

SEQUENCE OF OSSIFICATION IN THE SKELETON OF
GROWING LIZARD *CHALCIDES OCELLATUS* FORSCAL
(SCINCIDAE, REPTILIA)

By

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Key words: Lizard, Ossification Pattern.

ABSTRACT

The distribution of cartilaginous and ossification rudiments were described in the live-bearing lizards, *Chalcides ocellatus*, at birth, one-month-old, and 12-month-old. The skeletal elements investigated are: neurocranium, dermatocranium, visceral skeleton, vertebral column, ribs, sternum, appendicular skeleton and sesamoids and the ossification time for every skeletal element rudiment was recorded. Some variation occurs in sequence of ossification. The present results were compared with those reported for other reptiles.

INTRODUCTION

Many studies have been made on the osteology of lizard skeleton, head region structure (Kamal, 1965; DeBeer, 1937; Bellairs and Kamal, 1981), vertebral components (Williams; 1959; Winchester and Bellairs, 1977), appendicular skeleton (Sewertzoff, 1908; Holmgren, 1933; Romer, 1956; Burke and Alberch, 1985) and ossification types in reptiles (Haines, 1969). Development of a wide variety of vertebrate tissues, bone and cartilaginous skeletal elements, is characterized by a precise sequence of events or interactions which control differentiation and morphogenesis (Hall, 1984).

The present study describes the ossification of the skeletal elements at birth and those appearing after birth of the live-bearing lizard, *Chalcides ocellatus* Forskal. The knowledge of ossification timing in the present lizard may shed light on phylogenetic relationship among different reptiles and allows for comparing this timing and sequence of skeletal elements ossification with those of other reptiles.

MATERIALS AND METHODS

Specimens of *Chalcides ocellatus* were obtained from gardens in Umm-Salal-Mohammed in the State of Qatar. All lizards were reared in the laboratory at $28^{\circ}\text{C} \pm 2$, a photoperiod of 12 hr/day and mean relative humidity of 48% and fed on tomato and cucumbers.

Samples of 5 or 6 lizards were studied on birth day, one-month-Old (1MO) and 12-month-Old (12MO). For describing the ossification pattern in the skeletal elements, specimens were stained with alcian blue (McCann, 1971) followed by alizarin red S (Dawson, 1926) and examined using stereoscopic microscope at a magnification of X30.

For general histological examination, specimens at birth and at 1MO were fixed in Bouin's solution, the fore and hind limbs were removed, embedded in paraffin, sectioned at $7\ \mu\text{m}$, and stained with haematoxylin and eosin. For more detailed characterization of epiphysis at 1MO, the proximal humerus end was examined using the basic techniques of Mallory trichrome stain. Whenever possible, the nomenclature of DeBeer (1937), Romer (1956) and Bellairs and Kamal (1981) was adopted in the present study.

RESULTS

Head skeleton (Figs. 1 - 3)

At birth, the skull pattern is visible since each rudiment appears as a cartilaginous or ossification centre. In the neurocranium, ossification occurs in the basioccipital, exoccipital, supraoccipital, opisthotic, prootic, orbitosphenoid, sclerotic plates, parietal, frontal, nasal, septomaxilla, lacrimal, prefrontal, postfrontal, supratemporal, squamosal, jugal, vomer, and parasphenoid. In the splanchnocranium, ossification is identified in the premaxilla, maxilla, palatine, pterygoid, mid of epipterygoid, ectopterygoid and a large part of quadrate. Also, ossification occurs in the angular, dentary and coronoid of the mandible arch. Meckel's cartilage remains cartilaginous and much of it is ensheathed by bones. Only ceratobranchial-1 is ossified in the hyoid apparatus.

At One-month-Old, the pterygoid surface adjacent to the basipterygoid and the columella tip and around its footplate are still cartilaginous. There are cartilaginous zones between certain ossified bones: between prootic and opisthotic, between basisphenoid and basioccipital, and between basioccipital and opisthotic. In the lower jaw, the Meckel's cartilage and the articular surface are still cartilaginous. The hyoid body is ossified entirely while the free end of the processus lingualis is still cartilaginous. The three cornua of the hyoid are ossified except for their free ends which remains as cartilaginous rudiments.

