Phylogenetic and paleogeographic relationships of the varasichthyid group (Teleostei) from the Late Jurassic of Central and South America

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ABSTRACT

The phylogenetic and geographic relationships of certain Jurassic teleosts are studied using cladistic methodology. According to current evidence the Late Jurassic fishes *Domeykos*, *Protoclupea*, and *Varasichthys* from Chile and *Luisichthys* from Cuba form a monophyletic group, the varasichthyid group. The monophyly of this group is supported by five synapomorphies. *Ascalabos voithii* from the Late Jurassic of southern Germany is its sister group This sister group relationship is supported by two synapomorphies. The Ichthyodectiformes and the varasichthyid group are the only monophyletic assemblages that can be identified among Jurassic teleosts. The phylogenetic relationships among *Ascalabos, Domeykos, Protoclupea, Varasichthys,* and *Luisichthys* provide evidence of a biogeographic relationship between Europe (southern Germany), Central America (Cuba), and southern South America (Chile) through the Tethys seaway during the Late Jurassic.

Key words: Teleostean fishes, Varasichthys, Protoclupea, Domeykos, Luisichthys, Systematics, Chile, Cuba, Germany, Tethys seaway, Late Jurassic.

RESUMEN

Relaciones filogenéticas y paleogeográficas del grupo varasíctido en el Jurásico tardío de América Central y Sudamérica. Se estudian las relaciones filogenéticas y geográficas de ciertos peces teleósteos usando la metodología cladista. Los peces teleósteos del Jurásico Tardío de Chile, *Domeykos, Protoclupea y Varasichthys*, y *Luisichthys* de Cuba, forman un grupo monofilético (grupo varasíctido), el que se basa en cinco sinapomorfías. *Ascalabos voithii* del Jurásico tardío de Alemania es el grupo hermano del grupo varasíctido; ambos comparten dos sinapomorfías. Los Ichthyodectiformes y el grupo varasíctido son los únicos grupos monofiléticos de teleósteos que se pueden identificar durante el Jurásico. Las relaciones filogenéticas entre *Ascalabos, Domeykos, Protoclupea, Varasichthys* y *Luisichthys* proporcionan evidencia acerca de una relación biogeográfica entre Europa (sur de Alemania), América Central (Cuba) y el extremo sur de América del Sur, a través del Mar de Tethys durante el Jurásico tardío.

Palabras claves: Peces teleósteos, Varasichthys, Protoclupea, Domeykos, Luisichthys, Sistemática, Chile, Cuba, Alemania, Mar de Tethys, Jurásico tardío.

INTRODUCTION

Fossil fishes are known from a few Chilean localities ranging from the Paleozoic to the Tertiary. The oldest record refers to palaeoniscoid scales from the Chinches Formation, Early Carboniferous, north–

ern Chile (Bell, 1985). An almost complete palaeoniscoid fish is currently under description by Richter and Breitkreuz (in press). Although no formal description of a Triassic fish is published, a possible semionotid from Quebrada de San Pedrito was mentioned by Chong and Gasparini (1976). The only formal description of Cretaceous fishes is that by Schultze (1981) of a pycnodont dentition from the Early Cretaceous of El Volcán region, SE of Santiago. Other Cretaceous fishes are known from saurichthyid-like bones found in Lomas Negras and an undetermined teleost from Tierra Amarilla, Copiapó (Covacevich, personal communication; Arratia, personal observation). A few advanced teleosts, *e.g.*, complete perciforms, catfishes, and characiform teeth, are recorded from Tertiary localities in Cordillera de Lonquimay (Chang *et al.*, 1978; Arratia, 1982a; Rubilar and Abad, 1990; Rubilar, 1994).

The most outstanding Chilean fish localities are those from Jurassic strata (Sinemurian, Oxfordian, Kimmeridgian) in northern Chile, *e.g.*, Cerritos Bayos, Quebrada Vaquillas Altas, Quebrada del Profeta, and Sandón (Table 1). The fossil fish faunas are outstanding for their excellent preservation of bones and soft structures such as muscles, blood vessels, gut, and melanophores (see Schultze, 1989, for details).

The fishes of Quebrada del Profeta comprise a diversified fauna of neopterygians (*e.g.*, semionotids, pycnodontids, pachycormids: Arratia, 1987a), the halecostome *Atacamichthys* (Arratia and Schultze, 1987), one ?pholidophorid, six genera with seven species of teleosts (Arratia, 1981, 1982b, 1986a, 1987a; Arratia and Schultze, 1985), and two forms which were identified as Teleost sp. 1 and Teleost sp. 2 by Arratia (1991). This assemblage makes Quebra-

TABLE 1. LIST OF CHILEAN JURASSIC FISHES, THEIR LOCALITIES NEAR ANTOFAGASTA, NORTHERN CHILE, AND GEOLOGICAL AGES.

Taxa	Locality	Geological Age
Pycnodontiformes		
Pycnodontiformes indet.	Quebrada Vaquillas Altas Quebrada del Profeta, Cordillera de Domeyko	Sinemurian Oxfordian
Halecostomi		
Atacamichthys greeni	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Lepidotes indet.	Cerritos Bayos	Oxfordian ('formation 05' of Biese, 1961)
Pachycormiformes indet.	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Pachycormus indet.	Cerritos Bayos	Oxfordian ('formation 05' of Biese, 1961)
?*Pholidophorus domeykanus*	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Teleostei		
Antofagastaichthys mandibularis	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Bobbichthys opercularis	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Chongichthys dentatus	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Domeykos profetaensis	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Proleptolepids indet.	Quebrada Vaquillas Altas, Cordillera de Domeyko	Early Sinemurian
Protoclupea atacamensis	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Protoclupea chilensis	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Protoclupea sp.	Cerritos Bayos, Cerro Blanco	middle-late Oxfordian
Varasichthys ariasi	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Teleost sp. 1	Quebrada del Profeta, Cordillera de Domeyko	Oxfordian
Teleost sp. 2	Cerritos Bayos	Oxfordian
Indeterminate teleosts (= *Thrissops* of Biese and others)	Cerritos Bayos	Kimmeridgian
Indeterminate teleosts	Sandón	Oxfordian

da del Profeta the best known and richest fish locality in the Jurassic of South America, and one of the most important ones in the world.

The fishes from other Jurassic localities in northern Chile are partially known. For instance, Biese (1961) mentioned the presence of *Lepidotus (=Lepidotes)* and *Pachicornius (=Pachycormus)* in the Early Callovian and in the Oxfordian of Cerritos Bayos. Biese (1957, 1961) named '*Trissops* - Kal' or 'calizas de *Trissops*' one stratum bearing fishes he identified as *Trissops (= Thrissops)*. According to Arratia (1987a) these fishes are not *Thrissops* and should be considered as undetermined teleosts. One teleost collected in the west sector of Cerritos Bayos, in Cerro Blanco, was identified as *Protoclupea*, a genus first described from Quebrada del Profeta (Arratia *et al.*, 1975). Based on the presence of *Protoclupea*, Baeza (1976, 1979) assigned the horizon bearing this fish in Cerro Blanco to the middle-late Oxfordian by correlation with the occurrence of *Protoclupea* in Quebrada del Profeta.

One characteristic of most teleostean genera from Quebrada del Profeta is endemism, a condition that is common to most Jurassic teleostean genera from different continents. Furthermore, differences in faunal composition are found even in neighboring regions such as Chile and Argentina. As Arratia (1986b, 1987a) and Cione and Pereira (1987) noted, no common teleostean genus is known from the Late Jurassic of Chile and Argentina. As result of this endemism, paleobiogeographical hypotheses based on Jurassic teleostean faunas have not been proposed. In contrast, semionotids (*e.g.*, *Lepidotes*), have a world wide distribution.

Recently, Arratia (1991, and in press a) proposed two hypotheses of phylogenetic relationships of certain fossil (including several Chilean Jurassic fishes) and Recent teleosts. There are differences in the phylogenetic relationships between the Chilean fishes in both hypotheses: these differences result from the use of a different set of characters considered to build the matrices used in both analyses.

The goals of this paper are to present the phylogenetic relationships of some of the best known teleosts of Quebrada del Profeta (*e.g.*, *Varasichthys*, *Protoclupea*, and *Domeykos*), to test previous hypotheses proposed by the author, and to discuss their probable biogeographic implications.

MATERIAL AND METHODS

MATERIAL EXAMINED

Fossil teleostean species belonging to 15 genera were examined; the material is deposited in the institutions listed in the acknowledgments (a complete list of the studied material can be obtained from the author). A new fish from the Late Jurassic (Tithonian: Malm Zeta 3) of Germany is identified herein as Teleost n. gen. (Arratia, manuscript in progress).

The examined Chilean and Cuban Jurassic species are listed alphabetically:

Domeykos profetaensis Arratia and Schultze from the Oxfordian of Quebrada del Profeta, Chile. Text-Fig. 1B; Pl. 1, Fig. A.

Luisichthys vinalensis White from the Late Jurassic, probably Kimmeridgian, of Pinar del Río, Cuba. Pl. 2, Fig. A.

Protoclupea chilensis Arratia, Chang, and Chong and *Protoclupea atacamensis* Arratia and Schultze from the Oxfordian of Quebrada del Profeta, and *Protoclupea* sp. from Cerritos Bayos, Chile. Pl. 3.

Teleost n. sp. 1 *sensu* Arratia (1991) from the Oxfordian of Quebrada del Profeta, Chile.

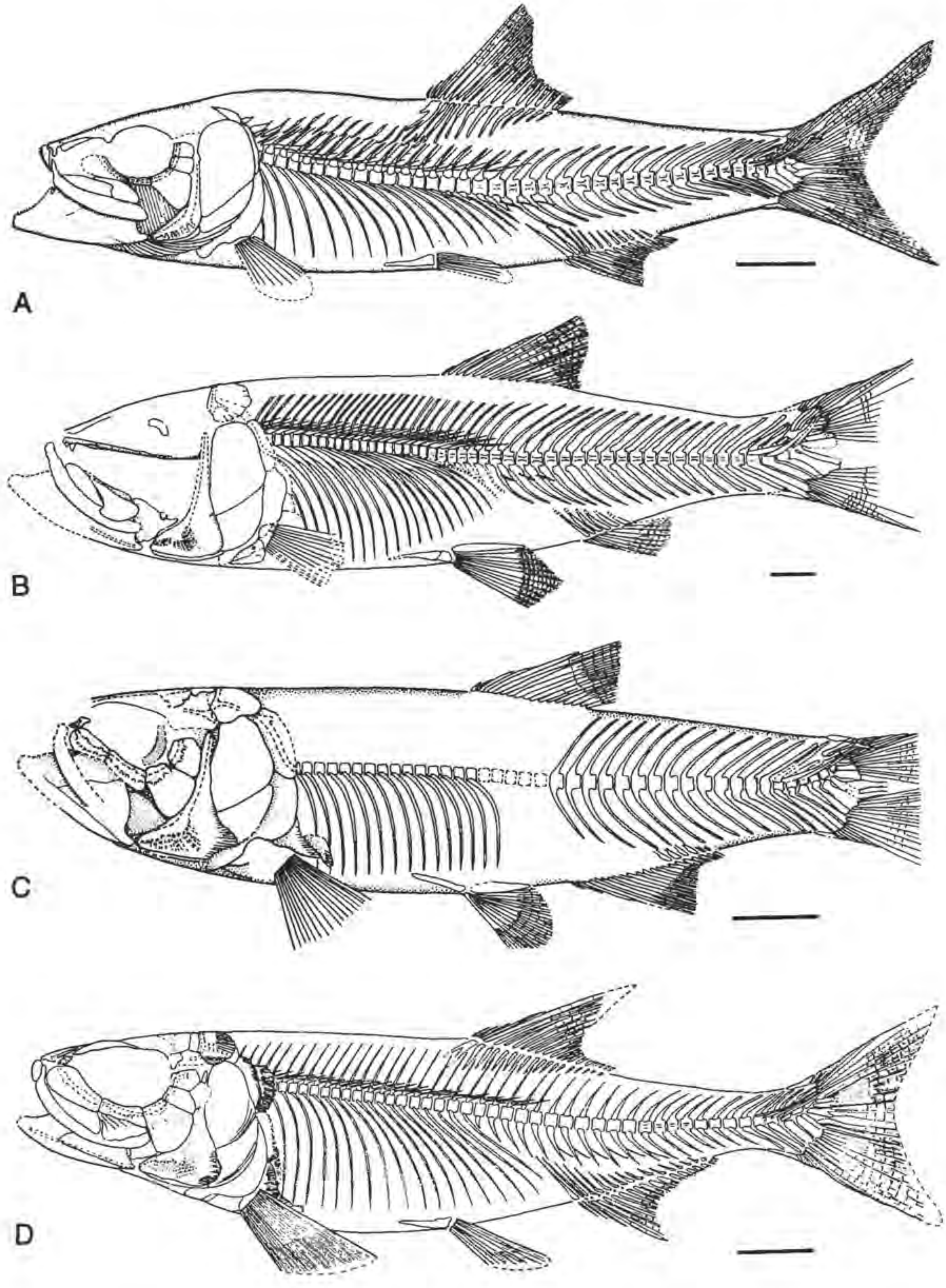
Varasichthys ariasi Arratia from the Oxfordian of Quebrada del Profeta, Chile. Text-Fig. 1D; Pl. 4.

The following species were considered for comparative studies to build the data matrix used in the phylogenetic analyses:

Allothrissops salmoneous (Blainville) from the Tithonian of Solnhofen, Bavaria, Germany; *Allothrissops mesogaster* (Agassiz) from the Tithonian of Kelheim, Bavaria, Germany; *Allothrissops* sp., incomplete specimens not assigned to species. These species are representatives of the Ichthyodectiformes *sensu* Patterson and Rosen (1977).

Anaethalion angustus (Münster) from the Tithonian of Eichstätt and Solnhofen; *Anaethalion angustissimus* (Münster) from Kelheim, Nusplingen, and Solnhofen; *Anaethalion knorri* (Blainville) from Eichstätt, Kelheim, and Solnhofen; *Anaethalion* cf. *A. subovatus* (Münster) from Eichstätt, Kelheim, and Solnhofen.

Ascalabos voithii Münster, from Solnhofen, Bavaria, Germany. Text-Fig. 1A.



Text-FIG. 1. Restoration in lateral view of certain Jurassic teleosts. A- *Ascalabos voithii* from Solnhofen, southern Germany (after Arratia, in press a); B- *Domeykos profetaensis* from Quebrada del Profeta, northern Chile (after Arratia, in press a); C- *Protoclupea chilensis* from Quebrada del Profeta, northern Chile (slightly modified from Arratia and Schultze, 1985); D- *Varasichthys ariasi* from Quebrada del Profeta, northern Chile (after Arratia, in press a). Scales = 1 cm.

Leptolepis coryphaenoides (Bronn) from the Lias of Neudingen and Salzgitter, Lower Saxonia, Germany.

'*Leptolepis*' *albragarensis* Woodward, from the Middle Jurassic of Talbragar, New South Wales, Australia.

Leptolepides sprattiformis (Blainville) from Solnhofen, Bavaria, Germany.

Lycoptera davidi (Sauvage) from the ?Late Jurassic of Lingyuan, China; *Lycoptera middendorffi* Müller from the ?Late Jurassic of Mongolia.

Orthogonikleithrus leichi Arratia from the Tithonian of Zandt, Germany.

Teleost n. gen. et sp. from the Tithonian of Mülheim and Daiting, Bavaria, Germany.

Tharsis dubius (Blainville) from Solnhofen, Bavaria, Germany.

GENERAL METHODOLOGY

Some fossil specimens were mechanically prepared; others were acid-prepared (with acetic acid and HCl 1-5%) following a modification of Toombs and Rixon's (1953) technique. Some of the acid-prepared specimens, *e.g.*, isolated bones, were studied under a Scanning Electron Microscope (SEM), Phillips 501. Serial cross sections of some caudal vertebrae were prepared to investigate their microstructure. The preparation of the specimens as well as of the illustrations were done by the author.

CLADISTIC METHODOLOGY

The interrelationships of the taxa of the ingroup were explored using cladistic phylogenetic principles (Hennig, 1966; Wiley, 1981; Ax, 1987). The analyses were conducted using PAUP (Phylogenetic Analysis Using Parsimony) software (version 3.0) of Swofford (1992) on a Macintosh computer.

All the characters have the same weight and are unordered. Characters coded as '9' on the matrix denote nonapplicable, missing, or unclear conditions due to preservation. In the text, *e.g.*, 'List of characters', the number of each character is followed by the character state in parentheses (*e.g*, 1[2] is character state 2 of character 1). Multistate characters were run unordered. Character optimization used DELTRAN.

The primitive state [0] of the characters was determined by outgroup comparison following Maddison *et al.* (1984). The outgroups were selected following the hypotheses of phylogenetic relationships by Patterson (1977) and Patterson and Rosen (1977). Therefore, the combined outgroup includes *Pholidophorus* spp., *Pholidolepis* sp. and *Proleptolepis* spp. The author did not consider aspidorhynchiformes and pachycormiforms to be part of the outgroup because of her observations on those fishes and information from recent literature (*e.g.*, Brito, 1992; Lambers, 1992; Arratia and Lambers, in press) question their position within the Teleostei *sensu* Patterson (1973, 1977).

