Paleosuchus

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In 1950 Federico Medem arrived in Colombia and set about studying the crocodilians of that country. By the time of his death in 1984 Fred Medem had contributed significantly to studies of all species of South American crocodilians (Medem 1981a, 1983). However, he will probably be best remembered for his pioneering work on the genus *Paleosuchus*. When I started studying *Paleosuchus* in 1979 the ground work had been laid and any basic information I could not find in his publications Fred provided in correspondence. This paper is largely a review of the literature, most of which was written by Federico Medem. It is unfortunate that Fred could not write it himself. I am also grateful to Andy Ross who provided much literature not available in Brasil. The work was financed by the Instituto Nacional de Pesquisas da Amazonia and by grant number 40.5055/83 from the Brazilian Conselho Nacional de Desenvolvimento Cientifico e Tecnologico to W. E. Magnusson.

NOMENCLATURE

Biochemical analyses (Densmore 1983) support the status of *Paleosuchus* as a distinct genus within the Alligatorinae. The problems associated with *Paleosuchus* nomenclature are complex and have been detailed by Mook and Mook (1940). However, since Medem's (1958) revision there has been almost universal acceptance of the names *Paleosuchus trigonatus* and *P. palpebrosus* for the two South American species of dwarf caimans. The only modern point of contention is the allocation of *Jacaretinga moschifer* Spix to synonymy with one of the species of *Paleosuchus*. The type specimen of *J. moschifer* was destroyed during World War II. However, the description of *J. moschifer* is accompanied by a figure of a crocodilian with a snout shape similar to that of *P. trigonatus*. Vaillant (1898) considered *J. moschifer* to be synonymous with *P. palpebrosus* based on the description which specifically mentions four rows of dorsal scutes between the hind legs. Medem (1958) considered *J. moschifer* to be a composite, the description based on *P. palpebrosus* and the figure based on a *P. trigonatus*, and so synonymized *J. moschifer* with *P. trigonatus*. The synonomy would not be important except that *J. moschifer* was described from Bahia, an area which has several confirmed reports of *P. trigonatus* (Magnusson 1987). For zoogeographic reasons I agree with Vaillant (1898) that *J. moschifer* is a synonym for *P. palpebrosus*. Also, Muller (1923), a specialist familiar with the species of *Paleosuchus*, identified and catalogued the type specimen as *P. palpebrosus*.

Medem (1983) considered Seba's plate 105, Figs. 3 and 4, of the specimen on which Schneider based his description of *P. trigonatus*, to represent the species we now call *P. palpebrosus* but did not suggest that the names of the two species be switched. In the interest of nomenclatural stability it may be necessary to designate a neotype for Schneider's *Crocodilus trigonatus*.

MORPHOLOGY

Species in the genus *Paleosuchus* are among the smallest of the Crocodilia. Medem (1981a) encountered male *P. trigonatus* up to 136 cm snout-vent length (SVL), however most adult males are in the size range 75-90 cm SVL. Females reach about 75 cm SVL. Few data are available for *P. palpebrosus* but it is generally considered that they mature at smaller sizes than *P. trigonatus*. Medem (1981a) records male *P. palpebrosus* up to 90 cm SVL and females up to 68 cm SVL. *Paleosuchus* tend to have short tails, at least in comparison to *Caiman crocodilus* (Vanzolin and Gomes 1979).

Distinctive features of the skull are the lack of distinct supratemporal fossae (small fossae are present in juvenile *P. trigonatus*), 8 teeth in the premaxilla, and the lack of an interorbital ridge. Three bones form a plate over the orbit and almost obscure it when the skull is viewed from above. The shape of the skull of *P. trigonatus* is that of a generalized crocodilian, but *P. palpebrosus* has a high smooth "dog-like" skull (Medem 1958, 1981a). Some individuals have body characteristics of *P. palpebrosus* but head shape and color of *P. trigonatus*. Medem (1970, 1981a) considered these to be hybrids. The best feature to distinguish between skulls of the two species is the relative size of the external mandibular foramen. In *P. trigonatus* the maximum width of the foramen (measured perpendicular to the long axis) is equal to or greater than the distance from the foramen to the inferior edge of the angular. The width of the external mandibular foramen is less than the distance from the foramen to the inferior edge of the angular in *P. palpebrosus*.

