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SHORT COMMUNICATION

FIRST FOSSIL RECORD (MIDDLE MIOCENE) OF THE VIPER SHARK *TRIGONOGNATHUS* MOCHIZUKI AND OHE, 1990, IN THE MEDITERRANEAN REALM

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The genus *Trigonognathus* Mochizuki and Ohe, 1990, is a monospecific taxon of 'lantern sharks' (i.e., family Etmopteridae), a group of small-sized bioluminescent deep-sea chondrichthyans, ranging in mature male specimens between 42–47 cm total length, and at least 52 cm for females (Ebert et al., 2021). This shark inhabits the upper continental slopes as well as the uppermost slope of seamounts, often at the bottom, at depths ranging between 250–1000 m, but has been caught at 150 m and 270 m in deep open waters (Mochizuki and Ohe, 1990; Compagno et al., 2005; Ebert et al., 2021). Only two species have been described thus far, the extant species *Trigonognathus kabeyai* Mochizuki and Ohe, 1990, and the extinct †*Trigonognathus virginiae* from the middle Eocene of France (Cappetta and Adnet, 2001). *Trigonognathus kabeyai* exhibits a combination of morphological characteristics that are unique among Squaliformes, like a highly protrudable jaw articulation (Shirai and Okamura, 1992; Straube et al., 2010), and a lack of dignathic heterodonty. Additionally, the tearing-type dentition, and strong monognathic heterodonty with hypertrophied anterior teeth, differentiate it from the genus *Squalus* and *Cirrigaleus* (with cutting-type dentition), and *Centroscyllium* and *Aculeola* (with no monognathic heterodonty and clutching-type dentition) (Cappetta and Adnet, 2001). The geographic distribution of *T. kabeyai* is restricted to the Pacific Ocean, in the Wakayama and Tokushima coasts of Japan (Mochizuki and Ohe, 1990; Shirai and Okamura, 1992; Ebert et al., 2021), Taiwan (Ebert et al., 2013), and in the north-west of Hawaii (Wetherbee and Kajiura, 2000). However, the fossil record of the genus *Trigonognathus* indicates a broader geographic distribution in the past (Aguilera and Rodriguez de Aguilera, 2001; Cappetta and Adnet, 2001; Carrillo-Briceño et al., 2015). These findings include †*T. virginiae* from the middle Eocene of Landes (eastern Atlantic), south-western France (Cappetta and Adnet, 2001), and two isolated teeth assigned to *Trigonognathus* sp. and *Trigonognathus* aff. *kabeyai* from the Upper Miocene of Panama (Carrillo-Briceño et al., 2015) and the Upper Miocene–Lower Pliocene of

Venezuela (Caribbean Sea) (Aguilera and Rodriguez de Aguilera, 2001), respectively.

Given the apparent rarity of this elusive taxon, any new finding, especially in the fossil record, is of note and increases our knowledge of this genus. Herein we describe a Middle Miocene locality with the first known record of *Trigonognathus* in the Mediterranean realm (south-eastern Spain), which offers new insight into the paleoenvironmental and paleobiogeographic history of this shark. In addition, with the objective of providing new information about possible diagnostic characteristics of the genus, the first description of its internal tooth histology is provided.

MATERIALS AND METHODS

A total of 77 isolated teeth from the El Ferriol outcrop have been assigned to *Trigonognathus* sp. The area of study, locally known for more than 30 years, has historically been the source of numerous elasmobranch and osteichthyan remains recovered by fossil collectors (Marín, 1992; Mendiola, 1996), but a systematic and rigorous study of the locality has not been undertaken.

The outcrop occurs at the outskirts of an old quarry (38.320070°N, 0.687791°W) that is located approximately 3 km north from the small locality of Bonavista (Alicante, Spain) (Fig. 1). The fossils are of Serravallian age (Middle Miocene) based on the presence of the foraminifer *Globoturborotalita occlusa* (Blow and Banner, 1962). A 25 kg sample of a calcarenitic-marlstone bed (1 m thick) rich in glauconite was disaggregated with acetic acid (ca. 5–10%), and the resulting concentrate was hand-picked for microfossil remains. A selection of the best-preserved specimens was photographed (Fig. 2) using a Hitachi S4800 scanning electron microscope to facilitate our morphological description. The specimens discussed herein are housed at the Museu de la Universitat de València d'Història Natural (Valencia, Spain), with the acronym MGVU. The systematic classification follows Cappetta (2012). Anatomical and taxonomic identification was based on bibliographical review (Mochizuki and Ohe, 1990; Shirai and Okamura, 1992; Wetherbee and Kajiura, 2000; Aguilera and Rodriguez de Aguilera, 2001; Cappetta and Adnet, 2001; Yano et al., 2003; Cappetta, 2012; Carrillo-Briceño et al., 2015), and comparison to fossil

