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Editor: Linda Trueb
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PRINTED BY
UNIVERSITY OF KANSAS PRINTING SERVICE
LAWRENCE, KANSAS

OCCASIONAL PAPERS

of the MUSEUM OF NATURAL HISTORY The University of Kansas Lawrence, Kansas

NUMBER 164, PAGES 1–37 26 JANUARY 1994

A New Early Cretaceous Gonorynchiform Fish (Teleostei: Ostariophysi) from Las Hoyas (Cuenca, Spain)

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ABSTRACT *Gordichthys conquensis* nov. gen. nov. sp. is a small gonorynchiform teleost only known from the recently discovered Early Cretaceous outcrop of Las Hoyas (Cuenca, Spain), which is Late Hauterivian–Early Barremian in age. This new fish is characterized by the following features: a short, triangular head; a mouth cleft that is directed dorsally; edentulous premaxilla, maxilla, and mandible, but toothed parasphenoid and vomer; a moderately deep body; a short-based, high dorsal fin; a robust caudal peduncle; an unforked caudal fin that is higher than long; last hypural in contact with U2, and neural spine of PU2, epurals, uroneurals, and last four hypurals in contact with each other. The supraoccipital bone partially separates the parietals; this condition is termed "mesoparietal." In addition, *Gordichthys* possesses the synapomorphies of the superorder Ostariophysi and of the order Gonorynchiformes in most of the characters that can be verified. It is similar to the members of the family Chanidae in several cranial and caudal endoskeletal features. However, it is considered as a gonorynchiform *incertae sedis* until a cladistic analysis is attempted. *Gordichthys conquensis* strikingly resembles the other Spanish Early Cretaceous ostariophysan teleost, *Rubiesichthys gregalis* Wenz, 1984, but the taxa can be distinguished on the basis of morphometric features of the body, head, and caudal fin, and by several anatomical characters.

Key words: Early Cretaceous, Spain, Anatomy, Systematics, Teleostei, Gonorynchiformes, New genus and species.

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 ISSN:0091-7958

RESUMEN *Gordichthys conquensis* nov. gen. nov. sp. es un pequeño pez teleósteo gonorynchiforme, conocido hasta la fecha únicamente en el recientemente descubierto yacimiento del Cretácico inferior de Las Hoyas (provincia de Cuenca, España), cuya edad se ha estimado como Hauteriviense superior–Barremiense inferior. Este nuevo pez está caracterizado por los siguientes rasgos: cabeza corta y triangular; apertura bucal dirigida dorsalmente; premaxilar, maxilar y mandíbula sin dientes, pero paraesfenoides y vómer dentados; cuerpo moderadamente alto; aleta dorsal corta y alta; pedúnculo caudal robusto; aleta caudal más alta que larga, sin ahorquillar; último hipural en contacto con U2, y espina neural de PU2, epurales, uroneurales y últimos cuatro hipurales en contacto entre sí. El supraoccipital separa parcialmente los parietales; se propone el término "mesoparietal" para nombrar esta condición craneal. *Gordichthys* posee, además, las sinapomorfías del superorden Ostariophysi y del orden Gonorynchiformes en casi todos los caracteres que pueden ser verificados. Se asemeja a los miembros de la familia Chanidae en varios caracteres craneales y del endoesqueleto caudal; sin embargo, se le considera gonorynchiforme *incertae sedis* hasta que se realice un análisis cladístico. *Gordichthys conquensis* es especialmente similar al otro teleósteo ostariofisio del Cretácico inferior español, *Rubiesichthys gregalis* Wenz, 1984, pero ambos pueden distinguirse en base a rasgos morfométricos del cuerpo, cabeza y aleta caudal, y a varios caracteres anatómicos.

Palabras claves: Cretácico inferior, España, Anatomía, Sistemática, Teleostei, Gonorynchiformes, Nuevo género y especie.

The Spanish Early Cretaceous outcrop of Las Hoyas, located in the province of Cuenca, about 200 km SE of Madrid, was discovered a few years ago and is proving to be one of the most important Early Cretaceous European outcrops (Sanz et al., 1988; Sanz, 1989; Sanz and Poyato-Ariza, in press). The Las Hoyas carbonate sediments have been dated within the Late Hauterivian–Early Barremian time span and contain copious, well-preserved remains of plants and animals; plants such as ferns, *Zamites*, and *Montsechia*, are abundant, as are crustaceans and insects (Odonata, Hemiptera, Hymenoptera, Orthoptera, Coleoptera, etc.). The vertebrate fauna is very rich, containing anurans, caudates, chelonians, saurians, crocodilians, dinosaurs, and at least two new birds—*Iberomesornis romerali*, which is the sister taxon of the Ornithurae (Sanz et al., 1988; Sanz and Bonaparte, 1992) and *Concornis lacustris* (Sanz and Buscalioni, 1992). An up-dated account of the flora and fauna of Las Hoyas was provided by Sanz and Poyato-Ariza (in press).

Fish are the most common vertebrates of the Las Hoyas fauna and are represented by many specimens of semionotiforms, pycnodontiforms, amiiforms, and pleuropholids. Non-gonorynchiform teleosts are especially abundant, including numerous new forms whose juvenile specimens occasionally are found clumped together throughout the formation (Poyato-Ariza, 1989; Poyato-Ariza and Wenz, 1990; Wenz and Poyato-Ariza, in press). Herein, an endemic new genus and species of gonorynchiform fish is described from Las Hoyas.

MATERIALS AND METHODS

In addition to the holotype and the 39 paratypes, there are 54 topotypes accounting for the total of 94 individuals of the new species found to date at Las Hoyas. Specimens designated as "A/B" are represented by a part and counterpart, whereas in those designated as "AB," the part and counterpart are restored on the same slab; absence of both "A" and "B" indicates that no counterpart was preserved. Specimens were prepared mechanically or treated locally with acid, as necessary (usually 2–3% acetic acid).

Most of the Las Hoyas specimens examined are in the collections of the Museo Provincial de Cuenca (MPC), provisionally housed at the Universidad Autónoma de Madrid (UAM). A few are from the private collection of Mr. Armando Díaz Romeral (R) and the Division of Vertebrate Paleontology of The University of Kansas Museum of Natural History (KUVP).

SYSTEMATIC PALEONTOLOGY

Subdivision Teleostei
Supercohort Elopocephala
Cohort Clupeocephala
Subcohort Euteleostei
Infracohort Ostariophysi
Series Anotophysi
Order Gonorynchiformes *incertae sedis*

Gordichthys nov. gen.

Type and only species.—*Gordichthys conquensis.*

Diagnosis.—Small teleost with relatively deep body; triangular head and small orbit. Relatively small parietals, partially separated by supraoccipital; frontals only slightly narrower anteriorly. Terminal mouth; mouth cleft directed dorsally; quadratomandibular articulation located anterior to orbit. High coronoid process (about 50% mandibular length); "leptolepid" notch present. Dentary anteriorly elongate, narrow, and slightly curved downward. Retroarticular free, not forming part of articulation with quadrate. Maxilla with broad posterior blade and long, curved, stout anterior process. Premaxilla broad and thin, with long oral process and no ascending process. Supramaxillae absent. Upper and lower jaws edentate; vomer and parasphenoid toothed. Large opercle; preopercular limbs with broad expansion on posterior edge and forming acute angle with one another.

Neural and haemal arches fused to their centra, at least in caudal region; two most anterior centra shorter than others. Anterior three neural arches

Fig. 1. *Gordichthys conquensis*. Holotype (LH 1228 R), right lateral view; 30.2 mm SL. Photo by D. Serrete.

enlarged and in contact with each other. First supraneural expanded, with a posterior process. Few, delicate epipleurals present between precaudal and caudal regions. Lateral line piercing across the length of supracleithrum. Pelvic bones in contact both proximally and distally. Robust caudal peduncle, one-eighth to one-sixth standard length (SL). Caudal fin higher than long, unforked. One or two neural and haemal arches and spines on Preural Centrum 2. Two independent ural centra. Two short uroneurals, two epurals, and six autogenous hypurals. Last hypural articulating with U2. Neural spine of PU2, epurals, uroneurals and Hypurals 3–6 in contact with each other. Caudal scutes absent.

Etymology.—From the Spanish adjective *gordo*, meaning fat, and the Greek substantive *ichthys*, meaning fish.

Gordichthys conquensis nov. sp.

(Figs. 1–2; Table 1)

Holotype.—MPC: LH 1228 R, provisionally housed at the UAM.

Paratypes.—MPC (provisionally housed at UAM): AB LH 477; A/B LH 480 (complete, well-preserved juvenile); A/B LH 509; A/B LH 550; A/B LH 598; A/B LH 602; AB LH 631; A/B LH 643 (complete, well-preserved juvenile); A/B LH 700 (almost complete, well-preserved); AB LH 735; A/B LH 739; LH 818; A/B LH 843; AB LH 928; A/B LH 929 (complete); A/B LH 951 (complete, well-preserved); AB LH 960; LH 985; A/B LH 1225 (complete, well-preserved); A/B LH 1279 (complete, well-preserved); A/B LH 1305; AB LH 1407; AB LH 1414; AB LH 1415; AB LH 1417; LH 1421; A/B LH 1585; A/B LH 1613; AB LH 1708; A/B LH 1725 (complete, well-preserved).

R: A/B LH 2179 R (complete, well-preserved); LH 4986 R (complete, well-preserved); LH 4989 R (complete, well-preserved).

KUVP: LH 1017 (KUVP 123102); A/B LH 1402 (KUVP 123105); A/B LH 1409 (KUVP 123103).

Horizon and locality.—Late Hauterivian–Early Barremian limestones of Las Hoyas, province of Cuenca, Spain.

Diagnosis.—Small size, up to 38 mm SL. Body depth 33% SL. Thirty-four to 40 vertebrae, 14–18 of them caudals. Ten or 11 pectoral fin rays; 9 or 10 pelvic rays; 9 or 10 dorsal rays; 8 to 10 anal rays. Anterior end of pelvic fin located at about 60% SL. Dorsal fin high and short-based, situated at about same level as, or posterior to, pelvic fins. Anal fin short, located at 75% SL.

Etymology.—The specific name is an adjective derived from the Latin *Conca*, the roman name of the Spanish province of Cuenca, in which the species was discovered. (*Gordichthys conquensis* means "fat fish from Cuenca.")

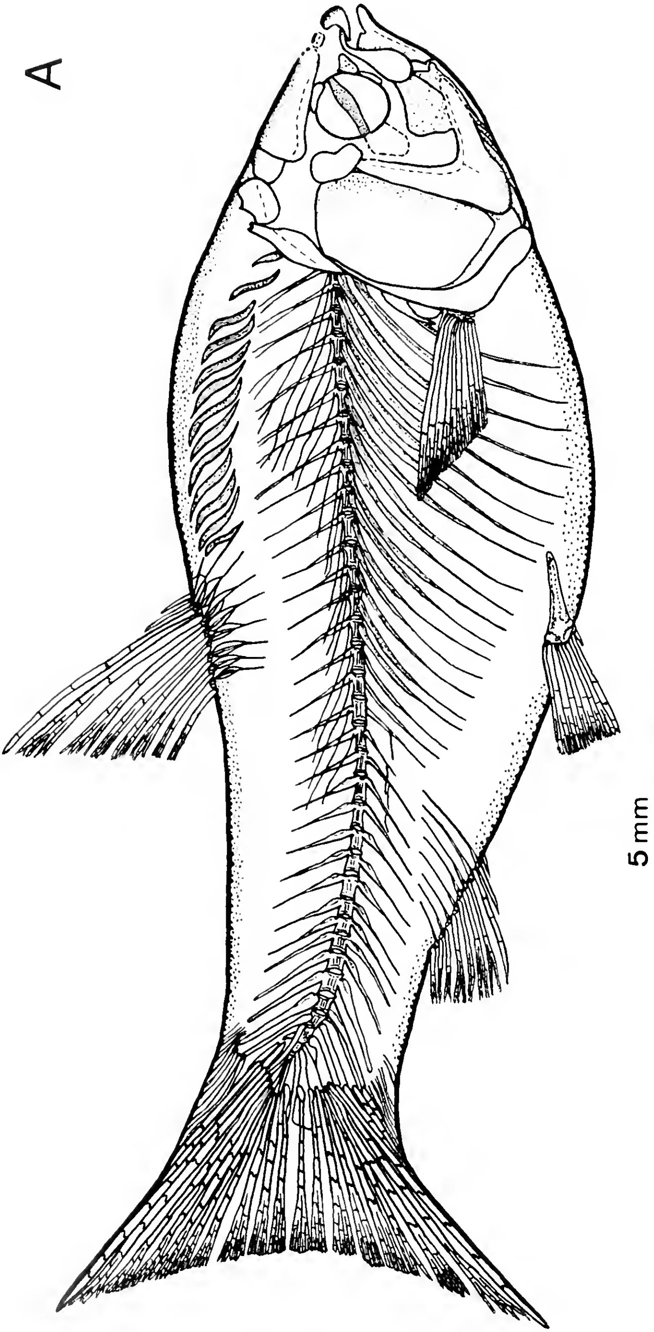

Fig. 2A. Restoration of *Gordichthys conquensis* in right lateral view. Based on the holotype and most of the paratypes.

