

THE TRIASSIC GLIDING REPTILE  
*ICAROSAURUS*

EDWIN HARRIS COLBERT

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## INTRODUCTION

THE DIAGNOSIS and a preliminary description of *Icarosaurus siefkeri*, collected from the Lockatong Formation of the Newark Group at the so-called Granton Quarry in northern New Jersey (fig. 1), have already been published (Colbert, 1966). The salient characters of *Icarosaurus*, a small reptile obviously highly adapted for gliding, were outlined, and some general comparisons were made with the related gliding reptile *Kuehneosaurus*, which was collected from the Keuper fissure fillings of the Bristol Channel region of England and briefly described by Pamela Robinson in 1962.

The purpose of the present work is to offer a detailed description of *Icarosaurus*, particularly as it can now be viewed against the background of Robinson's monograph now in preparation, on *Kuehneosaurus*, the manuscript and numerous illustrations of which have been made available to the author. An additional purpose of the present paper is to attempt some analyses and

interpretations of the special adaptations in *Icarosaurus*, of the aerodynamic problems that bear on such specializations, and of the taxonomic and geologic relationships of this reptile. *Icarosaurus*, as does its close relative *Kuehneosaurus*, deserves the attention that already has been given to the European genus; both forms represent important and surprising additions to our knowledge of Triassic life.

The circumstances of the discovery of *Icarosaurus siefkeri* were outlined in a previous paper (Colbert, 1966). An earlier paper, which also included a description of a phytosaur skull found in the Lockatong beds at the Granton Quarry (Colbert, 1965), described the geological relationships of the sediments in which *Icarosaurus* was found. *Icarosaurus siefkeri* is at present known only from the type, an almost complete, articulated skeleton, discovered by Alfred Siefker and two companions, Michael Bandrowski and Joseph Geiler, at the Granton Quarry in



FIG. 1. Map of the Hudson River shores of Manhattan Island (right) and New Jersey (left). Location of the Granton Quarry (upper left) and the American Museum of Natural History (lower right) shown in heavy-lined rectangles. Scale: 2 inches = 1 mile. From Colbert (1965).

1960. Furthermore, as indicated in my 1965 paper, the sediments making up the lower portion of the Granton Quarry (now almost completely removed) are definitely of the Lockatong Formation, and may be equated with Lockatong and related beds as exposed in eastern Pennsylvania, and with the Cumnock Formation of North Carolina.

I wish to acknowledge valuable help given me during the prosecution of the detailed studies of *Icarosaurus*. Particular thanks are due to Dr. Pamela Lamplugh Robinson of the University of London for her assistance and advice, and especially for her making available to me the manuscript of her monograph on *Kuehneosaurus* as well as photographic copies of many of the figures she used in her study.

I also wish to express my appreciation to

Profs. Bruno A. Boley and Morton B. Friedman of Columbia University for much-needed advice concerning aerodynamic problems. In addition I wish again to acknowledge my indebtedness to Messrs. Siefker, Bandrowski, and Geiler for the persistence of effort and acuity of vision that led to the discovery of the specimen, as well as to their interest in its development; to Mr. Gilbert Stucker of the laboratory staff of the Department of Vertebrate Paleontology of the American Museum of Natural History for his skillful work of preparation; to Mr. Michael Insinna and Miss Jennifer Perrott for drawings, most of them new in this paper; and to Mr. Chester Tarka for photographs.

This paper is the third in my "Studies of the Granton Tetrapod Fauna."

# TAXONOMY AND REVISED DIAGNOSIS OF *ICAROSAURUS SIEFKERI*

## CLASS REPTILIA ORDER SQUAMATA SUBORDER LACERTILIA<sup>1</sup> INFRAORDER EOLACERTILIA

**DIAGNOSIS:** Skull typified by paired midline bones of skull roof. Postfrontal and postorbital bones separate. Lacrimal large and may be excluded from orbital border. Quadrate with a dorsal head articulating with squamosal; paroccipital not forming part of joint; squamosal with well-developed dorsal ramus. Numerous palatal teeth, except on ectopterygoid. Ventral process of opisthotic extending down to intervene laterally between basisphenoid and basioccipital; no vidian canal. Inner wall of braincase may be unossified in region of vestibule. No fenestra rotunda. Prearticular in some cases not fused to articular. Astragalus and calcaneum usually not fused. Vertebrae usually amphicoelous or platycoelous. Ribs may be double-headed in cervical region. (From Robinson.)

### FAMILY KUEHNEOSAURIDAE

**REVISED DIAGNOSIS:** Eolacertilians with transverse processes of dorsal vertebrae widely expanded, bearing enormously elongated mid-dorsal ribs. In life these ribs probably supported a membrane adapted for gliding flight. Bones of skeleton light, many of them hollow. Limbs slender; hind limb longer than forelimb. Skull relatively short, with large orbit and transversely broad supratemporal fenestra. Maxilla forming portion of orbital border, but lacrimal excluded from orbit. Jugal lacking posterior process; temporal region widely open ventrally. Quadrate completely free ventrally, movable on its articulation with squamosal; with well-developed lateral lamina. Pterygoids elongated. Jaw slender, with a weak symphysis, and well-developed retroarticular process. Teeth simple, numerous, subpleurodont, and homodont.

### ICAROSAURUS COLBERT

*Icarosaurus* COLBERT, 1966, p. 5.

**TYPE SPECIES:** *Icarosaurus siefkeri* Colbert.

**REVISED DIAGNOSIS:** A small reptile, presacral length, including skull, about 100 mm. Bones thin-walled and hollow. Orbits large; frontals elongated; parietals separate. Upper temporal

opening broad. Quadrate with high ascending ramus, movably articulated with squamosal; jugal a crescentic bone with no posterior ramus. No quadratojugal and no supratemporal. Nasal opening large, seemingly not divided by a median premaxillary-nasal bar. Jaws long, mandible slender and closely set with simple, homodont teeth in sockets. Palatal teeth abundantly present. Twenty-four presacral vertebrae and two sacrals. As indicated by four caudals preserved in type specimen, tail long. Vertebral centra strongly constricted in middle, neural arches high. First nine vertebrae distinct from those that follow, and evidently having slender ribs. Tenth and eleventh vertebrae with short, broad ribs, approximating in shape transverse processes of following vertebrae. Next 10 vertebrae with greatly elongated and broadened transverse processes, to which are articulated on each side single-headed, enormously elongated, and, for most part, curved ribs, longest of which considerably exceeding total length of presacral series. Scapula short and strong; coracoid plate-like. Ilium deep, articulating with pubis and ischium by sutures in a closed acetabulum. Lower bones of pelvis distally expanded. Limbs long and slender, relationship in length of femur to humerus showing that hind limb is much longer than forelimb. Humerus characterized by strong proximal process and ectepicondylar foramen. Manus with five elongated digits of specialized structure and narrow, deep unguals.

### *Icarosaurus siefkeri* Colbert

*Icarosaurus siefkeri* COLBERT, 1966, p. 6.

**TYPE:** A.M.N.H. No. 2101, a complete skeleton except for portion of tail, some ribs, left manus, and lower segments of hind limbs.

**HORIZON AND LOCALITY:** Lockatong Formation of the Newark Group, Upper Triassic. From the former Belmont-Gurnee, or "Grantton," Quarry immediately west of Tonnele Avenue and about opposite Hamilton Avenue, North Bergen, New Jersey. The layer from which the specimen was obtained has been removed; its former position now is about 6 or 7 meters above the present ground surface and is occupied by buildings and parking lots. (See Colbert, 1965, 1966, for detailed descriptions of the geologic relationships of this site.)

**DIAGNOSIS:** Same as for the genus.

<sup>1</sup>For a diagnosis of this suborder, see Romer (1956).



FIG. 2. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Skeleton as preserved, dorsal view.  $\times 1$ .

## OSTEOLOGY OF *ICAROSAURUS*

### GENERAL FEATURES

AS NOTED in the preceding diagnoses, *Icarosaurus* and *Kuehneosaurus*, the two genera presently comprising the family Kuehneosauridae, are characterized most significantly and spectacularly by the light construction of the skeleton and the enormous elongation of the ribs on each side, such specializations obviously indicating adaptations for gliding flight. Consequently these extinct genera, the oldest known lacertilians, are compared in detail with the modern gliding lizard of the Orient, *Draco*. Such comparisons are fully justified, for, although the similarities between the ancient kuehneosaurs and the modern "flying dragons," which are agamids, probably represent close parallelisms in evolution rather than lineal descent, the adaptations of the extinct genera have been so closely followed by the living genus that the latter may be utilized for interpreting the former—a fortunate situation not always available to the paleontologist.

*Icarosaurus* (fig. 2) is a small reptile, with a total presacral length slightly less than 100 mm. As only four caudal vertebrae are preserved in the specimen, the length of the tail is conjectural, but, by their individual lengths, these vertebrae indicate that the tail was quite long, as expected by analogy with the modern *Draco*. For example, the presacral length of *Draco* is no more than one-third of the total length, and, if a similar ratio held for *Icarosaurus*, one could suppose that the fossil reptile had a total length of at least 300 mm., possibly more. Of course, such a total length indicates a reptile considerably larger than the typical species of *Draco*, in which total lengths are about 200 mm., and generally comparable with the giant species of the modern genus, *Draco maximus*. Conversely, the comparisons of individual bones show that *Icarosaurus* was markedly smaller than its European contemporary, *Kuehneosaurus*.

No particulars beyond these characters of size and the light construction of the skeleton need be added to the consideration of the general features of *Icarosaurus*. This reptile shows such remarkable specializations that a discussion of its osteology is necessarily largely concerned with them.

### SKULL AND JAWS

Most, if not all, of the bones of the skull are

present in the type skeleton of *Icarosaurus* (figs. 3 and 4). Unfortunately, however, the skull was disarticulated during the process of burial and fossilization, so that the separate elements are jumbled together in a confusing pile of small, delicate bones. It was not feasible to try to separate these skull bones and remove them, one by one, from the matrix for the purpose of study because they are too delicate for such treatment, even by the most sophisticated methods of modern preparation. Consequently the interpretation of the skull has been to a considerable degree an exercise in mental as well as physical manipulation, a process of lifting the bones pictorially from their resting places and trying to put them together again in their proper relationships. In so doing, the inevitable problems of bone identifications arise, for, although most of the elements can be readily identified, there are certain doubts concerning some of them (figs. 5 and 6).

In order to carry out this work, photographic enlargements, eight times natural size, were utilized. Particular credit is due to Mr. Chester Tarka of the Department of Vertebrate Paleontology for his skill in photographing the specimen and making these enlargements. Tracings of the skull bones were made from the photographs, as far as possible, and these were used for reconstructing the skull. In many cases, however, the bones were inevitably at angles to the plane of the photograph, so that there was distortion of individual bones as they appeared in the enlargements. Corrections of such distortions were attempted as much as possible. In this connection, it was found helpful to trace the bones on thin wax plates and to cut out such tracings. These wax replicas could then be bent to reproduce the original shapes and curves of the bones. In this way it was possible to arrive at a three-dimensional concept of the skull that may have a considerable degree of validity.

The skull of *Icarosaurus* is similar to that of *Kuehneosaurus* in its general proportions (figs. 7 and 8). In dorsal aspect it is triangular, with its broadest portion at the posterior borders of the orbits. This dimension is only slightly less than the total skull length. Consequently the skull appears to be very broad in occipital view, but in lateral aspect it has considerable depth. The mandibular ramus is comparatively slender.



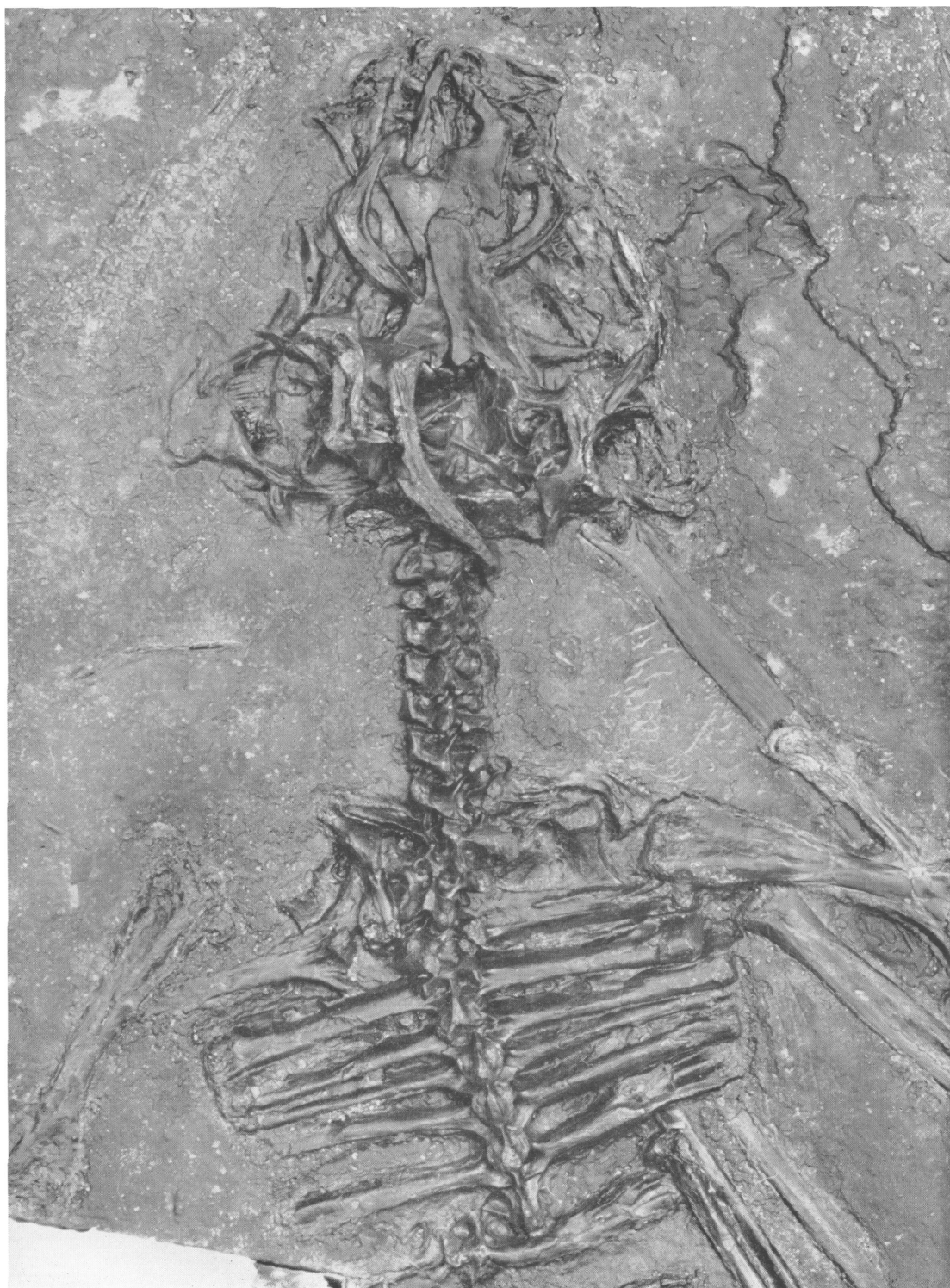


FIG. 3. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Anterior portion of skeleton, dorsal view.  $\times 3$ .



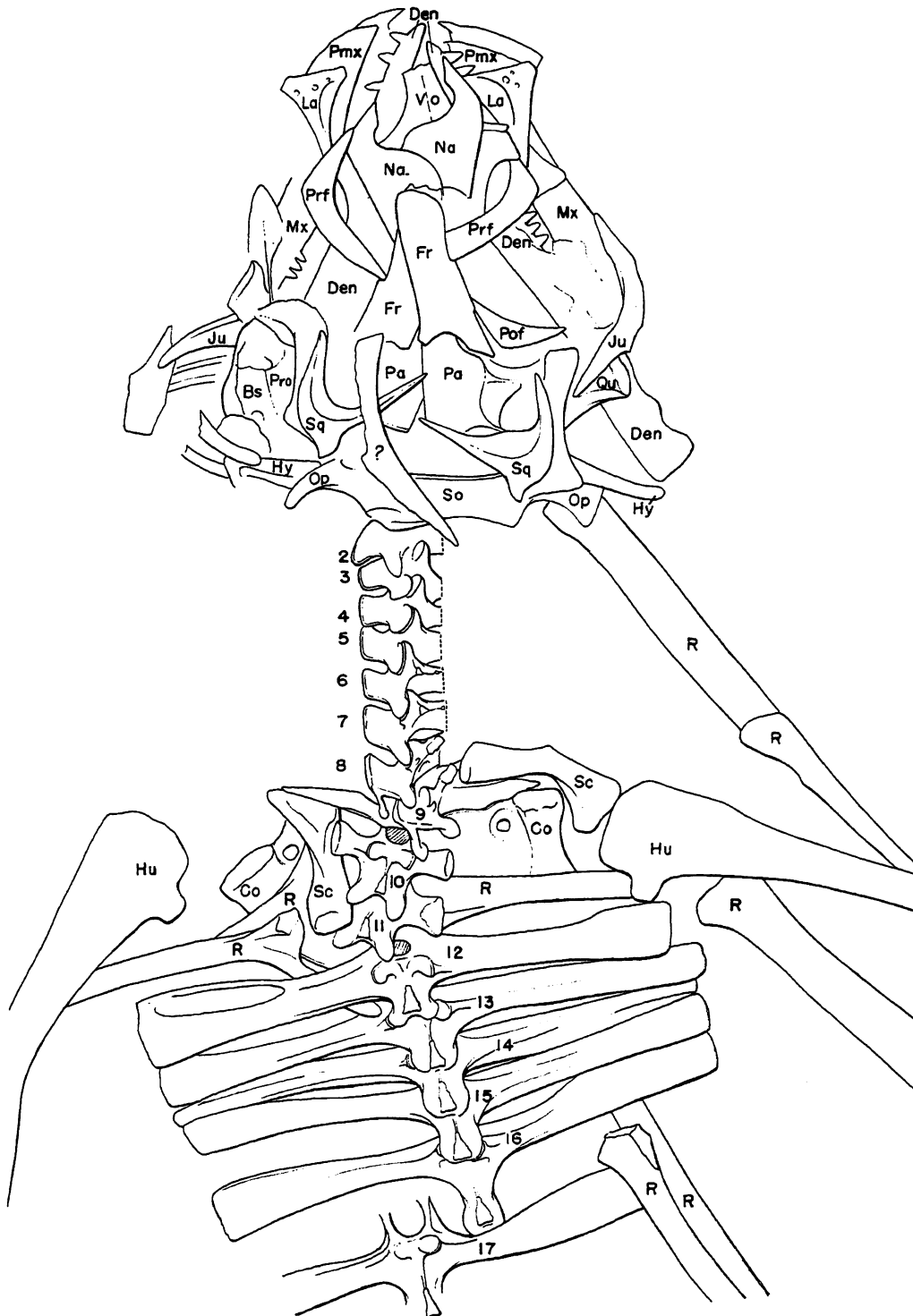


FIG. 4. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Identification of bones shown in figure 3. Numbers indicate vertebrae in presacral series. Key: Bs, basisphenoid; Co, coracoid; Den, dentary; Fr, frontal; Hu, humerus; Hy, hyoid; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Op, opisthotic; Pa, parietal; Pmx, premaxilla; Pof, postfrontal; Prf, prefrontal; Pro, prootic; Qu, quadrate; R, rib; Sc, scapula; So, supraoccipital; Sq, squamosal; Vo, vomer. Modified from Colbert (1966).

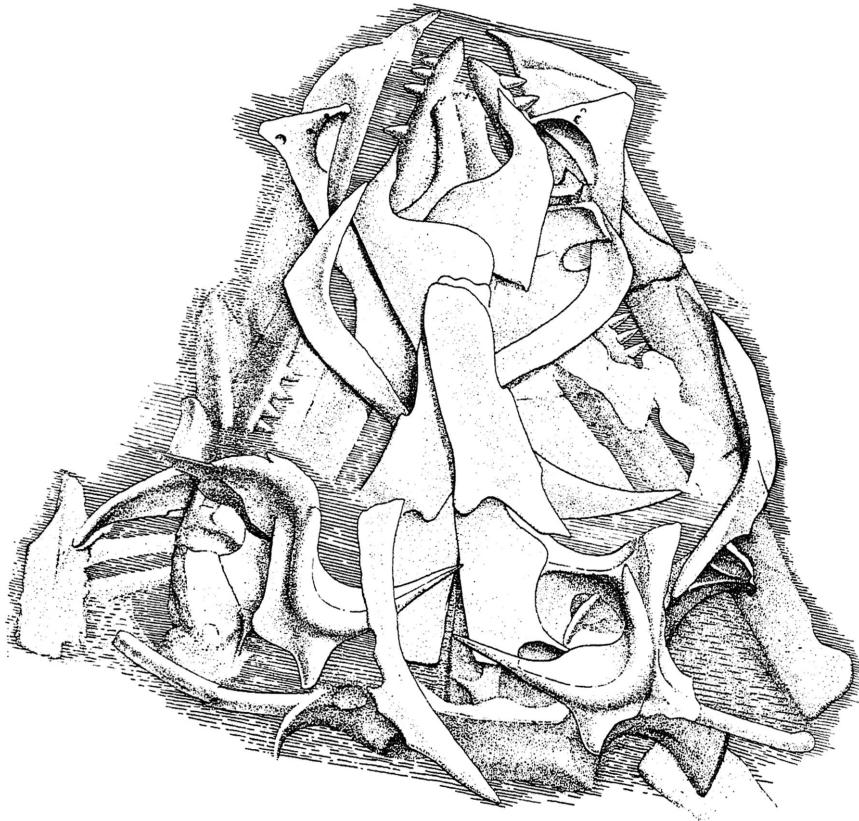


FIG. 5. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Skull and lower jaws as preserved, dorsal view.  $\times 4$ .

