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The Triassic Dinosaur Genera *Podokesaurus* and *Coelophysis*

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INTRODUCTION

As one aspect of a large study of the North American Triassic dinosaurs, it has been necessary to investigate very carefully the status of the several included genera. Not many genera are involved in the revision that is at present under way, yet there are problems of definition and of status, derived to a large degree from the sad fact that some of the taxa are based on rather inadequate materials. *Podokesaurus holyokensis* Talbot is one of the forms of which the type fossil is far from satisfactory, and the more this monotypic genus (the type species of which was founded on a single fragmentary skeleton long since destroyed) is studied, the more surely does it appear that *Podokesaurus* is synonymous with the genus *Coelophysis*. The purpose of the present paper is to set forth evidence and arguments for such a conclusion.

It is thought advisable to discuss this particular matter separately, rather than to wait for completion of the comprehensive study. *Podokesaurus* is a name widely established in the literature and has long been recognized as the type of a family of coelurosaurian theropods. The name "*Podokesaurus*" is consequently significant in works on Triassic dinosaurs, and its status should be clarified as much as possible.

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THE PROBLEM

The problem involves, of course, both *Podokesaurus* and *Coelophysis*. The latter is by far the older of the two genera, so it is considered first.

The name "*Coelophysis*" was proposed by Cope in 1889 as the generic designation for three reptilian species that he had named two years previously within the genera *Coelurus* and *Tanystrophaeus*. To be more specific, Cope described *Coelurus bauri* and *Coelurus longicollis* in the American Naturalist in 1887, and later in that same year *Tanystrophaeus willistoni*, in the Proceedings of the American Philosophical Society. In this latter publication he referred the two species, previously assigned to *Coelurus*, to the genus *Tanystrophaeus*.

In short, the nomenclatorial sequence was as follows:

- Coelurus bauri* Cope, 1887
- Coelurus longicollis* Cope, 1887
- Tanystrophaeus willistoni* Cope, 1887
- Tanystrophaeus bauri* (Cope), 1887
- Tanystrophaeus longicollis* (Cope), 1887
- Coelophysis bauri* (Cope), 1889
- Coelophysis longicollis* (Cope), 1889
- Coelophysis willistoni* (Cope), 1889

All the materials, numerous though fragmentary, on which the three species were based came from two localities (or more probably from one locality) in northern New Mexico, and almost certainly from a single horizon. Von Huene, in a review of Cope's New Mexican Triassic fossils published in 1915, indicated that the type materials of the three named species of *Coelophysis* had been found at two localities, in Rio Arriba County, New Mexico, one near the little settlement of Gallina, the other along Arroyo Seco, a tributary of the Chama River, perhaps some 25 miles to the east of Gallina. Von Huene evidently based his conclusions that these two localities were the sites where the type materials of the three species under consideration had been found on the work of Williston, Case, and himself in Rio Arriba County in 1911, and on the labels written by David Baldwin, who collected the fossils in 1881 for Cope. Williston and Case in 1911 found bones of *Coelophysis* just north of Cerro Blanco, near Gallina, a colorful ridge of lemon yellow sandstones topped by a rather dazzling white gypsum, all of Jurassic age. "The horizon of these remains can hardly be less than one hundred feet above the basal Upper Trias sandstones, and, in all probability, the original types came from the immediate locality whence the fragments were found by the junior author" (Williston and Case, 1912, p. 11).

This may be true, because it is known that Baldwin prospected the beds in this region. But Baldwin also worked along Arroyo Seco, and from the evidence of his labels it seems likely that he found bones of *Coelophysis* on the land now included within Ghost Ranch, northwest of Abiquiu, New Mexico. Ghost Ranch, in recent past years the property of Mr. Arthur Pack, is now owned by the Presbyterian Church.

One of the labels associated with the fossils on which the three species of *Coelophysis* were based reads, in Baldwin's handwriting: "Label Sack 2 Box 1 Prof. E. D. Cope. Contains Triassic or Jurassic bones all small and tender. Those marked little bones are many of them almost microscopic. All in this sack found in same place about four hundred feet below gypsum stratum 'Arroyo Seco' Rio Arriba Co., New Mexico. February 1881. No feet—no head—only one tooth. D. Baldwin—Abiquiu."