Characters were polarized by analysing character state distribution within the combined outgroup; thus the author reconstructed an ancestral character state for each feature. Ambiguous ancestral character states, *i.e.* not polarized, are coded '9' (Table 2).

A set of 75 characters was used to build the matrix for the cladistic analyses. These characters are based on the author's observations and on the following literature: Arratia (1981, 1984, 1987b, c, 1991, and in press a), Arratia and Schultze (1985), Cavender (1970), Gaudant (1968), Greenwood (1970), Ma (1987), Nybelin (1966, 1974), Patterson and Rosen (1977), and Schultze (1966). Two cladistic analyses were performed. Analysis 1 included 14 Jurassic teleostean genera known from a variety of morphological structures. Analysis 2 included the same 14 genera plus one Chilean form (Teleost sp. 1) known only from its caudal region.

The cladistic vicariance method is used for biogeographic analysis following Nelson and Platnick (1980, 1981), Wiley (1981), Grande (1990), and Grande and Micklich (1993).

ANALYSIS OF CHARACTERS

Most characters used in the phylogenetic analyses are osteological characters that are preserved in the fossil material. The general morphology, and its variation, characteristic of Jurassic teleosts is presented below to illustrate the current knowledge and interpretation of certain characters; the discussion

TABLE 2. DATA MATRIX OF 75 MORPHOLOGICAL CHARACTERS FOR 15 GENERA OF JURASSIC TELEOSTEAN FISHES.

Taxa	Character states
	111111111122222222223333333333444444444455555555556666666666777777 123456789012345678901234567890123456789012345678901234567890123456789012345
Outgroup	000000000000000000000000000000000000000000090000900000000000000000000000000
Allothrissops	109929910101000000111090201000092200010100000000000011000000000120111000009
Anaethalion	109920991101100200101010219999001110000001021102111011000000000211011190001
Ascalabos	1999299900010099001910102110090011000000000000100000000000010000120111000019
Domeykos	1199290900990910001910102900112911000100000001000000000000010000920100001011
Leptolepis coryphaenoides	000010000000000090000000100000001911000000000000100000000000010000110011000000
'Leptolepis' talbragarensis	9999999010100990919001010900999190009000000001000100900000090000919011090000
Leptolepides	101120010101000110190010211000001101000000021112111011000000010221111000001
Luisichthys	191129010109009909191010219999992200000010021100001000000120000921100090019
Lycoptera	909920990111009901191010202099911100011000110102110111100090000321122110100
Orthogonikleithrus	199929990901009911191010211099992211110110022102111111100000010221111101090
Protoclupea	199929999009001000191090290011292200000910020100001010000000000920100990011
Teleost n. gen	101121110901019919991111219009901200000110021102111211111021101211001011009
Teleost sp.1	99999999999999999999999999999999900000999000000090009111000100009001100999099
Tharsis	101120010101000900101010219000002210000000000101000010000000000110011900000
Varasichthys	111120010000001910191010210111202200091110100100000999999000000199100090011

Note: Combined outgroup ncludes: *Pholidophorus* spp., *Pholidolepis* sp., and *Proleptolepis* spp., **0**- plesiomorphic character state; **1-3**, apomorphic character states; **9**- unclear owing to preservation of the specimens or not applicable.

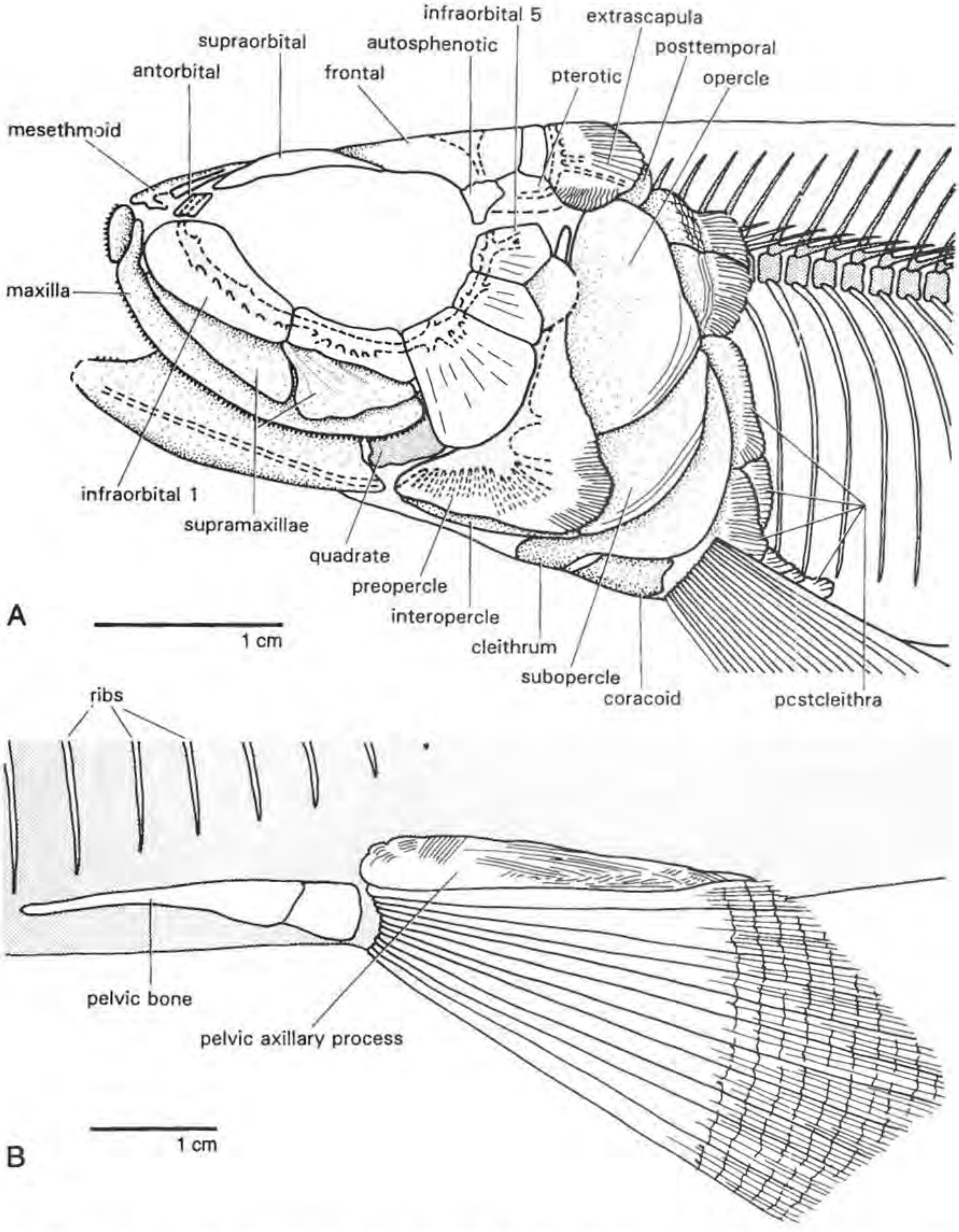
is centered mainly on the Chilean forms (Teleost sp. 1, *Domeykos, Protoclupea,* and *Varasichthys*) and the Cuban fish *Luisichthys*, and then compared with the condition(s) found in other Jurassic teleosts.

Some morphological features of the head, vertebral column and intermuscular bones, girdles and axillary processes, caudal skeleton and fin, and scutes and scales are presented and discussed below.

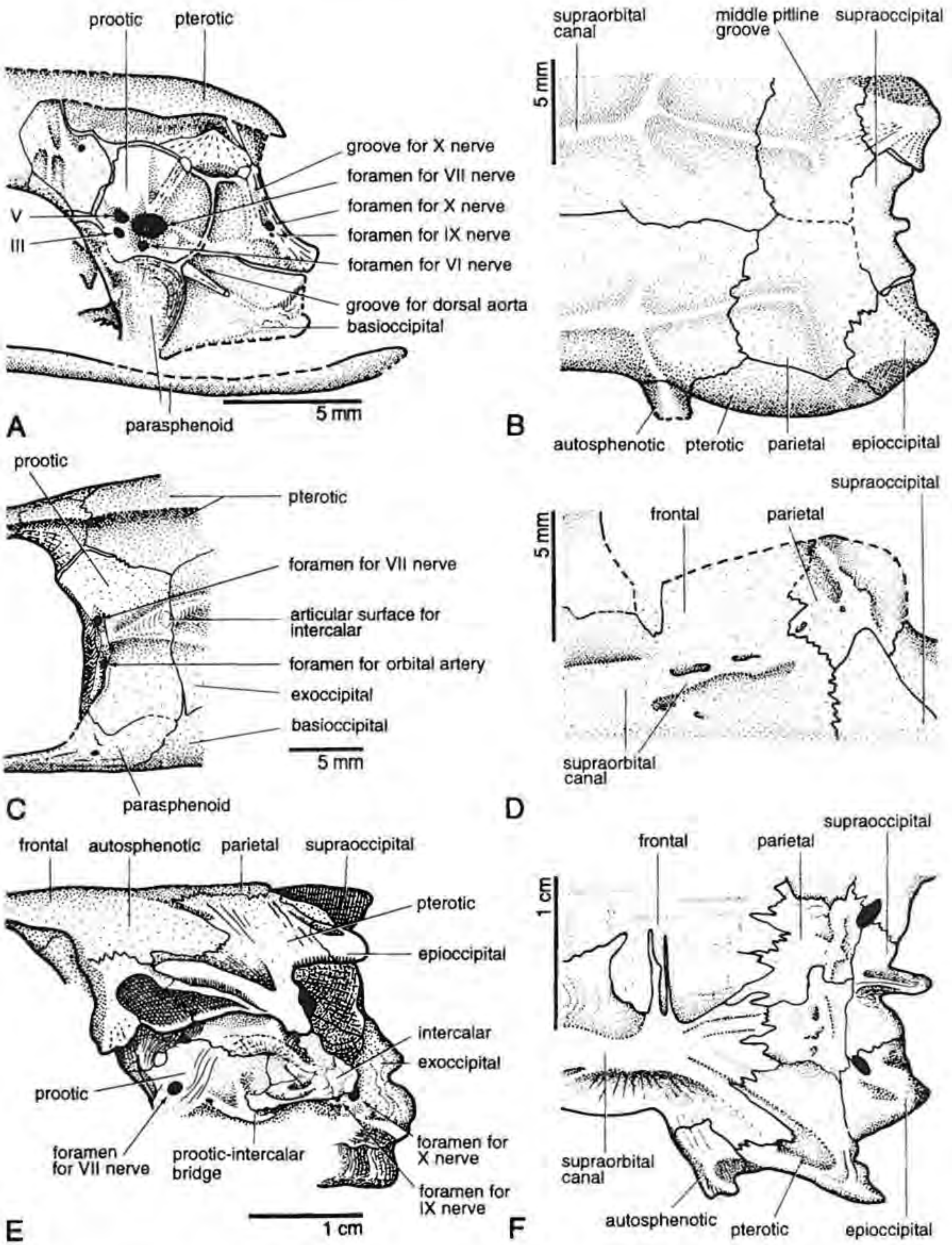
HEAD

The available information about head structures of the species examined is incomplete due to preservation of the fossil material. For instance, information on the braincase is available for a few species only, *e.g., Varasichthys* (text-Figs. 2A, 3A-B; Pl. 5, Fig. A; Arratia, 1981, text-Fig. 11; Arratia, 1984, Figs. 1A-B, 2), *Domeykos* and *Luisichthys* (text-Fig. 3C-F; Pl. 2, Figs. A-C; Arratia and Schultze, 1985, text-Figs. 13A-C, 18A-C), and *Chongichthys* (Arratia, 1982a, Figs. 3, 4). Outside the Chilean and Cuban fishes, the braincase of Jurassic teleosts is known in *Leptolepis coryphaenoides* (Rayner, 1948; Patterson, 1975; personal observation), *Tharsis* and *Leptolepides* (Patterson, 1975; personal observation).

The braincases of *Varasichthys* and *Luisichthys* are better preserved than that of *Domeykos* (text-Fig. 3A, C, E). There are some features common to the three genera such as the presence of sutures between chondral bones throughout life, and the absence of the following: an ossified aortic canal, a canal for occipital arteries in the basioccipital bone, and a spiracular canal. On the other hand, there are some interesting differences in the braincases of *Varasichthys, Luisichthys,* and *Domeykos.* For instance: **1-** the type of sutures joining the cranial bones. Well developed interdigitating sutures (dentata and/or serrata) are present between the bones of the braincase in *Luisichthys* (text-Fig. 3E, F). Slightly interdigitating sutures are present in *Domeykos* (text-Fig. 3C, D), whereas the bones are mainly connected by smooth (harmonica) sutures or a few slightly interdigitating sutures in *Varasichthys* (text-Fig. 3A, B) and *Protoclupea.* **2-** the size and position of



Text-FIG. 2. Restoration of some Jurassic teleosts from northern Chile. A- Lateral view of head and pectoral girdle of *Varasichthys ariasi* (slightly modified from Arratia, 1987a); B- Pelvic axillary process and pelvic fin of *Domeykos profetaensis* (based on specimens LBUCH 12-260972a, b and LBUCH 1-210277-13a).



Text-FIG. 3. Restoration of the lateral view of the neurocranium (left) and of the skull roof (right) of some Jurassic teleosts. **A-, B-** *Varasichthys ariasi* (based on specimens LBUCH 16-260977b and LBUCH 012378a); **C-, D-** *Domeykos profetaensis* (based on acid-prepared specimen LBUCH 1-210277); **E-, F-** *Luisichthys vinalensis* (based on acid-prepared specimen USNM 18656).

foramina for nerves and blood vessels differ among the three genera (compare text-Figs. 3A, C, and E). **3-** the presence of a foramen framed by the epioccipital, exoccipital, and parietal bones in *Luisichthys* which has not been observed in the other Jurassic teleosts examined. **4-** the presence of the intercalar bone in *Luisichthys* which is absent in *Varasichthys*, whereas the condition is unknown in *Domeykos*. **5-** a well developed intercalar-prootic bridge in *Luisichthys;* a poorly developed prootic bridge is known in *Domeykos*.

The braincase provides data about presence or absence of sutures between certain bones (character 1), the presence or absence of certain bones (character 5), position, size, and relationships between bones, the exit of foramina of some nerves and blood vessels (characters 7, 8), trajectory of sensory canals and grooves for pit lines (characters 9, 10 respectively), among others. These data may be phylogenetically important or may be useful as taxonomic tools at different hierarchic levels in certain teleostean clades.

The middle pit line groove (character 10) does not extend onto the pterotic in *Luisichthys* (text-Fig. 3F), whereas it does in *Domeykos, Varasichthys* (text-Fig. 3B), *Protoclupea,* and more primitive taxa such as *Leptolepis coryphaenoides* (Nybelin, 1974; Patterson 1975), *Proleptolepis furcata* (Nybelin, 1974), and pholidophorids (Nybelin, 1966). It does not extend onto the pterotic in *Tharsis* (Nybelin, 1974; Patterson 1975) and *Allothrissops* (Patterson and Rosen, 1977). Therefore a middle pit line groove extending onto the parietal and pterotic bones is interpreted here as the primitive character state.

At the base of the braincase, a short parasphenoid (text-Fig. 3C) not extending posterior to the basioccipital region, is observed in the examined Jurassic fishes with the exception of *Varasichthys* (text-Fig. 3A; Pl. 5, Fig. A). This feature was interpreted as a derived character of *Varasichthys* by Arratia (1981) by comparison with other Jurassic teleosts. Teeth on the parasphenoid (character 2), a primitive condition among teleosts, are found in *Leptolepis coryphaenoides, Tharsis, Anaethalion, Leptolepides,* and *Lycoptera*, whereas an edentelous parasphenoid is present in *Domeykos* and *Varasichthys*. The condition is unknown in *Protoclupea, Luisichthys,* and *Ascalabos*.

The pattern of bones of the cranial roof is similar among most of the teleostean genera studied. In primitive teleosts, the parietals are large and separate the frontal bones from the supraoccipital bone as illustrated by *Varasichthys* and *Luisichthys* (text-Fig. 3B, F). The supraoccipital bone may extend anteriorly below the parietals as it does in *Varasichthys* (Pl. 5, Fig. B). In contrast, small parietals separated completely by the supraoccipital bone is the condition shown by *Domeykos* (text-Fig. 3D; acid-prepared specimen LBUCH 1-210277); this feature is an autapomorphy of *Domeykos* among the teleosts examined. The supraoccipital crest (text-Figs. 2A, 3B) is rudimentary in most Jurassic teleosts such as *Domeykos, Protoclupea, Varasichthys, Leptolepis coryphaenoides*, and *Tharsis*. The supraoccipital crest is moderately projected posteriorly in *Luisichthys* (text-Fig. 3E, F; Pl. 2, Fig. C). It is large and projects posterodorsally in the ichthyodectiformes *Thrissops*, but not in other Jurassic ichthyodectiformes such as *Occithrissops* (Schaeffer and Patterson, 1984) and *Allothrissops* (Patterson and Rosen, 1977). Despite Biese's (1961) identification of *Thrissops* in Cerritos Bayos, northern Chile, a large supraoccipital crest has not been observed in any of the specimens from this locality and therefore this identification is probably incorrect.