In both genera the orbits are relatively large, as might be expected in such small reptiles, in which survival obviously depended to a great degree on acute vision. *Icarosaurus*, as does *Kuehneosaurus*, has a well-developed upper temporal opening, much broader than it is long. But the particularly striking feature of this skull, as is the case in *Kuehneosaurus*, is the absence of a ventral bar for the lateral temporal fenestra, with a correlative freeing of the quadrate so that it is capable of much movement at its articulation with the squamosal. In *Icarosaurus* the jugal, as seen from the side, is a sickle-shaped bone, with the ventral border between the horizontal and vertical rami broadly rounded and showing no remnant of a point to mark the position where a posteriorly directed jugal ramus might once have originated, in contrast to *Kuehneosaurus*, in which this portion of the jugal is sharply angular. Except for this minor difference, the jugals in the two genera are closely comparable, and in

this respect both forms are definitely lacertilian.

The frontals and parietals of *Icarosaurus* are similar in size and shape to the same bones in *Kuehneosaurus*, these characters being correlated with the very large orbits and the broad but anteroposteriorly short supratemporal fenestrae in both genera. In both genera, also, the bones are paired, a primitive feature, as contrasted with the fused frontals and parietals that characterize many modern lizards. In *Kuehneosaurus* there is a definite pineal foramen at the common junction of the paired frontals and parietals; this foramen is formed by a small notch in the corner of each bone. The presence of such a foramen in *Icarosaurus* cannot be established beyond all doubt, but the posterolateral corners of the frontals, which are clearly visible, indicate such to be the case. The frontal bones do not show sharp corners, but each bone in this region is obliquely truncated so that, if placed together in their proper relationships, the two truncations

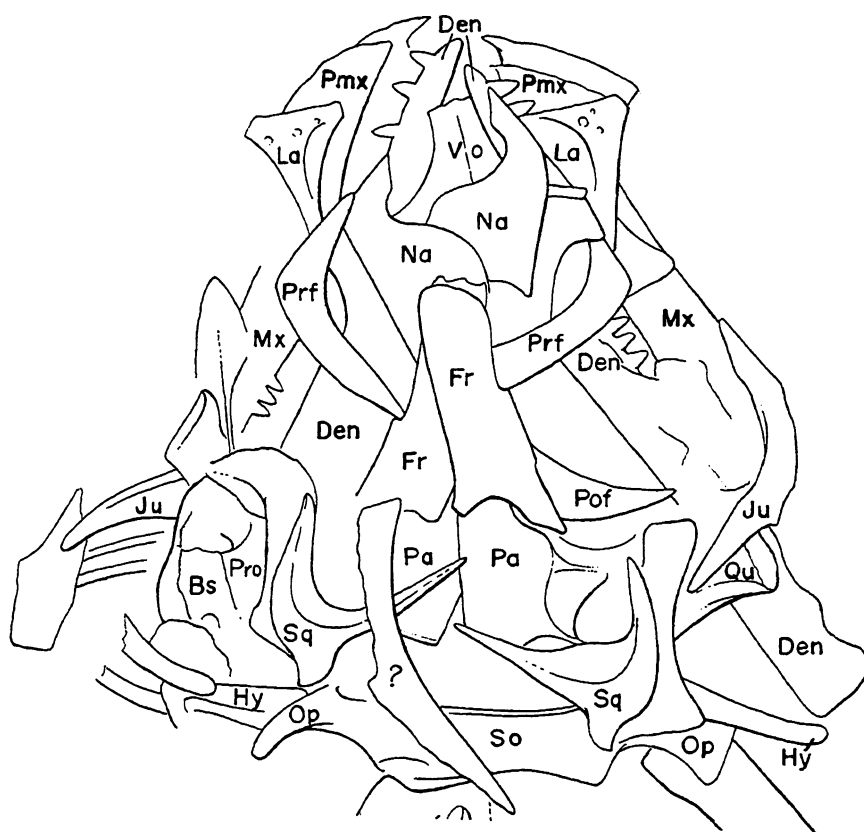


FIG. 6. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Identification of the bones shown in figure 5. Key: Bs, basisphenoid; Den, dentary; Fr, frontal; Hy, hyoid; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Op, opisthotic; Pa, parietal; Pmx, premaxilla; Pof, postfrontal; Prf, prefrontal; Pro, prootic; Qu, quadrate; So, supraoccipital; Sq, squamosal; Vo, vomer. Modified from Colbert (1966).

form a small notch. The contiguous areas of the parietals are covered by the overlying frontals, but it is reasonable to suppose that there might have been a matching notch in these bones. Thus the two notches would form, in effect, a small pineal opening. A pineal opening in this position is found in many modern lizards.

Together the paired frontals and parietals form a flat skull roof, but laterally each parietal descends obliquely to form a part of the lateral enclosure for the brain. The juncture between the flat dorsal and the curved lateral surfaces of the parietal is a semicircular edge that forms the internal border of the upper temporal fenestra. The posterior portion of this edge is in the form of a sharp curved ridge, or crest, separating the lateral wall of the braincase from the outer portion of the occipital wall, this, too, being

formed by a downbending of a part of the parietal surface. The anterolateral portion of each parietal is considerably extended laterally, probably to reach a medially extended ramus of the postorbital and to abut against a part of the postfrontal.

The postfrontal is a large, distinct bone, articulating medially with the frontal by a broad suture, and rapidly diminishing in size in its lateral extent, to come to a point in the posteroexternal region of the orbital border. Its long anterior edge forms part of the back of the orbit, and posteriorly it is in contact with the parietal and the postorbital. The large size and shape of the postfrontal in *Icarosaurus* indicate that the bone is probably of primitive form; in modern lizards the postfrontal is a small bone, or has even lost its identity by fusion with the

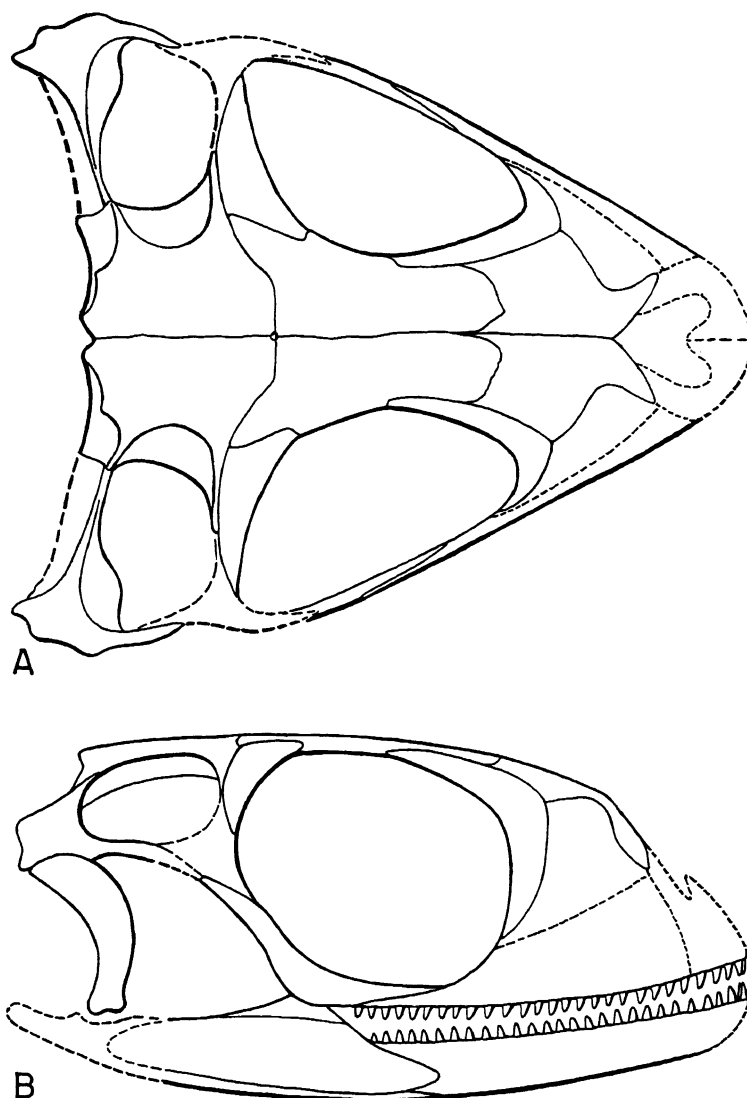


FIG. 7. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Restoration of skull and lower jaws. A. Dorsal view. B. Lateral view.  $\times 4$ .

postorbital. It is remarkably similar in shape and position to the same bone in *Prolacerta* and resembles it to a much greater degree than it does the same bone in *Kuehneosaurus*. Indeed, the resemblance between *Icarosaurus* and *Prolacerta* involves not only the shape and position of the postfrontal, but also the manner in which this bone articulates with its neighbors; for example, in both *Prolacerta* and *Icarosaurus* the frontals extend back laterally so that there is an extensive

articulation with the broad "base" of the postfrontal.

The prefrontals, as here identified, are long, crescentic bones similar to those of *Kuehneosaurus* in position and extent, but much more slender. The marked attenuation of the prefrontal in *Icarosaurus* perhaps may be correlated with the large orbit in this genus; certainly in this respect the development of the bone is more extreme than is the case in *Kuehneosaurus*.

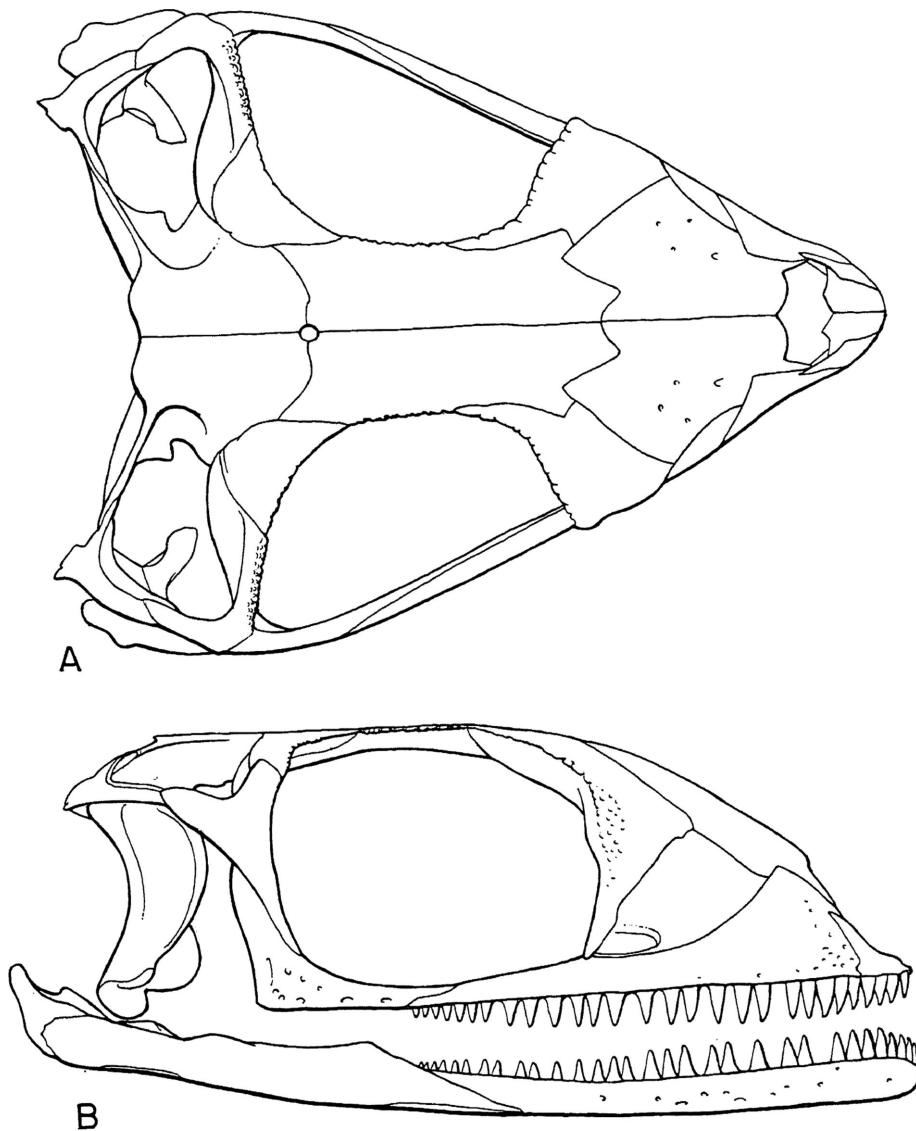


FIG. 8. *Kuehneosaurus* sp. Restoration of skull and lower jaws. A. Dorsal view. B. Lateral view (modified from Robinson, 1962).  $\times 4$ .

The lacrimals are large triangular-shaped bones, each of which shows, on its inner surface, near the lower border, a large, shallow, elliptical depression. This does not pierce the bone, therefore it cannot be regarded as a foramen for the lacrimal duct. It appears that the lacrimal bone is excluded from the orbit, as is the case in *Kuehneosaurus*. If this relationship of the bone is valid, it represents a rather remarkable specialization which would seem to be typical for the kuehneosaurs and at variance with other

reptiles. The lacrimal in primitive tetrapods extends from the orbit to the nasal region, but it is variously modified in the reptiles by adaptive radiation through time. The general trend is for the lacrimal to become reduced, as it is in most lizards, but to retain its basic position as a bone participating in the orbital margin and situated between the prefrontal above, the jugal below, and the vertical plate of the maxilla anteriorly. In the kuehneosaurs this relationship has been altered because of the great increase in size of

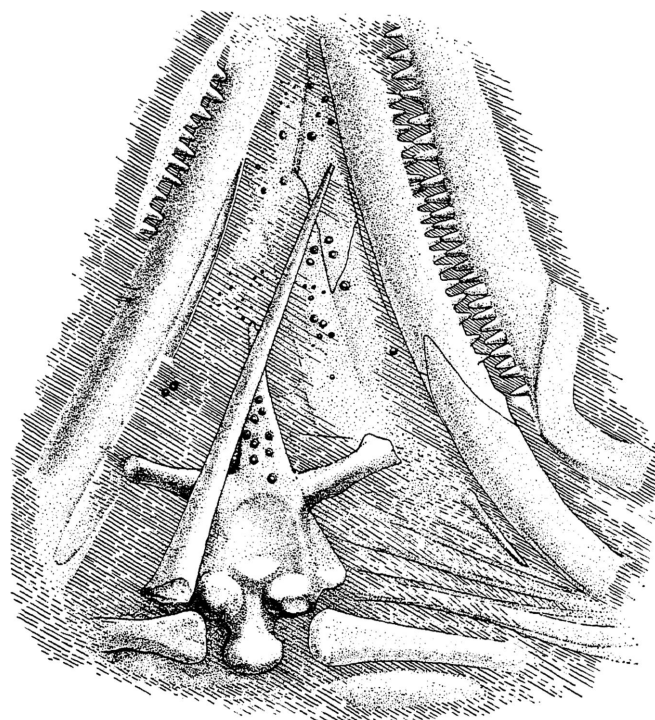


FIG. 9. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Skull and lower jaws as preserved, palatal view.  $\times 4$ .

the prefrontal, which thus makes up the anterior border of the orbit, and the backward extension of the maxilla, which makes up a part of the lower orbital border.

The nasal bones of *Icarosaurus* are large and of rather complex shape, broad posteriorly and having long edges that articulate with the prefrontals, but each narrowed anteriorly into a pointed process that extends forward above the lacrimal, presumably to reach the premaxilla. If the identification, interpretation, and orientation of these two bones are correct as described, then they partially enclose a very large nasal opening, perhaps larger in proportion than the external nares of *Kuehneosaurus*. The premaxillae are not wholly visible in *Icarosaurus*, but, judged from the structure of these bones in *Kuehneosaurus*, it is possible that the North American form, like its Old World relative, lacked the median premaxillary bar that separates the two nares in modern lizards and is characteristic of them.

The most logical interpretation of the nasals in *Icarosaurus* is based on the assumption that these bones are transposed in the specimen as

preserved. Certainly the straight edges of these bones, which have all the appearance of being median edges, are in general alignment with the straight, median edges of the frontals, which places the nasals in transposed positions (apparent in fig. 5). Only when such a shift (which supposedly took place during fossilization) is assumed can satisfactory relationships of the nasals with the contiguous skull bones be established. I am indebted to Dr. Robinson for this interpretation.

The premaxillae are not fully visible (figs. 5, 6, 9, and 10), and it is not possible from the manner in which they are exposed to determine much concerning their limits or shape. About all that can be said is that each bone contains several teeth.

More can be said, however, about the maxillae. The maxilla in *Icarosaurus* is a long bone, as it is in *Kuehneosaurus*, extending from near the front of the skull to a position beneath the middle or even the posterior portion of the orbit, thus being about half of the length of the skull. Throughout most of its extent it is slender, but it seems that anteriorly there is a deeper portion

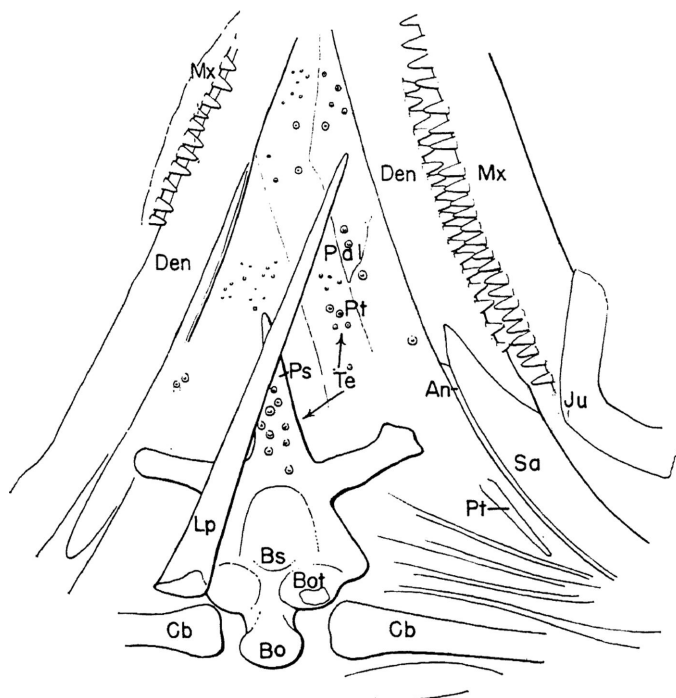


FIG. 10. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Identification of the bones shown in figure 9. Key: An, angular; Bo, basioccipital; Bot, basal tuber; Bs, basisphenoid; Cb, ceratobranchial; Den, dentary; Ju, jugal; Lp, lingual process of the corpus hyoideum; Mx, maxilla; Pal, palatine; Ps, parasphenoid; Pt, pterygoid; Sa, surangular; Te, palatal teeth.

that rises to meet the lacrimal and the nasal. This bone is set with a row of numerous small, simple, homodont teeth, perhaps about 27 or 28 in number. As indicated below, there are apparently about 30 teeth in the dentary, which should be opposed by an approximately similar number in the premaxilla and maxilla. The method of tooth implantation is not easy to distinguish, but seems to be of a subpleurodont type, trending toward a typical lacertilian pleurodont dentition from a subthecodont ancestral condition. The teeth are set very close together, to form a continuous row.

The postorbital is not definitely identifiable in *Icarosaurus*. Without much doubt it was a three-pronged bone of the usual diapsid type, articulating with the squamosal, the jugal, and the parietal.

Both squamosal bones are well preserved in the skeleton of *Icarosaurus*, thus giving some definite knowledge as to the articulation with the quadrate and the form of the posterior

border of the superior temporal fenestra. The squamosal in its middle portion is rather broad, with a large flange extending ventrally from the middle portion of its posterior margin. This broad part of the bone has on its ventral surface the concave depression, or cotylus, that houses the upper end of the movable quadrate. Two slender pointed rami extend from this middle portion of the squamosal, one forward to articulate with the postorbital and a long one internally to join the parietal, these two bones forming the back border of the temporal fenestra.

Robinson found no indication of a supratemporal bone in *Kuehneosaurus*, and certainly no bone that can be so identified is present in the skull of *Icarosaurus*.

