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Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull

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The fossil record is a unique source of evidence for important evolutionary phenomena such as transitions between major clades. Frustratingly, relevant fossils are still comparatively rare, most transitions have yet to be documented in detail and the mechanisms that underpin such events, typified by rapid large scale changes and for which microevolutionary processes seem insufficient, are still unclear. A new pterosaur (Mesozoic flying reptile) from the Middle Jurassic of China, *Darwinopterus modularis* gen. et sp. nov., provides the first insights into a prominent, but poorly understood transition between basal, predominantly long-tailed pterosaurs and the more derived, exclusively short-tailed pterodactyloids. *Darwinopterus* exhibits a remarkable 'modular' combination of characters: the skull and neck are typically pterodactyloid, exhibiting numerous derived character states, while the remainder of the skeleton is almost completely plesiomorphic and identical to that of basal pterosaurs. This pattern supports the idea that modules, tightly integrated complexes of characters with discrete, semi-independent and temporally persistent histories, were the principal focus of natural selection and played a leading role in evolutionary transitions.

Keywords: evolution; Middle Jurassic; China; Pterosauria; Pterodactyloidea; *Darwinopterus*

1. INTRODUCTION

In the *Origin of species*, Darwin (1859) emphasised the lack of intermediate forms linking principal groups of organisms as a key challenge to his theory of evolution. Darwin hoped that the fossil record would come to the rescue and provide evidence for these transitions, during which most evolutionary novelties are generated, and to some extent it has (Prothero 2007). Fossils such as the early bird *Archaeopteryx* (Wellnhofer 2008) and the proto-whale *Rodhocetus* (Gingerich *et al.* 2001) have proved critically important for understanding major transitions: not only do they link principal clades, but they also provide both a temporal context and insights into the nature and sequence of evolutionary events within these transitions. Interestingly, rather than exhibiting an array of intermediate character states, these and other transitional forms often consist of a mix of ancestral and derived states in a pattern termed mosaic evolution (Gould 1977). Frustratingly, the complexity of such patterns combined with the relative rarity of truly informative fossil intermediates has made it difficult to identify the mechanisms that underpin transitions. Normal microevolutionary processes seem insufficient to account for the rapid large scale changes that typify most transitions (Erwin 2000) but, at the same time, the operation, or even existence, of alternative macroevolutionary processes is uncertain and controversial (Gould 2002; Kemp 2007*a*).

Here we report on complete, well-preserved fossils of a new pterosaur from the Middle Jurassic of China that provides fresh insights into the nature of evolutionary transitions. The find documents in detail what was, until now, a poorly understood evolutionary transition from basal, predominantly long-tailed forms to derived short-tailed pterodactyloids (Plieninger 1901; Kuhn 1967; Wellnhofer 1978, 1991). More importantly, the unique almost perfectly modular distribution of characters in the new pterosaur allows us to pinpoint a macroevolutionary process, natural selection acting upon phenotypic modules (e.g. Raff 1996; Schlosser 2002, 2005), that may have played a lead role in facilitating the rapid large scale morphological changes that characterize this and many other transitions.

The pterosaur fossil record extends from the Upper Triassic to the end of the Cretaceous, 210–65 Ma (Wellnhofer 1978, 1991; Unwin 2005). The 65 Myr long Late Triassic–Late Jurassic interval seems to have been almost completely dominated by basal clades consisting of small to medium sized seemingly piscivorous or insectivorous pterosaurs (Wellnhofer 1975, 1978, 1991; Kellner 2003; Unwin 2003*a*,*b*, 2005). Typical characters of these pterosaurs include: separate nasal and antorbital openings in the skull, elongate cervical ribs, short metacarpus (less than 80% humerus length) and a fifth toe consisting of two elongate phalanges that supported a flight membrane (cruropatagium) stretched between the hind limbs (Unwin & Bakhurina 1994). Almost all basal forms also have a long tail (Unwin 2005), the only exception being anurognathids where it is reduced to a short stub (Bennett 2007). The skull, neck, body, limbs and tail form spatially distinct, well integrated anatomical modules that are temporally

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persistent and phylogenetically conserved (Kellner 2003; Unwin 2003*a*,*b*) and consistent with functional adaptations (feeding, flight) and developmental patterns (Bennett 1996).