The teleostean circumorbital series, as illustrated by *Varasichthys* (text-Fig. 2A), comprises the antorbital, infraorbital bones, and supraorbital(s) in most species studied. The common pattern of the infraorbital bones is the presence of an enlarged infraorbital 1 or lacrimal, a narrow infraorbital 2, a large infraorbital 3 which is usually the largest of the series, and smaller infraorbitals 4-6. This pattern can vary, *e.g.*, infraorbital 4 is the largest in *Allothrissops* (Patterson and Rosen, 1977, Fig. 5), and fusion of elements (character 11) probably occurred in *Lycoptera* and a few other teleosts.

The total number of infraorbital bones is nearly constant among the studied teleosts (text-Fig. 2A). Most of them have five infraorbitals, except for *Protoclupea* which lacks the fourth. This character has been interpreted as diagnostic for the genus. The information from the outgroup is equivocal, *e.g.*, seven infraorbitals are found in *Pholidophoroides limbata* (Nybelin, 1966) and five in *Pholidophorus bechei* (Nybelin, 1966) and *Proleptolepis megalops* (Nybelin, 1974). Because the author is uncertain of the phylogenetic meaning of this character, she did not include it in this study.

A suborbital bone (character 12) occurs in *Leptolepis coryphaenoides* (*e.g.*, Nybelin, 1974, text-Fig. 4; Arratia, in press a, Fig. 1D) and in *Varasichthys* (text-Fig. 2A; Arratia, 1984) among the genera examined. In *Varasichthys*, the suborbital bone is small and placed posterior to infraorbitals 4 and 5, extending onto the preopercle and probably reaching the opercle. In contrast, the suborbital bone is large, covering the lateral region of the head that extends ventral to the dermopterotic or pterotic, and between infraorbital 3 and the uppermost infraorbitals and the opercle and preopercle in pholidophorids such as *Pholidophorus bechei* and *Pholidophoroides limbata* (Nybelin, 1966) and proleptolepids and leptolepids such as *Proleptolepis megalops*, *Leptolepis normandica*, and *Leptolepis coryphaenoides* (Nybelin, 1974; Arratia 1984, and in press a). The suborbital bones in *Varasichthys* and pholidophorids, proleptolepids, and leptolepids are not homologous structures judging from the phylogeny (see below). According to Patterson and Rosen (1977, p. 100), a suborbital bone is present in an indeterminate specimen of *Thrissops* from the Late Jurassic of Dorset; this condition has not been described for other specimens of *Thrissops* (*e.g.*, Nybelin, 1964; personal observation), therefore presence of this suborbital bone could be interpreted as individual variation. Among Late Jurassic teleosts, the suborbital bone is known only from *Varasichthys*.

Most studied species have an upper jaw formed by a triangular premaxilla bearing a small ascending process, an elongate maxilla bearing a row of small conical teeth, and two supramaxillae. Most have a short lower jaw bearing a high coronoid process. The presence of all these elements represents the generalized condition in primitive teleosts as illustrated by *Varasichthys* (text-Fig. 2A).

A small triangular premaxilla without an ascending process is present in pholidophorids (Nybelin, 1966, Figs. 1, 9, 12). A similar premaxilla occurs in *Varasichthys* (text-Fig. 2A); the bone is unknown in *Domeykos* (text-Fig. 1B) and *Protoclupea* (text-Fig. 1C). The dorsoposterior margin of the premaxilla is broken in the available specimens of *Luisichthys* (*e.g.*, Arratia and Schultze, 1985, text-Fig. 19), but still the general shape of the bone is similar to that in *Varasichthys*. In contrast, the premaxilla is more elongate and bears a small ascending process in *Ascalabos* (text-Fig. 1A). Considering that the available information on the Chilean teleosts is incomplete, the author did not include this character in the phylogenetic analyses.

Jaws with a small conical teeth (character 13) represent the generalized condition among the studied teleosts (text-Fig. 2A). Elongate jaws with numerous villiform teeth are characteristic of *Anaethalion* among the genera examined; similar jaws are present in other Jurassic genera not included in this study such as *Daitingichthys* and *Eichstaettia* from the Tithonian of Germany (Arratia, 1987b, text-Fig. 22, Pls. 5B, 6). *Lycoptera* has elongate jaws with numerous large, conical teeth (this character was coded as '0' in table 2 to note that *Lycoptera* does not carry villiform teeth; still the dentition of *Lycoptera* differs from that of the outgroup). *Antofagastaichthys* has elongate jaws with few, large conical teeth.

The presence of two supramaxillae (text-Fig. 2A; character 14) represents the primitive condition among basal teleosts. The presence of one supramaxilla or its complete absence correspond to derived character states. One supramaxilla is present in *Lycoptera* among the studied teleosts and in *Antofagastaichthys* from northern Chile (Arratia, 1986a, text-Figs. 8, 9); supramaxillae are absent in Teleost n. gen. from Germany. In the analysis presented below, character 14 was coded as presence [0] *versus* absence [1]. There is no difference in the topology of the tree when the character is coded as presence of two [0], one [1], and absence of supramaxillae [2].

The lower jaw provides some important characters such as the composition of the articular facet for the quadrate (character 15), the fused or unfused condition of the angular, articular and retroarticular bones (character 16), the size of the postarticular process (character 17), and the position of the posterior opening for the mandibular canal (character 18). The last character is an important one in the evolution of teleosts (Arratia, in press a). The posterior opening placed lateral to the angular bone is a uniquely derived condition for osteoglossomorphs, clupeomorphs, esocoids, ostariophysans, salmonids, and other relatively advanced teleosts. Most primitive fishes such as the Jurassic teleosts from Chile have the posterior opening placed medial to the angular bone (*e.g.*, *Domeykos*), or posteriorly placed in the postarticular process (*e.g.*, *Varasichthys*).

A leptolepid notch in the ascending margin of the dentary is present in *Leptolepis coryphaenoides*, *Tharsis*, *Ascalabos*, *Domeykos*, and *Varasichthys*, but it is absent in ichthyodectiformes, *e.g.*, *Occi–*

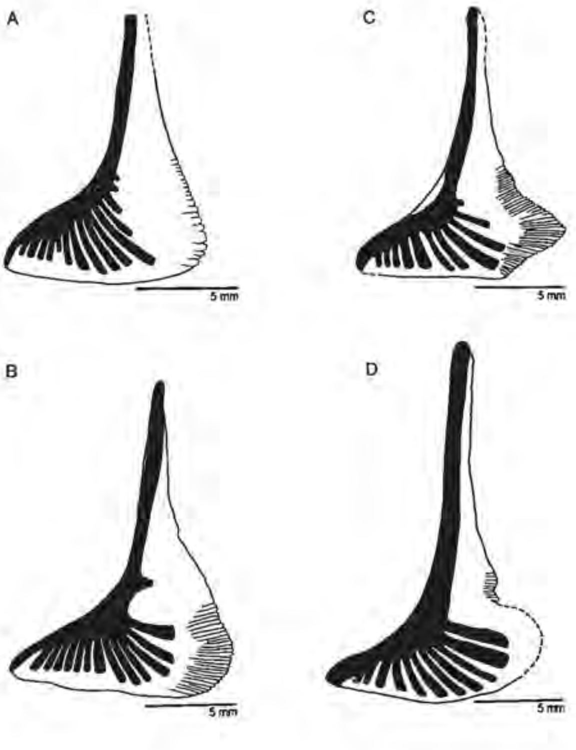
thrissops, Allothrissops, and *Thrissops*, and also in fishes with elongate jaws such as *Anaethalion* and *Antofagastaichthys*. The condition is unclear in *Leptolepides* and *Orthogonikleithrus*. The leptolepid notch is absent in some members of the outgroup, but it is present in *Proleptolepis* sp. (Nybelin, 1974, text-Fig. 16A). The leptolepid notch seems to be a synapomorphy at the basal level of the Teleostei.

The opercular apparatus of *Varasichthys* (text-Fig. 2A) represents the common condition present in most of the studied teleosts. However, an additional small bone, the suprapreopercle, is present in *Leptolepis coryphaenoides* (*e.g.*, Nybelin, 1974); a similar bone has not been observed in members of the varasichthyid group. Despite the general ressemblance of the opercular apparatus in the studied species, there are differences that deserve attention.

The preopercular canal gives off numerous branches in pholidophorids and in basal teleosts such as *Leptolepis coryphaenoides, Tharsis, Domeykos, Varasichthys, Protoclupea*, and *Luisichthys* (text-Fig. 4A-D). However, some of these fishes show variability in the number of branches as noted for *Leptolepis coryphaenoides* by Wenz (1968) and Nybelin (1974, text-Fig. 6A-L) and for *Varasichthys* by Arratia (1981, text-Fig. 12A-D). In contrast, few branches are observed in *Ascalabos* (text-Fig. 1A) and more advanced teleosts such as *Anaethalion, Leptolepides, Lycoptera*, and *Orthogonikleithrus*. There are some differences among fishes with a highly ramified preopercular canal. Sensory tubules of the preopercular canal are branching along the entire canal in *Leptolepis coryphaenoides*, thus the dorsal and ventral limbs of the bone bear sensory tubules. These sensory tubules are concentrated mainly on the ventral limb; they approach the ventroposterior margin of the preopercle (text-Figs. 1B-D, 2A 4A-D) in members of the varasichthyid group, but they are short in *Ascalabos* (text-Fig. 1A). The preopercular lower limb is broadly expanded in fishes with extensive ramification of the preopercular canal, *e.g.*, in members of the varasichthyid group (text-Figs. 1B-D, 2A, 4A-D; Pl. 1, Figs. A-B); it is unknown if the expansion of the bone and the ramification of the preopercular canal have evolved independently. In addition, the posterior margin of the ventral limb of the preopercle is crenulated in *Domeykos, Varasichthys, Protoclupea*, and *Luisichthys* (text-Fig. 4A-D), whereas this margin is smooth in other Jurassic teleosts. Because the evolutionary transformations of the preopercular bone and preopercular canal are not fully understood the author have not considered them in the cladistic analyses.

The bones of the pterygoid series are incompletely known in most of the species examined. A tooth bearing entopterygoid is only known from *Luisichthys*; this character is apparently an autapomorphy of this genus among the teleosts studied.

Branchial arches are important structures in the evolution of Recent teleosts, providing numerous diagnostic characters at different hierarchic levels (see Nelson, 1968, 1969; Rosen, 1973; Lauder and Liem, 1983). Regrettably they are unknown for most Jurassic teleosts, with a few exceptions such as *Tharsis dubius* (Nybelin, 1974, text-Fig. 26; personal observation) and *Allothrissops* (Patterson and Rosen,



Text-FIG. 4. Restorations of preopercles and of preopecular canal (black) of members of the varasichthyid group. **A**- *Domeykos profetaensis* (specimen LBUCH 12-260972a, b); **B**- *Varasichthys ariasi* (specimens LBUCH 16-260977a, b and LBUCH 02278a, b); **C**- *Protoclupea chilensis* (specimen R-369A, B); **D**- *Luisichthys vinalensis* (acid-prepared specimen USNM 18656).

1977). They are partially known in *Domeykos* (Pl. 1, Figs. A, B) and *Varasichthys* (Pl. 5, Fig. A).

A gular plate is present in *Varasichthys* (Arratia, 1981) and *Luisicnthys* (White, 1942; Arratia and Schultze, 1985), but its presence or absence has not been observed in *Domeykos* and *Protoclupea* because of preservational conditions. A gular plate is present in most Jurassic teleosts examined. The presence of this element is interpreted here as the plesiomorphic character state by comparison with the outgroup. A gular plate seems to be absent in teleosts such as *Leptolepides* and *Orthogonikleithrus*.

VERTEBRAL COLUMN AND INTERMUSCULAR BONES

It has been widely accepted that Jurassic teleosts above the level of pholidophorids have autogenous neural and haemal arches along the vertebral column. However, this condition varies depending on whether abdominal or caudal vertebrae are considered (characters 22 and 23). Previously the vertebral column was restored showing unfused neural and haemal arches in the caudal region, *e.g.*, *Leptolepis coryphaenoides* and *Allothrissops* (Taverne, 1975a, Fig. 1), *Anaethalion* (Gaudant, 1968, Fig. 1), *Ascalabos* (Taverne, 1975b, Fig. 1), and *Leptolepides* (Taverne, 1981, Fig. 1). In contrast, the author's observations of complete specimens (Pls. 3, 4; Pl. 6, Figs. A-D), studies of isolated vertebrae by Scanning Electron microscopy (Pl. 7, Figs. B, C), and investigation of serial cross sections of vertebrae (Pl. 7, Fig. D) confirm that neural and haemal arches of the caudal vertebrae are not always autogenous in Jurassic teleosts. Neural and haemal arches of most caudal vertebrae are fused in *Anaethalion* (Arratia, 1987b, text-Fig. 3A, B; in press a, Fig. 1A), *Ascalabos* (text-Fig. 1A; Arratia, in press a, Fig. 1B), *Daitingichthys* (Arratia 1987b, text-Fig. 23), *Domeykos* (text-Fig. 1B; Pls. 6, Fig. A; 7, Fig. A; Arratia and Schultze, 1985, text-Figs. 12, 16B), *Eichstaettia* (Arratia 1987b, text-Fig. 20), *Leptolepis coryphaenoides* (Arratia 1991, Pl. 5A-D; in press a, Fig. 1D), *'Leptolepis' talbragarensis* (Arratia 1991, Pl. 6A), *Leptolepides* (Arratia, in press a, Fig. 2A), *Protoclupea* (text-Fig. 1C; Arratia and Schultze, 1985, text-Fig. 2), *Varasichthys* (text-Fig. 1D; Pl. 6, Fig. B), and *Luisichthys* (Pl. 6, Figs. C, D). The autogenous condition of the neural arches in the abdominal region seems to be common in Jurassic teleosts, but not in the caudal region. In contrast, the presence of arches fused to the autocentrum in the caudal vertebrae is a synapomorphy at the level of *Leptolepis coryphaenoides* plus more advanced teleosts (Arratia, 1991 and below).

The surface of the vertebral centrum (character 21), smooth or sculptured, is an important character in phylogenetic analyses of teleosts (*e.g.*, Patterson and Rosen, 1977; Arratia, 1991 and in press a). Most Jurassic teleosts (including *Domeykos, Varasichthys, Protoclupea,* and *Luisichthys*) resemble Recent teleosts in having the surface of the caudal autocentra sculptured; the sculptur of the autocentrum may be represented by a longitudinal crest (*e.g., Domeykos*, Pl. 6, Fig. A), or a few longitudinal crests, or by numerous bony ridges (*e.g., Anaethalion*). In contrast, the surface of the autocentrum is smooth in *Leptolepis coryphaenoides* and in *Leptolepides*; the smooth condition in these two genera is interpreted as being derived independently, according to the distribution of this character state among teleosts (see below).

A thick, well ossified autocentrum is present along the entire vertebral column in *Domeykos, Varasichthys, Protoclupea,* and *Luisichthys.* The autocentrum is thin and without cavities for adipose tissue in *Leptolepis coryphaenoides* (Arratia, 1991, Pl. 4A); in contrast, the presence of a thick autocentrum with numerous cavities filled with adipose tissue (Pl. 7, Fig. D) is a synapomorphy shared by basal Jurassic teleosts above *Leptolepis coryphaenoides.* Arratia (1991) interpreted this character as a synapomorphy shared by teleosts above the level of *Leptolepis coryphaenoides + 'Leptolepis' talbragarensis.*

In the abdominal centra of most Jurassic teleosts, including *Domeykos, Varasichthys,* and *Luisichthys* (text-Fig. 1B, D; Arratia 1981; Arratia and Schultze 1985, text-Fig. 16A; Arratia, 1987b, text-Fig. 3B) the halves of the neural arches are unfused (character 24). In contrast, more advanced teleosts (*e.g.,* Teleost n. gen.) have both halves fused in a median neural spine along most of the abdominal region.

The notochord not constricted by the midcaudal autocentra (character 25) is considered the primitive condition present in *Leptolepis coryphaenoides.* In more advanced teleosts such as *Domeykos* (Pl. 6, Fig. B; Pl. 7, Fig. D), *Varasichthys,* and *Protoclupea* the notochord is strongly constricted by the midcaudal autocentra.

Intermuscular bones such as the epineurals are commonly found in Jurassic teleosts. They are thin, elongate projections of the lateroposterior wall of the neural arch on the abdominal and first caudal vertebrae (character 26). *Domeykos* and *Varasichthys* have a well developed epineural series (text-Fig. 1B, D). The presence or absence of epineurals is unknown in *Protoclupea* (text-Fig. 1C). Another series of small thin bones, the epipleurals, may be present in the anterior caudal region in some teleosts. Epipleural bones (text-Fig. 1B, D) are known from *Domeykos*, *Varasichthys*, and *Luisichthys*, whereas the condition is unknown in *Protoclupea* (text-Fig. 1C) because of insufficient preservation.

