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A New Triassic Procolophonid from Pennsylvania

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INTRODUCTION

The presence of Triassic procolophonid reptiles in North America was established by Gilmore in 1928 with his description of *Hypsognathus fenneri*, a name applied to a natural mold of a partial skeleton that had been discovered in a sandstone facies of the Brunswick formation of the Newark group at Clifton, New Jersey. Subsequently, in 1946, the present writer described an excellent skull and skeleton, and a second skull and some miscellaneous bones attributed to the same species, which had been unearthed in 1939 during some quarry operations in sandstones of the Brunswick formation, on the boundary line between Clifton and Passaic, New Jersey. This newer material of *Hypsognathus* was located no more than a mile or so from the type, but probably at a somewhat different level within the Brunswick formation from that of the first specimen. Although it was difficult to be positive as to the specific identity between the new materials and the type specimen, these new fossils were nevertheless regarded as probably the same as the type, particularly in view of the similarity in size, the common characters possessed by all the specimens, and the nearness of the two localities to each other. Because the new materials were so much more complete than the type specimen, they established many of the characters, especially those of the skull, that are now regarded as diagnostic for *Hypsognathus*. There are no compelling reasons for supposing that all these fossils from New Jersey represent more than a

single genus and species, so it seems justifiable to continue thinking of *Hypsognathus* materials from the Clifton-Passiac boundary, now in the American Museum of Natural History, as showing most of the salient characters typical of this genus and species.

In 1956 a small reptile skeleton was discovered by Norman Waltz in the Brunswick formation, near Bowmansville, in Lancaster County, Pennsylvania. Mr. Waltz very wisely presented the specimen to the North Museum of Franklin and Marshall College in Lancaster. A photograph of the specimen was then sent by John W. Price, Sr., Curator of the North Museum, to the United States National Museum, where the picture was identified by David Dunkle as very probably indicating a skeleton of *Hypsognathus fenneri*. Subsequently Dr. Price submitted the specimen to the present writer for study, the results of which are set forth in this paper. Later efforts to find more material at the locality where this specimen was discovered have met with little success.

I wish to express my great appreciation to Dr. Price for the opportunity to study and describe the specimen in the North Museum and thereby add more details to our growing knowledge concerning the anatomy and distribution of the Triassic procolophonids. Also much credit is due to Mr. Chester S. Tarka for the excellent photographs that illustrate this paper. Mr. Michael Insinna did the interpretive outlines under the author's supervision.

DESCRIPTION

SPHODROSAURUS,[1] NEW GENUS

GENERIC TYPE: *Sphodrosaurus pennsylvanicus*, new species.

DIAGNOSIS: See the diagnosis for the species, below.

Sphodrosaurus pennsylvanicus, new species

TYPE: North Museum No. 2321, a natural mold of a partial skeleton in the rock; A.M.N.H. No. 7601, a plaster cast of the original natural mold, and a latex positive made from the natural mold.

HORIZON AND LOCALITY: Brunswick formation, Newark group. Near Bowmansville, Lancaster County, Pennsylvania.

"The quarry [in which the specimen was found] is situated in the northeastern part of Lancaster County, Pennsylvania, about two miles east of Bowmansville. . . . The quarry, now abandoned, occurs in the baked portion of the Brunswick Shale; a large diabase intrusion to

[1] "Sphodros" (σφοδρος), robust; "sauros" (σαῦρος), lizard (or reptile).

the east was the source of heat that baked the shale. Scattered about the quarry are rounded masses of hornfels; the spheroidal weathering caused by exfoliation of thin layers gives these objects a concretionary aspect. The quarry contains a grey shale of the Brunswick Formation, Newark Series, Upper Triassic. The strike of the rock is N. 50 degrees E. and the dip is a gentle 25 degrees N.W." (Price, 1956, p. 168).

DIAGNOSIS: A small reptile of seemingly procolophonid relationships, closely comparable to *Hypsognathus* in size. The skull seems to have been unusually large in comparison to the size of the postcranial skeleton. The posterior portion of the skull is produced back into a "frill," as is common in the advanced procolophonids, this frill covering about five cervical vertebrae. There are 25 presacral vertebrae, to which are articulated widely spreading holocephalous ribs. The scapula is rather slender, the ilium seemingly deep. The pubis and ischium are plate-like bones, the former being proximally constricted and distally expanded. The hind limbs are large, the extended limb being approximately equal in length to the total length of the presacral series of vertebrae. In total length and in each of its component sections the linear dimensions in the hind limb are about double those in the fore limb. The metatarsals are rather slender, and long. The ungual phalanges of the pes are large, pointed claws.

