Morphometric Discriminant Analysis of isolated chondrichthyan scales for palaeoecological inferences: the Middle Triassic of the Iberian Chains (Spain) as a case of study

Inferencias paleoecológicas a partir del Análisis Morfométrico Discriminante de escamas aisladas de condrictios: el Triásico Medio de la Cordillera Ibérica (España) como caso de estudio

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Abstract

Palaeontological studies on exosqueletal disarticulated remains of chondrichthyans have focused on teeth and only less interest has been paid to scales due their limited taxonomic and systematic significance. However, classical works linking the morphology and the function of the squamation in extant sharks suggest that, despite their limited taxonomic value, the study of isolated scales can be a useful tool for palaeoenvironmental and palaeoecological inferences. Following this idea, we have analyzed the fossil record of shark scales from two Middle Triassic sections of the Iberian Chain (Spain), identifying different functional types by means of a morphometric discriminant analysis. From a total of 1136 isolated chondrichthyan scales, 25% were identified as abrasion resistant scales, 62% as drag reduction scales and 13% as scales of generalized functions. The elevated proportion of abrasion resistant scales suggests that this chondrichthyan palaeocommunity was highly dominated by benthic sharks that lived over a hard sea floor. However, one of the stratigraphical levels studied (He-20), presents statistically significant differences from the others, showing a lower percentage of abrasion resistant scales and a larger percentage of drag reduction scales. This level can be linked with punctuated changes in the bathymetry of the basin and changes in the structure of the chondrichthyan community with an increase in bentho-pelagic or pelagic forms. Finally, partial correlation analysis between relative abundances of functional scale types and tooth-based taxa from the same sections provide positive correlation between teeth of *Hybodus* and *Pseudodalatias* and drag reduction scales, and teeth of *Prolatodon* and abrasion strength scales.

Keywords: Triassic, Chondrichthyes, scales, teeth, Iberian Chain.

Resumen

Los estudios paleontológicos de restos desarticulados de condrictios se han centrado en los dientes, no prestando prácticamente interés al estudio de sus escamas debido a su limitada importancia taxonómica y sistemática. Sin embargo, algunos trabajos clásicos que han relacionado su morfología y función en base al estudio de la escamación de tiburones actuales, sugieren que, a pesar de su limitado valor taxonómico, el estudio de las escamas aisladas puede ser una herramienta útil para obtener inferencias paleoambientales y paleoecológicas. Siguiendo estas ideas, se ha analizado el registro fósil de escamas de tiburón de dos secciones del Triásico Medio de la Cordillera Ibérica (España), identificando diferentes tipos funcionales por medio de un análisis morfométrico discriminante. De un total de 1.136 escamas aisladas de condrictios, el 25% de ellas fueron identificadas como escamas resistentes a la abrasión, el 62% como de reducción de la resistencia y el 13% de las escamas como de función generalizada. La elevada proporción de las escalas resistentes a la abrasión sugiere que esta paleocomunidad de condrictios estaba claramente dominada por tiburones bentónicos que habitaban sobre un sustrato rocoso. Sin embargo, uno de los niveles estratigráficos estudiados (He-20), presenta diferencias estadísticamente significativas con los demás, mostrando un porcentaje más bajo de escamas resistentes a la abrasión y un porcentaje mayor de las escamas de reducción de la resistencia. Este nivel se relaciona con cambios puntuales en la batimetría de la cuenca y por lo tanto con cambios en la estructura de la comunidad de condrictios, con un incremento de las formas bento-pelágicas o pelágicas. Por último, el análisis de correlación parcial entre la abundancia relativa de los tipos de escamas funcionales y taxones en basado dientes de las mismas secciones proporcionan una correlación positiva entre los dientes de *Hybodus* y *Pseudodalatias* y escamas de reducción de la resistencia, y diente de *Prolatodon* y escamas de resistencia a la abrasión.

Palabras clave: Triásico, condrictios, escamas, dientes, Cordillera Ibérica

1. Introduction

Due to the cartilaginous nature of the chondrichthyan endoskeleton, the fossil record of this group consists mainly of disarticulated remains such as teeth, scales and fin spines. Within these elements teeth are by far the most informative in terms of taxonomy, systematics or autecology. Most of the extinct species of Chondrichthyes are described on the basis of isolated teeth (see for example monographs of Cappetta, 1987, 2012; Ginter *et al*., 2010 and references therein). In contrast, isolated chondrichthyan scales that commonly occur together with disarticulated teeth, provide limited taxonomic information (especially Mesozoic and Cenozoic taxa, see Reif, 1985a; Karatajute-Talimaa, 1998; Leidner and Thies, 1999; Thies and Leidner, 2011) for three main reasons: the presence of a high morphological diversity of scales in different regions of the body, which has been documented in both extant and fossil specimens (see Reif, 1973, 1974, 1985a); the evolution of some scales of similar, or even, identical morphologies in distantly related species (Muñoz-Chápuli, 1985); and the occurrence of ontogenetic variability (Reif, 1973, 1978). As a consequence, palaeontological studies of disarticulated remains of chondrichthyans have focused on teeth and very little attention has been paid to scales. However we propose that, despite the lack of taxonomic and systematic significance, isolated scales could provide useful information regarding the palaeoecological and palaeoenvironmental conditions. Our proposal is based on the classic works of Reif (1982; 1985a) where the relationship between the shape and function of scales of extant sharks was pointed out. Reif (1982, 1985a) differentiated scales into five different functions: abrasion resistance, defense, drag reduction, bioluminescence and generalized functions, and indentified eight characteristic morphologies associated with these functional types. Abrasion resistant scales are found in demersal sharks, which inhabit rocky or coralline substrates and, generally, in small body regions that are often subject to abrasion in all other sharks, such as the mouth area. Scales of this type are knob-like and smooth (Morphology 1) or strongly ornamented (Morphology 2). Both types very frequently show scratch marks. Defensive scales are common in demersal sharks inhabiting muddy or sandy substrates, and protect them against ectoparasites and the settlement of epibionts. Scales of this functional type are thorn-shaped with the cusps pointing in an upward-posterior direction commonly accompanied by mucus (Morphology 3). Drag reduction scales cover most of the skin surface in fast swimming pelagic sharks. Scales of this functional type have riblets aligned in the direction of fluid flow (Morphology 4). The geometry and arrangement seem to play an important role in the drag reduction although the underlying mechanisms are not well understood yet (e.g. Bechert *et al*., 2000; Douglas-Dean, 2011; Raschi and Musick, 1986; Reif and Dinkelacker, 1982; Reif, 1985a). Scales associated to bioluminescence have evolved in some mesopelagic sharks, enabling the skin to carry photophores and permitting light to pass between them (Reif, 1985b). This functional type is represented by three different morphologies: square-shaped with concave facets (Morphology 5), bristle-shaped (Morphology 6) and thorn-shaped (Morphology 7). Scales with ridges and lateral cusps well developed but shorter than the principal cusp fulfill generalized functions and are found in almost all sharks (Morphology 8). Other functions related to hatching and feeding has been documented for shark scales (Grover, 1974; Reif, 1974; Southall and Sims, 2003), but they are very atypical and have not been found among our material.

