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North American fossil cryptobranchidae

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NORTH AMERICAN FOSSIL CRYPTOBRANCHIDAE

By

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INTRODUCTION

Fossil remains of salamanders of the family Cryptobranchidae are grouped at the present under four generic names; Andrias, Megalobatrachus, Cryptobranchus and Plicagnathus. Two of these generic names are also applied to the Recent forms: Cryptobranchus to the North American hellbender and Megalobatrachus to giant salamanders inhabiting Japan and China. The relationships of the North American cryptobranchid fossils described in this work will be considered within the context of the whole family; therefore, for convenience in discussion, each genus will be considered briefly below.

Genus Andrias

The Mid-European fossils grouped here have been recently revised by Westphal (1958). They include the most numerous and most completely preserved fossils of the family Cryptobranchidae. The history of fossils referred to this genus is a long one, extending back to the early 18th century. These fossils were discovered a century earlier, than the Recent representatives of the family.

The first report on these fossils was made by the physician Johan Jakob Scheuchzer in 1726. Scheuchzer thought that he had discovered, in the Öhningen quarry near where he lived, the pelvic girdle of a wicked little man who had perished in the Noachian deluge. In Scheuchzer's time deposition by the Universal Deluge was a popular explonation for fossils found on mountain tops and far inland.

More bones of Andrias were found in the Öhningen quarry, and Gessner (1758), after examining all available fossils, came to the conclusion that the bones were not of human origin. However, it was not until Cuvier did some preparation on the specimen of Scheuchzer's "Homo diluvii testis" that the fossil was correctly placed in the order Urodela. In 1837 Tschudi described the specimen and gave it its present name Andrias scheuchzeri.

Fossil remains of Andrias are known from six localities in Central Europe (Westphal, op. cit., page 24). Öhningen near the Bodensee, is the type locality, and this quarry proved to be the most fossiliferous of the six. Westphal describes twenty-three Andrias fossils from this locality and lists two others not available to

him. The age of these deposits is Late Miocene. Most of the fossils are fairly complete, with skulls, hyoids, part of the vertebral column and limb bones intact, but in most cases the skeletons are strongly compressed by the weight of sediment.

The locality at Preschen in Böhmen yielded the remains of about ten individuals, most of which are parts of the vertebral column: however, some skull remains have also been found. The age of the strata is Late Miocene. Based on the difference in age and on apparently a broader squamosal, these fossils were placed in a different species, Andrias bohemicus, by Laube, (1897). Westphal (ibid, page 23) found these fossils identical with the Ohningen ones and placed them in Andrias scheuchzeri.

Meyer (1859/61) describes a single relatively well-preserved salamander skeleton from Upper Mid. Oligocene strata of Rott, near Bonn, which he placed in still another species Andrias tschudi. Westphal found no morphological differences and placed them in the same species Andrias scheuchzeri.

Three less important localities yielding fragments of Andrias scheuchzeri are:

1. Reisenburg near Günzburg: a premaxilla of Late Miocene age.
2. Hochenberg near Jungau, north of Sigmaringen: two poorly preserved jaw fragments of uncertain geological age.
3. Brunn near Vösendorf: a thoracic vertebra and humerus, of Early Pliocene age.

The generic name Andrias is also applied by Westphal to the living Oriental giant salamanders usually placed in the genus Megalobatrachus. Westphal's classification rests on osteological studies, in which he studied variations in skeletons of Recent Asiatic giant salamanders and compared these with the fossils. The presumed specific and the generic differences given by the earlier authors were found to be within the wide range of variations of the Recent forms. Since the name Andrias had priority over Megalobatrachus, therefore Andrias is applied to both the Central European fossils and the Recent Asiatic giant salamanders. This conclusion is confirmed by osteologic studies undertaken in connection with this work, and the generic name Andrias will be applied also to the Recent Asiatic forms.

Genus Megalobatrachus

Shikama and Hasegawa (1962) report Late Pleistocene

cryptobranchid fossils from the limestone quarry, Shikimzu, Hijikawamura, Kita-gun, Japan. The salamander fossils were found in association with fossil remains of mammals, birds, frogs, toads, and fish. The cryptobranchid remains include: a right parietal, a right parasphenoid, three right dentaries and eight vertebrae. The remains are supposed to have come from four specimen, one was estimated to be around 500 mm., and the other three 900 mm. in total length. Even the largest was well below the maximum size of 1300 mm. attained by Recent animals. The authors found the fossils to differ from the Recent Japanese form only in having a proportionately longer vertebral centrum. The difference was not thought to be of specific value, and the fossils were referred to Megalobatrachus japonicus.

If Westphal's classification is accepted these fossil remains should also be included in Andrias.

Genus Plicagnathus

The name Plicagnathus matthewi was applied by H. Cook (1917) to a lower jaw fragment of a large cryptobranchid from the Upper Miocene Snake Creek beds* of Western

*Though Cook refers to the strata as Lower Pliocene, he never published the locality data or indicated the precise stratigraphic horizon of the fossil. It is, however, highly probable that it came from near the base of the section in Sinclair Draw, Nebraska, referred to as "Lower Snake Creek beds". (Dr. R. Estes, pers. comm., 1963).

Nebraska. He recognizes the relationship of this fossil to the Öhningen Andrias, but believed it to be distinct enough to be placed in a separate genus on the basis of the "folded appearance of the internal surface of the lower jaw", and its very large size. The total length of the animal was estimated by Cook to be around 5 feet (1524 mm.). Cook refers to the same genus another fossil specimen in the possession of Dr. F. B. Loomis. There is no mention as what part of the animal this fossil represented, and the specimen, presumed to have been in the Collection at Amherst College, has not been found.

The above two fossils are the only ones that have been referred to Plicagnathus in the literature.

Genus Cryptobranchus

All living North American cryptobranchids are grouped within this genus, commonly known as the hellbenders.

Two authors have referred fossil salamander remains to this genus: Peterson (1925/26) describes a vertebra of Pleistocene age from Frankstown Cave in Pennsylvania, which he referred to Cryptobranchus. The vertebra is considerably smaller than that of an adult Cryptobranchus. This vertebra was not seen by the author.

Tihen and Chandler (1963, in press) report a complete

right maxilla and an anterior portion of a left maxilla from the Valentine formation of Nebraska. They interpreted the fossils as agreeing closely with the living Cryptobranchus, though of somewhat larger size. On the basis of the size, lesser curvature of the maxilla, and greater number of maxillary teeth they placed it in a new species C. maccalli. Through the kindness of Dr. Tihen the holotype and paratype were available to the author and will be considered in detail below.