Fig. 2B. Tentative restoration of *Gordichthys conquensis* in life; right lateral view prepared by M. Antón. Colors loosely based on Recent tropical freshwater cyprinodontiforms.

Table 1. Measurements and proportions of *Gordicthys conquensis*. Abbreviations: CPH, caudal peduncle height; HH, head height; HL, head length; MXBH, maximum body height; OD, orbital diameter; PAL, preanal length; PDL, predorsal length; PPCL, prepectoral length; PPVL, prepelvic length; PROL, preorbital length; PSOL, postorbital length; SL, standard length.

	Measurement					
Specimen(s) and statistic	SL	PDL	PAL	PPCL	PPVL	MXBH
Holotype (LH 1228 R)	30.2	16.7	23.2	8.8	17.3	11.8
%SL	—	55.3	76.8	29.1	57.3	39.1
Adults ($n = 73$)						
Average	32.1	18.8	24.1	9.0	17.5	9.5
Range	28.5–37.9	16.0–22.2	20.8–29.9	7.1–11.5	14.9–22.3	7.1–12.0
Average %SL	—	59.1	75.8	28.7	55.1	31.3
Range %SL	—	52.5–65.9	69.4–81.4	25.4–32.4	47.2–63.2	24.9–39.1
Juveniles ($n = 20$)						
Average	23.0	13.8	17.5	6.6	12.7	6.5
Range	13.4–27.5	8.3–17.0	11.0–21.3	4.0–9.4	7.7–15.8	3.5–11.0
Average %SL	—	60.3	75.8	29.6	55.9	28.5
Range %SL	—	52.3–66.5	71.4–85.2	23.7–37.6	47.7–64.3	22.3–37.7

Table 1. Continued.

Specimen(s) and statistic	Measurement					
	CPH	HH	HL	OD	PROL	PSOL
Holotype (LH 1228 R)	4.7	8.0	7.6	2.0	1.8	3.8
% SL	15.6	26.5	25.2	6.6	6.0	12.6
Adults (n = 73)						
Average	3.8	7.0	8.4	2.0	1.9	4.0
Range	2.5–5.5	4.9–9.5	6.5–10.4	1.4–3.1	1.2–2.9	3.5–5.5
Average % SL	12.9	22.7	27.1	6.7	6.4	14.0
Range % SL	10.0–17.2	16.1–29.3	24.4–31.0	4.7–8.2	4.7–7.8	11.6–16.0
Juveniles (n = 20)						
Average	2.5	5.0	6.2	1.6	1.5	3.2
Range	1.3–4.1	3.5–7.8	4.3–8.8	1.0–2.5	0.8–2.5	1.7–4.4
Average % SL	11.9	22.4	27.9	7.4	6.5	13.9
Range % SL	6.9–15.5	17.6–29.4	21.2–35.2	4.3–10.3	3.5–10.0	9.5–17.3

ANATOMICAL DESCRIPTION

Morphometric Data

Measurements and proportions of the holotype and means and ranges of variation of adult and juvenile specimens are presented in Table 1. *Gordichthys conquensis* is small; the average standard length is 32 mm and the longest specimen (LH 4986 R) is 37.9 mm SL. The average maximum body depth (reached approximately midway between the head and the dorsal fin) is 10 mm, which represents about 32% SL; thus, the body is rather deep and not typically fusiform (Figs. 1–2). The maximum observed body depth is 12 mm (LH 237). The head is shallow (average = 7.0 mm; maximum observed height = 9.5 mm), short, and triangular in shape; the height and length of the head are 23% and 27% SL, respectively. The orbit is small—about 7% SL and 25% of the head length.

The dorsal fin is located just posterior to the midlength of the body, at approximately 60% SL. The pelvic fins are located near a vertical line from the dorsal fins; usually, they lie anterior, but in some specimens (e.g., holotype, A/B LH 598, and AB LH 928), the pelvic fins lie slightly posterior to that line and probably have been displaced. The anal fin lies midway between the dorsal and caudal fins, at 75% SL (Figs. 1–2, 12). The caudal peduncle is robust, its depth being about 13% SL; the depth of the peduncle ranges from one-eighth to more than one-sixth SL.

Age

Despite their small sizes, most specimens of *Gordichthys conquensis* are adult. Some (20) are noticeably smaller, having standard lengths of 20–25 mm. The smallest specimens (A/B LH 602, 13.4 mm; AB LH 1414, 19.7 mm; AB LH 1415, 14.5 mm) are less ossified and have single-branched lepidotrichia (pectoral fin of A/B LH 480); these are juvenile features. The other specimens are well ossified, and in those in which the distal borders of the lepidotrichia are visible, they are double- or triple-branched (e.g., A/B LH 2179 R). The anterior neural spines are unfused in the midline in juveniles; there are traces of fusion in larger specimens, which on the basis of degree of ossification and branching of lepidotrichia, are considered to be subadults or adults.

Skull

The skull (especially the neurocranium and snout) is the most poorly preserved region in these specimens. Although the skull is crushed in most of them, a composite restoration based on several specimens was prepared (Fig. 3).

The skull roof is partially preserved in external view in A/B LH 480 and

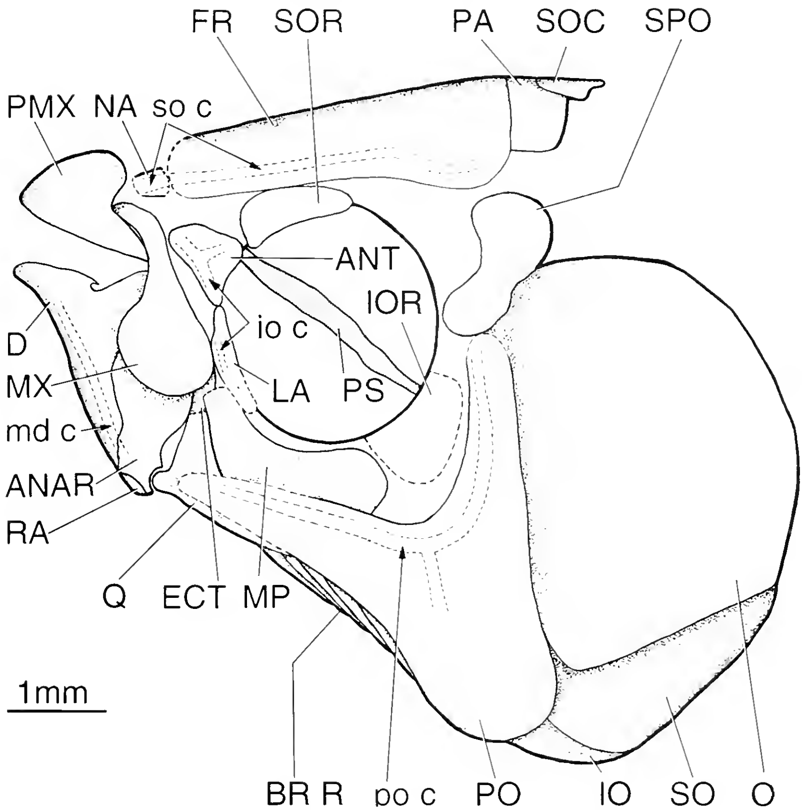

Fig. 3. *Gordichthys conquensis*. Schematic composite skull restoration in left lateral view. Based on most of the paratypes. Abbreviations: ANAR, anguloarticular; ANT, antorbital; BR R, branchiostegal rays; D, dentary; ECT, ectopterygoid; FR, frontal; io c, infraorbital sensory canal; IO, interopercle; IOR, infraorbital (three?); LA, lacrimal; md c, mandibular sensory canal; MP, metapterygoid; MX, maxilla; NA, nasal; O, opercle; PA, parietal; PMX, premaxilla; po c, preopercular sensory canal; PO, preopercle; PS, parasphenoid; Q, quadrate; RA, retroarticular; so c, supraorbital sensory canal; SO, subopercle; SOC, supraoccipital; SOR, supraorbital; SPO, suprapreopercle.

in internal view in A/B LH 1585. The frontals are rather broad, but slightly narrower anteriorly (A/B LH 2179 R; Figs. 3, 5) and bear a pitted ornamentation. The small nasal bone encloses the anterior portion of the supraorbital sensory canal. The canal seems unbranched throughout its length and is straight anteriorly; posterolaterally, it parallels the curved margin of the frontal and terminates before reaching the parietal bone (B LH 929). No connection has been observed between the supraorbital and infraorbital canals. The parietals are relatively small, nearly square, and partially sutured medially (in their anterior portions). The supraoccipital (Figs. 3, 9) is a relatively large bone located between the posterior parts of the parietals; because the supraoccipital partially separates the parietals (the posterior half of their midline), this cranial condition is described as "mesoparietal."

The stout parasphenoid is visible in lateral view as a straight bone that is inclined anterodorsally. The posterior part of the bone and its processes are not preserved in any of the specimens examined; some teeth are visible at the orbital level in A/B LH 794, A LH 2179, and KU 123102 (AB LH 1017). The small vomer is rectangular (preserved in ventral view in AB LH 1407) and bears at least two rows of teeth. Both the parasphenoid and vomerine teeth are small, conical, and circular in section.

The broad, thin premaxilla is hook-shaped and slightly concave (A/B LH 2179 R, LH 4986 R; Figs. 3, 5, 8). The premaxilla lacks an ascending process and its oral process is rather long. Supramaxillae are absent. The short maxilla is expanded posteriorly and slightly ornamented with small ridges and grooves (A LH 700, B LH 929; A/B LH 2179 R, LH 4986 R; Figs. 3, 5, 8). The anterior process of the maxilla is quite long (ca. 50% total maxillary length), stout, and strongly curved anteroventrally. The maxilla and premaxilla are edentulous.

The lower jaw is directed dorsally and forms an angle of approximately 45° to the horizontal plane of the skull in lateral view (Figs. 3–8). The

Fig. 4. *Gordichthys conquensis*. Head of LH 4986 R in left lateral view. Scale = 1 mm. Photo by D. Serrete.

