

*Cosesaurus aviceps*, *Sharovipteryx mirabilis* and *Longisquama insignis*

Reinterpreted

DAVID PETERS

Independent Researcher

12c San Miguel Drive, Saint Charles, Missouri, 63303, U.S.A.

[davidpeters@att.net](mailto:davidpeters@att.net)

314-323-7776

## **Key Words**

Pterosauria, Fenestrasauria, Triassic, Madygen Formation, Upper Muschelkalk, Origin of Active Flapping Flight

## **Abstract**

Currently the majority of pterosaur and archosaur workers maintain the traditional paradigms that pterosaurs appeared suddenly in the fossil record without obvious antecedent and that pterosaurs were most closely related to archosaurs because they shared an antorbital fenestra and a simple hinge ankle. Oddly, these hypotheses continue despite the widely accepted acknowledgement that no archosauriformes document a gradual accumulation of pterosaurian traits. The minority view provided four phylogenetic analyses that documented a gradual accumulation of pterosaurian traits in three fenestrasaurs, *Cosesaurus aviceps*, *Sharovipteryx mirabilis*, and *Longisquama insignis* and their ancestors. These three also had an antorbital fenestra and a simple hinge ankle by convergence. Unfortunately the minority view descriptions also included several misinterpretations. Those are corrected here. The revised descriptions add further support to the nesting of pterosaurs with fenestrasaurs, a clade that now nests within a new clade of lepidosaurs between Sphenodontia and Squamata. The new data sheds light on the genesis of active flapping flight in the nonvolant ancestors of pterosaurs.

## **Introduction**

The search for pterosaur precursor taxa continues with no consensus in sight. Hone and Benton (2007, 2008) summed up the majority view when they reported the Pterosauria

appeared suddenly in the fossil record without obvious antecedent. Representing the minority view, Peters (2000a) redescribed four pterosaur precursor candidates, *Langobardisaurus* (Renesto 1994, MCSNB 4860), *Cosesaurus* (Ellenberger & de Villalta 1974, MGB-V1), *Sharovipteryx* (Sharov 1971, PIN 2584/8) and *Longisquama* (Sharov 1970, PIN 2584/4, Figs. 1-12) and added these taxa to four prior phylogenetic analyses (Evans 1988, Jalil 1993, Bennett 1996 and Benton 1999). In each analysis pterosaurs nested with these four taxa rather than any included archosaur. Peters (2000a, 2002) showed that these taxa document a gradual accumulation of pterosaurian traits and erected the clade Fenestrasauria for *Cosesaurus*, *Sharovipteryx*, *Longisquama* and pterosaurs based on the synapomorphy of an antorbital fenestra without a fossa. Later workers (e.g. Brusatte et al. 2010, Nesbitt 2011) ignored these descriptions, analyses and taxa. Nesbitt (2011) cited the arguments of Hone and Benton (2007) for this exclusion (but see below). Brusatte et al. (2010: 10) preferred to, “follow the majority view,” and so did not include the above taxa in their archosaur study, nor did they delete their pterosaurs. Both studies nested pterosaurs within the Archosauriformes arising from the Parasuchia and Proterochampsidae. In recent phylogenetic analyses of the Pterosauria (Unwin 2003, Kellner 2003, Andres 2010 and all analyses derived from them) workers likewise ignored Peters (2000a). Instead they included only archosauriforms as outgroup taxa, treating them essentially as ‘all zero’ outgroups because none document a gradual accumulation of pterosaurian traits. Notably, pterosaur workers did not employ taxa from the Parasuchia or the Proterochampsidae as outgroups.

Prior Pterosaur Origin Phylogenetic Analyses and Hypotheses

Bennett (1996) nested pterosaurs with the small bipedal archosaur, *Scleromochlus* (Woodward 1907, Benton 1999). The suprageneric taxa Ornithosuchidae, Parasuchia and Suchia nested as successively more distant taxa. The nesting of bipedal *Scleromochlus*, with its tiny hands and vestigial lateral manual and pedal digits is at odds with a later work by Bennett (2008) in which he imagined a quadrupedal, arboreal, lizard-like proto-pterosaur with elongate lateral manual and pedal digits similar to another hypothetical model proposed by Wild (1978). Bennett (2008) imagined the first step toward the pterosaurian-grade was the supination of the forelimb, followed by the loss of the digit 4 ungual and the hyperextension digit 4 to fold against the dorsal (now supinated posterior) forelimb. Bennett (2008) did not explain how metacarpal 3 became detached from metacarpal 4 so the three medial metacarpals could migrate together across the palmar (now anterior) surface of the supinated manus where Bennett (2008) locates them in his reconstruction. Bennett (2008) gave no explanation for the appearance or evolution of other pterosaurian traits, such as the sternal complex, prepubis, attenuated tail and metapodial proximal phalanx of pedal digit five.

In a follow-up to his 1996 paper, Bennett (2012) declined to include pterosaur sister taxa recovered by Peters (2000a, see below). Instead Bennett reviewed his earlier taxon inclusion set, restricted to members of the Archosauromorpha. Peters (2000a) was mentioned only in regard to issues Bennett found with the Hone and Benton (2007) review of Peters (2000a), discussed below.

Benton (1999) nested pterosaurs between *Scleromochlus* and *Lagerpeton* and all three taxa were derived from *Euparkeria*, Proterochampsidae and Phytosauria (= Parasuchia) in order of decreasing distance. In counterpoint, Peters (2002) listed traits

*Scleromochlus* shared with basal bipedal crocodylomorphs, none of which were included in Benton (1999).

As mentioned earlier, Peters (2000a) added *Langobardisaurus*, *Cosesaurus*, *Sharovipteryx* and *Longisquama* to prior analyses by Evans (1988), Jalil (1993), Bennett (1996) and Benton (1999) and recovered these four as proximal sisters to pterosaurs.

Subsequent workers (Rieppel, Fraser & Nosotti 2003; Chatterjee & Templin 2004; Hone & Benton 2007) labeled this study as “heterodox.” They did not check the specimens. In this case, “heterodox” simply meant novel or different than orthodox.

Peters (2000a, 2002) showed that nearly every pterosaurian trait was already present in basal fenestrasaurs, except the elongation of the wing elements and the axial rotation of metacarpal 4. In those studies, basal pterosaurs shared with *Langobardisaurus*, *Cosesaurus*, *Sharovipteryx* and *Longisquama*: (1) posterior teeth differentiated from anterior teeth; (2) occiput at an obtuse angle to the jaw line; (3) pterygoids contact vomers; (4) palatines reduced; (5) cervical vertebrae descend from back of skull in simple curve (parallelogram-shaped cervicals); (6) procoelous presacral vertebrae; (7) posterior dorsal ribs straight and fused to transverse processes; (8) chevrons short, grading to long and parallel with each centrum distally, altogether producing an attenuated tail; (9) scapula low, grading to parasagittally elongate; (10) radius and ulna straight and closely appressed; (11) tibia and fibula straight and closely appressed; (12) fibula grading to splint-like; (13) distal tarsal 1 absent; (14) metatarsal 5 short; (15) pedal 5.1 metapodial.

In Peters (2000a, 2002), basal pterosaurs shared with *Cosesaurus*, *Sharovipteryx* and *Longisquama* (the Fenestrasauria): (1) antorbital fenestra; (2) anteriorly expanded lacrimal overhangs antorbital fenestra; (3) premaxilla elongate; (4) quadratojugal spur

appears; (5) dorsal vertebrae transverse processes enlarged; (6) at least four sacral vertebrae; (7) caudal ribs (transverse processes) reduced to seven; (8) clavicles overlap medially and do not extend dorsally; (9) interclavicle with anterior process; (10) anteriorly ilium elongated.

In Peters (2000a, 2002), basal pterosaurs shared with *Sharovipteryx*: (1) anterior [maxillary] teeth enlarged; (2) reduced torso equal to or shorter than skull plus cervicals; (3) mid and distal caudal vertebrae five times longer than tall; (4) humerus with crescentic deltopectoral crest; (5) manual digit 4 longer than humerus plus ulna; (6) tibia longer than femur; (7) dermal membranes (uropatagia) posterior to hind limbs.

In Peters (2000a, 2002), basal pterosaurs shared with *Longisquama*: (1) broad sternal complex formed of fused clavicles, interclavicle and sternum (Wild 1993). From the *Sharovipteryx* list, *Longisquama* also had 1) anterior teeth enlarged; 4) humerus with crescentic deltopectoral crest.

Several other synapomorphies listed in Peters (2000a, 2002) are not listed here because they were misinterpreted. Despite these problems, Peters (2000a, 2002) presented the first, and so far only, series of taxa that document a gradual accumulation of pterosaurian traits. That list has been expanded here (Fig. 12). See below.

In his PhD dissertation, Senter (2003) nested *Cosesaurus* with *Langobardisaurus*, *Sharovipteryx* and *Macrocnemus* as a sister clade to *Prolacerta* and *Protorosaurus*. Pterosaurs nested with *Scleromochlus* at the base of the Dinosauriformes derived from *Euparkeria* and *Proterosuchus*. *Longisquama* nested with the rib-glider *Coelurosauravus*. There are many scoring problems in Senter's analysis. As an example, Senter (2003, 2004) scored *Scleromochlus* with an elongated pedal 5.1 and a large sternum, but both are

absent. Senter (2003, 2004) followed Sharov (1970) in reporting dorsal tubercles on the skull of *Longisquama* and homologized them with the squamosal tubercles present in *Coelurosauravus*. In *Longisquama*, those “tubercles” are actually fused parietals divided medioposteriorly (Fig. 11). Senter (2003, 2004) considered the antorbital fenestra in *Longisquama* the result of damage. He denied the presence of antorbital fenestra in *Cosesaurus*, but traced it (Senter 2003, fig. 7).

In a two-part study Hone and Benton (2007, 2008) claimed they were going to test the “prolacertiform” origin of pterosaurs (as recovered in Peters 2000a) against the “archosaur” origin of pterosaurs (as recovered in Bennett 1996) by creating a supertree with a supermatrix of prior published work. That method does not require examining specimens either firsthand or with photographs. Despite being represented by complete and articulated fossils, *Cosesaurus* and *Langobardisaurus* were scored for less than a third of their character traits. *Longisquama* and *Sharovipteryx* were deleted from the inclusion set. In contrast to their stated objectives, the matrices presented by Peters (2000a) were deleted due to Hone and Benton’s (2007) inability to replicate Peters’ reanalysis of a modified Bennett (1996) dataset. Later Bennett (2012) reported their inability was the result of seven coding errors in retyping Peters’ published data matrix, along with other errors. In the second part of their two-part study, Hone and Benton (2008) omitted all references to Peters (2000a) and credited the competing “prolacertiform” hypothesis to Bennett (1996). Hone and Benton’s (2007, 2008) conclusions were self-described as ‘inconclusive’ as they were unable to recover any taxa that shared unambiguous pterosaurian traits. Their supermatrix also: 1) failed to nest four generic choristoderes with their taxon Choristodera; 2) failed to nest their taxon

Squamata with or within the Lepidosauromorpha; 3) failed to nest *Prolacerta* within the Prolacertiformes; 4) and nested the Pterosauria between the aquatic Proterosuchidae and the lumbering Erythrosuchidae.

Peters (2009) identified a pteroid and preaxial carpal in *Cosesaurus* along with fibers trailing the forelimbs, as in pterosaurs. Earlier Ellenberger (1993) illustrated these bones and soft tissues, but did not associate them with pterosaur anatomy.

#### Earlier Descriptions of the Three Basal Fenestrasaurs

All earlier workers (see below) had difficulties describing the three basal fenestrasaurs, *Cosesaurus*, *Sharovipteryx* and *Longisquama*. These difficulties can be attributed to initial bias, the crushed nature of the fossils themselves and lack of familiarity with sister taxa.

#### *Cosesaurus aviceps*

Ellenberger and de Villalta (1974, Figs. 1-4) described *Cosesaurus aviceps* as a small (14 cm snout to tail tip), Middle Triassic (Ladinian) reptile represented by the holotype and only known specimen, MGB-V1. Housed in the Museu de Geologia in Barcelona, the hand-sized plate contains the natural mold of the complete articulated skeleton and soft tissues in ventrolateral view together with an adhering medusa.

*Cosesaurus* was found in the Upper Muschelkalk of Alcover, Spain. That area is known for marine fossils with soft tissue preservation (Ellenberger 1978, 1993).

Prior interpretations of elements within the pectoral and pelvic girdles of *Cosesaurus* (Ellenberger and de Villalta 1974; Ellenberger 1978, 1993; Peters, 2000a)

were dissimilar to traits found in and shared by sister taxa recovered from prior analyses (Peters 2000a) and the present analysis (Fig. 12). *Cosesaurus* was reported to have a scapula acromion process (Ellenberger 1993; Fig. 2), but no candidate sister taxa have an acromion process. *Cosesaurus* was reported to have a deep interclavicle keel and enlarged, conjoined coracoids (Ellenberger 1993; Peters, 2000a, 2002), but no sister taxa have these. *Cosesaurus* was reported to lack a sternum (Ellenberger 1993; Peters 2000a, 2002), but all candidate sister taxa have a sternum. *Cosesaurus* appeared to have a stem-like process on its blade-like anterior ilium (Ellenberger 1993; Peters, 2000a, 2002), but no related forms share this trait.

Ellenberger (1993) reconstructed *Cosesaurus* as a digitigrade biped with lepidosaur and avian traits. He flipped the wrist and manus in order to make it appear that digit 2 was the longest, as in birds, rather than digit 4. That brought the two preaxial carpals to the postaxial side. A large, disarticulated sacral transverse process was considered an ischium and a gastralium was considered a retroverted pubis with an expanded articular ‘prepubis’ portion comprised largely of the anterior process of the ilium. Feather impressions were reported emanating from the tail. These avian interpretations were later dismissed (Milner 1985, Peters 2000a) as phylogenetic evidence mounted that birds were derived from small theropod dinosaurs (e.g. Gauthier 1986).

Sanz and López-Martínez (1984) crudely reconstructed *Cosesaurus* as a juvenile *Macrocnemus*, ignoring many traits (Fig. 1) not found in *Macrocnemus* (Peters 2000a). Using a supplied photograph of *Cosesaurus*, Senter (2003) was able to trace only a few crude outlines. He misidentified the coracoids as crescentic clavicles and denied the

presence of an antorbital fenestra, but his illustration Senter 2003, fig. 7) shows that he traced it.

Initial bias has played a part in prior interpretations of *Cosesaurus*. Ellenberger's (1978, 1993) views were influenced by his preconception of bird homologies. Sanz and López-Martínez (1984) clearly saw *Cosesaurus* as a juvenile *Macrocnemus*. Peters (2000a, b) recognized that an elongate pedal 5.1 (fifth digit, first phalanx) in *Cosesaurus* could be homologous with an elongate pedal 5.1 in pterosaurs, *Sharovipteryx*, *Langobardisaurus* and *Tanystropheus* (Bassani 1886, Peyer 1931, Wild 1973). Peters (2000a) agreed with Ellenberger (1978, 1993) on the presence in *Cosesaurus* of an antorbital fenestra, a posteriorly displaced naris, a spike-like quadratojugal, procoelus vertebrae, an elevated cervical series, four sacral vertebrae, an attenuated caudal series with chevrons parallel to each centrum, a blade-like anteriorly expanded ilium, a slender and appressed fibula, a simple hinge ankle joint, an elongate pedal 5.1, uropatagia trailing the hind limbs and fibers trailing the forelimbs. These traits are shared with pterosaurs, *Longisquama* and *Sharovipteryx*.

#### *Sharovipteryx mirabilis*

Originally *Podopteryx* [preoccupied] (Sharov 1971, Figs. 1, 5-9), *Sharovipteryx* is a small (~10 cm snout-vent, ~21cm snout-tail tip length), long-legged reptile represented by the only known specimen, PIN 2584/8 (plate and counterplate housed in the Paleontological Institute, Russian Academy of Sciences, Moscow, Russia). *Sharovipteryx* was found in the Madygen Formation (Ladinian–Carnian, Mid-Late Triassic), Dzailaichou, on the southwest edge of the Fergana valley in Kyrgyzstan. This area is

known for its fossil insects (Shcherbakov 2008) and soft tissue preservation in reptiles. While many elements are readily observable, magnified viewing of *Sharovipteryx* reveals additional details. Scales, structures similar to ‘hairs’ found in pterosaurs (Wang et al. 2002), later called pycnofibers (Kellner et al. 2010), and extradermal membranes obscure certain features and bone sutures. The middle area of the *Sharovipteryx* counterplate is missing, replaced with filler.

