The Osteology of *Compsognathus longipes* Wagner

by

JOHN H. OSTROM*)

With 16 text figures and plates 7—14

ABSTRACT

Detailed analysis of the holotype specimen of *Compsognathus longipes* — the classic or archtypical "coelurosaurian" theropod, does not substantiate the traditional carnosaur — coelurosaur subdivision of the Theropoda. Only in its diminutive size, is *Compsognathus* a typical coelurosaurian. The smallest of all known theropods, *Compsognathus* possesses a carnosaur-like large skull (perhaps a juvenile condition); a neck that is intermediate between the long cervical series of coelurosaurs and the short neck of carnosaurs; and forelimbs that are robust, but of intermediate length and bear carnosaur-like two-fingered hands. The hands, however, are unique among theropods, with a peculiar phalangeal formula of 2-2-0 for digits I, II and III. That condition excludes *Compsognathus* from an ancestral relationship with any known later theropod, as well as separating it from other presently known Late Jurassic theropods. The so-called impressions of integument and supposed skin armor are judged to be nothing more than solution-etched surfaces. The tiny skeleton preserved within the body cavity of *Compsognathus* is identifiable, and proves to be a small individual of the lacertilian *Bavarisaurus* (cf. *macrodactylus*), and n o t an embryo. Analysis of those stomach contents indicates a very long-tailed species, probably a highly cursorial ground-dwelling variety. This remarkable evidence establishes beyond any doubt that *Compsognathus* was a very agile and fleet-footed predator. On the basis of the unique construction of the hand, *Compsognathus* appears to belong to a dead-end lineage among theropods. On the same grounds, it is judged to be somewhat removed from the theropod line that earlier gave rise to *Archaeopteryx,* and ultimately to later birds.

KURZFASSUNG

Eine eingehende Analyse des Holotyps von *Compsognathus longipes,* dem klassischen und archaetypischen „coelurosauriden" Theropoden, stützt nicht die traditionelle Gliederung der Theropoda in Carnosauria und Coelurosauria. Nur hinsichtlich seiner geringen Größe ist *Compsognathus* ein typischer Coelurosaurier. Als kleinster bekannter Theropode besitzt *Compsognathus* einen carnosaurierartigen, großen Schädel (vielleicht ein juveniles Merkmal), einen Hals, dessen Länge zwischen der langen Cervicalreihe der Coelurosaurier und dem kurzen Hals der Carnosaurier liegt und Vordergliedmaßen, die kräftig, aber von intermediärer Länge sind, mit carnosaurierartigen, zweifingerigen Händen. Das Handskelett ist jedoch einzigartig unter den Theropoden und besitzt die eigenartige Phalangenformel 2-2-0 für die Finger I, II, und III. Diese Verhältnisse schließen *Compsognathus* von einer Verwandtschaft mit irgendeinem bekannten, späteren Theropoden aus; ebenso trennen sie ihn von anderen bis jetzt bekannten Oberjura-Theropoden.

Die sogenannten Hautabdrücke und der vermutete Hautpanzer werden für nichts anderes als angelöste Oberflächen gehalten. Das winzige, in der Leibeshöhle von *Compsognathus* erhaltene Skelett ist mit Sicherheit als ein kleines Individuum des Lacertiliers *Bavarisaurus* (cf. *macrodactylus*) zu bestimmen. Es ist k e i n Embryo. Die Analyse dieses Mageninhaltes deutet auf eine sehr langschwänzige Art hin, wahrscheinlich eine sehr schnelle, bodenlebende Form. Dies erlaubt die bemerkenswerte Feststellung, daß *Compsognathus* zweifellos ein sehr agiler und schnellfüßiger Räuber war. Aufgrund der einzigartigen Konstruktion der Hand, scheint *Compsognathus* im Hinblick auf die Phylogenie der Theropoden zu einer blind endenden Seitenlinie zu gehören. Es wird deshalb angenommen, daß seine stammesgeschichtliche Position etwas abseits von d e r Theropodenlinie lag, die früher zum Ursprung von *Archaeopteryx* und letztlich zu den späteren Vögeln führte.

*) Prof. Dr. J. H. Ostrom, Dept. of Geology and Geophysics, and Peabody Museum of Natural History, Yale University, New Haven, Conn., U.S.A.

TABLE OF CONTENTS

INTRODUCTION

For more than a century, *Compsognathus* has been one of the better-known dinosaurs — partly, for exactly the opposite reason that some other dinosaur kinds are well-known: *Compsognathus* is the smallest of all known dinosaurs. In life, it measured no more than 70 to 75 cm from snout tip to tail tip. In texts and popular writings, it has repeatedly been compared in size with the common chicken. *Compsognathus* also acquired fame because it was one of the first dinosaurian specimens discovered that was virtually complete, although, curiously enough, it was not originally identified as dinosaurian in the first report by Andreas Wagner (1861) — perhaps because it was so small, or because no one at that time really knew what dinosaur anatomy should be like. But perhaps more than anything else, the fame of *Compsognathus* was caused by Thomas Huxley's reference to it as a "bird-like reptile" in his speculations (1868, 1870) on the relationship between birds and dinosaurs.

Since Wagner's original description, this now classic specimen has been studied by many prominent scholars, including Huxley, Zittel, Marsh, Baur, Gegenbaur, von Huene and others, and has been the subject of several intriguing questions: the possibility of viviparity in dinosaurs, and the evolutionary relationship between dinosaurs and birds.

Until 1972, when a second very similar but larger specimen was reported (Bidar, Demay and Thomel) from southern France, the Munich specimen was unique. Except for three isolated "metatarsals" and an associated phalanx (Dames, 1884) sometimes referred to *Compsognathus*, no other specimens have been recovered from the Solnhofen Limestones, or elsewhere. (But see page 101—102).

The present study is a consequence of several factors: my persistent interest in dinosaurian biology and evolution; the recently re-recognized (and now reinforced) evidence of a probable dinosaurian origin of birds; the often-cited bird-like nature of *Compsognathus;* and finally, the need for a comprehensive detailed study of this classic specimen.

In the pages that follow, references are made to specimens that are housed in various paleontological collections. In those references, institutional names are abbreviated as follows:

A.M.N.H.   — American Museum of Natural History, New York.

B.S.P.   — Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich.

G.I.M.   — Geological Institute of Mongolia, Ulan Bator.

S.M.N.S.   — Staatliches Museum für Naturkunde Stuttgart.

U.S.N.M.   — United States National Museum, Washington, D.C.

SYSTEMATICS

Class Reptilia
Order Saurischia Seeley, 1887
Suborder Theropoda Marsh, 1881
Family Compsognathidae Marsh, 1882

D e f i n i t i o n : Small theropods with elongated hindlimbs, medium length forelimbs and large skull. Vertebral formula: 10 cervicals, 13 dorsals, 4 sacrals and more than 20 caudals. Cervical vertebrae opisthocoelous and pleurocoelous. Dorsal vertebrae amphyplatyan or platycoelous. Cervicals not elongated, rather approximating dorsal vertebral length. Pelvis of normal triradiate (propubic) organization. Pubis markedly longer than ischium and expanded distally. Ilium long and low. Tibia significantly longer than femur and metatarsals elongated. Tarsus and pes of normal theropod construction with I reduced and reverted and V vestigial. Pes digital formula: 2-3-4-5-0. Manus reduced to two functional digits, I and II, and vestigial metacarpal III. Digital formula: 2-2-0- - . Skull relatively very large, equal to or longer than femur. Two antorbital fenestrae and very large orbit. Mandible very slender. Dental count high: $\frac{3 + 15 \text{ or } 16.}{18}$ Anterior teeth with distinctly "bent", fang-like crowns.

D i s t r i b u t i o n : Malm of Europe: Solnhofen Lithographic Limestones of Bavaria and the lithographic Portlandian limestone of "Petit Plan", Canjuers, France.

I n c l u d e d t a x a : Compsognathus longipes Wagner, 1861, holotype specimen: B. S. P. A. S. I 563; and Compsognathus "corallestris" Bidar, Demay and Thomel, 1972.

D i s c u s s i o n : The systematic history of Compsognathus is rather interesting, especially as it relates to the early development of dinosaurian systematics. Although now widely viewed as the archtypical "coelurosaurian" dinosaur, curiously enough, Wagner (1861) gave no opinion on its systematic placement other than to refer to it as "einen Saurier". Huxley (1868) was the first to recognize that Compsognathus should be "placed among, or close to, the Dinosauria". As is well-known, the term Dinosauria was coined by Richard Owen (1842) as a reptilian order to encompass various extinct giant reptiles that had been unearthed in Britain. In 1887 and 1888, Seeley demonstrated that the "dinosaurs" then-known did not constitute a natural group, and proposed two distinctly different orders of dinosaurs — the Saurischia and Ornithischia — orders that are still generally accepted today. As a result, the term "Dinosauria" dropped from use as a formal taxon in classifications. Between the proposals by Owen and Seeley, a number of other schemes were proposed by various scholars. The more important of these classifications are summarized below:

Cope, 1866	Huxley, 1870	Marsh, 1878—84	Cope, 1883	Seeley, 1887
Orders	Suborders	Orders	Orders	Orders
		Stegosauria		
			Orthopoda	Ornithischia
Orthopoda		Ornithopoda		
	Dinosauria	Sauropoda	Opisthocoela	
Goniopoda		Theropoda	Goniopoda	Saurischia
Symphopoda	Compsognatha			
			Hallopoda	

Of special interest here is Huxley's classification, which established a new order, Ornithoscelida, containing two suborders, Dinosauria and Compsognatha. His suborder Dinosauria included all then known dinosaurs (Megalosauridae, Scelidosauridae, Iguanodontidae), including the Cetiosaurs (sauropods). The suborder Compsognatha was proposed by Huxley to include only *Compsognathus*, which he considered close to the Dinosauria in its "ornithic modifications", but different from them in the relatively greater length of the cervicals and a femur shorter than the tibia. The taxon Compsognatha persisted as a higher category of "dinosaurs" as late as 1896, when Marsh last listed it as a suborder of his order Theropoda. Marsh's classification of 1896 was as follows:

Class Reptilia
  Subclass Dinosauria
    Order Theropoda
      Suborder Coeluria
        Family Coeluridae
      Suborder Compsognatha
        Family Compsognathidae[1]
      Suborder Ceratosauria
        Family Ceratosauridae
        Family Ornithomimidae
      Suborder Hallopoda
        Family Hallopidae
    Order Theropoda (No sub-ordinal assignments)
      Family Megalosauridae
      Family Dryptosauridae
      Family Labrosauridae
      Family Plateosauridae
      Family Anchisauridae
    Order Sauropoda (Six families)
    Order Predentata (Equals Ornithischia)
      Suborder Stegosauria (Three families)

[1] Coincidentally, Marsh (1882) authored the family Compsognathidae.

      Suborder Ceratopsia (One family)
      Suborder Ornithopoda (Seven families)

Current traditional classifications subdivide the suborder Theropoda into two infraorders, Carnosauria and Coelurosauria, the former including the large carnivorous forms (Families Megalosauridae and Tyrannosauridae) and the latter all of the smaller and medium-sized theropods (Podokesauridae, Segisauridae, Coeluridae, Compsognathidae, Ornithomimidae and Oviraptoridae). *Compsognathus* has always been allied with the Coelurosauria, ever since its inception by von Huene in 1914. However, the general relationships among theropods have never been clear, and this is reflected in the numerous classification schemes and revisions of the Theropoda that have been proposed over the years (see Huene, 1909, 1914, 1920, 1921 b, 1926, 1928; Osborn, 1917; Gilmore, 1920; Matthew and Brown, 1922; Colbert, 1964; Charig, Attridge and Crompton, 1965; and Colbert and Russell, 1969).

In recent years, doubt has been expressed by some, as to the validity of this two-fold subdivision of the Theropoda. The discovery of *Deinonychus* (Ostrom, 1969a, 1969b), demonstrated once again that it is not always a simple matter to assign a particular taxon to one or the other of these infraorders. *Deinonychus* possesses anatomical features that are usually considered exclusively carnosaurian or coelurosaurian, but not common to both. Colbert and Russell (1969) resolved this problem by placing the Dromaeosauridae (including *Deinonychus*) in a third infraorder, Deinonychosauria. But the question remains: are the categories Coelurosauria and Carnosauria real and valid categories? For example, if the size factor is disregarded, can we justify them on purely anatomical grounds? *Deinocheirus* (Osmolska and Roniewicz, 1970), on anatomical grounds is an ornithomimid —

the classic coelurosaurian family —, but an ornithomimid of enormous size. Because of its huge size, Osmolska and Roniewicz placed it in its own family, Deinocheiridae, and assigned it to the Carnosauria. In 1972, I suggested that *Deinocheirus* was an overblown ornithomimid, but how could I justify placing it in the Coelurosauria? I could not, and therefore repeated the position I had taken earlier with *Deinonychus;* the infraordinal categories were omitted.

Most recently, Barsbold (1976) followed the same principle, but with a different twist. He proposed yet another revision of the Theropoda, wherein he recognizes s i x infraorders: Coelurosauria, Deinonychosauria, Oviraptorosauria, Ornithomimosauria, Carnosauria and Deinocheirosauria. This is comparable to the systematics implicit in my 1969 and 1972 papers, except that it is at a higher taxonomic level. Although I am not comfortable with the elevated rank, this arrangement, like my following "neutral" classification, simplifies some taxonomic assigments. At least as presently known, there are no difficulties in recognizing deinonychosaurs, oviraptorosaurs, ornithomimosaurs and deinocheirosaurs — i f d i a g - n o s t i c r e m a i n s a r e p r e s e r v e d. But if only non-diagnostic elements of these are available, we would be hard-pressed to assign them to any one of these categories. But even here with Barsbold's "neutral" classification, the Carnosauria and Coelurosauria still remain "mixed bags", with the implication that the carnosaurian Megalosauridae and Tyrannosauridae are more closely related to each other than either is to any other theropod group, and that all remaining small theropods (Segisauridae, Compsognathidae, Podokesauridae, Coeluridae, etc.) are likewise more closely related to each other. I prefer not to make that systematic judgement at this time, explicitly or implicitly. The data presented here on *Compsognathus* may provide new insight, but at the moment I believe that present evidence is inadequate for final conclusions. For these reasons, the following study is presented in the context of a conservative classification as follows:

Class Reptilia
  Subclass Archosauria
    Order Saurischia[2])
      Suborder Theropoda
        Family Podokesauridae
        Family Compsognathidae
        Family Segisauridae
        Family Coeluridae
        Family Dromaeosauridae
        Family Ornithomimidae
        Family Oviraptoridae

[2]) The suborder Sauropodomorpha is included, but not listed here.

Family Megalosauridae
Family Tyrannosauridae

Missing from this classification is the Family Hallopidae. The fragmentary (and only) specimen of *Hallopus* (Marsh, 1881, 1882), long considered as possibly closely related to *Compsognathus* and other "coelurosaurs", has been shown by Walker (1970) to be an early crocodilian. Thus, it is not considered further here.

Although not directly pertinent to the systematic placement of *Compsognathus*, two radical proposals have been published recently, that do involve the systematic assignment of the Theropoda. In 1974, Bakker and Galton reviewed certain anatomical evidence which led them to the conclusion that the Ornithischia and Saurischia were of monophyletic — common — ancestry, resurrecting Owen's "Dinosauria". Largely on their belief that all dinosaurs were endothermic and capable of high aerobic exercise metabolism (a popular, but unestablished hypothesis), they concluded that the "Dinosauria" deserved class rank. In their Class Dinosauria, the Theropoda is elevated to ordinal rank (thus returning to Marsh's classification of 1884), within the subclass Saurischia. Their most radical departure from conventional systematics, however, is their inclusion of birds as a subclass of the Dinosauria. This move was prompted by my studies (Ostrom, 1973 and work then in progress — 1976b) showing that *Archaeopteryx* probably was derived from a small theropod ancestor. Charig (1976), in a thorough review of the Bakker and Galton paper, correctly concludes that "until the case for endothermy in dinosaurs is proven (which is unlikely), there are no grounds for separating those reptiles into a different class from all others". As for the inclusion of birds as a subclass of Dinosauria, the possibility that *Archaeopteryx* evolved from a theropod ancestry (a theory that is not accepted by everyone), does not justify such radical departure from conventional classification. Moreover, their proposal fails to enhance the usefulness of the classification on either practical or theoretical grounds, and therefore should be rejected.

Of greater relevance here, is a paper by Thulborn (1975), which was generated by the Bakker — Galton paper. Thulborn argues persuasively (as did Charig, 1976), that existing evidence does not establish monophyly of the dinosaurs. He further rejects the speculation that dinosaurs were endothermic, but he does accept the theory that birds arose from theropods. This last conclusion prompts Thulborn to re-assign the Theropoda to the Class Aves, in order to put "full emphasis on the dinosaurian origin of birds". Desirable though that rationale may (or may not) be, classifying theropods such as *Tyrannosaurus* and *Allosau-*

rus as birds, will not add to the utility of vertebrate classification either, and therefore will not be accepted by the ornithological community or other systematists — even if the therapod-avian evolutionary relationships should achieve general acceptance. The conventional classification of the higher tetrapod classes Reptilia, Aves and Mammalia is adequate and flexible enough to accommodate these views, and I prefer to use the conservative subdivision of the Theropoda presented above, in the traditional Class Reptilia.

STRATIGRAPHIC AND LOCALITY DATA

Unfortunately, considerable doubt exists about the exact locality of *Compsognathus longipes,* with no apparent way to resolve it. The oldest surviving documentary record of the existence of this specimen, is Wagner's (1861) original description, which describes it as coming from the lithographic shales near Kelheim. A hand-written label glued to the underside of the *Compsognathus* case reads: "Compsognathus longipes Wagner — keine Eidechsen species — aus dem lithographischen Schiefer — im Altmühlthal bei Kelheim". The author of this label is unknown, but in all probability, it was the original owner, a Dr. Oberndorfer, a physician in Kelheim. However, another, more recent printed label gives different information. It reads: "Compsognathus longipes W a g n. — (Orig. Ex. z. Wagn. Abh. Bd. IX T. 3) — Lithograph. Schiefer. — Jachenhausen. Oberpfalz". Jachenhausen is a small village 15 km northwest of Kelheim.

No other records exist in the archives of the Bayerische Staatssammlung to explain these conflicting locality data, or why or by whom the locality Jachenhausen was first used. According to Professor Dehm, the printed label dates from before 1900, possibly during Zittel's time, but the author is unknown. The Oberndorfer collection was obtained by the Bayerische Staatssammlung in 1866, five years after Wagner described *Compsognathus.* Besides the specimen of *Compsognathus,* two other specimens of the Oberndorfer collection have labels with the same handwriting; a turtle *Eurysternum crassipes* and a pterosaur *Pterodactylus kochi.* This suggests that Oberndorfer probably authored these labels. The label for *Eurysternum* also reads "Kelheim".

It is presumed that Dr. Oberndorfer, as an amateur collector, obtained his specimens from a number of different Solnhofen quarries. It may be, that in order to protect his sources from other collectors, he con-

cealed the precise localities under the general description "bei Kelheim", and that the more specific locality of Jachenhausen is the correct locality of *Compsognathus.* But that is not supported by known stratigraphic evidence. Professor Dehm informed me that he attempted to identify the quarry site in the Jachenhausen area from which this specimen might have come. He was unsuccessful on two separate attempts, and reported to me that he was unable to find exposures of Solnhofen strata anywhere in the Jachenhausen area that corresponded with the lithology of the *Compsognathus* slab. Dr. Wellnhofer and I also attempted to re-establish the source of the *Compsognathus* specimen, and checked the large quarries north of the town of Jachenhausen. We also failed to discover any stratum that matched the lithology of the *Compsognathus* slab. Most important, is the fact that we failed to find a single specimen of the ubiquitous crinoid *Saccocoma* (half a dozen specimens of which are preserved on the *Compsognathus* slab) anywhere in the Jachenhausen area. Thus, neither the locality, or the stratigraphic provenance of *Compsognathus* can be determined now. All that can be said is that it came from lithographic facies of the Solnhofen Limestone — probably from somewhere in the Riedenburg — Kelheim area.

In order that this report be as complete as possible, it must be noted that both Marsh (1896) and von Huene (1923, 1925, 1932 and 1956) published that *Compsognathus* came from Solnhofen, but these seem to have been general references to the area in which the Solnhofen strata occur, rather than to the immediate vicinity of the town of Solnhofen. At least there is no surviving original record to substantiate a Solnhofen locality, and it is assumed here to be incorrect. Steel (1970) is the only author to publish the "Jachenhausen locality" as the source of *Compsognathus,* presumably having obtained this information from the printed label with the specimen.