RECENT COMPARATIVE MATERIALS

A. *Cryptobranchus a. alleganiensis*

MCZ no.	Locality	skull length in mm.*
2009-a	Cayuga L., N.Y.	44
2009-b	Cayuga L., N.Y.	44
2009-c	Cayuga L., N.Y.	42
2009-d	Cayuga L., N.Y.	45
1281-a	Headwaters of Allegheny R.	47
1281-b	Headwaters of Allegheny R.	51
17406	Pennsylvania	38
135	Ohio	36
129	Havre du Grace, Maryland	54
14846	Ohio R., at Madison, Indiana	40
247	New Harmony, Indiana	48
256	Charleston, South Carolina	46
134-	Missouri	
134-a	Missouri	
1845	no locality data	38
1320	no locality data	

———*The skull length was measured from the tip of the snout to the posterior border of the exoccipitals.

B. *C. a. bishopi*

MCZ no.	Locality	skull length in mm.
27792	Big Spring State Park, Missouri (skull only)	40

C. *Andrias j. japonicus*

40652	In captivity at U. of California	120
1887	Japan (mounted skeleton)	82
2393	Nagasaki, Japan	68
1896-a	Tokyo, Japan	37
1896-b	Tokyo, Japan	38
1896-c	Tokyo, Japan	35

D. *A. j. davidianus*

2852	Ya Chow, W. Szechuan, China	78
2489	Hung-ya-hsien, W. Szechuan, China	30

FOSSIL MATERIAL

A. Described North American fossils:

1. Plicagnathus matthewi, Cook, 1917 (Plastotype) USNM no. 8366, Lower Snake Creek beds, Nebraska, Upper Miocene, dentary.
2. Cryptobranchus maccalli, Tihen and Chantell, 1963, (Holotype and Paratype), Valentine formation, Nebraska, Uppermost Miocene or Lower Pliocene, right maxilla and fragment of the left maxilla.

B. Undescribed North American fossils:

1. UC no. 37165, left maxilla, Havorka Ranch, Marsland formation, Nebraska, Middle Miocene.
2. HC no. 1260*, lower jaw, in possession of Dr. Cook.
3. UK no. 12004, left maxilla, six vertebrae, two lower jaw fragments, right exoccipital, Quarry A, Pawnee Creek beds, Colorado, Middle Miocene.

C. Andrias scheuchzeri:

1. MCZ cast of an Ohningen specimen at the Zoologischen Museum of Zurich.

*Harold Cook considered this fossil to be a Plicagnathus matthewi.

D. North American fossils mentioned in literature and not seen by the author:

1. Plicagnathus matthewi, whereabouts and nature unknown, "in possession of Dr. Loomis", (Cook 1917).
2. Cryptobranchus sp., vertebra described by Peterson (1925/26), Frankstown Cave, Pennsylvania.

COMPARISON OF THE TWO GENERA OF RECENT CRYPTOBRANCHIDS

External features and Ecology

General

To obtain an idea of the differences which are considered generically significant in the Cryptobranchidae, the soft anatomy and bone structure of the two Recent genera of the family are here compared. The osteological differences observed between the two will be useful in the diagnosis of fossil remains and establishment of their taxonomic position within the family.

Cryptobranchus occurs only in large rivers and streams of the Eastern United States. It ranges from the southern part of New York state to as far south as Arkansas and Georgia; westward they extend into Missouri and Iowa (Bishop, 1943, page 59). Usually two living subspecies are recognized: C. a. alleganiensis and C. a. bishopi (Conant, 1958, page 197). The major differences between the two subspecies are in coloration. C. a. alleganiensis is as a rule gray, but may range from yellowish-brown to black, with irregular dark or light spots, while C. a. bishopi is gray with large prominent dark blotches on its back and

and lower lips. The single available skull of C. a. bishopi agreed in every detail with the skulls of C. a. alleganiensis. The two subspecies do not overlap each other geographically. C. a. bishopi occurs only at the western extremity of the species range, in Missouri and perhaps Arkansas (Bishop, 1943, page 63).

Living Andrias, usually called Megalobatrachus, occur in smaller streams than their American relatives. They are native to Japan and China. However, Myers (1951, page 179-180) reports on the capture of two giant salamanders in California, which appeared to be referable to Andrias. One from the Sacramento River was examined by Myers himself, and found to have a closed spiracle and a total length between 63-76 cm., above the average size for an adult Cryptobranchus. Myers believed that the animal probably escaped from captivity, but its unusual coloration (dark-brown with irregular yellow spots) made him consider the possibility that it may be native to this continent. He mentions in the same paper briefly that another specimen was captured by a frog firm in San Francisco in 1936-37.

External Features

Cryptobranchus and Andrias differ from each other

externally in possession by the former of an open spiracle for the ejection of water taken in during respiration, while in Andrias this opening is closed. Cryptobranchus is a much smaller animal than the Asiatic giant salamander; its size is between 290-510 mm. and the maximum size recorded is 740 mm. (Conant, 1958, page 59). Andrias attains a maximum size of 1350 mm. (Westphal, 1958, page 81). The largest one at my disposal measured 950 mm.

Skeletal anatomy

The Hyoid apparatus*

The greatest differences between the two Recent genera are exhibited in the hyoid apparatus. In Andrias only three visceral arches are retained in the adult individual, and ossification occurs only in the last one (Branchia II of Aoyama, 1929, page 148). Noble (1931, page 224) figures a small bone, just below the third visceral arch, which he calls epibranchial III. I was unable to find such a bone either in the specimens examined or mentioned in the literature. In Cryptobranchus five of the visceral arches are present in the adults. Westphal states that in

*There were no cleared and stained specimens available to me. My observations were made only on hyoids of dry skeletons --- not desirable materials for the study of the hyoid apparatus.

all five of the visceral arches some ossification occurs (1958, page 38), but Furbringer (1922, table 12) figures bone only in the first, third and fourth visceral arches, a situation confirmed in the material available to me. Rees, (1906, page 299) also agrees with the above statement.

Cranial Osteology

Andrias and Cryptobranchus have the same number of skull bones occupying similar positions in relation to each other. However, some of them do differ consistently in shape, proportion, and position, and set the two genera apart.

Figure A, B, C, table I, which compares the skulls of the two genera, will serve to show general orientation and the similarities of position and shape of bones. Only the differences are considered below.