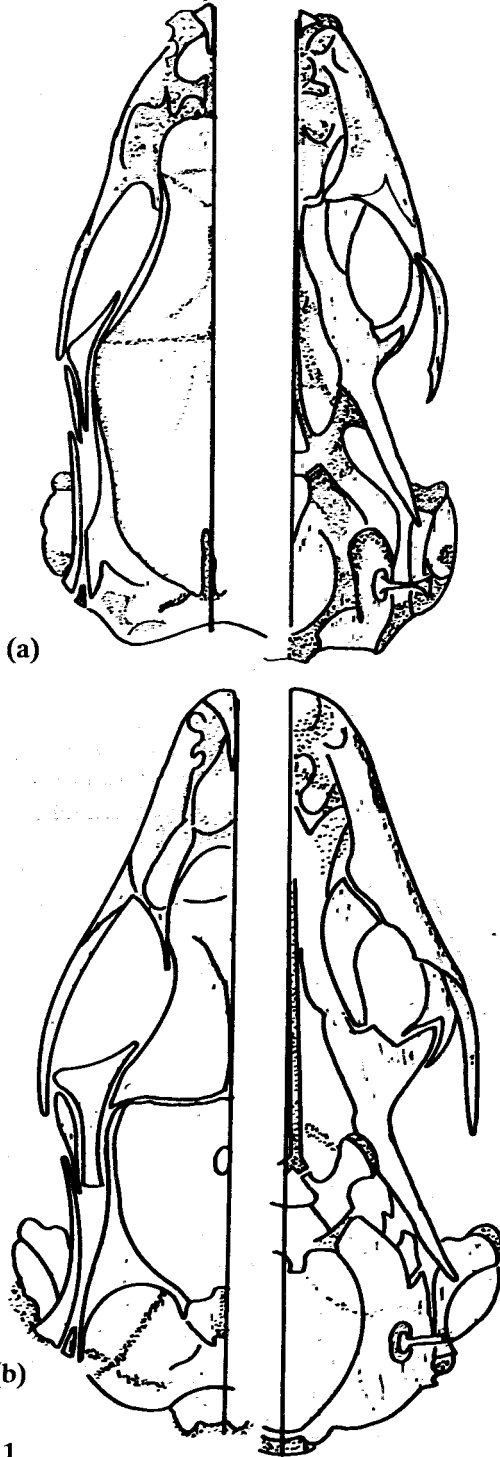


Fig. 1

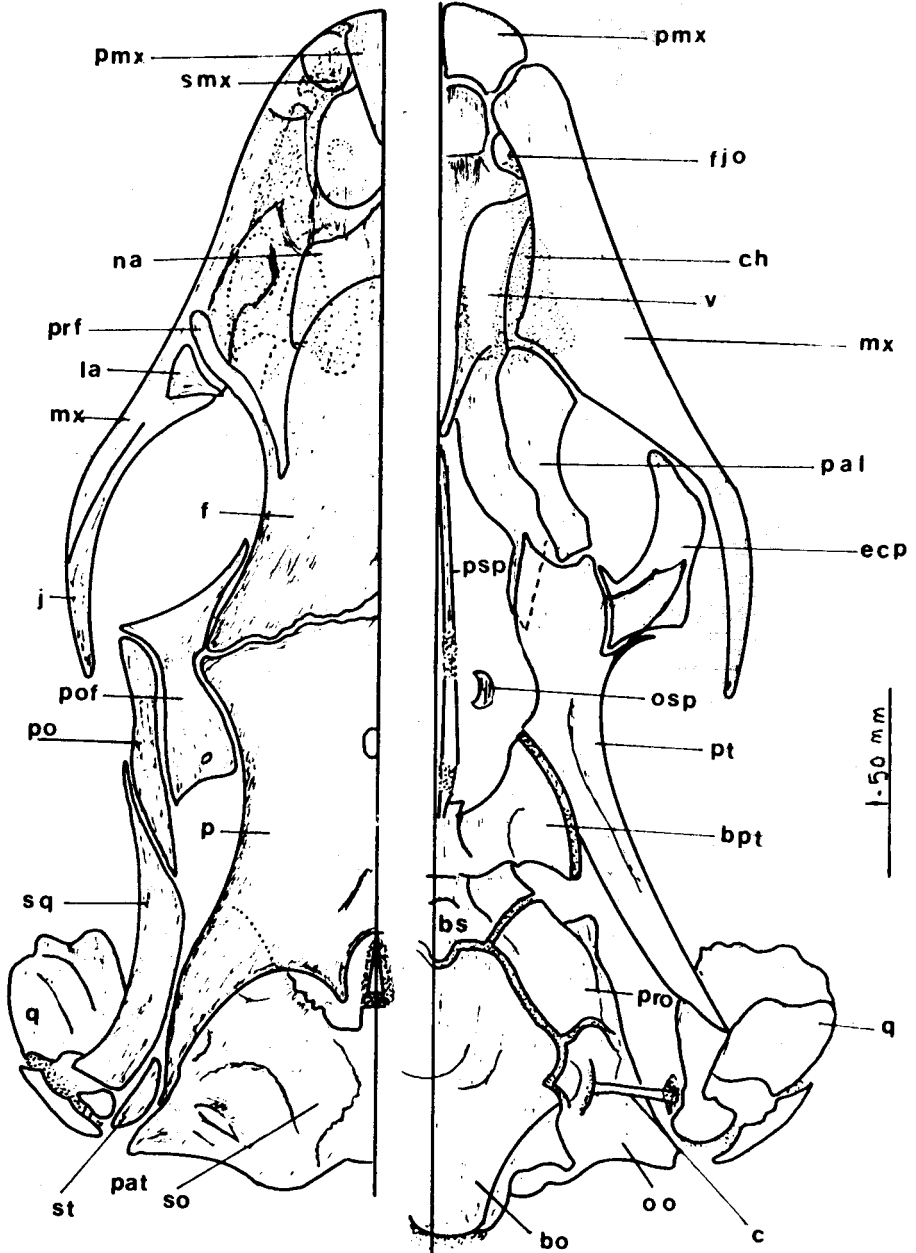


Fig. 1 - c

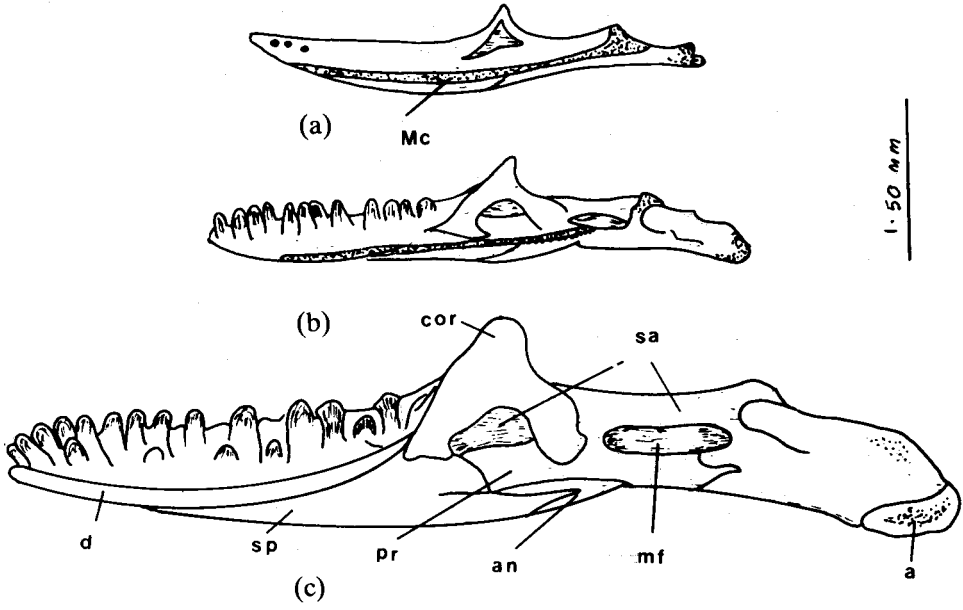


Fig. 2

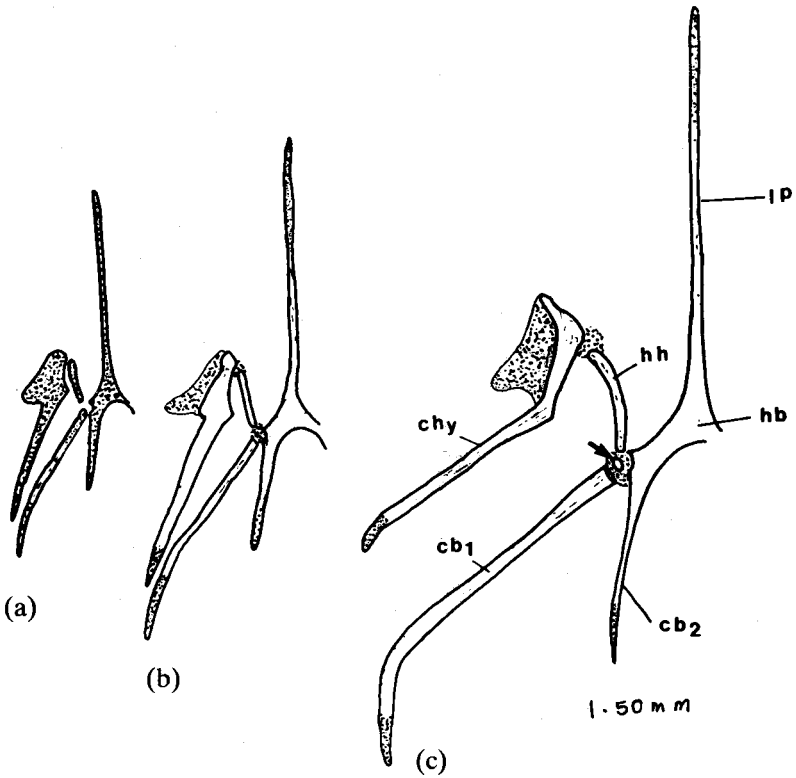


Fig. 3

At 12-Month-Old, the basipterygoid meniscus and the quadrate articulation surface are cartilaginous as is the columella tip and around its footplate. The cartilaginous zones at age 1MO noted above are still present. The region between ceratobranchial-1 and -2 and hyoid body has an ossified epiphysis. In the lower jaw, the articular bone still shows cartilage. At the same age, the ethmoid region retains its primitive cartilaginous character.

Vertebral column, ribs and sternum (Figs. 4 and 5)

At birth, the atlas consists of three unfused parts, a cartilaginous ventral intercentrum (i1) and two ossified neurapophyses. The axis bears two ossified intercentra (i2 and i3). The cartilaginous rudiments of intercentra i4, i5 and i6 are capped by a bony layer concealing them entirely. At 1MO, all the intercentra are clearly ossified. At 12MO, the intercentra are still unfused with their centra.

Between the birth day and 12MO, in the vertebrae of *C. ocellatus* a cranio-caudal gradient of development is observed; differentiation, chondrification and ossification occur later at progressively more caudal levels. Consequently, different vertebrae from the same individual may show different stages of development.

