



Loss of carpal elements in crocodylian limb evolution: morphogenetic model corroborated by palaeobiological data

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The comparison of bone homology between the manus of an Early Cretaceous fossil crocodile and that of the extant species *Alligator mississippiensis* supports explicitly, for the first time, the hypothesis of carpal loss in crocodylian limb evolution. This hypothesis, based on a developmental model of the organization of the tetrapod limb, is in accordance with the fossil evidence, and may supersede traditional Haeckelian views based on recapitulatory paradigms. The homologous relationships of carpal elements reveal the existence of two carpal patterns—one plesiomorphic and one apomorphic—in the crocodylian lineage. Phylogenetic change is explained causally by alterations of the osteogenesis of the distal carpals 2 and 3, which remain unossified in extant crocodile adults. This implies that crocodylian limb evolution is constrained by a process of paedomorphosis. This modification of the architecture of the crocodylian hand is a terminal event of its evolutionary history, affecting only eusuchian crocodiles. The results of this study contest the traditional view that the skeletal pattern of the crocodylian limb has been conserved unchanged since the Triassic.

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ADDITIONAL KEY WORDS—Archosauria – Crocodylia – palaeontology – embryology – limb evolution – heterochrony.

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INTRODUCTION

The homology of the carpal and tarsal elements in living archosaurs (crocodiles and birds) is an important and yet controversial evolutionary issue (Hinchliffe & Hecht, 1984; see also Shubin, 1994 for a detailed revision of the evolution of the phalangeal formula on the archosaurian hand). Although the theme has been widely discussed in birds, much less attention has been paid to the crocodiles. The present paper concentrates on the problem of the homology of the carpus of the crocodilian hand. Traditionally, recapitulatory paradigms were invoked in order to explain the evolution of the archosaurian limb (Holmgren, 1933; Romer, 1956; Romer & Parsons, 1981; Hinchliffe, 1985, 1991). These explanations argue that the embryonic carpal patterns recapitulate a generalized archetype (in number and skeletal elements), whereas a secondary set of fusions between carpal elements would produce the final adult pattern. According to the classical embryological studies 13 pre-cartilage condensations would represent the initial condition in the morphogenesis of the hand, and the subsequent fusions that take place during development would result in the reduced number of six carpals (Fig. 1A). As a result, diverse interpretations regarding the fusion processes were forwarded. One of the central issues of debate was the fate of distal carpals 1 and 2. The diverse scenarios propose that distal carpal 1 could alternatively become fused to: (a) its metacarpus, (b) the centrale, or (c) distal carpal 2, resulting in each case in different homological relationships (see Figs 1A and 2, and Müller & Alberch, 1990 for a discussion of this issue).

The alternative morphogenetic model proposes that a numerical reduction of the primary chondrogenetic condensations occurred in crocodilians, when compared with an ancestral reptilian condition (i.e. Chelonia) (Burke & Alberch, 1985; Müller & Alberch, 1990). The homological assumptions provided by this model are based on the sequence of appearance and connectivities between the chondrogenic elements during early development according to the morphogenetic rules governing the organization of the tetrapod limb (Shubin & Alberch, 1986). Based on the re-interpretation of carpal homology provided by this model, the crocodilian hand of the extant species *Alligator mississippiensis* initially has a lesser number of carpal elements, comprising a total of seven. During later development additional secondary modifications occur. Thus, the architecture of the adult hand would result both from primary pattern changes and from secondary remodelling during the final embryonic and postnatal ontogenetic stages (see Fig. 1B).

Therefore, the pattern of the adult manus of modern crocodiles is explained by very different processes depending on which hypothesis (recapitulationist or morphogenetic) is used. Neither of these opposing hypotheses have hitherto been tested in crocodiles using the fossil evidence. The central issue of this comparative study is to determine the pertinence of the carpal loss hypothesis and to elucidate the conflict on carpus homology in crocodilians. The objective is to confront palaeobiological and embryological data, with the assumption that the observed variability patterns (at genus and family levels) of the number of ossified carpals, when integrated with developmental mechanisms, may provide decisive information on the homology and evolutionary process of generation of the crocodilian manus.

