

Carpus in Mesozoic anurans: The Early Cretaceous anuran *Genibatrachus* from northeastern China

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ABSTRACT

The carpus (wrist) of fossil frogs is rarely preserved, because it consists of tiny skeletal elements that ossify only during the postmetamorphic life stage. The structure of the carpus is comparatively well-known in the temnospondyl ancestors of the Anura, but its changes during the transition to their anuran descendants are unknown due to the absence of transitional, presumably paedomorphic forms. The Early Cretaceous *Genibatrachus* from northeastern China is among the best-documented Mesozoic anurans, both regarding the number of preserved individuals and the representation of developmental stages. The latter aspect is especially important, because in its early developmental history, the anuran carpus is represented by cartilaginous nodules which may be the subject of various, often multiple fusions. Only later do the nodules or the fused elements ossify, enabling them to be preserved in fossils. This is why the carpus of adult fossil frogs is simpler than the foregoing larval period of cartilaginous carpus, not recordable in fossils. Nevertheless, the early development of the carpus may be reconstructed from the morphological details of its ultimate constituents. In this way, *Genibatrachus* may fill the gap in the evolutionary sequence of the carpus between Paleozoic temnospondyl amphibians and modern frogs.

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1. Introduction

According to the current view, anurans originated in paedomorphic temnospondyl amphibians (e.g. Shishkin, 1973; Bolt, 1977; Boy and Sues, 2000; Roček and Rage, 2000). If this is true, transitional forms had not preserved the skeletal elements that normally ossify only in adult, fully-grown individuals, among them tiny elements of the carpus. This is particularly regrettable because the key period of their development takes place when these elements are still cartilaginous. They originate as small, independent nodules, which may remain independent until adulthood. However, more often they fuse with their neighbours, giving rise to large elements which suggest only by their size and form that they have multiple origins (e.g. Schmalhausen, 1907; Jarošová, 1973; Fabrezi

and Alberch, 1996; Fabrezi and Barg, 2001). In many cases, early carpal elements cease to exist as independent structures before reaching the ossified stage. It is therefore obvious that the carpus of adult frogs is much simpler, compared with the cartilaginous carpus of tadpoles. In addition, the ultimate, ossified carpal elements may include different developmental constituents, often more than two. In spite of their different developmental origins, however, in adults they may bear the same name, which is the reason why carpal nomenclature is sometimes contentious. Thus, developmental data on the anuran carpus may help in assessing the homology of its elements. Reliable nomenclature, based on the homologous constituents of definitive carpal elements, is thus the most important in comparative analyses.

A significant source of information on the composition of the anuran carpus is its structure in temnospondyl ancestors, disregarding the aforementioned lack of knowledge on transitional forms. It is worth noting that one of the characteristic features of the anuran forelimb – namely that one digit, including its metacarpal, was reduced and ultimately lost – occurred as early as before the end of the Paleozoic (e.g. in *Balanerpeton*, *Dendrerpeton*,

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Eryops and *Dissorophus*; Gregory et al., 1923; Holmes et al., 1998; Milner and Sequeira, 1994). The structure of their carpus is best preserved in the early Permian *Eryops*, hence its generalised scheme (Dilkes, 2015, fig. 2A) may be taken as the starting point for the origin of the anuran carpus. It consisted of two proximal elements (ulnare and radiale) and two additional elements located between them (intermedium and one of the central elements, usually called centrale 4). At the level distal from the radiale was centrale 1, joined towards the ulnar side by centrale 2 and centrale 3. Then, there were four distal elements, termed the distal carpalia 1–4, each articulating with the base of the corresponding metacarpal. It should be noted that whereas in Paleozoic temnospondyls with four digits these are numbered 1–4, in anurans they are numbered 2–5, because it is assumed that the first digit was lost (Alberch and Gale, 1985).

In temnospondyl labyrinthodonts, all individual bones of the carpus can be recognised, but in fossil frogs the situation is different. They are rarely preserved, not only owing to their size, but mainly because their original identity is obscured by the above-mentioned processes that occur in the cartilaginous period of their development. Fusions of originally independent cartilaginous elements in fossil frogs can be reconstructed by means of similar processes, which can be studied in their extant relatives. In addition, information on the developmental history of ossified carpal elements can be inferred from their positional relations, their relative size and their shapes. Tentative results gained from isolated findings may become much more reliable if the number of fossil individuals is larger and if they are of various ontogenetic ages. In such rare cases it is possible to arrange individuals into developmental sequences that can reliably document the morphogenesis of the carpus.

One of these exceptional cases is a large series of the well-preserved fossil frog *Genibatrachus*, recently recovered from the Lower Cretaceous locality of Moqi in the province of Inner Mongolia, China (Gao and Chen, 2017). It includes both early metamorphosed froglets and postmetamorphic fully-grown adults and provides insights into the origins and development of various skeletal structures in these Lower Cretaceous frogs, including delicate ones like carpalia. Moreover, the skeletons of these specimens have been preserved in a range of positions, enabling assessments of individual variations in skeletal features and, based on these data, comparisons with available data from other Early Cretaceous anurans. The large number of these anuran fossils, their developmental range and their extraordinary good preservation make *Genibatrachus* the best-documented Mesozoic frog. Thus, the aim of the present paper is not only to describe the ossified carpus of fully-grown adult *Genibatrachus*, but also to reconstruct its final stages of development documented on ossified carpal elements. The results can provide the basis for comparisons with other adequately preserved Mesozoic anurans and ancestral temnospondyls as well as for understanding the developmental pattern of the carpus in all extant anurans.

