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A NEW GLIDING TETRAPOD (DIAPSIDA: ?ARCHOSAUMORPHA) FROM THE UPPER TRIASSIC (CARNIAN) OF VIRGINIA

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A new tetrapod taxon from the Upper Triassic Cow Branch Formation of Virginia is described solely on the basis of computed tomography (CT) scans of 2 individuals. The new form is characterized by the presence of extremely elongate thoracolumbar ribs that presumably supported a gliding membrane in life. It differs from all other known gliding tetrapods in possessing a very pronounced elongate neck. The grasping hindfoot is consistent with an arboreal habit.

A gliding habit has been reported in a handful of fossil reptiles, with the oldest occurrence in *Coelurosauravus* (Carroll, 1978; Evans, 1982; Evans and Haubold, 1987) from the Permian of Europe and Africa. Elongate ribs were originally described in this form and these were thought to have supported a gliding membrane in life, but it has since been shown that the membrane-supporting structures are not true ribs, but separate bundles of rodlike neomorph ossifications (Frey et al., 1997). However, 3 closely related forms (*Icarosaurus*, *Kuehneosaurus* and *Kuehneosuchus*) from the Upper Triassic of Europe and North America do have exceptionally elongate thoracolumbar ribs, and all have been referred to a single family, the Kuehneosauridae (Robinson, 1962; Colbert, 1970). They are further characterized by the ribs forming hinge joints with the markedly elongate transverse processes on the dorsal vertebrae. This contrasts with the living gliding agamid *Draco* (Colbert, 1970), in which the elongate thoracolumbar ribs are flexible and lack the hinge-joint with the vertebral transverse processes. A fourth Triassic tetrapod, *Sharovipteryx* from the Triassic of Kirghizia, also possessed a gliding membrane (Gans et al., 1987) but in this form it is stretched between the hind limbs. Here we describe a new Triassic tetrapod with elongate ribs that is comparable in size to the contemporaneous *Icarosaurus*, but differs significantly from kuehneosaurs in having a long neck, a character that is potentially very unstable in a gliding animal.

The 2 specimens of the new tetrapod were recovered from Carnian exposures at the Virginia Solite Quarry at Cascade, straddling the North Carolina-Virginia state line (Olsen, 1979). The locality comprises 3 separate quarries that together contain excellent exposures of the Cow Branch Formation (Fraser and Grimaldi, 2003). These exposures consist of sediments deposited in lake systems and showing periodic depth changes under the control of variations in the Earth's orbit (Milankovitch cycles) (Olsen, 1986). Although first described as rather unfossiliferous (Meyerton, 1963), the Solite sediments are now considered to represent some of the richest Triassic terrestrial sequences in the

world. Plants and vertebrates are well represented, but the diversity of insects is particularly important (Fraser and Grimaldi, 2003). The richest strata are microlaminated units showing no evidence of bioturbation. On the basis of geochemical analysis, these microlaminated units are thought to represent very shallow, marshlike marginal lake environments. One particular cycle, designated as SO/CB 2, has yielded the vast majority of the insects. Both specimens of the new gliding form originated in this cycle but in the horizon that is considered to represent the deepest part of the lake sequence. This particular level has yielded a number of fish including remains of the large palaeonisciform *Turseodus* and a coelacanth. No other tetrapods have been found in this horizon; the ubiquitous amphibious tetrapod *Tanytrachelos* occurs in sequences below and above this level and appears to be associated more with the lake margins (Fraser et al., 1996).

The new specimens are embedded in a hard dolomitized dark gray silty mudstone, and only faint impressions of the bones can be seen at the surface. Repeated attempts to remove the matrix using both mechanical and chemical techniques have been unsuccessful. The description of the new form is therefore based entirely on CT scans of both specimens.

Institutional Abbreviation—VMNH, Virginia Museum of Natural History.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903

?ARCHOSAUMORPHA von Huene, 1946

MECISTOTRACHELOS APEOROS, gen. et sp. nov.

