FIELDIANA · GEOLOGY

Published by

CHICAGO NATURAL HISTORY MUSEUM

Volume 10 | SEPTEMBER 22, 1958 | No. 33

NEW SALAMANDERS OF THE FAMILY SIRENIDAE

FROM THE CRETACEOUS OF NORTH AMERICA

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Since we published our first report on fossil salamanders of the family Sirenidae (Goin and Auffenberg, 1955) material has continued to accumulate. In addition to the species described in that paper, we have since described *Siren dunni* (Goin and Auffenberg, 1957) from the Eocene of Wyoming. These records were all from the Cenozoic. Thanks to the kindness of many friends who have let us work through unsorted microfossil material, we now have located two genera of Sirenidae from Mesozoic deposits.

The first of these genera was taken from the Trinity beds of the Lower Cretaceous of Texas.

Prosiren, new genus

Type species.—Prosiren elinorae, new species.

A genus of amphicoelous salamanders referred tentatively to the Sirenidae and characterized by moderately developed aliform processes; well-developed zygapophyseal ridges extending between the anterior and posterior zygapophyses; transverse processes, each formed of two plate-like structures, of which the upper fuses with the zygapophyseal ridge just posterior to the anterior zygapophysis; anterior glenoid cavity nearly round, just slightly higher than wide; a well-developed subcentral median ridge that has a nearly straight margin.

Diagnosis.—This genus differs from the genera *Siren* and *Pseudobranchus* in that it has a well-developed basapophyseal accessory

Library of Congress Catalog Card Number: 58-12179

process that originates on the lower plate of the transverse process slightly anterior to the subcentral foramen and extends downward and anteriorly to meet the anterior glenoid cavity near its lower margin. From the genus described below (p. 453), which also has basapophyseal processes, it differs in that the neural spine continues posteriorly between the aliform processes and in that these aliform processes are lower and thicker. Also, the dorsal margin of the aliform process slopes downward and backward from its point of contact with the neural spine rather than continuing posteriorly at about the same level for some distance, then turning down abruptly.

Prosiren elinorae, new species. Figure 187.

Type.—Chicago Natural History Museum PR 391, a dorsal vertebra.

Horizon and locality.—Turtle Gully, southwest portion of Greenwood Canyon Gully system, Lower Cretaceous, 2½ miles southwest of Forestburg, Montague County, Texas.

Referred material.—Two dorsal vertebrae, CNHM-PR 390, the same locality as the type, and PR 392, from Triconodont Gully, northeast portion of Greenwood Canyon Gully System, Lower Cretaceous, 2½ miles southwest of Forestburg, Montague County, Texas.

Diagnosis.—A sirenid with the neural spine extending posteriorly between the aliform processes and with well-developed basapophyseal accessory processes on the antero-ventral portion of the centrum.

It can be distinguished from all other Sirenidae, including the genus described below (p. 453), by the combination of well-developed basapophyseal accessory processes and a neural spine that extends between the arms of the aliform processes. It seems to differ from other Sirenidae also in the manner in which the dorsal margin of the aliform process slopes downward from the point at which it connects with the neural spine, so that the process appears somewhat triangular as seen from the side. In the other sirenids these processes continue posteriorly at a nearly uniform height until well over the postzygapophyses, at which point the dorsal margin turns downward at nearly a 90 degree angle in *Siren* and the genus described below and at least a 60 degree angle in *Pseudobranchus.* Thus, in these genera the aliform process as seen in profile appears to be more nearly rectangular than triangular.

Description of type.—Measurements (in mm.; measurements in parentheses are thousandths of length of centrum): Length of centrum along midventral line, 2.1. Width of vertebra at narrowest point of zygapophyseal ridges, 1.1 (0.524); height of vertebra from lower