1.1. Institutional abbreviations

CYGYB/CYH – Chaoyang Bird Fossil National Geopark, Chaoyang, Liaoning, China (朝阳鸟化石国家地质公园); DNM – Dalian Natural History Museum, Dalian, China (大连自然博物馆); GM – Geological Museum of China, Beijing, China (中国地质博物馆); HUJZ – Hebrew University, Jerusalem, Israel; IVPP – Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China (中国科学院古脊椎动物与古人类研究所); LPM – Liaoning Paleontology Museum, Shenyang, Liaoning, China (辽宁古生物博物馆); MNCN – Museo Nacional de Ciencias Naturales, Madrid, Spain; MACN – Museo Argentino de Ciencias

Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MV – Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences Nanjing, Jiangsu, China (中国科学院南京地质古生物研究所); PKUP – Peking University Paleontological Collections, Beijing, China; UFRJ-DG – Departamento de Geologia, Universidade Federal do Rio de Janeiro, Brazil.

2. Materials and methods

The fossil frog *Genibatrachus baoshanensis* was described by Gao and Chen (2017); their original collection involved nine adults including the holotype (PKUP V0401) and three juveniles, but was not available during our study. Our material comes from several outcrops which include the holotype locality, collectively named the Moqi locality (48°39′42.39N; 123°52′15.48E’), about 2 km east of Taipingqiao village and 17 km northwest of Baoshan township, Morin Dawa Daur Autonomous Banner, Hulunbuir, Inner Mongolia, China (see the map in Gao and Chen, 2017, fig. 1). Whereas Gao and Chen (2017) gave the age of the locality as 125 Ma (Barremian), recent dating of the volcanic horizon immediately above the fossil-bearing bed suggests 118 Ma, which is Aptian in age (Zhiqiang Yu, pers. comm. 2020).

Gao and Chen (2017) claimed *Genibatrachus* as a basal member of the Pipanura, with unresolved relationships with the Pipoidea and Acosmanura (Pelobatoidea + Neobatrachia). However, they based their phylogenetic conclusions on an incorrect determination of the vertebral centra as procoelous (as revealed by our CT scans, they are amphicoelous). Furthermore, they considered free ribs present on all presacral vertebrae except for V₁ in small individuals; if this were true, *Genibatrachus* would be a unique case among all anurans.

From the total number of specimens in our new collection (83 adults, most of them preserved as part and counterpart) now deposited in the IVPP, carpal elements were recorded in 37 individuals; moreover, in an additional individual (IVPP V22591, SVL 50.0 mm) the presence of an ossified carpus was highly probable, even if its elements could not be reasonably identified. All these individuals were adults, as inferred from the degree of ossification of the epiphyses of the metacarpals and other long bones, but some of them were not ‘fully-grown’, which means they did not reach maximum of their development. The size of these individuals, i.e. the snout-vent-length (SVL; measured in fossil frogs from the anterior end of the premaxillary symphysis to the posterior end of the urostyle), exceeded 50 mm, whereas in smaller specimens (= early postmetamorphic froglets) the carpal elements were not preserved even where adjacent skeletal elements (ulna, radius and metacarpals) were present. This means that their carpal elements were not yet ossified or calcified. The SVL of the largest individuals in our sample reached about 85 mm.

In some individuals it was possible to investigate the carpus of both the left and right sides (Fig. 1A1–A2); in the majority of them it was also possible to investigate the carpus in both the part and the counterpart (Fig. 1D1–D2, F1–F2, G1–G2, H1–H2, I1–I2). In several individuals (e.g. IVPP V24146), however, the forelimbs were not preserved in a natural position (i.e. directed anteriorly) and were instead stretched posterolaterally, sometimes even with the radioulna disarticulated from the humerus at the elbow joint and twisted along its long axis, so that the carpus’ general orientation could be inferred only from the position of the praepollex.

To compare the carpus in adult, fully-grown *Genibatrachus* with those in other Mesozoic anurans, we used the following material: *Eodiscoglossus santoniae* (MNCN-59173, Fig. 2B; see also Vergnaud-Grazzini and Weinz, 1975, fig. 5); *Neobatrachus gracilis* (originally *Cordicephalus*, but see Mahony, 2019; holotype, HUJZ F165, Fig. 2K, see also Nevo, 1968, fig. 6, pl. 9H; Trueb and Báez, 2006, fig. 1A);

