

A holistic approach to the palaeoecology of Las Hoyas *Konservat-Lagerstätte* (La Huérguina Formation, Lower Cretaceous, Iberian Ranges, Spain)

Una aproximación holística a la palaeoecología del *Konservat-Lagerstätte* de Las Hoyas (Formación La Huérguina, Cretácico Inferior, Cordillera Ibérica, España)

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Abstract

The Las Hoyas fossil site (Lower Cretaceous, Iberian Ranges, Spain) is a classic lacustrine *Fossil-Lagerstätte* that exemplifies the features predicted by the original concept of *Konservat-Lagerstätten* in relation to the quantity of remains, quality of preservation, completeness, and preservation by a combination of obrution, stagnation and, in this case, mainly bacterial sealing. Fossils are preserved in rhythmically laminated limestones deposited in a environment that underwent strong, climatically driven cyclical oscillations in water level within the framework of a seasonal, subtropical, regional-scale wetland. Extensive systematic layer-by-layer excavation and geological research have resulted in a comprehensive understanding of the stratigraphy and sedimentology of the locality and its regional palaeogeography. Two approaches have allowed the palaeoecology of the fossil association to be reconstructed. Firstly, autoecological reconstructions of the fossil groups are supplemented by palaeoenvironmental reconstructions based on the sedimentology. This considers taphonomic features and the ecological structure of the whole association, including vegetation and animals. The organization of the ecosystem resembles that of extant lentic ecosystems. It is dominated by obligate aquatic and amphibious organisms; facultative terrestrial organisms are scarce. Several lines of evidence from flora and fauna indicate strong seasonality and water stress. The second approach is dynamic and aims to unravel the information transferred to the fossil record about ecological dynamics and evolution by combining stratigraphical and palaeontological information and integrating this in a spatial and temporal framework. This analysis illustrates that Las Hoyas has a significant facies bias, reflecting alternating

wet and dry climatically controlled periods. The biotic response these wet and dry cycles produced a coupling of taphonomic and sedimentary processes that resulted in the characteristic cyclical arrangement of the stratigraphic and palaeontological record. Las Hoyas therefore represents a subtropical seasonal wetland impacted by cyclicity and ecological stress. This stress impeded short-term ecological evolution and resulted in a stable ecosystem that lasted for thousands of years. The results of this study also have implications for the concept of *Konservat-Lagerstätten* and its limitations. Whereas the former approach considers Las Hoyas as a canon of minimally biased information (as it is a *Konservat-Lagerstätte*), the latter approach reveals the biased characteristics of the association. The study illustrates that although all *Konservat-Lagerstätten* share similar preservational mechanisms, the paleoecological information that contain may differ.

Keywords: Las Hoyas, *Konservat-Lagerstätten*, Lentic Ecosystem, Paleoeological Dynamics, Facies Bias, Sedimentary and Taphonomic Cyclicity, Seasonal Wetlands, Lower Cretaceous

Resumen

El yacimiento de Las Hoyas (Cretácico Inferior, Cordillera Ibérica, España) es un clásico *Fossil-Lagerstätte* lacustre que encaja perfectamente con los rasgos que predice el concepto de *Konservat-Lagerstätte* en lo relativo a la abundancia de restos, calidad de conservación, completitud y génesis del depósito debido a la combinación de factores relacionados con el enterramiento rápido, el estancamiento y, en el caso particular de Las Hoyas, el sellado bacteriano. Los fósiles se conservan en calizas finamente laminadas que fueron depositadas en un ambiente que estuvo sujeto a fuertes oscilaciones cíclicas en el nivel de agua, climáticamente reguladas, en el marco de un humedal estacional y subtropical de escala regional. Las profusas excavaciones sistemáticas realizadas capa a capa, y la investigación geológica han dado lugar a un profundo conocimiento de la estratigrafía y sedimentología de la localidad y de su paleogeografía regional. Una doble aproximación a la interpretación de las asociaciones fósiles ha permitido la reconstrucción paleoecológica de la localidad. La primera parte de las reconstrucciones autoecológicas de los grupos fósiles retroalimentadas por la reconstrucción paleoambiental basada en la sedimentología. En esta aproximación se consideran las características tafonómicas y la estructura ecológica de la asociación completa, incluyendo la ecología vegetal y animal. La organización del ecosistema sigue un patrón semejante al de los ecosistemas lénticos actuales. Este ecosistema se caracteriza por la dominancia de organismos acuáticos obligados y de categorías anfibias y por la escasez de formas facultativas terrestres. Hay evidencias diversas, en la flora y en la fauna, de estrategias ecológicas vinculadas a la fuerte estacionalidad y al estrés hídrico. La segunda aproximación es dinámica, y pretende desvelar la información transferida al registro fósil en cuanto a la dinámica ecológica y su evolución mediante la combinación de información proporcionada por datos estratigráficos y paleontológicos, de modo que los datos son interpretados en términos de su marco y significado espacial y temporal. Este análisis muestra que Las Hoyas tiene un sesgo significativo de facies (*facies bias*), reflejando la alternancia de periodos húmedos y áridos controlados climáticamente. La respuesta biótica a estos ciclos húmedos y áridos produjo un acoplamiento entre los procesos tafonómicos y sedimentarios que da lugar a una estructura cíclica del registro estratigráfico y paleontológico de Las Hoyas. Por consiguiente, Las Hoyas representa un humedal subtropical estacional regido por la ciclicidad y por el estrés ecológico. Dicho estrés impide una evolución ecológica a corta escala dando lugar a un ecosistema estable que debió durar miles de años. El resultado de este estudio tiene algunas implicaciones en el concepto de *Konservat-Lagerstätten* y en sus limitaciones. Mientras que bajo la primera aproximación Las Hoyas se consideraría canon de información con un sesgo mínimo, puesto que es un depósito de conservación excepcional, la segunda aproximación pone de manifiesto el sesgo presente en la asociación. Este estudio ilustra que aunque todos los *Konservat-Lagerstätten* comparten mecanismos de conservación similares, la información paleoecológica que contienen difiere entre ellos.

Palabras clave: Las Hoyas, *Konservat-Lagerstätten*, Ecosistemas Lénticos, Dinámica Paleológica, *Facies Bias*, Ciclicidad sedimentaria y tafonómica, Humedales estacionales, Cretácico Inferior

1. Introduction

Konservat-Lagerstätten deposits are distinguished by the quality of preservation of soft-bodied organisms (Seilacher, 1990). *Konservat-Lagerstätten* have been considered as the “end member of a continuum” in the preservational spectrum (Allison and Briggs, 1991). Various factors and combinations thereof can be involved in the genesis of any deposit, but exceptional deposits have been explained within the framework of three parameters: obrution, stagnation and bacterial sealing. This background, provided by Seilacher *et al.* (1985), thus offers a

broad, simple classification. *Konservat-Lagerstätten* are usually interpreted as having resulted from the presence of specific palaeoecological and palaeoenvironmental factors, such as the presence of oxyclines or haloclines, biostratinomic factors involving rapid burial or factors related to necrolysis, such as the role of bacterial mats in slowing the rate of degradation of soft tissues and their authigenic replacement. Influenced by Seilacher’s model most studies use the preservational potential of a particular environment (e.g., anoxic bottom, early phosphatization, rapid burial, etc.) to explain why fossils are exceptionally well preserved (see for instance Stinnesbeck *et*

al. 2005 for the Late Cretaceous outcrop of El Rosario in Mexico). Concerning the relative abundance and absence of the preserved taxa, the composition of fossil assemblages is explained in ecological terms (environmental affinities and preferred habitats of species) rather than as taphonomic biases (see as an example Palci *et al.*, 2008 for the Kolmen, Slovenia Cenomanian Lagerstätte).

For many decades *Konservat-Lagerstätten* have been considered a canon with maximum information, exceptional places where palaeobiological information has been somehow frozen, the succession of singular “catastrophic events” of mass mortality being the commonest explanation for these exceptional deposits (Shipman, 1975).

Konservat-Lagerstätten have revealed the existence of organisms that never fossilize under other conditions, and the anatomical details of organic structures that would otherwise remain unknown; in summary they have provided specialists with abundant key evolutionary biological data. Little would be known about the early evolutionary stages of marine life if the Burgess Shale and Chengjiang did not exist. They may be thought of as windows onto the fossil record, through which the best approaches to the studying the Earth’s biological past can be pursued.

Assuming all these arguments are correct, it could also be argued that a realistic model of the representativity of this type of fossiliferous deposit with respect to palaeoecological aspects, among others, is methodologically handicapped. In other words, the *Konservat-Lagerstätte* model has become associated with a static or frozen view of palaeoecology that neglects the temporal sequence of events. In contrast a more dynamic perspective of a more holistic view, of the quality (i.e., preservation and bias) of the fossil record has been focused particularly in the marine realm, and structured within the sequence stratigraphic perspective (Holland, 2000). The advantage of this approach is that it accommodates many of the biases of the fossil record that vary over time and between environments.

It is not known yet if all of the *Konservat-Lagerstätten* are “palaeoecological windows” as they are for the studies on past biodiversity. It remains unclear what kind of palaeoecological information is transferred to the fossil record, that is, whether the *Lagerstätten* preserve their original dynamics and palaeoecological structure, and to what extent any bias is common to all *Konservat-Lagerstätten*.

Las Hoyas is a well-known Barremian (Lower Cretaceous) continental *Konservat-Lagerstätten*, acknowledged as one of the most important Lower Cretaceous *Lagerstätten* in the world (Sanz *et al.*, 2001). It is located

at the Serranía de Cuenca (Iberian Ranges, east-central Spain) and occurs within the La Huérguina Limestone Formation. Since it was discovered in 1985 it has yielded several thousand ichnofossils and body fossils, the latter including Bacteria, Fungi, Protista (Foraminifera), Algae, and a wide spectrum of Plant and Animal phyla (Buscalioni *et al.*, 2008; Fregenal-Martínez and Buscalioni, 2009, see below). It is especially well known as probably the best Mesozoic locality for fossil insects (Martínez-Delclós *et al.*, 2004). The locality has provided palaeontologists with information critical to understanding the early radiation of birds and the development of flight (Sanz *et al.*, 2002). It has also yielded significant information on the evolution and life habits of other organisms. For instance, articulated Characeae with their vegetative apparatus preserved were described first from Las Hoyas (Martin-Closas and Diéguez, 1998). The enigmatic *Montsechia vidali* has been interpreted as being an aquatic angiosperm on the basis of its ultrastructural preservation (Daviero-Gómez *et al.*, 2006). The replacement of “holostean” by early teleostean faunas may be documented at Las Hoyas (Poyato-Ariza, 2005). Some of the most significant discoveries relate to the anatomy of the albanerpetontid *Celtesdens* (McGowan and Evans, 1995), and the early evolution of Aves, for example the presence of a pygostyle in *Iberomesornis romeralli*. The earliest known alula was recorded in *Eoaulavis* (Sanz *et al.*, 1996; Sanz *et al.*, 2002) (see <http://www.yacimientolashoyas.es> for a list of cases and references).

Most of the fossils are fully articulated (excluding macrophytes) and many preserve soft tissues, and organic patterns and structures rarely found in the fossil record: patterns of colouring, nerviation, gut tracts, and ommatidium of insects, stomach contents and muscles of fishes, skin and integumentary tissues of such as frogs, salamanders, lizards, crocodiles and dinosaurs.

The sedimentary succession of Las Hoyas is a continuous, cyclical accumulation of finely laminated limestones deposited in an area that on a regional-scale was a wetland environment, strongly influenced by subtropical, seasonal climatic conditions.

The comprehensive palaeontological and stratigraphical records of Las Hoyas, and the large amount of data retrieved from many years of layer-by-layer excavation, have allowed us to adopt a dual approach to reconstructing the palaeoecology of the fossil assemblage. The goals of the current study are therefore two-fold. The first is to perform a palaeoecological analysis based on sedimentological data, the taphonomic features of the fossil association, and the recorded biota. Since Las Hoyas is a *Konservat-Lagerstätte*, this analysis will consider the entire fossiliferous lithosome as a unique, minimally bi-

ased, taphonomic unit. The second goal is to determine whether palaeoecological information can be interpreted in the context of ecological dynamics, especially evolutionary dynamics, by analyzing Las Hoyas in the actual temporal and spatial framework provided by its stratigraphic record. This approach aims to be the starting point for advances in the concepts and methodologies of palaeoecology, encouraging analyses of dynamics, while questioning some traditional assumptions in this area of research.

In the light of the conclusions obtained from the palaeoecological analysis of Las Hoyas the value and meaning of *Konservat-Lagerstätten* from the palaeoecological perspective is also revised.

2. Geological setting

The Serranía de Cuenca is part of the Iberian Ranges, a NW-SE oriented mountain chain that covers an extensive area in the eastern half of the Iberian Peninsula and was generated by the tectonic inversion of the Iberian Basin. The Iberian Basin was an intracratonic extensional basin formed during the Late Permian–Early Triassic that remained active throughout the Mesozoic until the Alpine Orogeny.

During the Late Jurassic–Early Cretaceous the Iberian Basin experienced a rifting phase related to the opening of the central Atlantic and the rotation of the Iberian Plate (Salas and Casas, 1993). Four palaeogeographic domains have been defined for the Early Cretaceous of the Iberian Basin (Soria *et al.*, 2000): Cameros, Central Iberian, Maestrazgo and South-western Iberian (Fig. 1A). Extensional tectonics divided each domain into many well-differentiated subbasins of graben and half-graben type.

The South-western Iberian Domain was limited by extensional fault systems running NW-SE (Vilas *et al.*, 1982, 1983, Mas *et al.*, 1982), with associated NE-SW systems of transfer faults that accommodated differences in extension rates.

The NE-SW Landete-Teruel transfer fault divides the South-western Iberian Domain into the Serranía de Cuenca and Valencia Basins. The Serranía de Cuenca Basin was in turn divided by the NW-SE extensional Hesperic fault to form two subsiding troughs (Uña-Las Hoyas and La Huérguina). The Uña-Las Hoyas Trough is composed of at least five small subbasins: Uña, Buenache, Los Aliagares, Las Hoyas and La Cierva (Fig. 1B).

Barremian sedimentation in the Serranía de Cuenca occurred under continental environmental conditions and no direct marine influence is observed (Poyato-Ariza *et al.*, 1998). Marine influence is restricted to the Valencia

Basin which was bounded by the Tethys Sea at its eastern edge (Mas *et al.*, 1982).

The climate of this area has always been considered to be seasonal subtropical with alternating wet and dry seasons. This interpretation is based on several sources of proxy climate data. Ziegler *et al.* (1983) performed a palaeogeographical and palaeoclimatic reconstruction and placed this area of the Western Tethys at the dry, divergent subtropical zone at a latitude of 25–30°N. Ziegler *et al.* (1987), on the basis of palaeobotanical data, proposed that seasonality occurred in tropical and subtropical areas, and a seasonal warm and semi-arid subtropical climate was assumed for the Iberian Plate during the Lower Cretaceous. Haywood *et al.* (2004) developed a model for Barremian Wealden climates of Western Europe using a Limited Area Model, which confirmed strong biannual seasonality of temperature, with mean cold-month temperatures of 4–8°C, and mean warm-month temperatures of 36–40°C. However, the model unexpectedly predicts an average precipitation rate of 4–8 mm/day for any one month, and more than 16 mm/day during the cold season. The model-predicted moisture budget results in very high evaporation rates, which greatly reduces moisture availability at ground level, thus accounting for the proxy data indicating dry conditions. Successive facies analyses of the Barremian deposits in different areas of the Serranía de Cuenca Basin have repeatedly shown sedimentological evidence of seasonality and highlighted climate as a extremely significant allocyclic control of sedimentation (Gierlowski-Kordesch *et al.*, 1991, Gómez-Fernández and Meléndez 1991, Fregenal-Martínez and Meléndez, 1993, Fregenal-Martínez 1998, Fregenal-Martínez and Meléndez, 2000).