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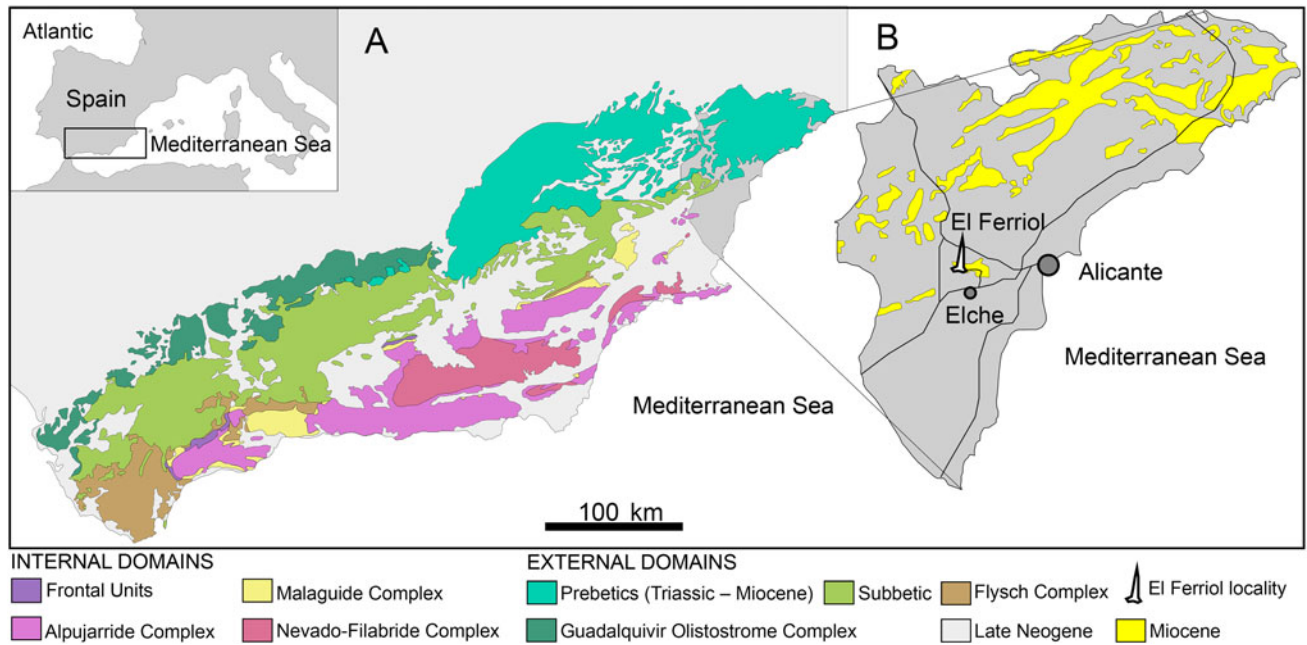


FIGURE 1. **A**, area of study in south-eastern Spain, highlighting the main geological divisions from the Betic Mountain Range, modified from Martínez-Pérez et al. (2018). **B**, location of the El Ferriol area of study (38.320070°N, 0.687791°W) in the Middle Miocene of the province of Alicante (SE Spain).

specimens from Panamá and Venezuela housed in the Palaeontological Institute and Museum at the University of Zurich, Switzerland (PIMUZ-A/I), and the Universidad Nacional Experimental Francisco de Miranda, Venezuela (UNEFM-PF), respectively.