In this study we firstly characterize the morphology of the five functional types proposed by Reif (1985a) using traditional morphometrics and discriminant analysis. Secondly we assign isolated placoid scales from synchronous levels of two stratigraphical sections (Middle Triassic) of the Iberian Chain (Spain), to these “functional” morphologies. The differential abundance of the functional types allow us to evaluate the structure of the chondrychtyan paleocommunity in terms of the relative dominance of more pelagic or benthic sharks and the properties of the physical environment they inhabited, such as the dominant substrate type, independently of the sedimentology.

2. Material provenance

The Middle Triassic (Anisian–Ladinian Muschelkalk) sediments in eastern Iberian Ranges comprise limestones and dolomites that represent epicontinental shallow-marine environments. It is composed of two carbonate units inferred as prograding carbonate ramps, related to shallow marine environments of epicontinental character. The upper Muschelkalk corresponds to the upper carbonate unit -with bioclastic and oolitic limestones, algal buildups and shallowing-upwards marl-limestone sequences- and represents the second and the most important marine transgression of the Middle Triassic in the southeast area of the Iberian range (meridional sector). López-Gómez and Arche (1992) have formally described the Dolomites and Limestones of Cañete Formation for the upper Muschelkalk units of this area.

A total of 1136 isolated scales were obtained after the dissolution of carbonate rocks with 10% acetic acid from the Bugarra and Henarejos sections of the Iberian Chain (Spain). Both sections expose dolomitic and limestone sediments of the Cañete Formation. According to López-Gómez and Arche (1992) and López-Gómez *et al.* (1987) it is of Ladinian age based on ammonites, bivalves, foraminiferas and conodonts (see Márquez-Aliaga *et al.*, 2004 and references therein).

The Henarejos section is located 1 km south-east of the village of Henarejos (Province of Cuenca). Ladinian molluscs have been reported by Marquez-Aliaga (1985) and López *et al.* (1987). The Bugarra section is close to the village Bugarra (Province of Valencia). Márquez-Aliaga *et al.* (1984) studied the stratigraphy and the invertebrate paleontological aspects of this section (Fig. 1). All specimens studied herein come from the uppermost member of the dolomites and limestones of the Cañete Formation (see Fig. 1) and are kept in the Museum of Geology of the University of Valencia (MGUV).

3. Methodology

In order to characterize the morphologies of each functional type proposed by Reif (1985a) we performed classical morphometric analysis of scales with known functions in extant sharks. Six variables (for explanation see Table 1) were measured on the dorsal surface of the scale crown from specimens figured in Reif (1985a) using ImageJ software. We used a total of 58 scales belonging to the eight scale morphologies. Each morphology was treated as a group. Discriminant analysis was performed to obtain maximum separation among the eight scale morphologies using SPSS Predictive Analytics Software Statistics (PASW) version 18.0. Three variables (LEN, WID and RID) were log-transformed to allow nonlinear combinations between them as sums or subtractions of logarithms in the discriminant functions (see below). Subsequently the fossil specimens were included in the discriminant analysis as unknown specimens and were assigned to one of the morphologies of functional types described by Reif (1985a) based on the similarity of their centroid values. Differential abundances of these functional types were statistically analyzed by Pearson's Chi-square test and Z-test using PASW software with the purpose of detecting differences between stratigraphic levels of the studied sections. Finally, we used Partial Correlation Analysis to compare the relative abundances of scale functional types *vs*. the relative abundances of tooth-based genera in the different stratigraphic levels (dates for tooth occurrences were taken from previous studies, see below). Partial Correlation Analysis allows the study of the relationship between two quantitative variables controlling the possible effect of another one that could mask correlations. Thus, the analysis was repeated four times controlling, in each case, the abundance of a concrete tooth-based genus.

4. Results and Discussion

4.1. Discriminant analysis using scales of extant sharks. Canonical variate analysis generated six discriminant functions. Coefficients, eigenvalues, proportion of explained variance and canonical correlation are presented in Tables 2 and 3. The first canonical discriminant function explains 53.6 % of the total variance while the second one accounts for 25.8% of the total variance (79.5% cumulative variance). The plot of the two canonical variables illustrates a good separation between the eight morphologies proposed by Reif (1985a) (Fig. 2). The discriminant analysis correctly classifies 100% of original cases, while the percentage of cross-validated grouped cases correctly classifies 93.1 % (i.e. 54 of the 58 scales) (Table 4). In this analysis, scales of morphologies 1, 2, 4 and 7 are the most correctly classified followed by scales of morphology 8. The least correctly classified are the scales of morphologies 3 and 6 (Table 3 and 4).

These results show that classical morphometric analysis is able to discriminate between the five functional types of chondrichthyan scales proposed by Reif (1985a) using six variables in the discriminant functions. In addition, we also tested other alternatives to the use of the classical morphometric analysis, like geometric morphometrics or Fourier analysis, but the results were not as good as expected. Due to the high morphological variability in scales, it was very difficult to set homologous points in the eight scale morphologies and, therefore, it was not possible to apply geometric morphometrics in an acceptable way. On the other hand, Fourier analysis only takes into account characters reflected in the contour of the scales without considering other features, as for example those related to the ridges, which might be useful to differentiate between groups. Although the results of this method are good, with the percentage of cross-validated grouped cases correctly classified ranging from 42.2-80% depending on the number of harmonics and the type of analysis (polar or elliptic), they are not as accurate as those obtained by classical morphometric analysis (Appendix 1 shows results obtained using Fourier analysis).

4.2. Discriminant analysis including fossil specimens. Once the discriminant analysis was established, the 1136 fossil scales from the Henarejos and Bugarra sections were included as unknowns. Following the predictions obtained, fossil scales were assigned to four morphologies belonging to three of Reif´s functional types (Fig. 3). 289 fossil specimens (25 %) were identified as abrasion resistant, 705 (62 %) as drag reducing and 142 (13 %) were identified as scales of generalized functions. None of the fossil scales were assigned to either bioluminescence type (morphologies 5, 6 and 7) or to the defense type (morphology 3). Abundances of each functional type by section and stratigraphic level are shown in Table 5.

When it is taken into consideration that in pelagic sharks scales for abrasion resistance are restricted only to small areas of the body (e.g. surrounding the mouth) representing less than 5% of the total body surface, the high proportion of scales with a protective function against abrasion present in our association become interesting for the interpretation of the data. It could be reasonably related with the presence of a high number of benthic sharks, in which (especially in those living on hard sea floor) abrasion resistant scales cover not only the mouth area but also half of the ventral part of the body and the ventral and anterior areas of the pectoral and pelvic fins (Reif, 1985a). Thus, our results indicate that the Middle Triassic chondrichthyan community from the Iberian Chain was dominated by benthic sharks. This suggests a palaeoenvironmental interpretation as an area of shallow marine waters, probably dominated by an abrasive substrate (such as a near-shore hard sea floor environment or some type of lagoon). This interpretation is in accordance with sedimentological data provided by Marquez-Aliaga *et al.* (1984) and López-Gómez *et al.* (1987).