The external nares in Cryptobranchus are usually surrounded by four bones: premaxilla, maxilla, nasal and frontal. In Andrias only three bones border the external nares: premaxilla, maxilla and nasal. The latter alone forms the posterior border of the nasal opening.* This arrangement also effects the number of bones that come in

*Westphal recognizes this diagnostic feature of Andrias and he has found an identical situation in the Ohningen and related fossils.

contact with the pars facialis of the maxilla. In Cryptobranchus only the frontal and prefrontal contact the pars facialis, while in Andrias the nasal also reaches the maxilla. The prefrontal is a broad, oval bone in Andrias. In Cryptobranchus this bone is long and narrow, extending as far back as the most posterior tip of the pars dentalis of the maxilla. In Andrias the prefrontal never reaches as far posteriorly as the posterior extremity of the pars dentalis. As a result of the short prefrontal, the parietal, which reaches anteriorly to contact the prefrontal, often takes part in the formation of the lateral border of the orbit. In cryptobranchids, as in all known salamanders, the posterior tip of the maxilla is not sutured to the pterygoid, but is connected to it by strong ligaments. This separation between the pterygoid and maxilla is relatively large in Cryptobranchus, but in Andrias the two bones are separated by only a very small gap. It is worthwhile to point out here that the two living subspecies of Andrias differ from each other in this respect. A. japonicus davidianus occupies a position intermediate between the wide separation seen in Cryptobranchus and the condition observed in A. japani-

cus japonicus, in which the two bones almost meet. An associated difference is reflected in the shape of the orbit, which in A. j. japonicus is oval and in A. j. davidianus is almost circular. These differences are especially evident in younger animals, since in larger individuals the skull becomes proportionately wider.

Among the fifteen Cryptobranchus skeletons at my disposal the frequency of minor variations in the skulls is high. Since some of these may cause a false diagnosis of fossil bones, the variations encountered will be enumerated below.

The premaxillary spines are usually long, and they extend to or beyond the posterior border of the external nares, but in five out of the sixteen specimens, the spines were short, reaching only to the middle of the external nares. In MCZ no. 1281, on the left side only three bones reached the border of the external nares, as in Andrias, while on the right side the usual four bones participate. Very often minute extra bones are present at the border of the external nares. These appear to have been pinched off from the frontal, but may be heterotopic. Such small bones may be present on one side, and be absent on the other. Such situation

was observed on MCZ nos. 129, 2009-a, 2009-b, and 1281. Also a separate small bone is found in the region of the premaxillary fontanelle which again may be present on one side or on both sides. Such bones were present in MCZ nos. 247 and 2009-d. Variations are especially apt to appear in larger individuals.

NORTH AMERICAN FOSSIL CRYPTOBRANCHIDAE

Individual cryptobranchid fossils from the Tertiary of North America have been described, such as Plicagnathus matthewi and Cryptobranchus maccalli, but there have been no attempts to treat all the available North American cryptobranchid material as a whole. The American fossils are by no means attractive, for in contrast to the European Andrias fossils, they are not entire skeletons, but mostly upper and lower jaw fragments and isolated vertebrae, all usually broken. Some of these single bones are, however, extremely well preserved and lend themselves to detailed osteological studies. Also in number the North American fossil cryptobranchids are inferior. European Andrias scheuchzeri skeletons, most of them almost complete, number in the thirties, while a thorough search for fossil American cryptobranchids resulted in: four maxilla, four fragments of lower jaws, six vertebrae and one exoccipital.* These fossils range from Early Mid. Miocene to Early Pliocene in age. Each fossil will be individually described below and compared with the other fossils and bones of recent repre-

*For North American cryptobranchid material not seen by the author see the section on materials.

sentatives of the family, in an attempt to establish the phylogenetic position of the North American fossil cryptobranchids.

DESCRIPTION OF FOSSILS

UC no. 37165, left maxilla.

Locality: Havorka Ranch, Marsland formation, Nebraska.

Age: Middle Miocene.

Description: The fossil specimen consists of an estremely well-preserved left maxilla, which is complete with the exception of a samll break on the tip of the pars facialis. The chord length of the maxilla is 101.7 mm.; the greatest distance between the chord length and the tooth row is 10 mm., indicating that the ventral border of the pars dentalis forms an average arc of between 45° and 50°.

Francis (1934, page) recognizes three distinct areas on the salamander maxilla: Pars facialis (ascending process), which overlays a lateral portion of the skull; Pars dentalis, which forms the ramus of the maxilla and bears the maxillary teeth; Pars palantine, a narrow area which comes in contact with the vomer and takes part in the formation of the palate. Each of these areas will be considered individually.

The pars facialis is located close to the anterior extremity of the maxilla and dorsal to the pars dentalis, its base length is 34 mm., about 1/3 of the total length

of the maxilla. The height as measured from the ventral border of the pars dentalis to the most posterior tip of the pars facialis, is 27 mm., but since the tip of the pars facialis is broken, this measurement is without much significance. The anterior portion of the pars facialis forms the postero-lateral border of the external naris, and a small curved process from this border projects medially, tending to form the dorsal border of the naris (Figure A, plate II). At its posterior border, close to its base, the pars facialis once again extends into a small triangular process, which forms a 45^{o} angle with the pars dentalis. Just below this process, between it and the pars dentalis, a prominent groove extends anteriorly. On the inside of the maxilla, at the poster-ventral border of the pars facialis, a prominent foramen is present, for the maxillary branch of the trigeminal nerve. The end branches of this nerve emerge through numerous small openings located on the pars dentalis, the foramen lateral nasi (Francis, 1934, plate I), of which there are nine on the pars dentalis of the Havorka fossil. The external surface of pars facialis is relatively smooth, surrounded at its base by a faint but distinct ridge which curves at first ventrad and then dorsad between the post-

erior and anterior process of the pars facialis. On the inner surface, where the pars facialis comes in contact with other bones of the skull, the surface is rough and irregular. Located anteriorly and bounded on both sides by strong ridges, a prominent triangular depression is present, the significance of which will be considered in the discussion.

The pars dentalis is essentially a horizontal bar, bearing teeth along its entire ventro-inner surface. The teeth, with the exception of a single damaged fragment, are missing, but the ridges indicating the number and position of teeth are well preserved and allow a fairly accurate tooth count of one hundred and seven. The dorsal portion of the pars dentalis extends inward to form a 90^{o} shelf over the tooth row. The pars dentalis maintains an almost uniform height through its entire length (it measures 15 mm. at the posterior border of the pars facialis and 13.2 mm., close to its posterior extremity), but tapers at its posterior end. At this point it shows numerous parallel ridges indicating the point of attachment of the ptergoid ligaments, which connect the maxilla with the ptergoid and to the suspensorium.