Sharov (1971, figs. 3-5) traced *Sharovipteryx* and reconstructed it as a glider. He also provided closer illustrations of the skull + neck and the torso + hind limb. Only the hyoids were identified in the skull + neck figure. Sharov mistakenly considered the fossil exposed in ventral view (Gans et al. 1987). He mistakenly identified the pubis as a retroverted posterior pelvic element. Here (Fig. 5) that area is identified as the proximal femur, displaced medially. Sharov (1971) tentatively, but correctly identified an elongated finger extending to the pelvic area, a tiny antebrachium (slightly longer than wide), carpals and an unidentified short curved line oriented medially that corresponds here to an ungual (Fig. 5). Disregarding portions of his own tracings, Sharov (1971) reconstructed *Sharovipteryx* along the lines of *Scleromochlus* with long, slender forelimbs and small hands with short fingers extending just beyond the outstretched knees. Sharov (1971) correctly traced small, convex, stiff, membranes anterior to the middle of each femur. However, his reconstruction transformed those into elastic membranes spanning the gap between the humerus and femur. Sharov (1971) identified pedal digit 1 as a boneless curve tipped by an ungual, here (Fig. 5) identified as soft tissue. Based on the presence of an elongate anterior ilium, Sharov considered

*Sharovipteryx* a 'pseudosuchian' (= advanced archosauriform) with possible affiliations to pterosaurs and/or *Scleromochlus*.

Halstead (1975) proposed that *Sharovipteryx* was a direct ancestor to pterosaurs basing his opinion on the presence in both of wing membranes. Confirming Sharov's (1971) figures, Gans et al. (1987) and Tatarinov (1989) reported the forelimbs were only one-third to one-quarter the length of the hind limbs (Fig. 5). Gans et al. (1987) and Dyke et al. (2006) both imagined the anterior membranes needed to stabilize *Sharovipteryx* in a gliding configuration without identifying them on the fossil. The reconstruction by Dyke et al. (2006) again attached the prefemoral membranes to the humerus, but Gans et al. (1987) did not. Gans et al. considered *Sharovipteryx* either a lepidosaur or a protorosaur with subtheodont teeth. Tatarinov (1989) considered *Sharovipteryx* a protorosaur (= prolacertiform).

Contra the present and all previously published studies, Unwin et al. (2000) reported the forelimbs 'have yet to be clearly identified.' They considered structures previously identified as forelimb elements as 'almost certainly remains of ribs' and supposed the forelimbs are still buried in the matrix. Unwin et al. (2000) agreed that *Sharovipteryx* was likely a prolacertiform based on the elongate cervical vertebrae and low neural spines, but also included a possible third trait, an incomplete lower temporal bar described earlier by Tatarinov (1994). Unwin et al. (2000) were unable to identify the tarsals or count the pedal phalanges, perhaps due to the displacement of the distal phalanges (Fig. 8). They mistakenly reported the presence of elongate penultimate phalanges on all digits. They reported the digits increased in length from one to five with 'intermediate' phalanges reduced, but those observations are not confirmed here. Unwin

et al. reported that digits 4 and 5 are subequal, as they appear *in situ* (Fig. 8), but a reconstruction shows that digit 4 extends far beyond digit 5 *in vivo*. Digit 5 is much longer than digit 4 when the disparate metatarsals are not included.

The skeleton of *Sharovipteryx* is preserved in a plate and a counterplate that often separates bones not at their surfaces, but through their shattered midsections. Peters (2000a) misinterpreted the posteriorly split cranial bones for pterygoids, assuming that the top of the skull was on the counterplate, exposing the palatal bones in dorsal view. No sister taxa had such robust palatal bones.

#### *Longisquama insignis*

Represented by the only known skeleton, PIN 2584/4 and its counterplate PIN 2584/5 (housed in the Paleontological Institute, Russian Academy of Sciences, Moscow, Russia), *Longisquama insignis* (Sharov 1970, Figs. 1, 10-11) was a small (13 cm snout-vent, 32 cm snout-tail tip length), reptile notable for its long dorsal plumes. A contemporary of *Sharovipteryx*, *Longisquama* was also found in the Madygen Formation.

Sharov (1970) provided simple tracings of *Longisquama* (Fig. 10d) that included the skull, cervicals, anterior dorsals, pectoral elements and forelimbs. Sharov traced soft tissue in the crook of the elbow, trailing the humerus and ulna, filling the throat area and a set of seven radiating plumes unlike those of any other reptile. The two “tubercle-like structures” Sharov traced at the back of the skull (Figs. 10, 11) are actually the fused parietals embayed posteromedially and rotated to a dorsal view. Sharov illustrated an elongate scapula and a manual digit 4 equivalent to the length of the humerus. Here (Fig. 10) that ‘digit’ is composed of jumbled phalanges from both hands, some aligned as

Sharov drew them. Sharov (1970) suggested the elongate plumes represented an early stage in the evolution of avian feathers, and that the clavicles represented an early avian furcula. He considered *Longisquama* a “pseudosuchian” on the basis of an antorbital fenestra (which is present) and a mandibular fenestra (which is not).

Agreeing with Sharov (1970), Haubold and Buffetaut (1987) reconstructed *Longisquama* with paired plumes oriented laterally for gliding or parachuting. However, when digital photographs of the plate and counterplate are aligned the left and right plates do not reveal paired plumes, only a single row. So it is difficult to understand how the concept of paired plumes arose other than to make them into parachutes. Jones et al. (2000) agreed with the paired plumes interpretation, that the plumes were proto-feathers and the clavicles were an avian furcula. Reisz & Sues (2000) and Prum et al. (2001) disagreed with both.

Unwin et al. (2000) also agreed that the plumes were aligned as pairs dorsally. Unwin et al. considered the skull holes of *Longisquama* the possible result of damage to the fossil. Instead of a furcula, Unwin et al. identified the bones as paired clavicles along with an interclavicle. They agreed with Sharov (1970) that *Longisquama* had acrodont teeth. These traits, they noted, were more typical of lepidosaurs. Unwin et al. observed only seven cervicals. All sister taxa have eight. One cervical, which may have been missed, is visible below the skull (Fig. 10c). Unwin et al. (2000) observed that only the anteriormost dorsal vertebrae were preserved. Sharov (1970) and all subsequent authors (including Peters 2000a) agreed, but closer examination reveals the entire vertebral column (Fig. 10). Unwin et al. (2000) reported a lack of cervical ribs, but they, too, are visible. Unwin et al. reported a long, narrow scapula, a rod-like coracoid and crescent-

shaped clavicles articulating with a well-developed interclavicle, but did not associate this suite of traits with pterosaurs. It is difficult to see how Unwin et al. were able to report elongate manual penultimate phalanges without reconstructing the manus, because the phalanges of one manus are on top of the other, scattered about (Fig. 10f, g). None of the digits have elongated penultimate phalanges in the present reconstructions.

Martin (2004) agreed that *Longisquama* had feathers and was capable of gliding with them. He provided an inaccurate skull drawing rather than a tracing (Fig. 11b). Fraser (2006) considered the plumes to be plant material accidentally preserved in coincidence with the vertebrae of *Longisquama*. Voight et al. (2009) and Buchwitz & Voigt (2012) argued against the plant hypothesis, explaining how the plumes developed in a feather-like process, convergent with avian dinosaurs. Due to inexperience working with difficult materials, Peters (2000a) provided a sophomoric tracing of the skull (Fig. 11) and anterior portion of the skeleton without realizing that some of the elements were palatal, occipital and from the hind limb. However, this was the first time a sternal complex similar to those of pterosaurs (Wild 1993) was identified in a non-pterosaur. In summary, virtually all work since Sharov (1970) has concentrated on the plumes with only one fresh illustration of the skeleton from Peters (2000a).

Every worker who described the above three fenestrasaurs shed new light on each specimen and made mistakes as well. Here those errors are corrected. The new interpretations add support to the Peters (2000a) hypothesis that pterosaurs were indeed derived from sister taxa to *Cosesaurus*, *Sharovipteryx* and *Longisquama* as all three had additional pterosaurian traits not listed in Peters (2000a, 2002, see below).

Recently *Kyrgyzsaurus* (Alifanov & Kurochkin 2011) has been added to the list of non-volant fenestrasaurs (Fig. 12) despite the fact that it was originally described as a drepanosaur.

The basalmost pterosaur, MPUM 6009 (Wild 1978, Museo di Paleontologia, Università di Milano, Italy) was originally considered a juvenile *Eudimorphodon* (Wild 1978) and later considered congeneric with *Carniadactylus* (Dalla Vecchia 2009) despite the size difference. In Peters (2007) MPUM 6009 nested with neither, but formed a transitional taxon between *Longisquama* and all other pterosaurs. *Carniadactylus* has a relatively larger sternal complex without posterior indentations, a straighter coracoid with a wider sternal articulation, and a longer scapula. The humerus of *Carniadactylus* has a terminal deltopectoral crest, but it is not terminal in MPUM 6009. The pes is smaller, relative to the tibia in MPUM 6009 and the metatarsus is also relatively smaller compared to the pedal digits.

A new phylogenetic analysis (Fig. 12) documents a gradual accumulation of pterosaurian traits arising within a new clade of lepidosaurs nesting between the Sphenodontia (Rhynchocephalia) and Squamata.

## **Materials and Methods**

The present taxon list of 24 is a subset of a larger taxon list of 389 taxa that includes several archosauriformes including generic members of the Parasuchia, Proterochampsidae and *Scleromochlus*. None of these nested with pterosaurs. That larger matrix originally included 228 characters. In the present subset 77 of those characters

were constant and 140 of the remaining 151 characters (Supp. Data) were parsimony informative. That results in 5.8:1 character/taxon ratio.

Although some characters used here are similar to those from various prior analyses, the present list of character traits (Supp. Data) was largely built from scratch. Characters were chosen or invented for their ability to lump and split clades and for a trait's visibility in a majority of taxa. Small and hard-to-see foramina were not included.

Due to the wide range and size of the inclusion set, data were collected from personal observation, photographs and the literature. I had direct access to the specimens of *Cosesaurus*, *Longisquama* and the counterplate of *Sharovipteryx* from which most of the present data were extracted. A first generation cast of *Cosesaurus* was a gift from Dr. Ellenberger.

Taxa and characters were compiled in MacClade 4.08 (Maddison and Maddison, 1990) then imported into PAUP\* 4.0b (Swofford, 2002) and analyzed using parsimony analysis with the heuristic search algorithm. All characters were treated as unordered and no character weighting was used. Bootstrap support figures were calculated (Fig. 12).

## **Results**

The present phylogenetic analysis of 24 taxa and 151 characters recovered a single optimal tree (Fig. 12) with a length of 403 steps, a Consistency Index (CI) of .529, a Retention Index (RI) of .727, a Rescaled Consistency Index (RC) of .384 and a Homoplasy Index (HI) of .471. All nodes in the lineage of pterosaurs had Bootstrap scores over 86.

The present analysis is the first to include 24 taxa that document a gradual

increase in pterosaurian traits. This falsifies prior claims (e.g., Hone and Benton 2007, 2008) that pterosaurs appeared in the fossil record without obvious antecedents. Prior workers had simply failed to include relevant taxa in their analyses and had looked elsewhere in vain. The following list of lepidosaurs (Fig. 12) document a gradual accumulation of pterosaur synapomorphies.

**A. *Homoeosaurus/Dalinghosaurus***

1) Frontal/parietal suture straight and longer than frontal/nasal suture; 2) caudal series longer than precaudal series; 3) pubic apron present and wide.

**B. *Carusia/Meyasaurus***

4) Naris longer than 2x height; 5) last maxillary tooth at mid orbit.

**C. *Bavarisaurus***

6) Naris displaced or posteriorly elongate; 7) caudal transverse processes absent beyond the eighth caudal; 8) proximal metatarsals subequal in width.

**D. *Lacertulus*/Daohugou lizard**

9) Premaxilla ascending process invades nasals; 10) premaxilla extends beyond nares; 11) postorbital tentatively contacts parietal; 12) quadratojugal gracile; 13) pterygoid narrow.

**E. *Tijubina***

14) Premaxilla ventral orientation horizontal (not transverse); 15) orbit less than rostral length; 16) jugal depth not gracile; 17) premaxillary teeth robust; 18) scapulocoracoid not fused; 19) metatarsal one greater than half of four.

**F. *Huehuecuetzpalli***

20) Skull table convex; 21) naris opening dorsolateral; 22) postfrontal does not contact upper temporal fenestra; 23) quadratojugal articulation with quadrate insecure; 24) olecranon process present; 25) fibula diameter not greater than half the tibia; 26) metatarsal five axially twisted.

**G. *Macrocnemus***

27) Preorbital skull length longer than postorbital length; 28) upper and lower temporal fenestra with both arches present; 29) quadratojugal extends from jugal ramus; 30) maxillary palatal processes present; 31) premaxillary teeth procumbent; 32) coronoid process low or tiny; 33) eight cervicals; 34) cervical ribs with free anterior processes; cervical rib orientation parallel to centra and elongate; 35) 25 or fewer presacral vertebrae; chevrons parallel to centra; 36) gastralia rod-like; 37) pubis orientation ventral; 38) fibula appressed to tibia.

**H. *Jesairosaurus***

39) Antorbital fenestra without maxillary fossa (tentative); 40) four premaxillary teeth;

41) dentary contributes to coronoid process; 42) three or more sacral vertebrae; 43) scapula larger than coracoid; 44) ilium posterior process not longer than anterior process.

**I. *Langobardisaurus***

45) Skull width less than 1.2x height at orbit; 46) prefrontal does not meet maxilla; 47) paroccipital angle transverse; 48) supratemporal and squamosal fused; 49) internal nares medial; 50) dorsal transverse processes present, some not shorter than centra; 51) second caudal transverse process longer than the centrum; 52) advanced mesotarsal tarsus.

**J. *Cosesaurus***

53) Antorbital fenestra without maxillary fossa; 54) naris not larger than antorbital fenestra; 55) premaxilla excluded from choana; 56) vomers narrow; 57) vomer teeth absent; 58) interclavicle fused to sternum; 59) coracoid reduced to strut; 60) ilium anterior process longer than acetabulum width; 61) prepubis present; 62) ventral pelvis without a thyroid fenestra (by convergence in *Jesairosaurus*); 63) tibia less than 2x ilium length.

**K. *Kyrgyzsaurus***

64) Major axis of naris greater than 30°; 65) nasals longer than frontals; 66) pineal foramen absent; 67) quadrate not posteriorly excavated; 68) no medial fusion of frontals and parietals; 69) postorbital posterior extends lateral to the medial posterior rim of parietal; 70) vomer contacts maxilla; 71) posterior mandible depth even.

**L. *Sharovipteryx***

72) Squamosal descending angle acute; 73) quadrate leans posteriorly; 74) internal nares not close to premaxillary teeth; 75) some maxillary teeth with multiple cusps; 76) five or more sacral vertebrae; 77) midcaudal centra 3x longer than tall; 78) radiale and ulnare block-like; 79) manus subequal to pes; 80) manual unguals 1-3 trenchant with long penultimate phalanges; 81) tibia/femur ratio not less than one; 82) metatarsus not compact; 83) pes shorter than half the tibia; 84) pedal 3.1 not longer than p2.1.

**M. *Longisquama***

85) Orbit does not enter anterior half of skull; 86) jugal quadratojugal process descends; 87) squamosal descends only to the dorsal cheek; 88) ectopterygoid fused to palatine; 89) palatal teeth absent; 90) retroarticular angle descends; 91) cervical height equals length; 92) cervicals decrease in height cranially; 93) midcervicals shorter than mid dorsal vertebrae; 94) reduced posterior dorsal ribs not present; 95) second caudal transverse process greater than width of centrum; 96) clavicles medially fused.

The following tested traits separate the basal pterosaur MPUM 6009 from proximal outgroup taxa.

**N. MPUM 6009, basal pterosaur**

1) Snout-occiput length not less than half the presacral length; 2) ventral aspect of premaxilla vs. rostrum, a third or greater; 3) lacrimal not deeper than maxilla; 4) humerus longer than femur; 5) forelimb longer than hind limb; 6) manus larger than pes; 7)

manual 4.4 longer than m4.3; 8) pedal digit five reduced to three phalanges (including ungual).

Pterosaurian traits not employed in the present phylogenetic analysis: 1) anterior rotation of the orbits: *Cosesaurus*; 2) anterior process of T-shaped interclavicle: tentatively in *Macrocnemus*, fully in *Cosesaurus*; 3) metacarpal 4 axially rotated, palmar side posterior: MPUM 6009 certainly, *Longisquama* less certainly; 4) ventral pelvis deeper than long: *Longisquama*.

