the Múzquiz localities which suggests that this fish was restricted to the open marine pelagic environment of Vallecillo, not entering the shallow water ramp areas in northern Coahuila. *Dixonanogmius*, a tselfatiiform fish similar to *Tselfatia*, is documented from Múzquiz. Further research could clarify if *Tselfatia* avoided the shallow environments of northern Coahuila to avoid competition for resources.

Two body shape types are here identified in *T. formosa* for the first time and associated with sexual shape dimorphism. Torpedo-shaped individuals are three times longer than wide (3:1), whereas trilliant-shaped individuals are twice as long as wide (2:1). Trilliant-shaped individuals are frequent in a range of 500 to 600 mm while torpedo-shaped specimens are abundant in small-sized individuals of 150 to 300 mm length. An increase of the body depth relative to the standard length is proposed by Patterson (1967) to occur during the ontogeny of *Tselfatia* but results presented here contrast this statement because no correlation is identified between size and shape. Torpedo- and trilliant-shaped individuals are both present in small- and large-sized specimens. Ontogeny is therefore excluded to explain the different outlines. Rather, the two types of body shape appear associated to foraging and reproduction. An increase of the abdominal cavity, as seen in trilliant-shaped individuals, is known from extant Carangidae and required for the accommodation of female reproductive organs, there allowing for maximized reproductive success as well as larval survival. Modern Carangidae (e.g. *Decapterus macrosoma*) exhibit bigger heads to maximize buccal volume to gain additional food needed to produce the eggs, while males need adaptations to succeed in male to male competition (Uba 2019). The preservation of stomach content is not frequent in *T. formosa* but is more common in trilliant-shaped individuals, thus adding evidence to the presented interpretation. Ambiguous specimens are not interpreted as transitional, e.g. caused by ontogenetic variation. These specimens are here interpreted as variations within *T. formosa*.

A taphonomic analysis of *Tselfatia formosa* is here conducted for the first time. Ifrim (2006) observed that specimens are complete and articulated but did not perform a taphonomic examination to support this statement. The author concluded that the teleost must have dwelled in deep water and that articulated individuals died beyond the buoyancy line which means that carcasses sank immediately after death, without a drifting phase (Ifrim 2006). The results presented here now support this assumption. *Tselfatia formosa* is frequently articulated and complete. The dorsal and anal fins are better preserved than the pectoral and pelvic fins and often erected. The column is majorly articulated and breakage is rare. Similar to *G. roberti* from Vallecillo, *T. formosa* is documented with spread fins and open mouths, pointing to respiratory stress. Embedding must have

been rapid preventing substantial decay and excluding a phase of flotation. The bones of disarticulated individuals remain in close distance to the body and did not drift away. Disarticulation caused by scavengers is not documented. Results therefore confirm the assumptions of Ifrim (2006) and Diedrich (2012) which associate *T. formosa* with deep-dwelling.

The function of the dorsal and anal fin was discussed by Giersch (2014) and Taverne (2000a). Both authors suggested that the teleost was able to fold back the dorsal and anal fins into a groove. Results presented here confirm this interpretation. *Tselfatia formosa* retracts the unpaired fins behind modified scales, as seen in recent fan fishes. These lateral plates, here documented for the first time, are preserved as skin shadow (Figure 28 A and B). Giersch (2014) argued that a skin between the fin rays is problematic due to overlapping fin rays and therefore suggested a similar appearance for *T. formosa* as seen in modern deep sea fish, e.g. Lophiiformes, but this is not seen in the taphonomic analyses presented here. Specimens with retracted fins show no major damage of the fin rays and the lepidotrichia remain in parallel arrangement (Figure 28 C). Preservation even supports the assumption of a membrane between the fin rays as a consistent arrangement is shown even in disarticulated individuals (Figure 28 D). Fins behave in a connected way, bending collectively, similar to a fan, as if exposed to a current (Figure 28 E and F). Regarding their massive size, this is astonishing, as fins would easily detach or break. Results therefore indicate that the membrane was still intact. It is concluded that *T. formosa* used the fins in a way similar to extant fan fishes (*Pteraclis* and *Pterycombus*). Fins are retracted to swim with high speed and erected to improve the maneuverability.

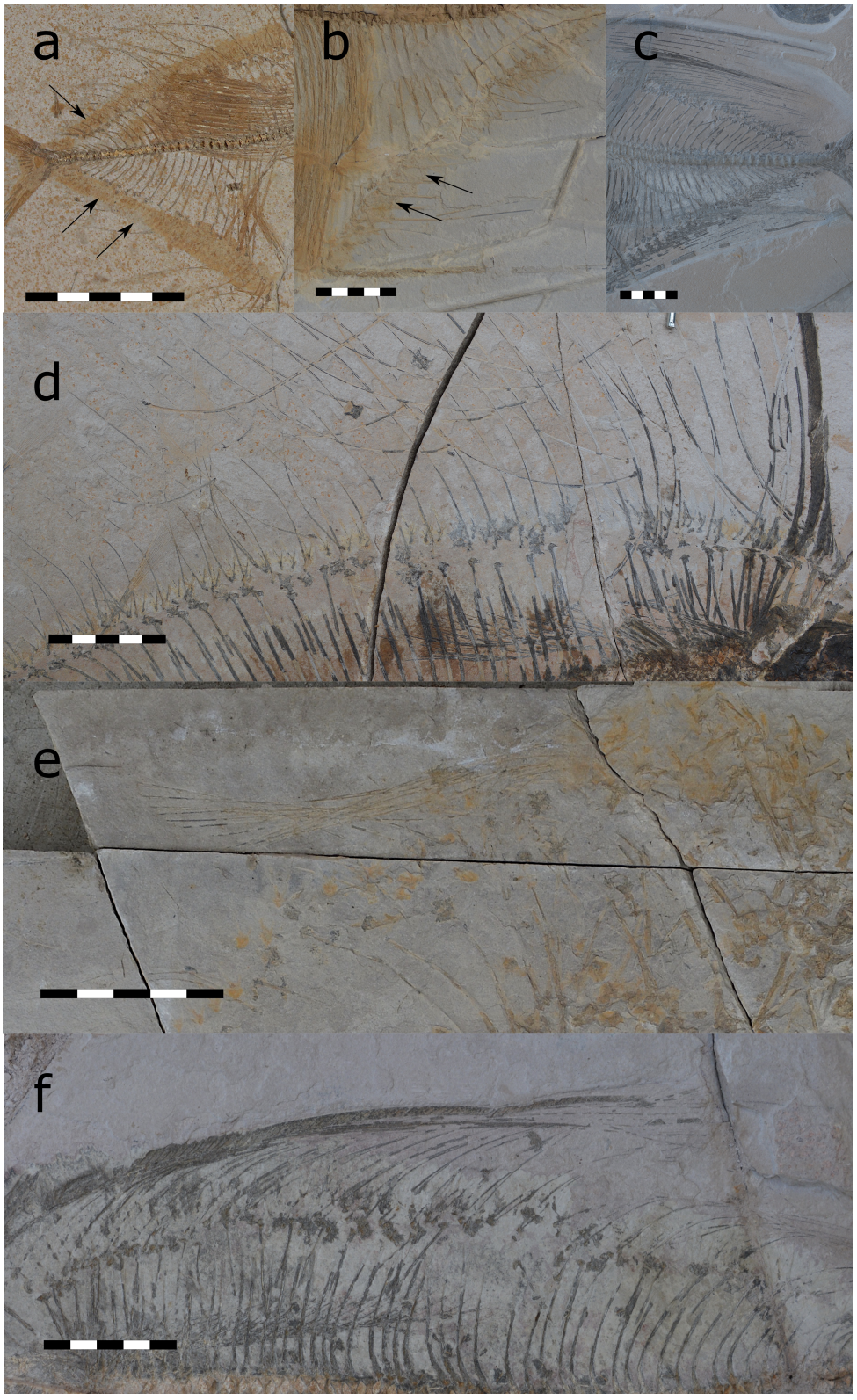

Figure 28: Preservation of the unpaired fins in *T. formosa* from Vallecillo. Lateral plates are preserved as skin shadow (A and B). Retracted dorsal fin without overlapping fin rays (C). Parallel arrangement of the fin rays (D) and collective bending of the rays indicating an intact membrane between the lepidotrichia (E and F). Scale bars 50 mm.

Chapter 6

Unpublished results and future research

For the present dissertation more than a thousand fish specimens were revised in the collection of Ing. Fernández Garza in Monterrey, the Museo del Desierto at Saltillo, and the Museo de Múzquiz in northern Coahuila. It is evident from this revision that these collections contain at least a dozen and perhaps two dozens, of new taxa, most of them fishes but also turtles, aigialosaurids and even pliosaurids. Most of this material is exceptionally well preserved and accessible through the above institutions. Taphonomic studies are still pending for this abundant material and even basic research is needed for most individuals. Deposits from northern Coahuila (Múzquiz) are even less explored and the number of undescribed fossils is equally large. Here are some informations regarding future investigations in Vallecillo.

6.1 *Vallecillichthys multivertebratum* Blanco and Cavin, 2003

Vallecillichthys multivertebratum is an endemic predator from Vallecillo that is mainly present by large sized individuals. A size range distribution presented here is based on 50 specimens and reveals an unimodal distribution of individuals ranging from 250 mm to 1800 mm length, with an abundance peak of specimens between 900 mm to 1400 mm length (Figure 29). These are interpreted as adults. Smaller specimens (juveniles), on the other hand, are extremely rare. This suggests that juveniles may have lived elsewhere.

No specimens have yet been discovered in the northern shallow marine deposits of Múzquiz.

Initial results on the taphonomy of *V. multivertebratum* provide evidence of different types of embedding and a frequent curvature of the vertebral column. The body is preserved either straight, J-bended (only one side bended, front or tail bended), S-shaped or crescent (U-shape) (Figure 30 A-D). Nevertheless 54% of the specimens are embedded straight. In 16% the body is slightly curved and only one side is J-bended, e.g. bending occurs directly behind the skull. 26% are preserved in a crescent position (U-shape). The

body is bended backwards, even forming a circle in extreme cases. The spine breaks into several compartments but specimens remain majorly articulated. A small percentage of 4% shows an S-shaped preservation (Figure 31).

Bending of the backbone is frequently seen in fishes and has been interpreted as evidence for tetany, as a post-mortem feature caused by overstretching of the spinal column due to gas accumulation in the abdominal cavity, or as the result of tension of the ligaments caused by dehydration in hypersaline waters (Seilacher et al. 1985; Viohl 1994; Chelouche et al. 2012; Anderson and Woods 2013; Pan et al. 2019). Nevertheless, spine curvation has also been observed in fishes that died in normal marine water. According to Weiler (1929) young individuals tend to bend more because their bones are less ossified and thus more flexible, but Pan et al. (2019) argued that the degree of curvature increases with the size of the individual, as larger specimens possess larger backbones. In *V. multivertebratum* several potential causes may have existed. There are specimens with a broken vertebral column, probably caused by gas pressure, while other individuals exist with an unbroken column which may have been flexible enough to resist. Gas pressure alone was probably not high enough to cause breakage of the backbone or lead to carcass flotation. High salinity levels causing dehydration and spine bending are not excluded regarding the extreme climatic conditions at the time of sediment deposition, but still appear less likely due to the open marine conditions in Vallecillo. High salinity levels as seen in lagoonal pools are clearly excluded. Spine bending resulting from dehydration would only have been possible in carcasses remaining floating at the water surface due to gas accumulation.

Another explanation for spine bending could be the elongated morphology of *V. multivertebratum*. The heaviest body part was presumably the skull; therefore, carcasses probably sunk head-first to the ground, thus increasing the probability for a J-bending and column breakage.

Bending of the vertebral column was already documented in *Goulmimichthys roberti* from Vallecillo (Stinnesbeck et al. 2020) and causally associated with tetany (together with open mouth and spread fins). In *Heckelichthys* sp., another Ichthyodectiform fish from Vallecillo with a similar elongated body shape, a curvature of the spinal column is also identified. Specimens show an S-shape or crescent (U-shape) curvature.

In *Gillicus arcuatus*, curvature of the spinal column is not documented although the fish shows a similarly elongated body. It is therefore assumed that the life style of the fishes contributes to the preservation, whether carcasses are embedded straight or bended.

Gut content in *V. multivertebratum* majorly consists of semi-digested *Rhynchodercetis yovanovitchi* specimens, a surface-dwelling taxon strikingly similar in appearance to modern needlefish. This suggests that *V. multivertebratum* hunted near the water surface and that gas accumulation was common due to e.g. higher water temperatures near the surface.

Vallecillichthys multivertebratum from Vallecillo is mostly embedded laterally but two

specimens show a dorsal and three a ventral embedding. Despite the fact that *V. multivertebratum* is an exceedingly elongated and slender fish, no loose heads or isolated body parts are documented in the museum material revised here. Disarticulated specimens persisted on the sea floor for some time and decomposed without the interference of scavengers. Their body broke into compartments but these isolated remains persisted in close distance to the main body. This suggests that the decay process took place at the sea floor and excludes an extensive phase of flotation and transportation. This result is surprising as *V. multivertebratum* is here interpreted as a surface dweller.

There is one specimen in the documented collections that preserved scales and color. Scales are rhombic in shape and a horizontal dark line, or band, is visible along the body side and interpreted as ornamentation (Figure 32 A and B). In addition, the fringe of the scales is dark grey colored. The dark-colored scales resemble the dorsal ornamentation seen in *Thrissops formosus* from Solnhofen. Punctae, as described by Blanco-Piñón and Alvarado-Ortega (2007), are not identified.

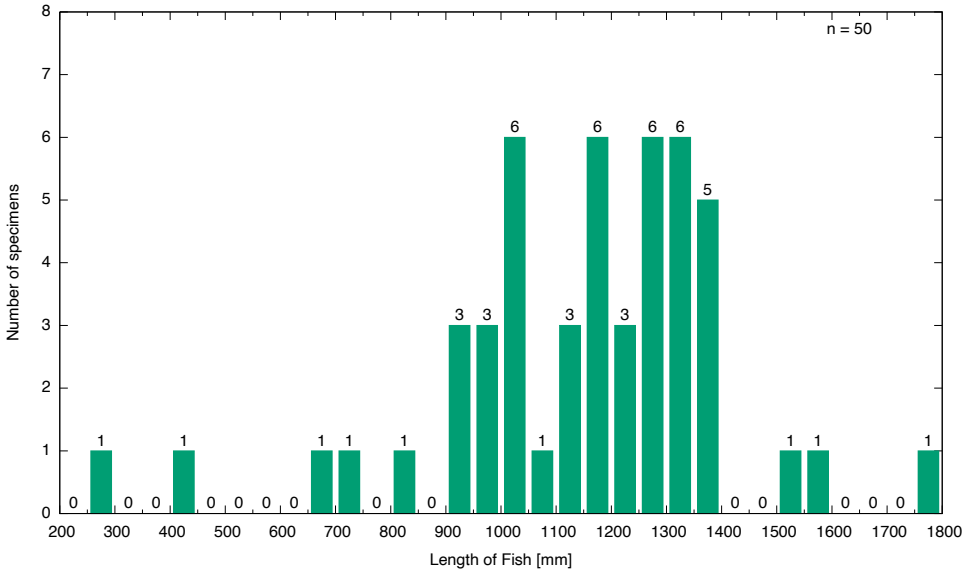

Figure 29: Unimodal size range distribution of *Vallecillichthys multivertebratum*.

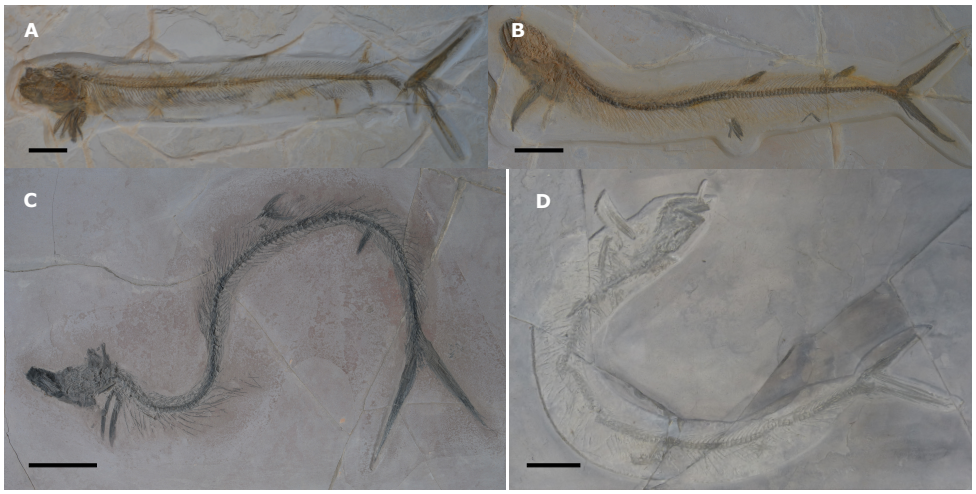

Figure 30: Different embedding forms in *Vallecillichthys multivertebratum* from Vallecillo. Straight embedding (A), J-formed beding (B), S-shape (C) and crescent shape (D). Scale bars 100 mm.

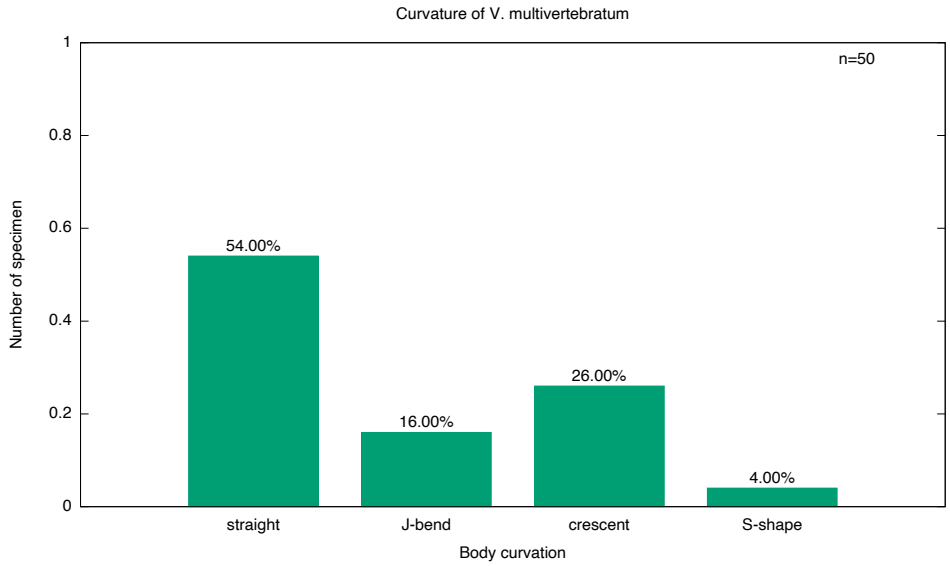

Figure 31: Embedding of *Vallecillichthys multivertebratum* in percent of the total number of individuals.

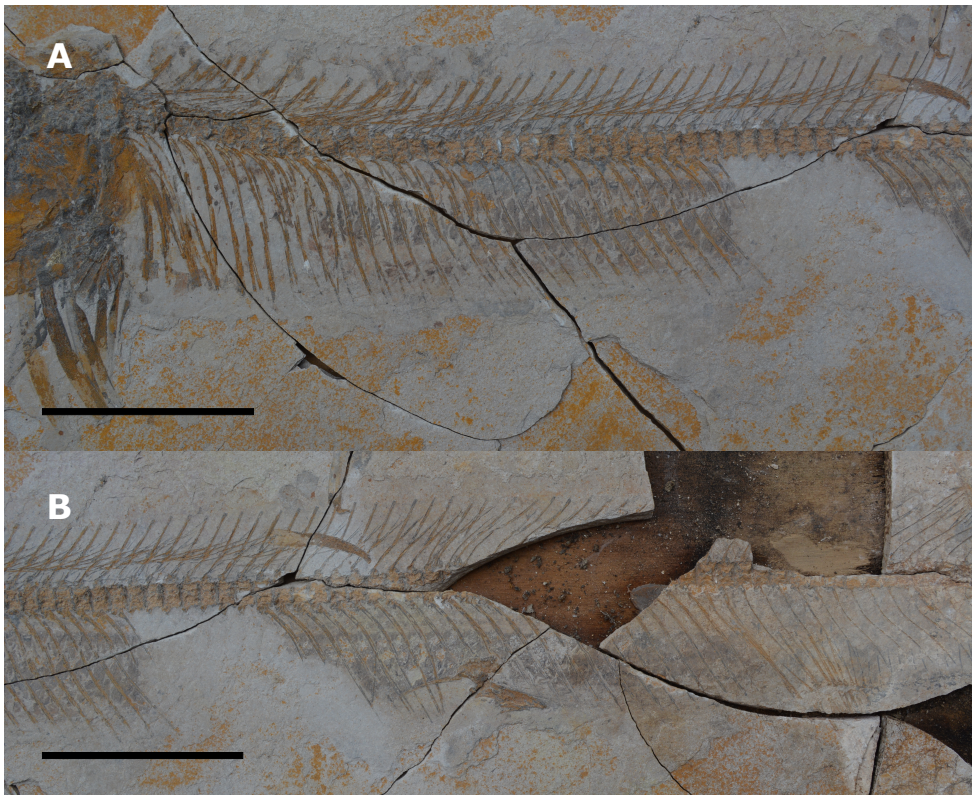

Figure 32: Color preservation in *Vallecillichthys multivertebratum*. Cranial part (A) and caudal part (B) of the animal with a horizontal dark band along the body. Scale bars 100 mm.

6.2 Pachycormiformes non det.

Pachycormiformes from Vallecillo reach a standard length of about 1 m. Small specimens (500 mm) are present but rare. Specimens are mostly laterally preserved and in two cases ventrally embedded. Most large individuals are articulated and complete, but small specimens are often decomposed. Small specimens did not drift to the surface; rather they remained on the sea floor prior to embedding and disarticulated there without the interaction of scavengers. Preservational differences between the two size classes are difficult to explain but large individuals may have sunken deeper into the substrate, thus improving their preservational potential. Alternatively, large specimens inhabited deeper water levels than small individuals. Nevertheless, this interpretation is only based on a single small individual and six large sized ones. A disarticulated individual from an unknown locality of Múzquiz is documented, too.

6.3 *Belonostomus longirostris* Lambe, 1902

A size range distribution based on 25 specimens of *Belonostomus longirostris* reveals an unimodal distribution (Figure 33). Specimens range from 350 to 1150 mm length but are frequently present between 600 and 900 mm length. Small specimens below 350 mm length are not documented. Juveniles may have populated shallow water habitats and migrated into the Vallecillo open sea as adults, but no juvenile *Belonostomus* are known to date from the shallow water Múzquiz localities to provide evidence for this assumption.

Preservation of *Belonostomus longirostris* includes specimens embedded straight, J-bend, crescent and S-shaped. The majority of the individuals shows a crescent preservation (U-shape) (52%). The body is bent backwards, as frequently seen in *V. multivertebratum*. 32% of the individuals are J-bended and only 12% are embedded straight. A minority of 4% is S-shaped (Figure 34). Specimens are usually nearly complete and slightly disarticulated. The body is occasionally split into separate compartments but scales and body parts remained in close distance to each other. There are no isolated skulls identified as in *Rhynchodercetis yovanovitchi*. The rectangular ganoid scales probably helped to maintain the body articulated and in one piece as described by Anderson and Woods (2013) for other fishes with ganoid scales. *Belonostomus longirostris* is interpreted as a surface dweller similar to modern Belonids but a phase of carcass flotation is excluded. Gas pressure was apparently not high enough to allow buoyancy and to let the body float to the water surface. Therefore, disarticulation majorly occurred on the sea bottom (Figure 35).

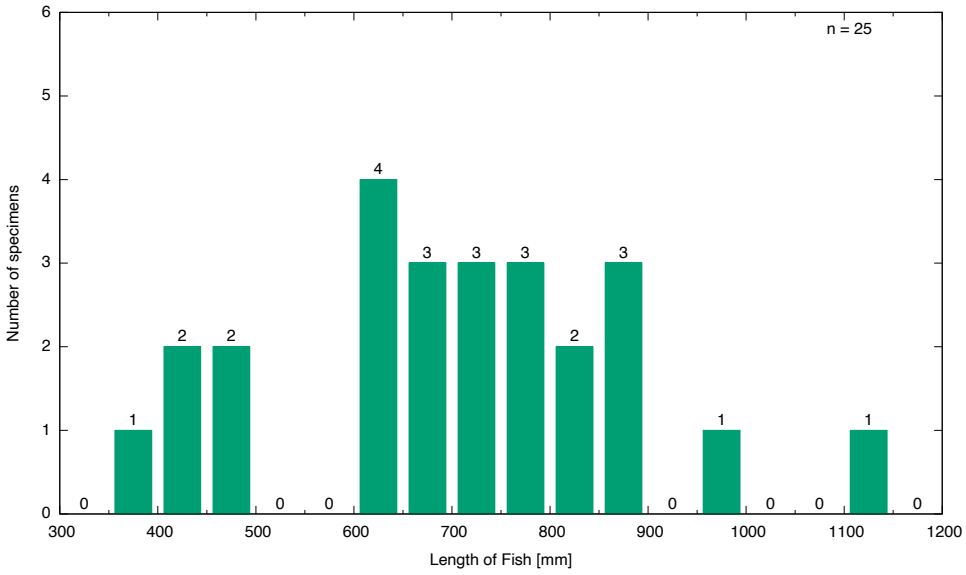

Figure 33: Size range distribution of *Belonostomus longirostris*.

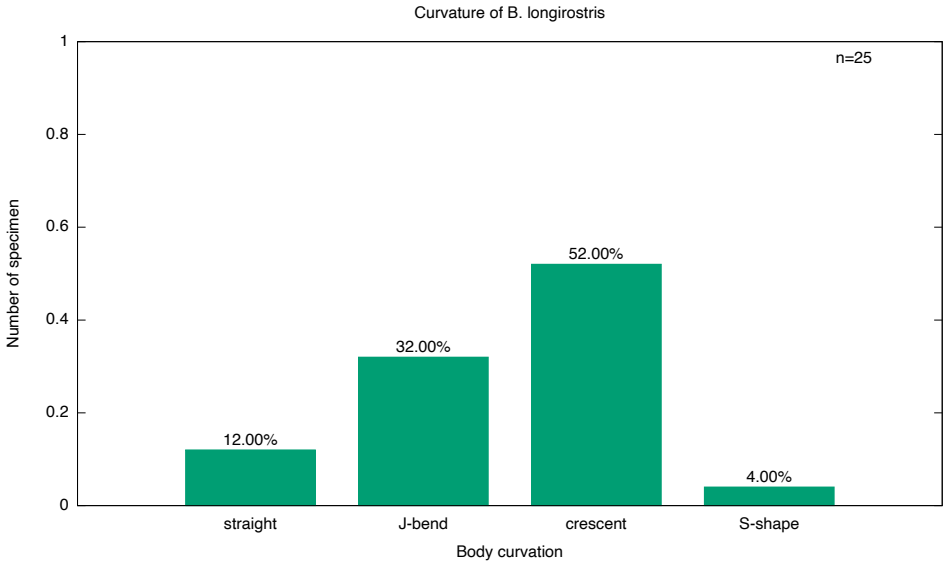

Figure 34: Embedding of *Belonostomus longirostris* in percent of the total number of individuals.

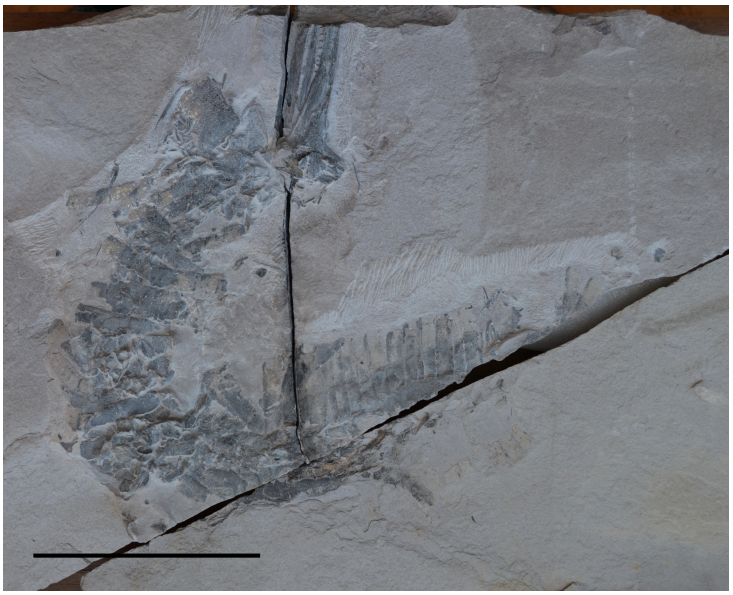

Figure 35: Disarticulated *Belonostomus longirostris* specimen from Vallecillo. Scale bar 100 mm.

6.4 Swordfish-like individuals

Six swordfish-like individuals here preliminary assigned to *"Protosphyraena" stebbingi* Woodward 1909 were documented. Three of them are nearly complete but in the other three specimens solely the skull is preserved. Apparently, the large and flat rostrum hampered lateral embedding and favored either a dorsal or ventral preservation. Disarticulated specimens and isolated skulls decomposed on the sea floor but carcasses may have floated at the surface for some time and lost the skull during this process. This appears likely as the skull is fixed to the heavy rostrum.

Chapter 7

Conclusions

The platy limestone deposit of Vallecillo is dated to the latest Cenomanian-middle Turonian and preserves a pelagic assemblage composed of reptiles, invertebrates and fishes. The deposit represents a mixture of species from the Western Interior Seaway and the Tethys, in addition to endemic taxa. Several fishes show close relatives, or are identical, to taxa from Northwest Africa (e.g. Morocco), which indicates that the Atlantic was sufficiently narrow to be crossed. Actinopterygians, Pachyrhizodont, Tselfatiiform, Aulopiform and Pycnodont fish dominate the Vallecillo assemblage.

The aim of this work was to understand the pelagic ecosystem found in Vallecillo and to reconstruct the former lifestyle of some of the most abundant fishes from the limestones. Therefore, it was critical to understand the preservation of the fossils and to conducting taphonomic analysis.

