

LATE JURASSIC TELEOSTS (ACTINOPTERYGII, PISCES) FROM NORTHERN CHILE AND CUBA

OBER-JURASSISCHE TELEOSTEER (ACTINOPTERYGII, PISCES) AUS N-CHILE UND KUBA

BY

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With 5 plates, 23 text-figures and 3 tables

Zusammenfassung

Zwei Teleosteer-Gattungen, *Protoclupea* ARRATIA et. al. 1975 b und *Domeykos* n. gen., mit drei Arten (*P. chilensis* ARRATIA et. al. 1975 b, *P. atacamensis* n. sp., *D. profetaensis* n. sp.) werden aus dem Oberen Jura (Oxfordium) der Cordillera de Domeyko in Nordchile beschrieben. *Luisichthys vinalesensis* WHITE 1942 aus dem Oberen Jura (Oxfordium) von Cuba ist neu untersucht.

Schlüsselwörter: Jura - Chile - Cuba - Teleostei - Morphologie.

Summary

Two teleostean genera, *Protoclupea* ARRATIA et al. 1975 and *Domeykos* n. gen., and three species (*P. chilensis* ARRATIA et al. 1975 b, *P. atacamensis* n. sp., *D. profetaensis* n. sp.) are described from the Oxfordian, Late Jurassic, of the Cordillera de Domeyko. *Luisichthys vinalesensis* WHITE 1942 from the Oxfordian, Late Jurassic, of Cuba is reinvestigated.

Key words: Jurassic - Chile - Cuba - Teleostei - morphology.

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Introduction

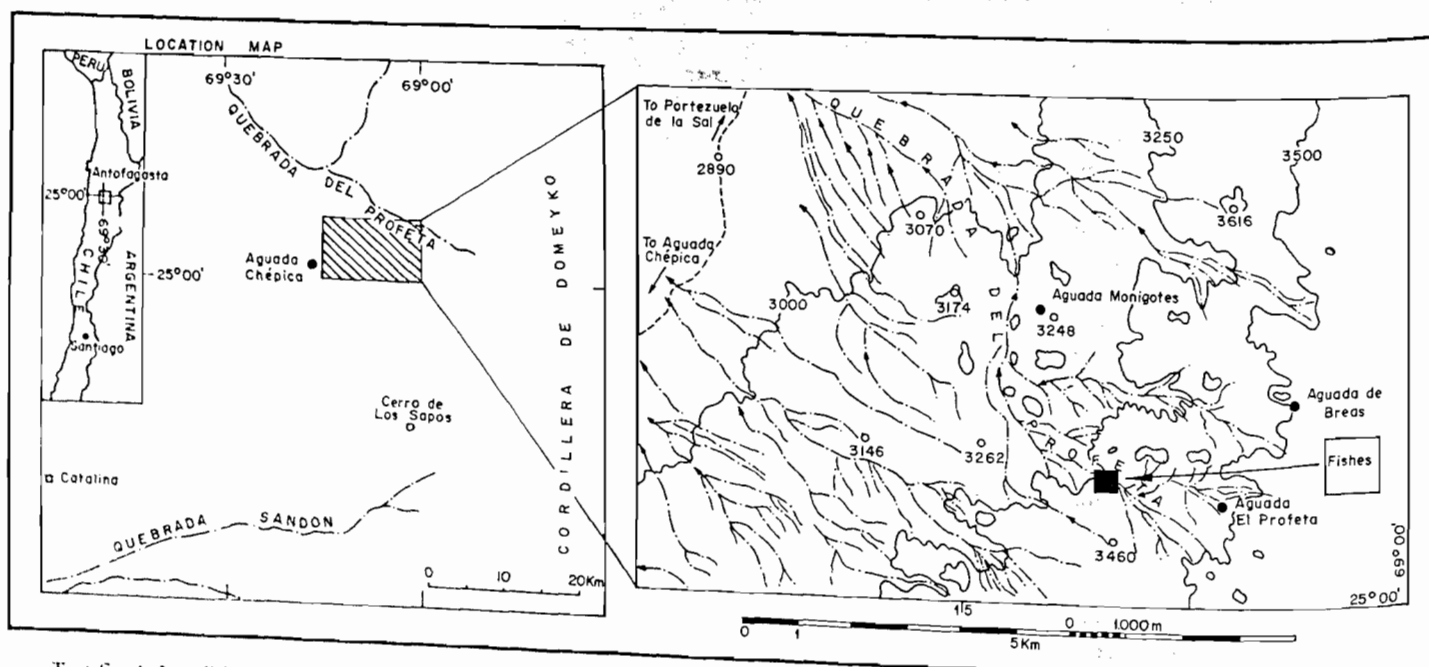
In recent years, many fossil teleostean fishes have been found at different localities in the Atacama desert in the north of Chile. The most diverse and well preserved teleosts have been discovered in Late Jurassic rocks at Aguada El Profeta, Cordillera de Domeyko, southeast of Antofagasta (text-fig. 1). Part of this material has been studied, and the following teleost species have been described: "*Leptolepis*" *opercularis* ARRATIA et al. (1975 a), *Protoclupea chilensis* ARRATIA et al. (1975 b), *Varasichthys ariasi* ARRATIA (1981), and *Chongichthys dentatus* ARRATIA (1982). Two additional teleosts will be described in this paper (*Protoclupea atacamensis* n. sp., and *Domeykos profetaensis* n. gen. and sp.). Soft tissue (muscles, vessels, swimbladder, melanophores, etc.) is preserved three-dimensionally in these fossils.

Protoclupea chilensis was described by ARRATIA et al. (1975 b) from unprepared material, and placed within the family Clupeidae as a preliminary approach. Further study of the holotype revealed additional teleostean features. At the same locality, there are other specimens with scales like those of *P. chilensis*; these belong to a new species of *Protoclupea* and to a new genus. *Leptolepides sprattiformis* (BLAINVILLE) from the Kimmeridgian of Bavaria and Cerin shares this type of scales (SCHULTZE 1966: fig. 40b) with the teleosts from Northern Chile. *Luisichthys* WHITE (1942), a Cuban Jurassic fish, has this feature, too. Therefore it is also included in this paper. Its revision is limited here to cranium, vertebrae and caudal skeleton.

Material and Methods

The material is deposited in the collections of the Departamento de Geología, Universidad de Chile, Santiago (R), of the Servicio de Geología y Minas, Santiago, Chile (I.I.G.), Laboratorio de Biología, Universidad de Chile, Santiago-Sur (LBUCH); Division of Ichthyology (KU) and Division of Vertebrate Paleontology (KUPV) of the Museum of Natural History, University of Kansas, and Division of Vertebrate Paleontology, National Museum of Natural History (U.S.M.N.), Smithsonian Institution, Washington, D. C.

The fossil Chilean material was collected along the one km north-south outcrop of one horizon within the Oxfordian rocks (HILLEBRANDT 1970, CHONG 1977) north of Quebrada El Profeta about 1 km east of Aguada Chica, Sierra de Varas, Cordillera de Domeyko, SE Antofagasta, Northern Chile at 24° 50' South, 69° 12' West (text-fig. 1). The holotypes described here were collected by ERNESTO PEREZ, Servicio de Geología y Minas, Santiago, Chile, (*Protoclupea chilensis*), by one of the authors, HANS-PETER SCHULTZE (*Protoclupea atacamensis* n. sp.), and by



Text-fig. 1. Localities of Jurassic fishes in Domeyko Range, northern Chile (provided by G. CHONG).

GUILLERMO CHONG, Universidad del Norte, Antofagasta (*Domeykos profetaensis* n. gen. et sp.). Paratypes and additional material were collected by the authors, and GUILLERMO CHONG, ARTURO QUINZIO and LUIS SANTANDER (Universidad del Norte, Antofagasta, Chile) in 1978. The Cuban fossil material described here was collected by D. H. DUNKLE and J. GALLARDO (March 1950) at different localities in the Province of Pinar del Río (see localities of *Luisichthys*), Cuba.

Some fossil Chilean material was prepared by the transfer technique (TOOMBS & RIXON 1959). Specimens of *Luisichthys* were acid prepared by Dr. D. H. DUNKLE. Latex peels were made by O. BONNER, Museum of Natural History, Lawrence, Kansas. Peels of scales of different regions of the body from all specimens were done following the technique of SCHULTZE (1966).

The number of Jurassic specimens studied is listed directly after the specific diagnosis of each species.

Some of the cleared and stained extant fishes used for comparisons were prepared using a modified version of the technique of DINGERKUS & UHLER (1977) to permit examination of both cartilage and bone. Illustrations were prepared by one of the authors, G. ARRATIA, by use of a WILD stereo-microscope equipped with a camera lucida; details were checked by using LEITZ and OLYMPUS microscopes with phase contrast of high resolution power.

Abbreviations used in Text-Figures

Ao	antorbital bone	Gp	gular plate	PH	parhypural
An	angular bone	H1-7	hypurals 1-7	p. i. b.	prootic-intercalar bridge
ar	articular bone	hs	haemal spine and arch	poc	preopercular sensory canal
arc	articular cavity for rib bone	Io1-5	infraorbitals 1-5 numbered from front to back	Pop	preopercular bone
art. i	articular facet for intercalar			PPH	processes of heads of upper hypurals
asp	autosphenotic bone	ioc	infraorbital sensory canal	pro	prootic bone
bo	basioccipital bone	Iop	interopercular bone	Psc1 1-2	postsupracleithra 1-2
BR 9	branched caudal fin-rays of upper lobe numbered from top downwards	it	intercalar bone	Psp	parasphenoid
		ll	main lateral line	pt	pterotic bone
cb	ceratobranchial	ln	"leptolepid" notch	PU 1	preural centra 1
ch. t	temporal chamber	mlc	main lateral line canal	q	quadrate
cfr	caudal fin rays	mo	membranous outgrowth of the first uroneural	rar	retroarticular bone
Cl	cleithrum	mplg	middle pit-line groove	ri	ribs
csc	caudal scute	msc	mandibular sensory canal	s	symplectic
D	dentary bone	mso	posterior opening of mandibular sensory canal	Scl	supracleithrum
drf	dorsal fin rays			Sm 1-2	supramaxillae 1-2
Dsp	dermosphenotic	Mx	maxillary bone	so	supraoccipital bone
Dt	dermethmoid	Na	nasal bone	soc	supraorbital sensory canal
E1-3	epurals 1-3	NPU 1	neural arch or spine of numbered preural centrum	Sop	subopercular bone
epb	epineural bone fused to the neural arch	ns	neural spine and arch	tc	temporal sensory canal
eo	epiotic bone	NU 1	neural arch of ural centrum 1	U 1-2	ural centra 1-2
Esc	extrascapular bone			UN 1-5	uroneurals 1-5
exo	exoccipital bone	Op	opercular bone	VII	foramen for hyomandibular trunk of facial nerve
F	frontal bone	Pa	parietal bone	IX	foramen for glossopharyngeal nerve
f.m	foramen magnum	parp	postarticular process of angular bone	X	foramen for vagus nerve
f. oa	foramen for orbital artery	Pcl 1-6	postcleithra 1-6		
f. p. j.	posterior opening of pars jugularis				

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Dr. J. CORVALÁN, Departamento de Geología, Universidad de Chile, Santiago, Chile, and Dr. N. HOTTON III and Mr. R. PURDY, National Museum of Natural History, Washington, D.C., U.S.A., were so kind to permit study of material in their care. The research has been done in the Division of vertebrate paleontology, Museum of Natural History, University of Kansas, Lawrence, Kansas. The authors are grateful for photographic help to Dr. J. CHORN, and for preparatory help to Mr. O. BONNER, both at the Museum of Natural History, Lawrence, Kansas.

The manuscript has been reviewed by Dr. C. PATTERSON, British Museum (Natural History), London, England for which we thank him very much. We thank cordially for the stylistic corrections by Dr. C. PATTERSON, London, and Mr. M. GOTTFRIED, Museum of Natural History, Lawrence, Kansas. We like to express our gratitude to Mrs. M. NOLTKÄMPER, Geologisch-Paläontologisches Institut und Museum, Göttingen, who typed the last part of the manuscript.

Systematic Paleontology

Subdivision Teleostei incertae sedis

Family indet.

Protoclupea ARRATIA et al. 1975 b

Diagnosis (emended): Elongate teleosts. Cranial roof without crests; parietals meeting in midline. Long and relatively deep infraorbitals; suborbital absent. Cephalic sensory canals enclosed by bone. Lower jaw with high coronoid process and "leptolepid" notch, without retroarticular, with elongate postarticular process, mandibular sensory canal opens medially. Ventroposterior angle of preopercle projecting posteriorly; preopercle with numerous elongate sensory tubules. Posttemporal small, covered by extrascapula. Lateral line on supracleithrum with two tubules and emerging in the posteroventral border of the large supracleithrum. Four to five postcleithra; postcleithrum 4 large, with crenulate posterior border. Elongate pelvic axillary process. Anal fin begins below last dorsal rays. Base of dorsal, anal and caudal fins covered by large oval scales, large oblong scales partially covering caudal fin rays and last dorsal rays. Autogenous neural and haemal arches. Five uroneurals inclined toward horizontal; first two uroneurals extending forward to PU 3-PU 4; three epurals. Scales with transversely oriented lines in the middle field; posterior field of scales smooth.

Type-species: *Protoclupea chilensis* ARRATIA et al. 1975 b

Text-fig. 2, 3 A-C, 4 A, 5 A, 6 A, 7 A, B, 8 A-C, 21 D, pl. 1, fig. A, B

Protoclupea chilensis ARRATIA et al. 1975 b: 10-11.

Protoclupea - CHONG 1977: 389.

Protoclupea chilensis ARRATIA et al. - GASPARINI 1979: 19, 29.

Protoclupea chilensis ARRATIA et al. (1975) - ARRATIA 1981: 108, 124.

Diagnosis: *Protoclupea* of about 15 cm standard length. Infraorbital 1 shorter than infraorbital 2; infraorbital sensory canal with short tubules. Articular excluded from postarticular process. Posteroventral angle of preopercle projecting caudally, forming a triangular posteroventral angle. Elongate triangular extrascapula and postcleithrum 4. Dorsal fin deeper than long. 44-46 vertebrae. Rays: more than 16 pectoral; 11 to 14 pelvic; about 14 principal dorsal rays plus 4 small unbranched rays; 19 principal anal rays plus 3 or 4 small unbranched rays; 37 caudal. Without scales on maxilla and infraorbital 1. Dorsal fin divided into two sets of rays by scale row.

Holotype: Part (R-396) and counterpart (R-396 A), nearly complete specimen, anterior end of head and posterior end of caudal rays missing; muscles preserved.

Paratypes: Part and counterpart (R-397 A): incomplete pectoral and caudal fins, poorly preserved. Specimen I.I.G. 2220173: posterior part of head and trunk, caudal fin missing, poorly preserved. Incomplete specimen I.I.G. 2011, missing anterior part of head and caudal fin, good preservation. Specimen I.I.G. 220173 a and its counterpart I.I.G. 220173 b cited as paratype in ARRATIA et al. (1975 b) does not belong to *Protoclupea chilensis* because the scales do not have the transversely oriented lines between the circuli in the middle field.

Table 1. Body relationships of *Protoclupea chilensis*, *Protoclupea atacamensis* n. sp. and *Domeykos profetaensis* n. gen. et sp.

	<i>Protoclupea chilensis</i>	<i>Protoclupea atacamensis</i>	<i>Domeykos profetaensis</i>
Standard length/head length	2.6–3.8	3.2	3
Standard length/predorsal length	1.7–1.9	1.8	1.8
Standard length/prepelvic length	1.6–1.9	1.8	1.7
Standard length/preanal length	1.3–1.4	–	1.2
Predorsal length/head length	1.8	1.8	1.7
Head length/head depth	1.4	1.5	1.4
Body depth/head depth	1.3	1.2	1.6
Head length/standard length (%)	25–39	31	33
Head length/predorsal length (%)	55	52	57
Head depth/Head length (%)	69	67	74
Peduncle depth/body depth (%)	48–49	–	–
Predorsal length/standard length (%)	54–60	57	56
Prepelvic length/standard length (%)	54–62	58	57
Preanal length/standard length (%)	73–80	85	–

Additional material: Part (KUV 71205 a) and counterpart (KUV 71205 b): nearly complete specimen missing anterior part of head and posterior part of caudal rays, trunk covered with muscles, good preservation. Part (LBUCH 3592 a) and counterpart (LBUCH 3592 B): displaced bones. Part (LBUCH 190179 a) and counterpart (LBUCH 190179 b): trunk including squamation and vertebrae, pelvic, dorsal, anal and caudal fins incompletely preserved.

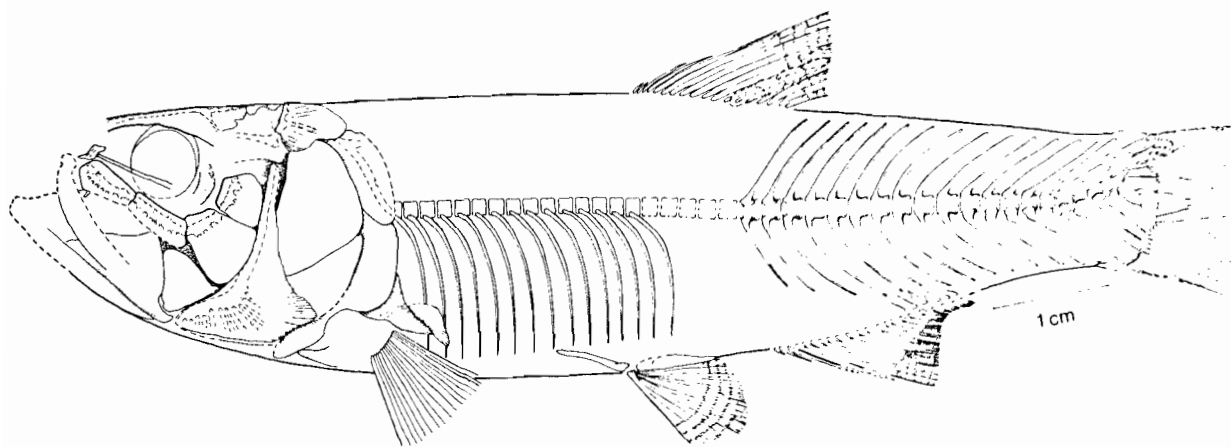
Locality and geological time: North of Quebrada El Profeta, about 1 km east of Aguada Chica, Sierra de Varas, Cordillera de Domeyko, southeast of Antofagasta, northern Chile at 24° 59'S, 69° 12'W; Oxfordian, Late Jurassic (text-fig. 1).