In addition, the best-preserved specimen (Fig. 2H) was scanned using the Synchrotron Radiation X-Ray Tomographic Microscopy (SRXTM) at the X02DA TOMCAT detector of the Swiss Light Source from the Paul Scherrer Institute (Villigen, Switzerland), which allowed us to reconstruct and analyse its internal histology. The specimen was scanned using a 10× objective, with an exposure time of 250 ms at 21 KeV, acquiring 1501 equiangular projections over 180°. The data was subsequently processed via re-gridding procedure (Marone et al., 2010) based on the Fourier transform method, resulting in volumetric data with voxel dimensions of 0.65 μm. The reconstructed files were then processed with the computer tomography software Avizo Lite 9.1© to generate a three-dimensional model of the tooth and characterize internal vascular channels and histological structure.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
 Superorder SQUALOMORPHII Compagno, 1973
 Order SQUALIFORMES Goodrich, 1909
 Family ETMOPTERIDAE Fowler, 1934
 Genus *TRIGONOGNATHUS* Mochizuki and Ohe, 1990
TRIGONOGNATHUS sp.
 (Fig. 2)

Referred Material—77 isolated and fragmented teeth, of which 27 are assigned to anterior positions and 50 to anterolateral or lateral positions. Nine figured specimens (MGUV-39022, MGUV-39021; MGUV-39024 to MGUV-39030); non-figured specimens are held in several slides under the register numbers MGUV-39023, MGUV-39031, and MGUV-39032.

Description—*Trigonognathus* teeth from the El Ferriol outcrop are generally poorly preserved, with the majority of the specimens represented only by their crown, and only two specimens retain remnants of the root (see Fig. 2H, I). The teeth consist of a monocuspidate crown that is rather symmetrical and very elongated, ranging between 5 and 6 mm in height, but strongly bent lingually (Cappetta, 2012), and showing in the most anterior positions a characteristic sigmoid curvature in profile view (e.g., Fig. 2C, D, F, J). Both the labial and lingual faces are transversally convex. The lingual face bears at least five or six robust ridges on the lower half of the tooth, although on some specimens can extend up to two-thirds of the tooth height. *Trigonognathus* exhibits monognathic heterodonty, with symphyseal and anterior teeth characterized by an elongated and clearly sigmoidal crown (Fig. 2J). This contrasts with shorter and wider teeth with weaker sigmoidal curvature in the lateral and posterior positions (Fig. 2F, G, H).

Of the only two teeth retaining part of the root (see Fig. 2H, I), only the medial section is present. This area has a clear and defined row of foramina that are aligned along the upper portion of the root, close to the crown-root junction, and extending all around the tooth base. In addition, a well-defined median labial foramen occurs on its basal face.

The tomographic analysis of the tooth shown in Fig. 2 (J–L) allowed the first characterization of tooth vascularization and histology. The analysis shows that the teeth we assigned to *Trigonognathus* sp. are characterized by an internal distribution of orthodontine and osteodontine that can be attributed to an orthodont histotype. The internal structure shows that the inner portion of the crown consists of orthodontine that fills the pulp cavity, whereas osteodontine is distributed all along the interior region of the root, which contains a complex network of vascular channels that merge as they extend towards the upper portion of the crown (Fig. 2K). The external vascularization of the preserved roots can be classified as anaulacorhize (Casier, 1947; Cappetta, 2012) due to the absence of a nutritive groove and the presence of