DISCUSSION

The specimen under consideration consists for the most part of a natural mold of a skeleton in the rock, with fragments of bone adhering in places. When viewing the original specimen in the rock, one is looking *down* upon the skeleton from above (see fig. 1). To facilitate the study of this fossil a flexible positive cast was made from the fossil, by Martin Cassidy of the Paleontological Laboratory, of black casting compound S.P. 16, thus reproducing in the round the various bones that in the fossil show as hollows in the rock. When viewing this cast, one is looking at the *ventral* aspect of the skeleton (see fig. 3). In addition, Cassidy made a plastic replica of the fossil, A.M.N.H. No. 7601.

The type specimen of *Sphodrosaurus* from Pennsylvania is very closely comparable in size to the two known skeletons of *Hypsognathus*, particularly to the American Museum specimen. In most part of the skeleton the size differences between the type of *Sphodrosaurus* and the American Museum specimen of *Hypsognathus* are so slight as to be quite insignificant, but in the skulls there does seem to be some difference between the two. The back portion of the skull of the Pennsylvania specimen appears to be wider by about one-third than the

FIG. 1. *Sphodrosaurus pennsylvanicus*, new genus and species. Type, North Mus. No. 2321. Natural mold of skeleton. In this mold the light color of the skeleton is due to natural discoloration of the rock. Very little of the original fossil remains. Dorsal view. × ⅔.

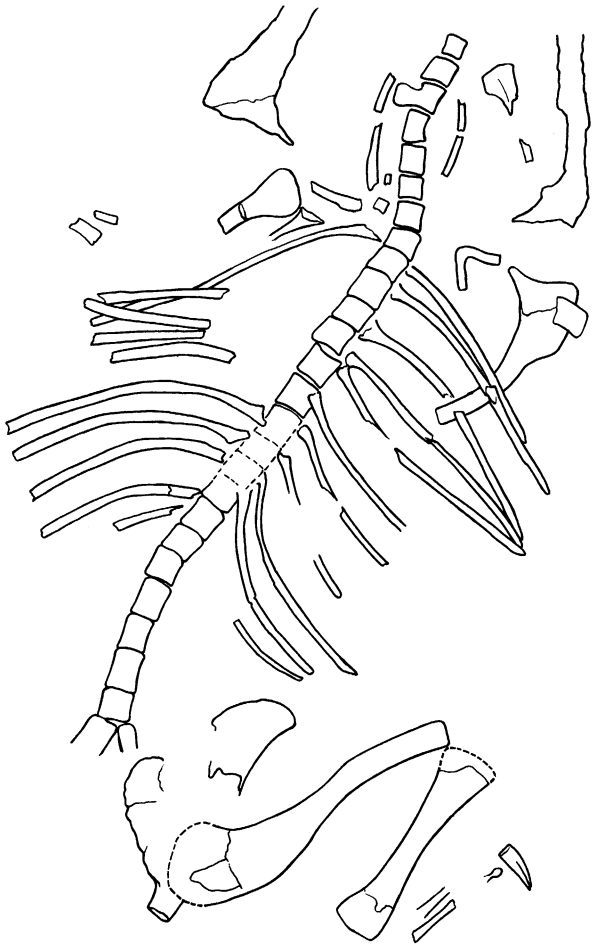

FIG. 2. The skeletal parts shown in figure 1, as seen in outline. A few minor elements have been omitted for the sake of clarity. × ⅔.

New Jersey specimen of *Hypsognathus*, which makes it seem inordinately large. Whether any of this difference can be attributed to crushing and flattening, thus adding to the apparent width of the skull, cannot be determined upon the basis of this particular fossil.

This similarity in size between the new fossil from Pennsylvania and the two skeletons of *Hypsognathus* immediately raises the question of the possibility that we are dealing with a third individual of *Hypsognathus fenneri* rather than with a different genus and species of procolophonid. The question is apropos, particularly in view of the

Fig. 3. *Sphodrosaurus pennsylvanicus*, new genus and species. Flexible positive cast (A.M.N.H. No. 7601) from type natural mold, ventral view. × 1.