Description: The fishes are elongate (text-fig. 2; pl. 1, fig. B) and reach about 15 cm standard length. The head is 25% to 39% of standard length (other body proportions in table 1); the low values belong to the holotype, a specimen of about 13 cm total length.

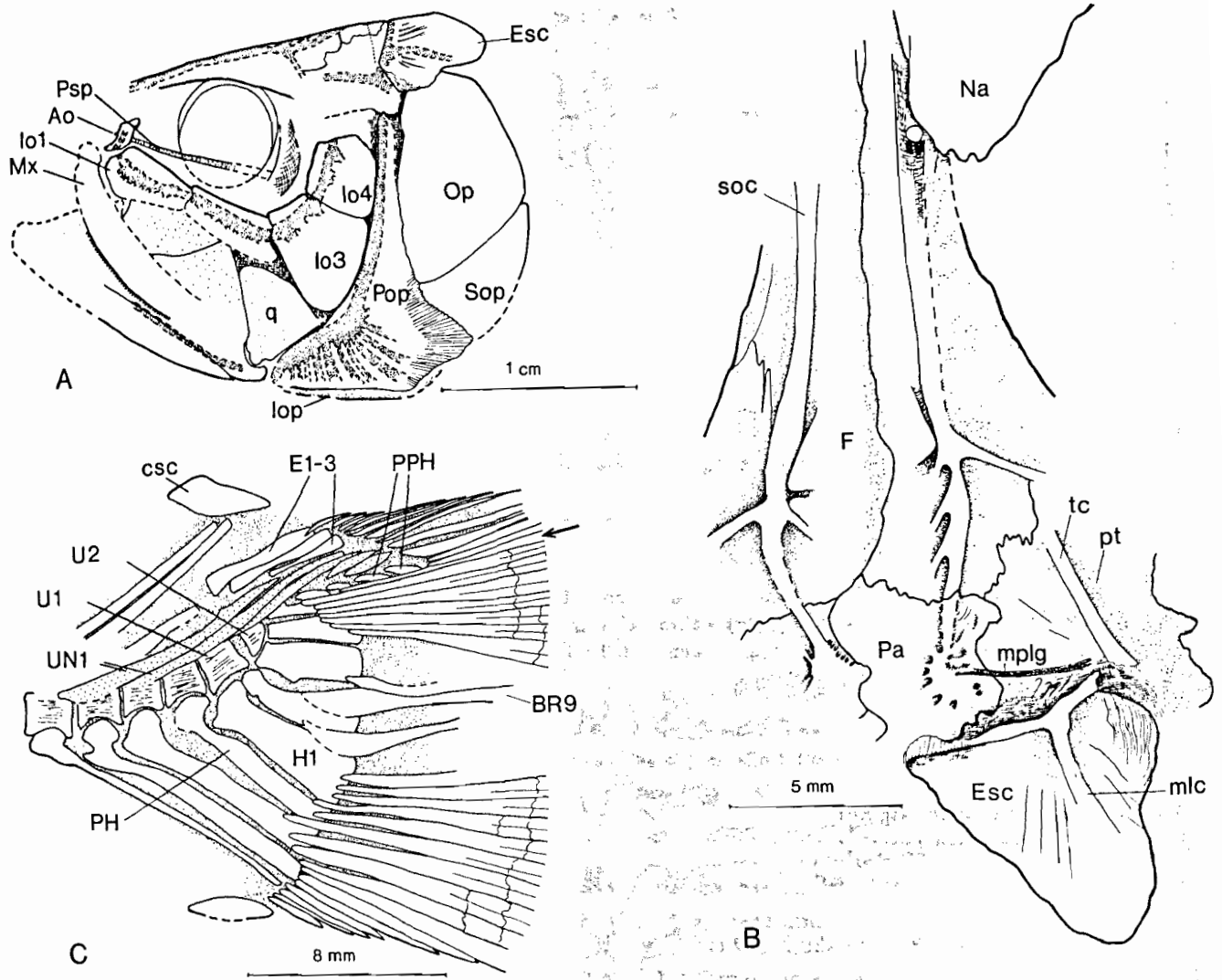
Skull roof (text-fig. 3 B): The skull roof is wide and flat. The bones are smooth and show no trace of ganoin. The anterior end of the cranial roof is not preserved. The anterior part of each frontal is partially overlapped by a broad flat bone that we interpret as the nasal. Most of the skull roof is formed by the frontals.

No dermosphenotic was found in any specimen; possibly *Protoclupea* had a small dermosphenotic contrary to the long bone present in leptolepids and Cretaceous clupeomorphs.

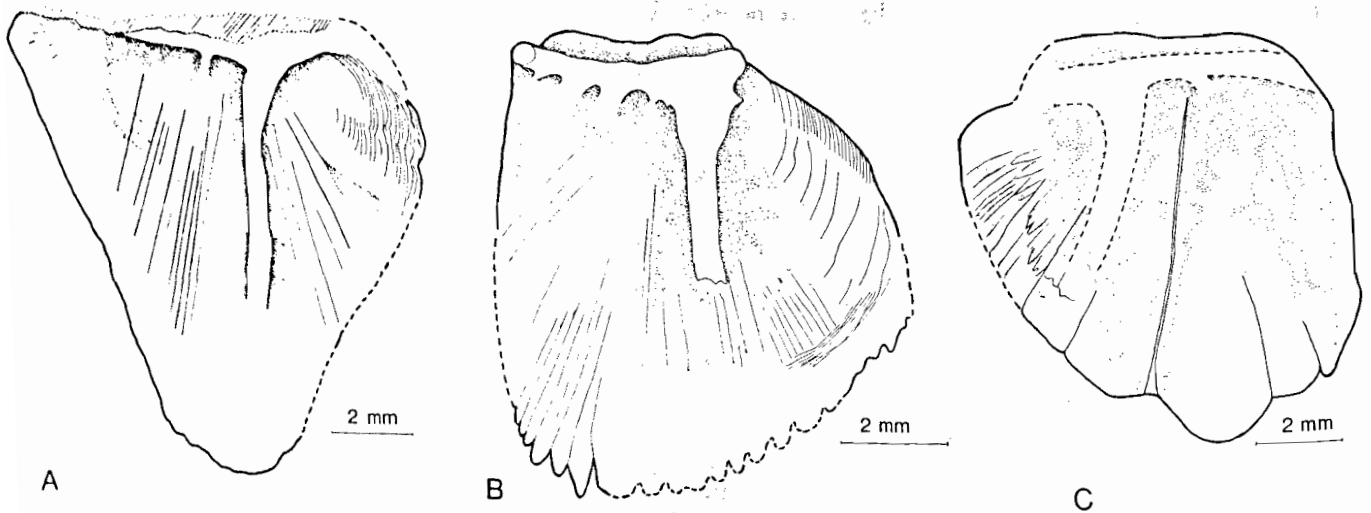
Both parietals are incompletely preserved. They are asymmetrical in that the supraorbital canal lies more laterally on the right one and in that the suture between both is moved to the left. The posterior portion of the pterotic is widened.



Text-fig. 2. *Protoclupea chilensis*. Restoration in lateral view based on many specimens; scales omitted.



Text-fig. 3. *Protoclupea chilensis*. A: Restoration of head in lateral view based mainly on holotype. B: Restoration of dorsal view of cranium. (holotype). C: Restoration of the caudal skeleton (holotype).



Text-fig. 4. Extrascapula. A: *Protoclupea chilensis* (holotype). B: *Protoclupea atacamensis* (KUV 71204 a, b). C: *Domeykos profetaensis* n. gen. et sp. (holotype).

The supraorbital sensory canal runs on the frontal in a bony tube and continues onto the parietal. The supraorbital canal gives off a few short tubules in the posterior part of the frontal and several very short tubules on the parietal. At the growth center of the frontal, the supraorbital canal gives off a branch towards the autosphenotic. The middle pit-line groove is deeply incised and extends from the radiation center of the parietal to the radiation center of the pterotic. The temporal sensory canal is incompletely preserved and the connection to the canal on the extrascapula is covered by rock. No opinion can be given about a recessus lateralis.

The extrascapula (text-fig. 4 A) is a large triangular bone; the ventroposterior margin shows some circuli. The supratemporal commissure and the main sensory canal are enclosed by bone. The main lateral sensory canal continues to the anterior margin of the extrascapula, but the connection to the temporal canal is covered by rock. A posttemporal bone has not been observed (it could be very small or totally missing).

Circumorbital series (text-fig. 3 A): The circumorbital series is incomplete dorsally; five bones are preserved. The antorbital is comma-shaped; its ventral border touches the anterodorsal margin of infraorbital 1. The infraorbital sensory canal ends on the antorbital.

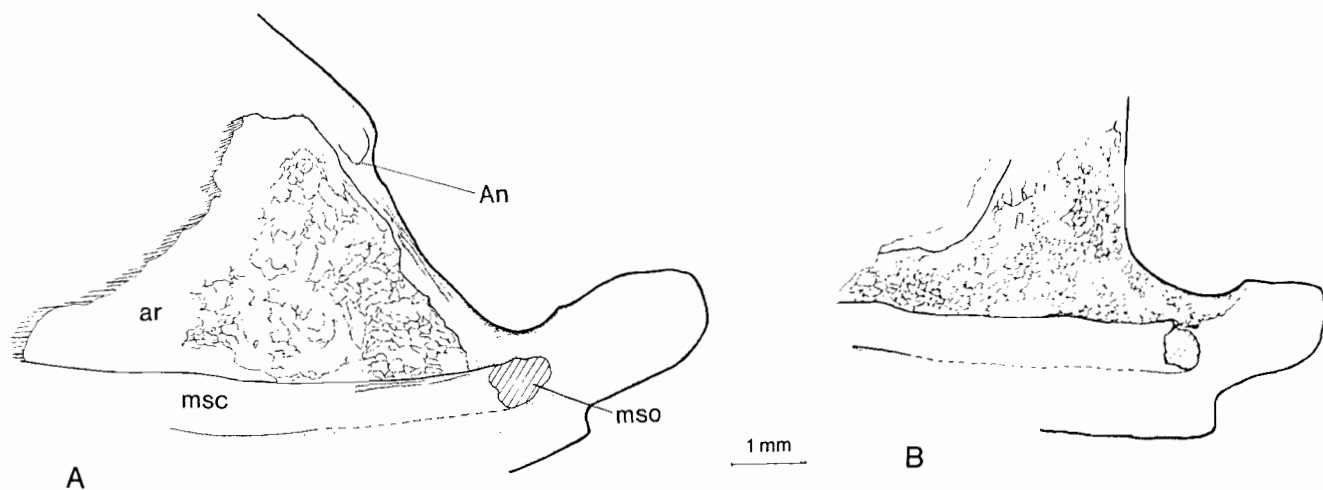
The lacrimal or infraorbital 1 is slightly oval and shorter than infraorbital 2. The infraorbital sensory canal passes through a tube along its centre and gives off several short tubules ventrally. Infraorbital 2 is the most elongate component of this series; the infraorbital sensory canal gives off about seven short tubules. The posterior margin of infraorbitals 3–4 reaches close to the anterior border of the preopercle. The infraorbital sensory canal gives off a few short tubules. Infraorbital 4 is the smallest infraorbital bone, and infraorbital 3 the largest, thus between infraorbital 1 and the largest bone of the series there is only one infraorbital. A fifth infraorbital is not preserved; if such bone was present, it was very small, judging from the space which is between infraorbital 4 and the pterotic.

There is no suborbital.

The sclerotic ring is ossified, but only one portion is preserved close to the posterior margin of the orbit. The limit of the eyeball is clearly visible in the holotype R-396 (pl. 1, fig. A, B).

Upper jaw (text-fig. 3 A): Only a small part of the maxilla is preserved; it bears a single row of small conical teeth.

Lower jaw (text-fig. 3 A, 5 A): The lower jaw is deep with a high coronoid process. The dentary lacks its anterior part, nevertheless a narrow, deep "leptolepid" notch is preserved between the ascending margin and the dorsal margin. On the posterior margin of the lower jaw, the articular is clearly distinguished from the dermal angular; it is slightly triangular in shape and its suture with the angular is clearly distinguishable. The articular does not project posteriorly below the articular facet. It seems that the angular alone forms the articular facet for the



Text-fig. 5. Posterior end of right lower jaw of *Protoclupea*, in medial view. A: *P. chilensis* (holotype). B: *P. atacamensis* n. sp. (holotype).

quadrate. The postarticular process is formed by the angular. There is no evidence of a retroarticular. The mandibular sensory canal opens medially.

Hyoid arch, branchiostegal rays and branchial skeleton: There are remains of the anterior and posterior ceratohyals and posterior branchiostegal rays. Part of the gill arch skeleton is preserved; no tooth plates are associated either with ceratobranchials or with epibranchials; the pharyngobranchials are not preserved.

Hyopalatine bones: There are remains of hyomandibular, metapterygoid, ectopterygoid and endopterygoid. The quadrate (text-fig. 3A) is a triangular bone with a slightly rounded upper border. The symplectic is not preserved.

Opercular bones (text-fig. 3A) and gular plate: The opercular series consists of preopercle, opercle, subopercle and interopercle (the latter poorly preserved); all these bones have a smooth surface.

The preopercle has a long dorsal limb and a relatively short ventral limb. The posteroventral angle of the bone is strongly projected back, forming a triangular margin which is finely crenulated. There is no notch in the upper part of the posterior edge of the preopercle. The preopercular sensory canal is broad and enclosed by bone; it runs near the anterior margin of the bone. The preopercular sensory canal gives off 11 tubules, most of them prolonged close to the ventroposterior margin of the bone. The tubules on the dorsal limb are the shortest. There is no evidence of a supraopercle.

The opercle has a rounded dorsal margin. There is an oblique suture between opercle and subopercle. Subopercular depth is about 45% of opercular depth. The interopercle is incompletely preserved in the holotype (R-396), but seems to be narrow.

There is no evidence of a gular plate.

Vertebral column and ribs: It is difficult to study the abdominal vertebrae because the preserved muscles cover them partially. 44 to 47 vertebrae are pierced centrally for the passage of the notochord. The caudal centra are markedly larger than the abdominal ones (text-fig. 2). All vertebral surfaces are apparently smooth, with delicate narrow longitudinal grooves. Both neural and haemal arches are autogenous. The needle-like neural and haemal spines are slightly inclined caudally.

It is not possible to determine precisely the number of abdominal vertebrae and ribs because of cover by muscles. That is the reason why the restoration of *Protoclupea chilensis* (text-fig. 2) presents an "open" area. The slightly curved ribs reach the ventral margin of the body.

The presence or absence of supraneurals, epineurals and epipleurals could not be determined because of insufficient preservation.

Pectoral girdle (text-fig. 2, 21 D) and fin: The supracleithrum is an elongate broad bone; its dorsal margin is covered by the extrascapula. The main lateral sensory canal gives off one secondary branch close to the dorsal margin of the bone. The posterior margin of the supracleithrum is incomplete preserved in most specimens. Postsupracleithra have not been observed. The cleithrum is large and broad; its dorsal end extends widely below the supracleithrum. The elongate postcleithra 1 to 3 present in most teleosts have not been observed. Nevertheless a triangular bone lies ventroposterior to the cleithrum which we interpret as postcleithrum 4. This bone has a finely crenulated posterior margin which projects far back. Posterior to postcleithrum 4, there is a small slightly triangular bone with a crenulated posterior margin that we interpret as postcleithrum 5. The scapula and radials are not preserved, but remains of the coracoid are found in specimen KUV 71205 a.

The pectoral fin has 16 or more broad, flattened pectoral rays, the distal ends of which are not preserved.