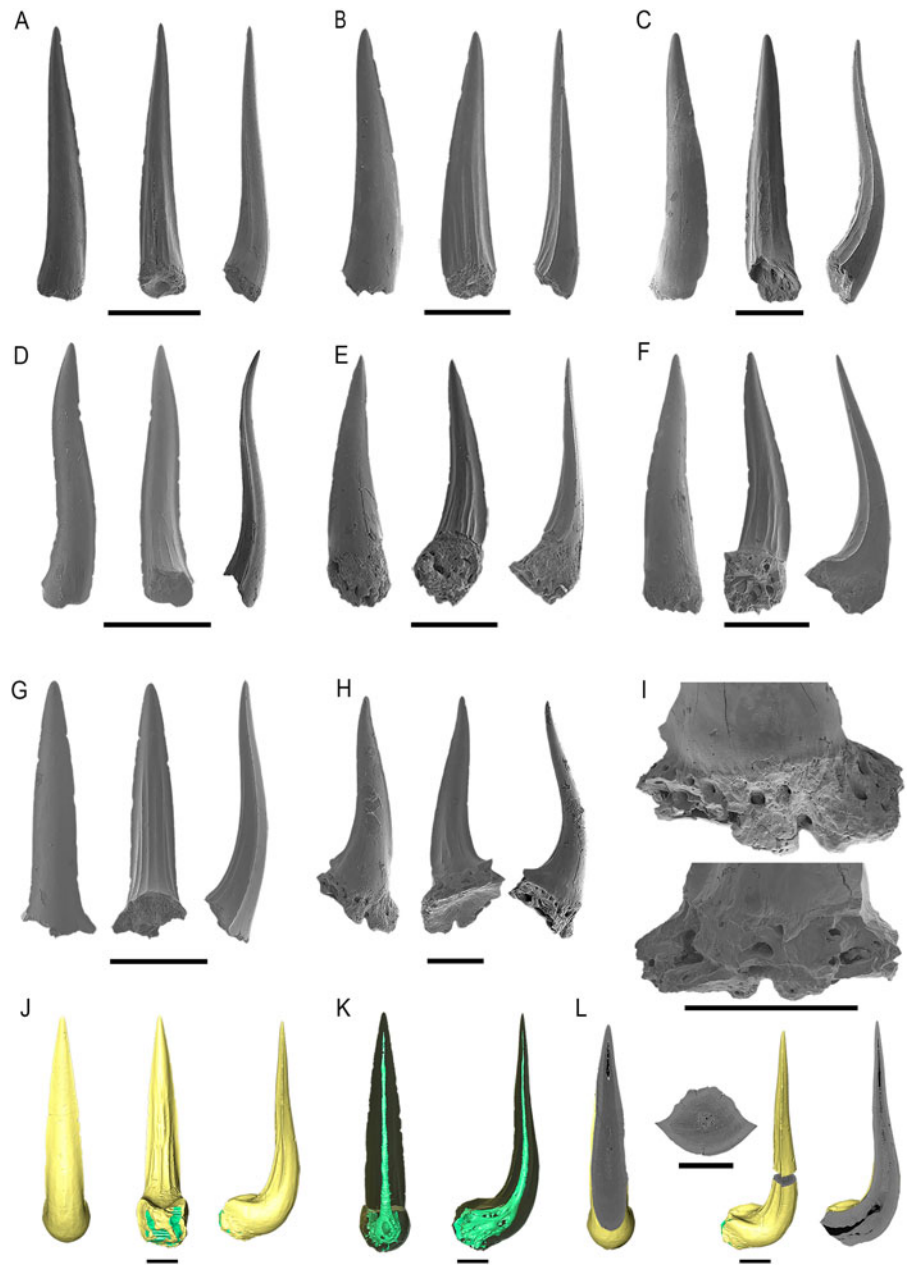


FIGURE 2. **A–H**, anterior (**A–D**), anterolateral (**E–G**), and mesio-distal (**H**) *Trigonognathus* sp. teeth from the Ferriol outcrop in labial, lingual, and profile views (MGUV-39026, MGUV-39027, MGUV-39024, MGUV-39022, MGUV-39025, MGUV-39029, MGUV-39030, and MGUV-39021 respectively). **I**, detail on the labial and lingual faces of the root of MGUV-39021. **J–L**, external isosurfaces, vascular network and virtual sections of MGUV-39028, in labial, lingual, and mesio-distal views, as well as an occlusal section of the mesial portion. Scale bars equal 1 mm (**A–H**), 500 μ m (**J–L**), 200 μ m (cross section of **L**).

vascular openings or pores in the basal face of the root (see Fig. 2H, I).

Comparative Remarks—*Trigonognathus* is easily identifiable by its moncuspidate teeth, which are high and narrow, with strongly marked folds present on the lingual surface, and the sigmoid curvature of the more anterior teeth, strongly developed on the base, which causes the teeth to bend toward the lingual face. In contrast with the majority of Squaliformes, *Trigonognathus* does not exhibit dignathic heterodonty, which many of the representatives in the order possess. In those other taxa, lower teeth have a cutting-type dentition with labiolingually compressed and slender upper teeth, but exceptions can be found in *Centroscyllium*, *Aculeola*, *Miroscyllium*, *Cirrigaleus*, or *Squalus* spp. (Cappetta and Adnet, 2001). Contrarily, *Trigonognathus* exhibits monognathic heterodonty and a tearing-type dentition. This general morphology is similar to other mesopelagic sharks, like the goblin shark *Mitsukurina*

