

THREE-DIMENSIONAL MUSCLE PRESERVATION IN JURASSIC FISHES OF CHILE

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ABSTRACT

Late Jurassic fishes of Northern Chile are preserved in calcareous concretions within black shales of Oxfordian age. Co-occurring invertebrates (decapod crustaceans, ostrean bivalves, and algae) indicate benthic life. Soft tissues of the fishes were impregnated by calcium phosphate during life, whereas the decay of the remaining soft tissue induced the formation of the calcareous concretions around the fishes. Occurrence of vitamin D₃ or a hydroxylated form of this vitamin is postulated to have occurred in the Jurassic phytoplankton; vitamin D₃ induced a break-down of the regulation of the calcium metabolism in the fishes as is the case in calcinosis of cattle. High concentration of phosphate in phytoplankton of the upwelling zone on the western margin of the shelf of South America could explain the additional supply of phosphate in the fossil fishes which is missing from surrounding concretions and sediment.

Key words: Preservation, Soft tissue, Impregnation in life (calcinosis), Teleostean fishes, Oxfordian, Northern Chile.

RESUMEN

Los peces del Jurásico Superior del norte de Chile están preservados en lutitas negras. La presencia de invertebrados (crustáceos decápodos, ostras y algas) junto con los peces es indicio de vida bentónica. Los tejidos blandos de los peces se impregnaron con fosfato de calcio en vida de los individuos, mientras que la descomposición de otros tejidos blandos indujo a la formación de concreciones calcáreas alrededor de los peces. Se postula la presencia de vitamina D₃ o de un compuesto hidroxilado de ella en el fitoplancton jurásico, lo que produjo el quiebre de la regulación del metabolismo del calcio en los peces; una situación similar a la presentada en la calcinosis en vacunos. El elevado contenido de fosfato, en el fitoplancton de la masa de agua vertical del borde oeste de la plataforma continental de América del Sur, explicaría el suplemento adicional de fosfato en el pez fósil, el que está faltando en las concreciones y en el sedimento.

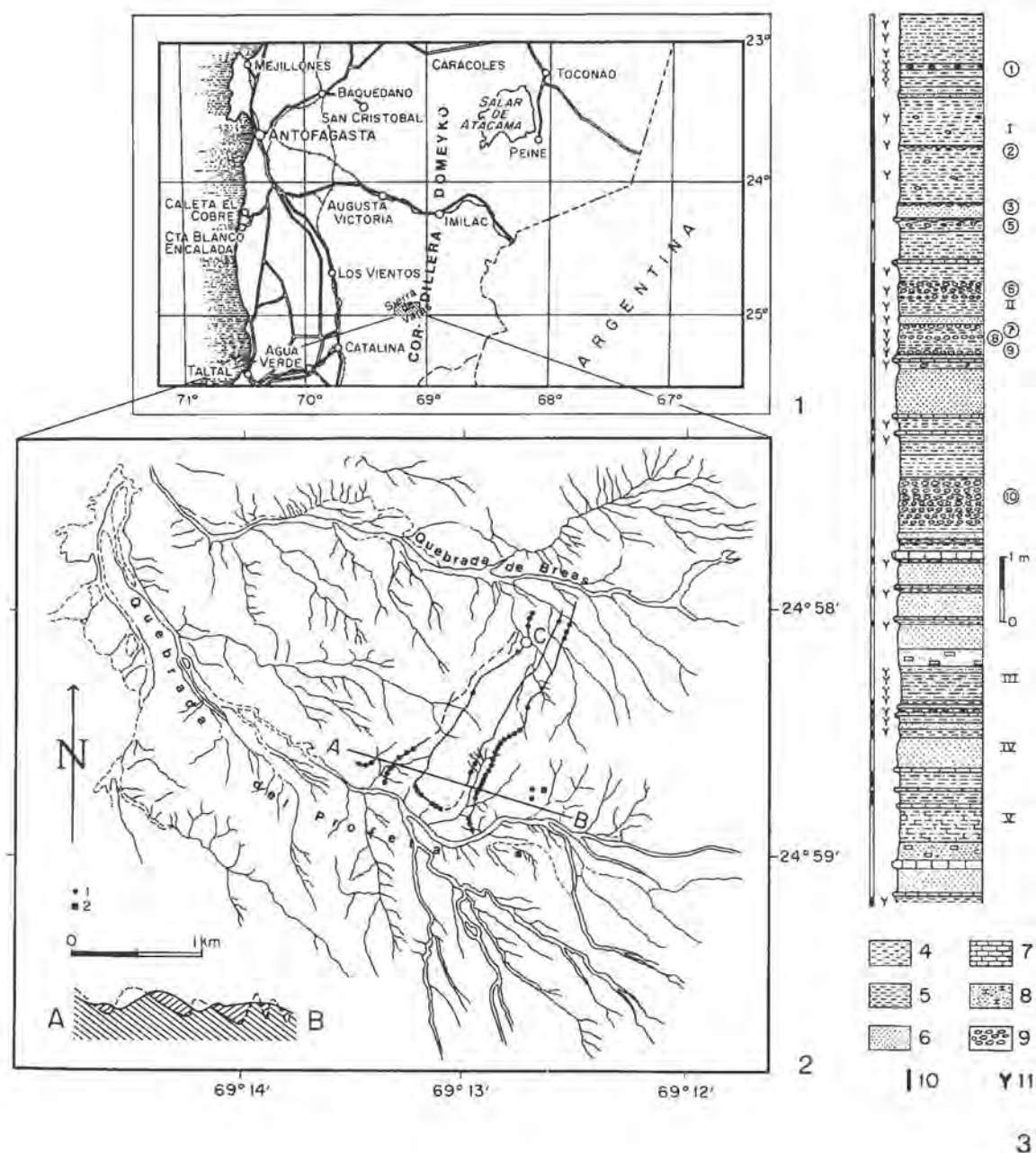
Palabras claves: Preservación, Tejidos blandos, Impregnación en vida (calcinosis), Peces teleósteos, Oxfordiano, Norte de Chile.

INTRODUCTION

Jurassic fishes have been known from northern Chile since the 1950's (Biese, 1957, 1961). In a southern continuation of Biese's localities (Cerritos Bayos, at the northern end of Cordillera Domeyko), Dr. G. Chong discovered, early in the 1970's, a rich new locality in the Sierra de Varas of the Cordillera de Domeyko. The first fish, the type specimen of *Bobbichthys opercularis*, was found by R. Arias. The diverse fish fauna was collected north of Quebrada del Profeta in different tributary valleys (approximate area from 24°58' to 24°59' S

and 69°12' to 69°14' W; Fig. 1) of the Quebrada del Profeta in the south and of the adjacent quebrada in the north. The following is a short outline of the geology, fauna and paleoenvironment of the locality.

The teleost fishes of the Cordillera de Domeyko are important in a phylogenetic context for studies of early teleosts (Arratia, 1984 and in press; Arratia and Schultze, 1985). In addition, they show exceptional preservation. Usually, only hard parts of organisms are preserved as fossils, but the fossil



FIGS. 1-3. Quebrada del Profeta, Sierra de Varas, Cordillera de Domeyko, northern Chile. **Fig. 1.** Geographic position of Quebrada del Profeta. **Fig. 2.** Outcrops of fish bearing layers. **A-B** : Section to demonstrate the reappearance of the same horizon by intersection between folds and topography; **C** : Section (Fig. 3) south of Quebrada de Breas with repetition of horizons with concretions (1-10); 1. Concretions with fossil fishes; 2. Concretions with reptile remains. **Fig. 3.** Section C with vertical distribution of concretions: 4. Siltstone; 5. Shales; 6. Fine-grained sandstone; 7. Limestone; 8. Calcareous sandstone; 9. Concretions; 10. Black colored rocks; 11. Gypsum; Encircled numbers (1-10): Horizons with concretions; Roman numbers (I-V): Sediment samples taken.

fishes of Cordillera de Domeyko, with three-dimensionally preserved muscles, look as if they had only recently died. Preserved are muscle fibers with mitochondria and nuclei, blood vessels, swim bladder, intestine and melanophores. These preserved soft tissues will be described, trying to explain how such unusual preservation could occur.

In 1978, the author collected in Quebrada de San Pedro, Caracoles, and in Quebrada del Profe-

ta, Sierra de Varas, with Professor G. Arratia, and Dr. A. Quinzio and Mr. L. Santander, both of the Departamento de Geología, Universidad el Norte, Antofagasta. Field work was organized by Dr. G. Chong, Departamento de Geociencias, Universidad del Norte, Antofagasta, and supported by the Alexander von Humboldt Foundation, Germany, and the Universidad del Norte, Antofagasta, Chile.

MATERIALS AND METHODS

All the material was found in concretions and collected in the Oxfordian rocks north of Quebrada del Profeta, Cordillera de Domeyko, northern Chile. The concretions were split in the field if they were not already opened by weathering. The material is deposited in three collections:

KUVP Division of Vertebrate Paleontology, Museum of Natural History, The University of Kansas, Lawrence, Kansas.

LBUCH Laboratorio de Biología, Universidad de Chile, Santiago-Sur (most specimens).

R Departamento de Geología, Universidad de Chile, Santiago, Chile.

A few of the specimens were prepared with acetic acid, and scanning electron microscope pictures were taken from these specimens at the Geologisch-Paläontologisches Institut, Universität Göttingen (SEM-prepared pieces of specimens and negatives were deposited at the department in Göttingen).

X-ray diffraction was performed on sediment samples I to V (Fig. 3), on one concretion (LBUCH 1-210277-13 = paratype of *Domeykos profetaensis*) and on muscles (LBUCH 1-210277-13 = paratype of *Domeykos profetaensis* and LBUCH 4277 = paratype of *Varasichthys ariasi*) and bones (LBUCH 1-210277-13 and 4277) at the Institut für Geologie und Dynamik der Lithosphäre, Göttingen.

For comparison, concretions of the Cretaceous Santana Formation of Brazil were studied at the Field Museum of Natural History, Chicago, Illinois (FMNH). Samples from concretions in the FMNH collection and from one sample from the American Museum of Natural History, New York (AMNH) were processed by X-ray diffraction.

Drawings were prepared by the author with drawing attachment to a WILD stereomicroscope M5A, photographs taken with a Nikon FM 35 mm camera.

GEOLOGY AND PALEOENVIRONMENT

Concretions which contain fishes occur in different horizons (Fig. 3) of the Oxfordian (Chong, 1977) sequence north of Quebrada del Profeta, Sierra de Varas. The author counted 10 horizons. Within these horizons, the frequency of concretions changes from north to south. Places with high numbers of concretions contain a low number of fossils. (The black dots in Fig. 2 mark the occurrences of concretions with fish fossils; concretions occur along the whole outcrop of the horizon.) The concretions occur in black sandy shales which are rich in gypsum (occurs as a secondary formation in thin layers within the shales

and sometimes around the concretions). These shales are intercalated by fine grained calcareous sandstones which predominate in the lower part of the section, and by thin limestone layers. The section (Fig. 3) has been measured in a tributary of the Quebrada de Breas, north of Quebrada del Profeta, where it was not obscured by debris from higher horizons. Here, the concretions (horizon 10) are all large (over 10 cm long and 4-8 cm thick), numerous and less fossiliferous than further south. In the southern part, just north of Quebrada del Profeta, one can distinguish a main horizon (Fig. 3, No. 10) with large grey concretions (up to 25 cm long,

15 cm wide and 8 cm thick), from two horizons with small black concretions (below 10 cm long, 7 cm wide, 4 cm thick). The horizon (Fig. 3, Nos. 7-9) with black concretions above the main horizon has many more fossil fishes than that below the main horizon. Reptile bones are present, but are only partially enclosed in concretions. The concretions were not *in situ*, having been collected from the surface of often steep slopes and therefore of unknown relationship to specific horizons in the section.

The same sequence appears on both sides of the deeply cut valleys and in consequent tributary valleys because the whole sequence is strongly folded (cross section A-B in Fig. 2) [and not mainly faulted as described by Chong (1977; *in* Arratia *et al.*, 1975b; *in* Chong and Förster, 1976)]. The folding is caused by compression from the east where Triassic rocks overthrust the Jurassic sequence, and Paleozoic volcanic and magmatic rocks overlie the Triassic sequence (Chong, 1977). The intensity of folding of the Jurassic rocks increases eastward within a short distance, so that one encounters many repetitions of the same horizon in the area where the reptile bones were found.

The fossiliferous beds are Oxfordian, but the whole ammonite fauna must be described in order to identify the zone within this stage. The age of the horizon was given as middle to late Oxfordian (Chong, 1977), but early to middle Oxfordian in Chong and Förster (1976). Within the sequence, Chong (*in* Arratia *et al.*, 1975b) cited different ammonites, those similar to *Perisphinctes* (Pl. 1, Fig. 5) occur in middle Oxfordian sediments in northern Chile (von Hillebrandt, 1988, written commun.). In Chong and Förster (1976), Chong cited *Evaspidoceras perarmatum* for middle Oxfordian *transversarium* zone, even though it could be correlated with the early Oxfordian *cordatum* zone.

The fauna of the main concretion-producing horizon (Fig. 3, No. 10) consists of crustaceans, fishes, ammonites, bivalves, teuthoids and *Lingula*, listed in order of decreasing frequency. One specimen of a decapod crustacean, *Chilenophoberus atacamensis*, was described as a unique specimen by Chong and Förster (1976). In contrast, it was found that decapod crustaceans are the most common fossils in the concretions. They occur together with the fishes as complete specimens (Arratia, 1987; Pl. 3, Fig. 1), but in most cases, as disintegrated parts which could be mistaken for

shriveled fish scales. The abdomen, telson and uropods (Pl. 1, Fig. 4) are frequently found between the shriveled segment parts of crustaceans. The ammonites (Pl. 1, Fig. 5) are three-dimensionally preserved, occur alone in concretions or together with other ammonites or fishes. They are preserved together with aptychus and siphon, sometimes the aptychi are found separately. Ostrean bivalves occur singly, but in most cases as clusters. Bivalves attached to ammonites were not observed; in some cases large ostreans occur with small perisphinct ammonites in the same concretion. Besides ostrean bivalves, '*Posidonia*' (Pl. 1, Fig. 3), in different sizes, cover horizons which are enclosed in the concretions. Very few teuthoids (Pl. 1, Fig. 2) have been discovered, they seem to represent *Plesiotheutis* or a closely related form. *Lingula* is known from a single specimen. Common within the concretions and on their outer surfaces are coprolitic masses without internal structure (Pl. 1, Fig. 6).