4.3. Pearson's Chi-square test and Z-test. Pearson's Chi-square test showed significant differences between levels of the Bugarra and Henarejos sections (p = 0.000 Table 5). Z-test allowed us to detect between what levels and in which concrete functional types significant differences occur (Table 6). The test show significant differences between level He-20 and the remaining levels. The percentage of abrasion resistant scales is significantly lower than in all others levels and the percentage of drag reduction scales is significantly higher than in four of the other seven levels (Bu 1-33, Bu 1-26, Bu1-26d and He-18). This suggests a change in the composition of the chondrichthyan community with an increase of the pelagic or bentho-pelagic forms. In fact the fraction of abrasion resistant scales (5.2%) is close to the expectation for pelagic sharks. Furthermore teeth of supposed benthic taxa (see below) do not occur in this level. These changes could be due to punctuated changes in the bathymetry of the basin related to transgressive-regressive pulses that produce a deepening and a displacement of the coastline where sediments of level He-20 were deposited.

Therefore, the analysis of scales allows us to detect changes in shark paleocommunities that indirectly may reflect environmental changes, in bathymetry or the predominant substrate, which could be tested by the sedimentology. Hence our results can be reinforced by future sedimentological works but are valid regardless of them.

4.4. Correlation with fossil teeth. Previous studies (Pla *et al.*, 2009; 2013) on isolated teeth from the same samples that the scales of this study identified the following tooth based species: *Palaeobates angustissimus* (Agassiz, 1838), *Pseudodalatias henarejensis* Botella, Plasencia, Márquez-Aliaga, Cuny and Dorka, 2010; *Hybodus bugarensis* Pla, Márquez-Aliaga and Botella, in press; *Prolatodon bucheri* (Cuny, Rieppel and Sander, 2001); *Prolatodon contrarius* (Johns, Barnes and Orchard, 1997); *Hybodus plicatilis* Agassiz, 1838; and *Lissodus* aff. *Lepagei* (Fig. 4). Partial correlation analysis between the relative abundances of functional types of scales and abundances of tooth-based taxa at generic level indicates positive correlation between teeth of *Hybodus* and *Pseudodalatias* and drag reduction scales, and teeth of *Prolatodon* and abrasion resistant scales. A negative correlation was present between teeth of *Prolatodon* and drag reduction scales (Table 7). Once more, these results are in agreement with the palaeobiological interpretations based on the tooth morphology (see Pla *et al.*, 2013). Thus, dentitions of *Prolatodon bucheri* and *Prolatodon contrarius* can be identified as belonging to a grasping-crushing feeding strategy (following the terminology of

Cappetta, 1986, 1987) with cuspidate anterior teeth and flat lateral teeth. This dental type (present generally in sharks of benthic habits) corresponds to a trophic adaptation for durophagy and indicates crustaceans, ostracods, or shelled invertebrates such as gastropods and bivalves as the preferred prey. In consequence, the obtained positive correlation between *Prolatodon* and abrasion strength scales is expected. In addition, *Pseudodalatias* exhibited a cutting-clutching dentition extremely similar to those of some extant neoselachian Dalatiidae (Gray, 1851). The feeding preferences of dalatiids consist of "parasitic" bites excising portions of flesh from large-size oceanic animals, including other sharks, marine mammals and bony fishes (Gasparini and Sazima, 1996; Soto and Mincarone, 2001; Heithaus, 2004; Heithaus and Vaudo, 2012). This trophic behavior is favoured by sharks with a bentho-pelagic swimming mode that look for prey in the water column. Therefore, the positive correlation between teeth of *Pseudodalatias* and drag reduction scales was also predictable. Finally, the multicuspidate teeth of hybodonts are considered to be adapted for a "grasping and swallowing" strategy (clutching- or tearing-type *sensu* Cappetta, 1987) that could include prey such us other small fishes, soft-bodied animals and arthropods. This strategy is present in both pelagic (as in some *Isurus*) and benthic sharks (such as Scyliorhinidae or Squatinidae, Cappetta, 1987). The positive correlation found between *Hybodus* teeth, which almost all belong to the species *H. plicatilis*, and scales of the drag reduction type indicate that this widespread shark – known from Germany (Agassiz, 1843), Switzerland (Meyer, 1849; Rieppel, 1981; Scheinpflug, 1984) Spain (Pla *et al.*, 2009; 2013) and Saudi Arabia (Vickers *et al*., 1999) was a bentho-pelagic to pelagic swimmer.

It is important to remark, that the good statistical correlation found between the abrasion resistant scales and durophag tooth-based taxa (that putatively belonging to benthonic sharks), and the high correlation between cutting teeth and drag reduction scales that could belong to more pelagic shark, strongly supports the idea that no taphonomic bias affect significantly the relative abundance of the different type scales, and hence our final results.

5. Conclusions

Classical morphometric analysis has been able to discriminate among the eight morphologies, included in five functional types, of chondrichthyan scales proposed by Reif (1985a). A high percentage of cross-validated grouped cases were correctly classified (93.1 %). This strongly supports a high possibility of correct identification when the discriminant functions are applied to isolated fossil scales.

A total number of 1136 isolated chondrichthyan scales were collected from two Middle Triassic sections (Henarejos and Bugarra) of the Iberian Chain. They were included in the discriminant analysis resulting in the identification of 25% as abrasion resistant, 62% as drag reduction and 13 % as scales of generalized functions. Neither the scales of the bioluminescent nor the defensive type defined by Reif (1985a) could be recognized. The elevated proportion of abrasion resistant scales indicates that the chondrichthyan palaeocommunity from the Middle Triassic of the Iberian Chain was dominated by sharks adapted to a benthic life-style. This is in agreement with palaeobiological interpretations provided by previous analyses of isolated chondrichthyan teeth from the same sections (Pla *et al*., 2013) which show that in terms of diversity, the chondrichtyan fauna was dominated by durophagous sharks most of them with grasping-crushing dentitions. Dentitions of this type imply feeding preferences including crustaceans, ostracods and shelled invertebrates (gastropods and bivalves), and they are currently present in sharks which live in close relationship with the substrate bottom looking for their prey. Thus, in our opinion, the high percentage of abrasion resistant scales (i.e. of benthic sharks) could be likely related with a palaeoenvironment of shallow marine waters, mostly dominated by a rough substrate, such as a rocky shore platform. Our dates are is in agreement with sedimentological and paleontological studies in the area (see e.g. Márquez-Aliaga *et al*., 1984; Márquez-Aliaga and López-Goméz, 1989; López-Gómez and Arche, 1992).

The statistical analyses results in differences between level He-20 (Henarejos section) and all other levels concerning the relative abundance of the functional types of scales. The percentage of the abrasion resistant type in this single level is significantly lower but that of drag reduction scales significantly higher. This can be linked with punctuated changes in the bathymetry of the basin -related to transgressive-regressive pulses- and changes in the structure of the chondrichthyan community with an increase in the pelagic forms. Finally, the partial correlation analysis between the relative abundances of functional types of scales and tooth-based taxa allowed the detection of a positive correlation between teeth of *Hybodus* and *Pseudodalatias* and drag reduction scales, and teeth of *Prolatodon* and scales of the abrasion resistant type.