The freely movable quadrate of *Icarosaurus* is nicely illustrated by the manner in which the specimen is preserved. As a result of burial and fossilization, the skull is flattened dorsoventrally. The quadrate, retaining its articulation with the squamosal and maintaining this joint as a pivot,



was rotated so that its free lower end described a forward arc of about 90 degrees. The bone is characterized by a long vertical ramus, the posterior surface of which is rather strongly concave from top to bottom, its opposite anterior surface convex. It is narrow from front to back, but rather broad, with a transversely broad articulation for the lower jaw. Of course, there is no quadratojugal.

As indicated, the crushing of the skull was dorsoventrally directed, so that its apparent width in the occipital region, for example, probably is not greatly different from the true width of the articulated skull. No particular details can be defined in this part of the skull, but apparently the exoccipital-opisthotic complex forms a transversely extended bar on each side of the foramen magnum. The opisthotic seems to be rather attenuated at its lateral extremity, but whether there is a strong ventral process, a feature quite characteristic of *Kuehneosaurus*, cannot be determined. The supraoccipital appears to be comparatively large, forming a broad and rather deep element, constituting the dorsal portion of the occiput.

The lateral wall of the cranium was well developed, as is seen by the presence of a rather large, platelike prootic, preserved on the left side of the skull. This bone is deep and ventrally shows a sutural junction with the basisphenoid. There is a very large notch for the trigeminal nerve, excavating the anterior border of the prootic.

The basioccipital of *Icarosaurus* is characterized not only by its well-rounded condyle, but also by the large and prominent basal tubera for the subvertebral muscles, each tuber being almost as large as the condyle itself (figs. 9 and 10). Whether the parasphenoid participates in the formation of the tubera is not definitely evident. The posterior portion of this bone in the vicinity of the tubera is broad, and from this region it narrows rapidly to the area of its articulation with the pterygoids, which is effected by a strong process on each side, running obliquely forward and laterally. Farther forward the parasphenoid is produced into a long cultriform process. Other bones of the palate are not clearly defined, except for some indication of rather broad vomers, as partially seen in the dorsal view of the skull, and the presence of large palatine and pterygoid bones, as indicated by the extensive deployment of palatal teeth in the ventral aspect of the skull.

The lower jaw is long and uniformly slender, as is also that of *Kuehneosaurus*, each dentary having a depth of little more than twice the height of the crowns of the teeth (figs. 9 and 10). The junction between the dentary and post-dentary bones is prominent, and it is reasonable to suppose that there may have been some movement in this region of the jaw. As mentioned above, there may have been as many as 30 dentary teeth; if so, the number is somewhat smaller than in *Kuehneosaurus*.

The surangular is a long, prominent bone, occupying much of the external surface of the mandibular ramus behind the dentary; this same situation is characteristic of *Kuehneosaurus*. A separate coronoid is not discernible, but this element may have been present as a small bone, now hidden by the matrix within which the type specimen of *Icarosaurus* is preserved. Beneath the surangular is a long, slender angular. On the inner surface of the right ramus a small section of the slender prearticular can be seen.

*Icarosaurus* obviously had a well-developed hyoid apparatus, as do most of the squamates. A long, straight, pointed element, its base near the right basal tuber, its pointed end projecting toward the left ramus of the mandible, may be identified as the lingual process of the corpus hyoideum. On each side of the basioccipital are the broad ends of two large elements, which evidently are the ceratobranchials. The size of these several bones indicates that the hyoid complex in *Icarosaurus* was large, evidently to serve as the base for a strong and perhaps long tongue.

#### DENTITION

As indicated, the teeth of *Icarosaurus* are small, simple, closely set, and homodont (fig. 11). They are subpleurodont as well, which is a primitive lacertilian condition, characteristic of those Triassic squamates that are designated herein as

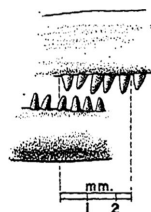


FIG. 11. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Detail to show spacing of teeth in maxilla (above) and dentary (below).  $\times 4$ .

eolacertilians. It is not possible to ascertain the total number of teeth on a side, above and below, in *Icarosaurus*, because in no area of the type specimen can one see the full extent of the upper and lower jaws, nor is it possible to combine the information from those regions that are visible to arrive at an unequivocal determination as to the exact number of teeth. The estimate of approximately 30 on a side, above and below, is conservative. Robinson (1962) showed about 37 premaxillary-maxillary teeth in *Kuehneosaurus* and more than 40 dentary teeth. Camp (1945) indicated fewer in *Pro-lacerta*: five premaxillary teeth, 14 to 16 maxillary teeth, and apparently fewer than 20 dentary teeth.

Evidently *Icarosaurus*, as is the related genus *Kuehneosaurus*, was abundantly supplied with teeth on the palate, these being present on the parasphenoid and on the apparently large palatine and pterygoid bones.

#### AXIAL SKELETON

Apparently there are 24 presacral vertebrae in the skeleton of *Icarosaurus siefkeri*. If this number is correct (there are good reasons for believing that it is), we see in *Icarosaurus* the retention of a primitive character for the lizards.

As preserved, the first 16 presacral vertebrae of *Icarosaurus* are in close articulation (figs. 3, 4). The next four vertebrae behind the sixteenth presacral have been separated from one another and displaced progressively toward the left, but they are so closely associated that there can be no doubt as to their several positions in the vertebral series. There is a considerable gap between the twentieth presacral and the one behind it, this gap being mostly in a lateral direction, with the vertebra following the twentieth displaced to the left. If lines are drawn at right angles to the vertebral axes, and tangential to the posterior and anterior articulations of the twentieth vertebra and the one following it, respectively, the distance between these lines is relatively small, approximately 3 mm., considerably less than the length of the vertebral centrum in this part of the column. Therefore it is here maintained that the vertebra behind the twentieth is the twenty-first, simply shifted to the left, and that no intervening vertebra has been lost.

Two more vertebrae closely follow number 21, although each has been rotated anteriorly to the

left, posteriorly to the right. These are obviously numbers 22 and 23. Then follows a gap, with the final presacral vertebra abutted against the first sacral, but at right angles to it. The gap between the twenty-third vertebra and the one behind it is, if one swings the latter vertebra and the one ahead of it into their proper positions, perhaps slightly less than the length of a centrum from this part of the column. Again it is maintained that there probably was no intervening vertebra, and that the gap represents a true vacuity caused by the displacement of the elements in the posterior part of the presacral series. Thus, according to this view, the last presacral preserved is number 24 (figs. 12 and 13).

The lengths of the centra of the vertebrae in the posterior part of the presacral series seem to reinforce the contention that there were only 24 presacral vertebrae. Thus the vertebrae numbered 19 to 21 inclusive make a graded series of increasing individual lengths; the twenty-first and twenty-second vertebrae are of approximately equal length, whereas 22 to 24 inclusive again make a graded series, but of decreasing lengths. The indication is that these vertebrae, although a bit scattered, are truly sequential and that no vertebrae are missing from the sequence.

Among Triassic eolacertilians, to use this term in a broad sense, *Macrocnemus* is stated to have 23 to 25 presacral vertebrae. In *Tanystropheus* there are 25 presacrals. *Kuehneosaurus* is credited with 28 presacrals, which may seem rather high. It should be noted, however, that in some modern lizards there are comparable numbers of presacral vertebrae—29 in *Varanus*, for example. *Draco*, the adaptations of which closely parallel those of *Icarosaurus* and *Kuehneosaurus*, shows 25 presacrals.

The presacral vertebrae of *Icarosaurus* are amphicoelus, and the centra, as seen ventrally, are spool-shaped (fig. 14), having expanded articulations and being much constricted through their middle portions. This character is not so pronounced in the first nine presacrals, which may be considered cervicals, but is very strongly developed in the succeeding presacral vertebrae, in which the centra becomes progressively longer as one proceeds from the anterior to the posterior part of the vertebral column.

The first nine presacrals have relatively short centra. In these vertebrae the neural arches are



FIG. 12. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Posterior portion of skeleton, dorsal view.  $\times 3$ .



FIG. 13. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Identification of bones shown in figure 12. Numbers indicate vertebrae in presacral region. *Key*: Caud, caudal vertebrae; Fe, femur; Il, ilium; Isch, ischium; Pu, pubis; R, rib; Sa 1 and Sa 2, sacral vertebrae. From Colbert (1966).



FIG. 14. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Centrum of middorsal vertebra, ventral view, showing spool-like character of vertebral centra.  $\times 4$ .

very high, but the neural spines are low. These latter are long from front to back, and, as might be expected, the spine of the atlas is longer than the spines of the vertebrae behind it (fig. 15). Its upper border is convexly curved, but in the other cervical vertebrae, as in the other presacrals that follow them, the spines have straight tops. The zygapophyses of the cervicals are expanded and flat, and the anterior and



FIG. 15. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Atlas-axis complex, right lateral view.  $\times 4$ .

posterior zygapophyses of adjacent vertebrae articulate along planes that are but slightly inclined from the horizontal. The anterior zygapophyses in each of these vertebrae are borne on strong, forwardly slanted pedicles, formed by the sides of the neural arch, whereas the posterior zygapophyses and the spine above them are carried back so that vertically they are situated in part behind the centrum.

The result of this construction of the vertebrae in the neck is that the zygapophyseal articulations are so arranged that they are above the articulations of the centra and intermediate between them. At the same time these articulations are carried laterally by an expansion of the upper portion of the neural arch. This expansion supports the posterior zygapophyses and an outward (as well as forward) sweep of the sides of the arch (the pedicles mentioned above) on which the anterior zygapophyses are placed. This arrangement gives to the neural arch in the cervical of *Icarosaurus* an expansion that is reminiscent of the arch in some of the cotylosaurs, except that in the genus herein described there has been a vertical growth, so that the zygapophyses are situated high above the centrum (fig. 16). This development in the



FIG. 16. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Sixth and seventh presacral vertebrae, right lateral view. Note well-defined facets for articulation of cervical ribs.  $\times 4$ .

cervical vertebrae of *Icarosaurus* is quite different from what is seen in *Kuehneosaurus*, in which the neural arch is relatively lower and certainly less expanded, in which the zygapophyses are not offset (as they are in the reptile from New Jersey), and in which the neural spine is relatively much higher. The specimens of *Kuehneosaurus* show the centra to be highly cancellous inside, as an adaptation for lightness. In view of the hollow nature of the transverse processes of *Icarosaurus* (described below), it seems reasonable to think that in this genus the centra were also lightened.

The structure of the vertebrae certainly must have provided *Icarosaurus* with a very strong neck. Perhaps such a strong neck was necessary because of the large head and strong jaw muscles, even though the skull was of a relatively light construction. Moreover, a strongly articulated neck would have been correlated with the greatly expanded and strongly articulated vertebrae of the anterior portion of the trunk.

Facets for cervical ribs are visible on the vertebrae behind the axis; such facets are not readily discernible on the second vertebrae, but supposedly they were present. Unfortunately no cervical ribs are to be seen associated with the specimen at hand, which is rather surprising, when the articulated nature of the skeleton and the fine preservation of detailed structures are considered.

*Kuehneosaurus*, as described in detail by Robinson, is remarkable in showing three rib facets on each cervical vertebra: a dorsal one on the neural arch, presumably the diapophysis; a lower one at the base of the neural arch, this facet being on a small process in the more posterior cervicals; and a ventral one on the anterior border of the centrum, about midway between its ventral and dorsal limits, this supposedly being the normal parapophysis. Possibly

three such facets may have been present in the cervical vertebrae of *Icarosaurus*, but there is no unequivocal evidence for them. In fact, only one definite facet can be seen in most of the vertebrae, situated anteriorly, apparently just above the boundary between the centrum and the neural arch. In the anterior cervical vertebrae of *Icarosaurus* the lateral surface of the neural arch is smooth above this visible rib facet, there being no transverse process. In the sixth cervical there is a short but strong process just beneath the anterior zygapophysis, but there is no indication that it bore a facet for the tuberculum of a rib. Indeed, it appears to be rounded, rather than faceted. In this vertebra, however, there are two facets on the centrum, a large one in line with the facets on the preceding vertebrae, and a small one beneath it. No good indications of facets are apparent on the seventh vertebra.

The evidence for rib facets on the cervical vertebrae of *Icarosaurus* is confusing. Possibly double-headed cervical ribs were present in *Icarosaurus*, as is normal in many reptiles. Whether there were triple-headed ribs, as in



FIG. 17. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Tenth presacral vertebra, dorsal view.  $\times 4$ .

*Kuehneosaurus*, is a moot point; such appears not to be the case.

The next two vertebrae, the tenth (fig. 17) and eleventh (fig. 18) of the presacral series, have centra that are longer than those in the preceding presacrals. They clearly show their spool shape, with the middle part of each centrum much constricted. The neural arches are high and the spines low, as in the other vertebrae described, but the zygapophyses are not flat and more or less horizontal in position but are curved upward. The transition from the flat to the curved zygapophyses is not sudden,

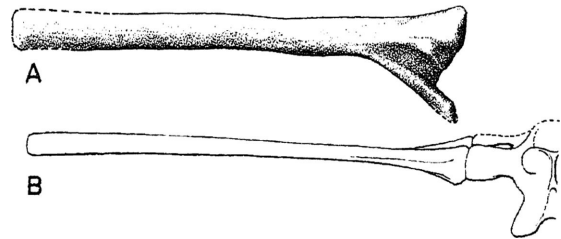


FIG. 18. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. A. Eleventh left rib, anterior view. B. Eleventh left presacral vertebra and rib, dorsal view.  $\times 4$ .

but involves several vertebrae, from about the eighth presacral and posteriorly. In the two vertebrae being described, the transverse processes are very strong, though short, and terminate in large, vertically expanded, articular surfaces. These transverse processes may be divided, each into a large upper and a smaller lower process, as is characteristic of the transverse processes in the tenth and eleventh vertebrae of *Kuehneosaurus*.

The ribs of the eleventh presacral vertebrae are quite unusual, being expanded and straight, and extending laterally from the vertebra to form elements that are remarkably similar to the elongated and expanded transverse processes of the twelfth presacral (fig. 19) and the vertebrae behind it. Yet it is quite clear that these large, pseudotransverse processes, if they may be so called, are true ribs. They have large, vertically expanded tubercles for articulation with the transverse processes of the vertebra described above, and in addition a slender process extends to a small capitulum. The resemblance between the ribs of the eleventh presacral vertebra and the transverse processes of the twelfth presacral are indeed close—an indication that the eleventh ribs must have been adapted to a very special function. (It is suggested that the purpose of these ribs, and probably of the ribs articulating with the tenth presacral vertebra as well, was to afford a base for strengthening the attachments of the iliocostalis muscles that were primarily involved



FIG. 19. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Twelfth presacral vertebra, dorsal view.  $\times 4$ .

in spreading and maintaining the tension on the wing during flight.)

The ribs of the tenth presacral vertebra seem to have had a similar form and function, although only the proximal portion of the left rib is visible. One has the impression, although this cannot definitely be documented, that the ribs of the tenth presacral were slightly less robust than those of the following vertebra and thus formed in effect a transition from the more normal, slender ribs of the anterior and middle cervical region with the single-headed, enormously elongated ribs of the thorax.

The first 11 presacral vertebrae and the ribs of the tenth and eleventh vertebrae are surpassed in adaptive transformations by the truly remarkable specializations of the next 10 vertebrae and their accompanying ribs. The twelfth presacral vertebra and its ribs epitomize the unusual adaptations that have developed in *Icarosaurus*. This vertebra has the spool-like centrum, the high neural arch, and the low spine described as characteristic for *Icarosaurus*, but it is particularly noteworthy because of the great development of its transverse processes, which are long, straight, hollow, and expanded. The length of these transverse processes is such that their ends are lateral to the articulations of the humeri with the pectoral girdle. The width of the twelfth vertebra, measured across the transverse processes, is thus considerably more than the length of the cervical series of vertebrae, and is somewhat more than a third of the entire length of the presacral series. The ends of these long and expanded transverse processes form on each side a large articulation for the single-headed rib. The anterior zygapophyses of the twelfth vertebra are expanded in such a way that together the two form the large part of a semicircle for articulation with the post-



FIG. 20. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Anterior view of prezygapophyses of twelfth presacral vertebra, showing semicircular form of zygapophyses, which permits rotation between vertebrae.  $\times 4$ .

zygapophyses of the preceding vertebra (fig. 20). This is a prominent character in the vertebra being described.

The next four vertebrae, which with the twelfth presacral form a closely articulated series, are similar to it in structure. In all, the transverse processes are straight, elongated, and expanded to such an extent that their ends are in contact with each other, or almost so. In all, the zygapophyseal articulations are curved, as in the articulations between the eleventh and twelfth presacrals, but the extreme development of these articulations as concentric semicircles decreases as one proceeds back along the column.

The development in these vertebrae of long transverse processes continues, but with decreasing emphasis, to the sacral region. The transverse processes become progressively shorter and less expanded from the sixteenth presacral posteriorly, so that their ends are no longer in close proximity, and they assume in the back portion of the presacral region more or less normal lengths. It should be said that in the progression from the twelfth presacral to the sacrum there is a steady increase in the length of the centra, and this, together with the reduction of the transverse processes, leads to the development in the posterior part of the back of a column that is of generally familiar form, with a construction that would allow for "lumbar" flexibility.

The flexibility of the column in this posterior segment would have been in decided contrast with what must have been a certain immobility in its "thoracic" portion. Certainly in that part of the back, from the twelfth to about the seventeenth vertebrae, there must have been a limited degree of horizontal flexibility, determined by the close apposition of the expanded transverse processes, especially those of the twelfth to sixteenth vertebrae inclusive. These processes, closely appressed to one another through the distal thirds of their lengths, would have formed a rather solid structure, which may be compared by analogy with the notarium of some of the flying reptiles.

The proximity of the ends of the transverse processes in the half-dozen vertebrae that form the anterior portion of the thoracic region limits horizontal movement in this part of the trunk, but this section of the vertebral column was not completely immobile. The zygapophyses indicate, by their almost semicircular articulating surfaces, that this part of the back probably was capable of a considerable degree of twisting,



that is, of a rotating of the vertebrae in relation to one another. Such rotational movements might have involved individual vertebrae to a limited extent, but more probably would have been participated in by the whole series of anterior trunk vertebrae, to elevate or depress one side of the body in relation to the other, perhaps frequently in differential degrees along the length of this portion of the column.

The presacral vertebrae of *Icarosaurus* are in many ways similar to comparable vertebrae of the genus *Kuehneosaurus*. As in the case of the cervical vertebrae, striking differences should be mentioned. *Kuehneosaurus* and *Icarosaurus* both have anterior "thoracic" vertebrae with greatly expanded transverse processes, but the expansion of these structures differs in the two genera. The processes are of comparable length, but in *Icarosaurus* the processes are hollow and their ends are so expanded that they are in close proximity. In *Kuehneosaurus* the transverse processes are broad but tilted, so that they have the form of elongated, obliquely vertical plates. Because they lack the fullness in their distal portions that is typical of *Icarosaurus*, the processes of *Kuehneosaurus* are not so close to one another distally. As seen in lateral view the processes of *Kuehneosaurus* consequently form a series of obliquely vertical, elongated ends, separated from one another, as contrasted with the row of contiguous articulations seen in *Icarosaurus*, at least in the first six or eight vertebrae behind the neck.

A more flexible thoracic region is therefore indicated in *Kuehneosaurus* than in the New World form—a back that in its forward part has less of the nature of a solid anchor for the "wing" and more of the nature of a normal vertebral column.

The highly specialized structural development of *Icarosaurus* for gliding is also indicated by the evidence in other parts of the skeleton. In some of the more anterior presacrals of *Kuehneosaurus*, notably the tenth, eleventh, and twelfth, the transverse processes are subdivided at their ends to form superior and inferior processes for articulation with the ribs. This character is a reflection of the carrying back from the cervical region of double-headed ribs—a condition that is paralleled to some extent in *Icarosaurus* by the remarkably expanded, double-headed ribs (like transverse processes) of the tenth and eleventh vertebrae. In the New Jersey gliding reptile the

break between double-headed ribs and more posterior single-headed ones occurs from the eleventh to the twelfth vertebrae. The same seems to be essentially true for *Kuehneosaurus*, as in this genus the transverse processes of the twelfth vertebra, although showing a distal subdivision, also show a secondary coalescence of the distal extremities of the processes to form an articulation that would have functioned for a single-headed rib.

As for other differences, the zygapophyseal facets in *Kuehneosaurus* do not show the semi-circular articulations that are so characteristic of the more anterior "thoracics" of *Icarosaurus*. Rather, the facets are steeply inclined planes. Also, the neural spines of the more anterior trunk vertebrae, at least, are relatively higher than those in *Icarosaurus*.

There are two sacral vertebrae in *Icarosaurus*, the centra of which are comparable in length with those of the posterior presacrals (fig. 21). These vertebrae are particularly noteworthy because of the distal expansions of their transverse processes to make firm and elongated

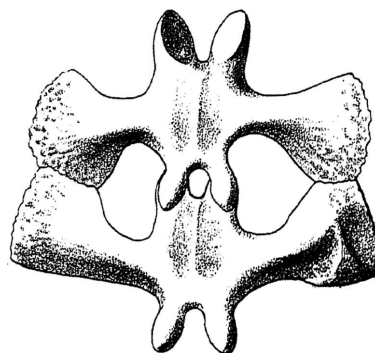


FIG. 21. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Sacral vertebrae, dorsal view.  $\times 4$ .

connections with the ilia on each side. In this respect the sacrals of *Icarosaurus* are similar to those of *Kuehneosaurus*, but the expansions of the transverse processes are even greater in the genus from New Jersey. Thus, in *Icarosaurus* the processes of the second sacral vertebra are fully as expanded as those of the first, which is not the case in *Kuehneosaurus*, an indication of the high specialization of this character in *Icarosaurus*.