The important component of the fauna is fishes (Arratia, 1987) of which the teleosts (Arratia *et al.*, 1975a, b, c; Arratia, 1981, 1982, 1984, 1986; Arratia and Schultze, 1985) and one halecostome (Arratia and Schultze, 1987) have been described. The fish fauna (compilations see Arratia and Chong, 1979; Gasparini, 1979; Arratia, 1985, 1987) includes:

- a. Undescribed pycnodonts (Arratia, 1987, Pl. 3, Fig. 3)
- b. Semionotid halecostome: *Lepidotes* sp. (Arratia, 1987, Pl. 4, Fig. 1)
- c. Large undescribed pachycormid
- d. Pachycormid halecostome (Arratia, 1987, Pl. 5, Fig. 1)
- e. Halecostome *Atacamichthys greeni* Arratia and Schultze, 1987 (Figs. 1-15, 16B, 19B)
- f. Teleosts (listed alphabetically):
 - *Antofagastaichthys mandibularis* Arratia, 1986 (Figs. 7-12, 13A, Pls. 3B, 4; Arratia, 1987, Fig. 3D)
 - *Bobbichthys opercularis* (Arratia, Chang and Chong, 1975) (Arratia *et al.*, 1975a, Figs. 2, 3, Láms. 1-2; Arratia, 1986, Figs. 1-5, 6D, Pls. 1, 2, 3A; 1987, Fig. 3B, Pl. 5, Fig. 3)
 - *Chongichthys dentatus* Arratia, 1982 (Figs. 2-14, 15A; Arratia, 1987, Figs. 4B, 5D, 9, Pl. 1, Fig. 6)
 - *Domeykos profetaensis* Arratia and Schultze, 1985 (Figs. 4C, 6C, 12-17, 21C, 22, 23A, Pls. 3,

- 4; Arratia, 1987, Figs. 5C, 8, Pl. 1, Fig. 5, Pl. 6 Fig. 1)
- *Pholidophorus domeykanus* Arratia, Chang and Chong, 1975 (Arratia *et al.*, 1975b, Fig. 3, Láms. 1, 2; Arratia, 1987, Pl. 6, Fig. 2)
 - *Protoclupea atacamensis* Arratia and Schultze, 1985 (Figs. 4B, 5B, 6B, 9-11, 21E, Pl. 2)
 - *Protoclupea chilensis* Arratia, Chang and Chong, 1975 (Arratia *et al.*, 1975c, Figs. 2, 4, 6, Láms. 1-4; Arratia, 1982, Fig. 15B; 1986, Fig. 6F; 1987, Figs. 3C, 4A, 5B, 7, Pl. 2, Fig. 2, Pl. 5, Fig. 4; Arratia and Schultze, 1985, Figs. 2-3, 4A, 5A, 6A, 7, 8, 21D, Pl. 1)
 - *Varasichthys ariasi* Arratia, 1981 (Figs. 2-19, Pl. 1-7; Arratia, 1982, Fig. 15C; 1984, Figs. 1-6, 7F, 10A, 11A; 1986, Fig. 6E; 1987, Figs. 3A, 5A, 6, Pl. 5, Fig. 2; Carroll, 1987, Figs. 7-16; Arratia and Schultze, 1987, Fig. 19C).

All teleosts, except *Protoclupea*, are unique to the localities north of Quebrada del Profeta. *Protoclupea* is the only teleost known from further north in Biese's localities in Cerritos Bayos (Arratia, 1987, Pl. 2, Fig. 4). At the north end of Cordillera de Domeyko in Quebrada de San Pedro at Caracoles (Fig. 1), the large undescribed pachycormid of Quebrada del Profeta occurs more frequently in the Oxfordian than in Quebrada del Profeta; in addition, pycnodonts, crocodiles and ichthyosaurs have been found in very large concretions at that locality. Ichthyosaur vertebrae and one large reptile bone are known from Quebrada del Profeta. The fishes in the small black concretions (Fig. 3, No. 7-9) are not yet studied. All are teleosts. The author found no invertebrates in these concretions.

The co-occurrence of crustaceans and fishes is not uncommon in the fossil record (Glaessner, 1965); another recently discovered locality is the Jurassic site in Osteno, Italy (Pinna, 1985). These fish-crustacean shales are not concretion locali-

ties and most of them preserve calcitic hard parts only as impressions. Pinna (1985) pointed out that the fauna of Osteno contains a large percentage of benthic elements (85.5%) so that benthic life must have been possible, and reducing conditions began within the sediment and not above it.

Black bituminous shales are usually interpreted as deposits of a sea basin with stagnant, oxygen deficient bottom waters (Seilacher and Westphal, 1971; Seilacher *et al.*, 1985). Since bottom conditions are hostile to most organisms, benthic forms may have been restricted to drifting woods or occurred as epizoans on ammonites. That was also the interpretation of Chong and Förster (1976) for the deposits at Quebrada del Profeta. However, we now know that decapod crustaceans are the most common fossils at the locality, and their preferred mode of locomotion, that of crawling on the substrate, indicates that they may have lived in the branched algae (Pl. 1, Fig. 1: *cf. Cladophora*, Chlorophyceae) growing on the sea floor. A further indication of bottom life are ostreans which are not attached to ammonites; they sometimes occur with ammonites in the same concretion. When they co-occur, the ostreans are larger than the small perisphincts. Most ammonites are thought to be bottom dwellers (Lehman, 1981, p. 179) more than free swimming forms. In summary, the presence of decapods, other invertebrates and algae, favors an interpretation of the paleoenvironment like that for the Posidonienschiefer in southern Germany by Kaufmann (1981) and Lehmann (1981) with bottom life. The oxic/anoxic boundary was within the sediment, so that benthic life was possible for the Oxfordian fish deposits in the Sierra de Varas. Only a careful recording of all sedimentological and paleontological data throughout the sequence will result in a more accurate interpretation of the paleoenvironment.

PRESERVATION OF SOFT ANATOMY

Fossils usually represent only the hard parts of an organism. Thus all additional information, such as color pattern, tracing of the soft body and especially preservation of soft tissues, gets special attention. The original soft tissue can be preserved under special conditions; the main requirement be-

ing stopping or retarding oxidation and bacterial activity by freezing or drying (mummies), or embedding (e.g. amber). In other cases, soft tissue is replaced and not preserved in its original composition. These replacements can occur post mortem by mineral infiltration or bacterial activity, and dur-

ing life (calcinosis).

Preservations of original tissue is found only in very recent deposits, Holocene and Pleistocene. Famous occurrences are the frozen mammoth cadavers with preserved muscles (Zimmermann and Tedford, 1976), but only some muscles retain identifiable histological structures whereas most tissues are completely disintegrated or partly replaced through decomposition. Further back in geologic time, the Eocene deposits (Geiseltal and Messel) of Germany present two kinds of preservation, not including preservation of original material such as hair in Messel (Richter and Storch, 1980) or keratin in Messel (Koenigswald *et al.*, 1981) and Geiseltal (Voigt, 1937). Wuttke (1983) demonstrated that the preserved 'soft tissue' in the deposits of Messel is only a ghost of the original tissue. Mineralized bacteria have pseudomorphosed the original soft tissue. A similar process of lithification has been demonstrated by Willems and Wuttke (1987) for 'soft tissue' preservation of Permian tetrapods of the Saar-Nahe-basin in W-Germany; there the substituted mineral is apatite. They argued that the ellipsoid shape of the spherulite is indicative of bacteria. The vertebrates in both localities (Messel and Saar-Nahe-basin) are flattened, and nearly two-dimensional. The same interpretation was given for three-dimensional muscle preservation in the Cretaceous concretions from Araripe, Brazil, by Martill (1988).

In contrast, a bacterial substitution is not feasible for the exceptionally well preserved soft tissue from the Eocene of Geiseltal. Cells with nuclei, melanophores, muscle striation, etc., appear much as they do in extant soft tissue (Voigt, 1934, 1935, 1936, 1937, 1938a, b, 1949; Brenner, 1939). Voigt (1937) postulated a two step process, first a kind of tanning, subsequently followed by silicification. Both processes are, of course, diagenetic processes found in reducing environments, and leading to nearly two-dimensionally preserved soft tissue.

Muscle fibers with striation have been described not only in Pleistocene and Tertiary deposits, but also in Cretaceous (Martill, 1988), Jurassic (Reis, 1888, 1893, 1895; Rauff, 1895; Ammon, 1896; Schweizer, 1964; Wykoff, 1972; Pinna, 1985), Carboniferous (Traquair, 1884) and Devonian (Jaekel, 1892; Dean, 1902, 1909) fishes. These muscles are always preserved as phosphate (apatite). The phosphate could have been

formed post mortem, the common explanation, or in the living organism (calcinosis).

POST MORTEM REPLACEMENT

Sea water has, even in upwelling zones, too low a concentration of phosphorus for precipitation of phosphate, therefore, the phosphorus must be enriched, possibly through decomposition of organic matter, either from carcasses or from fecal deposits (Burnett, 1977). A good example of such a relationship was given by Bate (1972) for the replacement of original calcium carbonate and chitin by apatite in ostracodes from the Cretaceous Santana Formation of Brazil. Only ostracods feeding on a fish carcass (two concretions of thousands) show the exceptional preservation, whereas other ostracodes lying outside the fish in the calcareous concretions do not show phosphatic preservation. Bate (1972) spoke of "chance mineralization under unique conditions". In this case, and other cases of exceptionally preserved arthropods, and especially in the muscles described in the present study, the phosphatization must have taken place before or immediately after death, prior to any considerable decay (Müller, 1979). The mineralization of muscles is not a simple replacement of one mineral by another as in the case of the ostracodes (Bate, 1972), but an infiltration of soft tissue by phosphate salts without distortion of the microstructure.

DECAY-INDUCED REPLACEMENT

Usually, soft tissue preservation is considered the result of mineral precipitation associated with incipient decay (beginning decomposition of carcasses). Calcium precipitation under such conditions is known from Recent fishes (Berner, 1968; Wilcox and Effler, 1981). Calcite precipitation is to be expected under marine conditions because concentrations of bicarbonate ions exceed those of phosphate in the sea and the sediment (Gulbrandson, 1969). In contrast, phosphate precipitation requires enrichment of the pore water in phosphate. The phosphate may be derived from decomposition of marine plankton (Gulbrandson, 1969) or other organisms (Burnett, 1977; Lucas and Prévôt, 1984), at the same time, anoxic conditions are necessary for precipitation. This process requires a very fine line between decomposition of soft tissue to produce the needed amount of phosphate

and precipitation of phosphate to preserve the soft tissue before its complete decay.

INFILTRATION

As a first condition, Reis (1893, 1895) argued that the base substances for his 'myophosphorit' (apatite) must be present shortly after the death of the animal before decomposition starts. Decomposition forms gases which distort the structures of the soft tissue. Second, Reis argued that the phosphate derived from the vertebrate remains in the intestine of fishes with preserved muscles, and he showed a connection between phosphatized muscle tissue and carnivorous behavior; only carnivorous fishes or reptiles feeding on other fish show muscle preservation. After discovering muscle preservation in pycnodonts, Reis (1898) argued then that pycnodonts with their crushing dentition for a bivalve diet, were partially carnivorous or were also feeding on carcasses.

REPLACEMENT BY BACTERIA

Early phosphatization by bacterial activity was thought to be responsible for the preservation of muscle tissue in fishes from the Cretaceous Santana Formation of Brazil (Martill, 1988). Martill (*op. cit.*) described a sequence from mass mortality, change of bottom water to anoxic conditions by decomposition of carcasses, to the covering of carcasses by a cyanobacterial ? mat. By sedimenta-

tion, the carcass passes through the oxic/anoxic boundary where phosphate is concentrated by bacterial breakdown of the original tissue. At the same time, bacteria deposit phosphate to preserve the fine structure of muscles.

Allison (1988) could not determine which of the three post-mortem processes (1. Decay-induced; 2. Bacterial fixation; 3. Formation of intermediate organic/inorganic complexes) is responsible for phosphatization of soft tissue; he argued an experimental approach to develop a model.

IMPREGNATION OF MUSCLES IN LIFE

The preservation of the microstructure of muscles, down to the cellular level, may be more readily explained by the phosphatic impregnation of muscle tissue in life. Such cases are known (calcinosis) in extant terrestrial mammals and are caused by feeding on plants which contain vitamin D₃ (Morris, 1982; Boland, 1986). Vitamin D₃ of plants breaks down the mechanism of phosphate regulation in the intestine so that the phosphate is absorbed and deposited in various soft tissues as apatite (Capen *et al.*, 1966). Vitamin D₃ is presently known to occur only in angiosperms within plants. The application of *in vivo* phosphatization as the mechanism for the preservation of phosphatic microstructure in marine environments postulates the occurrence of vitamin D₃ in plankton.