Pterodactyloids first appear in the Late Jurassic and persisted throughout the Cretaceous, during which they achieved considerable taxonomic and morphological diversity (Wellnhofer 1991; Unwin 2005; Andres & Ji 2008), and reached large and even giant size in several lineages (Hone & Benton 2007; Witton & Naish 2008). Pterodactyloids are characterized by many apomorphies including: single nasoantorbital opening, extreme reduction or loss of the cervical ribs, a short tail, long metacarpus and highly reduced or absent fifth toe reflecting a sharp reduction in the size of the cruropatagium (Wellnhofer 1978; Kellner 2003; Unwin 2003*a*, 2005; Andres & Ji 2008). The same principal anatomical modules evident in basal pterosaurs are easily recognized in pterodactyloids and tightly linked to function and development as shown, for example, by the differing allometric relationships evident in growth patterns for the skull, neck and post-cervical axial skeleton (Bennett 1996).

The major disparity between the morphotypes of basal pterosaurs and pterodactyloids highlights the large evolutionary gap between the two (Wellnhofer 1978, 1991; Unwin 2005). The transition that bridged this gap involved a fundamental restructuring of the pterosaur bauplan, documented here, for the first time, by a new species that, although it incorporates familiar anatomical features of basal forms and pterodactyloids, is completely different from all pterosaurs described so far.

2. SYSTEMATIC PALAEONTOLOGY

Pterosauria Kaup 1834.
Breviquartossa Unwin, 2003.
Darwinopterus modularis, new taxon.

(a) *Etymology*

Darwinopterus, for Darwin, honoring the anniversaries of his birth (200 years) and the publication of *On the origin of species* (150 years) and from *pteron* (Greek), winged; *modularis*, (Latin), meaning composed of interchangeable units.

(b) *Holotype*

ZMNH M8782, well-preserved skeleton (figures 1 and 2*a*,*b*,*e*; electronic supplementary material, figure S1) including cranium and mandibles, an almost complete vertebral column, partial sternum, shoulder girdles, pelvis, a partial left forelimb and elements of the hind limb, housed in the Zhejiang Museum of Natural History, Hanzhou, Zhejiang Province, China.

(c) *Referred specimen*

YH-2000, almost complete skeleton (figure 2*f*; electronic supplementary material, figures S2 and S3) lacking only parts of the skull, sternum and phalanges of manus digits i–iii and pes digits i–v, housed in the Yizhou Museum, Yixian, Liaoning Province, China.

Figure 1. Preserved skeletal remains of the holotype of *D. modularis* gen. et sp. nov. (ZMNH M8782).

(d) *Locality and horizon*

Linglengta, Jianchang County, Liaoning Province; Tiaojishan Formation, Middle Jurassic (Bureau of Geology and Mineral Resources of Liaoning Province 1989; see the electronic supplementary material).

(e) *Diagnosis*

Rostral dentition composed of 15 pairs of well-spaced, slender, spike-like teeth, the longest confined to the anterior half of the tooth row. This pterosaur is also distinguished by the unique combination of: confluent nasoantorbital fenestra; inclined quadrate; elongate cervical vertebrae with low neural spine and reduced or absent ribs; long tail of more than 20 caudals partially enclosed by filiform extensions of the pre- and postzygapophyses; glenoid located on the scapula; short metacarpus less than 66 per cent length of humerus and fifth toe with two elongate phalanges.

(f) *Description*

Preparation of ZMNH M8782 and YH-2000 by the Institute of Geology, Beijing, confirms that these fossils are genuine and not composited forgeries (a further four more or less complete specimens from the same locality and comparable to those described here, have not yet been accessioned in public collections). *Darwinopterus* is a relatively small pterosaur represented by two individuals (figures 1 and 2; electronic supplementary material figures S1–S3) with skull lengths of 0.14–0.19 m and forelimb lengths of 0.34–0.46 m (electronic supplementary material, table S1). Co-ossification in composite elements including the scapulocoracoids, proximal and distal syncarpals, the pelvis and the tibiotarsus, indicates that both individuals are osteologically mature.