(Fig. 1)

Holotype—VMNH 3649, the articulated skull, neck pectoral girdles, forelimbs and trunk complete as far as the pelvic girdle (Fig. 1A, B). The hindlimbs, tail, and most of the pelvic girdle were not preserved.

Referred Specimen—VMNH 3650, a complete skeleton missing only the distal tail and part of the left hindlimb (Fig. 1C, D).

Etymology—The generic and specific names are derived from the Greek 'mecistos' and 'trachy,' meaning longest neck; and 'apeoros,' meaning soaring.

Locality and Horizon—Solite Quarry, Pittsylvania County, Virginia, U.S.A. Cow Branch Formation, Carnian, Danville Basin, Virginia and North Carolina.

Diagnosis—A small diapsid reptile with exceptionally elongate thoracic ribs that are approximately half the total length of

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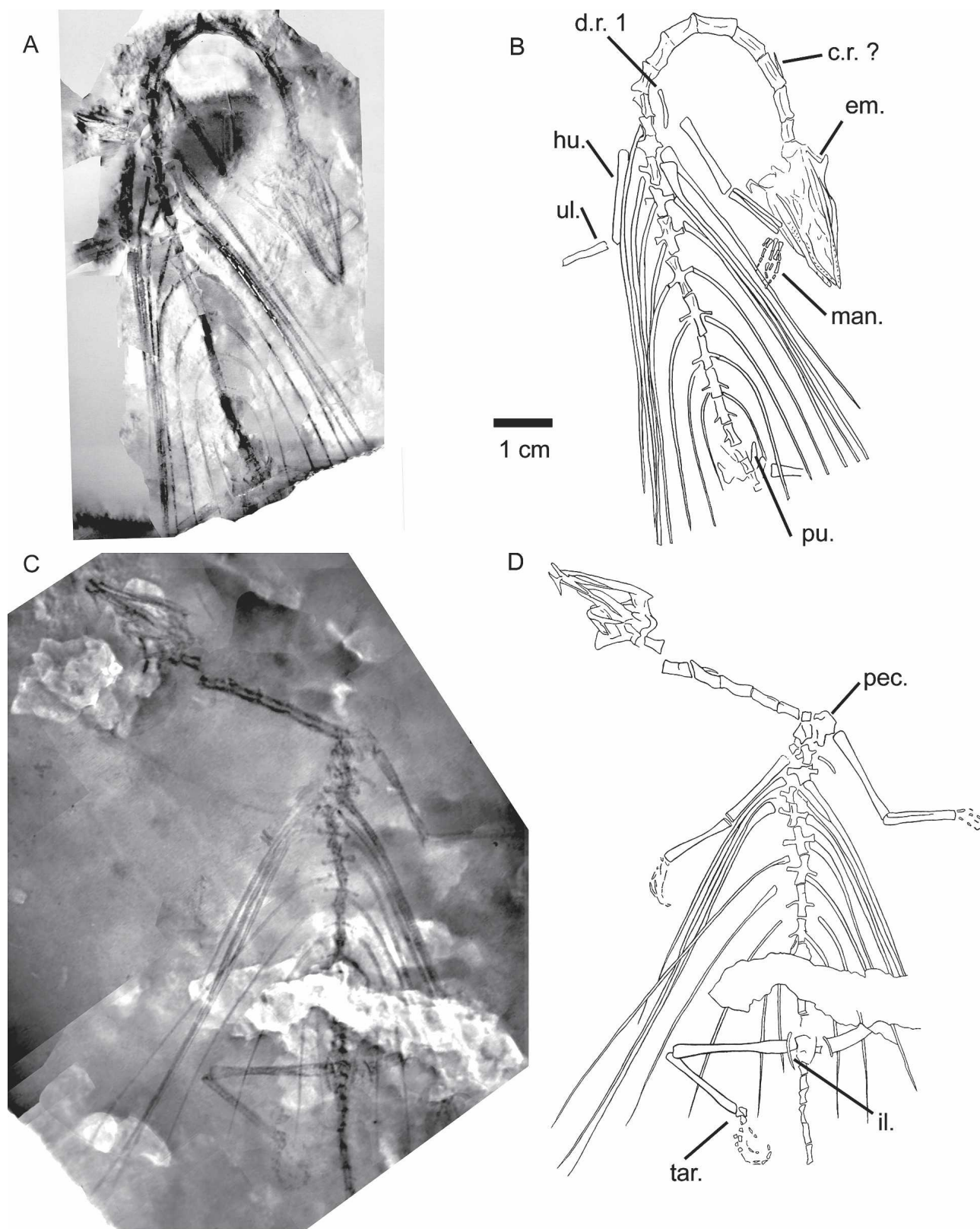