GENERAL DESCRIPTION

The classic specimen of *Compsognathus longipes* is well known, having been repeatedly illustrated and cited in numerous texts, technical papers and popular articles as the smallest dinosaur. Aside from its diminutive size (about that of a small partridge), it is remarkable for the completeness and quality of preservation. Although some regions are crushed, fractured or disarticulated, most of the skeleton is present,

Preserved bone (*Compsognathus*)
Bone impressions
Restored outline
Preserved bone (Small reptile)

30 mm

Figure 1: Camera lucida drawing of the specimen of *Compsognathus longipes*, showing preserved bone and bone impressions, together with my identifications. The parenthetic identifications of the hand elements are von Huene's (1925, 1926) interpretations for comparison with my interpretations of the same objects. The original drawing was made by me with a Wild binocular microscope and camera lucida at a magnification of 3.3. *Abbreviations:* Ac. — acromion; An. Cer. Ri. — anterior cervical rib; Ang. — angular; Art. — articular; Ast. — astragalus; At. Int. — atlas intercentrum; At. L. Ne. — atlas left neural arch; At. R. Ne. — atlas right neural arch; Ax. — axis; Ax. N. S. — axis neural spine; Br. C. — braincase; Ca. 1, 2, etc. — caudal vertebrae; Ca. n. S. — caudal neural spine; Cal. — calcaneum; Car. — carpal; Ce. 3, 4, etc. — Cervical vertebrae; Cer. Ri. 4. — cervical rib 4; Co. — coracoid; De. — dentary; Do. 1, 2, etc. — dorsal vertebrae; Do. Ri. 1, 2, etc. — dorsal ribs; Ep. — epipterygoid; Fe. — femur; Fib. — fibula; Fr. — frontal; Ga. — gastralia; Hu. — humerus; Hy. — hyoid; Il — ilium; In. Den. — inter dental plates; Is. — ischium; Jaw — mandible; La. — lachrymal L. — left; Max. — maxilla; Mt. — metatarsal; Mtc. — metacarpal; Na. — nasal; Pa. — parietal; Pal. — palatine; Pm. — premaxilla; Po. — postorbital; Po. Cer. Ri. — posterior cervical rib; Pt. — pterygoid; Pu. — pubis; Q. — quadrate; Qj. — quadratojugal; R. — right; Rad. — radius; Sa. 3, 4, etc. — sacral vertebrae; Sca. — scapula; Sp. — splenial; Sur. — surangular; Ta. — tarsal; Tib. — tibia; Ul. — ulna; Vo. — vomer; I, II, III, IV, V. — digit number; 1, 2, 3, 4, 5. — phalangeal number.
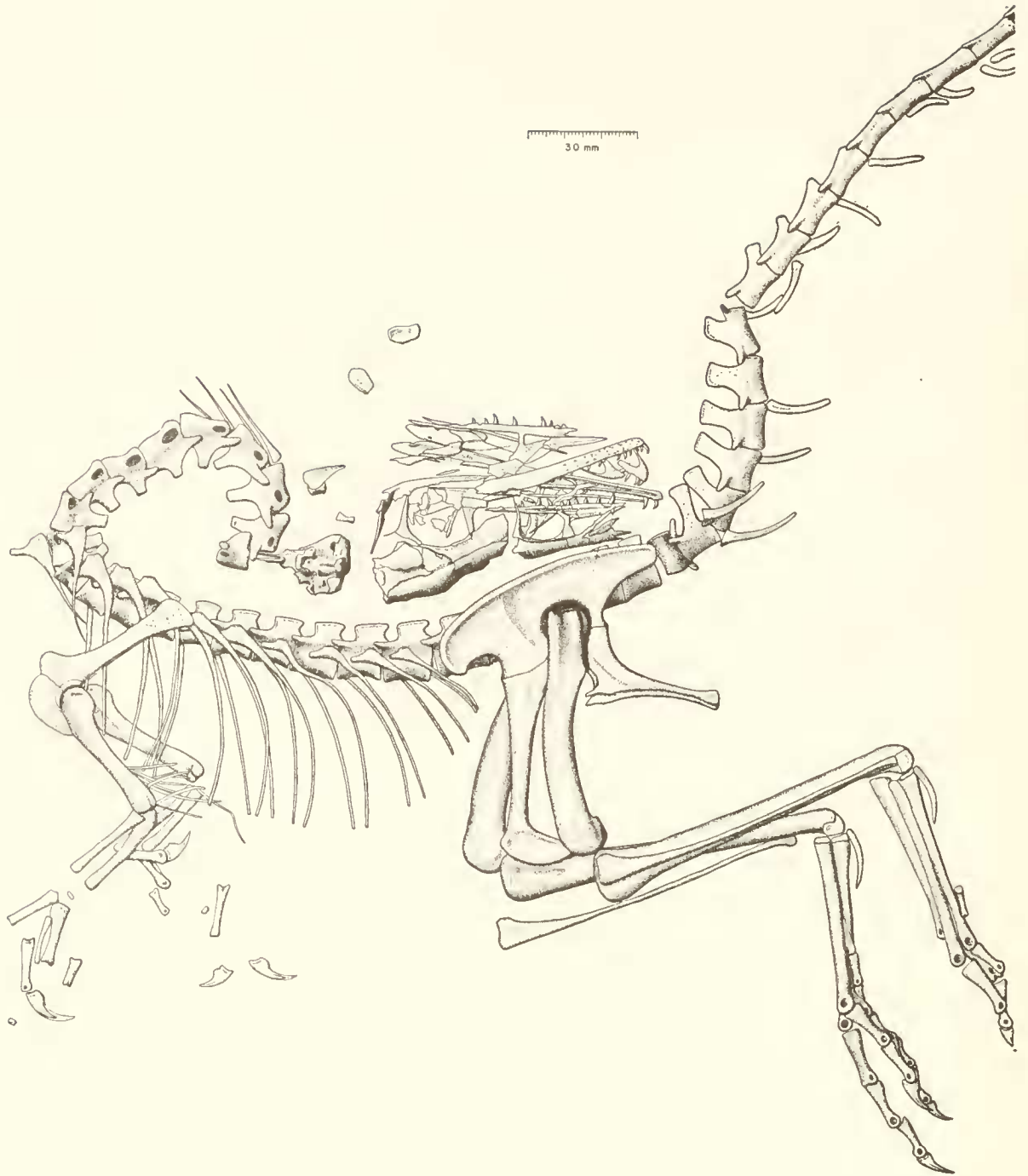
30 mm

Figure 2: Restoration of the skeleton of *Compsognathus* based on the camera lucida drawing of Figure 1.

either as actual bony elements or as impressions. A few areas have been obliterated by calcite crystals, especially in the lower part of the body cavity and the pelvis, or removed by solution. Apparently, the slab was situated close to the surface and subject to solution by sub-surface runoff: the importance of this will be discussed later. In spite of solution and crystallization, most of the bones are finely preserved, apparent-ly completely replaced by calcite with no recrystalli-zation and consequent distortion and loss of detail (see Plate 7.).

The specimen is preserved on its right side almost completely articulated. The only regions that have suffered some disarticulation are the hands, the skull, some of the cervical ribs and the posterior gastralia.

Why these particular regions have been disarranged is difficult to understand, although in the case of the gastralia there is some evidence that the stomach and body cavity were breached — perhaps due to build-up of gases generated within the rotting carcass. The posterior cervical ribs, the slightly displaced right fibula and the scattered phalanges of the hands may have been scattered by scavengers, but more likely they simply were drifted away from their original sites by gentle currents after connective tissues had decomposed.

The most peculiar aspect is its "death pose" — the highly contorted arrangement of the cervical series and the respective positions of the axis, braincase and dermal skull. The cervical column is looped back on itself almost a full 360 degree arc. This opisthotonic condition is not unusual, having been recorded in numerous pterosaur specimens (especially pterodactyloids), small theropods (see, for example, *Struthiomimus altus*, A. M. N. H. 5339, reported in Osborn, 1917, which is preserved in almost exactly the same pose as *Compsognathus*) and modern birds. It seems to be a common occurrence in carcasses of long-necked animals; notice, for example, that it is much less common in rhamphorhynchoid pterosaurs (than in pterodactyloids) and short-necked theropods. The most frequently invoked explanation of this backward distortion of the neck is shrinkage (due to drying) of the dorsal neck muscles and ligaments, particularly the ligamentum nuchae. However, that presumably requires that the carcass initially was exposed to sub-aerial conditions and perhaps even mummified, before being submersed, circumstances that are rejected by Rietschel (1976) for the several specimens of *Archaeopteryx* that are similarly contorted.

Whether or not desiccation is involved, contraction of dorsal muscles and/or ligaments appears to be the most probable explanation of this opisthotonic state. But in the case of *Compsognathus*, we are faced with a curious anomaly: the braincase and skull, to which these ligaments and muscles were firmly attached, are completely separated from the cervical column and each other. The braincase has been displaced backward, by more than its length, from the anterior end of the axis (and rotated 90 degrees about its longitudinal axis), while the dermal skull components have been displaced even further backward, and turned completely around (the braincase faces forward, but the skull faces backward). As one of the largest and strongest ligaments in the body, it seems unlikely that the connection of the ligamentum nuchae to the skull would have disintegrated before most other connective tissues. Yet that appears to be exactly what happened. The entire axial skeleton, except for the atlas and the skull, are preserved in close articulation. How this happened is unknown. There is no evidence

that the head was severed by scavenger action and currents strong enough to displace it surely would have disarranged the skeleton as well.

As for the skeleton itself, it is well formed and gives the impression of a fully developed individual (however, see later comments on this). The skull is relatively very large, a possible indication of immaturity. The neck is slightly shorter than the trunk. The caudal series extend off the end of the slab, so tail length is unknown. But from the very gradual reduction along the proximal caudals, the original tail length must have been more than twice as long as the preserved caudal series. The hind limbs are extraordinarily long and robust, while the forelimbs are of only medium length. *Compsognathus* clearly was an obligate biped and probably highly cursorial.

Cranial Skeleton

Skull.

Most of the skull and mandibles (see Plate 8) are present, but somewhat disarticulated. Certain regions are crushed and sufficiently damaged so as to make reconstruction difficult and uncertain. The fact that so many skull and jaw elements are separated from adjacent bones, while there was relatively little disarticulation in the post-cranium, suggests that either the skull was highly kinetic and very loosely bound together, or that this is a young individual in which the cranial elements had not yet become firmly united. The very small size of the specimen, the seemingly disproportionately long hind legs, and the relatively large orbit, support the juvenile explanation. But the fact that there are no textural differences, or differences in the degree of ossification between dermal and endochondral bones, plus the fact that all vertebral sutures apparently were closed, suggest that we are dealing with a mature individual.

The skull, as I have reconstructed it, is quite long (70—75 mm), very low and with a sharply tapered snout. The orbit was very large and nearly circular. Two antorbital fenestrae are present, one quite large about half the size of the orbit, and the other small. Both are sub-triangular in shape. The external nares were narrow, elliptical, and somewhat elongated. The temporal fenestrae have been obliterated by displacement of some bones and loss of others, but the lateral fenestra appears to have been quite high and narrow from front to back. In general appearance, the skull is most similar to that of *Archaeopteryx*. My reconstruction of the skull is given in Figure 3.

A convenient index of head size is the ratio of skull length to the length of the presacral vertebral column. Using a skull length of 72 mm and a presacral length of 235 mm, the ratio for *Compsognathus* is .30, somewhat higher than most "coelurosaurs", but not
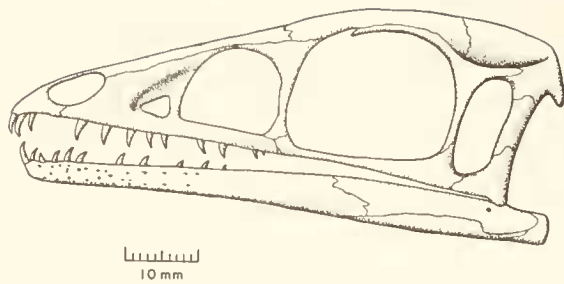
Figure 3: Reconstruction of the skull and jaws of *Compsognathus longipes*. The temporal region is largely hypothetical, as are the sutural details between the maxilla, jugal and lachrymal, the jugal and post-orbital, and the quadratojugal, quadrate and squamosal. The number of teeth shown is the absolute minimum, recording only those that are preserved in place or are indicated by tooth impressions. Empty alveoli due to tooth replacement or post mortem loss cannot be distinguished. The diastema at the premaxilla — maxilla suture is real.

significantly so. This higher ratio might be taken as further evidence that this specimen was immature. On the other hand, it might indicate a close affinity to the larger-headed "carnosaurs". A comparison of skull / presacral ratios in several other theropods with that of *Compsognathus*, is as follows:

Ornithomimus altus (A.M.N.H. 5339) .	.15
Gallimimus bullatus (ZPW-MgD-194 & GIM-DSP 100/11)	.16
Coelophysis longicollis (A.M.N.H. 7224)	.23
Ornitholestes hermanni (A.M.N.H. 619) .	.24
Allosaurus fragilis (U.S.N.M. 4734) . .	.28
Compsognathus longipes (B.S.P. AS I 563)	.30
Deinonychus antirrhopus (Reconstruction, various Y.P.M.)	.35 – .40
Tyrannosaurus rex (A.M.N.H. 5027) . .	.41

Not surprisingly, there seems to be an uninterrupted gradation between so-called "coelurosaurs" and "carnosaurs". Notice that *Compsognathus* has a ratio slightly greater than *Allosaurus*.

P r e m a x i l l a : Both premaxillae are present, displaced and lying between the extremities of the two dentaries. The lateral surface is exposed in both. The premaxilla is roughly triangular in shape, deeply emarginated posteriorly by the large external naris. The nasal process is long and very slender and does not appear to have been overlapped laterally or ventrally by the nasal. The maxillary process (missing in the right premaxilla) is much deeper and more robust. The end of this process is concealed beneath the left dentary, so the nature of the junction with the maxilla cannot be determined. The external premaxillary

surfaces are smooth and devoid of even tiny foramina. Premaxillary teeth number three, with the middle tooth the largest. Two teeth are preserved in place in the right premaxilla and a third lies slightly removed from the empty posterior alveolus. Only the middle tooth is preserved in place in the left premaxilla. A long diastema occurs behind these teeth, the entire maxillary process below the naris being devoid of alveoli. Preserved as they are, lying on their medial surfaces, little can be said about the nature of their mid-line articulation except that it must have been a flexible union.

M a x i l l a : The nearly complete left maxilla is displaced and lies below the rest of the skull and the mandibles. This exposes the inner surface of the less complete right maxilla situated close to its normal position. The maxilla is a rather delicate and thin bone with a surprisingly shallow tooth-bearing ramus. The jugal process seems to have tapered gradually to a very slender process less than 1 mm in depth, for what must have been an extremely weak (or flexible) junction with the jugal. Anteriorly, the maxilla is more robust, indicating a more extensive — and presumably stronger articulation with the premaxilla. The tapered anterior process of the maxilla, like the posterior maxillary process of the premaxilla, seems to have lacked teeth, although neither maxilla is well enough preserved to establish the absence of alveoli. However, it does appear that the upper diastema extended several mm behind the premaxillary-maxillary suture. The entire lower external surface, like that of the premaxilla, is free of foramina.

A thin sheet of bone extends upward from the premaxillary process, apparently forming most or all of the inferior-posterior margin of the external naris, although this region is not clearly preserved here. A small, triangular subsidiary antorbital fenestra is partly preserved here, separated by a robust vertical bony bar from the large sub-triangular antorbital fenestra behind.

The dentition extends over approximately two thirds of the maxilla length, reaching to a position just behind the main antorbital fenestra. The left maxilla still bears 6 teeth, plus 9 or 10 empty alveoli or tooth imprints. The right maxilla contains 5 teeth in situ, plus 6 clear tooth impressions or empty alveoli and 5 possible alveoli. Accordingly, the maxillary tooth count appears to have been 15, and possibly 16. The anterior extremity of the left maxilla shows several small triangular bony plates between some of the empty alveoli: these are interpreted as inter-dental plates.

N a s a l : The nasal bones are represented by several thin fragments and a long impression. The precise shape cannot be determined from these, but the paired nasals appear to have formed a straight, rather

broad and perhaps wedge-shaped, smooth-surfaced plate of bone extending between the premaxillae and the frontals. The contact with the frontals appears to have been squamous. The nasal contribution to the narial posterior border is not known, but it appears to have been small.

F r o n t a l : Much of the dorsal surface of the frontals is well-exposed, these bones having been rotated to lie almost parallel with the bedding plane. This permits an accurate measure of inter-orbital skull width (9.1 mm, minimum). It also shows that the frontals were firmly united, but not fused, along a very straight sagittal suture. The frontal plate is almost flat with only slight longitudinal convexities on either side of the midline, and of moderate thickness, as is shown along the posterior broken edge. The articulation with the parietals is not certain.

One interesting feature of the frontals is the presence of a short forward projection along the lateral margin, forming a unique feature of the superior orbital margin. It is faintly reminiscent of a palpebral or supra-orbital bone, but it projects forward rather than backward, and seems to be in contact with the main body of the frontal. It is well preserved on the right side, but is largely broken away on the left side. On both sides, it seems to have been continuous with the post-orbital, and may have been an anterior expansion of that element into the supra-orbital region. No comparable feature is known to me in other theropods.

P a r i e t a l : The parietals are represented by crushed, thin sheets of bone lying behind the frontals on both sides of the midline, and extensive impressions of their internal surfaces. The latter indicate that the sagittal suture persisted into the parietal area. Although not certified as such, the fronto-parietal union appears to have been positioned just behind the orbit. A slightly raised narrow ridge extends transversely in an irregular line across the large convex fragment of the left side that lies just behind the orbit. This appears to extend from a bone that I have interpreted as the left post-orbital. A corresponding linear feature shows faintly in the matrix impression of the internal surface of the right fronto-parietal. If these indeed are the fronto-parietal suture, it seems to reflect a very firm, solid union of these bones, a condition that is substantiated by the fact that they are preserved together with no apparent displacement and little distortion. That is in contrast to the disarticulated and displaced occurrence of most other cranial elements.

L a c h r y m a l : Both lachrymals are preserved close to their natural positions, but both are damaged sufficiently to preclude full description. The lachrymal appears to have been I-shaped, with a stout vertical shaft forming a narrow pre-orbital bar between the orbit and the antorbital fenestra. The upper and lower extremities seem to have been expanded, probably for firm union with the maxilla (and jugal?) and the nasal-frontal complex. Some or most of the upper expansion may have been composed of the pre-frontal, but this cannot be established. There is a distinct sutural facet on the inferior anterior edge of the left frontal, which I interpret as the articular facet for the pre-frontal.

P o s t o r b i t a l : This bone is easily recognized by its T-shape. Only the left has been identified here, forming the posterior margin of the orbit, slightly separated from the fronto-parietal. It appears to be a relatively thin sheet of bone with wedge-shaped anterior (frontal) and posterior (squamosal) processes above. The inferior process tapers gradually to an indeterminate articulation with the jugal.

J u g a l a n d Q u a d r a t o j u g a l : Neither of these bones has been identified with certainty, and apparently are lost, concealed beneath other bones, or so damaged as to be unrecognizable.

S q u a m o s a l : In all probability, the fragments overlying the postero-lateral region of the left parietal, represent what remains of the left squamosal. That is far from certain, though, as these fragments are so severely damaged that no details are discernible.

Q u a d r a t e : At the rear of the skull is a thin vertical lamina of bone which I interpret as the posterior part of the internal half of the left quadrate. The external half is missing. The upper extremity of this lamina ends in a broken surface and the lower part is concealed by the adjacent left pterygoid. If correctly identified, this portion of the quadrate is surprisingly slender and delicate, but the external part of the quadrate shaft must have been much more robust. Situated in the anterior part of the left orbit is an L-shaped fragment which may be part of this missing half of the quadrate, and perhaps part of the quadratojugal. The "ascending" shaft of this L-shaped fragment is quite stout and appears to have been either L, or C-shaped in cross section. The lower part is overlapped by a very thin sheet of bone (with broken edges), which may be the left quadratojugal.

P t e r y g o i d : The left pterygoid is conspicuous below the orbital and temporal regions, extending, forward from the quadrate to pass beneath the left dentary. The distinctive feature is the deeply concave cotylus of the basipterygoid articulation. Forward of this, the palatine ramus is straight and quite narrow, with a broadly convex ventral surface. Further anteriorly, this appears to expand in a broad, slightly concave bony sheet, but the lateral margin is not preserved. The medial margin is intact, though, showing that an interpterygoidal vacuity existed over most or all of the length of the pterygoids. Behind the basipterygoid articulation, the quadrate ramus extended

postero-laterally as a relatively high thin lamina at an angle of about 30 degrees to the palatine ramus. Unfortunately, the posterior extremity is missing.

The right pterygoid is not identifiable with certainty, but the several fragments in front of the quadrate-quadratojugal fragment, and in the orbit itself, probably represent remains of that element.

E c t o p t e r y g o i d : Not recognized.

E p i p t e r y g o i d : This element has rarely been reported in theropods, and its presence in *Compsognathus* is open to serious question. It is mentioned here only because one small bone closely associated with the skull and braincase, resembles the epipterygoids reported by Madsen (1976) in *Allosaurus*. It must be emphasized that this is an extremely tenuous identification. The bone in question is preserved between the cervicals and the left quadrate, just above the braincase. The preserved portion flares slightly to a gently convex oval surface which apparently was an articular surface. The opposite end, preserved as impression in the matrix, flares into a broad (thin ?) sheet of bone which terminates in a nearly straight edge. If this is indeed an epipterygoid, the latter must be the pterygoid process and the oval articular surface is for articulation with the laterosphenoid.

P a l a t i n e : Indeterminate.

V o m e r : Not recognized, with certainty.

B r a i n c a s e : The braincase is situated between the dermal skull on one side and the anterior cervical vertebrae on the other, completely separated from both. This peculiar circumstance has been noted by others, especially by Nopcsa (1903). It suggests a possible violent severing of the head from the neck, except for the fact that all components are preserved very close together.

Certain features of the braincase are clearly recognizable, but in other places it has been severely damaged and some bones are missing. Thus, the endocranium is not easily or fully interpreted. In addition, those regions that are recognizable, for the most part do not correspond closely with those of other theropods. Again, it is difficult to establish whether these differences are real, or due to damage and missing parts. (See Plate 9:1.)

In general, the endocranium is widely triangular in its ventral aspect, very broad behind at the occiput and tapering abruptly forward. The original width across the paraoccipital processes exceeded 16 mm and the basioccipital-basisphenoid length is about the same. Total preserved length of the basioccipital-basisphenoid-parasphenoid complex is 24.5 mm. Aside from the broad triangular form, the other distinctive aspect of this braincase is the nearly perpendicular relation between the ventral surfaces and the occiput.

The occipital condyle and the foramen magnum are the most obvious features. The condyle, however, is distinctly not theropod-like, being kidney-shaped rather than nearly spherical. The transverse width of the condyle is more than twice the sagittal dimension. Sutures clearly show that the lateral portions are formed of the exoccipitals, but the largest part is basioccipital. The exoccipitals do not meet in the mid-line, thus the basioccipital forms the ventral floor of the foramen magnum, as usual. The original shape and size of the foramen magnum are uncertain because of possible crushing and broken bone edges adjacent to the foramen, but it appears that it was much larger than the condyle, and perhaps oval in shape, with the transverse dimension the larger. If correct, these also are not typical of theropods, where the foramen is usually nearly circular and much smaller than the condyle. The dorsal margin of the foramen is formed by a smooth, transversely convex, sheet of bone that must be the supraoccipital. The upper part is concealed in matrix, but the height of this bone above the foramen magnum is at least 5 mm, which indicates that the foramen and condyle were positioned quite low on the occipital surface. The supraoccipital is oriented almost perpendicular to the basioccipital — basisphenoid surface.

Lateral to the condyle, several fragments of bone represent portions of the paraoccipital processes. No suture is evident separating the exoccipital and opisthotic. Although Nopcsa (1903) described this region as pierced by many foramina, as in birds, it is so fractured and damaged that only one doubtful foramen can now be recognized. I agree with Nopcsa, however, that this region is bird-like in its position and orientation. It lies almost entirely in the plane of the basioccipital-basisphenoid complex, although there is a dorsal expansion of unknown dimension more or less in the plane of the foramen magnum.

Anterior to the condyle, much of the basioccipital and basisphenoid have been lost, leaving only impressions of their internal surfaces. The impression shows that the floor of the endocranial cavity, at least in the region of the basioccipital, was traversed by a low sagittal ridge extending forward from the foramen magnum. A similar feature is present in some birds, but I am not aware of such a feature in other theropods, or in reptiles in general. In fact, very often there is a slight mid-line groove in the basioccipital and basisphenoid, which marks the position of the basal artery.

Anterior to this region are paired, but no longer symmetrical, lateral flanges that appear to have been crushed down onto the ventral surface of the braincase. These are quite prominent and apparently projected well below the endocranium. The most likely

interpretation of these structures is basipterygoid process of the basisphenoid. Nopcsa (1903), interpreted much smaller lateral projections further forward as the "pterygoid apophyses", but their position at the posterior end of the cultriform process of the parasphenoid, makes that interpretation unlikely.

Nopcsa (1903) puzzled over the paired, near-vertical longitudinal laminae at the anterior extremity of the braincase, postulating that they might be the pterygoids, palatines or the vomer. He finally decided, with some reservations, that they were the palatines. However, these laminae are unquestionably continuous with the other ventral elements of the braincase, and therefore cannot be any of the bones Nopcsa considered. Because of its double condition, Nopcsa was correct when he ruled out the presphenoid (which is rare in reptiles anyway). But it is quite obvious to me that these two lamina, which join in the mid-line, form the cultriform process of the parasphenoid, which normally is a double structure with an inverted V-shaped section.

Portions of the lateral wall of the braincase are present, and have been well-prepared (undoubtedly with great difficulty because of the narrow space between the braincase and other nearby elements). On the left side, there are two distinct foramina, piercing a slightly concave bone which I interpret to be the prootic. The larger foramen probably is the fenestra ovalis, and immediately anterior to it, a similar-sized foramen I take to be the trigeminal foramen. If correctly identified, the latter foramen must mark the approximate junction between the prootic and the laterosphenoid, but no suture is evident.

Mandible.

Both lower jaws are present, but disarticulated and slightly displaced. The most distinctive aspect of the mandible is its extremely slender form with nearly parallel upper and lower margins. No evidence has been recognized to indicate the presence of a coronoid process or of an external mandibular fenestra. Since all three of the lateral mandibular elements are nearly complete, I conclude that this fenestra probably was not present in *Compsognathus,* as is the case in *Ornitholestes.* However, the matter is beyond proof.