Soft tissue first appearance: 1) dorsal frill: *Huehucuetzpalli*; 2. cervical pycnofibers (pterosaur ‘hair’): *Sharovipteryx*; 3) caudal fibers (coalesce to form tail vane in certain pterosaurs): *Cosesaurus*; 4) fibers trailing forelimb (aktinofibrils in pterosaurs): *Cosesaurus*; 5) uropatagia: *Cosesaurus*; 6) volant wings and propatagium: preserved rarely in pterosaurs, but likely present in basal pterosaurs and precursor taxa with a pteroid.

## **Description**

Despite being known from complete and articulated fossils, *Cosesaurus*, *Sharovipteryx* and *Longisquama* are indeed difficult subjects. A cursory tracing or examination with preconceptions will fail to provide the amount of data available to the more patient, precise, experienced and unbiased observer familiar with their sister taxa. The following are incomplete descriptions, focusing primarily on the misinterpretations of Peters (2000a) and other workers.

## *Cosesaurus*

As Ellenberger (1978, 1993) indicated (contra Sanz and López-Martínez 1984; Peters 2000a), the scapula of *Cosesaurus* is indeed extremely narrow and posteriorly elongate (Fig. 1), almost rib-like. This morphology follows the pattern of pterosaurs, *Longisquama*, *Sharovipteryx* and *Kyrgyzsaurus*, and to a lesser extent *Langobardisaurus*, *Tanytrachelos* (Olsen 1979) and *Jesairosaurus* (Jalil 1997). *In situ* the scapula impressions appear undisturbed beneath the dorsal ribs and ventral gastralia (Fig. 2). Neither scapula includes an acromion process (contra Ellenberger 1978, 1993).

The rim of the reported median “keel” in *Cosesaurus* (Ellenberger & de Villalta 1974; Ellenberger 1978, 1993; Peters 2000a, 2002; Fig. 2) is reinterpreted here as the narrow, quadrant-shaped stem of a disarticulated coracoid (Fig. 3). Overall it is distinct from the disc-like coracoids of *Macrocnemus* and *Langobardisaurus*, but similar to the crescentic coracoids of *Sharovipteryx*, *Longisquama* and basal pterosaurs. There is a gap between the purported plane of the see-through “keel” and the thicker “rim” (Fig. 2). What lies beneath is reinterpreted as the anterior process of a cruciform interclavicle beneath the crescentic coracoid that forms the thicker ‘rim.’ The *in vivo* dorsal portion of the left coracoid lies on top of the sternum and interclavicle. The dorsal portion is expanded for articulation with the scapula, as in pterosaurs. The similar right coracoid extends *in situ* laterally with articular surfaces preserved closer to both the right scapula and the middle of the interclavicle. The right coracoid mimics the shape and position of a rim of the *Macrocnemus* scapula, hence my earlier misinterpretation (Peters 2000a; Fig.

2c). Ellenberger (1978, 1993; Fig. 2b) misinterpreted this curved bone as the acromion process of the scapula.

The *Cosesaurus* interclavicle (Figs. 1-3) is cruciform, with an anterior process not found in its phylogenetic precursor, *Huehuecuetzpalli* (Reynoso 1998), and only tentatively developed in *Macrocnemus* (Peyer 1937). A large anterior process is also present in *Longisquama* and basal pterosaurs where it produces a typically shallow keel. In *Cosesaurus* the interclavicle is flat. The transverse processes are robust.

As in most basal tetrapods, the medial clavicles of *Huehuecuetzpalli* and *Macrocnemus* articulate with the interclavicle, then curve dorsally to rim the anterior coracoids and scapulae (Fig. 3a, b). This changes in *Cosesaurus* where the shorter straighter clavicles do not extend dorsally, but rim only the anterior margin of the trapezoidal sternum coincident with the transverse processes of the interclavicle. In *Longisquama* and pterosaurs (Fig. 3d, e) the clavicles wrap around the sternum rim lateroposteriorly (Wild 1993; Fig. 3), distinct from all other tetrapods.

Previously mistaken for conjoined coracoids (Ellenberger and de Villalta 1974; Ellenberger 1978, 1993; Peters 2000a, 2002; Fig. 2), the thinly ossified sternum of *Cosesaurus* is twice as wide as long. The sternal shape of *Cosesaurus* most closely resembles that of *Macrocnemus* (Fig. 3b), but the placement, dorsal to the interclavicle (Fig. 3c), is more like that of *Longisquama* and pterosaurs. Scattered ribs give the false appearance of curved sternal borders in the impressed fossil.

Previously considered a stem-like process on the blade-like anterior of the birdlike-like pubis (Ellenberger 1993) or pterosaur-like ilium (Peters 2000a), a disarticulated fan-shaped prepubis (Fig. 4) rests on the expanded blade of the anterior

ilium beneath it. The other dislocated prepubis is beneath the right femur. Much of it remains visible due to crushing and breakage of the hollow limb. These pterosaur-like fenestrated prepubes are 3 mm in length, about as long as the anterior process of the ilium, with a blade similar in size to the pubis. Prepubes are unknown in the more primitive *Macrocnemus* and *Langobardisaurus*. Larger prepubes are present in *Sharovipteryx*, *Longisquama* and pterosaurs. Based on available data, the prepubis appears to be a new bone rather than a modified gastralium as no gastralium in more primitive taxa are robust or articulate with the pubis.

#### *Kyrgyzsaurus bukhanchenkoi*

Published eleven years after Peters (2000a) and originally considered an odd sort of drepanosaur, *Kyrgyzsaurus bukhanchenkoi* (Fig. 1) nests between *Cosesaurus* and *Sharovipteryx* in phylogenetic analysis (Fig. 12). Larger than its sisters, *Kyrgyzsaurus* is known from a skull, neck and pectoral girdle more robust than in *Cosesaurus*, but of similar morphology. Note the parallelogram-shaped cervicals raising the skull over the shoulders. As in other fenestrasaurs, extradermal soft tissue was also found dorsal to the skeleton of *Kyrgyzsaurus*.

#### *Sharovipteryx mirabilis*

On the plate, the small, crushed skull of *Sharovipteryx mirabilis* (PIN 2584/8, Figs. 1, 5-9) is exposed in dorsal view with the occiput and quadrates falling open in medial view (Fig. 6). The mandible is largely hidden beneath the skull. Palatal elements appear at the margins and through the posterior cranial split.

The reconstructed skull of *Sharovipteryx* greatly resembles those of *Cosesaurus*, *Kyrgyzsaurus*, *Longisquama* and the basal pterosaur, MPUM 6009 (Fig. 1) sharing a short rostrum, elongate posteriorly displaced naris, triangular antorbital fenestra, large orbit, narrow temporal fenestrae and a straight jawline.

The premaxilla of *Sharovipteryx* is acutely pointed with a short jawline exposure. The four tiny premaxillary teeth are about the size of the scales that layer its dorsal surface. At mid-length the premaxilla expands laterally posterior to the naris, cutting off most nasal contact. The ascending process continues as a narrow strip to the mid nasals. The slit-like and posteriorly displaced naris extends for less than a quarter of the premaxilla length. The nasals are twice the length of the frontals and are concave laterally to accommodate the strip-like prefrontals that border laterally. The frontals are wider than the nasals and include posterior lateral processes that substantially broaden the cranium and accommodate small triangular postfrontals that do not contact the upper temporal fenestrae. The frontal/parietal suture is obtuse, pointed posteriorly. The broad parietals are slightly broader posteriorly and longer medially.

The *Sharovipteryx* maxilla ventral margin is straight and accommodates approximately 17 teeth of various sizes. All are larger than those in *Cosesaurus*. The largest anterior teeth are recurved. The ascending process of the maxilla arises at a shallow angle ( $\sim 25^\circ$ ) and contacts the nasal, prefrontal and lacrimal. These frame a triangular antorbital fenestra without a fossa, as in pterosaurs. Gans et al. (1987) considered the antorbital fenestra absent, but they did not attempt a reconstruction. Due to crushing and slight scattering, the antorbital fenestra only becomes apparent with a reconstruction, but phylogenetic bracketing also indicates its presence. Forming the

posterior margin of the antorbital fenestra, the lacrimal is a curved, anteriorly leaning T-shape, concave along the orbit rim. The L-shaped jugal has an obtuse postorbital process. While beetles dot the matrix, a previously overlooked wasp-like insect resides inside the left orbit (Fig. 6). Unlike *Cosesaurus*, the jugal of *Sharovipteryx* lacks a quadratojugal process. The quadratojugal is a short spur arising from the base of the jugal, but not in contact with the quadrate. The postorbital is triradiate and half as tall as the orbit. The squamosal is strongly curved in dorsal view and does not include a descending process, unless it was broken off. The quadrate is a tall gently curved bone that leaned posteriorly in life.

The paired vomers of *Sharovipteryx* are narrow rectangular strips. The strip-like ectopterygoid and strip-like palatine probably combine to form an L-shaped bone, the ectopalatine, but their intersection is hidden by overlying bone. Both sinusoidal pterygoids are broken, but otherwise in place. They are more robust approaching the quadrates. The paired basipterygoid processes of the basisphenoid are elongate and narrow, as in *Cosesaurus*. The cultriform process is short and narrow. The supraoccipital is tall and narrow. The small opisthotics are greatly expanded laterally. Together with the supraoccipital they frame large posttemporal fenestrae.

The dentary is straight and narrows to a sharp Gothic tip in dorsal view. A few large recurved teeth, twice as tall as other dentary teeth, appear below the premaxilla/maxilla suture. The coronoid is low. The angular is less than half the depth of the mandible. The retroarticular process (articular) turns up slightly.

A set of elongate and tapering hyoids emerges from below the base of the skull. The longest extends to the fifth cervical. Their asymmetrical preservation suggests they were mobile.

In *Sharovipteryx* there are eight procoelus cervicals, probably seventeen dorsals, seven sacrals and about forty caudals. The presacral count matches that of *Cosesaurus*. Cervicals 3-6 are elongate, like those of long-necked pterosaurs, with very low to absent neural spines. *Langobardisaurus* also has a long neck, but proximal sister taxa (Figs. 5, 12) do not. As in pterosaurs, the morphology of the cervicals permits substantial dorsoventral mobility, but little movement to the left and right. Extremely gracile cervical ribs are oriented parallel to and are the length of each centrum.

The shorter dorsal vertebrae have short neural spines and short transverse processes. The first dorsal rib is gracile. The next seven are wide and flat distally. Together they form a disc in dorsal view. The next seven ribs are not preserved, but were likely extremely gracile (if present at all) as there is little room for any other shape. The two posterior dorsals do not have ribs. Gracile gastralia are barely perceptible. Seven sacrals are aligned between the elongated ilia. Their ribs (sacral transverse processes) are robust and expand distally. There is no sacral fusion.

Overall the tail of *Sharovipteryx* is extremely attenuate and stiff. The anterior four or five caudals are hidden beneath a rectangular patch of tiny scales, the product of a dorsal 'kink' (Gans et al. 1987) that raised the tail base. The first visible caudal is a robust bone with elongate articular surfaces permitting great dorsoventral flexion. The next one is narrower and elongate, like a cervical, with similar articular surfaces. The remaining caudals vary from three to seven times longer than tall. The posterior caudals

gradually decrease in diameter and length, likely to the tail tip, which is missing from the broken edge of the plate. Most caudal chevrons are subequal to and parallel each centrum.

The strap-like scapula is covered with a layer of scaly epidermis that looks like netting. It is longer than the stem-like coracoid, which lies beneath the ribs. The scapula and coracoid are unfused and widest at their suture. The ventral coracoid includes a posteriorly directed articular surface, probably connected to the unexposed sternal complex. The shape of the *Sharovipteryx* sternal complex can be estimated by phylogenetic bracketing, taking the rectangular sternal complex of *Cosesaurus* or the triangular one of MPUM 6009 and modifying either to fit the first few dorsal ribs of *Sharovipteryx* (Fig. 7). This hypothetical sternal complex would have been wider than long, narrowing anteriorly. In like fashion, the sternal complex also narrows anteriorly in *Longisquama* (Peters 2000a, 2002) and the basal pterosaur MPUM 6009 (Fig. 1).

In contrast to prior workers, Unwin et al. (2000) considered the forelimbs of *Sharovipteryx* buried or missing. The radius and ulna do indeed have a similar shape to the paddle-like rib tips, but all of the actual rib tips are accounted for. The right ulna and radius are oriented parallel to the ribs, but none of the other forelimb elements resemble ribs. The present interpretation (Fig. 1) matches and enhances what Sharov (1971) and Peters (2002) traced and Tatarinov (1994) described. Here the left and right elements match and all elements share traits and proportions with *Cosesaurus*, *Longisquama* and pterosaurs (Fig. 1). The tiny forelimbs of *Sharovipteryx* are best considered vestiges.

The short, robust humerus of *Sharovipteryx* has a large deltopectoral crest and a prominent capitulum/trochlea with flattened articular surfaces. So the elbow was likely

inflexible. The antebrachium is slightly longer than wide with an appressed radius and ulna incapable of pronation or supination, as in pterosaurs. The radiale and ulnare are block-like as in pterosaurs. The distal carpals are proportional to the proximal metacarpals. The pteroid is a short pawn-shaped bone that would have anchored a tiny propatagium if present. The square preaxial carpal is also preserved. Metacarpals 1-3 increase in length laterally with more asymmetry than in *Cosesaurus*. As in pterosaurs and *Longisquama*, metacarpal 4 is more robust than the others with an expanded distal articular surface. In pterosaurs metacarpal 4 rotates axially 90° (Peters 2002) so the finger flexes in the plane of the manus (contra Bennett 2008). In *Sharovipteryx*, if any rotation were present, it would have been minor because the PILs (parallel interphalangeal lines, Peters 2000b, 2010, Fig. 3) were continuous across all four medial digits. These lines indicate that digit 4 phalanges flexed in sets with their medial counterparts. In pterosaurs PILs are not continuous with digit 4 because it flexes independently in the plane of the manus and is so much larger. In *Sharovipteryx*, digits 1-4 are slender and elongate, increasing in length from 1 to 4 and all had trenchant unguis.

In *Sharovipteryx* the ilial processes are much longer. The pubis and ischium of the right pelvis are visible through the sacrals (Fig. 5). The left ventral pelvis is largely buried beneath uropatagia, so its shape can only be determined by the contours of the soft tissue that blankets them. As in *Cosesaurus*, the ventral pelvic elements of *Sharovipteryx* appear to be sutured, not fused, and without a thyroid fenestra.

Based on subtle surface contours, one prepubis appears to be buried beneath the fingers of the right hand (Fig. 5). If so, it is similar in shape to those found in *Cosesaurus* and MPUM 6009 and proportional to the *Sharovipteryx* femur, which makes the prepubis

appear large compared to the pelvis (Figs. 1, 7). If I have not correctly identified and outlined the prepubis, phylogenetic bracketing between *Cosesaurus* and MPUM 6009 provides *Sharovipteryx* with this shape and size of a prepubis.

The *Sharovipteryx* femur is as long as the glenoid-acetabulum length. That is more than twice the relative length present in *Cosesaurus* (Fig. 1). The basal pterosaur, MPUM 6009, has a femur nearly as long as the glenoid-acetabulum length. Most derived pterosaurs do not have such a long femur (exceptions include stork-like azhdarchids). The distal end of the *Sharovipteryx* femur expands anteriorly to form a pulley-like process (Unwin et al. 2000), which also acts as a stop to prevent overextension. Distinct from *Cosesaurus*, the tibia/fibula in *Sharovipteryx* is slightly longer than the femur, as in *Longisquama* and pterosaurs. Substantial soft tissue at the knee fills the gap between the femur and tibia, permitting great flexibility. A simple hinge ankle joint is present with two proximal tarsals (broader astragalus and spool-shaped calcaneum) along with three distal tarsals (centrale, distal tarsal 3 and distal tarsal 4; Peters 2000a).

Distinct from *Cosesaurus* the metatarsals in *Sharovipteryx*, *Longisquama* and MPUM 6009 (Fig. 1), spread widely, framing interdigital membranes. In situ pedal digit 1 is displaced lateral to metatarsal 2 and also displaced proximally, similar to the displacement of the other distal phalanges. In the new pedal reconstruction metatarsal four is longer than the others, as in *Cosesaurus* and basal pterosaurs. Here the interdigital membranes and uropatagium extend to the penultimate phalanges, further than in either *Cosesaurus* or pterosaurs. Pedal digit 4 is subequal to metatarsal 4 in *Cosesaurus*. Digit 4 is slightly longer in *Sharovipteryx* and much longer in MPUM 6009. As in *Cosesaurus*

and pterosaurs, pedal 5.1 is metapodial and digit 5 includes an ungual. Pedal 5.2 and p5.3 remain distinct in *Cosesaurus*, *Sharovipteryx* and *Longisquama*, but fuse in pterosaurs.