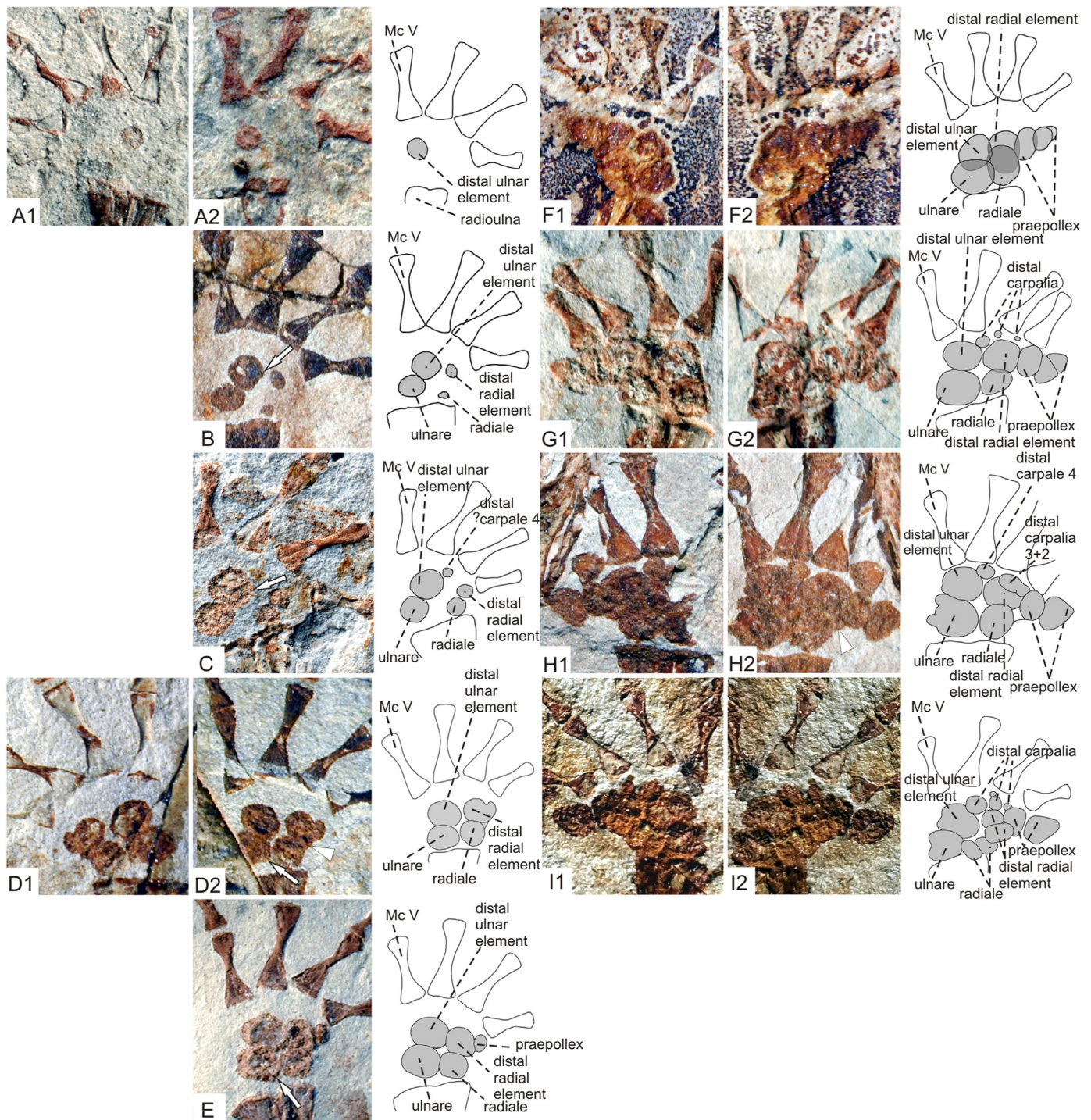


Fig. 1. Ossification sequence of the carpus in Early Cretaceous *Genibatrachus*. A – Left carpus (A1 – ventral aspect, IVPP V19272A–3, SVL 66.5 mm; A2 – dorsal aspect, IVPP V19272B–3). B – Left carpus, dorsal aspect, IVPP V20789B, SVL 67.2 mm. White arrow marks extension of distal ulnar element. C – Left carpus, dorsal aspect, IVPP V19238A, SVL 73.7 mm. D – Left carpus (D1 – ventral aspect, IVPP V24115A, SVL 75.4 mm; D2 – dorsal aspect, IVPP V24115B). White arrow marks extension of ulnare. Note small element between radiale and distal radial element (marked by white arrowhead). E – Right carpus, ventral aspect, IVPP V23303A, SVL 82.4 mm. F – Right carpus (F1 – ventral aspect, IVPP V19232A, SVL 61.6 mm; F2 – dorsal aspect, IVPP V19232B). Some elements overlap each other (indicated by dark shading). G – Left carpus (G1 – ventral aspect, IVPP V24096A, SVL 60.0 mm; G2 – dorsal aspect, IVPP V24096B). H – Right carpus (H1 – dorsal aspect, IVPP V24144B, SVL 67.8 mm; H2 – ventral aspect, IVPP V24144A). Small element between radiale and distal radial element is marked by white arrowhead. I – Right carpus (I1 – dorsal aspect, IVPP V19250A, reversed; I2 – ventral aspect, IVPP V19250A); posterior part of skeleton not preserved. Interpretative drawings on the right are all in dorsal aspect. Mc V – Metacarpal V. Not to scale.