D e n t a r y : The dentary is long and surprisingly slender, with nearly parallel upper and lower margins. It deepens slightly toward the rear. Externally, it appears to have been slightly convex dorso-ventrally. In its anterior part, the external surface is pierced by a large number of very fine pores, many of which are arranged in two parallel rows, an upper row just beneath the alveolar margin and a lower row close to the inferior margin. Other foramina are scattered in between. The upper foramina do not seem to coincide with tooth alveoli, either in number or position. The medial surface of the right dentary reveals a deep and very prominent Meckelian canal, bordered above and below by stout ridges. Much or all of this canal presumably was covered by the splenial, but there are no distinct articular scars for this bone, except posteriorly near the end of the dentary. Thus, it is possible that the Meckelian canal was open anteriorly. The symphysis is quite short, and appears to have formed a relatively loose or flexible union between the two mandibles. Tiny interdental plates are present between alveoli along the entire inner side of the tooth row. These occur as separate wedges of bone at each interalveolar position.

The tooth row, as measured on the left dentary, is quite long (26.2 mm), perhaps slightly longer than the maxillary row. There are 11 teeth preserved in place (or slightly dislocated) in the left dentary and seven empty alveoli. The right dentary has 16 empty sockets, plus two anterior teeth in place. Thus, the dentary tooth count is 18, which is one of the higher counts among theropods, exceeded only by that of *Coelophysis* (25) among theropod taxa known to me.

S p l e n i a l : These elements are questionably identified here (see Fig. 1), largely on the basis of their location and shape. They are preserved as thin sheets of bone or impressions which indicate a rather long and narrowly tapered bone. The shape and dimensions correspond approximately with those of the posterior part of the Meckelian canal. Both elements are located close to the dentaries — apparently lying in between them. One (the left ?) overlies the upper ramus of the left maxilla and the other (the right ?) seems to lie beneath that maxilla.

S u r a n g u l a r : Both surangulars are easily recognized lying side by side next to the left maxilla. Both bones show the external surface, the right surangular having been turned over. The surangular foramen is evident in both. Also clearly preserved in the right surangular is the articular cotylus for the distal end of the quadrate. The position of this cotylus clearly establishes that the retroarticular process was quite long (more than 5 mm) and the articular may have extended beyond the surangular extremity.

The external surface appears to have been almost planar. Dorsally, a stout angulation separates the lateral and dorsal surfaces, as in most other theropods, so they are oriented nearly perpendicular to each other. A faint antero-posterior ridge parallels the lower margin, marking the upper boundary of the articulation surface for the angular.

A n g u l a r : The left angular, incomplete, lies immediately adjacent and parallel to the left surangular, only slightly removed from its articulation with

that bone. Most of the lateral lamella is missing, but part of its original shape can be determined from the articulation scar on the surangular. Extending back from this is a very slender, slightly tapered process which articulated with the lower edge of the surangular all the way to its posterior extremity. Thus the retroarticular process was constructed of at least three elements, the surangular and angular in addition to the articular. The right angular possibly is represented by two fragmentary sheets of bone that overlie the right surangular, but no distinctive features are preserved. The form of the anterior end of the angular is not known, but presumably it overlapped the posterior end of the dentary in a squamous articulation.

Prearticular: Not recognized.

Articular?: Two sub-rectangular bones, which at first glance look like dermal scutes, lie one to two cm away from the two surangulars. Their identity cannot be verified, but I believe them to be the two articulars. My belief stems from their preserved location close to the surangulars, their size and shape, and the fact that there are two of them and they are paired. Although they seem to have slightly different shapes, perhaps due to differential crushing and somewhat different positions in the matrix, the exposed surfaces clearly are mirror images of each other. If my identification is correct, the exposed surface is the surangular or external surface. Each bone shows a prominent ridge which bifurcates into two lesser ridges at one end. This feature divides the exposed surface into two unequal areas, the larger of which I interpret as the articular surface for the surangular. The smaller surface is probably for the posterior process of the angular (see Plate 10:3).

Dentition.

Stromer (1934), presented a detailed description of the dentition of *Compsognathus*, together with a summary comparison with the teeth of selected other theropods. There is little that can be added to Stromer's study and what follows here is in part taken from his work, in order that this study of *Compsognathus* be complete.

As noted elsewhere in this report, the tooth count for *Compsognathus* is $\frac{3+15 \text{ or } 16}{18}$. Stromer (1934) gave it as $\frac{3+15+}{18}$, but it looks to me as though there might have been 16 tooth positions in the maxilla. Upper and lower teeth are quite similar at equivalent positions in the tooth rows, but there is gradational change in tooth morphology and size along the tooth rows.

The premaxillary teeth, and the anterior teeth in the dentary, are long and slender, tapering gradually to sharp points. The lower two thirds of the crown is straight, but the tip is bent sharply backward at an angle of 30 to 40 degrees. The crown is nearly circular or slightly oval in section, with the transverse diameter slightly greater than the longitudinal dimension. The crown is completely devoid of serrations or carina. The first premaxillary tooth appears to have been slightly procumbent, but probably not as sharply as Stromer (1934) illustrated.

The first two or three dentary teeth (Plate 9:2) are almost exactly the same as the premaxillary teeth, both in size and shape, and the first is slightly procumbent like its counterpart above. The next three or four teeth are similar, but instead of the sharply bent tip, the entire crown curves backward in a continuous curve. These teeth also lack a serrated edge, but where the forward-most dentary teeth are slightly compressed in their anterior and posterior surfaces, these are slightly compressed latero-medially, so that the greatest crown diameter is longitudinal. There is slight variation in size among these teeth as well. The remaining posterior dentary teeth become progressively smaller (shorter) and more compressed transversely, toward the rear of the tooth row. These posterior dentary teeth also become progressively less curved toward the back, becoming more nearly triangular in lateral profile, the rear edge being almost straight and perpendicular to the dentary with the anterior surface curving, gently back to meet it at the apex.

With only a few maxillary teeth well preserved, it is difficult to reconstruct the complete nature of the upper dentition. However, those that are present seem to parallel the posterior dentary teeth in form and size, becoming progressively shorter and less curved toward the back. And like their dentary counterparts, they are also laterally compressed and oval in section, with short serrated posterior carinae.

It is not possible to say very much about tooth replacement because so many teeth are missing. There are at least eight loose teeth scattered around the jaw elements, and numerous impressions of now missing teeth occur along all tooth rows. The left dentary perhaps gives the best evidence of the replacement pattern. Eleven teeth are present, six of which are crowded together in the anterior-most region (7 mm). The remaining five teeth are somewhat irregularly spaced over the next 18 mm of the tooth row. No indisputable tooth impressions are present at the now empty alveoli of the left dentary, so the existing eleven teeth still in situ represent the minimum number of functional dentary teeth when this specimen was buried. There could have been more. The overall distribution of these eleven remaining teeth is as follows: × × × × × × O O × O × O O × O × O × (where "O" is an empty socket and "×" a tooth in place). As we might have expected, this pattern suggests tooth replacement at alternating positions.

Hyoid Apparatus.

Hyoid elements have been recovered in a number of dinosaurs, but in most instances these have been ornithischians. Marsh (1896) and Gilmore (1920), reported the presence of possible ossified hyoid bones in *Ceratosaurus nasicornus* (U. S. N. M. No. 4735), and I recall seeing what appeared to me to be possible hyoid elements in some of the American Museum specimens of *Coelophysis longicollis*. With these exceptions, the hyoid apparatus appears to be unknown in theropods. For that reason, the identification of possible hyoid bones in *Compsognathus* must be considered as very tentative. But the two bones in question do not fit any other alternative skull element.

In so far as can be seen from their shapes, size and lengths, they are the same, and thus appear to have been paired. Both are very long, slender and straight bones nearly 30 mm long. One is located between the right dentary and maxilla, extending parallel to those two tooth rows. Imprints of maxillary teeth are pressed into it, indicating that it lies beneath (external to) the maxilla. The second one overlaps (lies external to) the left maxilla at a slight angle to its tooth row. Both of these objects are parallel-edged, flat ribbon-like bones, as preserved, but they may have been rod-like and only flattened after burial by sediment compaction. I doubt this, though, because similar-sized ribs in this specimen do not show a comparable degree of flattening. The fact that both bones seem to lie external to the maxillae is troublesome, since the hyoid apparatus in life is situated between the mandibles, and thus lies inside, or medial to, the maxillae. How they b o t h could have been displaced to lie outside of the maxillae, is the critical question against their being hyoid elements. But, in view of the disarticulation and dislocation of many other skull elements, that identification is not precluded, and on morphological grounds it seems most probably correct.

Axial Skeleton

Vertebral Column.

The vertebral column is complete, except for an unknown number of caudals distal to the fifteenth, and two segments in the dorso-sacral region that are represented only by impressions. The pre-sacral count totals 23, and the pre-sacral length approximates 23.6 cm, of which less than half (10.5 cm) is cervical length. There are 10 cervicals, 13 dorsals, 4 sacrals and more than 15 (probably more than 30) caudals.

C e r v i c a l v e r t e b r a e : The cervical series consists of 10 segments, including the atlas, and is complete, although not all of the atlas has been recognized. Von Huene (1908) reported 12 cervicals and 11 dorsals, without giving any detailed explanation, but later (1925) he specified 10 cervicals and 13 dor-

sals[3]). As noted previously, the neck is highly arched backward, with the atlas and skull separated from the cervicals. Only the intercentrum of the atlas has been (questionably) recognized here, together with two thin fragments that I suspect might be the atlas neurapophyses, (see Fig. 1). No sign of the odontoid has been detected. The atlas intercentrum is situated in the area between the skull, braincase and anterior cervicals, with its posterior and ventral surfaces exposed. The posterior surface is gently convex transversely, and strongly convex dorso-ventrally. The ventral surface is also convex transversely, but slightly concave longitudinally. Its upper part is concealed by a thin triangular sheet of bone (the right atlas neurapophysis ?), so that part of the intercentrum cannot be determined, but presumably it was strongly concave so as to fit beneath the odontoid. The transverse width of the intercentrum (4.45 mm) is the largest dimension and is close to that of the occipital condyle (4.6 mm). Little can be said about the questionable neurapophyseal fragments, except that they are very thin, concavo-convex, triangular sheets of bone with original lengths of something more than 10 mm.

The axis is situated just to the left of the braincase and slightly removed from the third cervical. I am not certain, but there appears to be a very thin axis intercentrum fused to its anterior end. The axis centrum is distinctly shorter than those of succeeding cervicals, but like all the following cervicals, it is marked by a conspicuous small oval pleurocoel in its anterior lateral surface. The axis centrum also is slightly opisthocoelous. The neural arch is damaged, but appears to have been long and of moderate height.

Although the quality of preservation varies from one segment to another, the remaining eight cervicals appear to have been quite similar to each other. The centra increease in length to a maximum of 12.7 mm for the sixth and seventh segments, then length diminishes progressively to 10.9 mm for the ninth and tenth. All cervicals are strongly opisthocoelous and centra are narrow-waisted with laterally facing, anteriorly placed pleurocoels. The neural arches are all severely damaged and difficult to interpret, but they appear to have been relatively low, long and massive, with stout zygapophyses. No diapophyses could be identified, although the double-headed design of the cervical ribs clearly establishes their original existence. Similarly, no cervical neural spines have been recognized.

D o r s a l v e r t e b r a e : In many instances, it is difficult to select a distinctive point of separation between the cervical and dorsal vertebrae, and in most cases it is decided on the basis of arbitrary features.

---

[3]) Von Huene's thirteenth dorsal, in fact, turns out to be the twelfth, a point that is discussed later.

The present specimen is no exception. I selected the point between the tenth and eleventh presacrals as the most appropriate place because there is a distinct change in the morphology of the ribs here and, although the preservation does not permit an absolute statement, there appears to be a change in vertebral morphology here as well. Although badly crushed and fractured, the eleventh presacral is much shorter (9.9 mm) than the tenth (10.9 mm). Also, the eleventh presacral seems to be the first in the series that lacks pleurocoels, although the crushed state of the centrum does not allow an unqualified statement on this. Most of the succeeding presacrals clearly are without pleurocoels. Finally, the rib (impression) adjacent to the eleventh presacral is more robust, although not much longer, than the preceeding cervical ribs and bears a well-defined, long-shafted capitular process like those of the succeeding thoracic ribs. On these criteria, there are 13 dorsal vertebrae, the last two of which are indicated only by impressions.

The second dorsal vertebra has a length of 9.4 mm, slightly shorter than the first, perhaps the result of distortion, whereas the rest have lengths very close to 10 mm. The centra appear to have been elongated, slightly narrow-waisted, spool-shaped structures. They are either amphiplatyan or slightly platycoelous. Because of the crushed state of many vertebrae, and the superimposed dorsal ribs, no sign of parapophyses or facets for the capituli are discernible. Even more surprising, in view of the widely separated capitulum and tuberculum of the dorsal ribs, is the apparent absence of prominent transverse processes.

The neural arches are all long and low, with stout zygapophyses. The neural spines also are low, rising less than 3 mm above the arches, but long — ranging from 7 to 9 mm in longitudinal dimension. These spines are situated at the rear of each segment, and in most instances overhang the anterior part of the succeeding vertebra. Anterior neural spines are nearly rectangular in shape, but posteriorly they become somewhat fan-shaped. All the dorsal spines have slightly thickened anterior margins (suggestive of well-developed interspinous ligaments), as well as lateral surfaces with distinctly sculptured texture. The latter may reflect muscular attachment, presumably slips of the M. lattisimus dorsi.

The zygapophyses are short, but stout and situated well above the centra. The postzygapophyses are positioned directly below the posterior margin of the neural spine, whereas the prezygapophyses project far forward of the neural spine. Because all zygapophyses are poorly preserved but still in close articulation, it is not possible to determine the attitude of the articular facets. Most probably, though, they were slightly inclined toward the mid-line.

A curious and inexplicable problem exists concer-ning Huene's (1925 & 1926) tally of the dorsal vertebrae. After concluding that there were ten cervical vertebrae, he then noted that these are followed by 12 dorsal vertebrae in front of the ilium and the neural process of the 13th is still to be seen above the anterior tip of the ilium. He then stated that five sacral vertebrae must follow this last. In other words, according to von Huene, the "neural process above the tip of the ilium" is the 23rd presacral segment, including an undetected atlas. According to my count, that same neural spine is the 2 2 n d presacral vertebra. I count the impression behind that "neural spine above the tip of the ilium" as the 13th dorsal, largely on the grounds that it (like its predecessor) is missing, and not preserved co-ossified with the sacrals behind. This last segment, von Huene obviously counted as one of his "five" sacrals, but that in no way explains how he counted 23 segments in front of this segment.

The relatively long and slender centra of the dorsal vertebrae, and the fan-shaped neural spines are unique among theropods, although a variety of "coelurosaurs" (i. e., *Coelophysis, Aristosuchus, Coelurus,* and to a lesser extent, ornithomimids) have moderately elongated dorsal vertebrae.

S a c r a l   v e r t e b r a e : The sacrum, unfortunately, is entirely obscured by solution, overlying portions of the ilium and femur, and growth of secondary calcite crystals. Consequently, nothing can be said about the morphology of the sacrum, or the sacral number with absolute certainty. However, using the lengths of the last dorsal, of about 12 mm (for the thirteenth dorsal by my count) and the first complete caudal preserved (the second caudal by my interpretation) of 11 mm, as indices, the sacrum probably consisted of only four segments, rather than five as von Huene (1908, 1925, 1926, 1932) and subsequent authors have cited. Unless the sacral segments of *Compsognathus* were much shorter than adjacent vertebrae in front and behind, the space available (41 mm) in this specimen simply is too short to have contained five sacral vertebrae. Yet, I cannot prove that the sacral number was four rather than five. Two vertebrae are missing (although preserved poorly as impressions) at the dorsal — sacral "junction", as was noted above. Their absence suggests that they were not co-ossified with the segments behind, and therefore are best considered as the 12th and 13th dorsals. Two co-ossified centra are partly visible behind the acetabulum. These are interpreted here as the 3rd and 4th sacrals (on the dimensional grounds listed above). The next vertebra behind is displaced, turned almost 90 degrees to the sacral and caudal series, and thus clearly not co-ossified with the sacrum. I assume this to be the first of the caudal vertebrae.

C a u d a l   v e r t e b r a e : The caudal series is represented by 16 segments, the last seven of which are only impressions. The centra of the proximal caudals are strikingly similar to the dorsal centra; long, slender, slightly narrow-waisted, spool-shaped elements. There are no pleurocoels, and no transverse processes — not even on the most anterior segments. This last feature, is a most unusual condition, and raises questions about the organization of the tail musculature and the function of the tail. It is not certain, but the preserved centra all appear to be amphiplatyan. The centra become progressively longer distally, with the last preserved vertebra (the tenth), the longest. This suggests a very long tail.

All neural arches have been destroyed by a large fracture which follows the course of the caudal series. The neural spines on the first few caudals are taller and narrower (shorter in the anterior-posterior dimension) than those of the dorsal vertebrae, but still are fan-shaped and erect. At the seventh caudal, the neural spine is inclined slightly backward, and succeeding spines slope progressively further backward and are successively shorter until at the tenth caudal only a low nubbin remains.

C h e v r o n s : Chevrons are present throughout the preserved portion of the caudal series. The first is preserved in place between the second and third caudals. All are similar in form and size, with very little apparent progressive diminution distally. They are slender, parallel-edged and slightly curved bones that taper only very slightly toward their extremities. The fact that the most distal chevron preserved (the tenth) is not much shorter than the first, suggests that the tail was unusually long and that the preserved part represents only a small fraction — perhaps less than a third — of the original tail length. This is supported by the relative sizes and lengths of the last preserved caudals and the proximal elements. On the other hand, the complete absence of transverse processes on the caudals could be interpreted as evidence of a relatively short tail, but I consider that unlikely.

Dorsal Ribs.

C e r v i c a l   r i b s : A total of 14 cervical ribs can be identified about the slab. Four of these clearly are paired and situated adjacent to the ventral surfaces of the fifth and sixth cervical vertebrae, presumably close to their natural positions. These seem best interpreted as the ribs of the fourth and fifth cervicals, in view of the fact that there are no ribs closely associated with the next five vertebrae and there are ten similar ribs scattered about in the area of the neck (see Fig. 1). From this scattered occurrence, it is obvious that the cervical ribs were free. All cervical ribs feature broad, triangular proximal portions with widely separated capitular and tubercular heads.

Posteriorly, they taper abruptly into long (up to 30 mm or more), hair-like filaments (diameter, 0.2 mm or less). The anterior-most ribs are less delicate and are straight, whereas those that are scattered about (and have been attributed to the posterior cervical segments) are very delicate and distinctly curved. Presumably, this curvature reflects a degree of "permanent" natural curvature of that part of the neck.

T h o r a c i c   r i b s : One or both members of eleven pairs of thoracic ribs are discernible, either as fragments of bone, or as impressions. In most instances, only the proximal third or half is present, the distal portions having been broken away or obscured by crystal masses in the lower regions of the body cavity. A few fragments of distal portions (fourth and fifth ribs of the left side) indicate the approximate complete length of some. All were double headed, with the tuberculum and capitulum widely separated, the latter at the end of a long narrow process. The rib shafts are slightly curved, tapering abruptly proximally to a nearly uniform thickness over half or two thirds of rib length. The distal third tapers very slightly. The shafts appear to have been oval in cross section and perhaps hollow, since nearly all preserved ribs have collapsed due to compaction into a figure 8 cross section.

Gastralia.

A number of small rod-like bones adjacent to the humerus represent part of the gastralia cuirasse, and marks the position of the ventral surface of the body. Additional displaced gastralia are scattered close to the knee. These last suggest that the ventral body wall ruptured, perhaps due to decomposition gases built up within the body cavity. Further evidence of that is the isolated tiny lower jaw preserved together with these displaced gastralia elements, that presumably belongs to the small skeleton within the body cavity of Compsognathus. None of these elements are complete, so original shapes and lengths are indeterminate. Some of them are more than 15 mm long, most are cylindrical or slightly compressed and nearly all are curved, either uniformly or variably. Most elements seem not to have been symmetrical, suggesting that most were lateral (but not necessarily paired) components of a two (or three) rowed structure, perhaps similar to the arrangement illustrated by Lambe (1917) and Gilmore (1920). A few fragments look as though they might have been symmetrical, and thus components of a median row of gastralia. The ventral body wall region has been disturbed by solution and crystal growth, so it is not possible to reconstruct accurately the original arrangement or dimensions of the gastralia cuirasse. It is presumed to have extended from near the sternal region close to the pectoral girdle back close to the distal extremity of

the pubis, but there seem to be far too few elements preserved here to form such a long structure. The gastralia close to the humerus seem to be little disturbed, showing that this region was sheathed ventrally by these dermal bones. The displaced gastralia back close to the pubis suggest, but certainly do not prove, that they may have extended this far back.

Appendicular Skeleton: Pectoral Girdle and Forelimb

Both forelimbs and the pectoral girdle are incompletely represented by impressions and partial or complete elements. Despite being incomplete, most of the important features are discernible. In contrast to the hindlimb, the forelimb total length is quite short, little more than one third (approximately .37) the hindlimb length, unusually short for a "coelurosaur". The forelimb is moderately robust, though.

Pectoral girdle.

As with the pelvis, portions of the pectoral girdle are completely missing or concealed and other parts are represented only by impressions. Only the upper portions of the scapulae and the anterior margins of the coracoids are preserved. Consequently, the morphology of the complete shoulder girdle cannot be reconstructed.

S c a p u l a : The scapular blade was a very thin, narrow sheet of bone slightly expanded at its dorsal extremity. In the lower part, the blade was somewhat thicker and parallel-edged. An impression of the lower part of the right scapula shows a distinct convex dorsal margin which, from its shape and location, is interpreted here as the acromion. If that is correct, Compsognathus possessed an unusually large acromion for a theropod. Presumably, this reflects the one time existence of relatively large deltoideus musculature, which would correlate with the robust construction of the forelimb.

C o r a c o i d : Situated at the upper end of the humerus, and lying beneath it, are two very thin, sheet-like fragments of bone. The anterior margins of both are alike and uniformly convex. The margin of the underlying right fragment appears to be continuous with a curved impression margin that extends dorsally and meets the anterior extremity of the acromion mentioned above. This junction presumably marks the position of the coracoid — scapula suture, as in most theropods. Unfortunately, nothing can be determined about the posterior or lateral portions of the coracoid, but what is preserved indicates a relatively large semi-circular anterior portion. The glenoid is completely unknown.

Forelimb.

H u m e r u s : Only the left humerus is present, the right being represented only by an incomplete impression. Unfortunately, the proximal 10 to 20 per cent of the humerus is missing, so no information is available about the nature of the proximal articulation, the deltopectoral crest, or humeral length. I estimate the original length to have been 38 to 40 mm, but it might have been as great as 45 mm. Von Huene (1932) estimated a maximum length of 52 mm, but that seems excessive. In non-tyrannosaurid theropods, the radius ranges from two thirds to three fourths of humeral length. On the basis of the radius length in Compsognathus (24.7 mm), the humerus should have been between 32.8 and 36.9 mm long. I suspect it may have been slightly longer. The shaft was hollow (it is now crushed almost flat), straight and probably nearly cylindrical. No details pertaining to the distal condyles, which face down into the matrix, can be determined, but the preserved conformation of the crushed posterior surface suggests that the radial condyle (as usual) was larger than the ulnar condyle. Contrary to von Huene's (1925) remark that the processus lateralis extends two thirds of the length of the humerus[4]), the deltopectoral crest seems to have been quite short. Its preserved length is less than 8 mm (out of a preserved humeral length of 33 mm). This is relatively short compared with other theropods where the deltopectoral crest usually approximates one third of humeral length (much less in ornithomimids), but in no instance that I am aware of, does it reach two thirds. However, in the absence of the proximal end of the humerus, it is quite possible that the deltopectoral crest of Compsognathus was of normal proportions.