Four caudal vertebrae are preserved in the *Icarosaurus* skeleton. These are certainly anterior

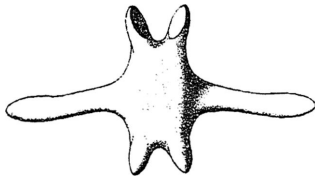


FIG. 22. *Icarosaurus siefkeri*, A.M.N.H. No. 2101.  
Anterior caudal vertebra, dorsal view.  $\times 4$ .

caudals (fig. 22), and the anterior three are in close articulation. The fourth, the last in the series, is slightly separated from the other vertebrae and is rotated somewhat. These vertebrae have long centra, nearly comparable in length with those of the sacra and not quite so long as the centra of the last few presacra. The centra increase somewhat in length from the front to the back in this series of four vertebrae. The transverse processes are also long and slender and project at about right angles to the centra. There was evidently a very low and elongated neural spine on each of the caudals preserved, as is evident from the materials, although the vertebrae are not fully preserved in their dorsal portions.

From the evidence of these four anterior caudals, it seems probable that *Icarosaurus* had a long, slender tail. The vertebrae are more slender and have longer transverse processes than do comparable vertebrae in *Kuehneosaurus*, and in these features they resemble in a general way the anterior caudal vertebrae of *Draco*. It is probable that a long tail in *Icarosaurus* was important as a means of controlling, in part, certain aspects of gliding.

There are 10 greatly elongated ribs on each side of the body of *Icarosaurus*, articulating by single heads with the expanded and elongated transverse processes of the twelfth to the twenty-first presacral vertebrae (fig. 23). The heads of the ribs, which match the ends of the transverse processes, are, among the anterior ribs, each in the form of an elongated triangle, with its long point directed ventrally. The more anterior of these ribs are exceedingly long, and, except for the first rib, show various degrees of curvature. The first elongated rib is straight. The curves are most pronounced in the fifth and sixth ribs, and seem to decrease from this point forward and backward. Apparently the first six ribs are of about the same length, with the first rib slightly shorter than the second rib. The longest of these

ribs is considerably more than twice the length of the presacral series; indeed, it is longer than the combined length of the skull and the presacral vertebrae. Behind the sixth rib, the lengths of the last four ribs show a rapid decrease, so that the last of the elongated ribs, the tenth, which is articulated with the twenty-first presacral vertebra, is only about a fifth as long as the longest of the ribs. The shapes of the rib heads and of the ends of the transverse processes of the more anterior ribs, alluded to above, indicate that the concave edges of the curved ribs were ventral (fig. 24).

It appears that the ribs of *Kuehneosaurus*, although greatly elongated, are for the most part much straighter than the ribs of *Icarosaurus*.

#### APPENDICULAR SKELETON

Unfortunately the pectoral girdle, although well preserved and in place, is to a considerable extent covered by the bones that normally lie above it—the vertebrae, with their expanded transverse processes, and the ribs (figs. 3 and 4). Consequently, certain features of the girdle, notably of the coracoid, are hidden, and there is no way, because of the fragility of the specimen and the virtual impossibility of removing the bones above the girdle, to see some of the details of these bones. The two scapulae are well exposed. There are no undoubted indications of clavicles and an interclavicle.

The scapula is heavy, robust, and short (fig. 25). Each scapula is bent, so that its upper portion is at a strong angle to the lower portion. The bend in this bone is very sharp, and anterolaterally, where it occurs, there is a rather prominent angle. Below this point the anterior surface of the scapula is flat and smooth, expanding ventrally to the large glenoid articular surface. Immediately above the point, which is about midway between the proximal and distal ends of the bone, the blade is rounded in cross section, but as it extends upward it becomes broadened and flattened, so that the vertebral border is rather wide. On the posterior side of the bone there is a continuous but strong curve, running from the edge of the glenoid articulation to a region opposite the anterolateral point, from which region this posterior border of the scapula continues as a rather straight line to the posterior edge of the vertebral border of the bone. In summary, the bone is noteworthy

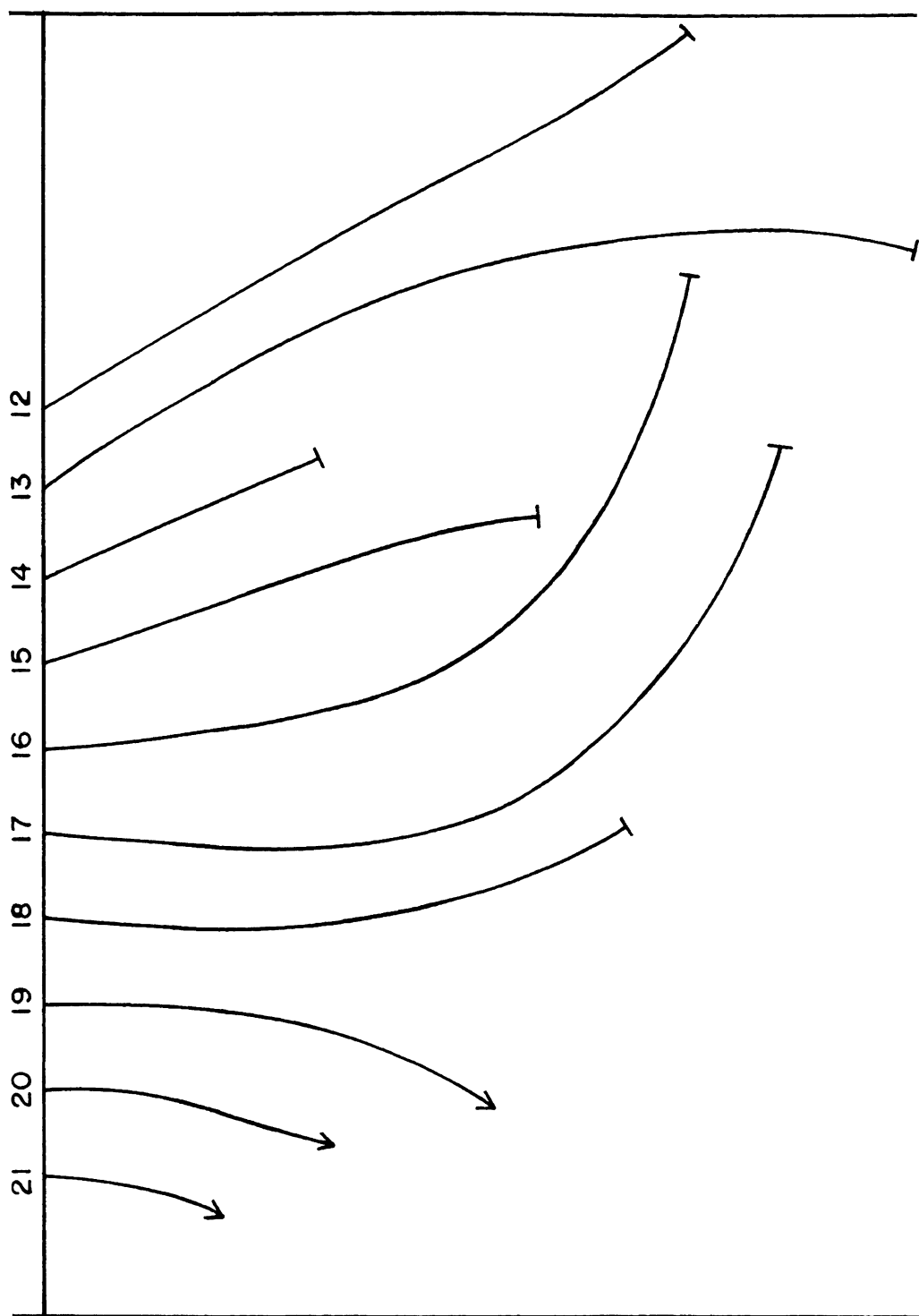


FIG. 23. *Icarosaurus sieffleri*, A.M.N.H. No. 2101. Lengths and curvatures of ribs of right side, as preserved. Lines terminating in small cross bars indicate incomplete ribs; those with points (ribs of the nineteenth to twenty-first presacral), complete ribs.  $\times 1$ .



FIG. 24. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Proximal portion of right rib of seventeenth presacral vertebra, anterior view. Note facet of single-headed rib, with a large dorsal rugosity for attachment of muscles.  $\times 4$ .



FIG. 25. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Right scapula, external lateral view.  $\times 4$ .

because of its short, stout form and because of the pronounced bend at the middle of its antero-lateral surface separating the upper and the lower portions of the bone.

This stout and strangely shaped scapula is not easily compared with the same bone in other reptiles. In many lizards the scapula is short and frequently heavy, but it is more generally in the form of a simple blade, although it may be expanded along its vertebral border, as it is in *Icarosaurus*. In *Draco*, for example, the scapula is a simple, vertical blade expanded along its vertebral edge. It curves around the side of the thorax anteriorly and makes a right angle with the essentially horizontal coracoid. In some other lizards, *Varanus*, for example, the scapula is proportionally much shorter and broader than it is in *Draco*, a condition carried over into the aquatic mosasaurs. In the pterosaurs the scapula is a long, straight blade, and the coracoid is likewise bladelike. In some of the advanced flying reptiles, such as *Pteranodon*, the vertebral edge of the scapula articulates with a long, median bone above the vertebrae to form the notarium, this in turn forming a strong anchor for the long wings. There is no evidence of a similar adaptation in *Icarosaurus*; the vertebral border of the scapula is elongated and was in life evidently in the normal position, lateral to the most anterior "thoracic" vertebrae, which, as described above, may have functioned in some

degree as a strong base for the wing. This scapula of *Icarosaurus* is a bone grown stout and heavy, perhaps as part of a very strong "landing gear" of an animal that came up against a tree trunk with some force after an aerial voyage from a neighboring tree.

Both coracoids are present, and, although neither is fully exposed, it is possible to obtain a fairly good idea of the form and position of these bones in *Icarosaurus*.

The coracoid in this reptile is a large, flat bone, horizontally placed beneath the anterior part of the thoracic region (fig. 26). A heavy,

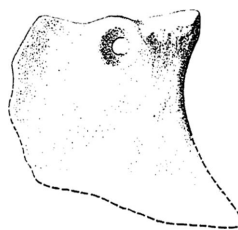


FIG. 26. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Right coracoid, dorsal view.  $\times 4$ .

expanded glenoid region shares the glenoid articulation with the contiguous part of the scapula, which extended vertically from this part of the coracoid. Close by, and medial to this glenoid, is a well-developed coracoid foramen separated only by a thin bony bridge from the anterior border of the coracoid. Posteriorly and medially the bone thins and flattens into a broad plate, with a concave lateral border and apparently a convex posterior border and a slightly convex or almost straight medial border. The two coracoids were evidently close to each other along the medial line.

In some respects the coracoid of *Icarosaurus* may be compared with the same bone in *Macrocnemus* (from the Triassic sediments of Monte San Giorgio, Switzerland), a genus in which the coracoid is a platelike bone, but the comparison is at best general. As in the case of the scapula, the coracoid of *Icarosaurus* is distinctive.

The coracoid of *Kuehneosaurus* is a large, plate-like structure that does not extend in front of the scapula and in which there is a well-developed foramen. In these respects it shows strong resemblance to the coracoid of *Icarosaurus*. The most noticeable difference between the two



FIG. 27. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Thoracic region of skeleton, showing right forelimb, dorsal view.  $\times 3$ .

genera is in the proportions of the coracoid. This bone seems to be longer in comparison with its width in *Kuehneosaurus* than it is in *Icarosaurus*.

The humerus of *Icarosaurus* is a long and slender bone, expanded at its ends and with a rather short, constricted section in its lower mid portion (figs. 27 and 28). Although relatively

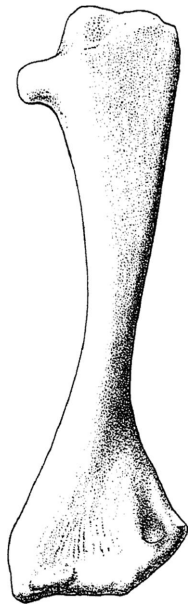


FIG. 28. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Right humerus, dorsal view. Note ectepicondylar foramen and prominent proximal process.  $\times 4$ .

long, this bone is considerably less than half of the length of the femur, which points up the fact that *Icarosaurus* was an animal with very long hind limbs.

The proximal expansion of the humerus begins at about the middle of the bone, and the increase in width continues to its culmination at the humeral head. Thus the articulation for the glenoid is rather elongated in a lateral direction. An especially interesting feature of this bone is the prominent knob, or trochanter, at the posterolateral surface, just below the head, which by virtue of its size and prominence is some indication of a powerful and perhaps specially adapted subcoracoscapularis muscle. The presence of such a large trochanter in *Icarosaurus* is but one of the many lepidosaurian characters seen in this reptile. Indeed, the expansion of the entire upper half of the humerus

indicates a strong complement of muscles inserting on this part of the bone.

Distally the humerus is also expanded in a lateral plane, to provide a wide but antero-posteriorly sharply rounded articulation for the radius and ulna. The capitellum for articulation with the radius is particularly prominent and is strongly convex. The trochlear area is rather heavily pitted, and it seems probable that the actual trochlear surface, for articulation with the ulna, has been eroded away. No entepicondylar foramen is present, but there is a well-developed ectepicondylar foramen, a distinct lacertilian character.

Strong resemblances are apparent between *Icarosaurus* and *Kuehneosaurus* in the shape and proportions of the slender humerus. In both, the shaft is slender, the ends are expanded, and there is an ectepicondylar foramen but no entepicondylar foramen. In *Kuehneosaurus* the humerus is "twisted" so that the ends are in different planes—a primitive character that is retained, for example, in *Sphenodon*. In *Icarosaurus*, however, it appears that there is no such twist in the humerus; it resembles the humerus of a lizard in this respect. It seems to show an advance beyond the condition typical of *Kuehneosaurus*, as do several other comparable characters in the two genera. The humerus of *Icarosaurus* is also specialized beyond the same bone in *Kuehneosaurus* by virtue of the development of the large proximal process mentioned above,

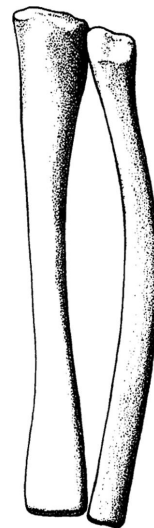


FIG. 29. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Right radius and ulna, dorsal view.  $\times 4$ .

although there is a small process in the same topographic location in the British forms.

The radius and ulna (fig. 29) are slightly shorter than the humerus. The radius is a slender, curved bone; the ulna is stouter and is straight. This latter bone shows some expansion of the ends, whereas the radius is more rodlike, with very little variation in the diameter of the bone throughout its length.

Part of the right manus (fig. 30) of *Icarosaurus* is present, with the bones in articulation. The

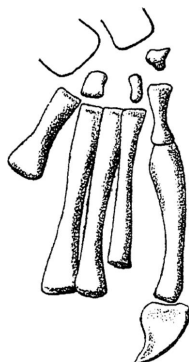


FIG. 30. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Bones of right manus as preserved, dorsal view.  $\times 4$ .

carpus is preserved after a fashion, but, unfortunately, fine details are difficult to distinguish, and only three carpal bones are definitely visible. Perhaps the carpus was to a large degree cartilaginous, or some of the bones were lost during the process of fossilization. Little can be said, therefore, with regard to the carpus in *Icarosaurus*. The metacarpals are all present, as are the phalanges of the first digit. All the other phalanges are missing.

One of the carpal bones that can be distinguished is a small element directly beneath the distal end of the radius, indicating that it is a small radiale. Of course it may be some other bone of the wrist that has been displaced. As to the other two bones, one is directly above the second metacarpal and one is above the fourth. These may be two of the distal carpals, or perhaps the one above the fourth metacarpal is an ulnare. Both bones are imperfectly preserved.

The metacarpals of *Icarosaurus* show an arrangement remarkably similar to that seen in *Draco*. The first metacarpal is relatively short, with its proximal end offset above the ends of the other metacarpals. The second metacarpal is long and slender but is considerably exceeded in

length by the third and fourth metacarpals, which are in turn of equal length and closely appressed to each other. It appears that these two digits may have acted more or less as a functional unit. The fifth metacarpal is short, comparable in this respect with the first metacarpal, but very heavy.

The proximal phalanx of the first digit is long and much expanded in its proximal portion, although the appearance of expansion of this phalanx may be in part the result of crushing. It articulates with a deep and narrow claw. These features of the phalanges of the first digit are so remarkably like the comparable phalanges in *Draco* that it is assumed that the phalanges of the other digits in the manus of *Icarosaurus*, unfortunately missing in the type specimen, were similar to those of *Draco* in general proportions and arrangement. They have been so restored in figure 31.

All the bones of the pelvis (figs. 12, 13, and 32) are preserved in the specimen of *Icarosaurus*, and on both sides the medial aspects of these bones are visible. When the animal was buried and the soft parts had decayed, the two halves of the pelvis separated at their sacroiliac joints,

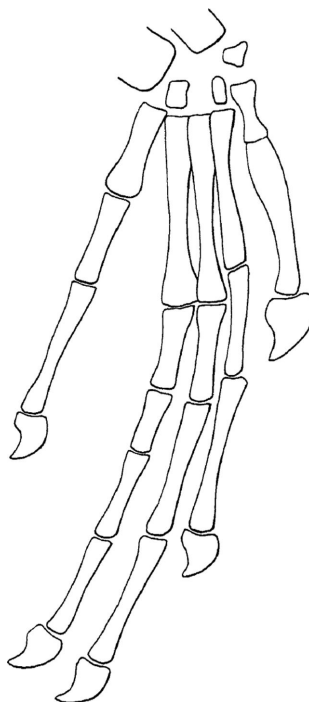


FIG. 31. *Icarosaurus siefkeri*, restoration of right manus, dorsal view.  $\times 4$ .



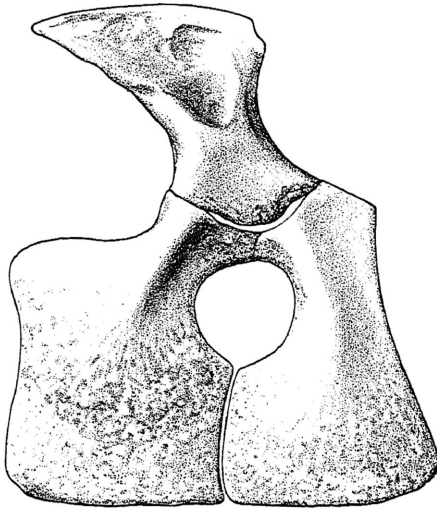


FIG. 32. *Icarosaurus siefkeri*, A.M.N.H. No. 2101.  
Left side of pelvis, internal lateral view.  $\times 4$ .

each half reclining in the sediment with its ilium lateral to the other two bones. In other words, the tops of the two halves of the pelvis fell away from each other.

This pelvis is rather small in relation to the size of the animal and in general form is modified somewhat from the primitive type of reptilian pelvis. The three bones of the pelvis on each side meet suturally in the acetabular region, with long sutures joining the two lower bones to the ilium.

The ilium is relatively high. It is expanded in its upper portion, but the posterior point does not extend far back to the same degree seen in *Kuehneosaurus*, or in many Permo-Triassic reptiles, so that the entire medial surface of the ilium in its upper portion was taken up with the sacral attachment. There is a large and deep depression on the medial surface of this bone, its lower border marked by a strong rim, extending around the ventral half of the depression, and situated on the narrowest part of the ilium. Dorsally this depression becomes shallow and broad and fades into the surface of the iliac blade.

The pubis and the ischium are expanded and platelike and are relatively large compared with the ilium. They are joined to each other proximally, below the acetabulum, by a short suture, and distally by a rather long sutural boundary. A large, rounded thyroid fenestra occupies a considerable portion of the boundary region

between the two bones, thus interrupting in this region the junction between them. An obturator foramen is not visible in the pubis, but whether its absence is real or only a result of fossilization is not definitely determinable at the present time. This bone is deep, proportionally much more so than is the case in the genus *Kuehneosaurus*. It has a relatively narrow neck in the region of the thyroid fenestra and a wide distal expansion of thin bone with a roughened surface. The ischium likewise is deep and distally expanded and rugose, with a narrow shaft or neck in the region of the thyroid fenestra. The two bones together give the lower moiety of the pelvis a rather quadrangular outline in lateral view: the pubis by reason of a sharp point anterior to the acetabulum and a well-developed angle rather than a rounded edge between its anterior and ventral edges; the ischium because of rounded posterior corners proximally and distally. Both lower bones of the pelvis are flat as preserved; it is possible that the two halves of the pelvis came together ventrally at a sharp angle, as in many living lizards, rather than in a rounded surface.