PALAEOBIOLOGICAL DATA

The carpus of Recent crocodiles is composed of a row of three proximal carpals (radiale, ulnare and pisiform), one cartilaginous central carpal, and a row of distal

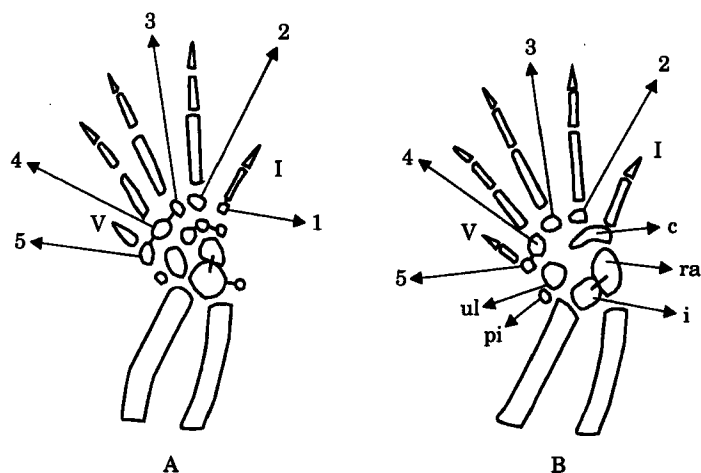


Figure 1. Schematic drawings of the chondrogenetic condensations and fusions in the crocodilian carpus. A, hypothesis generated by recapitulationist interpretations (after Müller & Alberch, 1990). B, the carpal loss hypothesis generated by Müller & Alberch (1990). Abbreviations: proximal carpals, ra(radiale), ul(ulnare) and pi (pisiform), i (intermedium); the central carpal c (centrale); the distal carpals (1-5), and the digits (I-V). Bars indicate secondary fusions of condensations.

TABLE 1. Sample of crocodilian fossil taxa in which the number and identification of distal carpals, taken from the literature, are recorded

Taxa	Number of ossified distal carpals	Identification
Crocodylomorpha:		
<i>Dibothrosuchus</i>	1	3 + 4; Wu & Chatterjee, 1993
<i>Terrestrosuchus</i>	1	3 + 4; Crush, 1984
Crocodyliformes:		
<i>Orthosuchus</i>	2	1 + c; 3 + 4; Nash, 1975
<i>Sichuanosuchus</i>	2	1 + c; 3 + 4; Peng, 1995
<i>Protosuchus</i>	1	3 + 4; Colbert & Mook, 1951
Mesocrocodylia:		
Atoposauridae		
<i>Atoposaurus oberndorferi</i>	3, 2 and 1	3
<i>Alligatorellus beaumonti</i>	1, and 2	none; Wellnhofer, 1971
<i>Alligatorium meyeri</i>	1	ib.
' <i>Alligatorium</i> ' <i>paintenensis</i> (attributed to a goniopholidid)	3	none; Wellnhofer, 1971
Thalattosuchia:		
<i>Steneosaurus bollensis</i>	3, 2 and 1	1
<i>Teleosaurus cadomensis</i>	3	3 + 4 + 5; Westphal, 1962
<i>Steneosaurus</i>	2	none; Deslonchamps, 1870
<i>Steneosaurus</i>	2	per. obs.
Eusuchia	1	3 + 4 + 5 or 3 + 4; Romer, 1956; Kalin, 1955

carpals. In the adult hand of extant crocodiles the distal row is composed of two elements, one cartilaginous lamella and one large ossified element. This row has been the subject of major controversy concerning its identification and homology and our analysis will be centred on this issue.

