Palaeoecology of the fishes from the Early Cretaceous lake of Las Hoyas, Cuenca, Spain, with a hypothesis of sexual dimorphism for the Chanidae *Rubiesichthys*

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**ABSTRACT**—The fishes from the Early Cretaceous (early Barremian) locality of Las Hoyas, in the Spanish province of Cuenca, are reviewed from a palaeoecological point of view. Las Hoyas was a permanent lake surrounded by actively interacting wetlands, with dry and humid cycles; no marine influence has been detected. A good number of the most generalized fishes from the lake, as well as small piscivore forms, would probably get into the wetlands in different extents throughout time, according to the availability of additional ecological space and food sources. Other fish taxa, such as the pycnodonts and the largest piscivores, must have had more physically restrained niches, probably somehow related with the humidity cycles in the palaeoenvironment. Juvenile fishes are largely represented in this locality, including events of mass mortality. The adults show a very interesting phenomenon of size reduction, probably related with environmental stress.

The ecomorphologic overview of the fishes from the permanent waters of the Las Hoyas lake confirms that they must have occupied different niches, which, according to the lacustrine ecological spaces, can be grouped into:

1) nekton related with the pleuston/plankton, such as the plankter *Pleuropholis* (Pholidophoriformes) or the surface insect-larvae eater *Gordichthys* (Chanidae), plus juvenile stages of many taxa, and possibly some other primitive teleosts that were plankton filters;

2) nekton in strict sense, including the piscivore *Caturus, Amiopsis, and Vidalamia* (Amiidae); the water-bug eater *Notagogus* (Macrosemiidae); the shrimp-eater *Lepidotes* (Semionotidae), and ram feeder *Rubiesichthys* (Chanidae), plus a large amount of primitive teleosts, which constituted the major component of the Las Hoyas fish biomass;

3) nekton related with the benthos, such as the predatory coelacanth *cf. Holophagus* and the pycnodonts *Stenamara* and *Turbomesodon*, adapted to a durophagous diet.

A hypothesis of sexual dimorphism for the chanid teleost *Rubiesichthys gregalis* is proposed. Both morphotypes are discriminated by their relative body height only, and do not differ in any other morphometric, meristic, or anatomic character. They both occur in the same levels of the same localities, in about a 50-50% ratio for adult individuals, and there is no difference between the morphotypes and specimens from both known populations, El Montsec and Las Hoyas. Consequently, the two morphotypes of *Rubiesichthys* are interpreted as sexual dimorphs of a single species, *R. gregalis*. According to the variation found in Recent fishes, the higher-bodied morphotype is proposed to be the female dimorph, and the lower-bodied morphotype, the male dimorph. Differentiation of sexual dimorphs begins at about 20 mm; all specimens below that length show slender bodies only, and are considered juvenile.
INTRODUCTION

This paper aims to present the fishes from Las Hoyas. This locality is placed in the Spanish province of Cuenca, some 160 Kms north-east of Madrid, in the region of Castilla-La Mancha. Here, fossils are very abundant, and most specimens are complete and in anatomic connection, with their organic structures extremely well preserved, thus showing many anatomic details. Las Hoyas is considered a preservational fossil-Lagerstätte, that is, a site that provides fossils in an outstanding state of conservation. The fossils yielded by the beds of laminated limestones from this locality provide an invaluable insight into the continental ecosystems of the Early Cretaceous. Some 200 animal, plant, and algae species (plus ichnospecies, that is, fossil prints, traces, or tracks) are known from this locality. Twenty-five of these species and ichnospecies were described from Las Hoyas for the first time ever, and are endemic, that is, known only from this locality in the whole globe. “In fact, the late Barremian freshwater ecosystem of Las Hoyas contains one of the most significant and diverse records of aquatic organisms described from the Early Cretaceous anywhere in the world” (Buscalioni and Fregenal, 2003: 15). That upper Barremian age was obtained biostratigraphically, which means by relative dating of fossil species, notably charophytes and ostracodes (Dieguez et al., 1995). That age implicates that the fossil-bearing beds are some 115 millions years old. Updated overviews of the fossils from Las Hoyas can be found in Sanz et al. (1999, 2000, 2001) and Ortega et al. (2003). In sum, this locality contains arguably the finest continental fossil record from the Cretaceous of Europe, and one of the most relevant global records of aquatic organisms from this age.

The present paper focuses on the ichthyofauna from this important fossil-Lagerstätte. The fishes of Las Hoyas are significant for several reasons. First of all, as for the rest of the fossils, for their fine preservation: most of them are complete and in full anatomic connection, showing the skeletal features, and occasionally some soft tissues, in exquisite detail. Secondly, this diversified ichthyofauna comes from a period, the Early Cretaceous, when primitive, non-teleostean actinopterygian taxa were being replaced by teleostean lineages, more derived. Hence the interest of the fishes from this locality within the evolutionary history of the Actinopterygii. Thirdly, because fishes are, by far, the most abundant and diversified vertebrates from this locality. And finally, as a consequence of this, they were fundamental components of the ecological niches and key elements of the trophic chains of the lake and of the surrounding wetlands.

In relation with this, the present paper aims to present the fishes from Las Hoyas from a palaeoecological point of view, instead of the more traditional taxonomic approach. To date, the ensemble of the fishes from Las Hoyas has been presented as a more or less extended taxonomical list (e.g., Sanz et al. 1988, 1999, 2000, 2001; Poyato-Ariza and Wenz, 1995; Ortega et al. 2003). It seems, then, interesting to attempt presenting them from another point of view. In addition, the current work at Las Hoyas includes new stratigraphic and taphonomic studies in order to refine the current palaeoecological hypotheses about this locality by integrating the freshwater ecosystem of Las Hoyas into the varied surrounding ecosystems throughout time (Buscalioni and Fregenal, 2003). A dynamic palaeoecological model of the ecosystem, rather than the traditional single unit representing a frozen window on the past, is currently envisaged for Las Hoyas (op. cit.; work in progress). Hence, a palaeoecological approach to the study of the fishes of this locality seems both pertinent and scientifically stimulating. This is attempted in the present paper to serve as a contribution to the broad dynamic palaeoecological model that is currently being developed.

The main objective of this paper is, then, to provide an insight to the ecology of the ichthyofauna from Las Hoyas according to their known possible food sources and to functional interpretations of the morphology of the different fish taxa, including comparisons with analogous Recent forms. This ecomorphologic approach acknowledges the causal connection that there is between the morphology and performance (function) on one hand, and between performance (function) and ecological patterns, on the other hand (e.g., Wainwright and Bellwood, 2002). Therefore, the fish taxa from Las Hoyas will be presented according to their ecological distribution in the ecosystem of this Cretaceous lake as it can be inferred from their morphology. But first, a few words need to be said about the fishes and the problems that their ecomorphologic studies present, especially when fossil forms are involved.

ECOMORPHOLOGY AND FOSSIL FISHES

1.- The ecomorphologic approach.