FIGURE 1. Composite CT scans and drawings of *Mecistotrachelos apeoros*, gen. et sp. nov. **A**, Composite CT scan of the holotype VMNH 3649 based on 90 slices. **B**, Specimen drawing of the holotype taken from the slices. All the scans were collected on an XTEK subsystem with energy settings of 150 kV and 0.150 mA. X and Y spacing of 0.055 mm and Z spacing of 0.06486 mm with 2400 views and 2 samples averaged per view. **C**, Composite scan of the referred specimen VMNH 3650 based on 37 slices. **D**, Specimen drawing of VMNH 3650 taken from the slices. The energy settings were 160 kV, 0.150 mA. X and Y spacing of 0.109 mm and Z spacing of 0.1254 mm. The CT images were digitally inverted to facilitate differentiation between bone and matrix. **Abbreviations:** **c.r. ?**, possible cervical rib; **d.r. 1**, first dorsal rib; **em.**, emargination of the jugal; **hu.**, humerus; **il.**, ilium; **man.**, manus; **pec.**, pectoral girdle; **pu.**, pubis; **tar.**, tarsus; **ul.**, ulna.

the entire skeleton; eight or nine cervical vertebrae that, with the exception of the atlas and axis, are at least twice as long as they are tall; dorsal vertebrae approximately equal in length to the cervicals; short metatarsals, length less than 1/5th the length of the tibia; foot adapted for grasping.

Description—The skull is preserved in both specimens and while details of individual elements are almost impossible to see, a few features are worth noting. Firstly, it is rather narrow, lightly built and bears a pointed rostrum. On the right side of the holotype, the slightly displaced jugal exhibits an emarginated posterior margin (Fig. 1A), and there is also evidence of additional fenestrations that appear to be situated in the temporal region of the skull roof (CT slice 45 of the holotype). Together these features are strongly suggestive of a diapsid condition. Numerous small teeth are preserved on the marginal tooth-bearing bones. The skull of the holotype is larger than in VMNH 3650 yet the forelimbs are shorter (Table 1). These proportional differences may be indicative of sexual dimorphism.

The holotype, VMNH 3649, would appear to have possessed either nine or possibly eight cervicals, although only eight are obviously preserved in the second specimen. This count is also based on the assumption that the atlas is very much reduced and not readily visible. The first identifiable vertebra, presumably the axis, is shorter than the remaining cervicals which are distinctly elongated, over twice as long (5.1 mm) as they are high (2.3 mm). For the most part neither specimen preserves obvious cervical ribs. This would be inconsistent with an archosauromorph identification. However, in VMNH 3650, the fifth vertebra has a short spur of bone that could be the remains of a short rib shaft. It is therefore possible that there are small and delicate ribs running along the bone that do not splay out prominently. At the same time, it is worth noting that the single specimen of *Icarosaurus* did not have cervical ribs preserved (Colbert, 1970), although facets for the ribs are still present. While the neck in VMNH 3650 as preserved is very straight, the holotype has a very marked curvature that is presumably indicative of the range of movement in life.