The skins of both species of *Paleosuchus* are heavily ossified, the bony osteoderms of the venter, dorsum and tail being so closely juxtaposed that the animal almost appears to be enclosed in a shell. Algae adhere to the skins of both species in captivity, and in some natural habitats (Medem 1958), giving the animals a green color. Medem (1981a) gives the sizes and meristics of individuals of each species collected in Colombia.

The eyes of *Paleosuchus* are a rich brown color. Medem (1981a) presents many color plates of each species. Adult *P. palpebrosus* have extensive dark pigment on the ventral surfaces and light-brown heads. Adult *P. trigonatus* have dark heads and generally lack pigment on the ventral surface. The dorsal surface of the head behind the eyes is light yellow in juveniles of each species (color photographs in Medem 1981a). Other aspects of coloration are variable and not very distinctive (Medem 1958).

The only other crocodilian genus with deep-brown eyes, heavily-armoured skin, heavily ossified palpebrals, and small adult size is the African crocodyline *Osteolaemus tetraspis*. Too little is known of the life histories of either genus to warrant speculation on the reasons for this morphological convergence but it may be significant that the distributions of both genera are centered on areas of tropical rainforest.

DISTRIBUTION

Paleosuchus trigonatus occurs throughout the Amazon and Orinoco drainage basins and the coastal rivers of the three Guianas. *P. palpebrosus* occurs over essentially the same range and extends south across the Brazilian shield to the Rio Parana and Rio Paraquay drainage basins. It also occurs in the Rio Sao Francisco drainage basin of the Brazilian states of Bahia and Minas Gerais. Medem (1983) gives detailed locality records. Two records for *P. trigonatus* (Aruana and Bahia) south of the Amazon Basin given by Medem (1983) are probably erroneous (Magnusson and Yamakoshi 1986). In Venezuela *P. trigonatus* is largely restricted to the southern, forested regions whereas *P. palpebrosus* occurs extensively over the northern "llanos" areas of the Rio Orinoco drainage (Gorzula 1987: Figs. 2 and 3).

Despite being sympatric over large areas, the two species of *Paleosuchus* are rarely syntopic. In water bodies in which they are found together one species is usually common and the other rare (Medem 1967, 1971a). The major habitat for *P. trigonatus* appears to be small forest streams (Medem 1967, Dixon et al. 1977, Magnusson 1985) and *P. palpebrosus* rarely occurs in that habitat. In the central Amazon Basin *P. palpebrosus* is found most commonly in inundation forests around the major rivers and lakes (Magnusson 1985). On the Brazilian shield, *P. palpebrosus* occurs in streams lined by gallery forests that run through savanna (Rebelo and Louzada 1984). Much of the confusion that surrounds the ecological distributions of the two species stems from the fact that it is difficult to work in small rainforest streams and gallery forest. Most observations (as distinct from occurrences) of *Paleosuchus* are made around large water bodies with easy access by boat. Individuals, especially large males and dispersing juveniles, are often found in such situations but to date there is no evidence that either species normally breeds around large water bodies. Large rivers and lakes are normally the major habitats for *C. crocodilus*, *Melanosuchus niger* and *Crocodylus intermedius*. Medem (1980) suggested that the occurrence of *Paleosuchus* in some habitats in Colombia increased after the larger, commerçially more valuable species, had been eliminated by overhunting.

Much more work needs to be done on the ecological distributions of the species of *Paleosuchus*, especially *P. palpebrosus*, but care must be taken to evaluate habitats for the presence of both sexes, nests and juveniles. Spotlight surveys from a boat as are used for most other species of crocodilians are probably of little use for evaluating populations of *Paleosuchus*. Gorzula (1987) suggests that the water bodies in which *P. trigonatus* occurs are chemically distinct from those in which *C. crocodilus* occurs, so limnological variables may be useful for distinguishing habitats.

FOOD

As with other crocodilians, *Paleosuchus* species eat a variety of vertebrate and invertebrate prey. Medem (1981a) lists the stomach contents of *Paleosuchus* taken in a variety of habitats in Colombia, Vanzolini and Gomes (1979) give stomach contents of *P. trigonatus* taken in Brazil, and Ruesta (1981) describes the stomach contents of 3 *P. trigonatus* from Peru. Large males of both species occasionally eat other crocodilians (Medem 1981a).