owstoni (Yano et al., 2003). Both genera have a jaw apparatus specialized for protrusion (Yano et al., 2003; Cappetta, 2012), and their tooth crowns share a high, slender, sigmoid cusp with ridges at the lingual face (similar ornamentation can be observed in some juveniles of *Mitsukurina*) (Cappetta, 2012). However these are more closely related to trophic ecology, with convergent development of ram feeding to catch small prey items through a wide gap in their mandibles (Yano et al., 2003, 2007). Compagno (1984) described the jaws of *M. owstoni* as specialized for quick projection to capture small prey, and the jaws of *Trigonognathus kabeyai* are capable of strong anteroventral protrusion that expands the oral cavity to capture prey (Shirai and Okamura, 1992), supporting the possibility of similar feeding modes between the two species (Wetherbee and Kajiuira, 2000). Despite dental similarities, *Trigonognathus* teeth can be distinguished from those of *Mitsukurina* by the weaker development of crown

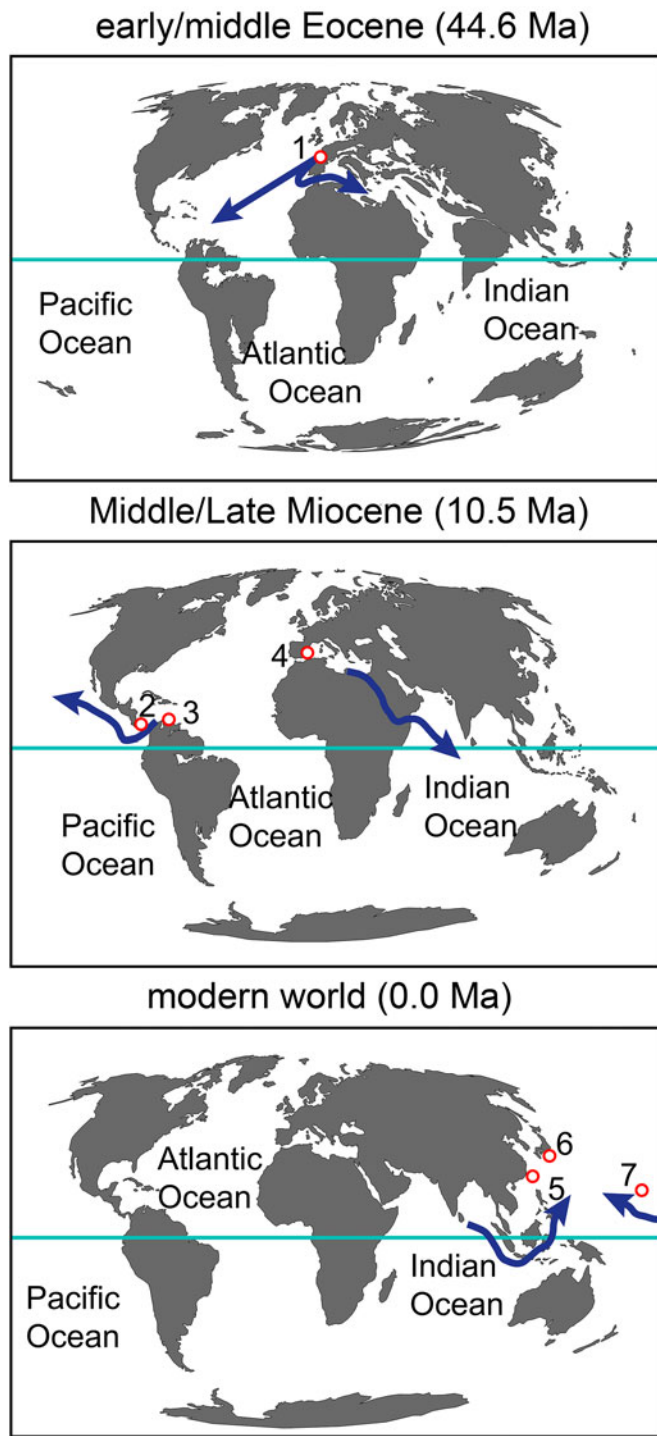


FIGURE 3. Worldwide distribution of fossil and extant *Trigonognathus* species. Maps (Mollweide projection) modified from Scotese (2014a, 2014b). 1, Cappetta and Adnet (2001); 2, Carrillo-Briceño et al. (2015); 3, Aguilera and Rodríguez de Aguilera (2001); 4, present work; 5, Ebert et al. (2013); 6, Mochizuki and Ohe (1990) and Yano et al. (2003); 7, Wetherbee and Kajiura (2000).

ornamentation and their root histology (see Cappetta, 2012: figs. 110, 175).