In the Serranía de Cuenca, Barremian sediments overlie Bathonian (Middle Jurassic) marine limestone unconformably (Fig. 1B); the latter underwent strong karstification during the Upper Jurassic and even during continental Early Cretaceous sedimentation.

Barremian continental deposits form two lithostratigraphic units linked by a lateral facies change: El Collado Sandstones Fm and La Huérguina Limestones Fm (Vilas *et al.*, 1982).

The Uña-Las Hoyas Trough exhibits little El Collado Fm, being filled mainly by deposits of the La Huérguina Fm. The thickest succession of the La Huérguina Fm occurs in the Las Hoyas Subbasin, which was infilled by almost 400 m of distal alluvial and palustrine-lacustrine deposits (Fregenal-Martínez 1998, Fregenal-Martínez and Meléndez, 2000). The sedimentary record of Las Hoyas has been divided into four sequences (Fig. 1C) separated by local unconformities or paraconformities and named

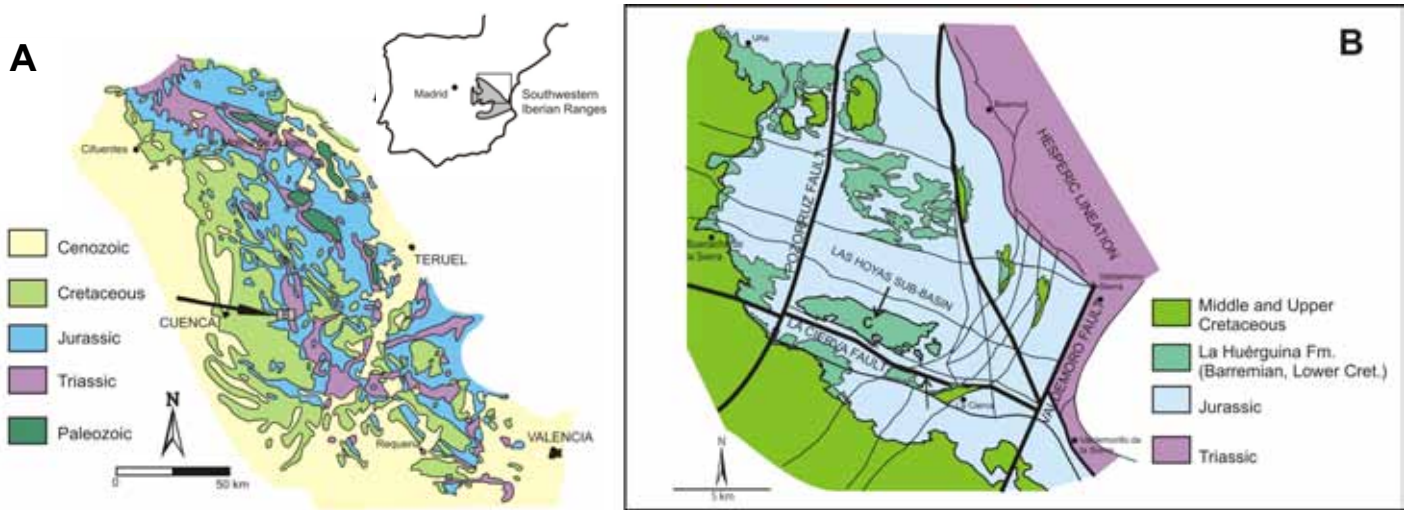


Fig. 1.-A. Location and general geological map of the Southwestern Iberian Ranges. B. Simplified geological map of Las Hoyas area. C. Detailed geological map of Las Hoyas sub-basin showing the position of Las Hoyas fossil site.

Fig. 1.-A. Localización y mapa geológico general de la Cordillera Ibérica Suroccidental. B. Mapa geológico simplificado del entorno de Las Hoyas. C. Mapa geológico detallado de la cubeta de Las Hoyas en el que se muestra la posición del yacimiento de Las Hoyas.

informally in ascending order as Rambla de Las Cruces I, Rambla de Las Cruces II, Pocillo del Pozuelo and Hoya de la Madre de las Latas (Fregenal-Martínez, 1998, Fregenal-Martínez and Meléndez, 2000).

The fossil-bearing rhythmically laminated limestones of the Las Hoyas *Konservat-Lagerstätte* occur in the Rambla de Las Cruces II Sequence, which is entirely composed of carbonates and characterized by the dominance of palustrine-lacustrine facies over distal alluvial and flood-plain facies.

3. Conceptual and methodological framework

The two objectives proposed in this work relate to two distinct conceptual frameworks. The results will illustrate that the two approaches are complementary.

The first approach assumes a “static” palaeoecological interpretation, and is based on sedimentology and supplemented by palaeobiology and taphonomy. It enhances the functional relationships and the congruence among

(i) the palaeoenvironmental hypothesis (addressed from the sedimentological analyses that establish the abiotic framework of the ecosystem), (ii) the taphonomic features of fossils (in terms of preservation of each fossil); and (iii) the relative abundance of fossils. The pattern of abundance refers herein not to the taxa themselves (as is common in this kind of study), but on the ecological categories that, according to the palaeoenvironmental hypothesis, should reflect a predicted structure. The use of ecological categories avoids the problem of rarity in species due to preservation, and furnishes the strong lines of the ecological structure, and it is thus likely to be a robust method of analysis. Epistemologically, the combination of the selected information about sedimentology, taphonomy and palaeobiology thus describes: 1) the potential for representativity, i.e., the fidelity of the composition of the palaeoecosystem, 2) the ecological dominance of the group of species that regulate the ecosystem, and 3) outstanding and significant palaeoecological processes that may explain the genesis of the deposit

and its potential biases.

The second approach is “dynamic” in that it interprets the taphonomic assemblages with respect to environment and time. In other words, the significance of the taphonomic data including their distribution within the fossiliferous lithosome will be explained in terms of the sedimentological meaning (environment) of the various facies that host each different taphonomic assemblage, and the stratigraphic architecture that the facies sequences display (sedimentary evolution over time).

Dynamic reading with respect to the environment will provide key evidence about what Holland (2000) identified “facies bias”, highlighting the environmental signal that controls differences in fossil abundance and richness. For this purpose the fossil associations present in all the facies have been compared.

Dynamic reading with respect to time will reveal the extent to which the structures of the fossil and sedimentary records are determined by the palaeoecological dynamics and whether there is an architectural taphonomic and sedimentary coupling. To this end, the succession of communities developed during every sedimentary sequence has been compared.

The taphonomic analysis performed to enable the dynamic reading includes the following criteria: the degree of demicity (*vs.* ademic) and autochthony (*vs.* allochthony) of the association (Fernandez-López, 1989). *Demicy* is a biological criterion, and is applied to those fossils that come from organisms that left ichnological traces or body parts, and/or that died in the same environment where they lived or that was their original habitat. Allochthonous is a taphonomic criterion applied to fossils that have been transported out of the place where the organism died or left any part. Whereas autochthonous refers to fossil that have been preserved where the organism died or left any part, no matter where they lived. For instance, in Solnhofen the famous horseshoe-crab fossil that left its trail before dying should be treated, applying those criteria, as ademic and autochthonous. This is the reason why Fernandez-López (1989, 1991) suggested that each criterion should be considered independently to maximize its heuristic potential, and herein we follow his criteria (*i.e.*, demicity and autochthony). The *spatial fidelity* concept used by Behrensmeyer *et al.* (2000) combines both sets of criteria (biological and taphonomic) without any explicit denomination of the weighting given to either, but the authors emphasised its relevance for understanding the preservational processes. Finally, this dynamic approach also gives a better appreciation of what has been called *temporal resolution* (Behrensmeyer *et al.*, 2000), which is the finest scale temporal category into which

the taphonomic association can be confidently assigned. Linked to temporal resolution is an evaluation of *time-averaging* (from virtually zero to millions of years), as the period of time represented by the biological components that comprise any fossil assemblage.

3.1. Data sampling and analyses

To deal with biases the primary requisite is to collect high quality data using appropriate fieldwork strategies. The database has been constructed using a systematic layer-by-layer sampling method. For each layer, the size and total number of specimens were first determined. Orientation was occasionally measured because Las Hoyas fossils are randomly distributed. Layer-by-layer excavation of square areas of 25 m² on average was carried out (Fig. 2). A total volume of more than 3000 m³ rocks was excavated.

To address the palaeobiological framework we used the complete taxonomic list of Las Hoyas, which includes information from systematic and random sampling methodologies. The taxonomic list is periodically improved by taxonomic revision carried out by specialists.

To address the sedimentary framework, the laminated limestones were exhaustively and continuously sampled. These limestones have a homogeneous appearance in the field and facies successions and associations have to be reconstructed under a petrographic microscope (Fig. 3). To this end, sampling covers the entire thickness of the excavated areas, and thin sections of rock sample were used for the microscopic description. Samples were taken while palaeontological excavation was being performed, in such a way that the fossil content of the sampled layers was always known. Herein we present the results of five years of excavations in which five contiguous areas were systematically sampled, each area being given the name of a colour (Figs. 2 and 4): 1) *pink 1996*, 2) *pink 1998*, 3) *lower black*, 4) *upper black* and 5) *lowermost black*. The sampled laminites were almost one metre thick in total and were composed of three elemental sequences (Fig. 4).

The raw data summarize the total number of fossils discovered (see Table 1 and Appendix 1). “N” takes into account only body fossils, although in the discussion other some relevant fossils are considered qualitatively, such as “worms”, coprolites and ichnofossils, that have not been quantitatively analysed because the sampling technique and taxonomical identifications progressively improved, and thus data accuracy differed slightly between areas. Consequently, neither plant remains nor other trace fossils such as coprolites and ichnofossils are included in the account provided in Table 1.

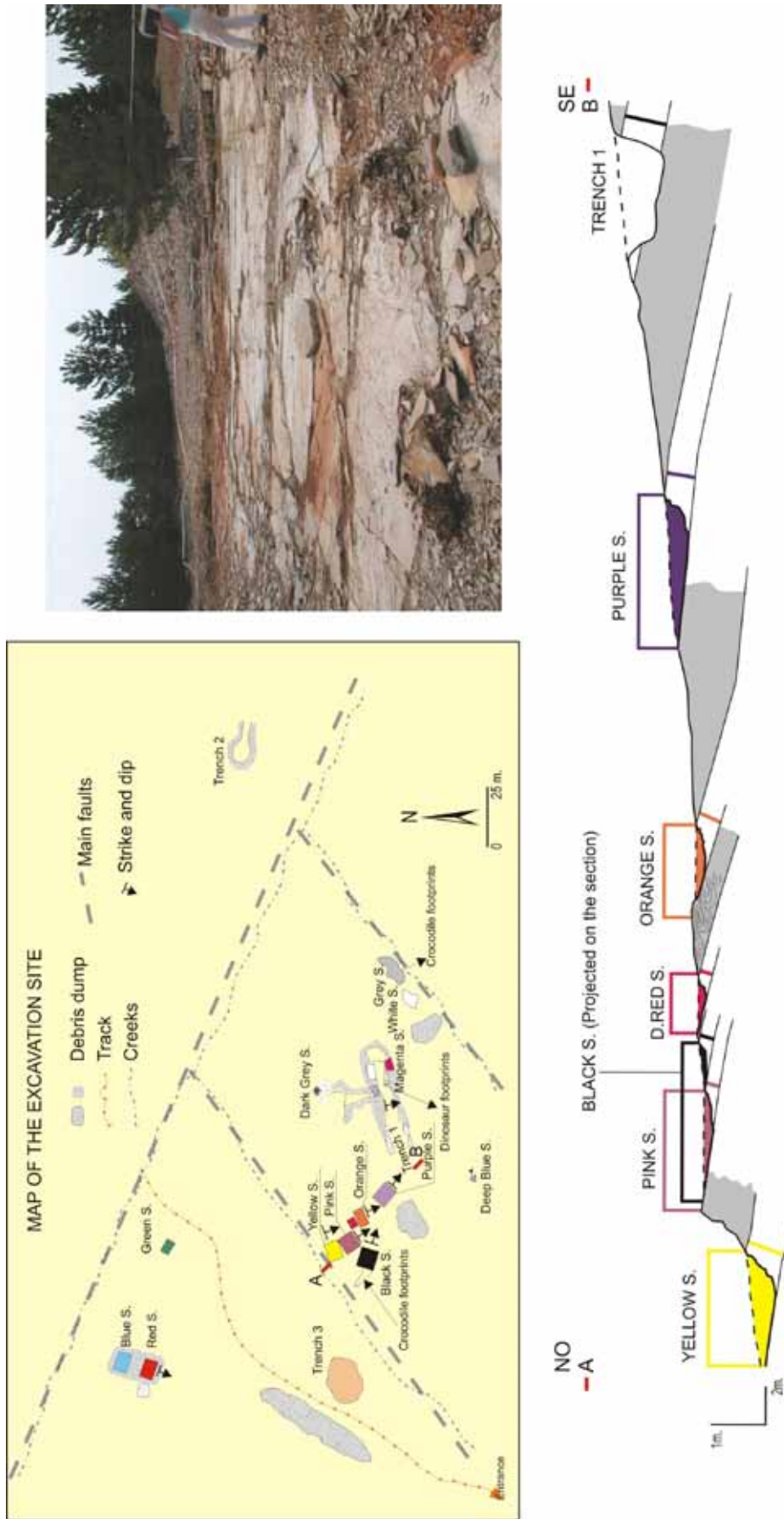


Fig. 2.- Updated map of the excavation at Las Hoyas fossil site; cross section shows the stratigraphic position of the sampled squares included in this study, and field view of the Black Square.

Fig. 2.- Mapa actualizado de la excavación del yacimiento de Las Hoyas, corte en el que se muestra la posición estratigráfica de las cuadrículas muestreadas e incluidas en este estudio y vista de campo de la Cuadrícula Negra.

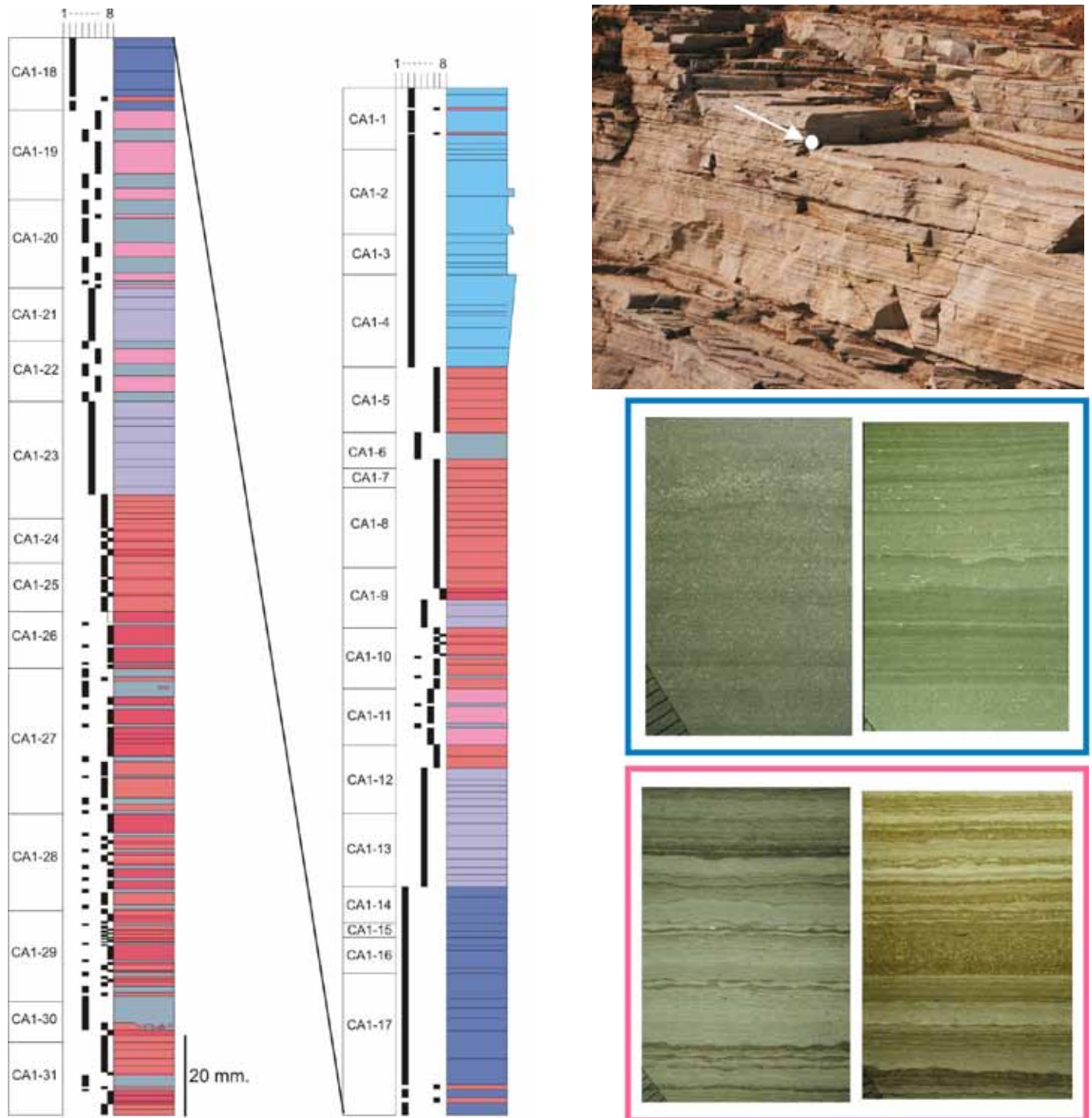


Fig. 3.- Close-up field view of laminated facies (white arrow points to a 2 euro coin for scale); reconstructed stratigraphic succession, obtained from thin sections, after a continuous layer by layer sampling. Up to eight different microfacies have been recognized numbered from 1 to 8 in the log at left and also represented by colors that range from deep blue to deep pink. The succession displays cyclical alternation of facies deposited during periods of wet (blue and bluish colored intervals) and dry (pink and pinkish colored intervals) environmental conditions. Two examples of each type of facies under the petrographic microscope are also shown, wet inside the blue framework and dry inside the pink framework. Scale division: 1 mm.