The pars palatine extends laterally from the base of the pars facialis (which it meets at almost a right angle), and joins the vomer in the formation of the palate. It is a very narrow process as measured from the base of the pars facialis to the point where it joins the vomer. Its maximum width is 5mm. The suture at which the pars palatine meets the vomer is 36 mm. long and is characterized by a broad, irregular surface.

Discussion: The pars facialis or ascending process of the Havorka maxilla closely resembles that of Recent Andrias. In Cryptobranchus this same area is almost an equilateral triangle with relatively smooth anterior and posterior borders, while in both the the Havorka specimen and in Recent Andrias it expands dorsally and is characterized by a numerous small processes along its dorsal border. The prominent anterior process of the pars facialis exhibited by the fossil is invariably present in all specimens of Recent Andrias, and is usually more prominent in larger individuals. Only one of the fifteen available specimens of Cryptobranchus (MCZ no. 1281) had such complex process. A posterior process on the pars facialis occurs in some individuals of both Recent genera but is much more prominent in Andrias japonicus.

In Recent Andrias skeletons the pars facialis of the maxilla overlaps three skull bones: nasal, frontal and prefrontal. Only a small portion of the nasal is covered by the anterior tip of the pars facialis. The nasal is followed by the frontal bone, of which the pars facialis overlaps a small triangular area. The remainder and the greater portion of the pars facialis covers the prefrontal in Recent specimens, in which the prefrontal expands and makes a strong anterior curve.underneath the pars facialis, and it alone meets the maxilla at the base of the pars facialis in a deep groove. The inner surface of the pars facialis is characterized by numerous ridges and depressions, the counterparts of which are observable on the three skull bones covered by this region of the maxilla. On close observation one can recognize a prominent triangular depression on the medial surface of the pars facialis, where the maxilla covers the frontal. Such a prominent depression also exists on the Havorka specimen, and is bounded on both sides by prominent ridges. On the basis of this observation one can assume the pars facialis of the fossil maxilla (as in Recent Andrias skeletons), covered the same three skull bones; nasal, frontal and prefrontal.

As previously pointed out in the description, the curvature of the maxilla in the Havorka specimen is less than either Cryptobranchus alleganiensis or in Recent* Andrias. This condition was also reported for Cryptobranchus maccalli (Tihen and Chantell, 1963, page 9). and will be discussed below.

Based on the chord length of the Havorka specimen, the total length of the salamander was around 1500 mm. Measurements on recent complete Andrias skeletons gave a ratio, of chord length of maxilla to total length, of between 1:15 to 1:16. With increasing total length the ratio appears to decrease, as indicated in the following table.

Table I

Specimen	Chord length	Total length	Ratio
MCZ no. 1887	47.0 mm.	700 mm.	1;14.9
MCZ no. 1896-a	18.7 mm.	290 mm.	1:15.5
MCZ no. 1896-b	17.5 mm.	280 mm.	1:16.0

The estimated length of 1500 mm. exceeds the maximum length recorded for living and fossil Andrias by about 150 mm. (See page 14)

The specimen is referable to Andrias on the basis of

———*See notes

the general appearance of the pars facialis of the maxilla and the apparent contact of this area with three skull bones: nasal, frontal and prefrontal, a situation not seen in Cryptobranchus. It differs from Recent representatives of the genus and from the European fossils in having less curved maxilla and a shallower sulcus dentalis (Hoffstetter, 1962, page 113).

It resembles Cryptobranchus in that the pars dentalis forms a horizontal shelf at right angle to the toothrow, rather than sloping dorsally as in Recent Andrias.

HC 1260

Locality: Upper part of so-called Marsland formation, Nebraska, (Runningwater formation of Cook, 1960).

Age: Middle Miocene.

Description: The specimen is the anterior half of the right dentary of a large cryptobranchid salamander. The maximum chord length of the specimen as preserved is 12 cm. The posterior height of the fragment is 28 mm., and it measures 21 mm. anteriorly. The break occurred at approximately at the point where the prearticular expands to cover the entire inner surface of the lower jaw. The prearticular was not preserved, however, the prominent depressions on both sides of Meckel's groove indicate the

area once covered by the prearticular. Meckel's groove is in the form of a deep triangular furrow, which narrows to a point, about 30 mm. from the anterior extremity of the dentary. Teeth are no longer present, but spaces are preserved for about one-hundred teeth. The space below the tooth row for replacement teeth (sulcus dentalis of Hoffstetter, 1962, page 113) is shallow. Ana area of 30 mm. on the sulcus dentalis (about midway along the tooth row) is covered with bone and a small canal appears to go through it. The symphysis is an elliptical area with a highly irregular surface. Located on it are two prominent knob like elevations, the more prominent of which represents the original axis of ossification of the dentary. It is located to the left and dorsal to the center of the symphysis. The other is located on the ventral border of the symphysis and appears to be a continuation of a strong ridge on the ventral portion of the labial side of the dentary. This ridge extends posteriorly less than one half the length of the fragment. Three large mental foramina (Westphal, 1958, page 29) and four small ones are arranged in a labial series along the long axis of the dentary side. The labial side of the dorsal border of the dentary is somewhat flattened.

Discussion: The salamander represented by this dentary fragment must have been very large. The portion preserved is somewhat more than half of the lower jaw and the total length of the animal is estimated from the chord length, (see above) at around 1800 mm. This exceeds the total estimated length of the Havorka specimen by about 300 mm.

The curvature of the dentary appears to be less than in Recent Andrias, resembling the Havorka maxilla in this character, and in the shallow sulcus dentalis. The ventral ridge on the labial surface of the dentary probably served for the attachment of the strong intermandibularis muscle. The fossil differs in no other observable characters from a recent Andrias dentary. However, minor variations were observed on the specimen examined. Both this fossil and the Havorka maxilla came from Middle Miocene strata of Nebraska. The identity of geological age and geographical occurance, along with the presence of common morphological characters, suggest that the two fossils represent the same species of Andrias.

Plicagnathus matthewi, Cook, 1917, Plastotype --- USNM no. 8366, left dentary.

Locality: Lower Snake Creek beds, Northwestern Nebraska.

Age: Late Miocene.

Description: The holotype of Plicagnathus matthewi has been lost, but two excellent casts of the type were made, one of which is presently at the American Museum and the other, used for description, is the property of the U.S. National Museum. A photograph of the original specimen, in the possession of Dr. Richard Estes, was also made available to me for comparison. The picture and the cast agree in every detail.