Kururubatrachus gondwanicus (holotype, UFRJ-DG 08, Fig. 2L; Agnolin et al., 2020, fig. 2); *Liaobatrachus beipiaoensis* (holotype, LPM 0030, Fig. 2F; DNM D2167, Fig. 2G, see also Dong et al., 2013, fig. 4B2; IVPP V12717, Fig. 2I; see also Dong et al., 2013, fig. 4C1);

Liaobatrachus sp. (LPM 0203, Fig. 2E); *Liaobatrachus grabaui* (holotype, GM V2126, Fig. 2C; see also Dong et al., 2013, fig. 3A2; MV 77; IVPP V11525, see also Dong et al., 2013, fig. 3B1; CYH 004); *Liaobatrachus macilentus* (IVPP V12510, Fig. 2H; see also Dong et al.,

2013, fig. 5B1); *Liobatrachus* sp. (CYGYB-002, Fig. 2J); *Notobatrachus degiustoi* (holotype, MACN 17720, Fig. 2A); and *Thoraciliacus rostriceps* (holotype, HUIJ F-93, see also Nevo, 1968, pl. 3A). Other taxa were compared based on published data.

Given that the anuran carpal nomenclature is still rather contentious, we prefer to use the neutral terms 'distal radial element' and 'distal ulnar element', rather than 'element Y' and 'distal carpale 5', respectively. Furthermore, the elements usually termed the 'ulnare' and the 'radiale' have a composite origin and involve transient elements that lose their identity before reaching the ossified stage, but their positions distal to the ulna and radius are so typical that it would be confusing to use other terms. The nomenclature of the centralia is derived from that used by Dilkes (2015) for temnospondyls. Short references are inserted where the composition of corresponding carpal elements is known in presumably related extant taxa (*Bombina*, *Discoglossus*, *Ascaphus*).

3. Results

3.1. Development of the carpus in *Genibatrachus*

The fossilised carpal elements of *Genibatrachus* are calcified or ossified nodules resembling centres of ossification that become larger with age in cartilaginous carpals of postmetamorphic living frogs. Due to variation in both the number and sizes of these nodules in a single carpus, we infer that the preserved individuals are of different ontogenetic ages. The largest recorded individual in our sample without any sign of a carpus is IVPP V20776 (SVL of 43.5 mm), whereas the smallest individual with a carpus is IVPP V18755 (SVL 55.8 mm). However, IVPP V22591 (SVL 50.0 mm) preserves vestiges of ossified elements in the area of the carpus, albeit not clearly recognisable. Thus, we posit that ossification of the carpus in *Genibatrachus* commenced when its SVL reached 50–55 mm.

The first ossified element of the carpus appears on the ulnar side, closer to metacarpal V than to the radioulna (Fig. 1A). Judging by its position and simple ovoid shape, this element could be the earliest nodule of the distal ulnar element. This earliest ossified element within the area of the distal ulnar element may be homologised with the centrale 3. The ulnare is not yet developed (the dark spot in Fig. 1A2 is a sand grain). The SVL of this individual is 68.2 mm, which when compared with all other adults in our sample, can be regarded as medium sized.

In another individual of almost the same size (IVPP V20789; SVL 68.3 mm), the ulnare is additionally preserved, accompanied by two much smaller elements on the radial side (Fig. 1B). The larger size of both elements on the ulnar side indicates that they are more advanced than the small elements on the radial side. Furthermore, the small proximal element on the radial side, identified as the radiale, appears to be the most recently developed of the four. It should be noted that the distal ulnar element (centrale 3 at this stage of development) bears a swelling on its medial side (marked by a white arrow in Fig. 1B), which may indicate an additional element fused with the original one illustrated in Fig. 1A. A similar swelling may be found in *Bombina*, where its relative position to centrale 3 suggests that it might be the centrale 4. In IVPP V19238A (Fig. 1C) and in later stages, the distal ulnar element (consisting of the centrale 3 and 4) is already transversely elongated (see white arrow in Fig. 1C), which may be explained by the integration of this additional element.

The elements on the radial side grow in size, but before reaching the dimensions of those on the ulnar side, the earliest (probably calcified) rudiment of the distal carpale 4 seems to appear adjacent to, but well separated from, the medial end of the distal ulnar

element (Fig. 1C). However, there is the possibility that it is just a fossilisation artefact. The latter interpretation is supported by the fact that ossified distal carpalia in other individuals of *Genibatrachus* appear only in adults with a well-ossified praepollex (Fig. 1G–I). Given this ambiguity, the identity of this element remains rather uncertain.

The developmental stages illustrated in Fig. 1A and B are each represented by only a single individual, yet the smaller sizes of the elements on the radial side (the radiale and the distal radial element) and the larger sizes of the two elements on the ulnar side also occur in IVPP V19238 (Fig. 1C), which is much larger (SVL 83.5 mm). This suggests that the development of the carpus commenced on the ulnar side.