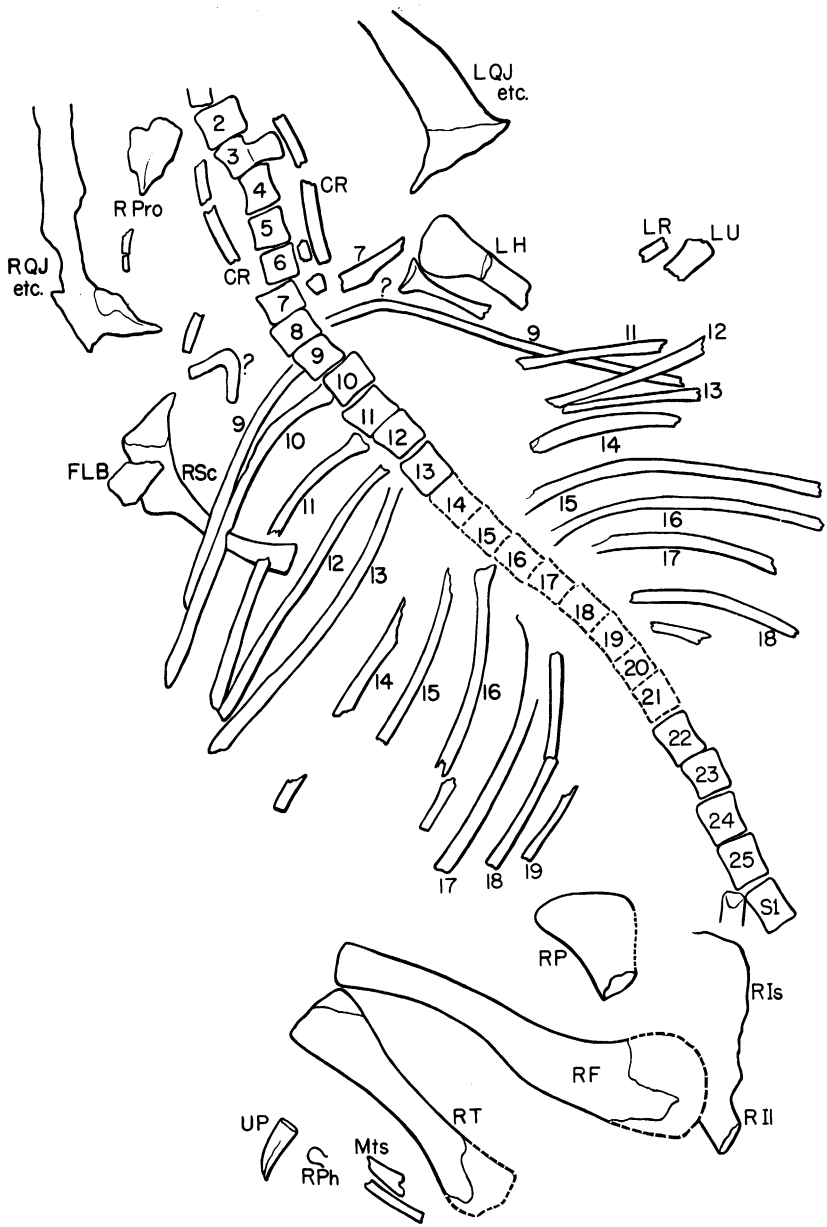

FIG. 4. Interpretation of figure 3. Presacral vertebrae and ribs numbered. *Symbols:* CR, cervical rib; FLB, fragment of limb bone; LH, left humerus; LR, left radius; LQJ, left quadratojugal; LU, left ulna; Mts, metatarsals; RF, right femur; RIl, right ilium; RIs, right ischium; RP, right pubis; RPh, right phalanges; RPro, right proötic; RQJ, right quadratojugal; RSc, right scapula-coracoid; RT, right tibia; S1, first sacral vertebra; UP, ungual phalanx. Slightly smaller than natural size.

fact that the new specimen may be equated stratigraphically with the described skeletons of *Hypsognathus*. Indeed, for some time the present writer considered this Pennsylvania fossil to be another skeleton of *Hypsognathus*.

But such a view has been difficult to maintain, in the light of certain very marked differences between this fossil and *Hypsognathus* as we know it. One would have to suppose a considerable latitude of specific differences within the genus *Hypsognathus* or a very great degree of variability within the type species to keep the Pennsylvania specimen within either of these taxonomic categories. A difficult taxonomic decision has had to be faced: Should a new procolophonid species, or even a new genus, be created for an incomplete skeleton from a formation in which the one described genus and species is based on materials that are admittedly scant?

The resolution of the problem has been facilitated during the past year by discoveries of procolophonids in the upper Triassic sediments of Nova Scotia by William Take of the Nova Scotia Museum of Science in Halifax and Donald Baird of Princeton University. In a comparatively small area along the shores of the Bay of Fundy, Take and Baird found fossils representing several distinct types of procolophonids, thereby indicating that these reptiles enjoyed a wide range of simultaneous adaptive radiation during late Triassic times in eastern North America. Such being the case, it seems quite justifiable to regard the differences between the Pennsylvania fossil considered herein and the described skeletons of *Hypsognathus* as very probably of full generic value. One can only wish that a complete skull had been found with this skeleton, to settle the question beyond all shadow of doubt.

As mentioned above, only the back portion of the skull is present in *Sphodrosaurus*, and even this is imperfectly preserved. One can see a long expanse of sculptured bone on each side, the two sections of bone diverging from each other posteriorly to reach the unusual width already noted. These two lateral regions are interpreted as the lower damaged edges of the quadratojugals, squamosals, and tabulars. It is assumed that in the American Museum *Hypsognathus* the quadratojugals carry horns or spikes that decorate the sides of the skull; in the new specimen no positive indications of such spikes or points can be seen. In *Sphodrosaurus* the back of the skull seems to extend as far back as about the fourth or fifth cervical vertebra, in accordance with the condition in the most advanced procolophonids, in which the back of the skull is produced posteriorly so that it overhangs the neck region somewhat as does the frill in a ceratopsian dinosaur. In *Hypsognathus*

the backward extension of the skull is less extreme, for it covers only two or three of the cervical vertebrae.