The plastotype represents a mesial fragment of a left dentary of a very large salamander. The anterior break appears to have occurred at the point where the anterior extremity of the prearticular was once located (now marked by flat triangular depressions on the fossil). The posterior break appears to be a short distance anterior to the region where the prearticular expands to take up the entire inner surface of the lower jaw in the Recent cryptobranchids. The deep triangular Meckel's groove extends along the entire length of the dentary

fragment. It measures 4 mm. at its posterior end, narrows to a point anteriorly, and is about 5 mm. deep at its posterior end. The chord length, as measured from the posterior ventral border to the anteroventral border of the dentary fragment, is 54 mm. The tooth row is 42 mm. long, and spaces for approximately 40 teeth are present. The sulcus dentalis is very narrow in comparison with that of Recent cryptobranchids. The height of the dentary fragments is 19 mm. anteriorly, and 22 mm. posteriorly.

Discussion: The type of Plicagnathus matthewi resembles very closely the Runningwater formation specimen, but a much smaller portion of the dentary is preserved. The two dentaries seem to have come from individuals of approximately the same size, but that represented by USNM no.8366 may have been somewhat smaller. Since the dentary portion is very fragmentary it is difficult to estimate the total length of the animal, but in comparison with HC no. 1260, P. matthewi appears to have been close to 1600 mm. Since there are no morphological differences between the two dentaries, Plicagnathus matthewi and the Runningwater formation specimen appear to represent the same species of Andrias.

This specimen is somewhat later in geological age from the previou two North American specimens. P. matthewi is Late Miocene in age, the others described were found in Mid-Miocene strata.

Cryptobranchus maccalli, Tihen and Chantell, 1963 Holotype --- UN no. 6100, right maxilla and Paratype --- UN no. 61001, left maxilla.

Locality: Valentine formation in Norden Bridge Quarry, Nebraska.

Age: Between Late Miocene and Early Pliocene (Tihen and Chantell, 1963, page 1).

Description: The holotype (consisting of a well-preserved right maxilla) was described in part by Tihen (1963 page 7) as follows: "chord length of 54 mm., ... length of the base of the ascending process* 17.3 mm.: straight-line height from ventral border to highest point of the ascending process 15.5 mm. No complete teeth remain, but the bases of many are intact; there were about 75 teeth in life ... The jaw is somewhat less strongly curved than in any specimen of alleganiensis." The curvature of the maxilla in Recent Andrias examined by Tihen was found also to be greater than in C. maccalli.

*Pars facialis of this paper (Francis 1934).

The sulcus dentalis below the tooth row is shallow. The pars dentalis maintains a nearly uniform height throughout its length and comes to a point posteriorly. The portion of the pars dentalis below the pars facialis is perforated by eleven foramina lateral nasi (Francis 1934, plate I). The pars facialis is an irregular triangular shape, its longest side being its base. The highest point of this triangle is formed by a prominent dorsal process which forms an angle of 45° with the pars dentalis. Close to its ventral posterior border the pars facialis gives off a posterior process. Below this process a well-marked furrow extends along the base of the pars facialis to the end of its anterior extremity. Caudad to this furrow a deep notch is located on the pars dentalis. The inner surface of the pars facialis is marked by a prominent ridge, which extends ventro-dorsad along the inner surface of the dorsal process, and marks the posterior border of a triangular depression. Only a suggestion of an anterior process is present.

The paratype according to Tihen (op. cit.) comprises "the anterior 8.5 mm. of a left maxilla. There are bases or spaces for 14 teeth." The pars facialis is broken dorsally, but a triangular area, bordered by two ridges

on its inner surface and similar to that seen in the holotype, is present. There are six foramina leteral nasi present on the maxilla fragment.

Discussion: This specimen resembles the Havorka maxilla closely, but is only about one-half its size. An estimation from the chord length of the maxilla gives a total length of 810 mm. according to Tihen. The pars facialis on both specimens is nearly identical in every observable detail.* C. maccalli and the Havorka specimen both show a mesial triangular depression on the inner surface of the pars facialis where at one time the maxilla covered the frontal bone. This indicates (see page 20) that probably three skull bones rather than two came in contact with the maxilla. Only in Andrias does the nasal reach the maxilla, and this may be considered a diagnostic feature of that genus. Tihen's specimens of "C. maccalli" also resemble Andrias in having a dorsal process which is tilted caudad, forming an angle of 45° with the pars dentalis, rather than being nearly vertical (90°) as in Cryptobranchus. The inner surface of the pars facialis resembles very closely a specimen of A. japanicus japonicus (MCZ no.

*The reader is reminded that the dorsal process of the pars facialis of the Havorka specimen is missing.

1896-a), in having a less curved maxilla, uniform height of pars dentalis, and a shallow sulcus dentalis. C. maccalli also resembles the Havorka specimen in these details. On the basis of the above observations, C. maccalli, along with the Havorka specimen, should be referred to Andrias.

UK no. 12004.

Locality: Quarry A, Pawnee Creek beds, Colorado.

Age: Early Mid. Miocene.

Description: UK no. 12004 was assigned to a number of cryptobranchid fragments representing the remains of more than one individual. The collection consist of: a left maxilla, two dentary fragments, one right exoccipital, and five vertebrae.

The maxilla is badly damaged, but its entire length is preserved. The chord length of the specimen is 30.4 mm. The entire pars facialis is broken off along with a small portion of the underlying pars dentalis. The break exposes the canal for the maxillary branch of the trigeminal nerve, which passes antero-ventrally through the maxilla from the posterior extremity of the base of the pars facialis. The pars palatine is 10 mm. long. The pars dentalis maintains a uniform height throughout

its length, but it comes to a point posteriorly. Two measurements of the width of the pars dentalis, one at the posterior extremity of the pars facialis and the second taken close to the posterior extremity of the pars dentalis both give a measurement of 4.6 mm. As a result of damage to the interior surface of the pars dentalis, a tooth count is not possible.

The larger fragment represents the anterior 14 mm. of a left dentary. There are bases or spaces for 15 teeth present. The symphysis is triangular in shape. Posterior to the symphysis the ramus of the left dentary forms a prominent platform below the tooth row.

The smaller dentary fragment has a maximum length of 9,3 mm., and probably represents the posterior extremity of the tooth-bearing portion of the bone. There are bases or spaces for 15 teeth present.