The premaxilla, shoulders and the base of the tail in *Sharovipteryx* are covered with scales. Long ‘hairs’ (pycnofibers in pterosaurs, Kellner et al. 2010) are visible on the scaleless skin surrounding the cervicals.

*Cosesaurus* and *Longisquama* both have dorsal plumes. Phylogenetic bracketing indicates that plumes should also be present in *Sharovipteryx*. A closer look reveals several short and gracile plumes in *Sharovipteryx* (Figs. 1, 6, 7) all slightly deeper than the torso. If we were looking at the same structures, Gans et al. (1987) described these as, “A series of grooves or folds suggests that a flap of skin may have attached to the dorsolateral surface of the trunk.” No propatagium or forelimb trailing membranes are visible, but phylogenetic bracketing and the presence of a short pteroid indicates that *Sharovipteryx* probably also had extradermal forelimb membranes. The fiber-enforced uropatagia are readily visible. Small, stiff pre-femoral membranes are also present, as traced by Sharov (1971). In a gliding configuration (Fig. 7) these would have filled the gap between the disc-like torso and the extended femora without connecting to the torso or forelimbs (Gans et al. 1987). In the pes interdigital membranes are visible between digits 4 and 5. Similar membranes were likely present between the medial pedal digits.

Considering the long list of traits shared by *Sharovipteryx* and pterosaurs, it is a wonder that they were never tested together in any published phylogenetic analysis other than Peters (2000a). The long forelimbs of pterosaurs and the short forelimbs of *Sharovipteryx* seem to have created an impasse. However, a variety of theropods, including several flightless birds, also vary widely in forelimb length.

*Longisquama insignis*

The skeleton of *Longisquama insignis* (PIN 2584/4) is severely crushed. Soft tissue is well preserved here, but it often obscures bones and sutures. Contra earlier reports (Sharov 1970; Unwin et al. 2000; Peters 2000a, 2002), the skeleton is complete (Fig. 10). The forequarters and the separated tail are largely articulated, but the left scapula + coracoid and the sternal complex are displaced anteriorly. The pelves are flipped posteriorly and the prepubes are displaced posteriorly. The posterior dorsal vertebrae rise sharply and the anterior sacrals descend sharply, as if they were taphonomically pulled between vertebrae #32 and #33. A set of posterior dorsal ribs is displaced near the mid caudals. The posterior 15 caudal vertebrae are preserved in a twisted spiral, as if they were the last to fall to the substrate, held aloft by the spinning vane at the tail tip. What Sharov (1970) illustrated as a displaced plume roughly parallel to the forelimbs is actually the left hind limb (Fig. 10). What Jones et al. (2000) and Buchwitz & Voigt (2012) considered plume stems dorsal to the dorsal vertebrae are actually metatarsals 1-5 of the left pes. The left pedal digits extend dorsally. The right hind limb is buried beneath posterior plumes. The left hand is essentially on top of the right one, which creates a jumble of digits. Even so, all the phalanges can be identified and both reconstructions match one another (Fig. 10). In essence, others have already seen many of the so-called “missing” post-cranial elements. They were hiding in plain sight, just misidentified. Here the elements are identified, segregated and reconstructed (Fig. 1).

With one *Longisquama* plume now identified as a hind limb, only six large plumes remain along with several smaller ones arising from the skull and cervicals. By homology with *Cosesaurus* and *Sharovipteryx*, the plumes are dorsal frills. No more dorsal frills are identified from the disturbed posterior torso and pelvic areas and no other dorsal frills are scattered about. So it is possible that only six large frills were present in *Longisquama*. They were sometimes shed (Sharov 1970, Buchwitz & Voigt 2012).

A V-shaped tail vane tips the tail. A scaly and hairy gular sac fills the throat area. A trachea is preserved (Fig. 11). As Sharov (1970) noted, membranes fill the crook of the arm (= propatagium) and trail the forelimb elements (= brachiopatagium). The uropatagia are detached from the hind limbs, covering some bones. Gastralia are present, but were thoroughly scattered when the torso and pelvis were disturbed. Nearly every aspect of the skeleton of *Longisquama* greatly resembles that of *Cosesaurus* and/or *Sharovipteryx*—only more exaggerated (Fig. 1).

A survey of past attempts at tracing the skull of *Longisquama* (Fig. 11) shows that Sharov (1970), Peters (2000a), Senter (2003) and Martin (2004) all struggled with tracing it or they opted not to go into detail. Those problems are rectified here (Fig. 11) with a more precise and labeled set of tracings and reconstructions.

The small, crushed skull of *Longisquama* is exposed largely in left lateral view on the plate (Fig. 11), missing only the pre-narial portion of the premaxilla and dentary. The L-shaped ectopalatines (fused ectopterygoid + palatine), vomers and sinusoidal pterygoids were rotated to the parasagittal plane during crushing, exposing their ventral surfaces while crossing the antorbital fenestra and orbit. The hyoids and occipital bones

were likewise rotated during crushing. Crushing exposed the dorsal surfaces of the fused parietals.

Of the premaxilla only the ascending process is preserved. It is a stem-like structure that rises as far as the anterior orbit. An impression of a posterior premaxilla tooth is also visible. The nasal anteriorly borders the posterior naris and extends slightly beyond the premaxilla ascending process. The maxilla includes a curved, wave-shaped ascending process that meets the lacrimal on the dorsal rim of the triangular antorbital fenestra. The maxilla includes 16 triangular to recurved teeth, deepest below the antorbital fenestra. Posterior maxillary teeth are either very closely appressed or multicusped. The jugal is slightly deeper than the maxilla. The lacrimal process of the jugal is small. The postorbital process of the jugal is twice as tall and leans posteriorly. The quadratojugal process of the jugal descends and produces a tiny, straight quadratojugal aligned parallel with the posteriorly tilted quadrate. The lacrimal is a slender splintered stem with a robust sloping T-shape top. The postfrontal is a narrow strip, narrower anteriorly, bordering the nasal and frontal. The frontal includes a narrow anterior process interdigitating between the nasal and prefrontal. The posterior frontal extends laterally in a tongue-like process to back a small triangular postfrontal not in contact with the upper temporal fenestra. The postorbital is gracile and triradiate with a long, straight jugal process/stem. The parietals are robust and fused together with large and deep upper temporal fenestrae. A deep medial embayment divides the posterior parietals. The squamosal borders the upper temporal fenestra and may contribute a descending process lateral to the quadrate, but this is difficult to determine in dorsal view.

The robust, tall right quadrate is undisturbed. The left quadrate is rotated  $\sim 80^\circ$  *in situ* with its articular surface in the middle of the orbit.

The gracile occipital bones were apparently fused together because they were preserved as a unit during taphonomic crushing. The supraoccipital portion is very tall and the opisthotics are elongate. These frame large, posttemporal fenestrae. The long basiptyergoid processes of the basisphenoid are more than twice the length of the short, gracile cultriform process.

The vomers are short narrow strips, extending from the premaxilla to contact the anterior pterygoids. The short rectangular ectopterygoid is fused to the narrow palatine probably creating an L-shaped ectopalatine, contacting the maxilla below the ascending process and the jugal suture. The pterygoids are gracile and sinusoidal. In palatal view the palatal elements produce a triangular rostrum. Several sets of hyoids are present. The Y-shaped hyoids are as long as the skull. More robust shorter hyoids are below the mandible. Two slender tapering bones cross the antorbital fenestra *in situ*, but probably were placed medially, between the other hyoids *in vivo*.

The mandible includes 13 conical teeth, several deeper than the gracile dentary. Posterior teeth are packed together so closely that some may represent multicusped teeth with multiple roots. The coronoid is not visible because it is obscured by the jugal, but the coronoid is not large in clade sisters. The surangular is nearly twice the depth of the angular. The ventral mandible margin is straight, but the posterior angular descends slightly.

In *Longisquama* there are eight small procoelus cervicals, 34 dorsals (two long ones between the anterior ilia), five sacrals and about 40 caudals. The presacral count is

nine more than in *Cosesaurus* (Fig. 1) contributing to a torso that is twice as long. The cervicals are much smaller than those in *Cosesaurus*, despite the greater size of *Longisquama* overall. Tiny cervical ribs are present. The anterior dorsals are similar in size to the cervicals. However the newly identified posterior dorsals, especially those between the elongate ilia, are increasingly longer and larger posteriorly. Based on the number of displaced dorsal ribs and the number of dorsal vertebrae without them, ribs attend every dorsal vertebra except those between the ilia. The longest ribs are at mid torso. There is no sacral fusion. Nor are the short sacral ribs expanded laterally, as in *Sharovipteryx*. The anterior three caudals have transverse ribs of increasing lengths, but the next three caudals reduce their transverse ribs caudally. Distinct from *Cosesaurus*, the transverse ribs in *Longisquama* are fused to each vertebra. The remaining caudals are elongate and apparently without ossified chevrons. Caudals 21 to 31 are extremely elongate. Thereafter the caudals gradually decrease in diameter and length to the tail tip, which is marked by an oval of eight tiny, sometimes paired ossifications supporting the tail vane. Overall the tail is extremely attenuate and apparently stiff for most of its length, but the in situ spiraling of the posterior 15 vertebrae suggests they were more flexible than in *Sharovipteryx* or pterosaurs.

The strap-like scapula of *Longisquama* is longer than the stem-like coracoid. Both are more robust than in *Cosesaurus* (Figs. 1, 3) and the coracoid has a straighter stem. The *Longisquama* sternal complex is crescentic with perhaps a very shallow anterior interclavicle keel. The clavicles overlap medially and rim the sternum posterolaterally, as in pterosaurs. The transverse processes of the interclavicle are likewise crescentic. By

way of expansion or embayment or both, the sternum develops a posteromedial process that creates a trident shape posteriorly, as in MPUM 6009, a basal pterosaur (Fig. 1).

The humerus of *Longisquama* is no larger than that of *Cosesaurus*, but it has a large deltopectoral crest and expanded distal condyles, as in basal pterosaurs (Fig. 1). The radius and ulna of *Longisquama* are likewise subequal to those in *Cosesaurus*. The radiale and ulnare are block-like, as in *Sharovipteryx* and pterosaurs. The pteroid and preaxial carpal are larger than in *Cosesaurus*. As in *Cosesaurus*, metacarpals 1-3 only slightly increase in length laterally. Distinct from *Cosesaurus*, and similar to *Sharovipteryx* and pterosaurs, metacarpal 4 in *Longisquama* is more robust than the others with an expanded distal articular surface. Here, as in *Sharovipteryx*, the manual PILs remained continuous with digit 4 joints, indicating that digit 4 phalanges still flexed in sets with their counterparts. Similar to *Sharovipteryx*, manual digit 4 in *Longisquama* is longer than digit 3 by two phalanges. Like MPUM 6009, digit 4 is more robust in *Longisquama*. The largest, most trenchant ungual in *Longisquama* is at the tip of manual digit 4. Like *Cosesaurus*, manual digit 5 in *Longisquama* is similar in length to the metacarpus and not a vestige, as in *Sharovipteryx* and pterosaurs (Fig. 1).

In *Longisquama* the short posterior process of the ilium rises 60°, much higher than in more primitive fenestrasaurs. This angle approaches that of the basal pterosaur MPUM 6009 (Fig. 1). Most derived pterosaurs revert to a lower posterior ilium angle of elevation. The pelvic elements (ilium, pubis, ischium) are all fused in *Longisquama* and the ventral elements are much deeper than in *Cosesaurus* and *Sharovipteryx*. One and a half prepubes are preserved. The other half is lost past the matrix break. The prepubis

articulates with the ventral pubis at an immobile butt joint (contra Claessens et al. 2009) and approaches the size and shape of the MPUM 6009 prepubis.

Relative to the torso, the femur of *Longisquama* is shorter than in *Cosesaurus*. No distinct femoral neck is present, as in sister taxa. The distal femur expands to form a concave cap for the convex proximal tibia. The tibia/fibula in *Longisquama* is longer than the femur. Distinct from all sister taxa, the tibia and fibula of *Longisquama* are robust. The fibula is slender, but not a splint. Tarsals have not been identified in the chaos of plume bases and vertebrae.

Distinct from sister taxa, the short, robust metatarsals of *Longisquama* are nearly subequal, only slightly increasing in length laterally. Metatarsal 5 is less than a third as long as metatarsal 4 (Fig. 1), as in sister taxa. The proximal phalanges on digits 1–3 are subequal to their metatarsals. The penultimate pedal phalanges are shorter. Digits 2–4 align distally as in MPUM 6009. The unguals are sharp, but not strongly curved. Pedal 5.1 is bent at mid-length with a distal trochlea articulation enabling retroverted distal phalanges, as in pterosaurs (Fig. 1). In *Longisquama* pedal 5.2 contacted the substrate on its dorsal surface, as in basal pterosaurs and the trackmaker of *Rotodactylus* (Peabody 1948, Peters 2000b, 2011). Pedal 5.2 is short. Pedal 5.3 is shorter and provided with an ungual (p5.4). Basal pterosaurs have one less phalanx than in *Longisquama* resulting from the fusion of pedal 5.2 and p5.3, maintaining the sum of their lengths.

### **Physiology and Behavior**

Pterosaurs were the first vertebrates to achieve powered flight. Here, based on additional data, are the surrounding environments and gradual changes that produced a wide

variety of anatomy, physiology and behavior in the Fenestrasauria, only one of which successfully culminated in powered flight.

## Environment

With only four known specimens, nonvolant fenestrasaurs are exceedingly rare in the fossil record. However, *Rotodactylus* ichnites, matched to fenestrasaur trackmakers (Peters 2000b), are more common. They are known from the lower Triassic of the Southwest United States, Europe and Algeria (Brusatte et al. 2011).

*Rotodactylus* tracks were formed on floodplains of large meandering rivers, far inland from the coast (Brusatte et al. 2011). *Cosesaurus* was washed out to marine sediments, which provide few clues to nearby terrains. The other three basal fenestrasaurs are all from the Madygen formation.

The Madygen megafauna was rich in pteridosperms (seed ferns). It also contained conifers, ferns, horsetails, and lycopsids (Shcherbakov 2008). In addition to the multitude of insects, freshwater bivalves, tadpole/shield shrimps and fish were also found there. A primitive cynodont, *Madysaurus* (Tatarinov 2005), was the only possible predator of the fenestrasaurs thus far discovered.

## Diet and Predation

Found in insect-laden sediments, fenestrasaurs were likely insectivores catching them on the substrate. In *Sharovipteryx* certain maxillary teeth were twice as large as others and recurved. These could have pierced the exoskeletons of insects. Posterior teeth were in contact with each other or multicusped for oral processing, a trait that continued

only to the end of the Triassic in pterosaurs. In palatal view (Figs. 7, 11) the rostrum of fenestrasaurs is broader cranially, providing a measure of binocular vision by rotating the orbits anteriorly. That would have been useful for judging distances to landing locations, prey, mates and rivals.

### Bipedal Locomotion and Flapping

In the basal lepidosaur, *Huehuecuetzpalli*, as in many living lizards, the ossified scapula is short, anteriorly fenestrated and dorsally truncated (Reynoso 1998). Impressions indicate that a cartilaginous extension, the suprascapula, extended the ossified portion, as in living lizards. Derived taxa took two paths. In *Macrocnemus* and *Tanystropheus* the scapula became short, not fenestrated, and without a trace of a suprascapula. This loss of fenestration has obscured their lepidosaurian affinities. Taking the other path, in *Tanytrachelos* and *Langobardisaurus* the continued erosion of the anterior rim gives the posterior remainder a strap-like appearance. In *Jesairosaurus* the scapula is also strap-like, but oriented vertically to the height of the neural spines, as in related drepanosaurs. In *Cosesaurus*, *Sharovipteryx*, *Kyrgyzsaurus*, *Longisquama* and pterosaurs the scapula is narrow and extends posterodorsally over several ribs. This change in morphology from ‘wide, short, mobile and vertical’ in *Huehuecuetzpalli* to ‘narrow, elongate, less mobile and diagonal’ in *Cosesaurus* signals a change in locomotion.

The evolution of the coracoid matches that of the scapula in this clade. In living lizards (and *Huehuecuetzpalli*) the coracoid is fenestrated. In *Macrocnemus* and *Tanystropheus* the coracoid fenestrae fill with bone, reverting back to a disc shape.