The skull is unusually large, almost twice the length of the dorsal + sacral vertebral series (DSV). This value is substantially greater than for any basal pterosaur and is high even for pterodactyloids (figure 3*a*). The skull construction is typically pterodactyloid, long and low, the

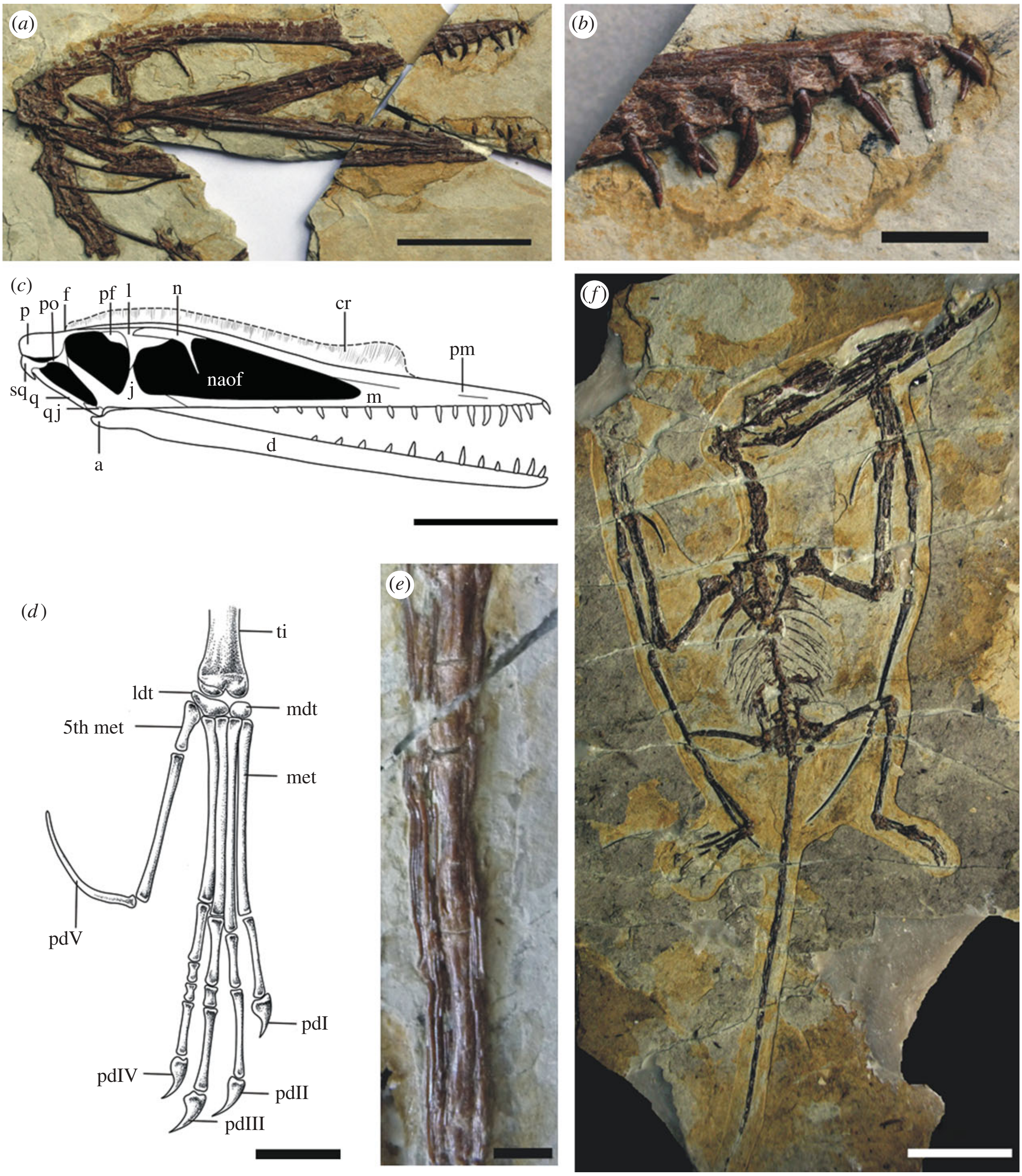

Figure 2. Holotype ZMNH M8782 (*a*,*b*,*e*) and referred specimen YH-2000 (*f*) of *D. modularis* gen. et sp. nov.: (*a*) cranium and mandibles in the right lateral view, cervicals 1–4 in the dorsal view, scale bar 5 cm; (*b*) details of the dentition in the anterior tip of the rostrum, scale bar 2 cm; (*c*) restoration of the skull, scale bar 5 cm; (*d*) restoration of the right pes in the anterior view, scale bar 2 cm; (*e*) details of the seventh to ninth caudal vertebrae and bony rods that enclose them, scale bar 0.5 cm; (*f*) complete skeleton seen in the ventral aspect, except for skull which is in the right lateral view, scale bar 5 cm. Abbreviations: a, articular; cr, cranial crest; d, dentary; f, frontal; j, jugal; l, lacrimal; ldt, lateral distal tarsal; m, maxilla; mdt, medial distal tarsal; met, metatarsal; n, nasal; naof, nasoantorbital fenestra; p, parietal; pd, pedal digit; pf, prefrontal; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; sq, squamosal; ti, tibia.

rostrum anterior to the orbit forming more than 80 per cent of total skull length (a derived condition restricted to certain pterodactyloids), with a confluent nasoantorbital fenestra, inclined quadrate and a short mandibular symphysis forming less than 20 per cent of total mandible length (Wellnhofer 1978, 1991; Kellner 2003; Unwin 2003*a*; Andres & Ji 2008). The dentition (figure 2*b*,*c*) corresponds closely to that which might be expected for a basal pterodactyloid and seems well suited for a gripping function. A long, low cranial crest with a serrate dorsal margin, similar to that of basal dsungaripteroids such as *Germanodactylus* (Wellnhofer 1970) and *Noripterus* (Lü *et al.* 2009), and some ctenochasmatoids (Wellnhofer 1970, 1978, 1991), extends from above the anterior end of the nasoantorbital opening to the apex of the cranium.