At birth, neural arch and much of the centrum of the trunk vertebrae are covered by a thin shell of perichondral bone; the arch and only the middle centrum may show some endochondral ossification. The junction between the neural arch halves is still cartilaginous. At 1MO, most of the neural spine epiphysis is ossified. At 12MO, the neural spine epiphysis and the ends of the centra are completely ossified. At the same age, the cartilaginous neurocentral suture becomes difficult to observe.

The two sacral vertebrae are unfused at the centra or arches but their cartilaginous pleurapophyses tips are fused. At 1MO, the pleurapophyses are ossified except for their cartilaginous fused edges which ossify at 12MO.

The first two caudal vertebrae bear well developed transverse cartilaginous processes with obvious cartilaginous chevrons. However, the first one is found in an intervertebral position between the third and fourth caudal vertebrae, Their size decreases towards the posterior part of the tail. At 12MO, the transverse processes and the chevrons are ossified except for their tips.

The 3rd, 4th, and 5th cervical vertebrae bear short ribs, and all trunk vertebrae possess long ribs but do not have intercentra. The thoracic ribs are attached to the sternum by a cartilaginous piece; 3 pairs attach to the sternum and two pairs to the xiphisternum. Posterior to the sternum, the symmetrical cartilaginous segments fuse with each other on the midventral line forming the parasternalia. The rib consists of two segments; a bony proximal segment and a cartilaginous distal one. At 1MO, an oval fenestra is developed in the xiphisternum, and at 12MO the first