When all four dominant elements of the carpus are approximately the same size, the praepollex begins to be different from the distal radial element (represented by a simple spherical element identified according to its position as the centrale 2) as a small nodule – probably partly overlapped by the larger element (Fig. 1D) – and later becomes completely separate (Fig. 1E). In the course of its further development, the praepollex differentiates into two and then three sections by the additional growth of the cartilaginous precursor, the terminal section being the smallest. In fully-grown adults, however, the praepollex consists of only two segments, of which the terminal becomes the largest and somewhat pointed (Fig. 1G–I). A hypothetical explanation is given in the Discussion. The last parts of the carpus to ossify are distal carpalia 2, 3 and 4 (if the uncertain structure illustrated in Fig. 1C is not taken as a precocious distal carpale). The distal carpalia appear only after the praepollex reaches its ultimate size (Fig. 1G–I). Distal carpale 4 ossifies first, followed by distal carpale 3, and finally distal carpale 2. Their ultimate sizes agree with the sequence of their appearance.

The next steps in the development of the ossified carpus (although not necessarily occurring in terminal developmental stages) involve fusions of some elements. This can be inferred from the observation that the originally separate ossified distal carpalia 2 and 3 possibly fuse with each other (Fig. 1H). However, the above-mentioned fusion of a small central element (presumably centrale 4, as suggested by *Bombina* and *Discoglossus*) with the earliest component of the distal ulnar element (Fig. 1B, C) occurs earlier. Furthermore, an extension of the medial side of the ulnare, indicated by the white arrows in Fig. 1D and E and resulting in its transversely elongate shape, suggests that change in shape might be caused by fusion with an additional element, probably the intermedium. A small, additional element is also present between the distal radial element (centrale 2) and the radiale between their medial outlines (marked by the white arrowhead in Fig. 1D2 and H2). It is not possible to ascertain whether this small element fuses with certain adjacent elements or remains independent, but because the distal radial element becomes extended medially (Fig. 1E), it can fuse with this small element. This small element may be a homologue of the centrale 1 in *Bombina* and *Discoglossus* (Jarošová, 1973; note, however, that she used another terminology).

The carpus of adult, fully-grown individuals of *Genibatrachus* is characterised by its praepollex consisting of only two segments, of which the terminal segment is extended as in *Discoglossus*, whereas the praepollex of younger individuals consists of three segments, the terminal one being the smallest, as in *Bombina*. Moreover, some elements seem to be subdivided in *Genibatrachus* (Fig. 1I). This can be seen clearly in the area of the radiale, where there are two elements instead of one; the same holds for the distal radial element. An additional element within the area of the radiale may be evidence of a free centrale 4, similar to *Notobatrachus* (see below).

3.2. Comparisons of *Genibatrachus* with other Mesozoic anurans

Our sample of 38 individuals with carpi in various stages of ossification allows us to select those that can presumably be interpreted as fully-grown adults (Fig. 1G–I). These can be compared with adults of other Mesozoic frogs.

The earliest known frog-like amphibian *Triadobatrachus* from the Early Triassic of Madagascar, which was the evolutionary stage preceding that of true frogs, had well-ossified proximal carpal and tarsal elements (Rage and Roček, 1989; Ascarrunz et al., 2016). Although the distal portion of its carpus is broken off, in the remaining proximal portion are remnants of four elements – the ulnare and the radiale, unequivocally identifiable according to their position relative to the ulna and the radius, as well as one element of almost the same size between them (probably the intermedium), and one smaller element at a level distal to this proximal row (which could be centrale 4). Thus, the proximal portion of the carpus in *Triadobatrachus* was essentially the same as in Paleozoic temnospondyls.

Unfortunately, the earliest known anurans from the Late Triassic (Stocker et al., 2019), as well as *Prosalirus* from the Early Jurassic (Shubin and Jenkins, 1995; Jenkins and Shubin, 1998) are represented by disarticulated skeletal elements, hence they do not provide any information about their carpus.

The earliest known anuran carpus belongs to the Middle–Late Jurassic (Callovian–Oxfordian) *Notobatrachus degiustoi* (Fig. 2A; see also Báez and Basso, 1996; Báez and Nicoli, 2004; Estes and Reig, 1973). In addition to the radiale and the ulnare, which are identifiable according to their positional relations to the ulna and the radius, there is a small element between them which, according to its topographical position, is the intermedium. Another, much larger element between the radiale and the ulnare was interpreted by Estes and Reig (1973) as centrale 4. To date, this is the only known example of an anuran preserving this carpal element independently. Distal to the ulnare is a large distal ulnar element which contacts metacarpal V, so it could be centrale 3 + distal carpale 5. Distal to the radiale is a similar large element, which in the holotype may be taken as consisting of two incompletely fused elements, explaining why it was interpreted as a fused centrale 2 and centrale 3 by Estes and Reig (1973). Alternatively, Báez and Basso (1996) claimed that this large element may be formed of two contiguous elements. In *Notobatrachus reigi*, there is only one large element (Báez and Nicoli, 2008). In any case, this part of the carpus of *Notobatrachus* seems to be rather variable (Fig. 2A2). On its medial side is a large praepollex, consisting of two elements, the distal one being the smaller. The remaining three elements are distal carpalia 2–4, which are well separated from each other and lie close to the bases of the corresponding metacarpals. The carpus of adult, fully-grown *Genibatrachus* basically corresponds to the majority of specimens of both species of *Notobatrachus* (disregarding the above-mentioned variation within the area of the distal radial element), except for the absence of an independent intermedium and centrale 4 (unless the latter is represented in IVPP V19250A; Fig. 1I) and the larger distal segment of the praepollex.