Direct, identifiable evidence of diet composition in fossils is extremely rare, so it needs to be deduced from morphologic observations. Not to mention the obvious impossibility of observing their mode of locomotion. It is therefore necessary to approach the ecological presentation of the Las Hoyas fishes from an ecomorphologic viewpoint.

Essentially, Ecomorphology is the integration of Functional Morphology and Ecology. In our case, it is
about inferring possible diet composition, feeding strategies, and type of locomotion (all that pointing to potential niches in the ecosystem) on the basis of morphologic observations on the fossil fish specimens. Ecomorphology is a very complex field of study, in which many factors and variables must be taken into account. It will not be possible to achieve a precise ecomorphologic analysis of the fishes from Las Hoyas in the present paper. First of all, because anatomic details need to be explored in depth for an accurate ecomorphologic study, and there is no room herein to attempt that for all the fishes in the locality. So, it is reckoned that the characters used in the present paper are scarce, general, maybe even superficial, but this is the way in which, at present, the first comprehensive approach to the palaeoecology of the Las Hoyas fishes can be attempted.

2.- Sources of variability in the diet of fishes.-

There are reasons for which the ecologic categorizations presented below for the fishes from Las Hoyas need to be considered lax and movable, and must not be regarded as utterly closed, completely distinct compartments. First of all, it is well known that the feeding patterns in fishes change, sometimes drastically, throughout individual ontogeny (e.g., LOWE-McCONNELL, 1987; WOOTTON, 1990; GRANADO-LORENCE, 1996). Changes in the diet during growth are a result of the modification in life stages, body size, and even muscles and bones shape, so that the feeding strategies, and therefore the diet composition, accordingly change. Even in the simplest case, where the same shape is maintained during ontogeny, the increasing size of the feeding apparatus results in a more effective performance on larger, and consequently different, food items. So, even throughout the most uncomplicated ontogenetic development, “changes in optimal or preferred prey size often result in changes in the taxonomic composition of the diet” (WAINWRIGHT and BELLWOOD, 2002: 50). For instance, in the Recent Serranidae, whose individual body morphology is very similar, and constant during ontogeny, the main composition of the diet changes with body size, and therefore changes throughout growth. Smallest individuals feed mostly on copepods; larger ones on prawns; larger ones on crabs; and the largest ones feed mostly on cephalopods (op. cit.).

Furthermore, direct evidence of diet in Recent fishes has shown the flexibility of feeding habits at species level. For instance, Gasterosteus aculeatus -the three-spined stickleback- can eat about 20 different categories of food within a single population (ALLEN and WOOTTON, 1984), which provides an idea of how potentially variable the diet of any fish can be. This variation can even depend on individual taste: a single Salmo trutta -the brown trout- can change preferences in its diet in only 30 minutes, and for a period of days (RINGLER, 1985). Even though ostracods are but a minor component on the diet of this fish, a single individual with a preferential taste for ostracods was on one occasion accounted to contain some 150,000 of them in its gut (WHATLEY, 1983).

Diet also changes according to the food availability. The effectiveness of the prey capture largely depends on prey density (e.g., GRANADO-LORENCE, 1996). Therefore, fish do switch from one type of prey to another when prey relative abundance changes, and this goes for generalist feeders and for specialized feeders as well (WOOTTON, 1990). In many cases, the variations in the food source are regularly seasonal (e.g., LOWE-McCONNELL, 1987); even the proportion of the vegetal and animal component of the diet can change seasonally (WOOTTON, 1990). Year-to-year changes are also frequent; for instance, brachiopods (lampshells) of the genus Lingula were the main component of the diet of the flatfish Cynoglossus in a certain year, whereas it “hardly appeared in the diet among the polychaetes and shrimps the preceding and subsequent years” (LOWE-McCONNELL, 1987: 274). Even lunar cycles are a source of plasticity in the diet of fishes, and the changes in diet may also be irregular (op. cit.).

One more reason to take the ecomorphologic approach with caution in fishes is that the morphology, and consequently the mechanics, of feeding acts on the food items through the behaviour of the animal. In fishes, forms with highly similar morphology do feed on different sources by living on different habitats, or, and this is most interesting for fossils, by behaving differently while sharing the same habitat. For instance, species of two sturgeonfishes, Ctenochaethus and Acathurus, may be sympatric, and yet feed on different algae because they have subtle differences in biting behaviour; even two different species of Acathurus that do feed on the same algae share the habitat by being territorially separated (WAINWRIGHT and BELLWOOD, 2002). The variation factors introduced by behaviour can be individual as well: single fishes do move to habitats of greater profitability, or do change their food preferences (WERNER et al., 1981). Even species with specialized morphological adaptations for a particular mode of feeding do show a surprising flexibility in their actual choice of food (WOOTTON, 1990).

Finally, it is important to remark that, in addition to all those sources of variation of the diet in fishes, many forms are essentially omnivorous, being able to adapt very effectively to very different food sources, thus becoming, in general, more widely distributed than specialist feeders (LOWE-McCONNELL, 1987).

In sum, actual diet in Recent fishes is highly variable so that ecomorphologic inferences need to be confirmed...
by direct evidence. This type of evidence is extremely scarce in fossils, so ecomorphologic inferences are to be taken with special caution when dealing with fossils.

3.- Niche categorization in Recent and fossil fishes.-

For all the reasons just explained above, the categorization of many Recent fish in terms of strictly defined trophic levels, such as primary carnivore, detritivore, zooplankter, herbivore, etc., cannot be accurately achieved (Wootton, 1990). The trophic categories, then, are used as general indicators of the overall preferences of the studied fishes. This obviously concerns fossil forms as well, so it is applied to the categories established below in the ecological presentation of the ichthyofauna from Las Hoyas.

However, in any case, the ecomorphologic approach has resulted on useful patterns of association between the morphology and the use of the habitat for inferring feeding habits and preys (Wainwright and Bellwood, 2002). We can be confident when using morphology to infer feeding habits because there is, in general, a strong correlation between the morphologic characters of a fish and its role in the trophic chain, since it is precisely its morphology what determines how the fish can feed (Wootton, 1990). And not only for feeding habits; ecomorphologic studies have provided constructive models of association between the body and fins shape and the locomotion in Recent fishes as well (Webb, 1984). Inferred locomotion habits, though, are also to be taken with caution in fossils, as experiments in order to observe the actual mode of swimming and to correlate it with observations of the fish in its original environment are obviously not possible. Brief, general patterns of niche preferences in fishes can be inferred from their morphology, but must be taken with caution, especially when dealing with fossils.