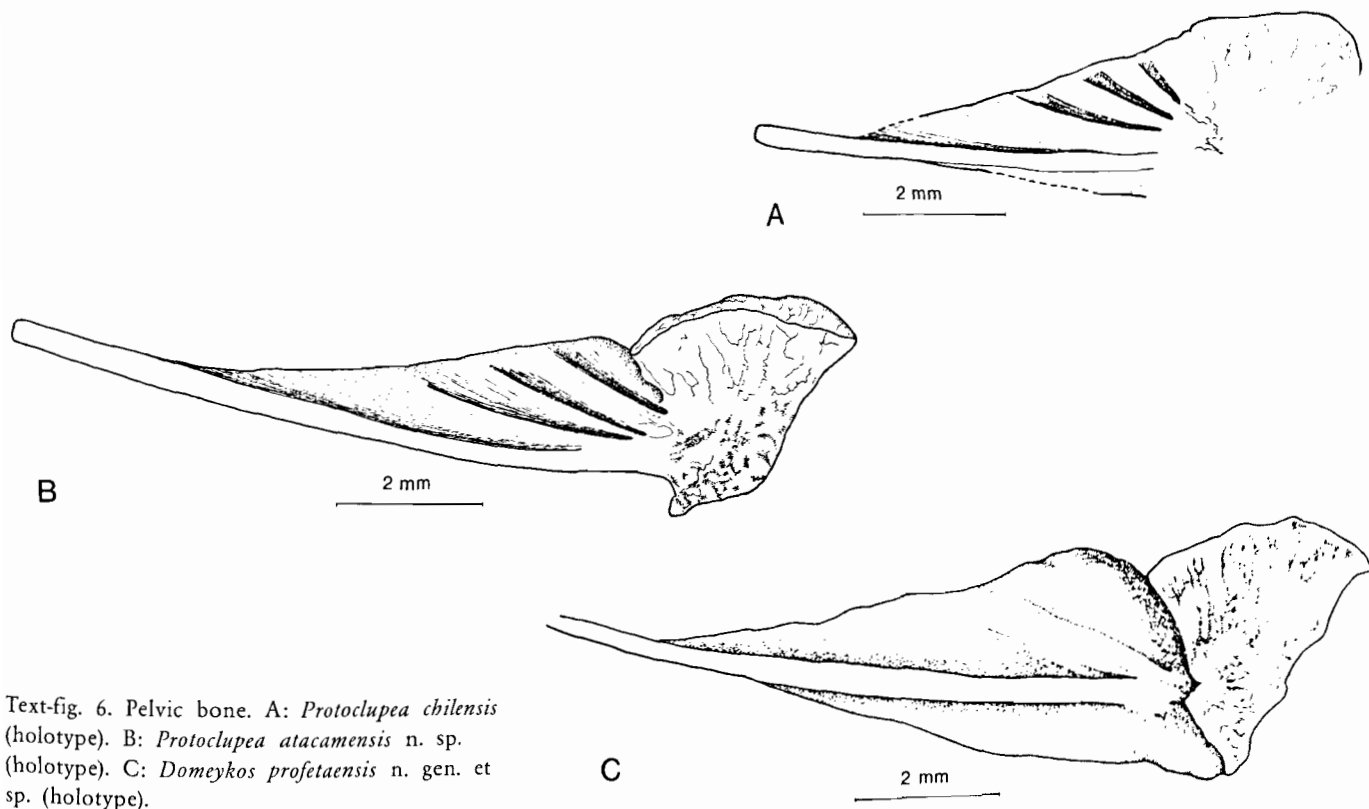
Pelvic girdle and fin: The poorly preserved, elongate triangular pelvic bone (text-fig. 6A) has an elevated ridge in the middle of the anterior part. No pelvic radials or splint have been seen. The 11 to 14 pelvic rays are broad, flattened, segmented and their distal ends are finely branched. Close to the first ray lies the axillary pelvic process, as long as the first pelvic ray (text-fig. 2); it is preserved as imprint so that it is not possible to decide if it is a scale-like bone or bone-like scale.

Dorsal and anal fins: The dorsal fin begins opposite or slightly behind the origin of the pelvic fin. The basal length is shorter than the longest ray. The dorsal fin is apparently divided into two portions separated from each other by a row of large oval scales (text-fig. 2); the first portion of the dorsal fin consists of 4 unbranched and 7 branched rays; the second portion formed by 7 shorter branched rays is partially covered by large scales (text-fig. 7A).

The anal fin starts behind the insertion of the last dorsal ray. The base of the anal is longer than the base of the dorsal fin. The fin is acuminate (text-fig. 2) and longer than deep. There are probably 4 unbranched rays; the third and fourth rays lack their ends. There are at least 19 branched rays, their bases covered by large scales similar to those of the dorsal fin (text-fig. 7A).

Caudal fin (text-fig. 3C): In all specimens the distal part of the caudal fin is missing. The caudal fin is small in proportion to the size of the fish.

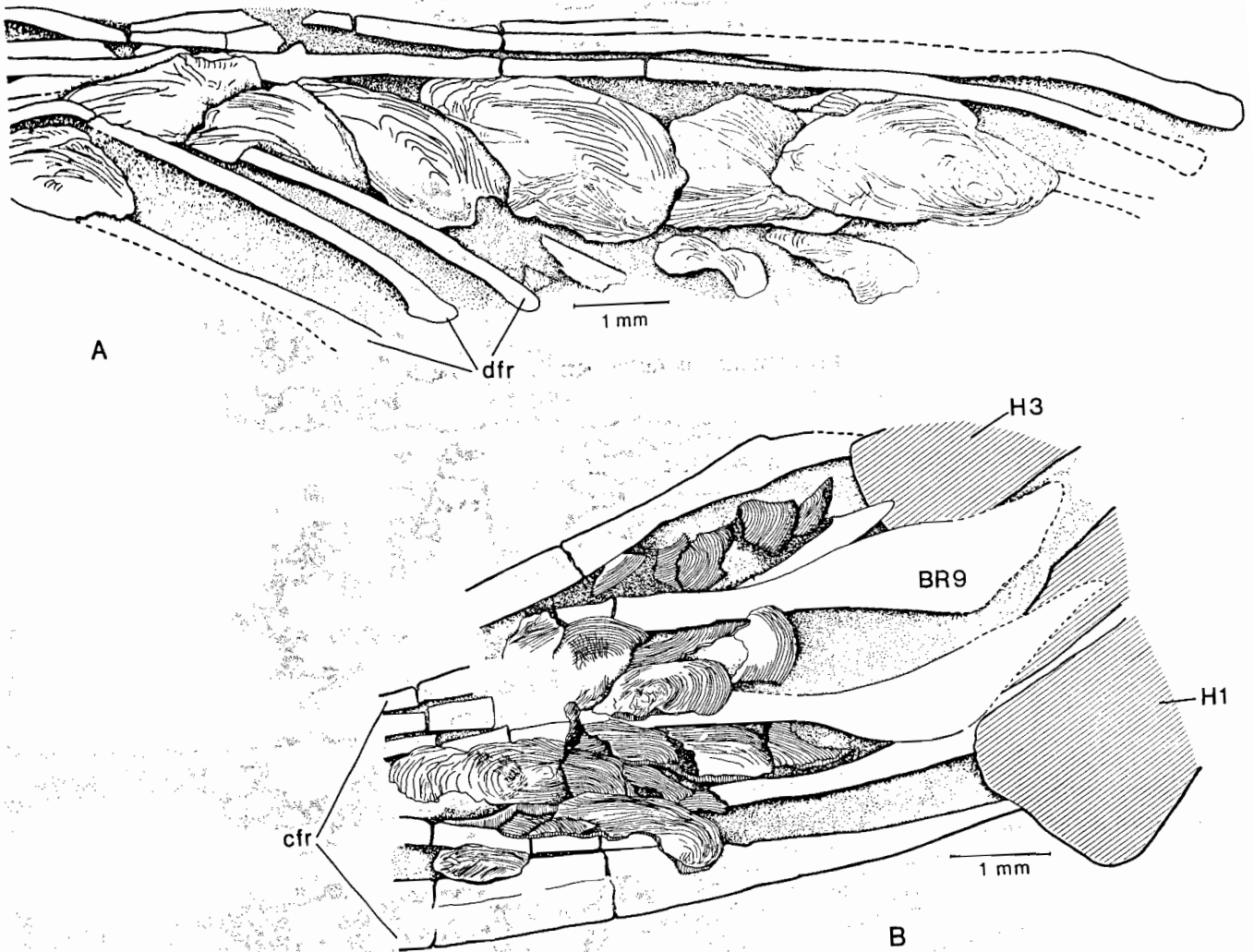
The haemal spines of preural centra 2–3 are wider than the haemal spines of the other caudal vertebrae. The haemal arches associated with preural centra 2–4 are autogenous and wide. The neural arches of preural centra 1–2 are absent or it could be that they were not fused. A neural arch over the first ural centrum is absent. The



Text-fig. 6. Pelvic bone. A: *Protoclupea chilensis* (holotype). B: *Protoclupea atacamensis* n. sp. (holotype). C: *Domeykos profetaensis* n. gen. et sp. (holotype).

parhypural is autogenous. There are six hypurals and remains of three additional ones. Hypurals 1 and 2 articulate with first ural centrum. Three epurals and five uroneurals are present; the uroneurals are inclined toward the horizontal and form two sets, two long anterior compound uroneurals followed by one medium-sized and two short fusiform bones. The longest uroneural reaches preural centrum 4; the anterior part of the second uroneural is not preserved but the bone probably reached preural centrum 4. The third uroneural partially overlaps first ural centrum and completely ural centrum 2. An anteriorly directed membranous outgrowth is developed from the anterodorsal margin of the first compound uroneural.

Thirty-seven caudal fin-rays can be counted in the holotype R-396; it seems that there are 10 upper and 11 lower principal caudal rays. One caudal scute precedes each lobe.



Text-fig. 7. Dorsal and caudal-fin rays and scales of *Protoclupea chilensis* (holotype). A: Scales located on the bases and in between the principal dorsal-fin rays. B: Scales covering the principal caudal-fin rays.

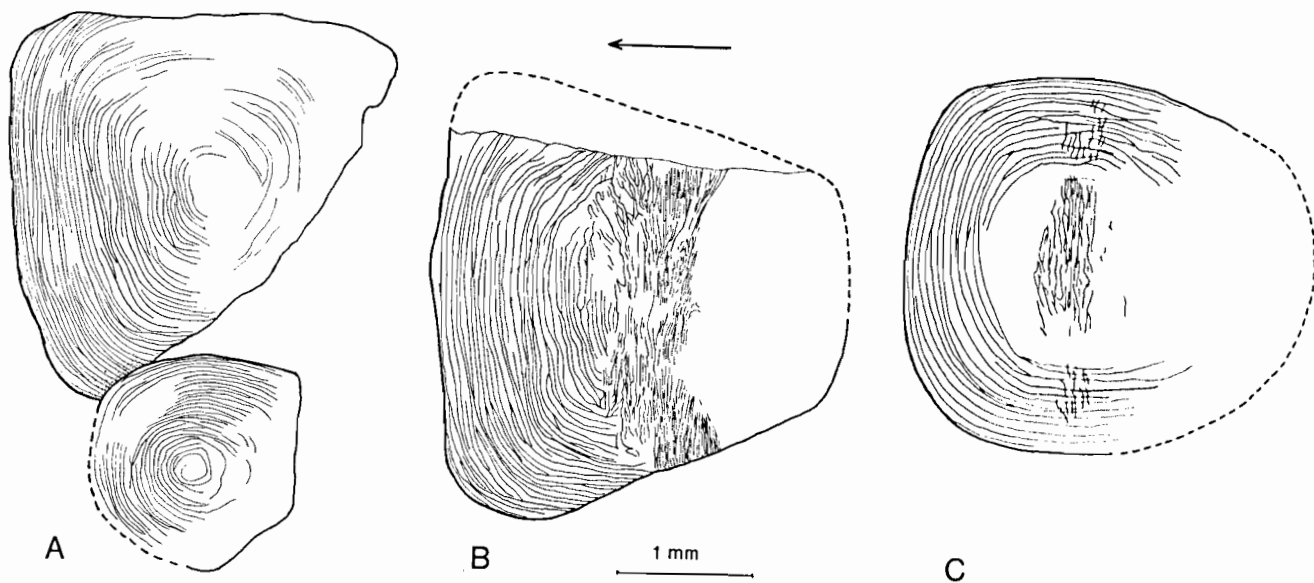
Squamation (text-fig. 8): The dorsal part of the head is covered by cycloid scales of different size and shape; the posterior field of these small scales shows no circuli. Contrary to the small scales in other regions, large scales lie behind the pectoral girdle; they present transversely oriented lines in the middle field, while the posterior field is smooth. The scales of the ventral part of the body are oval in shape and only rarely have transversely oriented lines. Large oblong scales with few circuli lie at the base and between the rays of dorsal and anal fins. The base of the caudal fin rays and part of the caudal rays (text-fig. 7B) are covered by very oblong large scales with many circuli in the anterior field and few transversely oriented lines in the middle field crossing the posterior part of the circuli.

A single lateral line runs along the flank. It is not possible to determine if it reaches the base of the caudal fin.

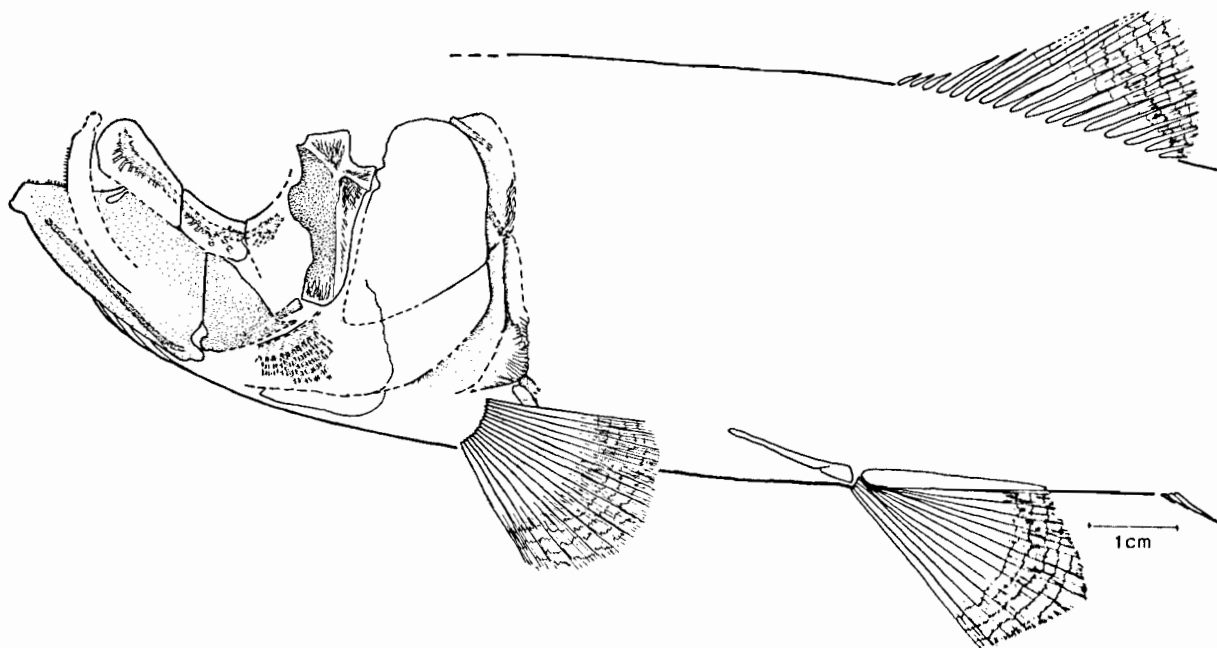
Protoclupea atacamensis n. sp.

Text-fig. 4B, 5B, 6B, 9, 10, 11 A-C, 21E, pl. 2, fig. A, B

Diagnosis: *Protoclupea* of about 26 cm standard length. Infraorbital 1 longer than infraorbital 2; infraorbital sensory canal with relatively long tubules. Small articular extends just to the posterior border of the lower jaw and projects into postarticular process. Broad, square postcleithrum 4. Dorsal fin longer than deep. Maxilla and infraorbital 1 scaled. No scale row dividing the dorsal fin into two sets of rays. Scales with transversely oriented lines in the middle field, smooth posterior field.



Text-fig. 8. Cycloid scales of *Protoclupea chilensis* (holotype). A: Posterodorsal part of head; B: Behind cleithrum; C: Ventral region of the body, in front of pelvic girdle. (Arrow points anteriorly).



Text-fig. 9. *Protoclupea atacamensis* n. sp., restoration in lateral view based in several specimens; scales omitted.

Etymology: The specific name refers to the Atacama desert where the specimens has been found in the Cordillera de Domeyko.

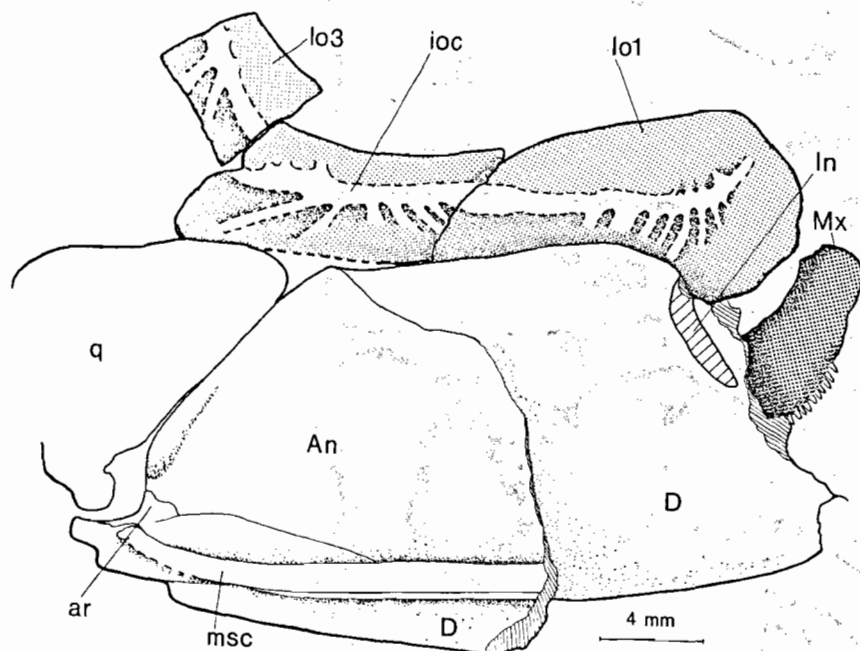
Holotype: Part (LBUCH 1-250277 a) and counterpart (LBUCH 1-250277 b): head incompletely preserved, part of the pectoral girdle and fin, pelvic girdle and incompletely preserved pelvic fin, dorsal fin and squamation; anal and caudal fin missing.