This backward extension of the posterior portion of the skull can be made clear by comparing, in *Sphodrosaurus* and *Hypsognathus*, the angle made by two lines connecting the parietal foramen with the back corners of the tabular bones on each side. (Although the parietal foramen is not present in the specimen of *Sphodrosaurus*, its position may be inferred with a fair degree of accuracy with relation to the occipital condyle.) In *Sphodrosaurus* this angle is about 90 degrees, an indication of the backward production of the tabulars; in *Hypsognathus* it is about 130 degrees.

There is a smooth surface of bone in the general basicranial region of this new specimen that extends out on the right side from the basicranium, narrowing into a bar that reaches back to expand again into a flattened surface at the posterior-lateral corner of the skull. This is taken to be in part the opisthotic, with perhaps other elements (perhaps the proötic) joining it.

There are 26 vertebrae in an articulated series between the skull and the pelvis. Watson (1914) considers that *Procolophon*, which he described, is characterized by 26 presacral vertebrae. Von Huene (1956) indicates that other genera in this family may have 24 or 25 presacral vertebrae, and Romer (1956) states that the Procolophonidae are characterized by 24 to 26 presacral vertebrae. The preserved vertebral series of *Sphodrosaurus* may be regarded either as all presacral in relationships, or as including one or two sacrals, but, as the last vertebra of the series is definitely longer than the one preceding it and as it appears that a short sacral rib joins this vertebra on the right side near its articulation with the preceding vertebra, this last vertebra is regarded as sacral. Consequently *Sphodrosaurus* may be considered as having 25 presacral vertebrae.

Most of these vertebrae are seen only in ventral view. It can be assumed that they had the swollen neural arches so typical of the procolophonids and of the cotylosaurs in general. Some of the cervical vertebrae have been twisted from their original position, so that they are seen in lateral view. These vertebrae are not very well preserved, but the second vertebra of the series shows a large broad spine arising from the centrum on the left side of the midline, which is interpreted as the neural spine of an axis seen in lateral view. No more can be said about the vertebrae in the Pennsylvania specimen, except that there is an increase in length of the centra among the posterior members of the series as compared with the middorsal and cervical vertebrae.