In summary, our analyses show that, despite their limited taxonomic value, isolated scales can be a useful tool for palaeoenvironmental and palaeoecological inferences of the chondrichthyan palaeocommunity. The good concordance of the results obtained from morphometric discriminant analysis of chondrichthyan scales from the Middle Triassic of the Iberian Chains with inferences based on isolated teeth and sedimentological data suggest that this methodology can be extrapolated for studies in other localities.

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7. References

Agassiz, L. (1833–44): *Recherches sur les poissons fossiles, 3*. Imprimerie de Petitpierre, Neuchâtel 32: 390 p.

Botella, H., Plasencia, P., Márquez-Aliaga, A., Cuny, G., Dorka, M. (2009): *Pseudodalatias henarejensis* nov. sp. A new Pseudodalatiid (Elasmobranchii) from the Middle Triassic of Spain. *Journal of Vertebrate Paleontology* 29(4), 1006-1012. doi: 10.1671/039.029.0425

Bechert, D. W., Bruse, M., Hage, W. (2000): Experiments with three-dimensional riblets as an idealized model of shark skin. *Experiments in Fluids* 28(5), 403-412. doi: 10.1007/s003480050400

Cappetta, H. (1986): Types dentaires adaptatifs chez les sélaciensactuels et post-paléozoiques. *Palaeovertebrata* 16, 57-76.

Cappetta, H. (1987): *Chondrichthyes II, Mesozoic and Cenozoic Elasmobranchii. Handbook of Paleoichthyology*. Verlag Dr. Friedrich Pfeil, München: 193 p.

Cappetta, H. (2012): *Chondrichthyes, Mesozoic and Cenozoic Elasmobranchii: Teeth. Handbook of Paleoichthyology*. Verlag Dr. Friedrich Pfeil, München: 521 p.

Cuny, G., Rieppel, O., Sander, P.M. (2001): The shark fauna from the Middle Triassic (Anisian) of North-Western Nevada. *Zoological Journal of the Linnean Society* 13, 285-30. doi: 10.1111/j.1096-3642.2001.tb00627.x

Douglas-Dean, B. (2011): *The effect of shark skin inspired riblet geometries on drag in rectangular duct flow*. Master thesis. Ohio: 86 p.

Gasparini, J. L., Sazima, I. (1996): A stranded melonheaded whale, *Peponocephala electra*, in southeastern Brazil, with comments on wounds from the cookiecutter shark *Isistius brasiliensis*. *Marine Mammal Science* 12, 308-312. doi: 10.1111/j.1748-7692.1996.tb00582.x

Ginter, M., Hampe, O., Duffin, C. J. (2010): *Chondrichthyes. Paleozoic Elasmobranchii: Teeth. Handbook of Paleoichthyology*. Verlag Dr. Friedrich Pfeil, München: 168 p.

Gray, J. E. (1851): *List of the specimens of fish in the collection of the British Museum. Part 1. Chondropterygii*. British Museum (Natural History), London: 160 p.

Grover, C. A. (1974): Juvenile denticles of the swell shark *Cephaloscyllium ventriosum*: function in hatching. *Canadian Journal of Zoology* 52, 359–363. doi: 10.1139/z74-043

Heithaus, M. R. (2004): Predator–prey interactions. In: J.C. Carrier, J.A. Musick, M.R. Heithaus (eds), *Biology of Sharks and their Relatives* CRC Press, Boca Raton, FL, USA: 487–521.

Heithaus M.R., Vaudo, J.J. (2012): Predator–prey interactions. In: J.C. Carrier, J.A. Musick, M.R. Heithaus (eds), *Biology of Sharks and their Relatives* CRC Press, Boca Raton, FL, USA: 505–546.

Johns, M. J., Barnes, C. R., Orchard M. J. (1997): Taxonomy and Biostratigraphy of Middle and Late Triassic elasmobranch ichthyoliths from northeastern British Columbia. *Geological Survey of Canada* 502, 1-235.

Karatajuté -Talimaa, V. (1998): Determination methods for the exoskeletal remains of early vertebrates. *Mitteilungen ausdem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe* 1, 21–52. doi:10.1002/mmng.19980010103

Leidner, A., Thies, D. (1999): Placoid scales and oral teeth of Late Jurassic elasmobranchs from Europe. *Mesozoic Fishes 2 - Systematics and Fossil Record*: 29-40.

López-Gómez, J., Arche, A. (1992): Las unidades litoestratigráficas del Pérmico y Triásico Inferior y Medio en el sector SE de la Cordillera Ibérica. *Estudios Geológicos* 48, 123-143.

López-Gómez, J., Márquez-Aliaga, A., Arche, A., Goy, A. (1987): La facies Muschelkalk de Henarejos (Cuenca): sedimentología y fauna del tramo superior. *Cuadernos de Geología Ibérica* 11, 665–676.

Márquez-Aliaga, A. 1985. *Bivalvos del Triásico Medio del Sector Meridional de la Cordillera Ibérica y de los Catalánides*. Colección Tesis Doctorales. Editorial de la Universidad Complutense de Madrid 40: 429 pp.

Márquez-Aliaga, A., De Santisteban, C., Márquez, L. (1984): Triásico Medio de Bugarra. *Estudios Geológicos* 40, 365-374.

Márquez-Aliaga, A., López Gómez, J. (1989): Paleontología y ambientes sedimentarios del Triásico medio, Muschelkalk, de la Cordillera Ibérica 1: Cuencas y Valencia. España. *Estudios geológicos* 45, 387-398.

Márquez-Aliaga, A., Valenzuela-Ríos, J.I., Plasencia, P., Ros, S. (2004): Los fósiles del Muschelkalk (Triásico Medio) en el sector oriental de la Península Ibérica. In: E. Baquedano, S. Rubio (eds.), *Miscelania en homenaje a Emiliano Aguirre. II: Paleontología*. Museo Arqueologico Regional de Alcalá de Henares: 276-291.

Meyer, H. von (1849): Fossile Fische aus dem Muschelkalk von Jena, Querfurt und Esperstädt. *Palaeontographica* 1, 195–208.

Muñoz-Chápuli, R. (1985): Sobre la clasificación tipológica del esqueleto dérmico de escualos. *Miscelánea Zoológica* 9, 396-400.

Pla, C., Marquéz-Aliaga, A., Botella, H. (2013): The chondrichthyan fauna from the Middle Triassic (Ladinian) of the Iberian Range (Spain). *Journal of Vertebrate Paleontology* 33, 770-785.

Pla, C., Plasencia, P., and Botella, H. (2009): Estudio preliminar de los condríctios del Ladiniense (Triásico Medio) de la sección de Bugarra (Valencia, España). *Paleolusitana* 1, 383-389.

Raschi, W., Musick, J. (1986): *Hydrodynamic aspects of shark scales*. NASA Contractor Report 3963: 123 p.

Reif, W. E. (1973): Ontogenese des Hautskelettes von *Heterodontus falcifer* (Selachii) aus dem Untertithon. *Stuttgarter Beitragezur Naturkunde* 7, 1–16.

