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A new and large monofenestratan reveals the evolutionary transition to the pterodactyloid pterosaurs

Highlights

- A new pterosaur, *Skiphosoura bavarica*, is named from the Jurassic of Germany

- The specimen is much larger than other known forms and is preserved in three dimensions

- The *Skiphosoura* helps document the transition from early pterosaurs to the pterodactyloids

- The tail is short but retains the supporting structures of earlier forms

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In brief

Hone et al. describe and name a new pterosaur, *Skiphosoura bavarica*, from the Jurassic of Southern Germany that is unusually large for the time and well preserved in three dimensions. This specimen, coupled with a new phylogenetic analysis, shows the stepwise accumulation of numerous characteristics from the early pterosaurs through to the derived pterodactyloids.

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A new and large monofenestratan reveals the evolutionary transition to the pterodactyloid pterosaurs

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SUMMARY

For over a century, there was a major gap in our understanding of the evolution of the flying Mesozoic reptiles, the pterosaurs, with a major morphological gap between the early forms and the derived pterodactyloids.[1] Recent discoveries have found a cluster of intermediate forms that have the head and neck of the pterodactyloids but the body of the early grade,[2] yet this still leaves fundamental gaps between these intermediates and both earlier and more derived pterosaurs. Here, we describe a new and large Jurassic pterosaur, *Skiphosoura bavarica* gen. et sp. nov., preserved in three dimensions, that helps bridge the gap between current intermediate pterosaurs and the pterodactyloids. A new phylogeny shows that there is a general progression of key characteristics of increasing head size, increasing length of neck and wing metacarpal, modification to the fifth toe that supports the rear wing membrane, and gradual reduction in tail length and complexity from earlier pterosaurs into the first pterodactyloids. This also shows a clear evolution of the increasing terrestrial competence of derived pterosaurs. Furthermore, this closes gaps between the intermediates and their ancestors and descendants, and it firmly marks the rhamphorhynchines and ctenochasmatid clades as, respectively, being the closest earliest and latest groups to this succession of transitional forms.

RESULTS AND DISCUSSION

Taxonomy

Pterosauria (Kaup, 1834)
  Breviquartossa (Unwin, 2003 sensu Andres et al.[3])
  Monofenestrata (Lü et al.[2] sensu Andres et al.[3])
  Pterodactyliformes[3]
  Skiphosoura gen. nov.
  S. bavarica sp. nov.

Diagnosis

A large, non-pterodactyloid pterodactyliform pterosaur (Figures 1 and S1–S11) with the following unique autapomorphies for this grade: raised margins of the alveoli in the maxillary dentition and laterally developed; variable tooth spacing with anterior teeth close together and posterior teeth much further apart in the upper jaw; postexapophyses present on cervical vertebrae; procoleous dorsal vertebrae; tail short but still retaining filiform supporting zygapophyses and chevrons; humerus shorter than femur; ulna more than 1.5 times the length of the humerus; robust pteroid that is gently curved along its length; and wing phalanx 2 is subequal to wing phalanx 3.

Etymology

Skiphosoura derives from "skyphos" and "oura," Ancient Greek for "sword" and "tail," in reference to the short, stiff, and tapering caudal series of the animal, with *bavarica* in reference to the Free State of Bavaria in Germany where the specimen was found.

Holotype

Specimen LF 4157—a near-complete but disarticulated specimen of a subadult animal that is missing only part of the skull, some vertebrae, and a few metapodial elements.

Locality information

The specimen was found in 2015 in the "visitor's section" of the Schaudiberg Quarry near Mühlheim, Bavaria, Germany, which has yielded other recent pterosaur finds[4] (Methods S1). The quarry is located near the town of Mühlheim at the western end of the district of Eichstätt, in Bavaria, Germany. The specimen was found in the "Dritter Kieselflinz Layer," just below the Hagende Wechselflinz layer of the Mörnsheim Formation, and was collected at the following coordinates: 48.859 89° north, 10.99 267° east, and with an elevation of 415 m. The Mörnsheim Formation was part of a complex series of isolated basins
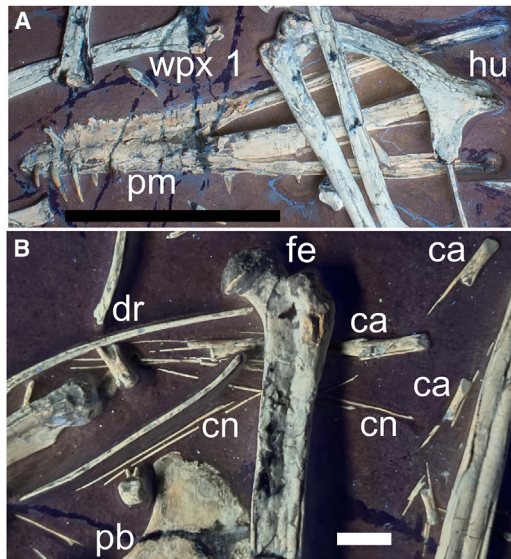
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Figure 1. Key elements of *Skiphosoura*
(A) The anterior part of the skull with the premaxillary crest and large teeth. Also seen is the humerus. Scale bar, 100 mm.
(B) The short caudal vertebrate with long zygapophyses and the elongate chevrons. Scale bar is 10 mm.
ca, caudal vertebra; cn, chevron; dr, dorsal rib; fe, femur; hu, humerus; pb, pubis; pm, premaxilla; wpx 1, wing phalanx 1.
See also Figures S1, S2, S7, and S9.

consisting of a series of laminated, lithographic limestones that are Lower Tithonian in age (Upper Jurassic)[5] and underlined by the Altmühltal Formation and overlain by the Usseltal Formation.[6]