In the central Amazon Basin *P. trigonatus* eats more terrestrial vertebrates than other crocodilians of similar size but *P. palpebrosus* eats similar foods (mainly invertebrates and fish) to *C. crocodilus* and *M. niger* in the same size range. Mammals and snakes are taken mainly by large *P. trigonatus* with fixed home ranges (Magnusson et al. 1987). The diet of *P. palpebrosus* in savanna gallery forest has not been studied.

REPRODUCTION

Medem (1981a), Dixon and Soini (1977), Ruesta (1981, 1982-83) and Magnusson et al. (1985) have described nests of *P. trigonatus*. Ruesta (1982-83) also described the embryos. The nests found by Ruesta and by Dixon and Soini in Peru were located 13 September and 14 August-30 November, respectively. The nest found by Medem in Colombia was located 13 February and had well developed embryos. Magnusson et al. (1985) found nests in the Manaus area between August and January. Egg laying apparently occurs at the end of the dry season and hatching at the beginning of the wet season. In the Manaus area *P. trigonatus* frequently make their nests beside or on top of termite mounds which elevate the temperatures of the eggs above that which they would otherwise attain (Magnusson et al. 1985). Medem (1981a) and Ruesta (1982-83) give egg dimensions. *P. trigonatus* has been bred in the Cincinnati Zoo (Jardine 1981).

Medem (1971b) recorded a nest of *P. palpebrosus* found in gallery forest in Colombia 1 November 1967, which hatched in December. Another nest found in the same area, but in a slightly more exposed site, had recently laid eggs 8 August 1970. That nest had a temperature of 31°C at 22cm depth. A third nest was located among four small trees on an elevated mound of earth formed by dry canals, 3km from a permanent canal, in August 1978 (Medem 1981a). Nest and egg dimensions of the three nests are given by Medem (1981a). Rebelo and Louzada (1984) found hatchlings near a nest in June-July in the Reserva Biologica Aguas Emendadas on the Brazilian Shield but the age of the nest could not be determined. Marc Hero (pers. comm.) encountered hatchling *P. palpebrosus* 13.2 cm and 14.2 cm SVL in the Rio Negro in October 1985, indicating nesting in the early dry season. The limited data coupled with the great climatic and geographical variation within the range of *P. palpebrosus* makes generalizations about its nesting season(s) presently inadvisable.

Medem (1981a) reports in detail the captive reproduction of a female that he considered to be a hybrid between *P. palpebrosus* and *P. trigonatus*. The female was mated by a *P. palpebrosus* and laid her eggs 27 September 1977. *P. palpebrosus* has also been bred in the Rio Grande Zoo, Albuquerque (A. Dale Belcher, pers. comm.).

Medem (1971b, 1981a) gives incubation periods of 90-92 and 147 days for *P. palpebrosus* eggs incubated artificially at variable temperatures. Ruesta (1982-83) reported incomplete incubation of *P. trigonatus* eggs after 3 months but the eggs had been moved and the final incubation temperature was not given. Jardine (1981) reported an incubation period of 114-118 days for eggs of *P. trigonatus* incubated artificially at 29-31°C. The data in Figure 1 indicate that the normal incubation period of *P. trigonatus* in the Manaus area is in excess of 100 days. This is longer than the incubation periods reported for all other alligatorines and most other crocodilians (Magnusson 1979).

PARASITES, DISEASES AND PREDATORS

Nothing is known of th effects of parasites, diseases and predators on populations of *Paleosuchus*. Magnusson (1985) reports variation in the frequency of parasitism by nematodes and leeches in different habitats in Amazonia and Medem (1981b) lists internal parasites found in