Based on the holotype there would appear to be either 13 or 14 dorsal vertebrae, making a total of between 21 and 23 presacals. This is consistent with many diapsids (although on the low side). The difficulty is determining where the sacrum begins in the holotype. VMNH 3650 provides no additional insight into the presacral count. While 11 dorsal vertebrae are preserved, there is a section missing in the posterior part of the column and as many as an additional 4 vertebrae may have been lost. In both specimens the first 3 dorsal vertebrae are relatively short with

prominent and quite robust transverse processes. The following 6 vertebrae are more elongate and are approximately equal in length to the main cervical series (Table 1). All but the last dorsal vertebra has a prominent transverse process that is comparable in proportions to that of the living *Draco*, but certainly not as elongate as in the kuehneosaurs.

Based on the holotype, the first dorsal vertebra bore a rib of standard length, but the next 8 have exceptionally elongate ‘thoracic’ ribs. The rib on dorsal vertebra 2 is complete and at 56 mm long is estimated to have been approximately equal to one third the total body length. The next 2 ribs are not complete in either specimen, but in VMNH 3650 they are approximately 70 mm long. In both specimens, the anterior 2 thoracic ribs have particularly robust proximal heads. This presumably allowed for the attachment of the musculature associated with rib movement. In VMNH 3650 the more posterior ribs are completely preserved and are approximately 35–45 mm long. The ‘thoracic’ ribs exhibit a shallow but definite posterior curvature in the proximal part of the shaft, but the distal two thirds of the shaft is almost straight. This contrasts sharply with the condition in *Icarosaurus*, where the distal portion of the rib shaft is curved, but the proximal part is straight. It is likely that this curvature in the proximal portion of the rib precluded the membrane from being stretched out completely perpendicular to the long axis of the vertebral column.

Details of the pectoral girdle cannot be discerned. Parts of the pelvic girdle can be seen in the scans of both specimens (Fig. 1A, C). No clear details are visible although an obturator foramen may be present in the pubis as seen in the CT scan of the holotype.

Both fore and hind limbs are relatively long and slender, with the forelimb about 88 percent the length of the hindlimb. The very slender humerus shows minimal development of the proximal and distal heads. VMNH 3650 preserves one hindlimb with the pes still in articulation.

Details of the manus and pes are difficult to discern and individual metacarpals, metatarsals and phalanges are indistinguishable. Nevertheless, a few general points are notable. The manus is best seen in the holotype, and although none of the carpals are visible parts of all 5 digits are preserved. Although there are discrete proximal tarsal bones, details are insufficient to comment on whether the new form is allied with the archosauromorphs or lepidosauromorphs. The fifth metatarsal was apparently short and subrectangular in shape. The pes, as preserved in the second specimen, had rather short metatarsals (only marginally longer than the proximal phalanges) reaching a maximum of one fifth the length of the tibia, while the digits are not spread out in a typical fashion but instead adopt a hooked posture, which suggests strong grasping capabilities. This ability, as well as the orientation of the metatarsals at right angles to the tibia, is highly suggestive of an arboreal habit.

The tail is completely missing in the holotype, and only the first 7 caudal vertebrae are preserved in VMNH 3560.

DISCUSSION

Taxonomic Position

Mecistotrachelos is a diapsid with elongate cervical vertebrae. The greatly elongated ‘thoracic’ ribs, which presumably supported a gliding membrane, are very reminiscent of the condition in kuehneosaurs. However, the kuehneosaurs (*Icarosaurus*, *Kuehneosaurus*, and *Kuehneosuchus*) have much shorter (and fewer) cervical vertebrae than *Mecistotrachelos*, and the skulls are also shorter and blunter (Fig. 2A). While the systematic position of kuehneosaurs has been the subject of some discussion, they are widely regarded as lepidosauromorphs.

The elongate cervical series and narrow pointed skull of *Me-*

TABLE 1. Measurements (in mm) of various skeletal elements in *Mecistotrachelos* (VMNH 3649 and 3650) and *Icarosaurus*.