JURASSIC FISHES OF NORTHERN CHILE

PRESERVED SOFT TISSUE

Different soft tissues are preserved in the Jurassic fishes of Quebrada del Profeta. Starting from outside to inside, we can observe skin, superficial muscles, myomeres, muscles of fins, blood vessels, swim bladder and intestine. Not every part is preserved in every fish; the most obvious structure preserved in nearly all fishes are the myomere muscles. Myomere muscles (Fig. 5; Pl. 2) appear in figures in the systematic descriptions of the following fishes: *Atacamichthys greeni* (Arratia and Schultze, 1987, Fig. 1), *Bobbichthys opercularis* (Arratia, 1986, Pl. 1, Fig. B), *Domeykos profetaensis* (Arratia, 1987, Pl. 6, Fig. 1), *Protoclupea chilensis* (Arratia *et al.*, 1975c, Lám. 4; Arratia and

Schultze, 1985; Pl. 1, Fig. B; Arratia, 1987, Pl. 2, Fig. 2; Pl. 5, Fig. 4), *Varasichthys ariasi* (Arratia, 1981, Pl. 3, Fig. B) and indet. (Arratia, 1987, Pl. 2, Figs. 1-3). The swim bladder can be seen in figures of *Protoclupea chilensis* (Arratia *et al.*, 1975c, Lám. 1; Arratia and Schultze, 1985, Pl. 1, Fig. B), and *Varasichthys ariasi* (Arratia, 1981, Pl. 3, Fig. 1). Intestine, blood vessels and melanophores (Arratia, 1987, Pl. 3, Fig. 2) are mentioned in Arratia (1987, p. 261).

SKIN

Below the scales lie a more or less structureless mass (Pl. 3, Fig. 2) which melanophores includes (Pl. 3, Fig. 1). It shows the impressions of the scales which may represent the inner side of

FIG. 4. Teleost indet. LBUCH 15-260972. Muscles of the dorsal fin. **de.d**: depressor dorsalis; **d.ra**: distal radial; **e.d**: erector dorsalis; **f.r. 1, 2**: fin ray 1, 2; **i.d**: inclinador dorsalis; **p.ra**: proximal radial; **pt**: pterygiophore.

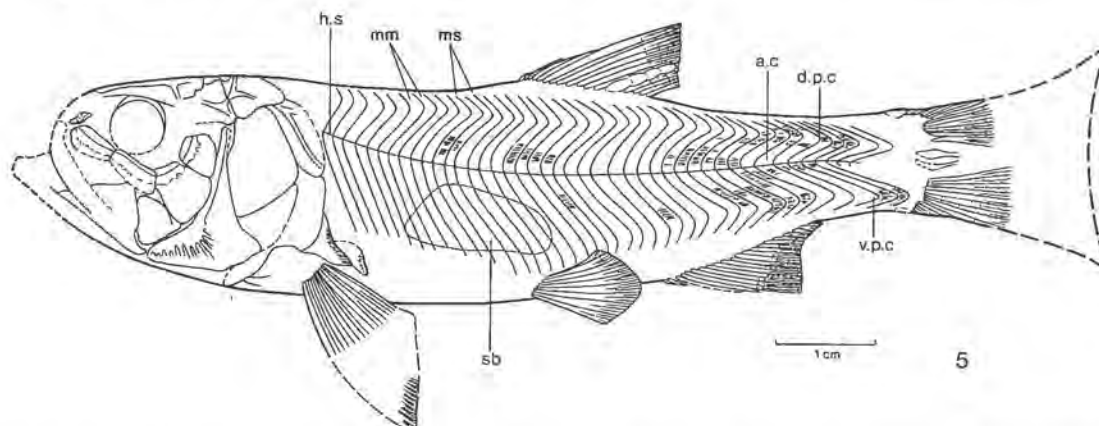
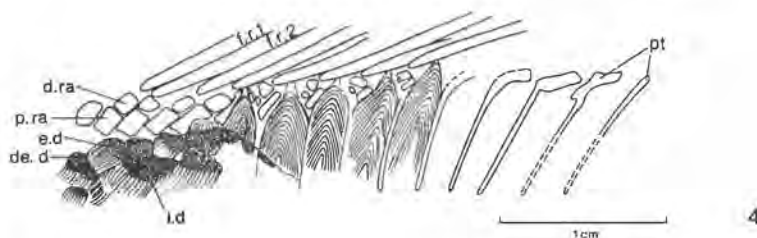


FIG. 5. *Protoclupea chilensis* Arratia et al., 1975c. Arrangement of myomeres in R-396 (holotype) and KUVF 71205b superimposed on reconstruction by Arratia and Schultze (1985, Fig. 2). **a.c**: anterior cone; **de.d**: depressor dorsalis; **d.p.c**: dorsal posterior cone; **d.ra**: distal radial; **e.d**: erector dorsalis; **f.r. 1, 2**: finray 1,2; **h.s**: horizontal septum; **i.d**: inclinador dorsalis; **mm**: myomere; **ms**: myoseptum; **sb**: swim bladder; **v.p.c**: ventral posterior cone; **p.ra**: proximal radial; **pt**: pterygiophore.

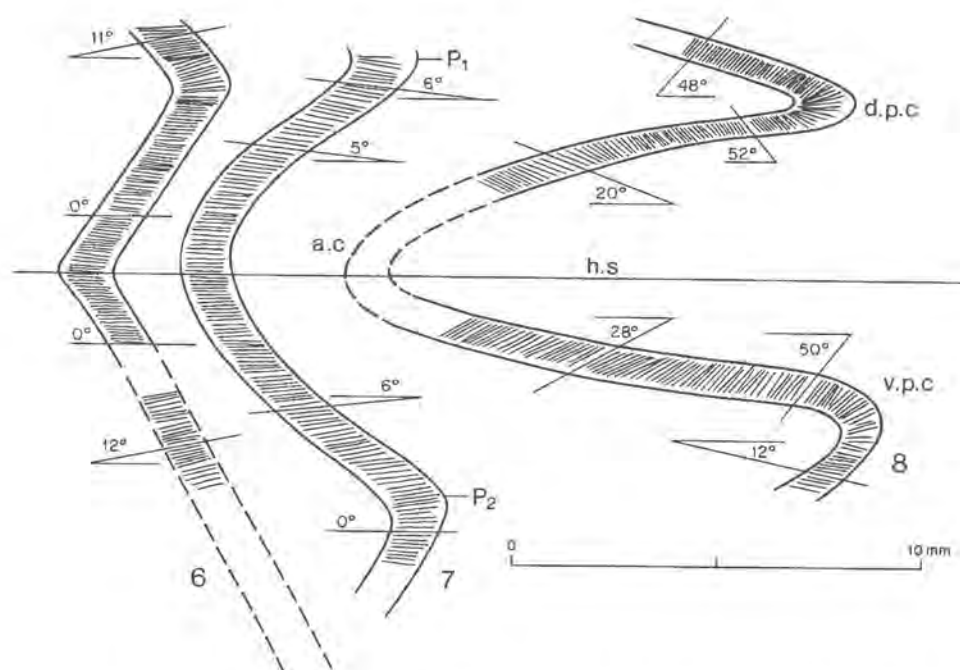
the scale pocket. The author has never observed this mass to cover the scales, so that only the lower part of the dermis with its melanophores seems to be preserved. The melanophores are always in a contracted phase. Below the deeper dermis, a thin layer of subcutaneous muscle appears (Pl. 3, Fig. 1); its fibers run dorso-ventrally.

MUSCLES

The best preserved muscles are those of the myomeres (Fig. 5, Pl. 2). They can be observed in most fishes from the locality in Quebrada del Profeta. The myomeres are typically Σ -shaped. The Σ -shape is displayed best in the caudal region. The horizontal septum runs in the middle of the body in the posterior abdominal and caudal regions; it runs anterodorsally in the anterior abdominal region. Each myomere is folded with cones alternatively directed anteriorly and posteriorly (Fig. 8). The ventral posterior cones are straightening out anteriorly, and in most cases they are not visible or preserved anterior to the pelvic fin (Fig.

6). The central anterior cone seems to be simple, not double, even in the caudal region. The dorsal posterior cone straightens out anteriorly, but is developed up to the head (Fig. 6). The myosepta are not preserved, they appear as rock(lime)-filled spaces. This space between the myomeres varies between specimens. This could indicate different stages of contraction or different degrees of mineralization. The distance between myomeres within each specimen are the same. Equal distance favors the interpretation of different degree of mineralization in different specimens. For each specimen a finite amount of calcium-phosphate was available; however, this amount varied from specimen to specimen.

Dietz (1913) introduced a ratio to express the folding of a single myomere. He related the length of a myomere to the direct distance from its dorsal to its ventral recurving. Here the shorter distance from the apex of the dorsal posterior cone (P_1) to the apex of the ventral posterior cone (P_2) is used, because the recurving ends of the myomeres are



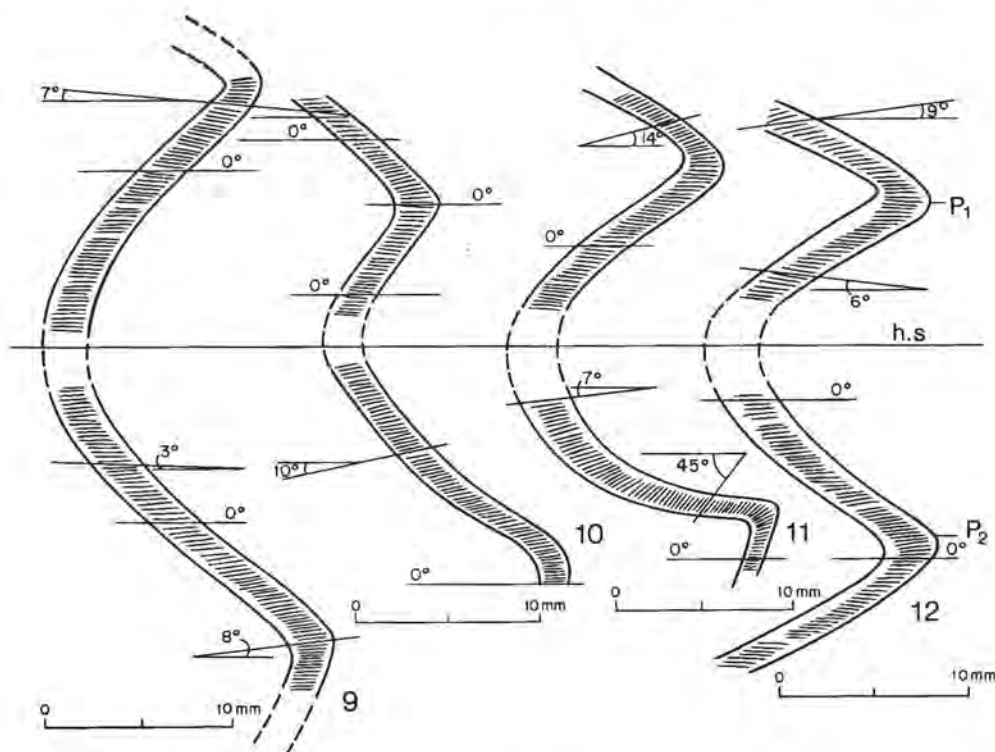
FIGS. 6-8. *Protoclupea chilensis* Arratia et al., 1975. Holotype R-396. Fig. 6. Myomere of anterior abdominal region. Fig. 7. Myomere of anterior caudal region behind dorsal fin and dorsal anterior part of anal fin. Fig. 8. Myomere of posterior caudal region. a.c: anterior cone; d.p.c: dorsal posterior cone; h.s: horizontal septum; P₁: apex of dorsal posterior cone; P₂: apex of ventral posterior cone; v.p.c: ventral posterior cone. To the left is anterior. Angles give deviation of direction of muscle fibers from direction of horizontal septum.

only rarely visible in fossil specimens. Consequently, this folding ratio is lower than that of Dietz (1913), i.e. Dietz's ratio (after his figures) of *Gadus morhua* is 1.15 for myotomes of the anterior abdominal region, 1.2 for myotomes of the posterior abdominal region, and 1.77 for myotomes of the tail region. Comparable ratios, using the shorter distance from the fossil fishes, are 1.0, 1.09 and 1.4, respectively.

The folding ratio in *Protoclupea chilensis* (Figs. 6-8) increases from the apdominal region (anterior abdominal region 1.1 to posterior abdominal region /anterior caudal region 1.38) to the tail region (3.29) much more than in *Gadus*. In comparing a myomere of the posterior abdominal region or anterior caudal region of four genera from Quebrada del Profeta (Figs. 9-12), differences in shape and degree of folding are obvious between them. *Protoclupea* and *Domeykos* have the lowest folding ratio (1.28 and 1.23, respectively), whereas the myomeres in this region of *Chongichthys* (1.47) and *Varasichthys* (1.59) are folded as much as those in the tail region of *Gadus* (1.4). The difference in

folding ratio corresponds, in part, to the body shape. In *Protoclupea* and *Domeykos*, the depth of the abdomen is reduced by about 20% from the region behind the head to the anterior abdominal region whereas in *Varasichthys* and *Chongichthys* body depth narrows by 33% between the two regions. An even larger difference in folding ratio between these two genera in the tail region is expected because *Varasichthys* has a very narrow peduncle. Unfortunately, no specimen of *Varasichthys* has a complete myomere preserved in the tail region.

The folding ratio gives only a general indication of similarity or dissimilarity of myomeres between species. The shape of the myomeres can be quite different with the same folding ratio. In *Protoclupea* (Figs. 7, 9) and *Chongichthys* (Fig. 12), myomeres of the posterior abdominal region are nearly symmetrically shaped dorsal and ventral to the horizontal septum, but myomeres of *Chongichthys* are more strongly folded in the posterior abdominal region, comparable to the degree for folding in the anterior caudal region of *Protoclupea*. *Domeykos*



FIGS. 9-12. Myomere from the anterior caudal region (behind dorsal fin and in front or above anterior part of anal fin). Fig. 9. *Protoclupea atacamensis* Arratia and Schultze, 1985, KUV 8124. Fig. 10. *Domeykos profetaensis* Arratia and Schultze, 1985, LBUCH 12-260912a. Fig. 11. *Varasichthys ariasi* Arratia, 1981, LBUCH 15-2609729. Fig. 12. *Chongichthys dentatus* Arratia, 1982, KUV 65038. h.s.: horizontal septum; P₁: apex of dorsal posterior cone; P₂: apex of ventral posterior cone. To the left is anterior. Angles give deviation of direction of muscle fibers from direction of horizontal septum.