*Jesairosaurus* and the proto-drepanosaur, *Hypuronector* (Olsen 1979), retain a coracoid embayment but more derived drepanosaurs do not. In *Cosesaurus* and later fenestrasaurs the anterior coracoid fenestrae expanded greatly, leaving only the quadrant shaped posterior rim. MPUM 6009 retains that quadrant-shaped coracoid. More derived pterosaurs more or less straighten out the coracoid stem (Fig. 3e).

In living lizards (and *Huehuecuetzpalli*) each scapulocoracoid is free to move anteroposteriorly (Jenkins & Goslow 1983), riding along the sliding joint bordered by the interclavicle stem and the anterior sternal rim. By contrast the narrow and posterodorsally elongate scapula of birds is relatively immobile, especially so owing to the great firmness of the ventral coracoid articulation to the sternum. Huntington (1918) reported the bird scapula combined great strength and rigidity, enabling a powerful ventro-appendicular musculature to move the anterior limb within a limited range in a few directions with great force, but not adapted to a wider extent of more diversified motion. In birds such a pectoral girdle serves as an anchor to the bones and muscles of the flapping wing. Analogous due to similarities in morphology, the strap-like scapula and stem-like coracoid in *Cosesaurus*, *Sharovipteryx*, *Longisquama* and basal pterosaurs would have likewise delivered great force over a limited range, especially so considering the socketing of the coracoid ventral stem to the sternal complex. Overall *Cosesaurus* had the proportions of a typical small quadrupedal lepidosaur (Fig.1), but the immobilization of the pectoral girdle must have had distinct behavioral and locomotory consequences.

Pterosaurs are universally considered flapping reptiles, capable of powered flight. As in birds, those similar pectoral girdles provided anchors for the muscles and bones that create thrust and lift in the forelimbs. That a basically identical pectoral girdle is

found in the tiny nonvolant pterosaur precursor, *Cosesaurus* attests to its nascent flapping ability. Obviously with such a short manus flight would have been impossible. Instead, perhaps *Cosesaurus* practiced some form of wing-assisted running (Dial 2003). The flapping winglets could have acted as secondary sexual signals or to intimidate rivals. Short trailing fibers on the forelimb of *Cosesaurus* (Ellenberger 1993, Peters 2009) were the precursors to the longer aktinofibrils that support pterosaur wing membranes. Even in their nascent stages they would have extended the surface area of the forelimbs, creating proto-wings. The presence of a tiny pteroid and preaxial carpal on *Cosesaurus* (Peters 2009) provides a starting point for the development of the pterosaur propatagium that Sharov (1970) illustrated (Fig. 1, 10) in *Longisquama*.

Among pterosaur workers there is universal agreement that a broad sternal complex with a robust anterior (interclavicle) process anchored the large pectoralis muscles of adduction that pterosaurs used for flapping (e.g. Wellnhofer 1991). A precursor sternal complex in *Cosesaurus* (Figs. 2, 3) and *Longisquama* (Fig. 1) would have been similarly muscled and used, even if less developed. The evolution of the sternal complex from the plesiomorphic state is well documented in fenestrasaurs (Peters 2002) and their lepidosaur ancestors.

In the basal lepidosaur, *Huehuecuetzpalli*, as in most tetrapods, the clavicles rise dorsolaterally to contact the anterior borders of the coracoid and scapula. In pterosaurs the clavicles extend posterolaterally to rim the sternum. The short straight clavicles in *Cosesaurus* represent a transitional phase between these two configurations (Peters 2000a, 2002). Since the dorsal orientation of the clavicles was lost in *Cosesaurus*, it is likely that any muscles anchored there were also lost or transferred in the process. As the

clavicles later expanded along the lateral rims of the sternum in *Longisquama* and pterosaurs, sternal muscles would have found new anchorage there.

The sternum of the basal lepidosaur, *Huehuecuetzpalli*, is rhomboidal and poorly ossified (Reynoso 1998, Fig. 3). It is located at the posterior tip of the interclavicle. In the more derived *Macrocnemus* the sternum is relatively smaller and without a pointed anterior or posterior, and it remains at the posterior tip of the interclavicle. In *Cosesaurus* the sternum is dorsal to the interclavicle without fusing to it. In *Longisquama* and pterosaurs the sternum is fused to the interclavicle and clavicles, creating anchors for strong flapping muscles.

Prepubes provide immobile ventral extensions to the pubis and medial anchors to muscles of femoral adduction (contra Claessens et al. 2009). Their appearance in fenestrasaurs coincides with the adoption of bipedal locomotion (Peters 2002). Pterosaur ichnites (Peters 2011) indicate that certain derived pterosaurs reverted to a secondary form of quadrupedal locomotion with their fingers oriented laterally to posteriorly. This could only occur when their forelimbs became long enough to reach the substrate (Peters 2000b, 2002). Note, that is not the case with the basal pterosaur, MPUM 6009 (Fig.1) with those long hind limbs. Rarely mentioned by other pterosaur workers, bipedal pterosaur tracks are known (Conrad et al. 1987, Lee et al. 2009, Peters 2011, Kim et al. 2012). A bipedal pose produced a long lever arm of the elevated torso, neck, head and forelimbs with its fulcrum at the first sacral vertebra. Without support the presacral region would tend to drop were it not for the ventral support provided by the gastralia and the prepubis, which guided compressive forces back to the pelvis.

Peters (2000b) found a match between the pes of *Cosesaurus* and certain *Rotodactylus* ichnites, which are typically digitigrade and narrow gauge with an extended pedal digit 5 planted behind the other digits (Peabody 1948). The tracks also demonstrate occasional bipedalism. The tiny forelimbs and elongate hind limbs of *Sharovipteryx* and *Longisquama* further attest to the practice of obligate bipedal locomotion in this clade (Peters 2000a, 2002). Torso elevation during bipedal standing and running would have freed the forelimbs to do something else, like flapping. A functionally bipedal configuration has no need for the sliding coracoid joint found in quadrupedal lepidosaur and tanystropheid pectoral girdles.

Early Triassic archosaurs or dinosaurs could not have made *Rotodactylus* and *Prorotodactylus* imprints (contra Brusatte et al. 2011). Based on relative toe lengths the better match is with macrocnemids and fenestrasaurs, taxa not considered by Brusatte et al. (2011).

*Sharovipteryx* was an obligate biped due to the great discrepancy in the length of its fore and hind limbs (Peters 2000a, 2002). The elongate ilium and seven sacral vertebrae provided support for the cantilevered forequarters leveraged over the fulcrum at the pelvis. *Sharovipteryx* would have been an able sprinter in the sprawling manner of living lizards capable of bipedal locomotion (Snyder 1954). Hollow leg bones kept their mass low. Major muscle anchors were concentrated at the pelvis and large prepubis. The distal femur and proximal tibia do not bear large muscle anchor scars or processes.

The unfused ankle of fenestrasaurs was a simple hinge joint, convergent with dinosaurs. This ankle morphology was inherited from a Late Permian sister to the basal lepidosaur, *Huehucuetzpalli* (Fig. 12), which also had unfused proximal tarsals

(Reynoso 1998), distinct from squamates and sphenodontids. Related tanystropheids retained an unfused tarsus, but drepanosaurs more derived than *Hypuronector* fused the proximal tarsal elements.

The metatarsals of *Sharovipteryx* could radiate 60° (Fig. 4), unlike the parallel metatarsals and toes of *Cosesaurus* and the trackmakers of *Rotodactylus* (Peabody 1948, Peters 2000b). Distinct from other fenestrasaurs, *Sharovipteryx* did not retrovert distal pedal digit 5, probably due to the more distal extent of its uropatagia, nearly to the tip of digit 5 (Fig. 8). Interdigital spaces were filled with membranes. Like web-footed ducks, *Sharovipteryx* would have walked on these fiber-reinforced membranes, creating unique ichnites. One wonders if *Sharovipteryx* could also run on water, like the living lizard, *Basiliscus basiliscus*.

Whether *Sharovipteryx* ever hopped is a mystery. Libby et al. (2012) described how leaping lizards use their tail for pitch control to redirect angular momentum from their bodies to their tails, stabilizing body attitude in the sagittal plane. Extant hopping mammals, like the kangaroo rat (Bartholomew & Caswell 1951, Biewener & Blickhan 1988) and the kangaroo (Alexander & Vernon 1975) approximate the gross morphology of *Sharovipteryx* with their short torso, long tail, short forelimbs and long hind limbs.

Odd little *Longisquama* has no analog in the present day, other than to some extent, the lemur, (e.g. *Propithecus*). Both share a small skull with large eyes, a short neck, a long, flexible torso, strong hind limbs and an attenuate tail typically elevated at the pelvis.

The tibia/fibula and feet of *Longisquama* are much more robust than in *Sharovipteryx* or basal pterosaurs (Fig. 1). A robust hind limb suggests that *Longisquama*

was a leaper or runner, not a gracile glider. The nearly subequal metatarsals of *Longisquama* radiated less than 30°, a product of its bipedal, narrow gauge configuration. That made the pes better suited for terrestrial locomotion. Relative to the metatarsals, the digits were much longer in *Longisquama*. Like most terrestrial amniotes, the penultimate pedal phalanges were relatively short. By contrast, in the pterosaur MPUM 6009, the pedal digits were much longer relative to the metatarsals and the unguals were more trenchant, ideal for tree clinging.

Like the trackmaker of *Rotodactylus* and pterosaurs, *Longisquama* had a retroverted, dorsal side down, distal pedal digit 5. Peters (2000a, 2002, 2011) showed how such a toe could be used as a universal wrench for perching on horizontal branches, along with keeping an elevated metatarsus steady on a flat substrate. The center of balance remained over the anterior toes, with relatively little pressure on the retroverted digit.

## Respiration and Metabolism

In the basal pterosaur MPUM 6009 the naris is much larger than in *Sharovipteryx* and *Cosesaurus*. Perhaps that reflects an increase in respiration to oxidize a higher energy lifestyle based on feeding the large muscles necessary to continuously flap the much larger wings. The larger naris could also represent weight savings on a larger skull.

As lepidosaurs, fenestrasaurs (including pterosaurs) may have lacked a diaphragm, so respiration was driven by expansion and contraction of the ribs (contra Claessens et al. 2009). In fenestrasaurs, the locking of the sternal complex to the anterior ribs prevented expansion of the anterior torso. So only the posterior ribs were free to

drive respiration in fenestrasaurs. The deeper pelvis and prepubis on *Longisquama* and MPUM 6009 made room for longer gastralia and longer posterior dorsal ribs. Thus, both deeper torso pterosaurs and longer torso longisquamids had a greater capacity for rib-driven respiration than shallow and short torso coesosaurs and sharovipterygids.

In basal tetrapods, including most lizards, an undulating torso constricts the ability of both lungs to fill and empty at the same time. As bipeds, basal fenestrasaurs were no longer tied to Carrier's constraint (Carrier 1987). They could breathe while running, an evolutionary novelty that was retained by pterosaurs, convergent with dinosaurs.

The presence of 'hair' on the neck skin of *Sharovipteryx* (Fig. 6) is the first indication of the pycnofibers that would eventually insulate the bodies of pterosaurs, as preserved in *Jeholopterus* (Wang et al. 2004, Kellner et al. 2010) and *Sordes* (Sharov 1971). Altogether the above traits point to a rising metabolic rate in this clade.

## Gliding

If *Sharovipteryx* prepared for a glide the way, the living rib-glider, *Draco volans*, does, then it would have reoriented itself head down on a vertical tree trunk (Fig. 9). In any orientation, glides would have been initiated with a coordinated leap to create initial airspeed (Gans et al. 1987).

While the gliding abilities of *Sharovipteryx* have been almost universally accepted (except by Tatarinov 1989), the anterior control surfaces that would have stabilized that glide have only been imagined (Sharov 1971, Gans et al. 1987, Dyke et al. 2006). A

closer look reveals there was never any need to imagine anterior membranes. Everything *Sharovipteryx* needed to glide is readily visible on the fossil (Figs. 5-7).

The vestigial forelimb canards of *Sharovipteryx* would have been only a minor component in the gliding and steering abilities of *Sharovipteryx*. Far more important was the lateral expansion of the extensible neck skin by the elongate hyoids (Figs. 6, 7). These provided *Sharovipteryx* with anterior strakes. When deployed, simply raising or lowering the long neck set pitch. In this way the strakes acted like horizontal elevators on an airplane, only in front of the main wing. Heretofore overlooked, the extensible neck skin of *Sharovipteryx* represents the long sought anterior control surface. Widespread ribs flattened the torso of *Sharovipteryx*, as in *Draco volans*. Stiff pre-femoral membranes filled gaps between the torso and hind limb creating a more or less continuous lifting surface.

The small uropatagia in *Cosesaurus* (Ellenberger 1978, 1993, Fig. 1) became greatly enlarged in long-legged *Sharovipteryx*. These fiber reinforced membranes created hind limb wings (Fig. 7). If each femur extended anteriorly 60° and each tibia extended from the femur 120° (similar to a reconstruction in Gans et al. 1987), the pedes would have aligned with the center of gravity, as in the bipedal configuration. The center of gravity of the hind limb wing would have passed just aft of the main spar, at the deepest camber of the wing, as in birds and pterosaurs.

While gliding, the webbed feet of *Sharovipteryx* became aerodynamic control surfaces. In flight, the pedes were configured near the center of gravity, outboard on the wing tips where they could act as ailerons and/or spoilers. By contrast, in pterosaurs the webbed toes were located far aft of the center of balance where they could act like twin

vertical stabilizers, flexing and extending at the tarsus to control yaw. In pterosaurs slightly flexing the webbed toes gave the pedal membranes camber that provided laterally directed lift (with sufficient airspeed) and so relieved the stress of extending the hind limbs laterally by muscle power alone. In the presence of large forelimb wings and the absence of neck strakes, pterosaurs retained small uropatagia to act as posterior horizontal stabilizers. Like *Sharovipteryx*, and distinct from illustrations in Peters (2002), pterosaurs would have extended their entire hind limbs laterally while flying.

The elevated posterior sacrals and posterior ilium of *Longisquama* kept the tail elevated, both to keep it from dragging and to provide an elevated staff enhanced with a decorative tail vane. The tail vane was not an aerodynamic control surface. Rather like feathers on an arrow or a weather vane, it kept the rest of the tail aligned with the rest of the body in the airstream (Peters 2002).

The small uropatagia in short-legged *Cosesaurus* (Ellenberger 1978, 1993) became greatly enlarged in long-legged *Sharovipteryx*, *Longisquama* and basal pterosaurs. Other than their decorative function, uropatagia in *Longisquama* might have helped dissipate metabolic heat from the large muscles in the hind limbs, acting like large surface area radiators. In long leaps trailing membranes might have added lift to extend those leaps and some measure of aerial braking to soften landings.

### Reproduction and Ontogeny

The tiny pelvic opening of *Cosesaurus* indicates that only tiny eggs could pass through it (Figs. 1). So *Cosesaurus* probably laid many tiny eggs at a time, whether buried or in a nest. A hypothetical hatchling from a 5 mm cosesaur egg would be about 1

cm in length or 1/14 the size of the adult. It would have been easy prey for most animals, whether insect or tetrapod. Only a moist leaf-litter environment would ensure that such tiny hatchlings would not die of desiccation (Hedges and Thomas 2001) due to their high surface area-to-volume ratio. *Sharovipteryx* had a deeper pelvic opening that could have produced a larger egg and a hatchling about 2 cm in length or 1/8 the size of the adult.

In *Longisquama* and pterosaurs reproductive strategies continue to evolve. Both *Longisquama* and MPUM 6009 had a much deeper pelvic opening capable of passing relatively much larger eggs. From such a large egg a hatchling could be 4cm in total length or 1/5 the size of the adult. In short-torso flying pterosaurs perhaps only one egg of this size at a time could be carried within a mother. In long-torso, nonvolant *Longisquama*, several more could be carried.

When only one young is produced at a time great care is usually given to that embryo/hatchling. The most protective place to develop is within the mother, especially when she has a high metabolism and the eggshell is extremely thin (Chiappe et al. 2004). These data support the hypothesis of egg retention in longisquamids and pterosaurs until just before hatching, a trait that often arises in lepidosaurs (Pyron & Burbrink 2013), but never in archosaurs. In support of this, pterosaur eggs preserved without an adult nearby include full term ossified embryos (Wang & Zhou 2004, Ji et al. 2004, Chiappe et al. 2004). These eggs have been conventionally laid and the adult has flown away. Pterosaur eggs preserved with an adult nearby do not include ossified embryos. In Lü et al. (2011) an immature egg was expelled upon the death of the mother. In Wang et al. (2014) immature eggs containing no ossified bones were fossilized along with the bones of adult pterosaurs. Likely each egg was inside a female at the time of her death, but became

scattered along with the rest of her bones during the weather event (perhaps a desert storm) that swept the colony to the bottom of the lake. Buried eggs would have been protected from such an event.