Eodiscoglossus santoniae (Fig. 2B) is known from the Early Cretaceous (late Berriasian to early Valanginian, about 140 Ma) of Spain. In our figured example, its carpus is well preserved, displaying four principal elements: the radiale, ulnare, elongated distal ulnar element (interpreted here as carpale 3 + distal carpale 5; but as the fused centrale 2 and distal carpale 5 according to Vergnaud-Grazzini and Weinz, 1975, fig. 5) and distal radial element (centrale 1 + 2; centrale 1 according to Vergnaud-Grazzini and Weinz, 1975). It also comprises an independent and well-defined distal carpalia 2, 3 and 4, as well as a praepollex adjacent to the distal radial element and consisting of two segments, the

distal larger than the proximal. All these features basically correspond to *Genibatrachus*. In the holotype of *Eodiscoglossus santoniae* (Báez and Sanchiz, 2007; fig. 5B; Báez and Gómez, 2016), the praepollex is much longer, consisting of three or four elements (see also Hecht, 1970). Worth mentioning is a small swelling on the medial surface of the ulnare (marked in Fig. 2B by the arrowhead in the interpretative line drawing made by Vergnaud-Grazzini and Weinz based on the original specimen). This swelling may suggest an incorporated intermedium.

Carpi also are preserved in the Early Cretaceous (early Barremian to early Aptian, about 128–125 Ma) anurans from Liaoning Province of northeastern China (Dong et al., 2013), namely in *Liaobatrachus grabaui* (Fig. 2C, D), *L. beipiaoensis* (Fig. 2F, G, I) and in *L. macilentus* (Fig. 2H). All have the same basic structural scheme as *Genibatrachus* and *Eodiscoglossus*, especially a large distal ulnar element (spherical or elongate) and separate distal carpalia 2, 3, 4, not coalesced with any other adjacent element. However, *L. grabaui* seems to differ from adult, fully-grown *Genibatrachus* by having its praepollex tapering towards its end. By contrast, the terminal segment of the praepollex of *L. beipiaoensis*, which differs from *L. grabaui* in its more toad-like appearance (e.g. tibiofibula shorter than femur), is markedly expanded. A praepollex consisting of two segments, of which the terminal one is expanded (possibly consisting of two fused, distal segments), is a shared character of *Genibatrachus*, *Liaobatrachus beipiaoensis* and *L. macilentus*.

The distal radial elements of most *Liaobatrachus* specimens (Fig. 2C, D, F, G, H) and also of *Eodiscoglossus* (Fig. 2B) and *Nevo-batrachus* (Fig. 2K) are extended proximo-medially, such that it seems that all include centrale 1. In *Liaobatrachus* sp. (Fig. 2E) it appears that centrale 1 is still independent. If it persists until adulthood (as seems to be supported by the high degree of ossification) this feature may be of taxonomic importance (see also the praepollex tapering towards its end). Also worth mentioning is that centrale 4 in several individuals of *Liaobatrachus* is more or less fused with the radiale (Fig. 2F, H).

Nevo-batrachus gracilis from the late Early Cretaceous (Aptian, c. 118 Ma) of Israel displays the complete carpus in dorsal aspect (Fig. 2K). Its main distinguishing characters are a radiale with a markedly swollen ulnar part, thus possibly including centrale 4 or (less probably) the intermedium, and another independent, medium-sized element between the ulnare and the radiale, which may be an independent intermedium. Furthermore, although the distal radial element is markedly extended proximally along the medial margin of the radiale as in other anurans, it is adjoined by a small, independent element adjacent to its distal portion (Fig. 2K) – which may be centrale 2 if the main body of the distal radial element is centrale 1 – and a small praepollex consisting of two segments and not extending beyond the level of metacarpal II. Additionally noteworthy is a slender, sigmoid distal ulnar element, which is in contact with the radiale by its long proximo-medial extension. Judging by its shape, this sigmoid distal ulnar element consists of two portions, probably centrale 3 and distal carpale 5. As a whole, the carpus of *Nevo-batrachus* recalls that of *Xenopus* (Jarošová, 1973, figs. 9, 10). Distal carpalia 3 and 4 are fused with each other. A small bone adjoining the base of metacarpal III probably represents distal carpale 2, because judging by the position of the praepollex, the carpus is rather disarticulated and displaced. The elongate metacarpals and the slender, sigmoid distal ulnar element confirm the assignment of this taxon to pipoids.