For the purpose of the present overview, the approach is, then, rather lenient. It is merely based on suggesting the most suitable habitats, locomotion, and feeding habits, and therefore niches, for the general morphology of the different fishes from Las Hoyas. That is, probably none of them is the “perfect paradigm” for any suggested locomotion or feeding strategy. The locomotion strategies are inferred from the overall body and fin morphology. Each of the feeding strategies is simply inferred from the food source that was available in their ecosystem, and from the morphology of body and jaws that is better suited among the fishes that are known from this fossil site. Despite the necessary cautions, this can be confidently attempted because the current knowledge on motion and feeding biomechanics in Recent fishes does allow to infer overall patterns of locomotion and feeding habits from anatomy only. And this can be applied to fossil fishes, with the necessary caution, to serve as a general reference within the framework of a comprehensive paleoecological study of their environment.

THE PALAEOECOSYSTEM OF LAS HOYAS

The ecosystem of the Las Hoyas area during the Barremian was that of a shallow lake with extensive, varied surrounding wetlands. These surrounding ecosystems are revealed by palustrine marls, meandriform river channels, and shallow lacustrine limestones and marls. They occupy extensive areas in the environs of the areas where the laminated fossiliferous limestones, formed in the deeper, permanent waters of the lake, are found (Fregenal-Martín, 1991, 1998; Fregenal-Martín and Meléndez, 1993, 1994; Poyato-Ariza et al., 1998; Martín-Closas et al., 2003). Therefore, the permanent waters of the lake were surrounded by extensive wetlands and other ecosystems, which must have interacted with the lacustrine ecosystem.

Both the lake and the surrounding environments fluctuated throughout time. The sedimentological analyses at this locality have revealed microfacies corresponding to humid and dry episodes (Fregenal-Martín, 1991, 1998). These fluctuating environmental conditions define, on one hand, a changing ecosystem, and, on the other hand, a taphonomic bias in the presence and in the relative abundance of specimens in the different fossiliferous beds from Las Hoyas. These dynamics are integrated in an ecological system that was globally very stable; this integration of general stability and dynamic changes could have been due to the occurrence of environmental conditions of stress (Buscalioni and Fregenal, 2003; Fregenal et al., work in progress).

It must be emphasized herein that no marine influence has ever been detected at Las Hoyas (e.g., Sanz et al., 1988, 2001; Fregenal-Martín, 1991, 1998; Fregenal-Martín and Meléndez, 1993, 1994, 1995; Talbot et al., 1995). This has been notably confirmed by multidisciplinary studies, including strontium isotope analyses of the fish fossils, which determined that the fishes originally grew and lived in a freshwater environment without marine influence (Poyato-Ariza et al., 1998; Poyato-Ariza, in press and this volume).

Concerning the precise environment of the fishes, it is obvious that these organisms dwelt in aquatic environments, that is, in our case, the lacustrine and wetland waters. The fishes lived essentially in the permanent waters of the lake, but they must have been present in the surrounding wetlands. Different taxa in variable quantities and distribution would have occupied the available
aquatic environments around the lake, taking advantage from, and adjusting to, the ecological fluctuations of the wetlands and their interaction with the lake, throughout time and according to the humidity cycles. We will focus on each of the lacustrine environments in order to integrate and facilitate the palaeoecological overview. We must bear in mind, though, that many of the fishes that we will see from the permanent waters of the lake must have also been present, in different degrees throughout time and space, in the freshwater ecosystems around the lake.

A general introduction to lacustrine ecosystems will be outlined next, as well as a presentation of the organisms -other than fishes- that dwell in each part of the lake, prior to presenting the fishes themselves. Since fishes did not obviously live on their own, their ecologic patterns need to be considered in relation to their environment and to the other organisms that shared each part of the ecosystem with them. We will consider them as associated organisms, which will be overviewed in each section before presenting and discussing the fishes.

THE FISHES FROM LAS HOYAS

In our presentation of the ichthyofauna from this fossil-Lagerstätte, we will follow the classic ecologic categorization of the fauna and flora in a lacustrine environment. These categories are not rigorous spatial divisions; they have more to do with the ecological habits of the organisms than with precise demarcations in the water body. There is a strong relationship, of course, between ecologic habits and spatial parts of the lake, but this relationship is not as rigidly strict as it may seem. For instance, the plankton is more abundant in shallow waters, but there is also plenty of planktonic organisms in midwaters, and even in deeper waters. This implies that some organisms with different ecologic habits may have occasionally shared physical spaces in the open waters of the lake, near the shore, and in the surrounding wetlands.

The definitions for ecological categories are adapted from Lincoln et al. (1982):

- Pleuston: formed by aquatic organisms that remain permanently at the water surface by their own buoyancy, normally positioned partly in the water and partly in the air.
- Plankton: formed by those organisms that are unable to maintain their position or distribution independent of the movement of the water mass.
- Nekton: formed by those actively swimming pelagic organisms able to move independently of water currents.
- Benthos: formed by those organisms attached to, living on, in, or near the lake floor.

According to these ecologic categories, there are, of course, no fishes in the pleuston or the plankton (except some eggs and very early larvae). In Las Hoyas, we know no remains of fishes with fully benthonic adaptations, e.g., dorsoventrally flattened. All the fishes of the lake are, strictly speaking, part of the nekton. However, they interact with other nektonic organisms and also with organisms with non-nektonic life habits. We will hence separate the most genuine nektonic fishes from those fishes of the nekton that are related with the pleuston-plankton, and from those fishes of the nekton that are related with the benthos, according mostly to the habitats of their inferred food sources.

In each of the following sections, the corresponding associated organisms will be briefly indicated. The corresponding information is compiled from Rabada, 1993; Martínez-Delclòs and Nel, 1995; Rodríguez-Lázaro, 1995; Garassino, 1997; Martín-Closas and Diéguez, 1998; Sanz et al., 1999, 2000, 2001; Martín-Closas et al., 2002, 2003; Ortega et al., 2003; Martín-Closas, 2003; and from personal observations. After the corresponding introduction to their accompanying organisms, the fishes will be presented and discussed in each section.

1. Fishes related with the pleuston-plankton. -

At Las Hoyas, the faunal pleuston is known from fossil remains of the hemipteran family Chresmodiidae; these are the water-striders, which are very abundant in Recent ecosystems of similar type. Floating parts of certain plants and floating larvae (see below) may arguably be considered pleuston as well. More significantly than nourishment, the plants would probably have provided shelter and protection for small fishes.

The phytoplankton from Las Hoyas is represented by relatively scarce chlorococcalean chlorophyte algae (Botryococcus, Pediasstrum). This is not surprising due to the lack of nutrients (especially phosphorous) in most calcareous lakes. The known zooplankton of largest size includes larvae and pupae of insect groups whose corresponding adults are free fliers: a varied array of Diptera: flies, mosquitoes, horseflies, and relatives; three families of Odonata, that is, dragonflies; and scarce remains of Ephemeroptera, the mayflies. Larval forms of aquatic insects may have also been part of the zooplankton. Smaller-sized zooplankton was formed probably by extremely abundant eggs and larvae of decapods, ostracods, pericarids, bivalves and gastropods, plus abundant fish and insect eggs. There is no fossil evidence of any of these so far, but they must obviously have been there, since the juveniles and adults are abundant, and the eggs and larval stages of most of these organisms are planktonic.

