

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2434

OCTOBER 22, 1970

The Cretaceous Teleostean Fish *Cimolichthys* from the Niobrara Formation of Kansas and the Pierre Shale of Wyoming

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INTRODUCTION

Representatives of the genus *Cimolichthys* occur in the Niobrara Formation (Coniacian-Santonian) of Kansas, in the Pierre Shale (Campanian) of Wyoming, and in equivalent horizons of Western Europe. (In addition, there is a single occurrence in the Pierre of Kansas and in the Pierre of Manitoba, Canada.) The type species, *Cimolichthys levesiensis* Leidy (1857, p. 95), is from the Chalk (Turonian-Senonian) of southern England; it is also present in the Chalk of Belgium and Holland (Leriche, 1902, 1906).

The Niobrara *Cimolichthys* was first described under the generic name *Empo* (*E. nepaholica* Cope, 1872a, p. 347), as well as *Cimolichthys* (*C. sulcatus* and *C. semianiceps*, Cope, 1872a, p. 351). Loomis in 1900 (p. 267), and Woodward in 1901 (p. 221), both recognized that the two genera were synonymous, but Hay in 1903 (p. 81), maintained that he could see no reason for abolishing the genus *Empo*.

Stewart published on the unique specimen of *Cimolichthys* (the type of *Empo lisbonensis*) from the Pierre of Kansas (1899, p. 111), and Lambe

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on the material (*Cimolichthys* sp.) from Manitoba (1916, p. 196). Until now, however, none of the *Cimolichthys* specimens from the Pierre Shale of Wyoming has been described, although they were remarked upon by Gill and Cobban (1966, p. 26). In a revision of certain representatives of the family Enchodontidae (*sensu* Woodward, 1901), I established the family Cimolichthyidae (Goody, 1969b, p. 36) to include the genus *Cimolichthys*. Reference to the North American material was omitted due to the absence of any workable specimens from either the Niobrara or the Pierre in any museum outside the United States. Thanks to the kindness of Dr. Bobb Schaeffer, I have been able to rectify the situation by studying the collections in the American Museum of Natural History (hereinafter abbreviated as A.M.N.H.).

Cope (1872a, 1872b, 1874, 1875) erected five species for the *Cimolichthys* material from the Niobrara Formation: *C. nepaholica*, *C. sulcatus*, *C. semianiceps*, *C. contracta*, and *C. merrillii*. Hay (1903, p. 85) reduced these to the single species *C. nepaholica*, which had priority of description. His determination is followed in the present paper, as there is no reason for retaining Cope's various species that are based mainly on isolated teeth and fragments of jaw bones. Additional specimens from the Pierre Shale of Wyoming have been examined, and I have concluded that the same species, *C. nepaholica*, is present in this deposit. The single North American species can readily be compared with the European species, *C. levesiensis*, and a congeneric status is justified. However, sufficient differences still exist to retain the specific differentiation.

SYSTEMATIC DESCRIPTION

ORDER SALMONIFORMES

SUBORDER CIMOLICHTHYOIDEI

FAMILY CIMOLICHTHYIDAE GOODY, 1969b

GENUS *CIMOLICHTHYS* LEIDY, 1857

GENERIC DIAGNOSIS (emended): Skull somewhat elongated and acutely pointed anteriorly. Palatine with two rows of teeth; ectopterygoid with a single row. Certain palatopterygoid teeth may show post-apical barb. Premaxilla elongate and ornamented, with vertical lamina supporting a single row of very small teeth. Maxilla long and slender, forming approximately one-half of the gape, never bearing teeth. Dentary shallow, but with a wide horizontal extent ventrally, and supporting three rows of teeth, the innermost being the largest. None of the dentary teeth barbed, but all recurved. Fifty to sixty vertebrae; approximately

half of these caudal. Dorsal fin short, situated midway along back; anal fin shorter than dorsal and close to caudal fin. Caudal skeleton without free ural vertebrae, with two elongate uroneurals and two expanded epurals. Hypurals 1 and 2 fused; 3, 4, and 5 fused; hypural 6 elongated and parallel to uroneurals. Caudal fin large, very deeply cleft, and exhibiting hypurostegy.

TYPE SPECIES: *Cimolichthys levesiensis* Leidy, 1857.

Cimolichthys nepaholica (Cope), 1872a

Figures 1-6, 7B, 8B

Empo nepaholica COPE, 1872a, p. 347 (original description); 1872b, p. 345. HAY, 1902, p. 387; 1903, p. 81, pl. 1, fig. 4, text figs. 69-72.

Empo nepaeolica: COPE, 1874, p. 46 (emended spelling); 1875, pp. 230, 279, pl. 49, fig. 9, pl. 50, fig. 8, pl. 52, fig. 1, pl. 53, figs. 3-5. STEWART, 1900, p. 332, pl. 59, figs. 1-9, pl. 61, figs. 2-5. MOODIE, 1911, p. 278, pl. 60, pl. 62, fig. 2; 1913, p. 249. KRUIZINGA, 1924, pp. 299, 311.

Cimolichthys nepaeolica: LOOMIS, 1900, p. 271, pl. 27, figs. 1-3. WOODWARD, 1901, p. 225, text figs. 8, 9. PRIEM, 1908, pp. 66, 67.

Cimolichthys nepaholica: HUSSAKOF, 1908, p. 66, fig. 35. COCKERELL, 1919, p. 184. HAY, 1929, p. 756.

Cimolichthys sulcatus COPE, 1872a, p. 351 (original description).

Empo sulcata: COPE, 1874, p. 46 (emended spelling).

Cimolichthys semianiceps COPE, 1872a, p. 351 (original description); 1872b, p. 326. LOOMIS, 1900, p. 273, pl. 27, figs. 4-6. WOODWARD, 1901, p. 228. HAY, 1929, p. 756.

Empo semianiceps: COPE, 1874, p. 46; 1875, pp. 233, 279, pl. 53, figs. 1, 2, 6-9. STEWART, 1900, p. 338, pl. 61, figs. 6-9. HAY, 1902, p. 387.

Empo contracta COPE, 1874, p. 46 (original description); 1875, pp. 232, 279, pl. 53, figs. 14-17. STEWART, 1900, p. 339. HAY, 1902, p. 387.

Cimolichthys contracta: LOOMIS, 1900, p. 273, pl. 27, figs. 8, 9.

Cimolichthys contractus: WOODWARD, 1901, p. 228 (emended spelling). HAY, 1929, p. 756.

Empo merrillii COPE, 1874, p. 46 (original description); 1875, pp. 232, 279, pl. 53, figs. 10-13. HAY, 1902, p. 387.

Cimolichthys merrillii: LOOMIS, 1900, p. 272, pl. 27, fig. 7. WOODWARD, 1901, p. 228. HAY, 1929, p. 756.

Empo lisbonensis STEWART, 1899, p. 111 (original description); 1900, p. 337, pl. 61, figs. 10a, 10b. HAY, 1902, p. 387.

Cimolichthys lisbonensis: WOODWARD, 1901, p. 228. HAY, 1929, p. 756.

Cimolichthys sp.: LAMBE, 1916, p. 196. GARDINER, 1966, p. 77.

SPECIFIC DIAGNOSIS (emended): Differs from type species, *C. levesiensis*, as follows: Neurocranium width equal to one-half its length; palatine without ventral longitudinal concavity; outer palatine tooth row more prominent than inner; at least two rows of teeth on vomer; supraorbital absent; 53 vertebrae (approximately).

HOLOTYPE: A.M.N.H. No. 1904, a small portion of the palatine bone from the Niobrara Formation of Kansas.¹

HORIZON AND LOCALITY: As Bardack (1965, p. 10) pointed out, locality records for Cope's material (1872a, 1872b, 1874, 1875) are poor. Most of the Niobrara material is from Gove, Logan, Trego, and Wallace counties, Kansas, and is Coniacian-Santonian in age. The specimens from the Pierre Shale of Wyoming come from near Mule Creek Junction and are Campanian in age. A single specimen is listed as coming from the "Lisbon shales, Fort Pierre Cretaceous" (Stewart, 1900, p. 337) of Logan County, Kansas.