The common predator *Goulmimichthys roberti* was selected as one of these species. It is an abundant taxon ranging from 250 to 450 mm length. Specimens are majorly articulated and complete, which excludes a time of carcass flotation. Carcasses showed different decay stages and fishes were laterally embedded in Vallecillo which suggests that the sediment must have been firm. There is substantial evidence of respiratory stress, likely provoked by the oxygen deficient to anoxic conditions at the sea floor. This anoxic bottom water excluded the presence of scavengers and favored fossil preservation of complete carcasses disintegrating *in situ*. In coeval localities in the Múzquiz area, approximately 400 km to the North of Vallecillo, on the other hand, *G. roberti* was rapidly covered by soft mud sediment in ventral and dorsal positions. Deposits in this latter region are therefore interpreted as more shallow. The presence of *G. roberti* in Múzquiz provides evidence for a wider geographical and ecological dispersal than previously known.

The first parasitic isopod from Vallecillo is documented on a specimen of *G. roberti*. It is attached to the skull of its host and probably fed on blood, tissue and mucus of the fish. The fossil isopod is the first documented from a pelagic environment and shows hook-like articles on all the appendages, allowing for an assignation to Cymothoidae. It is here assigned to a new species of the extant genus *Mothocya*, named *Mothocya vallecillae*. It is not known if *M. vallecillae* preferred *G. roberti* as host as only one individual was

found.

The analysis of the abundant teleost *Tselfatia formosa* revealed that this fish is present in two distinct morphological variations, a torpedo- and a trilliant-shaped body form. This is here interpreted as sexual shape dimorphism. Both types are present in small-sized and large-sized individuals, which excludes ontogenetic variation, but diamond-shaped (trilliant cut diamond) individuals interpreted as females dominate the assemblage. The fish is commonly represented by 500 to 600 mm long specimens which are well-articulated and complete, thus suggesting rapid burial without a time of carcass transportation to the surface or scavenger interference. The size range determined here extends previously known data by far and is based on the largest set ever documented (149 specimens). The taphonomical analysis also reveals new data on the extraordinary long dorsal and anal fins. The fin reconstruction provides positive evidence of a membrane between the lepidotrichia which allowed methods of high speed swimming and maneuverability. A lifestyle similar to extant fan fishes in deeper water is suggested.

Results of the taphonomic analysis are seen as a first approach to describe the decay and to document the exceptional preservation of Vallecillo fishes but several important questions e.g. regarding the potential existence of young *G. roberti* individuals in shallow marine regions, the dispersal of *M. vallecillae,* or the coeval existence of two very similar tselfatiiform species (*Tselfatia* and *Dixonanogmius*) in different environments of Mexico remain to be solved. More so, however, it also has become evident that the paleontological potential of the Vallecillo and Múzquiz plattenkalks is enormous, with only a small number of the fossil assemblages known to date and even less taxa formally described

Chapter 8

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2) Stinnesbeck, E.S., Wägele, J.W., Herder, F., Rust, J. and Stinnesbeck W. **A fish-parasitic isopod (Cymothoidae) on the pachyrhizodont *Goulmimichthys roberti* from the lower Turonian (Upper Cretaceous) Vallecillo plattenkalk, NE Mexico**. Cretaceous Research, 2021, 129.
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3) Stinnesbeck, E.S., Herder, F., Rust, J. and Stinnesbeck, W. **Taphonomy of the teleost *Tselfatia formosa* Arambourg, 1943 from Vallecillo, NE Mexico**. PlosOne, 2023, 18(2).
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Taphonomy and paleobiology of the Late Cretaceous (Cenomanian-Turonian) pachyrhizodont *Goulmimichthys roberti* from Vallecillo and Múzquiz, northeastern Mexico

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ABSTRACT

Upper Cretaceous (Cenomanian-Santonian) platy limestone deposits in northeastern Mexico contain diverse assemblages of fossil fishes including the pachyrhizodont *Goulmimichthys roberti*. A review of 177 individuals from new localities in the Múzquiz area of northern Coahuila and from Vallecillo (early-middle Turonian) of Nuevo León reveals an unimodal size distribution of the taxon and dominance of 250 to 450 mm long individuals at Vallecillo, while smaller (younger) and larger-sized specimens are markedly rare. Size distribution is similar in the Múzquiz localities. The taxon thus migrated into pelagic environments (e.g. Vallecillo) when maturity was reached. Carcass flotation is excluded for the material due to the abundance of complete and articulated specimens. The taphonomical decay analysis of *G. roberti* allows for a differentiation of four preservational stages and evidences environmental differences between Vallecillo and the Múzquiz area. *Goulmimichthys roberti* occupied a wider stratigraphic range and ecosystem variety than previously known, including both pelagic and shallow shelf settings.

1. Introduction

Near Vallecillo, located approximately 100 km north of Monterrey in north-eastern Mexico (Fig. 1), lower to middle Turonian (Upper Cretaceous) platy limestone yields well-preserved fishes including sarcopterygians, actinopterygians and cartilaginous taxa which indicate a marine open shelf depositional environment (Blanco-Piñón, 2003; Ifrim, 2006; Ifrim and Stinnesbeck, 2007; Ifrim et al., 2011b; Giersch, 2014). *Rhynchodercetis yovanovitchi*, *Tselfatia formosa* and *Nursallia gutturosum* are the most common fish species at Vallecillo (Ifrim, 2006; Ifrim et al., 2005; Ifrim and Stinnesbeck, 2007; Giersch et al., 2008; Giersch, 2014; Stinnesbeck et al., 2019). Nevertheless, pachyrhizodonts are also common and represented by at least three taxa (*Pachyrhizodus caninus*, *Tingitanichthys heterodon* and *Goulmimichthys roberti*). A random surface collection by Ifrim (2006) revealed the pachyrhizodont *Goulmimichthys roberti* to be the third-most frequent species after *T. formosa* (31%) and *N. gutturosum* (29%), comprising about 9% of the Vallecillo fish fauna.

The taxon was first described from Vallecillo as a new species, *Goulmimichthys roberti*, by Blanco-Piñón (2003) and Blanco and Cavin (2003). Giersch (2014) revised collections of actinopterygian fishes from northeastern Mexico, including Vallecillo, and revealed osteological features closely relating *G. roberti* with *Rhacolepis*. We agree with this interpretation of Giersch (2014) but here refer to the Vallecillo pachyrhizodont as *Goulmimichthys roberti*, because a taxonomical revision of the taxon is beyond the scope of this paper.

Pachyrhizodont fishes appeared in the Jurassic and reached a cosmopolitan distribution during the Cretaceous (Gayet et al., 2012). The genus *Rhacolepis* was described from the Lower Cretaceous Santana Formation of Brazil (Kellner et al., 1994) and the Albian Tlayua locality (González-Rodríguez et al., 2013; González-Rodríguez et al., 2016). *Goulmimichthys* is documented from the Turonian of Colombia (*G. gasparinii*), and from the Turonian Akrabou Formation of Morocco (*G. arambourgi*) (Cavin, 1995; Cavin, 2001; Páramo Fonseca, 2001; Blanco-Piñón, 2003; Alvarado-Ortega et al., 2006; González-Rodríguez et al., 2016).

Here we report on the taphonomy of well-preserved *Goulmimichthys roberti* from platy limestone deposits in northeastern Mexico (Fig. 2). The localities form a north-south trending transect across proximal to distal shelf conditions of the northwestern margin of the paleo-Gulf of

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Fig. 1. Geographic location of Vallecillo and outcrops in the Múzquiz area in northeastern Mexico (states of Nuevo León and Coahuila).

Mexico. Our material of the taxon was collected from little documented platy limestone deposits in the Múzquiz area (San Carlos, Temporales, Piedritas, Pilote and Carranza) that range from Cenomanian to Santonian times, and from the lower to middle Turonian Vallecillo locality (Fig. 1).

Vallecillo was located at about 400 km distance from the nearest Cretaceous coastline, while the planktic foraminiferal assemblage characterizes water depths of about 200 m (Ifrim et al., 2011a, 2011b). Localities in the Múzquiz region have been interpreted as significantly more proximal, representing shallow water deposits of only a few tens of meters depth (Ifrim, 2006; Ifrim et al., 2011a; Giersch, 2014). We suggest that the gradual increase in water depth towards the south, in this north-south transect of about 500 km distance (Fig. 1), may explain paleoecological and preservational differences of individuals, as well as the fish assemblage. These questions are here investigated for the pachyrhizodont *Goulmimichthys roberti*.

2. Sites and stratigraphic positions

Here we report on the well-known Vallecillo deposit (Figs. 1, 2a) and sparsely investigated localities with new findings of *Goulmimichthys roberti* from the region north of Múzquiz in northern Coahuila (Figs. 1, 2b–f; e.g. Stinnesbeck et al., 2005; Frey et al., 2006; Giersch et al., 2011; González-Rodríguez et al., 2013 and González-Rodríguez et al., 2016). To date, the age and most of these Múzquiz sediment sequences is still little constrained.

Vallecillo: The Vallecillo (26°39.32′N, 100°00.82′W) platy limestone deposit is dated to the latest Cenomanian-middle Turonian by Ifrim, 2006 and Ifrim and Stinnesbeck (2008) (Fig. 3). The pelagic vertebrate and invertebrate assemblage consists of a mixture of the Western Interior Seaway, the Tethys, and endemic species (Ifrim and Stinnesbeck, 2007). Twelve species of actinopterygian fishes are described to date (Giersch, 2014) but numerous others remain undetermined.

San Carlos: Based on thin section analysis of planktic foraminifera (e.g. abundance of heterohelicids, hedbergellids, whiteinellids, rotaloporids, but a notable absence of double-keeled globotruncanids), the sediment sequence at San Carlos (29°19.34′N, 102°39.28′W) is estimated to represent Cenomanian ages (Fig. 3). The locality is yet unknown to science. In addition to *Goulmimichthys roberti* we identified a yet undescribed pachycormid, a fragment of *Dixonanogmius*, *Rhynchodercetis yovanovitchi*, *Vallecillichthys multivertebratum*, and a coelacanth. The fish assemblage thus resembles that of Vallecillo. There is no evidence for bioturbation in the San Carlos platy limestone, nor for water current activity.

Piedritas: Based on planktic foraminiferal analysis in thin sections (e.g. presence of heterohelicids, hedbergellids, whiteinellids, rotaloporids, but absence of double-keeled globotruncanids), the Piedritas (29°14.57′N, 102°46.56′W) sediment sequence may represent a Cenomanian-Turonian age (Fig. 3). Platy limestone lithologies consist of finely laminated mud- and wackestone microfacies. The fish assemblage includes *Laminospondylus transversus*, *Goulmimichthys roberti*, and two possible enchodontid taxa.

El Pilote: Finely laminated platy limestone in the El Pilote (28°45.56′N 103°4.6′W) limestone quarry was tentatively dated to the Turonian by Vega et al. (2007) and González-Rodríguez et al. (2016), while Nyborg et al. (2014) suggested a middle Santonian age based on faunal similarities with the nearby Los Temporales locality (Fig. 3). The latter authors documented fishes inside an ammonite body chamber ("fish can"). Crustacean remains include stomatopods and *Cenomanocarcinus vanstraeleni*, as well as *Stramentum* sp. preserved on the ammonite *Forresteria* sp. (Vega et al., 2007). *Gillicus arcuatus* was documented by Alvarado-Ortega and Porras-Múzquiz (2009). We identified *Laminospondylus transversus*, *Goulmimichthys roberti*, *Enchodus* sp., as well as lamniform and *Ptychodus* sp. shark teeth. A chelonioid, a pterosaur wing finger and wood are also known from this locality but remain unstudied. Some fish specimens were probably embedded into soft sediment, as indicated by low pit-like depressions in the otherwise even sediment surface around these individuals. There is no evidence yet for bioturbation or currents from the sediment.

Carranza: The platy limestone at Carranza quarry (29°10.775′N, 102°27.193′W) is from the upper Turonian-lower Coniacian (Nyborg et al., 2014; Ifrim et al., 2019) (Fig. 3). Planktonic foraminifera indicate open marine shelf environments with water depths of > 50 m (Ifrim et al., 2011a). The fish assemblage currently comprises two unidentified enchodontids, *Goulmimichthys roberti*, and an unidentified acanthomorph. A chelonioid was also collected from the outcrop. Ammonoid shells with epizoic cirriped overgrowth and a wing fragment of the pterosaur *Muzquizopteryx coahuilensis* were also documented (Ifrim et al., 2011a; Ifrim et al., 2019). Thin sections preserve sediment lamination and planktic foraminifera are consistently present.

Los Temporales: According to Giersch et al. (2008) and Giersch (2014), the Los Temporales (28°57.23′N, 102°18.3′W) platy limestone is Middle-Late Santonian in age (Fig. 3). The author documented *Dixonanogmius* sp., *Goulmimichthys roberti* and other yet undetermined fishes, some of which show current alignment. Undetermined fishes were documented by Nyborg et al., (2014) as trapped in the empty body chambers of ammonites ("fish cans"). *Cenomanocarcinus vanstraeleni* and raninid crustaceans are also known from the location (Vega et al., 2007). A long-snouted lepisosteiform named *Herreraichthys coahuilensis* was described by Alvarado-Ortega et al. (2016). The quarry reveals finely laminated mud- and wackestone containing a diverse planktic foraminiferal assemblage (Vega et al., 2007; Nyborg et al., 2014).

González-Rodríguez et al. (2016) also mentioned *Goulmimichthys* sp. from the Cenomanian La Mula locality north of Múzquiz, but this

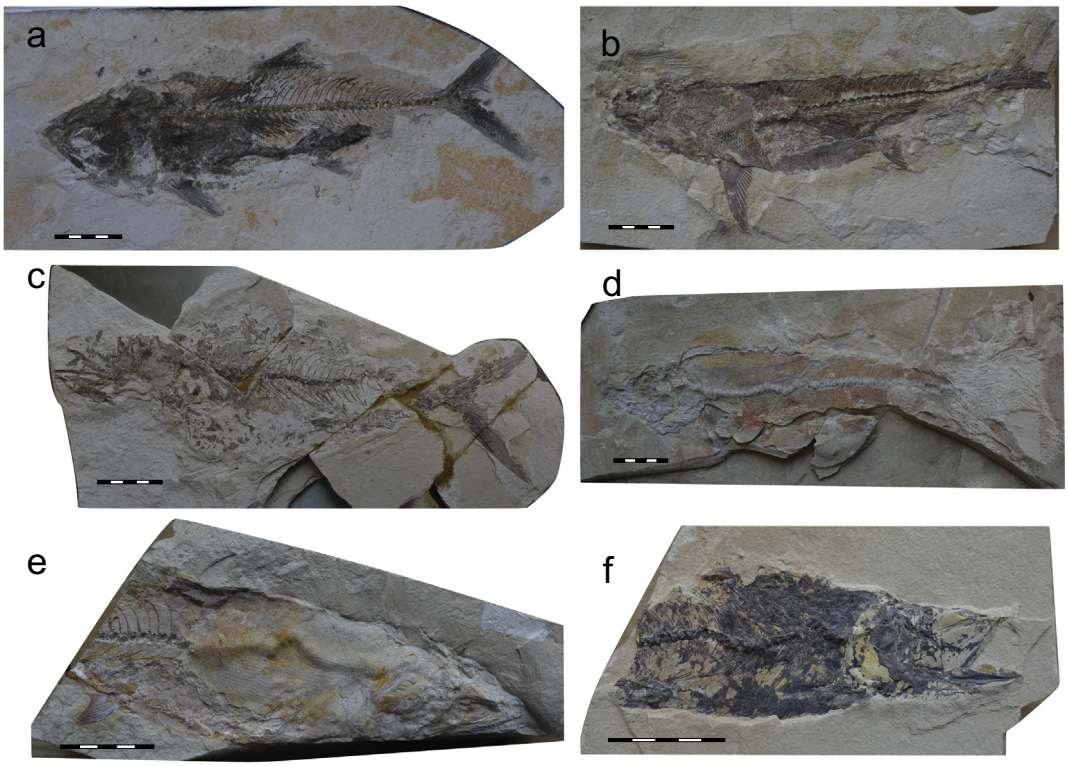

Fig. 2. *Goulmimichthys roberti* from Vallecillo; MVA-REG2544-PF196 (a) and Múzquiz (b–e). The pachyrhizodont is documented from San Carlos; CPC-476 (b), Temporales; MUZ-1 (c), Piedritas MUZ-1(d), Carranza; MUZ-REG1680 (e) and el Pilote; MUZ-212 (f). Scale 50 mm.

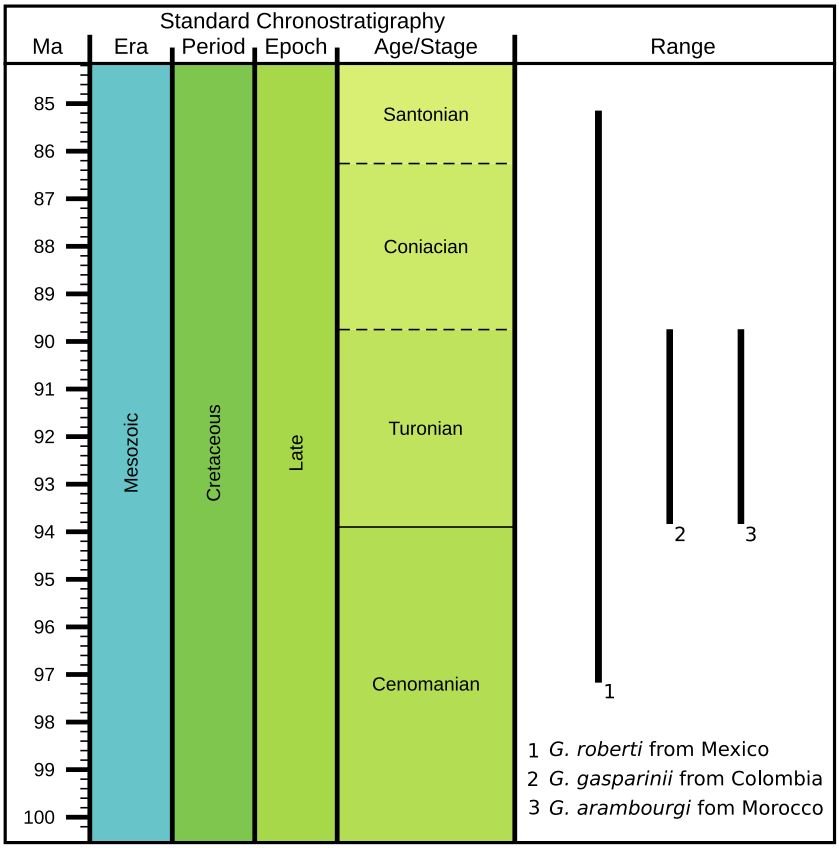

Fig. 3. Geological timescale of the Late Cretaceous visualizing the range of the Vallecillo individuals and specimens from Colombia and Morocco (Cavin, 1995; Cavin, 2001; Páramo-Fonseca, 2001).

assignation cannot be confirmed here. According to our review of fish material housed in the Museo de Paleontología de Múzquiz and in the Museo del Desierto, the La Mula assemblage is presently confined to *Scombroclupea occidentalis*, *Aspidopleurus kickapoo*, an undescribed acanthomorph and *Dixonanogmius* sp. This interpretation coincides with observations by Giersch (2014). Alvarado-Ortega et al. (2006) also documented *Saurodon* sp. from La Mula.

3. Materials and methods

The fossil material used for the present investigation on *Goulmimichthys roberti* consists of 166 specimens from Vallecillo and 11 individuals collected in platy limestone deposits of the Múzquiz area in northern Coahuila. The latter include three specimens from San Carlos, three from Temporales, and one from Piedritas. Four additional specimens were used for embedding classification and were collected at San Carlos (3) and Temporales (1). These specimens are housed in the Colección Paleontológica de Coahuila in the Museo del Desierto (MUDE) at Saltillo, the collection of Ing. Mauricio Fernández Garza in Monterrey (M) and the Museo de Paleontología de Múzquiz (MUZ). Our work is entirely based on these collections and no fieldwork was done here to collect material from the localities by ourselves.

The total length of individuals was measured following procedures described by Hastings et al. (2014), using the horizontal distance from the anterior-most point of the head to the tip of the longest lobe of the caudal fin. Photographs were taken with a Nikon D5200 camera.

Specimens missing significant parts of the skeleton due to breakage of the limestone slabs were not included in the taphonomic analysis. Missing parts were only tolerated when no significant information was lost (e.g. missing of the tip of the caudal fin).

Preservational and taphonomical characters of the analysis include articulation and completeness, the bending of the spinal column, mouth opening and fin preservation. Bending of the spinal column was classified into five groups: straight, bending in dorsal or ventral direction (aDV), lateral arched bending to the right or left (aRL), S-shape bending (Fig. 4a–d), and disarticulation (d). Breakage and disarticulation of the column, as also provoked by column bending (cbr), is documented separately, though only for Vallecillo specimens. Specimen embedding was classified into six types: lateral (L), dorsal (D), ventral (V), latero-dorsal (L-D), latero-ventral (L-V) and disarticulated (d). Individuals embedded latero-dorsally or latero-ventrally expose the dorsal or ventral body sides, respectively.

Articulation and completeness are differentiated; therefore, highly disarticulated but osteologically complete individuals are identified.

Bone dispersal is measured by five articulation groups: articulated (at), slightly disarticulated (sld), partially disarticulated (pd), mostly disarticulated (md) and strongly disarticulated (sd). Articulated specimens are well-preserved. Bones remain in their anatomical position. Slightly disarticulated specimens are characterized by detachment of single bones and single fins. Detached elements remain close to the body. Individuals interpreted as partially disarticulated show disarticulation by half, e.g. the skull, pectoral fins, and/or the dorsal fin are disarticulated, while other body parts remained in their original position. In general, the former position of the bones is identifiable and detached bones are close to the main body. The body can be disintegrated into parts that remained articulated. Mostly disarticulated individuals possess disarticulated parts at close distance to the main body. The former position of disarticulated body parts cannot be rearranged. Individuals interpreted as strongly disarticulated show bone disarticulation, without the perception of their former anatomical position. There are no detached parts that remain articulated in a compound.

Skeleton completeness is differentiated into four groups: complete (c), nearly complete (nc), partially complete (pc) and incomplete (ic). Complete individuals may lack a few ribs or fin rays. Nearly complete specimens lack ribs or single fins. The body remains mostly complete. Partially complete individuals are characterized by a loss of main body parts, e.g. the caudal fin, some vertebrae and posterior ribs. Specimens which lack more than half of the body, e.g. all fins and parts of the vertebrae, are considered as incomplete. The material reviewed here is characterized by the abundance of complete and near-to complete specimens, majorly categorized to the first three groups of completeness. This is probably attributed to the fact that our analysis is based on museum collections which are clearly biased towards complete specimens. The detachment and absence of scales was not included in the taphonomic range of articulation and completeness.

Fin preservation is classified into four groups: preservation not visible (nv), fins disarticulated (d), fins spread, and closed. Fins without visible preservation possess few articulated fin rays which do not allow for an identification as “spread” or “closed”. Disarticulated fins are characterized by detached fin rays, preventing further identification. Spread fins show a fan-like opening angle of 90° to the main body (Fig. 5a). Closed fins show fin rays without spreading. Rays are pressed together and oriented adjacent to the main body (Fig. 5b). Mouth

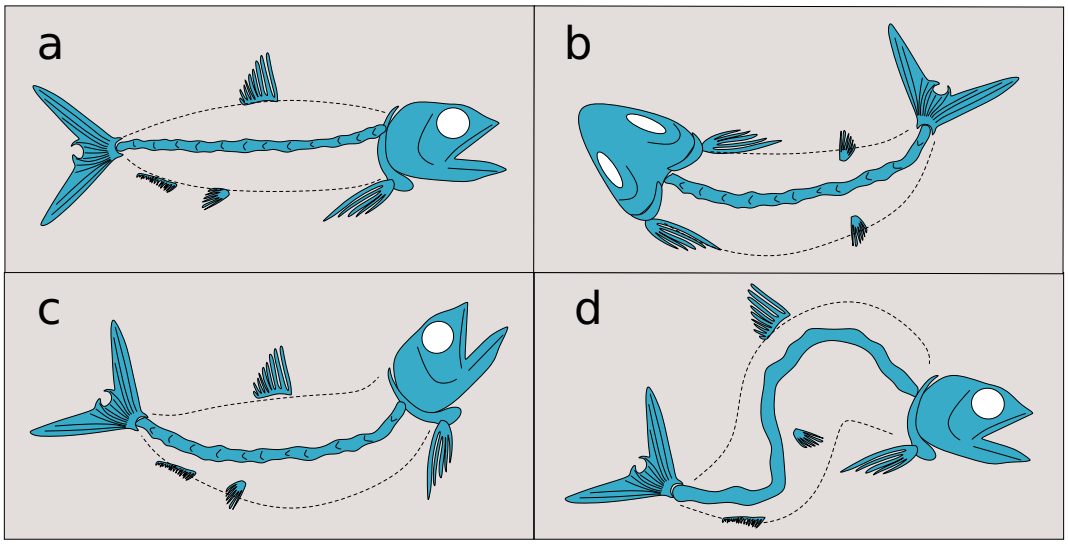

Fig. 4. Bending of the spinal column in *Goulmimichthys roberti*. Four types of bending are differentiated: (a) straight, (b) lateral arched bending to the right or left (aRL), (c) bending in dorsal or ventral direction (aDV), and (d) S-shape bending.

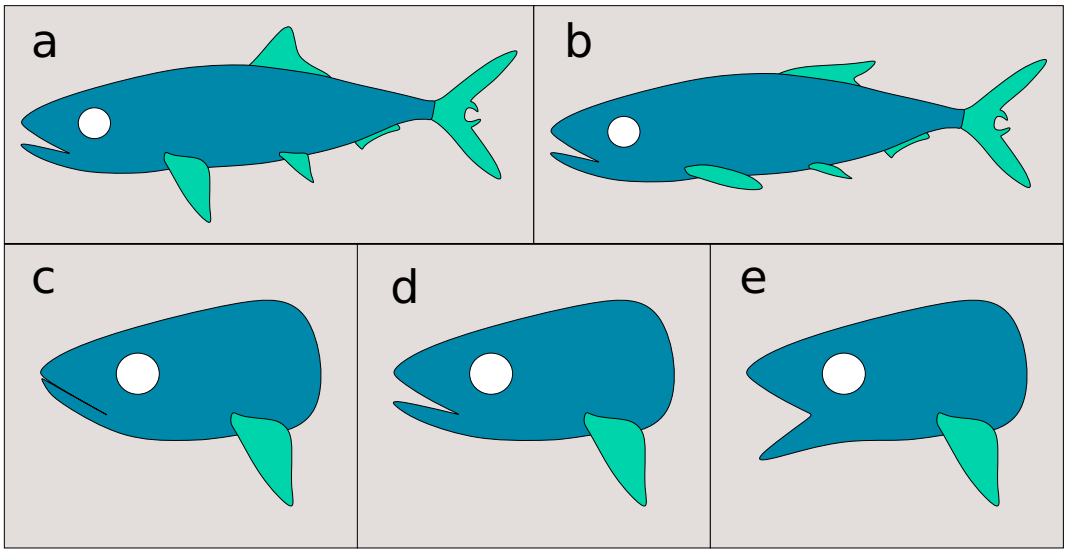

Fig. 5. Fin and mouth positions of *Goulmimichthys roberti*. Fins in a fan-like opening angle are interpreted as spread or flabellate (a). Fins with closed fin rays (b). Mouth closed (cl), moderately open (mo) and widely open (wo) (c–e).

opening was divided into three groups: closed (0°–10°) (cl), moderately open (11°–39°) (mo) and widely open (> 40°) (wo) (Fig. 5c–e). Disarticulated skulls, or those with significant bones missing (e.g. dentary), were not included in the present analysis.

Highly disarticulated or highly incomplete specimens were not included in the size range analysis but were used for taphonomical measurements. An exception was made for material in which the size could be properly reconstructed (e.g. caudal fin missing).

4. Results

4.1. Size range of Goulmimichthys roberti from Vallecillo and Múzquiz

The sizes of 163 specimens of *Goulmimichthys roberti* were measured to illustrate the size range distribution of the taxon. The collection is biased as it is based on material collected for private collections and museums. Distribution is markedly unimodal (Fig. 6), with a well-defined abundance peak of individuals between 250 and 450 mm length and a mode at 300–400 mm. Individuals ranging from 100 to 250 mm length are rare and interpreted as juveniles. Specimens smaller than 10 mm length have not been identified. Large-sized specimens ranging from 450 to 650 mm are equally rare; they are here interpreted to represent old individuals. The Vallecillo assemblage of *Goulmimichthys roberti* is dominated by individuals ranging from 250 to 450 mm total length, tentatively interpreted here as mature.

The size range distribution of 7 specimens from Múzquiz ranges from 200 to 400 mm length and thus represents a size distribution consistent with Vallecillo (Fig. 6). Specimens interpreted as juveniles ranging from 50 to 200 mm and adults from 400 to 650 mm are not present. The results for Múzquiz are taken with caution, because specimens were collected from different localities of distinct ages and do not represent one population.

4.2. Preservation and taphonomy of specimens from Vallecillo

Six embedding categories were differentiated for *Goulmimichthys roberti* from Vallecillo (Fig. 7a). Specimens are often embedded laterally (74.8%). In 11.7% of the assemblage, the body is preserved in a latero-dorsal and in 9.8% in a latero-ventral position, while fully ventral (1.2%) or dorsal (0.6%) positions are extremely rare (Fig. 7a). Only a small number of specimens (1.8%) was embedded disarticulated.