Another deep-water shark occurring at the El Ferriol site is *Chlamydoselachus* sp., a taxon with characteristic tricuspidate

teeth. These teeth are usually found as isolated broken fragments, and no complete tooth has been recovered from this site to date. *Chlamydoselachus* exhibits slender cusps that resemble those of *Trigonognathus*, possessing sharp edges and short, near vertical, ridges at the base (Cappetta, 2012). These features could cause possible misidentifications as broken *Trigonognathus* sp. crowns, but all the specimens identified as *Trigonognathus* clearly differ from *Chlamydoselachus* by a more circular cross section of the lower portion of the cusps. In contrast, *Trigonognathus* possesses a more slender cusp base when observed laterally, with a less convex lingual face. Additionally, specimens of *Chlamydoselachus lawleyi*, documented by Cigala-Fulgosi et al. (2009) and used by us as comparative material to *Trigonognathus*, show either strongly marked folds in the labial face of their cusplets (see Cigala-Fulgosi et al., 2009:fig. 6), or those folds are completely absent (see Cigala-Fulgosi et al., 2009:fig. 5). The folds on *Trigonognathus* are always present and conspicuous on the lingual face (see Fig. 2).

A row of well-developed foramina can be observed on the two specimens that partially preserve the root. These extend all around, from the labial to the lingual side and the proximal and distal lateral faces (Fig. 2H, I). This feature is similar to that seen in the anterolateral teeth of *T. kabeyai* (see Cappetta and Adnet, 2001:fig. 2, elements 7–11), but it appears to be absent, or at least much less defined, in the fossil species †*T. virginiae*, where they are less organized. Conversely, our specimens possess a medial lingual foramen on the basal face of the root (Fig. 2H, I), a feature that is also visible on the specimens of *T. virginiae* figured in Cappetta and Adnet (2001:fig. 4, elements 7 and 8), where it is even more strongly developed than in the El Ferriol specimens (Fig. 2I). These shared characters among extant and extinct species place the El Ferriol taxon as a possible intermediate species in the evolutionary lineage of the genus. Although we think that the new findings can represent a new chronospecies, the preservation of the teeth does not allow for analysis and distinction of a new species, and we therefore prefer to leave it in open nomenclature.

DISCUSSION

The study of the El Ferriol outcrop has yielded a rich and diverse fish assemblage (for a preliminary faunal list see Marín, 1992 and Mendiola, 1996), which include a significant collection of teeth assigned to *Trigonognathus*. Amongst the more than 1000 osteichthyan and 400 elasmobranch remains recovered from the site, at least seven elasmobranch orders and more than ten families are recognized (see Paleoenvironmental Inferences section). Although still under study, the paleodiversity and relative abundances of the elasmobranch teeth show the predominance of representatives of the families Etmopteridae (> 20%) and Chlamydoselachidae (ca. 20%), followed by Lamnidae, Carcharhinidae, and Dalatiidae (ca. 10%), with the remaining families (Centrophoridae, Hexanchidae, Mitsukurinidae, Pristiophoridae, Otodontidae, Hemigaleidae, and Odontaspidae) being represented by less than 5% each.

Our results highlight the abundance of fossil *Trigonognathus* remains. The El Ferriol locality represents the site with the highest concentration of specimens known to occur worldwide, as well as containing the first known Neogene record in the Mediterranean region.

Paleoenvironmental Inferences

As previously stated, the material we examined was obtained from a glauconitic calcarenitic marlstone layer, with glauconite formation resulting from authigenic diagenesis of biotite in shallow marine environments (Nichols, 2009). In addition, the marlstone also contains a high concentration of bioclasts with a mix of

fragmentary echinoderm, anthozoan and foraminiferal remains, and preserves a rich and diverse fish assemblage that is currently under study. Although the sedimentology indicates a shallow environment, our preliminary analysis of the faunal assemblage indicates a mixture of deep-water (Centrophoridae, Chlamydoselachidae, Dalatiidae, Etmopteridae, Hexanchidae, Mitsukurinidae, Pristiophoridae), pelagic (Carcharhinidae, Lamnidae, Otodontidae) and neritic (Carcharhinidae, Hemigaleidae, Lamnidae, Odontaspidae) elasmobranchs, as well as a diverse neritic bony fish record (Acanthuridae, Scaridae, Sparidae, Labridae).