The following fishes may have been related with the
pleuston-plankton of the lake:

1a.- *Gordichthys conquensis* (Fig. 1A).

This little fish is not very abundant, and appears generally as isolated specimens. The general shape of this fish strongly resembles the Recent cyprinodontiform genus *Gambusia*. They are only very distantly related, belonging to completely different superorders. However, they are morphologically convergent in a series of features (POYATO-ARIZA, 1991, 1994): similar small size (3-4cms); large abdomen; dorsal fin short, high, placed in the posterior part of the body; short and high caudal fin; and specially the antorbital position of the mandibular articulation (due to elongation of the suspensorium), and the large mouth cleft, directed upwards. All this convergent morphologic features suggest that *Gordichthys* was adapted to occupy a similar specialized niche than that of the Recent *Gambusia*, which feeds on planktonic larvae of Diptera, notably mosquitoes. Analogously to this genus, *Gordichthys* is supposed to have lived in narrow relationship with the pleuston-plankton, feeding on the numerous and relatively varied larvae of Diptera in the lake, and occasionally maybe also in the surrounding wetlands. It could have also fed on small non-aquatic insects that may have got stranded on the water surface. This interesting little fish is an endemism of Las Hoyas, that is, this locality is the only one in the world where it appears. Together with *Rubiesichthys*, described below (2b), *Gordichthys* forms the subfamily Rubiesichthyinae within the family Chaniidae of the ostariophysan order Gonorynchiformes (POYATO-ARIZA, 1996a, 1996b).

1b.- *Pleuropholis* sp. (Fig. 1B).

The little (3-4cms) and relatively rare specimens of fishes assessed to the genus *Pleuropholis* from Las Hoyas have not been studied in detail yet. This is a genus of medium-sized fishes of the order Pholidophoriformes (very primitive teleosts), known mostly from the Late Jurassic of Europe (Cerin, Solnhofen). Pending a sound anatomic description, some preliminary observations may be useful for our palaeoecological purposes. The relatively high, non-fusiform body, with a rounded head, straight dorsal and curved ventral contours, plus the dense cover of thick ganoid scales indicate that it was probably related with the water surface rather than a quick, openly nektonic swimmer. The mouth gape is very large, and the teeth are insignificant, both of which are features presented by plankter fishes. For our very general purposes, it can be considered as a good candidate for feeding on plankton.

1c.- Primitive teleosts.

Part of the adults of the primitive teleostean array mentioned below (2a) could fit the planktonic filtering anatomic model, as they show adaptations such as: small size; absent or tiny teeth; and well developed gill rakers that could act as a plankton filter, as is the case, for instance, of many Recent Clupeiformes (sardines and allies). Some specimens where the branchial arches are exposed show an extensive branchial basket which, together with the other features, strongly suggests that they were filtering organisms capable of feeding on the phyto and zooplankton of the lake and, occasionally, of the surrounding wetlands.

1d.- Juvenile fishes.

The youngest stages of many of the fishes from the lake, notably those of the primitive teleostceans (Figs. 1C-D; see 2a) were also very likely related with the plankton, feeding on it, probably inhabiting the most superficial layers of the shallowest waters of the lake, as Recent forms do. They also probably entered the surrounding wetlands whenever possible. These countless tiny juvenile teleostceans (sometimes under 10mm) often appear in mass mortality levels in distinctly recognizable layers of the outcrop. These events of mass mortality consist of thousands of specimens: a small plate about 47x17cms contains 166 individuals (PINARDO-MOYÁ et al., 1995). These individuals are mostly oriented due to some kind of flow (op. cit.), probably of low-energy type.

2.- Fishes with genuine nektonic habits.

The nekton is largely formed by fishes. In the Las Hoyas lake water body, the clearly nektonic animals that were not fishes are known from extremely abundant fossils of the Atyiidae decapod shrimp *Delocalia*, plus abundant actively swimming insects of the family Belostomidae, the water-bugs, known from adults and moults of various ontogenetic stages of several genera.

2a.- Primitive teleosts (Figs. 1E-F).

The largest fish biomass of Las Hoyas is represented by primitive teleosts, which constitute a relatively diversified ichthyofauna (POYATO-ARIZA, 1997). Some of them may have been plankters (see 1c), and most of them must have swam actively in the open nekton. The largest specimens are about a dozen cms. Their generalized body, fin, and mouth shape indicate a non-specialized locomotion and diet. Their mouth bones are primitive for teleostean fishes; the premaxilla is small, firmly attached to the snout, and the quadrate-mandibular articulation is very simple, not capable of projecting the lower jaw. However, the maxilla could rotate antero-ventrally, providing a big mouth gap, and consequently a large buccal cavity, that could be quickly expanded. This could result on a suction effect. As a matter of fact, many specimens have fossilized with their large mouths widely open. Therefore, and although jaw protrusion was certainly not as effective as in more derived teleosts,
Fig. 1. Some examples of the Las Hoyas ichthyofauna (I). All specimens belong to the collection of the Museo de las Ciencias de Castilla-La Mancha (MCCM). A-D, nektonic fishes related with the pleuston-plankton: A, *Gordichthys conquensis*, specimen MCCM LH 2179 R; B, *Pleuropholis* sp., specimen photographed during field works prior to labelling; C-D, mass mortality of juvenile teleostean fishes: C, layer photographed *in situ* during excavation; D, detail. E-H, openly nektonic fishes (I): E-F, primitive teleostean fishes, notice the large mouth gape; E, specimen photographed during field works prior to labelling; F, specimen MCCM LH 091 R a. photo Harre, Berlin. G, *Rubiesichthys gregalis*, specimen MCCM LH 11088; H: *Notagogus aff. N. ferrerii*, juvenile specimen photographed during field works prior to labelling. B, E, H: photos Sanz, Madrid.
suction must have been their feeding strategy for capturing small to medium sized food items by rapidly expanding the bucco-pharyngeal cavity, creating a pressure gradient (Wainwright and Bellwood, 2002). They would feed on all kinds of food particles of varied origins and size; mostly invertebrates, probably juvenile shrimps, water-bugs and other larvae and small invertebrates of all kinds, since the teeth of these fishes are usually tiny.

2b. **Rubiesichthys gregalis** (Fig. 1G).

This other chanid fish was initially described from the Early Cretaceous of El Montsec, Lérida, Spain (Wenz, 1984), later reported at Las Hoyas (Sanz et al., 1988), and consequently revised (Poyato-Ariza, 1991, 1996c). It is much more abundant than his family fellow described above (1a), which suggests, in principle, more generalized feeding habits. It was also very small (up to 40-45mm) and toothless. The mouth is completely terminal, but the mouth gape is remarkably smaller than in the teleosts just mentioned above. The suspensorium is very elongated. The body is elongated as well. These features make *Rubiesichthys* a good candidate for generalized ram, rather than suction, feeding on varied tiny particles in the water, which it would actively capture when rapidly swimming. In ram feeding, the fish may overtake the food items with a forward motion of the entire body (Wainwright and Bellwood, 2002). Effective protrusion is also used in ram feeding, but this was not the case of *Rubiesichthys*. The small body size of this fish and its edentulous -toothless- condition suggest that the items it fed on were quite smaller than those eaten by the teleosts of paragraph 2a above.

