OBSERVATIONS ON EGGS OF EUBLEPHARID LIZARDS, WITH COMMENTS ON THE EVOLUTION OF THE GEKKONOIDEA

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With one plate

CONTENTS

ABSTRACT

Captive specimens of *Coleonyx v. variegatus*, *C. v. bogerti*, *Eublepharis macularius* and *Hemitheconyx caudicinctus* laid parchment-shelled, moisture dependent eggs, resembling those of diplodactyline geckos and most lepidosaurians. Eublepharid eggs, including those of *Aeluroscalabotes* measured in radiographs, are twice as long as broad. Supporting and complementary evidence in the literature is considered. It is concluded that the Eublepharidae are a monophyletic group of the Gekkonoidea, retaining the primitive egg type. Functional and evolutionary aspects of various characteristics of different gekkonoid eggs are discussed, and conclusions drawn.

INTRODUCTION

Geckos constitute the superfamily Gekkonoidea, comprising three families: Eublepharidae (5 genera), Sphaerodactylidae (5 genera) and Gekkonidae: the last named family includes two subfamilies, Diplodactylinae and Gekkoninae (Underwood, 1954, 1955). The Diplodactylinae as recently redefined are restricted to Australasia (14 genera) while the nearly cosmopolitan Gekkoninae include the majority of geckos (some 50 genera) (Wermuth, 1965; Kluge, 1967; Bustard, 1968). Concerning the eggs, the whole superfamily Gekkonoidea has traditionally been regarded as characterized, among other things, by the brittle, hard-shelled eggs (Kluge, 1967 : 12; earlier references in Bustard, 1968). However, Shaw (1950 : 28) had already spoken of the "soft-shelled eggs of the gecko" *Coleonyx variegatus variegatus*. Actually, the geckos of the subfamily Diplodactylinae (sensu Kluge, 1967) lay pliable, parchment-shelled eggs similar to those of lizards and snakes in general. This is shown by the ample evidence provided and cited by Bustard (1965 : 298; 1967; 1968). The same has been suggested by Bustard (1967 : 283; 1968 : 163) to apply also to the Eublepharidae, on the basis of his knowledge of the eggs of *Coleonyx*, and Minton's (1966 : 73) observations on eggs of *Eublepharis*. The purpose of this contribution is to bring together miscellaneous additional records on eublepharid eggs, some of which confirm Bustard's suggestion, and to discuss certain evolutionary implications.

METHODS

Unless otherwise acknowledged, casual observations were made on lizards kept for other work in the vivarium of the Auditory Research Laboratories, Princeton University, from October 1967 to October 1968. During most of that period the lizard room was automatically lighted for 12 h daily by fluorescent and infra-red lamps. All eublepharids were in terraria more than 1 m from the infra-red lamps. Light and dark periods were coupled separately to thermostatic heating systems, but both the diurnal and the (lower) nocturnal temperatures varied seasonally, and to some extent between parts of the room. Prevalent temperature conditions will be described where pertinent. Food consisted of mealworms and, occasionally, grasshoppers obtained by grass-sweeping. Water in a small dish was always available.

Eggs were measured with callipers and are described in terms of their length, their greatest breadth (occurring at half-length), and their ellipticity (ratio breadth to length, Preston & Preston, 1953).

OBSERVATIONS AND REMARKS

Coleonyx variegatus variegatus (Baird)

Observations. — In 1966, Prof. H. Mendelssohn (Tel-Aviv University) presented me with two soft-shelled eggs, much like those of lacertids, laid by geckos which he had received from Dr. P. F. A. Maderson (then at the University of California, Riverside). The eggs had been discovered in the terrarium on 11 August 1966. I kept them between two sheets of moist cotton wool at (unrecorded) room temperature (in Jerusalem). One I opened on 23 August 1966. It contained a live advanced embryo, which I fixed in Boin's fluid (GK 427; after 2 years in alcohol: head and body, 28.5 mm; tail, 23.5 mm). The other hatched on 30 August 1966, carrying on its umbilicus a small remnant of yolk, and was fixed in formalin (GK 428; after 2 years in alcohol: head and body, 28 mm; tail, 21 mm). Prof. Mendelssohn informed me, that earlier clutches had been lost due to their drying up, because the staff had not expected that geckos would need a moist substratum for oviposition. Thereafter the sand was moistened.