Data about the number of ossified carpals are not infrequent from the fossil record. Table 1 reflects the variation in number of ossified distal carpals in the

crocodilian fossil record. Up to three ossified elements have been recorded. Their identities were postulated based on classic embryological studies and the assumption of the existence of an invariant number of distal carpals since the origin of the group during the Upper Triassic (Romer, 1956). The idea of a conservative hand was supported by the palaeobiological data, because the early crocodile *Protosuchus*, from the Lower Jurassic, had one large ossified distal carpal preserved (Colbert & Mook, 1951). Therefore, in instances when only one large ossified element was preserved, the palaeobiological evidence seemed to confirm the existence of the same number of carpal elements as in their living relatives (six carpals). The identification of the unique ossified element as a distal carpal follows the same homological relationship as present in extant species (the fusion of distal carpals 3+4; see the cases of *Terrestriusuchus* and *Dibothrosuchus* in Table 1). On the other hand, when two ossified elements are preserved their presence is taken as a diagnostic character of the species, and the extra element is identified as one of the fusions proposed (i. e. distal carpal 1 fused to the centrale; see Table 1 for the cases of the Upper Triassic crocodile *Orthosuchus* and the Jurassic and Early Cretaceous protosuchid *Sichuanosuchus*). Finally, a controversy emerges when three ossified elements appear in the distal row (see Table 1 for the cases of Atoposauridae, a dwarf lineage of neosuchian crocodiles from the Upper Jurassic and Lower Cretaceous, and the *Thalattosuchia*, neosuchian marine crocodiles). In these latter cases, no identification was proposed, pointing to a strong conflict between the embryological interpretations of extant species and the palaeobiological data. In the recapitulatory approaches in which the adult hand results from fusions of distal carpals 3+4+5, and the fusion of 1+2, or 1 plus its metacarpal (see Fig. 2), the presence of three distal carpals was not considered. The alternative was Romer's proposal (1956), in which the distal row should result from the fusion of the distal carpals 3+4, distal carpal 2 should be the unique constitutive element of the cartilage lamella, and distal carpal 1 becomes fused to the centrale. This fusion pattern is the only case in which three distal carpals can exist, although this was never suggested as a homological relationship in fossils. In summary, the occurrence of three distal ossified carpals was unexpected in the crocodilian hand, and their identification was highly controversial based on the prevailing embryological hypothesis.

The exceptional preservation of some new fossils allows a much more precise description of the spatial skeletal patterning of the early crocodilian hand (Fig. 3A). Such individuals represent key specimens for deep revisions of skeletal homology and evolutionary change (*Ichthyostega* and *Acanthostega*, Coates & Clack, 1990; *Archaeopteryx*, de Beer, 1954). One such the case is the tiny Barremian Las Hoyas crocodile, a subadult individual of about 15 cms of total length. The Las Hoyas crocodile (LH-7991) has gracile and parasagittal forelimbs, with notably elongated proximal carpals (radiale and ulnare) showing the diagnostic condition of codylomorphs. In this specimen, both hands have been preserved in an almost articulated condition. A flat ovoid pisiform rests at the side of the ulnare. There are three distal carpals, the largest one in contact with the ulnare. This distal carpal has two depressed surfaces on both sides of a tall crest, proximally articulating with the ulnare and distally and laterally with the metacarpals IV and V respectively. The other two distal carpals are independent elements. The most lateral one is placed between the largest distal carpal and the metacarpal III, while the other contacts the metacarpal II. The manus can be fully reconstructed, and it has the following phalangeal formula: 2/3/4/4/3 (Fig. 3B). Digit I is the shortest, probably