2c.- **Macrosemiidae** (Fig. 1H).

The fishes of this family of Halecostomi present a distinct, large dorsal fin divided in two lobes. The juvenile specimens of *Notagogus* cf. *N. ferreri* (Fig. 1H), about 2-3cms long, are very abundant, and a very conspicuous element of the Las Hoyas ichthyofauna, whereas adult specimens are extremely rare (Wenz and Poyato-Ariza, 1994). A detailed revision is needed to determine whether all adult specimens are actually *Notagogus* or there may be *Propeterus* as well, and also to determine whether this species is the same than the one known from El Montsec. In any case, their mouth gape is remarkably small, and their teeth are numerous, yet big, strong, and conical, smallest juvenile specimens comprised. These features strongly indicate specialized predatory insectivore habits. They could very well have fed on the abundant small water-bugs, which they would actively hunt when swimming in open waters, and also near the shores and probably into the wetlands as well.

2d.- **Lepidotes** (Figs. 2A-B).

This semionotiform is the fossil fish with the most extensive temporal and geographical record. Two endemic species have been described from Las Hoyas (Wenz, 2003): *Lepidotes microrhis* (Fig. 2A) and *Lepidotes tanyrhis* (Fig. 2B). These species are moderately abundant and small for this genus. Both species are under 16cms in largest adult individuals, whereas other species of the genus are up to about 2 meters long. The species from Las Hoyas present a high fusiform body, whose shape indicates a generalized locomotion (see Poyato-Ariza, this volume: fig. 2C); they were not specialists in any particular mode of swimming, but were apt to perform both active swimming and limited manoeuvring. They could swim well in open waters, near the shore and also amidst the bottom vegetal cover. Their mouth is small, but strong. The teeth are stout, yet high and relatively pointed both on the bones of the outer borders of the mouth (premaxilla, dentalosplenial) and on the more internal bones of the buccal cavity (vomer, demopalatines, coronoids; Wenz, 2003). These features all indicate that they could very well lurk as well as actively hunt small and moderately hard swimming nektonic animals; adults of the shrimp *Delclosia* and of water-bugs and beetles are suitable candidates to have been the chief preys of the Las Hoyas *Lepidotes*. If we had to infer a distinction at specific level, it would be, with the evidence currently available, based on hunting strategies and habitat (by different behaviour) rather than on diet or food source. This is so because both species have essentially the same dentition; *Lepidotes microrhis* has a higher body and shorter snout (Fig. 2A), suggesting that it would have been a relatively quicker swimming predator, maybe dwelling in more open waters.

2e.- **Piscivore fishes** (Fig. 2C).

Medium to large size; slender, fusiform body; powerful caudal fin and pedicle; large mouth gap; numerous long, sharp, pointed teeth; these are features of the fish-eating fishes. They are at the top of the fish trophic pyramid, although they could of course have been hunted by larger tetrapod predators. Being predators themselves, they are much more scarce than other fishes; and the bigger they are, the scarcer they become. Several piscivore fishes have been found at Las Hoyas, all of them belonging to the halecomorph order Amiiformes. The remains of *Caturus* are very rare, but both juvenile and adult specimens are known. This genus is well known from the Late Jurassic (e.g., Solnhofen). Also *Vidalamia* (Amiidae) is rare, and probably the largest fish known from Las Hoyas, as the adult specimens of this genus (also
Fig. 2. Some examples of the Las Hoyas ichthyofauna (II). All specimens belong to the collection of the Museo de las Ciencias de Castilla-La Mancha (MCCM). A-C. Openly nektonic fishes (II): A. Lepidotes microrhins, holotype, MCCM LH 8010 b; B. Lepidotes tanyrhis, holotype, MCCM LH 7410; notice the slender body and the more elongated snout when compared with the other species of the genus seen behind. C. Amiopsis sp., specimen photographed during field works prior to labelling, photo Sanz, Madrid. D-E. Nektonic fishes related with the benthos: D. Turbomesodon praeclarus, holotype, MCCM LH 16345, photo Serrette, Paris. E. Coelacanth cf. "Holophagus", specimen MCCM LH 607 R. F-H, sexual dimorphism and growth in Rubiesichthys gregalis: F. Growth series, specimens MCCM LH 1746, 3210 and 545, from smaller to larger, left to right, top to bottom. G-H, sexual dimorphs: high-bodied, interpreted as female, above; slender-bodied, interpreted as male, below; G. specimens MCCM LH 4992 R, female, and 545, male; H. Idealized life restorations, artwork by M. Antón for Poyato-Ariza (1991), previously unpublished. A, B, D, E, F: photos Serrette, Paris. A, B: photos courtesy S. Wenz, Paris.
known from El Montsec) may reach up to about 50cms. These two forms probably lived in the open waters of the deepest parts of the lake, and they might have been perhaps linked with the humid cycles. The most abundant piscivore fish from Las Hoyas is the ammīd *Amiopsis* (Fig. 2C), whose adults are smaller, up to about 20cms long. It could probably dwell in open, deep waters, but also nearer the shore, and even occasionally venture into the wetlands. The Recent *Amia* -the bowfin-, type genus of the family, is a very effective piscivore fish of North-America, dwelling in sluggish, clear, and lowland freshwaters that are preferably rich in vegetation (Lee et al., 1980 *fide Grande* and *Bemis*, 1998). It is a voracious predator whose primary food source are other fishes from the time it is about 10cm long (Schneberger, 1937 *fide Grande* and *Bemis*, 1998). It is interesting to note here, in relation with the ontogenetic changes in the diet of fishes mentioned above, that the specimens of *Amia calva* under 10cms, approximately, feed on smaller, very different animals that include adult and larval insects, ostracods, and other zooplankton and phytoplankton (op. cit.).

3.- Fishes related with the benthos. -

The benthic organisms represented in the fossil record from Las Hoyas are probably the most diversified, due to the taphonomic biases favouring the preservation of those creatures living on and in the sediments of the bottom of the lake. These organisms dwelt in a ground cover consisting of algae plus aquatic angiosperms (flowering plants). The algal flora of Las Hoyas was dominated by charophytes (stoneworts), which formed a dense cover in the shallow areas of the lake. They were abundant and diversified (*Charaxis, Clavatoraxis, Palaeonitella*) and formed at least two biocenosis, one living in permanent shallow waters, and another adapted to light-limited, deeper waters. Rare cyanobacteria and other algal groups, such as filamentous chlorophytes, were probably represented as well, but without a conclusive fossil record. Angiosperm record includes the buttercup-like *Ranunculus*, the waterlily-like *Proteaphyllum*, and the extremely abundant, yet enigmatic, *Monteschia*, initially assessed to the bryophytes, but whose reproductive structures suggest that it may be an angiosperm as well. Benthic animals include abundant crustaceans: ostracods (at least 16 different taxa), pericarids (isopods, speleogriphaceans), and the decapod *Austropotamonobius*, which is the same genus than a widespread Recent freshwater crayfish. Aquatic insects such as Coleoptera -beetles- larvae and adults of different groups occur as well, but they are not so abundant. Finally, only very few specimens of freshwater bivalve and gastropod molluscs are known. This scarcity could be due to palaeoecological factors, but maybe also to a taphonomic bias that did not favour the preservation of their calcitic shells.