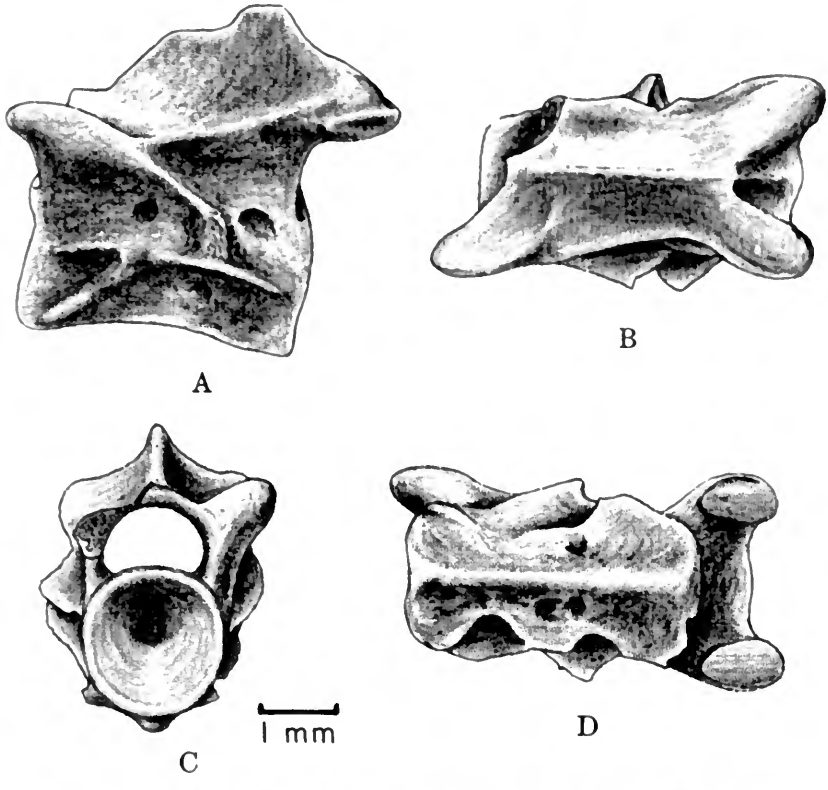

FIG. 187. *Prosiren elinorae*, type (CNHM-PR 391). A, Lateral view. B, Dorsal view. C, Anterior view. D, Ventral view.

margin of centrum to a line drawn between facets of postzygapophyses, 1.8 (0.857). Distance from tips of prezygapophyses to tips of postzygapophyses, 2.8 (1.333). Angle between aliform processes, 55°. Width of anterior glenoid cavity, 0.9 (0.429); height of anterior glenoid cavity, 1.0 (0.476). Width of neural canal, 0.8 (0.381); height of neural canal, 0.7 (0.333).

Centrum longer than high; glenoid cavity mildly ovate, slightly higher than wide. Centrum provided with an elevated, ridge-like, median ventral keel, on either side of which is found a moderate subcentral foramen. Margin of ventral keel slightly concave.

Total length of neural arch greater than length of centrum and its width at the narrowest portion of the zygapophyseal ridges slightly greater than width of centrum. Neural canal an inverted crescent anteriorly; about rounded posteriorly.

Articulating surface of prezygapophysis an elongate oval in shape, much longer than wide, directed more anteriorly than laterally. Articulating surface of postzygapophysis ovate. Zygapophyseal ridges well developed, slightly concave as seen from above, particularly posteriorly. As seen from the side the zygapophyseal ridge forms a very shallow V with the apex at the point where the dorsal portion of the transverse process meets the zygapophyseal ridge. It then continues posteriorly and somewhat dorsally to meet the posterior zygapophysis at the base of the aliform process.

Aliform processes but moderately developed, vertical in position; they are thicker and lower than in the genus *Siren*. As seen from above they form an anteriorly pointing V. A floor with a broadly crenate posterior margin is present between the aliform processes. The neural spine continues between the aliform processes for a distance to form a median ridge on the floor between them.

Neural spine well developed, higher than aliform processes. Its anterior margin broken so that its height anteriorly cannot be determined.

Transverse processes broken off; only their bases present. As in *Siren*, each is apparently composed of two plate-like portions of which the ventral is larger than the dorsal. The ventral portion a wing-like structure extending from close to the anterior margin of the side of the centrum posteriorly nearly the entire length of the centrum. The dorsal portion a flat plate extending from the zygapophyseal ridge, somewhat behind the posterior margin of the prezygapophysis, ventrally and posteriorly to meet the ventral portion to which it is fused. A well-developed basapophyseal accessory process originates on each side on the ventral surface of the lower portion of the transverse process. This process originates about one-third of the way back and extends downward and forward nearly to the point where the subcentral keel meets the margin of the glenoid cavity. Laterally a foramen is present in the angle between the dorsal and ventral portions of the transverse process and another lies somewhat ventral and posterior to the angle between the dorsal portion of the transverse process and the zygapophyseal ridge.