The preserved left excoccipital measures 11.5 mm. from its most anterior border to its posterior extremity. The greatest mediolateral diameter of the articulation surface is subcircular. On the left lateral surface a large foramen is present for the passage of the vagus nerve.

The vertebrae have been given letters a-e and will

be considered individually below.

Vertebra UK no. 12004-a. A trunk vertebra with a centrum length of 16.2 mm. The height of the centrum as measured between the dorsal and ventral borders of the cotyle is 12.4 mm. The angle formed by the neural spine with the centrum is 40°. The left transverse process is broken off almost at its base, but otherwise the specimen is well preserved, showing well-developed pre- and post-zygapophyses, nearly circular in shape. On the ventral midline of the centrum a large foramen is present. At the point where the ribs are attached the transverse process is 10 mm. high and 2 mm. wide.

Vertebra UK no. 12004-b. A trunk vertebra with a centrum 20 mm. long and 13.3 mm. high. The vertebra is badly damaged, and the neural arch is not preserved. The transverse processes are preserved but badly damaged. The right transverse process, at the point of rib attachment, is 9 mm. high and 3 mm. wide. The ventral foramen is located to the right of the midline.

Vertebra UK no 12004-c. A trunk vertebra with a centrum length of 13.8 mm., and a centrum height of 9.2 mm. The neura spine forms an angle of 30° with the centrum. Both of the pre- and one post-zygapophysis are

preserved and are slightly oval in shape. The right transverse process is missing; the left one at the rib attachment is 7 mm. high and 2 mm. wide. The ventral foramen is on the midline.

Vertebra UK no. 12004d. The centrum length of this trunk vertebra is 10.3 mm. and its centrum height measues 6.9 mm. The angle formed by the centrum and neural spine is 42°. All the zygapophysis are preserved and are round in outline. Both transverse processes are intact and give a measurement of 5 mm. and 2 mm. at the rib attachment. The ventral foramen is small and located on the midline.

Vertebra UK no 12004-e. A trunk vertebra with a centrum length of 9.3 mm. and centrum diameter of 5.9 mm. The angle formed by centrum and neural arch measures 23°. Pre- and post-zygapophysis with a slightly oval outline are preserved. The right transverse process is broken off at its base and the left one is damaged at the rib attachment. The ventral foramen is to the left of the midline.

Discussion: The Colorado collection represents the remains of at least four individuals, possibly more.

The maxilla resembles the Havorka specimen and the

Cryptobranchus maccalli in that the pars facialis has a uniform height along its entire length, and also in the very slight curvature exhibited by the ramus of the maxilla.

Vertebrae "a" and "b" appear to have come from the most anterior portion of the vertebral column, as suggested by their short centrum, but even in this case the length of the centrum is shorter in this vertebrae than in Recent Andrias, and the neural spines form a large (40°-42°) angle with the centrum; exceeding that of Recent Andrias, (maximum angle recorded 35°). The angle is much less in Cryptobranchus; the neural spine lies almost flat on top of the centrum. The high neural arches indicate that they probably represented a less flattened salamander than Cryptobranchus, and perhaps even less flattened than in the Recent Andrias.

The maxilla shows the same characters described in the other North American fossils. The exoccipital is typically cryptobranchid, but is not helpful in determening the genus. Vertebrae are also typically cryptobranchid and with their high neural arches suggest Andrias rather than Cryptobranchus.

CONCLUSION

Similar morphological characters shared by the North American fossil cryptobranchids seem to indicate the fact that they represent the same genus and species. Their occurance in a short spann of geological time and their close geographical distribution appears to strengthen the above assumption. The fossils range from Early Mid-Miocene to the Latest Miocene or Early Pliocene in Colorado and Nebraska.

To determine their relationship to the Recent genera of cryptobranchidae, the maxillae are helpful, since the two Recent genera exhibit definite osteological differences in this region. In Andrias the pars facialis of the maxilla contacts three skull bones: the nasal, the frontal and the prefrontal; in Cryptobranchus the nasal is not involved. The markings on the inner surface of the pars facialis of Cryptobranchid maccalli and the Havorka specimen appear to indicate the contact of three skull bones with this area. The dorsal process of the maxillae are also tilted caudad at about a 45° angle as in the case of Recent Andrias, and not rather than being nearly vertical as in that of Cryptobranchus. There is also a

strong general resemblance between the pars facialis of these specimens and that of Recent Andrias. The Colorado vertebrae with their neural spines projecting caudad at about 45° suggest also the Andrias condition rather than that of the flattened Cryptobranchus.

On the basis of the above observations the North American Mid-Cenozoic Cryptobranchid fossils are more closely related to Andrias than to Cryptobranchus, and therefore should be referred to that genus.

The North American Andrias are, however, not identical with Andrias scheuchzeri or A. japonicus. They differ from them in having a less curved maxilla and dentary, in having a shallow sulcus dentalis, and a horizontal shelf formed by the pars dentalis of the maxilla immediately at the base of the tooth row and at a right angle to it, and is therefore referred here to a different species.

Since Cook (1917) described the first North American cryptobranchid under the name of Plicagnathus matthewi, therefore the specific name matthewi should be retained for these fossils, which should now be referred to Andrias matthewi.

A summary of the known characters of this species follows.

General: The known specimens of this fossil salamander indicate individuals ranging between 450 mm. and 1800 mm. in total length.

Maxilla: The maxilla is less curved than in any other cryptobranchid so far described here. The sulcus dentalis is shallow. The pars dentalis forms a 90° shelf above the tooth row and maintains a uniform height throughout its entire length.

Dentary: Andrias matthewi also exhibits a lesser curvature in the dentary than any other member of the family, and the sulcus dentalis is also shallow here.

Vertebrae: The vertebrae have a somewhat shorter centrum length than in Recent Andrias or Cryptobranchus.

REFERENCES CITED

Aoyama, F.

1930. Die Entwicklungsgeschichte des Kopfskelettes des Cryptobranchus japonicus, Z. Anat. und Entwickl.- Gesch., 93, 107-181, 26 figs.

Bishop, Sherman C.

1947. Handbook of Salamanders. Ithaca, New York, Comstock Publishing Co., Inc., XIV + 555, 144 figs., 56 maps.

Conant, Roger

1958. A Field Guide to Reptiles and Amphibians of the United States and Canada, East of the 100th Meridian. Boston, Houghton Mifflin Co. 62 figs., 40 pls., 248 maps.

Cook, Harold J.