This label is the extent of the written evidence left to us by Baldwin as to the locality at which *Coelophysis* was found, and it seems highly probable to the present author that all the *Coelophysis* collected by Baldwin came from this one place. However, there can be but little doubt as to the contemporaneity of the type fossils; they were found in the Petrified Forest member of the Chinle Formation, which is exposed along Arroyo Seco beneath the towering cliffs of Jurassic sandstones and gypsum, and likewise along the north side of Cerro Blanco. There are other exposures as well in this general region.

Among the fossils collected by Baldwin are various parts of pelvic girdles, limb bones, foot bones, and vertebrae. These assorted bones are of varying sizes, and Cope, with his usual enthusiasm for making new names, set up the three species that are listed above. But even after he combined them in his new genus, *Coelophysis*, he did not select a type species. Nor did von Huene designate a type species in his 1915 review. Not until 1930 was a type species indicated, by O. P. Hay (1930), who chose *Coelophysis bauri*.

In 1947 and 1948 the present author and his associates collected a large series of *Coelophysis* skeletons from a quarry near the Arroyo Seco, on Ghost Ranch. It seems obvious that these materials were found very near to, if not immediately at, the spot mentioned by Baldwin in his label quoted above. The skeletons were found closely associated and intertwined, and many of them are complete. They represent animals of different ontogenetic ages, from small to large individuals. Therefore we now have excellent specimens of *Coelophysis*, constituting some of the most complete and significant dinosaurian skeletons ever discovered.

From these fossils it is quite obvious that the type materials for the three species described by Cope are nothing more nor less than bones that

represent individuals of varying ontogenetic ages. Since they were found at a single geologic horizon it seems that the only proper way in which to look at these original specimens is to regard them as indications of growth stages of a single species, *Coelophysis bauri*.

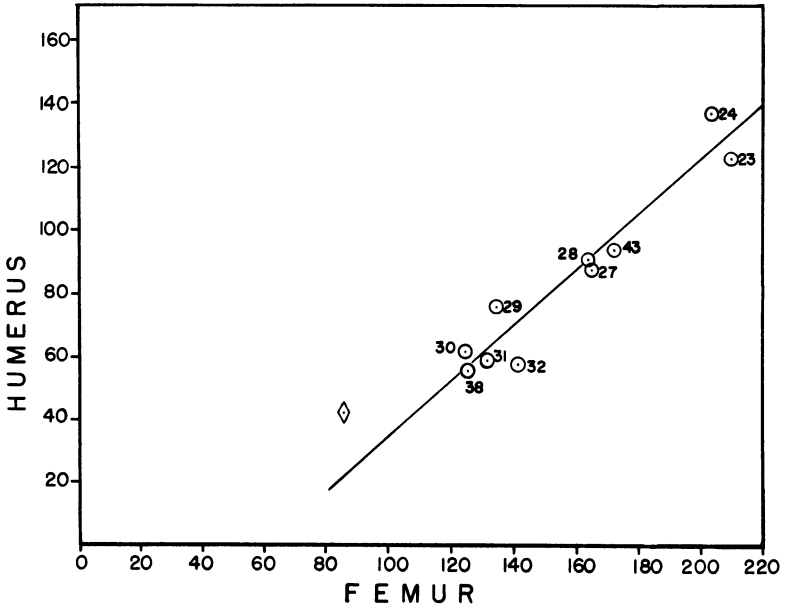


FIG. 1. The relationships of the length of the humerus (ordinate) to the length of the femur (abscissa) in *Coelophysis bauri*, as known from a series of specimens from a single quarry in the Chinle Formation at Ghost Ranch, New Mexico, and in *Coelophysis holyokensis* from the Newark beds of the Connecticut Valley. The Chinle specimens are indicated by circles and numbers, the numbers being the last two digits of the American Museum catalogue numbers as given in table 2. The Newark fossil is indicated by a diamond.