Reif, W. E. (1974): Morphogenese und Musterbildung des Hautzähnchen-Skelettes von *Heterodontus*. *Lethaia* 7, 25–42. doi:10.1111/j.1502-3931.1974.tb00882.x

Reif, W. E. (1978): Types of morphogenesis of the dermal skeleton in fossil sharks. *Paläontologische Zeitschrift* 52, 235–257. doi:10.1007/BF03006733

Reif, W. E. (1982): Morphogenesis and function of the squamation in sharks. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 164, 172–183.

Reif, W. E. (1985a): Squamation and Ecology of Sharks. *Courier Forschungsinstitut Senckenberg* 78, 1-255.

Reif, W. E. (1985b): Function of scales and photophores in mesopelagic luminescent sharks. *Acta Zoologica* 66, 111–118. doi:10.1111/j.1463-6395.1985.tb00829.x

Reif, W. E., Dinkelacker, A. (1982): Hydrodynamics of the squamation in fast swimming sharks. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 164, 184–187.

Rieppel, O. (1981): The Hybodont sharks from the Middle Triassic of Monte San Giorgio, Switzerland. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 161, 324–353.

Scheinpflug, R. (1984): Wirbeltierfunde im mainfränkischen Hauptmuschelkalk. *Aufschluss* 35, 21–36.

Soto, J., Mincarone, M. (2001): First record of kitefinshark, *Dalatias licha* (Bonnaterre, 1788) (Chondricthyes, Dalatiidae), in the south Atlantic. *Mare Magnum* 1, 26-26.

Southall, E.J, Sims, D.W. (2003): Shark skin: a function of feeding. *Proceedings of the Royal Society of London B* (Suppl.) 270, S47-S49. doi: 10.1098/rsbl.2003.0006 1471-2954

Thies, D., Leidner, A. (2011): Sharks and guitarfishes (Elasmobranchii) from the Late Jurassic of Europe. *Palaeodiversity* 4, 63-184.

Vickers-Rich, P., Rich, T.-H., Rieppel, O., Thulbom, R. A., McClure, H. A. (1999): A Middle Triassic Vertebrata Fauna from the Jilh Formation, Saudi Arabia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 213(2), 201–232.

Figure Captions

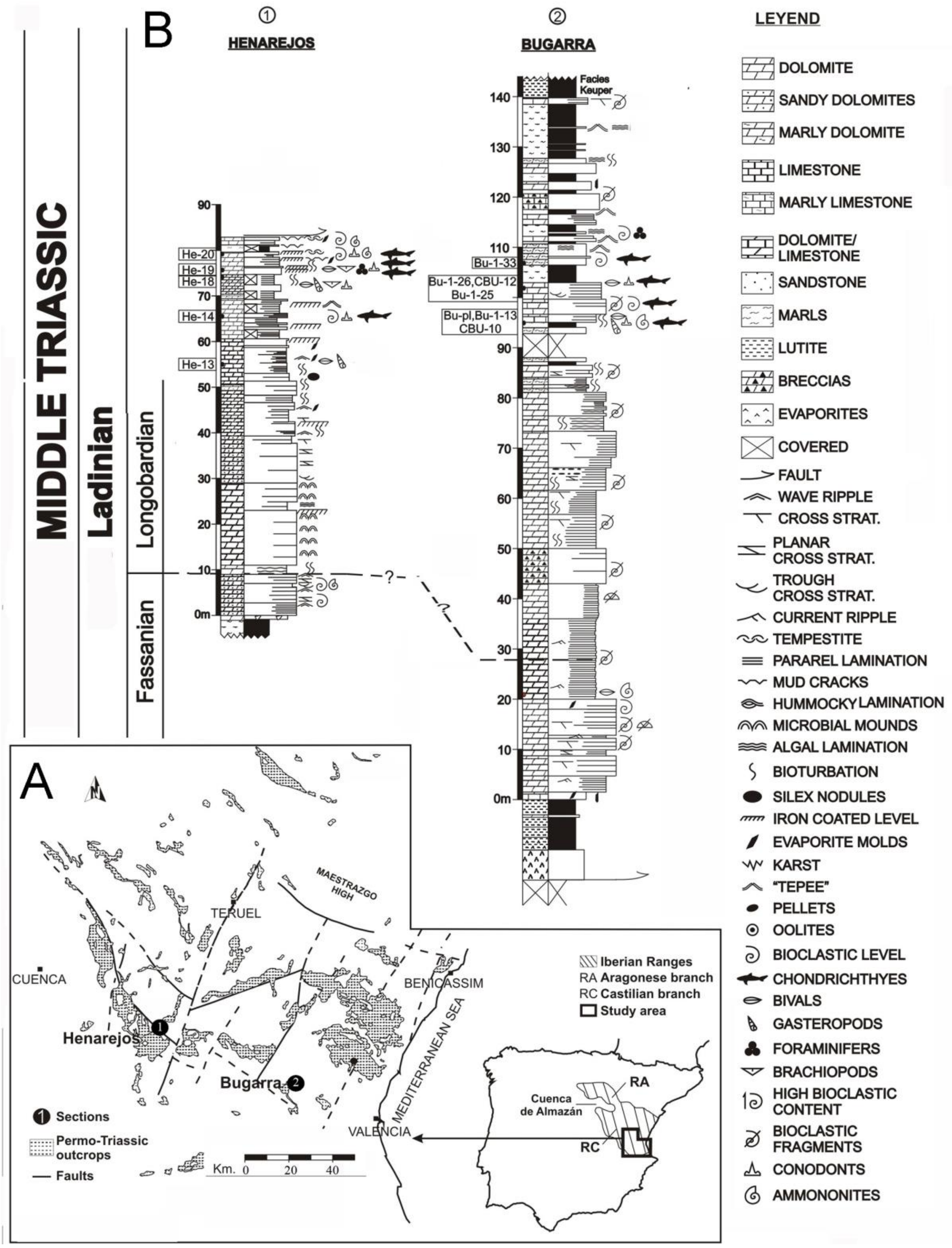

Fig. 1.- A. Geographical setting of the studied area with indication of the studied sections. B. Stratrigraphical column of Bugarra and Henarejos sections with a posible

Litho and biostratigraphical correlation between them and with indication of levels that yielded the material described in this work (modified from Pla *et al*., 2013).

Fig.1.- A. Localización geográfica del área estudiada con indicación de las secciones estudiadas. B. Columna estratigráfica de las secciones Bugarra y Henarejos con una posible correlación lito y bioestratigráfica entre ellas e indicación de los niveles que han librado el material descrito en este trabajo (modificado de Pla *et al*., 2013).