At Princeton, fourteen animals that had been collected by Prof. W. W. Mayhew and myself in the sand-dune country near Glamis, Imperial County, southern California, on 15 August 1967, were kept in terraria furnished with dry sand. Most of these animals were sacrificed for other work early in 1968. Three surviving pairs produced several eggs in the early summer of 1968. All were discovered too late in the dry sand, in a shrivelled condition, something which would never happen with the hard-shelled eggs of "typical geckos" (Gekkoninae). Hence more detailed data of these eggs are not available.

Remarks. — Shaw (1967) summarized his ample experience in breeding these geckos in the San Diego Zoo. The laying season is from late May to mid-September. During this time, a female produces usually two and sometimes three clutches, and one female produced four clutches in one season. A clutch consists of 1-3 (usually 2) eggs. The fresh eggs are very variable in size: length, 12.7-20.8 mm; width, 7.6-10.2 mm. This wide range is based on a rather large sample: nearly 100 clutches hatched. The shell is pliable, and size increases during incubation: length increased up to 21.9% and width up to 37.1%. Incubation lasted 59-81 days at "temperatures of about 80° F" (26.5° C). Neonati average 32 mm in snout-vent length with a tail of 30.5 mm.

Hence there is no doubt, that the parchment-like condition of the shell is normal in this species. Shaw's experiences are comparable to those usually made with lizard eggs. His observation of clutches containing three eggs is noteworthy and will be discussed later.

Fitch (1970 : 11-12) cites additional sources on reproduction in *Coleonyx*, including a claim for clutches of 3-4 in *Coleonyx elegans* in Chiapas, Mexico (Alvarez del Toro, 1960 : 74).

Coleonyx variegatus bogerti Klauber

Observations. — Several eggs were laid by animals purchased in the autumn of 1967 (from the "Pet Corral", Tucson, Arizona). The parchment-shelled eggs had been buried in the dry sand of the wooden terraria (by the females?), and were discovered in a dried and shrunken condition.

Eublepharis macularius (Blyth)

Observations. — Several pairs, all of which originated from West Pakistan (through various dealers) were kept at Princeton. Some of these had been obtained, half-grown, in 1963. Eggs were laid in the terraria repeatedly from 5 May 1968 (earliest oviposition) to 26 August 1968 (last oviposition). All eggs had pliable, parchment-like shells. Apparently clutches always contained one or (usually) two eggs. Each female must have produced two or three clutches in this time, and possibly more. Many of the eggs were discovered in the morning in a shrivelled, dried-up condition due to their pliable shell; they were usually laid at night between 1700 and 0900 h (local time) and the sand was mostly dry. Efforts were made to incubate eleven eggs, arranged between moist sand and cotton wool, at a room temperature fluctuating daily between ca. 24 and 27-32°C. All these attempts failed, due to mould or drying up, although some eggs survived for over forty days. During this time it sometimes happened that an egg started to dry up, developing an elongate 'dimple' parallel to its long axis. This could often be remedied by increasing the moisture of the covering cotton wool, or increasing the area of contact between the latter and the egg. The egg would imbibe water and resume its turgescence and shape.

Eight eggs that were measured when 1-2 days old, ranged in length from 26.5 to 34.0 mm (mean 29.7 mm); their breadth was 13.5-17.0 (mean, 15.3) mm; and their ellipticity was 0.462-0.561 (mean, 0.516).

Remarks. — The observations made by Minton (1966 : 73) similarly indicate a laying season from late April to mid-August. He observed a specific female laying three clutches with 3-4 week intervals. He already noted the pliable shell. The seven eggs he measured were 31-35 mm long and 13-16 mm broad. He, too, failed to have any eggs hatch, although some developed for four weeks. A remarkable observation of Minton's is that on 11 September a captive female laid three eggs.

Schifter (1967) likewise obtained from his captive pair eggs that failed to hatch, and comments on the parchment-like shell. The two clutches were laid in mid-July and on 24 August 1966. Oviposition occurred late in the evening. Schifter describes the size as 25 × 10 mm; this relatively small size may be due to the limited age of his animals, which had been bought as juveniles in the preceding year.

Hemitheconyx caudicinctus (Duméril) (plate 1, top fig.)