The only known adult/embryo pairing among pterosaurs is in the genus *Pterodaustro* (Chiappe et al. 2004; Chinsamy et al. 2008). The *Pterodaustro* embryo is 1/8 the size of the adult, reached sexual maturity after two years and full size in five years. If longisquamids and pterosaurs followed the pattern of other tetrapods, smaller genera, like *Longisquama* and MPUM 6009, probably reached sexual maturity more quickly and had shorter lifespans.

In fenestrasaurs, including *Longisquama*, mating probably occurred as it does in birds, by pressing the male cloaca against that of the female for sperm transfer. The raising of the tail base in *Longisquama* and basal pterosaurs, like MPUM 6009, may have facilitated mating in these bipeds. Hemipenes, a trait restricted to squamates, may or may not have been present because *Sphenodon* lacks these and the clade including *Huehuecuetzpalli* and fenestrasaurs nests between them (Peters 2007, Fig. 12).

#### Mating and territorial display rituals

Flapping probably originated as an addendum behavior to a suite of secondary sexual traits already in place. *Cosesaurus* had a dorsal frill, fibers trailing the forelimbs, uropatagia trailing the hind limbs and fibers (not feathers) emanating from the tail (Fig. 1). However, these are only small precursor decorations to the exotica found on *Longisquama*, in which the dorsal frill had greatly expanded to form elongate plumes. In the clade that produced pterosaurs, bigger wings, rather than longer plumes, enhanced

their display. At first the fore limb membranes may have signaled with a flash of bright membrane color (Peters 2002). Later, larger, flapping wings may have increased the height of leaps. Natural selection would have favored the best performers. A wagging tail tipped with a colorful vane may have been another secondary sexual trait in *Longisquama*. It is not impossible to imagine that fenestrasaurs also became vocal.

### Variation and Autapomorphies

While *Kyrgyzsaurus*, *Sharovipteryx* and *Longisquama* include many traits transitional between the primitive morphology of *Cosesaurus* and the derived morphology of pterosaurs (listed earlier, Peters 2002), it is clear that all three represent clades that split off from the direct line that led to pterosaurs. *Sharovipteryx* autapomorphies include the reduction of the forelimbs, elongation of the cervicals, development of neck strakes, flattening of the torso, elongation of the posterior ilium, development of pre-femoral membranes and the expansion of much larger uropatagia. *Longisquama* autapomorphies include the reduction of the cervicals, elongation of the torso, the increase in tibia diameter and the development of hyper-elongate plumes. The robust morphology of *Kyrgyzsaurus* represents a fourth evolutionary direction for cosesaurs, that of increased size, and probably with no propensity to glide or fly while retaining vigorous flapping as a secondary sexual or territorial behavior, judging by the size of its pectoral girdle. Given the proportions of *Cosesaurus* and MPUM 6009 (Fig. 1), especially in the forelimb, it seems likely that the development of the pterosaur wing did not involve a period of reduction, as seen in *Sharovipteryx* and *Longisquama*.

## Conclusions

Much has been learned about pterosaurs and their outgroup taxa since the publication of the minority view on pterosaur origins, which most workers have ignored. Earlier interpretations of *Cosesaurus*, *Sharovipteryx* and *Longisquama* are enhanced and corrected here. Odd autapomorphies are now replaced with synapomorphies linking these fenestrasaurs to their lepidosaurian precursors, their pterosaurian descendants and to each other. The pterosaur-like pectoral girdle of *Cosesaurus* gives new insights into the timing and development of characters associated with flapping flight in pterosaurs. These include support for the hypothesis of wing-assisted bipedal running along with energetic flapping during mating rituals and threat displays. The prepubis acted as an extension of the pubis providing new anchors for femoral adductor muscles used in bipedal locomotion. Despite its lack of large forelimbs, *Sharovipteryx* shared a suite of traits with pterosaurs. Other workers may have overlooked the hind limbs, posterior torso and tail of *Longisquama*, but it is clear from their data and figures, they did not provide the attention to detail provided here (Figs. 10-11).

Despite the long list of pterosaurian synapomorphies documented by these taxa (Fig. 12), paleontologists have been reticent to employ these taxa in phylogenetic analyses that include pterosaurs. Some of that reticence may be due to tradition and the widespread use of previously published matrices (even though included sister taxa do not demonstrate gradual accumulations of derived characters). Some of that reticence may be due to distrusting interpretation of difficult materials (even though phylogenetic bracketing recovers the same traits). It is time for the old paradigm to shift.

**Acknowledgements**— I am indebted to J. Gallemí, J. Gomez-Alba and the staff of the Museu de Geologia, Barcelona, for access to the holotype of *Cosesaurus*. D. Pruitt of The City Museum, St. Louis, along with V. Alifanov and A. Karhu of the Paleontological Institute, Moscow, permitted access to the holotypes of *Longisquama* and *Sharovipteryx*. I thank A. Tintori for providing valuable comments on an earlier version of the manuscript.

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## Figure Captions

Figure 1. Fenestrasaurs to scale. **A.** *Cosesaurus* in lateral view plus pelvis, hypothetical egg and hatchling, ventral view of pectoral girdle, dorsal view of right pes. **B.** *Sharovipteryx* in lateral view along with pes in dorsal view, hypothetical sternal complexes in ventral view, hypothetical egg and hatchling. **C.** *Longisquama* in lateral view including pectoral girdle in ventral view, manual unguals in anterior view, sacral area in dorsal view, right pes in dorsal view, hypothetical egg and hatchling. **D.** MPUM 6009 in lateral view along with pes in dorsal view, manus in dorsal and anterior views, sternal complex in ventral view, hypothetical egg and hatchling. **E.** *Kyrgyzsaurus* in lateral view, plus parietals in dorsal view, sternal complex as preserved and palate in palatal view. Soft tissue is gray. Scale bar equals 10 cm.

Figure 2. The pectoral girdle of *Cosesaurus aviceps*. **A.** The in situ specimen. **B.** Elements according to Ellenberger (1993) in which the clavicles are aligned transversely, the scapulae are posteriorly elongated and provided with a disc-like acromion process anteriorly, the coracoids are fused medially to form a ventral plate and a thick-rimmed keel is present medially. **C.** Interpretation of elements according to Peters (2000a) in which the clavicles are aligned transversely, the scapulae are short and crescentic, the coracoids are fused medially and a thick-rimmed interclavicle keel is present. **D.** Present reinterpretation in which the clavicles are aligned transversely, the scapulae are posteriorly elongated without an acromion process, the coracoids are quadrant-shaped, the interclavicle is flat and cruciform, the sternum is flat, broader than the interclavicle and dorsal to it. **Abbreviations:** **Ac**, acromion process of scapula; **Cl**, clavicle; **Co**, coracoid; **Hu**, humerus; **Keel**, interclavicle keel; **Ic**, interclavicle, **Pp**, prepubis; **Pt**, pteroid; **Sc**, scapula; and **St**, sternum. Black dots are preserved bubbles. Scale bar = 1 cm divided into 10 mm.

Figure 3. Comparison of pectoral girdles. **A.** The basal lizard, *Huehuecuetzpalli mixtecus* (IGM 7389 and IGM 4185, Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico; modified from Reynoso 1998). Here the clavicles and humerus of the larger specimen, IGM 7389, have been scaled down to fit the pectoral girdle of the smaller specimen, IGM 4185. **B.** The tanystropheid, *Macrocnemus bassanii*, (modified from Peyer 1937). **C.** The fenestrasaur, *Cosesaurus aviceps*. **D.** *Longisquama insignis*, traced in situ by Sharov (1970, above) and traced here (below). Note the taphonomic displacement of the sternal complex to a position that returns the clavicles to

the base of the neck, their plesiomorphic position in tetrapods. This has been a source of confusion regarding the affinity of these clavicles to the furcula in birds (Jones et al. 2000). **E.** Sternal complex of MCSNB 8950 (Museo Civico di Scienze Naturali, Bergamo; modified from Wild 1993). Abbreviations as in figure 1. Scale bars equal 3 mm.

Figure 4. *Cosesaurus* pelvic region. An earlier misinterpretation of the stem shape arising from the anterior ilium (Peters 2000a) is corrected here with the identification of two disarticulated and fenestrated prepubes, similar to those in basal pterosaurs. Scale bar equals 2 mm.

Figure 5. *Sharovipteryx mirabilis* in situ. **A.** Counterplate. **B.** Traced image of bones and soft tissues (center). **C.** Plate. Counterplate flipped to match plate. Note: The darkened middle of the plate is replaced with filler. Abbreviations: **1, 2, 3, 4**, manual digits; **Ca**, caudal vertebrae; **Ce**, cervical vertebrae; **Co**, coracoid; **DP**, dorsal plumes; **EDM**, extradermal membrane; **Fe**, femur; **Hu**, humerus; **Pt**, pteroid; **R/U**, radius/ulna; **Sc**, scapula; **Sk**, skull; **T/F**, tibia/fibula; **Ur**, uropatagium. Scale bar equals 1 cm. See figure 6 for skull details.

Figure 6. *Sharovipteryx mirabilis* plate, close-up of skull and cervicals in situ. **A.** Tracing of the plate. **B.** The plate. These interpretations correct earlier mistakes by Peters (2000a). Note the impression of a wasp-like insect in the left side of the skull. **Abbreviations:** **Bs**, basisphenoid; **De**, dentary; **Ect**, ectopterygoid; **Fr**, frontal; **Hy**, hyoid; **Ju**, jugal; **La**,

lacrimal; **Mx**, maxilla; **Na**, nasal; **Oc**, occipital bones; **Pal**, palatine; **Par**, parietal; **Pmx**, premaxilla; **Po**, postorbital; **Pof**, postfrontal; **Prf**, prefrontal; **Pt**, pterygoid; **Qj**, quadratojugal; **Qu**, quadrate; **Sq**, squamosal; **St**, stapes; **Vo**, vomer; (Scale bar equals 1 cm).

Figure 7. *Sharovipteryx* reconstructed. **A.** Dorsal view, left hind limb extended to gliding configuration, hyoids laterally extended creating neck skin strakes, vestigial fore limbs extended creating canard wings. Vertical arrow indicates hypothetical center of gravity.

**A1.** Hypothetical sternal complex in dorsal view, based on *Cosesaurus* (left) and MPUM 6009 (right) both distorted to match rib articulations in *Sharovipteryx*. **B.** Dorsal view of skull and neck, hyoids not laterally extended. **C.** Skull in dorsal, occipital, lateral and palatal views. **D.** Lateral view, bipedal configuration, note dorsal frill/plumes. Vertical arrow indicates center of gravity over the toes. **E.** Pelvis doubled in size in lateral view. **F.** Forelimb doubled in size. Unguals shown in lateral and anterior views. Trailing membrane is hypothetical based on phylogenetic bracketing between *Cosesaurus* and pterosaurs. **G.** Pes doubled in size. Interdigital membranes between digits 1 and 3 are hypothetical. Continuous PILs (parallel interphalangeal lines, Peters 2000b) indicate phalanges that operate in sets during flexion and extension. Scale bar equals 1 cm.

Figure 8. *Sharovipteryx* left pes in ventral view. Left: In situ tracing. Note distal elements have drifted proximally. Right: The same reconstructed, PILs added. Interdigital membrane between digits 1-4 based on 4-5 membrane. Note three distal tarsals (centrale,

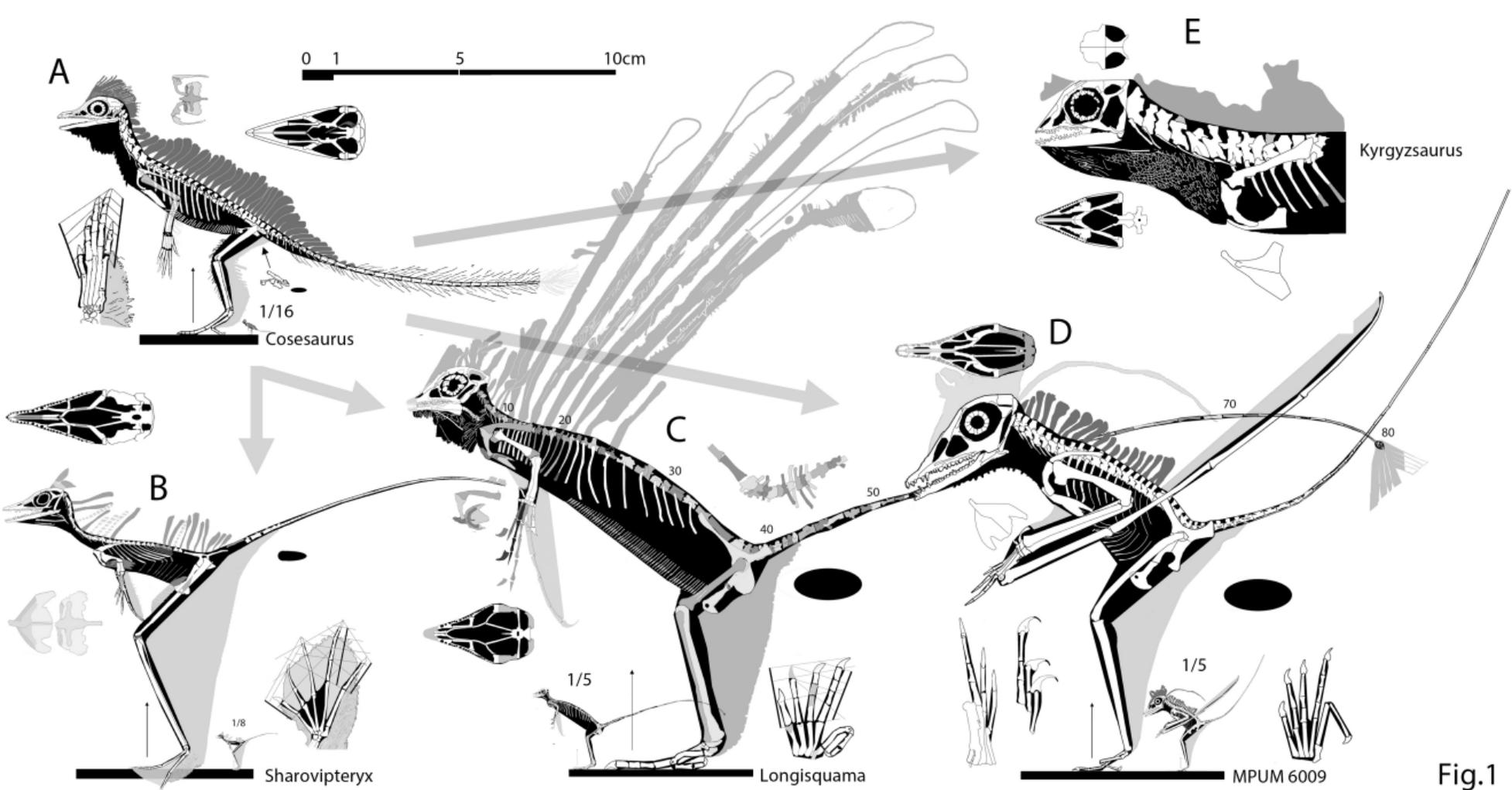
dt3 and dt4), plus an unfused astragalus and calcaneum comprise the tarsus, producing a simple hinge ankle joint. Scale bar equals 1 cm.

Figure 9. Three views of *Sharovipteryx* on a vertical surface. Here is how *Sharovipteryx* might have clung to and climbed on a seed fern trunk.

Figure 10. *Longisquama insignis* (PIN 2584/4, Sharov 1970). **A.** Plate. **B.** Traced image of right forelimb, soft tissue not included. **C.** Traced image of left forelimb and associated soft tissue. **D.** Tracings by Sharov (1970). Note the soft tissue trailing the forelimbs, anterior to the elbow, along the dorsal spine and filling the throat area. All are confirmed here. **E.** Current tracing of skeletal and soft tissue elements. Right appendicular elements are lightened for clarity. Sharov's lowest plume is actually the hind limb. Plume bases are beneath the left metatarsus. **F.** Reconstruction of left manus. **G.** Reconstruction of matching right manus. **H.** Reconstruction of pedal elements. Note pedal 3.2 (in gray) is hidden beneath pedal 2.2 *in situ*. **Abbreviations:** **1.1**, first manual phalanx of the first digit and other phalanges follow this pattern; circled numbers, pedal digits; reverse numbers, sacral vertebrae, other numbers, presacral and caudal vertebrae; **Co**, coracoid; **DP**, dorsal plumes; **DR**, dorsal ribs; **Fe**, femur; **Hu**, humerus; **Mc**, metacarpal; **Pl**, pelvis; **Pp**, prepubes; **Pt**, pteroid; **Pxc**, preaxial carpal; **Ra**, radius; **Re**, radiale; **S**, sternal complex; **Sc**, scapula; **Sk**, skull; **T/F**, tibia/fibula; **Ue**, ulnare; **Ul**, ulna; **Ur**, uropatagium. Scale bar equals 1 cm. See figure 3 for skull details and figure 1 for reconstruction.