GIRDLES AND AXILLARY PROCESSES

Characters of the girdles and axillary processes were first used by Arratia (in press a) in phylogenetic interpretations of primitive teleosts. Usually, information on these structures is incomplete due to insufficient preservation and therefore comparison is difficult, if not impossible. For instance, the supracleithrum is commonly hidden by the opercle so that its general size and shape and the trajectory of the lateral line canal are not available for all teleostean genera examined, nor for the members of the outgroup. The exit of the lateral line canal with respect to the supracleithrum (character 27) seems to be phylogenetically important within teleosts. The posteroventral exit of the canal is dorsally displaced in *Varasichthys* (text-Fig. 2A), the canal may exit at about the middle or at the upper third of the supracleithrum in other teleosts examined (*e.g.*, *Leptolepides*).

Structures such as the postcleithra (character 29) are not easily observed in the fossil material because of their position, commonly hidden by bones of the pectoral girdle, scales, and/or anterior ribs, and also because of their small size. Yet available information suggests that the common condition among teleosts is the presence of one to three postcleithra More than three postcleithra (text-Figs. 1B-D, 2A) are found in the Jurassic genera *Domeykos*, *Protoclupea*, *Varasichthys*, and supposedly *Luisichthys* (Arratia, 1984, and in press a; Arratia and Schultze, 1985, text-Fig. 21A, C-E; Gottfried, 1989). In addition, *Varasichthys* is unique among teleosts in having two postsupracleithra (text-Fig. 2A; character 28) lying medial to the posterior margin of the supracleithrum.

Pectoral and pelvic axillary processes (characters 30 and 31) are not well known in Recent teleosts, and they are less known in fossil forms. The lower series of postcleithra in *Domeykos*, *Varasichthys*, and *Protoclupea* resembles in shape and position the elements present in Recent *Elops*. The series of ventral modified postcleithra in *Elops* is interpreted as a pectoral axillary process by Arratia (in press a). The pectoral axillary process of the Chilean Jurassic forms is formed by modified bony elements. Remains of a fourth postcleitrum were reported in *Luisichthys* by Arratia and Schultze (1985); because it is unclear whether the element forms an axillary process, it is coded '9' in table 2. The presence of the pectoral axillary process formed by a series of modified bony elements is a unique character of the varasichthyid group among teleosts.

A pelvic axillary process has not been observed in most Jurassic teleosts; it is also poorly known among Recent teleosts. The pelvic axillary process has been observed in *Leptolepis coryphaenoides* (acid-prepared specimen, BGHan. 1957-5) and the Chilean Jurassic teleosts *Domeykos*, *Protoclupea*, and *Varasichthys* (text-Figs. 1B-D, 2B; Arratia and Schultze, 1985; Arratia, 1987a, and in press a) among Jurassic teleosts. Due to the differences in their structures, Arratia (in press a) interpreted the occurrence of the pelvic processes in *Leptolepis coryphaenoides* and in the Chilean teleosts *Domeykos*, *Protoclupea*, and *Varasichthys* as being independently acquired. An elongate bony axillary process (text-Figs. 1B-D, 2B) is present in members of the varasichthyid group; its absence in *Luisichthys* is interpreted as a reversal of the primitive condition.

CAUDAL SKELETON AND FIN

The caudal skeleton and fin are significant structures in the evolution of teleosts as shown by Gosline (1960), Nybelin (1963), Patterson (1968), Patterson and Rosen (1977), Lauder (1989), Schultze and Arratia (1989), Arratia (1991), and Arratia and Schultze (1992), among others. Despite numerous publications on the subject, many questions of the homology of certain elements of the caudal skeleton and fin still remain unanswered.

Structures such as the preural and ural centra and their arches, hypurals, epurals and uroneurals have undergone significant evolutionary transformations among fossil and Recent teleosts. The shape and length of the neural spines of preural and ural centra differ among basal teleosts (characters 36-41). Commonly, the neural spine of preural centrum 1 (text-Figs. 5A-C, 6) is short, shorter than that of preural centrum 2 in primitive teleosts (*e.g.*, in *Leptolepis coryphaenoides*, *Tharsis*, *Ascalabos*, Teleost sp. 1, *Domeykos*, *Protoclupea*, and *Luisichthys*). However, a long neural spine on preural centrum 1 is present in *Varasichthys* and *Lycoptera*, and it is interpreted as independently acquired in both genera.

Presence or absence of a neural spine and neural arch on the first ural centrum (characters 40 and 41) is important to be determined in basal teleosts. Teleost sp. 1, *Domeykos*, *Luisichthys* (text-Figs. 5A, C, 6; Arratia, 1991, Figs. 3, 5, 11) bear two neural arches on the first ural centrum, which is evidence of the compound origin of this centrum (fusion of ural centra 1 and 2). Some lycopterids (Greenwood 1970; Patterson and Rosen, 1977, Fig. 24; Arratia, in press b. Fig. 6) have two separate elements, ural centra 1 and 2, each bearing its neural arch. Other basal teleosts present an elongate first ural centrum but only one ural neural arch has been observed (*e.g.*, *Varasichthys, Ascalabos, Leptolepides*; Arratia, 1991, Figs. 9, 10).

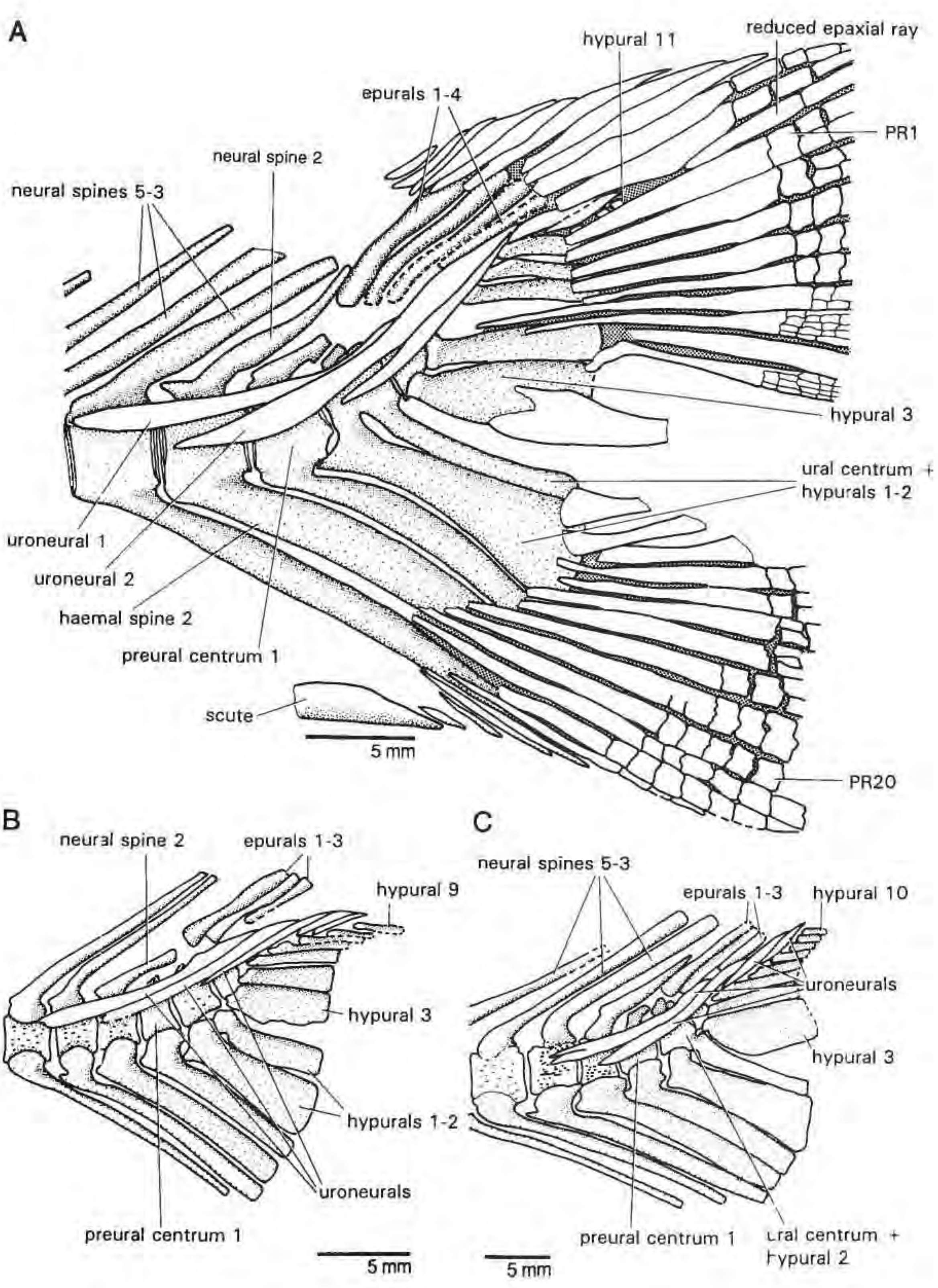
Teleosts usually have three epurals (character 43), however four epurals are present in basal teleosts such as *Domeykos* (text-Fig. 5A) and Teleost sp. 1 (text-Fig. 6). Four or more epurals are known from some pholidophorids (*e.g.*, *Pholidophorus bechei in* Patterson, 1968) and *Pleuropholis serrata* (Patterson, 1973). The presence of four or more epurals is interpreted here as the primitive condition. In contrast, *Varasichthys* and *Lycoptera* present only one epural which the author interpretes as a condition independently acquired in both genera, based on the phylogeny (see below).

Primitive teleosts such as *Leptolepis coryphaenoides, Ascalabos, Domeykos,* Teleost sp. 1, and others are characterized by a high number of uroneurals and hypurals (text-Figs. 5A-C, 6); however, a trend to reduce the number of these elements during the evolution of teleosts is observed. Eight uroneurals are present in primitive teleosts such as *Leptolepis coryphaenoides* (Arratia, 1991, Figs. 7, 24b), seven uroneurals in Teleost sp. 1, *Tharsis*, and *Ascalabos*, five uroneurals in *Domeykos, Protoclupea,* and *Leptolepides*, and four uroneurals in *Luisichthys*, among others. The trend to reduce the number of uroneurals (character 44) is achieved by fusion or loss of elements. The first uroneural in *Leptolepis coryphaenoides, Protoclupea,* and *Luisichthys* is the result of an incomplete fusion of uroneurals 1 and 2; the first uroneural in *Ortho–gonikleithrus* is supposed to be the result of the phylogenetic fusion of uroneurals 1-3. The second uroneural in *Domeykos* is interpreted as the result of the phylogenetic fusion of uroneurals 2 and 3 (Arratia, 1991). Loss of the most posterior uroneural(s) is observed in teleosts such as *Domeykos, Protoclupea, Luisichthys, Leptolepides, Orthogonikleithrus*, and others. Both processes, fusion and loss, can be found simultaneously in the same species (*e.g.*, in *Leptolepides sprattiformis*).

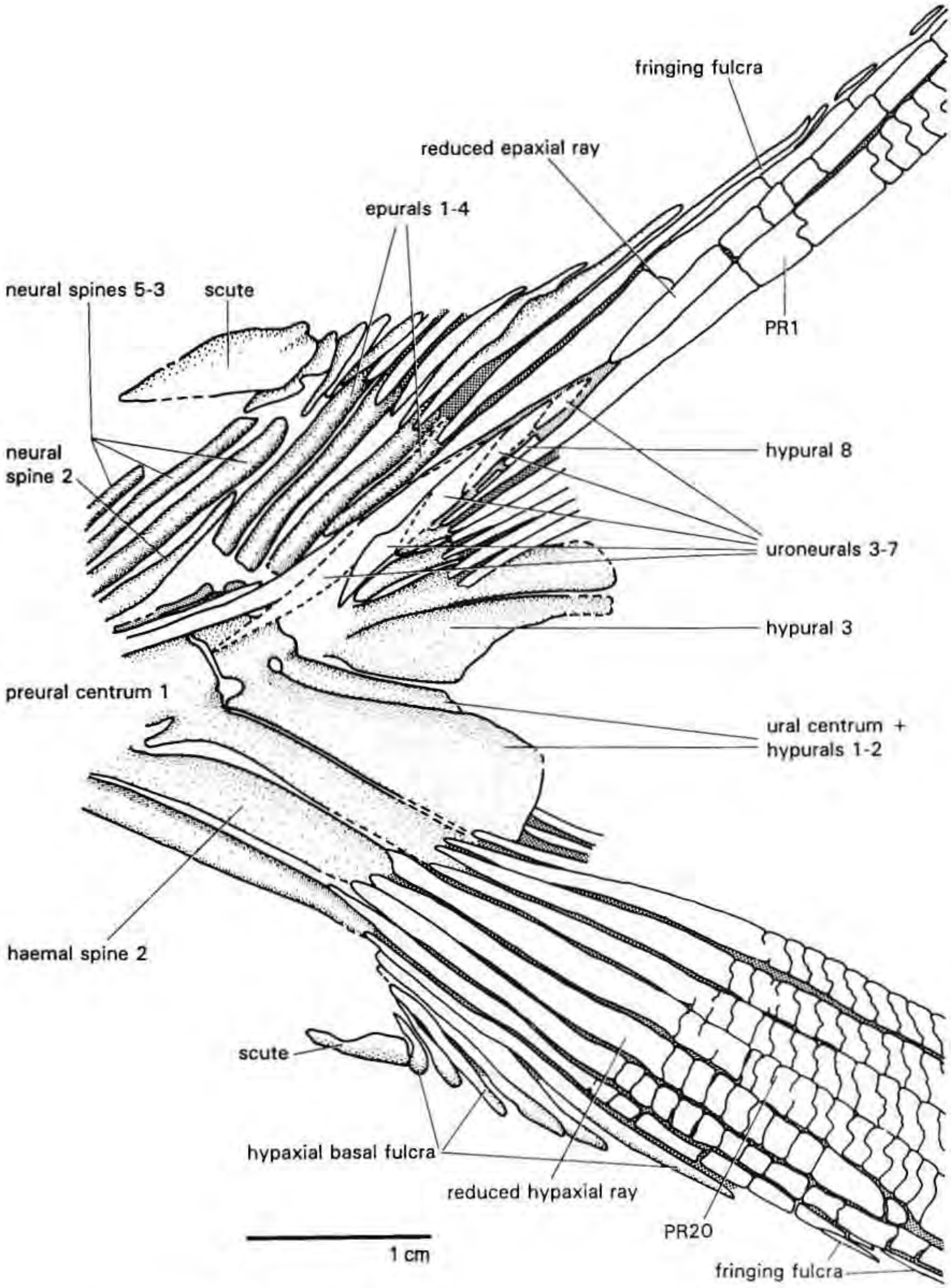
Shape and position of dorsal (*e.g.*, uroneurals, epurals) and of ventral (*e.g.*, hypurals) caudal elements vary among teleosts. The size of the first uroneurals and their relationships (characters 49-51) with preural centrum 4, 3, 2, and/or 1 are important in the evolution of the caudal skeleton of basal teleosts. In basal teleosts such as *Leptolepis coryphaenoides, Tharsis, Ascalabos, Domeykos* (text-Fig. 5A), *Varasichthys, Protoclupea* (text-Fig. 5B), and *Luisichthys* (text-Fig. 5C), the first uroneural reaches preural centrum 4 or 3; whereas in *Anaethalion, Leptolepides*, and *Orthogonikleithrus* it reaches preural centrum 2.

The length and number of uroneurals, their relation to each other, and their angle of inclination with respect to the horizontal (characters 45-51) seem to be phylogenetically significant in Jurassic teleosts. Members of the varasichthyid group and Teleost sp. 1 commonly present the primitive state of these characters.

Loss or fusion of elements is also observed within the hypurals (characters 52-57). Eight or more hypurals are present in *Ascalabos* (11), *Domeykos* (11), and Teleost sp. 1 (+8). The total number is unknown in *Varasichthys*. Seven hypurals are found in *Leptolepides* and six or less in Teleost n. gen. and in numerous extant teleosts. The number of hypurals is reduced among Jurassic teleosts by loss of the most posterior ones. Fusion of hypurals is rarely observed in Jurassic teleosts (one exception is *Daitingichthys*), whereas it is characteristic of more advanced teleosts such as some ostariophysans, perciforms, atherinomorphs, and others. The hypurals 1 and/or 2 may be laterally fused to their ural autocentra or unfused (characters 58-61); further fusion may also involve preural centrum 1.



Text-FIG. 5. Restoration of caudal skeleton in lateral view. **A**- *Domeykos profetaensis* (based on specimens LBUCH 3539, 012778a, b); **B**- *Protoclupea chilensis* (based on specimen DG-R 396A, B); **C**- *Luisichthys vinalensis* (based on specimen NMNH 18429).



Text-FIG. 6. Teleost sp. 1 from Quebrada del Profeta, northern Chile. Caudal skeleton in lateral view (based on specimen LBUCH 1987a, b).