Specimen	VMNH 3649	VMNH 3650	<i>Icarosaurus</i>
Skull length	23.6	19.2	24.8
Length cervical vertebra 6	6.4	5.15	1.2
Width/depth of cervical 6	2.6	1.92	
Length presacral 17	6.85		
Width/depth presacral 17	1.9		
Length 1st thoracolumbar rib	55.3	45.6	
Length 2nd thoracolumbar rib		>72.63	11.6
Length 3rd thoracolumbar rib		>69.63	108.0
Length 4th thoracolumbar rib		59.3	120.0
Length 5th thoracolumbar rib		49.7	126.0
Length 6th thoracolumbar rib		41.9	126.0
Length 7th thoracolumbar rib		35.0	123.0
Length 8th thoracolumbar rib		31.7	115.0
Length humerus	15.55	16.7	20.1
Length ulna	10.2	12.35	15.7
Length femur		19.9	34.7
Length tibia		15.6	23.0

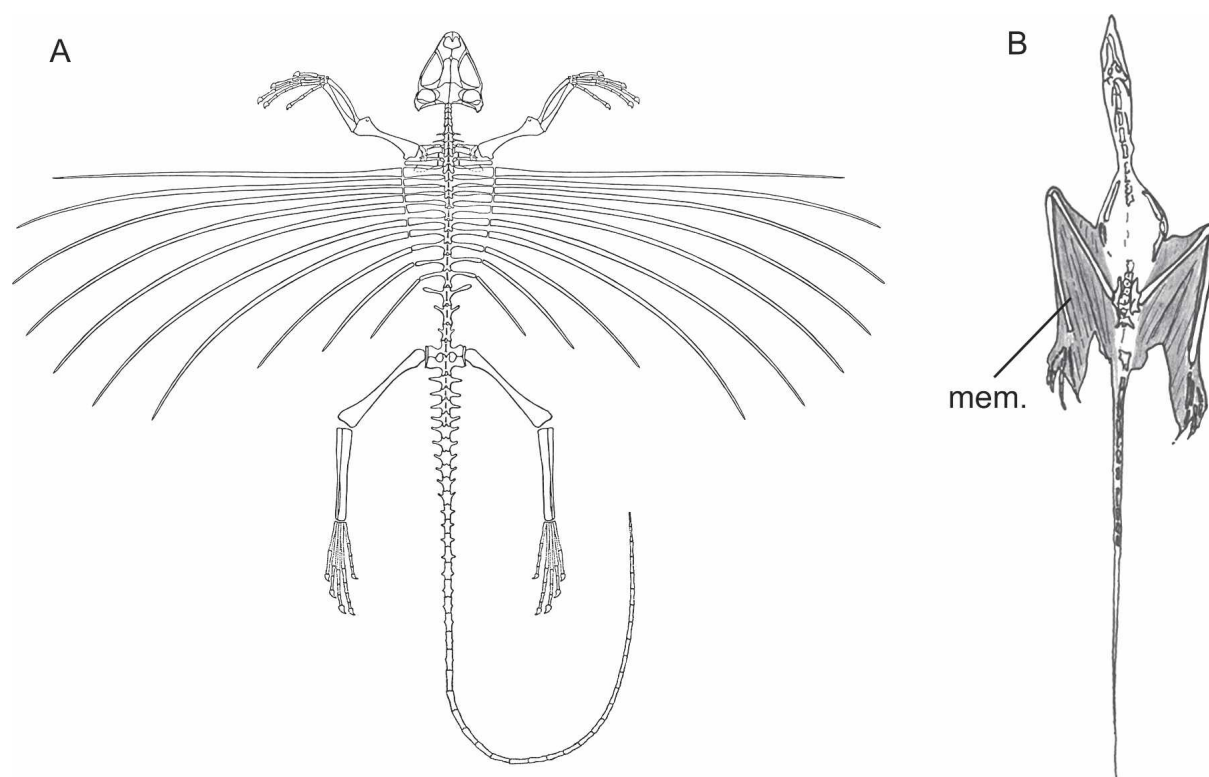


FIGURE 2. **A**, Restoration of the skeleton of *Icarosaurus* (after Colbert, 1970). **B**, The sole specimen of *Sharovipteryx* (after Unwin et al., 2000).

cistotrachelos are features shared by the enigmatic *Sharovipteryx* (Fig. 2B). On the basis of elongate cervical vertebrae with low neural spines, Unwin and colleagues (2000) considered *Sharovipteryx* to be a member of the Prolacertiformes. They also cited a possible incomplete lower temporal arcade, long and slender cervical ribs, straight femur, and the tibia longer than the femur as additional characters supporting prolacertiform affinities. However, it should be noted that the composition and diagnosis of Prolacertiformes (Protorosauria) is currently unclear (Rieppel et al., 2003).