(Fig. 10) and *Varasichthys* (Fig. 11) have myomeres arranged asymmetrically to the horizontal septum. In *Domeykos*, the dorsal portion is more folded than the ventral portion in the posterior abdominal region, the same is the case in the anterior abdomen. In *Varasichthys*, the ventral posterior cone is directed caudodorsally and not just caudally. It shows that the four genera differ in the shape of their myomeres, which does not closely correlate with differences in body shape. *Protoclupea* shows a high increase of myomeres folding in the tail region despite an evenly decreasing body depth (Fig. 5), but it indicates a powerful propulsion by the tail. Extensive folding of tail myomeres is indicated by the higher folding ratio in the posterior abdominal region of *Varasichthys* and *Chongichthys*, and what is preserved of the tail region in the holotype, indicates the same for *Domeykos*. Thus all four genera were active swimmers with powerful tail propulsion.

The direction of the muscle fibers changes along the body and within one myomere. The fibers run parallel to the body axis in the abdominal region, and at different angles towards the body in the caudal region. In *Protoclupea*, changes are minimal in the direction of the muscle fibers in the abdominal region (Figs. 6, 7) within one myomere. In the anterior caudal region, the muscle fibers are almost parallel near the horizontal septum (angle between 2-5°), whereas the angle (up to 15-20°) increases towards the dorsal and ventral posterior cones. The muscle fibers are directed posteriorly towards the horizontal septum between horizontal septum and posterior cones. They are directed anteriorly towards the horizontal septum dorsal and ventral of the posterior cones at a much steeper angle (up to 40°). The direction of muscle fibers deviates even more from the body axis with stronger folding of the myomeres in the tail region (Fig. 8). Muscle fibers in myomeres of the posterior ab-

dominal region of the four genera (Figs. 9-12) run more or less parallel to the horizontal septum, except in the differently shaped ventral posterior cone of *Varasichthys* (angle of 45°). In all four genera, the direction of muscle fibers in caudal myomeres deviates strongly from the body axis. Change in direction of muscle fibers is functionally necessary to permit a similar contraction of fibers in each myomere (Alexander, 1969).

Fortunately, in a few cases, the whole set of muscles are preserved at the base of the dorsal (Fig. 4) and anal fin. From the outside to the inside, inclinators, depressors and erectors are displayed. The erector is often quite obvious with its structure of cones packed into each other. These muscles attach to the proximal end of the fin rays, but the actual attachment point can rarely be observed.

Thus far, only body (axial) muscles have been observed, muscles could not be found in the head region of any fish or around the intestine. The microstructure of the axial muscles is preserved down to minute details. The muscle fibers are phosphatized but not the myosepta (Pl. 3, Fig. 3). Phosphate granules completely fill the muscle fibers or, in other cases, copy the striation (Pl. 3, Fig. 4). The granule size is variable; within the striations, two small granules (Pl. 3, Fig. 6) occupy the width of the bands, whereas those which completely fill vessels and fibers, can have twice the diameter. The phosphatized bands (between 0.6 and 1.15 μm wide) may represent the overlap area between thick (myosin) and thin (actin, troponin and tropomyosin) filaments where cross-bridges of the thick filament connect with the thin filament. These cross-bridges are Ca^{++} (thin filament) - Adenosine phosphate (ADP, ATP) connections, here the possibility for phosphate additions exists. Another explanation is also possible. The phosphatized bands may represent only the thin filaments, with Ca^{++} ions as attachment points for the phosphate surplus. The double appearance of the bands could then be explained as mineralization on both sides of the Z-line.

In cross-section (Pl. 3, Fig. 5; Pl. 4, Fig. 2), the muscle fibers appear blocky with cornered outline. The cross-section of the fibers usually appears structureless, but in a few cases a banding structure appears (Pl. 4, Fig. 2). This may represent the internal structure, or alternatively, large mitochondria. As in mitochondria, finger-like folds extend from the walls towards the center where they alter-

nate with each other. Another, not too common, structure in the Jurassic fishes from northern Chile is the nucleus (Pl. 4, Fig. 1). The volume of the nucleus is filled with Ca-phosphate; the figured nucleus has a length of about 20 μm .

BLOOD VESSELS

Blood vessels can be observed together with muscles in cross-sections (Pl. 3, Fig. 5), longitudinal sections (Pl. 3, Fig. 4) or below the vertebral column (dorsal aorta). Swim bladder and intestine are identifiable in the abdominal cavity, but the author hesitates to interpret other partially preserved structures.

SWIM BLADDER

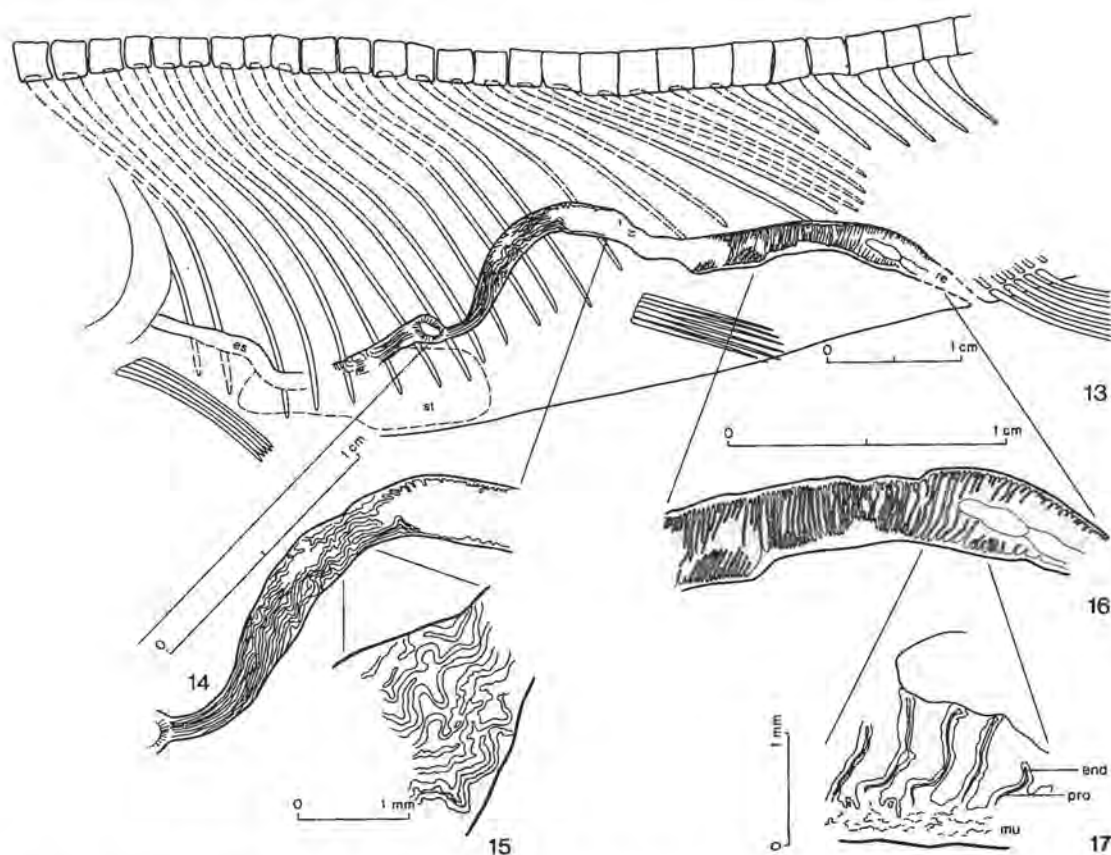
The swim bladder is preserved in three specimens of *Protoclupea chilensis* (holotype R-396; Pl. 5, Fig. 1) and of *Varasichthys ariasi* (15-260972 and LBUCH CH-3378). It ends above the base of the pelvic fin (R-396 and LBUCH CH-3378) or above the posterior half of the fin rays of the pelvic fin. The shape of one larger chamber is visible, but it is not clear how far it reaches anteriorly. Impressions of blood vessels run dorso-ventrally on the lateral wall of the swim bladder of specimen R-396B. A striated surface appears in the antero-dorsal part below the wall of the swim bladder in R-396B and LBUCH CH-3378. This may represent collagenous fibers or their impressions of the tunica externa or the smooth muscles of the tunica interna.

GILLS

In two specimens (LBUCH 12A-260972, *Chongichthys*, Pl. 6, Fig. 1, and in KUV 97765, teleost indet. in a small black concretion), the gills are preserved. They each surround a calcitic rod which seems to be a diagenetic formation. They are closely packed on the gill arches, with the exception of some very long filaments under the operculum of specimen LBUCH 12A-260972, that are spaced far from each other.

INTESTINE

The alimentary tract is preserved in a few specimens, mostly in the smaller black concretions (Fig. 3, Nos. 7-9). One specimen (KUV 97764, Figs. 13-17; Pl. 5, Fig. 2) shows nearly the complete alimentary tract whereas only part of the intestine is preserved in others (*Bobbichthys opercularis*: LBUCH 2-260972, KUV 83702; teleost



FIGS. 13-17. Alimentary tract in specimen KUVF 97764, teleost indet. Fig. 13. Abdominal region with alimentary tract. Fig. 14. Anterior part of intestine. Fig. 15. Enlargement of posterior portion of Fig. 14. Fig. 16. Posterior part of intestine. Fig. 17. Enlargement of posterior portion of Fig. 16. end: endodermal layer on folds; es: esophagus; mu: mucosa; pro: propria (mucosal center of villi); re: rectum; st: stomach.

indet.: LBUCH F5-61, CH-35900, 6-16, 5-1212). In specimen KUVF 97764, the esophagus is filled with an amorphous mass. The region of the stomach is indicated by a depression in the fossil, but definite boundaries cannot be determined. In contrast, the intestine is very well defined, it is an elongate organ without coiling. Internal structures (folds) and the mucosa are phosphatized whereas longitudinal and ring muscles are not preserved. The anterior part of the intestine (Fig. 14; Pl. 6, Fig. 2) has longitudinal mucous-membrane folds which posteriorly become complicated zig-zag folds (Fig. 15). A meshwork connects the zig-zag folds. A portion with only short folds follows the zig-zag folds. These give way to circular folds that occupy the posterior part of the intestine (Fig. 16). Anterior to the longitudinal folds, a few circular folds also appear (Fig. 14). Within the posterior part of the intestine, the circular folds diminish in length to-

wards the end of the intestine, where a crystallized space of a gas bubble reaches into the intestine (Fig. 16). The folds do not extend to the wall of the intestine in the posterior part of the intestine because the mucosa is also phosphatized (Fig. 17: mu); the mucosa reaches into the folds and forms their center (the propria; Fig. 17: pro). The layer around the center of the folds is thick relative to the whole diameter of the fold. This layer (Fig. 17: end) may represent the endodermal epithel only as seen in cross-sections of the teleost *Rutilus rutilus* by Al-Hussaini (1949, Figs. 5b-g). The rectum is not preserved, it must have occupied the short distance between the last preserved part of the intestine and the body margin, just in front of the anal fin.

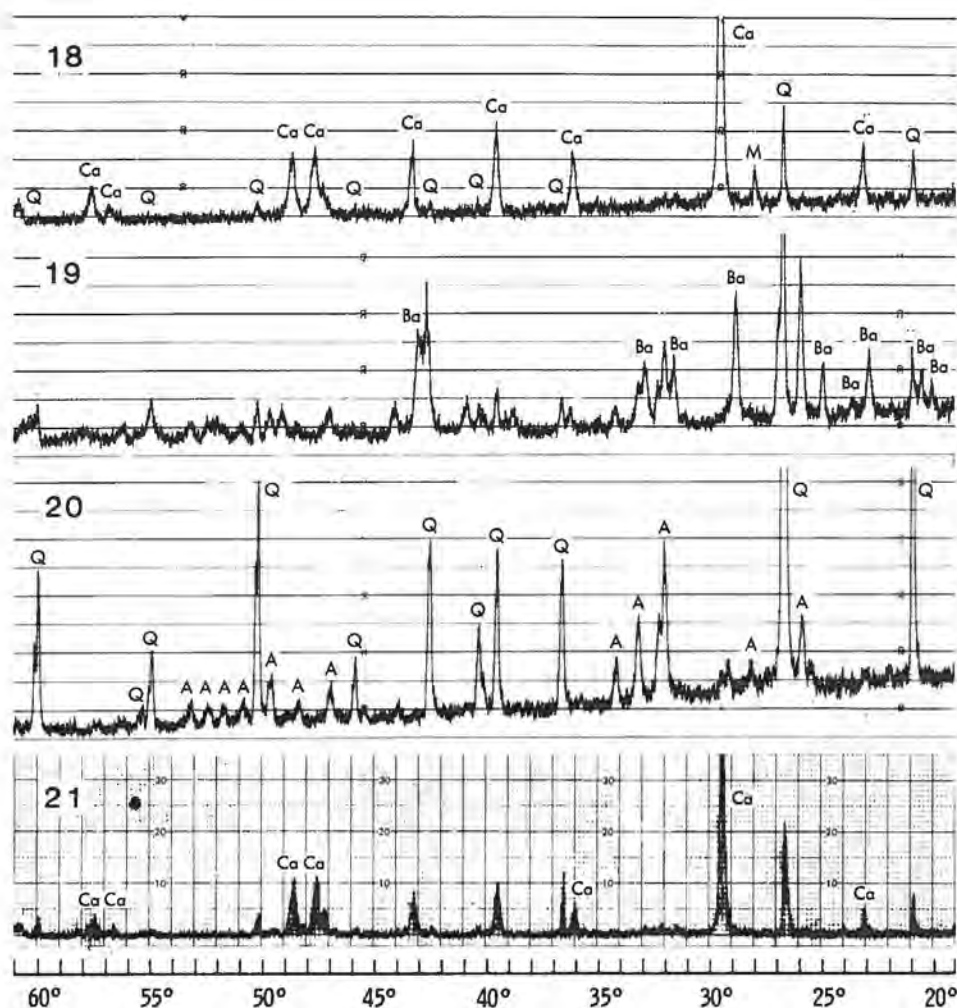
A straight intestine is primitive within actinopterygians (Nelson, 1972) and may be primitive within teleosts as well (Harder, 1980). The latter is sup-

ported by the specimen described above. It is not possible to determine from which side of the stomach on the intestine originates. It may pass the stomach on the right side as in primitive actinopterygians and most teleosts, or on the left, as in osteoglossomorphs. The combination of longitudinal with circular folds is found in some clupeomorph, whereas zig-zag folds are characteristic of *Esox* and the cyprinids (Eggeling, 1908; Jacobshagen, 1937). A satisfactory correlation between folding

and food preference has not yet been found (Harder, 1964). An intestine shorter than standard length is taken as an indication of carnivorous behavior.