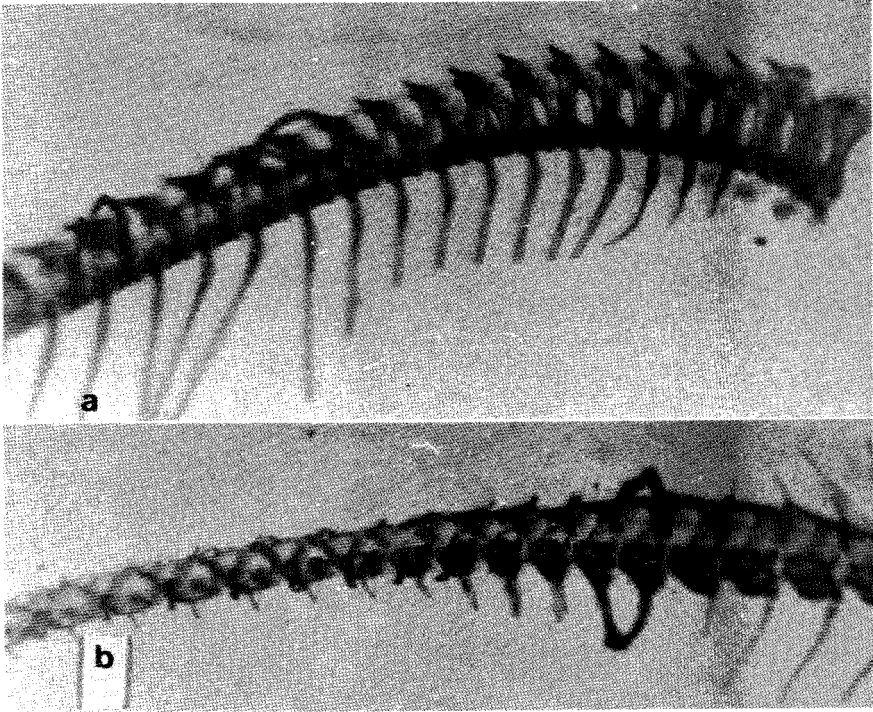


Fig. 4 - (a), (b)

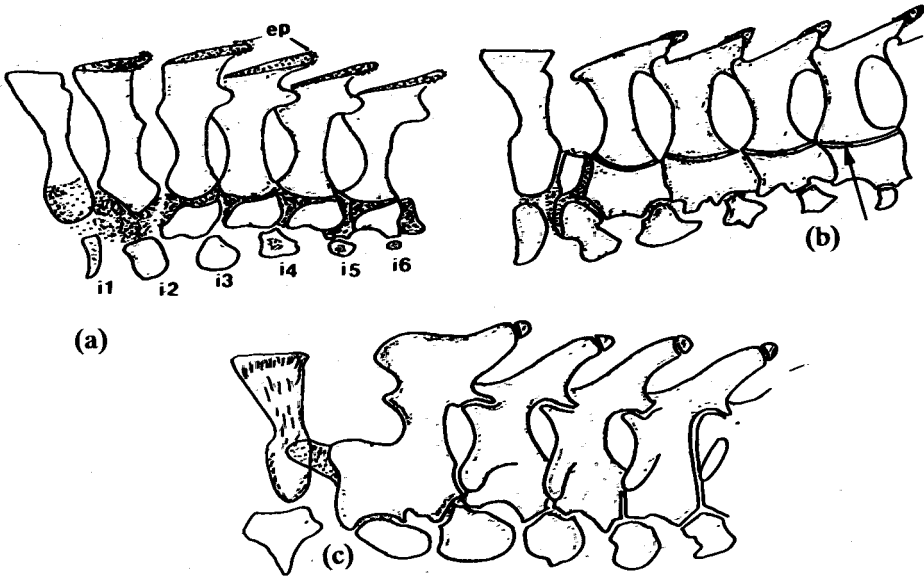


Fig. 5 - (a), (b), (c)

and second cartilaginous sternocostal segments show some ossification. The presacral vertebrae bear one pair of cartilaginous ribs which ossify at 1MO.

Pectoral girdle and fore limb (Figs. 6 and 7).

At birth, the scapula, clavicle, interclavicle, humerus, radius, ulna and phalanges are ossified. The coracoid rudiment shows some ossification. At 1MO, the radiale, ulnare centrale and carpalia 1 to 5 started to ossify. The epiphyses of humerus, radius and ulna show some ossification. At 12MO, the proximal humeral epiphysis has more than one ossification centre; the radiale has one epiphysis on the preaxial side and the ulnare has one on the postaxial side. All the carpalia and digits are fully ossified.

Pelvic girdle and hind limb (Figs 8 and 9).

At birth, ossification is observed in the ischium, pubis, femur, tibia, fibula, and all phalangeal digits. At 1MO, the 2 heads of the long bones show some ossification and the proximal tarsalia show ossification centres. Also, the distal tarsalia-3 and -4 and the ilium are ossified. At 12MO, the two proximal tarsalia are fused to form nearly one segment. The joint between the two pubis bones and between the two ischium bones are still unossified but the epipubis has an ossified rudiment.

Sesamoids (Figs 7 and 8).

At birth, there are no ossification centres. At 1MO, the pisiform shows some ossification. At 12MO, there is a large ossified lunula between the femur and tibia on the postaxial side and two smaller lunulae on the preaxial side and ulnar patella is present. Also, the pisiform is fully ossified. In the fore limb, there are two flattened ossified palmar sesamoids ventral to the carpalia. In the sole of the hind limb, there is one ossified sole sesamoid ventral to the tarsals.

Ossified epiphyseal centres (Figs. 10 - 12).

The epiphyses are always separated from the diaphyses by a cartilaginous zone, except for the distal epiphyses of the phalanges which are fused with the diaphyses. The epiphyses of the long bones ossify before those of the phalanges. In the humerus epiphysis at 1MO, the flattened cells of the growth zone become arranged in columns, and this arrangement is preserved as the cells hypertrophy. At this stage, the hypertrophied cartilage possesses irregularly scattered cells, and the marrow excavates blunt rounded cavities in the cartilage. The endochondral bone laid down by the marrow on the walls of the excavations follows their shape, and is correspondingly irregular in arrangement. The eroding marrow is guided by the cellular arrangement so that the formed cavities are longitudinally elongated and the endochondral bone laid down on the cavity walls is longitudinally arranged.