R a d i u s a n d U l n a : The radius and ulna are straight, slender bones with slightly expanded proximal and distal extremities — especially the proximal end of the ulna which bears a prominent olecranon. Both bones were hollow and seem to have been nearly circular in cross section. No details of the articulations can be seen. As shown in the table of dimensions, the radius is significantly shorter than the ulna, underscoring the prominence of the olecranon. In fact, relatively speaking, I am not aware of such an elongate olecranon in any other theropod. This must have provided unusual leverage for the M. triceps brachii for quick or powerful extension of the forearm, but it is not clear what adaptive significance this might have had.

C a r p u s : Curiously, the left manus is preserved separated from the radius and ulna by a gap of more than 6 mm, within which there is no evidence of any carpals. At first glance, this gap might be interpreted

[4]) Von Huene's statement is here attributed to the possibility that he misinterpreted the anterior portion of the right coracoid (see Fig. 1) as the left deltopectoral crest, but this thin sheet of bone is clearly separate from the humeral shaft, which in fact, overlies it.

TABLE 1

Measurements (in mm) of *Compsognathus longipes.*

Skull length	70—75 est.
Skull width	20 est.
Skull height	30 est.
Orbit length	19 est.
Orbit height	15 est.
Antorbital fenestra	11.8

	Left	Right
Dentary length	42.9	
Surangular length	29.9 +	29.8 +
Scapula length	38 est.	
Humerus length	38—40 est.	
Radius length	24.7	
Ulna length	28.5	
Mtc. I length	17.6	
Mtc. II length	13.95	
Mtc. III length	13.1	
Phalanx I—1 length	7.7	7.8
Phalanx I—2 length	9.6	9.7
Phalanx II—1 length	14.5	14.45
Phalanx II—2 length	10.4	10.4
Femur length		67 est
Tibia length	87.7	87.6
Fibula length		82.1
Pubis length	60 est.	
Ischium length	40 est.	
Mtt. I length		9.7
Mtt. II length	48.8 ?	50.4
Mtt. III length	56.0	55.95
Mtt. IV length	51.8	
Mtt. V length	16.0	15.9
Phalanx I—1 length	8.7	8.8
Phalanx I—2 length		4.5 +
Phalanx II—1 length	14.2	14.3
Phalanx II—2 length	13.7	13.65
Phalanx II—3 length		12.35
Phalanx III—1 length	17 est.	16.9
Phalanx III—2 length		13.65
Phalanx III—3 length		11.5
Phalanx III—4 length		10.2
Phalanx IV—1 length	10.5 est.	
Phalanx IV—2 length		10.6
Phalanx IV—3 length		9.1
Phalanx IV—4 length		10.5 est.
Phalanx IV—5 length		7.1

Vertebral lengths

Vertebral Number

Cervical 1 — —	Cervical 7 — 12.7
Cervical 2 — 8.7	Cervical 8 — 11.3
Cervical 3 — 9.5	Cervical 9 — 10.9
Cervical 4 — 11.0	Cervical 10 — 10.9
Cervical 5 — 12.3	Dorsal 1 — 9.9
Cervical 6 — 12.7	Dorsal 2 — 9.4

Dorsal	3 — 9.8 est.	Sacral	4 — 8.6
Dorsal	4 — 9.1 est.	Caudal	1 — —
Dorsal	5 — 9.7 est.	Caudal	2 — 10.9
Dorsal	6 — 9.9	Caudal	3 — 11.2
Dorsal	7 — 10.5	Caudal	4 — 11.5
Dorsal	8 — 10.2	Caudal	5 — 11.8
Dorsal	9 — 12.2 ?	Caudal	6 — 12.1
Dorsal	10 — 10.75	Caudal	7 — 12.6
Dorsal	11 — 11.4	Caudal	8 — 12.9
Dorsal	12 — 11.5 est	Caudal	9 — 13.2
Dorsal	13 — 12 est.	Caudal	10 — 13.3

Total sacral length 41.1

as evidence of a cartilagenous state of the carpals, but considering the highly ossified nature of the adjacent elements, that seems most unlikely. The right carpal area is concealed. It is certain that carpals were present during life, but whether they are preserved here and can be recognized is another matter. Three objects are present and seem to be of proper size. These are: first, a roughly rectangular impression 3.5 mm in maximum dimension is situated between the impressions of the left radius and ulna; second, there are two equal-sized and similarly shaped objects, one close to the prominent claw at the end of the left hand and the other, an impression, just to the right of the right hand next to the isolated long phalanx impression (see Fig. 1). The location of these three objects in the immediate vicinity of the two disarticulated hands, their size and shape, and the gap at the left wrist, all lead me to the conclusion that they are the missing carpals.

Recognizing the uncertainty of negative evidence, nevertheless, I suggest that the carpus of *Compsognathus* probably consisted of only two carpals because of the presence of only two distinct types among these three objects, and the absence of any other obvious carpal-like objects anywhere else on the slab. Such a wrist condition seems unlikely in view of the carpus construction in other theropods: four carpals in *Ornitholestes* and *Coelophysis* and five in *Allosaurus*, *Gorgosaurus* and *Ornithomimus*. But *Deinonychus* apparently had only two separate carpals, and *Velociraptor* also may have had only two wrist elements. Not much can be said about the morphology of these supposed carpals in *Compsognathus*, except that they are more or less rectangular, and apparently were relatively thin plates with at least one surface slightly concave.

M a n u s : In his original description of *Compsognathus*, Wagner (1861) was very careful not to specify the number of digits in the manus, but nearly everyone else who has since written about this unique specimen (Marsh, 1895, 1896; Zittel, 1895, 1911, 1918; von Huene, 1932, 1956; Romer, 1956; Steel,

1970) has specified three functional digits in the hand. I disagree. Both hands are partly disarticulated, but the elements are not widely scattered over the slab. Close inspection reveals that only 14 elements are present, including four claws of two kinds. These are preserved either as impressions or actual bones. Further inspection shows that there are only s e v e n different kinds of elements represented — each of which is duplicated. There are no extra or unmatched bones. In the left hand, there are three relatively long bones, one quite robust, another slightly less robust, and a third that is very slender. On the bases of their location, sizes and proximal articular surfaces, these appear to be metacarpals. They are preserved in the proximal region in both hands. In addition, the left
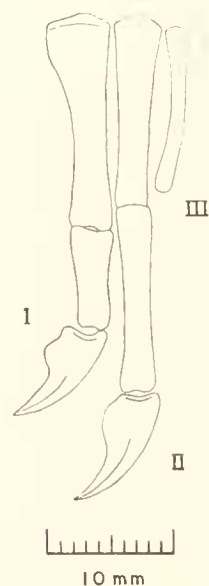

Figure 4: Reconstruction of the left hand of *Compsognathus longipes* in dorsal aspect, according to my interpretation of the hand elements as registered in Figure 1. As explained in the text, it is highly improbable that additional phalanges were originally present, but then lost in the specimen. The reduced formula of II (two phalanges instead of three) is unique, clearly separating *Compsognathus* from all other two-fingered theropods.

hand contains two phalanges of quite disparate lengths and one claw very close to the longer of the two phalanges. These same three elements of the right hand are preserved displaced and separated to the right of the forelimbs. Among the four claws, only two sizes and shapes are present, as is shown in Figure 1 and Plate 9:3 and 9:4.

I interpret the most robust metacarpal as the first, largely because of the basal expansion on one side, which clearly did not adjoin an adjacent metacarpal and therefore must have been either an external or internal surface of the metacarpus. This expansion is quite similar to the basal internal expansion of metacarpal I in *Deinonychus, Velociraptor, Ornitholestes, Struthiomimus* and other theropods, hence I conclude this must be metacarpal I. The very slender element is interpreted as metacarpal III, and apparently was vestigial. That leaves the remaining element as metacarpal II. On the basis of their relative widths proximally, I believe the short phalanx to be the proximal phalanx of the first digit and the long phalanx to be the proximal phalanx of II. Because of the preserved relation in the left hand, I interpret the longer of the two claw types to belong to the second digit. Since there are no unmatched extra phalanges or claws, and it seems highly improbable that o n l y corresponding elements would be missing from both hands, I conclude that there could only have been two functional digits in the hand of *Compsognathus*, plus a remnant (metacarpal) of a third, non-functional digit.

Von Huene (1926) interpreted the hand elements preserved here somewhat differently, apparently believing that some phalanges were missing. In the left hand, he interpreted the long phalanx as the proximal phalanx of digit I, but in the right hand, the impression of the long phalanx, which has exactly the same length and shaft width, he interpreted as the second phalanx of digit II. I consider these to be the same bone (II-1) from opposite hands. He also interpreted the massive broken bone adjacent to the ulna, which has a claw impression a p p a r e n t l y articulated with it, as I-1, but its size and position adjacent to the other metacarpals indicate it is metacarpal I. Von Huene's interpretation of the hand has been included in Figure 1, together with mine, because of the importance of evaluating his and my reconstructions of the hand. In my opinion, the organization of the hand, perhaps is the most critical evidence available for judging the proper systematic placement of *Compsognathus*.

I recognize that there may well be several phalanges missing, but this seems highly unlikely since all seven kinds that are preserved are matched by a mate. If any elements are missing, then the same bones would have to be missing from both hands. Thus, the digital formulae appear to have been 2—2—0, with digits IV
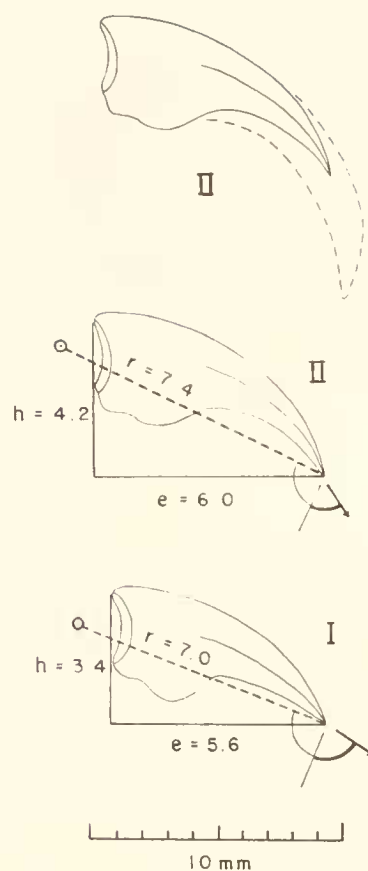

Figure 5: Profile of the first and second unguals of the hand of *Compsognathus* for comparison with the ungual form of other theropods (see Fig. 77, Ostrom, 1969b). The orientation is standard, with the chord of the articular facet arc oriented vertically. This chord has been extended (h = height) to meet a perpendicular (e = extension) from the ungual extremity. The ratios of height to extension (.61 and .70) are relatively low, and the radius (r = heavy dashed line) of ungual rotation has a low inclination similar to that of *Ornitholestes* and *Ornithomimus*. The arrows indicate the projected traces of the inner cutting edges of each ungual compared with the tangents to the arcs of ungual rotation (see Figure 6). — The upper figure shows the bony ungual of the second digit with the outline (dashed line) of the horny sheath (see also Plate 9:5).

and V completely lost. The position and very slender construction of the bone that I interpret as metacarpal III, seems to eliminate the possibility of a functional third digit. (It is also possible that this slender metacarpal is the first, rather than the third, but this would be contrary to patterns in all other theropods.)

If my reconstruction is correct, the hand of *Compsognathus* is unique among theropods, although it is somewhat similar to that of *Albertosaurus (Gorgosaurus), Tyrannosaurus* and *Tarbosaurus*. But unlike these larger theropods with two fingered hands, a complete third metacarpal is present, the second digit is shortened, and the forelimb is not so extremely
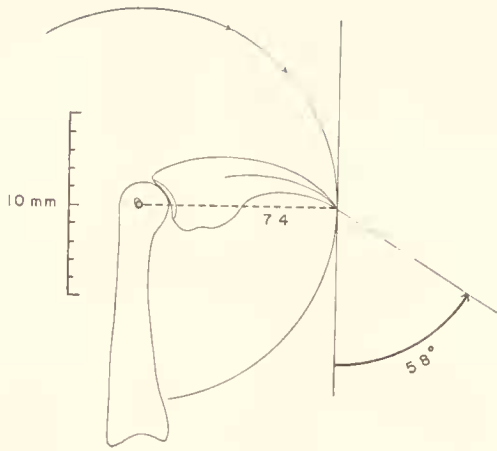
Figure 6: Mechanics of the ungual and penultimate phalanx of the second digit of the manus in *Compsognathus*, showing the angular relationship of the "cutting edge" of the bony ungual to the arc of ungual rotation. This angle is a very large 58 degrees, which compares with the 60 degree angle of the third ungual of *Ornitholestes*. (The "cutting edge" of the horny claw would be much smaller, and thus more efficient, as can be judged from the upper figure of Figure 5, but since the horny claw is so rarely preserved, I apply this technique to the bony ungual for comparsion with other theropods.) The large "cutting angle" in *Compsognathus* suggests that the hand claws were less suited for cutting or piercing than were those of *Deinonychus*, or even *Allosaurus* (see Fig. 78, Ostrom, 1969b).

shortened in *Compsognathus*. In another respect, the hand of *Compsognathus* resembles that of ornithomimids (and *Deinocheirus*), with its three similar lengthed metacarpals. In all other theropods, the first metacarpal is much shorter than the second.

Another interesting aspect of the hand is the design of the terminal phalanges. The claw of the second left finger is particularly well preserved (see Plate 9:5), including parts of the horny sheath that covered the bony ungual. The latter was about 50 per cent longer than the supporting ungual. In my *Deinonychus* study (Ostrom, 1969 b), I utilized a number of parameters by which claw shapes could be compared and described. Applying these parameters to the bony unguals of *Compsognathus*, reveals that they are not strongly curved as compared with some other theropod manual unguals. They have only a moderately high ratio of height to extension and a short height relative to the radius. This suggests to me that the manual claws were not purely raptorial or grasping, and certainly not piercing or cutting structures. This interpretation seems to be substantiated by the angular relationship between the ventral "cutting" edge of the ungual tip and a tangent to the arc through which the ungual tip passed during flexion

against the proximal phalanx (Fig. 6). This angle is a large 58 degrees. In all these parameters, the bony claws of *Compsognathus* most closely resemble that of digit III of *Ornitholestes hermanni* (A. M. N. H. 587). Compare these features of *Compsognathus* (Fig. 5 and 6) with those of Figures 77 and 78 in Ostrom, 1969 b.

Appendicular Skeleton: Pelvis and Hindlimb

Although neither one is completely preserved, the hindlimbs are one of the most distinctive features of *Compsognathus*, being very robust and surprisingly long. With a total length of more than 27 cm, the hindlimb is much more than twice the length of the forelimb, and is at least 10 per cent longer than the presacral vertebral length. *Compsognathus* was a very long-legged creature. The pelvis is less complete, but what is preserved is of typical theropod organization.

Pelvis.

The pelvis has suffered extensive post-preservational damage, particularly to the ilia. All elements were originally present in natural articulation, but now most of the left ilium is missing and only the impression of the upper border of the right ilium remains, the shaft of the left pubis is broken away and only the ischia are still nearly intact. The pelvis was of normal theropod design with the ischia projecting down and to the rear and the pubes extending antero-ventrally.

In past years, no special attention to pubic — ischiadic orientations would have been considered necessary in describing a theropod pelvis. But several recent discoveries have changed all that. The Harvard specimen of *Deinonychus* (Ostrom, 1976 a) clearly shows that in that taxon (at least), the pubes projected downward and slightly — or perhaps sharply — backward, perhaps even parallel to the ischium. Barsbold (pers. com.) has reported that in *Velociraptor* the pubes project backward parallel and immediately adjacent to the ischia. A similar, bird-like pubic arrangement also appears to have been present in *Oviraptor* (Barsbold, pers. com.). No such ornithic pelvic traits are evident in the *Compsognathus* remains.

I l i u m : From the fragmentary evidence pertaining to the ilia, these bones appear to have been quite long (between 5 and 6 cm)., shallow in height, and positioned quite close to the mid-line. The impression of the upper border of the right ilium gives the best evidence of length and shape. It shows a nearly straight, but gently convex upward profile, the highest point of which occurs above the level of the sacral neural spines. The original length of the ilium is indeterminate, but the anterior process appears to have been slightly longer than the posterior iliac process. The original shapes of these processes are unknown.

Pubis: The pubes have been slightly displaced from each other, with the left pubic shaft represented only by an incomplete impression, and the right shaft by several massive fragments. The incomplete proximal portion (of the left pubis) is massive in its construction, presumably for robust articulation with the ilium. Distally, the pubes narrow abruptly into slender, oval-in-section shafts, which join each other just above mid-length in a very narrow symphysis. The fused, distal extremities, are expanded longitudinally into the typical foot-like structure of all theropods. Due to breakage, the exact size and shape of this pubic "foot" is not determinate, but the preserved portion of the anterior part suggests that there was very little (if any) projection of this expansion anterior to the pubic shaft, as there is in most theropods (see *Struthiomimus, Deinonychus, Tyrannosaurus, Allosaurus,* for example).

Ischium: The two ischia are preserved together, one overlying the other. They are the best preserved elements of the pelvis. Compared with the long pubes, the ischia are surprisingly short — reminiscent of the condition in *Deinonychus* (Ostrom, 1976 a), although not so extreme. The proximal region is expanded dorsally and anteriorly for union with the ilium and pubis. Below this, the body of the ischium narrows markedly, with the anterior and upper margins distinctly concave. The anterior margin then expands forward into a delicate, sharply pointed obturator process, which is much more delicate and sharply tapered than in any other presently known theropod. From this process, the ischium tapers sharply backward into a narrow cylinder with a slight distal expansion. Because they are slightly displaced (as preserved), the underlying right ischium clearly reveals the symphysial suture surface extending over the ventral ischial length from the obturator process to the posterior extremity. The overall shape of the ischium — plate-like proximally and rod-like distally — most closely resembles that of *Tyrannosaurus,* differing only in the longer taper of the obturator process, the slighter distal expansion, and of course, in size.

Hindlimb.

Femur: Neither femur is complete, so few anatomical features can be reported. Fragments of the proximal end of the left femur (and the dorsal rim of the acetabulum) mark the upper extremity and the impression of the proximal end of the left tibia permit a reasonable length estimate (75 mm) for the femur. This estimate is corroborated by the preserved location of the distal end of the right femur, approximately 70 mm distant from the acetabulum. The clear impression of the left femur shows a rather thick, cylindrical shaft with slight antero-posterior curvature. No clear imprint or other evidence of a fourth

trochanter is discernible in this impression. The splintered and incomplete shaft of the right femur shows that the femora were hollow, and nearly circular in section. The most distinctive aspect of the femur, though, is its surprisingly stout or robust proportions.

Tibia: The tibia is slightly less robust, but much longer than the femur. It too is hollow and circular in section (as evidenced by the shaft impressions). The proximal ends of both are missing or incomplete, so the nature of the articular surfaces and the cnemial crest cannot be determined. But the distal end of the left tibia, and a good impression of that of the right, show some of the details of the tibia-tarsal construction. In contrast to the femur, the tibia is straight-shafted.

Fibula: The right fibula has separated completely from the tibia, showing that these elements were not fused at any point along their lengths. The fibula is an extremely slender long bone with a strongly concave medial shaft surface for close apposition against the tibia, and an equally convex external surface. The left tibia shaft shows a very narrow, faintly flattened strip along its antero-external surface, marking the area of fibular contact. Proximally, the fibula flares into a very broad (antero-posteriorly) head for articulation against the femur, while distally it is only slightly enlarged into a short rounded articular surface for union with the calcaneum. The most distinctive thing about the fibula, is its extremely slender shaft, which is in sharp contrast to the robust shaft of the tibia.

Tarsus: The tarsus clearly was of mesotarsal design, but unfortunately the exact details are no longer determinable. The distal extremity of the left tibia is present, more or less intact, showing its external aspect, including the extremity of the fibula next to it and a "proximal tarsal" in natural articulation closely appressed against the end of the tibia. The surprising feature of this left tarsus is the large anterior-posterior dimension of the "proximal tarsal", which is almost twice as broad as the fibular extremity. The impression in the matrix of the external surface of of the right tibia extremity seems to show the same condition — a very large (antero-posteriorly) "proximal tarsal" with a strongly rounded distal profile. The only difference here is that the right fibula is displaced, thereby revealing an underlying "ledge and shelf" articulation of this tarsal with the distal surface of the tibia (see Fig. 1). Unfortunately the anterior surface of the right tibia is poorly exposed, but what can be seen does n o t show an ascending process of the astragalus — this large "proximal tarsal".

Wagner (1861) made no mention of the tarsus, except to say that it was short, and Marsh (1895, 1896) gave no detailed description or illustration, but Baur (1882) described and figured a fragment of the

distal end of the right tibia which he removed from the specimen. Most unfortunately, this fragment, apparently with tarsal elements attached, no longer exists. Thus we are forced to rely on Baur's interpretations and illustrations, with no means of checking them. Furthermore, these illustrations (1882: Figs. 42 and 43) and descriptions are not as clear as we might like. For example, the lateral surface of Baur's fragment does not correspond with the impression left in the matrix, nor does it match the exposed lateral (equivalent) surface of the left tibia and tarsus, which are still present. The large, rounded "proximal tarsal" is not present in Baur's illustration, nor does he show any scar or articular facet for this element — which is most conspicuous on the left side. But perhaps the most important detail of Baur's paper is his interpretation of a narrow ridge-like feature that extends along his "anterior" surface of this now-lost tibial fragment. He identified this as the "Tibiale-aufsteigende Fortsatz" — the ascending process of the astragalus. I would accept this interpretation except for the fact, noted above, that Baur's figures do not match the preserved parts of the left leg, or the impression of the right — from which the missing fragment purportedly was removed.

Only two options are open to us. We either accept Baur's interpretations on faith, for they cannot be verified now, or we conclude that the construction of the tarsus in *Compsognathus* cannot be established in this specimen. It must be noted, however, that Baur's reconstruction of the astragalus is consistent with those known in other theropods.

But a nagging question remains: What is the large proximal tarsal? Is it the calcaneum, which it appears to be? If so, it is unusually large. Moreover, its relationship to the tibia is unusual for a theropod in that it clearly articulates with the distal surface of the tibia and not just its lateral surface, as in most theropods. This is quite evident in the impression of the left tarsus. But, on the other hand, it also clearly articulated with the fibula. If Baur (and Marsh) was correct in his interpretation, then it probably is the calcaneum. But at this point, I am not sure whether it is the calcaneum, the astragalus, or the lateral part of a fused astragalo-calcaneum. One thing is certain, though: the mesotarsal condyle of this proximal tarsal extends far in front of the anterior surface of the tibial shaft, much more than in any other theropod known to me. This would seem to indicate an unusually high degree of extension was possible at the ankle.

Baur (1882) detected three distal tarsals, which he labeled tarsals 2, 3 and 4—5. The latter is clearly recognizable as a flat disc closely articulated with the proximal end of the left metatarsal IV (see Pl. 10:1). It does not appear to have been co-ossified with the metatarsal, but it may have been. The other two

tarsals identified by Baur, are preserved as impressions and are not so unequivocal. As noted by Baur, the impression of the right metatarsus seems to show two convex cap-like elements at the upper extremities of metatarsals II and III. But in the left metatarsus, these same features appear to be just the proximal convex extremities of the two metatarsals. No clear suture or physical discontinuity separates these ends from the metatarsal shafts, but then the tarsals and metatarsals might have been fully co-ossified. Molds made of the impressions of the right metatarsus show the same condition, hence, if these two features are in fact distal tarsals, they w e r e completely co-ossified with metatarsals II and III. Since at least two distal tarsals, and usually three, are found in all other adequately known theropods, I strongly suspect that this last condition is the correct interpretation, but it must be pointed out that the present specimen does not permit certification.