In its total aspect the pelvis of *Icarosaurus* is very different from and somewhat more specialized than the pelvis of *Kuehneosaurus*. One might characterize the pelvis of this latter genus as generally conservative, of a type familiar among reptiles of Triassic age. The pelvis of *Icarosaurus*, by contrast, seems to be highly adapted. Once again, as in various other osteological features, *Icarosaurus* appears to be a genus advanced beyond *Kuehneosaurus* in the evolution of its osteological characters.

The right femur of *Icarosaurus* (fig. 33) is a long, straight, slender bone, approximately twice the length of the humerus, an indication that the hind limb in this little reptile was relatively long. The head of the bone is set at a small angle to the shaft, and of course the distal end of the bone is expanded for articulation with the tibia and fibula. This bone, which has been crushed to some extent, its walls being thin and fragile, lacks any prominent features. Below the head on the anterior side of the bone, which is the aspect seen, there seems to be a remnant of a faint longitudinal ridge, but whether this is natural or the result of crushing is difficult to determine. A large part of the left femur is also preserved, but it adds nothing to our knowledge.

A partial tibia is present, lateral to the right

femur, and because of its position (fig. 34) in the rock it is considered to be a right tibia. The upper end of the bone is missing, but an imprint in the rock shows the shape. The distal end of the bone is somewhat obscure, but it is believed

to be essentially complete. On the basis of these observations the tibia, which is a straight bone, is slightly more than two-thirds of the length of the femur. No traces of the hind feet have been found in the slab containing the skeleton.

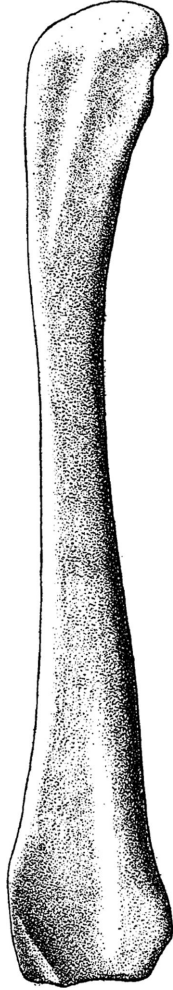


FIG. 33. *Icarosaurus siefkeri*, A.M.N.H. No. 2110.  
Right femur, ventral view.  $\times 4$ .



FIG. 34. *Icarosaurus siefkeri*, A.M.N.H. No. 2101.  
Right tibia.  $\times 4$ .

TABLE 1

COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF *Icarosaurus siefkeri* (TYPE), OF *Kuehneosaurus latus* (FROM SCALED FIGURES), AND OF *Draco spilopterus*

	<i>Icarosaurus siefkeri</i> A.M.N.H. No. 2101	<i>Kuehneosaurus</i> <i>latus</i>	<i>Draco spilopterus</i> A.M.N.H. No. 76572
Skull, total length as restored	24.8	27.1	13.0
Length, premaxilla to quadrate	22.5	26.2	11.0
Greatest width	21.4	21.2	8.7
Depth	9.0	9.2	5.6
Length of orbit	10.5	10.6	5.9
Length of temporal fenestra	3.7	4.1	3.7
Length of frontal (on midline)	7.7	9.4	5.7
Length of parietal (on midline)	5.0	5.2	1.4
Height of quadrate	5.3	7.3	2.1
Width at quadrates	—	20.7	6.9
Articular length of jaws	22.0	25.5	11.1
Total length of ramus	25.5 (est.)	29.4	13.2
Depth of ramus	1.8	—	1.5
Number of premaxillary teeth	4±	5	1
Number of maxillary teeth	27±	32	15
Number of dentary teeth	30±	41	16
Vertebrae			
Number of presacrals	24	28	25
Length of presacrals	74.0	—	52.0
Length of cervicals	17.0 <sup>a</sup>	—	10.0 <sup>b</sup>
Length of wing-bearing vertebrae	37.0 <sup>c</sup>	—	16.3 <sup>a</sup>
Sixth presacral			
Length of centrum	1.2	4.3	1.1
Anterior diameter of centrum	—	3.5	0.8
Height	4.3	10.2	2.0
Breadth, transverse process	—	7.1	1.6
Eleventh presacral			
Length of centrum	—	5.8	1.4
Anterior diameter of centrum	—	3.7	0.6
Height	—	10.1	1.8
Breadth, transverse process	6.4	19.8	2.6
Twelfth presacral			
Length of centrum	—	5.6	1.7
Anterior diameter of centrum	—	4.8	0.7
Height	—	10.2	1.8
Breadth, transverse process	26.1	21.8	3.5
Fifteenth presacral			
Length of centrum	—	5.7	3.2
Anterior diameter of centrum	—	4.5	0.7
Height	—	13.0 <sup>e</sup>	1.5
Breadth, transverse process	25.6	32.7	3.7
Twentieth presacral			
Length of centrum	6.3	6.3 <sup>f</sup>	3.0
Anterior diameter of centrum	—	4.2	0.7
Height	—	9.4	1.4
Breadth, transverse process	19.5	29.4	2.1
Twenty-third presacral			
Length of centrum	6.0	5.7	2.5
Anterior diameter of centrum	—	3.1	0.7
Height	3.9 <sup>g</sup>	7.6	1.5
Breadth, transverse process	7.6	21.8	1.8

TABLE 1—(Continued)

	<i>Icarosaurus siefkeri</i> A.M.N.H. No. 2101	<i>Kuehneosaurus</i> <i>latus</i>	<i>Draco spilopterus</i> A.M.N.H. No. 76572
First sacral			
Length of centrum	4.0	7.0	1.7
Anterior diameter of centrum	—	3.2	0.7
Height	—	8.9	1.5
Breadth, transverse process	12.0	14.4	3.6
Length of sacral series	8.2	13.3	3.2
Proximal caudal			
Length of centrum	4.8	6.2	1.8
Anterior diameter of centrum	—	5.0	0.7
Height	—	9.1	1.7
Breadth, transverse process	10.0	13.2	3.3
Length of ribs			
Presacral 11	11.6	—	30.3 <sup>a</sup>
Presacral 12 (wing rib 1)	108.0 <sup>c</sup>	—	31.1
Wing rib 2	120.0 <sup>c</sup>	—	33.0
Wing rib 3	126.0 <sup>c</sup>	—	32.0
Wing rib 4	126.0 <sup>c</sup>	—	31.2
Wing rib 5	123.0 <sup>c</sup>	—	27.0
Wing rib 6	115.0 <sup>c</sup>	—	—
Wing rib 7	89.0 <sup>d</sup>	—	—
Wing rib 8	63.0 <sup>d</sup>	—	—
Wing rib 9	42.0 <sup>d</sup>	—	—
Wing rib 10	26.0 <sup>d</sup>	—	—
Girdles			
Scapula, height	7.4	—	4.4
Coracoid			
Length	7 (est.)	—	4.2
Breadth	8 (est.)	—	2.0
Pelvis			
Height	16.0	23.5	3.3
Anteroposterior diameter	15.1	22.5	8.1
Ilium			
Height	7.9	14.2	1.0
Length, iliac crest	6.0	17.0	3.8
Pubis			
Height	8.3	9.2	—
Anteroposterior diameter	5.6	9.7	4.3
Ischium			
Height	9.0	9.2	2.1
Anteroposterior diameter	9.4	13.2	1.8
Forelimb			
Humerus			
Length	20.1	—	12.4
Distal breadth	6.3	—	2.0
Radius, length	15.5	—	10.0
Ulna, length	15.7	—	10.6
First digit, length	9.7	—	4.6
Manus, greatest length	—	—	10.0
Hind limb			
Length of femur	34.7	—	13.9
Distal breadth of femur	5.0	—	1.3
Length of tibia	23.0	—	10.9
Length of fibula	—	—	10.9
Greatest length of pes	—	—	14.4

TABLE 1—(Continued)

	<i>Icarosaurus siefkeri</i> A.M.N.H. No. 2101	<i>Kuehneosaurus</i> <i>latus</i>	<i>Draco spilopterus</i> A.M.N.H. No. 76572
Total presacral length	95.0	—	65.0
Total length	331 (est.)	—	153+
Wing span	272	—	60 (approx.)

<sup>a</sup>First nine presacrals.<sup>b</sup>First seven presacrals.<sup>c</sup>Nos. 12–21.<sup>d</sup>Nos. 12–17.<sup>e</sup>No. 16.<sup>f</sup>No. 21.<sup>g</sup>No. 24<sup>h</sup>The first wing rib in *Draco* articulates with the eleventh presacral vertebra.<sup>i</sup>As restored and along projected curves.<sup>j</sup>Ribs complete.

TABLE 2

COMPARATIVE MEASUREMENTS (IN MILLIMETERS) AND RATIOS OF THE TYPE OF *Icarosaurus siefkeri* AND AN ADULT *Draco whiteheadi*

	<i>Icarosaurus siefkeri</i> A.M.N.H. No. 2101	<i>Draco whiteheadi</i> A.M.N.H. No. 30917
MEASUREMENTS		
Weight in grams	40 (est.)	6.40
Total wing area in square cm.	173.90	12.44
Wing area, square cm. per gram	4.25	1.95
Wing loading, gram per square cm.	0.23	0.51
RATIOS		
Skull length/presacral length	33	25
Cervical length/postcervical-presacral length	30	24
Wing vertebrae length/presacral length	50	31
Humerus length/femur length	60	89

## ADAPTATIONS IN *ICAROSAURUS*

THE MOST STRIKING FEATURE of *Icarosaurus*, of course, is the tremendously elongated ribs (fig. 35), which are considered to be adaptations for the support of a membrane that would make on each side a flight surface, or wing, enabling *Icarosaurus* to glide from tree to tree. This interpretation of the elongated ribs in *Icarosaurus* is based on their close resemblance to the elongated ribs of the modern lizard *Draco*, an Oriental agamid. In view of the remarkable similarities in this regard between *Icarosaurus* and *Draco* (fig. 36), the supposition that the ribs were elongated as supports for a "wing" is abundantly justified; no other explanation for these long ribs need be seriously considered.

In *Draco* five, six, or seven ribs on each side are elongated for the support of the flight membrane; in *Icarosaurus* there are 10 such ribs. In *Draco* the ribs have been elongated to form a broad wing with a semicircular outline, a wing with no marked leading or trailing edges, and one in which the greatest lateral dimension is markedly less than its anteroposterior extent. In *Icarosaurus* the elongation of the ribs is of such nature as to form a much more highly developed wing, which is of much greater transverse extent, relatively speaking, than that of *Draco*, and is more restricted anteroposteriorly. The wing in *Icarosaurus* is characterized by a long, straight, leading edge, formed by the straight rib that articulates with the twelfth presacral vertebra and by a definite trailing edge resulting from the progressive reduction in length of the last four elongated ribs. Thus the differential elongation of the 10 ribs that support the flight membrane in *Icarosaurus* makes for a wing the length of which on each side is about twice the anteroposterior spread. These proportions are not unlike those in some of the soaring birds (fig. 37).

The adaptation of the wing in this reptile for efficient gliding involves, however, not only its outline but also its shape. As shown above in the osteological description, all the elongated ribs except the first one are curved, and the articulations of these single-headed ribs on the transverse processes show that the curves of the ribs were concave ventrally, convex dorsally. Con-

sequently the wing of *Icarosaurus* was shaped with a strongly concave under surface and a convex upper surface, which was aerodynamically advantageous (fig. 38).

Thus it is obvious that the adaptations in the ribs of *Icarosaurus* provided it with rather efficiently designed wings—certainly better than those seen in the modern lizard *Draco*. *Icarosaurus* must have been a skilled and precise glider, developing gliding to an even greater perfection than did *Draco*.

The single-headed ribs of *Icarosaurus* indicate that the wing was very flexible and movable and almost certainly could be folded back against the body when not in use, as can the wing in *Draco*. In the modern reptile the muscle control of the wing is comparatively simple (fig. 39). The first of the elongated ribs is pulled forward by strong slips of the iliocostalis muscles, and the same is true for the second elongated rib. The following three or four ribs are pulled forward mainly by ligaments, by which they are connected one to another, and by which the most anterior of these latter ribs is connected to the second elongated rib. In such a manner the wing is spread. Conversely, the ribs are folded back against the body mainly by the action of the intercostal muscles. In addition, slips of the intercostal muscles run along the length of each rib, and these, by varying tension, can control the curvature of the ribs, which are flexible.<sup>1</sup>

Probably the spreading and folding of the wing, as well as the varying of its surface aspects, were similarly accomplished in *Icarosaurus*. Such wing control would have augmented the efficiently shaped and generously proportioned wings of *Icarosaurus* in determining flight patterns and directions during gliding.

Although it may be assumed that the mechanics of wing extension and folding in *Icarosaurus* were in general similar to what is seen in *Draco*, there are necessarily differences that should be taken into account, owing in part, at least, to the different form and proportions of the wings in the two genera.

<sup>1</sup>For a description and analysis of wing musculature and function in *Draco*, see Colbert (1967).

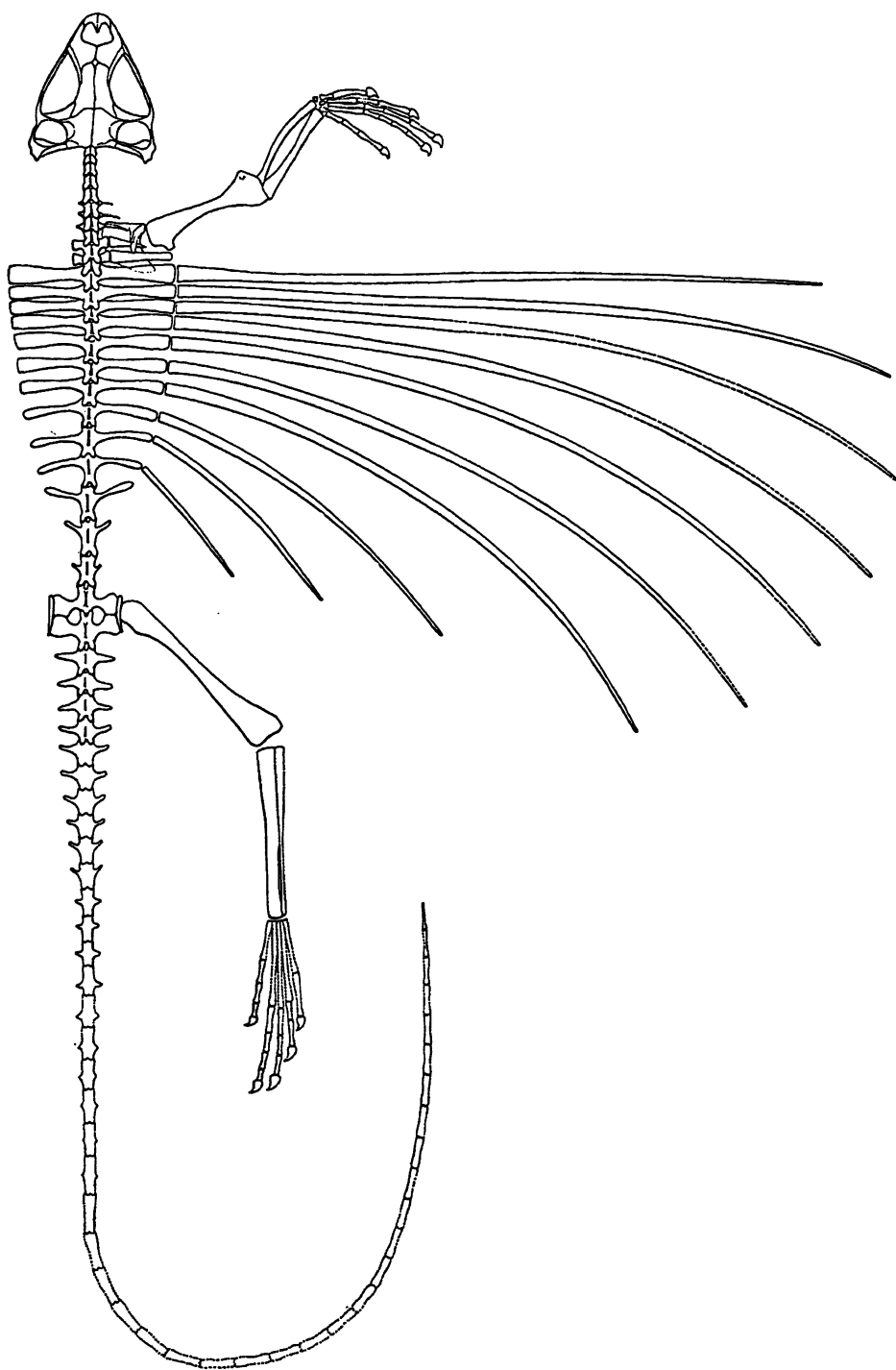


FIG. 35. *Icarosaurus siefkeri*, A.M.N.H. No. 2101. Restoration of skeleton, dorsal view.  $\times 4/5$ .

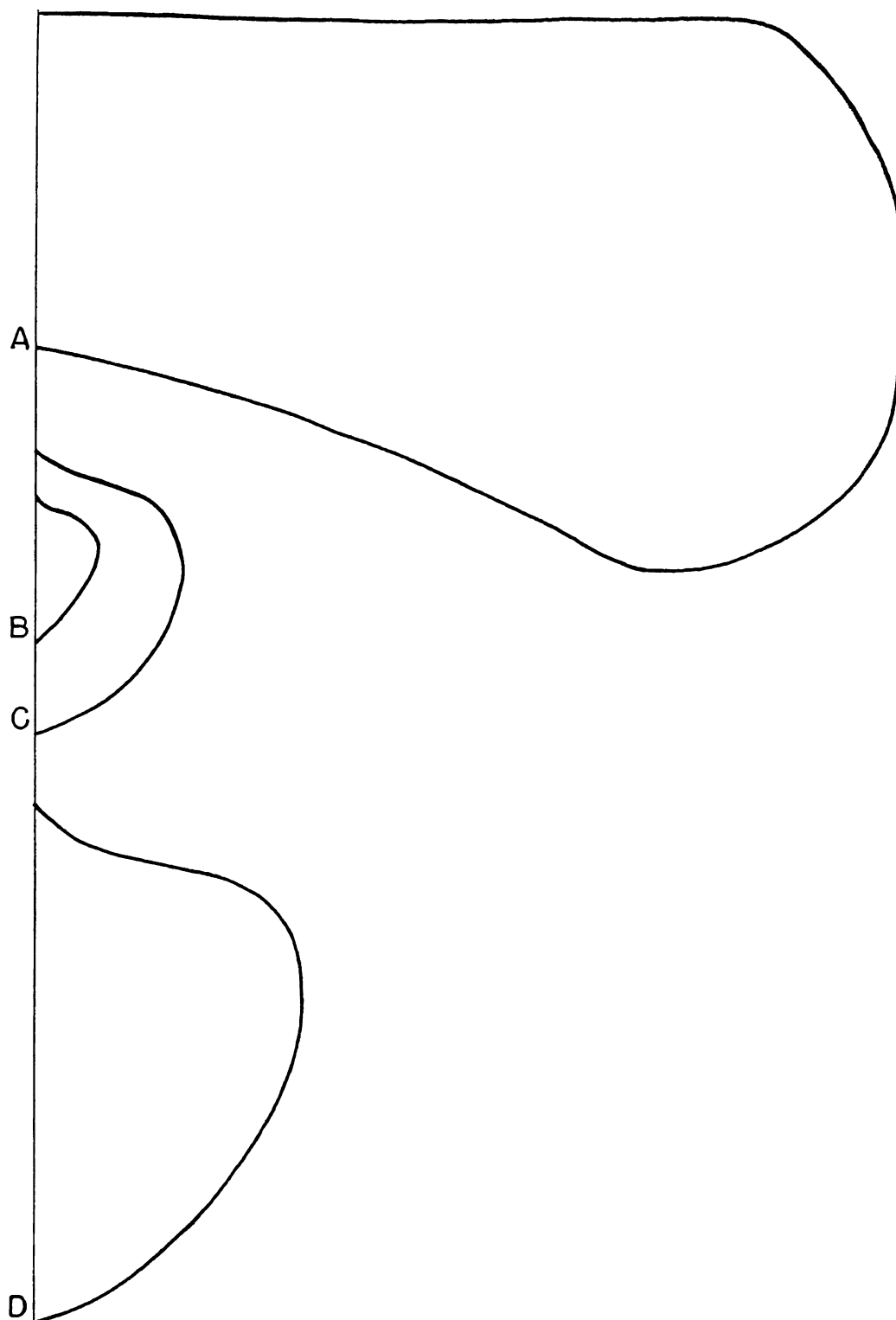


FIG. 36. Comparison of outlines of right wing, dorsal views. A. *Icarosaurus siefkeri*, A.M.N.H. No. 2101, as restored. B. *Draco whiteheadi*, juvenile, A.M.N.H. No. 30905. C. *Draco whiteheadi*, adult, A.M.N.H. No. 30917. D. *Draco maximus*, J. R. Hendrickson Collection No. 5338.  $\times 1$ .