Numerous urodermals or scale-like bones are found in members of the outgroup (*e.g.*, pholidophorids). Elements in the same position in Recent teleosts are tendon-bones and they were identified as 'urodermals' by Arratia and Schultze (1992) to note that they are not homologous with the urodermals. In contrast, one or two small elongate bones or 'urodermals' (character 64) occur lateral to the base of the first principal rays in fossil teleosts such as *Leptolepis coryphaenoides*, *Tharsis*, *Ascalabos*, and *Varasichthys*. The condition is unknown in *Domeykos*, *Protoclupea*, and *Luisichthys*.

Presence or absence of epaxial and hypaxial fulcra and of fringing fulcra (character 65) are important characters in the evolution of teleosts. However, a problem lies in how to distinguish between simple, unsegmented procurrent rays present in advanced teleosts and fulcra (Arratia, 1991). Losses of fulcra and fringing fulcra are interpreted as derived conditions among teleosts. Fringing fulcra in both lobes of the caudal fin (text-Fig. 6; Pl. 8, Fig. A) are only known in Teleost sp. 1 among the teleosts studied. An epaxial fringing fulcra is present in certain teleosts such as *Leptolepis coryphaenoides*, whereas the absence of the epaxial fringing fulcra is the common condition of primitive teleosts above the level of *Leptolepis coryphaenoides*.

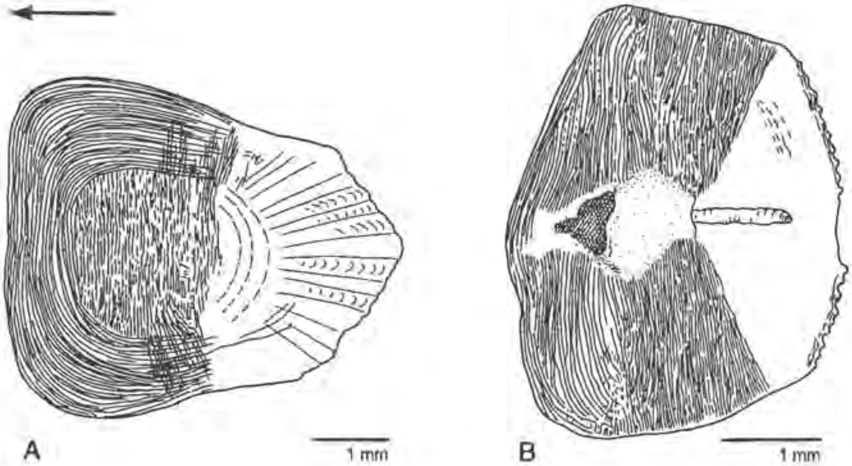
A reduced epaxial procurrent ray dorsolateral to the first principal ray (text-Figs. 5A, 6) is found in certain Jurassic teleosts such as Teleost sp. 1, *Ascalabos*, *Domeykos*, and *Varasichthys* (Arratia, 1991). A reduced epaxial ray is present in some members of the outgroup (*e.g.*, *Pholidophorus bechei* and *Pholidolepis dorsetensis*), whereas it is absent in *Pholidolepis ?dorsetensis*. The reduced epaxial ray is shorter in pholidophorids and pholidolepids than in the teleosts mentioned above; in addition, the ray is unsegmented in members of the outgroup. Because the structure of this element and its homology is still unclear, this character was not used in the analyses; however, a segmented epaxial procurrent ray may be another synapomorphy shared by *Ascalabos* and the varasichthyid group, and its loss in *Protoclupea* and *Luisichthys* another synapomorphy shared by these two genera within the varasichthyid group. This character may be phylogenetically important for interpretations of the relationships of Teleost sp. 1. This will depend on whether a segmented epaxial procurrent ray is homologous with the condition in pholidophorids. A reduced hypaxial ray (text-Fig. 6; Pl. 8, Figs. B, C) has only been observed in Teleost sp. 1 among the teleosts examined.

The total number of principal caudal rays, or the number of principal rays of the dorsal or ventral lobe of the caudal fin (characters 68, 69), seems to be important in analyses of phylogenetic relationhips of basal teleosts. Twenty or more principal caudal rays represent the primitive condition present in the outgroup and in teleosts (*e.g.*, in Teleost sp. 1, *Domeykos*, *Varasichthys*, *Protoclupea*, and *Luisichthys*). The presence of 19 principal rays is the most common condition found in teleosts (see Schultze and Arratia, 1989, table 1). Less than 19 principal rays is another derived condition found in certain advanced teleostean groups (*e.g.*, *Lycoptera*).

The structure of the caudal skeleton including composition of precaudal and ural centra, number of uroneurals, epurals, hypurals, number of principal caudal rays, scutes, fulcra, among others, shows a great diversity among teleosts. The important point is to understand the changes of the caudal skeleton and fin in different teleostean lineages, so homologous characters can be identified.

SCUTES AND SCALES

Information on scutes is available for most of the Jurassic teleostean species examined; in contrast, information on scales is incomplete due to condition of preservation. Fortunately, information on the scales of some teleosts is available from Schultze (1966), and for other teleosts the author prepared peels of the scales to study their characteristics and to prepare the illustrations. All teleosts examined have cycloid scales; still there are differences in the disposition of the circuli, radii, the presence of lines in the middle field of the scales, and other features that may be useful in identifying some groups. For instance, the scales of the ventral part of the body just posterior to the pectoral girdle in *Varasichthys* are unique among teleosts with the presence of a small peg (Arratia, 1981, text-Fig. 19C). Scales with circuli crossed by transverse lines in the middle field, are characteristic of *Ascalabos* and the varasichthyid group. *Ascalabos* (specimen JM SOS 2996a, b) has a well preserved squamation, with scales similar to those of *Domeykos* (see text-Fig. 7A). The transverse lines in the middle field in the scales of *Leptolepides* (text-Fig. 7B), or in some clupeomorphs, do not cross the circuli in the same manner as they do in *Ascalabos* and in the varasichthyid group, therefore they are interpreted here as different character states.



Text-FIG. 7.

Cycloid scales showing the middle field of the scale crossed by transverse lines. A- *Domeykos profetaensis* (after Arratia and Schultze, 1985); B- *Leptolepides sprattiformis* (after Schultze, 1966). Arrow points anteriorly.

CHARACTER TRANSFORMATION SERIES

The phylogenetic analyses are based on the following 75 morphological characters; the coding of the character states of each taxon is shown in table 2. Twenty morphological characters are from the head, six from the vertebral column and intermuscular bones, six from the pectoral girdle and axillary processes, 40 characters from the caudal skeleton and fin, and three are characters based on scutes and scales. Many characters were taken from the literature: characters 1, 3, 4, 5, 7, 8, 11, 26, and 41 are from Patterson and Rosen (1977). Characters 9, 12, 13, 15, 16, 17, 18, 22, 27, 29, 32, 74, and 75 are from Arratia (in press a). Characters 33, 34, 36, 37, 38, 39, 40, 43, 44, 45, 50, 52, 65, 66, 67, 68, 71, and 73 are from Arratia (1991).

1. Sutures between cartilage bones in braincase retained throughout life, rather than being lost ontogenetically: [0] absent; [1] present.
2. Parasphenoid bearing teeth: [0] present; [1] absent.
3. Ossified aortic canal: [0] present; [1] absent.
4. Canal for occipital arteries in basioccipital bone: [0] present; [1] absent.
5. Spiracular canal: [0] developed; [1] greatly reduced; [2] absent.
6. Basisphenoid: [0] present; [1] absent.
7. Separate openings in the prootic for the jugular vein, orbital artery, and the hyomandibular branch of the facial nerve: [0] present; [1] absent.
8. Foramen for the glossopharyngeal nerve in exoccipital, rather than in prootic: [0] absent; [1] present.
9. Ethmoidal commissure penetrating a broad mesethmoid and passing through the whole width of the bone: [0] absent; [1] present.
10. Middle pitline groove crossing the parietal and extending onto the pterotic: [0] present; [1] absent.
11. A large infraorbital bone representing the third and fourth of other teleosts: [0] absent; [1] present.
12. Suborbital bone(s): [0] present; [1] absent.
13. Elongate jaws bearing numerous villiform teeth: [0] absent; [1] present.
14. Supramaxillae: [0] present; [1] absent.
15. Retroarticular bone: [0] included in the joint facet for quadrate; [1] excluded from the joint facet for quadrate.
16. Articular bone: [0] fused with angular and retroarticular bones; [1] fused with angular; [2] partially fused with anguloarticular late in ontogeny.
17. Postarticular process of the lower jaw: [0] well developed; [1] poorly developed.
18. Posterior opening of the mandibular sensory canal: [0] placed medial; [1] placed lateral to the angular portion of the jaw.
19. Suprapreopercle: [0] present; [1] absent.
20. Tooth plates fused with endoskeletal gill arch elements: [0] present; [1] absent. (Modified from Lauder and Liem, 1983).
21. Caudal vertebrae with sculptured autocentra: [0] absent; [1] present.
22. Abdominal centra or abdominal autocentra: [0] with unfused neural arches; [1] with fused neural arches, except for the first five or six.
23. Middle caudal centra: [0] with unfused neural and haemal arches; [1] with fused neural and haemal arches.

24. Halves of neural arches: [0] separate along the abdominal vertebrae; [1] fused halves forming a median neural spine along most abdominal vertebrae, except the first four or five.
25. Midcaudal centra: [0] not constricting the notochord; [1] slightly constricting the notochord; [2] strongly constricting the notochord.
26. Epipleural intermuscular bones: [0] absent; [1] present (a few bones in the anterior caudal region). (Modified from Patterson and Rosen, 1977).
27. The main lateral line emerging from the supracleithrum: [0] at its posteroventral region; [1] at about its middle region; [2] at its upper third.
28. Postsupracleithra: [0] absent; [1] present.
29. Postcleithra: [0] three or less; [1] more than three.
30. Pectoral axillary process: [0] absent; [1] present; formed by bony elements.
31. Pelvic axillary process: [0] absent; [1] present; formed by a small bony element; [2] present; formed by an elongate bone (Figs. 1B-D, 2B).
32. First dorsal pterygiophore is: [0] bipartite or tripartite structure; [1] single structure.
33. Preural vertebrae (excluding preural centrum 1) of adult individuals with haemal arches: [0] autogenous; [1] laterally fused to their respective centra; [2] unfused laterally to their centra.
34. Parhypural in adults with haemal arch: [0] autogenous; [1] laterally fused to its centrum; [2] laterally unfused to its centrum.
35. Hypurapophysis (lateral process of the arch of the parhypural): [0] absent; [1] present.
36. Neural spines of preural vertebrae 5-3 distally expanded by fine anterior and posterior membranous outgrowths: [0] absent; [1] present.
37. Neural spine of preural vertebra 3: [0] inclined toward the horizontal at an angle of less than 45 degrees in relation to the dorsal margin of the centrum; [1] inclined toward the horizontal at an angle greater than 45 degrees.
38. Neural spine of preural centrum 2: [0] shorter than neural spine of preural centrum 3; [1] at least as long as neural spine of preural centrum 3.
39) Neural spine of preural centrum 1: [0] rudimentary or short; [1] long, close to, or reaching the dorsal margin of the body; [2] absent (Arratia, 1991).
40. Neural spines of ural centra 1 and 2 or 'first' ural centrum: [0] present; [1] absent. (Following Schultze and Arratia, 1989, and Arratia and Schultze, 1992, the usage of 'first'ural centrum here does not imply homology.)
41. Neural arch over first ural centrum: [0] complete; [1] reduced or absent.
42. A compound neural arch formed as a mass of cartilage over preural centrum 1 and ural centra early in ontogeny: [0] absent; [1] present. (For the explanation of the compound neural arch present in elopomorphs see Schultze and Arratia, 1988).
43. Number of epurals: [0] three or more; [1] one.
44. Number of ural neural arches modified as uroneurals: [0] seven or more; [1] six; [2] five or four.
45. Anterior uroneurals present as: [0] four or three long separate uroneurals (loss or fusion of one); [1] two long separate uroneurals (loss or fusion of two); [2] one long uroneural (loss or fusion of three).
46. Uroneurals: [0] progressively decreasing in length; [1] in two sets, a long anterior set and a short posterior set.
47. All uroneurals inclined towards the horizontal, or in a similar angle, one beside the other: [0] present; [1] absent.
48. Uppermost three uroneurals forming a series that overlaps, and lies at an angle to, longer anterior ones: [0] absent; [1] present; [2] other condition (less than three uppermost uroneurals present). (Modified from Patterson and Rosen, 1977).
49. The longest anterior uroneural(s) extending forward to preural centrum 2 or 3: [0] present; [1] absent.
50. First uroneural reaches: [0] preural centrum 3 or 4; [1] preural centrum 2.
51. Two uroneurals, rather than three or four, extending forward beyond the second ural centrum: [0] absent; [1] present. (Modified from Patterson and Rosen, 1977).
52. Number of hypurals in adult individuals: [0] ten, nine or eight; [1] seven; [2] six or less.
53. Hypural 10: [0] present; [1] absent.
54. Hypural 9: [0] present; [1] absent.
55. Hypural 8: [0] present; [1] absent.
56. Hypural 7: [0] present; [1] absent.
57. Hypural 6: [0] present; [1] absent.
58. Only second hypural fused with first ural centrum: [0] absent; [1] present.
59. In adults, both hypurals 1 and 2: [0] laterally unfused to ural centrum 1 and 2 or 'first' ural centrum; [1] laterally fused to 'first' ural centrum; [2] another condition.
60. Both hypurals 1 and 2 associated by fusion or articulation with a 'compound' centrum apparently formed by preural centrum 1 and ural centrum(tra): [0] absent; [1] present.
61. First uroneural fused with a 'compound' centrum apparently formed by preural centrum 1 and ural centrum(tra): [0] absent; [1] present.
62. Stegural: [0] absent; [1] present. (For explanation of stegural see Arratia and Schultze, 1992).
63. Pleurostyle: [0] absent; [1] present. (For explanation of pleurostyle see Monod, 1968, and Schultze and Arratia, 1989).

64. Urodermals and 'urodermals': [0] more than two urodermals; [1] two 'urodermals'; [2] one 'urodermal'; [3] none. (Modified from Arratia 1991, following terminology by Arratia and Schultze, 1992).
65. Fringring fulcra: [0] present in both lobes of caudal fin; [1] present in dorsal lobe of caudal fin; [2] absent in both lobes.
66. Proximity of the fulcra or dorsal procurrent rays to: [0] epurals and posterior uroneurals; [1] neural spines, epurals, and posterior uroneurals.
67. Long dorsal segmented procurrent ray(s): [0] absent; [1] present.
68. Number of principal caudal rays: [0] twenty or more; [1] nineteen; [2] less than nineteen.
69. Lower lobe of the caudal fin with: [0] more than nine principal rays; [1] nine principal rays; [2] less than nine principal rays.
70. Bases of the dorsalmost principal rays of the caudal fin: [0] crossing obliquely over the entire upper hypural series (save the last); [1] aligned with hypurals so that no fin-ray base overlies more than one hypural.
71. Dorsal processes of the bases of the innermost principal caudal rays of upper lobe: [0] present; [1] absent.
72. Abrupt dorsal flexion of the tail begins at preural centrum 1 or 'first' ural centrum: [0] absent; [1] present.
73. Dorsal scutes preceding caudal fin: [0] present; [1] absent.
74. Cycloid scales posterior to the pectoral girdle with circuli crossed by transverse lines in the middle field (text-Fig. 7A): [0] absent; [1] present.
75. Cycloid scales with crenulate posterior margin: [0] absent; [1] present.

RESULTS

PHYLOGENETIC ANALYSIS 1

The cladistic analysis presents the phylogenetic relationships among 14 genera of Jurassic teleosts, based on the 75 characters listed above and the character states in table 2. When these data are run with PAUP program, only one tree (text-Fig. 8) is obtained at 143 evolutionary steps. Its consistency index (CI) is 0.643. For characters supporting nodes see text-Fig. 8.

Node A represents the branching between *Leptolepis coryphaenoides* and more advanced teleosts. This node is supported by two uniquely derived features (midcaudal centra with fused neural and haemal arches and two 'urodermals') and six homoplastic characters.

The branching of *'Leptolepis' talbragarensis* and all other teleosts above node B is supported by one uniquely derived character (absence of suprapreopercle) and two homoplasies.

Node C corresponds to the branching between *Tharsis* and more advanced teleosts; six uniquely derived characters (sutures between cartilage bones, ossified aortic canal absent, canal for occipital arteries in basioccipital bone absent, spiracular canal absent, foramen for glossopharyngeal nerve in exoccipital, and a few epipleural intermuscular bones in the anterior caudal region of the body) and two homoplasies support this node.

Node D corresponds to the branching of two clades among Jurassic teleosts. One of them includes *Ascalabos* and the Chilean genera *Domeykos, Varasichthys*, and *Protoclupea* plus the Cuban genus *Luisichthys*; the other clade includes mainly genera from Europe and *Lycoptera* from Siberia, Mongolia, and China. Three homoplastic characters support this node.