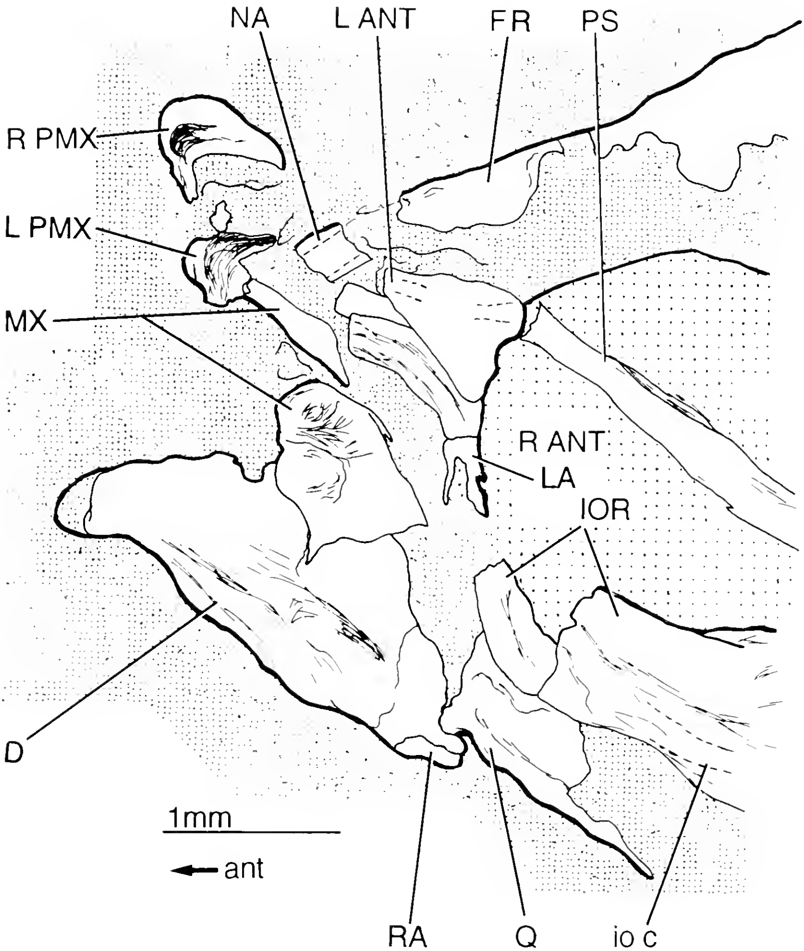

Fig. 5. *Gordichthys conquensis*. Anterior region of skull of A LH 2179 R in left lateral view. Abbreviations: D, dentary; FR, frontal; io c, infraorbital sensory canal; IOR, infraorbital bones; L ANT, left antorbital; L PMX, left premaxilla; LA, lacrimal; MD, mandible; MX, maxilla; n, notch; NA, nasal; Q, quadrate; PS, parasphenoid; RA, retroarticular; R ANT, right antorbital; R PMX, right premaxilla. Stippled areas represent matrix.

anguloarticular articulates with the quadrate just anterior to the orbit. The coronoid process is very high; the maximum height of the mandible is about one half of its length. The ventral margin of the lower jaw is slightly convex posteriorly and slightly concave anteriorly. The anterior portion of the mandible is long, quite low, and curved medially toward the symphysis (Figs. 6, 8). The upper border of the dentary presents a notch located just

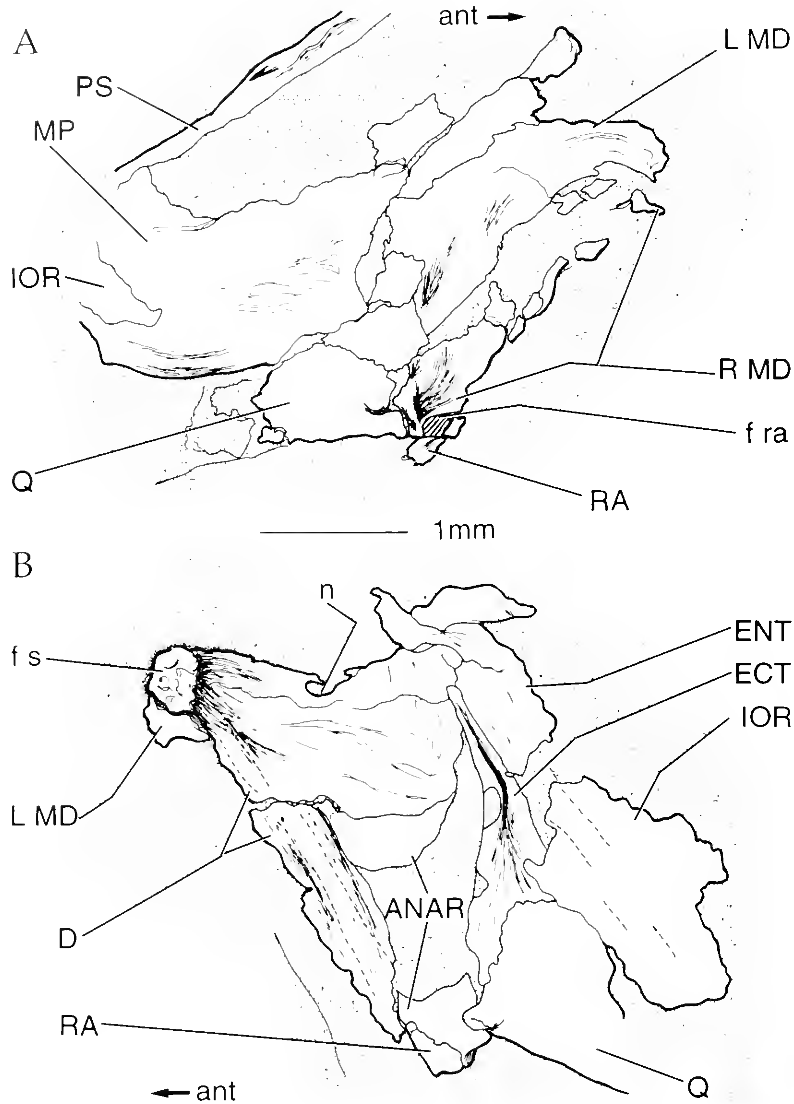

Fig. 6. *Gordichthys conquensis*. Mandibular region. **A.** Holotype, LH 1228 R, in right lateral view. **B.** A/B LH 1725 in right medial view. Abbreviations: ANAR, anguloarticular; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; f ra, facet for the articulation of the retroarticular; f s, surface for the symphysis articulation; IOR, infraorbital bones; L MD, left mandible; MP, metapterygoid; n, "leptolepid" notch; PS, parasphenoid; Q, quadrate; R MD, right mandible; RA, retroarticular. Stippled areas represent matrix.

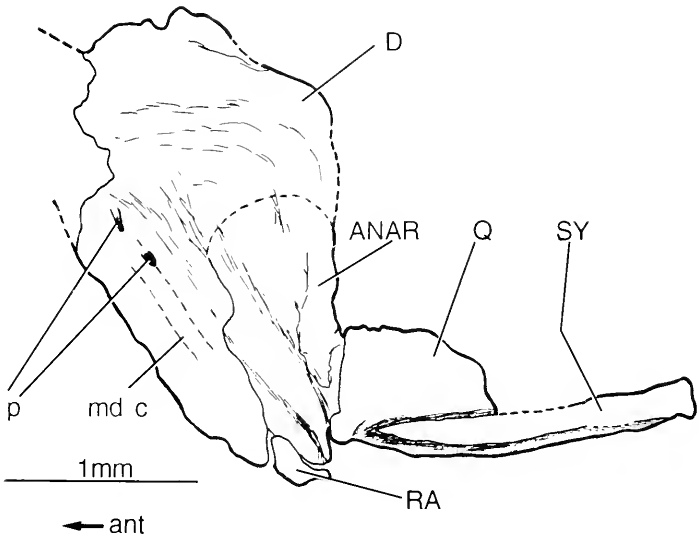

Fig. 7. *Gordichthys conquensis*. Right mandibular region of LH 985 in medial aspect. Abbreviations: ANAR, anguloarticular; D, dentary; md c, mandibular sensory canal; p, pores of the mandibular sensory canal; Q, quadrate; RA, retroarticular; SY, symplectic.

anterior to the coronoid process (Figs. 3, 5–6). This notch resembles that of more primitive teleosts, as pholidophorids and 'leptolepids' (leptolepid notch *sensu* Nybelin, 1966; 1974). The small, elongate retroarticular is not fused to other mandibular bones and does not participate in the articulation of the lower jaw with the quadrate (holotype; LH 818, LH 985, 1409A [KUVP 123103], AB LH 1417, B LH 1725; A/B LH 2179 R, LH 4986 R; Figs. 3, 5, 6–7). The dentary lacks teeth and encloses a mandibular sensory canal that extends along the ventral margin of the bone; the canal is only partially visible (Figs. 3, 7).

The triangular quadrate lies at the level of the orbit, because of the position of the articulation with the mandible. Its articular condyle is directed anteroventrally. The medial surface of the quadrate, along with the posteroventral process (*sensu* Arratia and Schultze, 1991) and symplectic, are visible in A/B LH 700, LH 985, and A/B LH 2179 R. The posteroventral process and the symplectic are rather elongate owing to the position of the quadrate-mandibular articulation, which, as mentioned above, is anterior to the orbit (Figs. 3, 5–7).

The metapterygoid is large; although the edges of the bone are not clear, a posterior expansion is evident (Figs. 3, 6). The anterior portion of the elongate, slightly curved ectopterygoid is narrower than the posterior part (Fig. 6B). The entopterygoid is broader than the ectopterygoid and lies

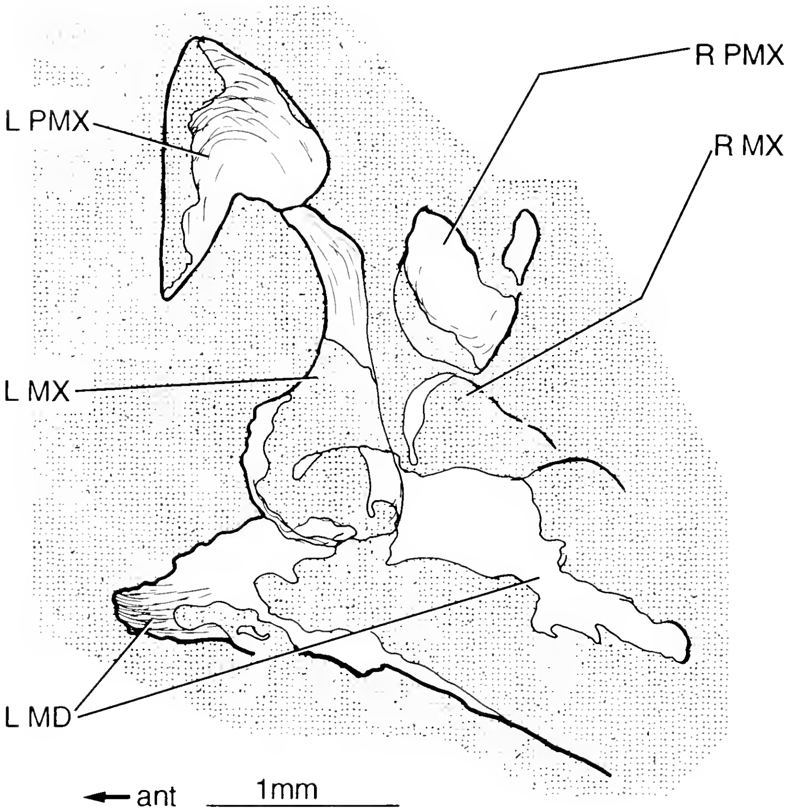

Fig. 8. *Gordichthys conquensis*. Oral region of LH 4986 R in left lateral view. Abbreviations: L MD, left mandible; L MX, left maxilla; L PMX, left premaxilla; R MX, right maxilla; R PMX, right premaxilla. Compare with Figure 4.

parallel to it (Fig. 6). Only fragments of the autopalatine are visible (A/B LH 700; B LH 3279 R), but it is apparent that the anterior portion of this bone overlies the entopterygoid and is in contact with the anterior part of the latter in the holotype.

The hyomandibula is partially visible in A/B LH 480, 735, and LH 4986 R. The opercular process is horizontal and articulates with the hyomandibular facet of the opercle; the rest of the bone is poorly preserved. The hyomandibula possesses a broad anterior blade, the exact size of which cannot be established. The hyomandibular articular head appears to be double in LH 4986 R. The remainder of the hyoid bones are not visible in any of the specimens. Although a fragment of the ceratohyal is present in B LH 2179 R, nothing can be said about the structure of the bone. Five short, thin branchiostegals are exposed in A LH 960.