This assemblage is similar to other warm-water faunas from Miocene sites documented in nearby outcrops of the Alicante province (see Martínez-Pérez et al., 2018; Ferrón et al., 2019). Examples of mixed shallow- and deep-water fish taxa are not uncommon in the fossil record (Aguilera and Rodríguez de Aguilera, 2001; Vialle et al., 2011; Carrillo-Briceño et al., 2015, 2016, 2020; Villafañá et al., 2020). Most of these examples are thought to have been the result of the migration of deep-water taxa to shallower areas during feeding and coastal upwelling processes, or elements being washed into deeper waters by turbidity currents or slumping (Vialle et al., 2011; Carrillo-Briceño et al., 2015, 2020; Martínez-Pérez et al., 2018).

It is well known that some deep-water shark taxa, such as *Isistius* (Laurito, 1997; Widder, 1998; de Figueiredo and de Carvalho, 2018 and references therein), *Squaliolus* (Seigel, 1978) or *Deania calcea* (Parker and Francis, 2012) undertake nocturnal migration to the surface in order to feed. This behavior has also been documented in extant *T. kabeyai* via capture by commercial purse seines at night, where individuals were caught near the surface (150 meters), in comparison to the usual bathymetric range of around 250–1000 meters (Ebert et al., 2021). In addition, stomach contents of the *T. kabeyai* specimens recovered by Yano et al. (2003) contained lantern fish, a taxon that also undertakes diel migrations. It is therefore plausible that extinct *Trigonognathus* representatives exhibited the same behavior, which could explain the presence of this taxon in nearshore deposits of the studied locality in association with epipelagic and neritic sharks. In any case, more detailed studies of the associated fauna, including the foraminiferal assemblage, and sedimentological analyses are needed in order to better ascertain whether the origin of these mixed faunas is caused by a feeding-related behavior or by turbidity currents or slumping that transported the elements into deeper waters.

Geographic Range and Evolution of the Genus

The discovery of *Trigonognathus* sp. in Middle Miocene deposits of the Mediterranean Sea highlights the differences between the current and past geographic distribution of the genus (Fig. 3). The living species, *T. kabeyai*, has only been found in deep waters of warm regions of the Pacific Ocean, such as Japan (Mochizuki and Ohe, 1990; Shirai and Okamura, 1992), Taiwan (Ebert et al., 2013), and Hawaii (Wetherbee and Kajiura, 2000). However, its fossil record indicates a wider paleogeographic distribution. The genus had an Atlantic distribution from the middle Eocene of France (Cappetta and Adnet, 2001) to the Late Miocene–early Pliocene of the Caribbean Sea (Aguilera and Rodríguez de Aguilera, 2001; Carrillo-Briceño et al., 2015), with the habitation of at least two additional marine basins (North Europe and Caribbean regions). The new finding broadens the geographic distribution of the genus to the Middle Miocene of the Mediterranean realm. These data suggest an Atlantic origin of *Trigonognathus* during the early/middle Eocene. Such an origin is supported by the appearance of early representatives of its family (Etmopteridae), such as †*Paraetmopterus nolfi* and †*Etmopterus cahuzaci* in European localities during the Eocene (Thies and Müller, 1993; Underwood and Mitchell, 1999; Adnet, 2000; Siverson and Cappetta,

2001; Adnet, 2006; Adnet et al., 2008; Straube et al., 2010, 2015; Flammensbeck et al., 2018), subsequently colonizing other sea basins. A plausible dispersal route for the genus could have been via the Atlantic basin and the proto-Caribbean Sea towards the Pacific Ocean, crossing the deep waters of the Central American Seaway (CAS) before its closure (Hoorn and Flantua, 2015; Montes et al., 2015). The interruption of deep-water flow in the CAS has been hypothesized to have occurred during the Middle Miocene, around 15–12 Ma ago (Montes et al., 2015; Jaramillo et al., 2017). Shallow marine connections (other than CAS) between the Caribbean and Pacific waters likely occurred in the Pliocene, when a permanent land barrier between the western Pacific and Atlantic oceans was established (Carrillo-Briceño et al., 2018).