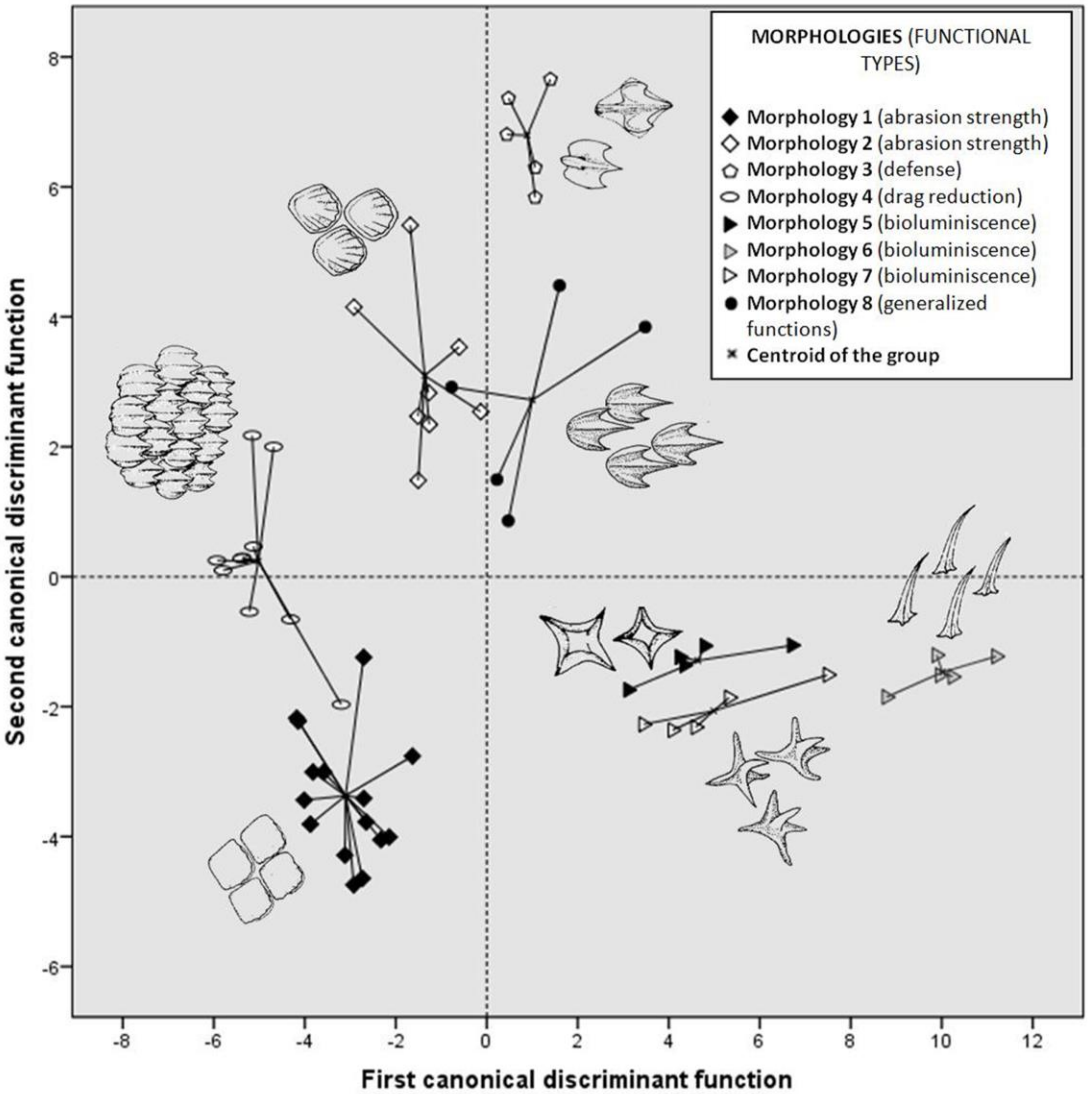

Fig. 2.- Scatter plot based on the first two discriminant functions, showing the eight scale morphologies and the five functional types.

Fig. 2.- Gráfico de dispersión de las dos primeras funciones discriminantes, mostrando las ocho morfologías y los cinco tipos funcionales.

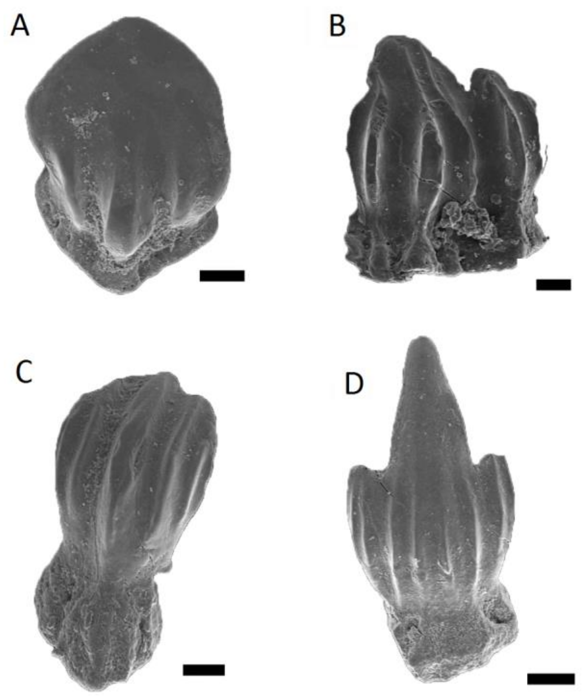

Fig. 3.- Morphologies of fossil scales from Henarejos and Bugarra sections. A: MGUV-24.804. Morphology 1 (Abrasion resistant scales) in upper-frontal view. B: MGUV-24.799. Morphology 2 (Abrasion resistant scales) in frontal view. C: MGUV-24.798. Morphology 4 (Drag reduction scales) in frontal view. D: MGUV- 24.803. Morphology 8 (Scales with generalized functions) in frontal view. Scales: A, C, 500 µm.; B, 100 µm.; D, 200 µm.

Fig. 3.- Morfologías de las escamas fósiles procedentes de las secciones Henarejos y Bugarra. A: MGUV-24.804. Morfología 1 (Escamas resistentes a la abrasión) en vista frontal-superior. B: MGUV-24.799. Morfología 2 (Escamas resistentes a la abrasión) en vista frontal. C: MGUV-24.798. Morfología 4 (Escamas con función hidrodinámica) en vista frontal. D: MGUV- 24.803. Morfología 8 (Escamas con funciones generalizadas) en vista frontal. Escala: A, C, 500 µm.; B, 100 µm., D, 200 µm.