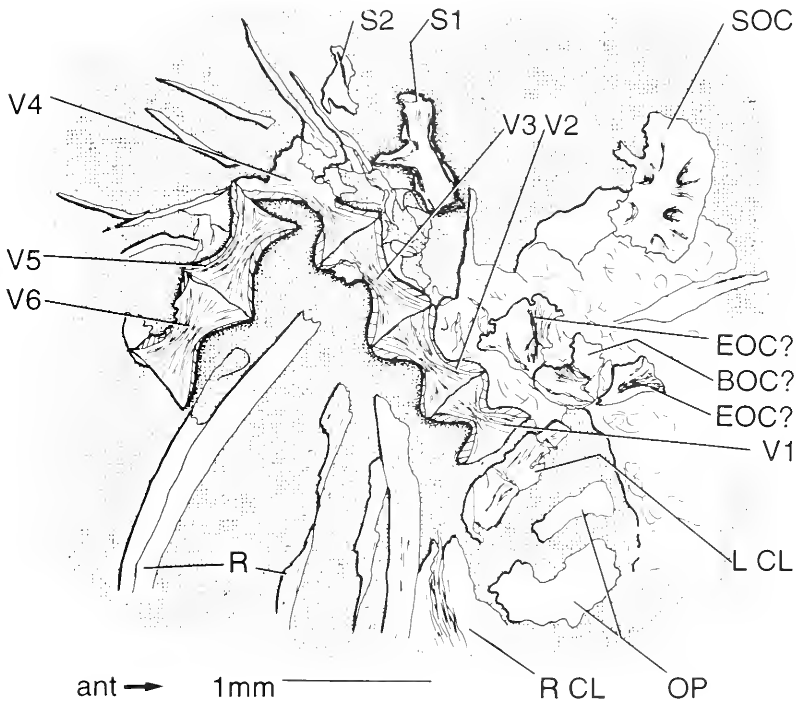

Fig. 9. *Gordichthys conquensis*. Most anterior vertebral region of A LH 929 in right lateral view. Abbreviations: BOC?, basioccipital?; EOC?, exoccipital?; L CL, left cleithrum; R CL, right cleithrum; R, ribs; S1–2, first and second supraneurals; SOC, supraoccipital; V1–6, first through sixth vertebral centra (preserved in longitudinal section). Stippled areas represent matrix.

The opercular apparatus is broad (Figs. 3–4). The large, ovoid opercle is thick and bears a strengthened anterior edge and a fine, pitted ornamentation like that of the frontal bones. The shape of the preopercle is peculiar. It bears a pair of narrow, straight limbs which form an acute angle with one another. Both the dorsal and the ventral preopercular limbs are directed anteriorly. The dorsal limb is narrower than the ventral limb (A/B LH 1279). The posterior margin and ventral margins of the dorsal and ventral limbs, respectively, are slightly concave at the bases of the limbs. The base of the preopercle presents a broad, conspicuous distal expansion. Although pitted ornamentation is absent on the preopercle, in one juvenile specimen (A LH 480), numerous growth lines parallel the edge. The preopercular sensory canal parallels the anterior margin of the bone; only one sensory branch has been observed (A LH 735), but there may be more. A relatively broad suprapreopercle is preserved in A/B LH 1414 and 1613 (Fig. 3). Although no traces of the preopercular sensory canal are visible in this bone, it is identified as a suprapreopercle on the basis of its extension and topographic position. The subopercle is rather narrow and bears an anterior ascending process (A LH 700; A/B LH 2179 R; Figs. 3–4). The interopercle is a small, triangular plate that is scarcely visible below the preopercle and subopercle.

The circumorbital region is preserved partially in A/B LH 700 and A LH 2179 R. The infraorbital series is preserved partially in B LH 1725 and A/B LH 2179 R (Figs. 5–6). The broad, stout supraorbital bone is preserved partially in A/B LH 700, A LH 794, and A/B LH 1407 (Fig. 3). The antorbital bone is moderately large and triangular with the base of the triangle forming the anterodorsal margin of the orbit and the apex directed anterodorsally (Figs. 3, 5). The first infraorbital bone (lacrimal) is long and narrow. Traces of the infraorbital sensory canal are present on the antorbital and first infraorbital bones. The canal on the antorbital bears a branch (antorbital branch) that is directed posterodorsally toward the supraorbital sensory canal on the frontal bone, although both canals are not connected to each other. A well-developed, relatively thick sclerotic ring that is formed by an undetermined number of elements is present.

Vertebral Column

There is an average of 37 vertebrae per specimen (range = 34–40, but most specimens have 36–38; Fig. 2A). The first three vertebrae are hidden by the opercular bones; however, they are visible in A/B LH 480, AB LH 735, LH 1017 (KUVP 123102) and LH 1421 (Figs. 9, 11). Well-developed ribs are associated with precaudal vertebrae 3–18/20. There are one or two transitional vertebrae between the precaudal and caudal vertebrae; transitional vertebrae may bear (1) small ribs, (2) an outline of an haemal arch, (3) both, or (4) neither. There are 14 or 15 true caudal vertebrae that possess well-developed haemal arches and spines. The vertebral formula of the holotype is:

37 = 21 precaudal + 1 transitional + 13 caudals + 2 urals

The autocentra are well ossified, although the walls are rather thin. There is a wide, open notochordal canal. The centra are longer than high, although at least PU1 and PU2 are higher than long. PU3 to PU5 are as high as they are long (Figs. 15, 16A). The external surface of each centrum has two or three lateral grooves, and there are small cavities for the articulation of the ribs and neural and haemal arches. The ribs insert on the anterior half of the centrum. In well-preserved caudal vertebrae, the neural and haemal arches, except those of the last caudals (the exact number of which cannot be determined), seem to be fused to the autocentra, at least laterally (Fig. 2A). This feature is not verifiable in precaudal vertebrae.

The most anterior neural spines (Fig. 2A) are unfused in the midline. During the development of young individuals, the neural spines seem to have fused progressively in a posterior-to-anterior direction, and fusion increases as development proceeds.

The proximally flattened ribs are quite long; they are as deep as the pleuroperitoneal cavity, which indicates that the abdominal morphology is not the result of preservational artifacts. The ribs articulate with the ventrolateral surface of the centrum via the inner face of their articular facet. Although the first rib always is preserved incompletely, it seems to be slightly enlarged and is associated with the third vertebral centrum (Figs. 9–11).

The epineural intermuscular bones are long structures that have been observed to be associated with all but the most anterior precaudal vertebrae (at least 2 or 3) and, occasionally, with the transitional vertebrae (Fig. 2A). There are a few short, delicate epipleural intermuscular bones associated with the transitional, last abdominal, and first caudal vertebrae. Their exact number cannot be established because they seldom are found and are poorly preserved (A/B LH 758). No epicentrals have been observed. There are 14 elongate, stout supraneural bones that lie between the cranium and the first dorsal pterygiophore; each bone possesses a central rod of chondral bone with an anterior and a posterior outgrowth of membranous bone (Figs. 2, 9–11). The first three of these bones lie at a lower level than the posterior members (A/B LH 1417).

Although the first three vertebrae and first two supraneurals usually are missing or covered by the cleithrum and the opercle, occasionally they are visible. The first vertebral centrum is shorter than the second, and the first and second shorter than all posterior centra (AB LH 631, A/B LH 843, A LH 1305; LH 4986 R; Fig. 9). At least the first three neural arches are slightly enlarged and in contact with their neighbors (Figs. 9, 11). There is no supraneural between the occiput and the first neural arch; the first supraneural lies between the first and second neural arches (Fig. 11). The first supraneural is not sigmoidal as the others are. It is remarkably large, but it is not in contact with the neural arches, and possesses an unusual, conspicuous middle process in the posterior border (A LH 929, A/B LH 1725; LH 4989 R; Figs. 9–11).

Fins and Girdles

Pectoral fin and girdle.—The 10 or 11 pectoral rays decrease in length from dorsal to ventral; thus, the fin is approximately triangular (Figs. 2A, 2B, 12). Every ray except the first is distally segmented and branched (single branch in the juvenile A/B LH 480).

The bones of the pectoral girdle are poorly preserved and crushed in all specimens examined. Part of the broad, trapezoidal posttemporal is visible

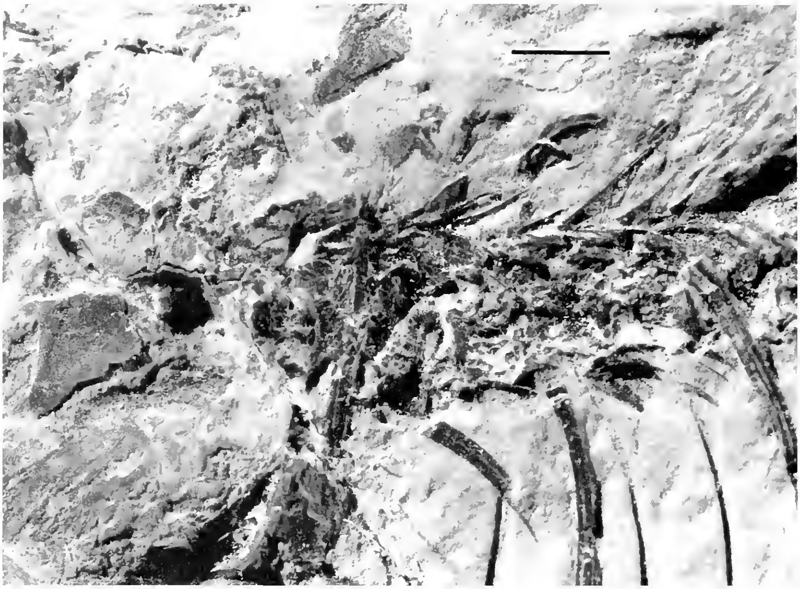

Fig. 10. *Gordichthys conquensis*. Anterior vertebrae of LH 4989 R in left lateral view. Compare with Figure 11. Scale = 1 mm. Photo by D. Serrete.

in AB LH 735 (Fig. 2A); the posterior margin is wavy and bears a point at its midlength, whereas the exposed parts of the remaining edges are approximately straight. The main lateral sensory canal is enclosed in the posttemporal and crosses the bone diagonally. The supracleithrum (Figs. 5, 13) is exposed almost completely in the holotype. The bone is leaf-shaped and truncate dorsally; the blunt ventral end overlaps the cleithrum (A LH 2179 R). The lateral line extends across the length of the supracleithrum, as it does in some more primitive teleosts, such as *Varasichthys* (Arratia, 1981; 1984). The robust cleithrum is curved and expanded ventrally. Although the posterior margin of the cleithrum is obscure, it seems to bear an expansion and a cavity for the insertion of the scapula and the coracoid. At least two postcleithra are preserved in AB LH 1708. The dorsal postcleithrum, displaced, is visible in AB LH 1407 and A LH 1708; the bone is flat and possesses an acuminate ventral process. The ventral postcleithrum is smaller (Figs. 2A, 13).

The endoskeletal girdle (Fig. 14A) is crushed and incomplete in all specimens. In A LH 2179 R, the scapula and coracoid are visible as subquadrangular, independent bones; however, it is not possible to determine the amount of separation between these elements owing to their displacement in this specimen. The scapula bears a relatively broad, elongate canal; as the upper edge of the bone is missing, the presence or absence

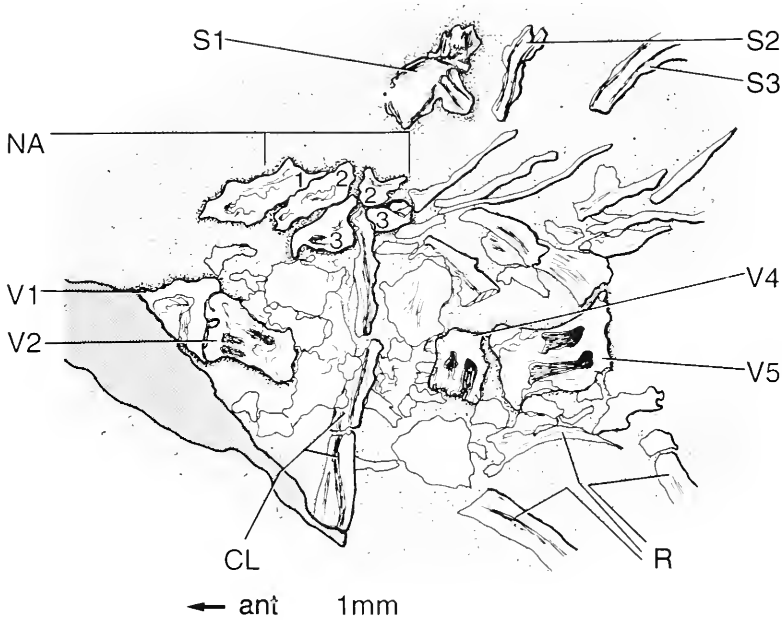

Fig. 11. *Gordichthys conquensis*. Most anterior vertebral region of LH 4989 R in left lateral view. Abbreviations: CL, cleithrum; NA1–3, neural arches 1–3; R, ribs; S1–3, first through third supraneurals; V1–5, abdominal vertebral centra 1–5. Stippled areas represent matrix. Compare with Figure 10.

of the mesocoracoid arch is unknown. The posterior border of the scapula and the coracoid (margo radialis) is nearly vertical, and four roughly quadrangular proximal pectoral radials lie adjacent to it (A LH 480). The distal pectoral radials are partially visible in the holotype; three are exposed and there may be an additional radial dorsally. They are triangular in shape; the ventral element seems to be very enlarged, elongate, and supports fin rays 4–10 (Fig. 14A). This unusual feature requires further confirmation.