3a.- Pycnodontiformes (Fig. 2D).-

Pycnodonts are rare in Las Hoyas. Only two specimens of *Stenamara mia* are known, the second one unearthed in 2003, and reported herein for the first time. Most of the pycnodont specimens of this locality belong to *Turbomesodon praeclarus* (Fig. 2D). Both genera are members of the large family Pycnodontidae. For additional anatomic and phylogenetic information on the pycnodonts from Las Hoyas, see Poyato-Ariza and Wenz (2000, 2002, 2004). The dentition of pycnodonts is traditionally interpreted as adapted to a durophagous diet. The variations and adaptations of their specialized dentition are explored by Poyato-Ariza (this volume). Both *Stenamara* and *Turbomesodon* present what in that paper is considered a “generalized pycnodont” dentition, meaning that the combination of their standard incisiform and molariform teeth would enable them to feed on a potentially varied hard food source. Hervibory, bizarre as it may seem, is also an interesting possibility to be explored for the Las Hoyas pycnodonts. Let us notice that the thalli of *Clavatoraxis robustus*, the most abundant charophyte alga, were reinforced with a coat of spine-cell rosettes, interpreted as a protection against hervibory (Martín-Closas and Díéguez, 1998). Although amphipods, coleopters, and crayfish do feed on charophytes in Recent similar environments (Proctor, 1996 *fide Martín-Closas* and Díéguez, 1998), such a hard vegetable food source might have been used by the Las Hoyas pycnodonts as well. Specially if we take into account their cutting-edged incisiform teeth and the possible animal hard-food sources available: on one hand, the crayfish, whose adult size is very large for the small mouth gape of the pycnodonts, and probably too hard to be broken with the delicate incisiform teeth of these fishes; and, on the other hand, the bivalves and gastropods, whose scarcity could be a taphonomic bias, but could also be a palaeoecological bias. An analysis of the fossils and fossil-facies associations, in the frame of the current palaeoecological work at Las Hoyas, will probably deliver more clues on their diet. In any case, the body shape of the pycnodonts from Las Hoyas indicate that they were specialized in manoeuvring (see Poyato-Ariza, this volume: fig. 2C), a clear indication that their preferred habitat in this lake would be the benthos with a dense ground vegetal cover. This could correspond to shallow and/or deep waters; this remains to be tested, although pycnodonts seem to be related with humidity cycles (Buscalioni, pers. comm. 2004).
specimens show the diagnostic characters of *Holophagus*. This genus is now restricted to the Lower Lias, so it probably belongs to a different one. Its scarcity and imperfect preservation prevent, though, a more precise taxonomic assignment for the time being. In any case, the coelacanth from Las Hoyas is very rare, and of moderate size for a fish of this group, up to about 30cms. Coelanchants, with their robust body and lobed fins, are well adapted to manoeuvring. The Recent coelacanth, *Latimeria*, lives in rocky bottoms, several hundred meters deep in the ocean, and is a big, voracious predator, but this was certainly not the case of the Las Hoyas lacustrine coelacanth. It must have dwelt amidst the dense vegetal cover of the deepest parts of the lake. Its more likely prey are juvenile and adult insects (beetles, water-bugs), crayfish, and maybe juvenile pycnodonts. It would be interesting to know whether it was somehow linked to the humid cycles.

3d.- Primitive teleosts.-

It is possible that some of the abundant, diversified primitive teleosts presented on paragraph 2a above were mud-filtering and detritivorous forms. A large mouth cleft, with projecting maxilla, and an extensive branchial basket would enable them to live on the particles that they may filter from the mud of the bottom of the lake, even though jaw protrusion was not possible for this teleosts with a relatively primitive oral anatomy. In any case, this specialized niche could probably not be occupied by any other fossil fish known from Las Hoyas, and it is likely that there were many detritivorous forms in this lake, for detritivorous fishes are very important in Recent tropical freshwaters (Lowe-McConnell, 1987).

**SEXUAL DIMORPHISM IN RUBIESICHTHYS GREGALIS**

It seems appropriate to include in the present paper some previously unpublished evidence of sexual dimorphism in one of the Las Hoyas fishes, *Rubiesichthys gregalis* (paragraph 2b). When this fish was revised (Poyato-Arzia, 1996c), empirical evidence of occurrence of two groups of adult individuals appeared (Appendix 1). While all of the smaller specimens are low-bodied (Fig. 2F), part of the larger individuals present the body as high as or lower than the head (Fig. 2G, below), and the other part, the body higher than the head (Fig. 2G, above). This difference is not preservational, since the ribs are slightly longer in all of the individuals with a higher body. Not a single other osteological difference is found between these two types; all of the specimens show the diagnostic characters of *Rubiesichthys gregalis* discussed by Wenz (1984) and Poyato-Arzia (1996c). In contrast, these distinct morphotypes are not found in *Gordichthys conquensis*, the sister-genus of *R. gregalis* (Poyato-Arzia, 1994, 1996a, 1996b; 1a above). Juvenile and subadult specimens of *Rubiesichthys* are known; the smallest known individual is 11.0mm in standard length. Numerous specimens form a growth series that can be considered continuous between 16 and 35mm (Wenz and Poyato-Arzia, 1994). The youngest specimens do not exhibit any morphometric difference, being all of them lower-bodied (Fig. 2F). The statistic analyses by Poyato-Arzia (1991), briefly outlined in Appendices 1 and 2, showed that the morphotypes can be confidently hypothesized to represent sexual dimorphs (Fig. 2H).

This hypothesis of sexual dimorphism is supported by all observations. As mentioned above, the difference in relative body height of the two groups of adult individuals is not due to preservational artifacts. Only two alternative hypotheses may explain this difference. The two morphotypes with different relative body height might be distinct taxa (hypothesis H1) or distinct morphotypes of the same species (alternative hypothesis, H2). The preferred hypothesis is H2. Firstly, because the results of all of the statistic analyses presented in Appendix 2 allow to reject hypothesis H1 and accept hypothesis H2. In addition, there are several biological arguments:

1) no anatomic differences were found;
2) no significant meristic differences were found;
3) no significant morphometric differences other than the relative body height were found;
4) both types of individuals coexisted temporally and spatially, since they appear in the same levels of the two outcrops where this fish is known, El Montsec and Las Hoyas; and
5) they occur in a roughly 50-50 ratio.