1917. First Recorded Amphibian from the Tertiary of Nebraska. Bull. Geo. Soc. Amer., 28, 213,.

1960. New Concepts of Late Tertiary Major Crustal Deformations in the Rocky Mountain Region of North America. Rept. 21st Internatl. Geol. Congr., part 7, 198-212, 1 fig., 1 map.

Francis, Eric T. B.

1934. The Anatomy of the Salamander. Oxford Univ. Press, Oxford, XXXI + 381, 84 figs,, 25 pls.

Furbringer, Max

1922. Das Zungenbein der Wirbeltiere insbesondere der Reptilien und Vögel. Abh. Heidelberger Akad. Wiss., Math.-Naturwiss., Kl. II, XII + 163, 271 figs., 12 pls.

Hoffstetter, Robert

1962. Additions a la faune reptilienne de l'Eocene Superieur de Mormont-Saint-Loup, Suisse. Bull. Soc. Geol. France, Ser. 7, 4, 109-117, 2 figs., 1pl.

Hyrtl, Josephus

1865. Cryptobranchus japonicus. Vindobonae, XII + 132, 14 tls.

Laube, G. C.

1897. Andriasreste aus der Böhmischen Braunkohlenformation, Abh. deutsch. naturw. med. Vereins Böhmen, 1, 25-32, 1 plt.

Meyer, H. v.

1859/61. Salamandrinen aus der Braunkohle am Rhein und in Böhmen. Palaeontographica, 7, 47-73 2pls.

Myers, G. S.

1951. Asiatic Giant Salamander caught in the Sacramento River, and an exotic skink near San Francisco. Copeia, 1951, no. 2, 179-180.

Noble, Gladwyn Kingsley

1931. The Biology of the Amphibia. London and New York, McGraw-Hill, XII + 577, 147 figs, 1 map.

Peterson, O. A.

1925/26. The fossils of the Frankstown Cave, Blair County, Pennsylvania. Ann. Carnegie Mus., 16, 249-314, 10 figs., 9 pls.

Reese, Albert M.

1906. Anatomy of Cryptobranchus allegheniensis. Amer. Natl., no. 40, 287.

Shikama, Tokio and Hasagawa, Yoshikazu

1962. Discovery of fossil giant salamander (Magalobatrachus) in Japan. Trans. Proc. Palaeont. Soc., Japan, N. S. no. 45, 197-200, 1 pl.

Tihen, J. A. and Chantell, Charles J.

1963. Urodela remains from the Valentine formation of Nebraska. In Press.

Tschudi, J. J.

1837. Über den Homo diluvii testis, Andrias scheuchzeri. Neues Jb. Mineral, 1837, 545-547.

Westphal, Frank

1958. Die Tertiaran und Rezenten Eurasiatischen Riesensalamander (Genus Andrias, Urodela, Amphibia). Palaeontogr. 110, nos. 1-3, 20-92, 4 figs, 6 pls.

Wiedersheim, Robert

1877. Das Kopfskelett der Urodelen. Ein Beitrag zur Vergleichenden Anatomie des Wirbelthierschadels. VII + 187, 6 figs., 9 pls.

Plate I

Three diagrams illustrating osteological differences between *Cryptobranchus alleganiensis* and the two recent subspecies of *Andrias*.

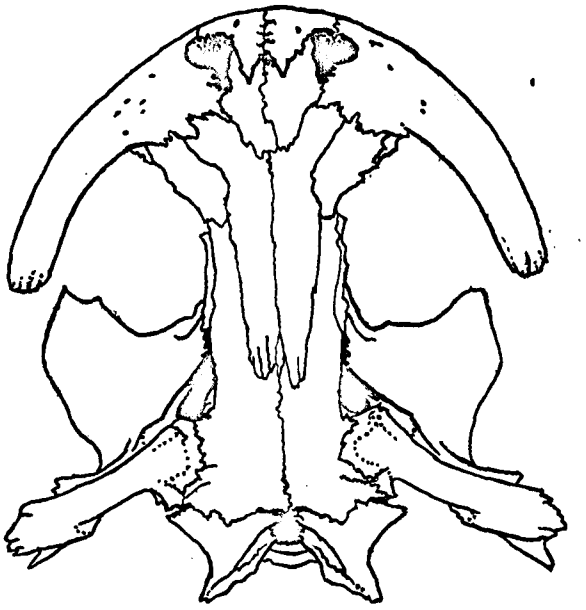
A. *Andrias japonicus davidianus* (x 1)

B. *A. j. japonicus* (x 1)

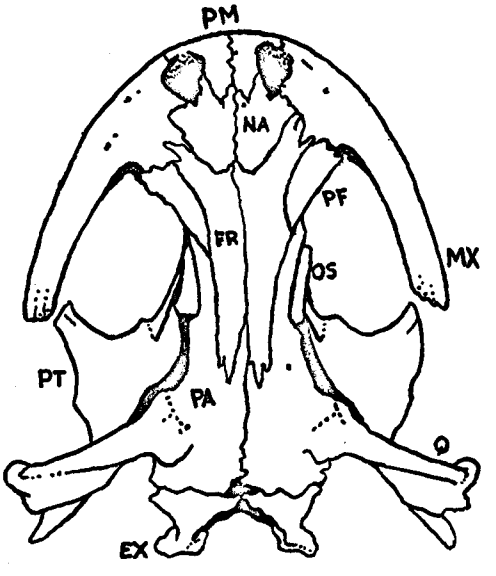
C. *Cryptobranchus alleganiensis* (x 2)

Note especially the number of bones contacted by the maxilla. Observe also the round orbits in *A. j. davidianus* and the oval ones in *A. j. japonicus*.

Abbreviations: Ex – exoccipital; Fr – frontal; Mx – maxilla; Na – nasal; Pa – parietal; Pm – premaxilla; Pt – ptergoid; Q – quadrate; Sq – sqamosal.



A



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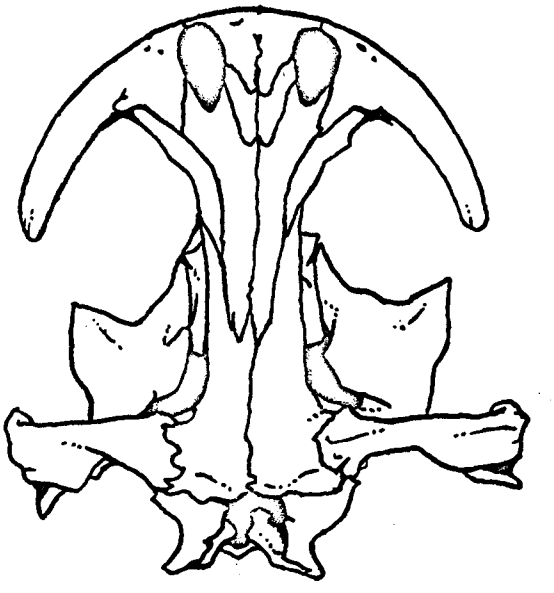


C

Plate I

Plate II

Illustration of similarities of maxillae of three Cryptobranchid salamanders.