Variation.—The two referred specimens are much more fragmented than is the type, but both seem to belong to this species. In characters that can be determined in them they agree with the type: in the slope of the posterior margin of the aliform processes; in the size and formation of the zygapophyses; and in the formation of the transverse processes. One of the specimens (CNHM-PR 392)

further agrees with the type in the formation of the basapophyseal processes, although they are better developed and extend below the lip of the glenoid cavity; in the form of the glenoid cavities of the centrum; and, as far as can be determined in this uncleaned specimen, in the shape of the neural canal. These three characters cannot be determined in the other specimen (CNHM-PR 390), but it agrees with the type in the formation of the neural spine and in the slope of the wings of the transverse process.

Both of these specimens have been excessively fragmented. In PR 392 the matrix itself seems to be holding the vertebra together; in PR 390 the matrix has separated and the specimen has fallen into discrete fragments.

Associated fauna.—In addition to these salamanders, the Forestburg stratum contains fragments representing fishes, other nondescript salamanders (Salamandridae?), and at least two families of frogs; there are also lizard jaws, and turtle and crocodile fragments, along with the remains of dinosaurs and of a primitive mammalian fauna. The mammals have been summarized by Patterson (1956).

The important Carnegie Museum collection of Upper Cretaceous vertebrate material, taken by J. B. Hatcher in 1900 from the Lance Formation in Niobrara County, Wyoming, has been examined for salamander remains. Included among the salamander fossils are two specimens that represent a large sirenid. These specimens differ from both the genus *Prosiren* described herein from the Lower Cretaceous and the Cenozoic genera *Siren* and *Pseudobranchus*. We therefore erect for them a new genus.

Adelphesiren, new genus

Type species.—*Adelphesiren olivae*, new species.

A genus of amphicoelous salamanders referred to the Sirenidae and characterized by well-developed aliform processes; well-developed zygapophyseal ridges extending between the anterior and posterior zygapophyses; transverse processes formed of two plate-like structures, the upper of which fuses with the zygapophyseal ridge just posterior to the anterior zygapophysis; anterior glenoid cavity nearly round, just slightly wider than high; a well-developed subcentral median ridge that has a nearly straight margin.

Diagnosis.—This genus differs from the genera *Siren* and *Pseudobranchus* in that it has well-developed basapophyseal accessory processes that originate on each side of the centrum just anterior to the subcentral foramen and extend anteriorly and slightly ventrally to