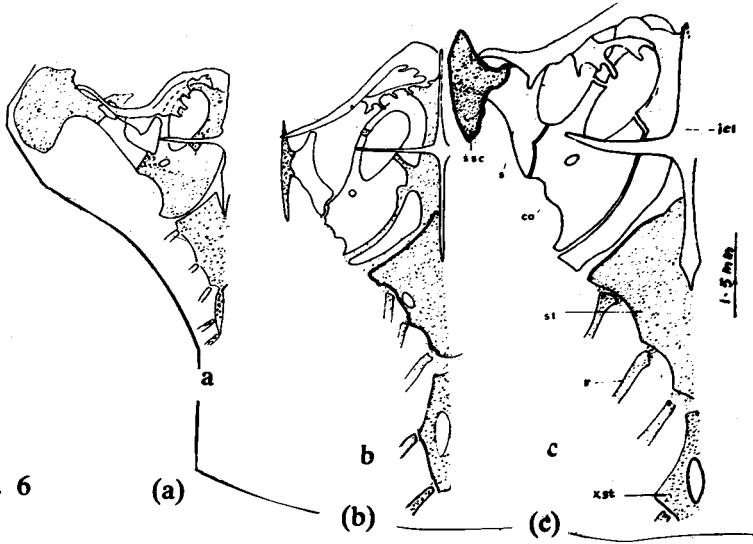


Fig. 6

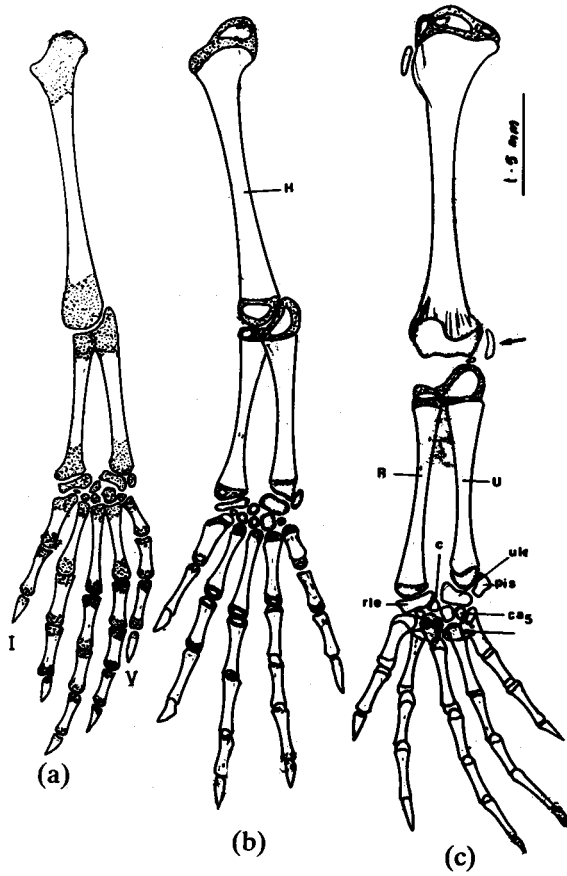


Fig. 7

Ossification in lizard

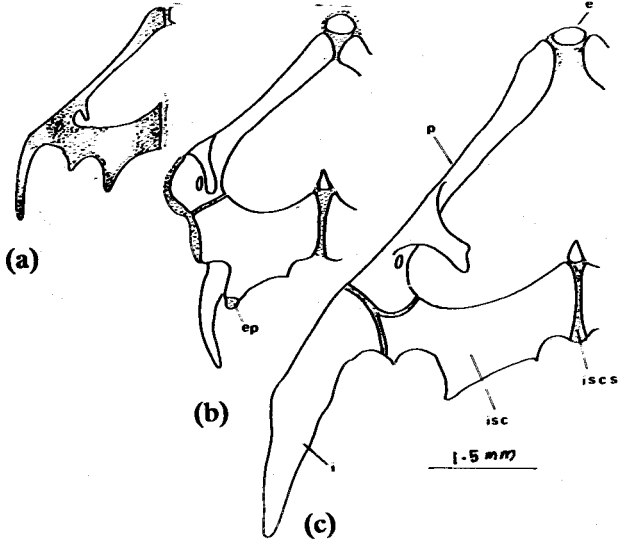


Fig. 8

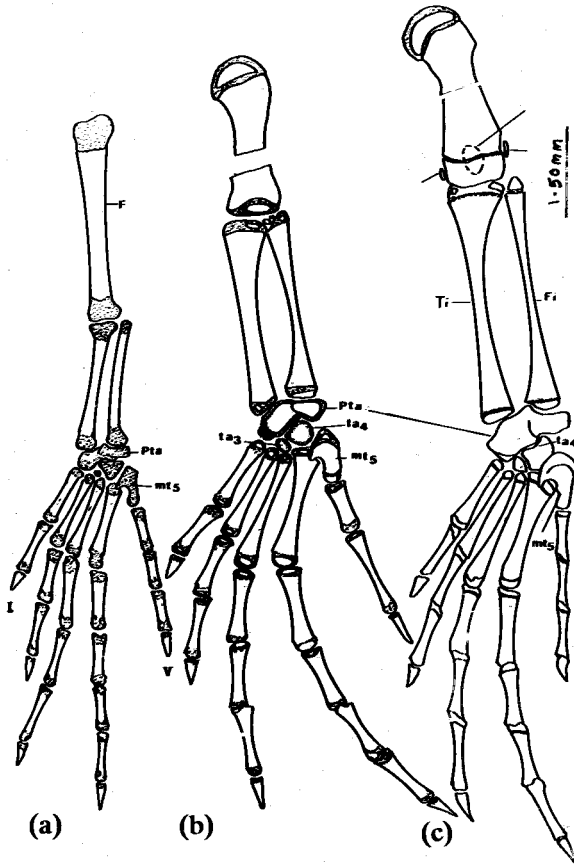


Fig. 9

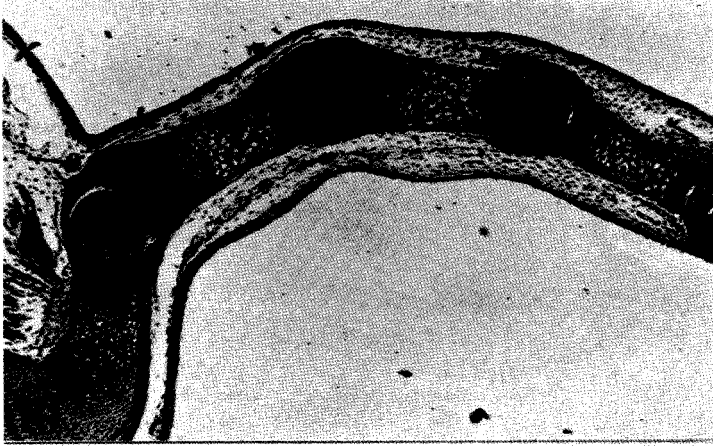


Fig. 10

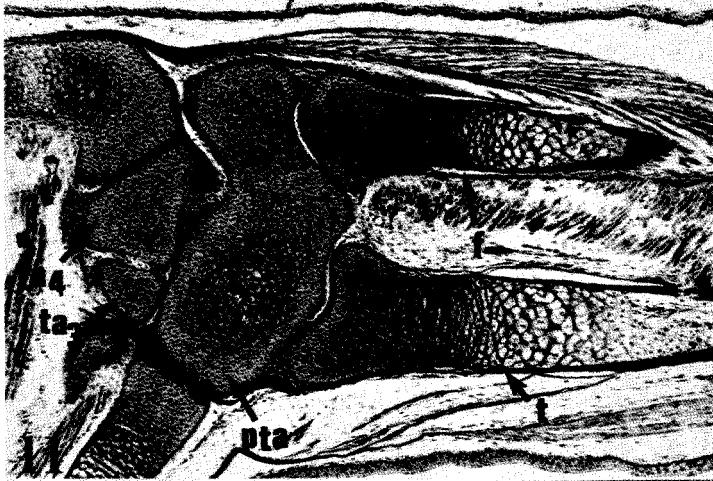


Fig. 11

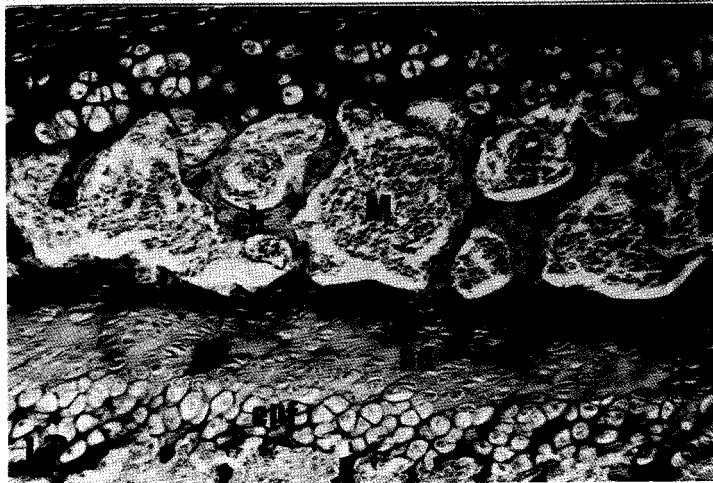


Fig. 12

DISCUSSION

At birth, the skull of *Chalcides ocellatus* is a well formed miniature of that in the adult. The skull ossification pattern shows homology with that of comparable skulls within the scincids and within the reptiles (Kamal, 1965; Bellairs and Kamal, 1981). Also at birth, the basiptyergoid, the quadrate articulation surface and the articular surface in the lower jaw are cartilaginous. Dollo (1884) found cartilaginous rudiments in several cranial bones, including the dorsal end of the quadrate, the basiptyergoid process and, in *Varanus*, the occipital condyle, while Moodie (1908) confirmed their existence in cleared preparations. Also, Jollie (1960) and Haines (1969) recorded bony epiphyses or secondary centres of ossification in a few skull bones in some lizards. In the adult gecko *Tarentola*, the quadrate articulation surface fails to ossify completely and thus appears irregularly notched in the dried skull (Rieppel, 1984). The presence of cartilaginous zones between certain bones seems to form a flexible brace between skull rudiments (Frazzetta, 1962; Wineski and Gans, 1984), or for skull growth (Moore, 1981).

Little information is available on the hyoid apparatus ossification, thus making detailed phylogenetic comparison difficult. In *C. ocellatus*, the middle of ceratobranchial 1 begins to ossify at birth, while the ceratobranchial 2 is ossified later. In turtles, the ceratobranchial 1 begins to ossify in the embryo (Schumacher, 1973). In *Trionyx*, the ossification begins at the proximal end of the ceratobranchial 1 with one centre of ossification, and, sometime later, the distal end ossified at two to eight centres (Ogushi, 1931). In *Lacerta*, Siebenrock (1894) described three centres of ossification in ceratobranchial 1. In *Varanus*, Schrivastava (1964) described also one centre in ceratobranchial 1. In *Coleonyx variegatus*, Kluge (1967) described the ossification of the lingual process and ceratobranchial 1.