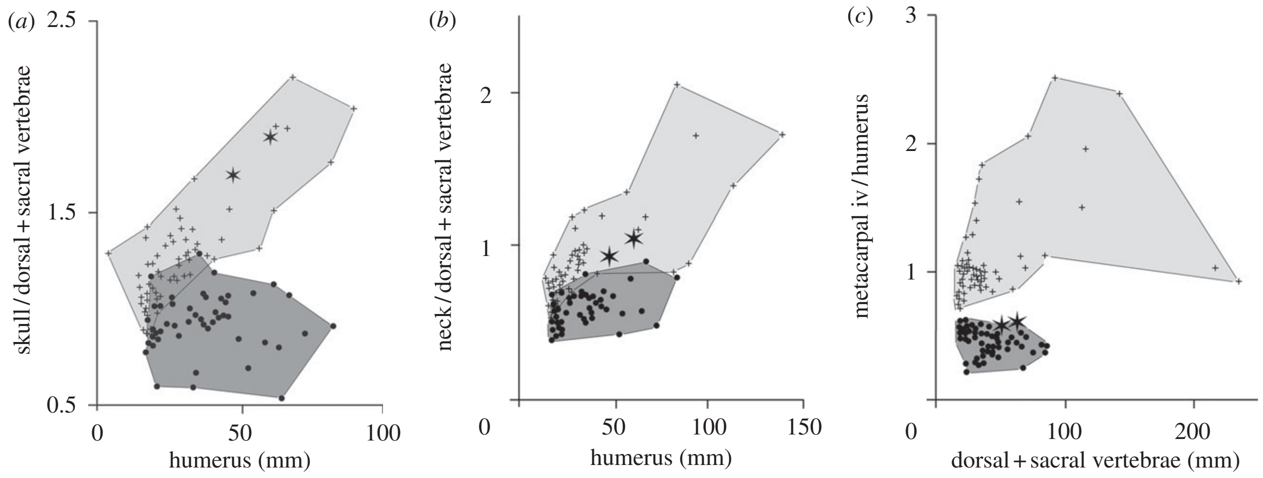

Figure 3. Comparison of *D. modularis* gen. et. sp. nov. to other pterosaurs: (*a*) skull as a proportion of body length (DSV) plotted against a proxy for size (length of the humerus in mm); (*b*) relative length of the neck; (*c*) relative length of metacarpus. Filled circles, basal forms; crosses, pterodactyloids; stars, *Darwinopterus*.

Darwinopterus exhibits the plesiomorphic condition of 27 precaudal vertebrae (Wellnhofer 1978; Bennett 2001). As typical for pterosaurs there are nine cervicals (Wellnhofer 1978, 1991; Bennett 2001; Unwin 2005), but the neck is relatively elongate, almost equivalent to or slightly exceeding the length of the DSV, a proportion only met with in pterodactyloids (figure 3*b*). The long neck results from elongation of cervicals three to seven, which have a length/width ratio of 2 : 1, a proportion typical of pterodactyloids, but not basal forms where these vertebrae are shorter and stockier (Wellnhofer 1975; Howse 1986). The same cervicals also appear to lack ribs and have a very low neural spine. These characters, only found among pterodactyloids and one unusual basal clade, Anurognathidae (Bennett 2007), appear to signal greater flexibility of the neck than in most basal forms. In sharp contrast to the derived morphology of the skull and neck, the tail of *Darwinopterus* is identical to that of most basal clades, consisting of more than 20 caudals which, apart from the first three or four vertebrae, are long and rod-like and enclosed by a sheath of bony filaments composed of highly elongated ossified extensions of the zygapophyses and hypapophyses (figure 2*e*) (Wellnhofer 1975, 1978).

The morphology and proportions of the pectoral and pelvic girdles and limbs also compare closely to those of basal pterosaurs and, apart from the relatively elongate pteroid, do not exhibit any pterodactyloid characters. The glenoid is located on the scapula rather than equally shared by the scapula and coracoid as in pterodactyloids (Wellnhofer 1978). The metacarpus is less than 70 per cent the length of the humerus, a universal feature of basal pterosaurs (figure 3*c*), and instead of a decline in the length of the second and consecutive phalanges of manus digit four, as found in many diapsids, all pterodactyloids and anurognathids, *Darwinopterus* corresponds to the condition in all long-tailed pterosaurs where phalanges two and three are of similar dimensions and exceed the length of the first and fourth phalanges (Wellnhofer 1975, 1978; Kellner 2003). Finally, the fifth toe consists of two elongate phalanges (figure 2*d*; electronic supplementary material, figure S3), as in all basal pterosaurs, and the distal phalanx is sharply recurved, a condition only met with in some rhamphorhynchids (Kellner 2003; Unwin 2003*a*,*b*).

3. DISCUSSION

(a) *Phylogeny and modularity*

Phylogenetic analysis (see the electronic supplementary material) of a taxon/character matrix consisting of 56 terminal taxa and 117 characters, the largest comprehensive dataset yet compiled for pterosaurs, yielded most parsimonious trees whose basic structure (figure 4*a*) is broadly in agreement with the results of previous studies (Kellner 2003; Unwin 2003*a*,*b*; Lü & Ji 2006; Andres & Ji 2008; Lü *et al.* 2008). The analysis found strong support for a sister group relationship between *Darwinopterus* and Pterodactyloidea. This clade is exclusively diagnosed by characters of the cervical vertebrae and skull, prominent among which is the presence of a confluent nasoantorbital fenestra from which we derive the clade name 'Monofenestrata'. We retain the phylogenetic definition and content of Pterodactyloidea used by other recent studies (Kellner 2003; Unwin 2003*a*; Lü *et al.* 2006; Andres & Ji 2008; Lü *et al.* 2008), but adopt a diagnosis that is restricted to postcranial characters.