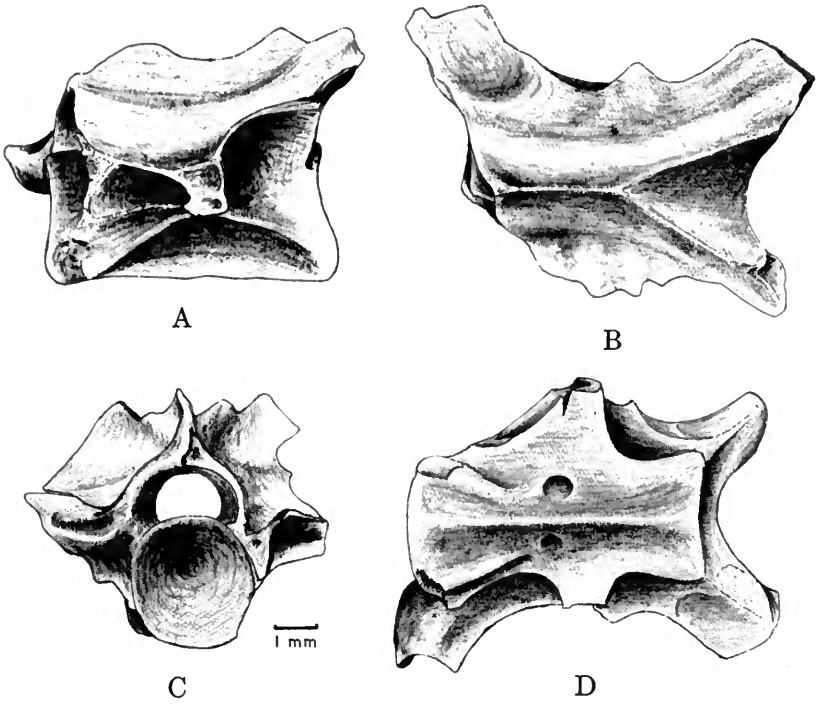

FIG. 188. *Adelphesiren olivae*, type (CM 6467). A, Lateral view. B, Dorsal view. C, Anterior view. D, Ventral view.

meet the glenoid cavity near its lower margin. From *Prosiren*, which has similar basapophyseal processes, it differs in that the aliform processes are higher and thinner, as in the genus *Siren*, and in that the neural spine terminates at the point of origin of the aliform processes rather than extending between them as it does in *Prosiren*.

Adelphesiren olivae, new species. Figures 188, 189.

Type.—Carnegie Museum no. 6467, a dorsal vertebra.

Horizon and locality.—Lance Formation, Upper Cretaceous, Niobrara County, Wyoming.

Referred material.—A single dorsal vertebra (CM 6448) with the same data as the type.

Diagnosis.—A large sirenid with well-developed basapophyseal accessory processes, with high, well-developed aliform processes that do not have the neural spine extending between them, and with a nearly round glenoid cavity.

It differs from the genus and species described above in its larger size, in that there is no evidence of neural spine between the aliform processes, and in that the dorsal margins of the aliform processes do not slant downward posteriorly but rather are nearly horizontal. From all the species of *Siren* and *Pseudobranchus* it differs in that it has well-developed basapophyseal accessory processes on the anteroventral surface of the centrum and from *Pseudobranchus* and all known species of *Siren* except *lacertina* in its larger size.

Description of type.—Measurements (in mm.): Length of centrum along midventral line, 8.0. Height of vertebra from lower margin of centrum to a line drawn between facets of postzygapophyses, 4.5 (0.563). Distance from tips of prezygapophyses to tips of postzygapophyses, 10.8 (1.350). Angle between aliform processes, 36°. Width of anterior glenoid cavity, 3.0 (0.375); height of anterior glenoid cavity, 2.8 (0.350). Width of neural canal, 3.1 (0.388); height of neural canal, 1.6 (0.200).

Centrum longer than high; glenoid cavity nearly round, but slightly wider than high. Centrum provided with a well-developed, elevated, ridge-like median ventral keel, on either side of which is found a relatively large, subcentral foramen. Margin of ventral keel nearly straight.

Total length of neural arch greater than length of centrum and its width at the narrowest portion of the zygapophyseal ridges greater than width of centrum. Neural canal an inverted crescent anteriorly; broadly oblong posteriorly; provided with a weakly developed, very low median epapophyseal ridge on the floor.

Articulating surfaces of prezygapophyses broadly oval in shape, only slightly longer than wide, and directed but slightly more laterally than anteriorly. Articulating surfaces of postzygapophyses ovate. Zygapophyseal ridges well developed, markedly concave as seen from above. As seen from the side the zygapophyseal ridge forms a very shallow "step" at the point where the dorsal portion of the transverse process meets the zygapophyseal ridge, with the posterior portion about a millimeter higher than the anterior portion.

Aliform processes well developed, vertical in position, their dorsal margins eroded so that neither their height nor their original profile can be determined. As seen from above they form an anteriorly pointing V. Floor between aliform processes present, with a broadly rounded, apparently eroded, posterior margin.

Neural spine well developed; dorsal margin eroded but still higher than the aliform processes.

Transverse processes obviously well developed and composed of two plate-like portions; the processes are broken near their bases. The ventral portion, a wing-like structure, extends from close to the anterior margin of the side of the centrum for about two-thirds of the length of the centrum, then continues posteriorly to the end of the centrum as a very low ridge. The dorsal portion extends from the zygapophyseal ridge somewhat behind the posterior margin of the prezygapophysis ventrally and posteriorly to the posterior margin of the ventral portion, to which it is fused. Its lateral extent cannot be determined because of fracture. What remains of the posterior margin of the transverse process is approximately perpendicular to the axis of the centrum.