Figure 11. *Longisquama insignis* skull. **A.** According to Sharov (1970). **B.** According to Martin (2004). **C.** According to Senter (2003). **D.** According to Peters (2000a). **E.** Tracing of the plate, skull elements ghosted to clarify palatal and occipital elements. **F.** Tracing of the plate, palatal and occipital elements omitted for clarity. **G.** Skull reconstructed, dorsal view; **H.** Skull reconstructed, lateral view; **I.** Skull reconstructed, palatal view. **J.** Fused occipital bones. These interpretations correct earlier mistakes by Peters (2000a). **Abbreviations:** **Bs**, basipterygoid process of the basisphenoid; **De**, dentary; **Ep**, ectopalatine (ectopterygoid + palatine); **Fr**, frontal; **Hy**, hyoid; **Ju**, jugal; **La**, lacrimal; **Mx**, maxilla; **Na**, nasal; **Oc**, occiput; **Par**, parietal; **Pmx**, premaxilla; **Po**, postorbital; **Pof**, postfrontal; **Prf**, prefrontal; **Pt**, pterygoid; **Qj**, quadratojugal; **Qu**, quadrate; **ScR**, sclerotic ring; **Sq**, squamosal; **Vo**, vomer.

Figure 12. Accumulation of pterosaurian traits in precursor taxa. The following taxa document a gradual accumulation of pterosaurian traits unmatched by any series of archosauriforms. Letters reference nodes. Bootstrap scores indicated. See text for list of gradually accumulating pterosaurian traits at each node.



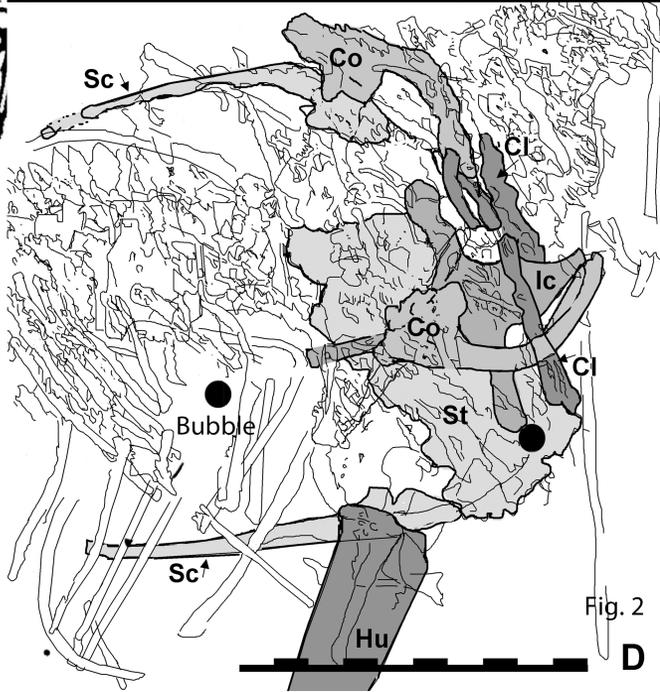
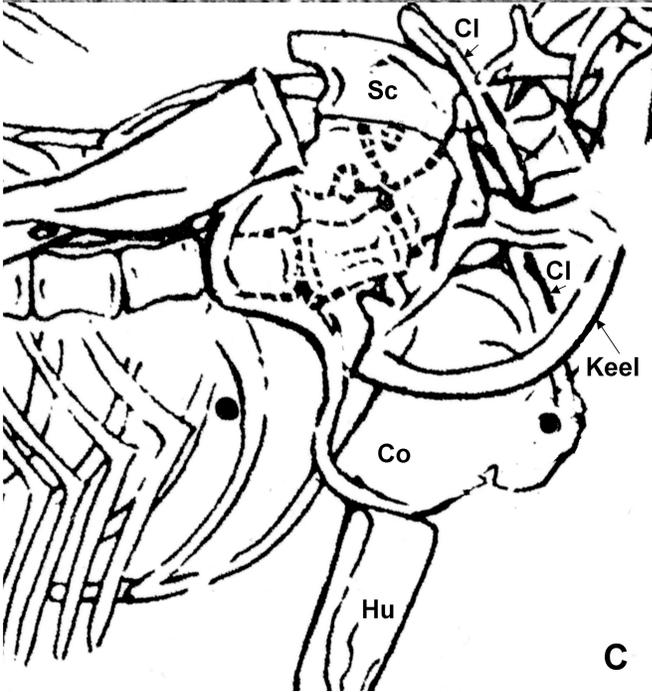
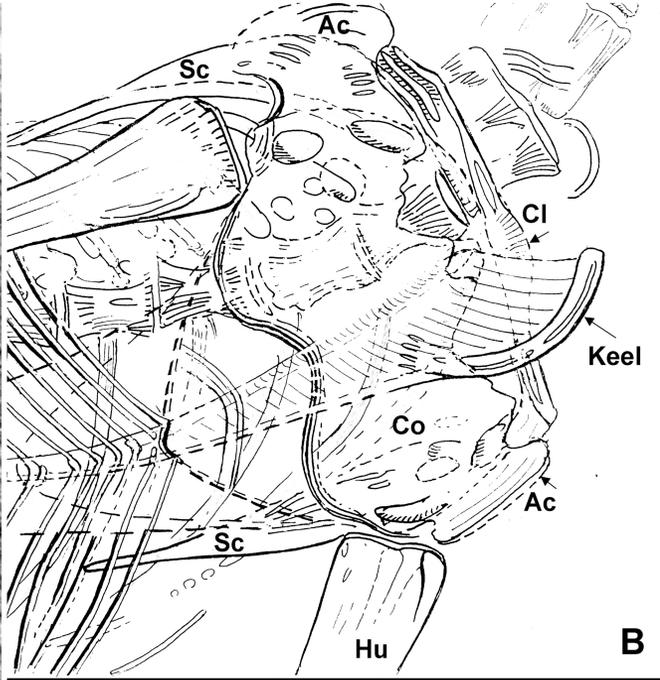
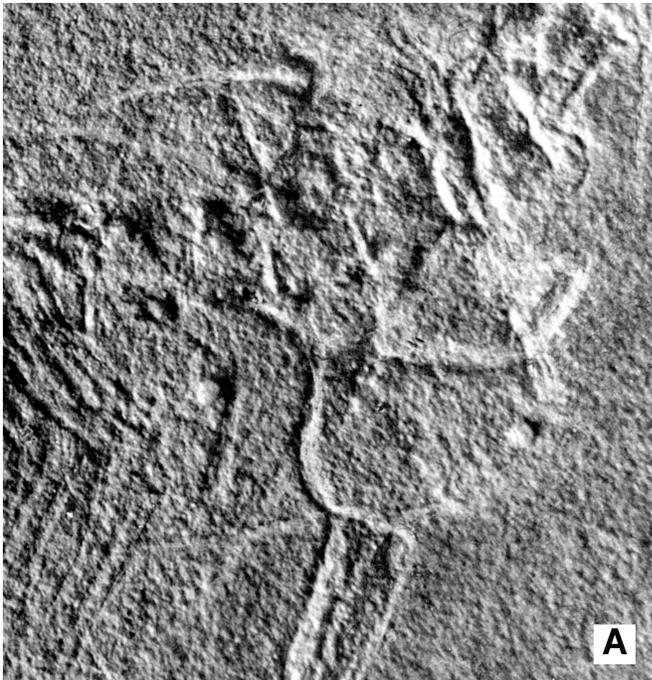


Fig. 2

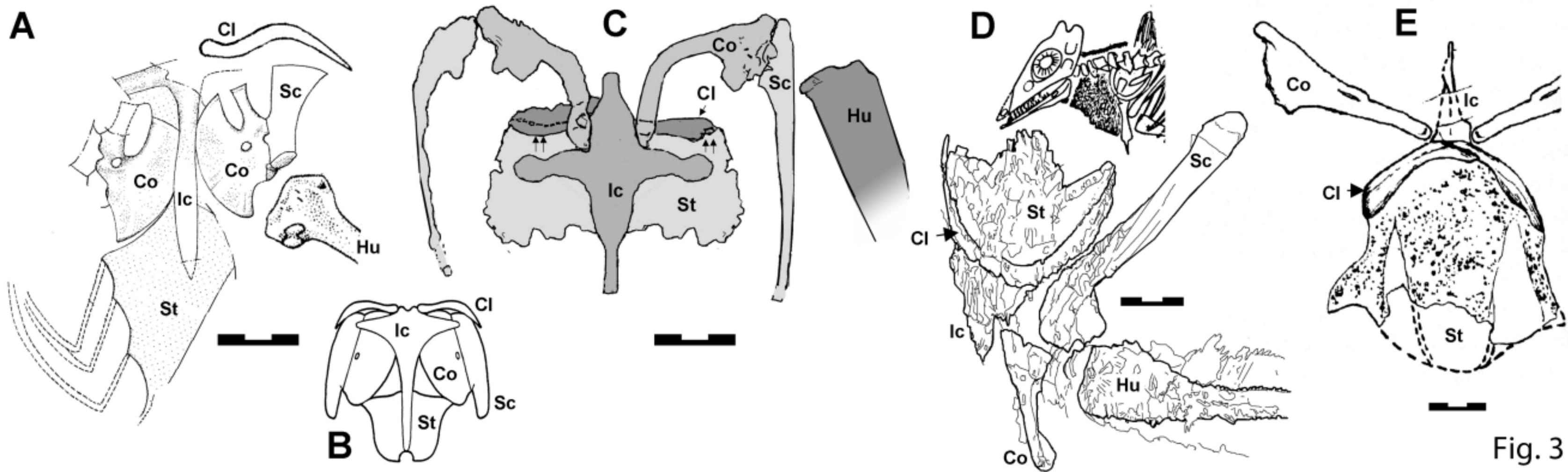
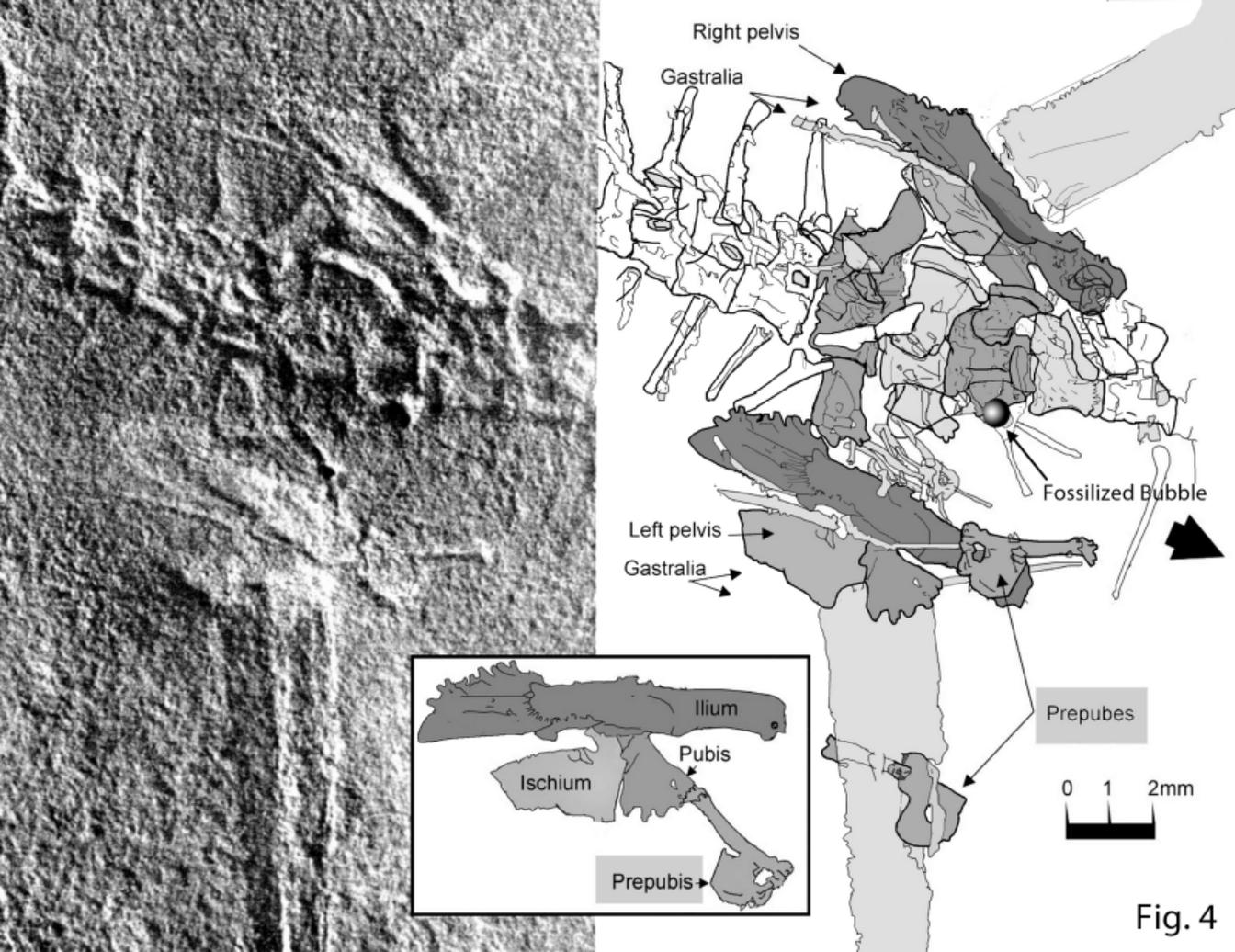