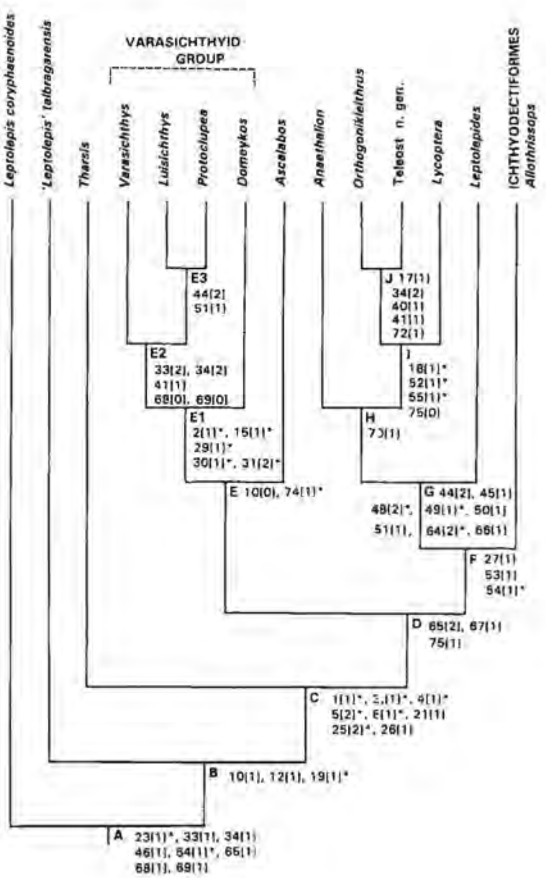
The sister group relationships (node E) between *Ascalabos* and the varasichthyid group is supported by one uniquely derived character (cycloid scales with circuli crossed by transverse lines in the middle field) and one reversal (character 10[0]). Node E1 corresponds to the branching between *Domeykos* and [*Varasichthys* + [*Protoclupea* + *Luisichthys*]]. This sister group relationship is supported by five uniquely derived characters. Node E2, the branching between *Varasichthys* and [*Protoclupea* + *Luisichthys*] is supported by five homoplasies. Node E3 [*Protoclupea* + *Luisichthys*] is supported by two homoplastic characters.

Node F, the branching between *Allothrissops* and more advanced teleosts, is supported by one unique derived character (loss of hypural 9) and two homoplasies. Node G represents the branching of *Leptolepides* and more advanced teleosts. This node is supported by three unique derived characters (uppermost series of three uroneurals lost, the longest anterior uroneural[s] reaching preural centrum 2, one 'urodermal') and five homoplastic characters. Node H, the branching of *Anaethalion* and [*Lycoptera* +

[*Orthogonikleithrus* + Teleost n. gen.]], is supported by one homoplasy. For other nodes see text-Fig. 8.

When the author added another character (leptolepid notch absent [0] *versus* present [1]), the presence of the notch was interpreted as a synapomorphy of primitive teleosts such as *Proleptolepis*, *Leptolepis coryphaneoides* and more advanced teleosts, and the absence as a synapomorphy (reversal) of node F.

Characters which are interpreted as autapomorphies of *Ascalabos* and of members of the varasichthyic group are listed in table 3.



Text-FIG. 8. Hypothesis of phylogenetic relationships of certain Jurassic teleosts. For explanation of characters and character states see text and table 2. Unique derived characters are indicated with an asterisk (*). The combined outgroup includes *Pholidophorus* spp., *Pholidolepis* sp., and *Proleptolepis* spp.

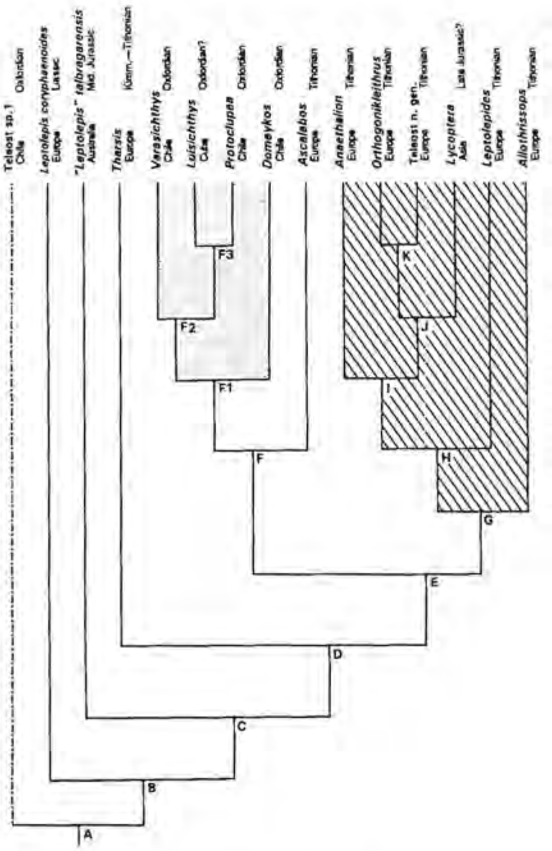
TABLE 3. HOMOPLASTIC AND UNIQUELY DERIVED CHARACTERS (*) THAT ARE INTERPRETED AS AUTAPOMORPHIES OF MEMBERS OF THE VARASICHTHYID GROUP IN ANALYSIS 1.

Taxa	**Characters**	
Domeykos	38[1]	preural vertebrae with haemal arches laterally fused to their respective centra (Fig. 5A)
	59[1]	both hypurals 1 and 2 laterally fused to 'first' ural centrum (Fig. 5A)
	72[1]	abrupt dorsal flexion of the tail begins at preural centrum 1 or 'first' ural centrum (Fig. 5A)
Luisichthys	2[0]	parasphenoid bearing teeth (Pl. 2, Fig. C)
	10[1]	middle pitline groove crossing the parietal only
	45[1]	two long anterior uroneurals (result of loss or fusion of two) (Fig. 5C)
	58[1]*	only second hypural fused with first ural centrum (Fig. 5C)
	66[1]	proximity of epaxial basal fulcra or dorsal procurrent rays to neural spines, epurals, and posterior uroneurals
Protoclupea	53[1]	hypural 10 absent (Fig. 5B)
Varasichthys	12[0]	suborbital bone present (Fig. 2A)
	17[1]	postarticular process of the lower jaw poorly developed (Fig. 2A)
	28[1]*	two postsupracleithra present (Fig. 2A)
	39[1]	neural spine of preural centrum 1 long
	40[1]	neural spine of ural centrum 1+2 absent
	43[21	one epural

PHYLOGENETIC ANALYSIS 2

Analysis 2 is the study of the phylogenetic relationships of the same genera included in analysis 1 plus one Chilean fish, Teleosts sp. 1, which is only known from the caudal skeleton and fin. Text-Fig. 9 represents the only topology at 150 evolutionary steps; the consistency index is 0.620.

The tree is identical to that in text-Fig. 8 at nodes A to J. Teleosts sp. 1 appears as the plesiomorphic sister group of *Leptolepis coryphaenoides* plus more advanced teleosts.



Text-FIG. 9. Hypothesis of phylogenetic relationships of certain Jurassic teleosts and their geographic distribution and ages. For explanation of characters and character states see text and table 2. Unique derived characters are indicated with an asterisk (*). The combined outgroup includes *Pholidophorus* spp., *Pholidolepis* sp., and *Proleptolepis* spp.

PHYLOGENETIC RELATIONSHIPS OF TELEOST SP. 1 AND OF THE VARASICHTHYID GROUP

TELEOST SP. 1

The caudal skeleton (text-Fig. 6; Pl. 8, Figs. A, C) of Teleost sp. 1 shows a unique combination of primitive features among teleosts with the presence of epaxial and hypaxial basal fulcra, fringing fulcra in both the dorsal and ventral lobes of the caudal fin, a reduced epaxial procurrent ray, a reduced hypaxial ray, four epurals, seven uroneurals, at least eight hypurals, and 20 principal caudal rays. However, Teleost sp. 1 also presents derived characters such as heavily ossified caudal autocentra which are fused to their neural and haemal arches and autocentra constricting the notochord.

In the phylogenetic hypothesis of teleostean relationships by Arratia (1991, Fig. 26), Teleost sp. 1 appeared as the sister group of *Domeykos*, immediately above the clade [*Leptolepis coryphaenoides* + *'Leptolepis' talbragarensis*]. That hypothesis was based on characters of the caudal vertebrae and caudal skeleton and fin. In the present analysis, the phylogenetic position of Teleost sp. 1 changed (text-Fig. 9: node A); it appeared as the plesiomorphic sister group of *Leptolepis coryphaenoides* plus more advanced teleosts. This is not surprising considering the unique combination of primitive features of the caudal skeleton characterizing Teleost sp. 1 (text-Fig. 6; Pl. 8, Figs. A, B; Arratia, 1991); however this phylogenetic arrangement is in conflict with the age of the fishes because Teleost sp. 1 is known from the Oxfordian, whereas *Leptolepis coryphaenoides* is known from the Liassic and *'Leptolepis' talbragarensis* from the Middle Jurassic (text-Fig. 9).

VARASICHTHYID GROUP

The name varasichthyid group is used here to include the following Late Jurassic fossil genera: *Domeykos, Varasichthys,* and *Protoclupea* from Chile and *Luisichthys* from Cuba. The monophyly of this group is supported by seven synapomorphies. These are: parasphenoid without teeth; retroarticular bone excluded from the joint facet for the quadrate; more than three postcleithra present; pectoral axillary process formed by bony elements; pelvic axillary process formed by an elongate bone; 20 principal caudal fin-rays; and lower lobe of the caudal fin with 10 principal fin-rays (a reversal). At present the author is studying new fossil fishes which may belong to the varasichthyid group; she will give a formal taxonomic status to the varasichthyid group after the new material from Chile and Cuba has been studied.

The taxonomic position and phylogenetic interpretations of *Domeykos, Varasichthys, Protoclupea,* and *Luisichthys* have changed in recent years. A short presentation of these taxonomic assignments and phylogenetic hypotheses is given below and contrasted with the present results.

Domeykos

Domeykos Arratia and Schultze (text-Fig. 1B; Pl. 1, Fig. A) is a monotypic genus only known from the Oxfordian of Quebrada del Profeta, off northern Chile. The original generic diagnosis is based mainly on a combination of primitive characters; the present cladistic study interprets several homoplastic features and probably one autapomorphy, *e.g.*, the complete separation of parietals by the supraoccipital bone (text-Fig. 3D) as characteristics of *Domeykos* (see table 3). Though *Domeykos* is a relatively well known form, it can be best identified by a combination of primitive features which separate it from other Jurassic forms.

Because of its combination of characters, *Domeykos* was considered as a Teleostei *incertae sedis* by Arratia and Schultze (1985). As explained above, *Domeykos* appeared in a position above the clade [*Leptolepis coryphaenoides* + *'Leptolepis' talbragarensis*] in a hypothesis of phylogenetic relationships among fossil teleosts by Arratia (1991) which was based on characters of the caudal region. *Domeykos* appeared as the plesiomorphic sister group of *Varasichthys* + [*Protoclupea* + *Luisichthys*] in the phylogenetic hypothesis by Arratia (in press a) and in the present paper, a hypothesis generated using characters from the head and whole body.

Varasichthys

Varasichthys Arratia (text-Fig. 1D; Pl. 4) is another monotypic genus only known from the Oxfordian of Quebrada del Profeta, off northern Chile; it is at present, one of the best known Late Jurassic teleosts. Its original generic diagnosis is based mainly on a combination of primitive characters and a few unique characters such as a long, slender parasphenoid extending posterior to the basioccipital, a small suborbital bone, and small, round cycloid scales on the ventral part of the body bearing a small peg. The presence of the suborbital bone and of the small scales bearing a peg were previously interpreted as primitive features by comparison with more primitive forms (Arratia, 1981, 1984). The present analysis interprets the suborbital of *Varasichthys* as being derived independently from the suborbital present in *Leptolepis coryphaenoides*. The condition of the scales is reinterpreted as uniquely derived among teleosts. In addition, the present cladistic analysis reveals a few autapomorphies of *Varasichthys* which are listed in table 3.

Arratia (1981) interpreted *Varasichthys* as a taxon that evolved in parallel to the European forms *Leptolepis coryphaenoides, Allothrissops, Tharsis,* and others. In Arratia's (1991) phylogenetic hypothesis, *Varasichthys* is placed above *Ascalabos*, in an unresolved position together with *Allothrissops* + [*Pachythrissops* + *Tharsis*]. Arratia's (in press a, and present paper) phylogenetic hypotheses suggest that *Varasichthys* is a member of a monophyletic clade, the varasichthyid group, and *Varasichthys* is the sister group of [*Protoclupea* + *Luisichthys*]. This clade, along with *Ascalabos*, is the sister group of another clade mainly composed of European forms (see text-Fig. 9).

Protoclupea

Protoclupea Arratia *et al.* (text-Fig. 1C; Pl. 3) is the only genus known from more than one species among the Late Jurassic teleosts of northern Chile. The original generic diagnosis and the amended diagnosis by Arratia and Schultze (1985) are based mainly on a combination of primitive characters; the present analysis interprets one homoplastic character (53[1]) as a feature of *Protoclupea* (Table 3). Arratia and Schultze (1985) interpreted the large nasal bone found in *Protoclupea* as a primitive feature by comparison with the large nasal bone in pholidophorids (Nybelin, 1966). This feature of *Protoclupea* may be considered as a reversal of the primitive condition present in the outgroup, it is an autapomorphy of *Protoclupea* within the varasichthyid group.

The taxonomic history of *Protoclupea* is complex. First it was considered to be a primitive clupeomorph by Arratia *et al.* (1975) based on certain similarities shared with *Clupea (Strangomera) bentincki*, a Recent clupeid from the southern Pacific Ocean. Further studies on new material showed that the combination of characters of *Protoclupea* does not correspond to those of the Clupeomorpha and the genus was considered to be another Teleostei *incertae sedis* by Arratia and Schultze (1985). In Arratia's (1991) phylogenetic hypothesis, based on the caudal vertebrae and caudal skeleton and fin, *Protoclupea* appeared above the clade [*Allothrissops* + [*Pachythrissops* + *Tharsis*]]. *Protoclupea* is interpreted as a member of the varasichthyid group by Arratia (in press a) and in the present study, and the sister group of the Cuban teleost *Luisichthys*.

Luisichthys

Luisichthys White (Pl. 2, Fig. A) is a monotypic genus only known from the Late Jurassic of Pinar del Río, in Cuba. Its original generic diagnosis is based on a combination of primitive characters; the amended diagnosis provided by Arratia and Schultze (1985) is based on a combination of primitive and advanced features such as the presence of a deep subtemporal fossa, a large foramen framed by the parietal, epioccipital, and exoccipital, a well developed prootic-intercalar bridge, and denticulated entopterygoid (text-Fig. 3E, F; Pl. 2, Figs. A-C). The present cladistic study interprets several homoplastic characters and one autapomorphy (the second hypural fused with 'first' ural centrum) as synapomorphies of *Luisichthys* (see table 3).

Luisichthys was considered first a leptolepiform by White (1942) and tentatively assigned to the Clupeomorpha by Arratia and Schultze (1985). This assignment to the Clupeomorpha was based on the fusion of the second hypural to the first ural centrum (text-Fig. 5C). Further studies have shown that this fusion evolved in parallel in *Luisichthys* and in the Division 2 of the Clupeomorpha (Arratia, in press a, b). In addition, *Luisichthys* lacks other clupeomorph synapomorphies proposed by Grande (1985, p. 252) such as presence of one or more scutes, each of a single element which crosses the ventral midline of the fish. Also lacking is the otophysic connection involving a diverticulum of the swimbladder that penetrates the exoccipital and extends into the prootic within the lateral wall of the braincase, forming ossified bullae in the prootic, and usually also in the pterotic; and the supratemporal commissure passing through parietals, or parietals and supraoccipital bones.

COMMENTS

Schaeffer and Patterson (1984, Table 3) listed *Varasichthys* and *Luisichthys* as belonging to the Leptolepidae *incertae sedis*, *Protoclupea* as ?Clupeocephala *incertae sedis*, and a *Pachythrissops* from the Oxfordian-Kimmeridgian of Chile somewhere between the Ichthyodectiformes and the Osteoglossomorpha. The placement of *Varasichthys* within the Leptolepidae is very curious because Patterson and Rosen (1977) and Schaeffer and Patterson (1984) acknowledged that there are no uniquely derived characters for the Leptolepidae *s.l.*, nor for the Leptolepidae *s.str.* (Nybelin, 1974); these families are based only on primitive characters. Members of the Leptolepidae *sensu* Nybelin (1974), *e.g.*, *Leptolepis*, *Tharsis*, *Ascalabos*, and *Leptolepides*, have different positions in the phylogenetic scheme of Patterson and Rosen (1977, Fig. 54) and Patterson (1977, Fig. 19), which demonstrates that the Leptolepidae *sensu* Nybelin (1974) is not a monophyletic group. Fishes such as *'Leptolepis' talbragarensis*, and *Ascalabos* were considered as Teleostei *incertae sedis* (more advanced than ichthyodectiformes) by Patterson and Rosen (1977), and *Leptolepides* was assigned to the Clupeocephala. According to Arratia (1991, in press a, present paper), *Leptolepis coryphaenoides*, *Tharsis*, *Ascalabos*, *Varasichthys*, *Luisichthys*, and *Leptolepides* have different phylogenetic positions among basal teleosts (text-Figs. 8, 9). Using the name Leptolepidae for taxa that are not related to *Leptolepis coryphaenoides* (which is the type-species of the genus and of the family) only creates confusion. *Domeykos*, *Varasichthys*, *Protoclupea*, and *Luisichthys* form a monophyletic group. *Pachythrissops* from the ?Oxfordian-Kimmeridgian from Chile is unknown to the author; therefore she considers it as an incorrect information by Schaeffer and Patterson (1984).