The Early Cretaceous anuran *Kururubatrachus gondwanicus* from Brazil (Fig. 2L; Agnolin et al., 2020) has a relatively well-preserved carpus, although moderately rotated along the long axis of the forelimb, such that it does not display a strictly dorsal aspect. Nevertheless, it is clear that the ulnare is the biggest element within the carpus, probably because it includes another element of

about the same size. The radiale is much smaller. Both the distal ulnar and the distal radial elements are probably embedded in the sediment and partly overlapped by adjacent elements, so their true shapes and sizes are difficult to assess. The same holds for the praepollex, which is distally obscured by metacarpal II. Three distal carpals may be recognised, all slightly displaced from their original position relative to the metacarpals. Most remarkable is a big ovoid element in the centre of the carpus, which is obviously independent from all the surrounding elements. It is probably one of the centralia, but because it articulates with the radiale as well as with both the distal ulnar and the distal radial elements, it is not possible to assess its identity more precisely. In any case, that large ovoid element markedly differs from *Genibatrachus*.

4. Discussion

The earliest studies of anuran carpi were conducted at the beginning of the 19th century, when Dugès (1834) described them in adult *Rana* and a metamorphosing tadpole of *Pelobates*, using terminology for human anatomy. The terms 'radiale' and 'ulnare', respectively, were only introduced later by Gegenbaur (1864) who also recognised the intermedium and observed (in newts) its fusion with the ulnare. Moreover, Gegenbaur also discovered an independent element in the centre of the carpus, for which he introduced the term 'centrale'. Finally, he introduced the name 'carpalia' for distal elements located close to the bases of the metacarpals. He numbered them from 2 to 5, not because he believed the first digit to be lost, but because he deemed the praepollex a vestigial digit. Gegenbaur applied these terms first to caudate amphibians and subsequently extended them to anurans. However, he did not try to denominate two distinct elements located distal to the ulnare and radiale, because he suspected that they originated in several cartilaginous primordia whose identities were unknown. Emery (1890) then interpreted the first digit of Gegenbaur (1864) to be a praepollex. A basic scheme of the anuran carpus was completed as a result.

Schmalhausen (1907) then elucidated the early development of the anuran carpus as a series of fusions of precartilaginous components and cartilaginous nodules that result in the reduction of the ultimate number of elements, and he also showed that fusions may differ across taxa. This means that the elements of adults may involve different developmental components, such that they are not homologous even if they bear the same names. Thus, even though development of the anuran carpus has been studied in reasonable detail, interpretations of its components differ and sometimes remains unsettled.

As regards the carpus in fossil *Genibatrachus*, one should first take into account that the available fossils only represent the concluding stages of their development. Advanced amounts of ossification suggest that the terminal adult stage was attained only in some of them (Fig. 1G–I). The sequence of ossification of the carpus documented in our fossils provide tantalizing hints of sequence of events that preceded ossification, thus are not preserved. The fact that the sequence of ossification within the carpus (evidenced in fossils by the different sizes of their ossification centres) corresponds to the sequence of chondrification may be supported by the late appearance of the praepollex (Fig. 1D–F) and the late fusions of the distal

carpalia (Fig. 11) in *Genibatrachus*, both of which correspond to their late appearance in the majority of extant anurans studied (e.g. Fabrezi and Alberch, 1996; Fabrezi and Barg, 2001).

The composite structure of the fossil carpal elements may be inferred from observations of Ritland (1955, fig. 8D, E), who illustrated ossification centres stained by alizarin in the carpi of two immature *Ascaphus*. There were two separate ossification centres in the proximal elements (ulnare + intermedium on the ulnar side; and radiale + undetermined centrale on the radial side) and two (and possibly three, according to Ritland) centres in the distal radial element. Only one ossification centre was found in the distal ulnar element. The elements with two centres were elongate, suggesting that they had originated in more than one centre. The proximal ulnar element (ulnare + intermedium) of fully ossified adults (Ritland, 1955, fig. 8B, C) still manifested the presence of an incorporated intermedium as a distinct convexity on its surface. Similarly, a single ossification centre in the distal ulnar element corresponded to this element's quasi-circular shape, both in immature and mature individuals. These observations in *Ascaphus* suggest that spherical carpal elements of *Genibatrachus* also represent ossification centres.

The development of the carpus of *Genibatrachus* as a whole begins on the ulnar side, as is the case with *Bombina* (Roček et al., 2021) and, with some variation, other anurans (Fabrezi and Barg, 2001). The ulnare, or the first nodule of the distal ulnar element, appears when all four metacarpals are already ossified. The distal ulnar element is ovoid in shape but soon begins to extend on its radial side (Fig. 1B, C), probably indicating the inclusion of an additional element which, according to its position, could be identified as centrale 4. A similar extension may be found in the ulnare (Fig. 1D2, E), where it reflects the inclusion of the intermedium. As a consequence, both the distal ulnar element and the ulnare acquire a transversely elongated form, exactly as is the case with extant *Bombina* and *Discoglossus* (Jarošová, 1973, figs. 11, 12). In the largest individuals (Fig. 1H, I), the distal ulnar element expands towards the proximal end of metacarpal V. This process is not clearly discernible on the shape of the distal ulnar element, but because it fills the space between the distal ulnar element and metacarpal V (and by analogy with *Bombina* and *Discoglossus*; Roček et al., 2021; Jarošová, 1973) it can be inferred that distal carpal 5 was incorporated into the distal ulnar element. This is preceded by or simultaneous with distal carpal 4.