A. Havorka fossil (x 1)

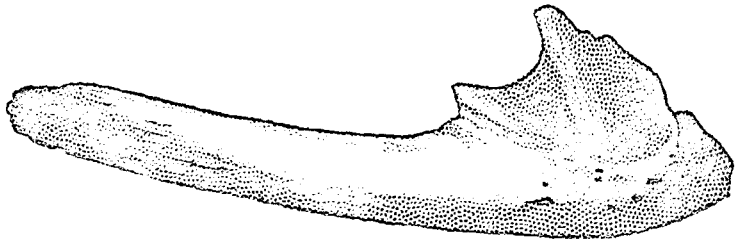
B. Recent Andrias japonicus japonicus (x 1)

C. Fossil Cryptobranchus maccalli (x 2)

Note especially the similarities exhibited by the pars facialis. (The dorsal process of the Havorka maxilla is broken.)

A

B



C

Plate I

Plate III

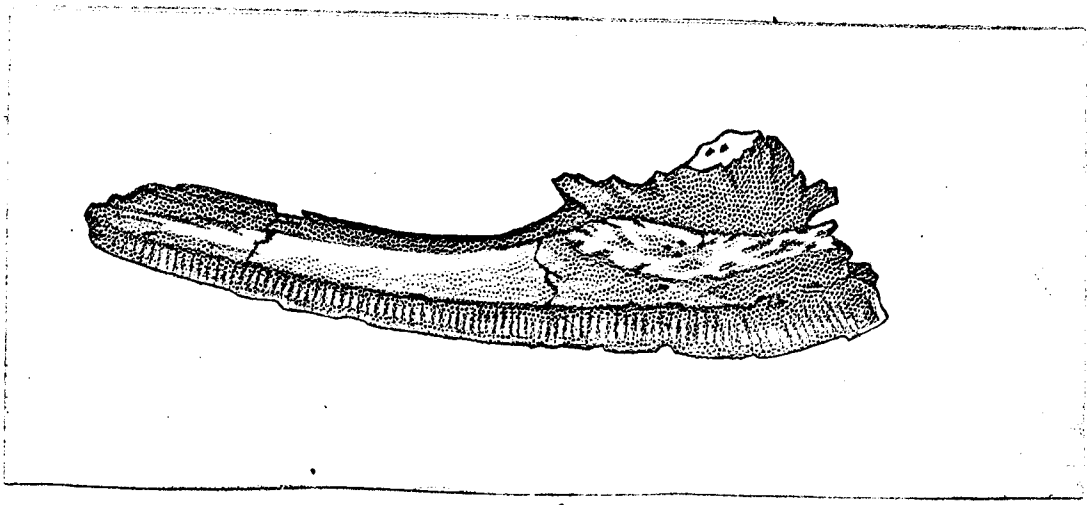
Illustration of the lingual view of three fossil specimens.

A. Havorka specimen (left maxilla)

B. Plastotype of Plicagnathus matthewi (left dentary)

C. HC 1260 (right dentary)

Note the triangular mesial depression on the pars facialis of fig. A., and also the similarities between the two dentaries B. and C.



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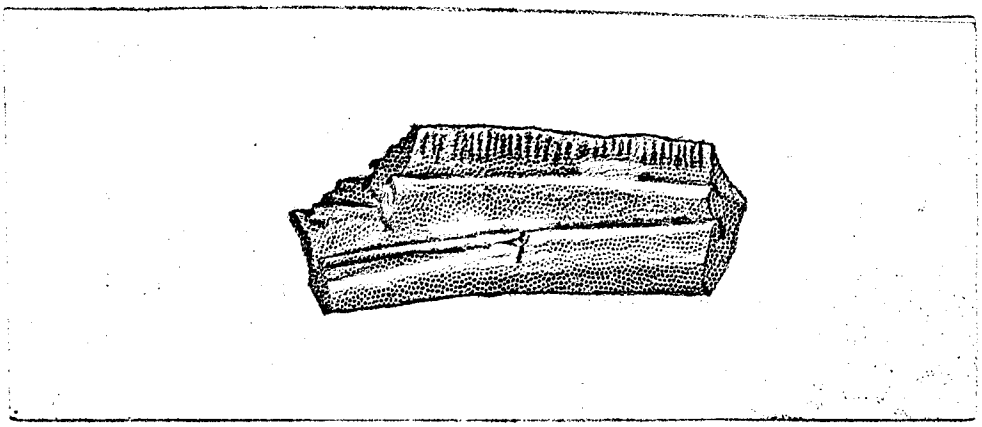

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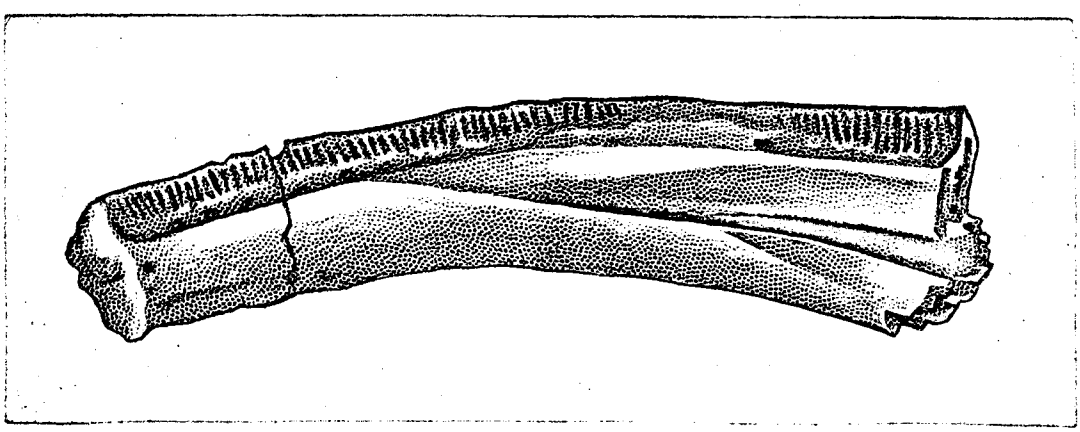

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