Phylogenetics
Our phylogenetic analysis (see STAR Methods and Methods S1) yielded a single most parsimonious trees of branch length 2,346, with a consistency index of 0.318 and a retention index of 0.778 (see the supplemental figures and references for node synapomorphies). *Skiphosoura* is recovered among taxa that are closest to, but not within, Pterodactyloidea (Figure 2). We recover the non-pterodactyloid taxa with a nasoantorbital fenestra as a grade (as with, e.g., Zhou et al., Andres and Myers, and Wang et al.[7–9]) and not predominantly a clade representing a radiation prior to the origin of the pterodactyloids (as with, e.g., Martin-Silverstone et al.[10]). *Skiphosoura* is one of the most derived of these taxa and close to the origin of the pterodactyloids alongside other Solnhofen-area non-pterodactyloid monofenestratans (Figure 2). We find that Archaeopterodactyloidea are sibling to Azhdarchoidea and Ornithocheiromorpha. We also find that the rhamphorhynchines are the closest non-monofenestratan pterosaurs to the Monofenestrata, especially the derived large-headed taxa *Dearc*[11] and *Angustinaripterus*.

Our analysis yielded several differences from previous versions of this dataset (unless stated otherwise, this refers to Zhou et al., Britt et al., and Dalla Vecchia[7,12,13]). The greatest differences in this analysis lie in the topology of Novialoidea (*Campylognathoides* + Pterodactyloidea). A well-supported grade of taxa traditionally considered "rhamphorhynchids" lies

around Monofenestrata (including Pterodactyloidea). Most notably, the closest relatives of Monofenestrata are all taxa traditionally called "rhamphorhynchines." A valid Rhamphorhynchini is recovered, and *Dearc* and *Angustinaripterus* represent the closest relatives of Monofenestrata. The earliest member of Monofenestrata remains *Pterorhynchus*, and Wukongopteridae now only includes *Wukongopterus* (Figure S12). All other former members of Wukongopteridae form a highly nested relationship around members of Pterodactyloidea. The genera *Darwinopterus* and *Kunpengopterus* are polyphyletic and include various crested or non-crested forms. *Kunpengopterus sinensis* itself is found to be paraphyletic, with the holotype being more closely related to Pterodactyloidea than the referred specimen IVPP V 23674, and similarly, various species of *Darwinopterus* are not found together (Figure 2).

In summary, though many "traditional" clades are recovered, they exist primarily as grades around Pterodactyloidea, often with a retained, if reduced, monophyletic component to the exclusion of Pterodactyloidea. With these grades, *Skiphosoura*, "Rhamphodactylus," and *Propterodactylus* represent the closest relatives of Pterodactyloidea.

Transitional characteristics
At least some traits from other diagnoses show up here in *Skiphosoura*, and features that were previously considered unique are being found in newly recovered material. This does show at least something of a mosaic of traits being present across these taxa and suggests that the evolution of the traits from non-pterodactyloids to pterodactyloids was not likely a simple step-wise accretion of characteristics. Others, however, do show a clear transition from the rhamphorhynchines through to the pterodactyloids.

The original discovery of *Darwinopterus* as an intermediate between the non-pterodactyloids and the pterodactyloids[14] bridged a critical gap in our understanding of pterosaur evolution. The near-perfect match of a pterodactyloid-type head and neck and the non-pterodactyloid body showed that the anterior portion of these animals derived before the posterior "caught up." But it also meant that there was no clear progression of the details of these features across these (now two) gaps. Our analysis demonstrates that the "rhamphorhynchines" *Dearc* and *Angustinaripterus* and the monofenestratans *Pterorhynchus* and *"Darwinopterus" robustodens* fill the gap between non-monofenestratans and *D. modularis*, and *Skiphosoura* and the remaining non-pterodactyloid monofenestratans fill the gap between *D. modularis* and Pterodactyloidea. This also means we see a clear set of transitions of major features from the earlier diverging pterosaurs right through to the early pterodactyloids and show that the "modularity" of *Darwinopterus* was due to its central position in the early Monofenestrata, which here contains Pterodactyloidea (Figure 3; Table 1).