MATERIAL: From the Upper Cretaceous Niobrara Formation of western Kansas: A.M.N.H. No. 1737 (type of *Cimolichthys* [*Empo*] *merrillii*), partial palatines, vomer and ?entopterygoid; A.M.N.H. No. 1738 (type of *Cimolichthys* [*Empo*] *contracta*), partial palatines, vomer, dentaries; A.M.N.H. No. 1741, skull elements; A.M.N.H. No. 1748, skull fragments; A.M.N.H. No. 1751, caudal fin, skull fragments; A.M.N.H. No. 1776, skull, vertebrae, base of pectoral fin; A.M.N.H. No. 1882 (type of *Cimolichthys sulcatus*), left dentary with teeth; A.M.N.H. No. 1904 (holotype of *Cimolichthys* [*Empo*] *nepaholica*), imperfect palatine; A.M.N.H. No. 1967, skull elements; A.M.N.H. No. 1969, neurocranium; A.M.N.H. No. 1989 (type of *Cimolichthys semianiceps*), vertebrae, palatine, dentaries with teeth; A.M.N.H. No. 2032, caudal fin and vertebrae; A.M.N.H. No. 2369, caudal fin and vertebrae; A.M.N.H. No. 2522, neurocranium and jaws; A.M.N.H. No. 3889, premaxilla; A.M.N.H. No. 6412, posterior neurocranium; A.M.N.H. No. 6422, posterior neurocranium; A.M.N.H. No. 8348, skull fragments and vertebrae; A.M.N.H. No. 8363, right lower jaw. From the Upper Cretaceous Pierre Shale, Mule Creek Junction, Wyoming: A.M.N.H. No. 1774, neurocranium and anterior part of body; A.M.N.H. No. 6406, posterior neurocranium, vertebrae and miscellaneous fragments; A.M.N.H. No. 6410, partial skull and skeleton; A.M.N.H. No. 8270, skull. From "Lisbon shales, Fort Pierre Cretaceous" of Logan County, Kansas: Kansas University Museum of Vertebrate Paleontology No. 328 (type of *Cimolichthys* [*Empo*] *lisbonensis*), left palatine.

DESCRIPTION

NEUROCRANIUM: The skull of *Cimolichthys nepaholica* has been superficially described and figured by Loomis (1900, p. 267, pl. 27, figs. 1, 4,

¹ According to Cope (1872a, p. 348), "the precise locality . . . has been mislaid." The specimen label for A.M.N.H. No. 1904 in O. P. Hay's handwriting gives the locality as "near Fossil Spring, Kansas," which was near Fort Wallace, Wallace County, Kansas.

5), Stewart (1900, p. 336, pl. 59, figs. 1, 2), and Hay (1903, p. 85, figs. 69–71). The type material of Cope (1872a) and the material used by Hay (1903) has been reexamined. A.M.N.H. No. 1969 (the specimen used by Hay, 1903, fig. 71, for the ventral view of the neurocranium) was prepared in acetic acid to give a more complete interpretation of the skull roof. *Cimolichthys nepaholica* differs in a limited number of ways from *C. levesiensis* from the English Chalk, described and figured by Goody (1969b, p. 37, figs. 16–21). The following description is thus limited to those features in which some degree of difference is shown.

The dorsal surface of the neurocranium (fig. 1) is especially well shown in A.M.N.H. No. 1969 (fig. 2). The ornamentation on the enormous frontals extends both anteriorly and posteriorly from the centers of ossification above the sphenotics. The most prominent anterior ridge lies above the tube that housed the supraorbital sensory canal and extends forward curving slightly medially. The posterior ridges are arranged in a fan, terminating at the posterior end of the frontal where it covers the more posterior roofing bones. In this posterior series of bones the supraoccipital only just appears on the roof, but the parietals are difficult to distinguish. Hay (1903, p. 85) noticed a narrow band of bone behind the rear of the frontal that extends laterally from the supraoccipital, but could find no distinct suture between the parietal and epiotic, so he surmised that it may have been present. The parietals in *C. levesiensis* (Goody, 1969b, p. 40) are "narrow transversely orientated strips of bone which laterally form part of the medial wall of the post temporal fossa meeting the pterotic anteriorly and the epiotic posteriorly." Although the suture between the parietal and the epiotic is difficult to determine, the epiotic in part is clearly defined. The whole occipital border of the roof is angled backward on each side from the supraoccipital. At the outer angles, the epiotics form prominent thickened knobs on either side of the skull; these supported the dorsal limbs of the post temporals (A.M.N.H. No. 2522).

There is no longitudinal crest apparent on the dorsal surface of the sphenotic as there is in *C. levesiensis*. The ornamented region of the pterotic (dermopterotic) rests on top of the smooth sphenotic (auto-sphenotic—the dermosphenotic is not represented). The dorsal surface of the pterotic in A.M.N.H. No. 6422 is ornamented with irregular shallow ridges of bone, unlike that of *C. levesiensis*. Toward the posterior end of the bone there is a lateral excavation of the ornamented layer which indicates the point of entry of the sensory canal from the preoperculum. This presumably connected with the otic branch of the infraorbital canal within the pterotic. As in *C. levesiensis*, there is a very

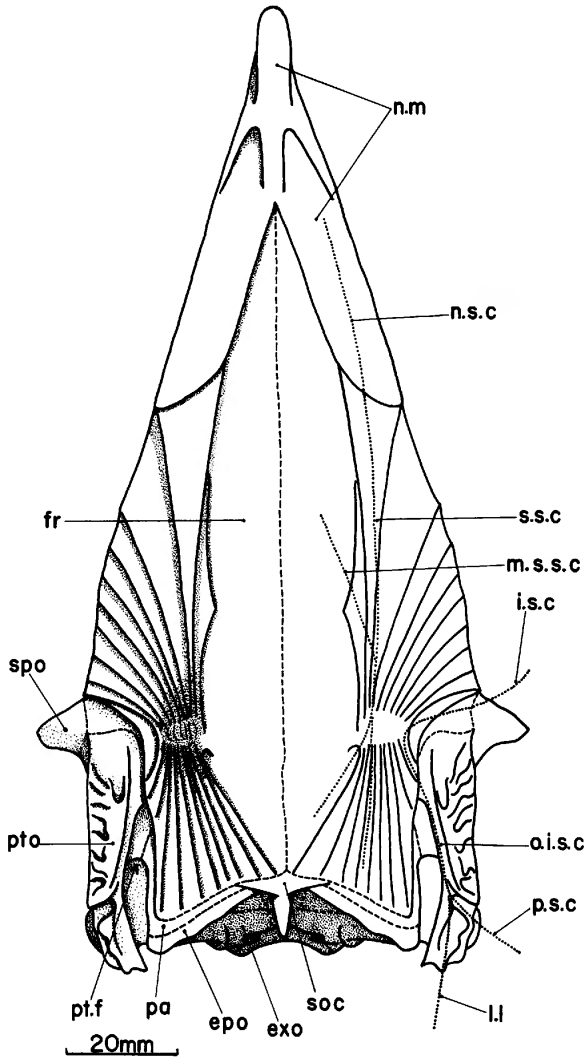


FIG. 1. *Cimolichthys nepaholica* (Cope), reconstruction of skull roof.

Abbreviations: epo, epiotic; exo, exoccipital; fr, frontal; i.s.c, infraorbital sensory canal; l.l, lateral line sensory canal; m.s.s.c, branch of supraorbital sensory canal onto medial region of skull roof; n.m, nasomesethmoid; n.s.c, nasal sensory canal; o.i.s.c, otic branch of infraorbital sensory canal; pa, parietal; p.s.c, preopercular sensory canal; pt.f, post-temporal fossa; pto, pterotic; soc, supraorbital; spo, sphenotic; s.s.c, supraorbital sensory canal.