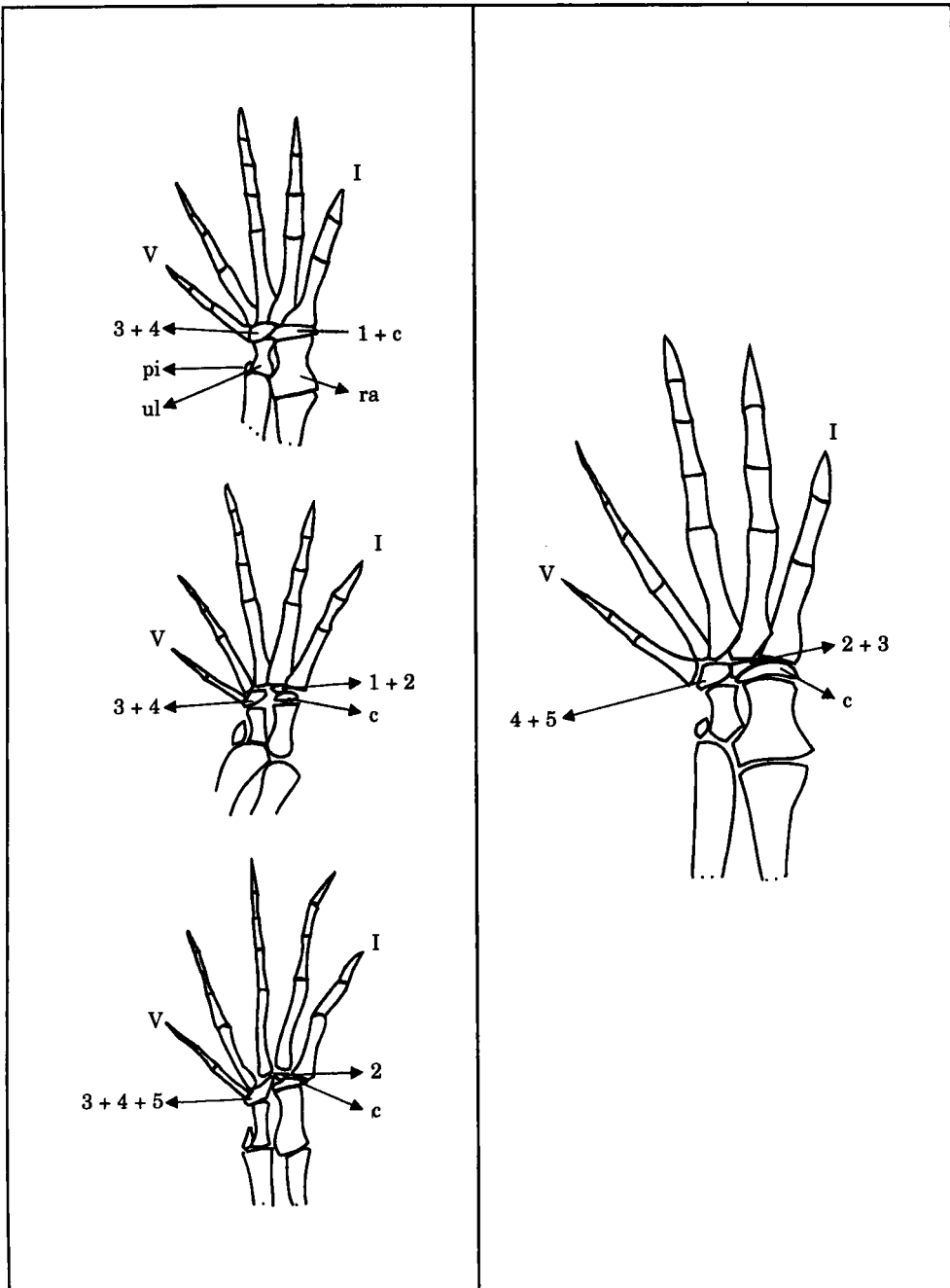


Figure 2. Different proposals for the identification of carpal elements in the adult manus of recent crocodiles. At left, from top to bottom: Romer (1956); Romer & Parsons (1981), and Kälin (1955). The representation on the right corresponds to Müller & Alberch (1990).