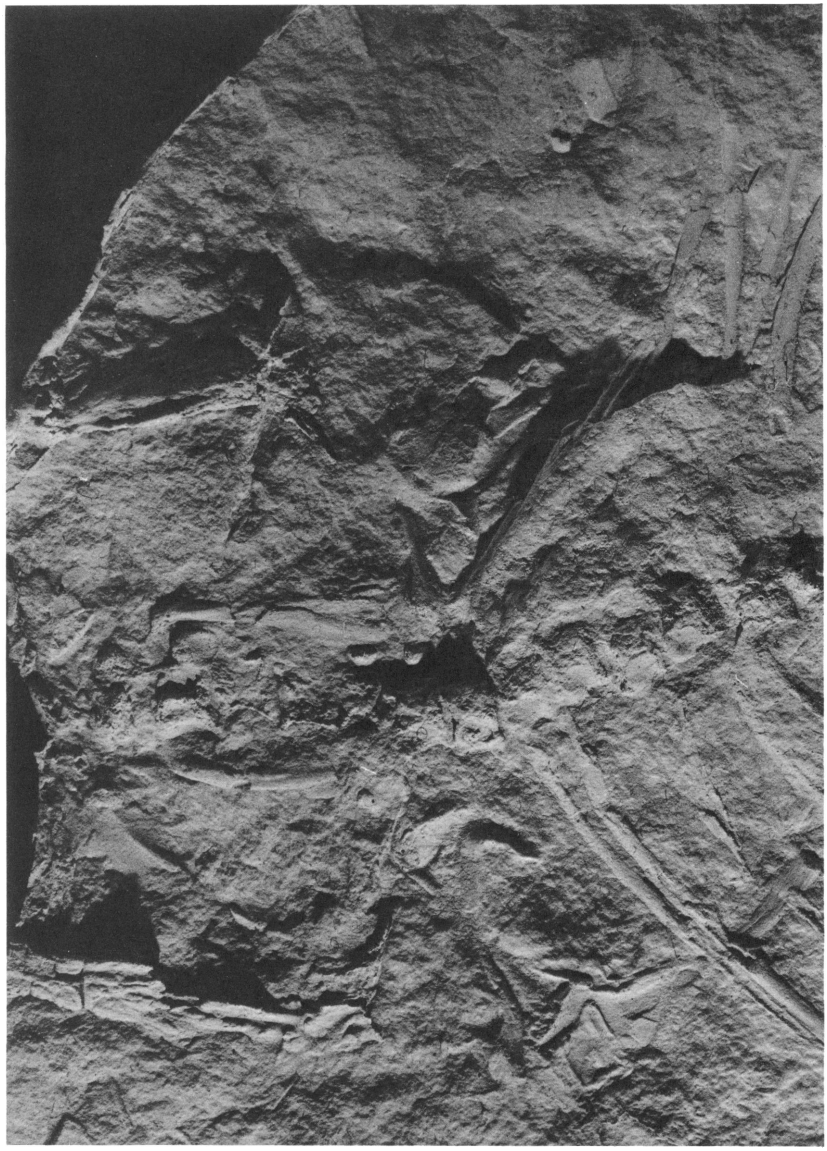

FIG. 5. *Sphodrosaurus pennsylvanicus*, new genus and species. Positive cast (A.M.N.H. No. 7601) from type, anterior portion of skeleton, ventral view. × 1½.

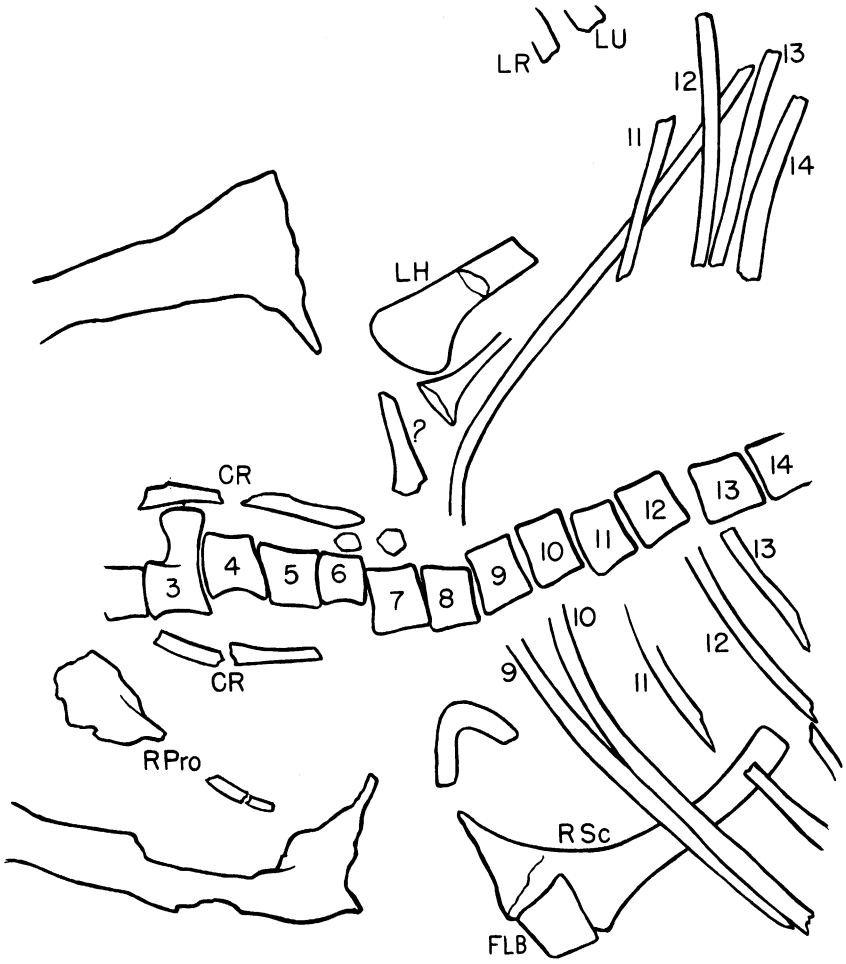

FIG. 6. Interpretation of figure 5. Presacral vertebrae and ribs numbered. *Symbols:* CR, cervical rib; FLB, fragment of limb bone; LH, left humerus; LR, left radius; LU, left ulna; RPro, right proötic; RSc, right scapulacoracoid. About × 1½.

In the Procolophonidae the ribs are holocephalous and articulate in each instance by a single articulation, borne in part by the arch and in part by the centrum of the individual vertebra. Although the heads of the ribs are not visible in *Sphodrosaurus*, it is obvious that their articulation with the vertebral column follows this pattern.