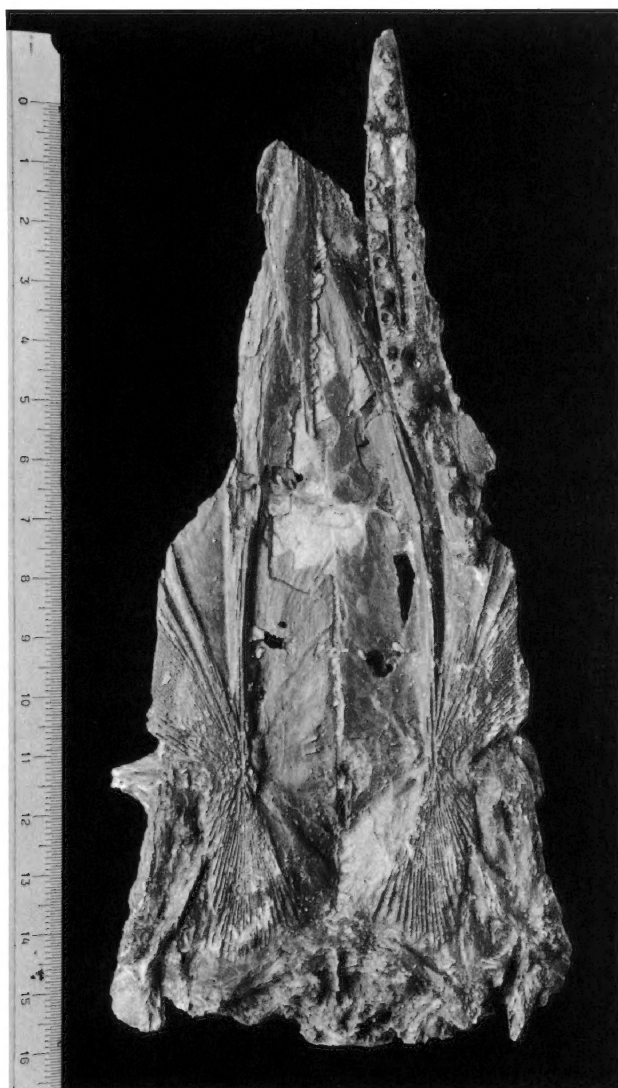


FIG. 2. *Cimolichthys nepaholica* (Cope), A.M.N.H. No. 1969, dorsal view of flattened skull.

shallow crest which originates beneath the frontal and extends posterolaterally where it forms the posterior margin of the incompletely roofed post-temporal fossa. This fossa is small (A.M.N.H. Nos. 1969, 2522, and 6422); it is formed medially from the frontal, parietal and epiotic, and laterally from the pterotic.

As mentioned above, the course of the supraorbital sensory canal is marked anteriorly by the most prominent ridge on the frontal surface. The sensory canal was continued anteriorly on the surface of the nasomesethmoid. The infraorbital sensory canal passed across the sphenotic to connect with the otic branch from the pterotic beneath the ornamented layer of the frontal, but there does not seem to have been any connection with the supraorbital canal.

There is a small ornamented supraorbital above the anterodorsal region of the orbit in *C. levesiensis*, but there is no trace of a bone in this area in *C. nepaholica*. A.M.N.H. Nos. 1969 and 2522 both show the composite nasomesethmoid formed, presumably, from the fusion of the nasals with the mesethmoid. Hay (1903, p. 86) in error, thought that the nasals were distinct bones. The composite structure has an anterior prominence of dense bone fused to the upper surface of the vomer, and two divergent laminae extending backward, flanking the anterolateral edges of the frontals. The lateral edges of the nasomesethmoid lie along the dorsomedial parts of each palatine and appear to aid in their support.

Cimolichthys levesiensis was reported to have a large, wide vomer (Goody, 1969b, p. 42, fig. 17), but this was in error. The vomer in *C. nepaholica* (A.M.N.H. No. 8348) is small and composed of very dense bone fused to the underside of the anteriormost part of the nasomesethmoid (fig. 3). These two bones together form a solid pointed mass, and the suture between them is impossible to determine. The vomer is narrow and bears an irregular set of teeth with normally two rows. It never has a single row, as in *C. levesiensis*.

The lateral ethmoid of the left side is visible in A.M.N.H. No. 1776, and the area of the palatine to which it was attached in life is somewhat expanded. No posterodorsal expansion of the palatine is evident in *C. levesiensis* (Goody, 1969b, fig. 20). The parasphenoid (fig. 3) is greatly expanded anterior to the orbit (A.M.N.H. No. 1969), where it contacts the palatines on either side. Farther back the parasphenoid tapers below the orbits (a condition resembling that in *C. levesiensis*), forming the floor of the posterior myodome, which opens posteriorly below the occipital condyle. The condyle itself is formed solely of the basioccipital, as in *C. levesiensis*; the exoccipitals meet each other above the condyle in the floor of the foramen magnum (A.M.N.H. No. 1748). The foramen that passed the vagus nerve lies lateral to the condyle in the exoccipital (A.M.N.H. No. 1969).

The prootic has been described in some detail for *C. levesiensis* (Goody, 1969b, fig. 18), and does not differ from that of *C. nepaholica*. A long

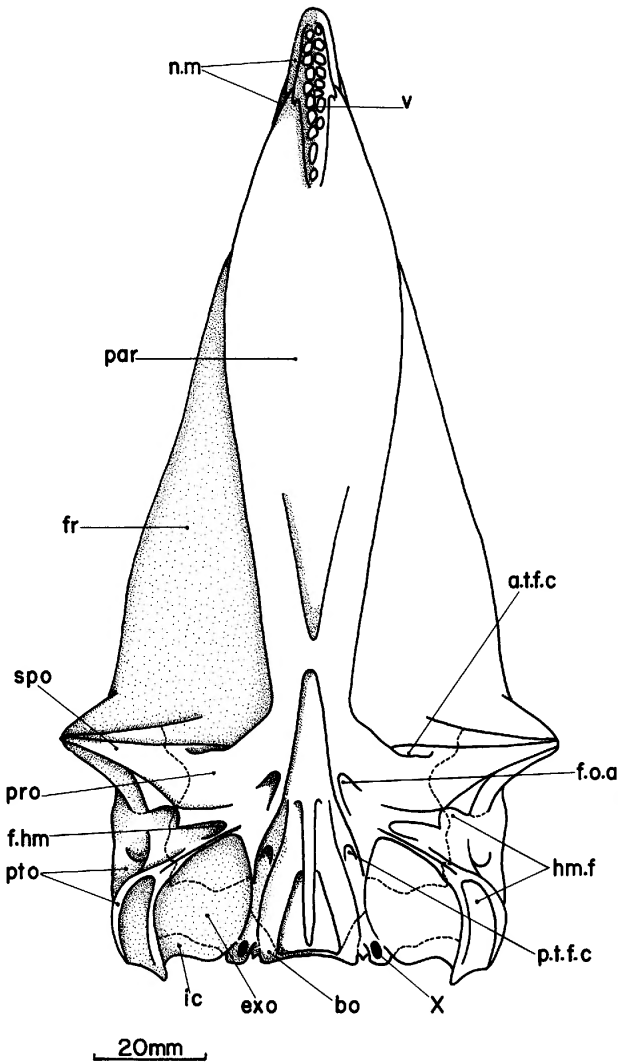


FIG. 3. *Cimolichthys nepaholica* (Cope), reconstruction of neurocranium, ventral view.

Abbreviations: a.t.f.c, anterior opening of trigeminofacialis chamber; bo, basioccipital; exo, exoccipital; f.hm, foramen for hyomandibular branch of facial nerve; f.o.a, foramen for orbital artery; fr, frontal; hm.f, hyomandibular facet; ic, intercalar; n.m, nasomesethmoid; par, parasphenoid; pro, prootic; p.t.f.c, posterior opening of jugular canal; pto, pterotic; spo, sphenotic; v, vomer; X, foramen for vagus nerve.

jugular canal is present, the posterior opening is at the hind end of the prootic (A.M.N.H. No. 6422). The foramen that transmitted the hyomandibular branch of the facial nerve out of the pars jugularis and the foramen which passed the orbital artery into the pars jugularis can be seen above and below the jugular canal respectively (A.M.N.H. No. 1969).

The hyomandibular facet is characteristically shaped (fig. 3); it is in two distinct parts (A.M.N.H. Nos. 1969, 6412, and 6422). The more prominent posterior part is a well-defined pterotic groove, whereas the anterior part is a cup-shaped facet formed from the sphenotic and prootic. A clearly defined oval dilatator fossa is visible in *C. levesiensis* (Goody, 1969b, fig. 18), but not in *C. nepaholica*. In the latter species the dilatator operculi muscles would have inserted onto the undersurface of the pterotic and sphenotic above the hyomandibular facet.