Specimens are frequently articulated and complete. While 21.5%

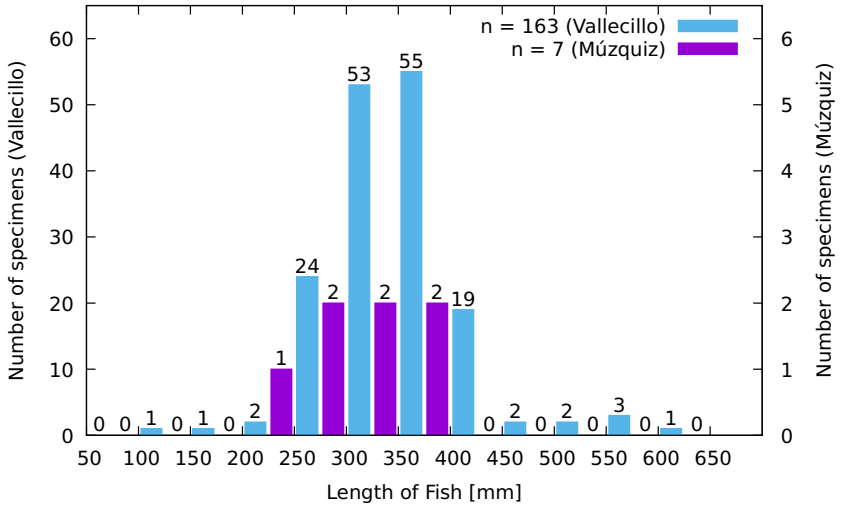

Fig. 6. Size range distribution of 163 individuals from Vallecillo and 7 specimens from Múzquiz sites.

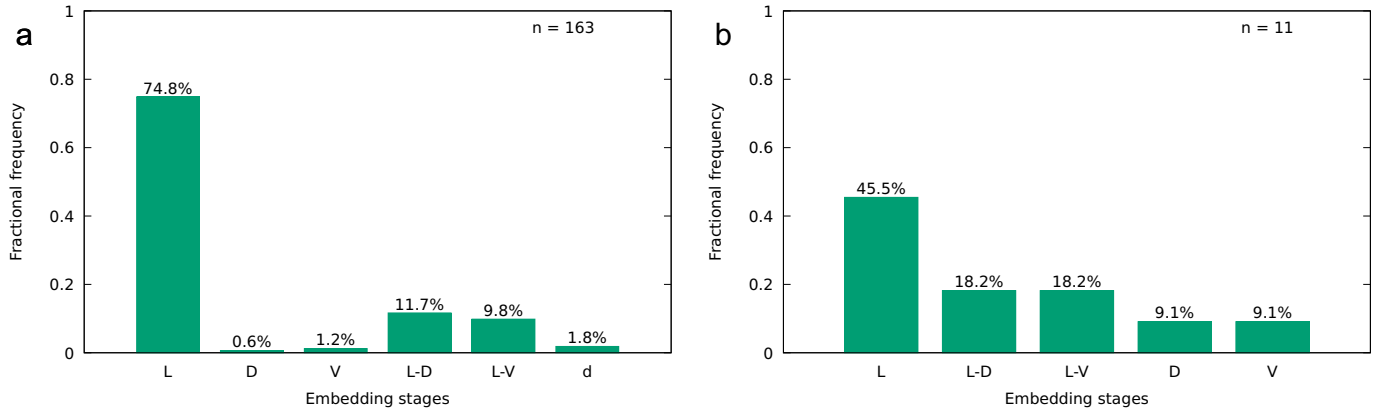

Fig. 7. Embedding of *Goulmimichthys roberti* from Vallecillo (a) and Múzquiz (b), in percent of the total number of individuals. Lateral, dorsal and ventral preservation (L, D and V) as well as latero-dorsal (L-D), latero-ventral (L-V) and disarticulated individuals (d).

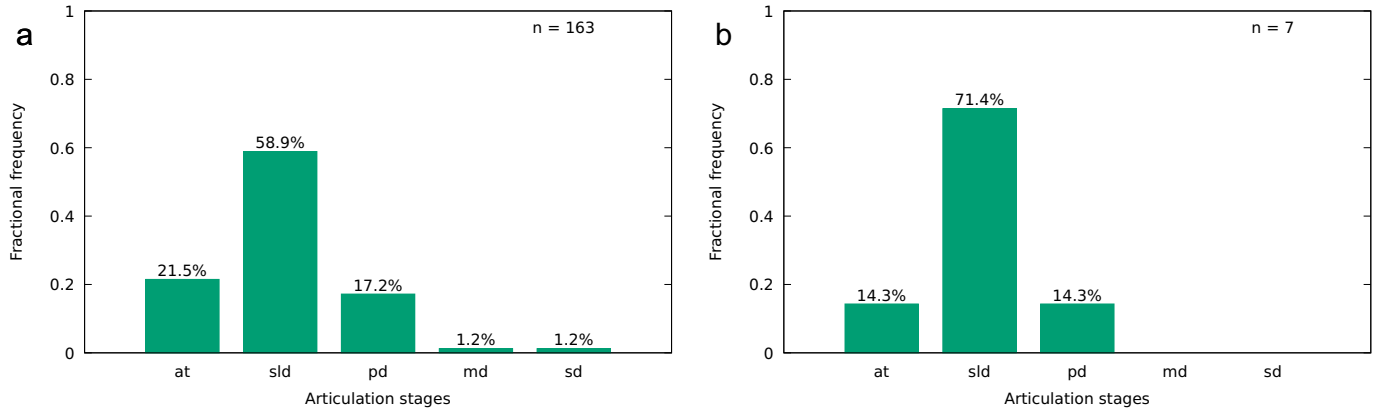

Fig. 8. Articulation of *Goulmimichthys roberti* from Vallecillo (a) and Múzquiz (b), in percent of the total number of individuals. Articulated (at), slightly disarticulated (sld), partly disarticulated (pd), mostly disarticulated (md) and strongly disarticulated (sd) individuals.

are well articulated, most of the present material is classified here as slightly disarticulated (58.9%) (Fig. 8a), with only a few detached bones. Partially disarticulated individuals (17.2%) are abundant, while mostly disarticulated (1.2%) and strongly disarticulated (1.2%) specimens are rare.

71.8% of the specimens are identified as nearly complete (Fig. 9a), while 20.9% are partially complete. Both fully complete (6.1%) and incomplete specimens (1.2%) are comparably rare (Fig. 9a). Specimens are frequently better articulated than complete.

The curvature of the spinal column of *Goulmimichthys roberti* is classified into five categories (Fig. 10a). The broad majority of specimens is embedded straight (87.7%), without any bend of the body. A curvature of the column towards an either dorsal or ventral direction is visible in 6.7%. Lateral column bending to the right or left (aRL), and an S-shape curvature of the column and column disarticulation (d), are rare (both reach 1.8% of individuals) (Fig. 10a).

Specimens embedded without any breakage of the vertebral column are documented in 53.4% (Fig. 11a). Nevertheless, documented column break reaches 43.6%. Column break due to curvature (cbr) is identified in only 2.5% of the specimens. Disarticulated specimens are almost

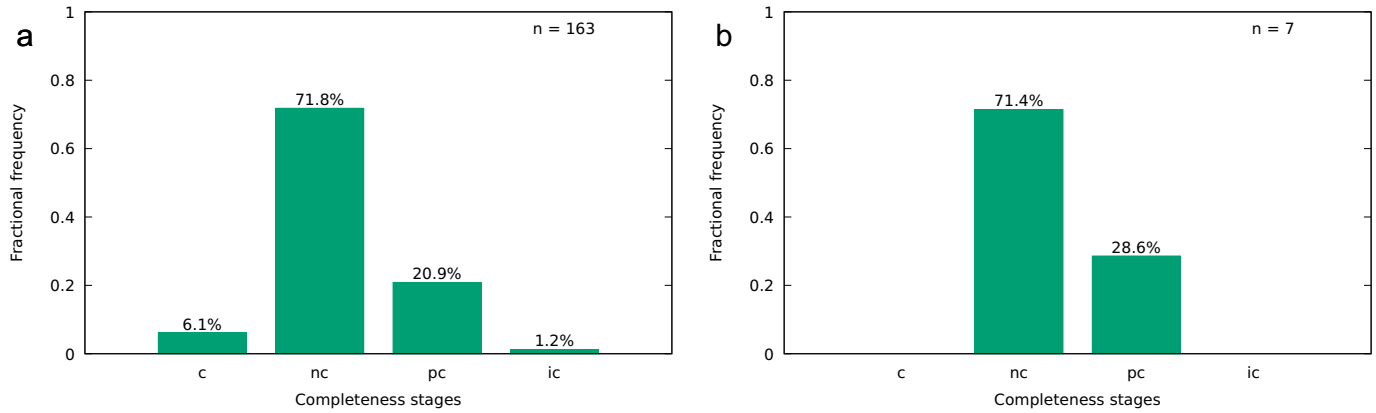

Fig. 9. Completeness of *Goulmimichthys roberti* from Vallecillo (a) and Múzquiz (b), in percent of the total number of individuals. Fully complete (c), nearly complete (nc), partially complete (pc) and incomplete (ic) individuals.

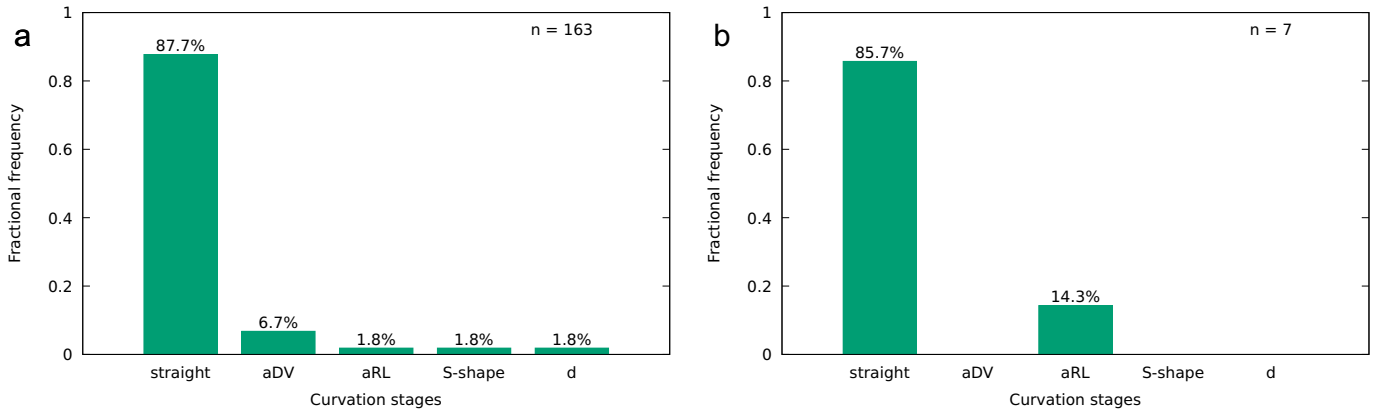

Fig. 10. Spinal column curvature of *Goulmimichthys roberti* from Vallecillo (a) and Múzquiz (b), in percent of the total number of individuals. Straight, arching of the spinal column in dorsal/ventral direction (aDV), to the right/left (aRL), s-shaped, and disarticulated specimens (d).

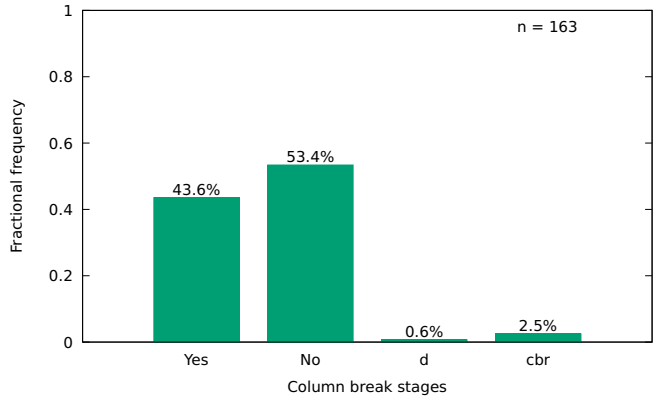

Fig. 11. Vertebral column breakage in individuals from Vallecillo, as percentage of the total number. Column break due to curvature (cbr) and disarticulation (d).

absent (0.6%).

A closed mouth is preserved in 30.1% of the individuals (Fig. 12a). Disarticulation is identified in 17.2%, while in 8% identification of the mouth position was not possible/ visible (nv) (e.g. dorsal preservation). An open mouth position was identified in 44.8% of the individuals, while a moderately open mouth position is seen in 30.7% of the material. Individuals with a wide mouth opening represent 14.1% (Fig. 12a).

Fin preservation was catalogued for the dorsal fin, pectoral fins and pelvic fins. The caudal fin is frequently preserved in a spread-out position. The anal fin is majorly missing, disarticulated, or identification was prevented by preservation. Pectoral fins are majorly preserved in a spread position (60.1%) (Fig. 13a). In 17.2% of the material pectorals are not identified due to the presence of only a few fin rays, while in 15.3% the pectoral fins are identified as closed. Disarticulated pectoral fins are rare and detected in only 7.4%.

Pelvic fins are also frequently spread (58.3%), whereas a closed position is seen in 22.1% of the material (Fig. 13c). In 11.04% of the assemblage the pelvic fins were not visible, and in 8.6% they were disarticulated. The dorsal fin was spread in 32.5% of the individuals and closed in 41.1% (Fig. 13e), while in 14.1% of the specimens the fin was not preserved (np). Disarticulated dorsal fins (9.2%) are rare, as is the category “not visible” (nv) (3.1%).

A decay pathway was reconstructed based on recurring features interpreted as successive decay stages (Fig. 14). These include the detachment of the dorsal fin, breakage of the vertebral column, and disintegration of the body into mainly articulated segments.

In the beginning of this decay process individuals were articulated and complete (Fig. 14a). Decay usually initiated with the detachment of the dorsal fin while the rest of the specimen remained complete and mostly articulated (Fig. 14b). Then, the vertebral column started to disarticulate. Vertebrae remained majorly articulated and complete (Fig. 14c). A break of the column is frequently observed behind the skull, anterior to the dorsal fin at about the height of the anal fin. The body is subdivided through the breakage of the column, yet these parts remain mostly complete and articulated (Fig. 14d). Therefore, isolated body parts decomposed independently from each other losing their

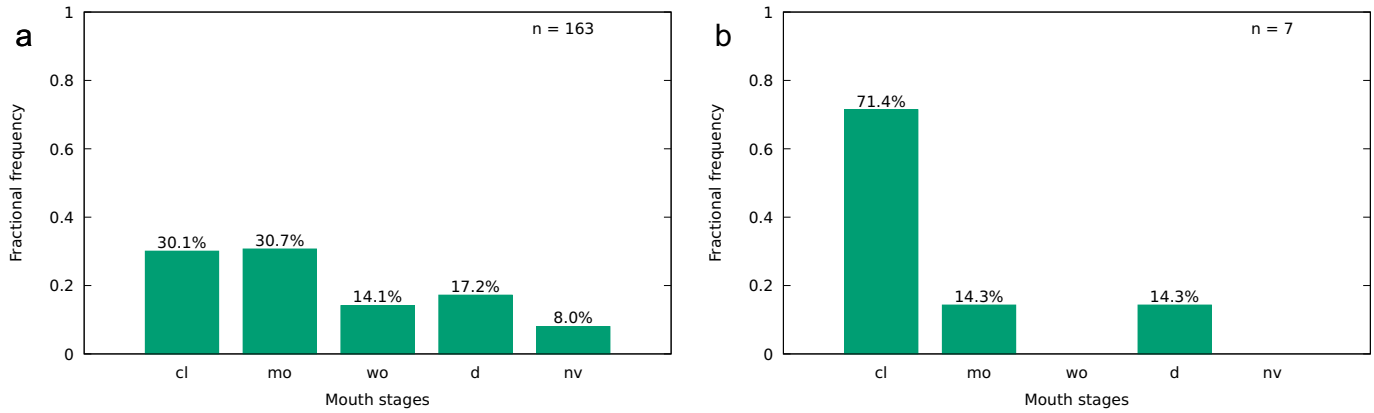

Fig. 12. Mouth opening of *Goulmimichthys roberti* from Vallecillo (a) and Múzquiz (b), in percent of the total number of individuals. Closed mouth (cl), moderately open mouth (mo), wide open (wo), disarticulated (d) and not visible (nv).

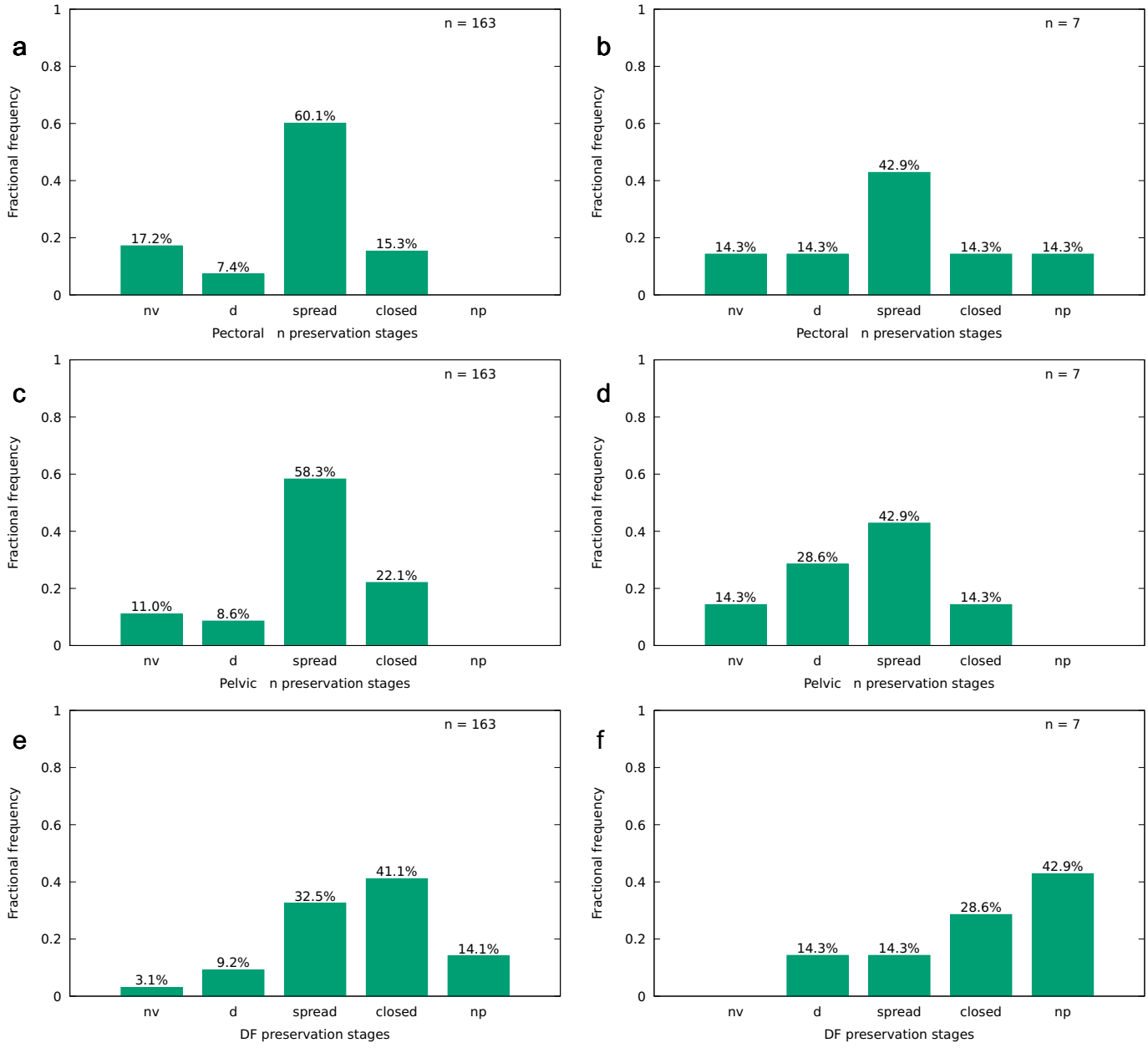

Fig. 13. Pectoral fin, pelvic fin and dorsal fin preservation of *Goulmimichthys roberti* from Vallecillo (a, c, e) and Múzquiz (b, d, f), in percent of the total number of individuals. Not visible (nv), disarticulated (d), spread fins, closed fins, not preserved (np).

detachment (Fig. 14e–f).

Occasionally, there are features documented without a restriction to previously described decay stages (decay pathway). Complete and articulated specimens can possess a disarticulated skull, or vertebrae, while other parts of the body do not present evident decay. In these cases, decay initially affected the skull or the vertebral column, while the rest of the carcass remained articulated and complete.

Another example of decay refers to specimens in which only the body outline and fins (except for the caudal fin) were affected by decay. These specimens are summarized in the category "other" (Fig. 15a). Two fully disarticulated specimens were added to this category, due to their extensive disarticulation and incompleteness, which is not represented by the four decay stages presented above (14a-d). Decay stages following stage four (Fig. 14d) are here summarized in the category "other" (Fig. 15).

Stage 1 is identified in 28.2% of the individuals; they are complete and articulated without any evidence of decay (Fig. 14a). Stage 2 is represented by 38.7% of the individuals and refers to specimens with detached dorsal fins. Stage 3 was identified in 12.9% of the individuals and is characterized by specimens with a detached dorsal fin and a broken vertebral column. Some vertebrae are disarticulated but the main body remained majorly articulated and complete. Stage 4 is documented in 8.6% of the material and refers to individuals in which the body is split into isolated parts (Fig. 14d). "Other" decay stages (e.g. disarticulated skull; Fig. 14e and f) comprise 11.7% of the faunal assemblage (Fig. 15a).

4.3. Gut contents of specimens from Vallecillo

Gut content was only identified in specimens from Vallecillo. It is preserved as recrystallized dark, compacted, three-dimensional calcite mass without identifiable matter, or as undigested skeletal remains. The latter comprise vertebrae and ribs of unidentifiable fish, although spinal column length of some individuals suggests that *Rhynchodercetis*

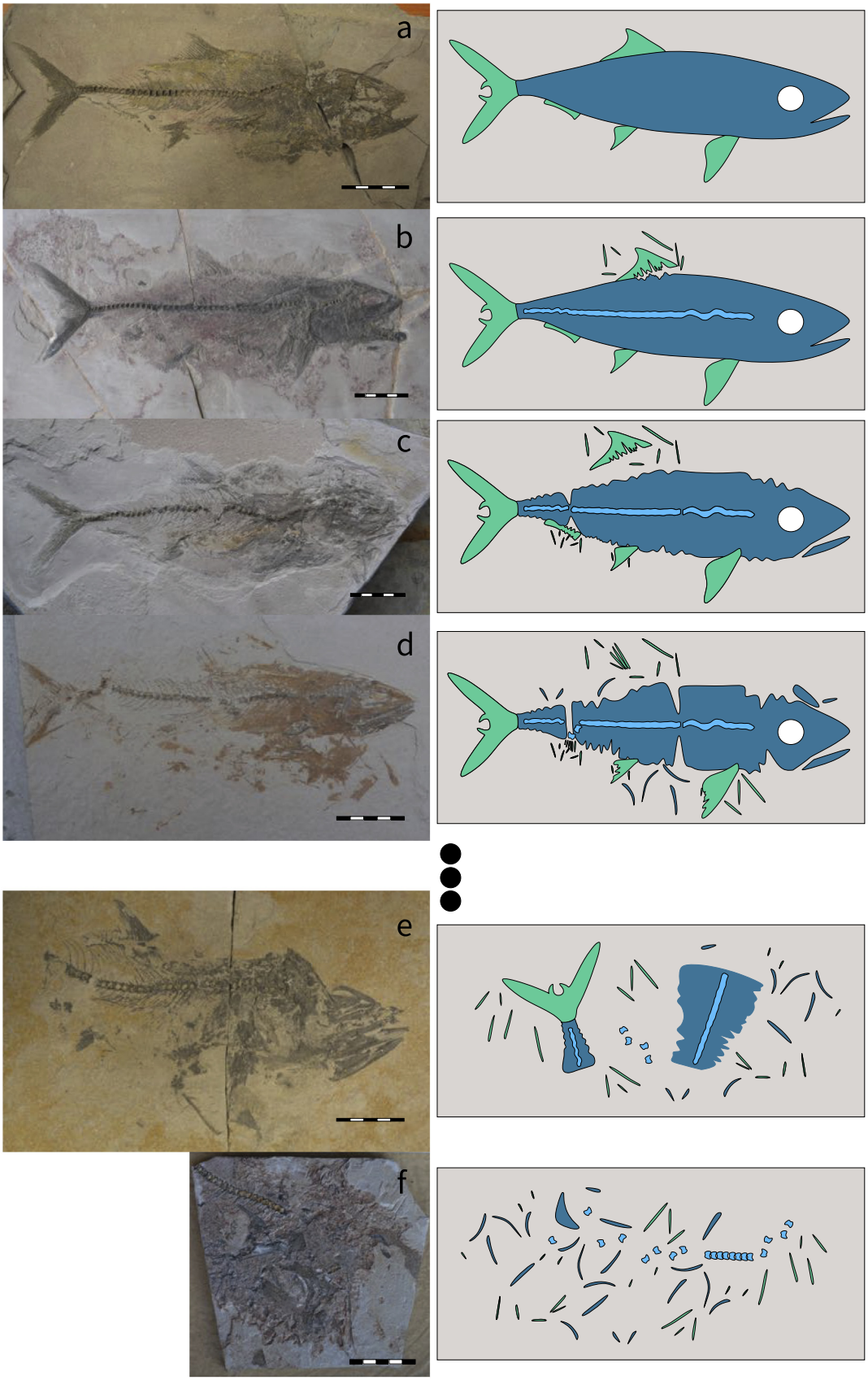

Fig. 14. Decay pathway of *Goulmimichthys roberti* from Vallecillo based on recurring features interpreted as successive decay stages. (a) Complete and articulated individual. (b) Decay starts with the detachment of the dorsal fin and slight disarticulation of the vertebral column. (c) A breakage of the vertebral column is frequently observed behind the skull, anterior to the dorsal fin and about the height of the anal fin. Skull disarticulation is observed but not restricted to this stage. (d) The body breaks up but fragments remain majorly complete and articulated. (e) Detached body parts decompose independently after losing their attachment. (f) Disarticulated and incomplete specimens.

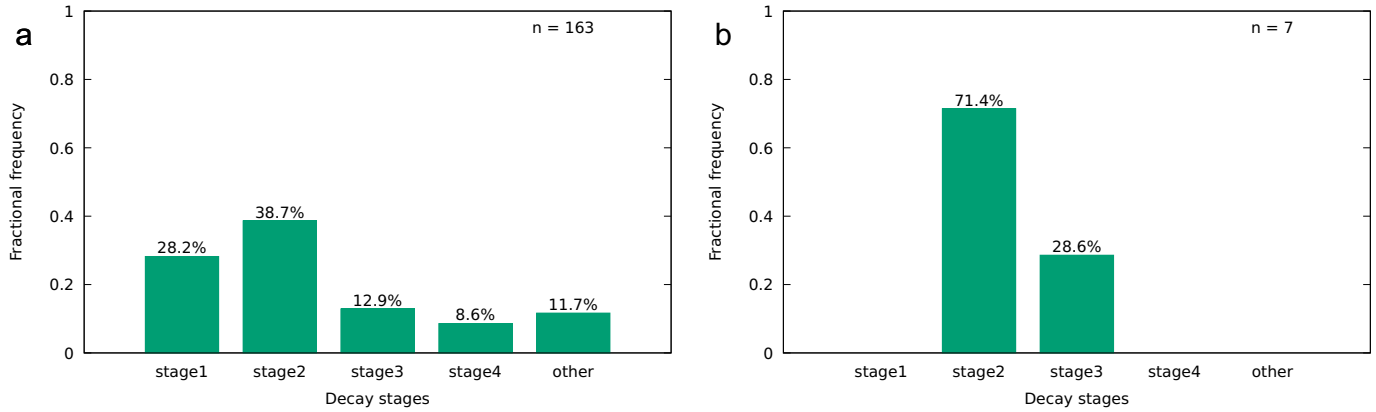

Fig. 15. Decay stages of *Goulmimichthys roberti* from Vallecillo (a) and Múzquiz (b), in percent of the total number of individuals. Stages are illustrated in Fig. 14.

yovanovitchi was an occasional prey. With only a single exception, these fishes were swallowed head-first. Compacted gut content is frequently preserved and forms curved or straight tubes, reflecting the digestive tract. 73 individuals are preserved without any gut content, but 85 specimens exhibit a compacted mass. In only eight individuals gut content is preserved as skeletal remains. It is not known why Múzquiz individuals lack stomach contents.

4.4. Preservation and taphonomy of specimens from Múzquiz outcrops in northern Coahuila

Goulmimichthys roberti is here documented for the first time from outcrops of the Múzquiz area in northern Coahuila, but the number of specimens collected is yet exceedingly small when compared to Vallecillo. In consequence, the statistical significance of data presented here for the Múzquiz area is low and results need to be taken with caution.

Three specimens have been revised from the Cenomanian San Carlos deposit. These are well articulated and complete. All specimens were identified as slightly disarticulated, which correlates with the degree in articulation seen at Vallecillo. Completeness is also similar to that interpreted for Vallecillo, ranging from “nearly complete” to “partially complete”. Embedding is characterized by frequent “dorsal preservation” of the body, although latero-dorsal, latero-ventral and fully ventral embeddings are also recorded. Embedding thus differs from the range identified for Vallecillo, where most specimens were embedded laterally (Fig. 7a).

Individuals from San Carlos are frequently preserved straight, with only a single laterally curved specimen (aRL) identified. These results resemble those from Vallecillo, where a dominance of straight embedded specimens was also observed. A break of the vertebral column was only documented in a single specimen. The mouth was closed in all specimens from San Carlos. A decay pathway was not identifiable, because of the low number of specimens.

The three specimens from the Santonian Los Temporales locality range from “articulated” to “partially disarticulated”, and from “nearly complete” to “partially complete”. All individuals were embedded laterally and straight, without any curvature of the vertebral column, or break. Closed, moderately open and disarticulated mouth positions were registered here.

A single specimen from Las Piedritas (Cenomanian-Turonian) is nearly articulated and nearly complete. The individual is preserved in a straight laterally embedded position, with a break of the vertebral column. The mouth is closed.

Specimens from the Múzquiz localities are majorly embedded straight (85.7%), without a curvature of the vertebral column (Fig. 10b). Individuals with a vertebral column arched to the right or left, are rare (14.3%). Other types of curvature (e.g. S-shape) are not present.

In total, specimens are nearly complete (71.4%) and only slightly disarticulated (Fig. 9b). Articulated and partly articulated specimens comprise 14.3% of the assemblage, whereas 28.6% are partially complete (Figs. 8b and 9b). Majorly disarticulated (md) and strongly disarticulated (sd) specimens are not present. Complete and incomplete specimens are also absent (Fig. 9b).