Paratypes: Part (KUVF 71204 a) and counterpart (KUVF 71204 b); trunk, pectoral, pelvic, dorsal and anal fins, muscles and squamation preserved. Part and counterpart (KUVF 81241): incomplete preserved specimen, anterior part of head and tail missing. Part (LBUCH 116-180173 a) and counterpart (LBUCH 116-180173 b): some isolated head bones, trunk, pelvic, dorsal and anal fins incompletely preserved, and squamation. Part (LBUCH 210277-1 a) and counterpart (LBUCH 210277-1 b): posterior part of head, trunk and pectoral, pelvic, dorsal and anal fins, vessels and scales preserved. Specimen LBUCH 210277-3: imprint of posterior part of trunk, incompletely preserved dorsal and anal fins, and squamation.

Locality und geological time: Same as *Protoclupea chilensis* (page 33, text-fig. 1).

Description: The fish reaches approximately 26 cm standard length. The head is about 31% of standard length (proportions in table 1).

Circumorbital bones (text-fig. 9, 10, pl. 2, fig. B): Remains of only three infraorbital bones are preserved. Infraorbitals 1 and 2 are relatively deep. Infraorbital 1 is longer than deep and roughly oval. The infraorbital sensory canal passes through a tube near the upper edge of the bone, giving off four short tubules dorsally and eight tubules ventrally. The infraorbital sensory canal passes through a tube along the center of infraorbital 2 and gives off six tubules ventrally and three tubules dorsally. Infraorbital 3 is incomplete; it is expanded posteriorly; the infraorbital sensory canal runs close to the orbital margin of the bone and there are four preserved tubules; probably this number could be a little higher.



Text-fig. 10. *Protoclupea atacamensis* n. sp. incompletely preserved infraorbital bones, maxilla, lower jaw and quadrate (holotype).

Upper jaw: A portion of the strongly curved maxilla (text-fig. 10, pl. 2, fig. B) is preserved; it bears a row of small conical teeth.

Lower jaw (text-fig. 5 B, 10, pl. 2, fig. A, B): The lower jaw is deep, with a high coronoid process. It is formed by dentary, angular and articular. The retroarticular is absent and there is no evidence of its presence by displacement of the bone.

The dentary bears a single row of small conical teeth; a deep and narrow "leptolepid" notch is developed between the ascending margin and the dorsal margin, the ventral margin is slightly curved, and the bone extends posteroventrally close to the articular facet for the quadrate. The quadrate mandibular articulation is slightly anterior to the posterior margin of the orbit. In the posterior region of the lower jaw the dermal angular and the endochondral articular are clearly distinguishable; a suture between both bones is preserved anteriorly. The articular seems to form most of the articular facet for the quadrate; it extends posterodorsally and covers a small section of the inner side of the postarticular process; most of the postarticular process is formed by the angular. The mandibular sensory canal opens medially.

Branchiostegal rays and branchial skeleton: There are remains of eleven branchiostegal rays (pl. 2, fig. A). Fragments of the gill arch skeleton are visible but they show nothing remarkable. The ceratobranchials are not associated with tooth plates.

Hyopalatine bones: The hyomandibular is vertically placed; the head of the bone (text-fig. 9) is undivided; the opercular process lies in the upper third of the bone; there is no preopercular process. Remains of ectopterygoid and endopterygoid are preserved; both bones are toothless. The symplectic is a splint-like bone. The quadrate is inclined forward; its anterodorsal angle is prolonged dorsally.

Opercular series (text-fig. 9, pl. 2, fig. B) and **gular plate:** Only the ventral limb of the preopercle is preserved in LBUCH 116–180173a. It projects far back and it bears a wide preopercular sensory canal with relatively long sensory tubules.

The opercle and subopercle are partially preserved. The opercle has a rounded upper edge, and an articular process for the hyomandibular. Subopercular depth is about 33% of opercular depth. The interopercle, completely preserved in LBUCH 116–180173a, is a deep and proportionally short bone.

There is no evidence of a gular plate.

Vertebral column: Some abdominal centra similar to those of *Domeykos profetaensis* n. gen. et sp. are preserved. The neural arches are covered by muscles. Remains of some ribs appear close to the ventral border of the body; their inclination is similar to that of *P. chilensis*. Most caudal centra are covered by muscles.

Pectoral girdle (text-fig. 9; 21 E) and **fin:** The extrascapula (text-fig. 4 B) is a large bone, broader distally than in the anterior margin; the supratemporal commissure gives off three or four tubules. Supracleithrum, cleithrum and postcleithra are partially preserved. The supracleithrum (text-fig. 9) is a large and broad bone widely covering the cleithrum; the lateral line canal branches into two tubules; a short dorsal one, and the main canal running to the posterior margin of the bone. Postsupracleithra have not been observed in any specimen. The cleithrum is missing its ventral portion in all specimens. Postcleithrum 1 has a crenulated posterior border. Two other elongate postcleithra lie close to the ventral border of the body, we interpret them as postcleithra 2 and 3. Postcleithrum 4, a broad triangular bone with a finely crenulated posterior border, lies between the cleithrum and postcleithrum 2.

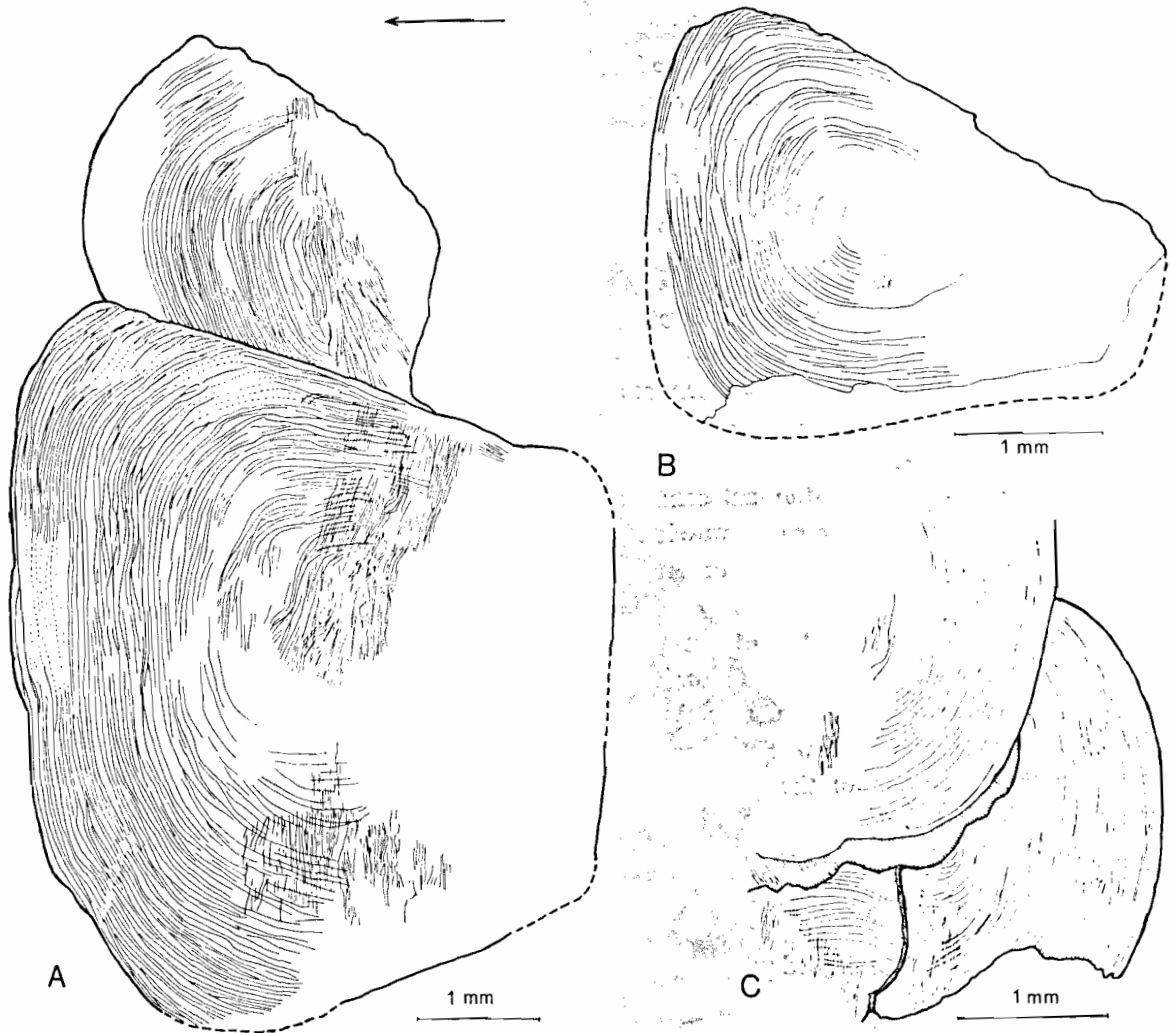
Sixteen to seventeen broad flattened pectoral rays are preserved in LBUCH 210277–1 a, b; their distal ends are finely branched.

Pelvic girdle and fin: The pelvic girdle lies anterior to the dorsal fin. The pelvic bone (text-fig. 6 B) consists of an anteromedially inclined membranous bone, and a medial process of endochondral bone. No pelvic radials or pelvic splint have been seen. The length of the pelvic fin is less than that of the base of the dorsal fin. There are 12 or 13 broad flattened, distally finely branched rays. A scale, the axillary process, lies close to the shortest upper ray, it is as long as the first ray (text-fig. 9). The pelvic axillary process is preserved as imprint only in all specimens (text-fig. 9).

Dorsal and anal fins: The margin of the dorsal fin is slightly emarginated; the base of the dorsal fin is longer than the longest ray. The dorsal fin has five small unsegmented and unbranched rays followed by two segmented rays and at least ten branched rays, the last one partially covered by oblong large scales like those on the base of the dorsal fin. The dorsal fin starts just in front of the origin of the pelvic fin. The anal fin is incompletely preserved in all specimens. Three or four small rays and nine long rays are preserved but it is not possible to decide which is the first segmented ray.

Squamation: Large oval cycloid scales lie on infraorbital 1 and the maxilla. Large scales (text-fig. 11 B) lie on the posterior part of the cranial roof. These have circuli in the posterior field, a few transversely oriented lines in the middle field and no ornamentation on the posterior field. Larger scales with many transversely oriented lines are located behind the cleithrum and supracleithrum (text-fig. 11 A). Large oval scales with complete circuli lie in the anterior part of the trunk below the lateral line; the circuli are crossed by transversely oriented lines (text-fig. 11 C).

There is only one lateral line on the middle of the flank.



Text-fig. 11. *Protoclupea atacamensis* n. sp., cycloid scales (holotype). A: Behind cleithrum. B: Posterodorsal region of head. C: Middle trunk, below lateral line. (Arrow points anteriorly).

Domeykos n. gen.

Diagnosis: Fusiform teleosts with flat cranial roof; parietals separated by supraoccipital. Cephalic sensory canals enclosed in bone or running partially within a bony groove. Deep neurocranium. Subtemporal fossa absent. Few elongate vomerine teeth; parasphenoid toothless. Two supramaxillae. Lower jaw with high coronoid process; without retroarticular; elongate postarticular process; mandibular sensory canal opens medially. Posteroventral angle of preopercle moderately projecting posteriorly; preopercular sensory canal with numerous elongate sensory tubules. Undivided lateral line on supracleithrum. Narrow, elongate postcleithrum 4. Abdominal vertebrae with smooth surface and autogenous neural arches; caudal vertebrae with longitudinal lateral ridges and fused neural and haemal arches. Scales with transversely oriented lines in the middle field, posterior field smooth; rounded or oval small scales without circuli and without transversely oriented lines at dorsal margin of body.

Etymology: *Domeykos* refers to Cordillera de Domeyko where the fossil fishes were collected.

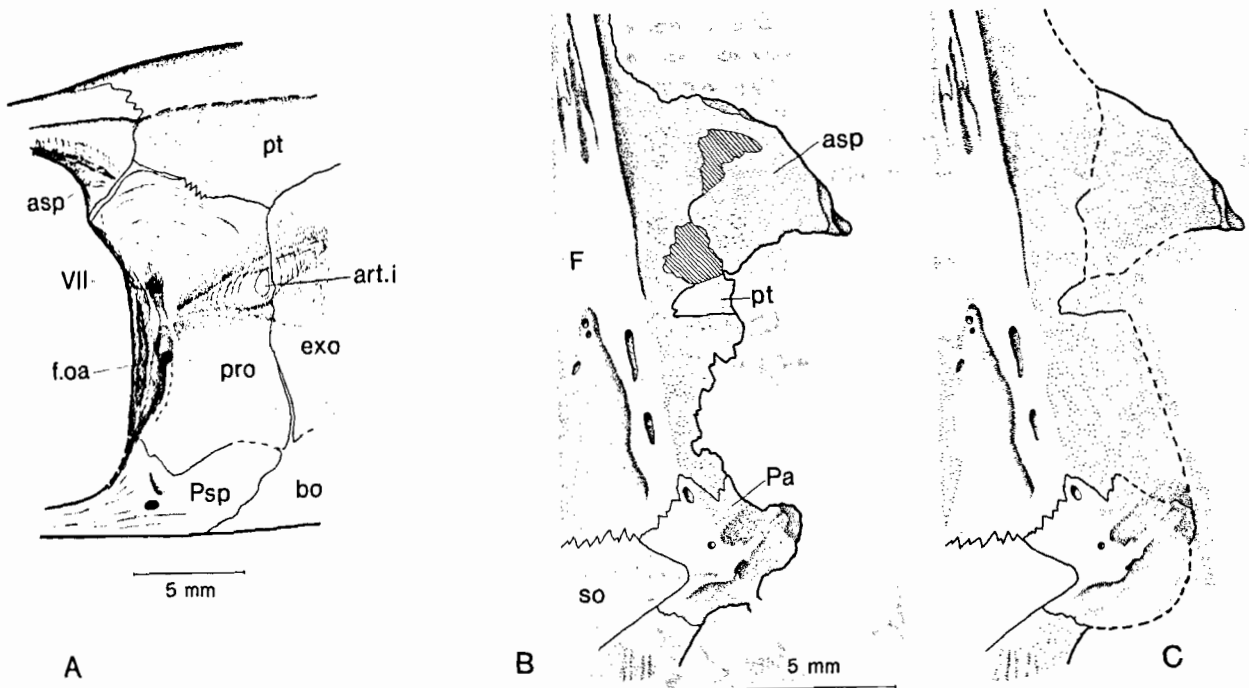
Type species: *Domeykos profetaensis* n. sp.

Text-fig. 4C, 6C, 12, 13 A-C, 14, 15 A-E, 16 A, B, 17 A-G, 21 C, 22, 23 A, pl. 3, fig. A, B, pl. 4, fig. A

Diagnosis: Same as generic diagnosis.

Etymology: The specific name refers to the locality Quebrada El Profeta in the Cordillera de Domeyko.

Holotype: Part (LBUCH 12-260972 a) and counterpart (LBUCH 12-260972 b); nearly complete specimen; caudal fin missing.



Text-fig. 13. *Domeykos profetaensis* n. gen. et sp. A: Restoration of neurocranium in lateral view, (holotype). B, C: Skull roof of acid prepared paratype LBUCH 1-210277. C: Restoration of skull roof after preserved part shown in B.

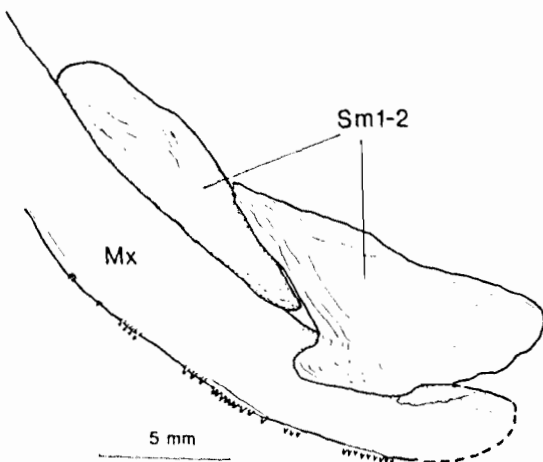
foramen for the trigeminal nerve is preserved on the orbital face of the prootic in the acid prepared LBUCH 1-210277. A deep groove lies on the orbital face of the prootic.

The exoccipital is not completely preserved. It is slightly inflated ventrally and forms the outer wall of the saccular recess together with the prootic and basioccipital. The lateral side of the neurocranium does not show any distinguishable fossa.

The basioccipital is incompletely preserved in the holotype, LBUCH 12-260972; it is relatively short dorsolaterally, and barely meets the prootic. The basioccipital projects anteriorly between the wings of the parasphenoid on the ventral side of the neurocranium.

The intercalar is displaced in the holotype LBUCH 12-260972. It is a slightly rhomboidal bone with elongate dorsal, lateral and ventral outgrowths or struts. We suppose that the intercalar contributes to a prootic-intercalar bridge because of the length of its lateral outgrowth or strut.

The ventral anteromedial region of the neurocranium is open, we were not able to find a basisphenoid.



Text-fig. 14. Supramaxillae and maxilla of *Domeykos profetaensis* n. gen. et sp. (holotype).

Circumorbital bones: Circumorbital bones are not preserved, only a portion of an ossified sclerotic.

Palate: The vomer is closely attached to the ventral side of the mesethmoid. Anteriorly the vomer ends in a lateral rounded projection (where the maxilla articulates). The vomer sends a long posterior shaft back below the parasphenoid. Two large conical teeth are preserved on the palatal surface of the vomer in the holotype.