A well-developed basapophyseal accessory process originates on each side of the centrum just anterior to the subcentral foramen and extends anteriorly and slightly ventrally to the margin of the anterior glenoid cavity. It becomes both wider and higher as it progresses anteriorly.

Laterally a foramen is present in the angle between the dorsal and ventral portions of the transverse process.

Variation.—A single vertebra (CM 6448), with the same data as the type, is somewhat larger (centrum length 9.5 mm.) but in the characters that can be ascertained it is essentially a duplicate of the type. Only one zygapophysis, the right posterior, remains, but it indicates that the shape of the articulating surfaces and the flare of the zygapophyses are essentially the same in the two specimens. Likewise, the structure of the aliform processes and the floor between them, the zygapophyseal ridges, the subcentral keel, the shape of the neural canal, and the form of the basapophyseal processes indicate a striking degree of similarity between the two specimens. In fact, only in that the posterior glenoid cavity seems to be slightly higher than wide does it appear to differ essentially from the type and even here the margin of the cavity is broken in the larger specimen so that its exact size and shape cannot be determined.

Associated fauna.—A genus of salamanders allied to the Salamandridae and a single vertebra of a snake were in the same lot that contained the specimens of *Adelphesiren*. The mammals of this collection have been reported by Simpson (1929).

DISCUSSION

The discovery of these new sirenids from the Upper Mesozoic greatly broadens our knowledge of the fossil history of the family

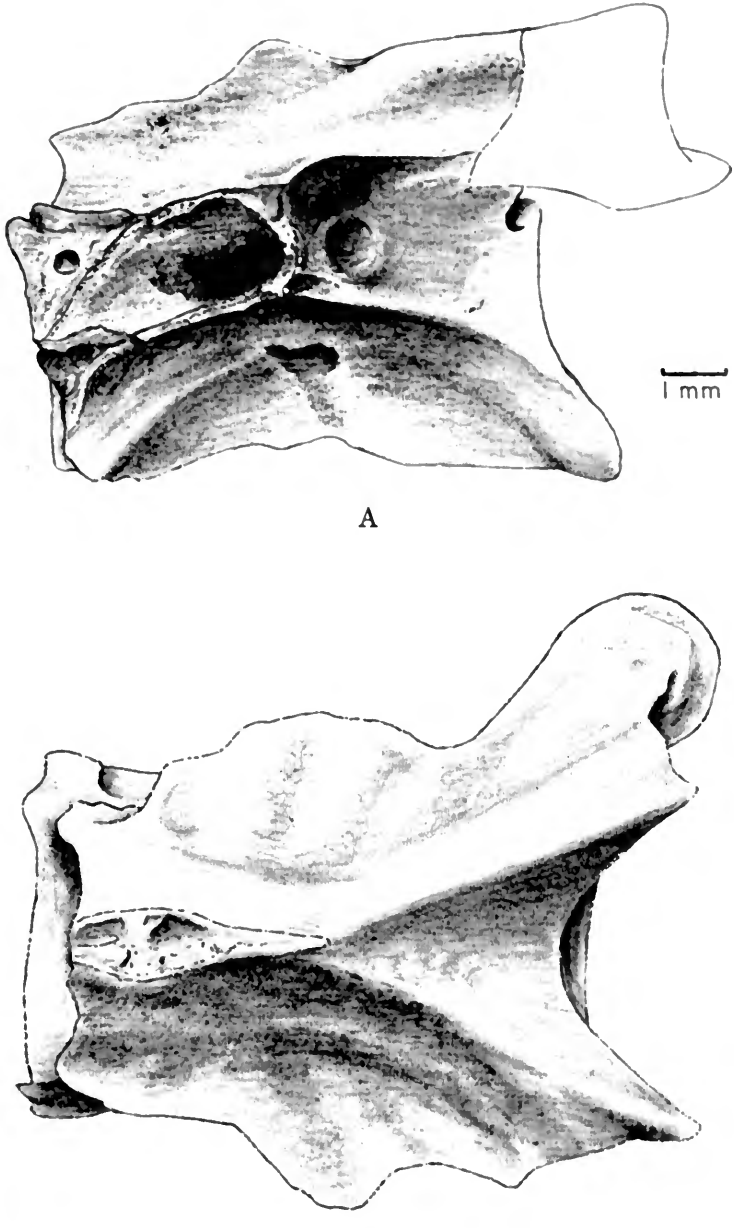

FIG. 189. *Adelphesiren olivae* (CM 6448). A, Lateral view. B, Dorsal view.

but, it must be admitted, does not entirely clarify our information concerning the lineage of these salamanders.