P e s : The pes is greatly elongated, with the metatarsal length somewhat greater than the median toe
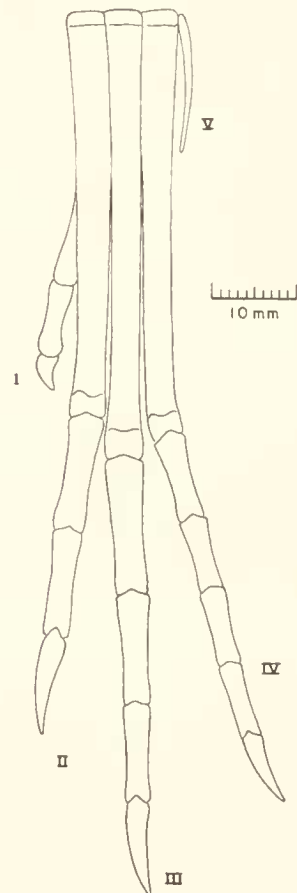

Figure 7: Reconstruction of the left foot of *Compsognathus longipes* in dorsal or anterior aspect. Notice the great length and very slender design, reminiscent of *Archaeopteryx* and later birds, and suggestive of high cursorial ability.

length. The central metatarsals (II, III, and IV) are stout and closely appressed together. Their respective lengths, where determinable, are given in the table of dimensions. Metatarsal I consists of a stout wedge-shaped bone fixed against the posterior surface of the shaft of metatarsal II just below mid-length. Its upper end fails to reach the tarsus by more than 20 mm, and there is no sign of a proximal portion, as has been found in *Allosaurus* (Gilmore, 1920; Madsen, 1976). The fifth metatarsal is a slender curved splint-like bone extending some 15 mm from the tarsus down the postero-lateral aspect of metatarsal IV. There are no distal elements of digit V. All of the first four metatarsals have well-developed distal ginglymoid facets and deep collateral ligament fossae, indicative of strong, precise toe actions, and perhaps cursorial habits (Plate 10:1).

The foot digits have the normal theropod formulae (2-3-4-5-0) and show the usual proportions, with the third toe the longest and II and IV somewhat shorter and nearly equal in length, and the first toe extremely short (it does not even reach the lower end of metatarsal II), and reverted to the back. The hallux ungual is preserved oriented like those of the other toes. However, this seems to be an artifact, as the proximal phalanx and the ungual obviously have been rotated about their long axes by more than 90 degrees, as is evidenced by the disparate orientations of the collateral ligament fossae on metatarsal I and the proximal phalanx of the first digit. (The penultimate phalanx of digit III has been similarly rotated about its long axis by about 180 degrees, without separation from adjacent phalanges: see Plate 10:2.) All pedal phalanges are quite robust, with pronounced collateral ligament fossae and strongly ginglymoid distal articulations. Where observable, the proximal phalanx always is the longest element in each toe. The unguals are obviously straighter than those of the manus, and broader, with a more triangular cross-section and less pronounced flexor tubercles. The ungual of digit I is very short and stubby, suggesting an almost vestigial state.

Mystery Bone.

There are a number of bone fragments, especially in the area around the skull, that I have not been able to identify with certainty. Most of these are too fragmentary, or contain no diagnostic features. One bone, however, appears to be complete, and does have distinctive features. Yet, I have not been able to identify it. This mystery bone (Plate 10:4) lies quite isolated, well above the skull and close to two cervical ribs. It is roughly quadrangular in shape, with a rounded articular process at one end. At first glance, it resembles the proximal end of a dicocephalous rib, with the articular process the capitulum and the adjacent "shoulder" the tuberculum. However, the other end, which is only 4.5 mm distant, is not a broken end, but rather is a distinct articular surface. The total length of this object is 5.85 mm, and its maximum and minimum widths are 3.8 and 2.4 mm, and it is complete. Its form does not match any bone that I am familiar with, and I have no suggestions other than that it may be a cranial element — perhaps the ectopterygoid.

SUPPOSED SKIN-ARMOR OF *COMPSOGNATHUS*

Von Huene (1901) made much of a series of surface irregularities, which he described as polygons, in the prominent depressions along the ventral regions of the trunk and abdomen. In the circular depression between the scapula and the left humerus, he claimed that 15 "polygons" could be seen, most of which were six-sided. In the oval depression just behind this, he saw impressions of 10 more similar but larger polygons arranged in rows. Because of their shape, and what he termed their regularity of arrangement, he concluded that these surface impressions were evidence of horny skin armor in *Compsognathus*. Von Huene acknowledged that no such plates are preserved along the back, where we would most expect skin armor, but he did claim that the neural spines of the trunk and tail are elongated lengthwise and strongly thickened transversely in their upper edges, forming a row of broadened platform-supports for the (missing) dorsal scutes. In support of this inaccurate description (the dorsal neural spines are not thickened distally) and supposed dorsal armor plates, Huene alluded to the dozen or so irregularly shaped bony ossicles found associated with some of the caudal neural spines in *Ceratosaurus* (U. S. N. M. 4735), reported by Gilmore (1920), as evidence of dermal armor in theropods. Nopcsa (1903) rejected both of these interpretations of Huene's, but interpreted other features as evidence of skin and muscle impressions.

I have examined the areas on the *Compsognathus* slab specified by von Huene under high magnification and various lighting conditions and have concluded that his evidence is very doubtful. As I have attempted to show in Plate 11:1, the surface configuration in these areas is unusual and different from that of other areas on the slab. But I do not see any consistent regularity of form or arrangement in any of the sites mentioned by von Huene. It is evident, though, that the regions concerned with von Huene's "polygons"

have been subjected to a very different history of solution and precipitation than other regions of the specimen. First of all, there are the peculiar depressions along the ventral part of the body of *Compsognathus*, with their irregular "hummocky" surfaces that appear to have been etched into the matrix. This is in sharp contrast to the usual, very smooth, planar, and sometimes almost glassy surfaces characteristic of other parts of the slab. Secondly, throughout these "etched depressions", there are irregular masses of very fine druzy crystals, mostly of calcite, but also (surprisingly) some of quartz. In some places it can be seen that these masses of druzy crystals coincide with the borders of the so-called "polygons", suggesting that these polygonal patterns reflect some aspect of crystal growth rather than impressions of skin armor. The general appearance of the ventral part of the body region and the area anterior to the sacrum, is that of a series solution cavities — vugs — dissolved into this slab along the bedding plane containing the skeleton of *Compsognathus*. This solution must have occurred long before the slab was excavated. Following formation of these solution cavities, masses of druzy calcite and occasional quartz crystals formed along the walls of these vugs, as they did within the hollow limb bones. In short, the hummocky "polygon" surfaces are the result of differential solution.

Further evidence in support of this explanation is the fact that the *Compsognathus* slab is traversed by a number of fractures. One prominent fracture extends the length of the trunk and abdomen of *Compsognathus* (see Plate 7), directly through the series of "etched" depressions or solution cavities, then follows along the trace of the tibia and across the left foot. A second fracture branches off this first one in the abdominal region and extends up through the "solution" cavity at the anterior part of the sacrum and then follows along the course of the caudal vertebrae. Throughout almost the entire courses of these fractures, the fracture edges are rounded — clear evidence of solution. This is especially evident in the trunk and abdominal regions and along much of the caudal series. Several other fractures present on the slab are characterized by sharp edges, and apparently are of more recent origin, not having been subjected to solution.

I suggest that prior to its excavation, the *Compsognathus* slab was situated quite close to the surface where it was subjected to solution by periodic ground water percolations through these fractures. Solution and subsequent crystalization resulted along parts of these fracture traces, resulting in crystal-lined vug-like cavities on this slab, and thus von Huene's "skin armor" is nothing more than the etched walls of these solution cavities. That these "polygon"-lined cavities are secondary in origin (contrary to von Huene's

interpretation) is clearly established by the unexpected presence of tiny, well-formed quartz crystals scattered about on these vug walls. Hückel (1974) reported the quartz content of the Solnhofen limestones varies up to a maximum of 0.4 % of total matrix, the quartz occurring in the form of sponge spicules, tiny well-rounded grains and rare perfect crystals. Barthel (1976) found the rounded quartz grains (usually less than 10 microns) to be widespread in the Solnhofen deposits and concluded that they were eolian in origin. The unabraded crystals, however, must be autogenic, and most probably post-diagenic crystallization derived from sources external to the Solnhofen matrix and introduced via bedding planes and fractures, such as described above (see Plate 10:6).

Nopcsa (1903) dismissed von Huene's "skin-armor" for much the same reasons, but maintained that skin impressions and traces of muscle fibers were preserved in several areas around the skeleton of *Compsognathus*. His "skin impressions" are curious, finely granular textured areas, and his "muscle fibers" occur as faint traces of "parallel irregular fibers" at several locations (but not everywhere he mentioned). Nopcsa illustrated both of these features in a drawing of *Compsognathus* (1903, Plate XVIII).

The granular texture is very evident throughout most of the rib cage (except within the polygon-lined depressions discussed earlier), between the femora, around the skull and especially close to the left humerus (see Plate 11:3). The contrast between this granular-textured surface and the more normal surface texture typical of other areas on the slab, is shown in Plate 11:4. Nopcsa may have been correct in his interpretation of this feature, but I have serious doubts. First of all, this granular texture occurs over much of the orbit! — as well as within the open jaws, areas that I would hardly expect to find scaly integument. Moreover, this same texture is present, perhaps less distinctly, surrounding all scattered and isolated bones and is not confined to the general region of the body. For example, it is quite clear in the areas surrounding the several scattered phalanges of the hands, as well as around the displaced cervical ribs. Obviously, this is not consistent with the integument explanation, but suggests that the bones themselves are the controlling factor in the distribution of this curious textural pattern. I suspect that this texture is also the result of solution etching along the bedding plane and is localized around three-dimensional objects lying on that plane. Evidence for that is the presence of what appears to be the same texture surrounding some of the specimens of the small crinoid *Saccocoma*. Notice that this granular texture is most prominently developed around the skeletal remains and *Saccocoma* specimens that are situated closest to the fractures that served as solution channels. Also notice that this

texture seems to grade imperceptibly into normal surface textures, rather than an abrupt transition at well-defined boundaries. The organic objects on this slab appear to have acted as centers of solution and / or chemical activity, resulting in this granular-textured surface. Whatever its origin, though, the integument theory of Nopcsa does not explain its occurrence around the specimens of *Saccocoma*.

Concerning the "parallel and irregular fibers" seen by Nopcsa, I must admit that I was unable to see most of the examples he cited (Nopcsa listed seven specific areas in which these were present). The "fibers" between the femur and ischium, and between the femur and tibia, and those along the base of the tail, simply are not there! Nor are "fibers" evident above the dorsal vertebrae, near the cervicals, or distally along the tail. A striated or linear textural pattern does occur proximally at the lower edge of the ischium, and also between the right radius and ulna (see Plate 11:2). In both of these sites, the striations are parallel to the adjacent bone edges. There also appears to be a very faint lineation along the dorsal region of the proximal caudals close to the tip of the right dentary. Nopcsa's "fibers" may well represent impressions of soft tissues, including muscle fibers. Such occurrences are not uncommon in Solnhofen specimens. Most notable are the feather impressions in the several specimens of *Archaeopteryx* and wing membrane impressions in numerous pterosaur specimens (but see also Reis, 1893). However, I am inclined to think that these striations are merely lineated granular texture etched into these surfaces, with the lineations being due to the local influence of the adjacent parallel bone margins.

COMPARISON WITH OTHER SPECIMENS REFERRED TO *COMPSOGNATHUS*

At the present time, only two other specimens have been recorded in the literature as possibly referrable to *Compsognathus*. The first of these consists of three metatarsals and a single phalanx, now in the Humboldt Museum für Naturkunde, East Berlin. The second is a nearly complete skeleton, *Compsognathus corallestris*, from Portlandian limestones of southern France. This specimen is in the Muséum d'Histoire Naturelle of Nice, France.

The Humboldt Specimen.

This specimen was first reported by Dames (1884) and has been cited subsequently by von Huene (1925, 1926 and 1932) as questionably referrable to *Compsognathus*. As shown in Plate 10:5, the specimen consists of four bones, three of which appear to be metatarsals and the fourth a proximal phalanx. These are preserved on counterpart slabs. First of all, it is important to mention that it is impossible to determine from these remains the exact nature of the complete metatarsus — whether it was composed of three, four or five metatarsals. So it is not possible to say which metatarsals are preserved here (and indeed whether these are metatarsals rather than metacarpals). The specimen is preserved with the shortest bone in the middle, a condition not known in the metapodials of any tetrapod, but Dames concluded (correctly, I think) that the longest element had been displaced and interpreted the three as follows: mtt. I = 54 mm; mtt. II = 60 mm; mtt III = 68 mm. This configuration does not correspond with the metatarsus of *C. longipes,* and on the basis of other tetrapod metatarsal construction, implies that a fourth, and perhaps a fifth metatarsal are

missing. In *C. longipes,* metatarsal I is incompletely formed, and metatarsals II, III and IV have lengths respectively of 50.4, 56.0 and 51.8 mm.

If we assume that the three long bones of the Humboldt specimen are metatarsals II, III and IV, and that the longest element is metatarsal III (as in *Compsognathus*), the relative lengths do not compare closely with those of either *C. longipes* or the Nice specimen (both of which are close in these proportions. A comparison of metatarsal ratios in the three specimens is as follows:

	C. longipes	*Nice specimen*	*Humboldt specimen*
Mtt III / Mtt II	— 1.11	1.14	1.27
Mtt III / Mtt IV	— 1.08	1.12	1.13
Mtt IV/ Mtt II	— 1.03	1.02	1.11

Considering the fact that the Humboldt specimen is intermediate in size between the Nice specimen and *C. longipes,* these ratios suggest that the Humboldt specimen is not referrable to *Compsognathus,* the same conclusion reached by Dames. The longest bone is too long relative to the others. This conclusion seems to be reinforced by the single phalanx that appears to be articulated with the shortest of the three metatarsals (II ?). If that articulation is correct, then its length (20 mm) is much greater relatively than that of the proximal phalanx of the second toe in *C. longipes.* Consequently, my conclusion is that the Humboldt specimen is not assignable to *Compsognathus longipes.*

TABLE 2

Comparative Anatomical Dimensions of *Compsognathus longipes*
(Dimensions in mm.)

	Type specimen	Nice specimen (C. "corallestris")	C. c. / C. l.*
Skull length	70—75 est.	110 est.	1.42
Orbit length	19 est.	27 est.	1.52
Humerus length	38—40 est.	67 est.	1.76
Radius length	24.7	42	1.70
Ulna length	28.5	45	1.57
Scapula length	38 est.		
Femur length	67 est.	110	1.49
Tibia + astragalus	87.7	135.5	1.54
Fibula length	82.1		
Mtt. II length	50.4	70.5	1.39
Mtt. III length	56.0	81.0	1.44
Mtt. IV length	51.8	72.0	1.39
Pubis length	60 est.	95 est.	1.58
Ischium length	40 est.	70 est.	1.75
Hindlimb length	264	377	1.42
Forelimb length	102	?	
Hand length	39	?	
Presacral column	236	310 + two = 342	1 44

Anatomical Proportions

Femur / Tibia	.76	.81	
Mtt. III / Tibia	.64	.59	
Humerus / Femur	.56	.61	
Humerus / Tibia	.43	.50	
Forelimb / Hindlimb	.38		
Skull / Presacral	.30	.32	
Forelimb / Presacral	.43		
Hindlimb / Presacral	1.11	1.10	
Skull-Orbital-Length Index	26	24	

* Ratio of *Compsognathus* "corallestris" / *Compsognathus longipes*.

The Nice Specimen.

In 1972, Bidar, Demay and Thomel reported the discovery of a nearly complete skeleton of a small theropod from Portlandian lithographic limestones (Petit Plan) at Canjuers, some 60 km west of Nice, which they assigned to a new species, *Compsognathus corallestris*. This new specimen (see Plate 12) is extremely similar anatomically to *C. longipes,* but is approximately 50 % larger. It also is preserved in a pose that is astonishingly similar to that of the Munich specimen, including the parallel flexed hind legs, the upswept tail, the 360 degree opisthotonic arc of the cervical series, the severed head in an upside down position pointing backward, and even the presence of stomach contents within the rib cage. So remarkably similar are the positions of the two skeletons, one cannot help wondering if this represents some obscure clue about the living habits of these specimens.

I was fortunate to be able to examine the Nice specimen in some detail in 1973, thanks to the kindness of Dr. Demay. It is not my intention here to give a full analysis of this specimen, the original authors have provided that. However, I think it is necessary to examine the criteria they adopted in establishing a new species.

In their diagnosis of *C. corallestris,* the authors emphasized the larger size of this specimen and cited varying size differences between corresponding elements as rationale for the establishment of a new species. Another key factor was their interpretation of the forelimb as a flipper-like appendage. In Table 2, I have listed a number of dimensions that are available from both specimens, together with some estimated dimensions, and calculated the ratios of *C. longipes* to *C. corallestris.* The dimensions given are mine, and in a few instances they differ from those given by Bidar,

Demay and Thomel. All measurements given in this report were made by me (unless otherwise indicated), with a Helios dial caliper with scale divisions to 0.05 mm. The data in Table 2 show that the various skeletal elements of *C. corallestris* range from about 40 % to 75 % larger than the corresponding element of *C. longipes*. Apparently, it was this varying difference that led the authors to conclude that the Nice specimen was distinct from *C. longipes* (together with the flipper forelimb). But these varying differences might simply reflect differing allometric growth of different parts of the skeleton, and thus are not reliable criteria for establishing a new taxon — especially since there are only two specimens available for comparison.

Unfortunately, their interpretation of the forelimb as a flipper-like structure is also highly questionable. The forelimb of the Nice specimen is very poorly preserved. In fact, it is so poorly preserved that it is extremely difficult — indeed impossible — to decipher the various components with absolute certainty. Most of the forelimb elements are represented by impressions only, many of which are indistinct, and their identities doubtful. The construction of the metatarsus and manus are entirely unknown. Finally, their evidence for a flipper consists of several "wrinkle-like" linear undulations paralleling the forelimb along its anterior margin. These surface features might represent the impression of soft parts, but it certainly does not look that way to me. Moreover, similar "wrinkle-like" surface irregularities occur further up on the slab which *continue the same exact trace* as their "flipper imprint". These can be seen extending away from the loop of cervical vertebrae, to the left and almost parallel to the lower jaw. This "wrinkle" along side the forearm, thus seems to be part of a much longer linear trace that extends well beyond the skeleton and therefore cannot be part of the specimen at all. I consider the flipper interpretation of the forelimb by Bidar, Demay and Thomel to be poorly founded and highly improbable. (See Plate 12.)

Beyond the size differences and the questionable flipper like forelimb, a considerable volume of anatomical evidence raises serious question about the validity of *Compsognathus corallestris*. In short, the two specimens are nearly identical, within the limits of imperfect preservation. In the skull, corresponding available elements, such as the premaxillae, maxillae, lacrymal, are the same. The dentaries also are alike, being long, very narrow and parallel-sided. The chief difference between the tooth-bearing elements of the two specimens is the greater number of teeth that are preserved in place in the Nice specimen, but I have already remarked about the numerous displaced teeth in the Munich specimen. Concerning the teeth, of particular importance is the "bent" shape of the

anterior teeth of the premaxilla and dentary that is so distinctive of *C. longipes*. The same tooth form is present in the Nice specimen.

Because of the poor preservation of the forelimb in the Nice specimen, no comparison with *C. longipes* is possible. But the hind limbs are comparable, and the striking similarities are most obvious, down to the detailed construction of the pes and even the identical form of the metatarsus — including the shape of the vestigial fifth metatarsal. In the pelvis, the ischium is exactly the same in both (the authors clearly misinterpreted the lower ischial margin, placing it much too low), with a narrow, slightly club-ended posterior extremity and an anteriorly placed, delicate, triangular obturator process. The pubis, contrary to their statement, is not much longer relatively than it is in the genotype specimen. As in the Munich specimen, the pubis is about the same length as the femur (notice that the distal extremities of the pubis and femur coincide in both specimens). Furthermore, although Bidar, Demay and Thomel reconstruct a much longer distal pubic "foot" than I believe is warranted by the specimen, the overall shape is very much like that in *C. longipes,* with long narrow cylindrical shafts and a large distal expansion. The ilium too, was long and low, as in *C. longipes* although no further comparisons can be made since only the upper margin is preserved in the type specimen. Finally, there are no distinctions preserved in the cervical or dorsal vertebral column that justify specific separation of these specimens, whereas the proximal caudals are virtually identical, with low neural spines and an absence of transverse processes. Even the chevrons are the same in both specimens.

On the bases of all these striking anatomical similarities, I see no justification for placing the Nice specimen in a separate species, especially considering the very doubtful nature of the criteria cited by the authors as their rationale. Accordingly, I consider the binomial *C. corallestris* to be a junior synonym of *Compsognathus longipes*, and refer the Nice specimen to that taxon.

Casamiquela (1975), described a very fragmentary specimen from the Middle Jurassic Lotena Formation (Callovian) of Neuquen Province, Argentina, which he referred to the Family Compsognathidae and assigned to a new genus and species, *Herbstosaurus pygmaeus*. The specimen consists of impressions or fragments of a sacrum, the right ilium and ischium, both femora a phalanx, and other unidentified fragments. Unfortunately, it is difficult to identify with certainty the several elements that are illustrated in the two unlabeled photographs of Casamiquela's report. However, if the lowermost long bone on those two photographs is a femur (as I believe the author interpreted it to be), then this specimen almost certainly can not be

referred to any presently known theropod species because the "shaft" of that bone curves in the transverse plane of the medially directed "femoral head", rather than in a para-sagittal plane as in all theropods. On that basis alone, I consider it highly unlikely that *Herbstosaurus pygmaeus* is closely allied with *Compsognathus,* or with any other theropod. (I suspect that this specimen may actually be pterosaurian, because of this unusual design of the "femur", plus the long and unusually shallow form of the ilium — an opinion that is shared by J. F. Bonaparte [personal communication]).

THE SUPPOSED EMBRYO WITHIN *COMPSOGNATHUS*

The Munich specimen of *Compsognathus* is remarkable in a number of features — its small size, completeness, quality of preservation and certain bird-like characters —, but perhaps the most remarkable feature is the tiny skeleton of a small reptile well-preserved within the rib cage of *Compsognathus.* In some ways, this tiny skeleton is one of the most important features of this specimen, for it either demonstrates viviparity in theropods (as Marsh claimed), or it provides direct evidence of feeding habits. Marsh (1881, 1883, 1895, 1896) was the first to notice the presence of this small skeleton and promptly concluded that "This unique fossil affords the only c o n c l u s i v e evidence that dinosaurs were viviparous." (My emphasis.) A few years later, Nopcsa (1903) discussed these important "gastronomic" remains at some length and provided the first illustration (1903, Plate XVII). He concluded that this small skeleton probably was not an embryo on the following grounds:

1) The estimated length of 8 cm was too large for the body cavity of *Compsognathus* which could not have been more than 11 cm in length.

2) The proportions of femur to tibia.

3) The proportions of humerus to lower jaw.

4) The position of the tail and hind foot.

5) The shapes of the upper and lower jaws.

6) The shape of the pelvis.

7) Single headed ribs.

8) The strongly ossified and well-formed articulations. Nopcsa concluded that this specimen probably was lacertilian.

I arrived at the same conclusions prior to reading Nopcsa's paper, for most of the same reasons, plus a number of others. I did not arrive at a definite identification until somewhat later, but at this point it can be stated quite categorically that the small skeleton within the rib cage of *Compsognathus* is p o s i t i - v e l y n o t an embryo, or even a young individual of *Compsognathus.* In addition to Nopcsa's points (with the exception of ♯ 3, which cannot be determined precisely in *Compsognathus,* and ♯ 4, which is of no significance), the following features preclude this specimen being an embryo:

1) The large astragalo-calcaneum.

2) Long transverse processes on the proximal caudals.