The genus *Podokesaurus* was established in 1911, the type species, based on a fragmentary skeleton, being *Podokesaurus holyokensis* Talbot. This skeleton was noticed in a Triassic boulder (not in place) on the campus of Mt. Holyoke College, Holyoke, Massachusetts, and was described by Mignon Talbot of that institution. It was installed in the museum of the college, and casts were made, one being deposited in the Peabody Museum of Natural History at Yale University. Subsequently the type specimen was destroyed by fire, so that our knowledge of the species, apart from the first description based on the original specimen, must of necessity rest on

the cast in the Yale museum, on any other such casts as may be in existence, and on a copy of the Yale cast, which is now in the American Museum of Natural History.

Podokesaurus holyokensis was based on a part of a skeleton. This specimen, which was contained within its original matrix, consisted of a series of posterior presacral vertebrae, separated by a long gap from a series of posterior caudal vertebrae. There were in addition a partial humerus, some ribs, a pubis and ischium, a right femur and a part of a left femur, the left tibia and fibula and a metatarsal, portions of right metatarsals, some foot bones, and a few other scattered bone fragments, including what seems to have been a few questionable skull elements. Most of the bones were rather poorly preserved, and it was not possible to see many details of the skeletal elements. Now that only the casts are available, it is hardly possible to get more than a general impression of those parts of the skeleton preserved, and some evidence as to their proportions to one another.

Nevertheless this skeleton, imperfect as it was, seemed at the time to constitute the most satisfactory evidence available for a delineation of the characters of the coelurosaurian family to which it belonged. *Podokesaurus* was accordingly designated as the type of the Podokesauridae. This name was established by von Huene in 1914 and has since become firmly established in the literature.

The synonymy of *Podokesaurus* with *Coelophysis* had been suspected, and this suspicion was stated by Colbert and Baird in 1958 as a result of their study of coelurosaurian bone casts from the Connecticut Valley. They compared the relationships of the lengths of the tibia to those of the pubis in various specimens of *Coelophysis*, and found that a regression line could be established into which the data for the two bones in *Podokesaurus* could be nicely fitted. Consequently they concluded, "this may indicate a rather close relationship between *Podokesaurus* and *Coelophysis* and raises a question as to the validity of the genus *Podokesaurus*" (Colbert and Baird, 1958, p. 7).

COELOPHYSIS AND PODOKESAURUS COMPARED

A list of selected diagnostic characters for *Coelophysis* based on associated skeletons referred to *Coelophysis bauri*, is given in table 1. Such characters as are known in the type materials of *Coelophysis* are compared with the same characters, so far as they are known, in *Podokesaurus*. Since both *Coelophysis* and *Podokesaurus* are monotypic genera, the characters compared are those for the genus and for the type species in each case.

As is readily apparent from table 1, virtually no differences can be drawn between *Podokesaurus* and *Coelophysis* on the basis of the known characters in the former genus. As is often the case in paleontology, a decision must be based on data that are all too incomplete, in this case

TABLE 1
COMPARISON OF DIAGNOSTIC CHARACTERS IN *Coelophysis bauri* AND
Podokesaurus holyokensis

<i>Coelophysis bauri</i>	<i>Podokesaurus holyokensis</i>
Lightly built, with hollow bones	The same
Maximum length about 3 meters; smallest known specimen about 1 meter in length	About 1 meter, estimated
Skull long, low, narrow	Unknown
Large antorbital fenestra	Unknown
Teeth laterally compressed, serrated	Unknown
About 26 upper, 25 lower, teeth	Unknown
Vertebrae amphicoelous	The same
Wide transverse processes, low spines	The same, so far as can be seen
Ten elongated cervicals, 13 dorsals	Number indeterminate
Five fused sacrals	Unknown
About 40 caudals, elongated posteriorly	Number unknown, elongated
Forelimb about one-half of length of hind limb	The same
Carpals present	Unknown
Manus functionally tridactyl, digit 4 reduced	Unknown
Ilium elongated	Unknown
Pubes equal to or longer than femur	The same
Pubes flattened, distally thickened	Seemingly the same
Ischia rod-like, proximally expanded	The same
Femur curved, large external trochanter	The same, so far as can be seen
Tibia-fibula slightly longer than femur	The same
Calcaneum-astragalus without ascending process	Probably the same
Pes functionally tridactyl, bird-like, long	The same
First digit reduced, and with claw	Unknown
Fifth digit a splint-like metatarsal	Unknown

evanescent, and such decision is always open to question. It seems, however, that the synonymy of *Podokesaurus* with *Coelophysis* is indicated as the most reasonable solution of the problem.