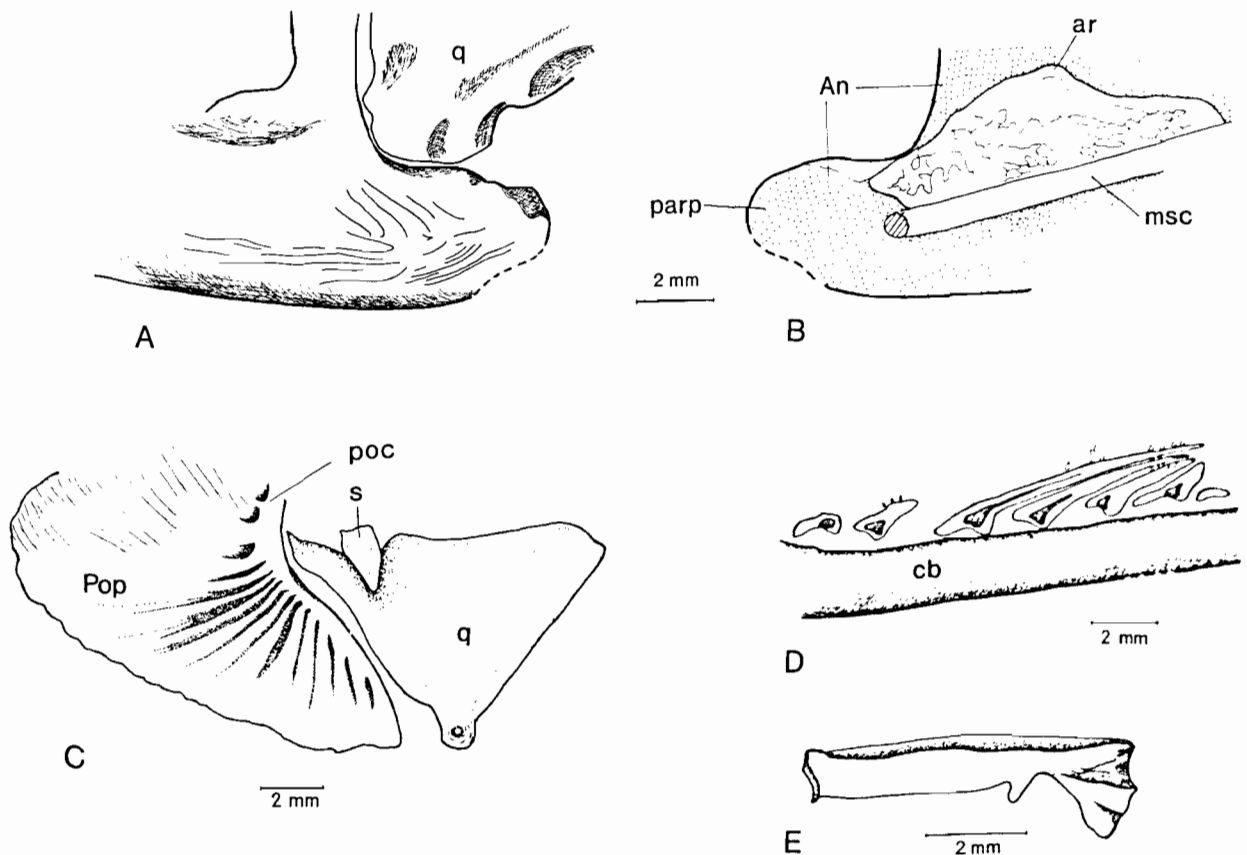
The parasphenoid narrows from the vomer backwards beneath the orbit, and expands again at the level of the ascending process. The parasphenoid is relatively short and it is without teeth. There is no evidence of a basipterygoid process.

The hyopalatine bones are incompletely preserved. The convex oral surface of the endopterygoid does not bear teeth. The posterior margin of the quadrate is thickened and slightly prolonged posteriorly. The symplectic is small (text-fig. 15 C), and triangular.

Upper jaw (text-fig. 14, pl. 3, fig. A): The upper jaw has preserved the maxilla and two supramaxillae. The maxilla is strongly curved in the anteromedially directed part; the ventral margin is smoothly convex with a row of small conical teeth. The two supramaxillae have the same general shape as in *Leptolepis*, *Leptolepides*, and *Tharsis*. The anterodorsal process of supramaxilla 2 is elongate; this bone shows a slightly ornamented surface.

Lower jaw (text-fig. 15 A, B, pl. 3, fig. A, B): The mandible is deep with a high coronoid process; the anterior part of the dentary is not preserved. The mandible is composed of dentary, angular and articular; a retroarticular is absent.

The ventral part of the dentary reaches far posteriorly below the postarticular process. A suture between the articular and angular bones is clearly defined in the holotype LBUCH 12-260972 b. The postarticular process is elongate and slightly ornamented; the sensory canal opens medially.



Text-fig. 15. *Domeykos profetaensis* n. gen. et sp. (holotype). A: External view of the posterior end of the lower jaw, and articular condyle of quadrate. B: Medial view of the posterior end of the lower jaw. C: Ventral limb of preopercle, symplectic and quadrate. D: Section of ceratobranchial. E: Hypobranchial.

Branchiostegal rays and branchial skeleton: Remains of eleven branchiostegal rays are preserved (pl. 3, fig. A, B). Fragments of the gill arch skeleton and some complete ceratobranchials and hypobranchials (text-fig. 15D-E) are visible. The pharyngobranchials are not visible.

Opercular series (text-fig. 12) and gular plate: The opercular series is composed by preopercle, opercle, subopercle and interopercle; these bones are not ornamented. The preopercle is composed of two limbs; the posteroventral angle of the bone is not as widely expanded as in *Protoclupea chilensis*. There is no evidence of a notch in the upper part of the posterior edge of the preopercle. The preopercular sensory canal is enclosed by bone and runs along the anterior margin of the bone. The preopercular sensory canal gives off 14 tubules (pl. 3, fig. B), the shortest in the dorsal limb; most of the tubules are prolonged close to the ventral and posteroventral margin of the bone.

The opercle has a rounded dorsal margin; the posterior margin runs ventroposteriorly, the ventral border anteroventrally. The subopercle is about 2.4 of opercular depth.

There is no evidence of a gular plate.

Vertebral column, ribs (text-fig. 12, 16A, B, pl. 4, fig. A) and intermuscular bones: The vertebral column is composed of more than 50 vertebrae which show two strongly different morphological pattern in the abdominal and caudal regions.

Each centrum is pierced by the notochord and is deeper than long. The caudal centra are larger than the abdominal ones. The vertebrae are partially covered by muscles just in front of the dorsal fin, therefore we cannot determine the precise number of abdominal vertebrae. Approximately the first 30 vertebrae (text-fig. 16A) have autogenous neural arches; the neural spines remain separated halves; the surface of most abdominal vertebrae is smooth. The caudal vertebrae (text-fig. 16B) show an advanced teleostean pattern with the neural and haemal arches fused to the centrum; the centrum has a well developed longitudinal crest. The lateral halves of the neural and haemal spines of the caudal vertebrae fuse to form a median neural or haemal spine. From the third abdominal vertebra on, each abdominal centrum has two relatively wide, deep, ventrolateral cavities. The long ribs are smoothly curved and are wider close to the articular condyle. The last ribs are not preserved.

Epineural bones fused with the neural arches are present at least until the thirtieth vertebra. The epineurals lie parallel to the vertebral column and the last ones are proportionally longer. A few small thin epipleural bones can be seen close to the haemal spines in front of the anal pterygiophores in the acid prepared LBUCH 1-210277. There is no evidence of supraneural bones.

Pectoral girdle (text-fig. 12; 21C, pl. 3, fig. A, B) and fin: The extrascapula (text-fig. 4C) is large, thin and its posterior border undulates. The supratemporal commissure and main lateral sensory canal are enclosed by bone. One tubule branches off the supratemporal commissure in the extrascapula. The main lateral sensory canal makes a sharp lateral curve. The main part of the posttemporal and the elongate dorsal process are preserved. The main lateral sensory canal runs in the middle of the bone and gives off three short tubules.

The partially preserved elongate supracleithrum (text-fig. 12) is not very wide; it is shorter than the opercle. The main lateral sensory canal is enclosed by bone and emerges distally at the ventroposterior margin to continue as a single lateral line. Postsupracleithra 1-2 have not been observed. The supracleithrum overlaps the cleithrum; the latter is the largest element of the pectoral girdle. Three postcleithra are preserved, postcleithra 1, 2 and 4. The elongate postcleithrum 1 lacks its posterior margin; postcleithrum 2 has a finely crenulated posterior margin; postcleithrum 4 lacks its posterior part but seems to be a narrow elongate bone.

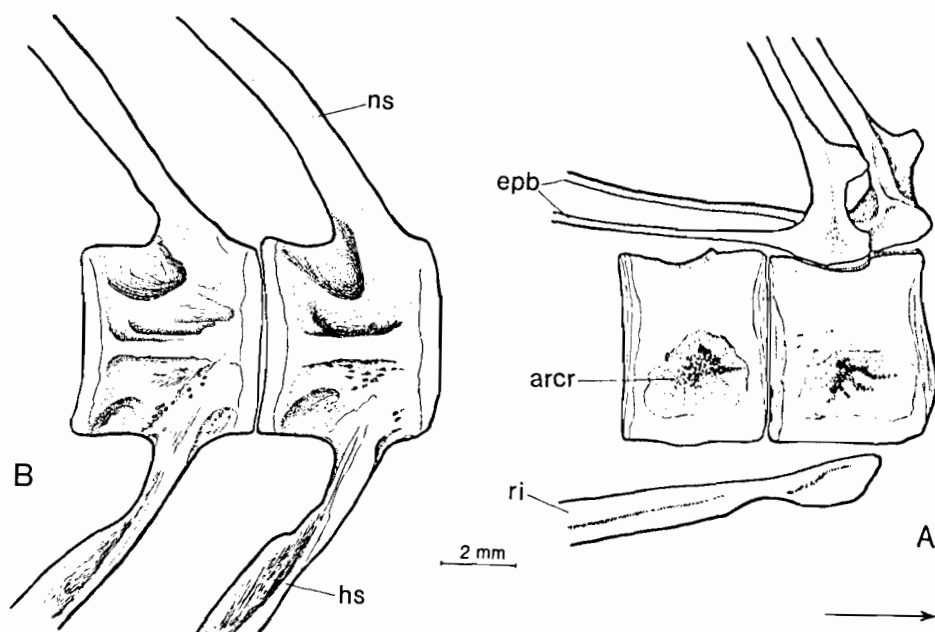
The scapula is preserved in the acid prepared LBUCH 1-210277 (pl. 4, fig. A); the scapular foramen lies entirely within the scapula, and there is the usual large facet on the bone for the foremost pectoral ray. The elongate coracoid presents a foramen close to the posterodorsal margin. Remains of two proximal radials are present.

The pectoral fin is not well preserved; it contains 12 flattened and distally finely branched rays; they do not show segmentation.

Pelvic girdle (text-fig. 6C) and fin: The elongate pelvic girdle is proportionally narrower than that of *Varasichthys ariasi* (ARRATIA 1981: text-fig. 17). There is no evidence of pelvic radials or pelvic splint.

Text-fig. 16. *Domeykos profetaensis* n. gen. et sp., vertebrae and ribs, in acid prepared specimen LBUCH 1-210277.

A: Abdominal centra, autogenous neural arches and ribs; epineural bones fused to neural arch, both halves of the neural arch not fused in midline.
B: Caudal vertebrae with neural and haemal arches fused to the centra.



The pelvic fin contains 10 to 12 rays; one pelvic fin has one ray more than the other one in the holotype LBUCH 12-260972 a, b. All pelvic rays are flattened, segmented, and finely branched distally. The pelvic axillary process, as long as the first ray, is preserved close to the uppermost ray; this is a flat, scale-like bone (LBUCH 1-210277), similar in structure to the postcleithra.

Dorsal fin (text-fig. 12): The dorsal fin starts just in front of the origin of the pelvic fin. The dorsal fin is slightly emarginated and a little longer than deep. It consists of 3-5 small unsegmented and unbranched rays and 12 principal rays. The dorsal pterygiophores are not preserved in the holotype (LBUCH 12-260972 a, b); some of them are displaced and isolated in the acid prepared LBUCH 1-210277. Large scales cover the base of the dorsal fin and partially cover the last dorsal rays.

Anal fin (text-fig. 12): The origin of the anal fin is behind the insertion of the last dorsal fin ray. The fin is not completely preserved in any specimen. 3 or 4 small unsegmented and unbranched rays and 9 branched rays are preserved. Six thin pterygiophores are preserved; the first one is not markedly strong, and is not prolonged close to the vertebral column.

The caudal fin is not preserved.

Squamation: Cranial roof, cheek and opercular apparatus are scaleless.

There are large scales (text-fig. 17 A, B) just behind the pectoral girdle; these scales show transversely oriented lines crossing the circuli in the middle field; the posterior field does not have any ornamentation. The scales placed dorsally just behind the neurocranium have a similar structure but are proportionally smaller. Large scales (text-fig. 23 A) with transversely oriented lines between the circuli lie in the middle of the flank of the trunk; the posterior field of these scales is undulated. The scales become smaller and rounded caudally along the midline. Elongate, slightly oval scales with circuli in the anterior part and without ornament in the posterior field (text-fig. 17D-F) lie on the ventral part of the body, and in front of the pelvic fin. Most of these scales have only some weak transversely oriented lines between the circuli.

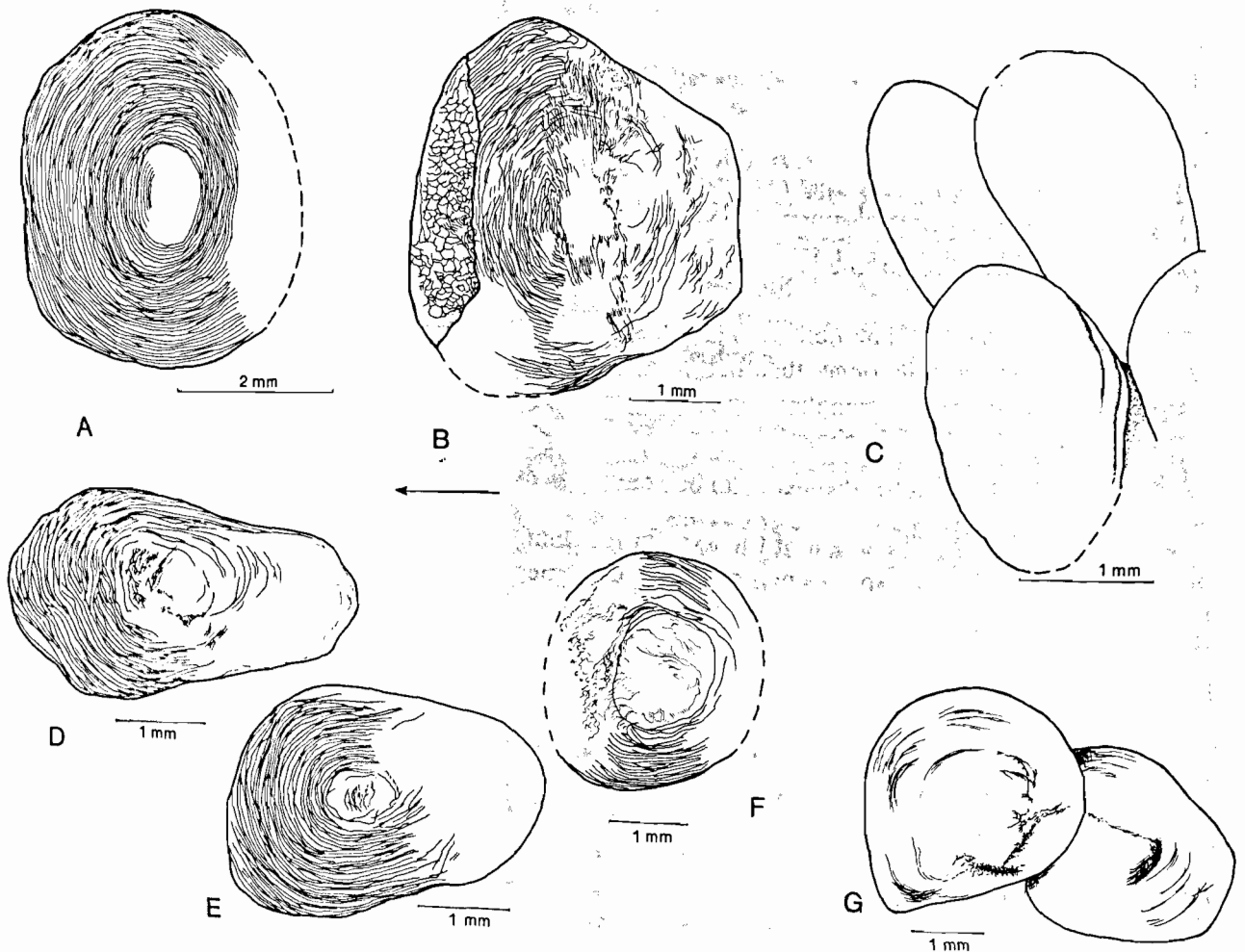
The scales at the dorsal margin, in front of the dorsal fin, are oval and without ornament; the scales at the dorsal margin posterior to the dorsal fin show some incomplete deep circuli (text-fig. 17C, G).

Subdivision: Téléostei
Cohort: Clupeocephala
Subcohort: ?Clupeomorpha

Family indet.

Luisichthys WHITE 1942

Diagnosis (emended): Large, deep-bodied, fusiform teleost with flat cranial roof; parietals joined in the midline. Deep neurocranium. Deep subtemporal fossa. Large foramen limited by pterotic, epiotic and exoccipital. Intercalar incorporated into the neurocranium. Well developed prootic-intercalar bridge. Foramina of trigeminal, abducens and oculomotor nerves in the anterior face of prootic; foramen for glossopharyngeal nerve in exoccipital. Toothed pterygoid bones. Two supramaxillae. Lower jaw with high coronoid process. Abdominal and caudal vertebrae with smooth surface; abdominal centra with autogenous neural arches; caudal centra with fused neural and haemal arches. Cycloid scales with transversely oriented lines in the middle field.



Text-fig. 17. *Domcykos profitaensis* n. gen. et sp., cycloid scales (holotype). A: Just behind supracleithrum. B: Just behind postcleithrum 1. C: At the dorsal margin of the body between skull roof and start of dorsal fin. D: At ventral region of body, just behind pectoral girdle. E: At ventral region of body in front of pelvic girdle. F: Below lateral line, in front of anal fin. G: On the dorsal margin of the body, behind dorsal fin.