Half of the documented individuals are embedded straight (45.5%), while 18.2% are latero-dorsally or latero-ventrally embedded, and 9.1% are preserved in an either dorsal or ventral position (Fig. 7b). Consequently, embedding of the Múzquiz specimens of *Goulmimichthys roberti* appears to present a higher variability than that detected for Vallecillo.

Most specimens exhibit a closed mouth position (71.4%) (Fig. 12b). Only in 14.3% of the assemblage moderately open or “disarticulated” mouth positions were identified (Fig. 12b).

The caudal fin is frequently preserved, in contrast to the anal fin which is commonly missing. Pectoral fins are spread in 42.9%, and thus almost half of specimens (Fig. 13b), as compared to 14.3% each for visible, disarticulated, closed, or absent pectoral fins. Specimens are frequently preserved with a spread-out pelvic fin (42.9%) (Fig. 13b), while 28.6% of the pelvic fins are disarticulated and 14.3% are not visible or closed. The dorsal fin is not preserved in 42.9% of the specimens (Fig. 13b). 28.6% of the individuals have a closed dorsal fin, while it is spread in 14.3%, and disarticulated in 14.3%.

The decay pathway visible in individuals from Vallecillo was adapted to the material from Múzquiz, suggesting similar pathways of decomposition. Most specimens belong to stage 2 and show detached dorsal fins (71.4%) (Fig. 15b). A minority of 28.6% represents stage 3, characterized by dorsal fin loss and breakage of the vertebral column. Stages 1, 4 and the category “others” are not present in the material.

5. Discussions

5.1. Size range distribution

The markedly unimodal size range identified for *Goulmimichthys roberti* from Vallecillo indicates that individuals ranging from 250 to 450 mm length populated this distal shelf region of the Paleo-Gulf of Mexico. Young individuals, with a body length of < 250 mm, are surprisingly rare and only comprise 4 out of 163 individuals (Fig. 6). We suggest that the taxon migrated into the pelagic Vallecillo area with a minimum size of 250 mm body length, likely when reaching maturity. A preservational hiatus, due to potential diagenetic loss of dissolution-sensitive bone material of juveniles (< 250 mm) appears unlikely, as abundant small-sized actinopterygian fishes are known from both Vallecillo and the Múzquiz area (e.g. Giersch, 2014; Stinnesbeck et al., 2019). Large-sized adults of > 450 mm length and up to 650 mm are also rare, either suggesting that only few individuals survived to grow

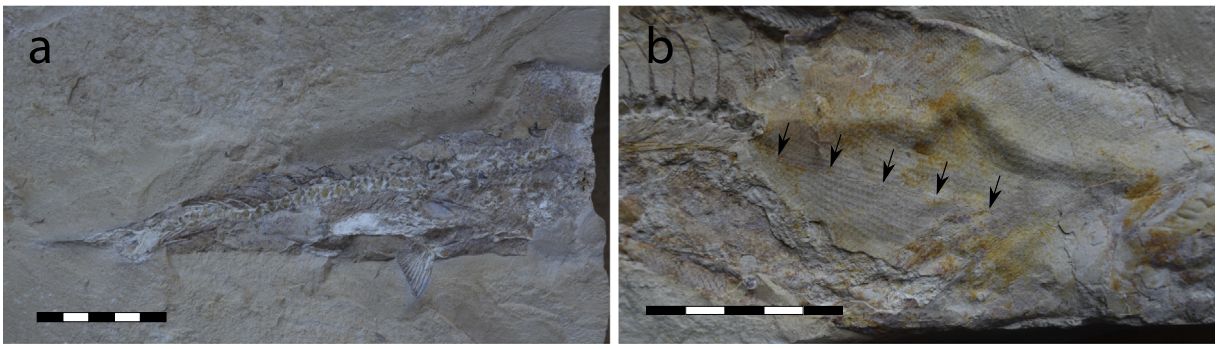

Fig. 16. Preservation of *Goulmimichthys roberti* from Múzquiz. Note that specimens are phosphatized, thus favoring the preservation of soft tissues. (a) Specimen CPC-TE5 from Los Temporales. This individual is embedded ventrally in soft sediment, which prevented a turnover of the carcass into a lateral position. (b) Specimen MUZ-REG1680 from Carranza. Note preservation of the lateral line canal. Scale 50 mm.

to these sizes, or that large-sized adults again migrated out of the region, except for a few solitary large specimens. Recent pelagic scombrids, e.g. *Thunnus alalonga*, are known to execute wide seasonal migrations throughout their life (Childers et al., 2011). An equivalent migration behavior is therefore a likely scenario for *Goulmimichthys roberti.* Repeated seasonal migration in and out of the Vallecillo area, as documented for *Nursallia gutturosum* by Stinnesbeck et al. (2019), is nevertheless excluded by the data presented here.

Individual sizes of Múzquiz specimens are here documented to range from 200 to 400 mm total length, which roughly corresponds to most Vallecillo specimens (Fig. 6). Our data from Múzquiz does therefore not provide evidence for a larger percentage of juveniles (< 250 mm), nor for very large adults > 450 mm. This result is unexpected, as the northern Coahuila Múzquiz area reflects a more proximal and notably more shallow area of the Cretaceous shelf than Vallecillo. Even so, the region did apparently not host schools of young *Goulmimichthys roberti*. It should nevertheless be noted that our material from Múzquiz is low in individuals from different locations and that numerous quarries are yet unknown to science.

The sizes documented here (100 to 650 mm) for the Vallecillo pachyrhizodont double the 300-to-400-mm length range described by Blanco and Cavin (2003) and Blanco and Cavin (2003). Size was probably underestimated because of only a few specimens available for these early studies. *Goulmimichthys arambourgi* from Morocco exhibits a standard length of < 300 mm (Cavin, 2001, 2004) and is thus notably smaller than the Vallecillo and Múzquiz *Goulmimichthys roberti*. No sexual dimorphism, or ontogenetic differences related to ontogenetic stages, have yet been identified in the Mexican material.

5.2. Remarks on biology

The fusiform body shape and markedly forked caudal fin of *Goulmimichthys roberti* resemble that of recent streamlined scombrids, such as tunas or mackerels, and are likely associated with sustained high-speed swimming (Fletcher et al., 2014). Propulsion is generated through the caudal fin. We assume a similar fast-swimming, open water schooling behavior for this Mexican pachyrhizodont.

5.3. Taphonomy

5.3.1. Embedding

Most *Goulmimichthys roberti* from Múzquiz are preserved as “slightly disarticulated” and “nearly complete” individuals. These results coincide with values for articulation and completeness determined at Vallecillo and provide evidence for the good preservation potential of this pachyrhizodontid. Another reason for the good preservation of the present material is probably due to the fact that our analysis is based on museum collections. Specimens from Múzquiz are embedded straight, as at Vallecillo. Even so, there is a higher variability regarding body orientation than at Vallecillo, where 74.8% of the individuals are laterally embedded. Adding four incomplete individuals from San Carlos (3) and Temporales (1), laterally embedded individuals in the Múzquiz area only reach < 50% of the assemblage (Fig. 7b). Even though the number of individuals is yet small, Múzquiz specimens are often not embedded laterally.

We therefore suggest that depositional conditions between the two outcrop regions may have differed. This is especially evident for San Carlos where only one out of six specimens were embedded laterally (three incomplete individuals added). Embedding differences between Vallecillo and Múzquiz may relate to the shallower setting of the northern (Múzquiz) localities, potentially allowing bottom currents to move carcasses on the sea floor. Even though, there is no evidence for current activity associated with the fish fossils and even small detached bones of disarticulated individuals remained close to the main body.

Alternatively, gas formation inside the carcass could have produced buoyancy and shifting of the body position, or rotation (Pan et al., 2015). Nevertheless, the abundance of complete and articulated specimens in both the Vallecillo and Múzquiz areas, opposes this latter scenario and further excludes a potential phase of carcass flotation (Stinnesbeck et al., 2019). In recent scombrids, which are morphologically and ecologically analogous to *G. roberti*, a swim bladder is frequently absent (Collette and Nauen, 1983). These fishes would instantaneously sink to the bottom due to higher density. In addition, there is no preference to a dorsal or ventral embedding, as seen in taxa in which gas inside the gut would turn the belly upwards (Pan et al., 2015, 2019). For instance, this pattern is assumed for *Laminospondylus transversus*, an abundant fish in the Múzquiz area which is almost always preserved in a ventral position (Giersch, 2014, and personal observation).

Specimens from Múzquiz are often buried in a fine mud sediment, with a small pit-like depression around the individual in an otherwise even slab surface (Fig. 16a). We suggest that these fishes were instantly covered by sediment after arriving on the sea bottom, without tumbling over into a lateral position. This scenario would best explain the variety of ventral and dorsal embeddings depending on the body movement when touching the ground.

Alternatively, the carcasses were rapidly overgrown by microbial mats, thus allowing for a stabilization of the body (Pan et al., 2015). The microbial mats would have required rapid growth, as documented from the Albian Tlayua quarry in the state of Puebla (Alvarado-Ortega et al., 2007). In the absence of solid data regarding the potential presence of microbial mats, we favor an explanation of rapid burial into soft sediment, or slight water movements causing distinct embedding forms, as there is some evidence of soft sediment to support this latter scenario. Disarticulated specimens probably remained uncovered on the sea floor for some time (Chelouche et al., 2012), disintegrating slowly as reflected by the decay pathway (Figs. 14, 15a) established for Vallecillo. As rapid embedding into soft sediment is not evidenced for

Vallecillo individuals, the sea bottom there must have been substantially more consolidated than in Múzquiz localities.

5.3.2. Decay pathway

Articulated and complete individuals from Vallecillo are summarized in stage 1, comprising 28.2% (Figs. 14, 15a). Decay initially starts with the detachment of the dorsal fin, while pectorals and pelvic fins, the anal and the caudal fin, are still articulated and complete (stage 2; Fig. 14b). In occasions, the vertebral column is slightly disarticulated, but without a break.

Stage 3 (Fig. 14c) comprises features of stage 2, but with advanced disintegration of the fins and body outline. Skull disarticulation may occur but is not restricted to a single stage. There are, however, individuals assigned here to stage 3, with a major body disintegration but articulated skull. A column break is frequently documented above the first anal fin ray (at about the 8th vertebra before the caudal fin) and beneath the dorsal fin.

During stage 4 (Fig. 14d), the body splits into several segments which nevertheless remain majorly articulated and complete. The vertebral column disarticulates sequentially. Subsequent decay stages (after stage 4) are not documented in the present material, likely due to collection bias. As these specimens were collected for purposes of public display, there was no intention to collect disintegrated fish fossils. We nevertheless suggest that decay processes would have led to further detachment of body parts (Fig. 14e), ultimately leading to the full disarticulation of specimens (Fig. 14f). This is assumed from a few incomplete and disarticulated specimens representing final decay stages (Fig. 14f).

Individuals from Múzquiz majorly exhibit the 2nd stage of the decay pathway presented above (71.4%) (Fig. 15b). Only two individuals represent stage 3 (28.6%). Specimens from Vallecillo are mostly classified as stages 2 (38.7%) and 1 (28.2%) and thus comprise stages that are less common in Múzquiz (Fig. 15). The remaining stages of the decay pathway are yet absent from Múzquiz, but this may relate to the small number of specimens.

5.3.3. Mouth and fins

Specimens from Múzquiz are majorly preserved with a closed mouth (71.4%), opposing 44.8% individuals from Vallecillo with an open mouth. Pectoral fins and pelvic fins are majorly spread-out in the Vallecillo material, with 60.1% and 58.3%. These results coincide well with the material from Múzquiz, where spread-out pectoral and pelvic fins reach 42.7%. The dorsal fin is closed in 28.6% of the specimens from Múzquiz and in 41.1% of Vallecillo specimens.

In fishes, spread fins and open mouths have often been associated with abrupt mortality, suffocation, or tetany (Bieńkowska-Wasiluk, 2010; Chelouche et al., 2012; Pan et al., 2019). Muscular contractions, causing gaping mouths and spread fins, are caused by respiratory stress, heat shock, salinity or alkalinity shock (Pan et al., 2015). A bend spinal column has been interpreted to reflect osmotic dehydration caused by a salinity or alkalinity shock. We dismiss this last scenario due to the common straight preservation of specimens in both localities, despite the abundance of gasping mouths in the Vallecillo material. Separate interpretations of flabellate fins and closed mouth are not available. An environmental interpretation based on flabellate fins is difficult, due to the potential association with social behavior. The latter often invokes spread fins, e.g. during mating, but this interpretation is refused here. For Múzquiz, we thus lack an answer to our results and need more material.

For Vallecillo, nevertheless, the frequency of open mouths and spread fins points towards respiratory stress. It is already well known that oxygen-deficient conditions prevailed on the Vallecillo seafloor (e.g. Ifrim et al., 2011b), but *Goulmimichthys roberti* was an open water fast-swimming fish that could easily avoid these hostile bottom conditions during life. On the other hand, individuals struggling with death may easily have ended up in deep levels of the water column, and thus the dysoxic "death" zone. The open mouths and spread fins of these Vallecillo individuals may well reflect their agony. Even though, we decline a scenario invoking major mass mortality events for Vallecillo causing the repeated sudden death of these specimens, e.g. by oxygen deficiency, as there are only few sediment layers known to date from the outcrop exposing fish concentrations. For the moment, we suggest that more taphonomical research is needed on other common Vallecillo species, e.g. *Vallecillichthys multivertebratum*, or *Tselfatia formosa*, to evaluate this question.

5.4. Gut content

Juveniles of the same species, but also other fish (e.g. *Santanichthys*) and arthropod remains are already documented as gut content of *Rhacolepis* (Wilby and Martill, 1992; Maisey, 1994; Kellner et al., 1994). *G. arambourgi* from Morocco is documented to have preyed on juvenile *Enchodus venator* (Cavin, 2004).

5.5. Environment and preservation

Goulmimichthys roberti from Múzquiz is generally phosphatized and occasionally preserved three-dimensionally, with anterior scales and the lateral line canal preserved (Fig. 16b), as well as soft tissue including scales, gut contents, or gill filaments. Preservation is thus notably better than at Vallecillo, where all vertebrate fossils are secondarily recrystallized to calcite comprising slab and counter-slab (e.g. Ifrim, 2006; Giersch, 2014; Stinnesbeck et al., 2019). Scale coverage is similar in the two outcrop areas and comparable to modern scombrids, possessing an anterior corselet. A corselet area behind the skull can be covered by large scales while the rest of the body remains naked (Collette and Nauen, 1983).

Abundant decapod crustaceans have been reported by Vega et al. (2007) from the El Pilote and Temporales localities north of Múzquiz. According to the authors, the presence of *Cenomanocarcinus vanstraeleni* suggests that water depth was < 50 m. Appendages of *C. vanstraeleni* and two raninids are flattened, suggesting that these crustaceans either covered their carapaces with fine mud, thus indicating a benthonic lifestyle, or that they populated floating algae (Vega et al., 2007). The latter scenario appears less likely due to the size of these specimens reaching to about 100 mm carapace diameter. The excellent preservation, articulation and abundance of these crustaceans therefore suggests oxygenated bottom water conditions and a shallow shelf setting for these Múzquiz localities, different to Vallecillo. Anoxic water conditions, excluding scavengers, likely favored the good preservation of fishes in the deep shelf of Vallecillo (Ifrim, 2006; Ifrim and Stinnesbeck, 2007; Ifrim et al., 2011a; Stinnesbeck et al., 2019), while excellent fossil preservation in the Múzquiz area was the result of rapid phosphatization and coverage of carcasses by soft mud sediment (Fig. 16a). Similar results have already been documented for the upper Turonian-lower Coniacian platy limestone of El Rosario in the Múzquiz area by Stinnesbeck et al. (2005).

5.6. Distribution

Goulmimichthys roberti is here documented from five Cenomanian to Santonian platy limestone deposits in the Múzquiz outcrop region of northern Coahuila and from the lower to middle Turonian Vallecillo deposit. Our material thus coincides with the known geographic range of *Goulmimichthys* from Colombia and Morocco to northeastern Mexico, but notably extends the stratigraphic range from the Cenomanian to Santonian (Fig. 3). We also propose a wider environmental range from the pelagic to shallow shelf habitats. The presence of the pachyrhizodont in north-eastern Mexico reveals a long-lasting, persistent range in the Western hemisphere.

6. Conclusions

We here review the taphonomy of 177 individuals of the pachyrhizodont fish *Goulmimichthys roberti* from Upper Cretaceous platy limestone in northeastern Mexico. While most individuals (166) were collected from the lower to middle Turonian Vallecillo site in northern Nuevo Leon, we also include 11 specimens from little known Cenomanian to Santonian localities in the Múzquiz area of northern Coahuila. Our sites form a 500 km long north-south trending transect across proximal to distal shelf conditions of the northwestern margin of the Paleo-Gulf of Mexico. Our data extends both stratigraphic and environmental ranges known to date for *G. roberti*. In the area, the size distribution of *G. roberti* is unimodal, with a well-defined peak of individuals between 250 and 450 mm length and a mode at 300 to 400 mm. The rarity of both juveniles < 250 mm length and large-sized specimens from 450 to 650 mm, indicate that *G. roberti* migrated into the pelagic Vallecillo area when reaching maturity. Large-sized adults migrated out of the region, except for a few solitary large specimens. The abundance of complete and articulated individuals of *G. roberti* in both the Vallecillo and Múzquiz areas excludes a potential phase of carcass flotation and favors the absence of a swim bladder in this fast-swimming fish. Laterally embedded specimens of *G. roberti* are more abundant in Vallecillo than in northern (Múzquiz) localities. Ventral and dorsal embeddings are frequent in Múzquiz, suggesting minor differences, e.g. a substantially more consolidated sea bottom in Vallecillo as compared to Múzquiz localities. About half of the Vallecillo individuals are preserved with open mouths and spread-out dorsal, pectoral and pelvic fins. These characteristics are interpreted to result from respiratory stress, likely provoked by the oxygen-deficient conditions at the Vallecillo seafloor. They may reflect the agony of individuals struggling with death in deep anoxic levels of the water column. Anoxic water conditions exclude scavengers, which likely favored good preservation of Vallecillo fishes, whereas the fossil preservation in the Múzquiz area was the result of rapid phosphatization and coverage of carcasses by soft mud sediment.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Colection and material number	Analysis
MUDE-VAD-4, REG1089,PJ	Size range, gut content
MUDE-VAD-62, K-48	Size range, gut content
MUDE-VAD-58, CPC-477, 790	Taphonomy, size range, gut content
MUDE-VAD-6, S-52, REG1089,PJ942	Taphonomy, size range, gut content
MUDE-VAD-7	Taphonomy, size range, gut content
MUDE-VAD-9	Taphonomy, size range, gut content
MUDE-VAD-15, S-51	Taphonomy, size range, gut content
MUDE-VAD-16	Taphonomy, size range, gut content
MUDE-VAD-17	Taphonomy, gut content
MUDE-VAD-18, REG1089, PJ660, CPC-311	Taphonomy, size range, gut content
MUDE-VAD-30, 921	Taphonomy, size range, gut content
MUDE-VAD-33	Taphonomy, size range, gut content
MUDE-VAD-34, K46	Taphonomy, size range, gut content
MUDE-VAD-35, 1057	Taphonomy, size range, gut content
MUDE-VAD-38, VC156	Taphonomy, size range, gut content
MUDE-VAD-39, CPC-529, 948	Taphonomy, size range, gut content
MUDE-VAD-40, CPC-528, VCV45b	Taphonomy, size range, gut content
MUDE-VAD-43, 997, CPC-532	Taphonomy, gut content
MUDE-VAD-65, 216	Taphonomy, size range, gut content
MUDE-VAD-66	Taphonomy, gut content
MUDE-VAD-95, S-6	Taphonomy, size range, gut content
M-VA-51, NE18	Taphonomy, gut content
M-VA-57, NE12	Taphonomy, size range, gut content
M-VA-79	Taphonomy, size range, gut content
M-VA-81	Taphonomy, size range, gut content
M-VA-89	Taphonomy, size range, gut content
M-VA-92 A and B	Taphonomy, size range, gut content
M-VA-93	Taphonomy, size range, gut content
M-VA-95	Taphonomy, size range, gut content
M-VA-96	Taphonomy, size range, gut content
M-VA-98	Taphonomy, size range, gut content
M-VA-104,M1DSC0010	Taphonomy, size range, gut content
M-VA-105, S-83	Taphonomy, size range, gut content
M-VA-112	Taphonomy, size range, gut content
M-VA-113	Taphonomy, size range, gut content
M-VA-129, M164	Taphonomy, size range, gut content
M-VA-130, M173	Taphonomy, size range, gut content
M-VA-134	Taphonomy, size range, gut content
M-VA-135	Taphonomy, size range, gut content
M-VA-146	Taphonomy, size range, gut content
M-VA-158	Taphonomy, size range, gut content

M-VA-165, M27	Taphonomy, size range, gut content
M-VA-166	Taphonomy, size range, gut content
M-VA-167	Taphonomy, size range, gut content
M-VA-168, M331,REG2544, PF199	Taphonomy, size range, gut content
M-VA-171, M47,MRG2544,PF205	Taphonomy, size range, gut content
M-VA-181, M65,REG2544,PF250	Taphonomy, size range, gut content
M-VA-182,REG2544;PF250	Taphonomy, size range, gut content
M-VA-183	Taphonomy, size range, gut content
M-VA-184, M77	Taphonomy, size range, gut content
M-VA-187	Taphonomy, size range, gut content
M-VA-203/613,MD6,REG2544,PF196BA	Taphonomy, size range, gut content
M-VA-204,	Taphonomy, size range, gut content
M-VA-208	Taphonomy, size range, gut content
M-VA-209,M50	Taphonomy, size range, gut content
M-VA-210,M49, REG2544, PF180	Taphonomy, size range, gut content
M-VA-211,M8,REG2544,TF264	Taphonomy, size range, gut content
M-VA-219, M10,REG2544,PF244	Taphonomy, size range, gut content
M-VA-221,REG2544,PF170,M44	Taphonomy, size range, gut content
M-VA-224,REG2544,PF257,M26	Taphonomy, size range, gut content
M-VA-226, REG2544,PF186,M8	Taphonomy, size range, gut content
M-VA-227, M5, REG2544,PF193	Taphonomy, size range, gut content
M-VA-229, M40,REG2544,PF178	Taphonomy, size range, gut content
M-VA-230, M46,REG2544,PF171	Taphonomy, size range, gut content
M-VA-232, M48	Taphonomy, size range, gut content
M-VA-235,REG2544,PF174, M41	Taphonomy, size range, gut content
M-VA-239	Taphonomy, size range, gut content
M-VA-243	Taphonomy, size range, gut content
M-VA-244	Taphonomy, size range, gut content
M-VA-245, M134SR	Taphonomy, size range, gut content
M-VA-246, M51,REG2544,PF172	Taphonomy, size range, gut content
M-VA-247, REG2544,PF32	Taphonomy, size range, gut content
M-VA-252	Taphonomy, size range, gut content
M-VA-274, M35,REG2544,PF292	Taphonomy, size range, gut content
M-VA-277	Taphonomy, size range, gut content
M-VA-279	Taphonomy, size range, gut content
M-VA-283	Taphonomy, size range, gut content
M-VA-284	Taphonomy, size range, gut content
M-VA-287	Taphonomy, size range, gut content
M-VA-288	Taphonomy, size range, gut content
M-VA-289	Taphonomy, size range, gut content
M-VA-291	Taphonomy, size range, gut content
M-VA-293	Taphonomy, size range, gut content
M-VA-296	Taphonomy, size range, gut content
M-VA-302, REG2544, PF175, M42	Taphonomy, size range, gut content
M-VA-304	Taphonomy, size range, gut content
M-VA-317	Taphonomy, size range, gut content
M-VA-328	Taphonomy, size range, gut content
M-VA-338	Taphonomy, size range, gut content
M-VA-341	Taphonomy, size range, gut content
M-VA-342, REG2544,PF61	Taphonomy, gut content
M-VA-344	Taphonomy, size range, gut content
M-VA-349	Taphonomy, size range, gut content
M-VA-605, REG2544, PF176	Taphonomy, size range, gut content
M-VA-606, REG2544, PF181	Taphonomy, size range, gut content
M-VA-607	Taphonomy, size range, gut content
M-VA-350	Taphonomy, size range, gut content
M-VA-610	Taphonomy, size range, gut content
M-VA-360, M11, REG2544, PF197	Taphonomy, size range, gut content
M-VA-614, PF 198, M60	Taphonomy, size range, gut content
M-VA-361, REG2544, PF165,X41	Taphonomy, size range, gut content
M-VA-363	Taphonomy, size range, gut content
M-VA-364, REG2544, PF164; AB	Taphonomy, size range, gut content
M-VA-367, M36	Taphonomy, size range, gut content
M-VA-368, X29, REG2544, PF144	Taphonomy, size range, gut content
M-VA-369AB, REG2544, PF191, MD7AB	Taphonomy, size range, gut content
M-VA-615, REG2544, PF189, M20	Taphonomy, size range, gut content
M-VA-617, REG2544, PF140, X36	Taphonomy, size range, gut content
M-VA-618, M34, REG2544, PF190	Taphonomy, size range, gut content
M-VA-621	Taphonomy, size range, gut content
M-VA-622, ME159	Taphonomy, size range, gut content
M-VA-623, REG2544, PF125	Taphonomy, size range, gut content
M-VA-624, M153	Taphonomy, size range, gut content
M-VA-625, M133	Taphonomy, size range, gut content
M-VA-626, M152	Taphonomy, size range, gut content
M-VA-627, M150	Taphonomy, size range, gut content
M-VA-628, M154	Taphonomy, size range, gut content
M-VA-629, MSR95	Taphonomy, size range, gut content
M-VA-630, NE23	Taphonomy, size range, gut content
M-VA-631	Taphonomy, size range, gut content
M-VA-633	Taphonomy, size range, gut content

M-VA-401	Taphonomy, size range, gut content
M-VA-634	Taphonomy, size range, gut content
M-VA-635	Taphonomy, size range, gut content
M-VA-405	Taphonomy, size range, gut content
M-VA-638, M151	Taphonomy, size range, gut content
M-VA-639	Taphonomy, size range, gut content
M-VA-411, REG2544, PF109	Taphonomy, size range, gut content
M-VA-641, G34	Taphonomy, size range, gut content
M-VA-642, MD5AB	Taphonomy, size range, gut content
M-VA-416	Taphonomy, size range, gut content
M-VA-418, M16	Taphonomy, size range, gut content
M-VA-425	Taphonomy, size range, gut content
M-VA-426	Taphonomy, size range, gut content
M-VA-664	Taphonomy, size range, gut content
M-VA-428	Taphonomy, size range, gut content
M-VA-646	Taphonomy, size range, gut content
M-VA-647	Taphonomy, size range, gut content
M-VA-433	Taphonomy, size range, gut content
M-VA-648	Taphonomy, size range, gut content
M-VA-438	Taphonomy, size range, gut content
M-VA-439, REG2544, PF158	Taphonomy, size range, gut content
M-VA-440	Taphonomy, size range, gut content
M-VA-649	Taphonomy, size range, gut content
M-VA-650	Taphonomy, size range, gut content
M-VA-651, REG2544, PF157	Taphonomy, size range, gut content
M-VA-652, REG2544, PF14, M71	Taphonomy, size range, gut content
M-VA-445, REG2544, PF131, G35	Taphonomy, size range, gut content
M-VA-448, M155	Taphonomy, size range, gut content
M-VA-654, REG2544, PF15, M71	Taphonomy, size range, gut content
M-VA-452, REG2544, PF9,M69	Taphonomy, size range, gut content
M-VA-454, REG2544, PF28	Taphonomy, size range, gut content
M-VA-655	Taphonomy, size range, gut content
M-VA-656	Taphonomy, size range, gut content
M-VA-473	Taphonomy, size range, gut content
M-VA-477, M171	Taphonomy, size range, gut content
M-VA-482, M170	Taphonomy, size range, gut content
M-VA- 484, M179	Taphonomy, size range, gut content
M-VA-486, REG2544, PF-106, PE20	Taphonomy, size range, gut content
M-VA-532	Taphonomy, size range, gut content
M-VA-534	Taphonomy, size range, gut content
M-VA-539, REG2544, PF260	Taphonomy, size range, gut content
M-VA-540, PF291	Taphonomy, size range, gut content
M-VA-548, REG2544, PF238	Taphonomy, size range, gut content
M-VA-56, NE8, RF2544 PF51	Taphonomy, size range, gut content
M-VA-613, REG2544, PF196A	Size range, gut content
MUDE-TED, CPC-475, 44Temporales	Taphonomy, size range
MUZ-TE-1; Temporales	Taphonomy, size range
MUZ-TE; Temporales; ohne No	Taphonomy, size range
MUDE-TED-7/T-5-Temporales	Taphonomy
MUZ-SC; San Carlos-ohne No	Taphonomy, size range
M-SC-2; San Carlos	Taphonomy, size range
MUDE, SCD-2, CPC-476; San Carlos	Taphonomy, size range
MUDE, SCD-1; San Carlos	Taphonomy
M-SC-31; San Carlos	Taphonomy
MUZ-SC1-San Carlos	Taphonomy
MUZ-Pi-1; Piedritas	Taphonomy, size range

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A fish-parasitic isopod (Cymothoidae) on the pachyrhizodont *Goulmimichthys roberti* from the lower Turonian (Upper Cretaceous) Vallecillo plattenkalk, NE Mexico

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ABSTRACT

The platy limestone (plattenkalk) deposit of Vallecillo in northeastern Mexico is widely known for its well preserved and diverse fish and marine reptilian assemblage dated to the early–middle Turonian (Late Cretaceous). A single specimen of the pachyrhizodont *G. roberti* revealed the first Cretaceous isopod (Crustacea, Arthropoda) attached to a fish host. Preservation allows for the interpretation of the entire body and most appendages. A parasitic lifestyle of the isopod is inferred based on the specimen's morphology including claw-like dactyli, but is also inferred based on the anoxic bottom conditions variously interpreted for the Vallecillo plattenkalk deposit, which excluded scavengers. The individual is here referred to the family Cymothoidae and described as *Mothocya vallecillae* n. sp.