Observations. — On 27 December 1967 I purchased (from "Noah's Ark", Princeton, New Jersey) two male and two female adults of this West African species. Together with the animals I received two eggs, which had been found in their cage. These were typical pliable-shelled squamate eggs, each 27 mm long, but so caved-in due to desiccation that the width could only be guessed at. One was discoloured, yellowish. Since the other inhabitants of that cage were only several *Anolis carolinensis* and some *Tarentola* sp. and small *Hemidactylus* sp., the eggs had obviously been laid by the *Hemitheconyx*. In the laboratory I buried these eggs in moist sand, and by the next day both had expanded to a breadth of 13 mm, retaining the length of 27 mm. Their ellipticity was thus 0.481. They later grew mouldy and were discarded.

Remarks. — This appears to be the first record of the eggs of any African eublepharid.

Only one of these animals had the broad, whitish, vertebral stripe (Loveridge, 1947: 27). The other three had the dark crossbands accentuated by whitish edges.

Aeluroscalabotes felineus (Günther) (plate 1, bottom fig.)

Observations. — Few herpetologists have seen this unusual gecko of Malaya and the Indo-Australian Archipelago alive and I am not among them. But I have been so fortunate as to be permitted to radiograph a series of 130 specimens in the Field Museum of Natural History, Chicago. These had been collected on Borneo, near Nanga Tekalit, Kapit District, Third Division, Sarawak, during several months of 1962-1963, by F. W. King. They had been caught in the evening (1845-2045 h, mostly) on shrubs along the Mengiong River and its tributaries.

On the radiographs it was easy to ascertain the sexes of the adult and subadult animals by the appearance of post-anal bones in the males, which are well developed in this genus, as in most geckos (Brongersma, 1934 : 162-167). Of 83 females, large ovarial or oviducal eggs were evident in 49. Among these, 16 females contained 20 oviducal eggs with already well-formed shells, indicating full size. These varied in length from 17.0 to 21.2 mm (mean, 19.2 mm); their width was 9.5-12.5 mm (mean, 11.1 mm); and their ellipticity was 0.477-0.646 (mean, 0.577). (Nine additional oviducal eggs with very thin shells were excluded from this computation.)

As to clutch size, of 36 females that carried large oviducal eggs, four had one egg in the right oviduct only. The remaining 32 had one egg in each oviduct, but in many females the left egg was smaller or younger (without, or with thinner, shell) than the right egg.

Remarks. — Evidently, this is the same material used by Inger & Greenberg (1966) in their study of the reproductive cycles in lizards of the Bornean rain forest. However, they state (1966, tables 4, 5) that among 80 females, 32 were gravid, each with two eggs. The discrepancies could arise in various ways; for example, as to clutch size, since they opened the specimens along the left flank, they may have caused the loss of left-hand oviducal eggs in a few cases.

Inger & Greenberg's work implies that this population of *Aeluroscalabotes* reproduces throughout the year; gravid females were absent only from the monthly sample of June (during the year 10 September 1962-10 September 1963).

There may be some doubt as to the correct identification of these *Aeluroscalabotes* (*felineus* or *dorsalis*), as they do have numerous tiny tubercles on the back (Boulenger, 1855).

Discussion

Eggs of Eublepharidae

The season of oviposition of eublepharid geckos roughly resembles that of most other geckos, and reptiles in general, in the same ecological area. Contrasting examples are provided, i.a., by the observations of Minton (1966) in a southern Palearctic desert, (including *Eublepharis*), and the study of Inger & Greenberg (1966) in an Oriental rain forest (including *Aeluroscalabotes*). It is not surprising that Nearctic *Coleonyx* and Palearctic *Eublepharis* oviposit during the later spring and most of the summer of the northern hemisphere, and that the Oriental, tropical *Aeluroscalabotes* reproduces almost throughout the year. Whether the *Hemitheconyx* that laid eggs, in captivity at Princeton, in December, did this in accord with their original West African annual cycle, is unknown. From observations on Australian geckos transferred to Jerusalem, I suspect that this may indeed be the case.

The long incubation period found by Shaw (as cited above) in *Coleonyx*, and inferred by Minton and by myself for *Eublepharis*, is likewise in keeping with the habits of other geckos, and reptiles in general. This is easily seen by referring to the data presented by Klingelhöffer (1959 : 329-330) and

Mayhew (1968 : 275-276). In this context one should note, that many incubation times are recorded at room (or even thermostat) temperatures that may be lower than those in nature; and that an average difference of only one degree Celsius may suffice to make a difference of 4-5 days in incubation time (Bellairs, 1969: 444; and pers. obs. on *Ptyodactylus hasselquistii guttatus*).