TYPES OF PRESERVATION

Soft structures have been described in such detail to demonstrate that a diagenetic or even bacterial transformation is very unlikely. In both



FIGS. 18-21. X-ray diffractometer records. Fig. 8-20: *Domeykos profetaensis* Arratia and Schultze, 1985; LBUCH 1-210277-13. Oxfordian, Upper Jurassic; Quebrada del Profeta, Sierra de Varas, Cordillera de Domeyko, northern Chile. Fig. 18. Sample from concretion surrounding the specimen. Fig. 19. Vertebrae (Quartz added). Fig. 20. Muscles (Quartz added). Fig. 21. *Notelops brama* (Agassiz, 1841); AMNH 11753) = Martill, 1988, Pl. 1, Fig. 2). Santana Formation (Upper Aptian?); Chapada do Araripe, northeast Brazil. Dorsal abdominal muscles (Quartz added). A: fluorapatite; Ba: barite; Ca: calcite; M: mica; Q: quartz.

cases, one would expect indication of decay. But, in contrast, soft parts with most abundant blood supply are best preserved and even such delicate structures as gills and villi in the intestine are completely preserved. These structures would decay immediately, especially the intestine with its bacterial flora, before transforming bacteria could reach the intestine. The fibers in the myomeres are three-dimensionally preserved throughout the depth of the myomeres. This is in contrast to the preservation of muscles in the Ceará concretions from Brazil, where muscle fibers are visible on the outside, whereas the mass becomes structureless with depth (inside).

MINERALOGY

The concretions occur in a calcareous sandy to shaley sequence (Fig. 3). The lower part of the sequence is richer in calcite. Based on X-ray diffraction, samples V, IV and III (Fig. 3) can be described as calcareous sandstones to siltstones. The upper part of the section contains more shales (samples II and I: plagioclase, feldspar, quartz and light colored micas) where the calcite is concentrated within the concretions. Gypsum occurs as a secondary formation resulting from the weathering of sulfides throughout the section; it often occurs in veins which run with the bedding plan or across it. Sample I contains jarosite, an iron sulfate, which occurs in the oxidation zone of mineral deposits. It is also a secondary formation.

The concretions are calcareous (limestone) with quartz and some mica (Fig. 18). They do not contain apatite. Fluorapatite is restricted to bones (Fig. 19) and muscles (Fig. 20), other soft tissues and coprolites. Barite occurs in the vertebrae (Fig. 19) of *Domeykos profetaensis* (LBUCH 1-210277-13) and muscles of *Varasichthys ariasi* (LBUCH 4277), whereas it has not been discovered in 10 analyzed sediment samples nor in the concretions. The deposition of barite in bones and muscles is unusual, it may indicate that barite distribution in the Late Jurassic was not uniform and that, like today, its highest concentration was in the southern East Pacific.

PRESERVATION

The fishes in the Upper Jurassic concretions from Quebrada del Profeta are preserved three-dimensionally although somewhat flattened. Most concretions enclose the body, with the anterior

(head) and posterior (tail) portions missing. Sometimes they contain the whole fish except the snout and the posterior, distal parts of the caudal fin. The body is usually intact with soft and hard parts in their anatomical position - disregarding those specimens which have been mechanically disturbed - even though the space in between the phosphatized soft tissues is filled with lime or calcite crystals (Pl. 6, Fig. 3). Never a case was observed where the parts show post mortem displacement within the body. This is in contrast to that observed by Martill (1988, Fig. 5) in the fishes from Ceará, Brazil, where the vertebral column falls to the 'bottom' of the body cavity (Pl. 6, Fig. 4).

The muscles cover the skeletal structures of the body. They have to be removed ('dissected') to see vertebrae, caudal skeleton, etc. These cut windows have been figured in specimens of *Protoclupea chilensis* (Arratia and Schultze, 1985, Pl. 1, Fig. B = Arratia, 1987, Pl. 5, Fig. 4; Arratia, 1987, Pl. 3, Fig. 2), *Atacamichthys greeni* (Arratia, 1987, Pl. 4, Fig. 3; Arratia and Schultze, 1987, Fig. 1) and *Domeykos profetaensis* (Arratia, 1987, Pl. 6, Fig. 1).

In cases where the fish was destroyed mechanically after deposition on the sea floor, bones and muscles behaved in the same way. Fragments of muscles are spread around like bones (Pl. 4, Fig. 3). The fragments of muscles have sharp edges, and they do not show any sign of decay at the margins. That indicates that the fish was exposed to currents or wave actions before the specimen was enclosed in the concretion, but after the muscles were phosphatized. However, to induce formation of the calcareous concretions, some of the decomposing products must have been present. Therefore, it seems unlikely that the separation of parts occurred by reworking of sediments after the fish was first covered by sediment followed by phosphatization of muscles.

COMPARISONS

Martill (1988) described muscle preservation in Cretaceous concretions from Ceará, Brazil. He supposed that these muscles are preserved in phosphate (p. 6: "cryptocrystalline francolite"), and developed a model explaining the phosphatization by bacterial activity. Phosphatization has been described for ostracodes (Bate, 1972) and copepods (Cressey and Patterson, 1973) in the

Brazilian concretions, but these are singular cases (Bate, 1972: two in thousands) where the phosphatized organism lies close to a phosphate source, e.g., the content of an intestine or a coprolite. In these cases, chitin and original calcitic shells are encapsulated or replaced by phosphate. In contrast, the muscles in the Brazilian concretions are preserved in calcite as shown by analysis of thin sections and by X-Ray diffraction of muscle tissue of *Microdon penalvai* (FMNH PF 12663) and *Notelops brama* (Fig. 21, AMNH 11753 = Martill, 1988, Pl. 1, Fig. 2). The muscles appear white in contrast to the yellowish-brown of the skeletal parts and scales; muscle fibers are distinct on the outside but the white mass becomes structureless internally. The white mass also appears between the scales. The calcification of superficial tissue and the change of structure in the muscle tissue from the outside to the inside indicate a process of infiltration from the outside of the fish. It is a presedimentary or very early syngenetic (during sedimentation) process, because the decay of muscle tissue is not complete; decomposing processes have progressed only on the inside of the fish so that hard structures are no longer in place (Pl. 6, Fig. 4). Post mortem calcification of muscle tissue is known from Recent fishes. Calcium is bound by fatty acids under supersaturated calcium conditions in an anaerobic environment (Wilcox and Effler, 1981) or in a high pH microenvironment even without supersaturated calcium conditions (Berner, 1968). The occurrence of such calcified fishes is known from marine environments (Wells and Erickson, 1933; Faber and Krejci-Graf, 1936), as well as from the marine fishes such as the alewife in freshwater lakes (Wilcox and Effler, 1981). Preservation of muscle tissue in calcite and preservation of essentially only superficial parts of muscles do not permit a comparison with the muscle preservation in the Late Jurassic fishes from northern Chile. Other localities may have phosphatized muscle preservation with microstructure, as described by Martill (1988) from Ceará, but attention is called about the use of shape and size of sphaerulites as an indication of bacterial formation. These structures could be explained as crystal formation under special environmental conditions.

Phosphatization of soft tissue was described by Willems and Wuttke (1987) and Reis (1893,

1895, 1898). Willems and Wuttke (1987) explained the phosphatic preservation of a ghost of the soft tissue in Permian amphibians as resulting from bacterial activities. The Permian amphibians do not show three-dimensionally preserved soft tissues in contrast to the fishes in the Late Jurassic of southern Germany (Reis 1893, 1895, 1898) and those from northern Chile.

Reis (1893) explained the phosphatization of muscle tissue and skin in the Late Jurassic fishes and reptiles of southern Germany by diffusion of Ca-phosphate from the stomach and intestine to other soft tissues at the beginning of decomposition. He argued that carnivorous forms collect enough bone material in their intestine to account for the amount of Ca-phosphate deposited within muscles. The postulated mechanism is diffusion from the intestine to the muscles. This mechanism does not explain the observed selective phosphatization of some but not all structures in the Chilean or German Jurassic fishes. In addition, one would expect deposition of dissolved phosphate around soft structures and not replacement of soft structures themselves. In contrast, Reis (1893) spoke of a complete anorganic replica of the microscopic structure of muscles. The preserved soft tissue in Late Jurassic fishes from southern Germany is thin, only 0.5 to 2.5 mm thick in fishes of up to 1 m total length. That is quite different from the Late Jurassic fishes in northern Chile. In addition, the occurrence of phosphatized muscle tissue in Late Jurassic fishes from southern Germany should be restudied, the author has not seen muscle tissue in any acid prepared specimen. In contrast to the findings of Reis (1893) for the fishes from Germany, muscle tissue is preserved in nearly every fish in the Upper Jurassic of northern Chile and is not restricted to carnivorous fishes. Only one Late Jurassic fish (undescribed) from northern Chile has been observed with a teleost head in its stomach.

In conclusion, bacterial replacement or diffusion of phosphate from intestine to muscle tissue are doubtful mechanisms when used to explain fine preservation of the soft anatomy of fishes. Both mechanisms are processes active at the beginning of the decomposition process and unlikely to explain the detailed preservation of the Chilean material. Another mechanism must have been active there.

INTERPRETATION

Phosphatization of soft tissue has always been interpreted as a syngenetic (during sedimentation) or diagenetic process in fossils. Nevertheless, published explanations (Reis, 1893, 1895; Martill, 1988; Allison, 1988) for fossil preserved muscle tissue seem not to be applicable to the Late Jurassic fishes from Chile. A process preceding syngenetic phosphatization is required to explain the described circumstances of these extremely well preserved soft tissue.

Today, phosphatization of living muscle tissue is known as calcinosis, an endemic sickness of grazing animals in different parts of the world (Morris, 1982). Calcinosis is induced by different plants which produce vitamin D₃ or its compounds (Boland, 1986). In vertebrates, vitamin D₃ is important for regulating calcium metabolism. Vitamin D₃ is hydroxylated in the liver to 25-hydroxyvitamin D₃ (24[OH]₂D₃), and then by the kidney to 1,25-dihydroxyvitamin D₃ (1,25[OH]₂D₃). The latter form is the main regulator of calcium metabolism. Its formation corresponds to calcium and phosphorus needs in the body. This regulation is bypassed as soon as vitamin D₃ or one of the hydroxylated forms are absorbed by the intestine. The consequent surplus of the metabolite leads to precipitation of calcium phosphate in bones and soft tissues. Vitamin D₃ plays a role in the regulation of muscle cells Ca metabolism and PO₄ fluxes (Boland, 1985), so that it is understandable that a change of the metabolite has effect on the soft tissue. An intake as low as 0.1 percent of the whole diet can produce calcinosis in cattle (Okada *et al.*, 1977).

The importance of vitamin D₃ for the calcium phosphate metabolism in fishes has only recently been shown (Henry and Norman, 1975). Also only

recently, vitamin D₃ has been discovered in plants (Worker and Carillo, 1967; Dobereiner *et al.*, 1971) and previtamin D very recently in phytoplankton (Holick *et al.*, 1982). Effects of vitamin D₃ in phytoplankton on fishes have not yet been described. Still, that premise in combination with high phosphate production by phytoplankton in an upwelling zone like the western coast of South America, can be used to postulate that the same or a process similar to calcinosis in cattle, was induced in the Jurassic fishes. The proposed explanation postulates the following scenario:

1. An upwelling zone with high production of phytoplankton which was rich in phosphate, was present in the Late Jurassic on the western margin of the shelf of South America, *i.e.*, conditions similar to the present day.
2. The phytoplankton containing vitamin D₃ or a hydroxylated form of it, was consumed by the fishes. Normal calcium phosphate metabolism of the fishes broke down, and additional ingested phosphate-rich phytoplankton induced an even higher rate of precipitation of phosphate in the soft tissue of the fishes than occurs in cattle.
3. The fishes that died of calcinosis on the continental shelf, sunk onto the floor of the epicontinental sea where black shales were deposited. The fishes were, in some cases, first destroyed before they were covered by sediment devoid of phosphate. Chemical processes associated with decay of the remaining soft tissue were sufficient to induce the formation of calcareous concretions.

This scenario explains co-occurrence of fishes with phosphatized soft tissue in phosphate-free concretions and sediment.

CONCLUSIONS

Fishes with exceptionally well preserved soft tissue occur in calcareous concretions in Upper Jurassic black shales of Northern Chile. Calcareous shells of invertebrates occur together with phosphatic bones and soft tissue of vertebrates. The invertebrate fauna of the black shales indicates that bottom life existed and that the boundary between oxidation and reduction was within the sediment. The fishes which sunk to the floor of the epicontinental sea were sometimes not immediately

imbedded, but partly disarticulated before they were enclosed in calcareous concretions. Muscles are spread out, as were the bones, which indicates that the muscles were phosphatized before embedding.