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1. Introduction

Isopoda form a highly diverse order of crustacean arthropods that inhabit marine, freshwater and terrestrial habitats. They developed a variety of different lifestyles ranging from free-living to scavenging and parasitic forms (Wilson et al., 2011; Nagler et al., 2017). The latter are temporarily or permanently attached to the host and consume their blood (hematophagous), but also mucous, epithelium and subcutaneous tissues (Smit et al., 2014). Preferences are identified to specific hosts, feeding strategies and even attachment positions (e.g. gill chambers) (Smit et al., 2014). Although scarce, the fossil record of isopods ranges back to the Carboniferous (Schram, 1970), while the first parasitic isopods date to the Jurassic and are assigned to Cymothoidae, with records from Germany (Solnhofen and Bethel-Bielefeld) (Nagler et al., 2016; Nagler et al., 2017).

Fossil parasitic cymothoid isopods are rarely associated directly to a fish host, although cases have been documented, e.g. from Germany and Italy (Nagler et al., 2016; Robin et al., 2019). From Mexico, fossil isopods of the Cretaceous have been documented from the Barranca el Gavilán locality in Puebla (Valanginian–Hauterivian), the upper Albian el Espinal and the Tzu-tzu localities of Chiapas (Albian) and the Albian (Lower Cretaceous) Tlayúa plattenkalk in Puebla (Wieder and Feldmann 1992; Feldmann et al., 1998; Vega et al., 2018; Vega et al., 2019). In these localities isopod specimens are documented by exuvia or body parts without the presence of a vertebrate host. Tlayúa specimens have been referred to as either ectoparasites or scavengers (Feldmann et al., 1998) and are associated with a diverse fish assemblage.

Here we report on a fairly well-preserved cymothoid isopod of the lower to middle Turonian (Upper Cretaceous) platy limestone (plattenkalk) of Vallecillo in northeastern Mexico. The site is well known for the abundance of well-preserved fishes, including

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sarcopterygians, actinopterygians and cartilaginous taxa (Blanco-Piñón 2003; Ifrim et al., 2007; Giersch 2014; Stinnesbeck et al., 2019, 2020; Vullo et al., 2021). The faunal assemblage indicates that Vallecillo was an open marine ecosystem dominated by fast swimming predators (Ifrim 2006; Ifrim et al., 2007; Giersch 2014; Stinnesbeck et al., 2020). The isopod discussed here from Vallecillo is associated with the pachyrhizodont fish *Goulmimichthys roberti* and is interpreted as parasitic to this host.

1.1. Geological setting

Vallecillo is located approximately 100 km north of Monterrey, the capital city of Nuevo León (Fig. 1A). Shallow quarries to the south of Vallecillo yield yellow to light grey platy limestone assigned to the Agua Nueva Formation (Cenomanian-Turonian); these lithologies are extracted at Vallecillo for flagstones, floors and walls. The limestone contains a diverse vertebrate and invertebrate faunal assemblage representing a mixture of elements from the western Gulf of Mexico, the Western Interior Seaway, the Tethys, and endemic species (Ifrim 2006; Ifrim and Stinnesbeck 2007; Giersch 2014). The most common fish species are *Rhynchodercetis yovanovitchi*, *Tselfatia formosa* and the pycnodont *Nursallia gutturosum* (Ifrim 2006; Giersch 2014; Stinnesbeck et al., 2019), but the pachyrhizodont *Goulmimichthys roberti* (Blanco and Cavin 2003) is also frequent (Stinnesbeck et al., 2020). The only crustacean previously documented from Vallecillo is the sessile cirriped *Stramentum* that grew on ammonite shells of *Pseudaspidoceras flexuosum* (Fig. 1B) and cf. *Vascoceras*. Several authors excluded post-mortem colonization by *Stramentum* due to the excellent preservation of infested ammonoid shells (Ifrim 2006; Ifrim and Stinnesbeck 2007; Ifrim et al., 2011a). The cirripeds were therefore likely embedded alive (Ifrim and Stinnesbeck 2007; Ifrim et al., 2011a). The scarce record of crustaceans from Vallecillo contrasts with their abundance in approximately coeval plattenkalk localities north of Múzquiz (e.g. El Pilote, El Rosario, Temporales), some 300 km NW of Vallecillo. Here, both decapod crustaceans and *Stramentum* are frequent (Vega et al., 2007; Ifrim et al., 2011a), thus indicating that oxygen-depleted bottom conditions were less adverse towards the north.

1.2. Preservation

In Vallecillo, vertebrate fossils are recrystallized to calcite and specimens comprise a slab and counter-slab preservation. Individuals were rapidly buried and anoxic bottom water conditions likely favored good preservation (Ifrim 2006; Ifrim et al., 2007). This is also the case for the near-complete and well-articulated individual of *G. roberti* hosting the isopod discussed here. The body of the host is laterally embedded, a character which is also identified in most other individuals of the taxon from Vallecillo (Stinnesbeck et al., 2020). The mouth is open and fins are spread, a feature often seen in fishes exposed to respiratory stress (e.g. suffocation). Gut content is identified as a dark recrystallized mass without identifiable matter. No diagenetic deformations are identified apart from the compression.

2. Materials and methods

The isopod specimen introduced here from Vallecillo is attached to a 380 mm long individual (INAH-REG2544-PF196AB; CPC2798) of *Goulmimichthys roberti* (Blanco and Cavin, 2003). It was identified on the dorso-lateral part of the skull of the fish on the parietal bone (Fig. 2A–C). The isopod measures 13 mm total length and a maximum width of 5 mm. It is preserved in dorsal view but with a slight twist to the left, thus exposing part the right body side. The specimen is oriented vertical to the host's longitudinal axis, with the head directed towards and in short distance to the gills (Fig. 2B–C).

The isopod specimen was identified by the first author while revising 166 *G. roberti* individuals from Vallecillo in the collection of Ing. Mauricio Fernández Garza, at San Pedro Garza García, Mexico. The limestone slab and counter-slab contains both, the fish described by Stinnesbeck et al. (2020) and the associated isopod documented here. Photographs were taken with a Nikon D5200.

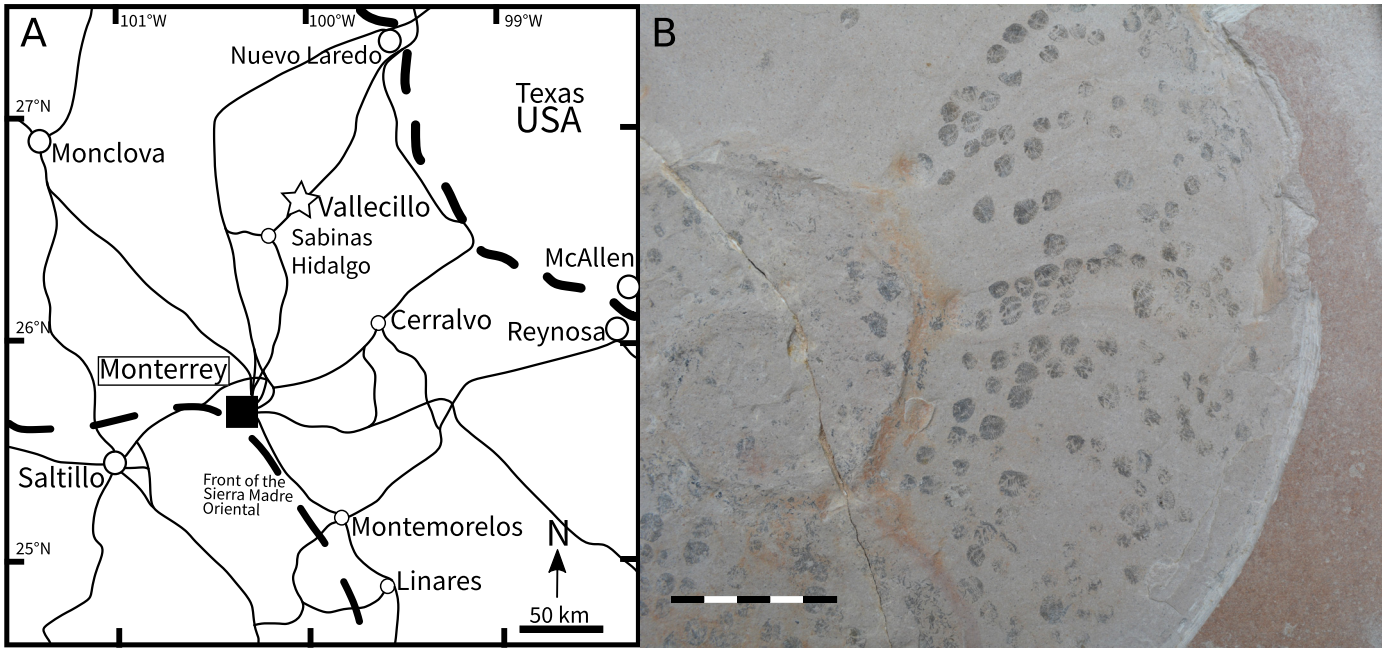

Fig. 1. A, Geographic location of Vallecillo in northeastern Mexico. B, Stramentid cirripeds overgrowing the ammonoid shell of *Pseudaspidoceras flexuosum*. Scale bar 50 mm.

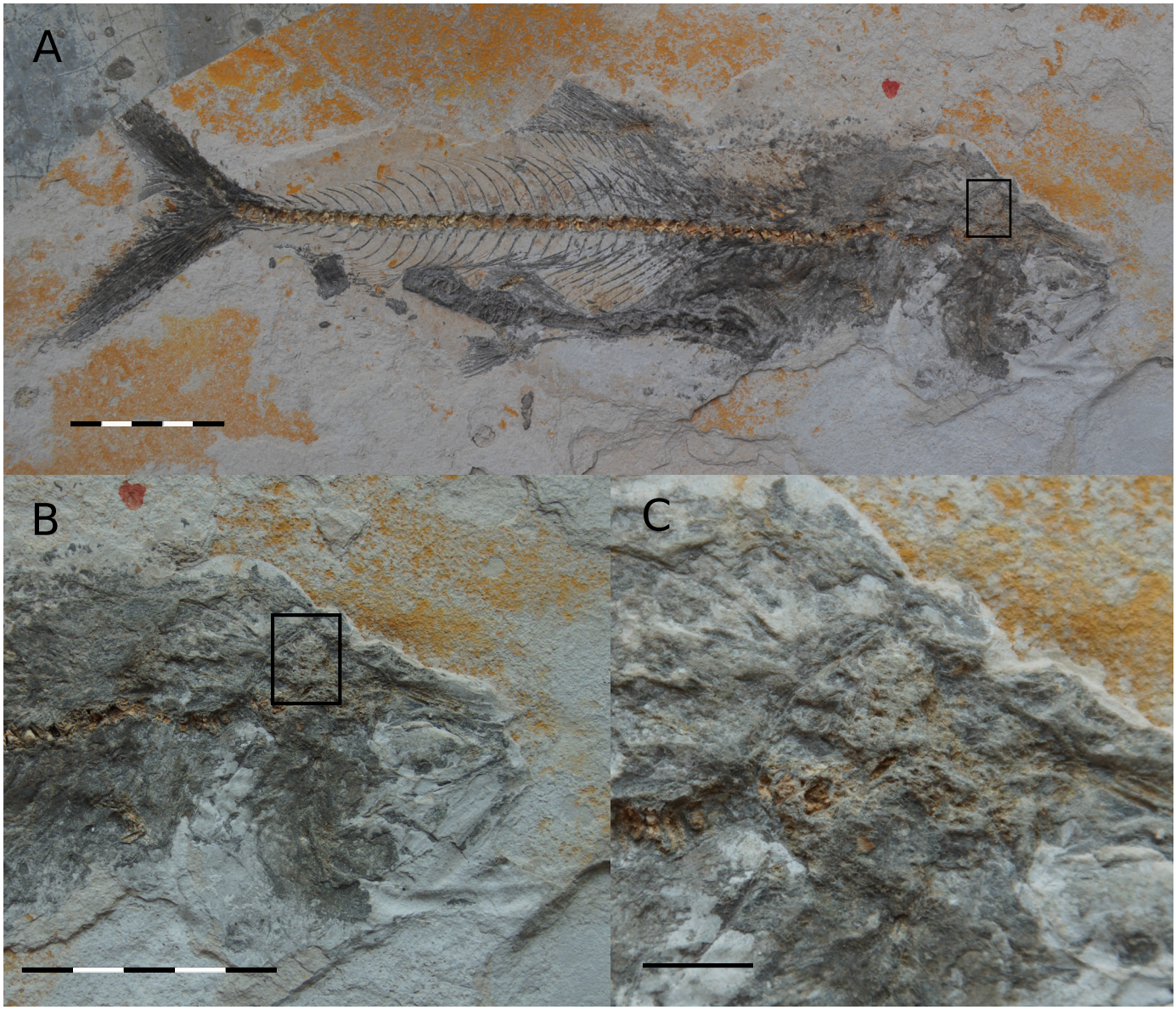

Fig. 2. A, *Goulmimichthys roberti* specimen INAH-REG2544-PF196/CPC2798 with attached isopod. B–C, Close-ups of the skull.

Specimen REG2544-PF196AB; CPC2798 was discovered in an active limestone quarry at Vallecillo and donated by a quarry worker to the fossil collector Ing. Mauricio Fernández Garza (Monterrey). The fossil was registered by the Instituto Nacional de Antropología (INAM) under the number REG2544-PF196AB. In the process of this publication the specimen was also registered at the Museo del Desierto (MUDE), Saltillo, Mexico, where it is housed under the number CPC 2798 and is publicly accessible.

2.1. Systematic palaeontology

Suborder PACHYRHIZODONTOIDEI Forey, 1977
Family PACHYRHIZODONTOIDAE Cope, 1872
Genus *GOULMIMICHTHYS* Cavin, 1995
Type species: *Goulmimichthys roberti* Blanco & Cavin, 2003

Goulmimichthys roberti is a frequent taxon in Vallecillo comprising 9% of the fish assemblage (Ifrim 2006). Its taphonomy has recently been revised by Stinnesbeck et al. (2020). The fusiform body shape and forked tail support the interpretation of *G. roberti* as a high speed swimmer adapted to open marine environments. Specimens from Vallecillo range from 250 to 450 mm length and likely formed schools (Stinnesbeck et al., 2020). The abundance of well-preserved, articulated and complete individuals, including INAH-REG2544-PF196AB/CPC2798, opposes a potential phase of carcass flotation. Rather, carcasses directly sank to the sea floor and were embedded rapidly. Anoxic bottom water conditions excluded scavengers in the Vallecillo locality, thus also favoring the excellent preservation of fishes in a micritic lime mud sediment (Ifrim 2006; Ifrim and Stinnesbeck 2007).

Order ISOPODA Latreille, 1817
Suborder CYMOTHOIDA Wägele, 1989
CYMOTHOOIDEA Leach, 1814
CYMOTHOIDAE Leach 1818
Mothocya Costa, in Hope, 1851

Diagnosis. Following the revision of *Mothocya* by Bruce (1986): Posterior margin of the cephalon never sinuate. Coxae nearly as

long as or longer than respective segment, broad and well visible in dorsal view. Pleon partly overlapped laterally by pereonite 7. Antennule larger and more robust than antenna. Maxilliped article 3 is robust lacking setae. Pereopods similar except for 4 to 7 which are longer compared with 1–3. Pereopod dactyli are long and robust. Uropod exopod longer than endopod.

Type species: *Mothocya epimerica* Costa, in Hope, 1851; by subsequent designation (Bruce 1986).

Remarks. Species of the family Cymothoidae are obligate fish parasites characterized through a mandible without or reduced molar process or lacinia, with an acute incisor, maxilla 2 endites with hooked setae and a maxilliped palp of only 2–3 articles. All pereopods are prehensile with dactylus longer than propodus, pleopods and uropods lacking marginal setae (Brandt and Poore 2003; Ravichandran et al., 2019).

***Mothocya vallecillae* n. sp.**

Derivation of name. Name refers to Vallecillo, the village where the specimen was found.

Diagnosis. External fish parasite (Fig. 3A–B) with cephalon wider than long, anterior margin rounded, no projecting rostrum, posterior margin nearly straight. Head not deeply immersed in pereonite 1. Pereon tergites laterally narrowing in pereonites 3 and 4, projecting posterolaterally in pereonites 5 and 6. Pereonite 7 distinctly shorter and less wide than preceding segments. Coxal plates visible in dorsal view (preserved in pereonites 3–6 in the holotype), lateral margins rounded. Pleon segments (1–5) are narrow and together as long as pereonite 7 and about as wide as pereonite 7. Pleotelsons posterior margin of oval shape. Uropods surpass posterior telson margin, rami of lunate shape, endopod distinctly longer than exopod.

Material (Fig. 3A–B). INAH-REG2544-PF196, housed in the Museo del Desierto (MUDE) in Saltillo, Coahuila, Mexico, under the number CPC2798.

Description. Specimen is 13 mm long and about three times longer than wide. Body dorsoventrally compressed and moderately vaulted.

Head: The small head is not deeply set into pereonite 1, but pereonite 1 may laterally reach beyond the posterior margin of the cephalon. It is rectangular to oval shaped and twice as wide (1 mm) as long (0.5 mm). A rostrum is not visible (either absent or bent ventrally). The head bears the antennule (1st) and the antenna (2nd) of the right side, and the antennule of the left side. No segmentation of these appendages is observed. Mouthparts and compound eyes are not identified.

Pereon: The pereon measures 8 mm in total length. Each segment is 1–1.5 mm long and 4–5 mm wide. Pereonite 1 is half as wide as pereonite 2 and pereonite 5 is wider than 4 and overlapping 6. All seven segments of the pereon show shapes resembling the characteristic outlines of many of the extant cymothoids, i.e. tergites are laterally bent in pereonites 4–6, with narrowing rounded and caudally directed tips of coxal plates. Segments are slightly shortening towards the pleotelson, with a compression of the 7th segment. Laterally rounded coxal plates are identified on the right thoracical half, attached to tergites. The coxal plates are 1 mm long and wide. They are unequal in shape and appear to be compressed due to diagenetic compaction. Coxae are shorter than respective pereonites. Pereopods are distinguished on both body sides and allow for the differentiation of leg articles i.e. basis, ischium, merus, carpus, propodus and dactylus. Coxal plate connections to pereopods 3, 5, 6 and 7 are visible on the right body side.

Pereopods: Pereopods 2 to 7 are identified on the right pereon side with two different orientations. On the left side, the appendages 4–7 are preserved. 4 is directed anteriorly and 5–7 are posteriorly-directed. With one exception (pereopod 6, left side), appendages are connected to the main body (pereon). Pereopod 2 from the right body side seems to be incomplete and displaced beneath the pereon. Pereopod 6 is longer than 7. All appendages appear to end in curved tips interpreted as hook-like elongated dactyli. Pereopods 3 and 7 from the right body side and 4 and 7 from the left side are completely preserved and joints between leg articles are visible. The basis of the right pereopod 3 is adjacent to pereonite 3 and seems articulated and complete. It is broad and slightly flattened, without any distinguishable ridges. Ischium, merus and carpus of

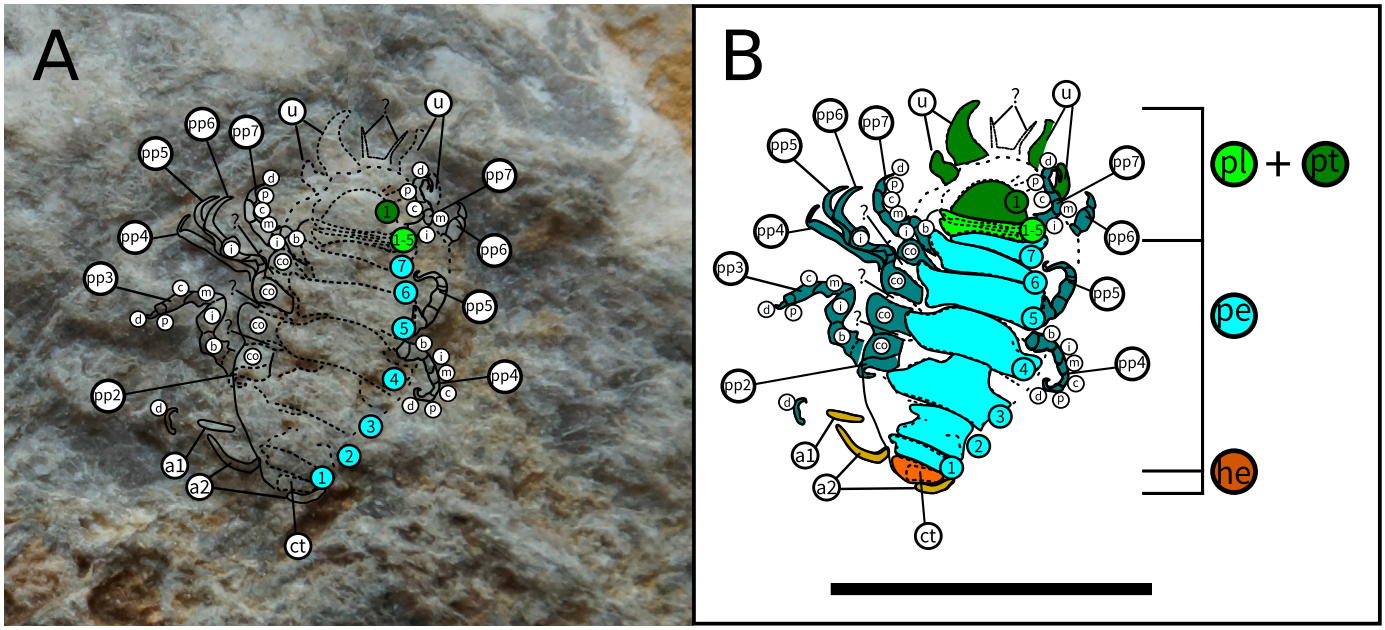

Fig. 3. A, Dorsal view of the isopod from Vallecillo, INAH-REG2544-PF196/CPC2798, A–B, Photograph of the specimen with anatomical interpretation. Body parts colored. *Abbreviations*: a1, antennule; a2, antenna; b, basis; co, coxa; c, carpus; ct, cephalothorax; d, dactylus; h, head; i, ischium; m, merus; pp, pereopod; pl, pleon; p, propodus; pe, pereon; pt, pleotelson; pl, pleon; u, uropod. Scale bar 10 mm.

this pereopod are laterally compressed. The propodus appears oval in shape and the ischium outline resembles a small cudgel. The same outline of the ischium is also identified in pereopods with no visible joints (e.g. pereopod 6 from the right body side). Pereopod 7 from the right side is smaller than the anterior pereopod 3. The pereopod 7 is laterally compressed and ischium and merus appear to be fused, due to fossilization. The dactylus of pereopod 7 is longer in comparison to the dactylus of pereopod 3. Pereopod 4 from the left side is slightly curved. Ischium, merus and carpus are similar in length. Ischium is similar in shape to pereopod 3. Pereopod 7 from the left side is curved posteriorly. The basis is not visible but ischium, merus, carpus, propodus and dactylus are preserved.

Pleon and Pleotelson: Pleon and pleotelson combined are 5 mm long. Pleonites 1–5 are together as long as pereonite 7 and as in pereonites their lateral tips are pointed posteriorly. Their short length resembles the pleon outline known from extant adult Cymothoida (especially mature females). The segments overlap each other, even though they are quite short. Segments are half the width (2.5 mm) of pereonites, without any visible dorsal grooves on each plate. Margins are visible and allow for the differentiation of the five segments. Preservation prevents further description of additional details due to overlapping of the pleon segments.

The pleotelson is distally rounded and slightly triangular in outline, broadest anteriorly. No details of the surface or margins are identified.

The uropods are 2 mm long; they are not covered by the pleotelson and appear to be disconnected from the body, although they are usually less prone to detach. This displacement is tentatively interpreted as caused by fossilization. Preservation does not allow further differentiation of details. Uropods are preserved as imprints in the micritic limestone and are lunate-shaped as known from extant Cymothoidae. Both the endo- and exopod are markedly large compared to extant specimens. The endopod is longer than the exopod and not covered by the pleotelson. Margins of both rami are medially concave. The uropodal protopod, which connects to the exo- and endopod, is not identified. There are two furca-like appendages of unknown nature between the endopods posterior to the telson margin; such filaments are not known in other Isopoda.

Occurrence and stratigraphical range. The Vallecillo plattenkalk member of the Agua Nueva Formation is early to middle Turonian in age (Ifrim, 2006; Ifrim and Stinnesbeck 2007). The Vallecillo locality is located approximately 100 km north of Monterrey, the capital city of Nuevo León.

Remarks. We affiliate the specimen from Vallecillo with Cymothoinae (Schioedte and Meinert 1884) due to a posterior margin of the cephalothorax that is not trilobed as in *Anilocrinae* (Schioedte and Meinert 1881). Within Cymothoinae, the Vallecillo specimen shows characteristics documented from *Mothocya* (Costa, in Hope, 1851). Characters typically seen in this extant taxon include a pleon that is slightly immersed in pereonite 7. The coxal plates are posteriorly acute, nearly as wide as pereonites and well developed. *M. vallecillae* resembles *M. renardi* by a narrow pleon and uropods extending the pleotelson (Hadfield et al., 2015). Coxae of *M. affinis* are large and wide, extending the pleon, a character also seen in the Vallecillo specimen. The pleon of *M. vallecillae* is partly overlapped by pereonite 7 and the pleotelson is longer than the pleon, as described for *M. melanosticta* (Vigneshwaran et al., 2018). The Vallecillo specimen differs significantly from e.g. *Mothocya plagulophora, M. parvostis, M. melanosticta, or M. collettei,* which possess a large and wide pleon and pleotelson and short uropods (Bruce 1986; Hadfield et al., 2015). Uropods of *M. vallecillae* are lunate-shaped and markedly large in comparison to the majority of extant *Mothocya*. *M. vallecillae* also differs from *M. epimerica*, *M. belonae*, *M. rosea* and *M. ihi*, due to a pleon and pleotelson that is unusually short in proportion to the rest of the body. The Vallecillo fossil thus shows unique features and is here referred to as a new species, *M. vallecillae*.

3. Discussion

Isopod attachment on the host offers important information, e.g. on feeding preference and host specificity. Recent cymothoids from the tropics are highly diverse. While they are usually specialized to specific fish families as hosts, and even specific genera or species, cymothoids from temperate environments are less specialized (Smit et al., 2014). Preferences for a precise attachment site on hosts are determined by specific needs of the parasite (Smit et al., 2014). Nagler et al. (2016) discussed characteristic features to determine a parasitic *versus* scavenging lifestyle of fossil isopods. These are here used as reference for our interpretative discussion of the Vallecillo isopod as a parasite:

1. There is only a single individual of isopod associated with *G. roberti* (INAH-REG2544-PF196AB/CPC2798) from Vallecillo. This scarcity contrasts with fossil isopod findings interpreted as unequivocal scavengers. For instance, numerous individuals infested the carcass of *Pachyrhizodus marathonensis* from the Santonian of Australia (Wilson et al., 2011). The abundance of isopods appears likely as food falls are unpredictable events at the sea bottom and may attract large numbers of scavengers, resulting in a high inter- and intraspecific competition on a carcass (Barradas-Ortiz et al., 2003). We therefore expect a higher number of individuals on a carcass although it is not impossible to find a single scavenger.
2. Orientation of the isopod in direction to current has repeatedly been observed in extant parasitic isopods and was interpreted as a strategy to reduce the danger of removal or grip loosing during host swimming. This is not seen in our specimen, which is oriented in direction to the gills instead of the swimming direction of the host, which could indicate movement after the hosts death. Therefore we can only infer that the isopod is clearly attached to the host but expect that scavenging isopods are frequently found in a random position with regard to the host.
3. The isopod infesting *G. roberti* is preserved above the gills on the skull top. In extant parasitic isopods, the position upon the host is markedly species and genus-specific (Brusca 1981; Smit et al., 2014). Animals of the genus *Anilocra,* for example, use multiple attachment positions: on top of the head, on the caudal peduncle, near the pectoral fins, or posterodorsally to the eye of the host (Fogelman 2005). However, conclusions based on the preserved position of the individual must be taken with caution because the parasite can freely move around on the host body.
4. The twisted body position of the Vallecillo isopod may represent a case of growth response due to host attachment, as described by Nagler et al. (2016). It suggests a permanent living phase of the adult isopod on the host.
5. All pereopods of our individual are modified to hook-like appendages.
6. Carcasses that lie on the sea floor without being covered by sediment generally show signs of decay. Bone dispersal in multiple directions indicates scavenging in comparison to e.g. dispersal in one specific direction, indicating a current. This is not the case in *G. roberti*, which is articulated and complete (Fig. 2A). We therefore propose that the fish specimen was rapidly brought out of the range of scavengers, e.g. by anoxic bottom conditions or rapid embedding. Completeness and articulation of the fish thus opposes an interpretation of our isopod as a scavenging taxon. The parasite did not detach after

the hosts death, possibly due to the rapid effect of toxic bottom water.

Out of 166 well preserved individuals of *G. roberti* from Vallecillo (Stinnesbeck et al., 2020), INAH-REG2544-PF196AB/CPC2798 is the only specimen that exhibits an attached isopod. Parasitic isopods are also unreported from other actinopterygian species examined from the site (e.g. Blanco 2003; Giersch 2014). For instance, Stinnesbeck et al. (2019) revised 90 specimens of *Nursallia gutturosum*, without detecting any isopods. Therefore, the question of a taxon-selective infestation cannot be answered to date.

3.1. Ecological comparison of the Vallecillo isopod

The Vallecillo specimen shows ecological features characterizing Cymothoidae (suborder Cymothoida). Cymothoidae are obligate fish parasites that permanently attach to the host as adults and lose the ability to swim. An assignment to Cirolanidae, Aegidae, Bopyridae, Cryptoniscoidea and Gnathiidae is excluded. Cirolanidae are scavengers and predators but not obligate parasitic. Aegidae parasitize fishes temporarily during immature and adult stages; they possess three anterior claw-like pereopods used for attachment. Bopyridae and Cryptoniscoidea preferentially parasitize crustaceans while tick-like Gnathiidae parasitize fishes only as larvae (Dohrn 1870; Mouchet 1928; Wägele 1988; Nagler and Haug 2016; Smit et al., 2019). *M. vallecillae* can be excluded as a host for Gnathiidae due to a well-developed pereopod 7 and pereonite 7 excluding a larval or manca stage and clearly pointing to an adult individual. Corallanidae exert a temporary parasitic lifestyle, possess a vestigial maxilla, a mandible provided with a narrow incisor process, while only the first three pereopods are prehensile and suited for host attachment (strong propodus, hooked dactyli) (Hale 1925; Bruce et al., 1982; Müller 1991).