Reanalysis of *Darwinopterus* treating all characters of this pterosaur, except those for the head and neck, as unknown (scored as '?'), resulted in its relocation to a position within Pterodactyloidea, as a sister taxon to Ornithocheiroidea (figure 4*a*, D1). Conversely, treating head and neck characters as unknown prompted the migration of *Darwinopterus* to a position within basal pterosaurs as a sister taxon to Rhamphorhynchidae (figure 4*a*, D2).

These contrasting results emphasize two key aspects of *Darwinopterus*: the complete absence of 'intermediate' character states that fall between those states found either in basal pterosaurs or in pterodactyloids (figure 3), and the almost perfect modularity exhibited by the mosaic pattern of character state distributions found in this pterosaur. The skull and neck are dominated by derived states confined to pterodactyloids, while the opposite is true for the body plus limbs,

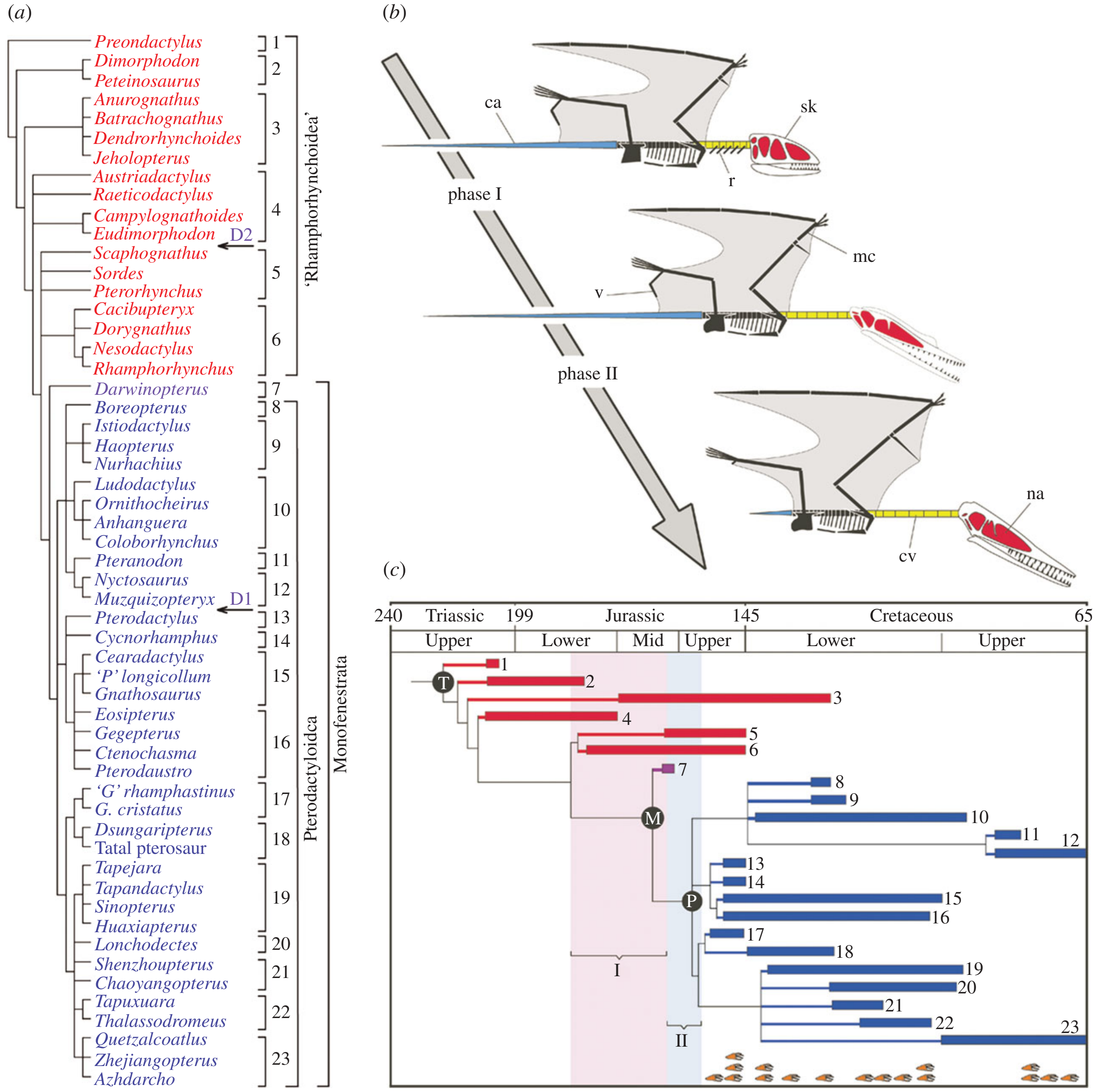

Figure 4. Phylogenetic relationships and evolutionary context of *Darwinopterus*. (*a*) Phylogenetic analysis of Pterosauria (see the electronic supplementary material for details), possible alternative locations for *Darwinopterus* indicated by D1 and D2. (*b*) Schematic restorations of a basal pterosaur (above), *Darwinopterus* (middle) and a pterodactyloid (below) standardized to the length of the DSV, the arrow indicates direction of evolutionary transformations; modules: skull (red), neck (yellow), body and limbs (monochrome), tail (blue); I, transition phase one; II, transition phase two. (*c*) Time-calibrated phylogeny showing the temporal range of the main pterosaur clades; basal clades in red, pterodactyloids in blue; known ranges of clades indicated by solid bar, inferred 'ghost' range by coloured line; footprint symbols indicate approximate age of principal pterosaur track sites based on Lockley *et al.