Pelvic fin and girdle.—There are nine or ten rays that are approximately equal in length and a short, stout pelvic splint. All lepidotrichia are distally segmented and branched except the first, which is segmented but unbranched. They all are the same length. The pelvic fins are approximately rectangular and shorter than the pectoral fins (Figs. 1–2, 12B). The pelvic bones are triangular, narrow, and long. Although there is a narrow separation between the bones, they are in contact anteriorly and posteriorly (Fig. 14B). Each pelvic bone bears a complex articular surface, which supports the lepidotrichia, on the posterolateral surface and a medial process that meets its antimere in the midline; lateral and posterior processes

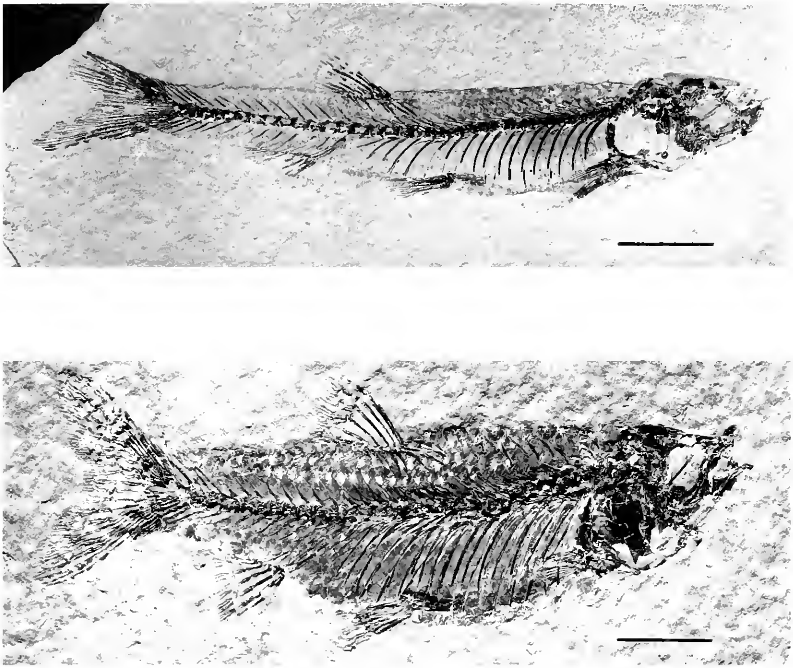

Fig. 12. *Rubiesichthys gregalis* (top; LH 545) and *Gordichthys conquensis* (bottom; LH 2179 R). Scale = 5 mm. Photos by G. Kurtz.

are absent. The anterior shaft of the pelvic bone is composed of a thin medial blade separated by a groove and flanked laterally by a robust ridge on each side; the shaft of each pelvic bone articulates with its counterpart at the anterior apex of the pelvic bone (Fig. 14B). Although only two pelvic radials are exposed in A/B LH 598, there probably are more.

Dorsal fin.—There usually are nine or ten rays, of which the first one or two are short, unsegmented and unbranched (Figs. 2A, 12B). The first segmented ray is the longest and is unbranched; all remaining rays are segmented and branched. The lepidotrichia decrease in length posterior to the first branched lepidotrichium. The dorsal fin is trapezoidal and about twice as high as long. There are eight or nine pterygiophores, of which the first is always double.

Anal fin.—There are one or two procurrent rays in addition to seven (usually) or eight principal rays. Unlike the dorsal fin, the trapezoidal anal fin is only slightly higher than it is long (Figs. 2A, 12B). The principal rays are segmented and branched; from the long first ray, which is the only unbranched one, posterior rays gradually decrease in size. There are six to nine (commonly 7 or 8) single pterygiophores.

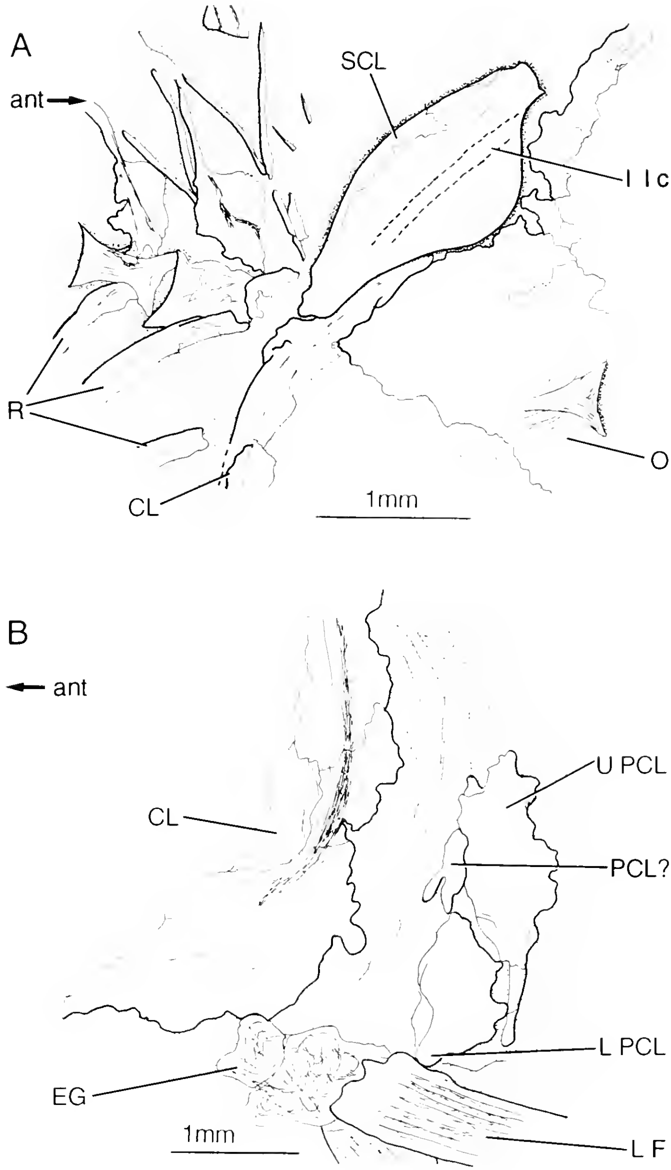

Fig. 13. *Gordichthys conquensis*. Pectoral region. **A.** Supracleithrum of the holotype (LH 1228 R) in right lateral view. **B.** Left lateral view of A LH 1708. Abbreviations: CL, cleithrum (fragmented); EG, endoskeletal pectoral girdle; l l c, lateral line canal; L PCL, lower postcleithrum (postcleithrum 3?); L F, left pectoral fin; O, opercle; PCL?, postcleithrum?; R, ribs; SCL, supracleithrum; U PCL, upper postcleithrum (postcleithrum 2?). Stippled areas represent matrix.

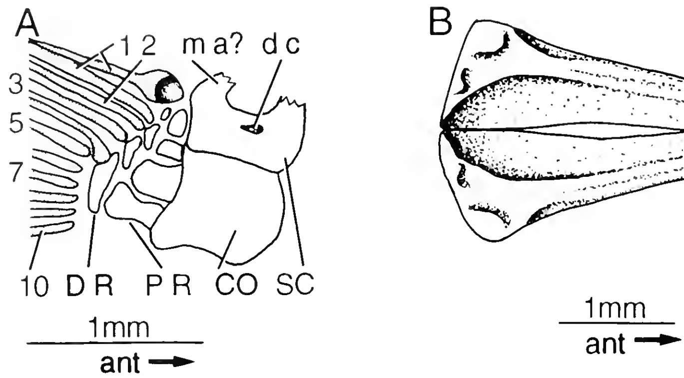

Fig. 14. *Gordichthys conquensis*. Girdle restorations. **A.** Lateral aspect of right endoskeletal pectoral girdle based primarily on A/B LH 480, LH 1228 R, and A/B LH 2179 R. **B.** Pelvic bones in ventral view based mainly on LH 1228 R. Radials are not depicted because their number could not be determined. Abbreviations: CO, coracoid; d c, diazonal canal; D R, distal radials; m a?, mesocoracoid arch?; P R, proximal radials; SC, scapula.

Caudal Fin and Endoskeleton

The caudal fin (Figs. 12B, 15–17) is preserved almost entirely in the holotype and AB LH 509, whereas it is preserved partially in the paratypes AB LH 477, A/B LH 480, AB LH 735, A/B LH 929, and A/B LH 2179 R. The fin is short but deep and greatly expanded, being at least 120% of the maximum body depth (B LH 509). The length of the fin is less than half of its height. The posterior margin is not forked or emarginate, but only slightly curved.

There are 49 caudal fin rays in the holotype. The dorsal lobe has 15 procurrent rays, at least the last two of which are segmented. The first principal ray is segmented and unbranched; it is followed by nine segmented and branched principal rays. In the ventral lobe, the first principal ray is segmented and unbranched and there are eight segmented and branched principal rays. Of the 15 lower procurrent rays, the three longest are segmented. In total, there are 19 principal rays in all specimens examined—ten in the upper lobe and nine in the lower. The number of procurrent rays varies individually. Proximally all rays have an acute base except the central rays, which bear an expanded base (A/B LH 2179 R). The base of the rays covers about two-thirds of the hypural bones.

Caudal endoskeleton.—Following Schultze and Arratia (1989), Arratia (1991), and Arratia and Schultze (1992), the numbering of the ural centra, uroneurals, and epurals does not necessarily imply homology.

Vertebral centra: The preural and ural centra are well ossified and all but

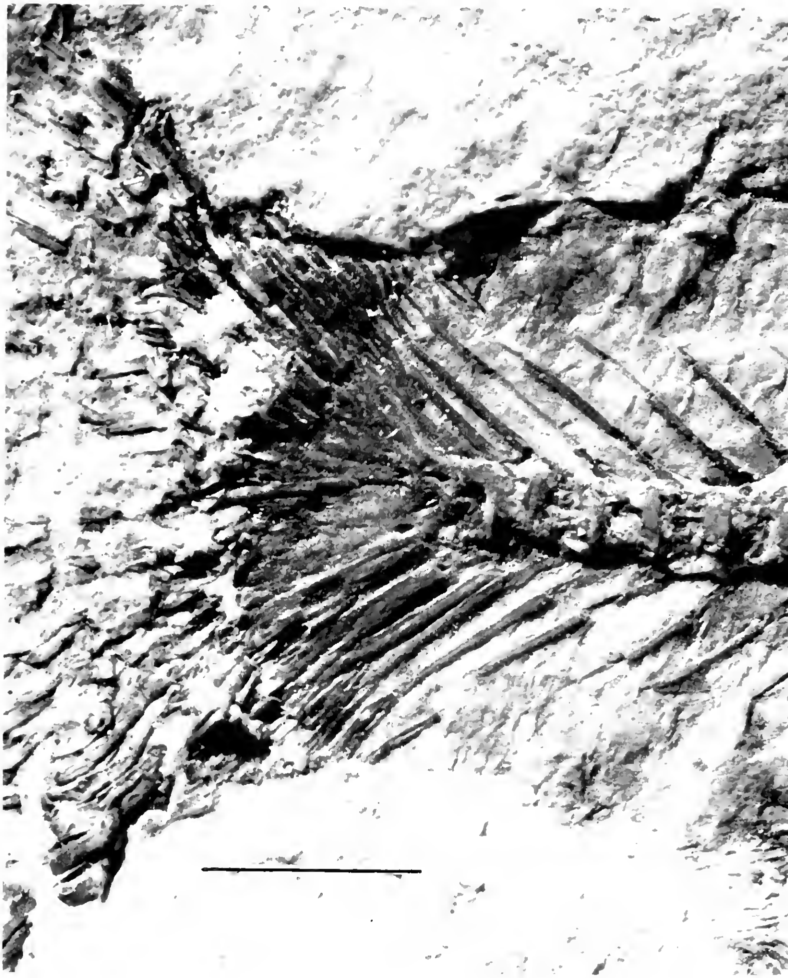

Fig. 15. *Gordichthys conquensis*. Caudal skeleton of the holotype (LH 1228 R) in right lateral view. Scale = 2 mm. Photo by D. Serrete.