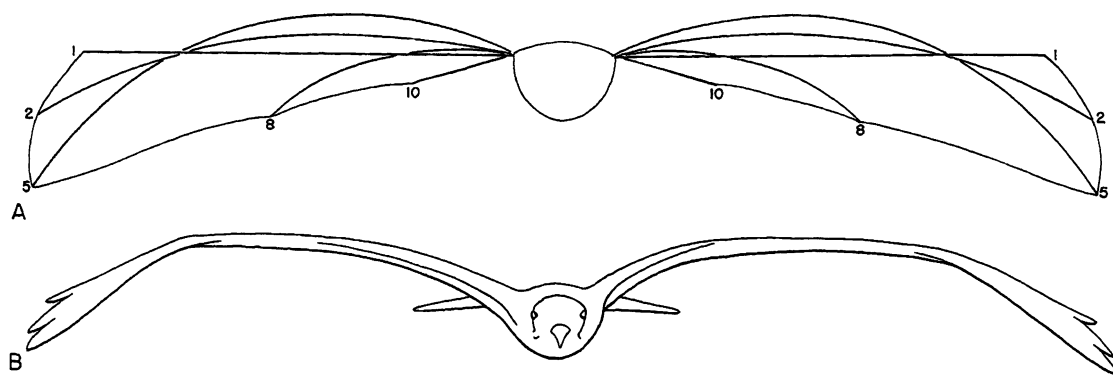


FIG. 37. A. Schematic diagram of wings of *Icarosaurus siefkeri*, anterior view, showing curvatures of wing ribs 1, 2, 5, 8, 10 attached, respectively, to presacral vertebrae 12, 13, 16, 19, 21. B. Silhouette of a kite, soaring, anterior view (modified from Vinogradov, 1951). Note rather close similarity between curve of wing rib 5 of *Icarosaurus* and wing curvature of the bird. Rib 2 forms one of the transition ribs between the straight leading edge of the wing, formed by the first wing rib, and rib 5. Wing ribs 8 and 10 indicate the trend from the long, strongly curved ribs of the middle portion of the wing to the trailing edge.

In *Draco*, for example, the five or six vertebrae that carry the elongated ribs have rather long centra, so that the transverse processes are well separated from one another. Consequently the folding of the wing in this reptile is a simple operation; the iliocostalis muscles are relaxed, and the ribs are pulled inward serially against the body mainly by the contraction of the intercostal muscles. In *Icarosaurus* the process of folding the wings (fig. 40) must have been somewhat more complex because the dorsal centra are proportionally shorter than those in *Draco*, so that the greatly expanded transverse processes are close to one another, especially in the anterior five vertebrae of the rib-bearing series. Therefore a simple horizontal folding back of the ribs as in *Draco* would have involved difficulties because of interference between the ribs in their more proximal portions, particularly as the ends of the virtually contiguous transverse processes are almost in alignment.

Apparently this difficulty was obviated for the most part by the curvature of the ribs in the fossil genus. Experiments with a three-dimensional model (figs. 49 and 50) indicate that, if the curves of the ribs have been correctly restored, their anterior portions would have been directed obliquely upward as the wing was folded back against the body, rising proximally from the rib articulations to successively higher points above the pelvic region, and then descending again distally to about the midline of

the body, above the forepart of the tail. Consequently there would have been no interference between them, although their articular ends were close to each other. In short, the curved ribs of *Icarosaurus*, when folded back (fig. 41), would have nested within one another in a series of concentric arcs. This system of wing folding and "stowage" holds for all but the first two elongated ribs.

Because the first rib is interpreted as having been virtually straight, to form the leading edge of the wing, and because the second rib has a relatively gentle curve, to make the transition from the straight first rib to the rather strongly curved ribs of the middle portion of the wing, these two do not fit into the concentric arrangement so nicely shown by all the other ribs, when the wing is in its folded position. What positions, then, did the first two ribs assume when the wing was folded back?

There are only two possibilities. Either the first two ribs were pulled back to positions lateral to the other ribs, or they were moved back to positions dorsal to the other ribs. It is difficult to bring these two ribs into positions lateral to the other ribs in the folded wing because of interference of their proximal portions with those of the following ribs; to move the first two ribs into such positions does violence to their articulations with the transverse processes. In other words, it is necessary to pull the heads of the first two ribs away from the trans-

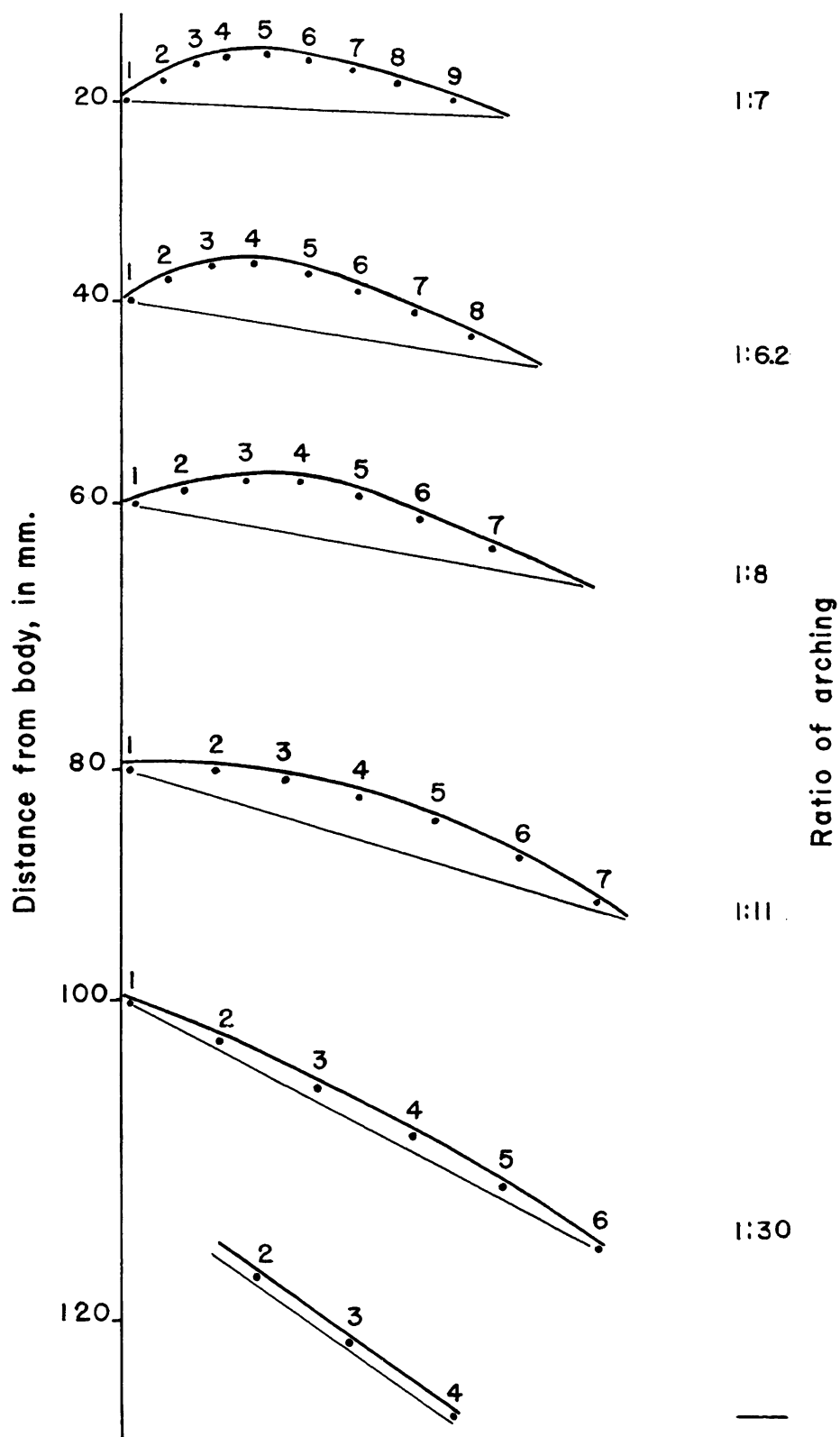


FIG. 38. Cross section of wing of *Icarosaurus siefkeri* at intervals of 20 mm. from body to position near wing tip, showing positions (dots) of ribs, identified by numbers.  $\times 1$ .

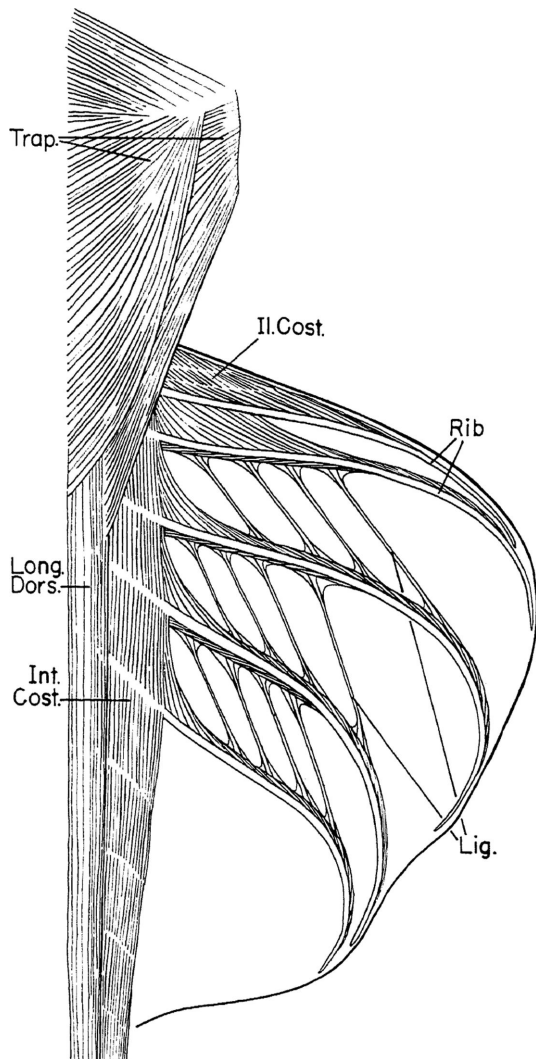


FIG. 39. Musculature of wing in *Draco whiteheadi*. Note strong muscles for pulling forward first two elongated ribs, and series of ligaments that pull posterior ribs forward in concert with anterior ribs. Similar arrangement of muscles for expanding wing possibly present in *Icarosaurus*. Key: Il.Cost., iliocostalis muscles; Int. Cost., intercostal muscles; Lig, ligaments between ribs; Long. Dors., longissimus dorsi muscle; Trap., trapezius muscle. From Colbert (1967).

verse processes in order to bring these ribs into such positions lateral to the third rib as would have been allowed by the extent of the membrane connecting them. Therefore it seems more likely that the first two ribs were moved back to

positions dorsal to the other ribs. Such movements and positionings of these two ribs would allow their proximal portions to fall into place above, or more properly in front of, the third rib without interference and would bring the middle and distal portions of the two ribs into positions considerably above the other ribs, but still within the limits allowed by the wing membranes. The folded wing is envisaged as rising above the midline of the back, the last eight ribs being close together in concentric arrangements, with the wing membranes folded between them, the ends of the first two ribs rising vertically above the other ribs to about the extreme limits allowed by the intervening wing membrane. Possibly the two wings were folded against each other over the midline of the back, so that in this position they together formed a rather high sort of sail or crest over the middle of the animal. At first sight such an arrangement appears clumsy, but in actuality the midline crest so formed would probably be no more disadvantageous than comparable but, of course, not homologous midline crests in certain modern lizards—*Basiliscus*, for example.

Certainly in such a position the wings would be virtually out of the way when the animal was climbing about in the trees, and from such a position these wings could be almost instantaneously pulled into position for flight.

The adaptations of the 10 elongated ribs on each side for support of the wings is clear enough. What is to be said about the two short ribs articulating with the tenth and eleventh presacrals? These ribs are much like the expanded transverse processes of the vertebrae that immediately follow the axial skeleton. Is it not possible that these ribs afforded additional anchorage for a very strong iliocostalis muscle in an area immediately in front of the leading edge of the wing where such an insertion would be particularly advantageous? Of course one may suppose that the iliocostalis muscle extended anterior to this region, to insert on the vertebrae of the neck region, but it is suggested that perhaps the bulk of this musculature was inserted on the two transverse-like ribs, so peculiarly developed in *Icarosaurus*.

Naturally the vertebrae that served as the base for the wings in *Icarosaurus* are strongly modified in conjunction with the unusual adaptations that have affected the ribs to make them controlled and perhaps flexible struts that

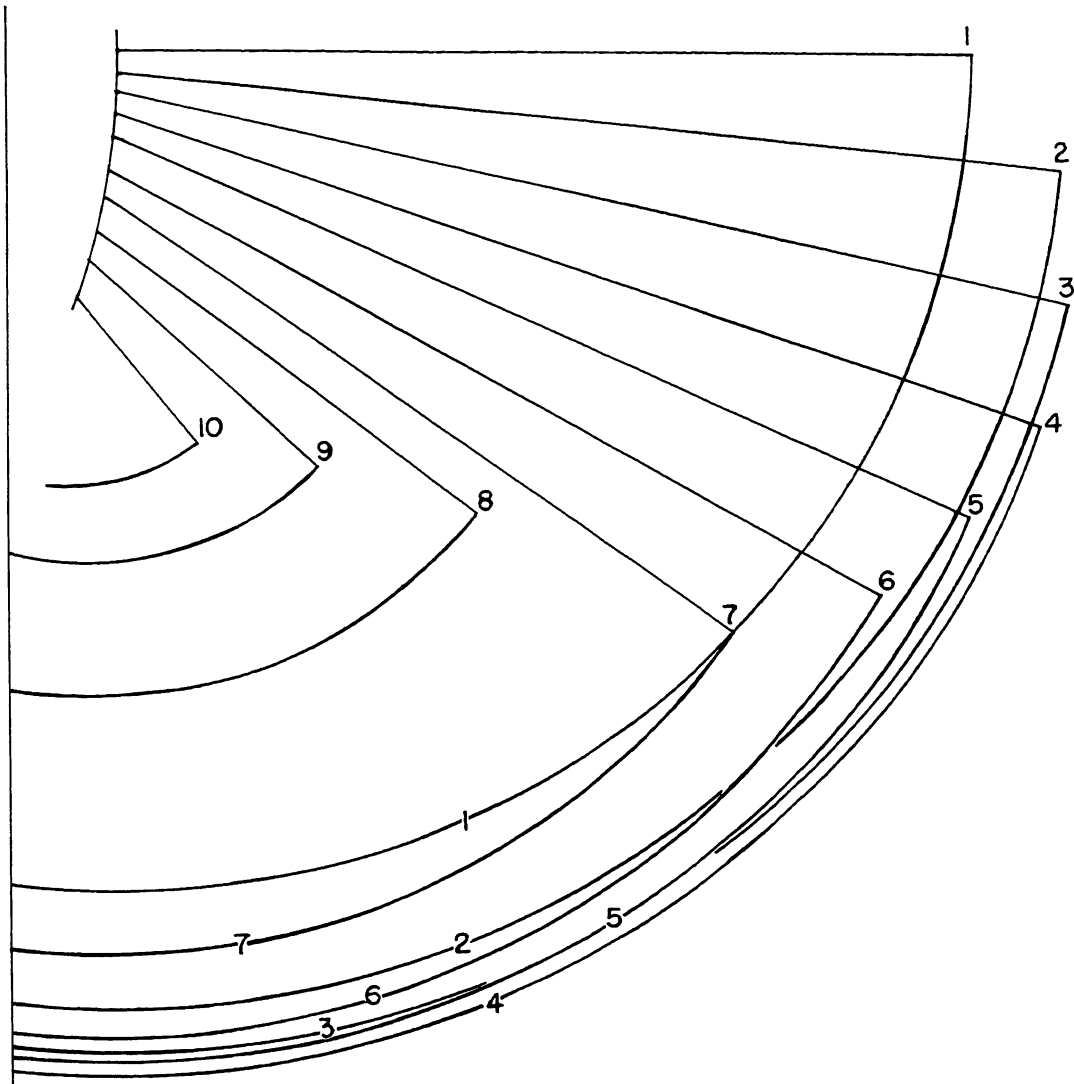


FIG. 40. Arcs described by tips of wing ribs of *Icarosaurus siefkeri* during folding of wing against body, dorsal view. Tips of ribs in extended position are joined to their respective vertebral articulations by straight lines.  $\times 1$ .

were pulled forward to expand and to stretch taut the extended wing, and pulled back to fold this wing against the body. The development of these anterior "dorsal" vertebrae suggests that they functioned not only as a strong base for support of the large wings, but also, and simultaneously, as a flexible base that operated in a dynamic manner partially to control the attitudes of the wings during flight (figs. 42 and 43). Large and well-formed wings such as are

characteristic of *Icarosaurus* would necessarily involve structural modifications in skeletal elements in addition to the ribs.

The great expansion of the transverse processes of the vertebrae that support the elongated ribs is a feature seen in *Kuehneosaurus* as well as in *Icarosaurus*. In both genera the transverse processes extend laterally to a remarkable degree—in *Kuehneosaurus* the width of the vertebrae with the most widely extended processes, measured

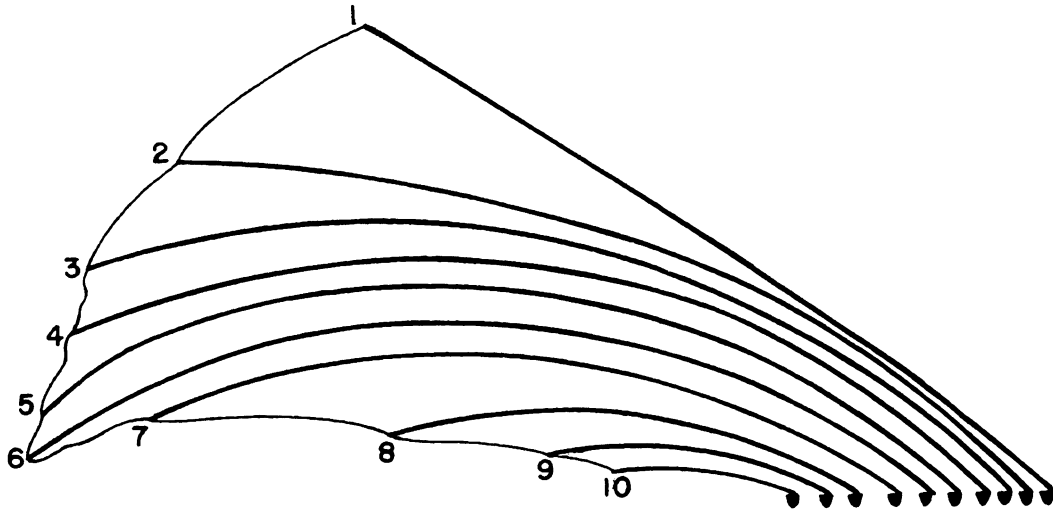


FIG. 41. Suggested positions of ribs in folded wing of *Icarosaurus siefkeri*, lateral view.  $\times 1$ .

across the transverse processes, is about six times the length of the centrum, and in *Icarosaurus* this width is as much as eight times the length of the centrum. In *Draco* the comparable transverse measurement is only about one-and-a-half times the length of the centrum. Consequently the lines of attachment of the wings to the thorax are widely separated from each other; the upper part of the body in this region is broad, relatively flat, and strong. It might be compared to top of the fuselage of a small, high-wing monoplane or a glider. Such an adaptation provides large areas for the insertion of strong muscles.

Although the expanded transverse processes of *Icarosaurus* and *Kuehneosaurus* are comparable in general proportions, they show many differences in detail. The transverse processes of *Kuehneosaurus*, although very broad, are nevertheless separated from one another when the vertebrae are in articulation. In effect they form a succession of oblique plates in series, the ends of which, in each case, are vertically elongated, but anteroposteriorly constricted for the articulation of the expanded rib heads, and well within the projected planes of central articulations. The expansion of the transverse processes in *Icarosaurus* takes the form of a general enlargement of each process, so that it forms a hollow structure of such dimensions that, in the first five vertebrae with such processes, the ends of

the processes are almost in contact with one another. The close approximation of the processes in the first five vertebrae that support elongated ribs makes of this sequence something of a "notarium," in effect, and it is difficult to imagine that there could have been much, if any, lateral flexion of the body in this particular region. The forepart of the wing must have had a strong anchor indeed, which would have been particularly advantageous for that part of the wing comprising the leading edge and the portion with the longest ribs.

These vertebrae have strong, semicircular, zygapophyseal articulations that allow them to rotate upon one another, although there was strong restriction of lateral flexion, but such rotation would have had the effect of warping the wings—a factor of great importance for flight control. Experiments with, and eyewitness accounts of, *Draco* have shown that this modern lizard exerts remarkable control over the direction of its glides. One can conjecture that *Icarosaurus*, with its well-developed wings capable of being warped by the rotation of the vertebrae, may have possessed an ability of flight control even surpassing that of the modern flying dragon.