Head
Dearc shows a head that is apparently a similar length to the torso, and this is otherwise absent in the rhamphorhynchines, suggesting that this is the first trait to begin to evolve as this is present outside of the Monofenestrata. All later taxa have a head that is as long or longer than the body.[2] Notably, the Monofenestrata merges the external naris and the antorbital fenestra into a nasoantorbital fenestra, originally described as a feature
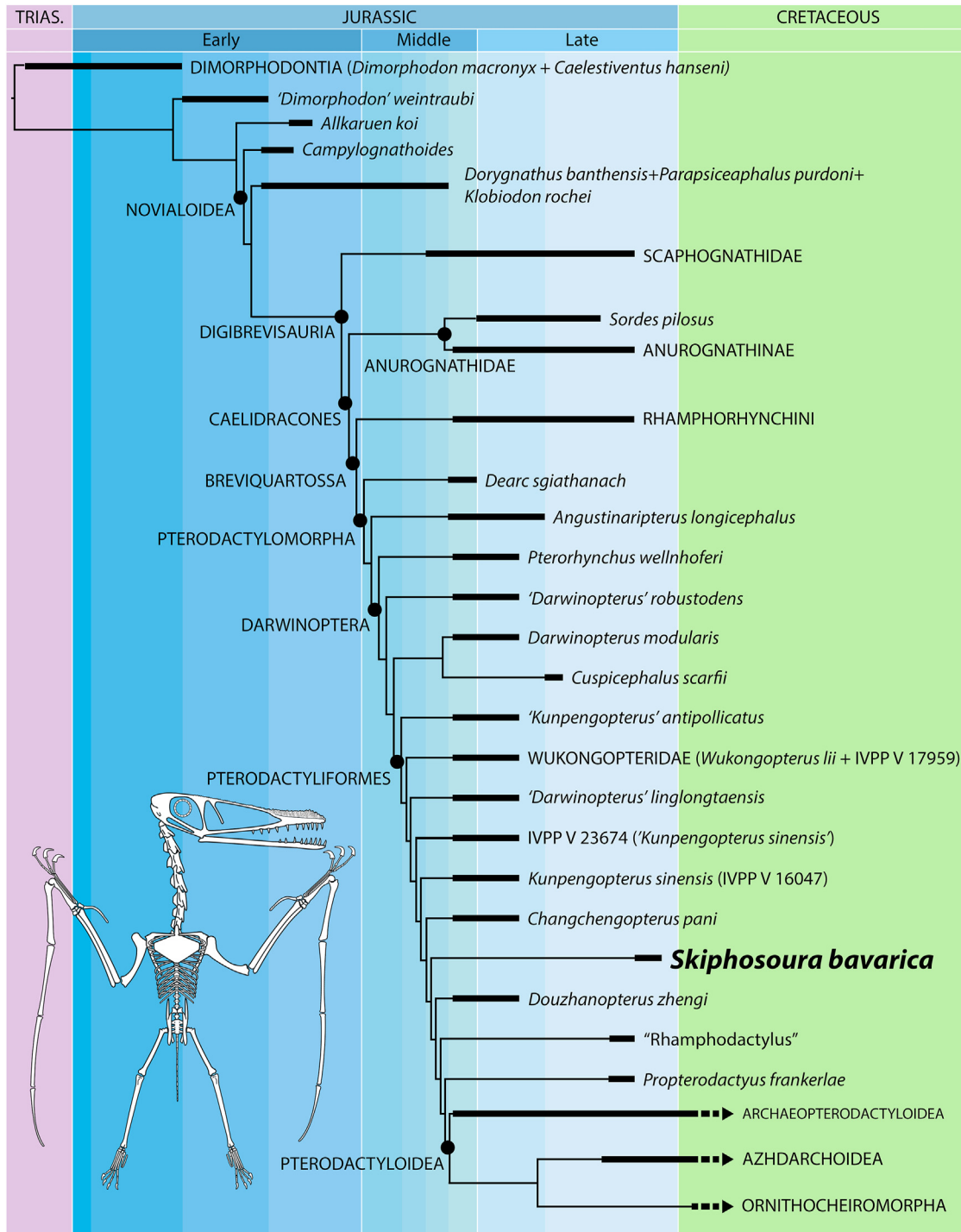
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Figure 2. Simplified phylogeny of Macronychoptera showing the phylogenetic placement of *Skiphosoura bavarica* gen. et sp. nov

The new taxon is recovered outside of Pterodactyloidea as a late-diverging member of a grade of non-pterodactyloid monofenestratans. Note that Monofenestrata also lies within an earlier-diverging grade of "rhamphorhynchids" (*Dorygnathus* to *Angustinaripterus*) and that "rhamphorhynchines" (Rhamphorhynchini, *Dearc*, *Angustinaripterus*) here represent the closest relatives of Monofenestrata.

See also Figure S10 and Table S2.

exclusive to Pterodactyloidea. Despite this, the nasal descending process is retained in most monofenestratans, leaving the external naris and antorbital fenestra partially divided at their dorsal extent. Notably, the naris in the non-monofenestratan *Angustinaripterus* is enlarged, perhaps as a prelude to it merging to form a nasoantorbital fenestra (NAOF).
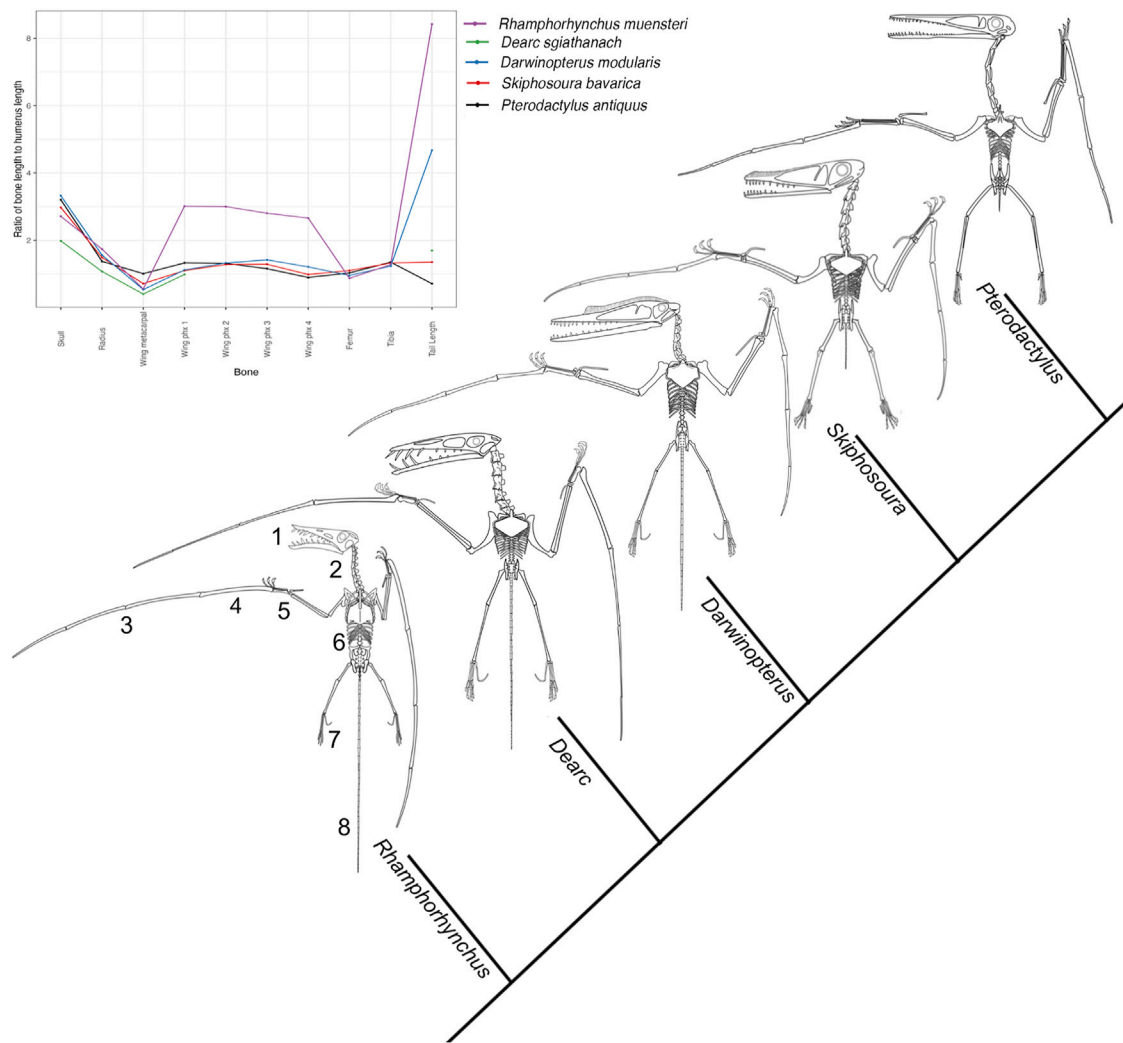
Figure 3. The transition of pterosaur proportions across the transition from early pterosaurs to the pterodactyloids