JAW APPARATUS: This complex, like the neurocranium, differs little from that of *C. levesiensis* (Goody 1969b, figs. 20, 21). A.M.N.H. No. 1776 shows that the dermal upper jaw (fig. 8B) is quite similar to that of *C. levesiensis* (fig. 8A), except that the maxilla is somewhat stouter in *C. nepaholica*. The anteriormost part of the maxilla lies in a shallow oblique groove on the lateral face of the palatine and is curved in toward the midline over the dorsolateral surface of this bone. The anterior edge of this inflected maxillary head has a groove along its length into which the posterior, obliquely inclined edge of the premaxilla fits. The supramaxilla is of a shape similar to that of *C. levesiensis* (fig. 8A), but is slightly larger (fig. 8B) and has no external ornamentation. The mandibles are likewise practically indistinguishable in shape, pattern of ornamentation, and distribution of teeth, although there is a disparity in size. Three principal rows of teeth are present and none are barbed, although as Hay (1903, p. 84) pointed out, the crowns of the innermost row are almost always broken off, so that it is difficult to detect whether post-apical or pre-apical barbs were present.

The hyopalatine apparatus, although incompletely preserved particularly in respect of the hyomandibular and pterygoids, does not appear to differ significantly from that of *C. levesiensis*. A.M.N.H. No. 1967 is an isolated palatine bone that does not show the ventral longitudinal concavity seen in *C. levesiensis*, but agreement is reached in the possession of two rows of teeth. However, in *C. levesiensis* the innermost row is the more prominent, whereas in *C. nepaholica*, the outer row contains the larger teeth. The inner tooth row extends to the extreme anterior end of the palatine and consists of approximately 20 tooth bases, which decrease in size posteriorly. The tooth bases are crowded

together and represent functional teeth and their successors. At the posterior end of the inner tooth row there is a greatly enlarged base, four times the diameter of the other bases in the row. Thus, as in *C. levisensis*, the inner row is terminated by the largest tooth in the upper jaw. The outer row is the more prominent, with the first base next to the fourth of the inner row. There are 13 bases following this that are more irregularly disposed than those of the inner row and that extend farther posteriorly. Again, functional teeth and their replacements are represented.

As noted in the introduction, Cope (1872a, 1872b, 1874, 1875) based most of his specific designations on palatine structure and on palatine and dentary tooth structure. Hay (1903, pp. 82-85) indicated that there was so much variation among the specimens that the distinctions specified by Cope were of little, if any, value. One constant feature in all of the specimens examined is the greater prominence of the outer tooth row of the palatine. In this respect *Empo lisbonensis*, erected by Stewart (1899, p. 111) on a fragmentary specimen (Kansas University Museum of Vertebrate Paleontology No. 328) from the Lower Pierre Shale (Lisbon Shale) of Logan County, Kansas, although imperfectly described, appears to be synonymous with *Cimolichthys nepaholica*. Stewart (1900, p. 337, pl. 61, fig. 10a, b) indicated that *Empo lisbonensis* was a fish of about the size of *Cimolichthys nepaholica*, in which the outer row of palatine teeth was the most prominent.

The pterygoids are imperfectly seen in A.M.N.H. No. 1776. The ectopterygoid is firmly sutured to the posteroventral region of the palatine and bears a single row of teeth. The anteriormost tooth of this row is the largest, and its basal diameter is only slightly smaller than the largest tooth at the posterior end of the palatine. The quadrate of A.M.N.H. No. 1741 (figured by Cope, 1875, pl. 53, fig. 2) has a transversely arranged condyle and a thickened, angled posterior edge that lies against, and overlaps slightly, the anteroventral edge of the preoperculum. This lower end of the preoperculum is all that remains of the opercular cover, and it is somewhat expanded. It ends ventral to the articular facet of the mandible, and here the deep groove that housed the sensory canal is shown. The groove runs below the jaw joint and is continued as a tube forward along the articular and dentary.

The description so far has been confined to specimens from the Niobrara Formation. However, several specimens from the Pierre Shale are present in the American Museum collections: A.M.N.H. Nos. 1774, 8270, 6410, and 6406. A.M.N.H. No. 1774 carries no information regard-

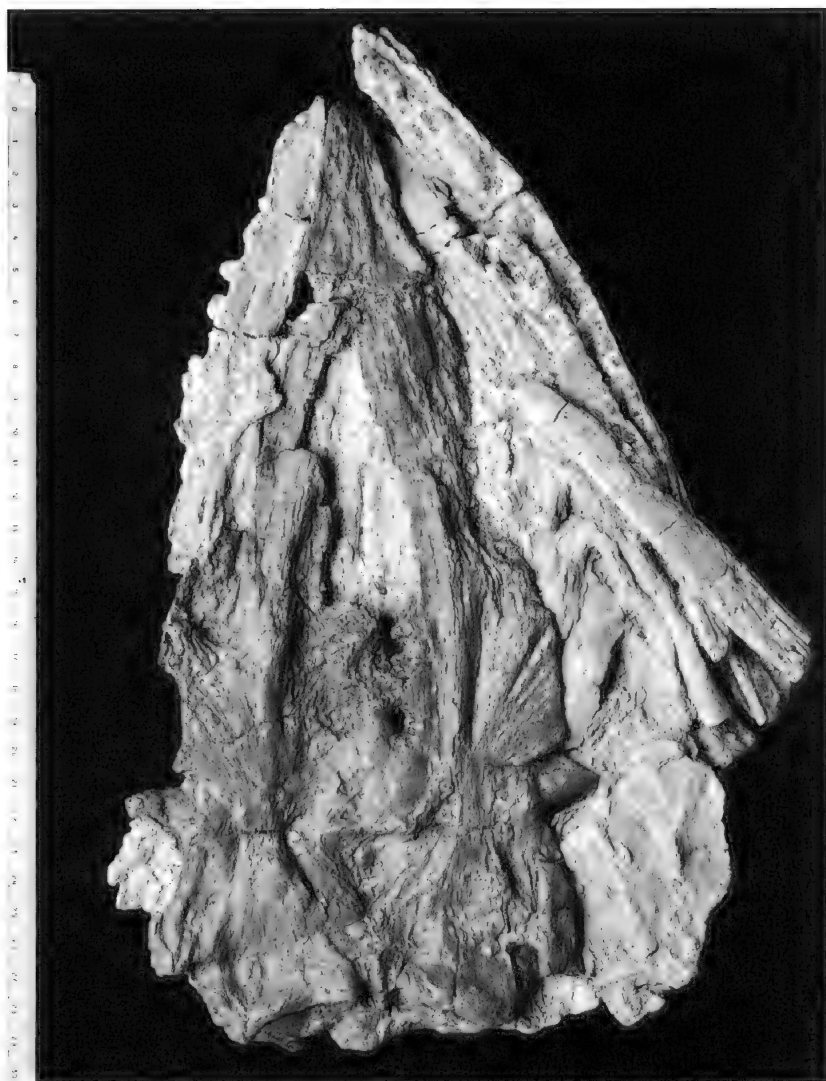


FIG. 4. *Cimolichthys nepaholica* (Cope), A.M.N.H. No. 1774, flattened skull, dorsal view.

ing horizon, but the remaining three, collected by Bobb Schaeffer, are all from the Sharon Springs Member of the Pierre Shale near Mule Creek Junction, Wyoming. Gill and Cobban (1966) published a detailed account of the Pierre Shale in this area, and they placed the age of this unit on the border between the Lower and Upper Campanian. The

Pierre specimens are of the skull region only. Although badly crushed and heavily impregnated with gypsum, they agree in all observable characters with *Cimolichthys nepaholica* from the Niobrara Formation.