The large size of the egg and hatchling, relative to adult size, is a peculiarity that eublepharids share with other geckos (Bustard, 1965: figs. 3-4; 1967: figs. 1-3; Werner, in press). This is obviously related to the small number of eggs per clutch, as compared to the habits of most other squamates. It is interesting that these features are rather consistent throughout the large and varied superfamily Gekkonoidea, while elsewhere considerable variation within a family may occur. For example, among Australian skinks, *Tiliqua scincoides* gives birth to up to twenty smallish offspring, whereas *Trachydosaurus* (= *Tiliqua*) *rugosus* produces one or two very large young (Bustard, 1970: 116-118, and figs. 66-67).

In this relation, eublepharids resemble other geckos and differ from most other squamates in the same areas, also in producing 2-4 clutches per year — and occasionally more (Werner, 1965; in press). Of course there are also cases of geckos laying only one clutch per year (Bustard, 1970 : 68).

Clutch size in geckos is normally two, except that it is only one in the Sphaerodactylidae and in a few of the smaller Gekkoninae (Werner, 1966 (*Tropiocolotes steudneri*); Bustard, 1968). Larger clutches have usually been explained as misunderstood cases of communal laying (e.g., Smith, 1935 : 27) and my own tendency has been to accept this interpretation. Other sources of error in this matter exist: for example, Mayhew (1968 : 271) attributes 1-3 eggs to *Phyllodactylus tuberculosus*; but the source he cites (Hoddenbach & Lannom, 1967: 295) included a single case of three ovarian follicles and did not exclude the possibility of later follicular atresia. However, as far as the Eublepharidae are concerned, clutches of three eggs seem indeed to occur. It is conspicuous that among the small number of herpetologists who have ever seen eggs of eublepharid geckos, both Shaw (for *Coleonyx*, cited above) and Minton (for *Eublepharis*, cited above) have specifically reported clutches of three.

The shape of gecko eggs in general (Gekkoninae and Sphaerodactylidae) tends to be rather less elongate than that of other squamate eggs. The eggs of many gekkonoid species are even nearly spherical, or, when pressed and adhering to the substratum, roughly hemispherical (Schreiber, 1912 : 557; Kopstein, 1938: pl. 25; Werner, 1965: fig. 8, and in press). The eggs of the eublepharid geckos, with average ellipticity values of 0.516 in *Eublepharis* *macularius*, 0.481 in *Hemitheconyx caudicinctus*, and 0.577 in *Aeluroscalabotes felineus*, are twice as long as wide. The same is true of the eggs of the diplodactyline genus *Oedura* (Bustard, 1967) but some diplodactyline eggs are not so elongate (Bustard, 1965 : 299-300, *Diplodactylus elderi*).

The egg-shell of geckos has usually been characterized as hard, brittle, although the Diplodactylinae have parchment-shelled eggs (references in introduction). Bustard (1967, 1968) already suggested that parchment-shelled eggs are characteristic of the Eublepharidae as well. Fitch (1970 : 11) made a statement to the same effect, without elaborating the evidence. From the observations reported and cited here it is clear that the eggs of *Coleonyx variegatus* sspp., *Eublepharis macularius*, and *Hemitheconyx caudicinctus*, have parchment-like shells. Moreover, eublepharid eggs can lose and regain water (as shown by my observations on *Eublepharis*), and they increase in size during embryonic development (as shown by Shaw's observations on *Coleonyx*, cited above). In these respects they resemble conventional squamate eggs (e.g., *Agama, Lacerta, Natrix*). The conclusion that eublepharids have typical, parchment-shelled, squamate eggs now appears justified.

Status of the Eublepharidae

Thus the Eublepharidae in their seasons of oviposition and incubation periods conform to the other Gekkonoidea and to reptiles generally, and in the size of their eggs and the number of clutches per year to other Gekkonoidea, in contradistinction to Squamata generally. In clutch size they agree with the Gekkonidae (the Sphaerodactylidae consistently lay one egg per clutch — Underwood, 1954; Bustard, 1968), except that the Eublepharidae are more prone to have clutches of three. On the other hand, the eublepharid egg shell differs from that of Sphaerodactylidae and Gekkoninae, resembling only that of Diplodactylinae; and the shape of the egg differs from that of Sphaerodactylidae and Gekkoninae, and is, as far as known, more consistently elongate than in the Diplodactylinae. These facts have a bearing on the disputed validity of the family Eublepharidae.