Upper left: Nopsca curves of the proportions of major elements of the skeleton scaled against the length of the humerus showing the transition of major proportions. Center: simplified phylogeny showing the transition of key characters in the evolution of pterodactyloids from the rhamphorhynchines and "through" the early monofenestratans. Skeletals showing the transition with representational taxa: *Rhamphorhynchus, Dearc, Darwinopterus, Skiphosoura,* and *Pterodactylus*. This shows the transitions of multiple features across the tree: (1) the increasing length of the skull and increase of the size of the naris before fusion to form the NAOF, (2) increase in the length of the cervical series, (3) proportional reduction in the length of the wingfinger and increase in the length of the proximal wing, (4) increase in the length of the first wing phalanx to be the longest of the four phalanges, (5) increase in the length of the wing metacarpal, (6) increase in the size of the prepubes, (7) reduction of the fifth toe, and (8) reduction and simplification of the tail. Reconstructions modified from Unwin,[15] Wellnhofer,[16] and Witton.[1] These are not to scale but are all set to a uniform torso length.

See also Figures S1–S8 and S11 and Table S1.

Cervical series

Dearc shows elongate cervical vertebrae,[11] so this feature has changed compared with the preceding rhamphorhynchines, and the series is lengthening but is not yet at the condition of the monofenestratans with a neck as long or longer than the body.[2] Early pterosaurs possess elongate, filiform cervical ribs (e.g., Padian and Cheng et al.[17,18]). Members of Caelidracones (Anurognathidae, Rhamphorhynchini, Monofenestrata) possess reduced, shorter cervical ribs. In *Propterodactylus* and Pterodactyloidea, cervical ribs are absent, which is generally regarded as a pterodactyloid trait.[2] The nature of the cervical ribs in *Skiphosoura* is unknown.

Prepubes

The *Dorygnathus* + Pterodactyloidea clade plesiomorphically has a prepubis consisting of a shaft and a slightly bifurcating (boot-like) blade. The monofenestratan prepubic blade does not bifurcate, however. *Dearc* similarly lacks bifurcation in its prepubic blade, extending the monofenestratan condition deeper into the tree and marking it as different from that seen in the Rhamphorhynchinae that have a unique H-shaped prepubic pair.[19]

Tail length

The tail is perhaps the most iconic distinction between pterodactyloids and early pterosaurs, with the latter being long-tailed and

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Table 1. Simplified description of major transitions in the origins of the pterodactyloids from earlier pterosaurs using exemplar taxa

Taxon	*Rhamphorhynchus*	*Dearc*	*Darwinopterus*	*Skiphosoura*	*Pterodactylus*
Skull size	smaller than torso	likely similar to the torso	longer than torso	longer than torso	longer than torso
Naris	small	large (based on *Angustinaripterus*)	fused into NAOF	fused into NAOF	fused into NAOF
Cervical series	shorter than torso	subequal to torso	subequal to torso	longer than torso	longer than torso
Prepubes	H-shape	small fan	large fan	large fan	large fan
Caudal series	long, elongate chevrons	inferred long, elongate chevrons	slightly shorter, elongate chevrons	much shorter, elongate chevrons	short, no elongate chevrons
Humerus and radius/ulna	a third of the length of the wingfinger	unknown	half the length of the wingfinger	half the length of the wingfinger	half the length of the wingfinger
Wing metacarpal	short	incomplete, condition unknown	slightly elongate	moderately elongate	long
First wing phalanx	shorter than phalanges 2 and 3	unknown	shorter than phalanges 2 and 3	shorter than phalanges 2 and 3	longest wing phalanx
Fifth toe	two elements, one long and curved	unknown	two elements, one long and curved	two elements, one short and reduced curvature	one element, very short

Various features begin to change at different times, but there is generally a clear progression from earlier to more derived taxa to get from the conditions seen in *Rhamphorhynchus* to those in *Pterodactylus*. See also Figure 2.

the former possessing a distinctly short tail.[2] Several anatomical changes underlie this traditional dichotomy, however, and do not align with a pterodactyloid:non-pterodactyloid split, as, e.g., the tail has already begun to reduce slightly in length in *Darwinopterus*.[20] The pterodactyloid tail is characterized by its lack of filiform hemaphophyses and being shorter than both the dorso-sacral vertebral series and the femur. The earliest diverging pterosaurs possess extremely long tail vertebrae, with the longest being over 2.5 times the length of the longest dorsal and remains longer than said dorsal until the Skiphosoura + Pterodactyloidea clade, when they become shorter. With respect to the entire caudal vertebral series, *Skiphosoura* retains a caudal vertebral series that is longer than its femur, but the vertebral series is shorter than any preceding taxa.