The arguments presented here in favor of regarding *Podokesaurus* as synonymous with *Coelophysis* are in line with the evidence of the bone casts from the Connecticut Valley, redescribed by Colbert and Baird in 1958. The authors could find no reasons for regarding the fossil they described, originally discovered a century ago, as anything other than *Coelophysis*.

Because the large bones (the redescribed specimen) and small bones (*Podokesaurus*) from the Connecticut Valley fall within the growth pattern of *Coelophysis*, it seems logical to regard these eastern specimens as generically the same as specimens from the west. (See figs. 1-3.)

TABLE 2
MEASUREMENTS IN MILLIMETERS

	Humerus	Femur	Tibia	Metatarsal III
<i>Podokesaurus holyokensis</i> (From Talbot, 1911)	42	86	104	65
<i>Coelophysis bauri</i>				
A.M.N.H. No. 7223	120	209	224	126
A.M.N.H. No. 7224	134	203	221	125
A.M.N.H. No. 7227	86	165	—	—
A.M.N.H. No. 7228	89	164	188	108
A.M.N.H. No. 7229	75	135	154	85
A.M.N.H. No. 7230	61	125	—	—
A.M.N.H. No. 7231	58	132	—	—
A.M.N.H. No. 7232	57	141	157	95
A.M.N.H. No. 7233	—	126	140	81
A.M.N.H. No. 7234	—	118	135	84
A.M.N.H. No. 7238	55	126	147	87
A.M.N.H. No. 7243	91	172	199	114
A.M.N.H. No. 7244	—	173	195	120
A.M.N.H. No. 7246	—	122	136	79
A.M.N.H. No. 7247	—	125	138	84
A.M.N.H. No. 7249	—	196	207	110
A.M.N.H. No. 7253	—	—	155	91
A.M.N.H. No. 7256	—	—	152	82

THE SPECIES

If the synonymy of *Podokesaurus* with *Coelophysis* is accepted, what then is the status of the species originally described as *Podokesaurus holyokensis*? Does it become a synonym of *Coelophysis bauri*, or is it a separate species of the genus? The answers to these questions are complicated by the fact that species differences as seen in the skeletons of reptiles, the evidence on which extinct species must of necessity be based, may be very subtle indeed.

One might argue that the graphs which have been presented to show the general correspondence between certain measurements of *Podokesaurus*