There are some long, flattened, cervical ribs on each side, their an-

TABLE 1

MEASUREMENTS (IN MILLIMETERS) AND RATIOS[a]

	Nyctiphruretus (Efremov, 1940)	*Procolophon* (Watson, 1914)	*Telerpeton* (von Huene, 1912)	*Hypsognathus* (Colbert, 1946)	*Sphodrosaurus*
Skull, length	54	49	52	50	—
Skull, width (posterior)	47	54	—	70.5	62
Presacrals, number	25	26	25	—	25
Presacrals, length	173	152	113	177[b]	150
Humerus, length	30	32	19	30	31[b]
Radius, length	15	21	16	22.3	23[b]
Manus, length	25	28	22	—	—
Fore limb, length	70	81	57	—	—
Femur, length	33	32	26	—	56
Tibia, length	16	17	18	—	42
Pes, length	30	34	24	—	38[b]
Hind limb, length	79	83	68	—	—
Ratio: skull length/presacrals length	*31*	*32*	*46*	*28*	—
Ratio: fore limb length/hind limb length	*89*	*98*	*84*	—	—

TABLE 1—(*Continued*)

	Nyctiphruretus (Efremov, 1940)	*Procolophon* (Watson, 1914)	*Telerpeton* (von Huene, 1912)	*Hypsognathus* (Colbert, 1946)	*Sphodrosaurus*
Ratio: humerus + radius/femur + tibia	*92*	*108*	*80*	—	*55*
Ratio: hind limb length/presacral length	*46*	*55*	*60*	—	*91*
Ratio: skull width/femur length	*142*	*169*	—	—	*111*
Ratio: femur length/presacral length	*19*	*21*	*23*	—	*37*
Ratio: humerus length/femur length	*91*	*100*	*73*	—	*55*
Ratio: femur length/humerus length	*110*	*100*	*137*	—	*180*
Ratio: tibia length/femur length	*49*	*53*	*69*	—	*75*
Length of femur in terms of posterior presacral verbrae	6	5	—	—	8

[a] The measurements from Efremov (1940), Watson (1914), and von Huene (1912) are for the most part taken from very careful measurements, made with the aid of a lens, of published scaled illustrations of the bones. Unfortunately these authors did not publish extensive tables of measurements.

[b] Estimated.

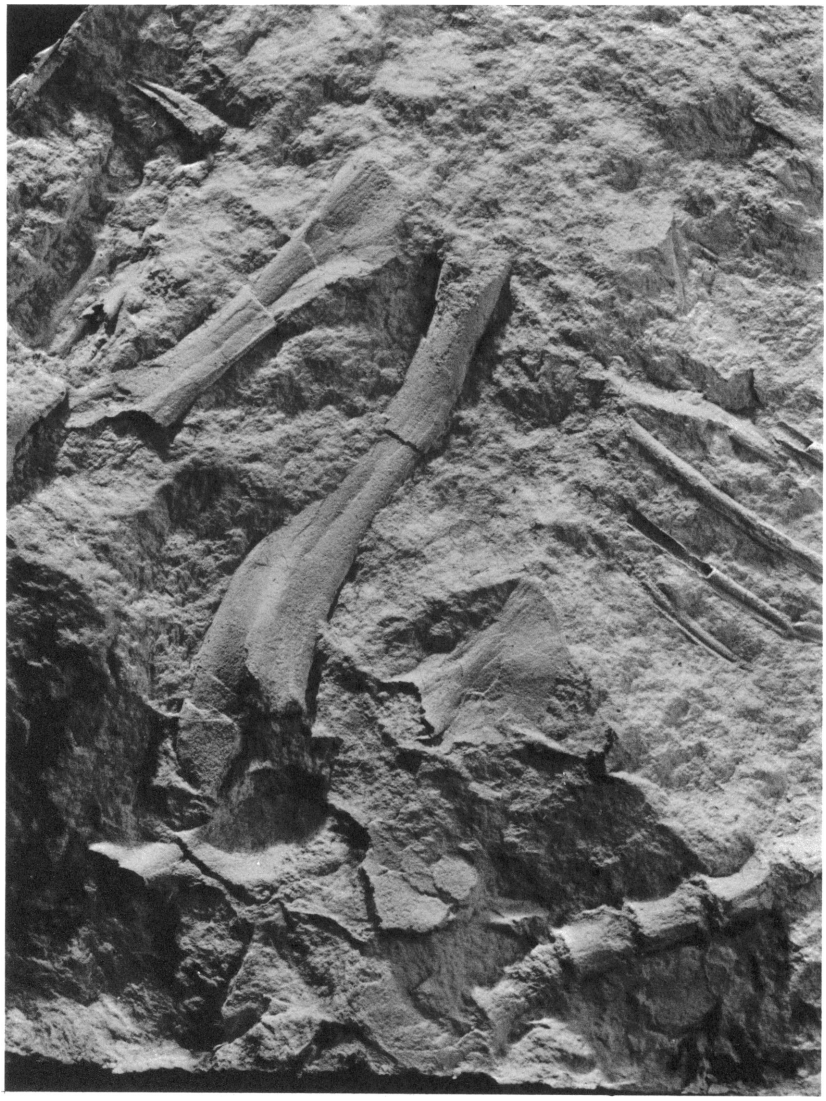

FIG. 7. *Sphodrosaurus pennsylvanicus*, new genus and species. Positive cast (A.M.N.H. No. 7601) from type, posterior portion of skeleton, ventral view. × 1½.