Cymothoidae characteristically possess seven pereopods with hook-like dactyli modified for host attachment, and a mandibular incisor modified into a blade-like cutting edge (Schioedte and Meinert, 1879–1884; Nierstrasz 1917). The body can be asymmetrical due to permanent attachment on the host, e.g. to fins. The short and oval-shaped cephalothorax of *M. vallecillae* resembles that of Aegidae and Cymothoidae. The individual from Vallecillo lacks eyes which may, however, have been very small sized or with a smooth surface. Their small size opposes an assignment to Aegidae in which eyes are generally large, but supports a placement within Cymothoidae. Pereonite tergites are narrower laterally and pointed posteriorly in pereonites 4–6, resembling those of some extant Cymothoidae. Conserved coxal plates (pereonites 3–6) are laterally rounded and visible in dorsal view. They are slender anteriorly and get posteriorly bigger as in Cymothoidae. Uropods are lunate-shaped as those of Cymothoidae and markedly large in comparison to extant species of this family. Family identification in isopods depends on the shape of pereopods apart from the mouthparts. In Corallanidae, pereopods 1–3 are prehensile, but lack the slender dagger-like dactyli, whereas in Aegidae hooked dactyli are only seen in the first three pereopods, while in Cymothoidae all legs have hooked dactyli. This latter modification is seen in the Vallecillo specimen which therefore supports an assignation to Cymothoidae. The shape of the body and the position on the host further support this conclusion.

3.1.1. Comparison within Cymothoidae

Species of Anilocrinae (e.g. *Anilocra* (Leach 1818), *Creniola* (Bruce 1987), *Pleopodias* (Richardson 1910), *Nerocila* (Leach 1818) and *Renocila* (Miers 1880)) are frequently attached to the body surface of a host (Bruce 1987; Aneesh et al., 2017; Welicky and Smit 2019; Aneesh et al., 2020). We compared these genera to the Vallecillo isopod, but see unique features to exclude an assignment to *Anilocrinae:* e.g. The cephalon margin is not trilobed. Uropods are not hidden under the pleotelson in the Vallecillo specimen as in *Nerocila* and the coxal plates are well visible, differing from *Creniola* (Bruce 1987). Pereopod 6 is similar in length to 7 in *Renocila* which is similar to our specimen, but pereopod 6 is more elongated than 7 in the Vallecillo fossil. Besides, Pereopod 7 of *Pleopodias* is longer and more elongated than other pereopods (Hadfield and Smit, 2017). *Pleopodias* has shorter uropods, a rectangular elongated pleotelson, large eyes, and a broad rostrum. In *Anilocra* pleon segments are longer and coxal plates are not well visible in dorsal view. Also, *Anilocra* species have a broad anteriorly projecting rostrum with a straight or rounded anterior margin. Coxal plates of *M. vallecillae* are more rounded and probably more laterally directed than in *Plotor* (Schioedte and Meinert 1881). As in *Amblycephalon* (Pillai 1954) the uropods are distinctly longer than the pleotelson. However, in *Amblycephalon* as in *Nerocila* and other cymothoids, the long ramus is the exopod, while in the fossil specimen from Vallecillo the endopod is longer. In *Bambalocra* (Bruce, Welicky, Hadfield and Smit 2019) coxal plates are not visible in dorsal view. These genera are therefore excluded.

3.1.2. Comparison to branchial and buccal inhabiting taxa

The Vallecillo isopod specimen is here assigned to Cymothoinae. External and buccal-inhabiting taxa of modern Cymothoinae are usually symmetrical in outline, while species inhabiting the gills of their hosts are asymmetrical (Smit et al., 2019; Hadfield et al., 2014). Nevertheless, a symmetrical body is visible for the fossil specimen from Vallecillo. *Mothocya* (Costa, in Hope, 1851) populates the branchial cavity and only exceptionally the buccal cavity of the host (Bruce 1986; van der Wal et al., 2019). The outline of *Mothocya* is highly variable, ranging from straight to twisted and narrow to broad. Coxal plates are posteriorly acute or rounded and dorsally visible, comparable to the Vallecillo specimen. The dactylus of the pereopods is long in *Mothocya* and the merus longer than the carpus, as identified in the fossil. The pleon is wide in extant *Mothocya* when compared to pereonite 5 and deeply overlapped by pereonite 7 (Bruce 1986). The latter is consistent with the Vallecillo specimen. Uropod rami often extend the posterior margin of the pleotelson in *Mothocya*, a feature seen in *M. vallecillae*. Nevertheless, *Mothocya* is a complicated taxon because antenna and antennules, mouthparts and pereopods are uniform, thus hampering a differentiation of individual species (Bruce 1986).

Elthusa (Schioedte and Meinert 1884) is another buccal-inhabiting extant member of Cymothoinae. In this taxon the antennulae are shorter or equal in length to the antennae, which is also seen in the Vallecillo specimen. The cephalon posterior margin is not trilobed and the pereopods possess short dactyli (van der Wal et al., 2019). The Vallecillo specimen thus shares more morphological features with *Mothocya* than with *Elthusa*. Extant *Mothocya* preferentially attaches to halfbeaks, belonids and silversides (Bruce 1986). There are also records of *Mothocya* on the blue flying fish *Exocoetus volitans* and the Indian sardine, *Sardinella sindensis* (Vigneshwaran et al., 2018). *Mothocya vallecilliae* is attached to a member of pachyrhizodontidae.

3.2. Remarks on biology and environment

3.2.1. Isopod attachment

There are reports of isopods abandoning their dying or stressed hosts (Brusca 1981). This phenomenon was already documented by Brusca (1981) for specimens of *Lironeca vulgaris* escaping from gill cavities of formalin-threatened pompanos within a few minutes. The Vallecillo specimen is preserved in close contact to the gills of *G. roberti*. Expecting a similar behavior for our specimen as observed in extant parasitic isopods abandoning their dying host,

we assume that the entry into the anoxic bottom zone of the Vallecillo ocean was fast, thereby reducing the possibility of the parasite to depart from its host.

3.2.2. Specimen interpretation

The extremities interpreted here as uropods (illustrated in green in Fig. 3A–B) and the slender appendages between them remain difficult to explain. We interprete these structures posteriorly as uropods based on the scenario that an interpretation of the flattened appendages as large antennae 2 appears unlikely. They are also excluded to represent pereopods because of the enormous size compared to the other pereopods. The slender appendages between the uropods (Fig. 3A–B) are also difficult to interpret. Similar structures are present in *Asellota* (styliform uropods), but members were never documented as parasitic. An interpretation as antennae is unlikely, because cymothoids do usually not hold these appendages anteriorly for hydrodynamical reasons. Also, the coxal plates and the pereonites are posteriorly bigger than anteriorly and bent caudally (in our interpretation), and thus resemble recent isopod species exposed to currents. We therefore consider the head of the specimen pointing downwards on the fish and suggest that the flattened structures represent uropods.

3.2.3. Isopod sex and maturity

Maturity is determined through the development of pereopod 7, pereonite 7, and the presence of mature reproductive structures such as oostegites of females, and the appendix masculina development of males. The second pair of pleopods and in some cases the first, are used to transfer sperm in male isopods. Such structures are not visible in our specimen. The Vallecillo individual shows a well-developed pereopod 7 and pereonite 7, which allows us to conclude on an adult stage of the specimen. The individual measures 13 mm length which is quite small for a female but common in males. Uropods are longer than the pleotelson and resemble the swimming "aegathoid" stage. The body is symmetrical. The Vallecillo species thus lacks features to determine the specimen undoubtedly as mature female.

3.2.4. Host shape

The fusiform body shape of *G. roberti* is associated with high speed swimming in an open marine environment (Giersch, 2014; Stinnesbeck et al., 2020). In general, slow-swimming fishes have rounded unlobed tails producing a large surface area for membrane stability (Fletcher et al., 2014). Fast swimming fishes, on the other hand, possess concave caudal fins with narrow lobes. In these cases, the peduncle is narrow and propulsion is primarily generated by undulations of the caudal fin (Fletcher et al., 2014). This is also the case for the caudal peduncle in *G. roberti* which is therefore interpreted as a fast swimmer. The structure of the fan shaped caudal fin ray flaps and hypural plates of *G. roberti* is similar to scombrids and we propose similar propulsion mechanics. A squamation focused on the anterior is also similar to scombrids.

3.2.5. Importance of the Vallecillo fossil

The isopod from Vallecillo is unique in several aspects. (1) It is the first isopod for Vallecillo. (2) It is dorsally preserved with appendages that allow for a differentiation of leg articles. The preservation of legs is generally rare in the fossil record. (3) The isopod is associated with the fish host specimen. A direct association of parasitic isopods to its vertebrate host/food is extremely rare in the fossil record and only documented from the lower Tithonian (Upper Jurassic) Solnhofen limestone, Germany (Nagler et al., 2016; parasitic isopods), potentially from the Eocene of Monte Postale, Italy (Robin et al., 2019; parasitic or scavenger isopods) and the Albian (Cretaceous) Toolebuc Formation, Australia (Wilson et al., 2011; scavenger isopods). For the Cretaceous, parasitic isopods directly attached to a host have not been reported to date, and only a few reports document isolated specimens, without a potential host, and thus without convincing evidence for a parasitic behavior. In the Coniacian Austin Chalk, for instance, Bowman (1971) documented the isopod *Palaega lamnae* in close distance to the mackerel shark *Lamna* sp., without immediate evidence for a parasitic or scavenging lifestyle (Wieder and Feldmann 1992; Robin et al., 2019). (4) Most isopods reported from the Cretaceous are from coastal shallow waters (Wieder and Feldmann 1992; Feldmann et al., 1998; Feldmann 2009; Wilson et al., 2011). This is not the case for the Vallecillo specimen, which was found in an open marine environment of about 200 m water depth and in about 400 km distance from the nearest Cretaceous coast (Ifrim 2006; Ifrim et al., 2011b). Pelagic isopods are extremely rare in the fossil record, as most findings come from restricted lagoonal environments. For example, one third of all Jurassic isopods known to date are from the famous Solnhofen Lagerstätte (Germany), but these specimens were probably washed into the lagoon from morphological heights surrounding the platy limestone environment (Etter 2014). This scenario of transport is excluded for the Vallecillo isopod, due to the articulation and completeness of both the host and the parasite, the latter being attached to the fish.

The bias of over-representation of shallow water isopods in the fossil record is probably linked to the fact that pelagic Lagerstätten are quite rare (e.g. the Cenomanian-Turonian Komen site from Slovenia). Most localities reflect quiet water restricted environments, e.g. Solnhofen (Tithonian) in Germany, Sahel Alma in Lebanon (Cenomanian and Santonian), Komen (Cenomanian–Turonian) in Slovenia, el Montsec and Las Hoyas (Berriasian–Barremian) in Spain and Santana (Albian) in Brazil (Cavin et al., 2000; Ifrim 2006; Selden and Nudds 2012). As locations reflecting open marine shelf or even pelagic conditions are scarce, fossil isopod species from these environments are rarely preserved, with Vallecillo representing an unusual exception.

4. Conclusion

The Vallecillo platy limestone deposit in northeastern Mexico provides the first Cretaceous record of a parasitic isopod directly associated with a fish host, an articulated and complete specimen of *Goulmimichthys roberti* interpreted as a fast swimming pachyrhizodont populating an open marine environment. The isopod specimen is also very complete, with most appendages preserved and articulated with the carapace, revealing morphological characteristics which allow for an assignation to a new species of Cymothoidae, *Mothocya vallecillae*. The parasitic lifestyle of this isopod is interpreted based on hook-like distal articles of the appendages and the position on the host. A scavenging lifestyle appears unlikely due to anoxic conditions prevailing at the Vallecillo sea floor. Benthic scavengers are generally unrecorded from the site to date. Articulation and completeness of *G. roberti* hosting the isopod, favor rapid embedding of the carcass without a phase of transport, e.g., floating at the surface. Therefore, the isopod is here interpreted as an open marine species.

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PLOS ONE

RESEARCH ARTICLE

Taphonomy of the teleost *Tselfatia formosa* Arambourg, 1943 from Vallecillo, NE Mexico

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Abstract

The platy limestone deposit of Vallecillo in northeastern Mexico is dated to the early-middle Turonian (Late Cretaceous) and known to contain a variety of well-preserved vertebrate fossils. One of the most common fish species is the teleost *Tselfatia formosa*. A review of 149 individuals reveals the presence of two types of body shapes (diamond-shaped and torpedo-shaped individuals) which is interpreted as sexual shape dimorphism (SSD). A unimodal size distribution illustrates a dominance of diamond-shaped specimens, but both body shape types are present in small (young) and big sized (old) individuals. The abundance of well-articulated and complete specimens suggests that *T. formosa* populated deep levels of the water column, which excluded buoyancy and flotation as well as carcass disintegration near the surface. The reconstruction of the dorsal and anal fins suggests the presence of a membrane between each fin ray and allows for ecological comparison of *T. formosa* with modern fan fishes.

1 Introduction

The teleost *Tselfatia formosa* was originally described by Arambourg [1, 2] from the Upper Cenomanian of Jebel Tselfat (Morocco) and is also known from the Upper Cenomanian of Cinto Eugeano in Italy [3], the Cenomanian-Turonian of Texas and Croatia [4], the Upper Cenomanian or Lower Turonian of Misburg in Germany [5], and the uppermost Cenomanian- middle Turonian Vallecillo locality in Mexico [6]. *T. formosa* is therefore presently restricted to the Cenomanian and Turonian. Individuals from the Austin Chalk (Coniacian-Santonian age) of Texas referred to *T. formosa* by Bardack and Teller-Marshall [4], differ from this taxon by lacking laterally keeled caudal vertebrae; they were assigned by Maisch und Lehmann [5] as *Tselfatia* sp. *T. dalmatia*, originally described from the Cenomanian-Turonian of Yugoslavia by Bardack and Teller-Marshall [4], is distinguished from *T. formosa* by a deeper and shorter body and a raised position of the pectoral fin in regard to the vertebral column [4, 5].

The systematic position of *Tselfatia formosa* was discussed by numerous authors. Taverne [7] proposed a close relationship to Bananogmiidae, instead of Beloniformes, Scombroidei or Osteoglossomorpha as previous suggested by Arambourg [1, 2] and Patterson [8], among others [4, 5]. The taxon is presently assigned to the order Tselfatiiformes (Bananogmiiformes)

which is split into the Eoplethodidae, Plethodidae and Protobramidae. *Tselfatia* is placed within Plethodidae and shares the characteristic segmented fulcra of the first anal and dorsal fin rays with *Dixonanogmius* [9, 10].

In Mexico fossil tselfatiiform fishes are represented by *Bananogmius*, *Dixonanogmius* and *Tselfatia*. *Bananogmius* was mentioned by González-Rodríguez et al. [11] to exist in the Albian Tlayúa locality in Puebla but has not yet been officially described. A similar fish to *Bananogmius* was reported by Applegate [12] from the quarries near Tepexi de Rodríguez in Puebla and a single specimen of *Bananogmius* was documented by Giersch [9] from the Turonian La Mula quarry in northern Coahuila but remains unpublished. We additionally suggest that *Dixonanogmius* is present in the Middle-Late Santonian Los Temporales locality (Fig 1A) and in the Cenomanian San Carlos quarry (Fig 1B and 1C). In addition to the abundant material from Vallecillo, *T. formosa* is here also documented from the Turonian Mesa las Tablas quarry in southern Coahuila (Fig 1D) and was already reported by Alvarado-Ortega et al. [13] from the Turonian Huehuetla quarry. *Tselfatia* sp. has been recorded from La Mula (Cenomanian-Turonian; Coahuila), Xilitla (Upper Turonian; San Luis Potosí) and the Turonian Arroyo las Bocas locality [14–16].

Tselfatia formosa from Vallecillo was first described by Blanco-Piñón [6]who identified various characters to characterize this species. These include a skull significantly higher than long, 65 vertebrae forming the vertebral column, small pectoral fins ventral to the vertebral column, a dorsal fin with 40 rays, an anal fin with 20 rays, a segmentation by pseudo-fulcra and

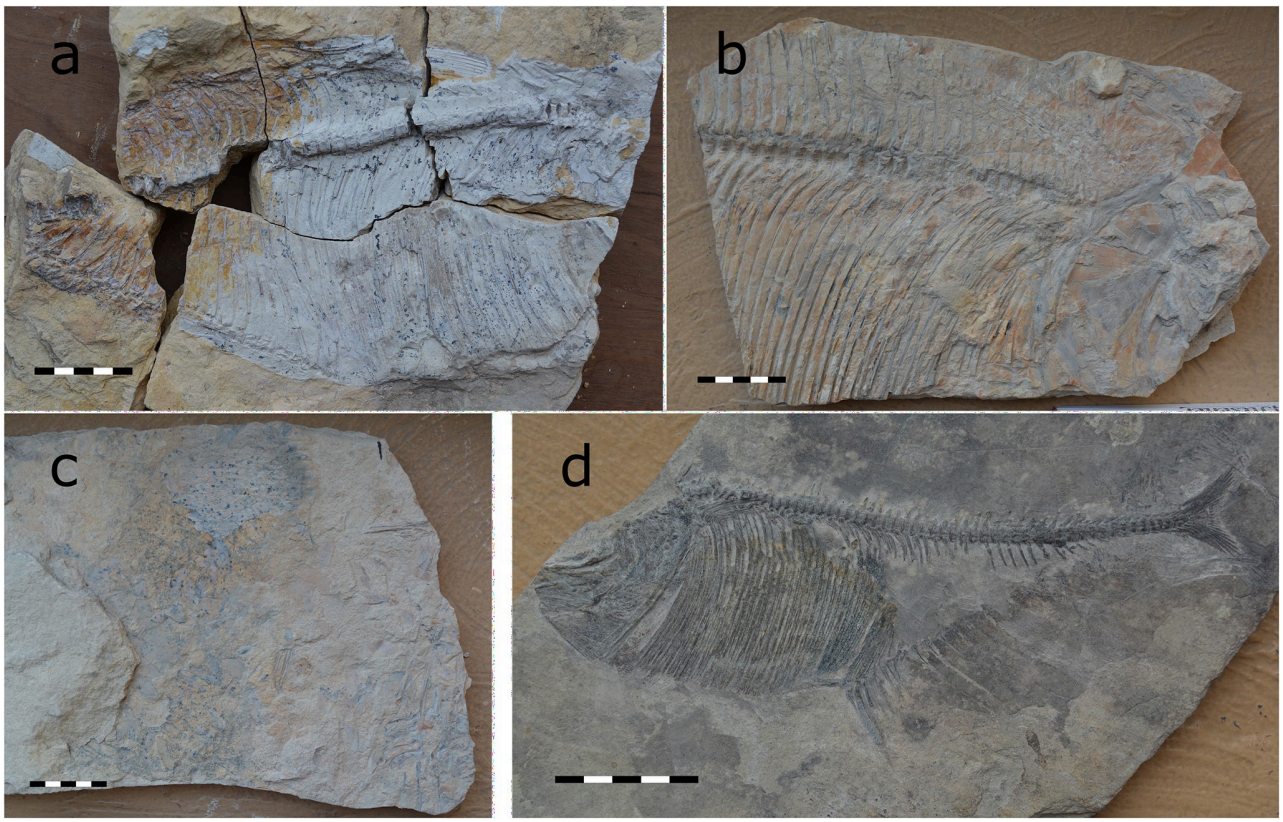

Fig 1. *Dixonanogmius* sp. from the Middle-Late Santonian Los Temporales locality (CPC-2837) (A) and from the Cenomanian San Carlos quarry (CPC-2838 and CPC-2836) (B and C). *T. formosa* from the Turonian Mesa Las Tablas quarry in southern Coahuila (CPC-2835) (D). All scales 50 mm.

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lepidotrichia on the 5th ray of the dorsal and the 3rd ray of the anal fin, and fused hypurals forming a fan-like structure [4, 7, 6]). The specimens presented here confirm this interpretation.

2 Materials and methods

The fossil material of *Tselfatia formosa* analyzed here consists of 149 individuals from Vallecillo. The collection is based on museum material and was not collected randomly from the surface of the outcrop. Fossils are housed in the Colección Paleontológica de Coahuila in the Museo del Desierto at Saltillo and in the collection of Ing. Mauricio Fernández Garza in Monterrey. The latter material will form part of a new paleontological museum in Monterrey dedicated to the Vallecillo fossil lagerstätte. This museum is currently under construction and will be opened 2023. The material of Mr. Fernández Garza will be housed in the museum of Saltillo until the new museum opens. All specimens received a catalog number of the museum of Saltillo (CPC) and in some cases from the Instituto Nacional de Antropología y Historia (REG). No permits were required for the described study, which complied with all relevant regulations.

Fragmentary specimens devoid of essential body compartments were not used for size range documentation and body shape analysis but were still used to obtain information about e.g. the dorsal or anal fins, the mouth, or the preservation of the vertebral column. The total length and the body depth of individuals was measured following the descriptions of Hastings et al. [17].

Articulation and completeness of *T. formosa* are differentiated allowing for the presence of highly disarticulated individuals that are osteologically complete. There are five groups identified in both fields, completeness and articulation. We distinguished complete (c), nearly complete (nc), partially complete (pc), mostly incomplete (mic) and incomplete (in) specimens. *Complete individuals* may lack only small osteological details such as single fins or ribs. Nearly complete individuals lack up to two fins, ribs and fin rays, but the body remains mostly complete. *Partially complete specimens* lack essential body parts such as the caudal fin, vertebrae, fins and ribs. To about half of the specimen is lost in this group. *Mostly incomplete specimens* are devoid of >50% of essential body parts. Specimens comprising only one body compartment (e.g. only the skull is present) are here considered as *incomplete*. The following five groups are differentiated regarding articulation: articulated (a), nearly articulated (na), partially articulated, mostly disarticulated (md) and disarticulated (d), as already discussed by Stinnesbeck et al. [18].

The preservation of **unpaired fins** is here classified into four groups: disarticulated (d), not spread (ns), spread to some extend (middle spread: ms) and fully spread (fs). Specimens with disarticulated dorsal or anal fin rays are classified as disarticulated (Fig 2A). Dorsal and anal fins which are retracted remain parallel to the main body reaching an angle of between 0˚—20˚ (Fig 2B). A middle spread dorsal or anal fin is here interpreted to range between 21˚—40˚ (Fig 2C). Fully erected fins reach to 90˚ (>41˚) (Fig 2D).

Highly disarticulated or incomplete specimens were not used for the determination of size range nor the analysis of body shape. Individuals used for the determination of size range were also used for body shape analysis and for the correlation of size and shape.

There are five categories for **column breaks**: disarticulation (d), no breaks (nb), break of column in the anterior region (head region: hr), break in the posterior region (tail region: tr) and break in both anterior and posterior region (head and tail region: htr). The anterior region of the body is defined as the distance from the most posterior point of the operculum to the first ray of the anal fin. Vertebrae located beneath the operculum are counted to the head

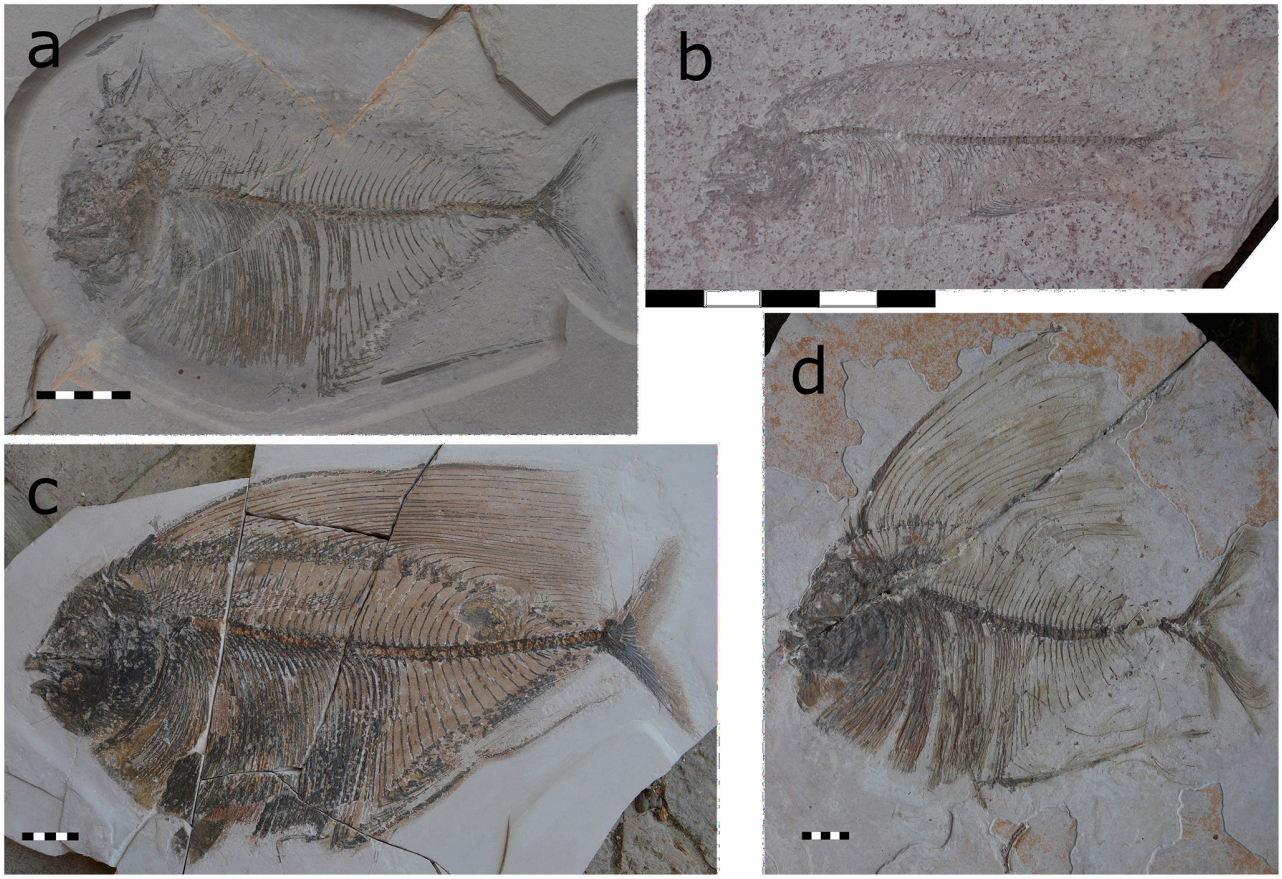

Fig 2. Preservational stages of the dorsal fin of *T. formosa*. Disarticulated dorsal fin (CPC-2892) (A). Folded dorsal fin classified as 'not spread' (ns) within a range of 0˚—20˚ (CPC-2841) (B). Middle spread dorsal fin (ms) within 21˚ to 40˚ (CPC-2948; REG2544 PF48) (C) and full spread (fs) dorsal fin (>41˚) (CPC-2839) (d). All scales 50 mm.

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region. The posterior region marks the distance from the first anal fin to the base of the caudal fin. Multiple column breaks anterior and posterior of the body are counted to the last category (head and tail region).

There are three positions identified for the **mouth**. Disarticulated (d), closed (c) and open (o) (> 0˚). Specimens with a disarticulated skull are counted as disarticulated.

The **body shape** of *T. formosa* is differentiated into two groups: diamond-shaped individuals (diamond) and torpedo-shaped specimens (torpedo), while disarticulated (d) and ambiguous individuals are also present. Diamond-shaped specimens are twice as long as wide, with a length to width body ratio of 2:1 (Fig 3A and 3B). Individuals show a curved back with a front higher than the tail. The attachment point of the fifth segmented ray at the skull forms the highest point of the back. Specimens show a notable "nook" between the pelvic and anal fins, which creates the deepest point of the ventral body and a rhombic shape (Fig 4A–4C). Torpedo-shaped individuals are three times longer than wide and thus present a length to width body ratio of 3:1 (Fig 3A and 3B). They are dorsally less curved when compared to diamond-shaped individuals, while the deeply keeled belly seen in diamond-shaped specimens is either absent, or faintly marked. The highest dorsal point is reached in the middle of the arched back and the deepest point before the anal fin (Fig 4D–4F). There are no other features identified

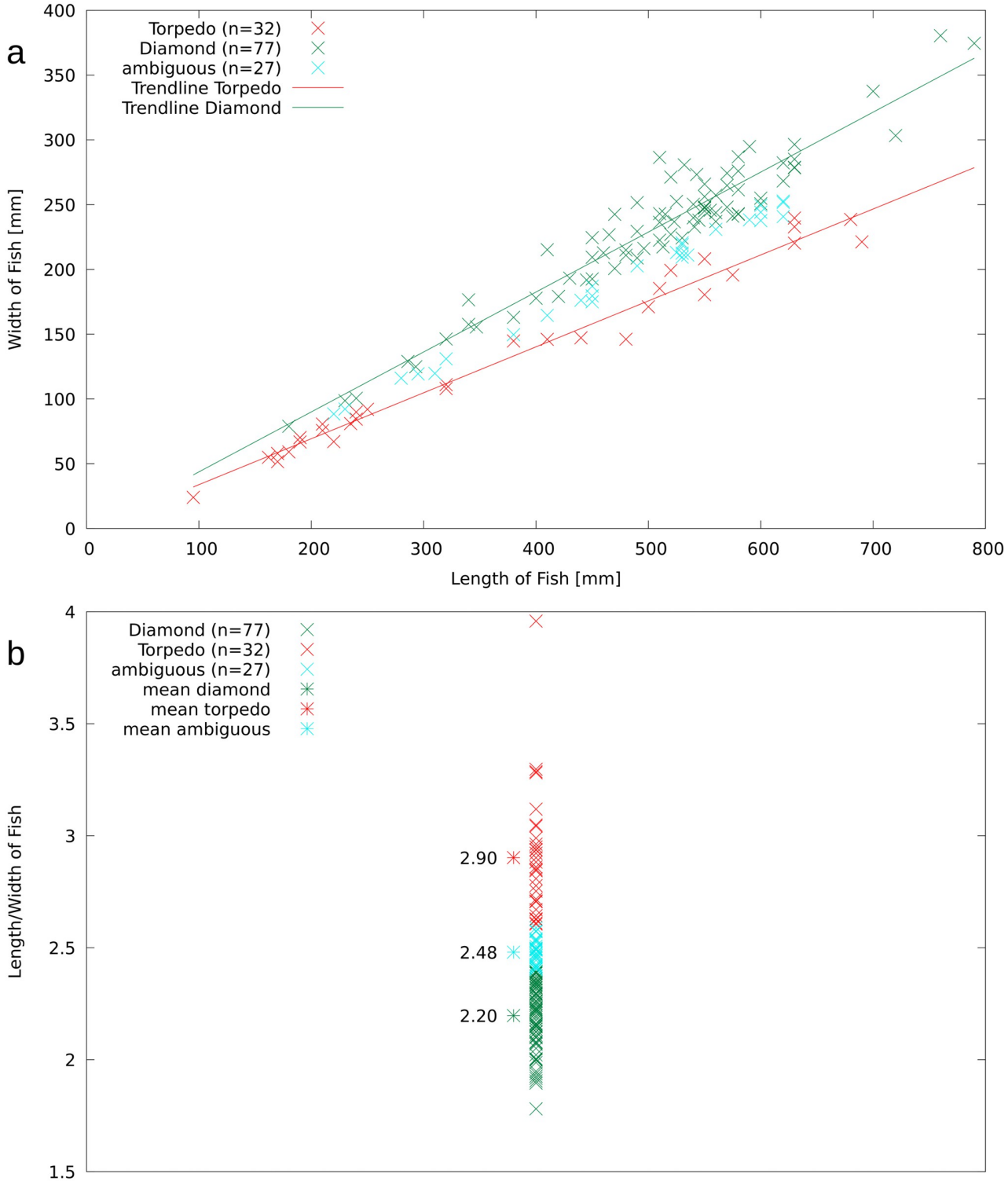

Fig 3. Body length of *T. formosa* in relation to body depth (A). Diamond-shaped individuals are deeply keeled and twice as long as wide, in contrast to torpedo-shaped individuals that are three times longer than wide with a more streamlined body outline (B).