The best preserved of the four specimens is A.M.N.H. No. 1774 (fig. 4); it shows a dorsoventrally crushed neurocranium. The proportions and ornamentation of the skull roof correspond exactly to those of the Niobrara specimens (compare figs. 2 and 4). The dorsal surface of the pterotic also shows the irregular ornamentation and the sensory canal exit as in the Niobrara forms. A.M.N.H. No. 6406 also shows the posterior end of the skull roof. The small vomer (A.M.N.H. No. 1774) has an irregular series of teeth aligned in two rows. This same specimen also clearly shows the enormously expanded parasphenoid and imperfect remains of the jaws. The palatine, like that of the Niobrara *C. nepaholica*, has no ventral longitudinal concavity, and the outer row of teeth is the more prominent. Part of the premaxilla and most of the dentary are seen in A.M.N.H. No. 8270; these features resemble those of the Niobrara specimens. This same specimen also shows a row of large, closely crowded, recurved teeth (five in number) at the anterior end of the ectopterygoid.

On the basis of the observable features, the *Cimolichthys* specimens from the Pierre Shale clearly belong to the species *C. nepaholica*.

CAUDAL SKELETON: Little of the caudal skeleton can be seen in any of the *Cimolichthys levisiensis* specimens (Goody, 1969b, p. 50); it is more distinctly observable in the *C. nepaholica* specimens. Hay (1903, p. 88, pl. 1, fig. 4) illustrated the caudal fin of A.M.N.H. No. 2032 to show the large size of the fin in relation to the size of the caudal vertebrae. He estimated the lobes of the fin to be 175 mm. long and remarked on its deeply cleft nature—the length of the rays in the midline of the fin are about 50 mm. (Hay, 1903, p. 88). The caudal skeleton is best observed in A.M.N.H. No. 1751, which was prepared in acetic acid (figs. 5, 6), and in A.M.N.H. No. 2369. The fin ray bases extend over much of the caudal skeleton, and the upper rays project down to the junction of the first and second preural vertebrae (using the terminology of Nybelin, 1963, p. 489). The lower rays extend more than halfway up the parhypural. There is a slight gap between the bases of the rays of the upper and lower lobes in the midline, exposing the junction between hypurals 2 and 3. There is no corresponding gap between the rays distally.

There are four free preural vertebrae involved in caudal support, preurals 2, 3, 4, and 5, along with a compound centrum formed from the fusion of preural centrum 1 and ural centrum 1, and probably ural

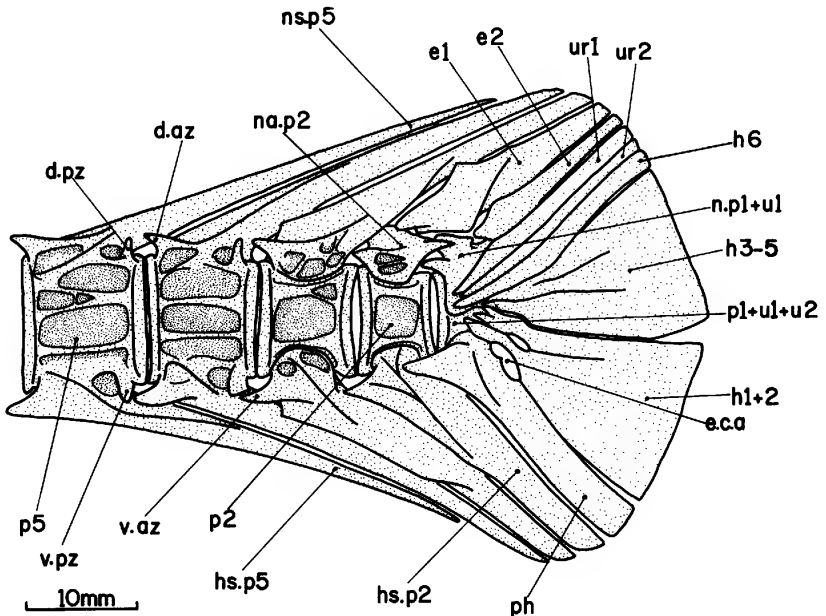


FIG. 5. *Cimolichthys nepaholica* (Cope), reconstruction of caudal skeleton from A.M.N.H. No. 1751.

Abbreviations: d.az, dorsal anterior zygapophysis; d.pz, dorsal posterior zygapophysis; e.c.a, foramen for exit of caudal artery; e1, e2, first and second epurals; hs.p2, hemal spine of second preural centrum; hs.p5, hemal spine of fifth preural centrum; h1 + 2, fusion of first and second hypurals; h3-5, fusion of third to fifth hypurals; h6, sixth hypural; n.p1 + u1, fused neural arches of first preural and first ural centrum; na.p2, neural arch of second preural centrum; ns.p5, neural spine of fifth preural centrum; ph, parhypural (hemal spine of first preural centrum); p1 + u1 + u2, compound centrum formed from fusion of first preural and ural centra; p2, p5, second and fifth preural centra; ur1, ur2, first and second uroneurals; v.az, ventral anterior zygapophysis; v.pz, ventral posterior zygapophysis.

centrum 2 (this last not represented as a free element). The free preural centra decrease in length posteriorly, and 2 and 3 are characterized by the presence of a very deep lateral fossa extending right into the body of the centrum. Preural centra 4 and 5 are characterized by a pair of longitudinal ridges of bone on their lateral faces, which separate a deep midlateral fossa from slightly shallower dorsolateral and ventrolateral fossae. The compound centrum is greatly reduced in length and almost hidden from view by the overlapping accessory structures.

Three neural and five hemal spines are involved in caudal ray sup-

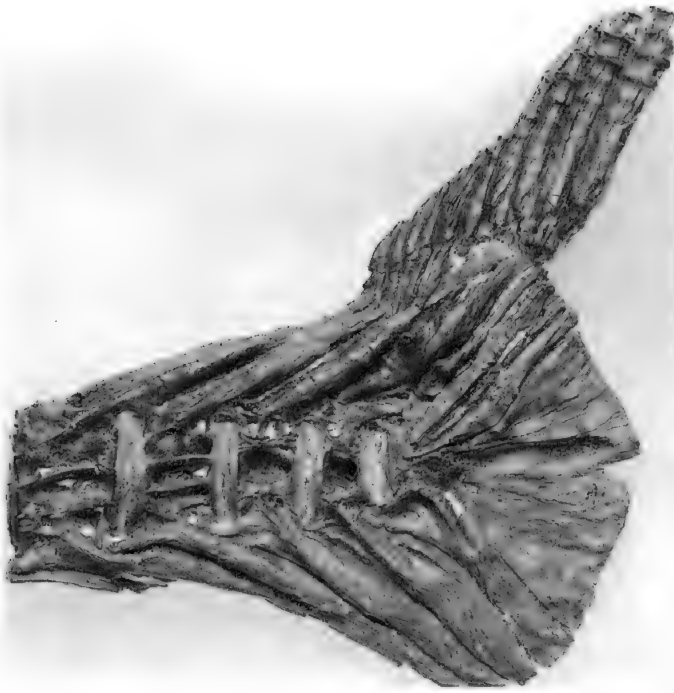


FIG. 6. *Cimolichthys nepaholica* (Cope), A.M.N.H. No. 1751, caudal skeleton.

port; preural centrum 2 and the compound centrum support neural arches without associated spines. The spines are noticeably stout, dorso-ventrally flattened, and inclined strongly backward. Both the neural and hemal arches of preurals 4 and 5 are fused to the centra, but the arches of preurals 2 and 3 are distinct ossifications the sutures of which are clearly visible above and below the deep lateral fossa. The hemal spine of preural 5 is the longest and most flattened; those of preurals 4, 3, and 2 become progressively shorter and fatter. The parhypural, that is, the hemal spine of preural 1 (Monod, 1967), resembles the spine of preural 2, but it is somewhat broader proximally and somewhat less broad distally. The caudal blood vessels bifurcated posterior to the hemal arch of the parhypural and their point of exit is indicated by a hole between this arch and the base of hypural 1. Complete neural spines on preurals 3, 4, and 5 are similar in form to the corresponding hemal spines. A clearly defined neural arch occurs on the second preural, but without a spine, and a neural arch is associated with the compound centrum, again without a neural spine. This latter arch is

expanded basally and extends down over the dorsolateral surface of the compound centrum and almost contacts the base of the parhypural, which extends over the ventrolateral surface of the centrum.