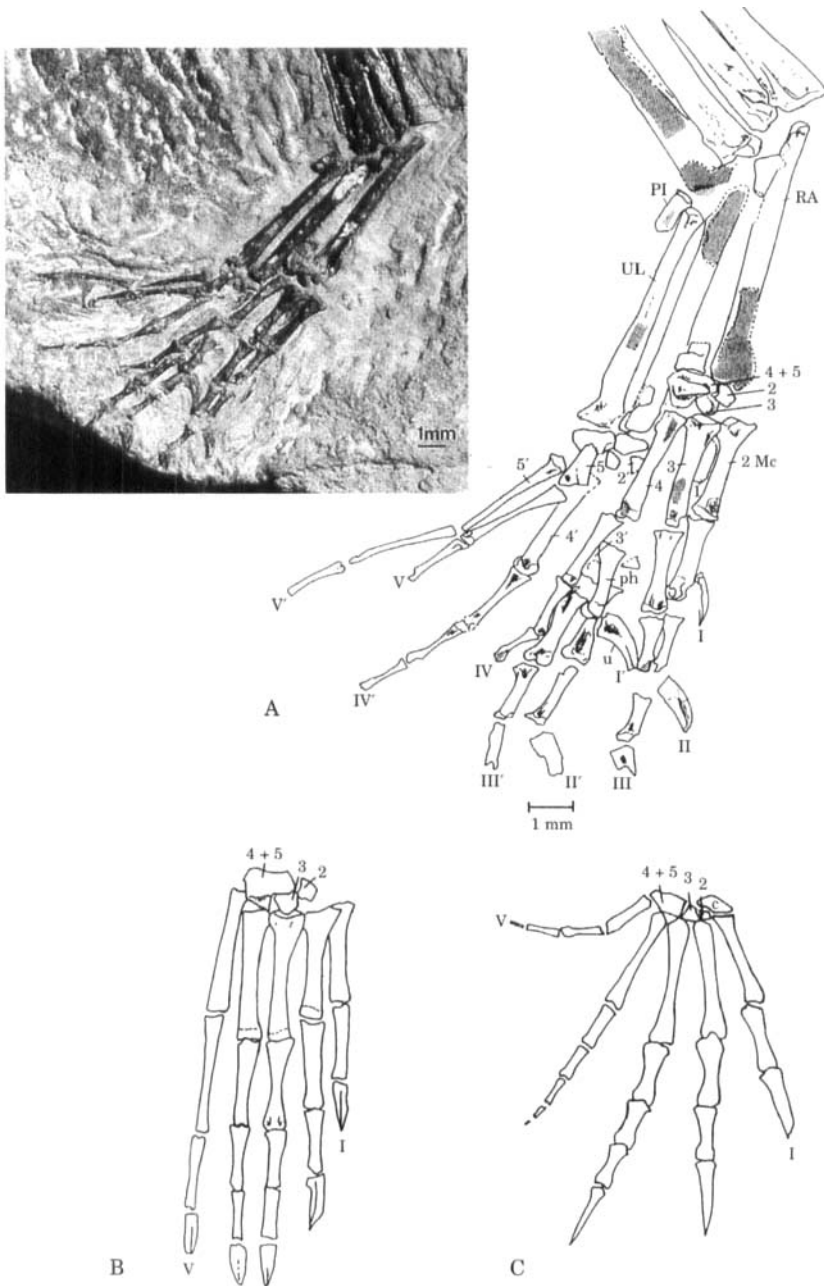


Figure 3. A, manus and carpal elements of the Las Hoyas crocodile (LH-7991) from the Lower Cretaceous (Upper Barremian) of Spain (province of Cuenca). Abbreviations as in Figure 1, and Mc, metacarpals (1–5 right hand, 1'–5' left hand); Ph, phalanx; u, unguis. B, reconstruction of the hand of LH-7991. C, hand of an *Alligator mississippiensis* embryo at stage 24 (modified from Müller & Alberch, 1990). Note that the centrale (c) of the embryonic limb remains as cartilage in the adult and would therefore not be preserved in the fossil record.

displaced palmarly from the remaining metacarpals, with a large unguis and a proximal phalanx developing asymmetrical condyles. Digit II is equal in length with digit V, and digits III and IV are the longest ones. All digits have slender and long phalanges, a feature even more accentuated in digit V.

The revision of extinct taxa in the lineage of crocodiles reveals that the variation in the carpal number is limited (see Table 1). The maximum number of ossified distal carpals is three. Preservational bias might exist in the cases in which one, two or three ossified elements are recorded, such as the protosuchids, the family Atoposauridae, and Thalattosuchia. On the other hand, modern crocodiles, that is the eusuchians, represent a homogeneous group in which all members of the clade only possess one large distal element.

HOMOLOGIES OF CARPAL BONES

The analysis of the early development of *Alligator mississippiensis* carried out by Müller & Alberch (1990) shows the digital arch as originating as an anterior branching of the primary axis (distal carpal 4 and metacarpal IV being components of it). The arch will give rise to distal carpals 3 and 2. Distal carpal 5 appears as a *de novo* condensation, while the distal carpal 1 completely fails to differentiate. During the final embryonic stages and postnatal life, remodelling of the primary pattern, ossification and fusion occur. Distal carpal 4 + 5 develops an osseous nucleus and distal carpals 2 and 3 together form a cartilaginous lamella.