In this connection, mention should be made of the evident development of a long tail in *Icarosaurus*. This, too, would have been of prime importance in the control of flight, especially in

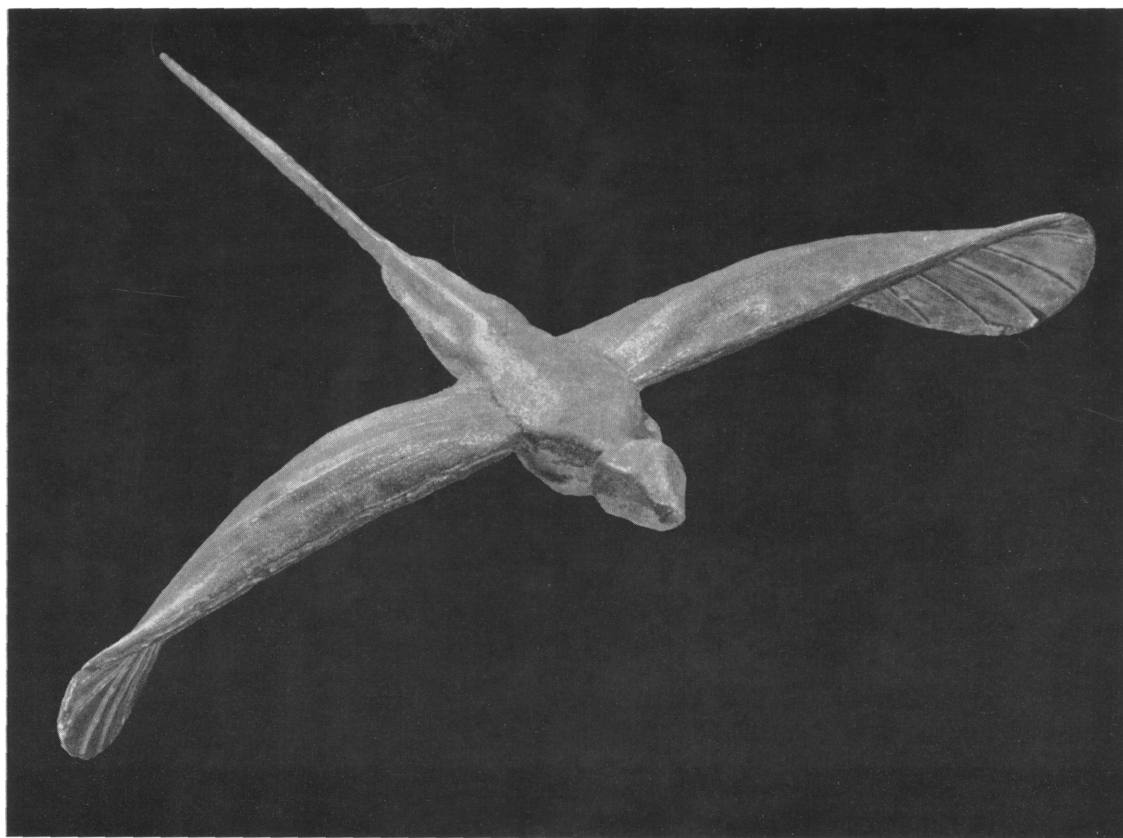


FIG. 42. *Icarosaurus siefkeri*. Model in oblique dorsal view, showing assumed position of wings during flight. Note straight leading edge of wing, formed by first elongated rib. For convenience, limbs have been modeled as pressed against the body; in life this reptile probably glided with the limbs widely extended, as does the "flying dragon" *Draco*. Length of tail conjectural. Not to scale.

the stabilization of the animal while it was in the air. Certainly such a function is obvious in the movement and the use of the long, slender tail in *Draco*.

The initiation of the glide and the landing at its termination must have been integral parts of the flight pattern in *Icarosaurus*, as they are in *Draco*. In the modern lizard the takeoff for a flight is accomplished by a sudden spring into space from a high point on a tree. As the animal launches itself with outstretched wings, the body is pointed down into a steep dive. This, as Klingel (1965) has shown, is the first or initial phase of the glide. This dive builds up kinetic energy for a long, almost horizontal flight, the second or main portion of the glide. At the end of the flight the animal swoops upward to land on the trunk of the tree toward which its glide

was directed, which is the third or final phase of the glide. The launching of *Draco* into its glide is accomplished by a strong push with its long hind limbs; the landing at the end of the glide involves a sudden stop against the tree trunk, the shock of which is probably absorbed to a considerable degree by the forelimbs.

Similar flight patterns may be envisaged for *Icarosaurus*. The long hind limbs of the Triassic genus certainly would have served to propel this animal with force into the initial phase of its glide. These limbs would, as in the case of *Draco*, have acted as a strong spring for the leap into space by virtue of the force engendered by sudden extension from a flexed or partially flexed attitude in which the advantages of long levers could be utilized.

The very heavy scapula and the large cora-

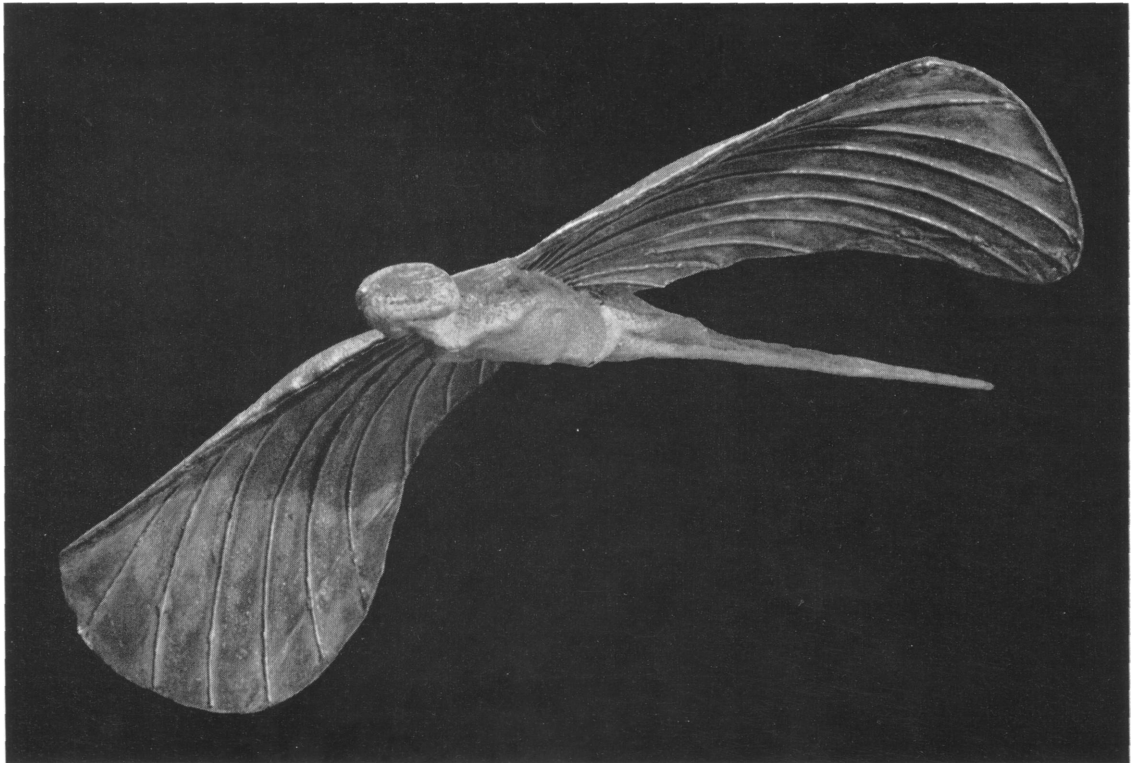


FIG. 43. *Icarosaurus siefkeri*. Model in oblique ventral view, showing spacing and curvatures of ribs that formed wing support. Not to scale.

coids of *Icarosaurus* appear to be, in part, a mechanism for absorbing the shock of landing. The heavy scapula in *Icarosaurus* may be compared in a general way with the strong scapula in modern frogs; the large, platelike coracoids might have served for the origins of strong pectoral muscles, affording at the same time strong support for the ventral part of the body in this region.

Of course the limbs of *Icarosaurus*, important though they might have been for takeoff and landing, were primarily adapted for earth-bound locomotion, probably mainly for clambering up, down, and around the trunks of trees. Consequently it is interesting to see that these limbs are similar to the limbs of modern lizards, including *Draco*. They are well adapted to running, and the hind limbs, as has been said, are much longer than the forelimbs.

The large posterolateral trochanter at the proximal end of the humerus indicates a very strong subcoracoscapularis muscle for the ad-

duction and rotation of the humerus. Although such a trochanter is a characteristic feature of the lepidosaurian humerus, its exceptional development in *Icarosaurus* is noteworthy; its significance is difficult to interpret.

The partially preserved hand of *Icarosaurus* indicates by its resemblances to the hand of *Draco* that the extinct reptile probably was well adapted for climbing on the trunks of trees, as is shown by the sharp, narrow but deep claw of the first digit of the manus preserved in *Icarosaurus*. A claw of this form would have been efficient for grasping small rugosities on trunks and limbs and would have had the necessary strength, in concert with the other claws of adjacent digits, to support the weight of the animal. It is to be supposed that similar adaptations characterized the pes in *Icarosaurus*.

Such were the adaptations of this reptile for locomotion, for running about on the trunks of trees, as is here postulated, and for gliding from one tree to another. The other adaptations in

*Icarosaurus* that may be inferred from the osteology are those for feeding and, to a limited degree, the development of sensory contact with the environment.

To consider the latter first, it may be assumed that *Icarosaurus* possessed a keen sense of sight, an assumption based on its large orbits. Similarly large orbits are also found in *Kuehneosaurus* and in the modern *Draco*. It seems axiomatic that sharp and precise eyesight was and is essential to these aerial reptiles. Gliding considerable distances from one tree to another, directing this flight, and making safe landings require the sharp definition of the distant target before the animal launches itself into the air. Indeed, the evolutionary success of these gliding reptiles in past ages and today has depended on visual acuity combined with the ability to glide.

The natural habitat of *Draco* is the dense rain forest of the Orient, where the treetops form a canopy beneath which there is a sort of twilight zone. This again is a condition that places a premium on large, light-gathering eyes. It seems probable that *Icarosaurus*, and perhaps *Kuehneosaurus* also, may have lived under environmental conditions similar to those for *Draco*.

Of course the ability to glide skillfully presupposes a delicate sense of balance, so it may be assumed that the middle ear was sensitive in *Icarosaurus*. Evidence as to the hearing ability of this extinct reptile is not available, but perhaps its auditory powers were similar to those of *Draco*. There may have been a well-developed sense of smell; certainly the narial openings are rather large.

The adaptations in *Icarosaurus* having to do with feeding are now considered. This reptile has a delicately constructed skull, which is surprising when one considers its relatively large size. Although the skull must have been lightly constructed, as excessive weight could not have been tolerated, its comparatively large size implies the presence of large jaw muscles of some weight, a conclusion that is supported by the differentiated neck vertebrae with their expanded, strong zygapophyses. Indeed, the marked differentiation of the neck indicates not only the strength necessary to support the skull but also a degree of cervical mobility that would have been of particular value to a fast-moving, predatory species. What were the adaptations in the skull of *Icarosaurus* to be correlated with the movement of the jaws during feeding?

The skulls of reptiles may be solidly constructed, or akinetic, with the bones immovably connected to one another, or they can be openly constructed, or kinetic, with at least some of the bones of the skull so connected that there is movement between them. The concept of kineticism, developed especially by Versluys, is succinctly analyzed and summarized by Robinson in her paper on the evolution of the Lacerilia (1967). The rather complex movements within the kinetic skull give it additional gape and biting power and clearly have been important in the evolutionary development of various lines of reptilian adaptive radiation.

Robinson showed that in *Kuehneosaurus* the skull, though potentially kinetic, is nevertheless restricted from any of the main types of kineticism by virtue of the interlocking joint between the pterygoids and the basiptyergoids. The preservation of the skull in *Icarosaurus* is such that no direct determination can be made regarding kineticism, but, in view of the many close resemblances between this genus and *Kuehneosaurus*, it seems probable that, as is that of the form from Britain, the skull of *Icarosaurus* was essentially akinetic.

In addition to the problem of kineticism in the reptilian skull there is the problem of streptostyly—the freeing of the quadrate so that it is movable with relation to the rest of the skull. This condition, highly developed in the modern squamates, is important in increasing the flexibility and gape of the jaws. In essence, streptostyly creates a sort of double jaw joint that has proved advantageous in the evolutionary radiation and adaptations among the squamates.

As Robinson has shown, streptostyly is achieved in part by the suppression of the lower border of the lateral temporal fenestra, commonly by the reduction or elimination of the jugal and quadratojugal bones, and in part, and more particularly, by the loss of the ventral ramus of the squamosal, which primitively hugs the lateral surface of the quadrate to form a splintlike joint that prevents movement between the two bones. Among the Eosuchia, which include such lizard-like forms as *Prolacerta* and *Pricea*, the strong union between the squamosal and quadrate persists, although the lower temporal arcade is interrupted. Among the Squamata, the most primitive members, the colacertilians, as represented by *Kuehneosaurus*



and *Icarosaurus*, show a complete suppression of the descending ramus of the squamosal and a consequent freedom of movement of the quadrate on the quadrate-squamosal joint.

In these early gliding reptiles the quadrate was able to swing back and forth in a manner similar to that in many of the modern lizards. In this connection it is interesting to note that the quadrate in *Draco* appears to be firmly fixed in place by a strong union between this bone and the end of the quadrate ramus of the pterygoid, which abuts against, and is joined to, the anterior border of the medial edge of the ascending ramus of the quadrate. The lower jaws of *Draco* evidently work against a solidly constructed skull.

In *Icarosaurus* and *Kuehneosaurus*, on the other hand, the jaws were evidently more mobile than they appear to be in *Draco*. *Draco* feeds on ants. The Triassic forms probably were insect eaters for the most part, but because of their large size and more mobile jaws they may have fed on larger prey. Perhaps they ate large insects and even small reptiles.

The numerous, simple, and homodont teeth in the Triassic forms would have been well adapted for an insectivorous or a micro-carnivorous diet. The large number of teeth set

around the margins of the jaws provided an extensive dental battery, which was supplemented by the numerous palatal teeth.

From the foregoing discussion the mode of life that characterized *Icarosaurus* may be reconstructed. It is suggested that this Triassic reptile was a denizen of the trees, as is the modern *Draco*, and that, like *Draco*, it probably seldom ventured down to the ground. Among the trees of a Triassic jungle in what is now New Jersey, a jungle that bordered a large lake, *Icarosaurus* climbed up and down and over the branches in search of food, which consisted of various large and small insects and perhaps small reptiles. Frequently it spread its wings and launched itself into the air to seek another tree—to escape from an enemy, to pursue a mate, or to search out a new feeding ground. Its mode of life was a successful one, and probably these little reptiles were numerous in the Triassic forests. Because of their habitat they were very rarely fossilized. At Granton Quarry in New Jersey, one individual of *Icarosaurus* fell into the quiet waters of the lake, and was covered by the fine muds in the shallow bottom. Thus was preserved a hitherto unknown member of a faunal assemblage. Its discovery has enhanced our reconstruction of Triassic life.

## AERODYNAMIC PROBLEMS OF ICAROSAURUS

THE OBVIOUS APPROACH to the problem of the anatomical adaptations of *Icarosaurus* for flight is by a comparison of *Icarosaurus* with *Draco*. The parallels between the Recent Oriental aerial reptile and *Icarosaurus* are so striking that many of the factors involved in the aerodynamics of one apply to the other. There are divergences, however, within these parallels, particularly because of differences in wing form. Further comparisons can be made between the extinct reptile and birds.

In my recent study (Colbert, 1967) on adaptations for gliding in *Draco*, the following points were made:

In relation to body weight, the wings of *Draco* are sufficiently large so that there is a low factor of wing loading. *Draco* has considerably more wing area than is necessary to enable it to glide efficiently, i.e., it has wing surface "to spare." Possibly this low wing loading is a corollary of the inefficient shape of the wing.

The wings in *Draco* are not particularly well designed for flight as far as shape is concerned. Each wing has a very broad base and is characterized by a semicircular outline, so that it has no well-defined leading or trailing edges and no

well-defined tip. Such a wing shape violates the requisites for efficient flight. Nevertheless *Draco* is an accomplished glider, quite able, as observations and experiments have shown, to perform flat glides over considerable distances and, what is particularly interesting, to direct its glides with remarkable precision.

The abilities of *Draco* as a glider are due, in addition to its low wing loading, to the curvatures of the ribs, controlled at least in part by the muscle slips running along the length of each rib. These curvatures give the wing a convex upper surface and a concave lower surface, in accordance with aerodynamic principles for successful flight.

In addition, *Draco* is able to direct its flight by muscular control of the attitudes of the wings, aided especially by the movements and attitudes of the long tail, which is a very important adjunct for flight.

Some of these considerations may be applied to *Icarosaurus*. The extinct reptile also had a low wing load, as can be seen in table 3. In this respect it is comparable to some of the smaller birds, such as the Rosebreasted Grosbeak and the Purple Martin, the latter of which is adept at

TABLE 3

COMPARATIVE MEASUREMENTS OF *Draco*, OF *Icarosaurus siefkeri*, AND OF VARIOUS BIRDS (FROM POOLE, 1938)

	Weight in Grams	Wing Area in Square Cm.	Wing Area, Square Cm. per Gram	Wing Loading, Gram per Square Cm.
<i>Draco whiteheadi</i>				
A.M.N.H. No. 30905	1.0	2.42	2.42	0.41
A.M.N.H. No. 30917	6.4	12.44	1.95	0.51
A.M.N.H. No. 30939	6.4	9.32	1.46	0.685
A.M.N.H. No. 30927	1.3	3.90	3.00	0.33
A.M.N.H. No. 30953	6.0	7.88	1.31	0.76
<i>Draco maximus</i> , J.R.H. <sup>a</sup> No. 5338	28.8	43.06	1.49	0.67
<i>Icarosaurus siefkeri</i> , A.M.N.H. No. 2101	40 (est.)	173.90	4.35	0.23
<i>Hedymeles ludovicianus</i> (Rosebreasted Grosbeak)	40.0	166.50	4.16	0.23
<i>Oceanodroma l. leucorhoa</i> (Leach's Petrel)	26.5	251.00	9.47	0.10
<i>Progne s. subis</i> (Purple Martin)	43.0	185.50	4.32	0.23
<i>Circus hudsonius</i> (Marsh Hawk)	414.0	1382.00	3.34	0.30
<i>Larus argentatus smithsonianus</i> (Herring Gull)	850.0	2006.00	2.40	0.42
<i>Cathartes aura septentrionalis</i> (Vulture)	2409.00	4356.00	1.81	0.55

<sup>a</sup>J. R. Hendrickson Collection, Honolulu, Hawaii.

gliding. It is interesting to note that the wing load of *Icarosaurus* is not very different from that of the Marsh Hawk, a soaring bird.

Apparently *Icarosaurus* had a wing that was strongly curved anteroposteriorly, especially in its more proximal section, as well as transversely, so that the upper surface was convex in both directions and the lower surface correlatively concave. This reconstruction of the wing is based on the curvatures of the ribs. It can be argued that there has been distortion, so that the ribs in life were not so strongly curved as they are in the fossil, but, even if there was distortion, it probably was not sufficient to have changed the ribs markedly from their original condition. This premise is based on the fact that the ribs as preserved show even, sweeping curves, with no apparent transverse breaks of consequence throughout their lengths. This view also is supported by the fact that the other bones of the skeleton, although in some cases displaced (as in the skull), are not appreciably distorted. Therefore it seems justifiable to assume that the curves of the ribs as preserved represent, to a large degree, their original condition.

The fore-and-aft curving of the wing of *Icarosaurus* seems to have been far from simple. The curve is very pronounced in the proximal portion of the wing for about half of its length. In fact, the ratio of arching to breadth of wing is about 1/7, or 1/8 in the proximal half of the wing, which is very great indeed when compared with a ratio of 1/10 in slow-gliding birds. Moreover, the strongest part of the curve is toward the anterior half of the wing—the more posterior portion is relatively flat. Toward the more distal part of the wing the surface seems to become progressively flatter, so that near the tip it has little curvature. It should be noted, however, that this more distal, flatter portion of the wing is considerably broader anteroposteriorly than the more narrow proximal part; the trailing edge is slightly oblique to the leading edge, so that the base is the narrowest part of the wing. If this reconstruction of the wing is correct, it indicates that the inner and outer halves of the structure achieved lift in rather different ways. Perhaps the inner portion of the wing was effective because of the strong fore-and-aft curve, whereas the outer part of the wing achieved its purpose by reason of its extensive surface. Together they formed a wing

that afforded considerable aerodynamic support for *Icarosaurus*.

The fore-and-aft curve of the wing in this extinct reptile would, of course, have provided the convex upper and concave lower wing surfaces that give lift, according to Bernoulli's theorem. But an aerodynamically efficient wing is one in which the leading edge is thicker than the trailing edge, and this condition was not met in *Icarosaurus*. Consequently it seems evident that the potential lift of the wing in this reptile was only imperfectly realized. Moreover, the strong curve of the wing in some of its areas may have created a certain degree of turbulence during gliding that would have decreased its efficiency. Nevertheless, it was a wing sufficient for the purpose it served. Indeed, the strong anteroposterior curves of the wing at various distances from body to wing tip and the strong lateral curves associated with the essential uniformity in the thickness of the wing, as well as the wide area of its flatter part, would have combined to give it some of the attributes of a parachute. Therefore one may envisage *Icarosaurus* as having the ability to glide and at the same time the ability to drift down slowly.