Consequently, the accepted hypothesis is H2: the lower and the higher-bodied morphotypes belong to the same taxon, *Rubiesichthys gregalis*. The most plausible kind of variation that explains the occurrence of two distinct morphotypes in individuals of the same species is obviously sexual variation.

Fishes, as most other Craniata, are dioecious, that is, the sexes are separate, although a good number of actinopterygian species are externally indistinguishable. The most common secondary sexual characters exhibited by living fishes are anatomical: color pattern, nuptial tubercles, contact organs, genital papillae, etc. (e.g., Laggler et al., 1977; Helfman et al., 1997). These characters are usually not preserved in fossil osteichthys. One remarkably exception is the basal actinopterygian *Pelopleurus nuptialis*, from the Triassic of Italy (Lombar-
Whenever sexual morphotypes do occur in Recent fishes, there are morphometric differences in the relative body height, the female presenting always a higher abdomen, as shown by Recent fishes. As a matter of fact, the mass of the ovaries can be up to 70% of the body weight, and it increases with body size of female individuals (Helfman et al., 1997). Studies of small living freshwater fishes presenting sexual morphotypes are congruent with those proposed for Rubiesichthys (see Poyato-Ariza, 1991, for a detailed account of taxa and references). It is therefore coherent to apply Rubiesichthys the criterion that, when sexual morphotypes occur, the female is the gender that exhibits a higher abdomen, as shown by Recent fishes. Thus, the morphotype with maximum body height equal or lesser than head height is interpreted herein as the male dimorph (Figs. 2G-H, below), and the morphotype with maximum body height greater than head height, as the female dimorph (Fig. 2G-H, above).

Empirical observation of the specimens of Rubiesichthys shows that the morphometric differentiation of the female (high bodied dimorphs) starts at 20mm in standard length. The morphotypes do not occur in the younger individuals (Fig. 2F), as they differ only from 20mm in standard length on, that is, the most juvenile specimens do not present distinct morphotypes. Therefore, we can assume that the sexual differentiation, that is, the development of recognizable gonadal structures, of Rubiesichthys gregalis used to start at 20mm in standard length on, at least in female individuals (in some fishes the male matures earlier than the female: Lagler et al., 1977). Sexual morphotypes cannot be distinguished in individuals under 20mm, so they can be confidently considered as juvenile ones. From 20mm on, the individuals could be considered as adult ones. The increase of the maximum body size, that is, in ovaries size, continues along the life of the female individuals, being anisometrically higher in larger females. Empirical observations also show that the females reach longer body size than the males in Rubiesichthys, which also happens in Recent fishes (e.g., Lagler et al., 1977; Helfman et al., 1997). It can also be deduced that, since both morphotypes occur in a roughly 50-50 ratio among sexually differentiated individuals, this fish was permanently dimorphic, as is the case of many Recent small freshwater genera (for instance, Poecilia and Cichlasoma: Helfman et al., 1997).

Studies of morphometric sexual dimorphism in fossil osteichthyan fishes are rare, since a statistic approach requires a significant number of well-preserved specimens. It is not usually testable if the morphotypes, provided that they occur, represent distinct genders of the same species, distinct species, or even distinct genera. The few known cases are consistent with the hypothesis presented herein for Rubiesichthys (e.g., Gaudant, 1973; Wilson, 1984).

CONCLUDING REMARKS

"Morphology is not a perfect predictor of prey-use patterns" (Wainwright and Bellwood, 2002: 44), especially when the approach is as general, superficial, and lenient as the one used in this paper. Even so, it can be noticed how the fishes from Las Hoyas tend to occupy distinct niches in the lake as soon as their morphology is used to predict possible preferences on their habitats and locomotion/feeding strategies. This is hardly surprising, of course, as it does happen in any Recent ecosystem, but is an indication that a cautious ecomorphologic approach is useful in fossil fishes.

The approach must be cautious because of the difficulties involving the actual ecologic characterization of fossil organisms, where remains of food in the digestive tract are just exceptionally preserved, and taphonomic factors do alter our perception of their original environment. In addition to this, when Recent forms are studied, it results evident that the diet composition in fishes can be very variable within a single species. It changes throughout growth; but even fully adult fishes may have an extremely varied diet, and cases of individual preferences are known. The diet is modified whenever the food sources change. Furthermore, fishes with similar morphology can feed on different organisms in the same habitat by behaving differently, and can even feed on the same organism in the same habitat, also by behaving differently. In both cases, the morphology is an indicator of the diet, but acts through the necessary filter of animal behaviour.

For all the reasons outlined above, the categorization of the Las Hoyas fishes presented here is far from strict. For instance, although primitive teleosts and Rubiesichthys are included in the fishes with purely nektonic habits, some of them may have actually been midwater zooplanktivores, and therefore would need to be included in the group of fishes related with the plankton as well. However, the purpose of this paper is not to achieve a strict ecomorphologic analysis or a rigorous niche categorization, but simply to show the potential possibilities for distinct niche preferences of the Las Hoyas fishes with the data currently available. In this sense, the main idea to retain is that the fishes from this Cretaceous lake can be arranged in distinct niches with different habitats and feeding strategies, at least potentially, and that this can serve as one more element for the study of the
palaeoecology of this fascinating locality.

The area of Las Hoyas was formed, during the Barremian, by a permanent lake surrounded by interacting, fluctuating wetlands. There were dry and humid cycles, and no marine influence. Some of the most generalized fishes from the lake, such as primitive teleosts, would probably get into the wetlands, and is possible that some small piscivore forms would do that as well. This would have occurred in different extent throughout time, according to the availability of the adequate aquatic ecological space and food sources. Some fish taxa, such as the pycnodonts and the largest piscivores, were probably much more restrained in space, and also perhaps in time. Their relationship with the humidity cycles in the lake is currently being explored (Fregenal et al., work in progress).

Juvenile specimens of most fish taxa are extensively present in Las Hoyas (Wenz and Poyato-Ariza, 1994). A good number of them, being plankton-related, probably occupied a different niche from that of the corresponding adults. Most Recent lacustrine juvenile fishes live in the most superficial part of the shallowest waters of the lakes, generally very near the shores, and amidst vegetation. Sudden changes in these restricted environments could explain the mass mortality events of juvenile teleosts consistently found at Las Hoyas. Growth in fishes is substantially affected by the temperature (e.g., Moyle and Cech, 1988; Wootton, 1990; Weatherley and Gill, 1987), so that juvenile fishes are very sensitive to changes in the temperature of the waters. A sudden change in temperature, among other possible physical and chemical changes, may have caused the mass mortality events.

Empic observation clearly shows that the adult fishes from Las Hoyas are considerably smaller than adult individuals of closely related taxa (e.g., Amiidae, Chanidae, Lepidotes, Pleuropholis). This suggests conditions of stress in the ecosystem, such as lake-level changes or frequent disruptions of the trophic chains. Small size could also be a physical advantage for adapting to dwell in the wetlands, even when water was very shallow. It confirms the preliminary evidences of, and fits well into, the currently developing palaeoecological model for Las Hoyas. This was an overall stable ecosystem, yet stressed, varied, and fluctuating throughout time, in a continental environment during the Barremian, 115 million years ago.