The three-dimensional preservation of soft tissue down to the cell nuclei is unparalleled in the fossil record. Diagenetic or syngenetic replacement or impregnation of soft tissue by calcium phosphate appears very unlikely because those

models require beginning decomposition of the cadaver to initiate the precipitation of calcium phosphate. There is no indication of incipient decay in the Jurassic fishes of Northern Chile. To the contrary, even structures such as abdominal organs, especially the intestine where the decay process starts and progresses very rapidly, are preserved down to the cellular level. The most recently proposed model by Martill (1988) for the 'phosphatization' of the cretaceous fishes from Brazil is unfounded because there muscles are preserved in calcium carbonate and not phosphate. Transformation of freshly killed fishes into calcareous mummies is known from fishes under marine and freshwater conditions (Wells and Erickson, 1933; Wilcox and Effler, 1981). In addition, the lack of phosphate in the concretions and surrounding sediments excludes diagenetic or syngenetic replacement. Phosphatization by bacteria can be excluded too; such a process leads to preservation of a

ghost of the soft tissue (Wuttke, 1983). In contrast, the soft tissue of the Late Jurassic fishes from Northern Chile is preserved three-dimensionally.

Therefore, the impregnation of soft tissue by calcium phosphate is explained here by a process in the living fish comparable to calcosis in cattle (Boland, 1986). Vitamin D₃ or a hydroxylated form of it is proposed to have occurred in the Late Jurassic phytoplankton. Intake of that phytoplankton induced a breakdown of the calcium metabolism in the fishes, and lead to precipitation of calcium phosphate in the soft tissue. The surplus of phosphate is derived from phosphate-rich phytoplankton in the upwelling zone at the west margin of the shelf of South America in the Jurassic. The exceptional preservation and the lack of phosphate in concretions and sediment indicate a predepositional precipitation of calcium phosphate in life for which calcosis in cattle is a modern analogue.

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REFERENCES

- Alexander, R.McN. 1969. The orientation of muscle fibers in the myomeres of fishes. *Journal of the Marine Biological Association of the United Kingdom*, Vol. 49, p. 263-290.
- Al-Hussaini, A.H. 1949. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits: Anatomy and histology. *Quarterly Journal of Microscopical Science*, Vol. 90, p. 109-139, 3 Pls.
- Allison, P.A. 1988. Phosphatized soft-bodied squids from the Jurassic Oxford Clay. *Lethaia*, Vol. 21, p. 403-420.
- Ammon, L. von. 1896. Ueber neue Stücke von *Ischyodus*. *Berichte des naturwissenschaftlichen Vereines zu Regensburg*, Vol. 5 (1894-1896), p. 252-263, 2 Pls.
- Arratia, G. 1981. *Varasichthys ariasi* n. gen. et sp. from the Upper Jurassic of Chile (Pisces, Teleostei, Varasichthyidae n. fam.). *Palaeontographica A*, Vol. 175, p. 107-139, 7 Pls.
- Arratia, G. 1982. *Chongichthys dentatus*, new genus and species, from the Late Jurassic of Chile (Pisces: Teleostei: Chongichthyidae, new family). *Journal of Vertebrate Paleontology*, Vol. 2, p. 133-149.
- Arratia, G. 1984. Some osteological features of *Varasichthys ariasi* Arratia (Pisces, Teleostei) from the Late Jurassic of Chile. *Paläontologische Zeitschrift*, Vol. 58, p. 149-163.
- Arratia, G. 1985. Peces del Jurásico de Chile y Argentina. *Ameghiniana*, Vol. 21, p. 205-210.
- Arratia, G. 1986. New Jurassic fishes (Teleostei) of Cordillera de Domeyko, Northern Chile. *Palaeontographica A*, Vol. 192, p. 75-91, 4 Pls.
- Arratia, G. 1987. Jurassic fishes from Chile and critical comments. In *Bioestratigrafía de los Sistemas Regionales del Jurásico y Cretácico de América del Sur* (Volkheimer, W.; Musacchio, E.A.; editors), Vol. 1. Jurásico anterior a los movimientos málmicos. *Comité Sudamericano del Jurásico y Cretácico*, p. 257-286, 6 Pls. Mendoza, Argentina.
- Arratia, G. (in press) The caudal skeleton of Jurassic teleosts; phylogenetic analysis. In *Symposium of early vertebrate studies and related problems in evolutionary biology*. Proceedings. Beijing, China, 18 Pls.
- Arratia, G.; Chang, A.; Chong, G. 1975a. *Leptolepis opercularis* n. sp. from the Jurassic of Chile. *Ameghiniana*, Vol. 12, p. 350-358, 2 Pls.
- Arratia, G.; Chang, A.; Chong, G. 1975b. *Pholidophorus domeykanus* n.sp. del Jurásico de Chile. *Revista Geológica de Chile*, No. 2, p. 1-9, 2 Láms.
- Arratia, G.; Chang, A.; Chong, G. 1975c. Sobre un pez fósil del Jurásico de Chile y sus posibles relaciones con clupeidos sudamericanos vivientes. *Revista Geológica de Chile*, No. 2, p. 10-21, 4 Láms.
- Arratia, G.; Chong, G. 1979. Los peces jurásicos de Chile. In *Congreso Geológico Chileno*, No. 2, Actas, Vol. 3, p. H125-144. Arica.
- Arratia, G.; Schultze, H.-P. 1985. Late Jurassic teleosts (Actinopterygii, Pisces) from Northern Chile and Cuba. *Palaeontographica A*, Vol. 189, p. 29-61, 5 Pls.
- Arratia, G.; Schultze, H.-P. 1987. A new halecostome fish (Actinopterygii, Osteichthyes) from the Late Jurassic of Chile and its relationships. *Dakoterra*, Vol. 3, p. 1-13.
- Bate, R.H. 1972. Phosphatized ostracods with appendages from the Lower Cretaceous of Brazil. *Palaeontology*, Vol. 15, p. 379-393, Pls. 66-71.
- Berner, R.A. 1968. Calcium carbonate concretions formed by the decomposition of organic matter. *Science*, Vol. 159, p. 195-197.
- Biese, W. 1957. Der Jura von Cerritos Bayos-Calama, República de Chile, Provinz Antofagasta. *Geologisches Jahrbuch*, Vol. 72, p. 439-494, 6 Pls.
- Biese, W. 1961. El Jurásico de Cerritos Bayos. *Universidad de Chile, Facultad de Ciencias Físicas y Matemáticas, Instituto de Geología, Publicación*, No. 19, 61 p., 6 Láms. Santiago.
- Boland, R.L. 1985. Does vitamin D perform a function in muscle? In *Vitamin D. Chemical, Biochemical and Clinical Update* (Norman, A.W.; Schaefer, K.; Grigoleit, H.-G.; Herrath, D. von; editors). *Walter de Gruyter*, p. 601-610. Berlin.
- Boland, R.L. 1986. Plants as a source of vitamin D₃ metabolites. *Nutrition Reviews*, Vol. 44, p. 1-8.
- Bremer, H. 1939. Paläophysiologische Untersuchungen an der fossilen Muskulatur aus der eozänen Braunkohle des Geiseltales bei Halle (Saale). *Nova Acta Leopoldina, Neue Folge*, Vol. 7, p. 95-118, 4 Pls.
- Burnett, W.C. 1977. Geochemistry and origin of phosphorite deposits from off Perú and Chile. *Bulletin of the Geological Society of America*, Vol. 88, p. 813-823.
- Capen, C.C.; Cole, C.R.; Hibbs, J.W. 1966. The pathology of hypervitaminosis D in cattle. *Pathologia Veterinaria*, Vol. 3, p. 350-378.
- Carroll, R.L. 1987. *Vertebrate Paleontology and Evolution*. *Freeman and Co.*, p. XIV + 698. New York.
- Chong, G. 1977. Contribution to the knowledge of the Domeyko Range in the Andes of Northern Chile. *Geologische Rundschau*, Vol. 66, p. 374-404.
- Chong, G.; Förster, R. 1976. *Chilenophoberus atacamenensis*, a new decapod crustacean from the Middle Oxfordian of the Cordillera de Domeyko, northern Chile. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, p. 145-156.
- Cressey, R.; Patterson, C. 1973. Fossil parasitic copepods from a Lower Cretaceous fish. *Science*, Vol. 180, p. 1283-1285.
- Dean, B. 1902. The preservation of muscle-fibres in sharks of the Cleveland Shale. *American Geologist*, Vol. 30, p. 273-278, 2 Pls.
- Dean, B. 1909. Studies on fossil fishes (sharks, chimaeroids and arthrodires). *Memoirs of the American Mus-*

- eum of Natural History*, Vol. 9, p. 211-287, Pls. 26-41.
- Dietz, P.A. 1913. Über die Form der Myotome der Teleostier und ihre Beziehung zur äusseren Leibesgestalt. *Anatomischer Anzeiger*, Vol. 44, p. 56-64.
- Dobereiner, J.; Tokarnia, C.H.; da Costa, J.B.; Campos, J.L.E.; de S Dayrell, M. 1971. 'Espichamento', intoxicación de bovinos por *Solanum malacoxylon*, no pastoral de Mato Grosso. *Pesquisa Agropecuaria Brasileira, Serie Veterinaria*, Vol. 6, p. 91-117.
- Eggeling, J. 1908. Dünndarmrelief und Ernährung bei Knochenfischen. *Jenaische Zeitschrift für Naturwissenschaft*, Vol. 43 (Neue Folge, Vol. 36), p. 417-529, Pls. 16-18.
- Faber, W.; Krejci-Graf, K. 1936. Zur Frage des geologischen Vorkommens organischer Kalkverbindungen. *Mineralogisch-Petrologische Mitteilungen*, Vol. 48, p. 305-360.
- Gasparini, Z. de. 1979. Comentarios críticos sobre los vertebrados mesozoicos de Chile. In *Congreso Geológico Chileno*, No. 2, Actas, Vol. 3, p. H15-32, 1 Lám.
- Glaessner, M.F. 1965. Vorkommen fossiler Dekapoden (Crustacea) in Fisch-Schiefern. *Senckenbergiana Lethaea*, Vol. 46a, p. 111-122.
- Gulbrandsen, R.A. 1969. Physical and chemical factors in the formation of marine apatite. *Economic Geology*, Vol. 64, p. 365-382.
- Harder, W. 1960. Vergleichende Untersuchungen zur Morphologie des Darmes bei Clupeoidea. *Zeitschrift für Wissenschaftliche Zoologie*, Vol. 163, 65-167.
- Harder, W. 1964. Anatomie der Fische. In *Handbuch der Binnenfischerei Mitteleuropas* (Demoll, R.; Maier, H. N.; Wundsch, H.H.; editors). *E. Schweizerbart'sche Verlagsbuchhandlung*, Vol. 2A (text), XIII + 308 p., Vol. 2B (figures), 96 p. Stuttgart.
- Henry, H.; Norman, A.W. 1975. Presence of renal 25-hydroxyvitamin-D-1-hydroxylase in species of all vertebrate classes. *Comparative Biochemistry and Physiology*, Vol. 50B, p. 431-434.
- Holick, M.F.; Adams, J.S.; Clemens, T.L.; MacLaughlin, J.; Horiuchi, H.; Smith, E.; Holick, S.A.; Nolan, J.; Hannifan, N. 1982. Photoendocrinology of Vitamin D: The Past, Present and Future. In *Chemical, Biochemical and Clinical Endocrinology of Calcium Metabolism* (Norman, A.W.; Schaefer, K.; Herrath, D. von; Grigoleit, H.G.; editors). *Walter de Gruyter*, p. 1151-1156. Berlin.
- Jacobshagen, E. 1937. Mittel- und Enddarm. In *Handbuch der vergleichenden Anatomie der Wirbeltiere* (Bolk, L.; Göppert, E.; Kallius, E.; Lubosch, W.; editors). *Urban & Schwarzenberg*, Vol. 3, p. 563-724. Berlin.
- Jaekel, O. 1892. *Cladodus* und seine Bedeutung für die Phylogenie der Extremitäten. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, p. 81-92.
- Kauffman, E.G. 1981. Ecological Reappraisal of the German Posidonienschiefer (Toarcian) and the Stagnant Basin Model. In *Communities of the Past* (Gray, J.; Boucot, A.J.; Berry, W.B.N.; editors). *Hutchinson Ross Publishing Company*, p. 311-381. Stroudsburg, Pennsylvania.
- Koenigswald, W. von; Richter, G.; Storch, G. 1981. Nachweis von Hornschuppen bei *Eomanis waldi* aus der "Grube Messel" bei Darmstadt (Mammalia, Pholidota). *Senckenbergiana Lethaea*, Vol. 61, p. 291-298.
- Lehman, U. 1981. The ammonites. Their life and their world. *Cambridge University Press*, p. XIV + 246, 12 Pls. New York.
- Lucas, J.; Prévôt, L. 1984. Synthèse de l'apatite par voie bactérienne à partir de matière organique phosphatée et de divers carbonates de calcium dans des eaux douces et marine naturelle. *Chemical Geology*, Vol. 42, p. 101-118.
- Martill, D.M. 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. *Palaeontology*, Vol. 31, p. 1-18, 4 Pls.
- Morris, K.M.L. 1982. Plant induced calcinosis: A review. *Veterinary and Human Toxicology*, Vol. 24, 34-48.
- Müller, K.J. 1979. Phosphatocopine ostracodes with preserved appendages from the Upper Cambrian of Sweden. *Lethaia*, Vol. 12, p. 1-127.
- Nelson, G.J. 1972. Observations on the gut of the Osteoglossomorpha. *Copeia*, p. 325-329.
- Okada, K.A.; Carillo, B.J.; Tilley, J.M.A. 1977. *Solanum malacoxylon* Sendtner: a toxic plant in Argentina. *Economic Botany*, Vol. 31, p. 225-236.
- Pinna, G. 1985. Exceptional preservation in the Jurassic of Osteno. *Philosophical Transactions of the Royal Society of London, Series B*, Vol. 311, p. 171-180, 3 Pls.
- Rauff, H. 1895. O. Reis: Untersuchungen über die Petrifizierung der Musculatur (Archiv für mikrosk. Anatomie. Bonn 1893, Vol. 41, p. 492-584, Pls. 29-31). *Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie*, Vol. 2, III. Referate, p. 151-159.
- Reis, O.M. 1888. Die Coelacanthinen, mit besonderer Berücksichtigung der im Weissen Jura Bayerns vorkommenden Gattungen. *Palaeontographica*, Vol. 35, p. 1-96, Pls. 1-5.
- Reis, O.M. 1893. Untersuchungen über die Petrifizierung der Muskulatur. *Archiv für Mikroskopische Anatomie*, Vol. 41, p. 492-584, Pls. 29-31.
- Reis, O.M. 1895. Ueber Phosphoritierung der Cutis, der Testikel und des Rückenmarks bei fossilen Fischen. *Archiv für Mikroskopische Anatomie*, Vol. 44, p. 87-119, 6 Pls.
- Reis, O.M. 1898. Neues über petrificirte Muskulatur etc. *Archiv für Mikroskopische Anatomie*, Vol. 52, p. 262-268.
- Richter, G.; Storch, G. 1980. Beiträge zur Ernährungsbiologie eozäner Fledermäuse aus der 'Grube Messel'. *Natur und Museum*, Vol. 110, p. 353-367.
- Schweizer, R. 1964. Die Elasmobranchier und Holocephalen aus den Nusplinger Plattenkalken. *Palaeontographica A.*, Vol. 123, p. 58-110, Pls. 7-12.