terior ends being opposite the front of the axis, which run back parallel to three or four of the cervical vertebrae. The dorsal ribs are slender, rather long, and only slightly curved, which indicates a wide spread,

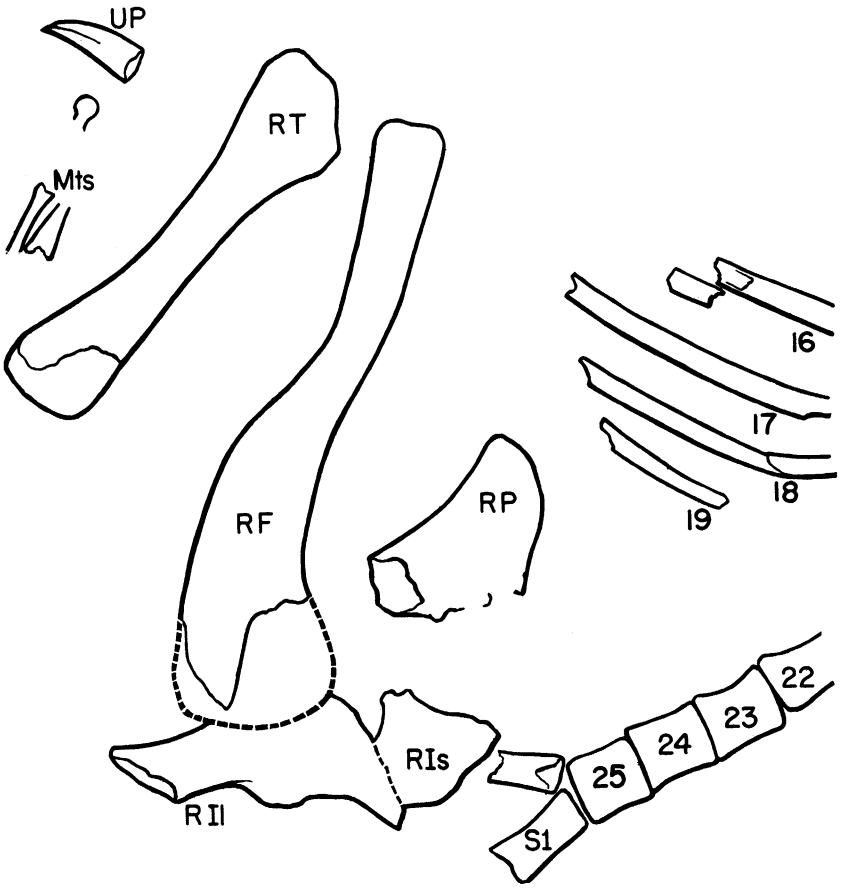

FIG. 8. Interpretation of figure 7. Presacral vertebrae and ribs numbered. *Symbols:* Mts, metatarsals; RF, right femur; RII, right ilium; RIs, right ischium; RP, right pubis; RT, right tibia; S1, first sacral vertebrae; UP, ungual phalanx. About × 1½.

in turn indicating a flat, broad body—a characteristic feature of the procolophonids.

The right shoulder girdle is preserved in part. It shows particularly well a long, blade-like, curved scapula, proximally broad and expanding at its lower end to articulate with the coracoid complex. A coracoid (probably the posterior one) is shown in an oblique cross section, and evidently it was a bone of some thickness in the glenoid region. Unfortunately sutures are not apparent, so that details of the scapula-coracoid juncture are not visible. The general shape of the scapula-

coracoid is readily apparent, however, and shows quite obviously that the shoulder girdle in *Sphodrosaurus* is slender, as compared for example with Watson's figure (1914) of the same complex in *Procolophon*, and is characterized especially by the long scapular blade. It is probable that two coracoids were present, as in other procolophonids. No indications of cleithrum, clavicles, and interclavicle are visible.

On the opposite side of the skeleton the proximal portion of the left humerus is partially preserved; the distal end disappears into the matrix. The upper end of this bone is broad. Somewhat displaced from it are to be seen the distal ends of the radius and ulna, the former a rod-like bone, the latter a broad, flat bone. The position of these bones indicates that if all the matrix could be removed they probably would be in articulation with the humerus. They indicate also that the elements of the fore limbs are considerably shorter and less robust than the corresponding elements of the hind limbs, the difference in this specimen being considerably greater than in other described procolophonids.

Perhaps the ilium was high, a procolophonid character. Nothing remains of this bone except a rather narrow but strong "neck" just above the acetabulum. The pubis is somewhat elongated, especially for a cotylosaur, with an expanded distal portion terminating in a curved edge. Near the acetabulum the pubis is narrowed into a "neck," and there appears to be a slight notch between this bone and the ischium. The small bit of ischium preserved indicates that this is a flat, plate-like bone.