The earliest known sirenid, *Prosiren*, which is here described, can at this time be but doubtfully referred to the Sirenidae. We include it here because it has rudimentary aliform processes and because the transverse processes seem to be of the same basic type as in the other sirenids, but it differs from all of them in that the aliform processes are low and heavy and slope down strikingly toward the margin of the postzygapophyses, whereas in all of the other sirenids the aliform processes are high and thin, like the neural spine. Also, the whole neural arch seems to stand higher and is more narrow than is typical of the sirenids. These characters seem to us to permit two possible interpretations. Either this is a very primitive sirenid, among the earliest of the line, and hence may be expected to be somewhat different from the later forms, or—a more likely interpretation, it seems to us—it is off the main evolutionary line and, while basically a sirenid, it probably does not represent at all the true ancestor of the modern sirenids.

Adelphesiren, on the other hand, seems to be quite typically sirenid. The high, thin, rectangular aliform processes are very *Siren*-like and, in fact, if it were not for the presence of well-developed basapophyseal accessory processes on the antero-ventral surface of the centrum, we would be inclined to include it in the genus *Siren*. The presence of these well-developed processes, however, indicates to us that it should be set off in a separate genus.

The early Eocene form, *Siren dunni*, is a typical *Siren* in every sense of the word, whereas the Miocene form, *Siren hesterna*, seems now not to fit in the general line of evolution, but to be somewhat of a side branch. With its short, stubby centrum and wide-flaring aliform processes, we just cannot conceive that it would be in between *Siren dunni* on the one hand and *Siren simpsoni*, or either of the recent species, on the other.

It is rather difficult to determine exactly what size means and how it should be interpreted in salamanders that have indeterminate growth, but it perhaps is worth mentioning that *Siren lacertina* has been, until this time, the only large sirenid, and it apparently came into existence in the late Pleistocene. Now, the presence of *Adelphesiren* from the Upper Cretaceous gives us two large forms. We do not mean to imply, of course, that they are necessarily closely related, but it does seem strange that all of the others, from the Lower Cretaceous, Eocene, Miocene and Pliocene, and the Recent species, *intermedia*, are small. This, as mentioned above, may not be significant,

but it may indicate that *Adelphesiren* itself is not on the line of sirenid evolution leading to the present species.

Also of some possible significance is the fact that nowhere below the Pliocene do we find two forms together. In the Pliocene, *Siren simpsoni* and *Pseudobranchus vetustus* occur, but from the Miocene, Eocene, Upper Cretaceous and Lower Cretaceous only single forms are known. This does not necessarily indicate that only single species were in existence at those times. It rather seems to us to indicate the fragmentary state of our knowledge and the inadequacy of our collections. If these were the only forms in existence at these times, it would be expected that one would lead logically to the other and that the sequence would be a smooth one from Lower Cretaceous to Recent. But at least two forms, *Prosiren* of Lower Cretaceous and *Siren hesterna* of the Miocene, seem to be definite sidelines, and the same may well be true of *Adelphesiren* from the Upper Cretaceous. It seems much more likely that we have just scratched the surface when it comes to collecting, and that many more data must accumulate before we can begin to work out the true evolutionary history of the family Sirenidae.

ACKNOWLEDGMENTS

We are indebted to Dr. M. Graham Netting and Dr. J. LeRoy Kay for making travel to Pittsburgh possible and for the privilege of sorting through Carnegie Museum's microvertebrate material. Dr. Rainer Zangerl has us in his debt for his kindness in sending us representative material from the Chicago Natural History Museum's microvertebrates from the Trinity beds of Texas so that we might sort through it here in Gainesville. Mrs. Olive B. Goin has been of material assistance in the preparation of this manuscript, typing it through several of its stages. To all of these we express our thanks.

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