With the new discovery from El Ferriol, an alternative dispersal route can be proposed for *Trigonognathus*, moving toward the Indian and Pacific oceans from the Atlantic Ocean through the Mediterranean Sea before the Indian Gateway closed during the Oligocene–Early Miocene (Rögl, 1997, 1999; Vara et al., 2013; Bialik et al., 2019; Torfstein and Steinberg, 2020), and then towards the Pacific before disappearing in the Atlantic and Mediterranean basins. New studies suggest the closure of the Miocene Indian Ocean Gateway to the Mediterranean by the Aquitanian stage, when the water-mass exchange between these basins was heavily reduced (Bialik et al., 2019). Although some connections may still have existed in some form during the Miocene (Segev et al., 2017), the feasibility of significant water-mass exchange via these connections is still being debated, and the dispersion of deep-water sharks would likely have occurred prior to the reduction of this water exchange.

Within this scenario, a deep-water elasmobranch such as *Trigonognathus* may have been affected by the degradation of the deep-sea environments in the Mediterranean basin during the Late Miocene and Pliocene due to the lack of water circulation and the lack of oxygen in lower bathymetric regions (Kouwenhoven et al., 1999; Sardá et al., 2004; Kouwenhoven and Van der Zwaan, 2006; Gallego-Torres et al., 2010). This situation could have been aggravated by the drastic changes that occurred during the Messinian Salinity Crisis (Hsü et al., 1973, 1977; Krijgsman et al., 1999; Garcia-Castellanos et al., 2009; Garcia-Castellanos and Villaseñor, 2011), which eliminated deep-sea environments and reduced available ecosystems, leading to extirpation or extinction of most deep-sea species (Coll et al., 2010). Perhaps the most important data supporting this hypothesis are the morphological similarities that the teeth recovered from El Ferriol have with both the Eocene *T. virginiae* and the extant *T. kabeyai* (see Comparative Remarks section). In any case, if the hypothesis of the Atlantic origin for *Trigonognathus* is correct, colonization of Pacific waters should have occurred before the closing of the seaways that connected the Atlantic, either via the proto-Caribbean or the Mediterranean and Indian Ocean during the Miocene, or both, later becoming extinct in both regions (Caribbean and Mediterranean), probably related with environmental changes that occurred in the Caribbean after the closure of the CAS (see Carrillo-Briceño et al., 2018, or in the Mediterranean after the Messinian Salinity Crisis, Martínez-Pérez et al., 2018).

Furthermore, we cannot rule out the possibility that the living species could be more widely distributed than the present data suggest, as it is difficult to establish the geographic distribution of deep-sea species because samples are largely dependent on the commercial fishing industry (Cappetta and Adnet, 2001). The discovery of *Trigonognathus* in the Mediterranean realm provides an alternative hypothesis for dispersal of the genus and its biogeographic history. In any case, sampling of more locations is needed to shed more light on the paleogeographic dynamics of this deep-sea genus of sharks, and to ascertain the accuracy of our interpretation of *Trigonognathus* distribution patterns during the Neogene.

CONCLUSIONS

The south-eastern Spain locality of El Ferriol preserves an abundance of fossil shark remains, including teeth and placoid scales. Among them, we stress the significant record of *Trigonognathus* teeth, showing the most abundant record for the genus worldwide, with 77 teeth recovered, as well as its first record in the Mediterranean Sea. The new *Trigonognathus* teeth from this locality present mixed characteristics between the Eocene and extant species, suggesting that this taxon could constitute a new morphological intermediate taxon. In addition, the new finding in the Miocene of the Mediterranean realm has allowed us to propose an alternative dispersal route through the Mediterranean to explain the geographic distribution of the extant genus, contrasting with the Atlantic–Central American Seaway Hypothesis. Ultimately, our discovery increases our knowledge of this poorly known deep-sea genus, including its evolutionary history.

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Author contributions: JLH, JDCB, and CMP conceived the study; JLH, JDCB, and CMP conducted the fieldwork, JLH, JDCB, SA, and CMP identified the specimens; JLH led the writing with assistance from HGF, JDCB, SA, HB, and CMP.

Data availability: All fossil remains described in this work are deposited at the Museu de la Universitat de València d'Història Natural.

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