Fig. 3.- Vista de detalle en campo de las facies laminadas (la flecha blanca señala una moneda de 2 euros como escala); sucesión estratigráfica reconstruida obtenida a partir de láminas delgadas realizadas de un muestreo de campo continuo capa a capa. Se han reconocido hasta ocho microfacies diferentes que aparecen numeradas de 1 a 8 en la columna de la izquierda y que están también representadas por una gama de colores que va del azul intenso al rosa intenso como extremos. La sucesión muestra la alternancia cíclica de facies depositadas durante periodos con condiciones ambientales húmedas (intervalos coloreados en tonos azulados) y áridas (intervalos coloreados en tonos rosados). También se incluyen dos ejemplos de cada conjunto de facies a escala microscópica, las húmedas dentro del marco azul y las áridas dentro del marco rosa.

4. Characterization of Las Hoyas *Konservat-Lagerstätte* and its ecosystem: "static" approach

4.1. Paleoenvironmental reconstruction and sedimentology of Las Hoyas deposits

The picture that emerges when palaeogeographical, stratigraphical and sedimentological data are analyzed in terms of a palaeoenvironmental reconstruction for the Barremian in the Serranía de Cuenca is that of an extensive subtropical (seasonal, winter wet), continental (freshwater) wetland system, dominated by carbonate sedimentation that overlay a low-relief karstic terrain. A flat, smooth, topography with localized ridges of Jurassic limestones at the edge of the sub-basins at the time of deposition was the general landscape. Consequently, the watershed, and source areas of sediments would have been mostly composed of carbonates.

The groundwater and surface waters draining the basin would therefore have contained a high concentration of dissolved calcium carbonate that enhanced the pedogenic and biological production of carbonate and maintained basic pH conditions in ephemeral and permanent water bodies. The wetland landscape comprises the typical environmental mosaic within these depositional systems: alluvial plains, marshy and swampy palustrine plains, different types of channels, sloughs, ponds and shallow permanent lakes.

Strong seasonal differences in landscape geomorphology reflect water availability, which was greater during the wet season. During this season ponds and lakes had their highest water levels, palustrine and alluvial plains were flooded and all channels were active. During the dry season most ponds dried out, lakes had low water levels, alluvial and palustrine plains were subaerially exposed and dominated by pedogenic processes, and ephemeral channels remained inactive.

As in modern subtropical wetlands fire was an active element in these environments, and charcoal is abundant in different facies. Charcoal in flash-flood deposits is of particular significance, and suggests an association between fire and strong seasonal storms followed by flooding. Blacked pebbles and charcoal associated with palustrine deposits indicate that the other common cause of fire in these environments was spontaneous combustion with inorganic-rich palustrine soils.

The paleogeographical distribution of the different elements of the environmental mosaic reflected local conditions and each sub-basin had its own specific set of environments, e.g., permanently flooded wetlands and lakes located in specific depocentres. The type of channels var-

ied depending on the proximity to watersheds and source areas, and palustrine and pedogenic environments were associated with non-subsiding areas, such as sub-basin margins.

The fossiliferous sediments of Las Hoyas are finely laminated limestones composed almost entirely of calcium carbonate with a small fraction of clays and organic matter. These sediments accumulated in a hard water, periphyton-dominated wetland, which was covered by thick microbial mats, and underwent strong, climatically driven cyclical oscillations of the water level.

Despite the homogeneous field appearance of laminated facies, two alternating facies associations, and several transitional facies between them have been distinguished petrographically (Fig. 3).

The first association is the result of sedimentation by traction and decantation of allochthonous detrital carbonate particles and vegetal debris, chemical and bio-induced precipitation of calcium carbonate, and accumulation of thin microbial mats (Fig. 3, blue framed). These were deposited during seasonal flooding and longer-term wet periods during which high water levels favoured more lacustrine conditions.

The second association reflects the autochthonous production of carbonate linked to the growth of microbial mats that grew massively during dry periods when the water column was drastically reduced to probably just a few centimetres deep. Microbial mats and laminae of very fine detrital carbonate sediments with debris of plants and other organic remains were transported during occasional floods and form sediments deposited during dry periods (Fig. 3, pink framed). The association of dry period sediments with dinosaur and crocodile trails and isolated tetrapod tracks, as well as the sparse presence of desiccation cracks, are indicative of extreme low water levels, and support strong water level oscillations between wet and dry periods. Preliminary geochemical data from carbon and oxygen isotopes (Talbot *et al.*, 1995) suggest that Las Hoyas sediments were derived from karstic water. Therefore, the groundwater might have maintained a thin persistent water cover, or at least a certain level of humidity in the sediments, thereby avoiding frequent complete desiccation. Some drought events are implied by the presence of desiccation cracks.

Preservation of laminated sediments requires a special set of environmental conditions; in particular destruction of lamination, mainly by bioturbation, must be avoided. Anoxia is often invoked to explain such conditions. Since thermal or chemical water stratification processes are unlikely to occur in shallow freshwater subtropical lakes and wetlands, it has been hypothesized that the warm

SL	F	Q	NAS	I	C	W	O	NF	NC	NI	NB	A	B	C	D	E	F	G	H	I	1	2	3	4	5	6	7	8
Ng102R	D	3	59	N	Y	N	N	5	46	9	1	45	0	0	2	7	0	0	0	0	0	0	0	0	0	5	0	0
Ng12A	W	2	1	N	N	N	N	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ng16A	W	2	1	N	N	N	N	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ng17A	W	2	7	N	N	N	N	4	0	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	4	0	0
Ng19A	W	2	1	N	N	N	N	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ng110R	D	2	47	N	Y	N	N	46	1	0	0	1	0	0	0	0	0	0	0	0	0	46	0	0	0	0	0	0
Ng111R	D	2	1	N	Y	N	N	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ng112R	D	2	31	Y	Y	N	N	19	8	4	0	8	0	0	2	1	0	0	0	0	0	19	0	0	0	0	0	0
Ng11314R	D	2	3	N	N	N	N	2	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Ng11415R	D	2	30	N	Y	Y	N	3	6	4	0	5	0	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0
NgS1A	W	3	0	N	Y	N	N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NgS2A	W	3	1	N	Y	N	N	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NgS4A	W	3	2	N	N	N	N	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
NgS5R	D	3	5	N	Y	N	N	1	2	1	0	2	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
NgS7R	D	3	3	N	Y	Y	N	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
NgS8R	D	3	2	N	N	N	N	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
NgS9R	D	3	41	N	N	Y	N	4	2	29	1	1	0	0	3	19	2	1	1	2	1	0	0	1	0	2	0	0
NgS1012A	W	2	3	N	Y	N	N	1	0	2	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
NgS14A	W	2	1	N	N	N	N	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
NSC1A	W	2	0	N	N	N	N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NSC3A	W	2	2	N	N	N	N	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
NSC45A	W	2	1	N	N	N	N	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
NSC6R	D	2	108	N	N	N	N	101	6	1	0	6	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	1
NSC7R	D	2	22	N	Y	Y	Y	13	4	2	0	4	0	0	2	0	0	0	0	0	13	0	0	0	0	0	0	0
NSC8R	D	2	12	Y	N	N	N	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	
NSC910R	D	2	51	Y	Y	N	Y	4	6	3	0	2	0	1	1	0	0	0	1	4	0	0	0	0	0	0	0	0
NSC11A	W	1	2	N	Y	N	N	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
RS0198A	W	1	4	N	N	N	N	1	0	3	0	0	0	0	2	1	0	0	0	0	0	0	0	0	1	0	0	0
RS298A	W	1	2	N	N	N	N	0	0	4	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0
RS3_498A	W	1	0	N	N	Y	N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RS598A	W	1	2	N	Y	Y	N	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
RS698*	D	1	1	N	Y	Y	N	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RS798*	D	1	0	Y	N	N	N	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RS1198*	D	1	8	N	Y	N	N	0	8	0	0	0	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RS1398R	D	1	8	N	N	N	N	0	6	0	2	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RS1498R	D	1	26	N	N	N	N	0	26	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RS1598R	D	1	5	N	N	N	N	0	4	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RS1698A	W	1	6	N	N	Y	N	0	0	6	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
RS1798A	W	1	29	N	Y	Y	N	5	5	18	0	3	2	0	1	6	1	0	1	0	2	0	0	0	0	1	0	0
RS1.196A	W	2	9	N	N	N	N	8	1	0	0	0	1	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0
RS296R	D	2	27	N	N	N	N	23	4	0	0	3	1	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0
RS396R	D	2	36	Y	Y	N	Y	22	13	2	0	4	6	2	0	0	0	0	0	21	0	0	1	0	0	0	0	0
RS496R	D	2	29	Y	Y	N	N	12	17	0	0	9	5	3	0	0	0	0	0	12	0	0	0	0	0	0	0	0
RS596R	D	2	275	Y	Y	Y	Y	212	59	2	2	32	4	13	0	0	0	0	0	208	1	1	2	0	0	0	0	0
RS696R	D	2	6	Y	Y	N	N	2	3	0	0	2	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0

Table 1. Raw data. SL. Sampling labels. F. Facies type: W (wet), D (dry). Q=sequence; NAS=total number of fossil sampled in the layer; I=ichnofossils; C=coprolites; W="worms"; O=ostracods; NF= total number of fish; NC=total number of crustaceans; NI=total number of insects; NB= total number of bivalves; crustaceans: *Delclosia* shrimps (A); peracarids-espeleogríficeans (B); austrapotamobius decapods (C); insects: coleopterans (D); belostomatids (E); chrisopids (F); kalligrammatids (G); ephemeropters (H); chresmodids (I). Fish: "leptolepids" (primitive teleostean juveniles) (1); pleuropholidids (2); amiidid (3); *Notagodus* (4); *Gordichthys* (5); *Lepidotes* (6); pycnodontiforms (7); *Rubiesichthys* (8)

Tabla 1. Datos brutos. SL. Etiquetas del muestreo. F. Tipo de facies W (húmeda), D (árida). Q=secuencia; NAS=número total de fósiles muestreados en la capa; I=icnofósiles; C=coprolitos; W="gusanos"; O=ostrácodos; NF=número total de peces; NC=número total de crustáceos; NI=número total de insectos; NB= número total de bivalvos; Crutáceos: gambas *Delclosia* (A); peracáridos-espeleogríficeos (B); decápodo *Austropotamobius* (C); Insectos: coleopteros (D); belostomátidos (E); crisópidos (F); kalligramátidos (G); efemerópteros; chresmódidos (I). Peces: "leptolépidos" (teleósteos primitivos juveniles) (1); pleurofolídidos (2); amiididos (3); *Notagodus* (4); *Gordichthys* (5); *Lepidotes* (6); pycnodontiformes (7); *Rubiesichthys* (8).

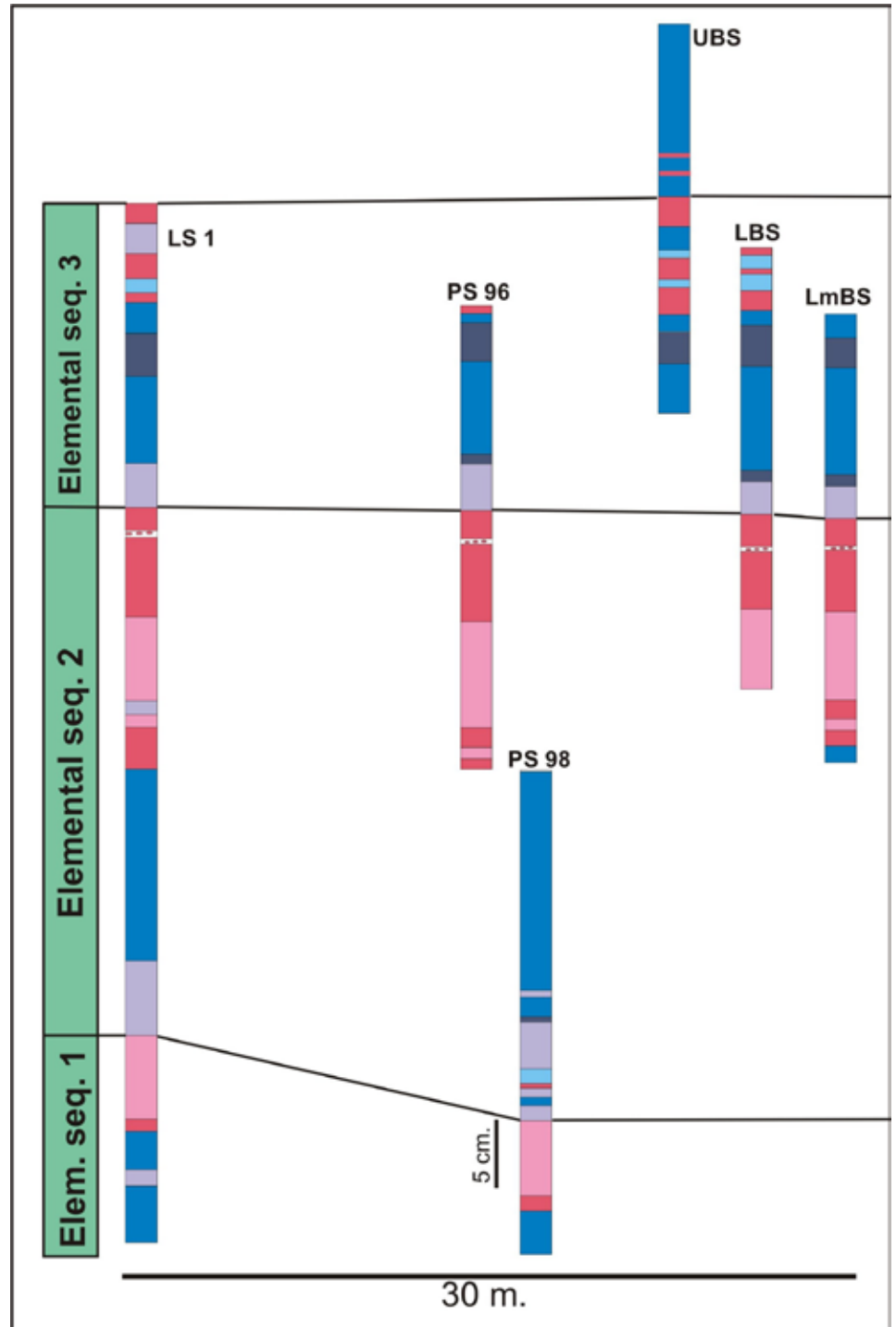
environment, prolonged periods of water stagnation, and the high rate of accumulation of organic debris carried by floods provided the conditions required to maintain anoxic to dysaerobic conditions in the sediments and bottom waters, and prevent reworking of sediments by bioturbators.