The femur is a long and strong bone. It is equal in length to at least eight of the posterior presacral vertebrae and is considerably longer than the tibia. It is somewhat curved and is proximally expanded into a large head that is directed dorsomedially. On the ventral surface of this bone, running down the shaft from the head, is a strong ridge, the ventral ridge that is typical of many cotylosaurs. Romer mentions the fact that in the procolophonids the "ventral ridge system [is] reduced; no fourth trochanter" (Romer, 1956, p. 486). There is obviously no fourth trochanter, but in this femur the ventral ridge is well developed.

The length and robustness of the femur in the new specimen from Pennsylvania are characters that distinguish it quite sharply from other known Procolophonids. For instance, whereas this bone is about the equivalent in length of eight posterior presacral vertebrae, the femur in *Procolophon* is equal in length to only about five posterior presacrals. Or again, its length is somewhat more than a third of that

of the entire presacral series, as compared with a femoral length of a fourth or a fifth of the length of the presacrals in other procolophonids. Its size is well illustrated in other respects, too; thus it is about twice the length of the humerus, whereas in other procolophonids the humerus is more nearly equal to the femur in length.

The tibia of *Sphodrosaurus* is likewise large, being about three-fourths of the length of the femur, whereas in other procolophonids the tibia is only a half or two-thirds as long as the femur. The tibia is a stout bone in this Pennsylvania fossil. The fibula is not visible; evidently it is lodged in the matrix beneath the tibia.

The pes is obviously long, probably about equal in length to the tibia, when extended. So it is that the combination of large femur and tibia and an elongated pes makes the hind limb of *Sphodrosaurus* very long indeed, almost as long as the total length of the presacral series of vertebrae. Such a length contrasts sharply with the condition in other procolophonids, in which the hind limb is either somewhat less, or perhaps a little more, than half of the length of the presacral series of vertebrae. Correlative is the fact that the hind limb is about twice as long as the fore limb, as compared with an approximate equality in length of hind limb and fore limb in other procolophonids.

The hind foot is imperfectly preserved in the type specimen of *Sphodrosaurus*, but a few bones are evident. Although no tarsal bones are to be seen, one broad metatarsal is visible, probably the third or fourth, and one narrow one, probably the fourth or fifth. At least two intermediate phalanges, very obscurely seen, are present below the heavy metatarsal. The ungual is nicely exposed and, quite surprisingly, is a long, straight, strong claw, not unlike a crocodilian claw in shape. A strong claw such as this is rather unexpected in a procolophonid.

CONCLUSIONS

The foregoing description has shown that *Sphodrosaurus* shows various resemblances to and certain differences from the several genera of procolophonids that have been described from late Paleozoic and Triassic strata in different parts of the world. Perhaps the most striking differences between this form and the established genera of procolophonids are in the great length and robust size of the hind limb in the Pennsylvania specimen, and the long, sharp claws of the pes. Such characters might lead one to doubt the true procolophonid relationships of *Sphodrosaurus*, but other characters, such as size, the obviously large skull, the extension of the back of the skull in a sort of frill over the cervical region, the evidently broad vertebral neural arches (as in-

dicated by the separation of the heads of the ribs), and the holocephalous, flaring ribs, are all characters that point to procolophonid affinities for *Sphodrosaurus*. Therefore it seems most reasonable on the basis of our known material to place *Sphodrosaurus* among the Procolophonidae as a late Triassic representative of the group. It is

TABLE 2

COMPARISONS BETWEEN *Sphodrosaurus* AND *Hypsognathus*

	Sphodrosaurus	*Hypsognathus*
Size	Equal to *Hypsognathus*	Equal to *Sphodrosaurus*
Skull	Very large, larger than that of *Hypsognathus*	Large
	Posterior portion extending over about 5 cervical vertebrae	Posterior portion extending over about 2 or 3 cervicals
	No evidence of spikes on quadratojugals	Spikes on quadratojugals
	Angles of lines from tabulars to parietal foramen about 90°	Angle of lines from tabulars to parietal foramen about 130°
Vertebrae	25 presacral	Number of presacrals not definite
	Neural arches broad	Neural arches broad
Ribs	Holocephalous and flaring	Holocephalous and flaring
Pectoral girdle	Scapula long and curved, proximally broad	Scapula long, proximally broad
Pelvic girdle	Ilium high, pubes and ischium plate-like	Not known
Limbs	Hind limb very large and robust, about twice the length of fore limb	Hind limb not known
Feet	Metatarsal elongated; unguals forming long, sharp claws	Hind limb not known

becoming apparent that at the end of Triassic times these reptiles went through a final stage of varied adaptive radiation in North America (and perhaps in other parts of the world as well). Like so many groups of animals, the history of which we are acquainted with in the fossil record, the procolophonids seem to have experienced a final "burst" of evolutionary development before their extinction, which coincided with the close of the Triassic period.

As a summary, a comparison between *Sphodrosaurus* and *Hypsognathus*, its nearest neighbor in time and space, is given in table 2.

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