Pteroid

In non-monofenestratan pterosaurs, the pteroid is typically short, being less than 40% the length of the ulna, while monofenestratans possess a pteroid longer than 40% of the ulnar length. Among the present sample, *Skiphosoura* is the only monofenestratan that differs from this, possessing the former, shorter condition. That said, the robusticity of the pteroid here differs from most pterosaurs, so it may have functioned differently from other taxa.

Wing metacarpal length

A classic feature of Pterodactyloidea is the elongate fourth (wing) metacarpal, typically quantified as being 80% or more of the humeral length. This feature remains unique to Pterodactyloidea, being absent in early monofenestratans, including *Skiphosoura*. However, as previously noted,[20] this may have begun to elongate in the Monofenestrata. The members of the IVPP V23674 + Pterodactyloidea clade, including *Skiphosoura*,

uniquely share a wing metacarpal that is over half the length of the first wing phalanx. As such, it does appear that the wing metacarpal did elongate prior to Pterodactyloidea and within the grade between *Darwinopterus* and Pterodactyloidea.

Femur

Members of Pterodactyloidea plesiomorphically possess a femur that is longer than its humerus, differing from the opposite in nearly all monofenestratan pterosaurs with the exception of *Skiphosoura*. Given its phylogenetic condition, the elongate femur of *Skiphosoura* appears to be an independent condition.

Fifth toe

The fifth toe is an elongate structure in most early pterosaurs, with the first phalanx of the digit alone typically being greater than or equal to 75% of the length of the fourth metatarsal. However, we see this phalanx has reduced in length to less than 75% of the length of the fourth metatarsal in the Kunpengopterus + Pterodactyloidea clade. The second phalanx of the toe follows a similar path of reduction. The earliest diverging monofenestratan to differ from this condition is "*Darwinopterus*" *linglongtaensis*, which possesses a reduction of the proximal portion of this digit such that the once-midlength bend is positioned proximally. *Skiphosoura*, *Douzhanopterus*, and *Propterodactylus*[21] represent the first of these taxa to reduce the phalanx to the point of losing a distinct bend entirely. This condition is extended in the Pterodactyloidea that lack the second phalanx entirely.[1]

Overall, it is clear that the head and neck did elongate early on in the origins of monofenestratans, and the major postcranial changes associated with the pterodactyloids were a later acquisition, so the "head and neck first" ideas of Lü et al.[2] remain fundamentally correct. But these were not the result of any kind of saltation, and we now see a larger head appearing in

the rhamphorhynchines prior to the first monofenestratans, and the tail shortening and wing metacarpal elongating before the earliest pterodactyloids, as well as the prepubes changing before the first monofenestratans. It remains likely that future discoveries will blur these lines further and show still more steps between the development of these traits (Figure 3).

However, as may be expected, this is not a simple steady progression with each trait increasing at each node on the phylogeny, and some show stasis or higher or lower values than may be expected. For example, the pteroid varies in length between various early monofenestratans, and *Douzhanopterus* has a reduced tail but one that is longer than *Skiphosoura*. Furthermore, *Skiphosoura* and the other Solnhofen region-derived non-pterodactyloid monofenestratans are contemporaneous with the ctenochasmatids in the Late Jurassic and so are not direct ancestors but late surviving members of this branch. Further discoveries are likely to increase the variations seen around this apparently simple transition.

Size and ecology
Skiphosoura is far larger than other currently known early monofenestratans. The wingspan (calculated as the sum of the humeri, ulnae, wing metacarpals, and wing phalanges) is 1.75 m, around 70% larger than the "Rhamphodactylus,"[22] which is the next largest known. (*Cuspicephalus* is likely a similar size to *Skiphosoura* based on the size of its skull,[23] though this is the only part of it preserved.) *Skiphosoura* is therefore a giant, at least relative to other monofenestratans, that are typically 1 m or less in wingspan, and given that it may not have finished growing, it may have been still larger at full osteological maturity. This size would also place *Skiphosoura* as one of the largest pterosaurs of its time. The earlier *Dearc* is c 2.5 m in wingspan,[11] but in the Solnhofen region there is one slightly larger *Rhamphorhynchus* specimen than this (NHM-UK 37002), but *Skiphosoura* is bigger than all other specimens of this genus, and all other Solnhofen region non-pterodactyloids, and only a few pterodactyloids of the local area approach or exceed a 2 m wingspan.[4] At the very least, we are seeing a progression in size with the larger taxa (*Skiphosoura*, *Cuspicephalus*, and "Rhamphodactylus") all appearing after the smaller forms of the Middle Jurassic, suggesting the occupation of increasing ecospace over time.