4.2. Fossil taphonomic features

Fossils from the laminated limestones of Las Hoyas show no evidences for having been transported over long distances, elements are not broken or abraded, indicating all were or produced close to their burial place (parauto-

Fig. 4.- Stratigraphic correlation, and division into three elemental sequences, of the succession of laminated facies that are included in this study. PS98- Pink Square 98; PS96- Pink Square 96; LmBS- Lowermost Black Square; LBS- Lower Black Square; UPS-Upper Black Square; LS- Lateral sampling that includes the whole stratigraphic span herein considered.

Fig. 4.- Correlación estratigráfica y división en tres secuencias elementales de la sucesión de facies laminadas que se incluyen en este estudio. PS98- Cuadrícula Rosa 98; PS96- Cuadrícula Rosa 96; LmBS- Cuadrícula Negra Basal; LBS- Cuadrícula Negra Inferior; UPS- Cuadrícula Negra Superior; LS- Muestreo lateral continuo que incluye todo el intervalo estratigráfico considerado en este trabajo.



chthonous). 70-80% of the fossils are fully articulated. The exoskeletons of crustaceans show few disarticulated appendages or antennae (Rabadà, 1993). Insects, which have been more extensively studied, are mostly articulated, especially aquatic species. Aquatic plants (*Charophytes*, the supposed angiosperm *Montsechia* and the fern *Weichselia*) have thalli, stems and fructifications preserved (Martín- Closas and Gomez, 2004). Fish scales preserved in situ and their axial columns and tails remain

articulated. Tetrapod skeletons show limited dispersion of body elements with respect to the degree of articulation and overlapping. The autochthonous condition of fossils is consistent with data from molecular taphonomy, suggesting a dominant aliphatic composition of fossil fish scales, plants and decapods, which probably arose from the incorporation of lipids from the original organic sources, indicating preservation by *in situ* polymerization of labile aliphatic components (Gupta *et al.*, 2008).

Early ontogenetic stages (juveniles) and adults are commonly present. Numerous moults (exuviae) of young individuals of the heteropterans belostomatid *Iberonepa romerali* have been noted (Martínez-Delclòs, *et al.*, 1995), and mayflies, flies and coleopteran larvae are quite frequently present (Soriano, 2006; Fregenal-Martínez *et al.*, 2007). Several juvenile salamanders, frogs and crocodylians have been discovered (Ortega *et al.*, 2003). The presence of juvenile and adult dwarf organisms such as fish and belostomatid insects is a common pattern at Las Hoyas, which shows a remarkable bias toward small fossils.

Las Hoyas is a *Konservat-Lagerstätte* that preserves a broad range of organic components: mineralised muscle, tissue imprints, chitin, cellulose, lignified cellulose, shelly and apatite skeletons (Fig. 5). Preserved eyeballs and peritoneal membranes in fish, and even white banding that may correspond to mineralised replicas of myomeres are quite common. Other examples are the mineralised muscle of the dinosaur *Pelecanimimus* (Briggs *et al.*, 1997), and the tissue imprints obtained from the albanerpetonidid *Celtesdens*. The scaly skin and eyelids, the fingers and toes tightly curled into the centre of the hands and feet, and the intact skin all suggest that this albanerpetonidid may have died and dried out (become mummified) before arriving at the burial place (McGowan and Evans, 1995). The crocodile *Montsecosuchus* has preserved scaly skin and *Eoalulavis* has limonitized feathers preserved.

Insects and crustaceans are preserved as moulds or mineralised replicas, or as impressions preserving organic matter (Delclòs *et al.* 2004). Some mecopterans and belostomatids preserve their colour pattern, and their tracheal and gut tracts. Some specimens of the *Delclossia* carid shrimp preserve digestive organs and eyes. Macroplants are preserved as impressions or as carbonaceous films. Articulated leaves and seeds are abundant, as are stems, twigs, cones and inflorescences. Palynomorphs have also been preserved.

Potential mechanisms that explain the taphonomic features of Las Hoyas are, in descending order of abundance: microbial mats (i.e., bacterial sealing), anoxia and rapid burial by sediments or rapid inclusion in microbial mats.

The contribution of microbial mats (cocoid and filamentous bacteria) has been directly observed in the preservation of tissue imprints in fish eyes (Gupta *et al.*, 2008) and in the dinosaur *Pelecanimimus polyodon* (Briggs *et al.*, 1997). In this latter, the existence of either a throat pouch or a soft occipital crest demonstrates the importance of microbial mats in preserving soft tissues. The presence of microbial mats might also be confirmed in aquatic insects (Delclòs pers. comm.). In belostomatids (*Iberonepa*), the inference of microbial mats arises from

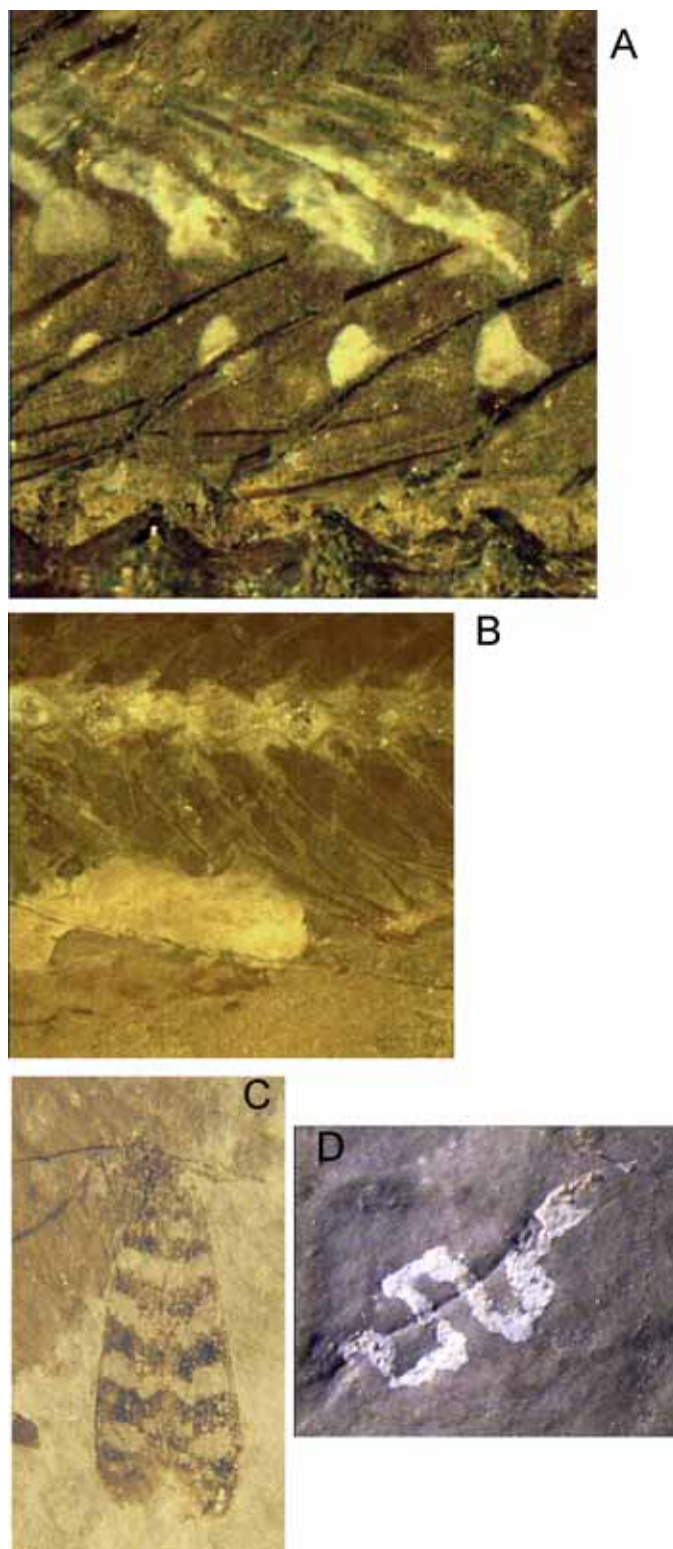


Fig. 5.- Examples of fossil preservation at Las Hoyas. A, white, banded, tissues representing mineralised replicas of fish myomeres. B, faecal mass in fish abdominal cavity. C, colour pattern preserved in Mecoptera wings. D, gut tract preserved in a belostomatid insect.

Fig. 5.- Ejemplos de conservación en los fósiles de Las Hoyas. A. El bandeado blanco corresponde a replicas mineralizadas de miómeros en un pez. B, masa fecal en la cavidad abdominal de un pez. C, patrón de coloración de las alas de un mecóptero. D, tracto digestivo de un insecto belostomátido.

the analysis of overlapping areas of a body. The mat prevents sediment infilling the cavities and spaces between body parts. The leg and abdomen of *Iberonepa* may be observed only in the absence of sediment. The confining effects of microbial mats and algae might also promote phosphatization of soft parts, such as gut tracts of fish and aquatic insects and of insect ommatidium.

The near-completeness of articulated appendages in carid decapods, such as the aquatic *Delclosia*, and bony elements in the terrestrial lizard *Hoyalacerta* and the aerial aves *Concornis*, suggest that burial events (or entombing inside microbial mats) were rapid. The comparison of the taphonomic features observed and the results of taphonomic experiments indicate that burial might have taken place in less than 20 days (Briggs, 1995; Cambra-Moo, 2003; Cambra-Moo and Buscalioni, 2003).

The initial results of a laboratory study using tanks to grow microbial mats under controlled conditions were reported by Iniesto *et al.*, (2009). Fish and insect carcasses are placed upon the mat to measure the time elapsed until embedding by the mat growth, and to observe the decay processes inside the mat. Rapid entombment occurs during this process, and in as little as two weeks individuals become completely covered. They remain fully articulated, retaining delicate anatomical details even after months of decay.

Preservation of body and trace fossils along with laminated facies requires a special set of environmental conditions. As discussed above anoxia is inferred from sedimentological and palaeoichnological analyses to account for such a preservation of fossils and sediments. Ichthyological analysis indicates that the Las Hoyas invertebrate ichnofauna (*Mermia ichnofacies*) displays evidence, such as dominance of superficial structures, the paucity of infaunal traces and a small size that indicate environmental stress due to lack of oxygen, (Buatois *et al.*, 2000) consistent with an environment with short periods of oxygenated bottom waters, but permanently anoxic interstitial waters.

4.3. Ecological structure

In terms of biodiversity, metazoans are represented by at least five or six phyla (Porifera, Mollusca, Arthropoda, Chordata and Vermiform animals, such as Nemertina and Annelida) and plants by four (Phycophyta, Bryophyta, Pteridophyta and Spermatophyta). Around 15 families and 17 genera of plants, and 50 families and 80 genera of metazoans have been documented, aquatic organisms being the most abundant. To date, the list of genera has yielded N=132, of which arthropods are by far the most diverse group, representing 45% of the genera from Las

Hoyas (Fig. 6). The arthropod Classes present are Arachnida, Diplopoda, Crustacea and Hexapoda. The hexapoda is represented by 13 orders (Ephemeroptera, Odonata, Blattodea, Isoptera, Orthoptera, Archaeorthoptera-Chresmodidae, Hemiptera, Coleoptera, Hymenoptera, Trichoptera, Neuroptera, Mecoptera and Diptera) and 40 families (Fregenal-Martínez *et al.*, 2007). The next most abundant groups are the Pteridophyta (15%) and Osteichthya (14%), while the others (Charophyte, Bryophyta, Mollusca, Amphibia, Squamata and Archosauria) make up the remaining percentage of the taxa identified so far (Fregenal-Martínez and Buscalioni, 2009). Thus, the bulk of the taxonomic diversity (67%) at Las Hoyas is based on arthropods (mainly insects) and plants (Pteridophytes, Spermatophytes, Bryophytes and Algae).

Consistent with sedimentological and palaeoenvironmental studies, our working hypothesis is that Las Hoyas was a shallow periphyton-dominated wetland that formed part of a regional-scale depositional system made up of seasonal tropical wetlands. Consequently we would expect the ecological structure to contain: 1) a complex vegetation structure, 2) animal ecology dominated by aquatic taxa, and 3) as wetlands are a mixture of transitional habitats, a hybrid of ecotones with aquatic to terrestrial plants and animals present. This broadly defines this ecosystem as an open system with no clear ecotones that generates a wide variety of microhabitats and environmental mosaicism linked to water availability. This definition is in accordance with the essence of modern wetlands provided by van der Valk (2006).

Complex vegetation structure and insects

Trophically modern wetland systems are based on the abundance of macrophytes, algae and organic detritus, and on the quality and relative abundance of insects as the second scale of primary production (Batzer *et al.*, 2006). As a wetland Las Hoyas is characterized by the extraordinary dominance of periphytons as revealed by features of its sediment and the exceptional fossil preservation.

The depositional system in which Las Hoyas was located would have been profusely vegetated (Martín-Closas, 2005). The complexity of the vegetation is characterized by the presence of submerged aquatic algae and plants. A very important part of the Las Hoyas fossil assemblage is comprised of aquatic plants. Two types of aquatic macrophytes are the most abundant: charophyte algae (Martín-Closas and Diéguez, 1998), and the early aquatic angiosperm *Montsechia* (Daviero *et al.*, 2006). Their taphonomic preservation and relative abundance reveals these to be autochthonous. Other aquatic hydrophytes such as the enigmatic *Ranunculus ferrerii*, or the floating plant *Proteaephyllum reniforme* are rare at Las Hoyas.