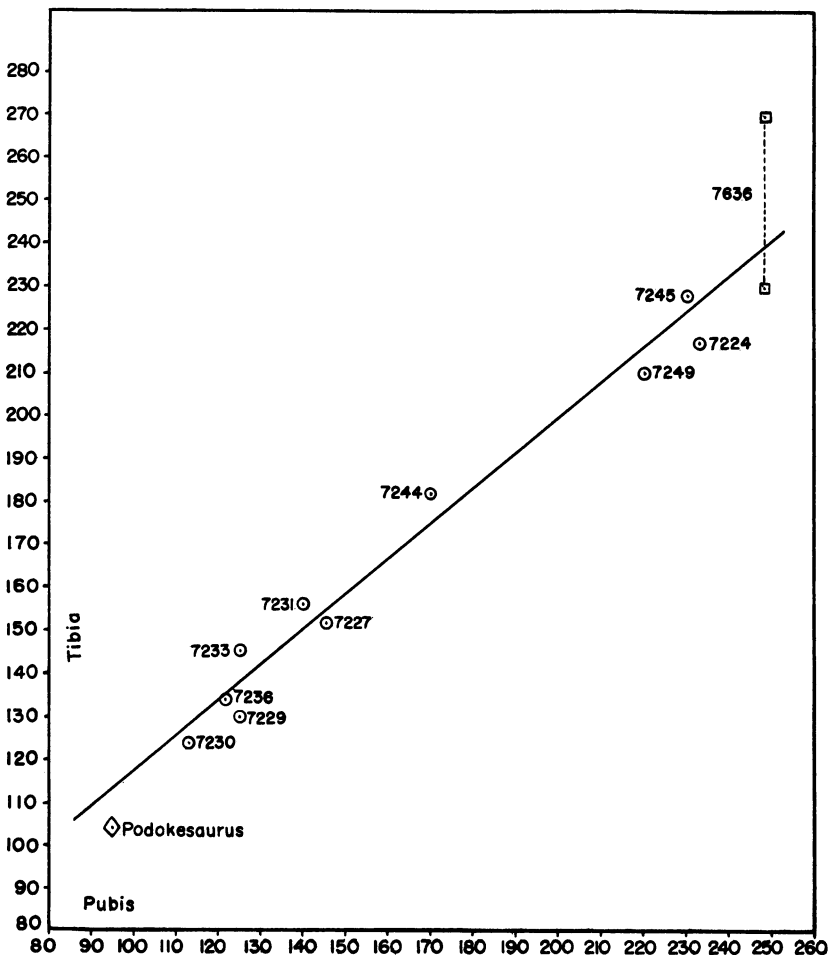


FIG. 2. The relationships of the length of the tibia (ordinate) to the length of the pubis (abscissa) in *Coelophysis bauri*, as known from a series of specimens from a single quarry in the Chinle Formation at Ghost Ranch, New Mexico, and in *Coelophysis holyokensis* (here labeled *Podokesaurus*) from the Newark beds of the Connecticut Valley. (From Colbert and Baird, 1958.)

(or as is here being argued, of *Coelophysis*) *holyokensis* with the trend of growth in *Coelophysis bauri* indicate a specific identity between these supposedly different forms. But the graphs may be interpreted in another way, namely, that they do show generic identity, but not necessarily specific resemblances.

There are, however, one or two characters in *Coelophysis holyokensis*

which, so far as can be seen in illustrations and casts of the type, seem to differ slightly from the same characters in *Coelophysis bauri*. Thus, the spines of the vertebrae in the former are not so long from front to back as they are in the latter, and the ischium of *Coelophysis holyokensis* appears to be a little different in shape from that of *Coelophysis bauri*. What is the significance of these characters?

In an attempt to check this, two genera of modern lizards were examined, each represented by two species. The vertebral column of *Varanus bengalensis* from India apparently differs from that of *Varanus exanthematicus* from Africa in that the vertebral spines are longer antero-posteriorly in the former than they are in the latter. This difference is the same as that observed between the vertebrae of *Coelophysis bauri* and those of the type specimen of *Podokesaurus holyokensis*, as mentioned above. In the two lizard species the pelvic girdles show very minor differences in proportions, which may be compared with the differences seen between the ischia of the two fossil forms under consideration. In the South American lizard *Tupinambis*, two species, *Tupinambis teguixin* and *Tupinambis nigropunctatus*, while not showing any appreciable differences in the vertebral spines, show recognizable differences in proportions in the pelvis, particularly of the pubes. These two species also show minor proportional differences in the pectoral girdle.

Although the observations on these lizard skeletons were limited to a few simple inspections and were not statistically analyzed, they indicate that small differences between reptilian species belonging to a single genus can be found in the postcranial skeleton, a subject to which not much attention has been given by herpetologists. On the basis of these limited observations, it is here suggested that those differences that are apparent between *Coelophysis bauri* and the type of *Podokesaurus holyokensis*, although not of such magnitude as to justify the perpetuation of two distinct genera, are sufficiently distinct to justify the probable recognition of two separate species, one in eastern North America and the other in the western part of the continent.

Thus it is proposed that the Triassic coelurosaurs of North America belonging to the family Podokesauridae be designated as follows:

Order Saurischia

Coelophysis bauri (Cope), Chinle Formation, western North America

Coelophysis holyokensis (Talbot), probably from the Portland Formation, Newark Group, eastern North America

It is suggested that the bones from the Connecticut Valley redescribed by Colbert and Baird as *Coelophysis* sp. belong to *Coelophysis holyokensis*.