3) Lepidosaurian design of the distal end of the humerus, with pronounced entepi- and ectepicondyles.

4) The very robust fibula.

5) Only two sacral vertebrae.

6) Autotomous caudal vertebrae.

In Figure 8, I have recorded the distribution of these remains, together with my identifications. The only important differences between Nopcsa's interpretations and mine, are his failure to recognize some elements of the left foot, fragments of the right tibia and fibula, the right astragalo-calcaneum, and his mistaking the right metatarsus for a metacarpus.

The prey object lies on its left side, with its head-end pointing toward the rear of *Compsognathus.* That it actually lies within the rib cage of *Compsognathus* is certain, as can be seen in Plate 13, which shows it overlying the right ribs of *Compsognathus* and overlain by the left ribs. Included are at least nine dorsal vertebrae, 11 pairs of dorsal ribs, the left humerus, parts of the pelvis, the entire left hindlimb and parts of the right, plus an extremely long caudal series including at least 50 segments. Lying out side of the body cavity of *Compsognathus,* is a left mandible which also probably belongs to this specimen. Nopcsa also identified a triangular impression just above this jaw and anterior to the right femur of *Compsognathus,* as a maxilla, but I am very doubtful of this identification — at least as the specimen now exists. The dimensions of the various elements of this tiny skeleton are given in Table 3.

The rib cage and dorsal vertebrae are little disturbed, although details of the vertebrae are difficult to interpret. The ribs themselves are robust, surprisingly so for such a small individual, but most distinctive is their single-headed articulation with the vertebrae. The sacrum consists of two, apparently co-ossified segments clearly discernible between the last rib-bearing vertebra and the first vertebra behind with elongated transverse processes. The proximal caudals

Figure 8: Camera lucida drawing of the small reptile skeleton inside the body cavity of *Compsognathus*. The original drawing was made by me at a magnification of 6.6, with a Wild binocular microscope and camera lucida. *Abbreviations:* Ast.—Calc. — astragalo-calcaneum; C. 1, 6, etc. — caudal vertebrae; Ca. Vert. — caudal vertebrae; D. Vert. — dorsal vertebrae; Fe. — femur; Fib. — fibula; Hu. — humerus; Hu. Im. — Imprint of the distal end of the humerus; L. — left; Mtt. — metatarsals; Pe. — pelvis; R. — right; Ra. — radius; Sa. 1. — first sacral vertebra; Tib. — tibia; Ul. — ulna.

TABLE 3

Comparative Measurements (in mm) of the small skeleton within *Compsognathus*, and the type specimen of *Bavarisaurus macrodactylus*.

	"stomach" contents	*Bavarisaurus macrodactylus**
Humerus length	14.0	15.3
Femur length	16.8—18.0	21.15
Tibia length	16.9	19.2
Fibula length	17.2	18.8
Mtt. I length	6.8—8.1	5.5 ?
Mtt. II length	9.2—10.4	9.2 ?
Mtt. III length	10.4—11.4	11.2
Mtt. IV length	8.9—10.1	11.15
Body length	47 est.	52
Tail length	190 +	

extend down toward the solution cavities described earlier, then cross over the right tarsus. At this point, the series is interrupted.

My initial attempts to decipher these stomach contents were frustrated by the presence of several long rows of bony elements in the posterior regions adjacent to the left foot. At first, these appeared to be rows of vertebrae, giving the impression that there were several small skeletons present within the body cavity of *Compsognathus*. Then, because of their flat form, and what appeared to be sculptured surfaces and paired arrangements, I concluded that they were
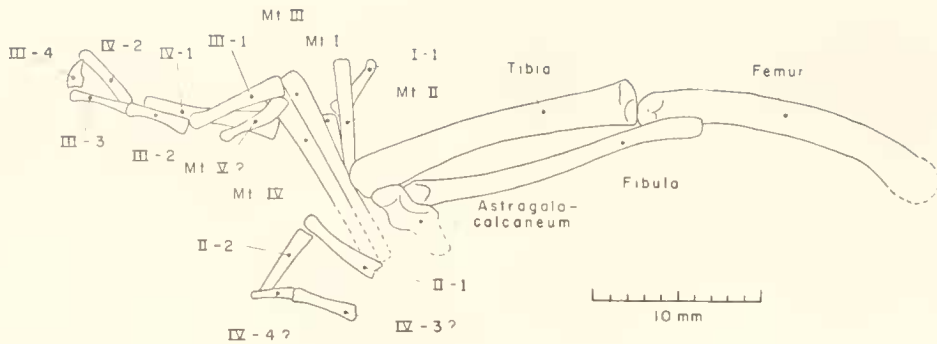
Figure 9: Camera lucida outline drawing of the restored left hindlimb of the small reptile shown in Figure 8, preserved within the body cavity of *Compsognathus*, together with my interpretations of the various elements.

rows of dermal scutes. The objects are very small, and preservation is not perfect, all of which complicates the matter. But now I am absolutely certain that these are rows of caudal vertebrae. Zygapophyseal processes are detectable at several places, but they are rarely distinct. The most distinctive features are the autotomy sutures dividing each centrum into subequal anterior and posterior halves. These are well-defined throughout most of the caudal series and appear to have been present on all caudals, except perhaps the first 8 or 10 segments. The caudal series appears to be nearly complete, with only a few elements missing in the vicinity of the tenth caudal, and perhaps a few others at several points. The tail is preserved folded back and forth on itself in four sub-parallel rows. At least 50 segments can be identified, with the total length exceeding 19 cm. That is extremely long, when compared with the hindlimb length (femur plus tibia equals 3.4 cm, approximately).

Adjacent to the sacrum, a large L-shaped plate of bone represents parts of the right pelvis, with the proximal end of the right femur still in almost full articulation with the acetabulum. Details are not clear, but there can be no question that the L-shaped bone is the right ilium, with perhaps a portion of the pubis. Next to the pelvic bones, is a well-preserved distal end of a left humerus. This, together with the autotomous caudal structure, is perhaps the most important clue to the identification of these remains. Very distinct here is a large radial condyle and a much smaller trochlea for the ulna. Also evident is a large and pronounced ventral supratrochlear fossa. But most important are the very large entepicondyle and somewhat less prominent ectepicondyle, which clearly show that this is not an archosaurian humerus (Plate 14:4).
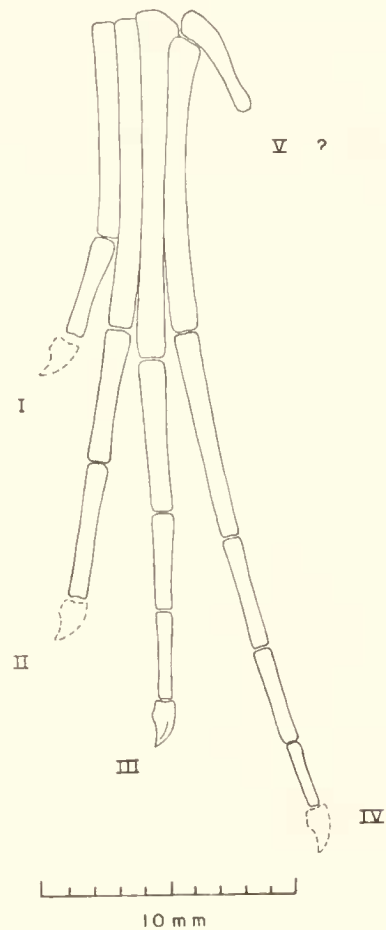

Figure 10: Reconstruction of the left foot (in dorsal aspect) of the small reptile, according to my identifications recorded in Figure 9. Although my identifications cannot be certified, this foot is readily distinguished from that of *Compsognathus* in the completely formed metatarsal I, the relatively more massive metatarsus, the stout and curved metatarsal V (?), the relatively longer toes, and the unusual length of the proximal (?) phalanx of the fourth digit.

The left hindlimb is nearly intact, although the foot bones are disarrayed. The femur and tibia are both stout and very nearly the same length. The tibia is straight, the femur slightly curved. The fibula is surprisingly robust. Articulated with the latter is an irregular-shaped bone which I interpret as a fused astragalo-calcaneum. Two articular facets are evident, which appear to have been for the two epipodials. The medial part, unfortunately, is concealed beneath some of the caudal vertebrae, but in the right ankle this region is exposed, showing what appears to be a stout expansion or process. This does not correspond to the calcaneal tuber of the crocodilian or pseudosuchian tarsus, either in form or position. No other tarsals are discernible in either ankle. The large size of this element, together with its proximal position articulated with the tibia and fibula, leave little doubt that it is the co-ossified astragalus and calcaneum. Important here is the fact that this bone is quite unlike the proximal tarsals of known theropods (see Welles and Long, 1974).

Closely associated with this tarsal bone are the somewhat disarrayed bones of the left foot. My identification of these foot bones is given in Figure 9. The respective positions of the main metatarsals, and the normal (expected) serial arrangement of the four phalanges associated with the middle metatarsal, leave little doubt that this is the third digit. The very long proximal phalanx beneath, and the shorter phalanx at its extremity, seem best linked with the fourth metatarsal. Other identifications are less certain. Figure 10 is my reconstruction of the foot according to the interpretations given in Figure 9. If correctly reconstructed, this foot is very distinct from that of Comp-
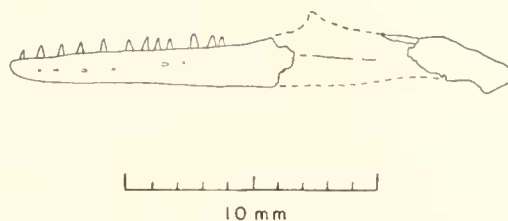

Figure 11: The isolated left mandible that is preserved outside of the body cavity of *Compsognathus*. As is shown in Figure 1, it is closely associated with a number of displaced gastralia of *Compsognathus*. Presumably, it belongs to the small reptile within *Compsognathus*. Notice that it bears a distinct coronoid process and that it is relatively less slender than that of *Compsognathus*. See also Plate 14:3.

sognathus, but it is surprisingly similar to that of another Solnhofen taxon.

The tiny jaw lying outside of *Compsognathus*' body cavity, most probably also belongs to this specimen, although that cannot be certified. In support of this, there are no other remains of small vertebrates on the *Compsognathus* slab, and the mandible is of appropriate size. Two features of this mandible distinguish it from that of *Compsognathus*: the presence of a well-developed coronoid process, and the greater degree of forward taper of the dentary. Tiny sharp, symmetrical, conical teeth are present, apparently with thecodont (or possibly pleurodont) implantation. No evidence of the "bent" tooth form of *Compsognathes* is visible. (See Plate 14:3.)

Now that I have emphatically rejected the "conclusive" evidence of Marsh, and his embryonic iden-
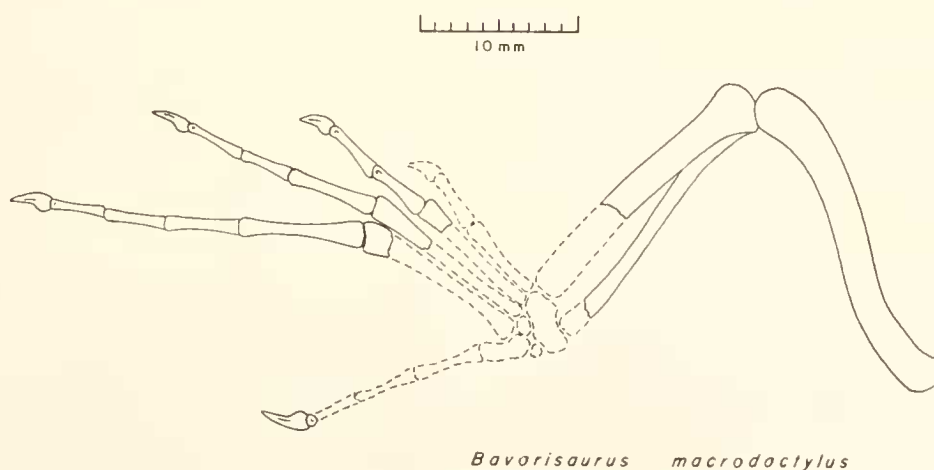

Bavarisaurus macrodactylus

Figure 12: Camera lucida drawing of the left hindlimb of the type specimen of *Bavarisaurus macrodactylus*, for comparison with the hindlimb elements of the small reptile illustrated in Figures 8, 9 and 10. The slight differences in pedal proportions may be due to erroneous interpretations of the foot elements in the *Compsognathus* stomach contents, or to ontogenetic differences, or, most likely, to taxonomic differences.

TABLE 4

Some Available Skeletal Proportions of the
Small Reptile Skeleton Inside *Compsognathus,* Compared
With Other Solnhofen Lower Tetrapods.

	Femur / Tibia	Femur / Humerus	Tibia / Mtt. III
"Stomach contents" of *Compsognathus*	1.00 — 1.06	1.20 — 1.28	1.48 — 1.66
Bavarisaurus macrodactylus (B. S. P. 1873 III 501)	1.10	1.38	1.76
Homaeosaurus brevipes (B. S. P. 1887 VI 2)	1.25	1.39	1.48
Homaeosaurus maximiliani (B. S. P. AS I 565)	1.06	1.19	1.39
Kallimodon pulchellus (B. S. P. 1887 VI 1)	1.24	1.30	1.43
Eichstaettisaurus schroederi (B. S. P. 1937 I 1)	1.40	1.32	1.46
Ardeosaurus digitatellus (B. S. P. 1923 I 501)	1.68	1.33	1.46
Palaeolacerta bavarica Mus. Maxberg	1.12 est.	1.32 est.	—
Alligatorellus beaumonti (B. S. P. 1937 I 26)	1.03	1.17	2.0
Atoposaurus oberndorferi (B. S. P. 1901 I 12)	1.03	1.13	1.97

tity of this skeleton, the question remains: What is it? Can it be identified? I believe that it is identifiable. After examining various other Solnhofen specimens, and reviewing the literature on other small tetrapods from the Solnhofen beds, I am convinced that these remains are those of a small individual of the lacertilian, *Bavarisaurus*. Recognizing that the small size of this specimen may be due to immaturity, comparison of limb proportions and other size factors must be viewed with skepticism. Nevertheless, the ratios of femur to tibia, femur to humerus and tibia to metatarsus (Table 4) agree quite closely with those of the type specimen of *Bavarisaurus macrodactylus* (Hoffstetter, 1953), and several species of *Homoeosaurus*. Reference of these remains to any species of *Homoeosaurus* is precluded by the thecodont (or perhaps pleurodont), rather than acrodont, dentition.

In addition to this dimensional evidence, further support for identifying these remains as *Bavarisaurus* is found in the several distinctive parts of the skeleton preserved. The foot, as I have reconstructed it in Figure 10, corresponds quite closely with that of *Bavarisaurus macrodactylus* (see Fig. 12), except for the unknown state of the fifth toe in the present specimen. In addition, *Bavarisaurus* possesses a large, irregular-shaped astragalo-calcaneum (see Fig. 40C of Cocude-Michel, 1963), although preservation does not permit recognition of close morphological similarities. These elements are illustrated in Plates 13 & 14. Also important here is the distal end of the humerus, which is

very similar to that of *Bavarisaurus* (see Fig. 2B, Hoffstetter, 1964), as I have attempted to show in Plate 14: 4 & 5. Finally, the construction of the numerous caudal vertebrae seem to provide the most compelling evidence of all for identifying these remains as *Bavarisaurus* cf. *macrodactylus*.

As shown in Figures 8 and 13, an extremely long series of caudal vertebrae are folded back and forth on itself into four sub-parallel rows. Microscopic examination of these vertebrae reveals that all except the most proximal centra are marked by complete and well-defined autotomy sutures. Each suture traverses the middle of the centrum in a nearly vertical course, then bends sharply forward in its upper part (Plate 14:1). This identical structure (see Plate 14:2), and what appears to be the same vertebral morphology, are found in all preserved caudal vertebrae of the type specimen of *Bavarisaurus macrodactylus* (see Fig. 1b, Hoffstetter, 1964). Furthermore, the morphology and disposition of the long transverse processes of the proximal caudals in the small specimen are like those of *Bavarisaurus*. The only apparent difference between the two specimens is the extremely long tail of the small individual and the apparently relatively short tail in the type of *Bavarisaurus*. The latter, however, looks as though it might have been shortened as a result of tail autotomy: the last distinct vertebra is still quite large, causing the tail extremity to have a somewhat "stubby" appearance. Also, there is a faint impression distal to the last recognizable caudal which
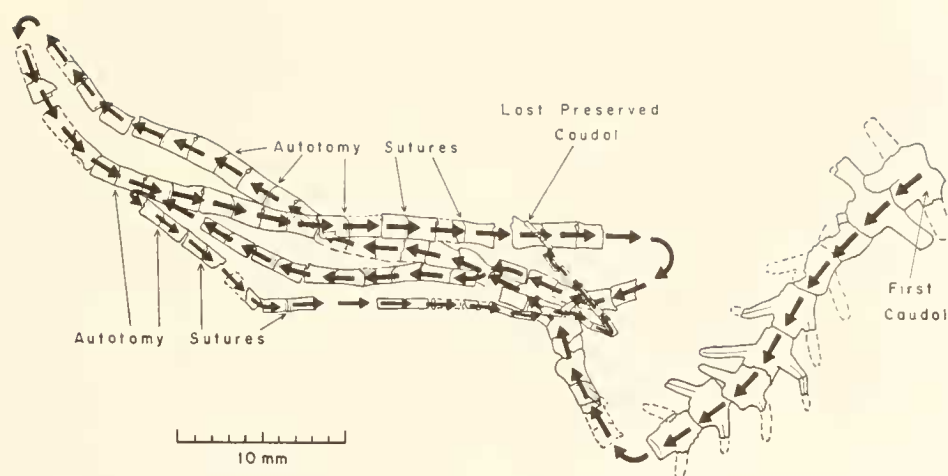
Figure 13: Outline drawing of the folded caudal series of the small reptile, taken from Figure 8. Missing segments are restored by dashed outline. The heavy arrows register my reconstruction of the caudal sequence, progressing from the first caudal to the extremity. Notice the forward flexure of the autotomy sutures.

looks to be that of a fleshy stump-like tail extremity, reminiscent of regenerated tail stumps that are commonly found in modern autotomous lizards. Another aspect of the caudal anatomy preserved in these two specimens that may be important is that a l l caudal centra, except the most proximal segments, seem to be autotomous. In most modern autotomous lizards, autotomy fracture planes occur throughout the caudal series (except for a few proximal segments), but functional autotomy may be confined to a limited region of the tail by progressive ontogenetic fusion at the autotomy cartilage septa throughout the other parts of the tail (Etheridge, 1967).

The extraordinary length of the tail in the specimen within *Compsognathus* appears highly improbable at first glance, but all I can do is to present the evidence as I see it. In Figure 13, I have traced the sequence of caudals (line of heavy arrows) as I interpret it, from the sacrum through four 180 degree bends, to the delicate tail extremity. A minimum of 50 segments can be discerned, and the total length of this folded series is not less than 19 cm. That is more than four times the probable body length of 46 mm (estimated from the proportions of the larger-sized type specimen of *Bavarisaurus*). Improbable though such an extreme tail length seems, I am convinced that it is correct. The only other possible explanation is that more than one caudal series is present among these stomach contents. Against that interpretation, I offer the following evidence: 1) There is no other evidence that more than one individual is preserved within the the body cavity of *Compsognathus;* 2) Notice that the complete sequence as interpreted in Figure 13 consists of progressively smaller vertebrae proceeding toward the tail

tip; 3) Notice also, that the dorsal flexure of the autotomy sutures consistently bend in a forward direction — toward the sacrum — showing that two of the four rows are oriented in one direction (with the anterior end toward the rib cage) and the other two rows are oriented in the opposite direction (with the anterior end pointing away from the rib cage). This verifies my interpretation that the "ends" of the vertebral rows actually are "folds" — 180 degree bends, as illustrated in Figure 13; 4) And finally, there is a physical break at an autotomy fracture plane at each of the three proximals folds in the tail. From these facts, I conclude that these parallel rows of vertebrae represent a folded, but nearly continuous caudal series of a single individual. Thus the extraordinary tail length is correct.

Other parts of the so-called *Compsognathus* embryo skeleton are much too fragmentary to be of reliable value in support of this identification, but the pelvic bone does seem to resemble the L-shaped ilium of the type specimen of *Bavarisaurus*. Also, the ribs of *Bavarisaurus* are quite robust in construction (but not pachyostostic), and are single-headed, as in the small specimen. A very small fragment of the anterior tip of the left dentary of *Bavarisaurus* preserves small, sharp, conical pleurodont teeth, which are very similar to the teeth in the tiny jaw on the *Compsognathus* slab. The latter, however, appear to be thecodont, although this mandible lies on its medial surface and a pleurodont implantation cannot be ruled out.

In summary, a surprising amount of anatomical and proportional evidence establishes the identity of *Compsognathus'* last meal as a young individual of *Bavarisaurus* (cf. *macrodactylus*).

COMPSOGNATHUS THE ANIMAL

The Munich Specimen: Adult or Juvenile?

Curiously enough, the small size of the type specimen of Compsognathus has never provoked published inquiry about the maturity of this individual, although the question has often been debated in classroom discussions. In fact, the literature on Compsognathus seems to meticulously avoid the subject, tacitly treating the matter as though there could be no question, and accepting the Munich specimen as an adult individual. That conclusion is far from established, as the discovery of the Nice specimen clearly demonstrates.

As was mentioned earlier, the Munich specimen gives the appearance of being a mature individual, at least in the texture and completeness of the bones of the skeleton and the apparently closed sutures of the vertebral column. However, other factors (besides its small size) suggest that it may not be a fully mature specimen. But with only two specimens available for comparison, no definitive statement can be made.

Three distinctive features of C. longipes suggest, but do not prove, that this is not a fully adult individual: 1) The relatively large skull; 2) The disproportionately large orbit; 3) The relatively long hindlimbs. As is well-known, the head is disproportionately large in all hatchling or new-born amniotes, but in some theropods (Megalosauridae, Tyrannosauridae) the skull remained disproportionately very large in the adult stage. A comparison of skull and post-cranial proportions of Compsognathus and various other theropods (given on page 82), unfortunately proves to be inconclusive as regards the relative ontogenetic age of the Munich specimen.

Even though the occipital and posterior portions of the temporal region are not preserved, the orbit can be seen to be relatively enormous compared with the estimated length of the skull (70 to 75 mm). Using

Kälin's (1933) skull — orbital — length index $\frac{(19\ mm \times 100)}{72\ mm}$ gives a relatively high value of 26, which by comparison with Kälin's numbers suggests a juvenile state. Skull — orbital — length indices for other theropods are given in Table 5, but again, comparisons with Compsognathus are not conclusive, because we are comparing different taxa rather than individuals known to be of differing ages, but belonging to the same species. Yet, the type specimen of Compsognathus does have one of the highest skull — orbital — length indexes among theropod specimens.

Finally, as was noted earlier, the hindlimb length of Compsognathus is relatively long (but not excessively for theropods) and is reminiscent of precocial limb proportions in the young of certain cursorial animals (horse, deer, antelope, etc.). Yet, for the simple reason that the hindlimb is not unusually long for a theropod (of any size) clearly indicates that we should not consider long limb length p e r s e as evidence of immaturity. Comparison with the only other specimen certifiably referrable to Compsognathus (the French specimen, "C. corallestris") offers little additional evidence in this regard. For example, the ratio of total hindlimb length to presacral length is approximately the same in "C. corallestris" and C. longipes (1.10 vs 1.11), even though the French specimen is 50% larger. (I obtained a different presacral length than the authors of "C. corallestris", measuring 31 cm, with two cervicals missing or unmeasurable. Adding an average vertebral length of 16 mm for each of the two missing segments, I estimated the total presacral length to be 34.2 cm.) Assuming my vertebral length estimate to be reasonably close, there is no difference in the relative hindlimb lengths of these two specimens. If these two specimens belong to the same species, as I believe, this indicates that either there was

TABLE 5

Skull — Orbital — Length Indexes of Some Theropods.