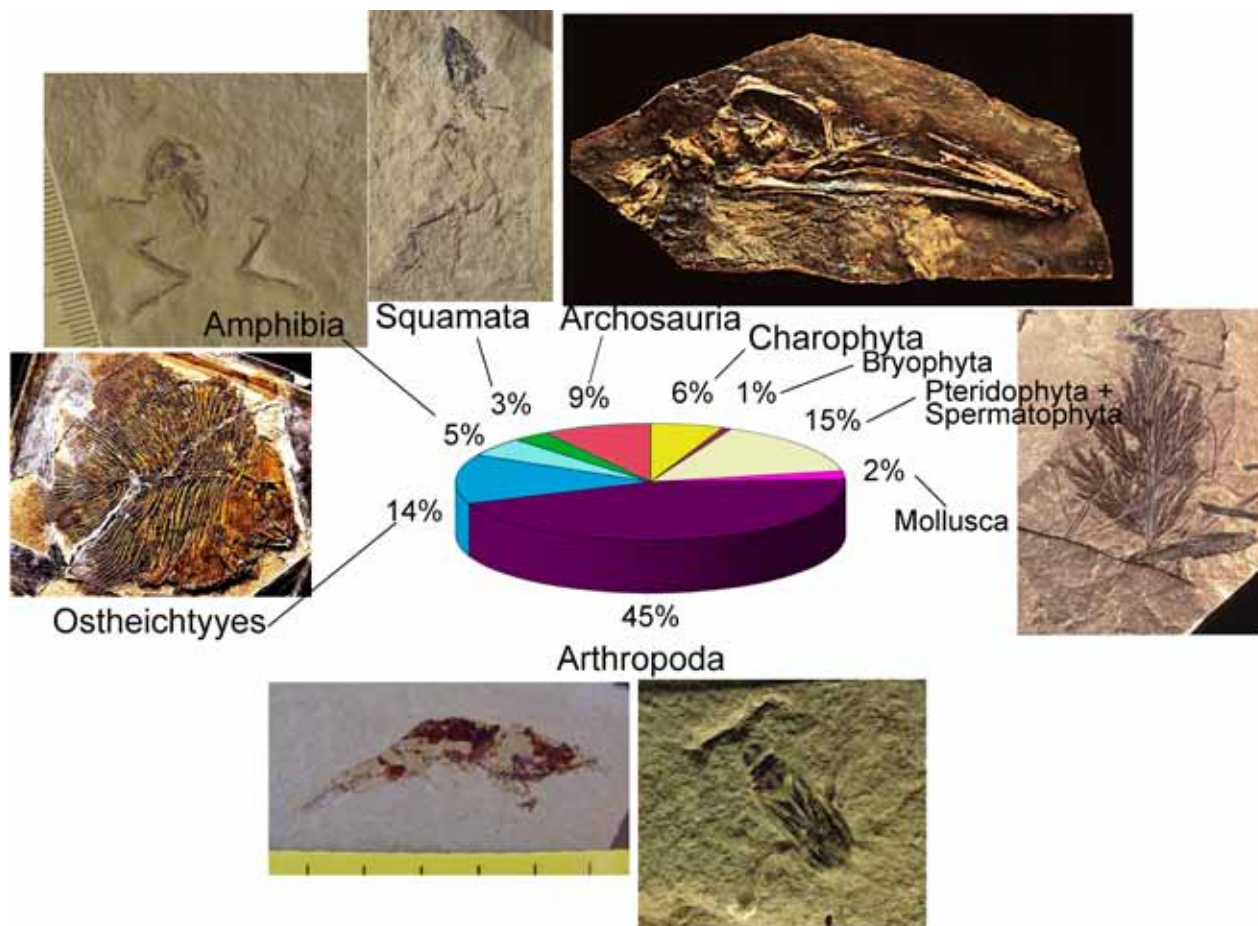


Fig. 6.-Diversity recorded in Las Hoyas. Specimens figured correspond: Osteichthyes-*Turbomesodon* MCCMLH-9266; Amphibia-*Eodiscoglossus*; Squamata-*Meyasaurus* MCCMLH-370; Dinosauria-*Pelecanimimus* MCCMLH-777; Dicksoniaceae: *Onychiopsis*; MCCMLH-29503; Heteroptera: *Iberonepa* MCCMLH-17087, and Caridea: *Declosia*. MCCMLH-280. Fossils housed at Museo de las Ciencias de Castilla-La Mancha in Cuenca (Spain)

Fig. 6.-Figura compuesta de la diversidad registrada en el yacimiento de Las Hoyas. Los especímenes figurados corresponden a: Osteichthyes-*Turbomesodon* MCCMLH-9266; Amphibia-*Eodiscoglossus*; Squamata-*Meyasaurus* MCCMLH-370; Dinosauria-*Pelecanimimus*; MCCMLH-777; Dicksoniaceae: *Onychiopsis* MCCMLH-29503; Heteroptera: *Iberonepa* MCCMLH-17087, and Caridea: *Declosia* MCCMLH-280. Fósiles pertenecientes a las colección del Museo de las Ciencias de Castilla-La Mancha en Cuenca (España).

There is a high diversity of terrestrial macrophytes. Of the heliophytic plants, conifers are the best represented, with a great diversity of Cheirolepidaceans, Taxodiaceans and *Podozamites* preserved as leaves, branches and cones. One of the most abundant is the Cheirolepidaceae *Frenelopsis*. Ferns are dominated by the Mantoniaceae species *Weichselia*, fossils of which vary in the type of preservation: articulated, fragments of pinnae and pinnules (occasionally burnt). Bryophytes (Thalites) and herbaceous ferns such as *Onychiopsis* are fairly abundant, while other herbaceous ferns, such as *Cladophlebis* and *Coniopteris*, are frequent to rare in the assemblage. Terrestrial angiosperms are rare, although several leaf types have been recorded in the locality (Barral-Cuesta and Gomez, 2009). *Frenelopsis* might be adapted to riparian habitats and grew in lacustrine environments (Gómez

et al., 2003), while ferns and mosses might form part of moist soil species, or form part of limestone outcrop communities.

High insect diversity and the wide spectrum of ecomorphotypes represented (zooplanktivorous, herbivorous, carnivorous, scavengers, xylophagous, saprophagous) reflect the environmental mosaicism of wetland systems. Abundance is biased towards aquatic insects that exhibit a wide range of ontogenetic stages (from larvae, pupae and exuviae to adults). Conversely, terrestrial forms are less abundant but more diverse, and in terms of preservation insects are represented by complete specimens and by isolated body parts mostly wings. This is demonstrated by coleopterans (Soriano, 2006) where abundance is concentrated in the aquatic family Coptoclavidae, but diversity increases in the terrestrial forms Cupedidae and

Scarabaeidae. Semi-aquatic insects and other groups living around vegetation and water bodies include grasshoppers, crickets, dragonflies, or neuropterans, caddis fly larvae and some larvae of the beetle Coptoclavidae (for details see Ponomarenko & Martínez-Delclòs 2000, Soriano *et al.* 2007). Parandrexidae beetles, Cupedid reticulated beetles, weevils and several forms of cockroaches and termites are associated with terrestrial environments, above all with wood and fungi (Martínez-Delclòs 1991, 1993, Zherikhin and Gratshev 2003, Soriano *et al.* 2006, Soriano and Delclòs 2006). Arachnids, particularly orb-weaver spiders, also form part of the terrestrial cluster (Selden and Penny, 2003).

Animal ecology

The lentic freshwater ecosystem of Las Hoyas contains one of the most significant records described for the Early Cretaceous (Sanz *et al.*, 2001). The organization of animal ecology at Las Hoyas has been analysed using the ecological categories defined for extant wetlands. The aim is to test to the extent to which an ancient ecosystem might correspond in composition and relative abundance those characteristics of modern systems. These categories are founded on the life cycles and the dependence of animals on wetland hydrology. The species can be grouped in the following categories: (1) obligate aquatic: found either in the water column or in flooded soils, (2) amphibious: species considered to spend at least part of their life cycle in wetlands and the remainder in some terrestrial environment, (3) facultative: species that may be found in wetlands and terrestrial environments, and (4) incidental: species occasionally found in wetlands.

Results from Buscalioni *et al.* (2008) reveal that Las Hoyas was dominated by obligate aquatic taxa (64%; in this previous study arthropods and macrophytes were excluded, although crustaceans, and some insects groups are also obligate aquatic), 24% of amphibious taxa, but fewer facultative to incidental forms (12%).

Of the obligate aquatic organisms, there are thousands of fish specimens. They are focal wetland animals because they are keystone species in terms of their ecological role, the productivity of wetlands being mainly based on fish biomass (Batzer *et al.*, 2006). As a general condition, most dominant fishes in modern wetlands are small-sized species and small individuals. Protected wetland areas, as seems to be the case for Las Hoyas, are places selected by fished for protection from predators and as nesting areas. This would explain the bias towards juvenile individuals at this locality. Las Hoyas is not special in this sense, since the most abundant individuals are small juveniles of *Notagodus* (Wenz and Poyato-Ariza, 1994), and a basal

teleostean fish, formerly related to "leptolepids" (Poyato-Ariza, 1997). Other teleostean species, such as the genera of the family Chanidae, *Gordichthys* and *Rubiesichthys*, are frequent, and are also small species. Species with a medium-to-large body size are less abundant. These include pycnodontiform fish like *Turbomesodon*, the coelacanth "*Holophagus*" (one of the largest), *Lepidotes*, and several amiiform species (*Vidalamia*, *Caturus* and *Amiopsis*) (Poyato-Ariza and Wenz, 2004).

The most abundant aquatic insect is the belostomatid *Iberonepa*, which has adaptations for active swimming, with its appendicular segments transformed into paddles. Less abundant although still frequent are insects that exhibit morphological aquatic adaptations for locomotion or feeding strategies, such as coptocloid coleopterans, chresmodids, dipterans larvae, odonates, anisopterans (see Fregenal-Martínez *et al.*, 2007 for a summary). Most aquatic insects depend on plant shelter. The presence of mayflies (Ephemeroptera), preserved as nymphs and adults at Las Hoyas, might indicate oxygenated waters, since oxygen stress prevents many aquatic animals groups from occupying poorly oxygenated wetlands (Mendelsohn and Batzer, 2006). This condition is supported by the absence of midges (Chironomids), which are the aquatic insects best adapted to low oxygen levels in modern wetlands (van der Valk, 2006).

Decapods are the most abundant invertebrates in Las Hoyas. Their trophic regimes range from omnivorous to scavenging (for the astacid decapod *Austropotamobius*, Garassino, 1996) to feeding on periphyton (as may be the case for the shrimp *Declosia*, since it occurs in modern relatives; Burns and Walker, 2000). The presence of peracarids, the minute spelaeogriffaceans, with a poor and patchy fossil record, and today live in fresh groundwater limestone caves should also be noted (Jaume, 2008). Other crustaceans, such as ostracods, have also been recovered at Las Hoyas, associated with mass mortality or invasion, as well as other invertebrates made up of a plethora of rather small- to medium-sized worm-like organisms whose taxonomy is difficult to establish because no fossil record is described for them.

Unionid bivalves and conchostraceans are also present and reveal that Las Hoyas water would have been alkaline, since the recent equivalents of these organisms typically live in alkaline waters, ranging in pH from 6.6 to 9.5 (for unionids see Good, 2004). Water alkalinity was deduced from independent criteria using sedimentological and geochemical sources (Poyato-Ariza *et al.*, 1998). The amphibious category gathers those species that are considered to spend at least part of their life cycle in wetlands and the remainder in a terrestrial environment;

albanerpetontids, anurans, caudates as well as chelonians and crocodylomorphs form part of this category. Albanerpetontids and crocodylomorphs are by far the most dominant groups. Turtles are rare (a new centrocryptodiran turtle is represented by three juvenile specimens that do not exceed 20 cm in body length). Within this category some taxa might be more terrestrial and less water-dependent. For instance, the albanerpetontid *Celtedens* had terrestrial adaptations. In contrast, the salamander '*Hylaeobatrachus*' retained its external gills and is therefore definitely fully aquatic (Evans and Milner, 1996). In the same sense, two groups of crocodylomorphs are included in this biota, one with terrestrial adaptations (a gobiosuchid, Buscalioni *et al.*, 1996, Ortega, 2004) and the other possessing aquatic life habits (advanced neosuchians). It is worth noting that most of the recovered specimens in the amphibious category are juveniles and/or small-sized species.

Facultative species are diverse but rare. Lizards and dinosaurs were facultative and incidental terrestrial components of this biota, respectively. The terrestrial habits of the Las Hoyas lizard biota include the runner *Meyasaurus* (the most abundant species), the climber *Scandensia* and the burrower *Hoyalacerta* (Evans and Barbadillo, 1998). Non-avian dinosaur body fossils are extremely rare, and the group comprises medium- to small-sized individuals, among including the ornithomimosaur *Pelecanimimus* (Pérez-Moreno *et al.*, 1994). Dinosaur ichnofossils are fairly common, although their presence seems to be linked to particular palaeoenvironmental settings (see below). Pterosaurs have also been categorized as facultative to incidental organisms. Fossils belonging to this group occur as isolated teeth and a partially articulated skull (Vullo *et al.*, 2009).

Birds, the other focal wetland animals, can be considered to fall within a wide range of categories from amphibious to incidentals. Las Hoyas has yielded a high diversity of Enantiornithes aves. Species recorded (*Iberomesornis romerali*, *Eoalulavis hoyasi* and *Concornis lacustris*) have interpreted as being perching enantiornithines of reduced size with enhanced flight capabilities, allowing low speed flight and good manoeuvrability (Sanz *et al.*, 2000, 2002; Ortega *et al.*, 1999). The life history of enantiornithes may be more strongly linked to wetland ecosystems than was previously thought. For instance, *Eoalulavis* (Sanz *et al.*, 1996) adopted limicol habits, feeding on worms and crustaceans at the shores of water bodies, and the morphology of these birds (e.g., long legs with long toes) might also represent limb adaptations as in modern wading birds.

4.4. Concluding remarks

In summary, the interplay among the sedimentary analyses, taphonomy and ecological structure confirms the palaeoenvironmental hypothesis that stresses four important features of the fossil record at Las Hoyas: 1) Compared with modern wetland ecosystems in terms of recorded phyla and diversity, Las Hoyas is highly representative, i.e., it has a high *fidelity* of composition: its fossil record "captures the original biological information faithfully, accurately, truthfully" (*sensu* Behrensmeier *et al.*, 2000). 2) When relative abundance is taken into account, macrophytes, arthropods (crustacean and aquatic insects), and small teleostean fish are the dominant taxa, as would be expected from the freshwater environmental setting. A diverse assemblage of animals including aquatic insects, ostracods, crayfish, and juvenile and small adult fishes depended on plant cover for their development and shelter. In fact, with respect to the obligate aquatics, the epibenthos and epiphyton of the Las Hoyas ecosystem is the habitat containing the greatest relative abundance. 3) The strong influence biofilms in the association are abundant and play a major role in fossil preservation. 4) Some groups in the fossil association corroborate or improve our knowledge of particular abiotic conditions of the ecosystem.

5. Assembling the taphonomic and stratigraphical records: assessing biases and interpreting dynamics. "Dynamic" approach

The palaeoecological reconstruction of Las Hoyas ecosystem outlined above is part of an integrated research effort. Many of the details that can be identified regarding particular morphological adaptations reflect the unique conditions of preservation of the *Konservat-Lagerstätten*. From this perspective, it may be said that Las Hoyas as a *Konservat-Lagerstätte* is a "canon" of preservation with maximum information, i.e., a minimally biased association in which information can be directly read because of the very high fidelity of its composition (Behrensmeier *et al.*, 2000). If this is true Las Hoyas might be used *a priori* as a reference or model to reconstruct the palaeobiology and palaeoecology of other, similar, Lower Cretaceous freshwater deposits.

Reconstructions made by considering the complete fossil content are essentially a "frozen picture" of the landscape with its flora and fauna. This "static" approach is compromised by the intuitive observation that ecological dynamics are never preserved as such. In effect, this method cannot avoid flattening the ecological and taphonomic

processes to a single entity, amalgamating data or processes that came from different ecological dynamics in the palaeoecological reconstruction. As no other sources of bias are taken into account, the diversity recorded might be distorted and result in an incongruent assemblage.

To address this problem, we employ a dynamic approach to palaeoecological reconstruction, and explore whether Las Hoyas in particular, and *Konservat-Lagerstätten* in general, behave as single entities. In other words, we attempt to establish whether Las Hoyas represents a unique ecosystem that can be regarded as a taphonomic unit. Therefore, we will place the palaeobiology and taphonomy of Las Hoyas within its actual spatio-temporal framework, and address the following key questions:

What is the specific bias of *Konservat-Lagerstätten* deposits? How can we prospect the *resolution* (temporal) and *fidelity* (spatial) of the “canon” itself? Does a unique taphonomic structure explain the abundance?

Is the total recorded diversity better explained in terms of time resolution? By this we mean: does Las Hoyas provide such temporal stratigraphic resolution that would reveal successive ecosystems? Alternatively, is the more general explanation in terms of spatial fidelity the better one? In other words, does Las Hoyas provide evidence of isochronous laterally coexisting ecosystems?

How are sedimentary *tempo* and, biological and/or ecological *tempo* related?

5.1. The stratigraphic record of Las Hoyas

Temporal distribution of palaeobiological information is strongly dependent on the structure of the stratigraphic record. An adequate palaeobiological interpretation requires a detailed understanding of the stratigraphical architecture in terms of time and sedimentary environments. However, this relationship has not always been well understood or given sufficient emphasis. Different approaches to assess either palaeobiological or stratigraphic completeness have been used (Kidwell, 1991, 1993). Holland (1997, 2000) showed how introducing sequence stratigraphy in macroevolutionary analyses results in a predictive model for bias in the large-scale structure of the fossil record.