The present observations in *C. ocellatus*, that the vertebral column develops in a cranio-caudal gradient and that all centres of ossification in the vertebrae are present at birth, are in agreement with the previous studies on *Lacerta vivipara*, *Anguis fragilis* and *Natrix natrix* (Winchester and Bellairs, 1977), *Lacerta agilis* (Borchwardt, 1977), and various lepidosaurian reptiles (Williams, 1959). In *C. ocellatus*, the cartilaginous spine epiphysis is ossified at 12MO. The spine ossification is a secondary centre (Haines, 1969).

In *C. ocellatus*, the intercentra are separated from their centra up to the age of 12 months and keep their intervertebral position. Hoffstetter and Gasc (1969) recorded the fusion of intercentra with their centra in mature *Chalcides*. This controversy may be explained by individual variation among the same group of *Chalcides* used in this study and/or the fact that fusion may vary with the specimen age.

The sacrum of *C. ocellatus* consists of two unfused sacral vertebrae with expanded sacral pleurapophyses similar to most inguanids, many agamids and some lacertids.

Hoffstetter and Gasc (1969) recorded that *Chalcides* sacrum consists of two fused vertebrae in the adult stage.

The changes occurring in the appendicular skeleton of *C. ocellatus* during ossification appear to resemble those in many lizards. The carpus is similar to that of *Calotes versicolor* (Mathur and Goel, 1976) and *Ascalabotes fascicularis* (Sewertzoff, 1908). However, in the lizard *Agama colonorum*, the developmental pattern seems very different but the carpus of the adult differs from that of adult *C. ocellatus* only in the absence of the carpalia-1 (Holmgren, 1933). Holmgren reports as many as twelve elements in the embryo as compared with seven in the adult; the centrale-1 fuses with the radiale, the centrale-3 and -4 and the intermedium fuse with the ulnare, and the carpalia-1 fuses with the metacarpal-1.

The tarsus of *C. ocellatus* at birth consists of three rudiments, proximal tarsal and distal tarsalia-3 and -4. The proximal tarsal shows two centres of ossification. Bruke and Alberch (1985) concluded that the tarsus in the turtle *Chrysemys* is the remnant of the proximal centrale, which merges with the intermedium to form the astragalus. This conclusion contrasts with a traditional view that the astragalus is made up of the intermedium and the tibiale (Sewertzoff, 1908), or that it represents only the tibiale or only the intermedium (Romer, 1956). Peabody (1951) has shown that in the primitive reptilian tarsus, the astragalus is made up of the tibiale, the proximal centrale, and the intermedium. Schaeffer (1941) has postulated that the tibiale has been lost from the tarsus of later reptiles. On the other hand, in *Agama*, Holmgren (1933) considers the proximal tarsal elements to be made of the astragalus (centrale-1 + intermedium), the fibulare (centrale-4), distal centrale (centrale-2), and probably the tarsalia-1 and -2. He implicitly remarks the absence of a real fibulare, but only implicitly considers the real astragalus absent.

In *C. ocellatus*, there are two elements in the distal row of tarsals, the tarsalia-3 and -4, these two elements appear separately. In *Agama*, Holmgren (1933) shows that tarsalia-4 is considered to incorporate centrale-2 whereas tarsalia-1 and -2, according to one explanation, are believed to be represented by an element lying in position of tarsalia-1 (meniscus of Sewertzoff, 1908). Holmgren, however, gave the following statement, "my material is too scarce to allow me to determine the origin and fate of these structures".

From the present investigations, the absence of tarsalia-5 lend support to the remarks of Romer (1956) who states, "It is often assumed to be fused with distal 4 or with metatarsal-5, but it more probably simply disappeared in most cases". It may be noted that in all the reptiles where metatarsal-5 is hooked, the tarsalia-5 is always missing although the reverse is not true. The present investigation conclusively shows that the hook of metatarsal-5 is not due to a fusion with the tarsalia-5 (Romer, 1956). Possibly, the absence is a means of adjusting a broad foot to the narrow tarsus, bringing the divergent fifth toe into line with the other digits (Romer, 1956), or to help broadening the base of the foot (Bellairs, 1969).

The fore limb of *C. ocellatus* has a pisiform rudiment in the palmar position relative to other carpal bones. This element is in every way comparable with the pisiform of anurans (Emery, 1894) and other reptiles (Holmgren, 1933; Schwartz, 1938). It appears to be a true carpal, since it occurred in all early tetrapods with well ossified hands (Haines, 1969). The other sesamoids are ulnar patella and lunulae. The patella is found in most lizards (Camp, 1923) and in many mammals at the knee and elbow (Retterer and Vallois, 1912). The lunulae appear in *Lacerta* and *Hemidactylus angularis* (Haines, 1969). In *Sphenodon*, there is a single lunula and they appear also in the varanus-like fossils (Nopcsa, 1903).

In *C. ocellatus*, the epiphyses are always separated from the diaphyses by a cartilaginous zone, except the distal epiphyses of the phalanges, which are fused with the diaphyses. This is in general agreement with typical reptilian condition, and supports observations that the phalanges grow only on their proximal ends (Haines, 1969). The epiphyses of the long bones ossified before those of the phalanges. This sequence confirmed Haines' (1969) suggestion that the larger epiphyses ossify before the smaller ones.

As the epiphysis of *C. ocellatus* matures, the flattened cells of the growth zone become arranged in columns, and this arrangement is preserved as the cells hypertrophy. Bausenhardt (1951) denied the existence of columns in crocodiles and turtles. In the epiphysis interior, the cells are not hypertrophied. Suzuki (1963) described a peculiar basophilic network in the matrix between the cell groups. The basophilia might be explained along the biochemical lines developed by Van den Hooff (1964) who found resting cartilage to be acidophilic owing to the preponderance of collagen fibers, and PAS-positive from the bonding of the fibers with each other. In *C. ocellatus*, the changes undergone by the cartilage cells passing from the epiphysis through the growth zone to the metaphysis appear to resemble those in the turtle, crocodiles and *Gallus* (Whiston, 1940; Wolbach and Hegsted, 1952). However, those who have studied endochondral bones (Heidsieck, 1928 in *Lacertilia* and Haines, 1969 in *Crocodylus*) report conditions similar to those observed in the present study.