The Las Hoyas crocodile shows the same spatial distal carpal patterning as the one described in the final embryonic stages (17–24) of the extant *Alligator*. This comparison is valid from a strict topological correspondence criterion. By comparing the topographic connections of the Las Hoyas crocodile with *Alligator* embryonic stages, the two small distal carpals of the fossil associated with metacarpals II and III, remaining independently differentiated elements, can be clearly identified as distal carpals 2 and 3. On the other hand, the largest distal carpal, the unique element linked to metacarpals IV and V, is identified as distal carpal 4 + 5 (see Fig. 3B,C).

The spatial relationships of distal carpals in the fossil strongly support the Müller & Alberch bone homology, in which three differentiated elements appear: distal carpals 2 and 3 are independent elements, and 4 and 5 become fused. This supports also the assumption that distal carpal 1 fails to differentiate in Crocodylomorpha. Based on this evidence, first, the restricted number of carpals found in the fossil record cannot be explained as a random event, and second, the similarity in the carpal patterning of the fossil and the embryonic stages of *Alligator* discards the possibility that other fusion events may have occurred, since the independence of dc2 and dc3 falsifies all the classic proposals.

HETEROCHRONY AND PHYLOGENETIC CHANGE

When the homology is considered, and the number of ossified distal carpals are mapped onto a phylogenetic hypothesis of the Crocodyliformes (see Figs 4 and 5), the most parsimonious interpretation asserts that there is a reduction in the number