Originally, Boulenger (1883) erected the family Eublepharidae to comprise the genera *Coleonyx, Eublepharis* and *Hemitheconyx* (= "*Psilodactylus*"), because they differed from other geckos in having procoelous vertebrae and a single parietal bone. He noted already at the time that "these three genera are very closely allied, not only in structure, but even in coloration." Later he (1885 : 229) commented that the scattered distribution of these genera (the procoelous vertebrae of *Aeluroscalabotes* were obviously unknown, and *Holodactylus* had not been described) appeared to be a remnant of an earlier wide distribution of the family. On the other hand Gadow

(1901: 512) asserted that this group was "undoubtedly a heterogeneous assembly, as indicated by the very scattered distribution of its few species...".

Meanwhile, any geckos that turned out to have procoelous vertebrae (e.g., *Lepidoblepharis*), were also assigned to the Eublepharidae, until Noble (1921) clarified that there existed a separate group of New World genera with procoelous vertebrae, viz., the Sphaerodactylidae. This complex situation deterred many authors from accepting any subdivision of the geckos (Klauber, 1945: 135; Romer, 1956: 540). Actually, both the Sphaerodactylidae and the Eublepharidae are very well defined not only morphologically (Underwood, 1954, 1955), but also by reproductive characteristics. The Sphaerodactylidae lay one single hard-shelled egg per clutch (Underwood, 1954: 480; Bustard, 1968). The eggs of the Eublepharidae have just been discussed, and the evidence from their eggs, based, as it is, on representatives from different continents, supports not only the claim for their separation from the Sphaerodactylidae and Gekkoninae, but also Boulenger's implied suggestion (1885) that the Eublepharidae constitute a monophyletic group.

Evolutionary aspects

Underwood (1954, 1955) proposed two alternative schemes for the evolutionary relationship between the four families and subfamilies of geckos. Accepting both his classification (1954) and his second evolutionary opinion (1955), to the effect that among geckos amphicoelous vertebrae are primitive, I proposed (1961) an evolutionary hypothesis involving reproductive traits. At the time, geckos were believed to have hard-shelled eggs, in common with dibamid lizards, crocodiles, many turtles, and birds. Hence this was suggestive of a primitive, common feature. But because the ovoviviparous New Zealand diplodactylines have particularly primitive skeletons (Stephenson & Stephenson, 1956), I proposed that the hard-shelled eggs might represent a secondary development from ovoviviparity, and that this sequence may explain the small and strictly fixed clutch size in geckos.

At present Kluge's (1967) conclusion that the Eublepharidae and Diplodactylinae are more primitive than the Gekkoninae and Sphaerodactylidae, seems correct. Kluge did not consider the egg-shell but the first two groups have pliable shells, the last two calcareous shells. Apparently, the pliable egg-shell is basic in the Squamata, and even in the Lepidosauria, because it occurs in *Sphenodon* too, as I was recently fortunate to verify. (Incidentally, monotreme eggs are pliable as well.) From this basic state the ovoviviparity of the endemic New Zealand genera *Heteropholis, Hoplodactylus* and *Naultinus* could easily have evolved, as it has in several other families (e.g., *Lacerta vivipara*). In the eublepharids a clutch of three (and perhaps four) sometimes occurs, and the same range of variation (1-3 eggs and perhaps 4) also occurs in the ovoviviparous Diplodactylinae (McCann, 1955: 33, 49). This is perhaps a remnant of a more primitive condition, before a stricter regulation of clutch size was perfected. On the other hand, the Gekkoninae, and perhaps independently the Sphaerodactylidae, increased the mineral content of the shell, making it brittle (Bustard, 1967 : 283).

A full treatment of gekkonoid evolution, considering all aspects, is outside the scope of this paper. But even considering the eggs only, some evidence in support of the last suggestion exists. In birds the developing embryo obtains most of its calcium from the inner layers of the egg-shell and, as far as known, the same is true in turtles. However, in the pliable eggs of squamates the embryo derives the required calcium from the particularly calcium-rich yolk. Interestingly, this arrangement appears to have been retained in the calcareous-shelled eggs of geckos (Bellairs, 1969 : 437-438).