Preural 1 and Urals 1–2 possess three longitudinal grooves laterally (Fig. 16A: holotype and A LH 735). Preural 1 and Ural 1 have a single large, deep lateral groove; Ural 2 lacks grooves. The preurals and both ural centra are free, lacking any traces of fusion between adjacent centra. The preural centra decrease in length caudally; Preural 1 is trapezoidal and, posteriorly, oriented upward in the same direction as Ural 1, which is about twice as long as it is high. The second ural is small and nearly triangular; it possesses an articular groove for Uroneural 2 and is oriented upward at a much greater angle than Preural 1 and the first ural. The second ural is

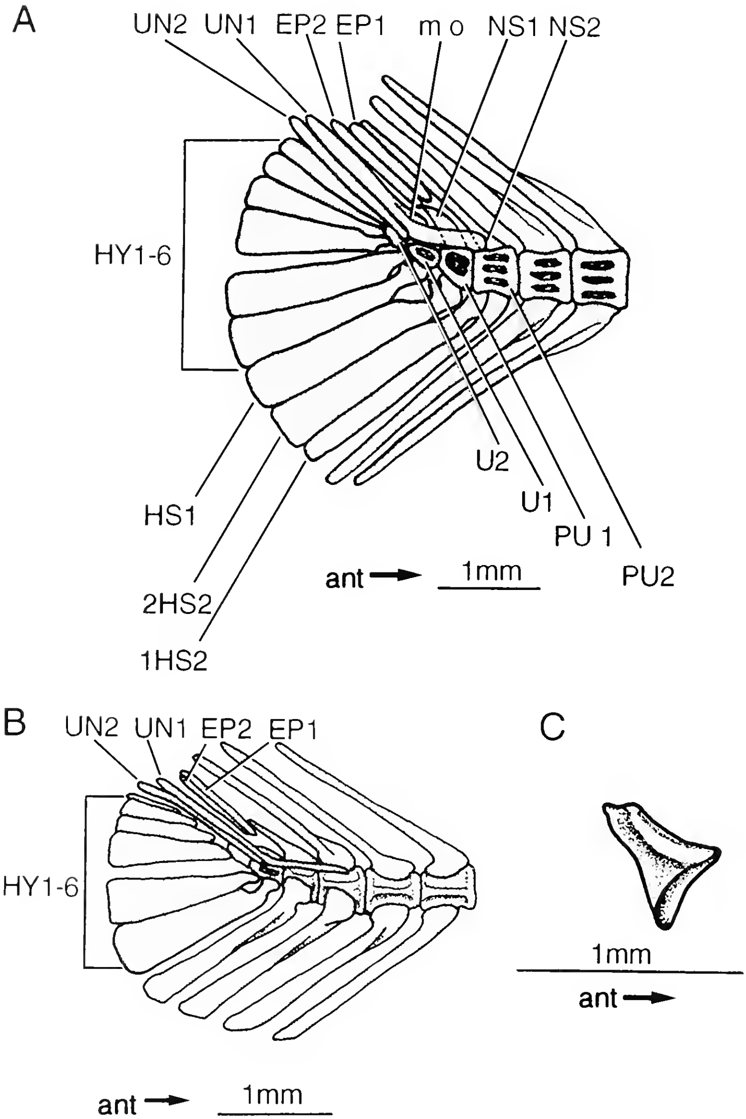

Fig. 16. Caudal endoskeletons. **A.** *Gordichthys conquensis;* restoration based mainly on the holotype, LH 1228 R. **B.** *Rubiesichthys gregalis* (after Wenz, 1984). **C.** *Gordichthys conquensis;* second ural centrum of A LH 735. Abbreviations: EP1–2, Epurals 1–2; 1HS2 and 2HS2, first and second haemal spines of Preural 2; HS1, haemal spine of Preural 1; HY1–6, Hypurals 1–6; m o, membranous outgrowth of Uroneural 1; NS1, neural spine of Preural 1; NS2, neural spine of Preural 2; PU1–2, Preural Centra 1–2; U1–2, Ural Centra 1–2; UN1–2, Uroneurals 1–2.

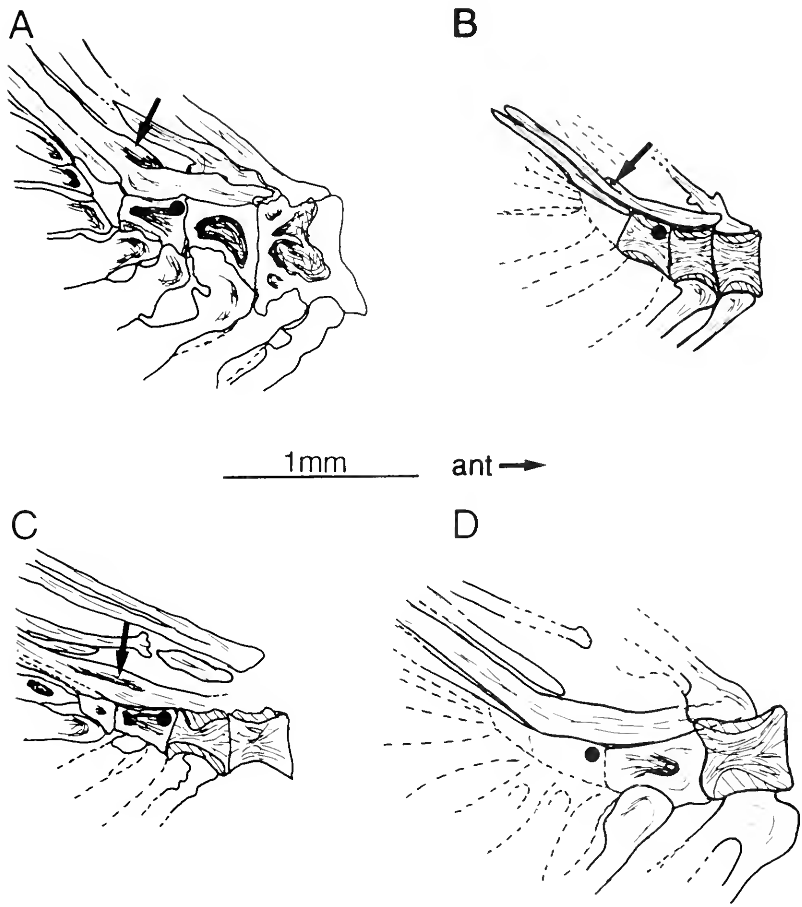

Fig. 17. *Gordichthys conquensis*. Individual variation in the membranous outgrowth of the first uroneural in the caudal endoskeleton. **A.** LH 1228 R (holotype). **B.** A LH 550. **C.** A LH 951. **D.** LH 985. The first ural centrum is indicated by a closed circle and the membranous outgrowth by an arrow.

partially covered laterally by Uroneural 2 and Hypurals 3–5; these observations were made in A LH 735, in which the second ural is preserved as an isolated element.

Epaxial elements: The preural neural arches are not fused to their centra. The neural spines in the preural region are slightly elongated and those of Preurals 5–3 are longer than those on the rest of the caudal vertebrae. Preural 2 may bear one or two neural arches and spines (Figs. 16A, 18). Reduction in the length of the neural spine(s) of Preural 2 also presents individual variation. In the holotype, the spine is only slightly shorter than that of Preural 3, whereas in A/B LH 929, the spine is extremely reduced, and in A/B LH 2179 R, the spines of both Preurals 2 and 3 are greatly reduced. (In all other specimens examined, the neural spine of Preural 3 is not reduced.)

The reduction in the lengths of the neural arch and neural spine of Preural 1 is evident in A LH 509, in which the arch is small and triangular, and the spine is short. The length of neural spine of Preural 1 is variable; it is slightly longer in the holotype and A/B LH 929 than it is in A LH 509 (Fig. 18).

There are two epurals and two uroneurals (Figs. 16A, 17). The first uroneural is strongly curved and relatively short, scarcely reaching Preural Centrum 2. The second uroneural is straight and short; it terminates at the level of the articulation between the first and second ural centra. The first uroneural partially covers the neural arch and spine of Preural 1 and possesses a small dorsal membranous outgrowth (holotype, B LH 509, A/B LH 700, B LH 758, A LH 951, A LH 1225, A/B LH 1402 [KUVP 123105], AB LH 1415, LH 4989 R; Figs. 4, 16A, 17A). However, there is considerable variation in the morphology of the first uroneural. The membranous outgrowth is displaced ventrally on the dorsal surface of the curvature in A LH 550, B LH 643, B LH 739, and A LH 951; it is reduced in size in A LH 550 and B LH 643, and enlarged in A LH 739 and A LH 951 (Fig. 17B, C). In B LH 787, LH 985, and AB LH 1414, the well-preserved first uroneural lack any membranous outgrowth (Fig. 17D).

The neural spine of Preural 2, the epurals, the uroneurals, and Hypurals 3–6 are in contact (Figs. 15, 16A, 17A, B).

Hypaxial elements: Haemal arches are not fused to the preural centra. The haemal spines of Preurals 5–3 become progressively longer and more expanded posteriorly relative to those of the midcaudal centra. There also is considerable variation in the numbers of haemal arches and spines associated with Preural 2. This centrum may have either one or two haemal

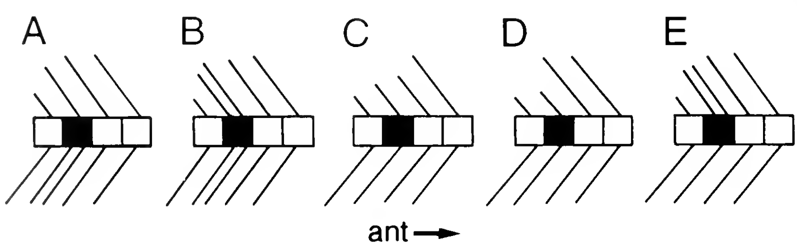

Fig. 18. Diagrams of the caudal endoskeleton of specimens of *Gordichthys conquensis* to illustrate the variation in the numbers and lengths of the spines on the second preural centrum (in black). **A.** LH 1228 R (holotype). **B.** LH 509. **C.** LH 2179 R. **D.** LH 929. **E.** LH 480.

arches and spines (Figs. 16A, 18). The presence of two neural and haemal arches and spines suggests that two vertebrae may have fused to form Preural 2; however, the centrum is normal in shape and size. Summarizing, the structural variations include Preural 2 with: one neural arch and spine, and two haemal arches and spines (holotype); two neural arches and spines, and two haemal arches and spines (AB LH 509); one neural arch and spine, and one haemal arch and spine (A/B LH 929; A/B LH 2179 R); or two neural arches and spines, and one haemal arch and spine (A/B LH 480) (Fig. 18). Younger specimens (e.g., A/B LH 480, AB LH 509) tend to possess higher numbers of arches and spines, which might suggest that elements fuse in older individuals.

The parhypural is robust and large. There are six triangular hypurals with thickened lateral borders (Fig. 16A). The configuration of the hypurals in lateral profile is fanlike, not more or less straight, as in most primitive teleosts. None of the hypurals is fused to an ural centrum. Each of Hypurals 1–4 possesses a strong articular arcocentrum that is concave along its anteroventral margin. Hypurals 1–3 are broad. Hypurals 1 and 2 articulate with the first ural centrum, whereas Hypurals 3–6 articulate with the second ural centrum. Hypural 2 is as large as Hypural 3, but longer; the bones are separated by a diastema. Hypurals 4 and 5 are nearly perfectly triangular, whereas Hypural 6 is a stout rod that reaches the distal tip of the second ural centrum. In other teleosts, such as *Leptolepis*, *Elops*, *Diplomystus*, *Chanos*, *Tharrhias*, *Gonorynchus*, and *Opsariichthys*, there is a gap between U2 and the last hypural(s).

The first principal ray is supported by Hypural 6, and the last principal ray is supported by the haemal spine of Preural 2 (LH 509). Caudal scutes are absent and no urodermals have been observed.