Type-species: *Luisichthys vinalesensis* WHITE 1942

Text-fig. 18 A-C, 19, 20, pl. 5, fig. A-C

Luisichthys vinalesensis WHITE 1942: 99; pl. 19, fig. A-F.

Luisichthys vidalis (error) - ARRATIA 1981: 109.

Luisichthys WHITE 1942 - ARRATIA 1981: 127, 130, 132-138.

Studied material: Cast of syntype MCZ 8344: bones, precaudal vertebrae and pectoral girdle; cast of syntype MCZ 8345: cranial bones and precaudal vertebrae; cast of syntype MCZ 8349: vertebral column and tail; specimen U.S.N.M. 18429: complete fish in part and counterpart; acid prepared specimen U.S.N.M. 18618: lateral view of head; acid prepared specimen U.S.N.M. 18656: skull and anterior part of the body.

Locality and geological time: Pinar del Río, Hoya de San Antonio and Hoya de la Sierra; Pinar del Río at Jagua Vieja, 10 km NE of Vinales, Cuba; Formación Jagua, Oxfordian, Late Jurassic.

Description: The acid prepared skull bones are without ornamentation, the sensory canals are enclosed in bone (except the supratemporal commissure) so that it is very difficult to follow them. The braincase is short and deep. A description of the ventral part of the skull is not possible because of preservation.

Skull roof (text-fig. 18 A; pl. 5, fig. C): A small section of the dermethmoid is present at the midline. The lateral ethmoid is slightly prolonged ventrolaterally, and it is sutured posterolaterally with the frontals which form most of the cranial roof. No fontanel is left between the frontals which join anteriorly by a smooth suture, while posteriorly, close to the autosphenotic, the suture is deeply interdigitated. The suture between both frontals and parietals is asymmetric. The supraorbital sensory canal makes a sigmoid curve close to the dermosphenotic, as in leptolepids or other Jurassic teleosts. Posteriorly, each frontal is sutured with the autosphenotic, pterotic and parietal. The autosphenotic is arched so strongly that it forms part of the lateral side of the braincase. The autosphenotic produces a ventral spine. A deep cavity lies posteriorly to the spine, partially roofed by the bone-enclosed temporal canal running through the pterotic. There is no evidence of any foramen (like the clupeomorph temporal foramen) and no evidence of a recessus lateralis.

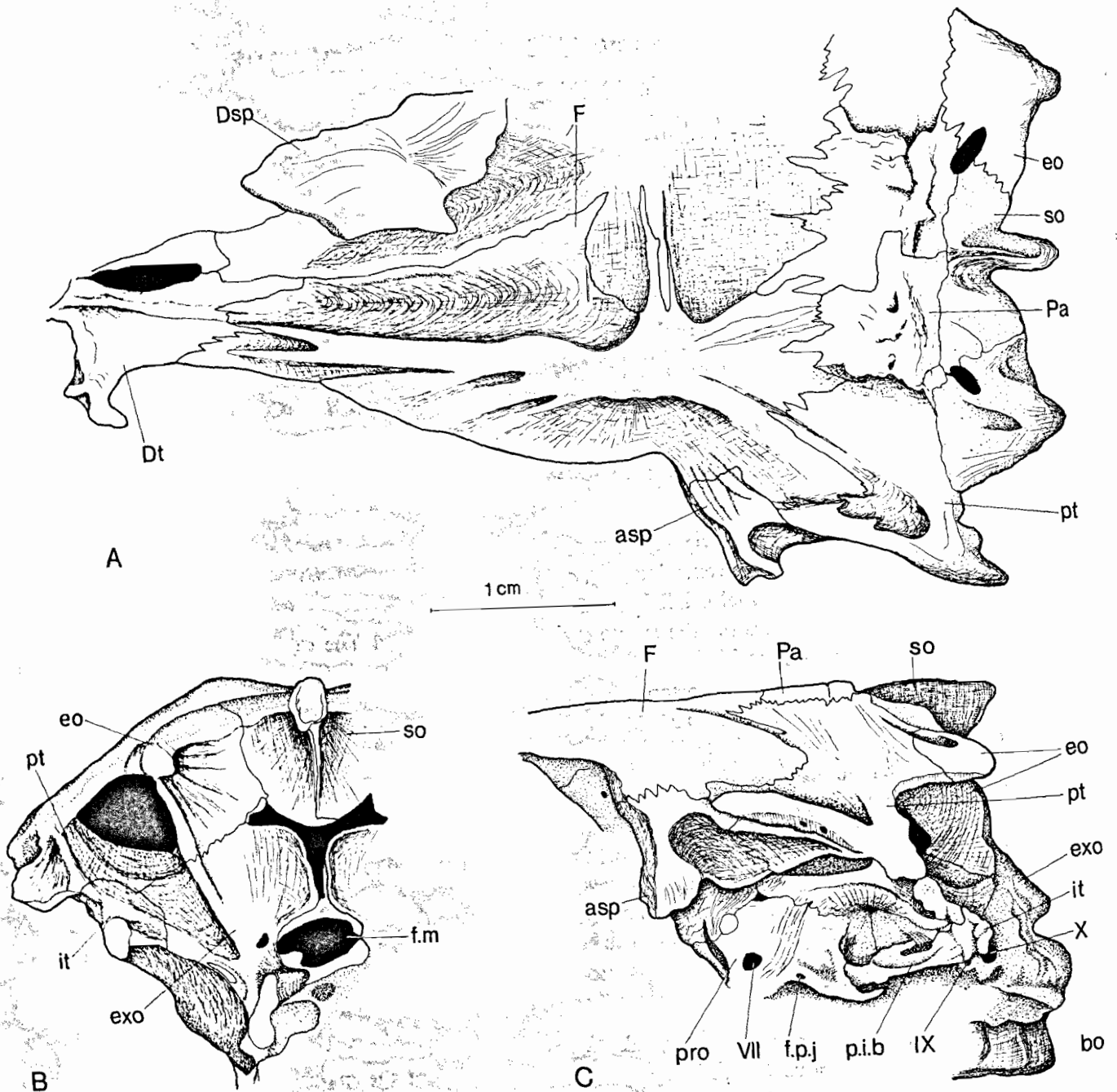
The pterotic forms the posterolateral part of the skull roof, and is abruptly arched ventrolaterally and posteroventrally. It is V-shaped, with the inner limb broader than the external one. The parietals are sutured in the midline, not separated by the supraoccipital.

The supraoccipital is a small bone, producing a narrow crest which does not rise above the level of the skull roof. The supraoccipital is sutured anterodorsally with the parietals and laterally with epiotics. An oval foramen lies at the junction of the epiotic, supraoccipital and parietal, as in *Clupea finta* (RIDEWOOD 1904: text-fig. 122).

Lateral view of braincase (text-fig. 18 C, pl. 5, fig. B): The autosphenotic and the lateral part of the pterotic form a steep roof above the dorsal part of the lateral side of the braincase. They cover the elongate articular facet for the hyomandibular. The most characteristic features of the lateral side of the braincase are the deep subtemporal fossa and the well developed prootic-intercalar bridge which forms the dorsal border of a deep jugular fossa. The bridge is formed mainly by the floor of the subtemporal fossa. A large part of pterotic, the prootic, and the exoccipital together with the intercalar form the subtemporal fossa. At the meeting point of the four bones, there is a small space. It is not possible to describe the ventral part of the braincase because the hyomandibular is displaced lying below the prootic-intercalar bridge.

The prootic is a large bone. It meets the autosphenotic dorsally on the lateral surface and on its anterior transversely oriented face. The latter bears three large rounded foramina (foramen of trigeminal nerve, of abducens nerve, and of oculomotor nerve). The lateral face of the prootic is pierced by the relatively small oval foramen for the hyomandibular trunk of the facial nerve. The prootic bears a horizontal arm which projects abruptly laterally articulating with the intercalar and forming a well developed prootic-intercalar bridge. The prootic projection of the bridge is directed posteriorly, external to the intercalar, producing a sharp tip.

The lateral face of the exoccipital forms a small part of the subtemporal fossa. Just below the posterior part of the intercalar, the exoccipital is pierced by two foramina, a large oval foramen for the vagus nerve and a smaller foramen for the glossopharyngeal nerve.

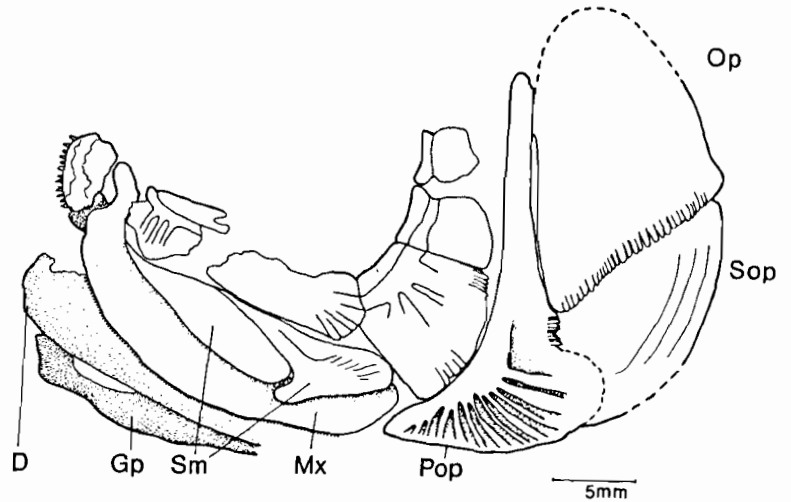


Text-fig. 18. *Luisichthys vinalesensis* (U.S.N.M. 18656). A: Skull roof. B: Posterior view of cranium. C: Lateral view of braincase.

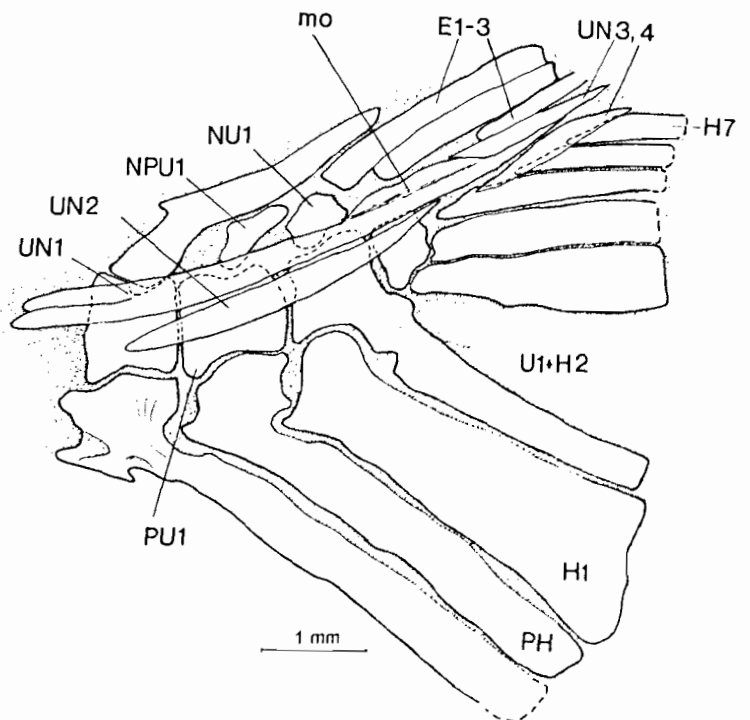
Posterior face of braincase (text-fig. 18 B, pl. 5, fig. A): The most remarkable feature is a large foramen (?post-temporal fossa) which opens widely into the braincase. Its borders are formed by the pterotic (lateral and dorsal borders), epiotic (medial border), and the exoccipital, just reaching the ventral border. A narrow-Y shaped space lies between supraoccipital, epiotics and exoccipitals. It does not open into the foramen magnum.

Circumorbital series (text-fig. 19): WHITE (1942: pl. 19, fig. A, B) figured five broad infraorbitals and no suborbital in the circumorbital series. Infraorbitals 2 and 3 are slightly crenulated as also the ventral margin of the opercle and probably the posterior margin of the preopercle (text-fig. 19). The acid prepared U.S.N.M. 18656 shows a broad, incompletely preserved dermosphenotic occupying the position of a supraorbital. WHITE (1942: pl. 19, fig. A) figured a small dermosphenotic.

Vertebral column and intermuscular bones: *Luisichthys*, like *Domeykos*, has two different kinds of vertebrae. The vertebra are as long as deep, and there is no obvious size difference between abdominal and caudal vertebrae as in *Protoclupea* and *Domeykos*. According to WHITE (1942: 99), the caudal centra have a lateral ridge, but the specimens studied here show no difference in the smooth surface of abdominal and caudal vertebrae, and the latter do not bear a lateral ridge. The abdominal vertebrae have autogenous neural arches, while the caudal vertebrae have fused neural and haemal arches with the exception of the most posterior vertebrae. There are elongate epineural bones fused with the neural arches of the abdominal vertebrae.



Text-fig. 19. *Luisichthys vinalesensis*, restoration of some head bones in lateral view, based on specimens U.S.N.M. 18429, 18618, 18656.



Text-fig. 20. *Luisichthys vinalesensis*, caudal skeleton (U.S.N.M. 18429).

Caudal fin (text-fig. 20): The haemal spines of the preural centra 2-3 are wider than the haemal spines of the other caudal vertebrae, and their haemal arches are autogenous. Preural centrum 1 and ural centrum 1 have small autogenous neural arches, but lack neural spines. The parhypural is autogenous. There are seven hypurals. Ural centra 1 and 2 are preserved completely in specimen U.S.N.M. 18429. Ural centrum 1 is as large as preural centrum 1, it is articulated with hypural 1 and fused with 2. Three epurals and four uroneurals are preserved. The

first compound uroneural (UN 1+2) is slightly bifid anteriorly and projects to preural centrum 3, a membranous outgrowth is developed on its anterodorsal margin. The second uroneural is shorter than the first. Uroneurals 3 and 4 are the shortest. Uroneural 3 lies in an unusual position on the dorsoposterior part of the first uroneural. All of them are slightly horizontal.

Thirty-six caudal fin-rays are counted; there are 10+10 principal caudal rays. One large caudal scute is incompletely preserved in the ventral lobe.

Scales: Few scales are preserved because they were removed by acid treatment. In U.S.N.M. 18429, some large scales are preserved on the ventral part of the body in front of the distal ends of the pectoral rays. All scales have transversely oriented lines in the middle field, like those already described for *Protoclupea* and *Domeykos*.

Comparison

Protoclupea

Revision of holotype, paratypes and additional specimens of *Protoclupea* permits us to emend the diagnosis of the genus and type species *P. chilensis*.

The generic diagnosis is based on a combination of advanced and primitive characters (table 2). The following five characters are present also in *Luisichthys* and *Leptolepides*: comma-shaped antorbital; loss of a suborbital bone; a membranous outgrowth developed on the anterodorsal margin of the first uroneural; neural arch over ural centrum 1 reduced or absent; scales with transversely oriented lines in the middle field (text-fig. 8 C, 11 A, 17 B). *Protoclupea* shares with *Luisichthys*, *Leptolepides* and other primitive teleosts the presence of two sets of uroneurals which are differentiated into anterior and posterior uroneurals. In *Protoclupea*, the posterior uroneurals lie in an angle to the anterior one (text-fig. 3 C). All uroneurals seem to be aligned in the same angle (text-fig. 20) in *Luisichthys*. Two long first uroneurals and a small portion of a third uroneural extend forward beyond ural centrum 2 in *Protoclupea* as in other primitive teleosts, e.g. in *Leptolepis coryphaenoides* and *Tharsis dubius*. In *Luisichthys* and *Leptolepides*, only two uroneurals extend forward beyond ural centrum 2. The presence of additional postcleithra (4-5) is an uncommon character for teleosts and separates both *Protoclupea* and *Domeykos* n. gen. from *Leptolepides*.

Both parietals meet in the midline in *Protoclupea* and *Luisichthys* (text-figs. 3 B, 18 A), a primitive condition present also in leptolepids and such fossil clupeomorphs as *Diplomystus*. Parietals are separated by the supraoccipital in *Domeykos* n. gen. (text-fig. 13 B, C).

The new species, *Protoclupea atacamensis*, shows some significant differences to *Protoclupea chilensis*. The articular participates in a small area of the articular facet for the quadrate in *P. chilensis* (text-fig. 5 A), while the articular participates extensively in the articular facet in *P. atacamensis* (text-fig. 5 B), and it extends partially onto the dorsal part of the postarticular process.

Domeykos n. gen.

The diagnosis of the new genus is based on a combination of primitive and advanced characters. The combination of two different kinds of vertebrae within the vertebral column is rare within teleosts: abdominal vertebrae with smooth surfaces, autogenous neural arches with paired neural spines, and caudal vertebrae with a longitudinal lateral ridge, fused neural and haemal arches, and fused neural and haemal spines (text-fig. 12). The vertebral column of *Domeykos* looks similar to that of *Luisichthys* and *Allothrissops*, a Jurassic ichthyodectiform. The vertebral columns of *Domeykos* and *Luisichthys* differ from that of *Allothrissops* where the haemal arches only are fused with the centra in most of the caudal region (PATTERSON & ROSEN 1977). In *Domeykos*, both, neural and haemal arches fuse with the caudal centra. Autogenous neural arches are present in many Jurassic fishes, e.g. be found in *Elops* (until the thirty fourth vertebra, according to TAVERNE 1974) and in some modern clupeomorphs as *Clupea (Strangomera) bentincki* and *Sardinops sagax* (at least on the anterior abdominal vertebrae). The epineural bones are fused to the neural arches in *Domeykos*, as in *Luisichthys*, pachyrhizodontoids (FOREY 1973 b),

Table 2. Some features of the four Jurassic fishes, *Protoclupea*, *Domeykos*, *Luisichthys* and *Leptolepides*. +: present or yes; -: absent or not; ?: unknown condition.