The wings are, in general, in proportion between *Skiphosoura* and other early monofenestratans (Table S2). However, those animals with similar proportions at different sizes would still produce different flight characteristics because of the square scaling of the area of the wing membrane but the cube scaling of mass, meaning that larger pterosaurs would have higher wing loading.[24] Therefore, despite the apparent similarity of proportions, *Skiphosoura* would fly somewhat differently to other members of this group. This idea is further supported by the pterodactyloid-like condition of a number of other flight-related features. The long wing metacarpal and the long pteroid would imply a different ability to control the shape of the wing in flight and alter the configuration of control surfaces, and the long femur would extend the brachiopatagium posteriorly to give a deeper wing chord. Most notably, the reduction of the fifth toe and the short tail would imply a considerable reduction in the size of the uropatagium between the hindlimbs,[25] which would alter the arrangement of the wing membranes to something much closer to that of pterodactyloids. This would also imply that the tail did not function as a rudder, as has been hypothesized for non-pterodactyloids.[26]

What is more unusual is the elongate femur seen here, although, as noted above, only the femur is long and the tibiotarsus is roughly in proportion to that seen in other early monofenestratans (Figure S11). More importantly, the long leg and long proximal wing (with the elongate metacarpal) would have given the animal a longer stride and implies a greater degree of terrestrial capability in *Skiphosoura* compared with earlier monofenestratans. Although early pterosaurs were not inept terrestrial locomotors,[27] it is generally regarded that the development of a reduced uropatagium freed up the hindlimbs and facilitated terrestrial locomotion in the pterodactyloids.[15] Thus the reduced uropatagium here would further support the idea that *Skiphosoura* was more terrestrially competent than its ancestors and that the shift to increased terrestrial competence occurred before the origin of the complete pterodactyloid bauplan.

This appears to be part of a trend seen in non-pterodactyloids to move away from the more marine environments occupied by early pterosaurs and into terrestrial settings. It was noted that *Dearc* may have inhabited a more inland setting than other rhamphorhynchines,[11] and we see the tibiotarsus elongating in the phylogeny with all taxa after *Darwinopterus robustodens*. Antungual sesamoids, which are regarded as increasing grip and so being linked to climbing, develop as a result of frequent hyperextension of the unguals is typical of scansorial taxa.[27] These are present in several of the more derived monofenestratans, and this suggests that some of these may have been scansorial and occupying a more terrestrial habitat and niche than preceding forms. The absence of these sesamoids in the later novialoids aligns with their shorter limbs and large recurved claws to indicate a shift to presumably exclusively climbing behavior (when not flying). Their absence in Pterodactyloidea and their closest relatives within Monofenestrata aligns with a reduction of the importance of climbing behavior in their shift to terrestriality. In this sense, antungual sesamoids appear to reflect the loss of, redevelopment of, and later specialization for, terrestrial behavior in pterosaurs.

Although the manual unguals are much larger than those of the pes in *Skiphosoura*, they do show overall similar levels of curvature, which is unusual in pterosaurs and suggests a similar degree of adaptation to gripping the substrate in each. Even though almost the entire specimen is disarticulated, even elements that do not normally come apart like the radius and ulna, metacarpals 1–3, and the pelvic plate have separated, and some of the manual and pedal unguals are still in articulation with the long penultimate phalanges of the digits, suggesting they have incredibly strong ligaments and held these elements in articulation. Strongly curved claws and long penultimate phalanges have been shown to be indicative of a strong grip[28] and suggest that *Skiphosoura* might have been a good climber, though with no evidence of any antungual sesamoids. Collectively though, this suggests that *Skiphosoura* might not have favored coastal areas normally and that they typically lived inland, and this matches the interpretation of this fauna from other sources. The preserved fauna in the Mörnsheim Formation is probably unrepresentative of the local area, with high representation of, e.g.,

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slow swimming fish and ammonites but low representation of faster swimmers and benthic animals, suggesting that the preserved animals had mostly washed into the basin and did not necessarily live there.[5] As with the local anurognathids,[29] this may mean that *Skiphosoura* and other early monofenestratans were common animals but were rarely captured in the lagoonal system of the region.

Remarks

Skiphosoura bridges the gaps between the early monofenestratans and the pterodactyloids, showing a lengthening wing metacarpal, reduced fifth toe, and reduced tail as the postcranial characters "catch up" with the early adoption of a large head and long neck. It also shows adaptations toward a more terrestrial lifestyle, which fits with the longstanding idea that pterodactyloids were more capable on the land than earlier pterosaurs.[30]

The very first pterosaur finds were from the Solnhofen region, and *Pterodactylus* and *Rhamphorhynchus* have been icons of pterosaur evolution for two centuries. Their names were used as the basis for the fundamental split in pterosaurs—the Pterodactyloidea and the "Rhamphorhynchoidea" (now non-pterodactyloids)—yet we now find that these animals are among the closest to each other. As such, the Solnhofen region remains central to our understanding of pterosaur evolution and these most famous genera actually tie together the most important transition in the history of the clade.

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the lead contact, David Hone (d.hone@qmul.ac.uk).

Materials availability
The specimen is permanently held with the Lauer Foundation (LF) for Paleontology, Science and Education (PSE) in Wheaton, Illinois, USA. Public access to type and figured specimens as well as specimens listed or cited in publications together with other scientifically important specimens is guaranteed.

Data and code availability
Data are publicly available as of the date of publication. The full matrix is available here: http://morphobank.org/permalink/?P5534.

This paper does not report original code.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Other		
Fossil specimen	Lauer Foundation	LF4157

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

The rock layers which contain the specimen consist primarily of chalk limestones with marly parts and siliceous layers of varying thickness. This means that the slab and the fossil elements had suffered various breaks and in places were misaligned. Prior to discovery the material has also suffered damage from water. Water widened cracks in the matrix and could gather in depressions, 'mellow' areas, leaving stains on the matrix (see below). More importantly, in some places the bones had dissolved and were largely left as natural casts in the matrix, and these areas were restored with resin.

METHOD DETAILS

Preparation of the specimen was conducted primarily using a binocular microscope with a X30 magnification and under UV illumination to highlight the differences between the matrix and the specimen. The bones were soft and flaky compared to the relatively hard matrix and so considerable amounts of consolidants were needed to stabilise these during preparation.