ACKNOWLEDGEMENTS

I should like to express my gratitude to Professor Galila M. Khalil, Head of the Zoology Department, Faculty of Science, University of Qatar for critically reading the manuscript and for valuable suggestions. All this work has been performed in the Department of Zoology, University of Qatar, State of Qatar.

FIGURES

Cartilage is shown by stippling. Scale = 1.50mm.

- Fig. 1: Diagrammatic illustration of the skull in *C. ocellatus* to show the distribution of cartilaginous and ossification rudiments. a, at the newly born lizard; b, at 1MO; c, at 12MO. Dorsal and ventral views. bo, basioccipital; bpt, basipterygoid; bs, basisphenoid (parabasisphenoid); c, columella auris; ch, choana (internal nostril); ecp, ectopterygoid; f, frontal; fJo, foramen for duct of Jacobson's organ; j, jugal; la, lacrimal; mx, maxilla; na, nasal; oo, otooccipital (opisthotic + exoccipital); Qsp, orbitosphenoid; p, parietal; pal, palatine; pat, ossified part of anterior process of tectum (ossified as supraoccipital); pfr, prefrontal; pif, pineal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; pro, prootic; psp, parasphenoid; pt, pterygoid; q, quadrate; smx, septomaxilla; so, supraoccipital; sq, squamosal; st, supratemporal; v, vomer.
- Fig. 2: Diagrammatic illustration of the lower jaw in *C. ocellatus*. a, at the newly born lizard; b, at 1MO; c, at 12MO. a, articular; an, angular; cor, coronoid; d, dentary; Mc, Meckel's cartilage; mf, mandibular fossa; pr, prearticular; sa, splenial.
- Fig. 3: Diagrammatic illustration of the hyobranchial skeleton in *C. ocellatus*. a, at the newly born lizard; b, at 1MO; c, at 12MO. cb1, cb2, ceratobranchial 1 and 2; chy, ceratohyal; hb, hyoid body; hh, hypohyal; lp, lingual process of hyoid. Arrow, a small body nodule representing hyobranchial.
- Fig. 4: Vertebral column preparation in the newly born *C. ocellatus* to show the craniocaudal gradient of vertebral development. Different vertebrae show different stages of ossification. a, cervical and trunk regions and b, presacral, sacral and caudal vertebrae with their processes.
- Fig. 5: Diagrammatic illustration showing ossification development of cervical vertebrae in *C. ocellatus*. a, at the newly born lizard; b, at 1MO; c, 12MO. ep, cartilaginous epiphysis; i1, i2, i3, i4, i5, i6, intercentrum 1, 2, 3, 4, 5 and 6 Arrow, neurocentral suture.
- Fig. 6: Diagrammatic illustration of the pectoral girdle and sternum in *C. ocellatus*. a, at the newly born lizard; b, at 1MO; c, at 12MO. cl, clavicle; co, coracoid; icl, interclavicle; r, rib; s, scapula; ssc, suprascapula; st, sternum; xst, xiphisternum.
- Fig. 7: Diagrammatic illustration of fore limb of *C. ocellatus* a, at the newly born lizard; b, at 1MO; c, at 12MO. c, centrale; ca5, carpalia 5; H, humerus;

pis; pisiform; R, radius; r, radiale; rle, radiale; U, ulna; ule, ulnare; Arrow, ulnare patella.

- Fig. 8: Diagrammatic illustration of the pelvic girdle of *C. ocellatus*. a, at the newly born lizard; b, at 1MO; C, AT 12MO. e, epipubic; ep cartilaginous process; i, ilium; isc, ischium; iscs, ischiamic symphysis.
- Fig. 9: Diagrammatic illustration of the hind limb of *C. ocellatus*. a, at the newly born lizard; b, at 1MO; c, at 12MO. F, femur; Fi, fibula; mt 5, metacarpal 5; pta, proximal tarsal element; ta3, ta4, tarsalia 3 and 4; Ti, tibia; Arrows, ossified lunulae.
- Fig. 10: Longitudinal section in fore limb of *C. ocellatus*. All phalanges start ossifying, their ends are of normal cartilage in the newly born lizard.
- Fig. 11: A longitudinal section through the hind limb of a newly born *C. ocellatus*. Perichondral ossification is taking place in the tibia and fibula shafts; toward the centre of the shaft the cartilage becomes hypertrophic. The proximal tarsal has two fused ossification centres. f, fibula; t, tibia; pta, proximal tarsus; ta3, ta4, tarsalia 3 and 4.
- Fig. 12: Longitudinal section through the distal end of the humerus of a 1MO *C. ocellatus*. A large diffusely ossified centre occupies the greater part of the interior of the epiphysis. eb, endochondral bone; epf, endochondral bone formation; hc, hypertrophic cartilage; M, marrow cells.

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تتابع التعظيم أثناء نمو الجهاز الهيكلية في السحلية كالسيدس أو سيلاقتس (سنسيدي - الزواحف)

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وصف توزيع التغضرف والتعظيم للجهاز الهيكلية في الزواحف كالسيدس أو سيلاقتس عند أعمار ثلاث هي : عند الوضع وعمر شهر وعمر ١٣ شهراً وذلك في عناصر الجمجمة العصبية ، الجمجمة الادمية ، الجهاز الحشوي العمود الفقري ، الضلوع ، القص ، الحزام الصدري والطرف الأمامي ، الحزام الحوضي ، والطرف الخلفي وكذلك القطع الهيكلية ذات الوضع الشاذ .
وأوضحت الدراسة تباين عناصر الجهاز الهيكلية في أزمنة تعظيمها .