The hypurals exhibit a high degree of fusion, so that functionally two hypural plates are produced, one to the lower and one to the upper caudal lobe. It can be seen where fusion has occurred between individual hypurals. Two hypurals form the lower plate, distinguishable basally where they articulate with the compound centrum. Hypural 1 is closely associated along its entire length with the posterior edge of the parhypural. Hypural 2 is a slightly smaller bone that extends up to the midline of the fin. The bases of these two hypurals extend onto the ventrolateral surface of the compound centrum and laterally contact the downgrowth of the neural arch. The hypurals to the upper lobe are fused into a plate that articulates basally with the posterior end of the compound centrum. Three hypurals—3, 4, and 5—enter into the composition of this plate, but only hypural 3 is visible basally as a separate bone. Another hypural component is described below.

Prominent uroneurals extend posterodorsally from a basal association with the dorsolateral part of the neural arch of the compound centrum. At first sight there appear to be three stout elongate uroneurals fitting closely together to form a stiffening brace to the upper caudal lobe. On closer examination, however, it is seen that the anterior two structures are definitely paired and are thus uroneurals. The third structure appears to be unpaired posteriorly. It seems to be the uppermost hypural (hypural 6), as its posterior edge is closely associated with the anterior edge of the uppermost part of the hypural plate. The second uroneural is the narrower of the two and is sandwiched between uroneural 1 and hypural 6. These latter two structures are slightly stouter than the second uroneural and are of approximately equal size. At their bases all three structures taper to points and end together on the neural arch at the same level.

Two epurals are present: the first is a greatly expanded element with its base lying above the neural arch of preural 2. Epural 2 is less massive and somewhat narrower, but it still has its base slightly expanded where it lies above the neural arch of the compound centrum.

DISCUSSION

Based on the specimens so far recovered, it is proposed that a single species of *Cimolichthys*, *C. nepaholica*, is represented in the Upper Cretaceous of North America. Gill and Cobban (1966) proposed that during

much of Late Cretaceous time the western interior of North America was the site of an epicontinental sea that extended from Mexico to the Arctic. This sea is thought to have been rather shallow, rarely exceeding 300 feet in depth (Schuchert, 1910). Gill and Cobban suggested that the western boundary of the sea migrated eastward, and that the first major retreat occurred during late Niobrara deposition and continued throughout the deposition of the Pierre Shale. In the vicinity of Red Bird (near Mule Creek Junction), Wyoming, the Pierre rests conformably on the Niobrara, which here terminates with a calcareous shale. The change in lithology from the soft yellow or white chalk of the Niobrara to the dark, organic fissile shale of the Pierre (Sharon Springs Member) may reflect a decrease in water depth. More likely it reflects, among other factors, the relative distances from the shoreline, the effects of currents, and the rate of deposition. Such factors would influence the composition of the deposit and the mode of preservation of the fauna, but they are not likely to have a marked effect on the distribution of an active, open-water predatory fish, such as *Cimolichthys* presumably was (see below). It is probable, then, that a single species spanned the entire time represented by both of these Cretaceous deposits.

The systematic description shows not only that a single species of *Cimolichthys* was present in the Upper Cretaceous of North America, but also that sufficient differences exist to warrant separation between this species, *C. nepaholica*, and the European *C. levesiensis*. Goody (1969b) grouped *Cimolichthys levesiensis* with *Dercetis* (*Benthesisikyme*), *Rhynchodercetis*, and *Pelargorhynchus* in the suborder Cimolichthyoidei within the order Salmoniformes (*sensu* Greenwood et al., 1966). The genus *Prionolepis*, known from the English Chalk and from the Lebanese Chalk, was considered a possibly related genus. The inclusion of *Prionolepis* in the Cimolichthyoidei seems to be supported on the basis of the affinity of certain features seen in *C. nepaholica*.

Goody (1969b) noted that the characteristic mesethmoid arrangement in *Prionolepis cataphractus* had little in common with that of *Cimolichthys levesiensis*. However, the nasomesethmoid of *Cimolichthys nepaholica* provides a possible link between these other two forms (fig. 7A-C): *C. levesiensis* shows two backwardly divergent laminae flanking the frontals; *C. nepaholica* shows the point of attachment of the two laminae being produced forward as a small rostral prominence; and *P. cataphractus* has two large posterolaterally arranged flattened wings together with a clearly defined anterior rodlike portion.

The structure of the dermal upper jaw (fig. 8A-C) is also similar in the three forms. Both *Cimolichthys* species and *Prionolepis* possess a long

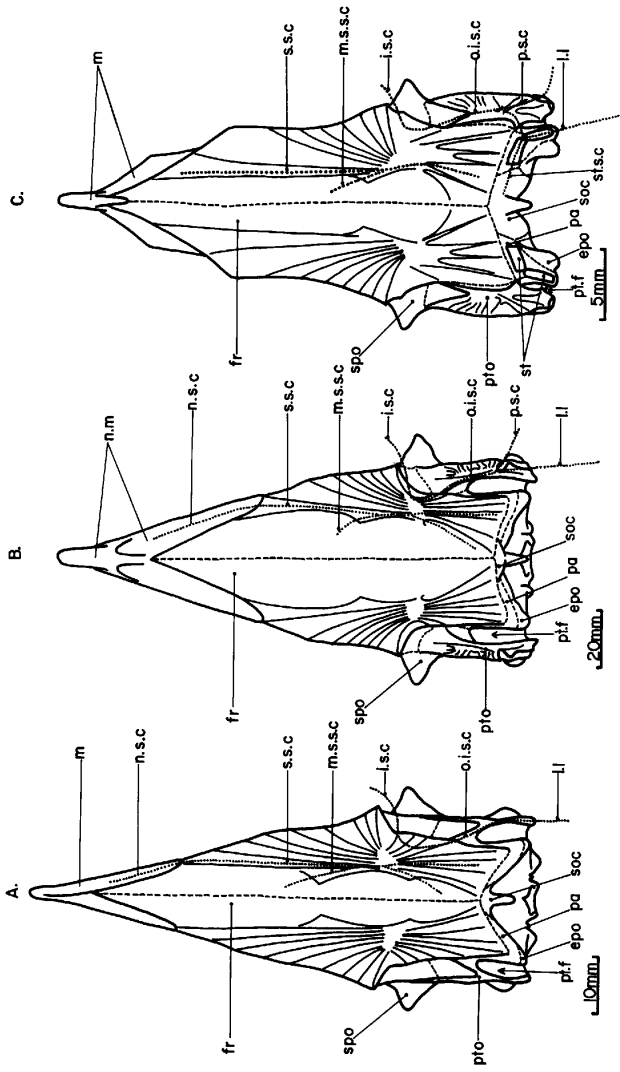


FIG. 7. Dorsal views of neurocranium. A. *Prionolepis cataphractus* (Pictet and Humbert). B. *Cimolichthys levisiensis* Leidy. C. *Cimolichthys nepaholica* (Cope).
 Abbreviations: epo, epiotic; exo, exoccipital; fr, frontal; i.s.c, infraorbital sensory canal; l.l, lateral line sensory canal; m, mesethmoid; m.s.s.c, branch of supraorbital sensory canal onto medial region of skull roof; n.m, nasomesethmoid; n.s.c, nasal sensory canal; o.i.s.c, otic branch of infraorbital sensory canal; pa, parietal; p.s.c, preopercular sensory canal; pt.f, post-temporal fossa; pto, pterotic; soc, supraorbital; spo, sphenotic; s.s.c, supraorbital sensory canal; st, supratemporal; st.s.c, supratemporal sensory canal.

shallow-toothed premaxilla of simple form, that is, without articular or ascending processes. The maxilla in *Prionolepis*, although extensively toothed and lacking a supramaxilla, has the same form as that in *Cimolichthys*; both are long and narrow. They rest on the dorsolateral surface of the palatine medial to the premaxilla and form approximately half of the mouth border.

There is a further similarity in the mandible, which in both genera has a lateral longitudinal shelf extending forward from the articular facet (fig. 8). When the jaws are closed, the maxilla rests on the surface of this shelf. Since articulatory processes on the premaxilla are lacking and there is little, if any, articulatory association between the maxilla and premaxilla, it is assumed that the dermal upper jaw was immobile (apart from probable lateral displacement during enlargement of the orobranchial chamber related to respiratory or feeding movements).