The order Ichthyodectiformes seems to be the other monophyletic group known from the Jurassic. As defined by Patterson and Rosen (1977, p. 115), the monophyly of the Ichthyodectiformes is supported by five synapomorphies. These are: ethmopalatine ossification in the floor of the nasal capsule articulating with the palatine; six or seven uroneurals, the first three or four extending anteroventrally to cover the entire lateral surface of the first, second, or third centra; teeth in a single series in the jaws; coracoid enlarged ventrally, meeting its fellow in a midventral coracoid symphysis; and anal fin long, falcate, opposed by a short remote dorsal fin. The presence of a single series of teeth on the jaws is also present in other Mesozoic teleosts. Yet this homoplastic character, in combination with the others, is diagnostic of ichthyodectiforms.

In Patterson and Rosen's (1977) phylogenetic hypothesis the ichthyodectiforms were placed between *Leptolepis coryphaenoides* (plesiomorphic sister group) and *Tharsis*. The present results do not corroborate such relationships (see text-Fig. 8). Ichthyodectiforms are interpreted here as teleosts more advanced than *Tharsis, Ascalabos,* and the varasichthyid group.

Members of the varasichthyid group share several synapomorphies listed above. *Domeykos*, the most generalized member, is difficult to diagnose on the basis of advanced characters alone; yet the pattern of the braincase of *Domeykos* (text-Fig. 3C, D) differs from that of *Varasichthys* (text-Fig. 3A, B), and *Luisichthys* (text-Fig. 3E-F) in the position of the parietals, the position of the prootic and its shape, the position of the foramina for nerves in the prootic, and the poorly developed prootic-intercalar bridge. The comparison of the braincase of *Varasichthys* and *Luisichthys* shows also strong differences between these two genera. Because of the extensive morphological differentiation of the braincase of each of these Jurassic genera, it is difficult to find synapomorphies, but it is easy to find autapomorphies of each genus. The comparison of these forms with other Jurassic teleosts is little help because the braincase of other teleosts (*e.g., Tharsis, Leptolepides,* and *Chongichthys*) also differ markledly from those in the varasichthyid group. Such comparisons also reveal that our understanding of the variability of the braincase and its evolutionary transformations among teleosts is inadequate. The differences found in the braincase, pectoral girdle, and other structures in the varasichthyid group and in other teleosts such as *Chongichthys* and *Antofagastaichthys* are of such magnitude that these Oxfordian forms must have diversified at least as far back as the Middle Jurassic. Unfortunately, a Chilean fossil fish record for the period between the Early Sinemurian and the Oxfordian is presently lacking.

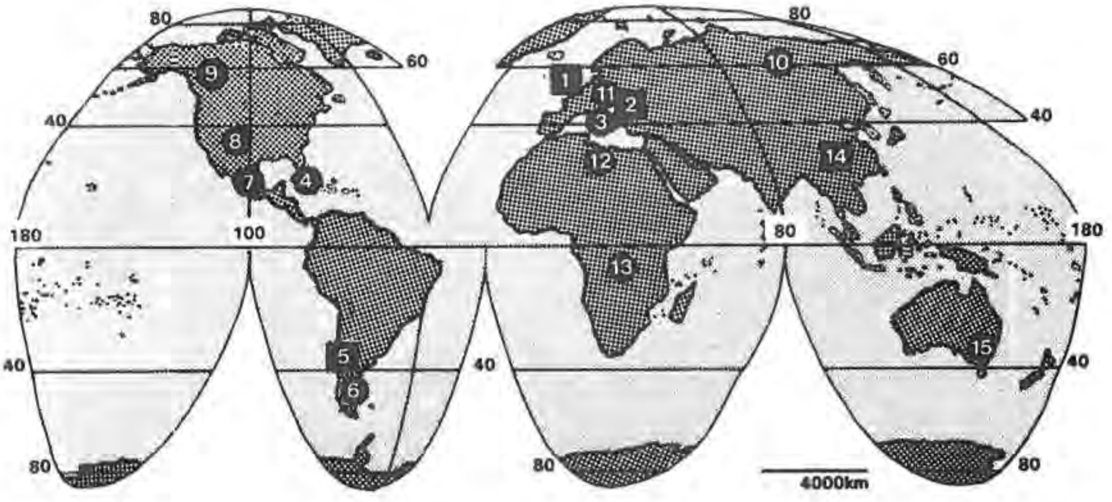
One interesting aspect is the presence of several homoplastic and a few unique derived features which are autapomorphies of members of the varasichthyid group. The combination of primitive characters clearly separates Teleost sp. 1 and *Domeykos* from other Jurassic forms. This illustrates the difficulties in defining basal forms on uniquely derived characters only, and confirms Ax's (1987) statement that some primitive features can be diagnostic characters as well.

PALEOGEOGRAPHIC RELATIONSHIPS OF THE VARASICHTHYID GROUP

About 20 fossil fish localities are known from the Jurassic (Schaeffer and Patterson, 1984, tables 3, 4; Arratia, in press b); most are marine deposits. However, numerous important non-marine deposits are known from China (Chang and Jin, in press), Argentina, and one from Australia. Presently, it is uncertain whether the age of the lacustrine deposits from China (and Siberia) is Late Jurassic or Early Cretaceous (Chang and Jin, in press).

About 15 important fossiliferous fish localities (text-Fig. 10) are recorded from the Late Jurassic; among them, the best known localities and the best known assemblages are those from Great Britain, Germany, and France. Outside Europe, only a few localities compare in fish diversity with those in Europe. Examples are Quebrada del Profeta in Cordillera de Domeyko, northern Chile, and Pinar del Río, in Cuba.

Information on the different Late Jurassic localities and their fish fauna is so diverse that comparisons between them have to be done with great precaution. The present study employs the cladistic vicariance method of biogeographic analysis, that 'is a rigorous two-phase method of finding relationships based on the relative relationships of taxa endemic to the areas being analyzed' (Grande and Micklich, 1993, p. 245).

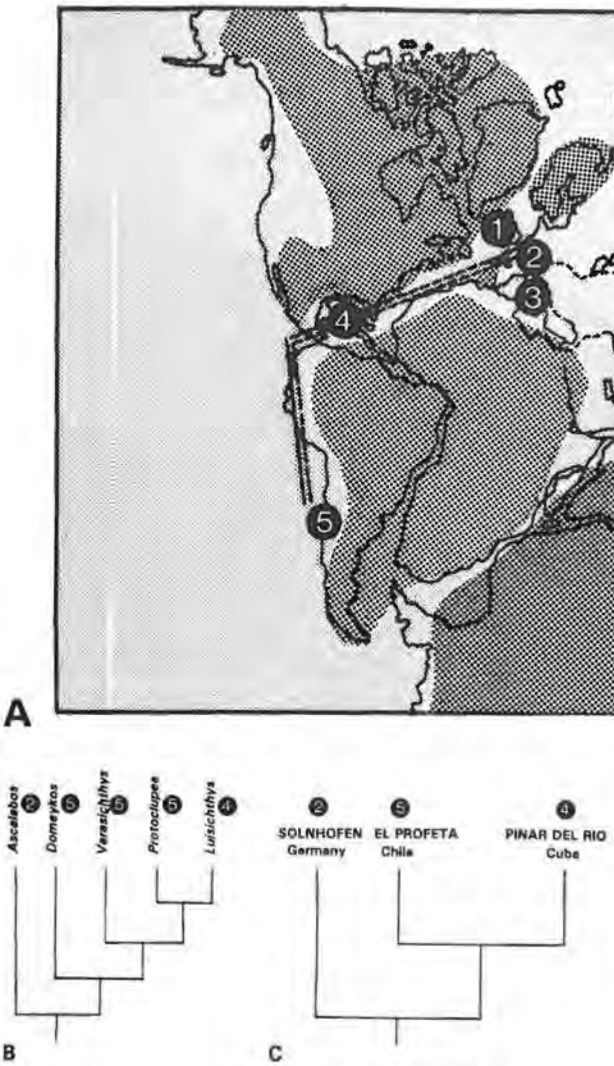


Text-FIG. 10. Important Middle and Late Jurassic localities with teleostean fishes. 1- Great Britain (*e.g.*, Dorset); 2- Germany (*e.g.*, Solnhofen, Eichstätt, Kelheim); 3- Italy; 4- Cuba (*e.g.*, Pinar del Rio, Vinales); 5- Northern Chile (*e.g.*, Quebrada del Profeta in Cordillera de Domeyko); 6- Argentina (*e.g.*, Cerro Côndor; non-marine deposits); 7- Mexico (*e.g.*, Nueva León); 8- United States of America (*e.g.*, Colorado, New Mexico, Wyoming); 9- Canada; 10- Siberia; 11- France (*e.g.*, Cerin); 12- North Africa (*e.g.*, Algeria, Morocco, and Tunisia); 13- Trans-Erythrean Trough (parts of Arabia, India, East Africa, and Madagascar); 14- China (*e.g.*, northern China; non-marine deposits). The age, Late Jurassic to/or Early Cretaceous is uncertain (Chang and Jin, in press);15- Australia (*e.g.*, Talbragar, New South Wales; non-marine deposit).

The first step of such an analysis is to generate a hypothesis of phylogenetic relationships of organisms, *e.g.*, fishes, based on synapomorphies. Such a hypothesis is provided above (text-Fig. 8). The second step is to transform the phylogenetic hypothesis (text-Fig. 11B) into an area relationship. For this purpose the author overlaps the geographic area (text-Fig. 11A) of the taxa onto the cladogram (text-Fig. 11C).

In the phylogenetic hypothesis (text-Fig. 11B) *Domeykos* is the sister group of *Varasichthys* + [*Protoclupea* + *Luisichthys*]. *Domeykos*, *Varasichthys*, and *Protoclupea* are known from Quebrada del Profeta, northern Chile (text-Fig. 11A, C: locality 5), whereas *Luisichthys* is known from Pinar del Rio, Cuba (text-Fig. 11, A, C: locality 4). Following the phylogenetic relationships of the genera, both areas are interpreted as sister areas. Since *Ascalabos* from southern Germany (text-Fig. 11A, C: locality 2) is the sister group of the varasichthyid group, southern Bavaria may be interpreted as the sister area of southern South America (Chile) plus Central America (Cuba). Connection of these areas through the Tethys seaway seems probable. This is evidence for a connection by the Tethys seaway between fish faunas of Europe, Central America, and South America during the Late Jurassic. A marine corridor (Hispanic or Caribbean corridor) has been postulated between the Western Tethys (European Tethys) and the East Pacific (west of South America) during the Late Jurassic (*e.g.*, Hallam, 1977, 1983); however new marine corridors arose as a consequence of the fragmentation of Laurasia and Gondwana (Hallam, 1983; Scotese, 1987; Riccardi, 1991). Late Jurassic marine vertebrates which could have used the Hispanic corridor include fishes (see above) and crocodiles such as a new crocodile found recently in the Oxfordian of Cuba (Iturrialde and Norell, 1992) and *Metriorhynchus* and *Geosaurus* which have been reported from the Tithonian of South America and Europe (see Gasparini, 1992).

The phylogenetic hypothesis (text-Fig. 9) shows that at least two clades evolved in both hemispheres during the Late Jurassic. The clade including [*Anaethalion* + [*Leptolepides* + [*Lycoptera* + [*Orthogonikleithrus* + Teleost n. gen.]]]] has evolved in the north, in Europe and Asia, whereas the varasichthyid group evolved in Central America and the Pacific side of South America. Whether these two clades are natural assemblages mainly restricted to northern and southern continents should be tested when additional Late Jurassic fossil taxa, now under study, are known and their phylogenetic relationships examined.



Text-FIG. 11. A- distribution of land (dark grey) and sea (light grey; from Schaeffer and Patterson, 1984) with location of Late Jurassic fish localities (indicated by black circles). 1- Great Britain; 2- Germany; 3- Italy; 4- Cuba, 5- Chile. B- scheme of phylogenetic relationships of *Ascalabos* and the varasichthyid group. C- simplified area cladogram of Solnhofen, Quebrada del Profeta, and Pinar del Río.

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PLATES 1-8

PLATE 1

Figures

Some Jurassic teleostean fishes in lateral view. Arrow points anteriorly.

A *Domeykos profetaensis*, Late Jurassic, Oxfordian, Quebrada del Profeta, Chile (specimen LBUCH 12-260972a).

B *Domeykos profetaensis*, latex cast of head and pectoral girdle and fin (specimen LBUCH 12-260972b) to show the vomerine dentition, details of the preopercular sensory canal, and parts of the branchial arches.

PLATE 1

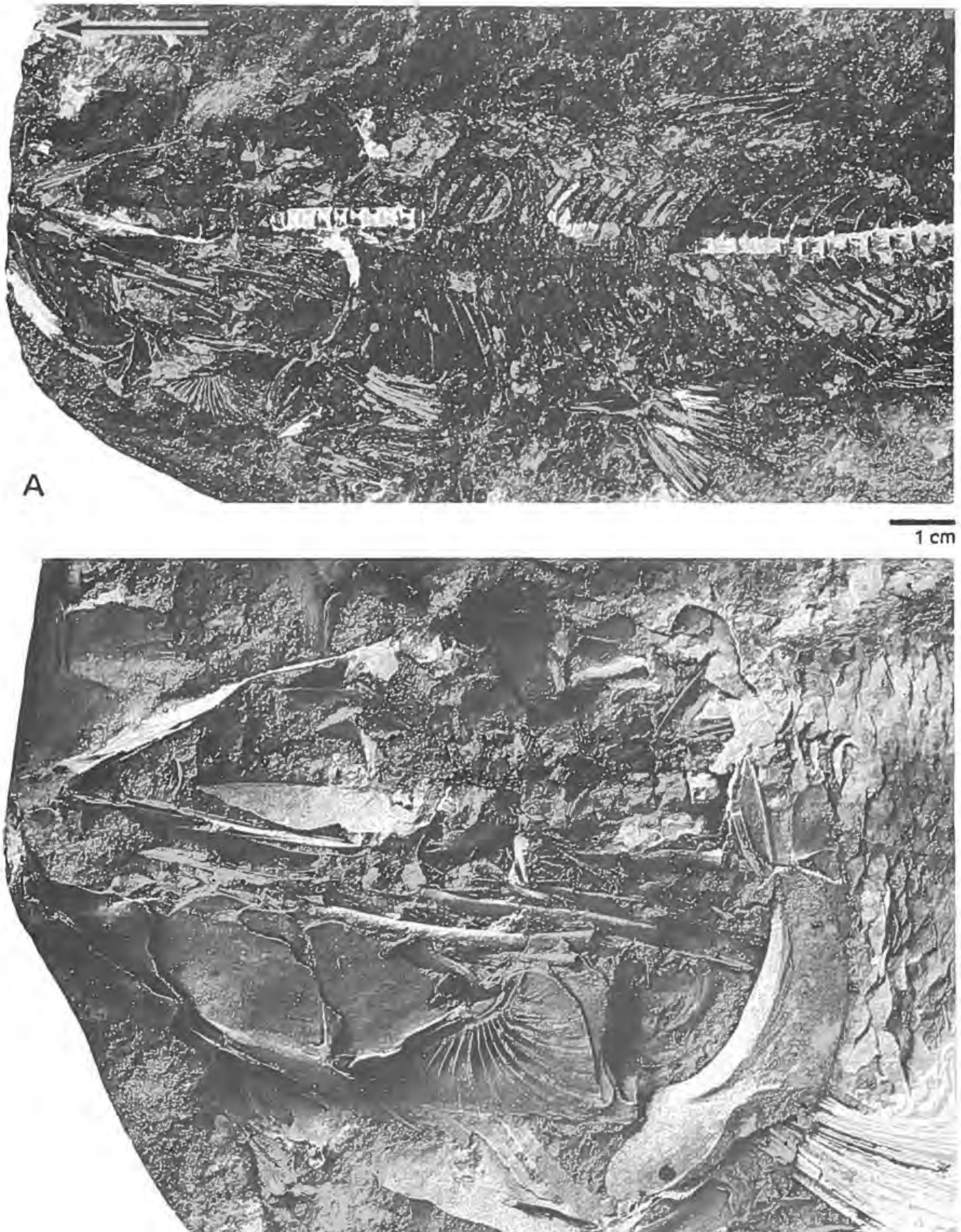

PLATE 2

Figures

Luisichthys vinalensis, Late Jurassic, Pinar del Río, Cuba (acid-prepared specimen USNM 18656; dusted with NH_4Cl).

A Head, pectoral girdle, and anterior abdominal vertebrae and associated elements. Arrow points to the ?posttemporal fossa.