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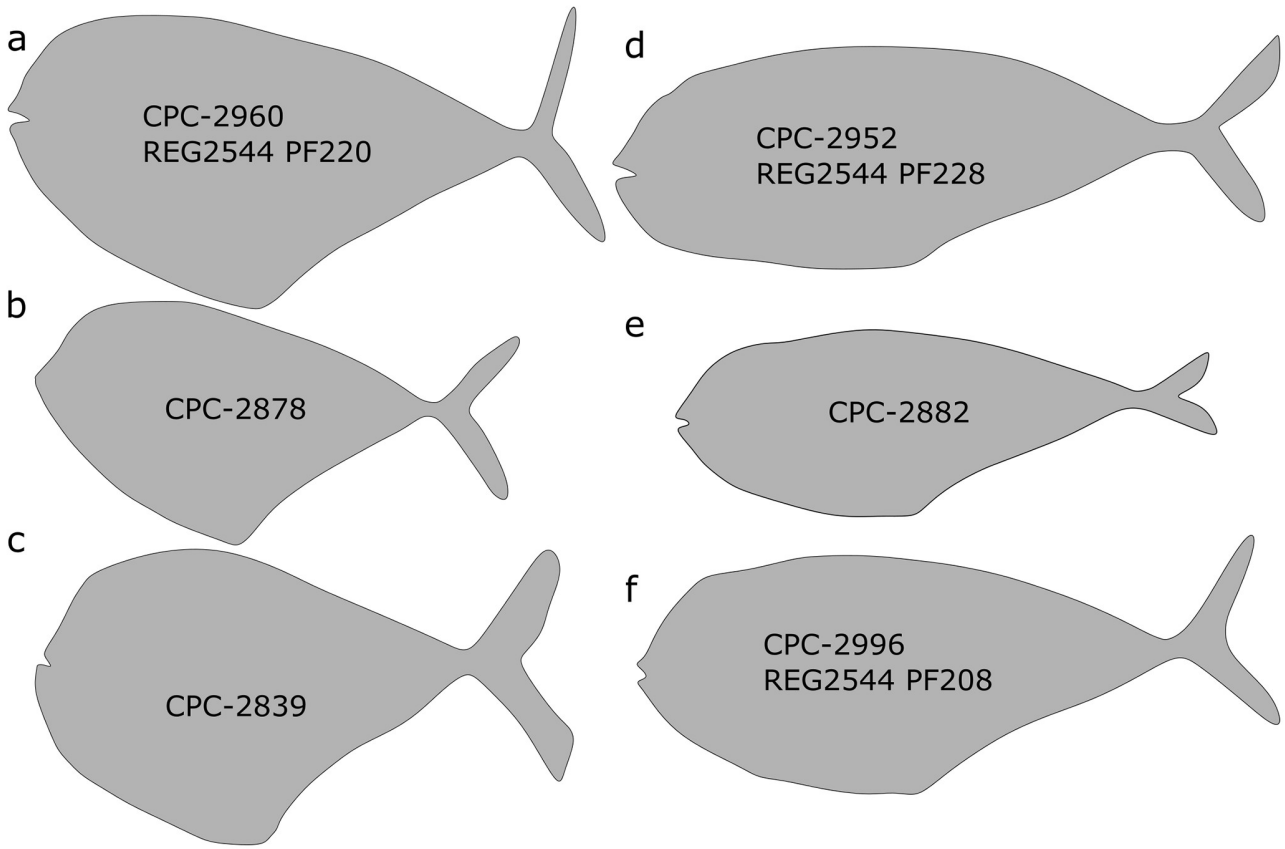

Fig 4. Body shape types documented in *T. formosa*. Diamond-shaped individuals are deeply keeled (A—C) while torpedo-shaped individuals show a streamlined body outline (D—F). The specimen collection numbers are placed inside each shape.

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here to distinguish the two body shapes and thus no traits that would justify the erection of two different *Tselfatia* species. Specimens described as ambiguous are not clearly differentiated as diamond or torpedo-shaped. These individuals are not keeled enough to distinguish a rhombic shape and not long enough to be interpreted as torpedo-shaped (Fig 3A and 3B).

3 Results

3.1 Body shape

53.8% of the individuals are here referred to the diamond-shaped type, whereas 23.1% are classified as torpedo-shaped (Fig 5). 4.2% of the individuals were disarticulated, thus not allowing for a precise classification of body shape and 18.9% are interpreted as ambiguous.

3.2 Size range and body shape

The size range distribution for *T. formosa* is illustrated based on the total body size of 143 specimens from the platy limestone deposit of Vallecillo (Fig 6). It should be noted that the material was collected for museum purposes and is thus selective. It was not collected randomly from the surface of the outcrop, but nevertheless no preference was given to large specimens as abundant small individuals are also present. The smallest specimen reaches a length of 95 mm,

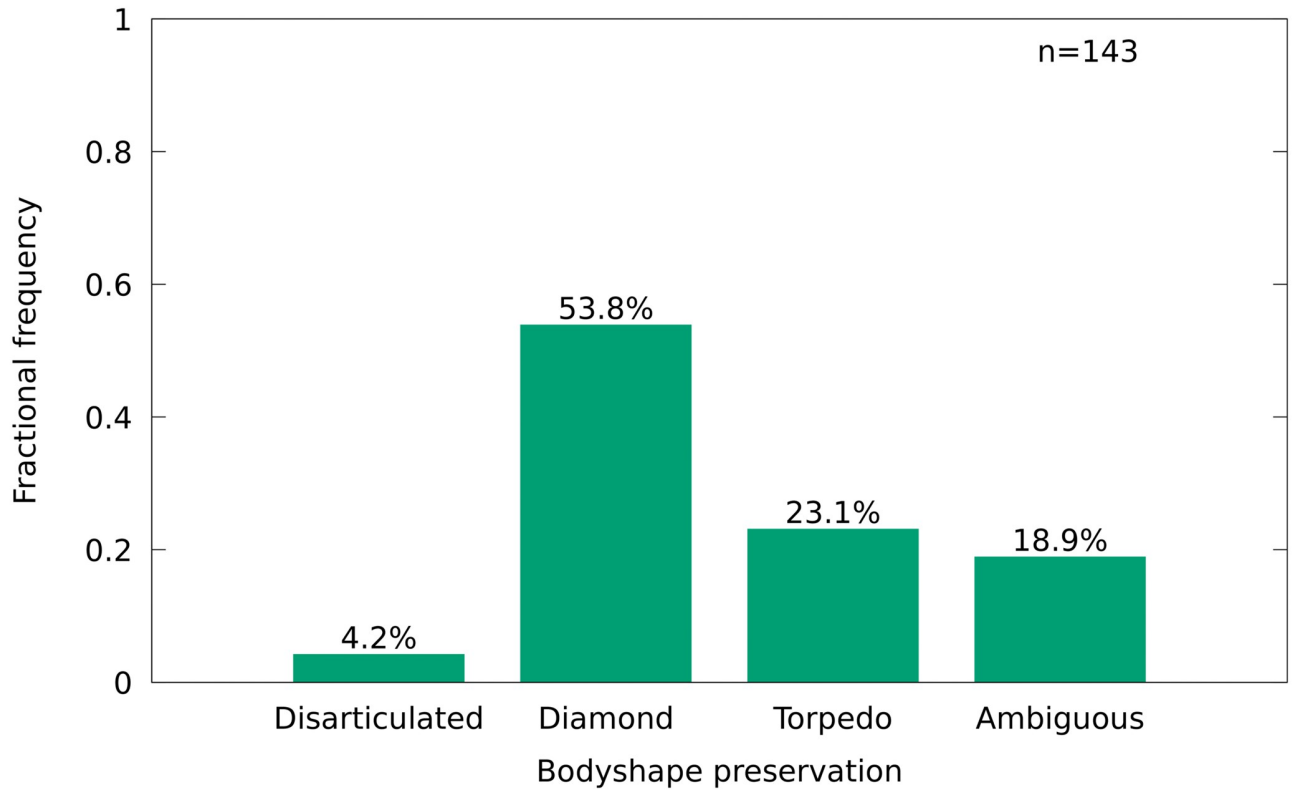

Fig 5. Diamond-shaped, torpedo-shaped and disarticulated individuals of *T. formosa* in percentage.

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while the largest is 790 mm long. Small individuals below 50 mm are not present, most likely as a result of diagenetic destruction or lack of preservation. A similar preservational bias has been described for *N. gutturosum* and *G. roberti* from Vallecillo lacking individuals smaller than 50 mm [18, 19]. A unimodal size distribution is illustrated in Fig 6 by an abundance peak of individuals between 500 to 600 mm length. According to these data, the former Vallecillo ocean was therefore predominantly populated by individuals ranging from 400 to 650 mm length, which are here interpreted as adults. Juvenile individuals ranging from 150 to 400 mm length are less abundant. Specimens ranging from 50–150 mm, 250–400 and 650 to 800 mm length are rare.

Regarding the two types of body shape, small individuals ranging from 150 to 250 mm length are frequently torpedo-shaped, whereas adult specimens of 450 to 600 mm length are majorly diamond-shaped. Nonetheless, both diamond or torpedo shaped specimens are identified in juveniles and adult individuals in the present material (Fig 6). Ambiguous individuals are majorly identified in the range of 500 to 600 mm length.

3.3 Taphonomy and preservation

3.3.1 Gut content. Gut content is preserved as compact recrystallized mass without identifiable matter, similar to the situation identified in *Goulmimichthys roberti* from Vallecillo [18]. This amorphous mass is often elliptical in outline, allowing for a distinction of the cloacal canal between the pelvic and anal fins. Nonetheless, stomach content is rare (20.2%) and a majority of specimens (79.0%) lacks intestinal remains.

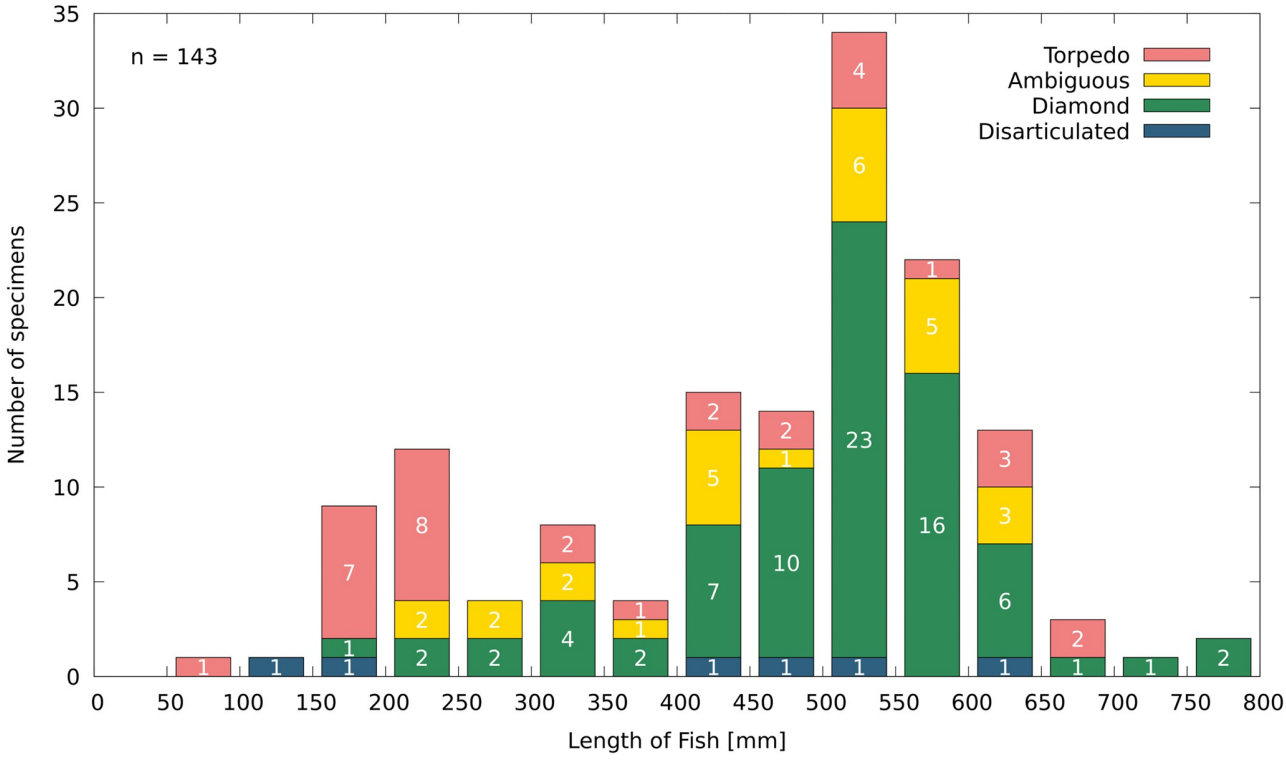

Fig 6. Size range distribution of 143 individuals of *T. formosa* from Vallecillo correlated to both body shape types. Torpedo-shaped individuals are marked in red and diamond-shaped specimens in green. Disarticulated individuals are presented in blue and ambiguous individuals in yellow.

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3.3.2 Scales and color. Scales are rhombic in shape and preserved as shadow imprints in three *T. formosa* specimens from Vallecillo (Fig 7A). One specimen interpreted as

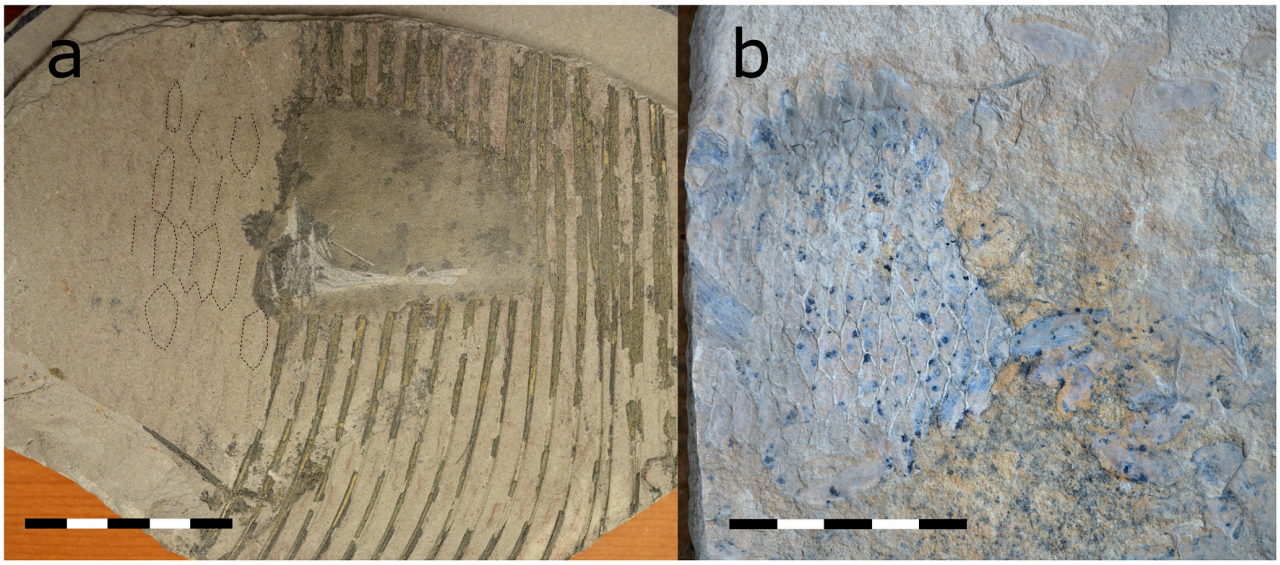

Fig 7. Scales of *T. formosa* from Vallecillo (CPC-2824) (A) in comparison to *Dixonanogmius* sp. from San Carlos (CPC-2836) (B). All scales 50 mm.

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Dixonanogmius sp. from the San Carlos locality (Cenomanian) in northern Coahuila shows a similar shape of scales as identified here in *Tselfatia formosa* from Vallecillo (Fig 7B). Horizontal color patterns forming stripes as described by Giersch [9] were not observed in the present material of *T. formosa*.

3.3.3 Completeness and articulation. All specimens of *T. formosa* presented here are laterally preserved. Most individuals are nearly complete (55.0%) or complete (27.9%) (Fig 8A), while 15.0% are partially complete. Only 1.4% of the individuals are mostly incomplete and 0.7% are incomplete.

The majority of the individuals are nearly articulated (41.4%) and 33.6% are articulated (Fig 8B), while 15.0% are partially articulated and 7.9% classified as mostly disarticulated. 2.1% of the specimens are disarticulated. Individuals are therefore mostly complete rather than articulated, and generally well preserved (disarticulation and incompleteness is rare). Even though, it needs to be emphasized that the collection analyzed here is biased, as mainly well preserved specimens have been collected for exhibition purposes.

3.3.4 Fin preservation. The dorsal fin of *T. formosa* is frequently preserved in a middle spread position (36.2%). A fully spread position of the dorsal fin is visible in 28.2%. In 24.8% of the specimens the dorsal fin was disarticulated and a minority of 10.7% lack any fin spreading (Fig 9A).

The anal fin is mostly spread in a middle position (43.0%). 27.5% possessed a disarticulated anal fin and 22.1% lacked fin spreading. Only 7.4% showed a full erection of the anal fin (Fig 9B). In conclusion, the dorsal fin is more frequently erected in the present material than the anal fin.

Pectoral fins are preserved in 47.0% of the specimens, but a majority of 51.0% lacks pectoral fins. In only 2.0% of the individuals the pectoral fin is disarticulated (Fig 9C).

In the majority of individuals the pelvic fins are not identified (59.7%). In 29.5% of the specimens the pelvic fins are preserved but 10.7% possess disarticulated pelvic fins (Fig 9D). Pectoral fins are better preserved than pelvic fins. It has not been possible to calculate the percentage of pectoral and pelvic fin spreading due to bad preservation.

3.3.5 Preservation of the vertebral column. The vertebral column is mostly straight, different to the frequent curvature identified in specimens of *Goulmimichthys roberti* from Vallecillo [18]. In 48.3% of the individuals the vertebral column is unbroken. In 20.3% the column

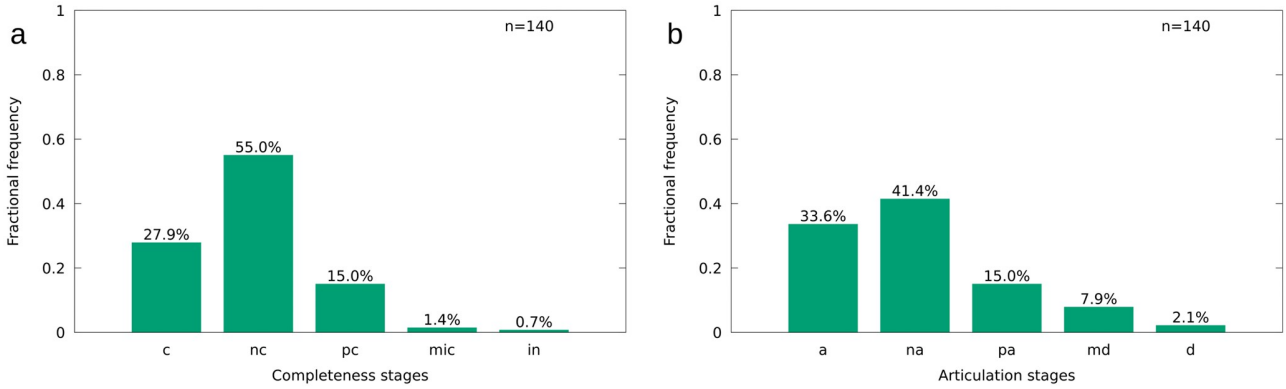

Fig 8. Completeness (A) and articulation (B) of *T. formosa* from Vallecillo in percent of the total number of individuals. Completeness stages differentiated here (Fig. 8A) include complete (c), nearly complete (nc), partially complete (pc), mostly incomplete (mic) and incomplete (in) specimens. Articulation stages differentiated (Fig. 8B) include articulated (a), nearly articulated (na), partially articulated (pa), mostly disarticulated (md) and disarticulated (d) individuals.

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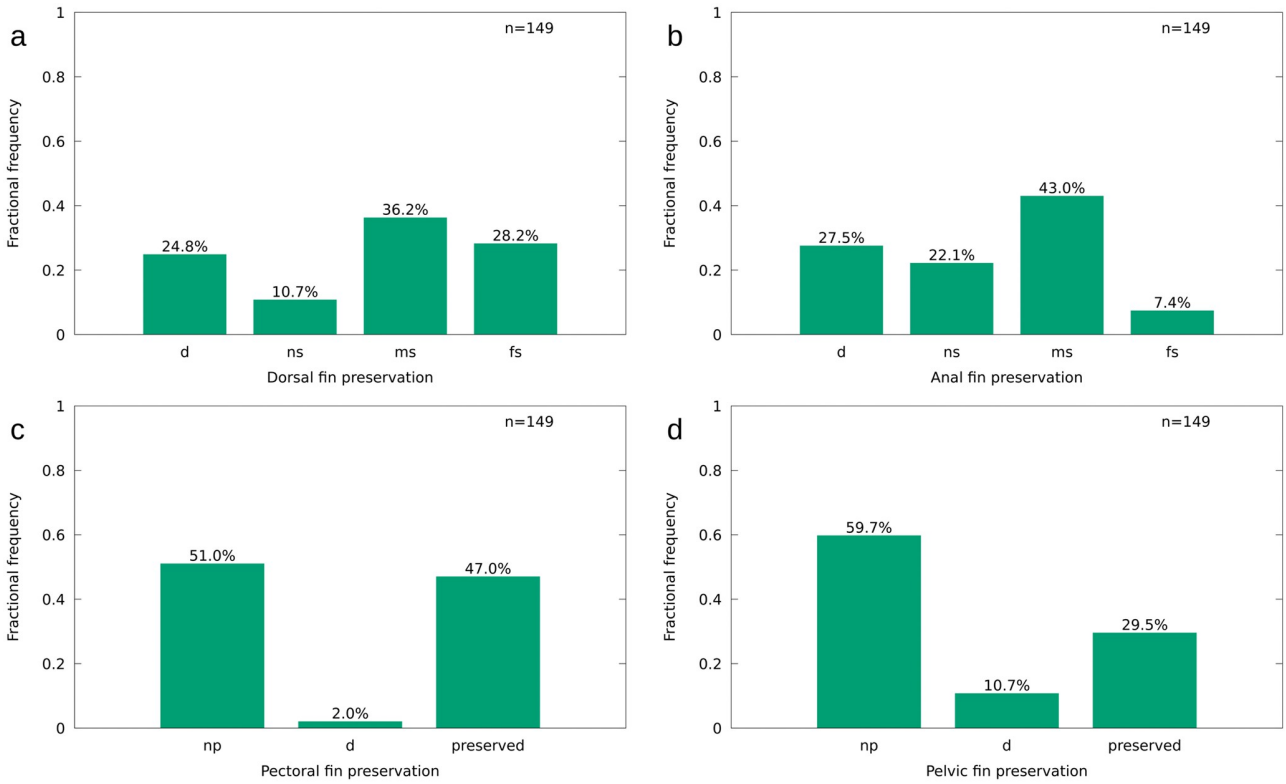

Fig 9. Preservation of the dorsal (A), anal (B), pectoral (C) and pelvic fins (D) of *T. formosa*, in percent of the total number of individuals. Disarticulated (d), not spread (ns), mostly spread (ms), fully spread (fs), not preserved (np) and preserved.

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is broken in the posterior region and in 16.78% in the anterior region, while 7.7% show fractures in both regions. In 7.0% of the specimens the vertebral column is disarticulated (Fig 10).

A break of the vertebral column is therefore identified in about 50% of the specimens but it is not particularly frequent in specific positions of the column. This differs from *G. roberti* from Vallecillo where breakage of the column was abundant in the tail region [18].

3.3.6 Reconstruction of the dorsal and anal fins. The major fin ray of both the anal and dorsal fin is exceedingly long, reaching the base of the caudal fin when retracted. The dorsal and anal fin rays of *T. formosa* are therefore much longer than described by Taverne [7] and Giersch [9]. To obtain a new reconstruction of both fins, we drew the contour of majorly complete fossils (Fig 11A and 11C) and rotated each fin ray at the basis to obtain a vertical erection of the fin (Fig 11B and 11D). This allows for a reconstruction of the original dimension of the dorsal and anal fins, which coincides with incomplete specimens of *T. formosa* (Fig 11E).

4 Discussion

4.1 Size range

The abundant material of *Tselfatia formosa* from Vallecillo ranges from 50 to 800 mm length. A unimodal distribution is identified similar to that found for *G. roberti* [18] from the locality. However, in contrast to *G. roberti* the highest abundance is here registered for individuals ranging between 500 and 600 mm length (Fig 6). These adult individuals, with total lengths of 400 to 650 mm, are notably more abundant than juvenile specimens ranging between 150 to

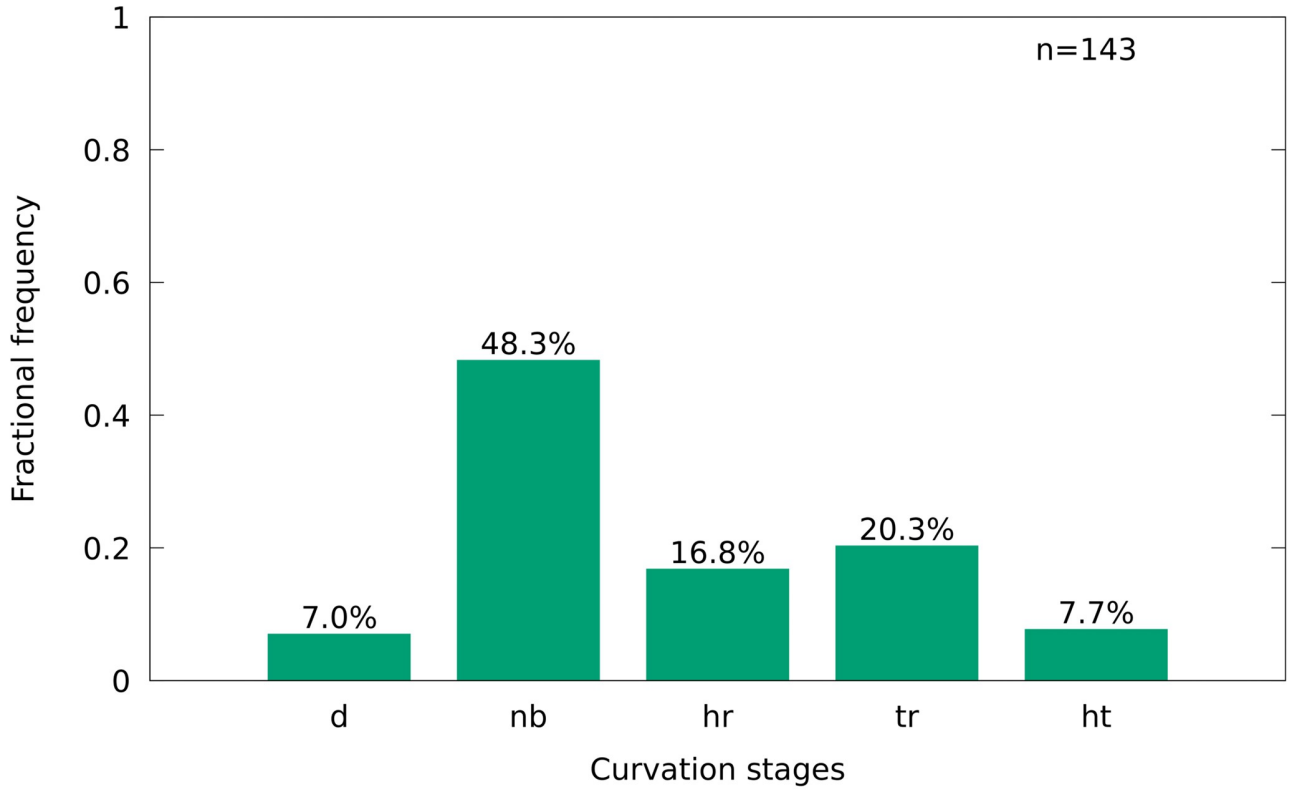

Fig 10. Preservation of the vertebral column in *T. formosa*, in percent of the total number. Disarticulated (d), no break (nb), break in head region (hr), break in tail region (tr), break in head and tail region (ht).