* (2008); stratigraphic units and age in millions of years based on Gradstein *et al.* (2005). 1, *Preondactylus*; 2, Dimorphodontidae; 3, Anurognathidae; 4, Campylognathoididae; 5, Scaphognathinae; 6, Rhamphorhynchinae; 7, *Darwinopterus*; 8, *Boreopterus*; 9, Istiodactylidae; 10, Ornithocheiridae; 11, *Pteranodon*; 12, Nyctosauridae; 13, *Pterodactylus*; 14, *Cycnorhamphus*; 15, Ctenochasmatinae; 16, Gnathosaurinae; 17, *Germanodactylus*; 18, Dsungaripteridae; 19, *Lonchodectes*; 20, Tapejaridae; 21, Chaoyangopteridae; 22, Thalassodromidae; 23, Azhdarchidae. Abbreviations: M, Monofenestrata; P, Pterodactyloidea; T, Pterosauria; ca, caudal vertebral series; cv, cervical vertebral series; mc, metacarpus; na, nasoantorbital fenestra; r, rib; sk, skull; v, fifth pedal digit.

and tail (figure 4*b*). These modules match those already listed above for other pterosaur clades. Moreover, their persistence, even during a major evolutionary transition, as demonstrated by *Darwinopterus*, points to the possibility that it was modules, rather than individual characters, that formed the principal (although not necessarily exclusive) units upon which natural selection acted during major evolutionary transformations (Brandon 1999). This mechanism has been widely mooted and discussed (e.g. Raff 1996; Schlosser 2002, 2005; Kemp 2007*a*) and, in contrast to microevolutionary processes, where the piecemeal accumulation of small changes requires long periods of time to bring about major transformations, could effect large-scale changes over relatively short time intervals. Until now, however, clear evidence for module selection has been lacking.