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I began writing this paper the day after 11-M, in my home in Madrid, very near Atocha train station; it is humbly dedicated to all the worldwide victims of terrorism and war, which inflict terrible inhuman pain to innocent human beings.

REFERENCES


APPENDIX 1

This Appendix briefly explains the morphometric and meristic characters measured and counted, respectively, during the study of the sexual dimorphism of *Rubiesichthys gregalis*, discussed in the text. The morphometric and the meristic characters are variable within narrow ranges, as given below. The list of material is in Poyato-Ariza (1996a, 1996b, 1996c).

1a.- Morphometric characters.

The morphometric measures studied are (in millimetres): standard length (11.0-42.1), predorsal length (6.7-24.8), preanal length (8.1-31.1), prepectoral length (3.4-11.0), prepelvic length (5.8-24.9), head height (2.0-6.7), maximum body height (1.5-6), caudal pedicle height (0.8-3.1), preorbital distance (0.7-2.0), orbital diameter (0.8-2.5), postorbital distance (1.5-6.0), and head length (3.0-10.5). In addition, these measures are used to calculate the following ratios (the range of the main values for adult individuals in percentage are presented in brackets): postoral length/head length (50-55%); head height/standard length (15-20%); head height/maximum body height (80-125%); head height/head length (60-65%); head length/standard length (25-29%); maximum body height/standard length (15-20%); predorsal length/standard length (55-60%); preanal length/standard length (70-75%); pelvic length/standard length (50-55%); and caudal pedicle height/maximum body height (40-50%). These variations are not significant (5% spans), except that of the ratio “maximum body height/head height”, which present a 45% span, being the only one that does not present a unimodal distribution. The variation in this ratio accounts for the observed morphotypes mentioned and discussed in the text.

1b.- Meristic characters.

The following meristic characters were counted for this study (the main values are presented in brackets): number of vertebrae (37-39); number of dorsal fin pterygiophores (8-9); number of segmented dorsal fin rays (7-8); number of anal fin pterygiophores (7-8); number of segmented anal fin rays (7). All these characters show unimodal variation. The pectoral and pelvic fin rays are not countable in a statistically significant number of specimens, so this character is not included in the statistic analyses below. It must be noticed, anyway, that it does not show relevant variation among the individuals where it is accessible (there are 9, only exceptionally 10 fin rays in the counted pectorals and pelvics). With this exception, all the morphometric and meristic characters are included in the statistic analyses of Appendix 2.

APPENDIX 2

This appendix outlines the previously unpublished statistic analyses by Poyato-Ariza (1991) and the additional ones that support the hypothesis of sexual dimorphism for *Rubiesichthys gregalis*.

The large number of adult specimens of *Rubiesichthys gregalis* unearthed at El Montsec and Las Hoyas allow a statistic approach to analyse the morphometric and
meristic variation. Only large individuals (above 25mm in standard length) were included in this set of analyses, so that the potential ontogenetic changes would not disturb the initial analyses.

The tests were separately carried out for each population of Rubiesichthys by using 117 large specimens from Montsec and 142 from Las Hoyas. The results were identical for both populations. The statistic tests consisted of:

A) Plotting the distribution of all of the available morphometric and meristic characters, in order to confirm their distribution. All of these characters (listed in Appendix 1 above) showed unimodal distribution. Only the ratio "maximum body height/head height" resulted non-unimodal.

B) Analysis of characters correlation to determine whether the relative body height covaries with any meristic character. This was attempted because most of the latter usually present two main values, close enough to determine a unimodal distribution, but since each peak value could be associated to one of the morphotypes, and not to the other, it was necessary to test the independence of the relative body height and each meristic character. For instance, the distribution of the number of dorsal axonosts is unimodal, but shows two main values, 8 and 9, so that one of the morphotypes could always present 8 rays, and the other morphotype, 9. If so, this difference might be significant enough to involve specific, or even generic, variation. This corresponds to hypothesis H1: the morphotypes belong to different taxa. Hence, the alternative hypothesis, H2 is: both morphotypes belong to the same taxon.

The null hypothesis for every test of independence was: "The ratio maximum body height to head height and the meristic character X are independent". The test of independence of variables used as statistic Pearson's Chi Square, with one freedom degree, and an alpha value of 0.05. The ratio maximum body height/head height was tested with all of the available meristic characters listed in Appendix 1 above. The result was that this ratio is not correlated with any meristic feature. In other words, all of the meristic features are evenly distributed in both higher-bodied and lower-bodied individuals. So, hypothesis H1 can be rejected, and hypothesis H2 can be accepted. This means that both morphotypes differ only in their relative body height, from which we confidently conclude that the variation is not specific or generic, and that both morphotypes belong to the same taxon, Rubiesichthys gregalis.

This was confirmed, for the present study, by a Principal Component Analysis on the SPSS program, which showed that the main source of variation among all of the analyzed variables is the ratio "maximum body height/head height", that is, the relative body height.

Added in proof: the recently published paper by Schultze and Soler-Gijón (2004) states that "Terrestrial forms like plants, spiders, insects, and reptiles cannot be used to reconstruct an aquatic depositional environment; their occurrences in the Lagerstätte are accidental (...in contrast to Poyato-Ariza et al. 1998)" (op. cit.: 334). The first part of this statement is quite obviously right, although it lacks a more strictly taphonomic approach. The second part, though, implies that the terrestrial taxa were the ones used for reconstructing the depositional environment of Las Hoyas, but this is simply not true. Firstly, the mentioned paper precisely emphasizes that "The palaeoecological evidence from Las Hoyas strongly indicates a continental environment, as evidenced not only by the majority of the taxa present at this locality, ..." (Poyato-Ariza et al., 1998: 72; underlining added for the present paper); the list of aquatic freshwater taxa known from literally thousands of specimens produced by demic organisms is impressive (Poyato-Ariza et al., 1998: 72; see brief outline in the different sections of the present paper). Secondly, the evidence for reconstructing the depositional environment comes precisely from geological and sedimentological data, which are obviously the relevant ones for this kind of study (Poyato-Ariza et al., 1998: 69-71), and not from palaeoecological inferences.

Thirdly, and most importantly, the combined evidence provided by palaeogeography, stratigraphy, sedimentology, taphonomy, palaeoecology and isotopic analyses (oxygen, carbon, and strontium) indicates that at Las Hoyas sediments were deposited and fossils were produced in a fresh water environment, free of marine influence (e. g., Poyato-Ariza et al., 1998; see this reference, the present paper, and Poyato-Ariza, this volume, for further data and citations). All other possible hypotheses about the palaeoenvironment of Las Hoyas during the Barremian are simply not based on actual scientific data.