Mecistotrachelos shares the elongate cervical vertebrae, straight and slender femur and the narrow pointed skull with *Sharovipteryx*. Details of the cranial elements are difficult to decipher in both taxa, but in *Mecistotrachelos* the posterior process of the jugal does not appear to have made contact with the quadratojugal, and it is likely that it too had an incomplete lower temporal arcade. On the other hand, while the cervical ribs are indistinct in *Mecistotrachelos* there is no evidence to suggest that they had long and slender shafts. Moreover, the tibia is shorter than the femur, and the support for the gliding membrane is clearly very different to that of *Sharovipteryx*. While it would seem that *Mecistotrachelos* exhibits closer affinities to *Sharovipteryx* than kuehneosaurs, there are still very distinct differences, and we consider it to belong to a separate clade of archosauromorphs.

Paleobiology

Such an elongate neck is unusual in a gliding form since there is a much greater potential for flight instability due to head movements. Some modern birds such as herons overcome this problem by holding the neck in an S-shape during flight. Given the rather long cervical vertebrae in *Mecistotrachelos* (a feature also shared by *Sharovipteryx*), their relatively low number and

apparently rather rigid intervertebral articulations, this was not an option.

A very different 'wing' shape was described for *Icarosaurus* in which the central elongate ribs had a marked ventral flexure that in turn would have produced a concave lower surface of the 'wing.' Even in *Coelurosauravus*, where the membrane was supported by neomorphic rod-like structures with no participation of the thoracolumbar ribs, the wing supports exhibit a distal flexure that would have produced a similar camber to the wing profile (Frey et al., 1997). The straight distal portions of the thoracolumbar ribs in *Mecistotrachelos* preclude any fixed cambering of the 'wing.' However, if differential vertical movements of the anterior and posterior ribs were possible, then *Mecistotrachelos* would have been capable of a variable camber wing. Moving the anterior rib down would increase the wing camber, increasing lift and drag. Moving the anterior rib up would flatten the wing, decreasing camber and decreasing lift and drag. This would make the first ribs functionally similar to the pteroid bone in pterosaurs, or even the alula in birds. In contrast, the wing in *Icarosaurus* would function more like a parachute. The robust rib heads of *Mecistotrachelos* are consistent with this theory.

While an aerial habit is almost certain, both specimens of *Mecistotrachelos* were recovered from sediments deposited in the deepest part of the lake, yet there is not a single adaptation for aquatic habit. Therefore it seems likely that both specimens were blown off course and out over the lake.

By comparison with *Icarosaurus*, the forelimbs in *Mecistotrachelos* are much longer relative to the hindlimbs (ratio of 0.62 in *Icarosaurus* and 0.82 in *Mecistotrachelos*). The gracile humerus also contrasts with the better developed proximal and distal humeral heads of *Icarosaurus*. This is probably linked with different foraging behaviors where perhaps the more powerful hindlimbs of *Icarosaurus* were the principal propulsive force to climb up the trunks of trees. We suggest that *Mecistotrachelos*

foraged for insects among the canopy and used its feet to grasp the narrower branches. The short metatarsals and phalanges and the preserved 'hooked' posture of the foot supports its arboreal habit. The numerous small teeth are indicative of an insectivore, and a number of terrestrial insects have been described from the same locality as *Mecistotrachelos* (Fraser et al., 1996).

The discovery of *Mecistotrachelos* shows that a gliding habit evolved in at least three very different Triassic tetrapod clades. The long neck coupled with the high ratio of forelimb to hindlimb length is unique among Triassic gliding reptiles.

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