It can be assumed that *Icarosaurus* was able to change the attitude of the wings by muscular control, as does *Draco*—important in determining the lengths and the directions of its flights. Because experiments have shown that the long tail of *Draco* is of particular importance in controlling the direction of the glide, both vertically and laterally, this same function may be attributed to the obviously long tail of *Icarosaurus*.

The differences between *Icarosaurus* and *Draco* in the shape of the wings is important. In this character the extinct reptile may be compared to a bird, as both have transversely extended wings, the lateral dimension of which considerably exceeds the longitudinal dimension—a wing with a long, straight leading edge, a long trailing edge, and a lateral portion that may be called a tip.

These characteristics give the wing of *Icarosaurus* a true aspect ratio, which can hardly be said for the peculiar semicircular wing of *Draco*. In its comparatively low aspect ratio, its wing loading, and its wing curvature, *Icarosaurus* shows resemblances to birds, such as the Marsh Hawk, that are capable of slow gliding and soaring without stalling. The several characters that

typify the wing in *Icarosaurus* indicate an animal capable of long, sustained, directed gliding, and perhaps even of slow "parachuting." Consequently *Icarosaurus* seems to have had the capacity for varied "flight," which would have given it much latitude during aerial locomotion;

this factor would have favored its success in an evolutionary sense.

All that is said in the foregoing paragraphs concerning *Icarosaurus* applies equally to *Kuehneosaurus*, the type genus for this interesting branch of Late Triassic reptiles.

## ZOOLOGIC RELATIONSHIPS OF *ICAROSAURUS*

THE CLOSE RELATIONSHIP between *Icarosaurus* and *Kuehneosaurus* fully justifies placing the two genera in a single family, the Kuehneosauridae, as first defined by Robinson in 1967. What is said herein must be considered supplementary to her remarks concerning the position of *Kuehneosaurus* among the reptiles. Briefly, the kuehneosaurs are Triassic lacertilians in which the dorsal vertebrae have widely extended transverse processes articulating with greatly elongated, single-headed ribs. The latter were obviously adapted for the support of a patagium, or flight membrane, capable of being folded back against the body when not in the extended position for gliding. The other characters that define kuehneosaurs are outlined above in the Revised Diagnosis.

The kuehneosaurs may be considered true lacertilians, and as such they are the earliest representatives of the suborder. They are, however, far from primitive; their adaptations for gliding surpass any such capacity seen among the modern gliding lizards. Nevertheless, they show various characters that indicate their descent from prolacertilian ancestors. In such features as the paired bones along the midline of the skull, the long frontals and short parietals, the broad supratemporal fenestra, the form and proportions of many of the bones in the temporal region, and the numerous palatal teeth, the kuehneosaurs closely resemble *Prolacerta*. It seems justifiable to separate the kuehneosaurs from other lizards as members of a distinct infraorder, the Eolacertilia. The characters diagnostic for the Eolacertilia are those that have been indicated for the Kuehneosauridae.

The evolution of the lacertilians may have been initiated by the appearance of the younginid eosuchians in the late Permian, and carried on to a step not far below the true lacertilian condition in the prolacertiform eosuchians of the early Triassic (fig. 44). The step from a

reptile such as *Prolacerta* to the first eolacertilians was not large, and the transition must have taken place during the passage from early to late Triassic time. The point in geologic time for this transition cannot be determined on the basis of present evidence; perhaps there were eolacertilians well established in the Middle Triassic. Certainly by Keuper time these reptiles had advanced to such a degree that they were highly specialized for a particular ecologic niche, as is indicated by the kuehneosaurs.

As to how long the kuehneosaurs (or the eolacertilians) persisted we can only conjecture. The eolacertilians possibly were caught up in the wave of reptilian extinction that marked the close of the Triassic; if so, they must have given rise to the later lizards before then. Conversely, they may have continued into the early Jurassic, when they became the ancestors of some of the lizards that appear as well-established forms in the late Jurassic.

It seems evident, however, that the kuehneosaurs are somewhat removed from the ancestry of later lacertilians. These highly specialized squamates were, on the basis of present evidence, peculiar to late Triassic history. They established a special mode of life in which they were successful for a time. Subsequently their particular adaptation, for gliding from tree to tree, was imitated, after a fashion, by those modern agamids of the genus *Draco*. There is no reason to think, however, that *Draco* is descended from the kuehneosaurs. The similar adaptations of the Triassic and modern forms represent, rather, successive parallelisms—a phenomenon often seen in the evolutionary history of the vertebrates.

The discovery of the kuehneosaurs has revealed a surprising aspect in the history of lepidosaurians, namely, that the first known true lacertilians, on the basis of present evidence, were highly adapted for a specialized mode of life.

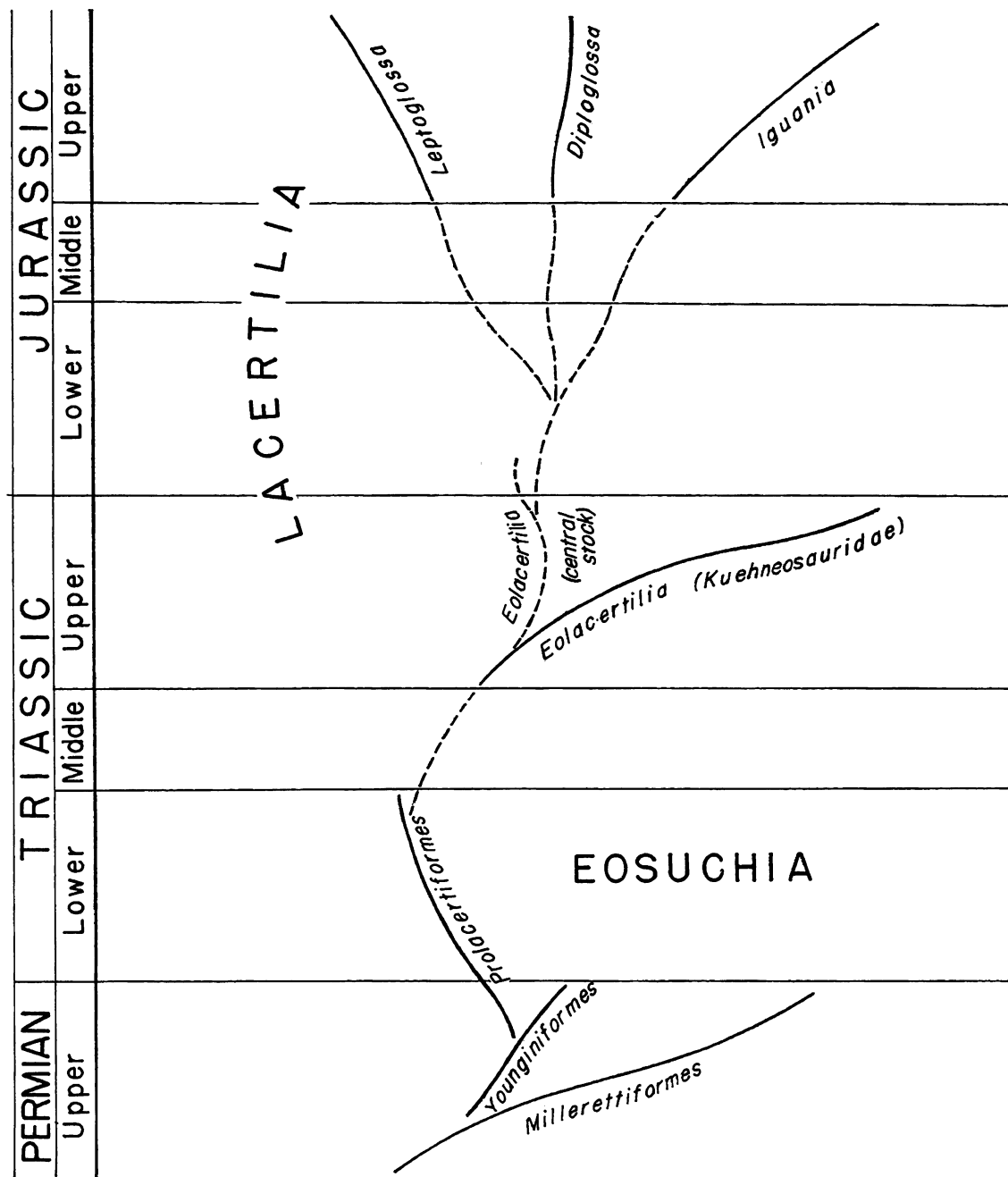


FIG. 44. A suggested phylogeny, indicating the position of the Kuehneosauridae with relation to the Eosuchia and the Lacertilia.

## GEOLOGIC AND GEOGRAPHIC RELATIONSHIPS OF *ICAROSAURUS*

IN PREVIOUS PAPERS by the present author (Colbert, 1965; 1966), the specific geological relationships of the so-called Granton Quarry were discussed (fig. 45), and it was shown that *Icarosaurus* and various other reptiles collected at that quarry occurred in black shales and argillites of the Lockatong Formation of the Newark Group, which represents the Upper Triassic along the eastern border of North America. The Lockatong Formation is a lacustrine deposit, which has been described by various authors, but particularly by McLaughlin (1939, 1945, 1948), McLaughlin and Willard (1949) and, more recently in detail, by Van Houten (1964, 1965). It is a facies intercalated between the Stockton Formation below and the Brunswick Formation above, and it can probably be correlated to a considerable degree with the lower portions of the Brunswick. In New Jersey the Lockatong conforms to the general northeast-southwest strike of the Triassic sediments, outcropping from a point across the Hudson River from Manhattan Island through the middle of the state and across the Delaware River into eastern Pennsylvania (fig. 46). The Lockatong beds at the Granton Quarry site are, of course, strictly correlated with the sediments in eastern Pennsylvania; the exposures represent cyclic deposition in a large lake that covered this region during late Triassic time. Continuing

southward, they can be closely correlated with the black shales of the Cumnock Formation in North Carolina.

Moreover, the Lockatong Formation of the Atlantic seaboard of North America can generally be correlated with the Petrified Forest Member of the Chinle Formation in Arizona, in whole or, more probably, in part.

These conclusions about the relationships of the North American Upper Triassic sediments are based particularly on the occurrence of phytosaurs. *Rutiodon carolinensis* is found in the Lockatong exposures of New Jersey and Pennsylvania, as well as in the Cumnock Formation of North Carolina, where the type specimen was discovered. *Rutiodon zunii*, which occurs in the lower position of the Petrified Forest Member of the Chinle Formation in Arizona, is a closely related species, so that this horizon in the southwestern Triassic is considered essentially equivalent to the sediments containing *R. carolinensis*.

The phytosaurs were first described from the Keuper beds of the type Triassic in southern Germany. These reptiles are found in the upper part of the German Keuper, in the Schilfsandstein, the Buntermergel, and the Stubensandstein horizons. The genus *Phytosaurus* occurs in all three levels, *Mystrisuchus* is found in the Buntermergel and Stubensandstein, and *Ebrach-*

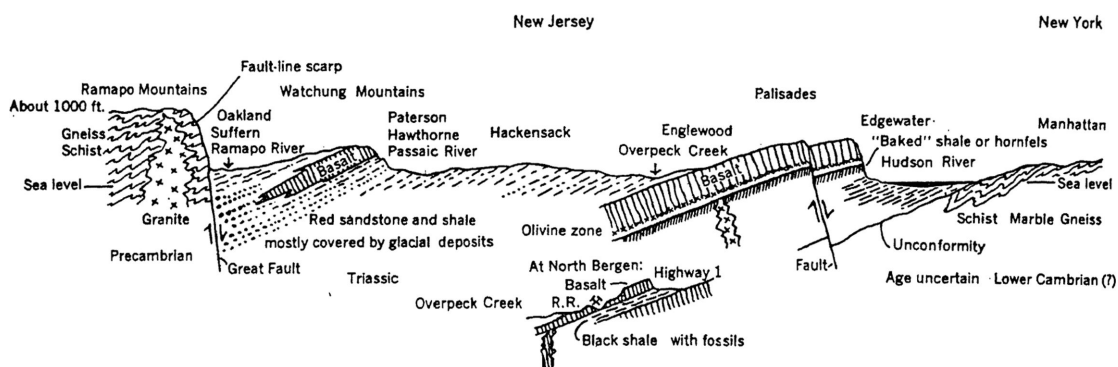


FIG. 45. Structure section from Manhattan westward to the Ramapo Mountains, with a detail (below showing the geologic relationships at the Granton Quarry (indicated by crossed hammers) at North Bergen, New Jersey. From Kay and Colbert (1965).

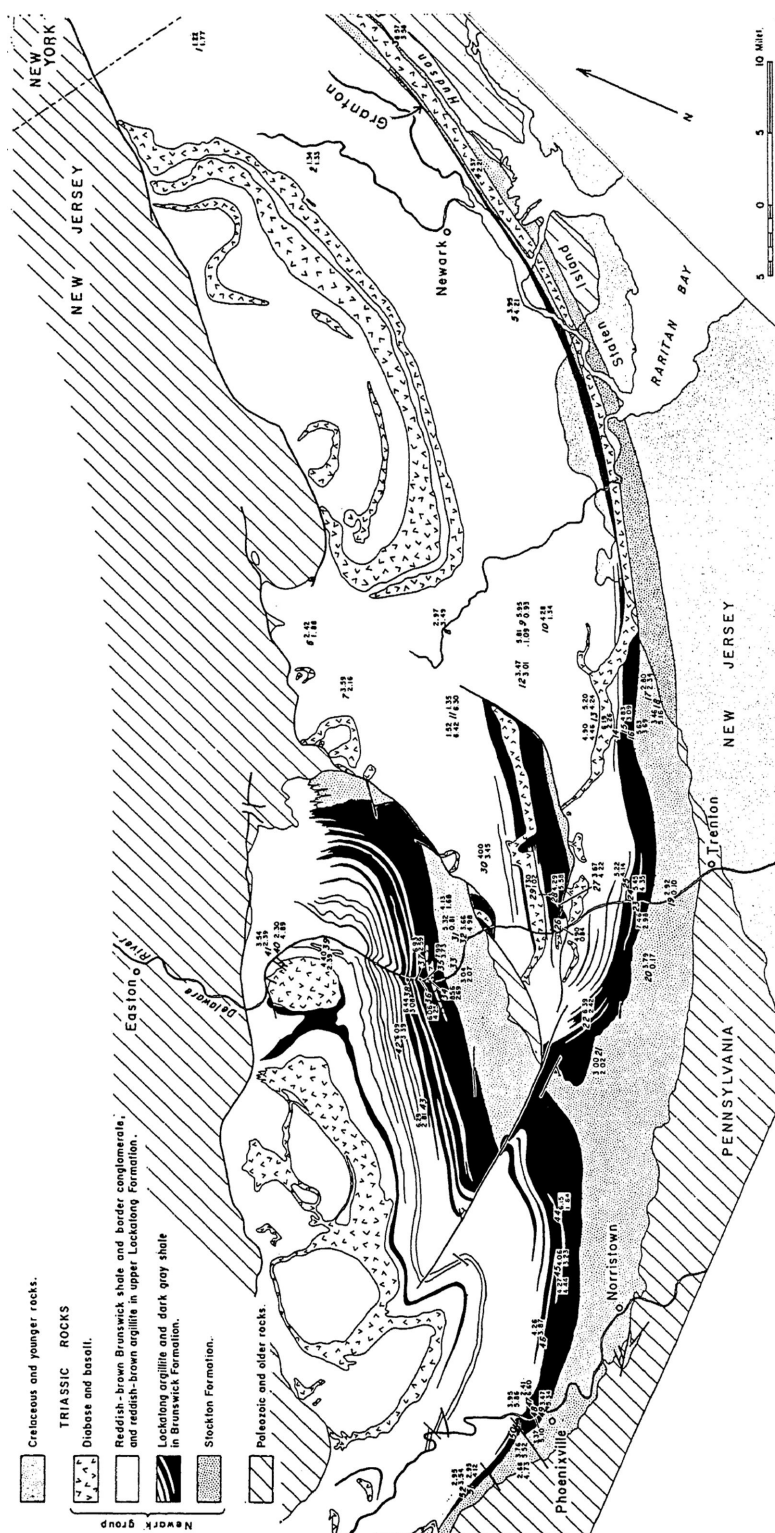


Fig. 46. The exposures of the Lockatong Formation (in solid black) of the Newark Group in New Jersey and Pennsylvania. Note the location of the Granton Quarry. The numbers refer to the  $\text{Na}_2\text{O}$  and  $\text{K}_2\text{O}$  content of the Triassic rocks. From Van Houten (1965).



*osuchus* in the Schilfsandstein. As Gregory (1962a, 1962b) has shown, *Rutiodon* is closely related to *Phytosaurus*, although it is generically distinct from the European genus. Therefore the Lockatong Formation, with *Rutiodon* as a characteristic reptile, may be equated with the upper portion of the Keuper (excluding the uppermost horizon, the Knollenmergel) of the type Triassic. Thus the age of *Icarosaurus* may be regarded as Keuper. Perhaps future discoveries will extend the stratigraphic range of this reptile, but on the basis of present knowledge it may be considered to have appeared during the late stages of Triassic history.

The age of *Kuehneosaurus* has been thoroughly discussed by Robinson (1957) in her description of the Mesozoic fissures of the Bristol Channel area. As she has shown, the Carboniferous limestone outcrops on each side of the Bristol Channel contain numerous fissures, some of which are filled with deposits of Keuper age, some with deposits of Rhaetic and Liassic age. It is from certain fissures containing Keuper deposits, specifically from the Batscombe and Emborough quarries in Somerset, that the numerous isolated bones of *Kuehneosaurus* have been collected. Robinson indicated that the fissure fills here are of late Keuper age, which would correlate them with the Lockatong Formation containing *Icarosaurus*.

*Icarosaurus* may have been widely distributed across the North American continent during late Triassic time, but preserved only in the fine,

black shales of the Newark Group. Or perhaps its specialized environment, here regarded as more or less comparable to a modern tropical rain forest, was actually limited during the Triassic, so that the presence of *Icarosaurus* in the Lockatong Formation represents the distribution of a restricted species. The latter situation, however, is not indicated. The discovery of *Kuehneosaurus*, to which *Icarosaurus* is closely related, in Britain indicates that these late Triassic gliding reptiles inhabited large areas of the northern Triassic continents. An analogy with the distribution of the modern flying dragon *Draco* is possibly relevant. The range of this modern genus (and here we are dealing with one genus in contrast with two from the Triassic) includes the Philippine Islands, much of the East Indies, the island of Hainan, and south through the mainland of southeastern Asia and west to the southern tip of India. Such a distribution extends through about 50 degrees of longitude and 30 degrees of latitude comprising an area that is as large as most of North America, or one that would extend from the eastern seaboard of North America across the Atlantic to include all of Great Britain and a part of the western European continent. The area that represents the distribution of *Draco* is sufficiently large to include all the localities at which the Triassic kuehneosaurs have been discovered. It is reasonable to assume, therefore, that these ancient reptiles were at least as widely distributed as their modern ecological counterparts.

## CONCLUSIONS

THIS STUDY, which supplements the original description of *Icarosaurus siefkeri* (Colbert, 1966), is a detailed description and interpretation of the skeleton of this late Triassic aerial reptile from the Lockatong Formation of the Newark Group at North Bergen, New Jersey. The discovery of *Icarosaurus* and of the closely related *Kuehneosaurus*, both representatives of the earliest known lacertilians (the Eolacertilia), has revealed new aspects of the reptilian faunas that lived during the Triassic. These highly specialized lizards, adapted for gliding over considerable distances, are but two taxa from a Triassic environment hitherto largely unknown. There is still much to be learned about the tetrapods that inhabited the earth during the first phase of Mesozoic history, and our present knowledge affords only an incomplete picture of what must have been rich and varied faunas living in a vast tropical world.

Of particular interest to the student of reptilian evolution is the fact that *Icarosaurus* and *Kuehneosaurus*, by far the earliest lacertilians now known, indicate that the advent of the lizards

was earlier than heretofore suspected, and that the initial radiation of the lacertilians proceeded with great speed—perhaps with almost explosive effect, as is often the case with new evolutionary lines. If the kuehneosaurs display such high degrees of specialization, one can assume that there must have been, prior to their appearance, a phase or rapid evolutionary development marked by the derivation of the late Triassic lizards from an early Triassic prolacertilian stock. Perhaps the transition from prolacertilian to lacertilian took place during the Middle Triassic. Certainly by late Triassic time the lizards were established—to such a degree that some of them, the kuehneosaurs, had become highly modified from a central eolacertilian stock.

At some future time, annectant eolacertilians intermediate between such genera as *Prolacerta*, on the one hand, and *Kuehneosaurus* and *Icarosaurus*, on the other, may be found. Perhaps they will point to the more central evolutionary path that led from the prolacertilians to the later lizards—the Jurassic ancestors of the lizards that inhabit the modern world.

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