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350 mm length. Specimens ranging from 50 to 150 mm, 250 to 300, 350 to 400 and 650 to 800 mm length, are underrepresented. The specimens presented here (n = 143) significantly extend both, the number of individuals of *T. formosa* recorded to date from Vallecillo and their size range (e.g. [6, 9, 20, 21]). Individuals recorded by Blanco [6] range from 160 to 610 mm length. Smaller and bigger-sized individuals were recorded by Ifrim [20] and Giersch [9]. Both authors presented a unimodal size range based on small specimen numbers. In general the size range presented here coincides with data presented by these latter authors, except for specimens between 180 and 280 mm length missing in the size range of Ifrim [20]. The material presented here is based on museum collections and was not collected randomly. The size range is nevertheless similar to that presented by Ifrim [20] which is based on randomly collected material. We therefore consider our results as unbiased. The total set of data indicates that the former Vallecillo ocean was majorly inhabited by adult individuals (>400 mm length). The abundance of big-sized specimens can also be interpreted to indicate high adult mortality. Seasonal migration of small specimens, as seen in *N. gutturosum* from Vallecillo [19], appears unlikely for *T. formosa*, due to the low number of small-sized individuals here interpreted as juveniles. These did apparently not persist in the Vallecillo region, which represents an open marine environment with water depths of about 200m [20, 22]. Rather, these juveniles may have populated shallow areas near the coast, although to date there is no positive evidence for this hypothesis. Future findings of small *T. formosa* in northern Coahuila (e.g. north of Múzquiz) could clarify this interpretation, as this region was placed in more shallow environments.

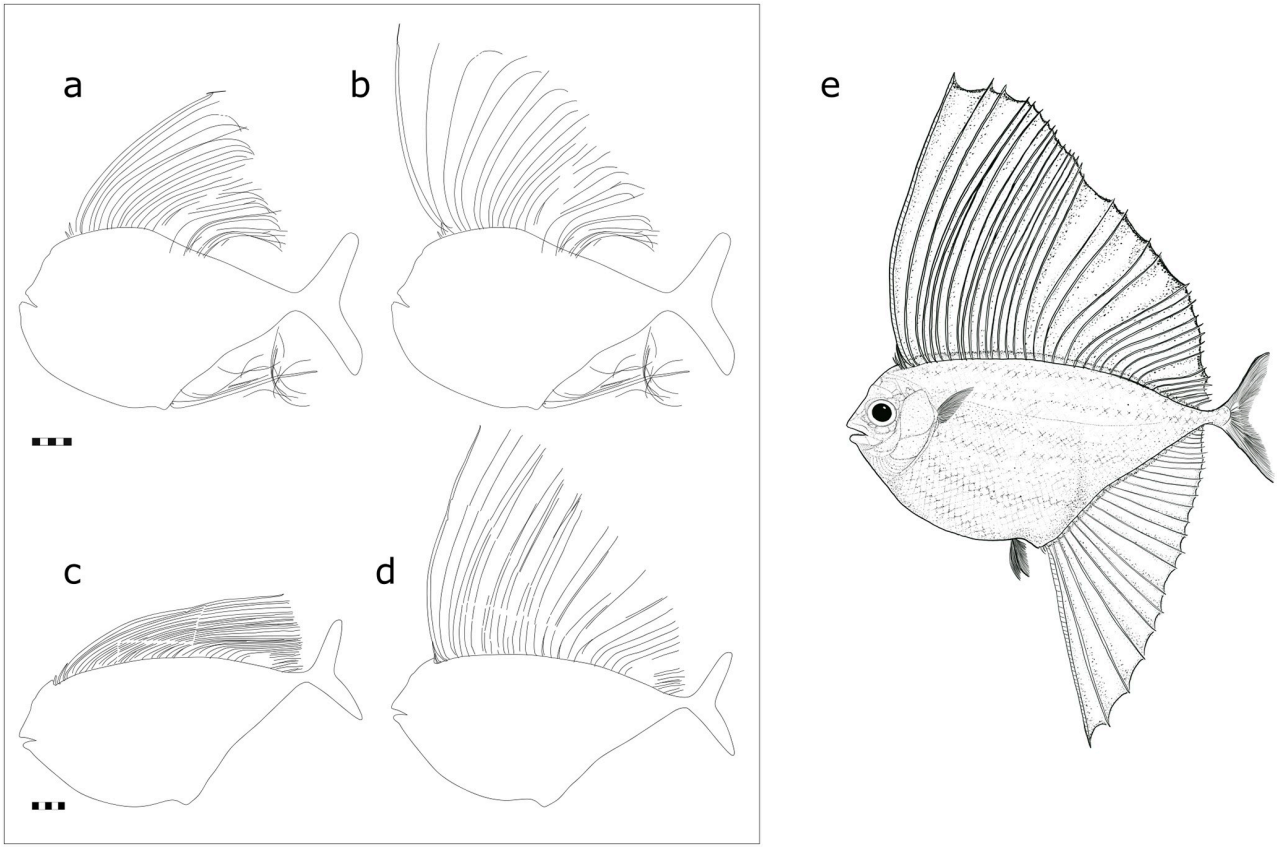

Fig 11. Reconstruction of the dorsal fin of *T. formosa*. Fossil outline as identified in CPC-2839 and CPC-2948; REG2544 PF48 with semi-erected dorsal fin (A and C) in comparison to its modification (B and D) with erected dorsal fin. Schematic reconstruction of the dorsal and anal fin including a membrane between the fin rays (E) and scale color as suggested by Giersch (2014). Both scales 50 mm.

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4.2 Body shape and sex

A torpedo-shaped and a diamond-shaped body type are here identified for *T. formosa* (Fig 4). There are no other osteological differences between the two forms, which are identified in both small and large-sized individuals (Fig 6). Torpedo shaped individuals show a length to width body ratio of 3:1, whereas in diamond shaped individuals the ratio is 2:1. Diamond-shaped individuals are more frequent in the length range of 500 to 600 mm, while torpedo-shaped specimens are abundant in smaller-sized individuals, ranging from 150 to 300 mm length (Fig 6). No study is known to us documenting these distinctly different body outlines in *T. formosa*, but an increase of body depth relative to the standard length was proposed by Patterson [8] to occur during the ontogeny of *Tselfatia*. For *T. dalmatica*, nevertheless, Maisch and Lehmann [5] argued that the differences in body proportions cannot be explained as an ontogenetic variation. Unfortunately, the authors provide no explanation for this conclusion nor do they discuss this in detail. However, if changes in body shapes were present during the ontogeny of *T. formosa*, one would expect a certain shape to be correlated to a certain size. Juvenile *Tselfatia* would then display a torpedo-like body shape during early ontogeny, changing into a diamond-like form when the adult stage is reached, or vice versa. Clearly, this is not the case in the Vallecillo material, as both torpedo- and diamond-shaped animals are represented by juvenile and adult specimens (Fig 3A). We therefore propose that the two body

shape types rather represent sexual dimorphism, as previously identified in *N. gutturosum* from Vallecillo [19]. Such differences in male and female appearance are scarce in the fossil record but well studied in extant fishes [23–29]. Sexual shape dimorphism (SSD) can reflect e.g. locomotion, foraging, mating behavior or habitat requirements [30–32]. A slender shape is frequently correlated to habitats in which greater swimming activities are needed [33], consequently leading to shape differences depending on the complexity of the habitat. Differing body shapes of *T. formosa* could therefore be the result of different habitat preferences within the water column of Vallecillo. *T. formosa* living in higher energetic upper stages of the water column could then display a more slender body shape, while individuals populating the low energy deeper water developed a diamond-shaped form. Nevertheless, this interpretation is opposed by the absence of preservational differences between diamond- and torpedo-shaped individuals, as articulation and completeness are similar in both groups. In animals populating shallow depths of the ocean, disarticulation of carcasses is a common taphonomic feature as these individuals are exposed to extended decay during drifting and floating [34]. Animals which lived in deeper zones of the water column or at the sea floor are, on the other hand, often preserved complete and articulated. Therefore, no water column preferences (agitated and quiet water conditions) are associated to one or the other body shape and both types must have populated deep water levels. Furthermore it has been suggested that fishes with deep bodies generally associate with complex environments requiring for high maneuverability [33, 27]. This is arguably not the case for diamond-shaped *T. formosa*, which shared the same open marine environment populated by torpedo-shaped individuals. More likely, the differing body outlines may relate to foraging or reproductive reasons. An increase of the abdominal cavity is required in fishes for the accommodation of female reproductive organs; it is then associated with higher fecundity [27, 31, 35]. This adaptation may be present in diamond shaped individuals to maximize reproductive success and improve larval survival. The strategy has been documented for extant Carangidae, e.g. *Decapterus macrosoma* [36]. Females of *D. macrosoma* exhibit a deeper body depth, broader belly, bigger head and wider caudal fins than males of this species, which are narrow-bodied with smaller heads and wider dorsal and caudal fins [36]. Females store energy to facilitate the production of offspring, while males present adaptations to succeed in male to male competition [31, 36]. Furthermore, females of *D. macrosoma* exhibit bigger heads to maximize buccal volume and suction velocity. This is needed to acquire additional food to produce the eggs [36]. This latter adaptation is not identified in *T. formosa* due to insufficient skull preservation but nevertheless, gut contents are majorly seen in diamond-shaped individuals. This observation favors the assumption that stomach content is more common in diamond-shaped individuals, as these potential females needed to swallow additional quantities of food, which is therefore preserved more often. Based on these observations we tentatively interpret diamond-shaped individuals as females and more slender specimens as males.

Ambiguous specimens are not interpreted as a transitional form between diamond and torpedo-shaped individuals. A shift from one shape to the other caused by e.g. ontogenetic variation is here excluded. Ambiguous individuals are rather interpreted as a variation within *T. formosa*. These individuals are not precisely assigned to either the diamond or the torpedo form.

4.3 Taphonomy

T. formosa from Vallecillo is frequently well articulated and complete (Fig 8A and 8B). Dorsal and anal fins are often better preserved than the pectoral and pelvic fins. The dorsal fin is majorly erected in a middle-spread position (36.2%), or fully spread (28.2%), whereas the anal

fin is majorly middle-spread (43.0%) or disarticulated (27.5%). The vertebral column is frequently articulated and breakage is rare (48.3% without break), without an indication of substantial weakness at the tail (posterior) or head (anterior) region. The mouth is frequently disarticulated (46.3%), but 47.0% of the specimens are documented with an open mouth (Fig 12). *T. formosa* is therefore regularly seen with spread fins and an open mouth, similar to *G. roberti* from Vallecillo [18].

Due to the abundance of well-articulated and complete individuals we propose that no transport or flotation phase of the carcasses existed and that arrival on the sea bottom was rapid. Fishes were rapidly buried, thereby preventing substantial decay. Even in the few disarticulated individuals, displaced bones generally remained close to the main body and did not drift away (Fig 13). Fin rays usually split in two halves resulting in two major fin rays lying next to each other. In highly disarticulated specimens the pseudo-fulcra of the major fin ray split into small parts similar to box knife blades. Disarticulation caused by scavengers is not documented from Vallecillo, and bone dispersal by currents is extremely rare. The excellent preservation of *T. formosa* thus points to a lifestyle in deeper water zones of the former Vallecillo ocean. This interpretation agrees with assumptions by Ifrim [20] and Diedrich [37], the latter associating medium sized *T. formosa* with cold water fish.

4.4 Function of the dorsal and anal fin

Giersch [9] and Taverne [38] suggested that *T. formosa* was able to fold back the dorsal and anal fin into a sulcus or groove. We agree with this interpretation. The strategy is comparable

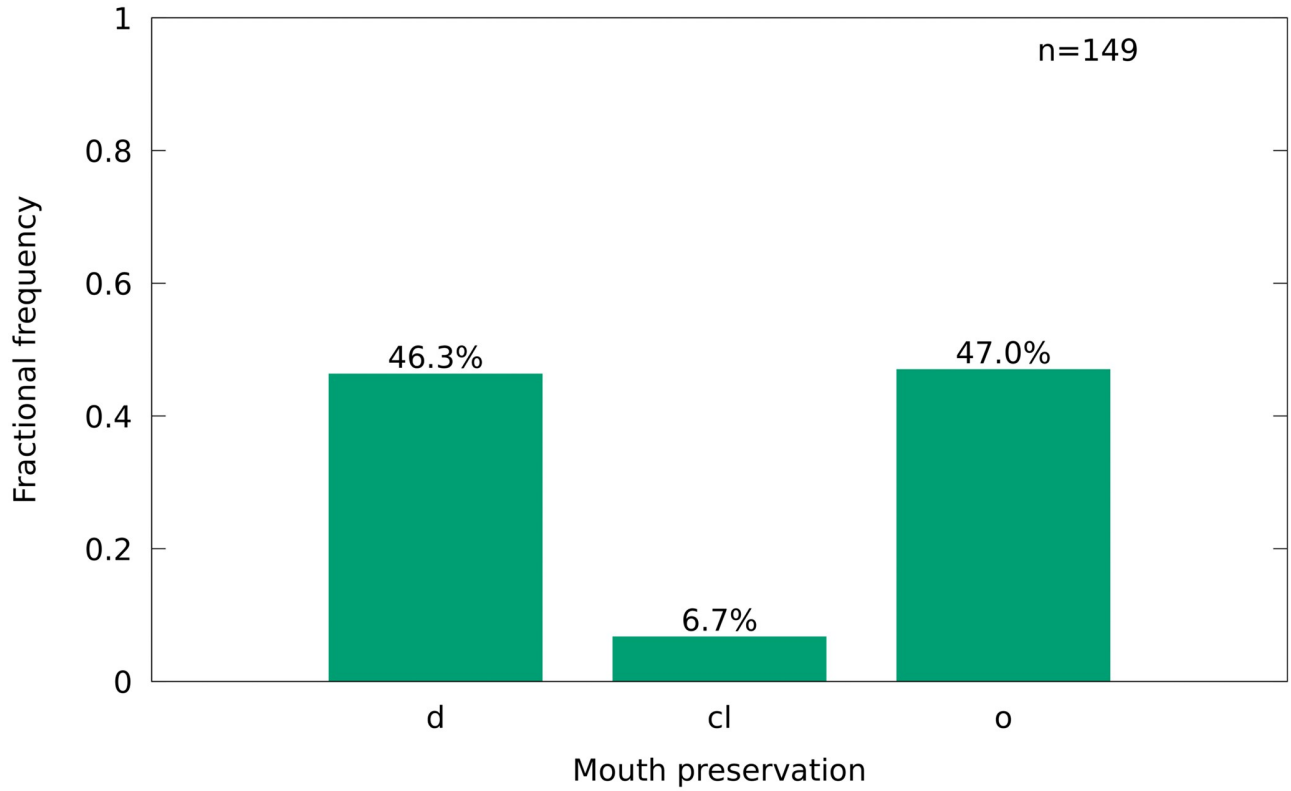

Fig 12. Mouth preservation of *T. formosa*, in percent of the total number. Disarticulated (d), closed (cl) and open (o).

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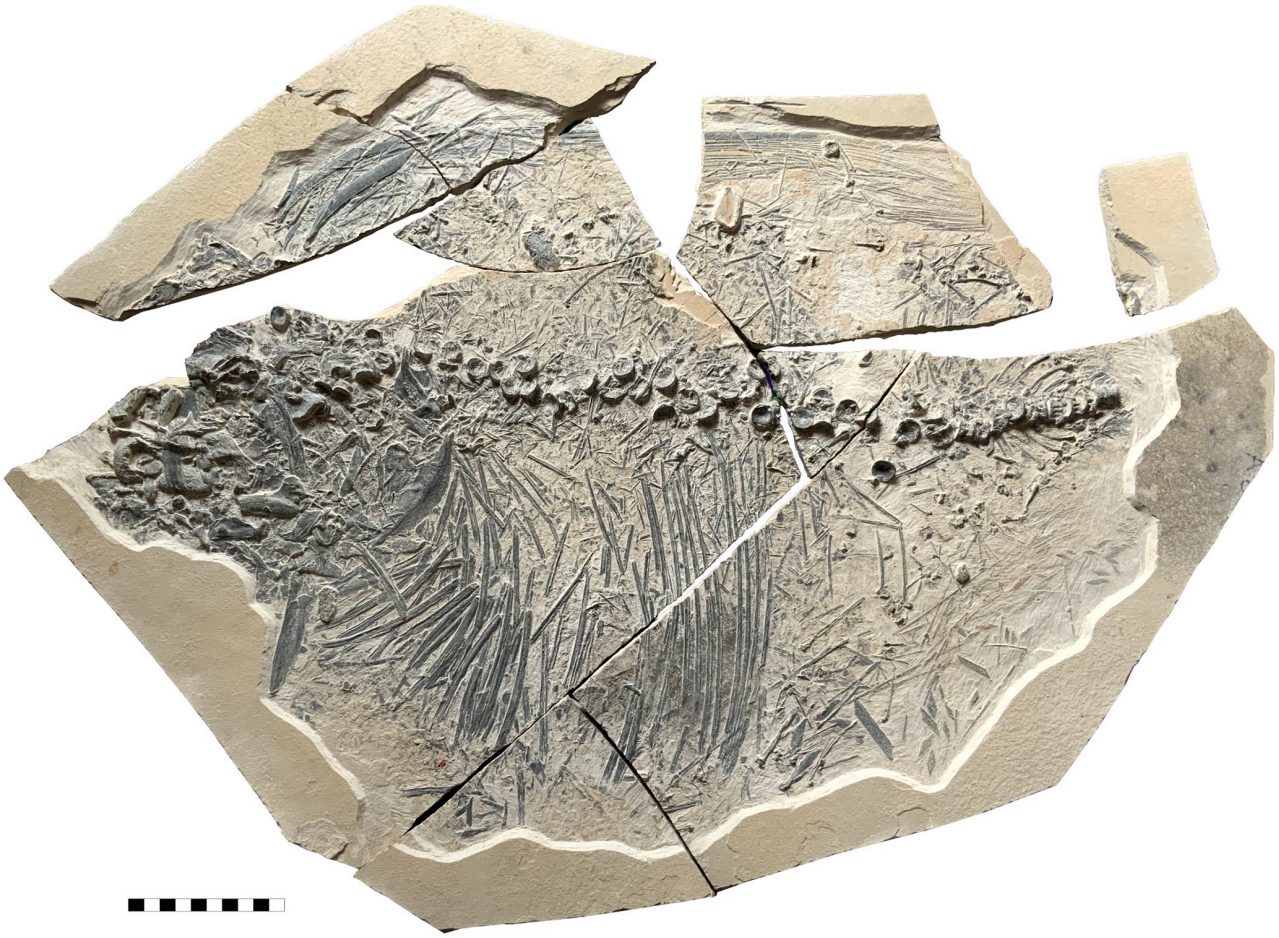

Fig 13. Disarticulated *T. formosa* (CPC-2833). The carcass disintegrated on the seafloor without bone dispersal caused by scavengers or currents. A phase of flotation is excluded. Scale 100 mm.

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with that of modern fan fishes which retract the anal and dorsal fins behind modified scales at the base of the medial fins [39]. The sulcus of *T. formosa* is here built by lateral plates in which the fin can be retracted (Fig 14A and 14B). The middle segment sits between the pterygiophore and lepidotrichia, as already described by Giersch [9]. Each lepidotrichia sits on top of the middle segment, thus allowing for the retraction of the fin (Fig 14C). These lateral plates are here documented as skin shadow at the base of the rays (Fig 15A and 15B). The body shape therefore appears slightly expanded, similar to that in extant fan fishes.

Giersch argued that a fan of the dorsal and anal fin, such as seen in modern swordfishes, would be functionally problematic in *T. formosa* due to overlapping fin rays. Folded skin between individual lepidotrichia would then hamper the retraction of the unpaired fins and even make this movement impossible. However, specimens with retracted dorsal and anal fins present no evidence of damage of the fin rays (Fig 15C). Lepidotrichia do not overlap each other but remain parallel arranged (Fig 15D). The documented preservation of the unpaired fins therefore supports our assumption of a membrane between the fin rays. These show a consistent arrangement, even in disarticulated specimens. The fin rays thus behave in a connected way, similar to a fan. Delicate fin rays, as present in *T. formosa*, would easily have lost stability

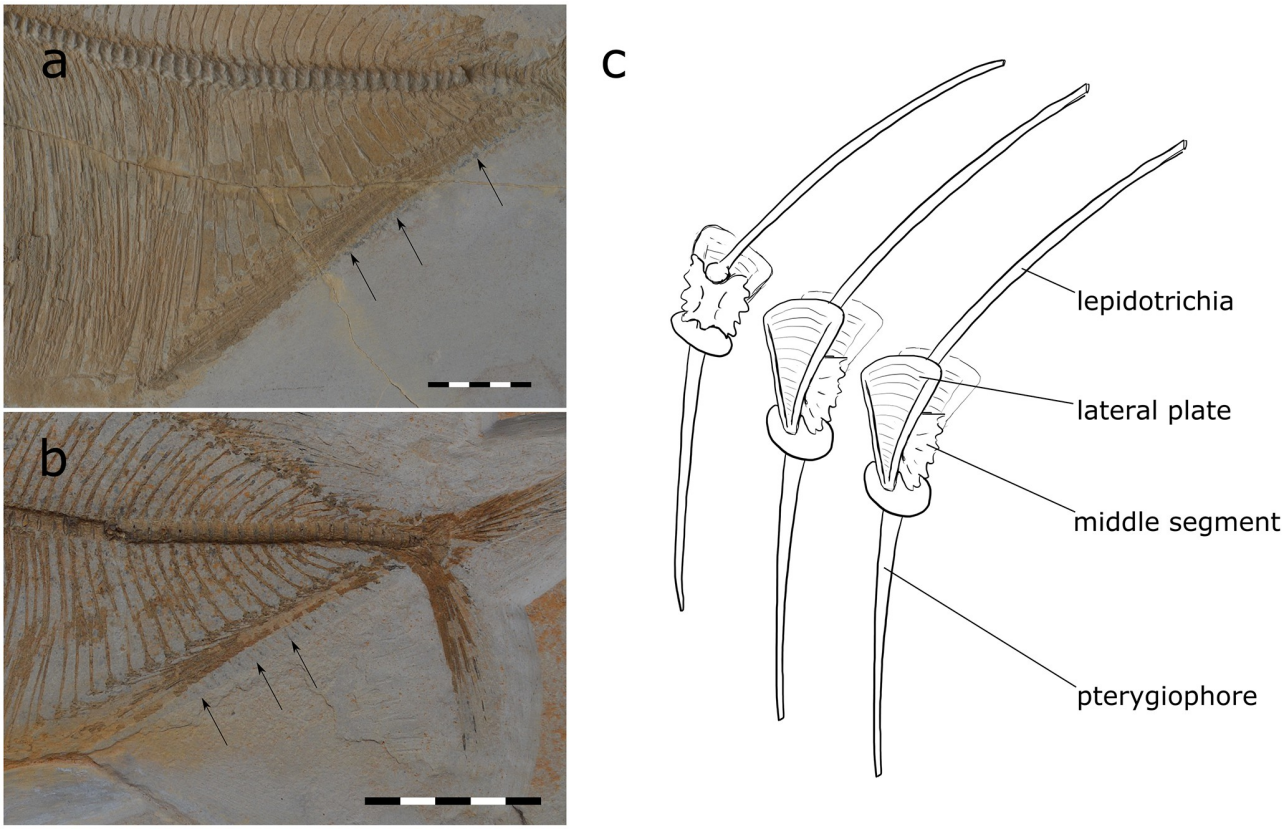

Fig 14. Retraction of the unpaired fins of *T. formosa* behind lateral plates (A and B) (CPC-2856 and CPC-2885). Reconstruction of the skeletal elements found in the unpaired fins (C). All scales 50 mm.

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without a skin behaving as a stabilizer. Regarding the massive fin size the fin rays would easily detach, break, or would disintegrate in a chaotic way. Rays would then spread into different directions overlapping each other, which is not the case in the fossil specimens described here. On the contrary, it rather appears that fins were connected, bending collectively into one direction (e.g. as if exposed to a current) (Fig 15E and 15F). This leads us to the interpretation that the membrane was still intact. Furthermore, the impressive size of the dorsal and anal fins is not an argument to us to exclude a membrane, as extant fan fishes possess fins comparable to *T. formosa* [40–42]. We therefore suggest a similar retraction of the unpaired fins as seen in modern fan fishes which possess a membrane between the lepidotrichia.

Extant fan fishes (*Pteraclis* and *Pterycombus*) use their extremely large fins to avoid predators and to catch prey [39]. They have adapted methods to swim with high speed when retracting the fins and to improve their maneuverability by erecting them [39]. Considering the similarities of the huge dorsal and anal fin and the body shape of *T. formosa* we assume a similar strategy. Active hunting of prey thus seems likely in *T. formosa* based on its body outline.

5. Conclusion

A review of 149 individuals of *Tselfatia formosa* from the Lower to Middle Turonian platy limestone deposit of Vallecillo, northeastern Mexico, reveals the presence of two different body shape types which are interpreted to represent sexual shape dimorphism (SSD). Both

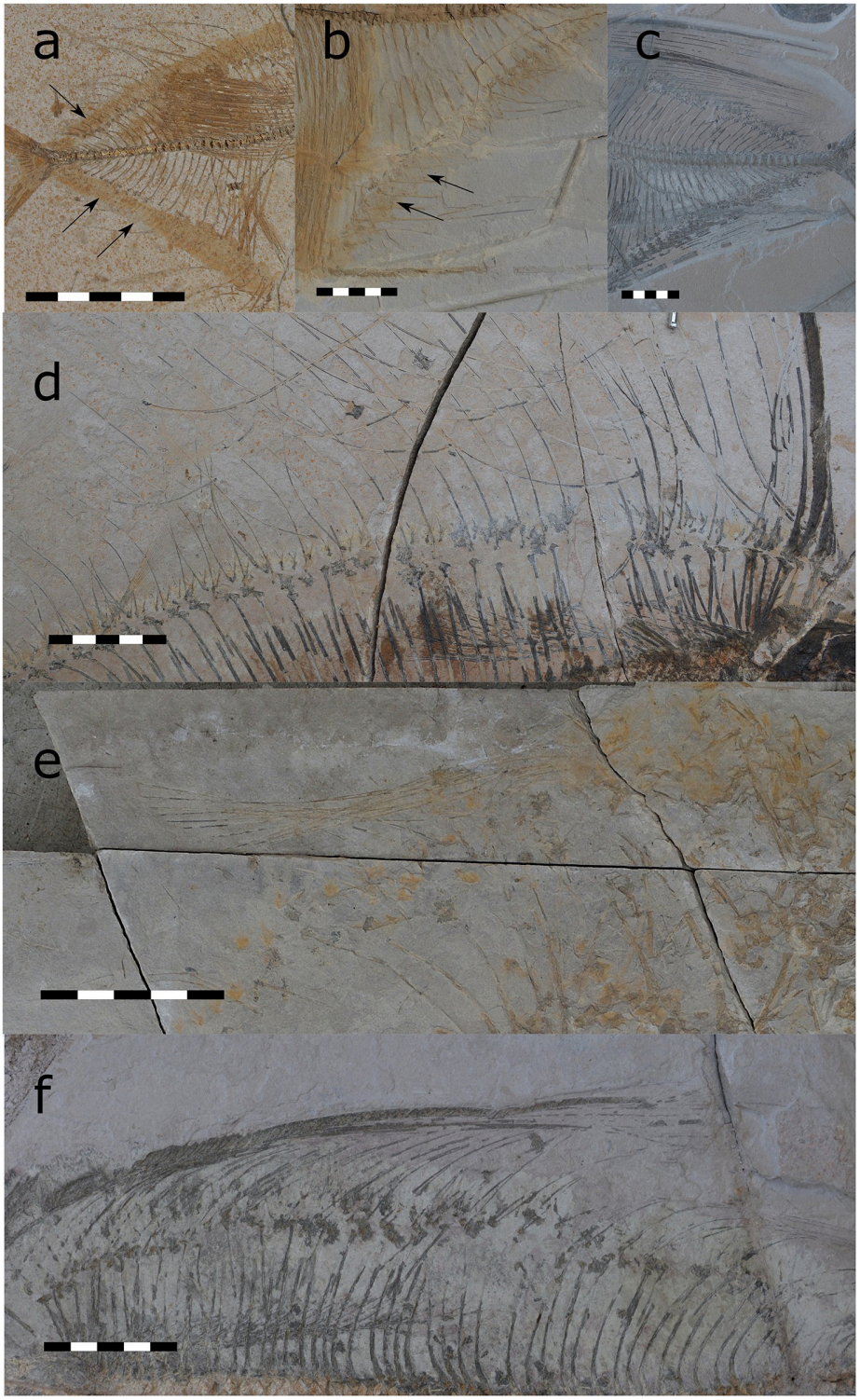

Fig 15. Preservation of the unpaired fins in *T. formosa*. A skin shadow (CPC-2832 and CPC-2883) (A and B) illustrates the sulcus to retract the dorsal and anal fin. Retracted dorsal fin without overlapping fin rays (CPC-2865) (C). Parallel arrangement of the dorsal fin rays (CPC-2960; REG2544 PF220) (D). Collective reaction of the fin rays similar to a fan indicating an intact membrane between the lepidotrichia (CPC-2902 and CPC-2871) (E and F). All scales 50 mm.

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types are present in small sized individuals interpreted as young and big sized specimens interpreted as adults. The unimodal size distribution of *T. formosa* illustrates one abundant peak between 500 and 600 mm length and a dominance of large and diamond-shaped individuals in the Vallecillo area. Diamond-shaped individuals are interpreted as deeply keeled females; they are twice as long as high compared to torpedo-shaped individuals interpreted as males with a length to width ratio of 3:1, thus being three times longer than wide. The abundance of well-articulated and complete specimens favors the rapid burial of carcasses, without an interference of scavengers and also excluding a phase of carcass flotation. The impressive dorsal and anal fins of *Tselfatia formosa* allow for comparison with modern fan fishes and a reconstruction of these fins with a membrane between each lepidotrichia. We therefore suggest that *T. formosa* inhabited a deep water environment and that its lifestyle resembled that of extant fan fishes.

Supporting information

S1 File.
(PDF)

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