Photography of the specimen was taken with a Nikon D4 DSLR using a 28 mm lens for the full slab images, and 105 mm macro lens for all other images. Visible light images were taken using a pair of Raleno video LCD panels, set at 5600K color temperature, with built in diffuser and a sheet of polarizing film over the LCD screen and a circular polarising filter on the lens. UV light images were taken with illumination from a Way Too Cool, "triple lamp" equipped with appropriate filters and three 95-watt bulbs which include UV A, UV B and UV C wavelengths, which were used together. Additional images were captured with each individual wavelength (UV A, B and C). An orange color filter was used on the lens for UV photography as this counteracts the purple tone of the UV lights to provide clearer recognition of ultraviolet induced fluorescence (UVIF) expressed in the visible light spectrum.

Description

The bones of LF 4157 are generally in very good condition, and some are preserved in three dimensions and apparently undistorted, though some elements are damaged. Nearly all of the elements are represented (see S3 for a full description and Figures S1, S2, S3, S4, S5, S6, S7, S8, S9, and S10). The specimen is almost entirely disarticulated, though some elements are in natural articulation or preserved close to neighbouring anatomical elements. Although the specimen is large (1.75 m in wingspan), but not fully osteologically mature. It bears numerous adult features (e.g., fully fused pelvic plates, fused extensor tendon processes).[31] However, the manual carpals are not fused (which normally happens early in ontogeny),[32] and the sacral vertebrae appear to have separated from each other. As such we refer to it here as a subadult.

Skull: The skull is proportionally large, estimated to be 275-330 mm. Although somewhat crushed, the skull would have been long and triangular in outline with a large (NAOF) occupying most of the space of the skull. The premaxillae are long and extend posteriorly to form the dorsal margin of the cranium (Figure 1). This shows the presence of a long but not tall filiform bony crest. The maxillae are large and make up a major part of the skull. The palatal extension of the right maxilla is clearly visible and implies that the skull would be over 20 mm wide at a point 100 mm from the anterior tip. The nasal descending process is present and angles anteroventrally into the nasoantorbital fenestra. A foramen pierces the lateral surface of the element, a characteristic exclusively found in members of Monofenestrata.[33] The right postorbital is a triradiate element. The left lacrimal is a T-shaped element exposed in lateral view.

Both splenials are preserved, and are extremely thin, laminar elements. They are notably far shorter than the mandible. The anterior portion of the pterygoid forms the majority of its anteroposterior length, only usually seen in macronychopteran pterosaurs.[34] A foramen pierces the dorsal surface of the pterygoid. The ventral margin of the quadrate is developed as an anteroposteriorly convex, mediolaterally concave articular surface for the mandible. The hyoids are present as a pair of very long and thin straight rods of bone.

The mandible is massive and robust unit and can be determined as 270 mm and approximately 65 mm wide. Anteriorly, the mandibular symphysis is 70 mm long.

There are three alveoli in each premaxilla, and at least nine in each of the maxilla. The margins of the alveoli are raised above the surface of the jaw margins, some by nearly 2 mm. The teeth are well spaced in both the upper and lower jaws and this extends along the tooth rows such that the teeth are closer together anteriorly and more spaced out posteriorly. In the dentaries, there are at least seven and probably eight alveoli on each side. The shape of the crowns varies along the tooth row with the anterior teeth being longer (up to 11.5 mm) and more slender and slightly curved, and the posteriormost teeth being shorter (as little as 4.5 mm) and proportionally more robust and less curved.

Axial column: Six cervical vertebrae are preserved, none of which bear cervical ribs as in some monofenestratans.[34] The cervical vertebrae are roughly twice as long as they are wide and appear to be relatively dorsoventrally short. The centra are procoelous and ventrally have paired ventrolaterally directed postexapophyses on the posterior face which are not seen in other monofenestratans.[35] The neural arch complex is broad, the neural spines are long and low.

Ten dorsal vertebrae are preserved. The centra are spindle-shaped, procoelous and faces that are wider than tall. The neural spines are thin and rectangular.

Four possible sacral / synsacral vertebrae are present. The centra of these are procoelous and 9.5 mm in diameter, immediately above the centrum is an oval neural canal that is wider than it is tall. The neural spine is roughly rectangular in outline being slightly longer than tall, and slightly posteriorly directed.

The tail is represented by at least 15 caudal vertebrae (Figure 1). These range from 6-10 mm in length. The anteriormost elements have only tiny zygapophyses, but the middle caudals have elongate and very narrow zygapophyses similar to those of other monofenestratans and earlier forms.[7] These are up to 8.5 mm long and so would fully overlap at least one other centrum in the series. There are similarly long and fine chevrons preserved. The longest of these is 49 mm and so would have typically overlapped four to five centra in the series. In total the tail is at least 125 mm long based on the total lengths of all of the available elements that can be measured.

Girdles: The scapula is an elongate element with a flat shaft that projects posteriorly at roughly 70 degree from the coracoid. The coracoid is longer than two thirds of the length of the scapula. Distal to the glenoid and these two projections, the coracoid expands posteriorly to form an elongate shaft. A sternal plate is preserved in ventral view but this is poorly preserved, it is a similar shape to that of other monofenestratans.[36]

The pelvis is present as two fused elements representing the left and right sides but both are seen in medial view. The ilium has a long and straight anterior ramus that is nearly half the total length of the pelvis, with the postacetabular ramus being much shorter. Ventrally the plate has a rounded margin with no apparent division on indention where the pubis and ischium meet. The two prepubes are present and similar to other monofenestratan pterosaurs (e.g., 'D.' linglongtaensis[33]) being roughly fan-shaped with a short projection.

There are numerous dorsal ribs and gastralia preserved on the specimen.

Forelimbs: The humeri are large and robust with limited curvature to the shaft and lack foramina. The deltopectoral crest of each is a long, deep, and tongue-shaped as in e.g., 'D.' linglongtaensis.[33] The distal condyles are large and robust.