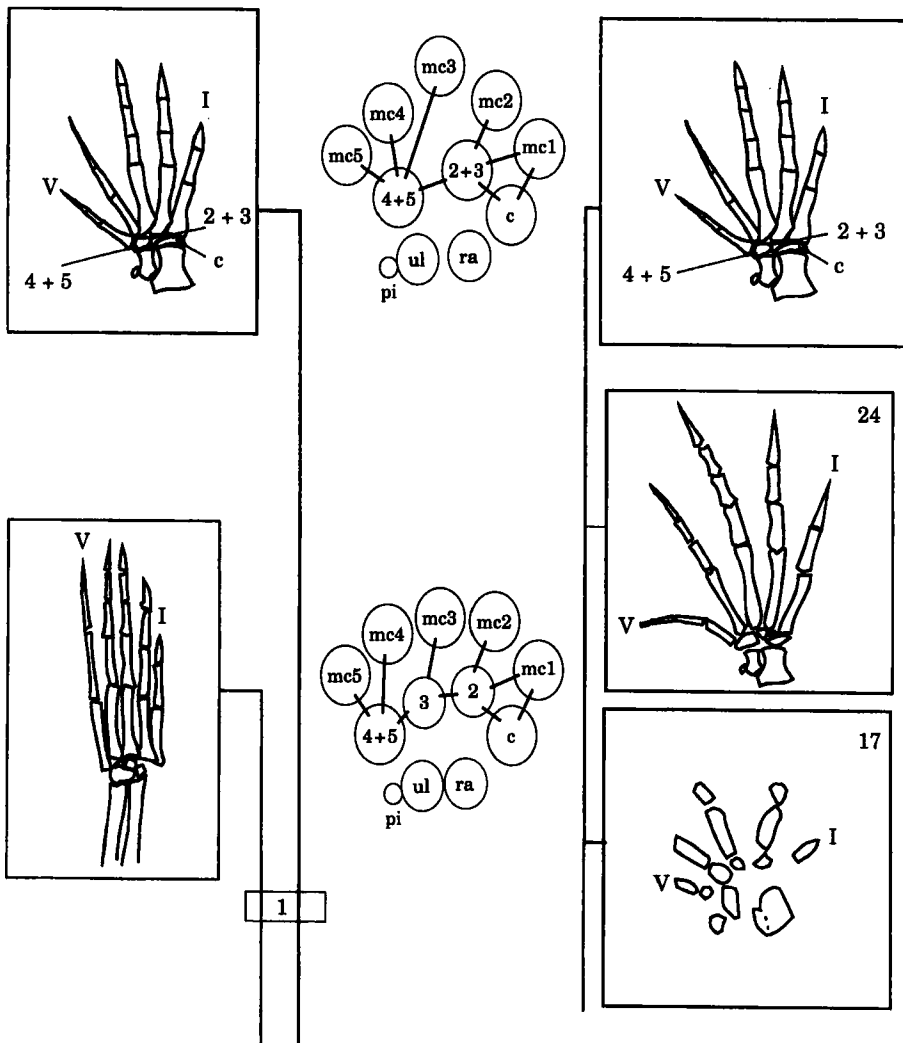


Figure 4. Schematic drawing showing the ontogeny of *Alligator mississippiensis* limbs (right), and the phylogeny of Crocodyliformes limbs (left) (node 1 is Crocodyliformes, see Figure 5 for a cladistic representation). The identification of carpal elements is based on topographical correspondence criteria. The topographic connections of the distal carpals reveal the similarities in spatial relationships of the fossil and the embryonic stages (17–24). Abbreviations: mc, metacarpals; c, centrale, 2,3,4 and 5, distal carpals; ra, radiale; ul, ulnare; pi, pisiform; I and V, digits.

of distal carpals (the dc1 fails to differentiate). This reduction implies a deviation from the ancestral condition, an evolutionary novelty shared by all the crocodyliforms. This evolutionary modification is based on a heterochronic alteration of the primary pattern of development of the crocodylian hand, the delay of the segmentation process that would have given rise to dc 1 in the digital arch (see Müller & Alberch, 1990; Müller, 1991).

Consequently, the presence of three ossified elements in the distal carpal row of crocodiles must be regarded as the plesiomorphic condition (Fig. 5). This condition

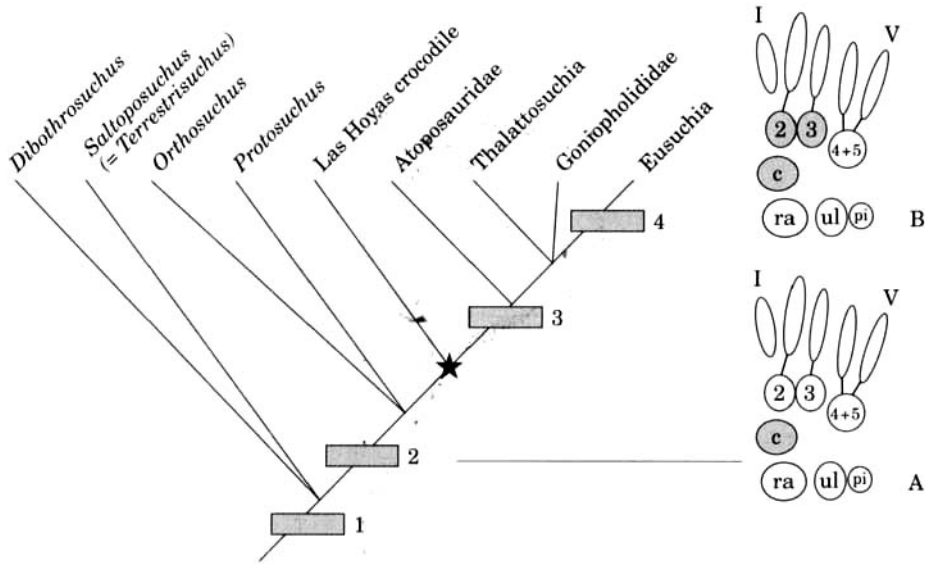


Figure 5. Cladogram showing the taxa utilized to evaluate the variation in the carpal number throughout the Crocodyliformes. The phylogenetic hypothesis is based on Clark (1994). In the depicted cladogram the original terminal taxa have been replaced by major monophyletic groups; taxa that do not contain information on the carpal number have been eliminated. Although *Sichuanosuchus* is absent in the cladogram, it is considered the sister taxon of *Protosuchus* after Wu & Sues (1995). The division of the main monophyletic clades from Clark (1994) are: Node 1, Crocodylomorpha; Node 2, Crocodyliformes; Node 3, Mesoeucrocodylia and Node 4, Eusuchia. According to the diagnoses of these nodes the Las Hoyas crocodile is phylogenetically placed as the sister taxon of Mesoeucrocodylia. It shares several apomorphies with the mesoeucrocodylians (i.e. the presence of fused frontals, and the basisphenoid shorter than the basioccipital), but it also shows a set of primitive characters that are derived in the members of this taxon (i.e. palatines do not form a secondary palate, and the anterior process of the ilium similar in length to the posterior process). See also Buscalioni et al. (1996), for a discussion of the phylogeny of the Las Hoyas crocodile.