Sedimentology is an essential tool for establishing the environmental context, the landscape of reconstructed fossil ecosystems, and for comparing data with the biostratigraphic hypothesis. For these reasons, it is currently considered extremely relevant in palaeoecology (Behrensmeyer *et al.*, 2000). Nevertheless, on reviewing the palaeoecological literature it becomes obvious that the potential when analyses of the stratigraphical architec-

ture, sedimentology and the fossil record are combined to provide palaeoecological hypotheses, has been underestimated. The stratigraphical record of each sedimentary basin has a specific set of features or patterns that, as in biostratigraphy, may contribute to creating or enhancing bias and artefacts at different scales. These may be relevant to our understanding of the dynamics of palaeoecological communities.

The record from Las Hoyas, as with other lacustrine localities, is an exceptional palaeoenvironmental archive with high temporal resolution (Cohen, 2003). The continuity and temporal resolution of the lacustrine deposits of Las Hoyas (low time averaging) and its unique palaeobiological and taphonomic features qualifies Las Hoyas as a natural laboratory where reconstruction of ancient Mesozoic continental ecosystems can be carried out within a dynamic context (Buscalioni and Fregenal-Martínez, 2003).

Las Hoyas is made up of two facies associations that correspond to sedimentation during wet and dry periods (see section 4.1 and Fig. 3).

The stratigraphic arrangement of facies follows a cyclic vertical pattern (Figs. 3 and 4), primarily controlled by the seasonal alternation of wet and dry environmental conditions. This basic alternation is arranged in elemental sequences made up of a variable number of single laminites, numbering up to several hundred (Figs. 3 and 4). These sequences are 20- to 50-cm-thick, laterally persistent sequences, with sharp and well defined lower and upper boundaries. The lower part is dominated by facies developed during a wet period, gradually moving upwards to facies representing drier periods. Thus, each elemental sequence is considered equivalent in terms of temporal meaning and tendency to other well-known cycles, such as metric to decimetric cycles made up of marls, charophyte limestones and palustrine limestones representing infilling and reduction of the depth of small lakes and ponds.

Wet and dry periods of the elemental sequences reflect cyclicity imposed over the annual seasonal cycles. Such long term cyclicity might have been controlled by a combination of climate and other allocyclical processes. Determining the time represented by each elemental cycle is not easy, but given their nature and origin, the order of 10^3 years might be a reasonable estimate (Buscalioni and Fregenal-Martínez, 2003).

5.2. Environmental dynamics: facies bias

Due to the specific nature of the sedimentation processes involved in forming Las Hoyas (continuity and

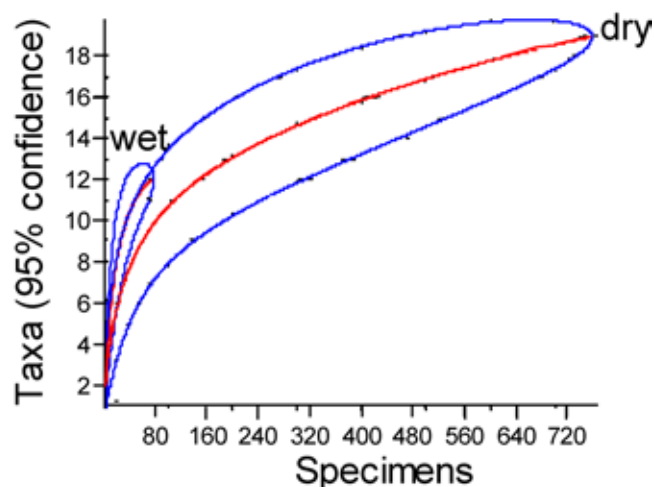


Fig. 7.- Rarefaction curves with 95% confidence intervals (“banana plot”) for the wet and dry associations calculated using PAST© program (Hammer and Harper, 2008).

Fig. 7.- Curvas de rarefacción con 95% de intervalo de confianza (“contorno de banana”) para las asociaciones húmedas y secas, calculadas usando el programa PAST© (Hammer and Harper, 2008).

high temporal resolution) each lamina is considered to represent a snapshot, with fairly instant (*census*) time averaging. Assuming this, we can infer associations (recognised by the presence of the same species in several assemblages) made of the piles of successive assemblages. Many associations at Las Hoyas are characterised by: i) instantaneous events such as daily activity (e.g., digestion, mass mortality), or ii) high proportion of demic organisms (e.g., with serial of ontogenetic stages) and autochthonous fossils accreted in short-scale events of fossil accumulation, all of which are of similar size and preservation type.

The relationships between the sedimentation during wet and dry periods and fossil associations in each facies have been compared independently of the elemental sedimentary cycle from which they were retrieved. The objective is to reveal the changes that each environmental signal produces in the pattern of association.

There were 764 fossil specimens in the dry association, and 76 in the wet association (Table 2). When coprolites and “worms” were considered the total number of sampled fossils was 829 and 93, respectively. This disparity in the results can be interpreted by using rarefaction curves (Fig. 7) that compare taxon counts in samples of different size. The curve shows that wet and dry facies have different rarefaction curves. Wet associations are richer despite their low abundance, while dry associations are strikingly abundant although homogeneous. Wet and dry episodes differ not only with respect to the total number of fossils

but also in their richness and taxon content. These peculiarities are reflected in the resulting richness and diversity indices (Table 2).

Characterisation of the association in dry facies follows its own model, in which time-averaging seems to be of a lesser order of magnitude than for wet periods. This rich association could be the by-product of dense microbial mats, probably acting under a shallow water layer. Fossils trapped by the microbial mat show that a reliable sequence of ecological events occurred in the wetland during periods of environmental stress: bioturbation (invertebrate traces), ostracod invasion, periodic storms, coprolite or “worm-larva” accumulations, and mass mortality of small juvenile basal teleosteans and/or crayfish. Accumulation by mass mortality and tetrapod traces contributes hundreds of elements.

The analysis of the fossil associations shows that demicity and autochthony are the major features of the dry associations. This can also be applied to shallow water inhabitants of the dry episodes formed by small juvenile teleostean fishes, carid shrimps (*Delclossia*), peracarid spelaegriphaceans and astacid decapods (*Austropotamobius*) together with the presence of the aquatic angiosperm *Montsechia*. Necktonic fish, epibenthonic shrimps, and peracarids are dominant elements (up to 65% and 25% of the total amount of body fossils in dry facies, respectively).

The fish association is characterised mainly by small animals (mean body length, 15 to 20 mm). In dry associations, juvenile basal teleosteans (“leptolepid-like”) are dominant elements whose ecomorphotypes have been associated with plankton filter organisms (Poyato-Ariza, 2005). Furthermore, the fish assemblage (i.e., “leptolepid-like”, *Notagogus*, *Pleuropholis*, *Rubieschthys* and *Gordichthys*) features low fusiform bodies, whose skeletons have led these species to being functionally interpreted as active swimmers (*Rubieschthys*), or dwellers of superficial waters (basal teleosteans and *Gordichthys*) (see Poyato-Ariza, 2005, for fish ecomorphology). One of the striking characteristics of the association is the low proportion of insects, as a whole (except for aquatic heteropterans), during long drier intervals. Finally, occasional exclusion between the aquatic plants, Charophytes and *Montsechia*, apparently occurs.

Wet facies are proportionally rich, because almost all specimens belong to different taxa (genera or species). Plant debris is the most commonly found type of remain. Fieldwork observations record “bad-preservation” for these fossils (in the Las Hoyas preservational context), and denote the presence of isolated elements such as scales, or non-articulated fish bones. Wet facies show dif-

1)

WET	0	0	5	4	25	6	0	44	3	3	0	4	16	4	2	1	0	12	0	0	0	0	8	1	0
DRY	8	4	15	6	473	222	7	62	124	45	30	11	29	2	1	2	3	453	1	1	7	1	7	0	1
VAR	I*	O*	C*	W*	NF	NC	NB	NI	A	B	C	D	E	F	G	H	I	1	2	3	4	5	6	7	8

2)

3	3	0	4	16	4	2	1	0	12	0	0	0	0	8	1	0	4	0	18	0	76	WET
124	45	30	11	29	2	1	2	3	453	1	1	7	1	7	0	1	2	23	14	7	764	DRY
A	B	C	D	E	F	G	H	I	1	2	3	4	5	6	7	8	FI	CI	II	BI	NASS	VAR

3)

0	wet	dry	Boot p(eq)	Perm p(eq)
Taxa S	12	19	0.615	0.888
Individuals	76	757	0	0
Dominance	0.1489	0.3932	0	0.001
Shannon H	2.127	1.465	0	0.001
Evenness e ^{H/S}	0.6994	0.2278	0	0
Simpson index	0.8511	0.6068	0	0.001
Menhinick	1.376	0.6906	0.256	0.139
Margalef	2.54	2.715	0.76	0.903
Equitability J	0.8561	0.4976	0	0
Fisher alpha	4.008	3.538	0.464	0.565
Berger-Parker	0.2368	0.5984	0	0

Table 2.- **1.** Total number of fossils in wet and dry associations. VAR= variables; NAS=total number of fossil sampled in the layer; I=ichnofossils; C=Coprolites; W="worms"; O=ostracods; * asterisk denotes number of observations, and it does not represent the total number of individuals recorded. NF= total number of fish; NC=total number of crustaceans; NI=total number of insects; NB= total number of bivalves; Crustaceans: *Delclosia* shrimps (A); peracarids-spelaeogriphaceans (B); *Austropotamobius* decapods (C); Insects: coleopterans (D); belostomatids (E); Chrysopids (F); Kalligrammatids (G); Ephemeropterans (H); Chremodids (I). Fish: "leptolepids" (primitive teleostean juveniles) (1); pleuropholidids (2); amiidid (3); *Notagogus* (4); *Gordichthys* (5); *Lepidotes* (6); pycnodontiforms (7); *Rubiesichthys* (8). **2.** Data used in the estimation of rarefaction curves. Data are represented in figure 6. FI= undetermined fish; CI= undetermined crustaceans, II= undetermined insects; BI= undetermined bivalves; NASS=total number of collected fossils. **3.** Richness and diversity indices for the two samples (wet and dry), with probabilities of equality $p < 0.05$. To evaluate species richness in the two samples, note that Menhinick richness index is higher in the wet association. This index attempts at compensating for sample size (Hammer and Harper, 2008). Other indices such as Dominance, Evenness and Berger-Parker, attempt to incorporate relative abundance. Note here that the higher abundance and homogeneous composition of the dry association result in greater values of Dominance and Berger-Parker indices. Results from PAST© program (Hammer and Harper, 2008).

Tabla 2.- **Arriba:** Número total de fósiles en las asociaciones secas y áridas. VAR= variables; NAS=número total de fósiles muestreados en la capa; I=icnofósiles; C=coprolitos; W="gusanos"; O=ostrácodos;*el asterisco señala el número de observaciones, pero no indica el número total de individuos registrados. NF= número tal de peces; NC= número total de crustáceos; NI= número total de insectos; NB= número total de bivalvos; Crustáceos: gamba *Delclosia* (A); peracáridos-espeleogripháceos (B); decápodo *Austropotamobius* (C); Insectos: coleopteros (D); belostomátidos (E); Crisópidos (F); Kalligrámmatidos (G); Efemeropteros (H); Cresmódidos (I). Peces: "leptolépidos" (teleosteos juveniles primitivos) (1); pleurofolididos (2); amiididos (3); *Notagogus* (4); *Gordichthys* (5); *Lepidotes* (6); pycnodontiformes (7); *Rubiesichthys* (8). **Abajo:** Datos utilizados en la estimación de las curvas de rarefacción. Los datos han sido representados en la figura 6. FI= peces sin identificar; CI= crustáceos indeterminados; II=insectos indeterminados; BI= bivalvos indeterminados; NASS= número total de fósiles recogidos. **3.** Índices de riqueza y de diversidad para las dos muestras (húmeda y árida), con probabilidades de semejanza $p < 0.05$. Para evaluar la riqueza de especies en las dos muestras, nótese que el índice de riqueza Menhinick es más alto en la asociación húmeda. Este índice intenta compensar el tamaño de la muestra (Hammer and Harper, 2008). Otros índices como el de Dominancia, Rareza y Berger-Parker incorpora la abundancia relativa. Nótese la alta abundancia y la composición homogénea de las asociación árida que dan valores mayores en los índices de Dominancia y de Berger-Parker. Resultados de PAST© (Hammer and Harper, 2008).

ferent fossil preservation compared with dry facies. Although the wet sample is limited, insects, *Lepidotes* and Pycnodontiform fish dominate wet assemblages. Fish have distinct bulky and globular body shapes characteristic of oscillatory locomotion, with average sizes of up to 55 mm at Las Hoyas (the largest individuals are about 500 mm). Insect distribution is bounded by wet episodes, i.e., they were collected in the wettest facies and in wet facies bounded by drier ones. Insects collected are either aquatic (*Iberonepa*, *Torcanepa*, Diptera, Ephemeroptera

and Odonata larvae) or terrestrial (Blattodea, Chresmodidae, Chrysopidae and Kalligrammatidae). The abundance of aquatic forms exceeds the terrestrial ones. Moulds of *Iberonepa* have also been retrieved, implying a demic production of these body fossils. The insect diversity (more than six species) in these facies is extraordinary. The increase in insect diversity in wetter facies is not unexpected since, as a general pattern, their life cycles are related to flooding or wetter periods in modern wetlands (Mendelssohn and Batzer, 2006).

SQ	F	NASS	NF	NC	A	B	C	1	2	3	4	5	6	7	8	NB	NI	D	E	F	G	H	I
NI02NS5_9	D	10.48	3.16	7.07	6.92	0	0	1.41	0	0	1	0	2.64	0	0	1.41	6.55	2.44	5.29	1.41	1	1.41	1.41
NI2NI9	W	3.1	2	0	0	0	0	0	0	0	0	0	2	0	0	0	2.44	1	1	1.41	1	0	0
NI10NI15	D	10.58	8.42	3.87	3.74	0	1	8.30	0	0	1	1	0	0	0	0	3	1.41	1	0	0	0	0
NS1NS4	W	1.73	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1.41	0	1.41	0	0	0	0
NS5NS9	D	7.14	2.23	2	1.73	0	0	1.41	0	0	1	0	1.41	0	0	1	5.83	2	4.58	1.41	1	1.41	1.41
NS10NS14	W	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1.73	1	1	0	1	0	0
NSC1NSC5	W	1.73	1.41	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0
NSC6NSC10	D	13.90	11	4	3.46	0	1	10.86	0	0	1.41	0	0	0	1	0	2.44	1.73	0	0	0	0	1
NSC11	W	1.41	1.41	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
R9801R985	W	3.16	1.41	0	0	0	0	1	0	0	0	0	1	0	0	0	2.82	1	2	1	0	0	0
R986R9815	D	6.92	0	6.70	0	5.29	3.16	0	0	0	0	0	0	0	0	1.73	0	0	0	0	0	0	0
R9816R9817	W	5.91	2.23	2.23	1.73	1.41	0	1.41	0	0	0	0	1	0	0	0	4.90	1	2.64	1	0	1	0
R961.1	W	3	2.82	1	0	1	0	2.82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R962R966	D	19.31	16.46	9.80	7.07	4.12	4.24	16.24	1	1	1.73	0	0	0	0	1.41	2	0	0	0	0	0	0

Table 3.- Root transformed data for Cluster Analysis. Leyend as in Table 1. See figure 8 for the resulting Cluster.

Tabla 3.- Datos transformados para el análisis de aglomeración. Leyenda como en la Tabla 1.

Neuston may represent 44% of the total sample in some cases, while nektonic organisms account for only 13%. During wet periods the positive water balance would promote more lacustrine conditions and a deeper water layer. The presence of big fishes in the association strengthens this assessment. Medium- to large-bodied fish are thought to be bottom dwellers (Pycnodontiforms), and show an efficient hydrodynamic design (*Lepidotes*) (Poyato-Ariza, 2005). Transport of materials, including potentially carcasses, is common in wet facies; some laminae have a tractive origin. Wet episodes might recover carcasses previously exposed subaerially (mummified in some cases) or in litter (i.e., plant debris), whereas dry episodes are able to capture organisms produced by means of microbial mats.