The radius and ulna are long, straight elements that are subequal in length. A total of six cuboid carpals are preserved showing that these have not fused into the adult pterosaur condition of a single large proximal and distal syncarpal in each wing. Both pteroids are preserved, and these are unusually robust and are shorter than the wing metacarpals. Metacarpals 1-3 are subequal in length to each other and slightly shorter than the wing metacarpal. Both wing metacarpals are preserved in anterior view and possess a large medial condyle at the proximal face. The wing metacarpal is proportionally the longest of any early monofenestratan with the exception of the "Rhamphodactylus"[22] which is very marginally longer.

The manual phalanges of the free fingers are well preserved but not all the elements are present for both hands. The phalanges are generally robust with well-developed condyles and a ventral expansion proximally. The unguals have prominent flexor tubercles and are strongly curved.

The wing phalanges are long and straight elements with expanded proximal and distal ends. The first wing phalanx has a large wing extensor process which is fully fused to the phalanx, and this is not curved as in a number of early monofenestratans.[37] Wing phalanges 2 and 3 are subequal in length. Wing phalanx 1 is shorter than 2 and 3, and phalanx 4 is the shortest in the wing. The fourth wing phalanx is curved along its length and these also taper to a near point distally.

Hindlimbs: The femur is a long and robust element and is unusual as it is slightly longer than the humerus and close to the length of the tibiotarsus. The femoral head is offset from the shaft at approximately 45 degrees on a stout neck. Distally there are a pair of condyles that are slightly wider than the shaft of the femur.

The tibiae are combined with the proximal tarsals into tibiotarsi. These are very long and straight elements that are about 25% longer than the femur. The shaft tapers such that ventrally, immediately before the condyles is only around 8 mm across. The left fibula is present alongside the tibiotarsus as a thin and splint-like element that is less than 2 mm in diameter. Two distal tarsals are present on the slab, these are small and indeterminate in shape.

The metatarsals are long and thin elements with metatarsals 2 or 3 being the longest. The fifth metatarsal is different being wider than it is long and bulbous with a short distal extension. The pedal phalanges are mostly long, straight and thin. The first pedal phalanx of the fifth toe is only slightly shorter than the second which is short and only slightly curved compared to many non-pterodactyloid pterosaurs. The pedal unguals are curved and sharp and are proportionally larger than the pedal unguals of most pterosaurs, though much smaller than those of the manus.

Additional methods
Phylogenetics
We added *Skiphosoura* to the dataset of Pêgas.[38] Several further modifications were made to the coding of the dataset (see Methods S1), including the addition of 15 new characters (521-535) and several taxa (in addition to *Skiphosoura bavarica*): *Allkaruen koi*, IVPP V 23674, and "Rhamphodactylus".[22] The analysis of this dataset was performed under TNT[39] using a new Technology Search was used for the first step (using Sectorial Search, Tree fusing, and default parameters). Whereas the previous analysis had no additive

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characters, the following characters are here considered additive: 1, 2, 3, 5, 14, 22, 25, 26, 31, 34, 44, 66, 76, 78, 105, 121, 130, 133, 135, 140, 141, 164, 180, 187, 239, 242, 243, 244, 245, 248, 253, 254, 302, 322, 340, 345, 346, 377, 378, 417, 418, 450, 451, 459, 461, 470, 479, 483, 485, 489, 491, 501, 518, 520, 522, 532, 534.

The *Kunpengopterus sinensis* operational taxonomic unit (OTU) now only represents the holotype (IVPP V 16047) due to the creation of a new OTU for the previously included specimen IVPP V 23674. Additionally, the proximity of the fossils that form the only specimen of *Kryptodrakon progenitor* - IVPP V18184, an assemblage of disarticulated bone fragments[41] - is a weak justification for their representing a single individual or taxon. As its diagnosis relies upon these elements representing the same taxon, we consider *Kryptodrakon progenitor* a nomen dubium, and it is deleted from this analysis.

A number of changes were made to the existing character constructions (see full changes in Methods S1). The most notable of these changes are as follows. [90] possesses a number of taxa coded for an unnamed state (5), but these taxa all possess state (4), "harpoon-shaped", so they are recoded accordingly. [155] featured an unnamed character for the condition found in *Torukjara bandeirae*, reflecting a supposedly different palatal ridge from that of other pterosaurs. However, the condition in this taxon is not found to be sufficiently different from state (4) here to code it as separate, and the coding of *T. bandeirae* is changed from (4) to (3) here. State (2) of [485] was also unlabeled but appears to reflect the deeply concave margin described in both Naish et al.[40] and Andres et al.,[3] and so [485(2)] is here labeled "deeply concave". An unnamed state (4) exists for [322], as well, but all taxa coded as such fit the description of state (3), "extremely elongate", and so all taxa coded as (4) were changed to (3). For character 479, taxa coded as state (2) actually possess state (1) "longer than the preacetabular process" and taxa coded as state (1) actually possess an omitted character state "shorter than the preacetabular process". These changes are incorporated, state (0) "approximately equal in size to the preacetabular process" is made to be the new intermediate state (1) and the character is made ordered to reflect that it is now a morphograde.

Five characters were deactivated. [236] was deactivated as it is a pseudoreplicate of [233]. [380] and [381] are pseudoreplicates of several characters, see below for more information on these characters and their deactivation. [414] appears to represent an incomplete version of [418], and as such, it is deactivated. Similarly, [433] codes for the same metric as [372], and it is deactivated.

See Table S3 for information on the specimens and references used for coding all included operational taxonomic units (OTUs) and Figure S12 for the full resultant phylogeny. Additional data on the specimen, analysis and interpretation is available in S4-S7.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA

IVPP, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China

LF, Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois, USA

NHM-UK, Natural History Museum, London, UK