Module selection also requires the operation of other ancillary processes such as dissociation (Raff 1996). This effectively permits decoupling of modules and allows them to evolve at different rates and with different evolutionary trajectories (Schlosser 2005). Contrasts between character state distributions of approximately homologous modules can reveal the action of this process. In pterosaurs, decoupled modules are demonstrated by the presence of both 'long' and 'short' tails in basal clades. Intriguingly, patterns of character distribution suggest that change *within* modules over time was highly coordinated, a phenomenon that bears comparison with correlated progression (Kemp 2007*b*). This is prompted by the observation that anatomical, functional and developmental components of particular modules seem to have been tightly integrated. For example, in ornithocheiroids (figure 4, clades 8–12) the forelimbs exhibit a suite of unique anatomical features (Unwin 2003*a*), possibly related to a predominantly soaring lifestyle (Wilkinson 2008), that, significantly, are found in all known members of this large and temporally long-lived clade, but not in any other pterosaur.

Ultimately, for module selection to be accepted as a real evolutionary process, and not merely an epiphenomenon, requires demonstration of a genetic basis. While this is beyond the scope of the present study, it is worth noting that the phenotypic modules identified here match closely to the expression domains of *Hox* genes (Holland 1992). This raises the possibility of a link between module selection and genetics and suggests a promising avenue for further exploration.

(b) *Documenting an evolutionary transition*

Darwinopterus provides, to our knowledge, the first detailed insights into the transition from basal pterosaurs to pterodactyloids and, when combined with our rapidly increasing knowledge of the pterosaur fossil record (Barrett *et al.* 2008), helps to pinpoint several key features regarding the nature and timing of this event (figure 4*c*). Two distinct phases are recognized. In the first, elongation of the skull, breaching of the bony bar separating the nasal and antorbital opening, reconfiguration of the cranium leading to an increase in the relative size and volume of the braincase and simplification of the dentition, together with changes to the shape of the cervical vertebrae and loss of the cervical ribs, culminated in the monofenestrate skull and modified neck inherited by *Darwinopterus* and all pterodactyloids (figure 4*b*). The exact functional and ecological significance of these features is still unclear, but based on details of the dentition, increased flexibility of the neck and likelihood of a highly restricted terrestrial ability (Unwin 2005), we suggest that *Darwinopterus* may have been an aerial predator, but note that this and more general ideas regarding diet and feeding mechanics in pterosaurs would benefit from further analysis. Contemporaneous fliers upon which *Darwinopterus* might have fed include pterosaurs (Lü *et al.* 2006; Lü 2009), feathered maniraptorans (Czerkas & Yuan 2002; Zhang *et al.* 2002; Xu *et al.* 2009) and gliding mammals (Meng *et al.* 2006). The geological age of *Darwinopterus* and earliest records for the clade Rhamphorhynchidae + Monofenestrata, constrain this first phase to the mid-Early to late Middle Jurassic (figure 4*c*).

In the second phase of the transition, modifications were confined to the post-cervical axial column, limb girdles and limbs. Key among these were shortening of the tail, elongation of the metacarpus and reduction of the fifth toe, changes that appear to have significantly improved the locomotory abilities of pterodactyloids (Unwin 2005). Critically, these permitted a much greater degree of agility on the ground (Witton & Naish 2008), facilitating the invasion of a variety of terrestrial habitats that were inaccessible to basal pterosaurs and *Darwinopterus* because of their more limited terrestrial ability, owing, in part, to the large cruropatagium which linked the hind limbs (Unwin & Bakhurina 1994; Unwin 2005; Bennett 2007). Assuming that these events postdated *Darwinopterus*, but predated the first appearance of pterodactyloids, which are certainly known from the mid- Upper Jurassic (Wellnhofer 1978, 1991; Unwin 2005), and possibly even slightly earlier (Buffetaut & Guibert 2001), then this second phase must have occurred in the late Middle to early Late Jurassic (figure 4*c*). This hypothesis is consistent with the seeming absence of pterodactyloids from Middle Jurassic (Stonesfield Slate, England; Cerro Condor, Argentina; Daohugou, China) or earliest Upper Jurassic (Karatau, Kazakhstan) pterosaur assemblages (Unwin & Bakhurina 1994; Unwin 1996; Lü *et al.* 2006; Codorniú & Gasparini 2007), and the sudden, widespread appearance of pterosaur tracks (all seemingly produced by pterodactyloids) in the Upper Jurassic (Lockley *et al.* 2008).

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