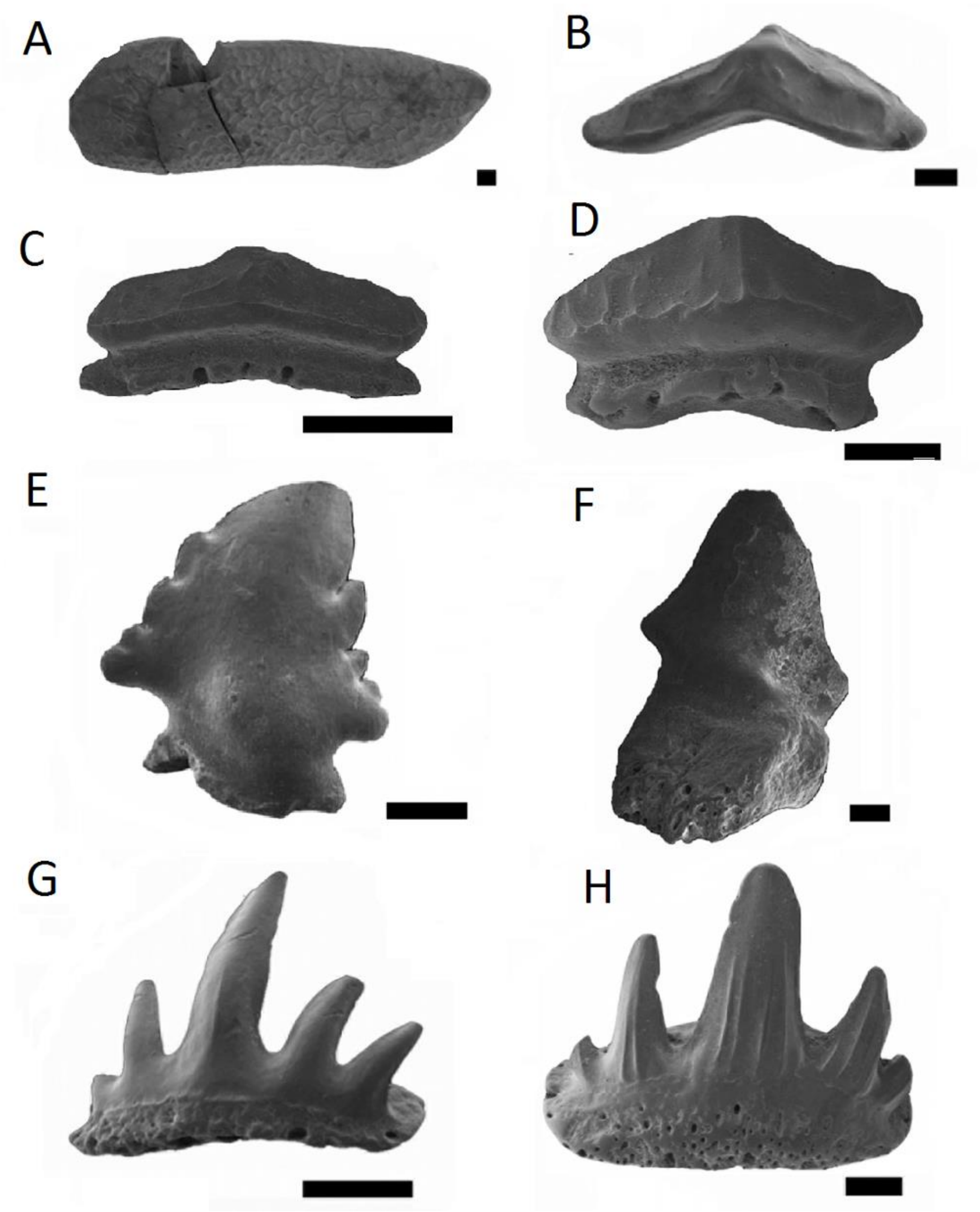

Fig. 4.- Fossil teeth from Henarejos and Bugarra sections (from Pla *et al.*, 2013). A: MGUV 25791. *Palaeobates angustissimus*, occlusal view, Bugarra section. B: MGUV 25854. *Lissodus* aff. *L. lepagei*, lingual view, Bugarra section. C: MGUV 25822. *Prolatodon contrarius*, labial view, Henarejos section. D: MGUV 25796. *Prolatodon bucheri*, labial view, Bugarra section. E: MGUV 25868. *Pseudodalatias henarejensis*, lower tooth in labial view, Henarejos section. F: MGUV 25869. *Pseudodalatias*

henarejensis, upper tooth in lingual view, Henarejos section. G: MGUV 25831. *Hybodus bugarensis*, labial view, Henarejos section. H: MGUV 25837. *Hybodus plicatilis*, labial view, Bugarra section. Scales: 200 µm.

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Fig. 4.- Dientes fósiles procedentes de las secciones Henarejos y Bugarra (de Pla *et al.*, 2013). A: MGUV 25791. *Palaeobates angustissimus*, vista oclusal, sección Bugarra. B: MGUV 25854. *Lissodus* aff. *L. lepagei*, vista lingual, sección Bugarra. C: MGUV 25822. *Prolatodon contrarius*, vista labial, sección Henarejos. D: MGUV 25796. *Prolatodon bucheri*, vista labial, sección Bugarra. E: MGUV 25868. *Pseudodalatias henarejensis*, diente de la mandíbula inferior en vista labial, sección Henarejos. F: MGUV 25869. *Pseudodalatias henarejensis*, diente de la mandíbula superior en vista lingual, sección Henarejos. G: MGUV 25831. *Hybodus bugarensis*, vista labial, sección Henarejos. H: MGUV 25837. *Hybodus plicatilis*, vista labial, sección Bugarra. Escalas: 200 µm

Table 1. Explanation and coded designations of measured scale characters.

Tabla 1. Explicación y códigos de designación de los caracteres de las escamas medidos.

CIR.	Circularity = 4Π (area/perimeter^2)
ANG.	Angle created between the two most lateral ridges / 2
PA	Presence or absence of ridges
LEN.	Maximum length of the scale
WID.	Maximum width of the scale
RID.	Average length of ridges

Table 2. Standarized canonical discriminant function coefficients.

Tabla 2. Coeficientes estandarizados de las funciones canónicas discriminantes.

	Function					
Variable	**1**	**2**	**3**	**4**	**5**	**6**
CIR.	-0,967	-0,304	0,179	-0,458	-0,168	0,187
ANG.	1,303	1,960	5,761	1,489	0,748	0,946
PA	7,460	-8,598	7,560	5,703	0,657	-7,984
Log (LEN.)	0,609	-0,389	0,656	-1,191	-1,061	-0,349
Log (WID.)	-0,391	0,175	-0,691	1,694	0,108	-0,229
Log (RID.)	-6,266	11,025	-1,864	-4,311	0,362	8,077

Table 3. Eigenvalues, proportion of explained variance and canonical correlation of the discriminant functions.

Tabla 3. Valores propios, proporción de varianza explicada y correlación canónica de las funciones discriminantes.

Function	Eigenvalue	% of Variance	Cumulative % of Variance	Canonical Correlation
1	23,079	53,6	53,6	0,979
2	11,115	25,8	79,5	0,958
3	5,124	11,9	91,4	0,915
4	2,910	6,8	98,1	0,863
5	0,639	1,5	99,6	0,624
6	0,168	0,4	100,0	0,379

Table 4. Count (Non-italic numbers) and percentages (Italic numbers) of cross-validated grouped cases correctly classified.

Tabla 4. Recuento (Números en tipo itálica) y porcentaje de casos clasificados correctamente mediante validación cruzada.