Fig. 3



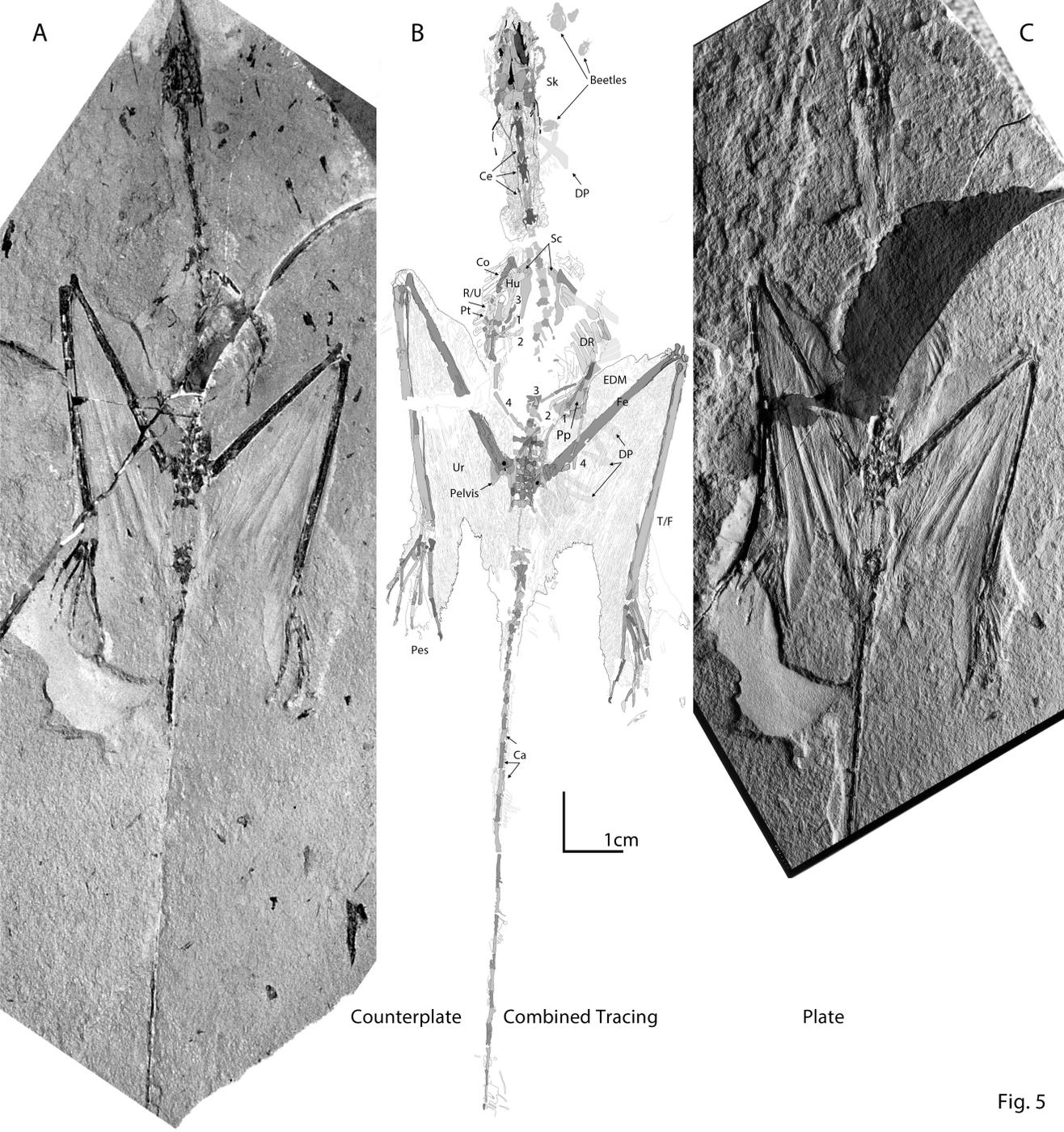


Fig. 5



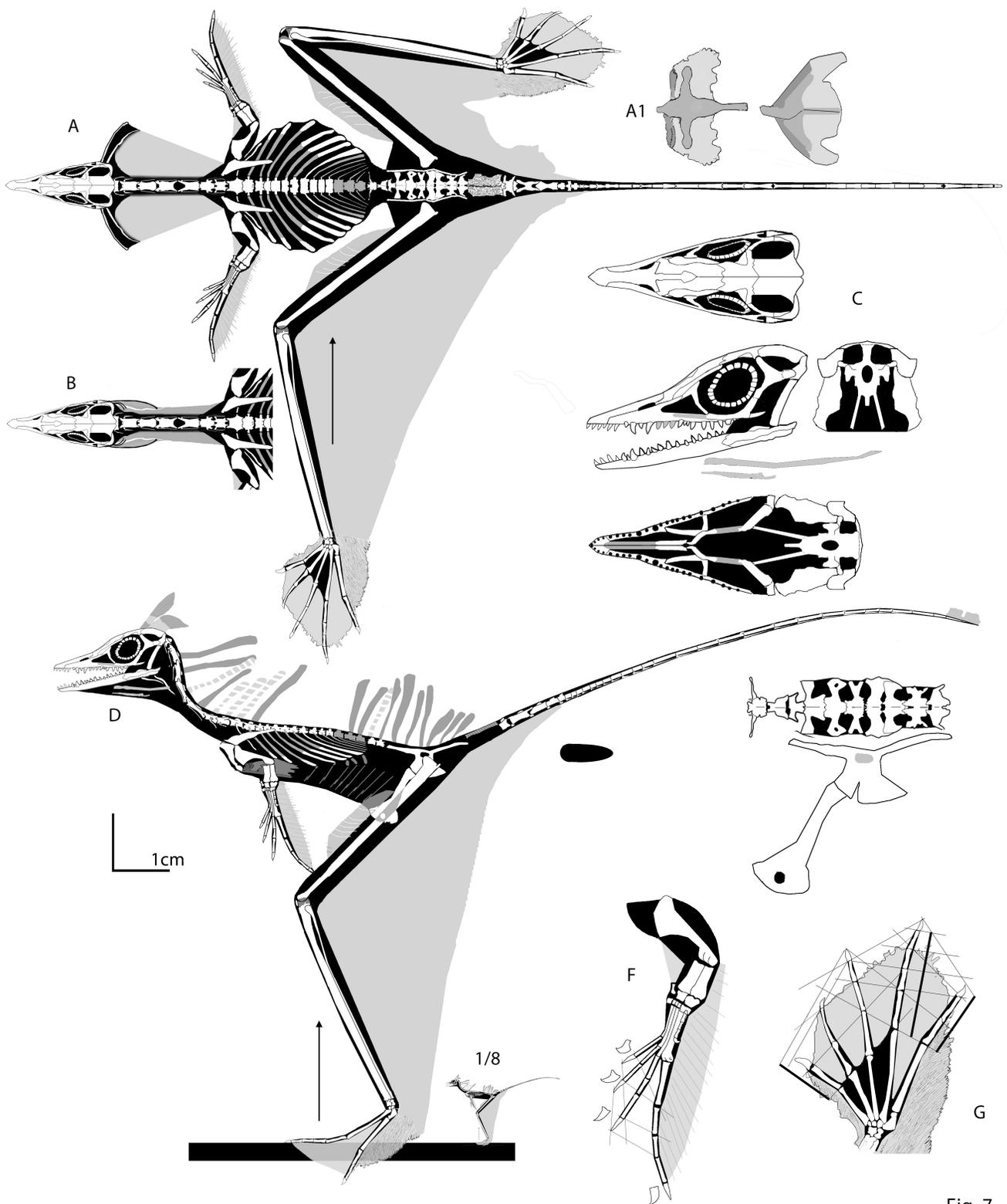
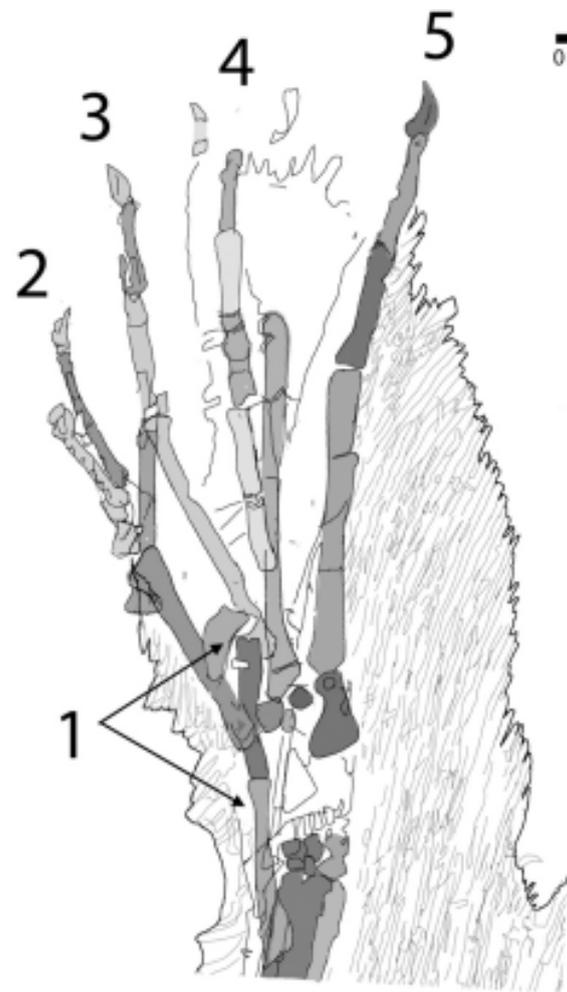


Fig. 7



0 1mm 1cm

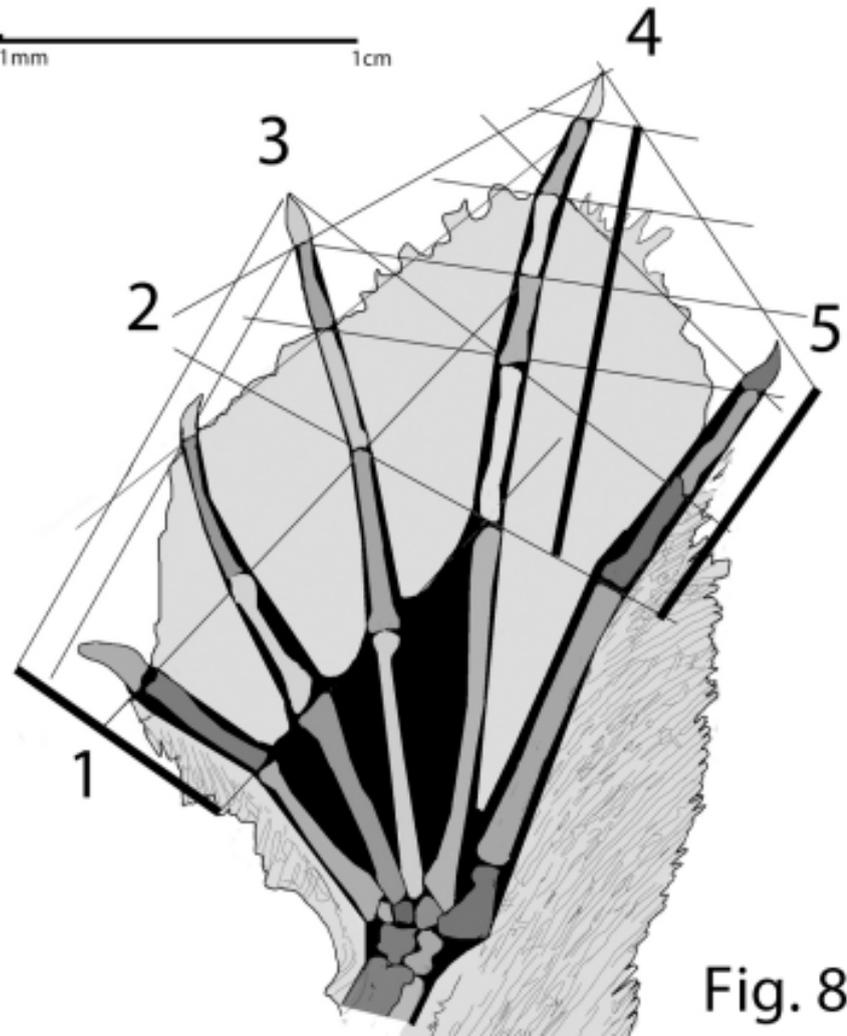


Fig. 8

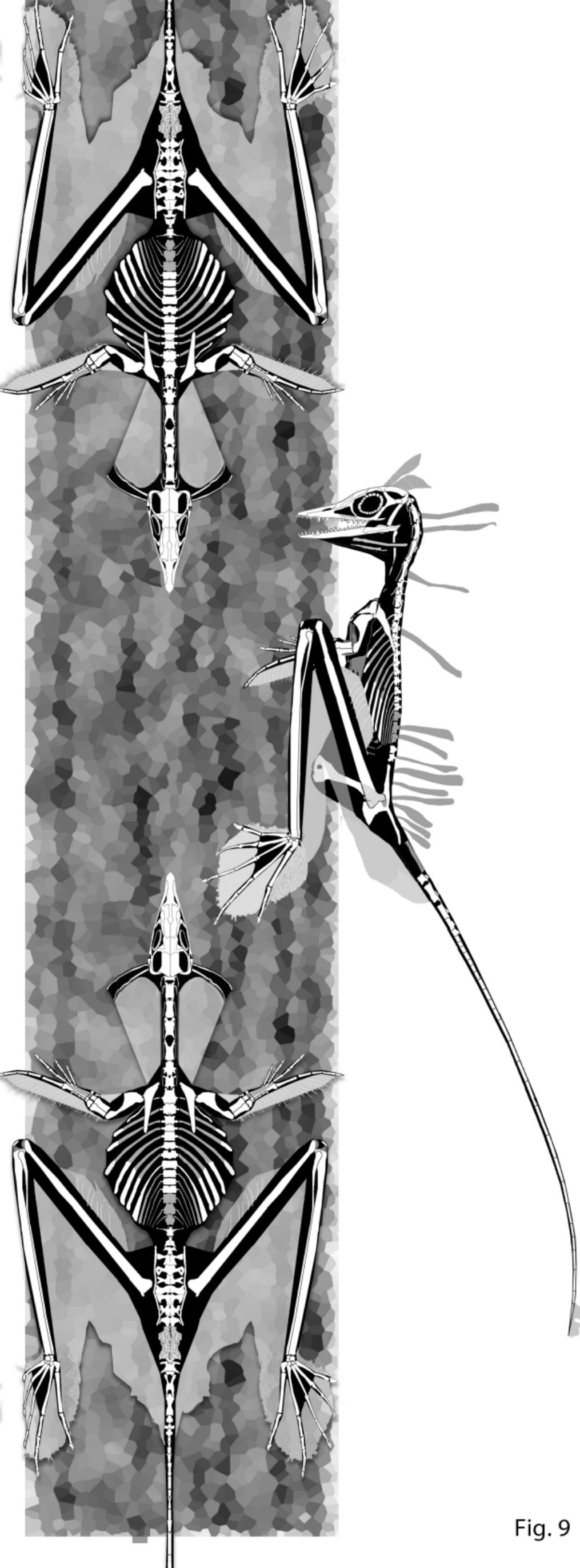


Fig. 9

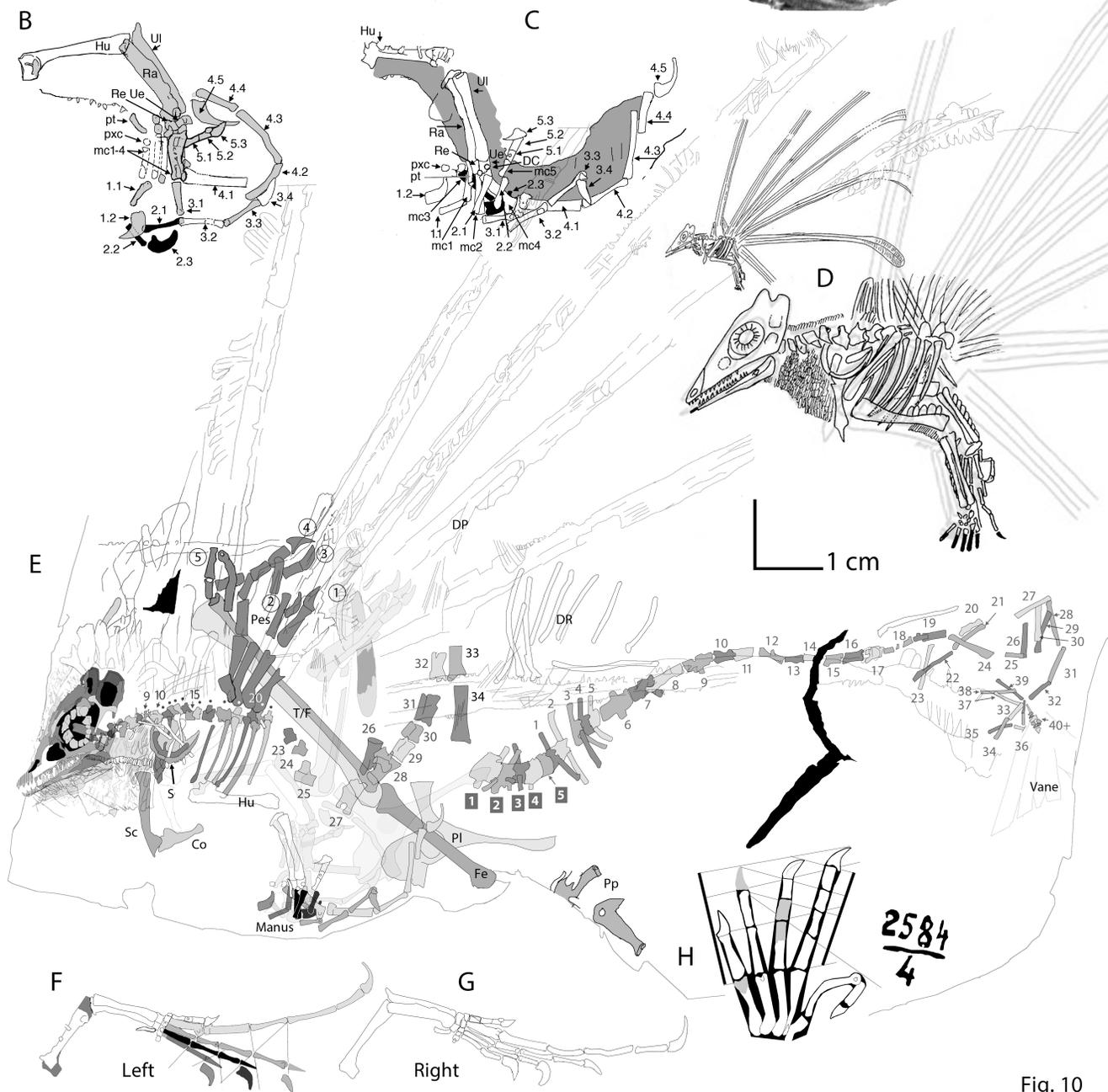


Fig. 10