Compsognathus longipes (Holotype)	26
Compsognathus longipes (Nice specimen)	24
Ornithomimus altus	26
Ornitholestes hermanni	25
Gallimimus bullatus	24
Velociraptor mongoliensis	23
Saurornithoides mongoliensis	22
Allosaurus fragilis	14
Tyrannosaurus rex	10

little allometric change in hindlimb length during growth, or both specimens are essentially mature. Thus, on the basis of just these two specimens, it is not possible to decide whether long hindlimb length is a juvenile condition or an adult cursorial adaptation.

Returning to skull size, on the basis of my estimates of skull length and presacral column length, the skull of "*C. corallestris*" appears to have been relatively larger (.35 of presacral length) than that of *C. longipes* (.30 of presacral length), even though the latter is smaller. The difference could well be due to errors in my estimates, rather than to an unlikely positive allometric skull growth. With regard to skull — orbit — length index, *C. longipes* and "*C. corallestris*" have fairly close indexes (26 and 24). The slightly lower index for the larger French specimen suggests more advanced maturity.

With such a limited sample, none of these parameters can be considered as conclusive evidence of relative age, but I am inclined to believe that the Munich specimen of *Compsognathus* is an immature, although probably not a juvenile, individual. That belief is based primarily on the enormous size of the orbit, the larger size of the Nice specimen, and the texture and fully ossified state of the skeleton.

Reconstruction and Life Habits

Attempts to reconstruct posture and life habits of extinct animals are educated guesses at best, and must always be viewed as such. The present effort is no exception. Speculations about the functional significance of particular skeletal features are even more suspect, unless one can point to a nearly identical modern analogue. Because of its chicken-size, (estimated live weight, 3-3.5 kg), and certain bird-like features in its skeleton (foot, hind leg, skull ?), there is a natural tendency to turn to modern ground-dwelling birds for our analogues in reconstructing life style and posture in *Compsognathus*. Certainly, that seems reasonable grounds for claiming bipedal carriage in this creature. But, as Figure 14 shows, there is much else about *Compsognathus* that is not bird-like, and this is where my reconstruction falters. Whether my reconstruction in Figure 14 is any closer to the truth than the earlier reconstuctions by Huxley in 1876 (see Marsh, 1895), Marsh (1895, 1896) and von Huene (1925) can never be known, but I offer it as my best estimate of the posture and skeletal organization of *Compsognathus longipes*.

The osteology of the hind and fore limbs establish conclusively that *Compsognathus* was a biped, and in all probability, an obligate biped. The length of the forelimb, although not as shortened as has been generally held (.43 of presacral column length), when considered against the greater length of the hindlimbs, makes a four-legged stance rather awkward, but perhaps not impossible. However, the reduced two-finger construction of the manus, while not short in the absolute sense, appears to be a specialized adaptation incompatible with quadrupedal locomotion. On the other hand, we can be quite certain that the forelimbs were used to some extent in raising the animal from a resting pose, as well as in predatory activities.

At first glance, the hindlimbs appear to be unusually long, but when compared with the length of the presacral column, they are comparable to those of other theropods. The relative proportions of femur to tibia and tibia to metatarsus suggest that *Compsognathus* may have been only a moderately fast cursorial biped. That interpretation, however, is strongly contradicted by the stomach contents, which are discussed later. Using my estimate of femur length of 67 mm, the femur / tibia ratio is a moderately low .76, which is less than that of *Ornithomimus* (= *Struthiomimus*) at .88, but still much greater than that of fleet-footed struthious birds such as *Struthio* (.46) and *Casuarius* (.57). The metatarsus / tibia ratio, the commonly accepted index of cursorial ability, is a moderate .63, close to that of *Ornithomimus* (.68) and *Ornitholestes* (.73), but well below that of *Struthio* (.95) and *Casuarius* (.85). So, contrary to earlier suppositions, *Compsognathus* appears not to have been as fleet-of-foot as some other "coelurosaurian" theropods. In fact, this last ratio is surprisingly close to that of graviportal "carnosaurian" theropods like *Albertosaurus* (= *Gorgosaurus*), although *Compsognathus* obviously cannot be categorized as graviportal. Perhaps this "graviportal" index, and the stomach contents of *Compsognathus*, are important reasons for us to re-examine the theoretical basis of designating certain limb element ratios as "graviportal" and others as "cursorial".

Compared with the hindlimb, the forelimb definitely is reduced, measuring only 38 % of hindlimb length and 43 % of presacral vertebral length. This compares with typical non-tyrannosaurid forelimb / presacral ratios that range from .50 to .60. Despite its somewhat reduced length, though, the forelimb elements of *Compsognathus* are quite robust and the hand equals almost 40 % of the total forelimb length. All of this suggests an active and powerful role for the anterior appendage. This interpretation is reinforced by the relatively large coracoids, the very prominent acromion and the stout scapula. The acromion and coracoids especially, suggest the presence of a powerful pectoral and deltoideus musculature, which in turn implies powerful antero-ventral adduction and flexion of the forelimb and hand, and strong elevation of the humerus. Presumably, these actions were critical in the prey-catching process, but exactly how is not clear.

The unique design of the manus — long, but reduced to just two functional fingers (one of which has
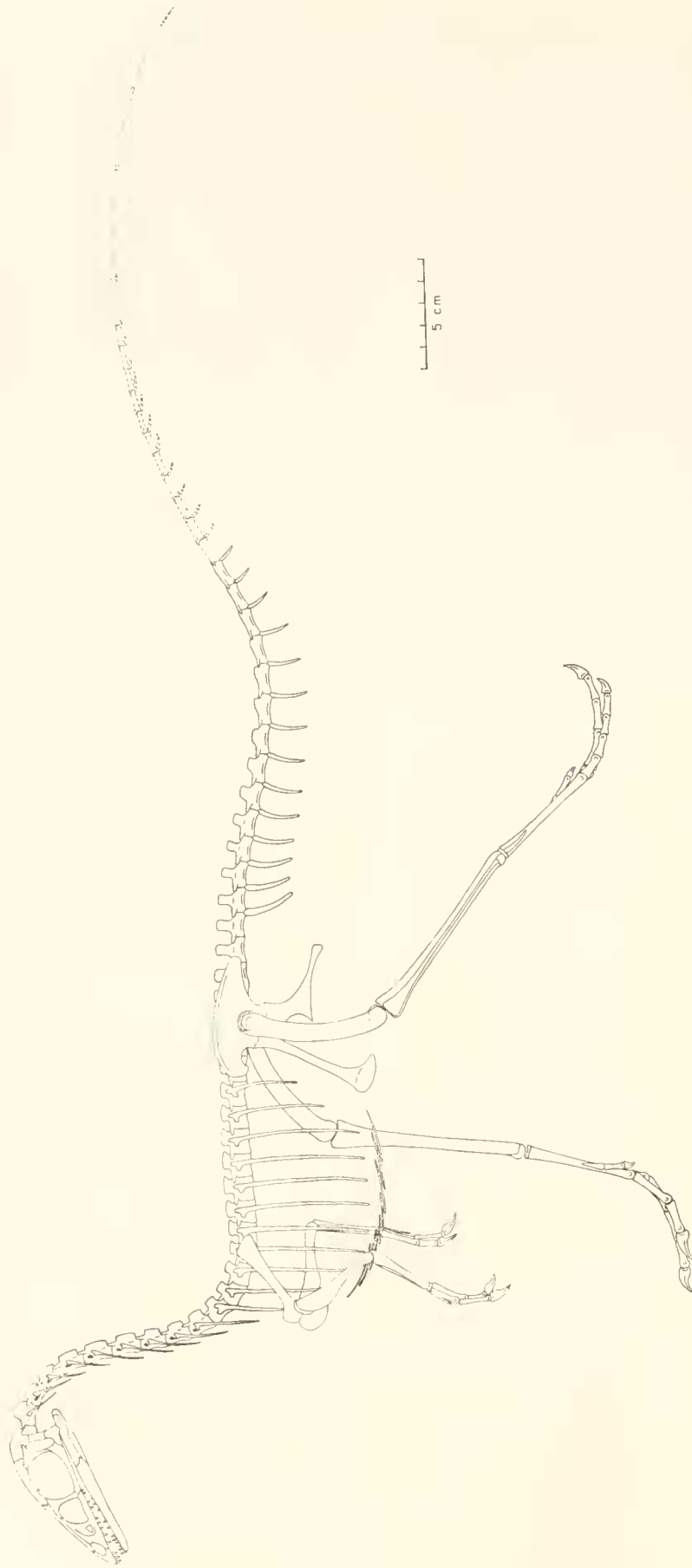
Figure 14: Skeletal reconstruction of *Compsognathus longipes*. The distal parts of the tail are hypothetical, as is the exact form of the ilium and the posterior part of the skull. Notice the large size of the head, the long hands, and the great length of the foot and metatarsus.

5 cm

a reduced phalangeal formula) — is difficult to understand, especially when considered in terms of the more usual three-fingered hands of most other theropods, or the more primitive five digit manus. First thoughts are that the manus of *Compsognathus* was not suited for raptorial activities, and this seems to be substantiated by the rather straight and short form of the unguals (see Figs. 5 and 6), and the reduced phalangeal count of digit II, as compared with the ungual form of other theropods. However, that interpretation seems to be in conflict with the robust construction of the arm and hand, and the prominent elements of the shoulder girdle. My conclusion is that the hand was specialized for some role, but probably not the usual prey-catching action usually envisioned for most theropods. But what kind of activity requires a long, stout, two-fingered hand? Is it possible that it served as a digging structure — to tear apart insect nests, ant hills or termite mounds? That seems unlikely in view of the stomach contents.

That *Compsognathus* was a predator, there can be no doubt. The dentition alone indicates that. Since virtually all modern flesh-eating vertebrates are opportunistic feeders, we can be certain that *Compsognathus* ate whatever small creatures it could find and catch. For that reason, and because of its small size, we should conclude that *Compsognathus* probably was insectivorous, at least in part. But in addition, the tiny skeleton preserved within *Compsognathus* is dramatic and indisputable evidence that *Compsognathus* preyed on small vertebrates as well. Identification of these stomach contents as *Bavarisaurus* (cf. *macrodactylus*) provides specific critical evidence about the food-seeking habits and skills and the food preferences of *Compsognathus* that go far beyond any previous intuitive deductions about the predatory habits of any other theropod (*Deinonychus* included). Dinosaur remains that contain recognizable stomach contents, let alone identifiable food items or prey remains, are extremely rare. So whatever can be deduced about the adaptations and live nature of *Bavarisaurus* provides unusual specific insight into the hunting skills and behavior of *Compsognathus*.

Overall, the relative proportions of the tail, the limbs and feet of *Bavarisaurus* are quite similar to those of modern lizards that are noted for their speed and/or agility, such as certain teiids, iguanids, lacertids and agamids. The type specimen of *Bavarisaurus macrodactylus* (B. S. P. 1873 III 501) displays the usual lacertilian disparity of hindlimb vs. forelimb length. But more important, is the fact that the pes is markedly longer than the manus. Most important of all, though, is the extremely long tail of *Bavarisaurus*, as can be seen in the remains preserved within *Compsognathus* (see Fig. 8 and Plate 13). Romer (1956) observed that long tails are most common among
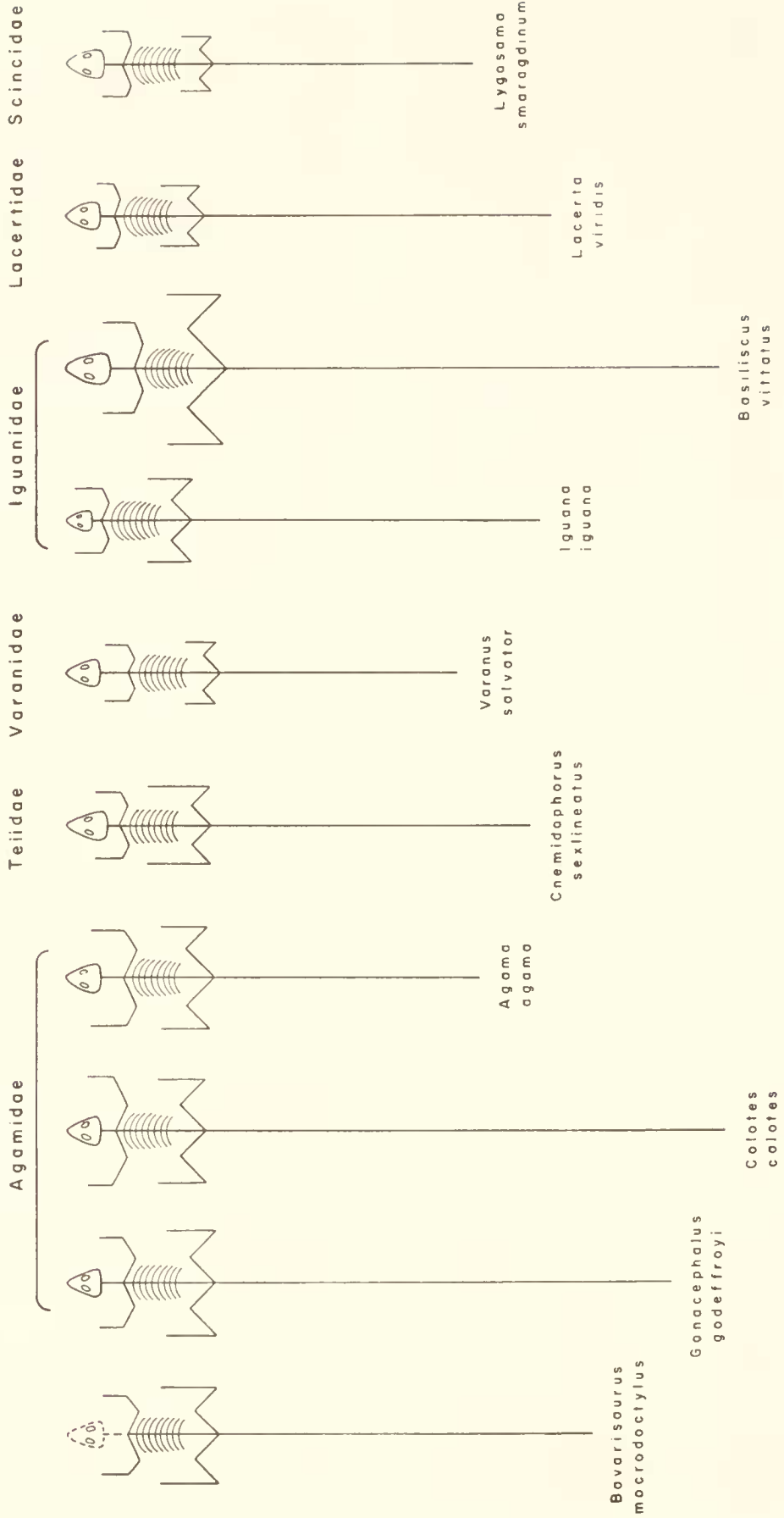
arboreal lizards. While that is true, long tails are also typical of many of the fastest-running ground-dwelling species, such as some teiids and iguanids.

In Figure 15, I have plotted the major body parameters of some of the longest-tailed living lacertilian species for comparison with those of *Bavarisaurus* (taken from both the type specimen and the remains within *Compsognathus*). Of interest here are the several species (and there must be others) in which the tail is relatively longer than in *Bavarisaurus*. For example, the agamids *Gonocephalus godeffroyi* and *Calotes calotes*, among the longest-tailed lizards known, are very active climbing and leaping forms. *Agama agama* also is an active climber, but perhaps not as quick as *Gonocephalus* and *Calotes*. *Iguana iguana* and *Lacerta viridis* also are long-tailed, although not to the extent of the two agamids included above, but the iguanid, *Basiliscus vittatus* has a tail length comparable to that of *Calotes calotes*. *Iguana iguana* is a good climber, but also is a fast runner. *Lacerta viridis* is predominantly a running form, as is the teiid *Cnemidophorus*. Mertens (1960) recorded that *Cnemidophorus limniscatus* was capable of speeds up to 15 miles (23 km) per hour over short distances. *Basiliscus* also is noted for its high running speed, and its ability at maximum velocity to run on its hind legs (notice [Fig. 15] the extreme disparity of hindlimb vs. forelimb length, as compared with another fast-running form, *Cnemidophorus sexlineatus*). From these data, I conclude that long tails from 3 to 5 times the body length, are found in both highly cursorial and active climbing lizards.

The question of interest here, is, can we determine whether *Bavarisaurus* was predominantly a fast-running ground-dweller, or an agile climber? I think we can.

Notice in Figure 15 that the hands and feet of climbing forms (the agamids and *Iguana*) are not so disproportionate, and in *Agama* they are of nearly equal length. Presumably, this is a reflection of the need for enhanced (enlarged) grasping powers of the manus in climbing species. In the highly cursorial species, on the other hand, the manus is conspicuously shorter than the pes — extremely so in *Cnemidophorus*, and somewhat less so in *Basiliscus* and *Lacerta*. On this basis, the elongated foot and relatively short hand of *Bavarisaurus* suggest that it probably was a fast-running ground lizard, rather than a habitual tree-dwelling or climbing species.

While the data of Figure 15 represent only a small sampling of the Lacertilia, and may be viewed as merely suggestive but not conclusive as regards the living habits of *Bavarisaurus*, one additional piece of evidence preserved in the "consumed" specimen strongly supports the cursorial interpretation. That evidence is the autotomy fracture septa of the caudal

Scincidae — *Lygosoma smaragdinum*

Lacertidae — *Lacerta viridis*

Iguanidae — *Basiliscus vittatus*

Iguana iguana

Varanidae — *Varanus salvator*

Teiidae — *Cnemidophorus sexlineatus*

Agamidae — *Agama agama*

Calotes calotes

Gonocephalus godeffroyi

Bavarisaurus macrodactylus

vertebrae. Autotomy is far from rare in modern lizards, but it does seem to occur most commonly in ground-dwelling species.

On the basis of the autotomous and very long tail, and the hand and foot proportions, the picture that emerges of *Bavarisaurus* is one of a very fast-running, predominantly ground-dwelling lizard, perhaps similar to the living species of *Cnemidophorus*. From this unusual evidence, it is clear that *Compsognathus* was equipped to pursue and catch very fast-running and agile prey. If you have ever attempted to run down and catch specimens of *Cnemidophorus* (as I have) or *Basiliscus*, you can appreciate what that involves — keen sight, rapid acceleration, high speed and quick reaction and maneuverability.

AFFINITIES OF *COMPSOGNATHUS*

Early attempts, especially those by Huxley (1870), to decipher the affinities of *Compsognathus*, were confounded by the facts that the tibia was significantly longer than the femur and the cervical vertebrae were viewed as "elongated", conditions that were unknown in other then-known dinosaurs. These conditions led Huxley to propose his higher taxon, Compsognatha, which he ranked equally with the Dinosauria. The problem was that almost no other remains of small dinosaurs, let alone what we would now identify as "coelurosaurian" theropods, were known at the time. Not until the 1880's did fragmentary remains of small theropods begin to surface: *Coelurosaurus*, 1865; *Coelurus*, 1879; *Hallopus*, 1881; *Thecospondylus*, 1882; *Aristosuchus*, 1887; *Coelophysis*, 1889; *Ornithomimus*, 1890; *Agrosaurus* and *Calamospondylus*, 1891. But none of these finds were anywhere near as complete as the specimen of *Compsognathus*. Most consisted of only a few vertebrae, or teeth, or limb fragments. Only the specimens of *Hallopus* and *Coelurus* preserved sufficient parts to permit meaningful comparisons. Thus, it is not surprising that early works often allied *Compsognathus* with *Hallopus*, and somewhat less frequently with *Coelu-*

rus. But, it is important here that proper credit be given to Huxley. Despite these facts, and its diminutive size, as early as 1868 Huxley perceived that the affinities of *Compsognathus* were among or close to the giant dinosaurs.

Walker (1970) established conclusively that *Hallopus* has nothing whatever to do with theropods, but is an early crocodilian. This leaves *Coelurus* and a relatively small number of adequately founded theropod taxa for comparison with *Compsognathus*, out of a total of 40-odd genera listed by Steel (1970) under the "Coelurosauria". These other taxa are: *Coelophysis*, *Coelurus*, *Halticosaurus*, *Ornitholestes*, *Procompsognathus* and *Segisaurus*. While the type specimens of other small theropods may be adequate bases for establishing the respective taxa, I consider the types of *Avipes*, *Velocipes*, *Agrosaurus*, *Aristosuchus*, *Calamospondylus*, *Caudocoelus*, *Coelurosaurus*, *Thecocoelurus* and *Thecospondylus* to be quite inadequate for assessing the affinities of *Compsognathus*. And for obvious reasons, there can be no c l o s e relationship between *Compsognathus* and oviraptorids, ornithomimids or dromaeosaurids, so these will not be reviewed here.

Figure 15: Diagramatic comparison of the main skeletal components of *Bavarisaurus* cf. *macrodactylus* (the stomach contents of *Compsognathus*) with those of selected modern, long-tailed lizards. All skeletons are represented with equal body lengths to facilitate comparison of relative tail lengths. Data on *Bavarisaurus* are derived from the type specimen (B. S. P. 1873 III 501) and the remains preserved within the rib cage of *Compsognathus*. Data on the recent lizard species were obtained from specimens in the Bayerische Zoologische Staatssammlung, through the courtesy of Dr. U. Gruber. The long-tailed agamids, *Gonocephalus* and *Calotes*, are extremely active and agile climbers. *Iguana* also is a good climber, but is a speedy ground runner as well. The other species illustrated are predominantly ground-dwelling forms, all of which are fast over short distances. Fastest of all, are the teiid *Cnemidophorus* and especially the iguanid *Basiliscus*. Long tails seem to be typical of highly active lacertilians and not distinctive p e r s e of either predominantly climbing species, or highly cursorial forms. However, there is other evidence in the data plotted here that is suggestive: there appears to be less disparity of fore and hind foot length in the climbing forms (agamids, *Iguana*) than there is in the fast-running ground dwelling kinds (*Cnemidophorus* and *Basiliscus*).

Compsognathus is distinct from each of six previously mentioned genera as follows:

1) *Coelophysis* (Late Triassic): High tooth count ($\frac{23}{12}$), deep mandible, four-fingered manus, femur and tibia sub-equal, no distal pubic expansion or expansion is very small, dorsal vertebrae are pleurocoelous.

2) *Halticosaurus* (Late Triassic): Deep mandible, five-fingered manus, femur longer than tibia, dorsal vertebrae possibly pleurocoelous.

3) *Procompsognathus* (Late Triassic): Broad apron-like pubic plates as in pseudosuchians, with a long mid-line symphysis and lacking a distal expansion.

4) *Segisaurus* (Late Triassic): Presence of clavicles and an interclavicle (?), three-fingered manus, and what appears to be a prominent calcaneal tuber.

5) *Coelurus* (Late Jurassic): Cavernously pleurocoelous dorsal vertebrae, and extremely elongated metatarsals.

6) *Ornitholestes* (Late Jurassic): Three-fingered manus, and femur longer than tibia.

The distinctive features of *Compsognathus* are: The very slender or shallow mandible, "bent" form of the anterior teeth, "sub-equal" length of cervical and dorsal vertebrae, pleurocoelus cervicals and non-pleurocoelous dorsals, very short ischium (relative to pubic length) and two-fingered construction of the hand. The most important of these, in my opinion, is the specialized design of the manus, and on that basis alone I place *Compsognathus* in its own separate family, Compsognathidae. My rationale for this is first, no other theropod is presently known which posesses this unique manus morphology, and second, this construction of the manus precludes *Compsognathus* being ancestral to any other known theropod. I have no doubt that some critics will point out that the exact design of the manus in *Compsognathus* is open to question, but I think it has been demonstrated above that the hand could not have consisted of more than two fingers, both of which apparently were constructed of two phalanges. Contrary to the view of some, that the phyletic loss of structures should not be considered as specialized or advanced conditions, I believe the two-fingered hand of *Compsognathus* does represent a specialized adaptation. But more important, the unique phalangeal formulae (2-2-0) establish that this is unrelated to the digital reduction characteristic of later deinodonts (*Albertosaurus*, *Tarbosaurus* and *Tyrannosaurus*), where the formulae are 2-3-0.