Scales

The scales are not well preserved. The squamation evident in AB LH 951, A/B LH 1725, and A/B LH 2179 R reveals the scales to be cycloid, large, ovoid, and strongly imbricated, and bearing relatively well marked circulii.

DISCUSSION

Gordichthys conquensis resembles the chanid genera *Aethalionopsis* (Gaudant, 1966; Taverne, 1981), *Dastilbe* (Silva-Santos, 1947; Blum, 1991a), *Parachanos* (Arambourg and Schneegans, 1935; Taverne, 1974), *Tharrhias* (Patterson, 1975; Oliveira, 1978; Blum, 1991b), and the Recent *Chanos* (Ridewood, 1904; Rabor, 1938; Patterson, 1975). It shares the following characters with these taxa: (1) Premaxilla thin and broad, slightly concave, with curved posterior edge, long oral process and no ascending process; (2) maxilla formed by broad posterior blade and long anterior process; (3) supramaxillae absent; (4) mandible with high coronoid process and dentary low and curved anteriorly; (5) edentulous premaxilla, maxilla, and mandible; (6) quadratomandibular articulation located anterior to orbit and suspensorium elongate with some elements (e.g., symplectic) oriented nearly horizontal to neurocranium; (7) opercle hypertrophied; (8) preopercle expanded posteroventrally; and (9) caudal skeleton similar to that of fossil forms, but more primitive than that of *Chanos*, in which the first uroneural, the first preural, and both urals are fused.

Comparison with *Rubiesichthys*

Gordichthys conquensis is especially similar to *Rubiesichthys gregalis* Wenz, 1984 (Fig. 12) with which it is found at Las Hoyas (Sanz et al., 1988; Poyato-Ariza, 1989; Poyato-Ariza and Wenz, 1990); *R. gregalis* first was found in Montsec (Lérida, Spain) (Wenz, 1984). A detailed comparison of these taxa is difficult because only a preliminary description exists for *Rubiesichthys* (Wenz, 1984); nonetheless, in addition to the cranial similarities described above and shared also by *Gordichthys* and *Rubiesichthys*, both genera have caudal endoskeletons that are nearly identical in the number and arrangement of epurals (2), uroneurals (2), and hypurals (6). Despite their resemblance, *Gordichthys conquensis* can be distinguished from *Rubiesichthys gregalis* and, therefore, be considered as a new taxon on the basis of the following combination of features: (1) *Gordichthys* has a remarkably high body in contrast to *Rubiesichthys;* the average ratio of maximum body height to standard length is 0.32 in the former and 0.15–0.20 in the latter. (2) *Gordichthys* possesses a short, triangular head and an opercle that covers three vertebrae, whereas in *Rubiesichthys* the head is elongated and the opercle more hypertrophied, covering four vertebrae. (3) The skull is mesoparietal in *Gordichthys* and lateroparietal in *Rubiesichthys*. (4) The articular process of the maxilla is incurved in both genera, but the curvature occurs closer to the base in *Rubiesichthys* than in *Gordichthys*. (5) *Gordichthys* possesses teeth on the parasphenoid and the vomer. The parasphenoid is edentulous in *Rubiesichthys*; its vomer has never been observed. (6) The ventral border of the dentary is slightly concave in *Gordichthys*, whereas it is almost straight in *Rubiesichthys*. (7) The symplectic and the posteroventral process of the quadrate are shorter in *Gordichthys*. (8) The cleithrum is more curved in *Rubiesichthys* than in *Gordichthys*. (9) The vertebral centra are comparatively shorter in *Gordichthys*. (10) *Gordichthys* has fewer vertebrae (mostly 36–38, $\bar{x}$ = 37) than *Rubiesichthys* (mostly 38–40, $\bar{x}$ = 39); see Figure 19. (11) The neural and haemal arches of *Gordichthys* seem to be fused to their centra, at least laterally and in the caudal region; they seem autogenous in *Rubiesichthys*. (12) The dorsal fin is higher in *Gordichthys*. (13) The pectoral fin is large and triangular in *Gordichthys*, and narrow, elongate, and

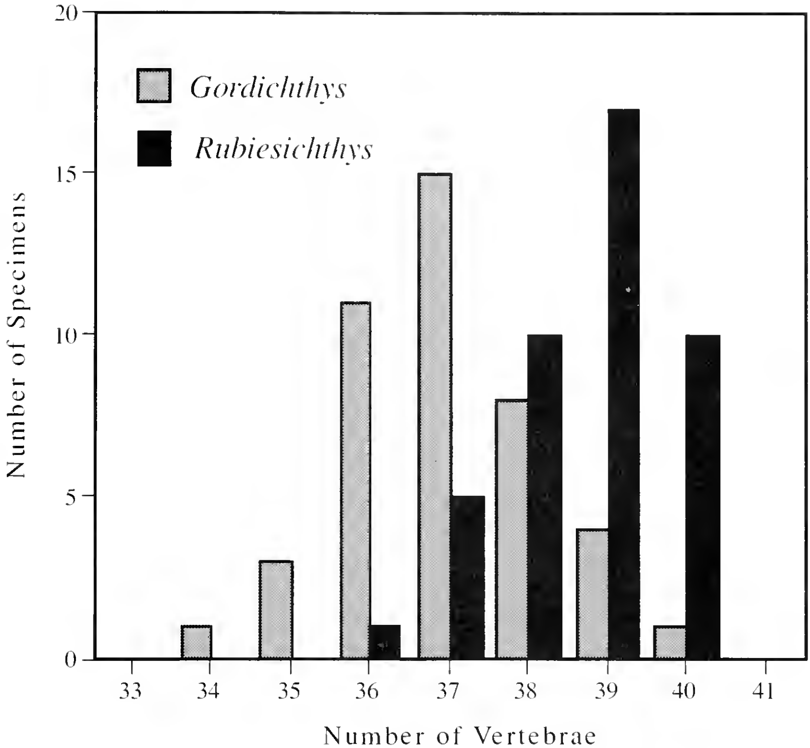

Fig. 19. Histogram showing the distribution of the number of vertebrae in 46 specimens of *Gordichthys* and 46 randomly chosen specimens of *Rubiesichthys* from Las Hoyas. Although some overlapping does occur, the distribution is bimodal.

quadrangular in *Rubiesichthys*. (14) The caudal fin is short, high, and unforked in *Gordichthys*, whereas in *Rubiesichthys*, it is longer, lower, and deeply forked. (15) The profile of the hypurals is broader and the angle described by Uroneural 1 greater in *Gordichthys* (Fig. 15, 16A, 17) than in *Rubiesichthys* (Fig. 16B). (16) In *Gordichthys* (Figs. 15, 16A, 17A), Hypurals 3–6 articulate with the second ural centrum, whereas in *Rubiesichthys* (Fig. 16B), only Hypurals 3 and 4 articulate with the second ural centrum (e.g., MSE 520 a; A LH 545; LH 4991 R). According to Wenz (1984; see Fig. 16B in this paper), only Hypural 3, and not Hypural 4, is in contact with the second ural centrum. A study of the specimens discovered after the publication of her paper reveals the condition described above. (17) The neural spine of PU2, the epurals, the uroneurals, and the last hypurals are separated in *Rubiesichthys* (Fig. 16B), whereas they all are in contact with one another in *Gordichthys* (Figs. 15, 16A, 17A, B).

Diagnosis

Gordichthys conquensis is a peculiar little fish that combines both primitive and advanced features. Some of its plesiomorphic traits are present in more primitive, non-Elopocephalan teleosts—e.g., supraoccipital in contact with parietals anteriorly; high coronoid process; "leptolepid" notch present; toothed vomer and parasphenoid; lateral line extending across the length of the supracleithrum; and independent caudal endoskeleton elements. Among the advanced features (at different hierarchical levels; see next section) of *Gordichthys* are: quadratomandibular articulation anterior to the orbit; retroarticular independent, not forming part of the articulation with the quadrate; morphology or premaxilla, maxilla, and mandible, which are edentulous; supramaxillae absent; expanded opercle; acute-angled preopercular limbs; neural and haemal arches fused to their centra, at least in caudal region; most anterior centra shortened; posterior process in expanded first supraneural; reduction in number of uroneurals, epurals, and hypurals; and caudal scutes absent. Autopomorphic features of *Gordichthys* include: body depth about one-third SL; short, triangular head; mouth cleft directed dorsally; pelvic bones in contact both anteriorly and posteriorly; morphology of dorsal and caudal fins; robust caudal pedicle, one-eighth to one-sixth SL; last hypural contacting U2; fanlike configuration of hypurals in lateral view; neural spine of PU2, epurals, uroneurals, and Hypurals 3–6 in contact with one another. This combination of features diagnoses *Gordichthys conquensis* and justifies the erection of this new genus and species.

Classification

Too little is known about the fossil chanid genera to which *Gordichthys* seems to be most closely allied (especially *Rubiesichthys*) to attempt a cladistic analysis of their relationships at this time. However, *Gordichthys* can be classified tentatively by comparison of its characters to the synapomorphies that diagnose the major teleostean clades (fide Patterson, 1977; Patterson and Rosen, 1977; Fink and Fink, 1981; Lauder and Liem, 1983). Only those characters that can be observed in *Gordichthys* are cited below.

Subdivision Teleostei.—Neural arches of caudal region elongated as uroneurals; premaxilla mobile.

Supercohort Elopocephala.—Fewer than two uroneurals extending forward beyond second ural centrum; epipleurals confined to middle part of trunk.

Cohort Clupeocephala.—Articular and angular fused; retroarticular excluded from quadratomandibular articular facet; neural arch on first ural centrum absent (or highly reduced); membranous outgrowth on the anterodorsal margin of Uroneural 1 (with individual variations in *Gordichthys*, as mentioned above). (See Arratia [1991] and Schultze and Arratia [1989], for variations and distribution of the last two characters.)

Subcohort Euteleostei.—The presence of an adipose fin and nuptial tubercles cannot be confirmed in *Gordichthys* and the species lacks a stegural and outgrowths of the neural arches and spines in the caudal endoskeleton—features that diagnose the Euteleostei. The evidence for the inclusion of *Gordichthys* in this subcohort is ambiguous, but as Patterson and Rosen (1977:126) and Lauder and Liem (1983:132) acknowledged, the " ... definition of euteleosteans is far from satisfactory." *Gordichthys* possesses some synapomorphies of other clades included in the Euteleostei and, more significantly, it lacks any of the synapomorphies diagnosing the Clupeomorpha (Grande, 1985); thus, pending further evidence, it seems most reasonable to include *Gordichthys* in the Euteleostei.

Superorder Ostariophysi.—Of the 15 synapomorphies diagnosing the Ostariophysi (Fink and Fink, 1981), *Gordichthys* possesses five—viz., Characters 41, 58, 63, 64, and 111. *Gordichthys* lacks supramaxillae (41) and a supraneural anterior to the neural arch of the most anterior vertebra (58). The anterior neural arches are expanded and abut one another (63). *Gordichthys* lacks an unattached neural arch anterior to the arch of the first vertebral centrum (64) and possesses haemal spines anterior to PU2 that are fused to the centra (111). Characters 7–8, 20, 54–57, 117–118, and 127 of Fink and Fink (1981) are not verifiable in any *Gordichthys* specimen.

Order Gonorynchiformes.—Of the 14 synapomorphies diagnosing the Gonorynchiformes (Fink and Fink, 1981), *Gordichthys* possesses five—viz., Characters 10, 29, 38, 42, and 115. The parietals are reduced, although not extremely in *Gordichthys* (10) and the suspensorium is elongated in a parasagittal plane (29). The premaxilla is thin and flat (38) and the jaws edentulous (42). There are two epurals (115). The other characters (nos. 6, 14, 46, 48, 65, and 125) are not verifiable. Character 96, the number of postcleithra reduced to one or none, is not considered to be significant, because it occurs independently in several teleostean lineages (Fink and Fink, 1981:345). In addition, *Gordichthys* does not possess any verifiable otophysan synapomorphies; therefore, the most congruent position for this taxon is in the order Gonorynchiformes.