In addition to these noticeable and presumably significant similarities, there are a number of minor skull agreements. The distribution of the sensory canals, excluding the supratemporal, which is absent in *Cimolichthys*, are similar, especially the supraorbital canal (fig. 7). The frontal bones, in which these canals lie, are arranged in much the same manner, extending back almost to the occipital border where they contact the supraoccipital and separate the parietals. In both *C. nepaholica* and *P. cataphractus* (fig. 7B, C) the dorsal surface of the pterotic is extensively ornamented and appears to represent a dermopterotic component; this is not true, however, of *C. levesiensis* (fig. 7A). There is even a lateral excavation of the ornamented layer in *C. nepaholica* and *P. cataphractus* that indicates the passage of the preopercular sensory canal. Goody (1969b) indicated a small posterior excavation of the roof in *Prionolepis*, which most probably represents the opening to an almost completely roofed post-temporal fossa. The same bones border the fossa, epiotic, parietal, frontal, and pterotic in *Prionolepis* as in *C. nepaholica*. In the orbital area *C. nepaholica* agrees with *P. cataphractus* in having lost the supraorbital bone; this element is still represented in *C. levesiensis*.

The jaw suspensorium is vertical in both genera. The quadrate condyle lies below the occiput and the broad hyomandibular has a distinctly double head. A factor possibly related to the upright suspensorium is the absence of an interoperculum in both genera. Schaeffer and Rosen (1961) stated that the interoperculum serves to converge the opercular series onto the interoperculo-mandibular ligament, so that contraction of the levator operculae muscles can also serve to depress the lower jaw. The absence of an interoperculum in *Cimolichthys*, *Priono-*

lepis, and in the other cimolichthyoids (*Dercetis*, *Rhynchodercetis*, and *Pelargorhynchus*), as well as in the enchodontoids (Goody, 1969b)—all forms with a vertical suspensorium—may indicate that if the ligament were present it ran from the suboperculum to the mandible. Or the more primitive method of jaw depression by the action of geniohyoid muscles from the hyoid arch (Schaeffer and Rosen, 1961) may have existed. The quadrates also show a degree of likeness in that the pos-

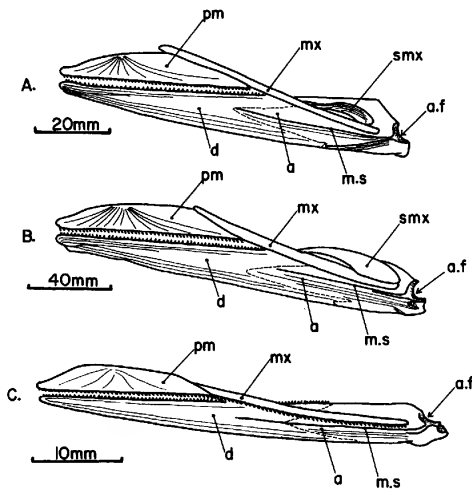


FIG. 8. Jaws, lateral views. A. *Cimolichthys levesiensis* Leidy. B. *Cimolichthys nepaholica* (Cope). C. *Prionolepis cataphractus* (Pictet and Humbert).

Abbreviations: a, articular; a.f, articular facet; d, dentary; m.s, lateral mandibular shelf; mx, maxilla; pm, premaxilla; smx, supramaxilla.

terior edges are thickened and angled laterally, tending to overlap the anterior edge of the lower end of the preoperculum.

These structural correspondences between *C. nepaholica* and *P. cataphractus* suggest a reasonably close relationship between the two genera. Additional similarities are discussed in the following consideration of the caudal skeleton.

The caudal skeleton of *Cimolichthys nepaholica* (figs. 5, 6) provides a further basis for the assignment of the family Cimolichthyidae to the Salmoniformes, as proposed by Goody (1969b). The basal salmoniforms, for example, *Salvelinus* (Gosline, 1960, fig. 2), retain the generalized teleostean arrangement of two ural centra (Patterson, 1968a). Within the order there is a tendency to reduce this number, either by fusion of the first ural centrum with the first preural centrum, leaving a single

free ural vertebra (argentinoids, Gosline, 1960, fig. 10; some stomiatooids, Weitzman, 1967; enchodontoids and halecoids, Goody, 1969b, figs. 42, 48, 64, 69; and many myctophoids, Gosline, 1961), or by the fusion of both ural centra to the first preural vertebra (galaxioids, Gosline, 1960, fig. 11; plecoglossoids, Gosline, 1960, fig. 12; and *Cimolichthys nepaholica*). It is of interest that Goody (1969b) noted a free second ural centrum in *Prionolepis cataphractus*. This fact, however, does not invalidate the conclusions as to the relationship between *Cimolichthys* and *Prionolepis* based on skull structure, as Weitzman (1967) has shown that in the stomiatooid genus *Borostomias* two species have fused centra and one species has a free second ural. Thus the presence or absence of a second ural centrum in some groups is merely a specific character and does not exclude a close relationship between two genera.

Gosline (1960) noticed the tendency in the salmonoids, argentinoids, and osmeroids for the most posterior neural and hemal spines to be laterally flattened, forming a keel both above and below the peduncle. In *Cimolichthys nepaholica*, however, there is a tendency for dorsoventral flattening to occur, and the spines are pressed quite closely together, tending to grip the centra firmly and imparting a pair of strengthening struts to the caudal peduncle. Cavender (1966) noticed a similar but more extreme condition in his "*Ichthyodectes*" type of caudal skeleton. This arrangement would impart some measure of strength and stability to the caudal peduncle, which is further enhanced by the presence of zygapophyses in *Cimolichthys nepaholica*. On the anterior regions of each of the five neural and hemal arches, there are forward projections overlapping the centrum in front. In addition to these, there are, on preural vertebrae 4 and 5, corresponding projections from the posterior ends of the arches in close approximation to the forward prominences (fig. 5). These dorsal and ventral zygapophyses would aid in preventing undue torsion of the caudal peduncle.

Cimolichthys nepaholica has two epurals representing detached neural spines. Patterson (1968a) pointed out that three epurals is the primitive teleostean number, and that the anteriormost can, in some instances (Norden, 1961), fuse to a neural arch to become indistinguishable from a normal neural spine. He also noted that the fusion of an epural with the neural arch of preural centrum 2 is a common occurrence among acanthopterygians, and that the primitive condition of the neural spine of preural vertebra 2 is shorter than its predecessor, as exemplified by *Elops* (among others). Goody (1969a) suggested this with reference to the reduced neural spine on the second preural of *Sedenhorstia*; it only appears to be reduced due to the elongation of the neural spines of

preurals 3 and 4 anterior to it. With the development of a more efficient caudal support, the backward extension and elongation of neural spines may have become necessary. Epurals, being detached neural spines, could have been utilized in this process by becoming reattached to neural arches. Possibly the neural spine of preural vertebra 3 in *Cimolichthys nepaholica* incorporates an epural. However, the low neural arch of preural vertebra 2 is an advanced condition according to Patterson (1968b), derived from a condition such as that in *Elops*, and it is difficult to ascertain why the process of epural reattachment did not occur on preural vertebra 2. The great expansion of the anterior epural in *Cimolichthys nepaholica* effectively fills out the space bounded by the neural spine of preural vertebra 3, the low neural arch of preural vertebra 2 and the second epural, which in turn completely fills the space between the first epural and the first uroneural. *Prionolepis cataphractus* also exhibits two epurals (Goody, 1969b), and, as in *Cimolichthys nepaholica*, the first is expanded.

It has been suggested that two elongated uroneurals formed from modified neural arches (Patterson, 1968a) are present in *Cimolichthys nepaholica*; this agrees with the general condition found in salmoniforms (Gosline, 1960; Weitzman, 1967; Greenwood et al., 1966; Goody, 1969b). It has also been suggested that the third elongated structure is the uppermost hypural and not a uroneural. This upper hypural extends anteroventrally along the hind edge of the second uroneural and is divided basally to produce a pair of processes lying on either side of the compound centrum, thus presumably paralleling the uroneurals functionally as well as morphologically. This modification of the uppermost hypural is a feature not normally associated with the salmoniform group, but it is encountered in the perciforms. Monod (1967, fig. 15) figured a caudal skeleton of *Acanthocybium* in which two hypural plates are present, with the uppermost hypural excluded and closely associated with the posterodorsal extension of the stegural. His figure also shows *Acanthocybium* as having two epurals, the anterior one slightly expanded, a low neural arch on preural vertebra 2 and a complete spine on preural vertebra 3. This is the condition described for *Cimolichthys nepaholica*. However, perciforms normally have five hypurals (Patterson, 1968b), whereas it is suggested here that *Cimolichthys nepaholica* has six.