It is admitted that no ironclad case can be made for the proposals and

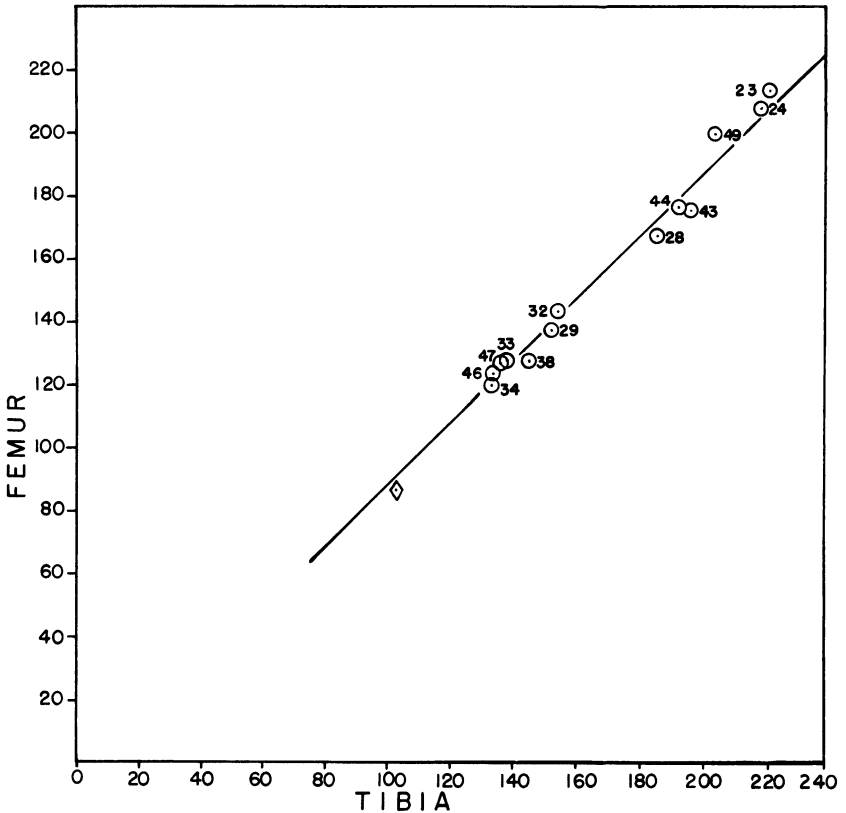


FIG. 3. The relationships of the length of the femur (ordinate) to the length of the tibia (abscissa) in *Coelophysis bauri*, as known from a series of specimens from a single quarry in the Chinle Formation at Ghost Ranch, New Mexico, and in *Coelophysis holyokensis* from the Newark beds of the Connecticut Valley. The Chinle specimens are indicated by circles and numbers, the numbers being the last two digits of the American Museum catalogue numbers as given in table 2. The Newark fossil is indicated by a diamond.

suggestions that are presented above. One might with logic argue that the type of *Podokesaurus holyokensis* is indeed generically distinct from *Coelophysis bauri*, and that more material from the Newark beds of eastern North America would bear this out. But the burden of proof is, seemingly, on the proponents of such a view. At the present time the probabilities appear to be in line with the suggestions made above.

It should be added that the presence of this single North American dinosaurian genus, with separate species east and west, accords very

nicely with the evidence of many recent reptiles. For example, Colbert and Imbrie (1956) have called attention to similar taxonomic and distributional patterns in the North American skink, *Eumeces*, and the soft-shelled turtle, *Amyda*.

THE FAMILY

The two species of *Coelophysis* are placed, above, in the family Podokesauridae. Even though, according to the present proposal, the genus *Podokesaurus* vanishes as a synonym of *Coelophysis*, the family name Podokesauridae remains. Article 40 of the revised International Code of Zoological Nomenclature, adopted by the XV International Congress of Zoology (1961), provides: "When, after 1960, a nominal type-genus is rejected as a junior synonym (objective or subjective), a family-group name based on it is not to be changed, but continues to be the valid name of the family-group taxon that continues both the senior and junior synonyms."

Consequently the complete classification of the coelurosaurian dinosaurs with which we are herein concerned is as follows:

Class Reptilia

Order Saurischia

Suborder Theropoda

Infraorder Coelurosauria

Family Podokesauridae

Genus *Coelophysis* Cope

Coelophysis bauri (Cope), 1887

Coelophysis holyokensis (Talbot), 1911

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