Family Chanidae.—Although some authors have dealt with this family recently (e.g., Taverne, 1974, 1981; Fink and Fink, 1981; Patterson, 1984; Blum, 1991a), the Chanidae lacks a diagnosis. *Gordichthys conquensis* might be included in this family based on the characters mentioned at the beginning of the Discussion. At least some of them may be synapomorphies that could support the monophyly of the family Chanidae, but until a cladistic analysis is made, *Gordichthys conquensis* will be provisionally considered as a Gonorynchiform *incertae sedis*.

CONCLUSIONS

Gordichthys conquensis resembles the chanid fishes from the European Early Cretaceous *Aethalionopsis robustus*, from Bernissart, Belgium (Traquair, 1910; Gaudant, 1966; Taverne, 1981), and *Rubiesichthys gregalis* from Montsec and Las Hoyas, Spain (Wenz, 1984; Sanz et al., 1988; Poyato-Ariza, in press a) in several cranial and caudal endoskeletal features. *Gordichthys* also shares significant similarities with other fossil genera of this family (*Dastilbe, Parachanos, Tharrhias*), as well as with the Recent *Chanos*, whose caudal endoskeleton is otherwise rather different and more derived, with fusions of Preural Centrum 1, ural centra, and first uroneural, all of which are independent in the fossil forms.

Insofar as the features can be verified, this new fish possesses the synapomorphies that characterize the Ostariophysi and Gonorynchiformes. However, some characters are not accessible in the specimens available and one character (presence of postcleithra) is somewhat controversial. The fish from Las Hoyas might be related to the family Chanidae, but the lack of a definition of this family on the base of synapomorphies does not allow a definitive assessment. Therefore, *Gordichthys conquensis* nov. gen. nov. sp. is classified provisionally as Gonorynchiformes *incertae sedis;* a cladistic analysis will be attempted as soon as a thorough study of *Rubiesichthys gregalis* and a revision of other Chanidae are conducted (Poyato-Ariza, in press a, b).

Acknowledgments: For their valuable criticisms of earlier drafts of this manuscript, I thank Sylvie Wenz (Muséum National d'Histoire Naturelle, Paris, France) and Gloria Arratia (The University of Kansas, Lawrence, Kansas, USA). Armando Díaz Romeral (Cuenca, Spain) generously made available specimens from his private collection for examination, inclduing the holotype. The Museo Provincial de Cuenca, represented by Jesús Madero, loaned its specimens to the Unidad de Paleontología, Universidad Autónoma de Madrid. I am indebted to M. Antón for his rendering of Figure 2B and to G. Kurtz and D. Serrette for their photographs. A 6-wk visit to The University of Kansas was supported by the F.P.I. trip fund from the Ministerio de Educación y Ciencia of Spain. Field work at Las Hoyas was supported by the Dirección General de la Junta de Comunidades de Castilla–La Mancha (Spain). This paper is a contribution of the projects CHRX-CT 93-0164 (E.E.C.) and CICYT PB 88-0174 (Spain). The manuscript was completed at The University of Kansas with a postdoctoral grant from the Spanish Ministerio de Educación y Ciencia, Programa Sectorial de Formación de Profesorado y Personal Investigador, Subprograma General en el Extranjero, ref. EX92 01119682.

LITERATURE CITED

ARAMBOURG, C., AND D. SCHNEEGANS. 1935. Poissons fossiles du Bassin Sédimentaire du Gabon. Ann. Paleontol. 24:139–160.

ARRATIA, G. 1981. *Varasichthys ariasi* n. gen. et sp. from the Upper Jurassic of Chile (Pisces, Teleostei, Varasichthyidae n. fam.). Palaeontographica Abt. A. 175:107–139.

ARRATIA, G. 1984. Some osteological features of *Varasichthys ariasi* Arratia (Pisces, Teleostei) from the Late Jurassic of Chile. Palaont. Z. 58:149–163.

ARRATIA, G. 1991 The caudal endoskeleton of Jurassic teleosts; a phylogenetic analysis. Pp. 249–340 *in* Chang, M.-M., Liu, H., and Zhang, G.- R. (eds.), *Early Vertebrates and Related Problems in Evolutionary Biology*. Beijing, Science Press.

ARRATIA, G. AND SCHULTZE, H.-P. 1991. Palatoquadrate and its ossifications: development and homology within osteichthyans. J. Morphol. 208:1–81.

ARRATIA, G. AND SCHULTZE, H.-P. 1992. Reevaluation of the caudal skeleton of certain actinopterygian fishes: III. Salmonidae. Homologization of caudal skeletal structures. J. Morphol. 214:187–249.

BLUM, S. 1991a. *Dastilbe* Jordan, 1910. Pp. 274–285 *in* Maisey, J. (ed.), *Santana Fossils. An Illustrated Atlas*. Neptune, New Jersey: T. F. H. Publications, Inc.

BLUM, S. 1991b. *Tharrhias* Jordan and Branner, 1908. Pp. 286–296 *in* Maisey, J. (ed.), *Santana Fossils. An Illustrated Atlas*. Neptune, New Jersey: T. F. H. Publications, Inc.

FINK, S. V., AND W. L. FINK. 1981. Interrelationships of the ostariophysan fishes (Teleostei). Zool. J. Linn. Soc. 72(4):297–353.

GAUDANT, J. 1966. Sur la nécessité d'une subdivision du genre *Anaethalion* White (Poisson Téléostéen). C. R. Somm. Séances Soc. Geol. France 8:308–310.

GRANDE, L. 1985. Recent and fossil clupeomorph fishes, with materials for the revision of the subgroups of clupeoids. Bull. Amer. Mus. Nat. Hist. 181(2):231–372.

LAUDER, G. V., AND K. F. LIEM. 1983. The evolution and interrelationships of the actinopterygian fishes. Bull. Mus. Comp. Zool. Harvard Univ. 150(3):95–197.

NYBELIN, O. 1966. On certain Triassic and Liassic representatives of the family Pholidophoridae s. str. Bull. Brit. Mus. Nat. Hist. Geol. 11:351–432.

NYBELIN, O. 1974. A revision of the leptolepid fishes. Act. Reg. Soc. Sci. Litt. Gothburg. Zool. 9:202 pp.

OLIVEIRA, A. F., DE. 1978. O gênero *Tharrhias* no Cretáceo de Chapada do Araripe. An. Acad. Bras. Cien. 50(4):537–552.

PATTERSON, C. 1975. The distribution of Mesozoic freshwater fishes. Mem. Mus. Nat. Hist. Nat. Paris, ser. A, 88:156–174

PATTERSON, C. 1977. The contribution of paleontology to teleostean phylogeny. Pp. 579–643 *in* Hecht, M. K., P. C. Goody, and B. M. Hecht (eds.), *Major Patterns in Vertebrate Evolution*. New York: Plenum Press.

PATTERSON, C. 1984. Family Chanidae and other teleostean fishes as living fossils. Pp. 132–139 *in* Eldredge, N., and S. M. Stanley (eds.), *Living Fossils*.

PATTERSON, C., AND D. E. ROSEN. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bull. Amer. Mus. Nat. Hist. 158(2):81–172.

POYATO-ARIZA, F. J. 1989. Ictiofauna del yacimiento de Las Hoyas. Pp. 83–124 *in* Sanz, J. L. (ed.), *La Fauna del Pasado en Cuenca. Actas del I Curso de Paleontología*. Actas Acad. Inst. "Juan de Valdés," No. 1, Cuenca, Spain.

POYATO-ARIZA, F. J. In press a. A revision of *Rubiesichthys gregalis* Wenz 1984 (Ostariophysi, Chanidae), from the Early Cretaceous of Spain. In Arratia, G., and Viohl, G.(eds.), *Mesozoic Fishes: Systematics and Paleoecology*. Proc. First Intern. Meet. Eichstätt. München, Dr. Pfeil.

POYATO-ARIZA, F. J. In press b. The phylogenetic position of *Rubiesichthys gregalis* and *Gordichthys conquensis* (Teleostei, Chanidae), from the Early Cretaceous of Spain. In Arratia, G., and Viohl, G.(eds.), *Mesozoic Fishes: Systematics and Paleoecology*. Proc. First Intern. Meet. Eichstätt. München, Dr. Pfeil.

POYATO-ARIZA, F. J., AND S. WENZ. 1990. La ictiofauna española del Cretácico inferior. Pp. 299–311 *in* Civis Llovera, J., and J. A. Flores (eds.), *Actas de Paleontología (Actas de las IV Jornadas de Paleontología)*. Acta Salmanticensia Bibl. Cien. No. 68.

RABOR, D. R. 1938. Studies on the anatomy of the bangos, *Chanos chanos* (Førskal). I. The skeletal system. Philipp. J. Sci. 67:351–377.

RIDEWOOD, W. G. 1904. On the cranial osteology of the clupeoid fishes. Proc. Zool. Soc. Lon., 2:361–372.

SANZ, J. L. (ed.). 1989. *La fauna del pasado en Cuenca. Actas del I Curso de Paleontología*. Actas Acad. Inst. "Juan de Valdés," No. 1, Cuenca, Spain.

SANZ, J. L., AND J. F. BONAPARTE. 1992. A new order of birds (class Aves) from the Lower Cretaceous of Spain. Pp. 36–50 *in* Campbell, K. (ed.), *Avian Paleontology and Evolution*. Sci. Ser. Nat. Hist. Mus. Los Angeles, no. 36.

SANZ, J. L., J. F. BONAPARTE, AND A. LACASA. 1988. Unusual Early Cretaceous birds from Spain. Nature 331(6155):433–435.

SANZ, J. L. AND A. D. BUSCALIONI. 1992. A new bird from the Early Cretaceous of Las Hoyas, Spain, and the early radiation of birds. Paleontology 35(4):829–845.

SANZ, J. L. AND F. J. POYATO-ARIZA (eds.). (In press). *Las Hoyas: un lago de tiempos remotos. Actas del III Curso de Paleontología*. Actas Acad. Inst. "Juan de Valdés," Cuenca, Spain.

SANZ, J. L., S. WENZ, A. YÉBENES, R. ESTES, X. MARTÍNEZ-DELCLÓS, E. JIMÉNEZ-FUENTES, C. DIÉGUEZ, A. D. BUSCALIONI, L. J. BARBADILLO, AND L. VÍA. 1988. An Early Cretaceous faunal and floral continental assemblage: Las Hoyas fossil site (Cuenca, Spain). Geobios 21(5):611–631.

SCHULTZE, H.-P., AND ARRATIA, G. 1989. The composition of the caudal skeleton of teleosts (Actinopterygii, Osteichthyes). Zool. Jour. Linn. Soc. 97:189–231.

SILVA-SANTOS, R., DA. 1947. Uma redescrição de *Dastilbe elongatus*, com algumas considerações sobre o gênero *Dastilbe*. Minist. Agric. Div. Geol. Mineral. Notas Prelim. Estud. (42):1–7.

TAVERNE, L. 1974. *Parachanos* Arambourg et Schneegans (Pisces Gonorynchiformes) du Crétacé inférieur du Gabon et de Guinée Equatoriale et l'origine des Téléostéens Ostariophysi. Rev. Zool. Afr. 88(3):683–688.

TAVERNE, L. 1981. Ostéologie et position systématique d'*Aethalionopsis robustus* (Pisces, Teleostei) du Crétacé inférieur de Bernissart (Belgique) et considérations sur les affinités des Gonorhynchiformes. Bull. Acad R. Belg. Cl. Sci. (Ser. 5) 67(12):958–982.

TRAQUAIR, R. H. 1910. Les poissons wealdiens de Bernissart. Mem. Mus. R. Hist. Nat. Belg. 5(1908):iv + 65 pp.

WENZ, S. 1984. *Rubiesichthys gregalis* n.g., n. sp., Pisces Gonorynchiformes, du Crétacé inférieur du Montsech (Province de Lérida, Espagne). Bull. Mus. Natl. Hist. Nat. Paris (Ser. 4, Sec. C) 3:275–285.

WENZ, S., AND F. J. POYATO-ARIZA. (In press). Métodos de trabajo en Paleoictiología. Nuevas aportaciones al estudio de la ictiofauna de Las Hoyas. *in* Sanz, J. L. and F. J. Poyato-Ariza (eds.): *Las Hoyas: un lago de tiempos remotos. Actas del III Curso de Paleontología*. Actas Acad. Inst. "Juan de Valdés," Cuenca, Spain.