Cluster analysis reveals the internal structure of the data (Table 3 and Fig. 8) segregating wet from dry cases. This result demonstrates that fossil association is sensitive to environmental conditions. Discriminant analysis (using the percentage of relative abundance for each variable) performed to classify each type of environment, yields equivalent results (Table 4). When cross-validation is carried out with respect to the discriminant predictors obtained, the fossil associations are correctly classified in 89% of cases (95% of wet cases N=20, and 90% of dry N=26 are well classified). Discriminant analysis is used to confirm visually the hypothesis that there are two distinct associations, whereby the wet association is characterized by higher insect diversity plus *Lepidotes* fish, while the dry association typically features an abundance of “leptolepid-like” fishes and crustaceans (Fig. 9 and Table 5).

The environmental conditions in wet and dry facies associations define two distinctly biased taphofacies. There are differences in fossil abundance, richness and preservation quality. Since facies characterisation documents

two ends of a spectrum of environmental conditions, a mixture of environmental conditions influencing ecological dynamics and determining the nature of the taphonomic bias is the more likely explanation. Environmental variation has a biotic response that can be read in wet and dry alternation as the dominance of one set of species over others: insects-*Lepidotes*-Pycnodontiform fish in wet periods and crustaceans-small basal teleosteans in dry periods. In addition, dry periods are related to periphyton dominance that affects the quality and abundance of preservation. Therefore, a sedimentological, taphonomic and palaeoecological coupling might be concluded at Las Hoyas.

5.3. Sequence dynamics

The succession of communities developed during an elemental sedimentary sequence (e.g. a cycle of environmental variation from wet to dry conditions in the order of 10^3 years of duration, see section 5.1) has been considered as a unit, and the sequences have been compared among them. Three complete sequences have been defined (Fig. 4), all of which show a strong commonality in their behaviour and faunal composition. Every elemental sequence records the average features of the dominant facies association.

The first sequence is poorly characterized and incomplete. Its association is characterised by wet periods with undetermined insects and, in addition, its dry periods are far less abundant in fossil content than the equivalent dry periods of other sequences. The second and third sequences do not have different fossil assemblages, and both are dominated by the abundance and frequency of “leptolepid-like-fish” and “belostomatid insects” (Fig. 10).

The succession of elemental sequences, herein considered, do not show any superimposed trend, neither sedi-

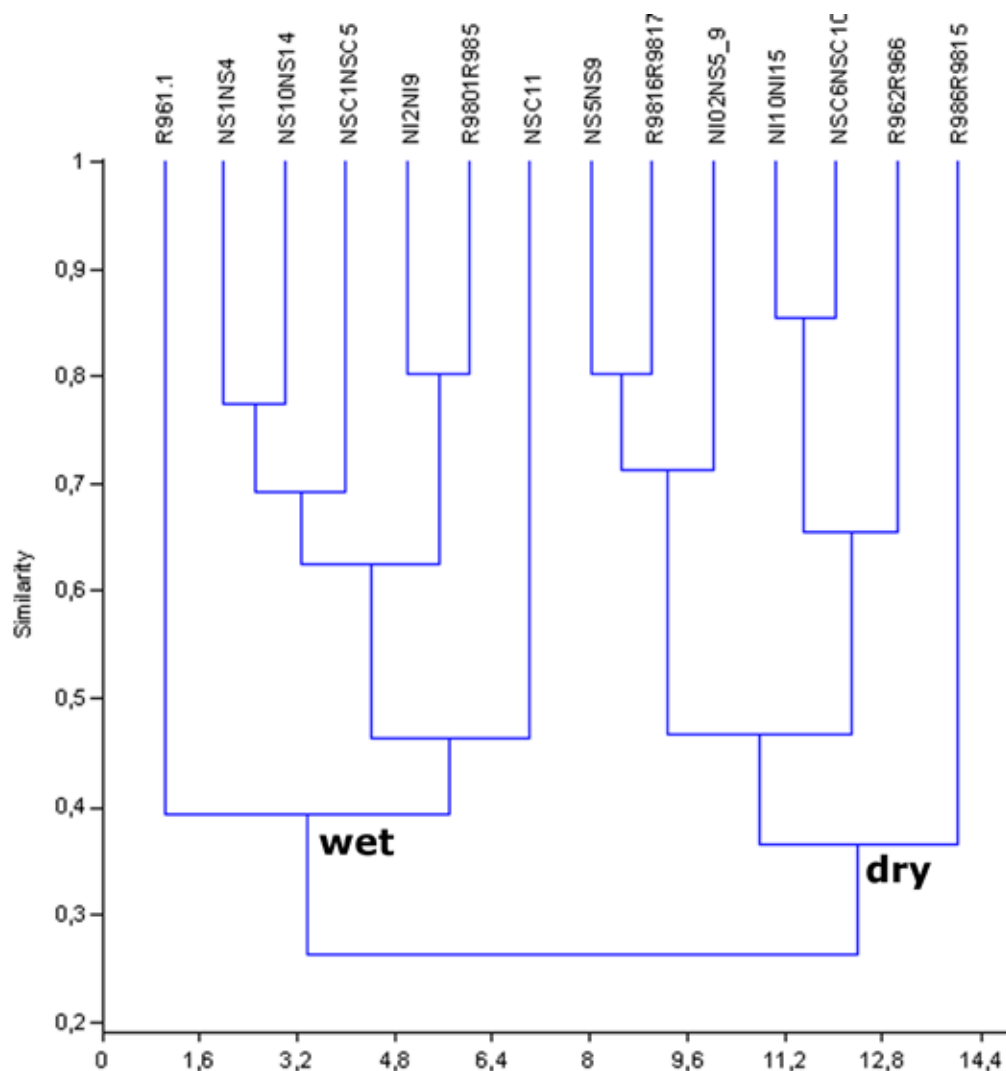


Fig. 8.- Hierarchical cluster of fossil association of dry (D) and wet (W) set of facies based on furthest linkage and Bray-Curtis similarity index using the PAST© program (Hammer and Harper, 2008). This method of scoring similarity was preferred over others because it satisfies those criteria that guarantee a balanced measure of similarity of species abundance (Clarke and Warwick, 2001). Before conducting the similarity test the abundance data was (\sqrt{y}) root transformed to downweight the importance of the highly abundant specimens. Case labels correspond to the sampled areas (R96, R98, NI, NS, y NSC, see Appendix 1 and Table 3). Cases are classified mainly according abundance and presence/absence of insects, fish and crustaceans (see figure 10 caption).

Fig. 8.-Aglomeración jerárquica de las asociaciones fósiles correspondientes al conjunto de facies áridas (D) y húmedas (W) obtenida con el vecino más lejano y el índice de semejanza Bray-Curtis usando el programa PAST© (Hammer and Harper, 2008). Este método para estimar la semejanza se ha preferido por que satisface aquellos criterios que garantizan un resultado balanceado (Clarke and Warwick, 2001). Antes de realizar el test de semejanza los datos de abundancia han sido transformados (\sqrt{y}) para disminuir la importancia de los especímenes de mayor abundancia. Las etiquetas de los casos corresponden a las áreas muestreadas (R96, R98, NI, NS, y NSC, véase Apéndice 1 and Tabla 3). Los casos se han clasificado principalmente de acuerdo a la abundancia y a la presencia/ausencia de insectos, peces y crustáceos.

mentary, nor taphonomic. In other words, taphonomic structure seems to be rather monotonous or homogeneous and taphonomic gradients are repeated cyclically. Accepting the idea of a coupling between taphonomy and palaeoecology means that ecological trends on the chosen scale of analysis are also monotonous or homogeneous. The palaeoecological dynamics that arise or that can be

inferred indicate an extremely stable ecological system.

There is a second hypothesis that might explain our findings, which depends on the accuracy of temporal resolution of the sedimentary record. If the resolution is assumed to be extremely near to biological timing, palaeoecological dynamics and events might be recorded with such temporal fidelity that either no significant macroeco-

SL	F	N	FI	A	B	C	1	2	3	4	5	6	NB	II	7	D	E	F	G	H	I	8	c
NgI02R	D	59	0	76.2	0	0	0	0	0	0	0	8.47	1.694	0	0	3.389	11.86	0	0	0	0	0	3
NgI2A	W	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	3
NgI6A	W	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	3
NgI7A	W	7	0	0	0	0	0	0	0	0	0	57.14	0	0	0	14.28	0	14.28	0	0	0	0	3
NgI9A	W	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	3
NgI10R	D	47	0	2.13	0	0	97.87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
NgI11R	D	1	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	2
NgI12R	D	31	0	25.8	0	0	61.2	0	0	0	0	0	0	3.225	0	6.451	3.225	0	0	0	0	0	2
NgI1314R	D	3	0	0	0	0	66.6	0	0	0	0	0	0	33.33	0	0	0	0	0	0	0	0	2
NgI1415R	D	30	0	16.6	0	3.33	6.66	0	0	3.33	0	0	0	13.33	0	0	0	0	0	0	0	0	2
NgS1A	W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
NgS2A	W	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
NgS4A	W	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	4
NgS5R	D	5	0	40	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	3
NgS7R	D	3	0	0	0	0	0	0	0	0	0	0	0	66.66	0	33.33	0	0	0	0	0	0	3
NgS8R	D	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	3
NgS9R	D	41	0	2.43	0	0	2.43	0	2.44	0	4.87	2.43	2.43	0	7.31	46.34	4.87	2.43	2.43	4.87	0	0	3
NgS1012A	W	3	33.3	0	0	0	0	0	0	0	0	0	0	0	0	33.33	0	0	33.33	0	0	0	3
NgS14A	W	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	3
NSC1A	W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
NSC3A	W	2	0	0	0	0	50	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	3
NSC45A	W	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	3
NSC6R	D	108	0	5.55	0	0	92.59	0	0	0	0	0	0	0.925	0	0	0	0	0	0	0	0.92	2
NSC7R	D	22	0	18.18	0	0	59.09	0	0	0	0	0	0	0	0	9.090	0	0	0	0	0	0	2
NSC8R	D	12	0	0	0	0	8.333	0	0	16.6	0	0	0	0	0	0	0	0	0	0	0	0	2
NSC910R	D	51	0	3.92	0	1.960	7.843	0	0	0	0	0	0	1.960	0	1.960	0	0	0	0	1.960	0	2
NSC11A	W	2	0	0	0	0	0	0	0	0	0	50	0	0	50	0	0	0	0	0	0	0	2
RS0198A	W	4	0	0	0	0	0	0	0	0	0	25	0	0	0	0	50	25	0	0	0	0	2
RS298A	W	4	0	0	0	0	0	0	0	0	0	0	0	25	0	25	50	0	0	0	0	0	2
RS3_498A	W	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
RS598A	W	2	0	0	0	0	50	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	2
RS698*	D	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
RS798*	D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
RS1198*	D	8	0	0	12.5	87.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
RS1398R	D	8	0	0	25	37.5	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	1
RS1498R	D	26	0	0	80.76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
RS1598R	D	5	0	0	80	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	1
RS1698A	W	6	0	0	0	0	0	0	0	0	0	0	0	83.33	0	0	16.66	0	0	0	0	0	1
RS1798A	W	29	0	10.34	6.89	0	6.89	0	0	0	0	3.44	0	31.03	0	3.44	20.6	3.44	0	3.44	0	0	1
RS1.196A	W	9	0	0	11.11	0	88.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
RS296R	D	27	0	11.11	3.70	0	77.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
RS396R	D	36	0	11.11	16.66	5.55	58.33	0	0	2.77	0	0	0	5.55	0	0	0	0	0	0	0	0	2
RS496R	D	29	0	31.03	17.24	10.34	41.37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
RS596R	D	275	0	11.63	1.45	4.72	75.63	0.36	0.363	0.72	0	0	0.72	0	0	0	0	0	0	0	0	0	2
RS696R	D	6	0	33.33	16.66	0	33.33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2

Table 4.- Data of the discriminant analysis. Variables are the same as Table 1, except for FI =undetermined fish. II=undetermined insects. c=cycles.

Tabla 4.- Datos para el análisis discriminante. Las variables son las mismas que en la Tabla 1, excepto FI y II que indican peces e insectos indeterminados, respectivamente; c=ciclos.

FI	A	B	C	1	2	3	4	5	6	NB	II	7	D	E	F	G	H	I	8
-0.0585	0.10853	0.053022	0.060514	0.030257	-0.20845	-0.20845	0.3605	0.056578	-0.10785	0.074483	-0.03394	0.011488	0.06540	-0.03378	-0.04671	-0.05868	-0.00739	1.4611	2.3516

Table 5.- Discriminant Function. Function offset constant =0.634897. Variables are the same than in Table 4.

Tabla 5.- Función discriminante.

logical trends occurred during formation of the whole site, or the stratigraphic interval and its corresponding temporal span analyzed are not long enough to document such trends. Beyond the actual evidence, the nature of the stratigraphic record itself makes this hypothesis unreliable or extremely unlikely. The first hypothesis suggests

that the evolution of these ecosystems has the ability to integrate fluctuating environmental episodes in which no successions of communities are detected. The hypothesis also supports the idea of a fairly stable (or it should be said “consistently unstable”) ecological system. Those stable ecosystems might be the result of stressed environ-

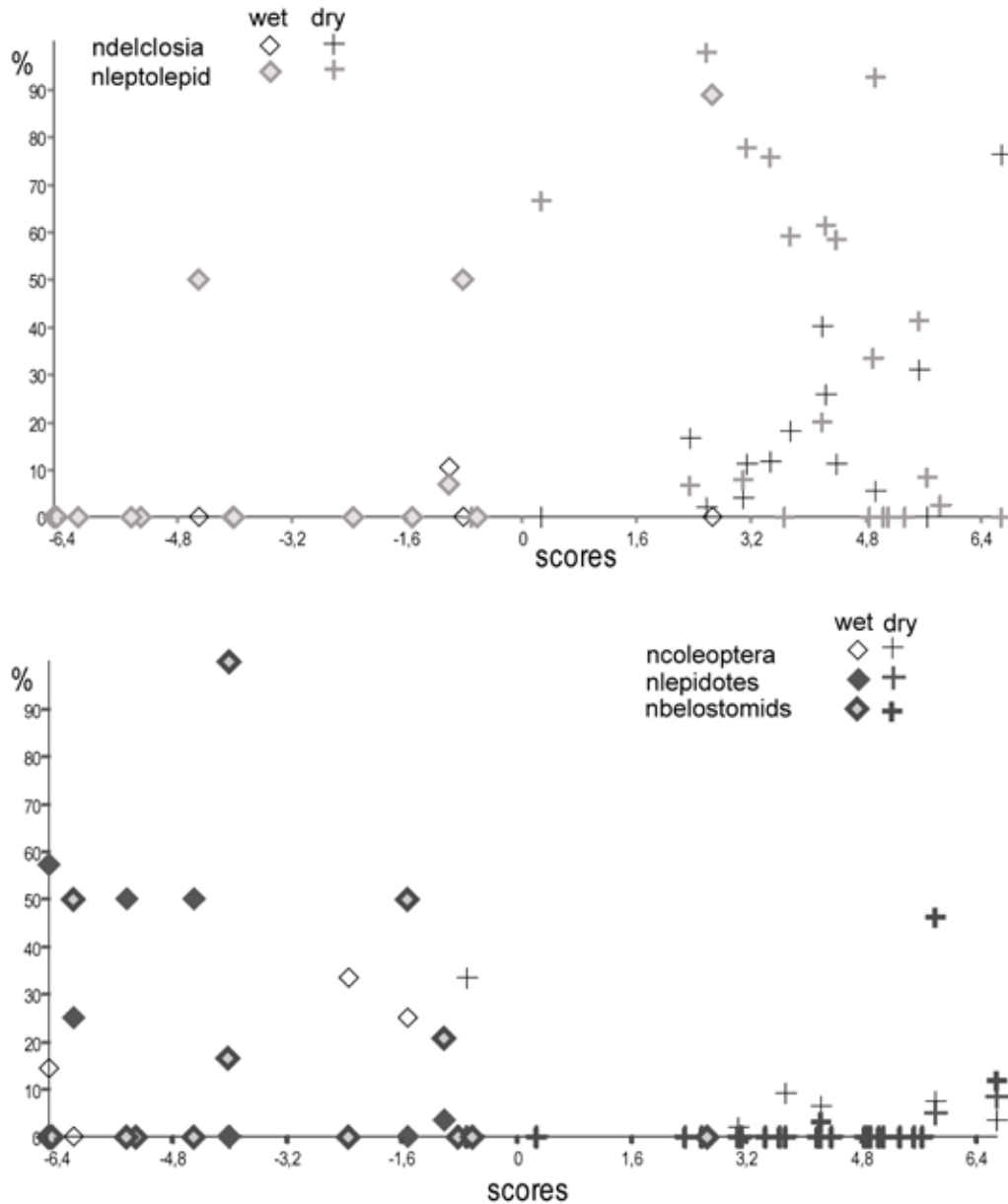


Fig. 9.- Two group discriminant analysis using PAST© program (Hammer and Harper, 2008). Discriminant function is calculated to explore how groups of facies (wet and dry) differ with respect to the fossil content. The abundance within each layer (percentage of the number of collected fossils per layer with respect to the total number of fossils) was not included in the analysis. To calculate the discriminant function, the equality of covariance matrices has been assumed. Hotelling t test had a value of $p=0.045$. The discriminant function is given in Table 5. The bivariate plots represent discriminant scores (using a cutoff of zero, as the midpoint between the means of the discriminant scores of the two groups) against the percentage of the most significant variables for wet (*Lepidotes* fish, belostomatid and coleopteran insects) and dry (“leptolepid-like” fish, *Delclosia*) facies. Negative values of the discriminant scores correspond with wet facies. Wet and dry layers are indicated by diamonds and crosses, respectively.