	<i>Protoclupea</i>	<i>Domeykos</i>	<i>Luisichthys</i>	<i>Leptolepides</i>
1. Large, broad nasal	+	?	-	-
2. Parietals joined in mid-line	+	-	+	+
3. Middle pit-line crossing pterotic	+	,	-	-
4. Prootic-intercalar bridge	?	poorly developed	well developed	-
5. Number of infraorbital bones	4	?	5	5
6. Infraorbital sensory canal ends on ...	antorbital	?	?	infraorbital 1
7. Small premaxilla lacking ascending process	?	?	+	-
8. Bones of the posterior part of the lower jaw	angular & articular	angular & articular	angular, articular & retro-articular	angular, articular & retro-articular
9. Separated angular and articular	+	+	?	-
10. Retroarticular included in the articular facet of lower jaw	-	-	?	+
11. Elongate postarticular process	+	+	-	+
12. Parasphenoid teeth	-	-	?	+
13. Pterygoid teeth	-	-	+	-
14. Gular plate	-	-	+	-
15. Additional postcleithra 4 & 5	+	+	4(?)	-
16. Lateral line emerging in posteroventral margin of supraopercle	+	+	?	-
17. Pelvic axillary process	+	+	-	-
18. Autogenous neural and haemal arches of caudal vertebrae	+	-	-	+
19. Longitudinal lateral ridge on caudal vertebrae	-	+	-	-
20. Epineural fused to the neural arch	?	+	+	-
21. Epipleurals	?	+	+(?)	+
22. Number of hypurals	9	?	7	7
23. Number of uroneurals	5	?	4	5
24. First two uroneurals extend forward beyond U2	-	?	+	+
25. Membranous outgrowth on anterodorsal margin of first uroneural	+	?	+	+
26. Hypural 2 fused with U1	-	?	+	-
27. Principal caudals rays of lower lobe	11	?	10	9
28. Scales with transversely oriented lines in middle field	+	+	+	+

Chongichthys (ARRATIA 1982) and some recent clupeomorphs as *Clupea* (*Strangomera*) *bentincki*. The caudal vertebrae of *Domeykos* show a modern configuration (pl. 4, fig. A) like various Recent teleosts.

Domeykos shares with *Protoclupea*, *Leptolepides* and *Luisichthys* the same kind of scales with transversely oriented lines in the middle field (text-fig. 8, 11, 23 A, B, C). *Domeykos* differs from *Protoclupea*, *Leptolepides* and *Luisichthys* in several features (table 2).

Luisichthys

Revision of material of *Luisichthys* permits us to emend the diagnosis of the genus and type-species *Luisichthys vinalesensis*. The emended diagnosis is based on a combination of primitive and advanced characters.

Luisichthys appears to be more similar to *Domeykos* than other Jurassic teleosts in the configuration of the centra, in fused epineural bones and in the presence of epipleural bones. Both genera differ in the gular plate (present in *Luisichthys* after WHITE 1942 and after this paper (text-fig. 19), absent in *Domeykos*), in the position of parietals (joined in *Luisichthys*, separated by supraoccipital in *Domeykos*) and in the presence of a deep subtemporal fossa in *Luisichthys* which is absent in *Domeykos* (for other differences see table 2). In *Proleptolepis* sp. and *Leptolepis coryphaenoides*, the post-temporal fossa and the fossa bridgei are confluent rather than separated by a transverse bony wall (PATTERSON 1975: 384), the fossa is roofed by parietal and dermopterotic as in *Allothrissops* (PATTERSON & ROSEN 1977: 96). In the Cretaceous ichthyodectiforms, the post-temporal fossa is partially roofed by contact

between epiotic and pterotic. A big hole in *Luisichthys* (text-fig. 18B; pl. 5, fig. A): the fossil state does not permit to decide if the hole (? post-temporal fossa) was closed off from the cranial cavity by a membrane or not. The posterior part of the braincase of other Jurassic teleosts is too poorly known to decide if such a hole as in *Luisichthys* occurs in other.

The glossopharyngeal foramen lies in the exoccipital (text-fig. 18C) of *Luisichthys* like in Upper Jurassic leptolepids, *Allothrissops*, *Varasichthys* and more advanced teleosts, and it does not pierce the prootic as in pholidophorids. No information is available from *Protoclupea*, *Domeykos* and from other Jurassic teleosts.

Luisichthys differ from all other Jurassic teleosts by presence of a hypural 2 fused with ural centrum 1, a character found in clupeomorphs; hypural 1 articulates with ural centrum 1 (as in the fossil clupeomorph *Diplomystus*) while in most adult Recent clupeomorphs it is separated by a space from ural centrum 1. The presence of a membranous outgrowth on the anterodorsal margin of the first uroneural (a clupeocephalan character) is also found in Jurassic teleosts as e. g. *Protoclupea* and *Leptolepides*. Although *Luisichthys* presents hypural 2 fused with ural centrum 1, it lacks other clupeomorph features as for instance a recessus lateralis, and scutes.

A detailed comparison of osteological characters of *Protoclupea*, *Domeykos*, *Luisichthys* and *Leptolepides* follows the arrangement in table 2:

1. Nasal: An exceptional large nasal bone (text-fig. 3B) is present in *Protoclupea chilensis*, in some pholidophorids as e. g. *Pholidophorus bechei*, *Pholidophoroides crenulata* and *Pholidophoropsis maculata* (NYBELIN 1966) and in the Recent *Denticeps* (GREENWOOD 1968, personal observation). The nasal bone is elongate in Jurassic and most Recent teleosts. The large nasal bone of *Protoclupea* may represent a primitive feature because of the occurrence in pholidophorids.

2. Parietal: Left and right parietal meet each other throughout their length in the midline. This pattern is found in *Pholidophorus* (NYBELIN 1966, PATTERSON 1975), *Pholidophoroides* (NYBELIN 1966), *Pholidophoropsis* (NYBELIN 1975), *Proleptolepis* (NYBELIN 1974), *Leptolepis* (NYBELIN 1966, PATTERSON 1975), *Tharsis* (NYBELIN 1966), *Leptolepides* (TAVERNE 1981), *Allothrissops* (PATTERSON & ROSEN, 1977), *Varasichthys* (ARRATIA 1984), *Protoclupea* (text-fig. 3B) and *Luisichthys* (text-fig. 18A). This pattern is primitive because of its distribution in pholidophorids and early teleosts. Contrary in *Domeykos* (text-fig. 13B, C), the parietals are separated by intrusion of the supraoccipital so that the frontal sutures posteriorly with the supraoccipital. The condition of *Domeykos* occurs in other Recent teleosts (e. g. clupeomorphs), it is advanced over the pattern in *Protoclupea* or *Luisichthys*. The advanced condition developed parallel in *Domeykos* and clupeomorphs.

3. Middle pitline: The groove of the middle pitline crosses the pterotic in *Protoclupea* like in pholidophorids (NYBELIN 1966), *Proleptolepis* (NYBELIN 1974) and *Varasichthys* (ARRATIA 1981, 1984). The groove of the middle pitline does not cross the pterotic in *Tharsis*, *Leptolepides*, *Luisichthys* and extant teleosts. The latter pattern is interpreted as the advanced one. This character separates *Protoclupea* from *Luisichthys*; the condition is unknown in *Domeykos*.

4. Prootic-intercalar bridge: *Domeykos* has an intercalar which does not form a well developed prootic-intercalar bridge. The condition is unknown in *Protoclupea*. A relative small intercalar is present in pholidophorids and leptolepids. It is not articulated with a prominent lateral process of the prootic, thus, a bridge formed by both bones is missing on the lateral face of the neurocranium. A well exposed intercalar is present in *Luisichthys* (text-fig. 18C, pl. 5, fig. B). It bears a long prominent anteriorly directed process which articulates with a short prominent process of the prootic forming a prootic-intercalar bridge also found in the Jurassic teleosts *Chongichthys* (ARRATIA 1982), in the Cretaceous *Notelops* (FOREY 1977) and in fossil and Recent elopiforms (FOREY 1973b, Taverne 1974). This prominent horizontal bridge found in some fossil and extant teleosts only has to be considered as specialization appearing parallel in these forms.

5. Number of infraorbitals: Four infraorbitals are present in *Protoclupea chilensis* and five in *Luisichthys*, leptolepids, *Leptolepides*, *Tharsis* and most extant teleosts. The loss of one infraorbital in *Protoclupea* is a specialization of the genus.

6. Antorbital: The infraorbital sensory canal of *Protoclupea* ends on the antorbital (a primitive condition) and on infraorbital 1 in *Leptolepides* (advanced condition). Comparison with *Domeykos* and *Luisichthys* is not possible.

7. Premaxilla: *Luisichthys* has a small, slightly triangular premaxilla without ascending process. The same is the case in *Pholidophorus bechei* (NYBELIN 1966), *Proleptolepis* (NYBELIN 1974), and *Varasichthys* (ARRATIA 1981). Thus, *Luisichthys* is considered primitive in this feature.

8, 9. Articular-angular and retroarticular: The posterior part of the lower jaw is formed by angular and articular only, there is no evidence of a retroarticular or of a surangular in *Protoclupea* and *Domeykos* (text-fig. 5; 15 A, B). We have no evidence to support the hypothesis that the retroarticular could be fused with articular or angular, therefore we suppose that *Protoclupea* and *Domeykos* lack a retroarticular as the Chilean Jurassic teleost *Chongichthys* and some extant New World engraulids. A separate retroarticular is found in *Luisichthys* (U.S.N.M. uncat.); thus, the feature separates *Protoclupea* and *Domeykos* from *Luisichthys* and other Jurassic teleosts (*Leptolepides*, *Tharsis*).

In *Proleptolepis*, the endoskeletal bone (articuloretroarticular) is topographically equivalent to both, articular and retroarticular of higher teleosts; and the bone is fused with the angular. A similar situation is found in adult *Leptolepis coryphaenoides* (PATTERSON & ROSEN 1977: fig. 32 A, B). In a young specimen of *Tharsis*, the three bones are separated; while angular and articular are fused in larger specimens of *Tharsis* (PATTERSON & ROSEN 1977: fig. 32 D, E). According to PATTERSON & ROSEN (1977: 118), "more apomorphous groups of Mesozoic teleosts such as ichthyodectids and *Tharsis* show lesser degree of fusion so that visible sutures between some of the bones remain even in large adults". The occurrence of three separate bones in juvenile specimens indicates that separate ossification of angular, articular and retroarticular is primitive. Fusions of two (anguloarticular in *Leptolepides* and adult *Tharsis*) or three bones (*Proleptolepis*) or loss of the retroarticular (*Protoclupea*, *Domeykos*, *Chongichthys*, engraulids) are independently occurring specializations over the primitive situation.

10. Articular facet: In Jurassic teleosts (*Proleptolepis*, *Leptolepis*, *Tharsis* and *Leptolepides*) and in the Recent *Elops* and *Orestias*, the retroarticular is included into the articular facet. It is the main component of the articular facet in *Orestias*. The retroarticular is not included into the articular facet in most Recent teleosts and in the Jurassic teleost *Varasichthys*. The condition is unknown in *Luisichthys*; the lack of a retroarticular means that it is not included in the articular facet in *Protoclupea* and *Domeykos*.

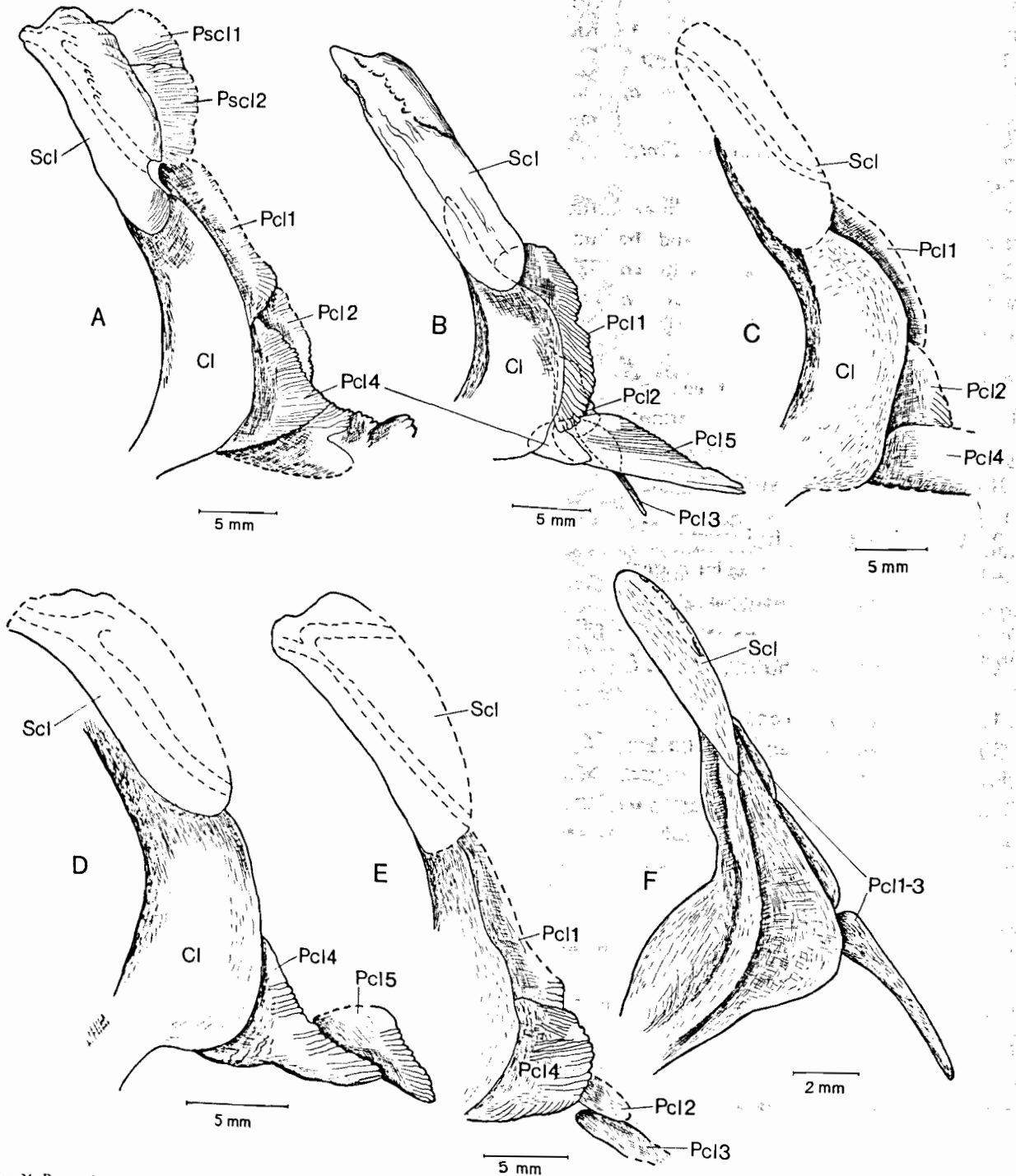
11. Postarticular process: The postarticular process of the posterior part of the lower jaw is elongate in *Protoclupea* and *Domeykos*, and short in *Luisichthys*. The feature separates the two Chilean genera from *Luisichthys*. A rudimentary postarticular process is present in *Proleptolepis* (PATTERSON & ROSEN 1977), *Varasichthys* (ARRATIA 1981), and in different lineages of extant teleosts as in the characid *Cheirodon*, in the perciform *Percichthys*, in the atherinid *Basilichthys*. The feature is difficult to evaluate since variation in length of the postarticular process occurs within one teleost group, e. g. an elongate postarticular process in the clupeomorph *Engraulis*, but a slightly developed elongate process in the clupeomorph *Sardinops* and even within ontogeny of one species (*Tharsis*: PATTERSON & ROSEN 1977, fig. 32 D, E).

Presence of a surangular bone, fused anguloarticular retroarticular, rudimentary postarticular process and posterior position of the opening of the mandibular sensory canal, have been interpreted as primitive for teleosts by PATTERSON & ROSEN (1977). *Protoclupea* and *Domeykos* are more advanced (loss of surangular and retroarticular, separate angular and articular, elongate postarticular process and medial opening of the mandibular sensory canal) in all these features than *Proleptolepis*. They share with *Leptolepis coryphaenoides*, *Tharsis dubius*, *Allothrissops* and *Leptolepides* loss of surangular, an elongate postarticular process, and a medial opening of the mandibular sensory canal, but not a separate retroarticular. *Varasichthys*, another primitive Jurassic teleost from Chile, is more primitive in fused anguloarticular, and short postarticular process, but shares with *Protoclupea* and *Domeykos* the loss of surangular and the medial position of the opening of the mandibular canal.

12, 13. Teeth on parasphenoid and endopterygoid: *Protoclupea* and *Domeykos* lack dentition on parasphenoid and endopterygoid. This feature separates these two genera from *Luisichthys* with a finely dentated

endopterygoid (pl. 5, fig. B, C); the ventral surface of the parasphenoid has not been seen. Lack of dentition in both bones is also found in few other Jurassic (*Tharsis* and *Varasichthys*) and in most extant teleosts. Teeth on parasphenoid are known in *Pholidophorus*, and the primitive teleosts *Leptolepis*, *Leptolepides* and *Allothrissops*. Dentated endopterygoid is not a common condition within fossil and extant teleosts.

14. Gular plate: A gular plate is present in *Luisichthys*, but is absent in *Protoclupea* and *Domeykos*, thus, the two Chilean genera are more advanced in this feature than *Luisichthys*, pholidophorids, and *Leptolepis*.