	Predicted group								
	Morphology 1	**Morphology 2**	**Morphology 3**	**Morphology 4**	**Morphology 5**	**Morphology 6**	**Morphology 7**	**Morphology 8**	**TOTAL**
Morphology 1	5	0	0	0	0	0	0	0	5
	(100,0)	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(100,0)*
Morphology 2	0	5	0	0	0	0	0	0	5
	(0,0)	*(100,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(100,0)*
Morphology 3	0	1	4	0	0	0	0	0	5
	(0,0)	*(20,0)*	*(80,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(100,0)*
Morphology 4	0	0	0	15	0	0	0	0	15
	(0,0)	*(0,0)*	*(0,0)*	*(100,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(100,0)*
Morphology 5	0	0	0	0	7	1	0	0	8
	(0,0)	*(0,0)*	*(0,0)*	*(0,0)*	*(87,5)*	*(12,5)*	*(0,0)*	*(0,0)*	*(100,0)*
Morphology 6	0	0	0	0	0	4	1	0	5
	(0,0)	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(80,0)*	*(20,0)*	*(0,0)*	*(100,0)*
Morphology 7	0	0	0	0	0	0	5	0	5
	(0,0)	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(100,0)*	*(0,0)*	*(100,0)*
Morphology 8	0	0	0	1	0	0	0	9	10
	(0,0)	*(0,0)*	*(0,0)*	*(10,0)*	*(0,0)*	*(0,0)*	*(0,0)*	*(90,0)*	*(100,0)*

Table 5. Count of scales (Non-italic numbers) and differential abundance (Italic numbers) of each functional type by levels and sections (A: Henarejos; B: Bugarra).

Tabla 5. Recuento de escamas (Números sin cursiva) y abundancia diferencial (Números en cursiva) de cada tipo funcional por niveles y secciones (A: Henarejos; B: Bugarra).

A		**Level**							
		He - 14		**He - 18**		**He - 19**		**He - 20**	
		Count	%	Count	%	Count	%	Count	%
Functional type	**Abrasion strength**	32	*22,9*	90	*46,2*	31	*16,4*	10	*5,2*
	Drag reduction	96	*68,6*	96	*49,2*	137	*72,5*	152	*79,6*
	Generalized functions	12	*8,6*	9	*4,6*	21	*11,1*	29	*15,2*
	TOTAL	140	*100*	195	*100*	189	*100*	191	*100*

B		**Level**							
		Bu 1 - 33		**Bu - pl**		**Bu 1 -26**		**Bu 1 – 26d**	
		Count	%	Count	%	Count	%	Count	%
	Abrasion strength	13	*39,4*	18	*21,7*	10	*41,7*	85	*30,2*
	Drag reduction	16	*48,5*	60	*72,3*	10	*41,7*	138	*49,1*

Functional type									
	Generalized functions	4	*12,1*	5	*6,0*	4	*16,7*	58	*20,6*
	TOTAL	33	100	83	100	24	100	281	100

Test of independence of functional types abundances and stratigraphic levels: χ^2 = 139,301; f.d. = 14; Sig. = 0,000.

Table 6. Z-test results based on two-sided tests with a significance level 0.05. For each significant pair, the key of the category with the smaller column proportion appears under the category with the larger column proportion.

Tabla 6. Resultados del test-Z basados en pruebas bilaterales con un nivel de significación 0,05. Para cada par significativo, la clave de la categoría con la proporción de columna menor aparece debajo de la categoría con mayor proporción de columna.

A		**Level**			
		He – 14 (A)	**He – 18 (B)**	**He – 19 (C)**	**He – 20 (D)**
Functional type	**Abrasion strength**	D	A, C, D	D	
	Drag reduction	B		B	B
	Generalized functions				B

B		**Level**			
		Bu 1 – 33 (A)	**Bu – pl (B)**	**Bu 1 -26 (C)**	**Bu 1 – 26d (D)**
Functional type	**Abrasion strength**				
	Drag reduction		C, D		
	Generalized functions				B

6b

		Level							
		Bu 1 -33 (A)	Bu – pl (B)	Bu 1 -26 (C)	Bu 1-26d (D)	He – 14 (E)	He – 18 (F)	He – 19 (G)	He – 20 (H)
Functional type	Abrasion strength	H	H	H	G,H	H	B,D,E,G,H	H	
	Drag reduction		D,F			D,F		D,F	A,C,D,F
	Generalized functions				E,F				F

Table 7. Partial correlation analysis results between fossil teeth and functional types of scales. Significant correlations are identified with a single asterisk (A: Control variable *Prolatodon*; B: Control variable *Lissodus*; C: Control variable *Pseudodalatias*; D: Control variable *Hybodus*).

Tabla 7. Resultados del análisis de correlación parcial entre los dientes fósiles y los tipos funcionales de escamas. Las correlaciones significativas se presentan con un asterisco (A: Variable control *Prolatodon*; B: Variable control *Lissodus*; C: Variable control *Pseudodalatias*; D: Variable control *Hybodus*).

A			**Teeth genera**		
			Hybodus	*Pseudodalatias*	*Lissodus*
	Abrasion strength	Correlation	-0,142	0,214	-0,171
		Significance	0,761	0,645	0,714
Functional type	**Drag reduction**	Correlation	-0,080	0,182	-0,225
		Significance	0,864	0,697	0,628
	Generalized functions	Correlation	0,358	-0,622	0,607
		Significance	0,431	0,136	0,148

B			**Teeth genera**		
			Hybodus	*Pseudodalatias*	*Polyacrodus*
	Abrasion strength	Correlation	-0,515	-0,269	0,775*
		Significance	0,237	0,560	0,041*
Functional	**Drag**	Correlation	0,431	0,451	-0,864*

type	**reduction**	Significance	0,335	0,310	0,012*
	Generalized functions	Correlation	0,303	-0,557	0,242
		Significance	0,509	0,175	0,601

C			**Teeth genera**		
			Hybodus	*Lissodus*	*Polyacrodus*
Functional type	**Abrasion strength**	Correlation	-0,668	-0,041	0,760*
		Significance	0,101	0,931	0,047*
	Drag reduction	Correlation	0,793*	-0,125	-0,825*
		Significance	0,033*	0,789	0,022*
	Generalized functions	Correlation	-0,198	0,519	-0,014
		Significance	0,670	0,233	0,977

D			**Teeth genera**		
			Pseudodalatias	*Lissodus*	*Polyacrodus*
Functional type	**Abrasion strength**	Correlation	-0,549	-0,043	0,673
		Significance	0,202	0,928	0,098
	Drag reduction	Correlation	0,809*	-0,249	-0,833*
		Significance	0,027*	0,590	0,020*
	Generalized functions	Correlation	-0,690	0,676	0,473
		Significance	0,086	0,095	0,284

Appendix 1. Percentages of original and cross-validated grouped cases correctly classified obtained using Fourier analysis (Polar and elliptical) with different number of harmonics (20, 40, 60 and 100).

Apéndice 1. Porcentajes de casos originales y por validación cruzada clasificados correctamente usando Análisis de Fourier (Polar y elíptico) con diferente número de harmónicos (20, 40, 60 y 100).

Original cases				
Number of harmonics	**20**	**40**	**60**	**100**
Polar Fourier Analysis	82 %	88 %	88 %	87 %
Elliptical Fourier Analysis	80 %	88 %	86 %	53,3 %

Cross-validated cases				
Number of harmonics	**20**	**40**	**60**	**100**
Polar Fourier Analysis	76 %	70 %	72 %	80 %
Elliptical Fourier Analysis	64 %	68 %	66 %	42,2 %