The remaining hypurals of *Cimolichthys nepaholica* have fused to the extent that two functional hypural plates result. Primitively there is a roughly vertical posterior edge to the hypural complex, but throughout teleostean evolution there has been a marked reduction in the asymmetry of the caudal endoskeleton. This is profoundly noticed in the hypural

complex of *C. nepaholica*, in which there has been a tendency for the upper hypurals (3–5) and the modified sixth to become functionally and structurally associated with the uroneurals to form a symmetrically disposed unit with its lower counterpart composed of hypurals 1 and 2 and the parhypural. These two roughly triangular functional units meet in the midline of the fin. With the achievement of internal symmetry the hypurals lose their vertical posterior edge; it inclines forward slightly above and below the midline (fig. 5). This condition is most noticeable in fish with deeply cleft tails, such as *Cimolichthys nepaholica*.

One last feature, which is characteristic of many salmoniforms, is the production of a stegural (Monod, 1967) from the first neural arch, the first preural neural arch, and the first uroneural. *Cimolichthys* shows the beginnings of such an element. The compound centrum bears an expanded neural arch that extends forward to contact the neural arch of preural vertebra 2; it is probably formed from the neural arches of preural vertebra 1 and ural vertebra 1. The first uroneural is, however, still a separate strap-shaped bone applied to the dorsolateral surface of this arch. Here seems to be the forerunner of a stegural, such as the one in *Sedenhorstia* (Goody, 1969a, fig. 2).

Some of these ideas can be correlated with those of Patterson (1968a) concerning the development of the teleostean tail from the pholidophorid tail (fig. 9). Patterson maintained that an oblique plane of weakness existed in the pholidophorid tail (fig. 9A) and in the ancestral teleostean tail at the level of the second ural segment. This weakness is emphasized by the termination of the preural neural spines anterior to the plane and the origin of the epurals posterior to it. Functional and structural obliteration of this "joint" is brought about initially by forward extension of the uroneurals (fig. 9B), which generally in primitive teleosts extend onto the first two or three preural centra (fig. 9C). In *Cimolichthys nepaholica* (fig. 9D) the uroneurals extend across the line onto the compound centrum, accompanied by the modified sixth hypural extended anteroventrally. Additional strengthening has been achieved by the strong backward slant and stoutness of the neural spines, which cross the line of weakness (fig. 9C and D), by the fusion of the first epural onto the neural arch of preural vertebra 3 crossing the line, and finally by the great expansion of the remaining two epurals that now also straddle the line. Thus a complete extension of bone dorsally obliterates the ancestral hinge to allow little or no flexion or torsion of the caudal fin.

The structure of the caudal skeleton seems to justify placing the cimolichthyoids in the order Salmoniformes, but it does not indicate

close relationship to any of the other salmoniform groups. The specializations noticed in the caudal structure, for example, hypurostegy—the covering of the hypurals by the bases of the caudal rays (Le Danois and Le Danois, 1964)—is seen in numerous other teleost groups, such as the scombroids (both Berg, 1940, and Le Danois and Le Danois, 1964, used hypurostegy in the definition of this group) and the plethodontids (Patterson, 1967b). Generally hypurostegy is accompanied by fusion of the hypurals into one or two large plates. This fusion is in part an expression of the trend in teleosts to simplify and increase the symmetry of the caudal endoskeleton, but obviously it has much functional sig-

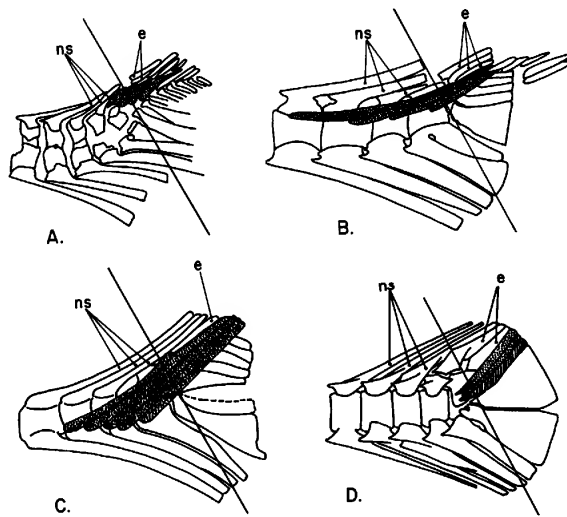


FIG. 9. Representative caudal skeletons illustrating obliteration of line of weakness present in pholidophorid and early teleostean tail. A. *Pholidolepis dorsetensis* Nybelin, after Patterson, 1968a. Plane of weakness indicated at level of second ural segment, with preural neural spines terminating anterior to it and epurals originating behind it. B. *Leptolepis dubia* (Blainville), after Patterson, 1967a. Plane of weakness partially obliterated by elongation and forward extension of uroneurals, preural neural spines, and epurals are still in same condition as in *Pholidolepis dorsetensis*. C. "*Ichthyodectes* type," after Cavender, 1966. Plane of weakness now obliterated by forward extension of uroneurals and backward extension of preural neural spines. D. *Cimolichthys nepaholica* (Cope). Plane of weakness obliterated by forward extension of both uroneurals, sixth hypural, and epurals and expansion of latter, together with backward extension of preural neural spines.

Abbreviations: e, epurals; ns, neural spines; oblique line represents plane of weakness; ural neural arches are stippled in A.; uroneurals are stippled in B., C., and D.; modified elongated hypural is crosshatched in D.

nificance, as the same trends are seen in the holostean *Pachycormus* (Wenz, 1963).

Lund (1967) pointed out that the entire locomotor system of *Pachycormus* is much like that of the scombroids. A deeply forked caudal fin held quite rigidly is characteristic of fishes capable of fast sustained swimming (Nursall, 1962). The deep cleft reduces the flexibility at the middle of the fin, where there is a tendency for the water stream to concentrate. In the deeply forked tail there is often a production of lateral keels on the caudal peduncle to counteract the tendency for the water stream to concentrate at the middle of the fin. The keels deflect water dorsally and ventrally to disperse its thrust over the entire fin (Nursall, 1963). These lateral keels are shown well in carangids and scombrids and also in many fossil forms with deeply cleft tails, for example, *Tselfatia* (Arambourg, 1954; Patterson, 1967b), *Enchodus* and *Prionolepis* (Goody, 1969b). Lateral keels were probably present in *Cimolichthys*, and the whole caudal fin suggests that *Cimolichthys* was a fast, active predator, an assumption also supported by the fusiform shape of the body.

CONCLUSION

From the foregoing it can be seen that there is only a single species of *Cimolichthys*, *C. nepaholica*, recovered from the North American Upper Cretaceous. It has also been shown that the skull structure of *C. nepaholica* differs little from that of *C. levesiensis*, the type species from the English Chalk. The skull structure also substantiates the association between the Cimolichthyidae and *Prionolepis* previously suggested by Goody (1969b). The structure of the caudal skeleton and fin is an addition to the knowledge of the genus as a whole, but, as Patterson indicated (1968b), the study of a single structural complex is unlikely to produce firm conclusions about relationships. This is evident in the case of *Cimolichthys nepaholica*, which has departed considerably from the basal teleost plan. The presence of an anteroventrally extended sixth hypural has been noticed as being a particularly advanced character and the compound centrum, the low neural arch on preural vertebra 2, and the fusion of the remaining hypurals are further specialized features generally associated with more advanced groups, such as the percoids, although they are also known in several advanced salmoniform groups. These specialized characters, together with hypurostegy, a deeply cleft fin and the strengthening of the caudal peduncle are all suggestive of a fish adapted for fast propulsion (Gregory and Conrad, 1937). The cleft caudal fin and the fusiform body seen in the Cimolichthyidae suggest

that this family was composed of pelagic fishes capable of sustained active swimming.

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