B Neurocranium in posterior view. Arrow points to the ?post temporal fossa. **B**, **C**, same scale.

C Neurocranium in lateral view. Arrows point to the entopterygoid.

PLATE 2

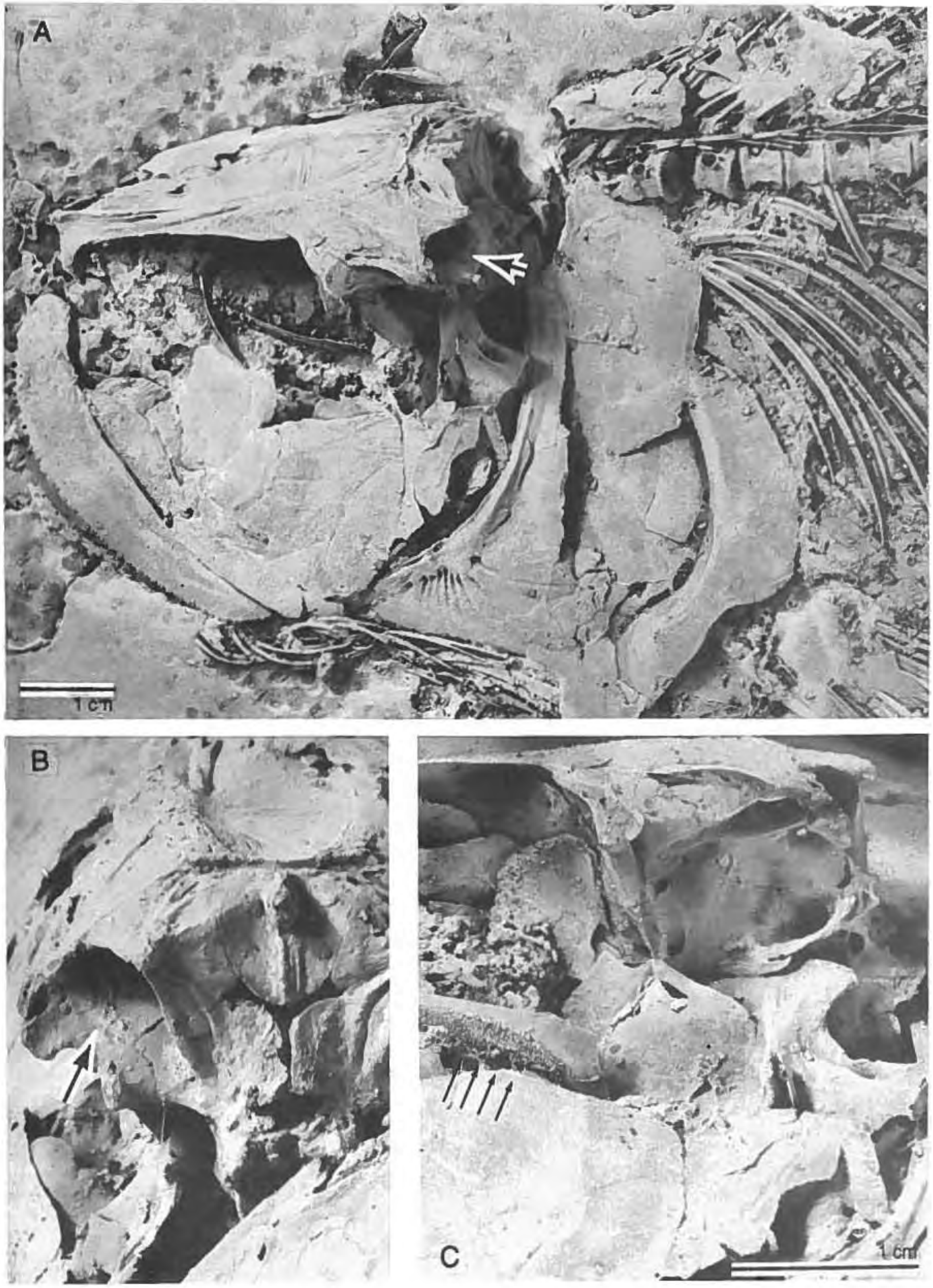

PLATE 3

Protoclupea chilensis, Late Jurassic, Oxfordian, Quebrada del Profeta, Chile (specimen DG-R 396).

PLATE 3

PLATE 4

Varasichthys ariasi, Late Jurassic, Oxfordian, Quebrada del Profeta, Chile (specimen LBUCH 16-260977a).

PLATE 4

PLATE 5

Figures

Varasichthys ariasi (specimen LBUCH 16-260977b). Large arrows point anteriorly.

A	Neurocranium in lateral view. Small arrow points to the posterior end of the parasphenoid; boc, basioccipital bone.
B	Cranial roof (specimen LBUCH 012378a, dusted with NH_4Cl). Note the extension of the basioccipital bone below the parietals.

PLATE 5

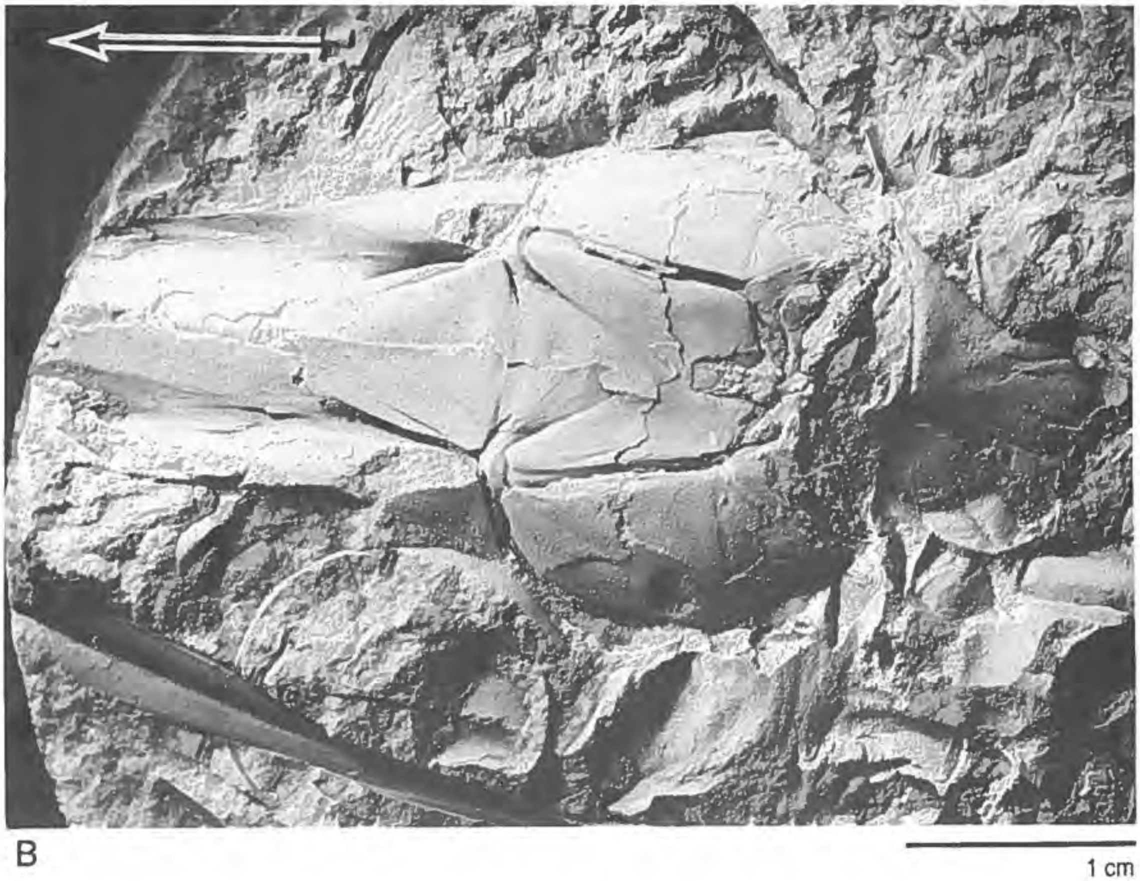

PLATE 6

Figures

Vertebral column in some members of the varasichthyid group.

A	*Domeykos profetaensis* (acid-prepared specimen LBUCH 260972a).
B	*Varasichthys ariasi* (specimen LBUCH 1-270a). The arrow points to the hourglass-like chordacentrum which is observed in the region with the autocentrum removed.
C	*Luisichthys vinalensis*. Caudal vertebrae in lateral view (specimen NMNH 18429 under alcohol).
D	*Luisichthys vinalensis*. Enlargement of a caudal vertebrae in lateral view (specimen NMNH 18429, dusted with NH_4Cl).

PLATE 6

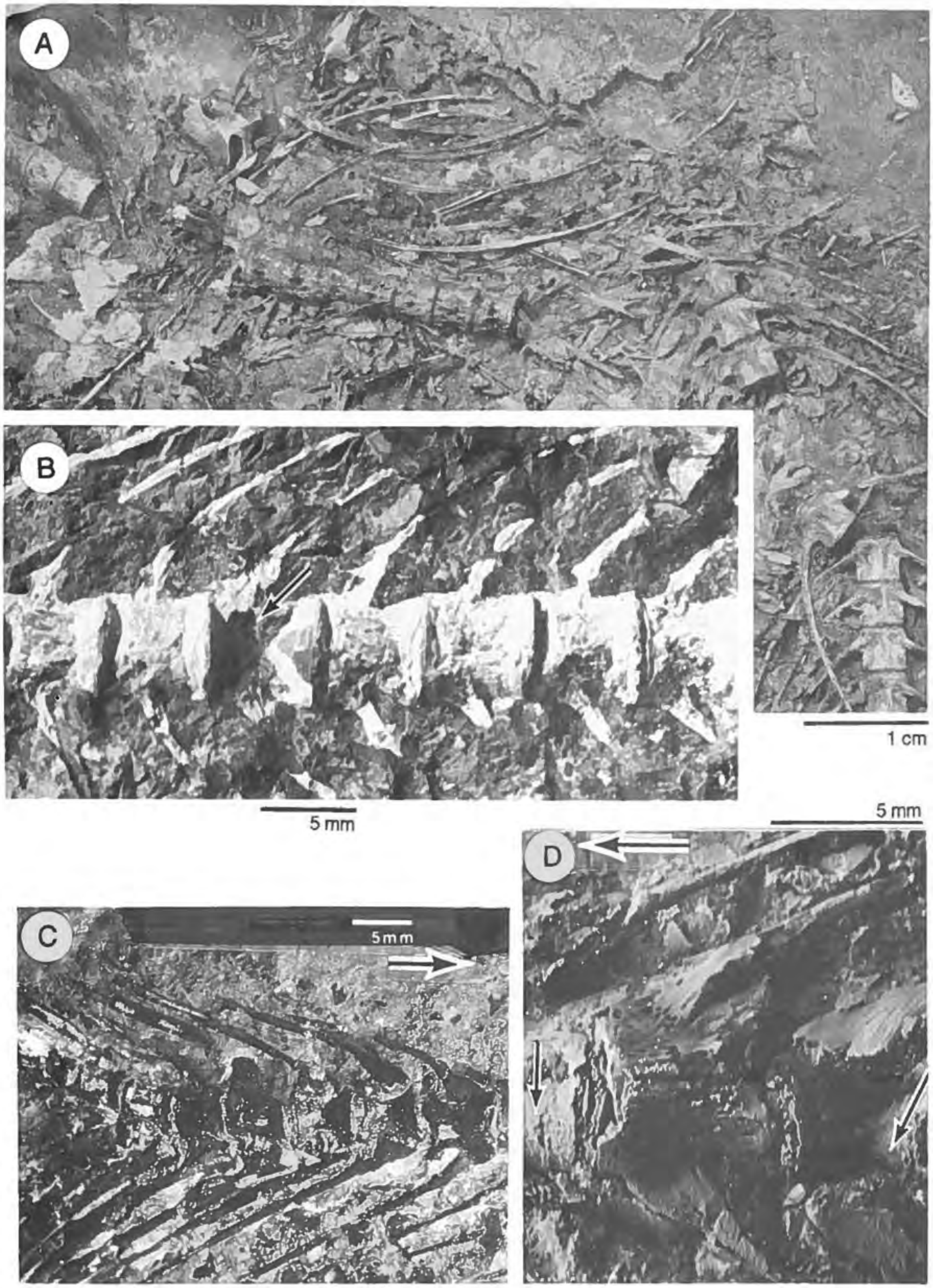

PLATE 7

Figures

Vertebral centra in certain Jurassic teleosts.

A	Caudal region of *Domeykos profetaensis* (specimen LBUCH 012778a). Arrow points anteriorly.
B, C	SEM of vertebral caudal centra of *Leptolepis coryphaenoides* (specimens KUVP 91012) showing fusion of the arches and the autocentrum (40x and 68x, respectively).
D	Cross section of a midcaudal vertebrae of *Domeykos profetaensis* showing the fusion of the arches and the autocentrum (KUVP 97044). Small arrows point to cavities for adipose tissue.

PLATE 7

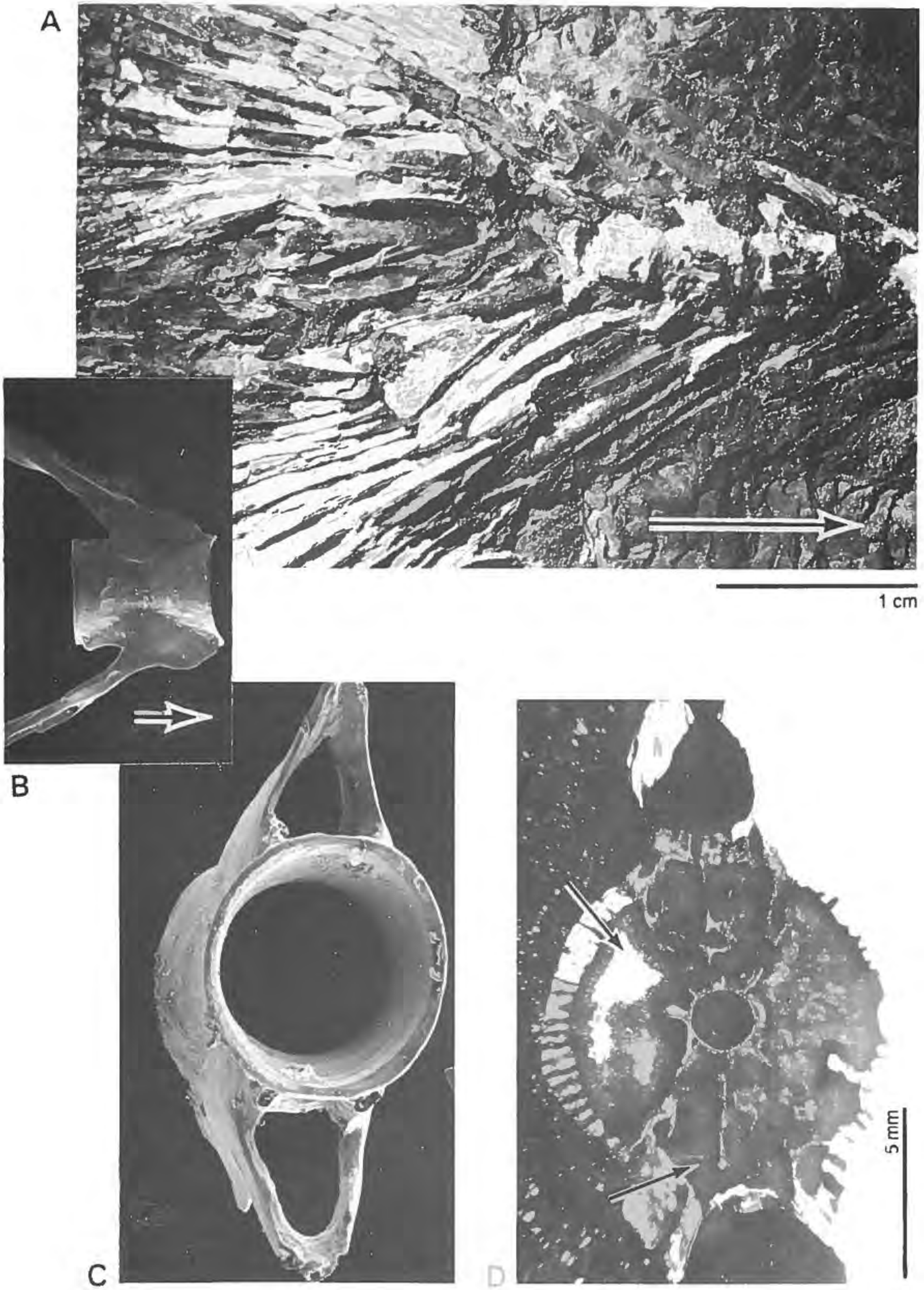

PLATE 8

Figures

Teleost sp. 1 *sensu* Arratia (1991). Caudal skeleton in lateral view (specimen LBUCH 1987b).

A Caudal skeleton and fin. Arrow points anteriorly.

B Enlargement of a section of the rays in the ventral lobe of the caudal fin of the specimen in figure A. Arrows point to the reduced hypaxial ray.

PLATE 8