Fig. 9.- El análisis discriminante para dos grupos se ha realizado utilizando el programa PAST© (Hammer and Harper, 2008). La función discriminante se calculó para explorar cómo los grupos de facies (húmeda y seca) difieren en su contenido fósil. La abundancia registrada en cada capa (porcentaje de fósiles recogidos por capa respecto al número total de fósiles obtenidos) no ha sido incluida en el análisis. Para el cálculo de la función discriminante, se ha asumido la igualdad en las matrices de covarianza. El valor p para el test t de Hotelling es de 0.045. La función discriminante se describe en la Tabla 5. En las gráficas bivariantes se representa las puntuaciones del discriminante (utilizando un corte en cero como punto medio entre las medias de las puntuaciones discriminantes de ambos grupos clasificados) frente al porcentaje de las variables más significativas obtenidas para el grupo húmedo (pez *Lepidotes*, los insectos belostomátidos y coleópteros) y para el grupo de facies secas (los peces “tipo-leptolépid”, y la gamba *Delclosia*). Los valores negativos de las puntuaciones discriminantes corresponden a los clasificados como facies húmedas. Los símbolos utilizados en forma de diamante corresponden a facies húmedas, mientras que las cruces se refieren a las facies secas.

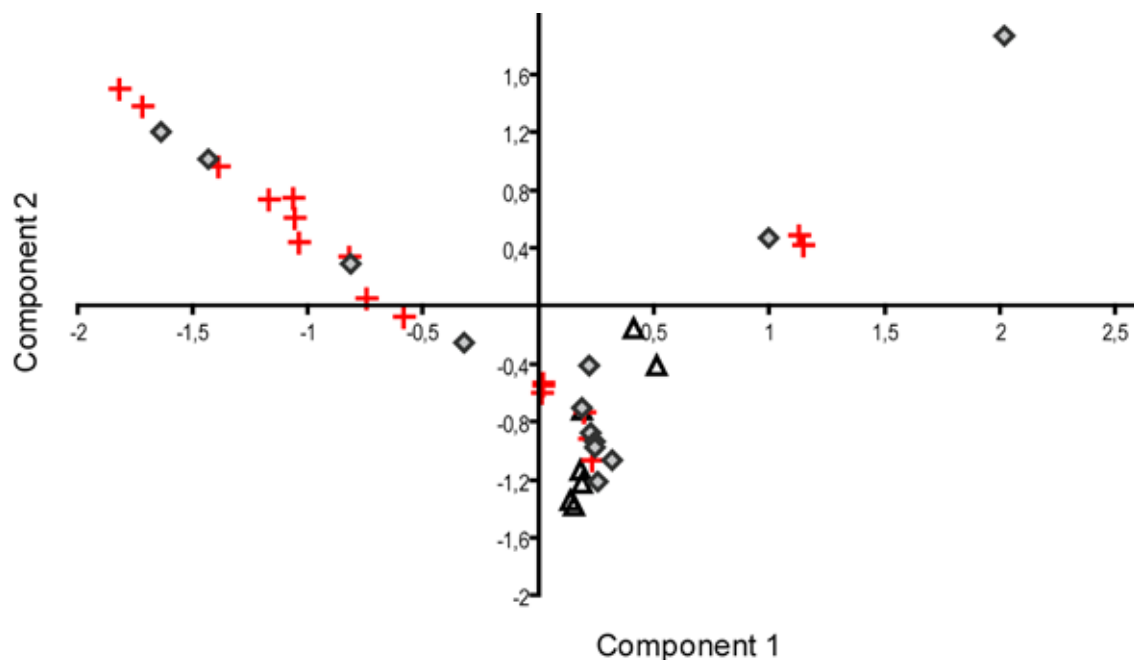


Fig. 10.- Principal Component Analysis showing the distribution of sequences 1 to 3. PC1 explains 31% of the variance. The major factor loadings for PC1 are “belostomatids” (towards positive values) and “leptolepid-like” (towards negative values). PC2 explains 18% of total variance. The first, second and third sequence layers are represented by triangles, crosses and diamonds, respectively. Note that the first cycle is poorly represented and it is placed in one quadrant, while the second and the third have equivalent distributions.

Fig. 10.-Análisis de Componentes Principales mostrando la distribución de secuencias de los ciclos 1 a 3. El 1PC explica el 31% de la varianza. Los factores de carga principales del 1PC se refieren a los insectos belostomátidos (positivos) y peces de tipo “leptolépidos” (negativos). El 2PC explica un 17,9% de la varianza total. Los triángulos corresponden a las asociaciones incluidas en el primer ciclo, las cruces a las del segundo, y la forma de diamante a las del tercero. Nótese cómo el ciclo primero está peor representado y se distribuye preferentemente en el cuadrante inferior, mientras que el segundo y tercero muestra una distribución equivalente.

mental conditions, whereby the stress itself prevents the ecological climax being reached, or sustained development and evolution over time towards a new ecosystem. Palaeobiological evidence is needed to account for these stressed-stable ecosystems, wherein dramatic variations in water budget and insolation from the rainy to dry seasons cause hydrological stress, anoxia in ponds and small lakes, as well as changes in nutrient availability, biomass and diversity. In these ecosystems it would take thousands of years to reach the ecological climax.

The estimate of the possible time span represented by the sequences studied herein (each of the order of 10^3 years), suggests that stability of the ecological dynamic might have been of an order of magnitude of thousands to tens of thousands of years. Whether the system was stable for the whole time span represented needs to be checked. However, not yet fully analysed data from the quarry (same facies and fossil association throughout the site) supports and predicts the long-term (tens of thousands years) stability hypothesis concerning functional relationships, whereas cases of specific taxonomic replacement are expected.

5.4. Conclusion

The model described above is the result of placing data from the Las Hoyas *Konservat-Lagerstätte* in spatial and temporal framework. This “dynamic” approach helps to reveal that the ecological reconstruction of Las Hoyas based on a “static” approach masks biases and reflect false biases. The frozen picture (that amalgamates dry and wet association) is a good representation of the palaeoecology of dry periods corresponding to the maximum abundance that should explain why some taxa are neither dominant nor ever retrieved. For instance, the scarcity and rareness of medium to large fish species might be thought to be a taphonomic bias (differential potential of preservation) linked to size. Thus, it should be expected that other large sized species were had not been preserved as well.

The dynamic approach shows that the two collections of fossil associations that are significantly coupled with facies yields two very different pictures of abundance and richness. This could imply that there were two different ecosystems or, indicate effects of a differing taphonomic bias on the same original faunal and floral structure. Ac-

cepting the idea of a link between taphonomy, ecological composition and sedimentology (differences in the taphonomic associations and ecological composition are closely related to environmental conditions), the best supported hypothesis would be the existence of two alternating ecosystems. The ecological trends on the chosen scale of sequence analysis are also monotonous or homogeneous, as the three complete sequences delimited all show a strong commonality of behaviour and faunal composition.

Therefore, effort is required to develop methods and concepts for extracting dynamic information from the fossil record, avoiding static reconstruction wherever possible.

6. The palaeoecological meaning of *Konservat-Lagerstätten*

The study reported here has also raised some implications and new questions concerning the real meaning of Las Hoyas and other *Konservat-Lagerstätten* and the assumptions underpinning the concept of *Konservat-Lagerstätten*.

Our analysis clearly shows that this type of fossil occurrence cannot be considered as result of dramatic, unusual, sedimentary processes. The mechanisms that generated Las Hoyas are anything but dramatic events on a geological scale. Sediments and their stratigraphic arrangement are easily explained by a stratigraphic framework dominated by background sedimentation. Bacterial mats, and subordinately anoxia and rapid burial, mainly due to the fast growth of mats, account for almost all of the processes involved in the genesis of the site following the classification of Seilacher *et al.* (1985). Since those processes may occur over a broad spectrum of depositional environments developed at any geological time, and within sedimentary basins constrained by different climate and tectonics conditions, the model is not very specific as a predictive tool. Thus, the classification provides a collection of cases that, despite being similar in the model, are independent and lacking a common pattern of causation.

Many attempts at classifying *Konservat-Lagerstätten* (Briggs and Crowther, 1990) with respect to various criteria such as type of sedimentary basin, depositional system and geological age, among others, have failed to capture the actual spectrum of known *lagerstätten* and to give the original concept a concrete and universal meaning from a genetic, palaeoecological and palaeobiological point of view. This can be easily understood if we accept that apart from taphonomic genetic processes included in Seilacher's classification and the unusual amount of pal-

aeobiological information (anatomical details, evolutionary novelties and unusual taxa) they might not share any palaeoecological commonality.

Following this line of reasoning we need to reconsider whether all those "windows" onto the fossil record are equally sized or equivalent, i.e., whether palaeoecological information, or information about taphonomic trends and other types of palaeontological information are maximized to the same extent in *Konservat-Lagerstätten* as the information about body fossils seems to be.

To address this issue requires every case to be reviewed in greater depth. For example, whereas Las Hoyas seems to be a clear example placed at the end of a spectrum due to its palaeontological, stratigraphic and environmental features, others can be placed within a wide scope. For instance, in Solnhofen the information about dynamic and functional palaeoecology is troublesome. Likewise, obrution *Konservat-Lagerstätten* linked to geological catastrophic events, such as Pompey, are severely biased by randomness. In fact, these are effectively frozen pictures of determinate ecosystems since they reflect maximum composition fidelity, and, in the case of Pompey, even great spatial fidelity (i.e., demic and autochthonous humans). In these deposits, which were produced by a "series of catastrophic events" that yielded accumulations with mass mortality (Shipman, 1975), a fine-scale census of the original biological community might be studied. In this particular case, they can be considered to be a unique taphonomic unit. Knowing the genesis of the deposit and the catastrophe the biases are under control and we would be equally justified in interpreting the taphonomic association with a static as with a dynamic approach.

Considered from this point of view, many *Konservat-Lagerstätten* might be closer to palaeontological occurrences that are not classified as *Konservat-Lagerstätten* as exceptional "windows" on the fossil record. Conversely, some fossil associations preserved in taphonomic environments, which result in worse preservational quality, contain better quality palaeoecological information than some *Konservat-Lagerstätten*. This is the case for some microfossil assemblages of La Huérguina Limestone Formation located close to Las Hoyas, whose paleoecology is similar to that revealed by the Las Hoyas analysis (Buscalioni *et al.*, 2008). In this sense, it would be worth comparing Las Hoyas to other fossil localities with respect to their palaeogeography and age, in an attempt to determine whether they share taphonomic and palaeobiological commonalities that can contribute to our understanding of the potential megabias during the Lower Cretaceous and to contrast the dynamic hypothesis of long-term ecological stability.

7. Conclusions and prospects

-Las Hoyas is a *Konservat-Lagerstätten* in the sense of the concept defined by Seilacher *et al.* (1985). Further, it can be considered a “*paleoecological Lagerstätten*” that holds information that, if read in its spatial and temporal framework, and by integrating stratigraphic with palaeontological information, reveals a dynamic and evolutionary ecological picture of the original ecosystem that is not available from traditional palaeoecological analysis.

-Taphonomic structure of Las Hoyas *Konservat-Lagerstätte* is ecologically induced. The biotic response to environmental cycles induced a coupling between taphonomic and sedimentary processes that resulted in the characteristic cyclical arrangement of the stratigraphic and palaeontological record of Las Hoyas. Therefore Las Hoyas shows a significant *facies bias* that allows us to build a predictive model with which any newly recovered sample might be tested.

-The results of the dual approach used to reconstruct Las Hoyas ecosystem are not contradictory. Nonetheless, while the traditional approach leads to something of a dead end by providing a frozen picture of the ecosystem, the second approach moves frontiers forward, and generates new hypotheses about ecological dynamics.

-Las Hoyas was a subtropical seasonal wetland that is heavily influenced by ecological stress that impeded short-term ecological evolution and resulted in a stable ecosystem that lasted for thousands of years. The organization of the ecosystem follows a similar pattern to that of extant lentic ecosystems. It is characterized by the dominance of obligate aquatic and amphibious organisms and by the scarcity of facultative terrestrial organisms. There are multiple lines of evidence from flora and fauna of ecological strategies linked to strong seasonality and water stress. Despite the presence of shallow lakes, ecological lacustrine structures cannot be clearly recognized and Las Hoyas shows a strong bias towards wetland ecological conditions.

-The dynamic approach for the analysis of other similar preserved biotas is encouraged in order to improve the knowledge on the paleoecological meaning of *Konservat-Lagerstätten*.

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Appendix

Data. Raw data were obtained by sampling the fossil association layer-by-layer (Table 1). Each sampling area is denoted by a colour: pink 1996 (*Rosa 96*), pink 1998 (*Rosa 98*), lower black (*Negra I, inferior*), upper black (*Negra S, superior*), and lowermost black (*Negra S/C*). The layer itself is herein named in Spanish as *capa* and numbered (0 or 0.1, 0.2, 1, 2, etc.). Since the objective is to test the taphonomic association for each facies type, the layers have been grouped accordingly. For instance, *NegraIcapa02* to *NegraScapa* from layers 5 to 9 correspond with dry facies. The table below summarizes the total number of fossils found according the above variables and the groups formed by the layers, by facies types (dry or wet).

Groups of layers-	Facies types	Number of fossils in association
NegraIcapa02NegraScapa5-9	Dry	110
NegraIcapa2-NegraIcapa9	Wet	10
NegraIcapa10-NegraIcapa15	Dry	112
NegraScapa1-NegraScapa4	Wet	3
NegraScapa5-NegraScapa9	Dry	51
NegraScapa10NegraScapa14	Wet	4
NegraS/Ccapa1-NegraS/Ccapa5	Wet	3
NegraS/Ccapa6-NegraS/Ccapa10	Dry	193
NegraS/Ccapa11	Wet	2
Rosa98capa01Rosa98capa5	Wet	10
Rosa98capa6Rosa98capa15	Dry	48
Rosa98capa16Rosa98capa17	Wet	35
Rosa96capa 1.1	Wet	9
Rosa96capa2Rosa96capa6	Dry	373