If the evidence for close relationship between *Compsognathus* and known "contemporaneous", or later theropods is preclusive, as I believe it is, then evidence for close affinity with earlier taxa is less conclusive, although suggestive. The presence of a two-fingered manus precludes "close" relationship with later three-fingered forms, but it does not negate proximity to preceding three-(or more)-fingered kinds. Among the pre-*Compsognathus* theropods mentioned above, *Procompsognathus triassicus* is the most interesting. The type specimen (S. M. N. S. 12 591), named but not described by Fraas (1913), consists of a dorso-ventrally crushed incomplete skull and mandibles, a complete right hindlimb and foot, left femur, both pubes, the left scapulo-coracoid, a radius and ulna, ten dorsal vertebrae plus ribs, five or six cervicals and eight or nine caudals. Additional material (S. M. N. S. 12 352) found later, consisting of an incomplete manus and pre-orbital parts of a somewhat larger skull, were referred to this species by von Huene (1921 a), but his referral must be viewed with skepticism.

In several respects, the type remains are quite similar to those of *Compsognathus longipes*, most notably in the construction and proportions of the foot and dorsal vertebrae, and to a lesser extent, the hindlimb. The chief differences lie in the distinctly primitive design of the pubes (broad transverse plates meeting in a long mid-line symphysis with no distal expansion) and the long transverse processes of the proximal caudal vertebrae. The femur to tibia ratio also differs slightly (.83 in *Procompsognathus* to .76 in *Compsognathus*). Although the pubis is relatively much longer than in most pseudosuchians, approaching the length of the femur as in theropods, its broad transverse, apron-like form is reminiscent of the pseudosuchian condition. This primitive design of the pubis contrasts with the advanced design of the foot, which is remarkably similar to that of *Compsognathus* (see Fig. 16).

The type skull of *Procompsognathus* is moderately crushed dorso-ventrally, making comparison with the laterally crushed skull of *Compsognathus* somewhat difficult. The nares are indistinct, a large triangular antorbital fossa is present containing what appears to be two disparate sized fenestrae, and the orbit is quite large. The mandibles appear to be very shallow, as in *Compsognathus*, but the teeth are of typical theropod form, with no sign of the "bent" shape characteristic of the anterior teeth of *Compsognathus*.

Von Huene (1921 a), considered *Procompsognathus* to be a "coelurosaur" — presumably close to *Compsognathus* — and over the ensuing years it has consistently been placed with other small or lightly-built Triassic theropods (or presumed theropods, such as *Hallopus*). That would seem to be a reasonable assignment in view of the distinctly theropod-like design of the pes. But the apparently pseudosuchian-like construction of the pubis, together with the indeterminate condition of the acetabulum and the absence of
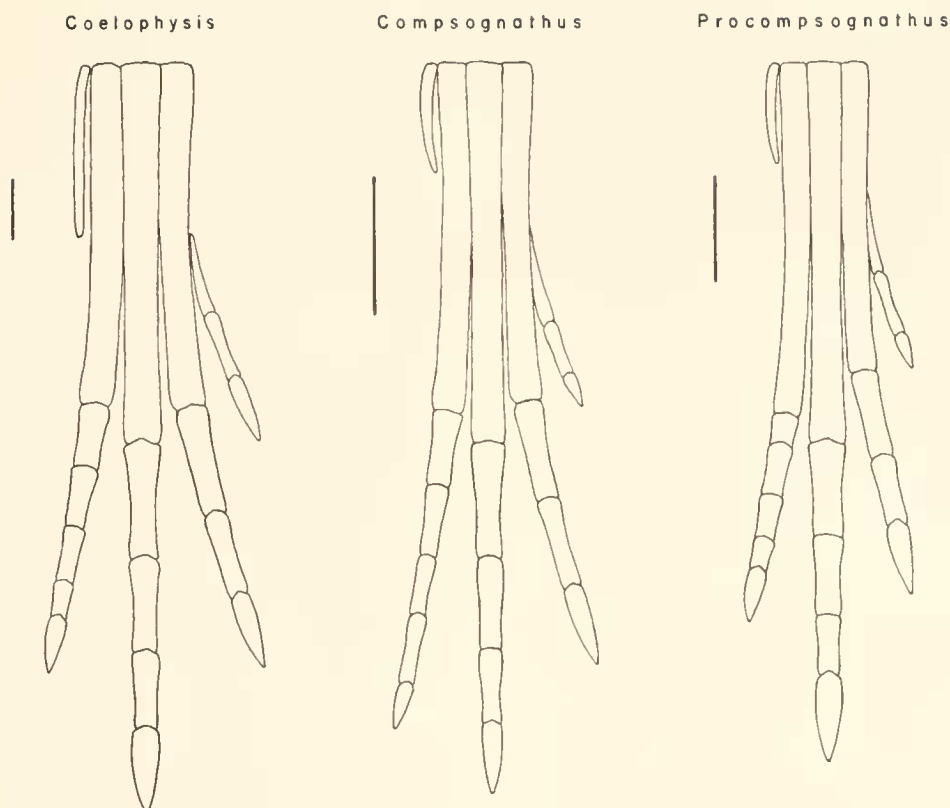
Coelophysis   Compsognathus   Procompsognathus

Figure 16: Comparison of foot morphology in *Compsognathus longipes, Procompsognathus triassicus* (S. M. N. S. 12 591) and *Coelophysis longicollis* (A. M. N. H. 7223). All three are drawn with the third metatarsals equal in length to eliminate size differences and to show the relative proportions of the digits to the metatarsus. The similarities are obvious. The foot of *Compsognathus* might have been derived from either *Procompsognathus* or *Coelophysis* — or a common ancestor of these Triassic forms. The vertical lines equal 20 mm for all three specimens, to show relative sizes.

other pelvic bones, raises the question as to whether this specimen is truely theropodan, or perhaps thecodontian. That question takes on added significance in the light of recent discoveries of the small pseudosuchians (?) *Lagosuchus* and *Lagerpeton* (Romer, 1971, 1972) from the Middle Triassic of Argentina. Both of these taxa possess an elongated foot with reduced digits I and V, and what appears to be near meso-tarsal grade ankle joints.

Until a very much needed, new and detailed analysis of *Procompsognathus* is available, little can be said about its placement, or its possible relationship to *Compsognathus*. However, I suspect that these remains represent those of a late, but advanced (in foot structure) pseudosuchian not ancestral to any theropod. *Compsognathus* appears to represent a dead-end theropod line derived from the primitive podokesaurids (*Coelophysis, Halticosaurus*). The foot of podokesaurs is typical theropod in its construction and comparable to that of *Procompsognathus* (see Fig. 16), but the pelvis is more advanced than that of *Procomp-*

sognathus, at least in the form of the pubis. This last point, together with overall primitive theropodan anatomy of *Coelophysis* (as the best-known podokesaurid), qualify podokesaurids as possibly ancestral to *Compsognathus*, coelurids and perhaps other theropods.

One final observation concerning the possible affinities of *Compsognathus*, is required here. Elsewhere (Ostrom, 1973, 1976b), I have argued that *Archaeopteryx* and later birds evolved from a "coelurosaurian" ancestry, and I raised a speculative question (1974) "whether some small theropod dinosaurs might have had feathers". As a small theropod, *Compsognathus* cannot be very far removed from the theropod line that gave rise to birds, but its reduced manus, as well as its contemporaneous occurrence with *Archaeopteryx*, exclude it from direct ancestry of *Archaeopteryx* and later birds.

If the speculative question about feathered "coelurosaurs" can ever be answered, the Munich specimen

of *Compsognathus* is the critical specimen to examine. It is the smallest of known theropods and it comes from the same Solnhofen limestones (but not exactly the same facies) as the specimens of *Archaeopteryx* with their distinct feather impressions. There are n o feather impressions — nor any evidence whatever that is suggestive of feathers — anywhere on the *Compsognathus* slab. The reader can be sure that I made an exhaustive examination, under various lighting conditions, in search of evidence for feathers, but to no avail. If feathers had been present in *Compsognathus*, it is inconceivable to me that no evidence of them would be preserved, considering the complete and almost undisturbed manner in which the skeleton is preserved, the fine details of the skeleton, and the presence of portions of one horny claw. But the fine-grained matrix shows nothing. Thus, I conclude that *Compsognathus* almost certainly was not feathered.

LITERATURE CITED

BAKKER, R. T., & GALTON, P. M. (1974): Dinosaur monophyly and a new class of vertebrates. — Nature, 248 (5444): 168—172, 4 Figs.; London.

BARSBOLD, R. (1976): Zur Evolution und Systematik spätmesozoischer Raub-Dinosaurier. — Paläont. und Biostrat. d. Mongolei Trudy, Ausg. 3: 68—75; Moskau.

BARTHEL, K. W. (1976): Coccolithen, Flugstaub und Gehalt an organischen Substanzen in Oberjura—Plattenkalken Bayerns und SE. Frankreichs. — Eclogae Geol. Helv., 69: 627—639, 2 Abb., 4 Taf.; Basel.

BAUR, J. G. (1882): Der Tarsus der Vögel und Dinosaurier. — Morphol. Jb., 8: 5—44, 2 Taf.; Leipzig.

BIDAR, A., Demay, L. & Thomel, G. (1972): Compsognathus corallestris nouvelle espèce de dinosaurien théropode du Portlandien de Canjuers. — Ann. Mus. d'Hist. Natur. Nice, I (1): 3—34, 21 Abb., 3 Tab.; Nice.

CASAMIQUELA, R. M. (1975): Herbstosaurus pigmaeus (Coeluria, Compsognathidae) n. gen. n. sp. del Jurásico medio del Neuquén (Patagonia septentrional). Uno de los más pequeños dinosaurios conocidos. — Act. Internat. Congr. Paleont. & Biostratig., Tucuman. Vol. 1: 87—101, 2 Figs., 1 Taf.; Tucumàn, Argentina.

CHARIG, A. J. (1976): "Dinosaur monophyly and a new class of vertebrates": a critical review. — In: Bellairs, A. d' A., & Cox, C. B. (1976): Morphology and Biology of Reptiles. — Linnean Soc. Symp., Ser. 3: 65—104, 10 Figs.; London.

CHARIG, A. J., ATTRIDGE, J., & CROMPTON, A. W. (1965): On the origin of the sauropods and the classification of the Saurischia. — Proc. Linnean Soc. London, 176 (2): 197—221, 2 Pls.; London.

COCOUDE-MICHEL, M. (1963): Les Rhynchocéphales et les Sauriens des calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. — Nouv. Arch. Mus. Hist. natur. Lyon, 7: 1—187, 41 Abb., 34 Taf.; Lyon.

COLBERT, E. H. (1964): Relationships of the saurischian dinosaurs. — Amer. Mus. Natur. Hist. Novitates 2181: 1—24, 6 Figs.; New York.

COLBERT, E. H., & RUSSELL, D. A. (1969): The small Cretaceous dinosaur Dromaeosaurus. — Amer. Mus. Natur. Hist. Novitates 2380: 1—49, 15 Figs., 3 Taf.; New York.

COPE, E. D. (1866): [Remarks on Laelaps]. — Proc. Acad. Natur. Sci. Philadelphia, 1866: 316—317; Philadelphia.

— — (1867): [Account of extinct reptiles which approach birds]. — Proc. Acad. Natur. Sci. Philadelphia., 1867: 234—235; Philadelphia.

DAMES, W. (1884): [Über Metatarsen eines Compsognathus-ähnlichen Reptils von Solnhofen]. — Sitz-Ber. Ges. Naturforsch., 1884: 179—180; Berlin.

ETHERIDGE, R. (1967): Lizard caudal vertebrae. — Copeia, 1967, No. 4: 699—721.

FRAAS, E. (1913): Die neueste Dinosaurierfunde in der schwäbischen Trias. — Naturwiss., I, 45: 1097 bis 1100; Berlin.

GILMORE, C. W. (1920): Osteology of the carnivorous dinosauria in the United States National Museum, with special reference to the genera Antrodemus (Allosaurus) and Ceratosaurus. — Bull. U. S. Nat. Mus., 110: 1—159, 79 Figs., 36 Pls.; Washington D. C.

HOFFSTETTER, R. (1953): Les Sauriens anté-crétacés. — Bull. Mus. nat. Hist. natur., (2) 25: 345—352, 1. Abb.; Paris.

— — (1964): Les Sauria du Jurassique superieur et specialement les Gekkota de Baviere et de Mandchourie. — Senckenberg biol., 45: 281—324, 4 Abb., 8 Taf.; Frankfurt.

HÜCKEL, U. (1974): Vergleich des Mineralbestandes der Plattenkalke Solnhofens und des Libanon mit anderen Kalken. — N. Jb. Geol. Paläont. u. Mineral., 145: 153—182, 17 Abb.; Stuttgart.

HUENE, F. von (1901): Der vermutliche Hautpanzer des Compsognathus longipes Wagner. — N. Jb. Mineral. Geol. u. Paläont., 1901: 157—160, 1 Abb., 1 Taf.; Stuttgart.

— — (1908): Die Dinosaurier der europäischen Triasformation mit Berücksichtigung der außereuropäischen Vorkommnisse. — Geol. Paläont. Abh. Suppl., Bd. 1: 1—419, 315 Abb.; Jena.

— — (1909): Skizze zu einer Systematik und Stammesgeschichte der Dinosaurier. — Clb. Mineral. Geol. u. Paläont. Jg., Abt. B (1): 12—22; Stuttgart.

— — (1914): Das natürliche System der Saurischia. — Clb. Mineral. Geol. u. Paläont. Jg., Abt. B (5): 154 bis 158, 1 Abb.; Stuttgart.

— — (1920): Stammesgeschichtliche Ergebnisse einiger Untersuchungen an Trias-Reptilien. — Z. f. induktive Abstammungs- und Vererbungslehre, Bd. 24, H. 2: 159—163, 1. Taf.; Berlin.

— — (1921 a): Neue Pseudosuchier und Coelurosaurier aus dem Württembergischen Keuper. — Acta Zool., Bd. II, 1921: 329—403, 35 Abb., 4 Taf.; Stockholm.

— — (1921b): Coelurosaurier-Reste aus dem obersten Keuper von Halberstadt. — Clb. Mineral. Geol. u. Paläont. Jg. (10): 315—320. 6 Abb.; Stuttgart.

— — (1923): Carnivorous Saurischia in Europe since the Triassic. — Bull. Geol. Soc. Amer., 34: 449—468, 3 Figs.; New York.

— — (1925): Eine neue Rekonstruktion von Compsognathus longipes. — Clb. Mineral. Geol. u. Paläont. Jg. 1925, Abt. B (5): 157—160, 1 Abb.; Stuttgart.

— — (1926): The carnivorous Saurischia in the Jura and Cretaceous formations, principally in Europe. — Rev. Mus. La Plata, 29: 35—114, 56 Figs.; 2 Pls.; Buenos Aires.

— — (1928): Kurze Übersicht über die Saurischia und ihre natürlichen Zusammenhänge. — Paläont. Z., Bd. II (3): 269—273; Berlin.

— — (1932): Die fossile Reptilordnung Saurischia. — Monogr. Geol. u. Paläont., Bd. I (4): 1—361, 56 Taf.; Leipzig.

— — (1956): Paläontologie und Phylogenie der Niederen Tetrapoden. — 716 S., 690 Abb.; Jena (Fischer).

HUXLEY, T. H. (1868): On the animals which are most nearly intermediate between birds and reptiles. — Ann. Mag. natur. Hist. (4) 2: 66—75; London.

— — (1870 a): Further evidence of the affinity between the dinosaurian reptiles and birds. — Quart. J. Geol. Soc. London, 26: 12—31; London.

— — (1870 b): The classification and affinities of the Dinosauria. — Quart. J. Geol. Soc. London, 26: 32—51; London.

118

Kälin, J. A. (1933): Beiträge zur vergleichenden Osteologie des Crocodilidenschädels. — Zool. Jb. Abt. Anat. u. Ontog. der Tiere, Bd. 57: 535—714, 29 Abb., 6 Taf.; Jena.

Lambe, L. M. (1917): The Cretaceous theropodous dinosaur Gorgosaurus. — Mem. Canadian Geol. Surv., Dept. of Mines, 100: 1—84, 48 Figs.; Ottawa.

Madsen, J. H., Jr. (1976): Allosaurus fragilis: A revised osteology. — Bull. Utah Geol. Mineral. Surv., 109: 1—163, 26 Figs., 55 Pls.; Salt Lake City.

Marsh, O. C. (1878): Principal characters of American Jurassic dinosaurs, Part I. — Amer. J. Sci. (3) 16: 411—416, 6 Pls.; New Haven.

— — (1881 a): Principal characters of American Jurassic dinosaurs, Part V. — Amer. J. Sci. (3) 21: 417 bis 423, 7 Pls., New Haven.

— — (1881 b); Jurassic birds and their allies. — Amer. J. Sci. (3) 22: 337—340, New Haven.

— — (1882): Classification of the Dinosauria. — Amer. J. Sci. (3) 23: 81—86, New Haven.

— — (1883): Principal characters of American Jurassic dinosaurs, Part VIII; The order Theropoda. — Amer. J. Sci. (3) 26: 81—85, 1 Pl., New Haven.

— — (1884): Principal characters of American Jurassic dinosaurs, Part VIII; The order Theropoda. — Amer. J. Sci. (3) 27: 329—340, 7 Pls., New Haven.

— — (1895): Restoration of some European dinosaurs with suggestions as to their place among the Reptilia. — Amer. J. Sci. (3) 50: 407—412, 1 Fig., 4 Pls., New Haven.

— — (1896): Dinosaurs of North America. — 16th Ann. Rep't. U. S. Geol. Surv., 133—415, 66 Figs., 84 Pls. Washington D. C.

Matthew, W. D., & Brown, B. (1922): The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. — Bull. Amer. Mus. Natur. Hist., 46: 367—385, 1 Fig., New York.

Mertens, R. (1960): The World of Amphibians and Reptiles. — G. G. Harrap & Co., pp. 1—207, 80 Pl., London.

Nopcsa, F. (1903): Neues über Compsognathus. — N. Jb. Mineral. Geol. u. Paläont., 16: 476—494, 4 Abb., 2 Taf., Stuttgart.

Osborn, H. F. (1917): Skeletal adaptations of Ornitholestes, Struthiomimus, Tyrannosaurus. — Bull. Amer. Mus. Natur. Hist., 35: 733—771, 21 Figs., 4 Pls., New York.

Osmolska, H., & Roniewicz, E. (1970): Deinocheiridae, a new family of theropod dinosaurs. — Palaeont. Polonica, 21: 5—19, 2 Figs., Warsaw.

Ostrom, J. H. (1969a): A new theropod dinosaur from the Lower Cretaceous of Montana. — Postilla (Peabody Mus. Natur. Hist., Yale Univ.) 128: 1—17, 8 Figs., New Haven.

— — (1969b): Osteology of Deinonychus antirrhopus, an unusual theropod from the Lower Cretaceous of Montana. — Bull. Peabody Mus. Natur. Hist. 30: 1—165, 83 Figs., New Haven.

— — (1972): Carnivorous dinosaurs. — In, McGraw-Hill Encyclopedia of Science and Technology (1971—1972), by Lapedes, D., p. 176, 2 Figs., New York.

— — (1973): The ancestry of Birds. — Nature, 242 (5393): 136, London.

— — (1974): Reply to "Dinosaurs as reptiles". — Evolution, 28: 491—493, Lawrence, Kansas.

— — (1976a): On a new specimen of the Lower Cretaceous theropod dinosaur Deinonychus antirrhopus. — Breviora (Mus. Comp. Zool., Harvard Univ.) 439: 1—21, 8 Figs., Cambridge, Mass.

— — (1976b): Archaeopteryx and the origin of birds. — Biol. J. Linnean Soc. London, 8 (2): 91—182, 36 Figs.

Owen, R. (1842): Report on British Fossil Reptiles. — Rep't. Brit. Assoc. Adv. Sci. 11th Mtg., 60—204, Plymouth.

Reis, O. M. (1893): Untersuchungen über die Petrificirung der Muskulatur. — Archiv mikroskop. Anat., Bd. 41: 492—584, 3 Taf., Bonn.

Rietschel, S. (1976): Archaeopteryx — Tod und Einbettung. — Natur u. Mus., 106: 280—286, 9 Abb., Frankfurt.

Romer, A. S. (1956): Osteology of the reptiles. — Univ. Chicago Press, pp. 1—772, 248 Figs., Chicago.

— — (1971): The Chañares (Argentina) Triassic reptile fauna X. Two new but incompletely known long-limbed pseudosuchians. — Breviora (Mus. Comp. Zool., Harvard Univ.) 378: 1—10, 3 Figs., Cambridge, Mass.

— — (1972): The Chañares (Argentina) Triassic reptile fauna XV. Further remains of the thecodonts Lagerpeton and Lagosuchus. — Breviora (Mus. Comp. Zool., Harvard Univ.) 394: 1—7, 6 Figs., Cambridge, Mass.

Seeley, H. G. (1887): On the classification of the fossil animals commonly named Dinosauria. — Proc. Roy. Soc. London, 43 (260): 165—171, London.

— — (1888): The classification of the Dinosauria. — Rep't. Brit. Assoc. Adv. Sci. 57th Mtg., 698—699, Manchester.

Steel, R. (1970): Saurischia. — In, Handbuch der Paläoherpetologie, Teil 14: 1—87, 23 Figs., Stuttgart.

Stromer, E. (1934): Die Zähne des Compsognathus und Bemerkungen über das Gebiß der Theropoda. — Clb. Mineral. Geol. u. Paläont. Jg., Abt. B, 1934: 74—85, 1 Abb., Stuttgart.

Thulborn, R. A. (1975): Dinosaur polyphyly and the classification of archosaurs and birds. — Australian J. Zool. 23 (2): 249—270, 5 Figs., Melbourne.

Wagner, A. (1861): Neue Beiträge zur Kenntnis der urweltlichen Fauna des lithographischen Schiefers; V. Compsognathus longipes Wagn. — Abh. bayer. Akad. Wiss., Bd. 9: 30—38, 3 Taf., München.

Walker, A. D. (1970): A revision of the Jurassic reptile Hallopus victor (Marsh), with remarks on the classification of crocodiles. — Phil. Trans. Roy. Soc. London (B), 257: 323—372, 13 Figs., 1 Pl., London.

Welles, S., & Long, R. A. (1974): The tarsus of theropod dinosaurs. — Ann. So. Afr. Mus., 64: 191—218, 13 Figs., Capetown.

Zittel, K. A. (1890): Handbuch der Paläontologie, Abt. I, Paläozoologie Bd. III; Vertebrata (Pisces, Amphibia, Reptils u. Aves). — S. 1—900, 719 Abb., München & Leipzig.

— — (1895): Grundzüge der Paläontologie (Paläozoologie). — S. 1—971, 2048 Abb., München & Leipzig.

— — (1911): Grundzüge der Paläontologie (Paläozoologie); 2nd Ed. (Revised by Broili, F., Koken, E., & Schlosser, M.); Abt. II, Vertebrata. — S. 143—308, Abb. 265—456, München & Leipzig.

— — (1918): Grundzüge der Paläontologie (Paläozoologie); 3rd Ed. (Revised by Broili, F., & Schlosser, M.); Abt. II, Vertebrata. — S. 1—675, 786 Abb., München & Berlin.