The functional advantage of the calcified egg-shell is evident: whereas the eggs of eublepharids are strictly moisture-dependent (as described), and the same is true of diplodactyline eggs (Bustard, 1965 : 298-299, 1967 : 277), hard-shelled gekkonine eggs are drought-resistant (Bustard, 1967 : 283; pers. obs.). Since both eublepharids and diplodactylines successfully inhabit desert areas, it is unlikely that the need for the hard shell arises from lack of moisture in the ground. Rather, it is probably related to the climbing habit, and to the advantage in depositing the eggs within the realm of the vertical habitat, hard and well aerated as it often is (e.g., rock crevices), without recourse to the ground and its moist substratum, in which the eggs could be enveloped closely.

In gekkonines the freshly-laid egg is pliable, but it promptly hardens, and then it cannot expand any more as it would in other lizards. Hence if the neonatus has to be large (perhaps because of its food, Fitch, 1970 : 200-201), the egg must be rather large already when laid. But among geckos the relative size of pliable-shelled eggs appears to be fully as great as that of calcareous-shelled ones (Bustard, 1967 : 283-284). Thus the small clutch size and large egg size of Eublepharidae and Diplodactylinae may be regarded by some as a kind of "preadaptation" to the later evolution of the rigid shell.

The broader, more nearly spherical, shape of the hard-shelled eggs, as compared to that of pliable-shelled ones, probably functions in two ways: 1. Pliable-shelled gekkonoid eggs expand unevenly during development so that the growing embryo is afforded a capsule not only bigger, but relatively much broader than the freshly-laid egg (Bustard, 1965, 1967; Shaw, 1967). The rigid-shelled egg should obviously conform to the broad terminal shape, not the initial narrow shape, of the pliable-shelled egg. 2. For a given volume the sphere represents the least surface area. Hence spherical eggs would (a) be subject to the slowest possible rate of temperature change. (b) They also would occupy the least portion of the substratum, the adequate area of which may be limited. (When, rarely, eggs stuck on rocky substratum are elongate rather than hemispherical, it is their long axis that parallels the rock surface, as I recently observed in the Namib desert.) (c) Perhaps most important, a spherical shape requires the least quantity of calcium (and other materials) for a given volume and a given shell consistency.

The actual, physiological, importance of these self-evident aspects of egg shape may be, and should be, examined, in various ways. However, it is piquant that the single calcareous-shelled egg of the skink-like *Dibamus* ever reported, appeared to constitute a clutch of one, suggesting a relatively large size (Fitch, 1970: 200). In addition, it "was broad in proportion to its length, but not circular." Finally, it was found not in the ground, but in a dead tree trunk (Boulenger, 1912: 99-100). The whole combination of conditions appears to parallel that in geckos.

CONCLUSIONS

1. Eublepharidae resemble the other Gekkonoidea in their (a) seasons of oviposition, (b) incubation periods, (c) consistent relatively large size of eggs and (d) relatively large number of clutches per year. Gekkonoidea differ from other Squamata in (c) and (d).

2. Eublepharidae resemble Diplodactylinae and Lepidosauria in general in their parchment-shelled, moisture-dependent eggs, representing the primitive lepidosaurian condition. In this they differ from Gekkoninae and Sphaerodactylidae, among geckos.

3. Eublepharidae resemble Gekkonidae in their usual clutch size of two, but occasionally have larger clutches, probably a primitive feature, in common with the ovoviviparous Diplodactylinae of New Zealand.

4. Eggs of Eublepharidae are much narrower, more elongate, than those of Gekkoninae and Sphaerodactylidae. Eggs of Diplodactylinae are almost as narrow. All these pliable eggs expand unevenly to become wider.

5. (a) The calcareous, drought-resistent egg-shell of Gekkoninae and Sphaerodactylidae, probably evolved in connection with the climbing habit. (b) The relatively spherical shape of this rigid egg both affords adequate space for the embryo and reduces the requirements in calcium. (c) The original large size of pliable-shelled gecko eggs, and hence the small clutch size, serve as a "preadaptation" for the rigid-shelled eggs that nevertheless hatch a large neonatus.

6. The characteristics of eublepharid eggs support the idea that the Eublepharidae are a monophyletic group of gekkonoids, best accorded family rank.