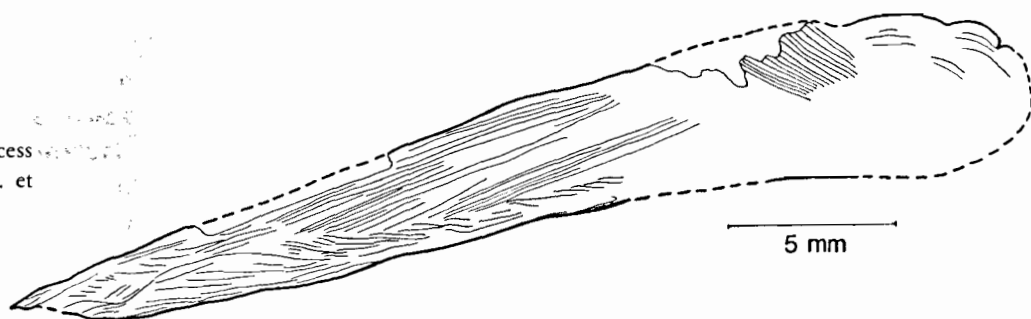
Text-fig. 21. Part of pectoral girdle in external view of some fossil and Recent teleosts. A: *Varasichthys ariasi* (after ARRATIA 1984). B: *Elops saurus atacamensis* (KUVP 71204 a, b). C: *Domeykos profetaensis* (several specimens). D: *Protoclupea chilensis* (mainly KUVP 71205 a, b). E: *Protoclupea atacamensis* (KUVP 71204 a, b). F: *Leptolepides sprattiformis* (after TAVERNE 1981).

15. Postcleithra: *Protoclupea*, *Domeykos* and *Luisichthys*, like most known fossil and Recent teleosts, lack postsupracleithra 1 and 2. These two bones are present in *Varasichthys*, while postsupracleithrum 2 is found only in some Recent teleosts (ARRATIA 1984). *Protoclupea* (text-fig. 21 D, E) and *Domeykos* (text-fig. 21 C) possess the additional postcleithra 4 and 5 which are also present in *Varasichthys* (text-fig. 21 A; at least six postcleithra according to ARRATIA 1984) and in the Recent teleosts *Elops* (text-fig. 21 B; TAVERNE 1974, ARRATIA 1984). Remains of a probable postcleithrum 4 have been discovered in one specimen (U.S.N.M. 18656) of *Luisichthys*, but we are not sure about this feature in this fish because of poor preservation. No additional postcleithra have been described in other fossil or Recent teleosts; three, fewer, or no postcleithra is the common situation. The presence of additional postcleithra has been interpreted as a primitive feature by ARRATIA (1984), therefore *Protoclupea* and *Domeykos* are more primitive than *Leptolepis*, *Leptolepides* and other known European Jurassic teleosts in this character.

16. Lateral line: Information about the point of emergence of the lateral line canal on the supracleithrum in Jurassic teleosts is rare. The lateral line canal emerges from the posteroventral margin of the supracleithrum (text-fig. 21 A, C, D, E) in *Varasichthys*, *Protoclupea* and *Domeykos*, while it emerges in the middle region, or close to the upper third of the supracleithrum in *Leptolepides* (text-fig. 21 F), *Allothrissops* (PATTERSON & ROSEN 1977: fig. 10), *Elops* (text-fig. 21 B). We interpret the presence of a broad, large supracleithrum carrying a lateral line canal emerging on the lower third of the bone, as the primitive condition.

17. Pelvic axillary process: In teleosts such as elopiforms, clupeomorphs (with exception of *Denticeps*), and atherinids, the pelvic fin is associated with an elongate element which lies in a skin fold at the base of the uppermost ray. This element is the pelvic axillary process (text-fig. 22), its structure and length varies in teleosts. The pelvic axillary process is formed by bone in *Domeykos* (text-fig. 22), probably although in *Protoclupea*, and in *Elops*, while it is formed by scales (or only by one scale) in clupeomorphs and atherinids. A pelvic axillary process was not found in *Luisichthys*. We do not know of any other Jurassic teleost with this structure.

Text-fig. 22. Pelvic axillary process of *Domeykos profetaensis* n. gen. et sp. (LBUCH 1-210277-13 a).



18. Neural and haemal arches: Abdominal vertebrae of *Protoclupea*, *Domeykos* (text-fig. 16 A, pl. 4, fig. A) and *Luisichthys* (pl. 5, fig. C) have a similar configuration: a smooth surface, autogenous neural arches and paired neural spines. Autogenous neural arches and paired neural spines are found in *Leptolepis*, *Leptolepides*, *Allothrissops*, *Chongichthys*, and in *Elops*. Autogenous neural and haemal arches in the caudal region occur in *Leptolepis*, *Ascalabos* and *Leptolepides*. Autogenous neural arches and fused haemal arches characterize most of the caudal region of *Allothrissops*. *Domeykos* and *Luisichthys* differ from all other Jurassic teleosts in that neural and haemal arches are fused with the centra (except the last ones) in the caudal region. *Protoclupea* presents a more primitive vertebral column with autogenous neural and haemal arches.

19. Lateral ridge on caudal vertebrae: The caudal vertebrae of *Domeykos* have a longitudinal lateral ridge which is missing in *Luisichthys*. The caudal vertebrae of *Domeykos* and *Luisichthys* constrict strongly the notochord while a weak constriction is produced by abdominal vertebrae.

20. Epineurals: Long epineural bones fused to the neural arches are present in *Domeykos* and *Luisichthys* like in pachyrhizodontoids (FOREY 1977), *Chongichthys* (ARRATIA 1982) and extant clupeomorphs as *Clupea* (*Strangomera*) *bentincki*. Epineural bones attached to the neural arches can be found in *Leptolepis* and *Leptolepides*. Epineural bones fused to the neural arches – or as an outgrowth of the neural arches – are a derived condition which has evolved parallel in different teleost groups.

21. Epipleurals: Few small epipleural bones occur in the middle region of the body in *Domeykos* and probably in *Luisichthys*, a situation like in *Tharsis* and higher teleosts after PATTERSON & ROSEN (1977), nevertheless many euteleostean groups lack the character even in their most primitive members (e. g. Siluriformes). The condition is unknown in *Protoclupea*.

22. Hypurals: The number of hypurals (nine) in *Protoclupea* is identical with that in *Leptolepis coryphaenoides* and higher than that in *Luisichthys* (seven). Pholidophorids have more than ten hypurals. Reduction of the number of hypurals either by fusion or loss is the trend within teleosts. *Protoclupea* shows the primitive condition for teleosts, while *Luisichthys* is closer to extant teleosts (six or five hypurals), where few groups possess still seven hypurals (e. g. *Hiodon alosoides*).

23. Uroneurals: The number of uroneurals varies strongly within teleosts. Eight uroneurals are found in *Pholidophorus bechei*, seven in *Tharsis dubius*, six in *Leptolepis macrophthalmus* and *L. talbragarensis*, five in *Protoclupea* and *Leptolepides*, four in *Luisichthys* and some *Anaethalion*-species (three in others). Three or fewer uroneurals occur in different extant teleost groups. The listing shows that reduction of the number of uroneurals is the trend within teleosts.

24. Extension of first two uroneurals: *Protoclupea* looks more primitive than *Luisichthys* in having two long uroneurals and a small portion of a third one extending forward beyond ural centrum 2. Only the first two uroneurals extend forward beyond ural centrum 2 in *Luisichthys*, a condition defining the supercohort Elopeocephala.

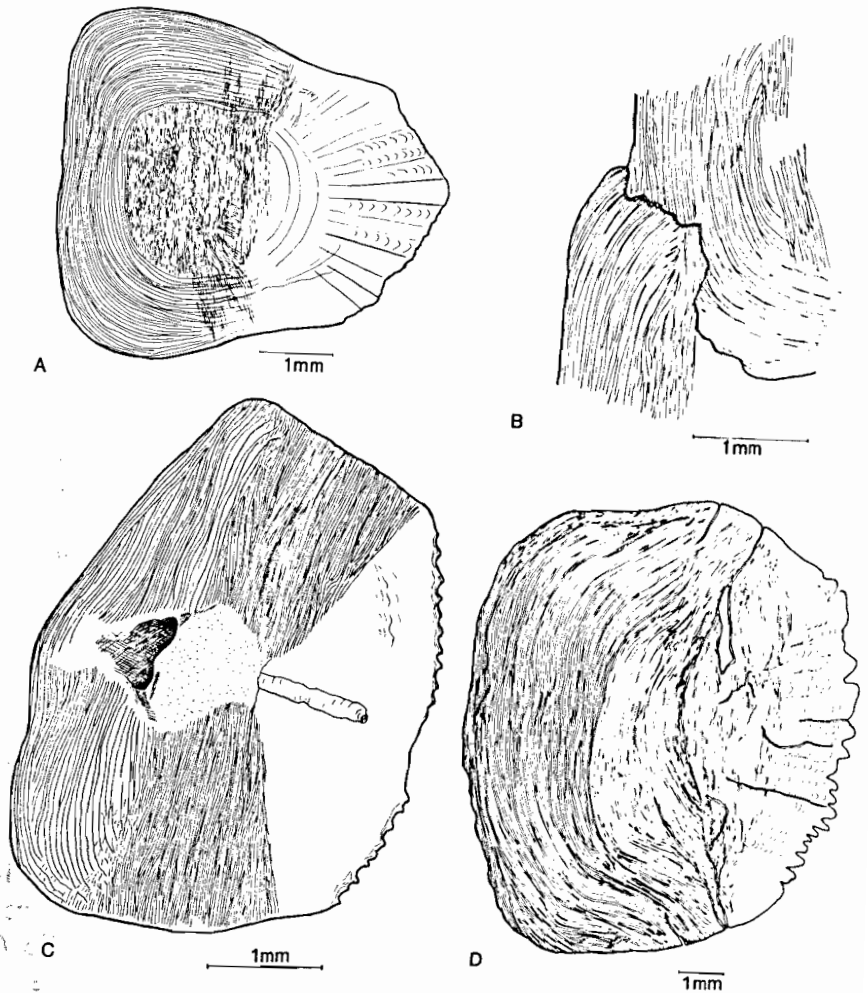
25. Membranous outgrowth: A well developed membranous outgrowth is present on the anterodorsal margin of the first uroneural in *Luisichthys*; a very small membranous outgrowth in *Protoclupea*. A membranous outgrowth characterizes members of the cohort Clupeocephala after PATTERSON & ROSEN (1977). This feature should be checked in other Jurassic teleosts considered as incertae sedis by PATTERSON & ROSEN (1977) before using it as characteristic feature of one group. The variation may be greater than supported at present. For example "*Leptolepis*" *talbragarensis* do not present a membranous outgrowth in the specimen figured by CAVENDER (1970: fig. 1B) while a well developed outgrowth is shown in fig. 46A by PATTERSON & ROSEN (1977).

26. Hypural 2 and ural centrum 1: Hypural 2 is fused with ural centrum 1 in *Luisichthys*; this is a feature found in clupeomorphs. The relationship of hypurals 1 and 2 to ural centrum 1 in *Luisichthys* resembles even more that in the fossil clupeomorphs *Ellimmichthys longicostatus* (PATTERSON & ROSEN 1977: fig. 37) and *Diplomystus* (TAVERNE 1976, GRANDE 1982).

27. Principal caudal rays: The number of principal caudal rays of the lower lobe of the caudal fin in *Protoclupea* (eleven) and in *Luisichthys* (ten) is higher than that of *Leptolepis coryphaenoides* (nine), and closer to that of pholidophorids.

28. Scales: The scales of the teleosts described here from the Late Jurassic of Chile have, in common with *Leptolepides* from the Late Jurassic of Europe (SCHULTZE 1966: fig. 40B, and text-fig. 23C), fine transversely oriented lines crossing the scales from dorsal to ventral border between the anterior and posterior field. These lines are especially conspicuous on flank scales (text-fig. 11A, 17B) while they are restricted to the center of scales from the dorsal or ventral region (text-fig. 17D, E); they can be lacking on scales from some regions. These lines are not

Text-fig. 23. Scales of some fossil and Recent teleosts (lateral line scales or just posterior pectoral girdle). A: *Domeykos profetaensis* n. gen. et sp. (acid prepared specimen LBUCH 1-210277-13). B: *Luisichthys vinalesensis* (U.S.N.M.). C: *Leptolepides sprattiformis* (after SCHULTZE 1966), D: *Dorosoma cepedianum* (KU 0017).



continuous, like the circuli, but interrupted, bifurcating and undulated. The scales of *Luisichthys* show the same feature (text-fig. 23 B).

The lines on the anterior field of clupeomorph scales take the same dorso-ventral direction (text-fig. 23 D) and are commonly compared with the circuli of other teleosts. Nevertheless the scales of some clupeomorphs (text-fig. 23 D, pl. 4, fig. B, C) show both circuli and transversely oriented lines. Here the transversely oriented lines have the same properties as the transverse lines in the middle field of *Leptolepides*.

The comparison shows that *Protoclupea*, *Domeykos* and *Luisichthys* are more advanced in characters 2, 4, 5, 9, 10, 11, 12, 17, 18, 20 and 26 than *Leptolepides*, while *Leptolepides* is more advanced in characters 1, 6, 8, 13, 14, 15, 16, 23 and 27; and the four genera have the same level of development in 3, 13, 14 (*Protoclupea* and *Domeykos*), 21, 23 (*Luisichthys*), 24, 25, and 28. The polarity of many of these characters is unknown. They are only partly identical with those used by PATTERSON & ROSEN (1977) in their phylogenetic arrangement of teleosts. Using the characterization of higher categories of teleosts by PATTERSON & ROSEN (1977: 126), the three genera *Protoclupea*, *Domeykos* and *Luisichthys* are set apart from each other (table 3). *Luisichthys* is more advanced than *Leptolepides*, and has to be placed within the cohort Clupeocephala, or even in the subcohort Clupeomorpha. The problem is only that not all important characters are known in *Luisichthys*, and that *Luisichthys* has still some very primitive characters. The number of principal rays of the lower caudal lobe (character 23 in PATTERSON & ROSEN 1977: 129) is higher even than in *Leptolepis coryphaenoides*, and the number of hypurals equals that of osteoglossomorphs (character 37 in PATTERSON & ROSEN 1977: 130).

These two characters only interfere with a position of *Luisichthys* within Clupeomorpha, contrary *Protoclupea* and *Domeykos* show a mixture of advanced and primitive characters. We will leave *Domeykos* out of further consideration because the most important structure for teleost phylogeny, the caudal skeleton is unknown. *Protoclupea* has a free proximal hypural 1 like clupeomorphs, but the hypural 2 is not fused with ural centrum 1

Table 3. Concordance (+), discordance (–) of features of *Protoclupea*, *Domeykos* n. gen. and *Luisichthys* with those of higher teleosts (according to PATTERSON & ROSEN 1977:126). ?: unknown; §: other condition.

	<i>Protoclupea</i>	<i>Domeykos</i>	<i>Luisichthys</i>
Supercohort Elopocephala:			
1. Only two uroneurals extend forward beyond U2	–	?	+
2. Epipleural bones well developed	?	+ (poorly developed)	+ (uncertain)
Cohort Clupeocephala:			
1. Angular and articular fused	–	–	?
2. Retroarticular excluded from the articular facet for the quadrate	§	§	?
3. Tooth-plates fused with first three pharyngobranchials and fifth ceratobranchial	?	?	?
4. Neural arch over U1 reduced or absent	+	?	+
5. Anteriorly directed membranous outgrowth developed from the anterodorsal margin of first uroneural	+	?	+
6. Six hypurals	–(9)	?	–(7)
Subcohort Clupeomorpha:			
1. Second hypural fused with U1/ first hypural free proximally	–/+	?	+/+
2. Supratemporal commissure passing through parietal	§	§	– (over and behind)
3. Otophysic connection involving a diverticulum of the swimbladder that penetrates the braincase	?	?	?

and the supratemporal commissure seems to pass further posteriorly over the extrascapulars (the same in *Domeykos*). *Protoclupea* possess two characters of clupeocephalans, but is much more primitive in having nine hypurals instead of six. The retroarticular is not developed or lost in *Protoclupea* and *Domeykos* so that clupeocephalan characters 41 and 42 of PATTERSON & ROSEN (1977) cannot be evaluated. *Protoclupea* with three uroneurals extending forward beyond ural centrum 2 does not fulfill even the basic character of the supercohort Elopocephala so that the clupeocephalan characters have to be explained as parallel, and the lack of retroarticular as an autapomorphy of *Protoclupea* and *Domeykos*. *Protoclupea* possess one osteoglossomorph character, but is more primitive in another. Where known, *Protoclupea* has the characters of *Tharsis* with exception of character 33 and 31 (PATTERSON & ROSEN 1977:129) while *Domeykos* agrees with *Tharsis* here, too. In conclusion, *Protoclupea* and *Domeykos* occupy a position like *Tharsis dubius* in the scheme of PATTERSON & ROSEN (1977:fig. 54).

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Legends of Plates

Plate 1

Protoclupea chilensis (holotype). A: Head. B: Complete specimen. (Scales equal 1 cm).

Plate 2

Protoclupea atacamensis n. sp. (holotype). A: Head. B: Counterpart. (Scales equal 1 cm).

Plate 3

Domeykos profetaensis n. gen. et sp. (holotype). A: Latex cast of complete specimen, dusted with NH₄Cl. B: Head of counterpart under alcohol. (Scales equal 1 cm).

Plate 4

Domeykos profetaensis n. gen. et sp. A: Cranium and vertebrae (acid prepared specimen LBUCH 260972 a). B–C: *Diplomystus dentatus* (KUVF 17365), scales of lateral side in the middle part of the body (dusted with NH₄Cl).

Plate 5

Luisichthys vinalesensis (U.S.N.M. 18656). A: Neurocranium in posterior view. B: Neurocranium in lateral view. C: Head with pectoral girdle. (Dusted with NH₄Cl; scales equal 1 cm).