At nodes 2 (Crocodyliformes) and 4 (Eusuchia), the number and nature of distal carpals are graphically represented assuming the most parsimonious distribution of these features in the clade. A shows the plesiomorphic condition, and B the apomorphic one. These diagrams contain the proximal carpals (ra, ul and pi), the central one (c), distal carpals 2–5 and metacarpals I–V. The cartilaginous elements are shadowed. The phylogenetic change depicts a pedomorphosis event, because distal carpals 2 and 3 are ossified in the plesiomorphic hand while osteogenesis is truncated in the descendant lineage (Eusuchia), in which these two distal carpals remain unossified and became fused into a singular cartilaginous lamella in the adult hand.

should be defined as follows: three proximal carpals, one centrale, and three ossified distal carpals (2, 3 and 4 + 5). In contrast, the apomorphic condition has a reduction in distal carpal number, 2 + 3 and 4 + 5 being the former cartilaginous pairs. An alternative, less parsimonious solution should explain the presence of three ossified elements in the neosuchians Atoposauridae and Thalattosuchia as a homoplastic condition reflecting, nonetheless, the ancestral one.

The carpal pattern of the Las Hoyas crocodile suggests how this transformation took place in the evolution of the crocodylian hand (Fig. 5). Since osteogenesis of distal carpals 2 and 3 is altered throughout phylogeny (from fully ossified, in non-Eusuchia taxa, to unossified, in Eusuchia), the major mechanism operating in the evolution of the crocodylian hand seems to be pedomorphosis. An earlier termination

of the developmental processes occurs in the extant lineage of Eusuchia (see also Müller, 1991).

The evolutionary change in eusuchians is accomplished throughout the modification of the primary pattern during later stages of ontogeny. This modification affects the initial number of carpal elements through the fusion of the two unossified distal carpal elements 2 and 3. Thus, the final differentiation that takes place to produce the adult hand of the extant species must actually be considered as an evolutionary novelty of this clade.

Therefore, the phylogenetic changes that occur in the crocodylian limb evolution are bounded by two sequential morphological novelties dealing with loss of carpal elements; the first concerns the early developmental phases of limb organization, and the second the later stages of ontogeny. Underlying these transformations are heterochronic alterations of the hand morphogenetic processes considered causal in the generation of the morphological novelties; an apparently common occurrence in the transformations of the skeletal organization in vertebrate limb evolution (Müller, 1990, 1991; Müller & Wagner, 1991).

CONCLUSIONS

The information provided by palaeobiological data is found to be a powerful tool. The use of this information has been advocated because variability patterns, phylogeny and embryological transformational sequences are mutually contrasted (Patterson, 1981; Shubin & Wake, 1996). The combination of ontogenetic and palaeobiological data in the present study has three main implications:

- (1) Corroboration of the homological relationships of carpal identity in crocodiles proposed by the hypothesis of carpal loss by Müller & Alberch (1990), based on studies of *Alligator mississippiensis* development.
- (2) Refutation of the general view that the crocodylian limb skeleton is a conservative structure since the Triassic.
- (3) Suggestion that two carpal patterns (one plesiomorphic and one apomorphic) exist in the crocodylian hand, representing the phylogenetic change constrained by an alteration of the developmental process.

This new picture replaces the traditional view of a conservative evolution of the crocodylian limb with a more dynamic one, in which the hand of modern crocodiles is explained and considered as a highly derived structure. The fact that the carpal pattern of living crocodiles is apomorphic within the Crocodylomorpha must be born in mind when using extant species as direct representatives for all crocodylomorphs, and might also affect further interpretations of developmental studies in archosaurs.

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