Dedication and acknowledgements

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Notes added in proof

(1) It might be expected, especially in desert reptiles, that it is advantageous for the neonatus to contain a reserve of water, which might increase the neonatus' weight above that of the egg. Water imbibed by the egg could thus serve for this purpose and also increase the space available to the embryo, which in this case would indeed require more space. However, after this paper went to press I learned that, at least in some cases, water imbibed by the egg functions differently. Badham (1971) found that all the water imbibed by the eggs of *Amphibolurus barbatus* (Agamidae) serves to produce an albumen layer around the yolk. This albumen remains until hatching time, when it oozes out. Her findings explain why the squamate hatchling, as a rule, does not exceed the initial weight of the egg, even where the latter increased its weight several times during incubation (*Amphibolurus barbatus*; Bustard, 1966; other references in Badham, 1971). It remains to be seen to what extent Badham's observations apply to geckos. Although usually the gecko hatchling, Diplodactylinae included, weighs less than the initial weight of the egg, Bustard (1965: 299) lists a neonatus of *Diplodactylus elderi* that weighed 0.42 g, whereas the egg (with shell) had weighed initially only 0.39 g. My suggestion that the large size of the pliable-shelled egg was a prerequisite for the evolution of the rigid shell, probably remains largely correct; but now we understand that the large size of the pliable-shelled egg is indeed required for the production of a large hatchling, because the latter can exceed the initial weight of the egg by only a little. The main functional difference between the two types of eggs is that in the pliable-shelled egg partial drought-protection is given by the watery albumen envelope, and this is replaced in the rigid-shelled egg by the more efficient calcareous shell.

(2) Just recently Hofmann (1972) gave a popular, well illustrated, account of successfully breeding and rearing *Eublepharis macularius* in captivity.

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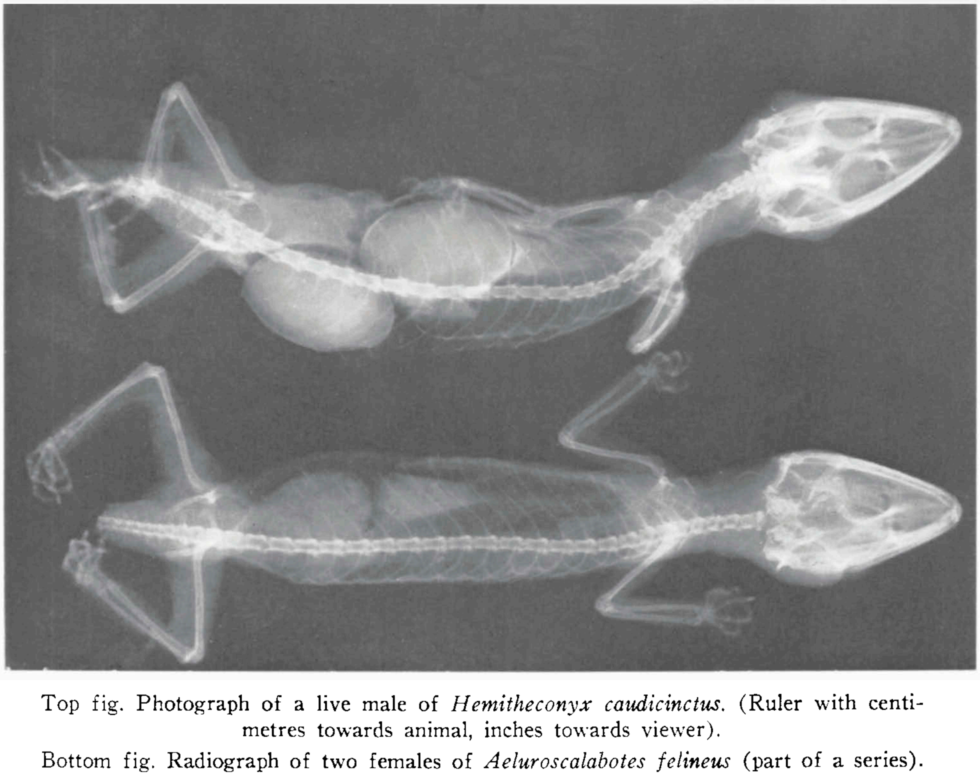

Top fig. Photograph of a live male of *Hemitheconyx caudicinctus*. (Ruler with centimetres towards animal, inches towards viewer).

Bottom fig. Radiograph of two females of *Aeluroscalabotes felineus* (part of a series). Upper, FMNH 146054 carrying two oviducal eggs with well developed shells; lower, FMNH 146092 without oviducal or advanced ovarian eggs. Scale, × 0.98 of original contact radiograph.