- Seilacher, A.; Westphal, F. 1971. Fossil Lagerstätten. In Sedimentology of parts of Central Europe. Guidebook 8. *International Sedimentological Congress, No. 8*, p. 327-335. Heidelberg.
- Seilacher, A.; Reif, W.-E.; Westphal, F. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London, Series B*, Vol. 311, p. 5-23.
- Traquair, R.H. 1884. Description of a fossil shark (*Ctenacanthus costellatus*) from the Lower Carboniferous rocks of Eskdale, Dumfriesshire. *Geological Magazine, New Series, Decade III*, Vol. 1, p. 3-8, 2 Pls.
- Voigt, E. 1934. Die Fische aus der mitteleozänen Braunkohle des Geiseltales. *Nova Acta Leopoldina, Neue Folge*, Vol. 2, p. 21-146, 14 Pls.
- Voigt, E. 1935. Die Erhaltung von Epithelzellen mit Zellkernen, von Chromatophoren und Corium in fossiler Froschhaut aus der mitteleozänen Braunkohle des Geiseltales. *Nova Acta Leopoldina, Neue Folge*, Vol. 3, p. 339-360, 3 Pls.
- Voigt, E. 1936. Weichteile an Säugetieren aus der eozänen Braunkohle des Geiseltales. *Nova Acta Leopoldina, Neue Folge*, Vol. 4, p. 301-310, 2 Pls.
- Voigt, E. 1937. Weichteile an Fischen, Amphibien und Reptilien aus der eozänen Braunkohle des Geiseltales. *Nova Acta Leopoldina, Neue Folge*, Vol. 5, p. 115-142, 5 Pls.
- Voigt, E. 1938a. Tierische Weichteile aus der Braunkohle des Geiseltales bei Halle/S. *Natur und Volk*, Vol. 68, p. 11-117.
- Voigt, E. 1938b. Weichteile an fossilen Insekten aus der eozänen Braunkohle des Geiseltales bei Halle (Saale). *Nova Acta Leopoldina, Neue Folge*, Vol. 6, p. 3-38, 7 Pls.
- Voigt, E. 1949. Mikroskopische Untersuchungen an fossilen tierischen Weichteilen und ihre Bedeutung für Systematik und Paläobiologie. *Zeitschrift der Deutschen Geologischen Gesellschaft*, Vol. 101, p. 99-104.
- Wells, R.D.; Erickson, E.T. 1933. The analysis and composition of fatty material produced by the decomposition of herring in sea water. *Journal of the American Chemical Society*, Vol. 55, p. 338-341.
- Wilcox, D.A.; Effler, S.W. 1981. Formation of alewife concretions in polluted Onondaga Lake. *Environmental Pollution, Ser. B*, Vol. 2, p. 203-215.
- Willems, H.; Wuttke, M. 1987. Lithogenese lakustriner Dolomite und mikrobiell induzierte Weichteil-Erhärtung bei Tetrapoden des Unter-Rotliegenden (Perm, Saar-Nahe-Becken, SW-Deutschland). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, Vol. 174, p. 213-238.
- Worker, N.A.; Carillo, B.J. 1967. 'Enteque seco', calcification and wasting in grazing animals in the Argentine. *Nature*, Vol. 215, p. 72-74.
- Wuttke, M. 1983. 'Weichteil-Erhaltung' durch lithifizierte Mikroorganismen bei mittel-eozänen Vertebraten aus den Ölschiefern der 'Grube Messel' bei Darmstadt. *Senckenbergiana Lethaea*, Vol. 64, p. 509-527, 2 Pls.
- Wykoff, R.W.G. 1972. The biochemistry of animal fossils. *Williams and Wilkins Co.*, 152 p. Baltimore.
- Zimmermann, M.R.; Tedford, R.H. 1976. Histologic structures preserved for 27,300 years. *Science*, Vol. 194, p. 183-184.

PLATES 1 - 6

PLATE 1

Figures

Plants and invertebrates from the Oxfordian (Upper Jurassic) north of Quebrada del Profeta, Sierra de Varas, Cordillera de Domeyko, northern Chile. Scale: 1 cm.

- 1 Cladophore algae. x 1.
- 2 Cuttlefish *Plesiotheutis* sp., posterior half of the shell. x 1.
- 3 Bivalve "*Posidonia*". x 1.
- 4 Decapod crustacean *Chilenophoberus atacamensis* Chong and Förster, 1976; abdomen and uropod. x 3.
- 5 Ammonite *Perisphinctes* sp. x 1.
- 6 Coprolite on top of small concretion. x 1.
Scale: always 1 cm.

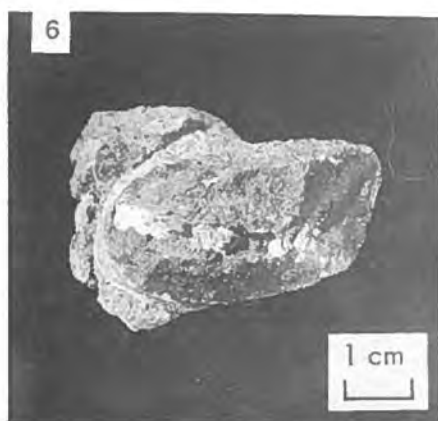
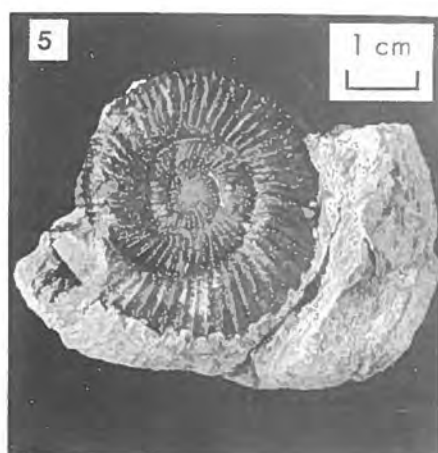
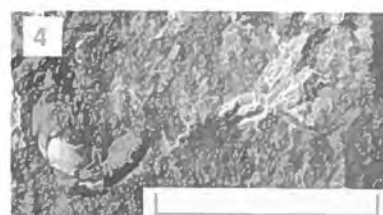
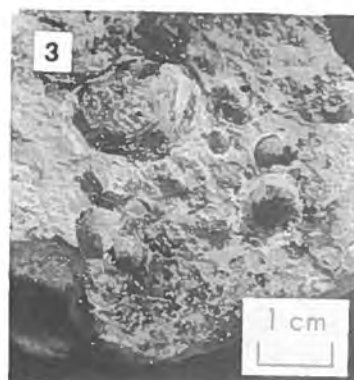
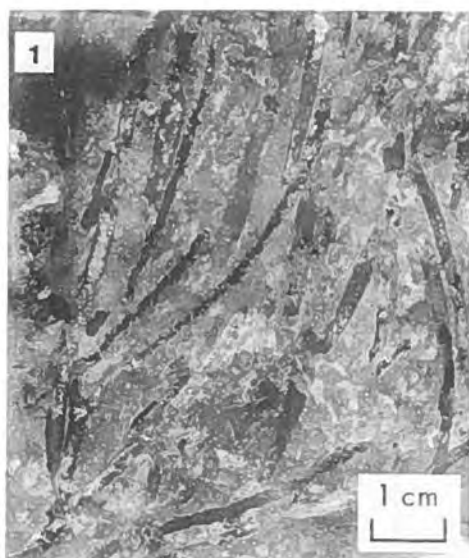


PLATE 2

Protoclupea chilensis Arratia, Chang and Chong, 1975. KUV 71205b; postcranial portion with partly removed scale cover to show muscle myomeres below dorsal fin, and myomeres taken off partly to show the vertebrae; Quebrada del Profeta, Sierra de Varas, Cordillera de Domeyko, northern Chile. Oxfordian, Upper Jurassic. About x 2. Scale: 1 cm.

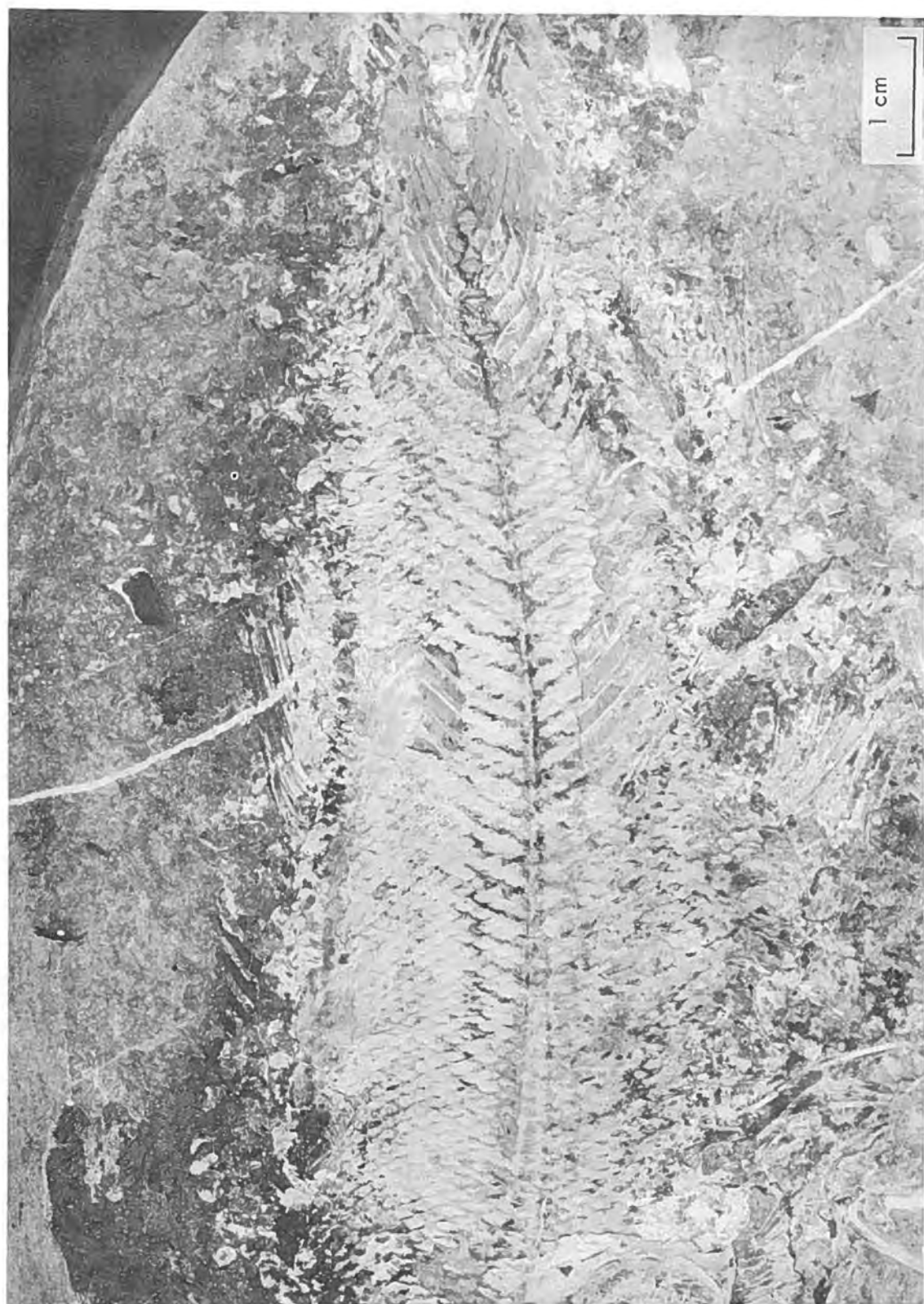


PLATE 3

Figures

Skin and muscles in fishes from Oxfordian (Upper Jurassic) north of Quebrada del Profeta, Sierra de Varas, Cordillera de Domeyko, northern Chile.

- 1 *Protoclupea chilensis* Arratia, Chang and Chong, 1975. KUVJ 71205b; posterior ventral abdominal region between pelvic and anal fins showing myomeres overlaid by dorso-ventrally running subcutaneous muscles, dermis with melanophores and scale impressions. x 9. Scale: 1 mm.
- 2 *Varasichthys ariasi* Arratia, 1981. LBUCH 4277a (Paratype; Arratia, 1981, p. 11). SEM 21568, skin. x 176. Scale: 0.1 mm.
- 3 - 6 *Domeykos profetaensis* Arratia and Schultze, 1985. LBUCH 1-210277-13 (Paratype, Arratia and Schultze, 1985, p. 43), etched by acetic acid.
 3. SEM 21581; muscle fibers of two myomeres along a space representing the separating myoseptum. x 82. Scale: 0.1 mm.
 4. SEM 21598; muscle fibers with and without striation. x 60. Scale: 0.1 mm.
 5. SEM 21586; cross sections of muscle fibers and vessels (ve). x 437. Scale: 0.1 mm.
 6. SEM 21588; muscle striation. x 1914. Scale: 0.01 mm.