The development on the radial side is markedly delayed, but similar. The distal radial element grows in size as a single nodule, simultaneously with the radiale. Then the space between the two becomes filled with a mass that is difficult to differentiate from the adjacent elements (Fig. 1D2), but as may be inferred by analogy with *Discoglossus* (Jarošová 1973, pl. VIII, figs. 2, 3), it can be (or it can become) a part of the distal radial element. The main body (and originally the earliest part) of the distal radial element may be interpreted as the centrale 2. The ultimate ossified distal radial element consists at least of centrale 2 + centrale 1, + a proximal extension, which Jarošová termed the 'carpal praepollicis' (and 'element Y' by Schmalhausen, 1907). One can only speculate about the identity of the two elements in the area of the radiale in some adults (Fig. 11), because it has no analogue in other extant frogs;

of fragmentary skeleton. D – *Liaobatrachus grabaui*, right carpus in dorsal aspect, MV 77, reversed for comparisons (see also Dong et al., 2013, fig. 3C1). SVL 77.3 mm. E – *Liaobatrachus* sp., right carpus in ventral aspect, LPM 0203. SVL 76.8 mm. F – *Liaobatrachus beipiaoensis*, right carpus in ventral view, holotype LPM 0030. SVL ca. 60.0 mm. G – *Liaobatrachus beipiaoensis*, right carpus preserved as natural cast, DNM D2167 (see also Dong et al., 2013, fig. 4B1, B2). SVL 65.8 mm. H – *Liaobatrachus macilentus*, right carpus in ventral aspect, IVPP V12510 (see also Dong et al., 2013, fig. 5B1). SVL 56.7 mm. I – *Liaobatrachus beipiaoensis*, right carpus in ventral aspect, IVPP V12717 (see also Dong et al., 2013, fig. 4C1). SVL 76.2 mm. J – *Liaobatrachus* sp., right carpus in dorsal aspect, reversed (CYGYB-002). SVL 86.8 mm. K – *Nevobatrachus gracilis*, holotype, left carpus in dorsal view (HUJZ F165). SVL ca. 27.5 mm. L – *Kururubatrachus gondwanicus*, holotype (UFRJ-DG 08), left carpus in dorso-lateral aspect. SVL 41.3 mm. Image courtesy Federico Agnolin. Mc V – metacarpal V, given for orientation. Except for A, interpretative drawings are on the right. Not to scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

only the Early Jurassic *Notobatrachus* (Fig. 2A2) has an additional element between the ulnare and the radiale, which was considered to be centrale 4 by Estes and Reig (1973, fig. 1–6) and Báez and Nicoli (2008, fig. 3–5).

The formation of the definitive distal radial element was simultaneous with the development of the praepollex, which seems to bud from its radial side (Fig. 1D2, E). It later differentiates, probably by additional growth, into three segments, of which the distal one is the smallest (Fig. 1F). This praepollex is similar to adult *Bombina* (Roček et al., 2021, fig. 7) and to *Liaobatrachus* (Fig. 2D, E). However, fully-grown adults of *Genibatrachus* (judging by the complete series of distal carpalia 2–4, some of which are even fused together; Fig. 1H, I) have a different praepollex, consisting of only two segments, the proximal smaller and the distal larger and triangular in shape. This praepollex is similar to that of *Discoglossus* (Jarošová, 1973) and most of *Liaobatrachus*. Thus, the question arises as to how the tripartite praepollex of adult but not fully-grown *Genibatrachus* could develop into the definitive shape of the praepollex in fully-grown *Genibatrachus*. A possible answer is that the large, distal, shovel-like segment could arise by fusion of the two distal segments, but there is no palaeontological evidence of this. Conversely, the carpus of *Bombina* with a tripartite praepollex can easily be derived from discoglossoid ancestors (*Eodiscoglossus*, *Latonia*) by simple abbreviation of the development of its carpus.

5. Conclusions

There were four dominant elements in the carpus of adult *Genibatrachus*, all approximately spherical in shape. Using the terminology applied to temnospondyls, which are considered ancestral to anurans, the ulnare is in fact the ulnare itself + intermedium, the distal ulnar element consists of centrale 3 + distal carpal 5 and the distal radial element ('element Y' according to some authors) consists of centrale 2 + centrale 1, the latter characterised by its comparatively long proximo-medial extension. The radiale in *Genibatrachus* consists of a single element, but this can be accompanied by an independent centrale 4 in some individuals. A praepollex consisting of two segments (large terminal and small proximal) is characteristic for adult, fully-grown *Genibatrachus* (Fig. 1G–I) but may be also found in some, but not all, Early Cretaceous *Liaobatrachus* (Fig. 2F–H), *Eodiscoglossus* (Fig. 2B), and in extant *Discoglossus*. Given that the carpus of temnospondyls comprised larger number of ossified elements than the anuran carpus, it may be hypothesized that origin of frogs was associated with reduction of the carpals either by their fusion with adjacent elements or by their disappearance in the pre-ossified period of development. This process can be elucidated by size and morphology of preserved carpal elements in *Genibatrachus*.

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