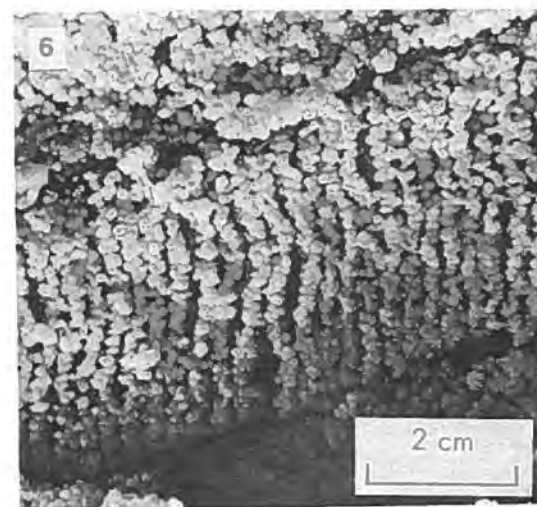
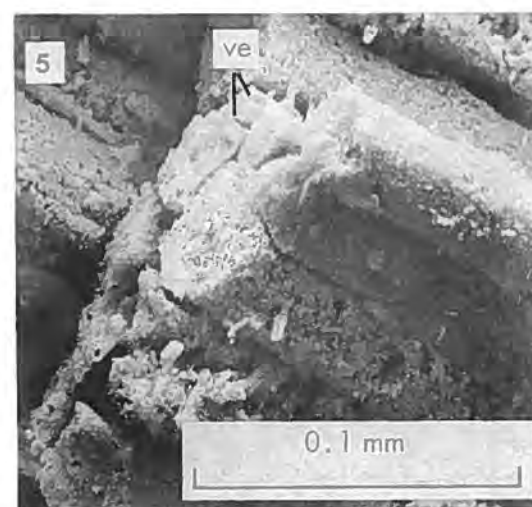
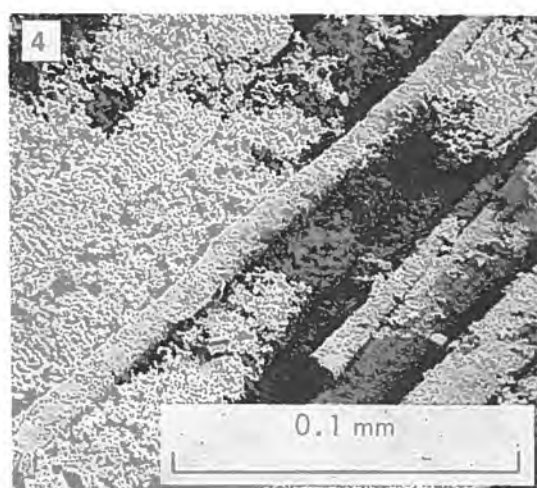
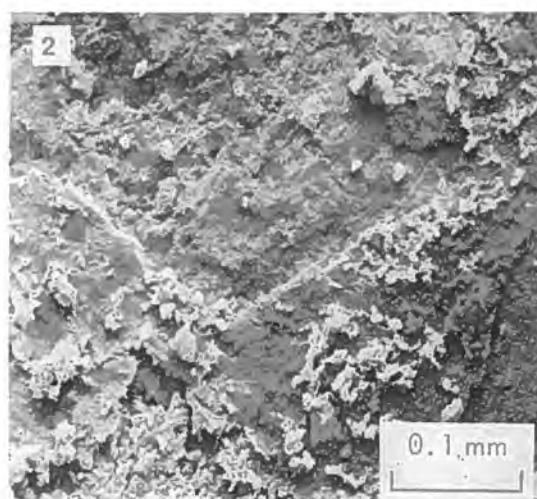
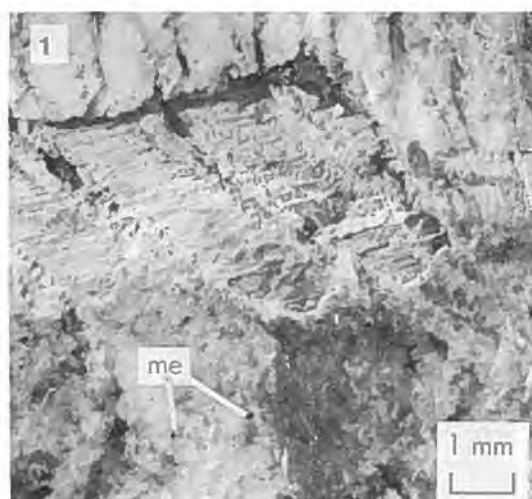


PLATE 4

Figures

Muscle preservation in fishes from Oxfordian (Upper Jurassic) north of Quebrada del Profeta, Sierra de Varas, Cordillera de Domeyko, northern Chile.

1 - 2

Domeykos profetaensis Arratia and Schultze, 1985, LBUCH 1-210277-13 (Paratype, Arratia and Schultze, 1985, p. 43); etched by acetic acid.

1. SEM 21584; striated muscle fiber with nucleus. x 1030. Scale: 0.01 mm.
2. SEM 21596; mitochondria. x 960. Scale 0.01 mm.

3

Teleost indet. LBUCH 13-260972. Muscles myomeres partially intact, partially distributed over the surface like the bones. x 1. Scale: 1 cm.

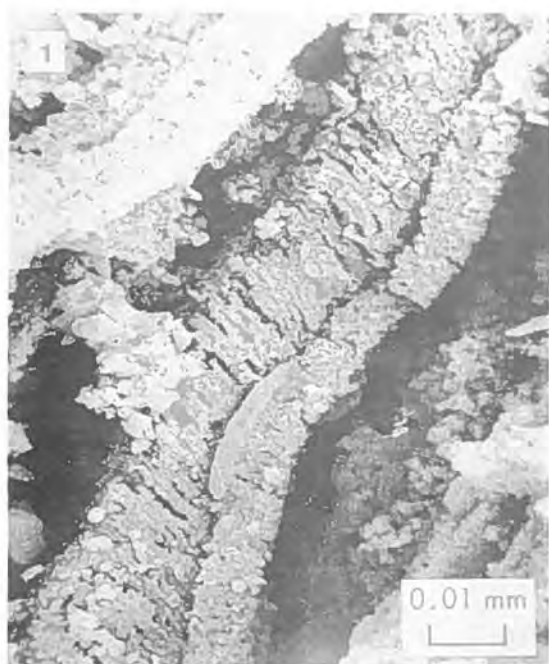


PLATE 5

Figures

Organs of the abdominal cavity in fishes from Oxfordian (Upper Jurassic) north of Quebrada del Profeta, Sierra de Varas, Cordillera de Domeyko, northern Chile.

1

Protoclupea chilensis Arratia, Chang and Chong, 1975. Holotype, R-396B, swim bladder (**sb**). x 3.1. Scale: 1 cm.

2

Teleost indet. KUV 97764; alimentary tract (compare Fig. 13); **a.int**: anterior region of intestine; **p.int**: posterior region of intestine. x 3. Scale: 1 cm. Arrow points anteriorly.

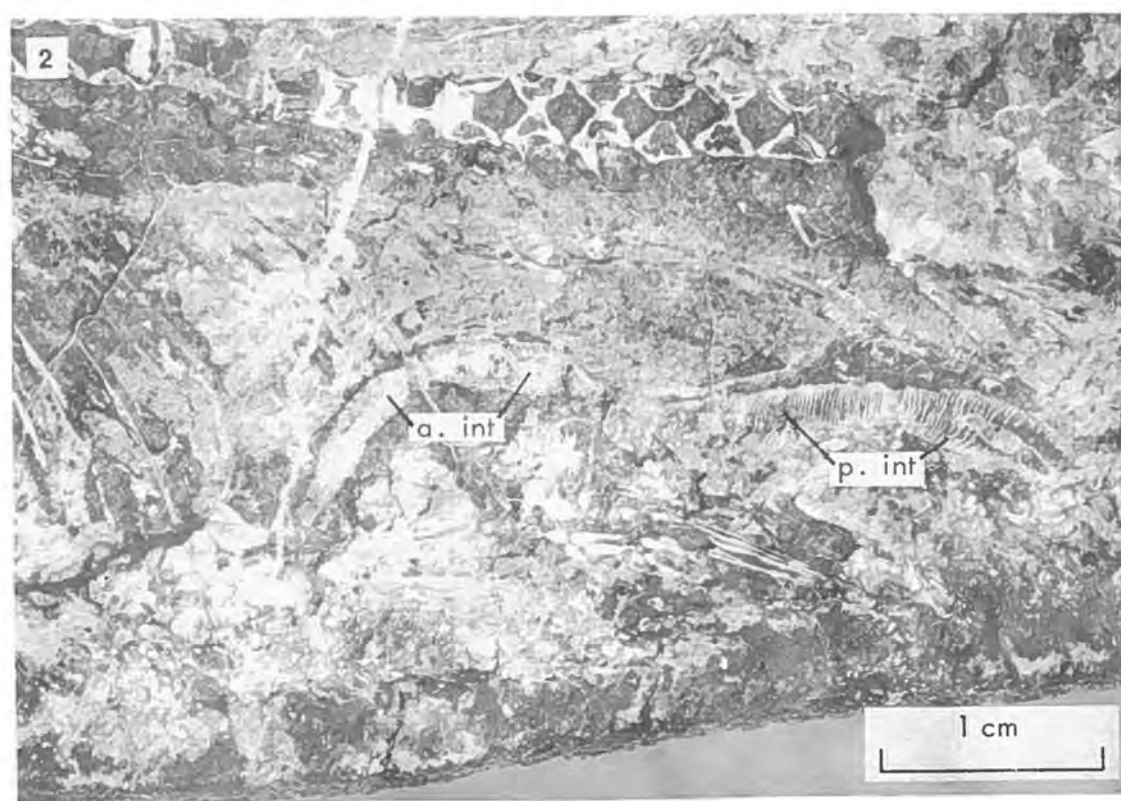
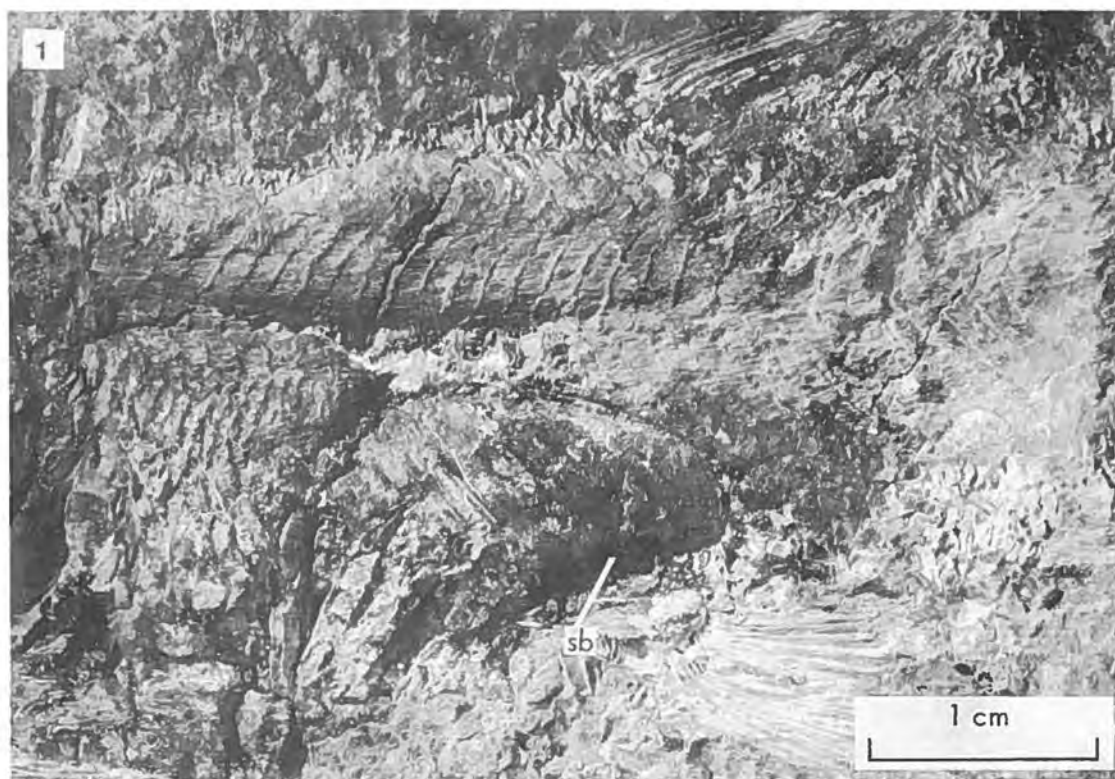


PLATE 6

Figures

- 1 - 3 Fishes from Oxfordian (Upper Jurassic) north of Quebrada del Profeta, Sierra de Varas, Cordillera de Domeyko, northern Chile.
1. *Chongichthys dentatus* Arratia, 1982. LBUCH 12A-260972; opercular region with gills. x 3. Scale: 1 cm.
 2. *Bobbichthys opercularis* Arratia, Chang and Chong, 1975. KUVF 83702 cross section through anterior region of intestine. x 1.6. Scale: 1 mm.
 3. Teleost indet. KUVF 99300; cross section through compressed caudal region above anal fin. x 4. Scale: 1 cm. Arrow points dorsally.
- 4 *Rhacolepis buccalis* Agassiz, 1844. FMNH P12174; axial cross section (= Martill, 1988, Fig. 5) with calcite filled abdomen, cavities with calcite crystals at dorsal margin, vertebrae and muscles at ventral side of body. x 9. Scale: 1 cm. Arrow points anteriorly. Santana Formation (Upper Aptian?); Chapada do Araripe, northeast Brazil. Sediment structures in oblique angles to specimen.