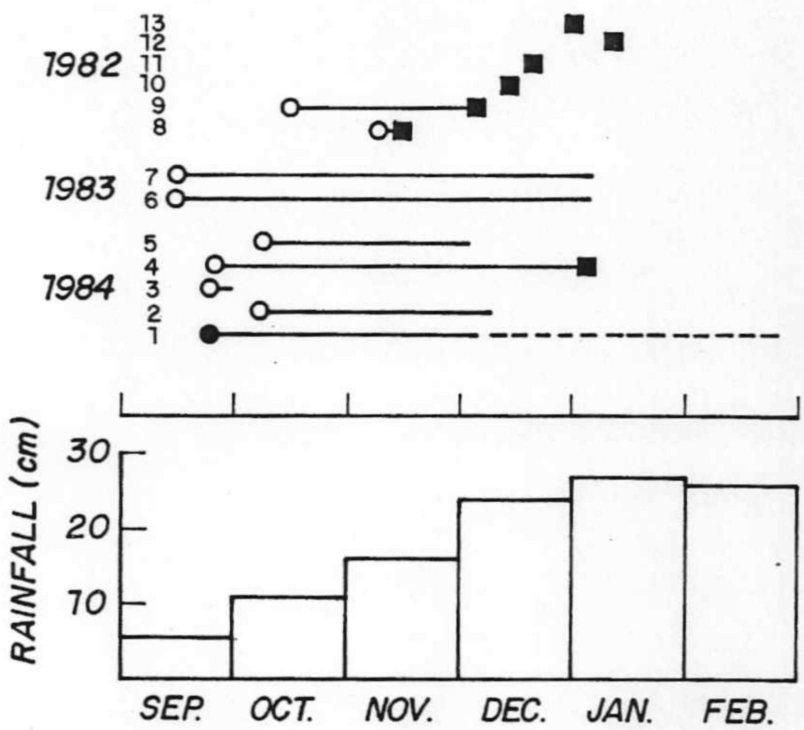

Figure 1. Dates of laying (solid circles), hatchling (solid squares), first encountering (open circles), and periods with incubating eggs (lines), for 13 nests in the Manaus area. The dates of death of eggs in nest #1 are not known and the period of uncertainly is indicated by the broken line. Rainfall records are means (1910-1975) for the city of Manaus.

Paleosuchus in Colombia. Medem (1981a, 1981b) reports attacks by tabanid flies on animals restrained on shore near the banks of rivers during daylight hours.

There are no reports of diseases in wild *Paleosuchus* and the only confirmed predators of *Paleosuchus* are man, anacondas (*Eunectes murinus*) and other crocodilians (Medem 1983). However, jaguars (*Panthera onca*) regularly eat *C. crocodilus* (Medem 1981a) and other reptiles (Louise Emmons, pers. comm.). There is no reason to believe that they do not also eat *Paleosuchus*. The only large *P. trigonatus* (approx. 65 cm SVL) that I have found dead was eaten by a large cat (*P. onca* or *Felis concolor*). It is likely that the cat killed the *P. trigonatus* as, apart from a conspecific, there are no other predators in the area that are likely to be capable of killing a large *P. trigonatus* close to water.

Most of the nests of *P. trigonatus* I studied in 1983 and 1984 were destroyed by predators. However, I believe the high rate of predation may be related to interference with nests while measuring temperatures. None of the nests studied in 1982, which were all discovered late in incubation, suffered predation. Ruesta (1981) and Medem (1983) list probable nest predators of South American crocodilians but, apart from humans, no predators have been caught in the act of robbing *Paleosuchus* nests.

BEHAVIOR

Little is known of the behavior of either species of *Paleosuchus* and they are not good candidates for behavioral research as they are much more shy in the presence of humans than most crocodilians. My coworkers and I have caught one female *P. trigonatus* several times in a shallow stream in front of a nest with incubating eggs, and tracks in front of another nest indicate that a female was in attendance. We have never been attacked when opening nests but have noted altered behavior by females associated with hatchlings. Twice females have left their refuges and approached us when we were catching hatchlings near nests and on one occasion a female, which was accompanied by a hatchling group and that had been noosed around the back legs, chased us out of the stream. We have not observed aggressive behavior towards humans by *Paleosuchus* in any other situation. Medem (1981a) describes aggressive behavior by a captive female *Paleosuchus* defending a nest and Gorzula (1984) describes having his inflatable boat sunk by a *P. trigonatus* which responded to human initiations of hatchling *C. crocodilus* calls.

All successful nests in my study area were opened by a crocodilian and females with hatchling groups were found in front of four recently opened nests. One nest, constructed in the home range of an adult male but far from the normal area of activity of any female, was found recently opened and the hatchling group was accompanied by the adult male. No female was found in the area despite intensive searching. A female (64 cm SVL) had been caught at that site the preceding August but no female had been seen there before or after so it seems likely that the male opened the nest and released the young. Eggs in some nests in the Manaus area are encased in hard termite workings by the end of incubation (Magnusson et al. 1985). Nest opening by an adult is probably essential for successful hatching of those eggs. More detailed observations will probably show *Paleosuchus* to have the same range of nest-guarding, nest-opening and hatching-defense behaviors found in other crocodilians.

After heavy rain *P. trigonatus* are often found in rapids or small waterfalls; sitting perpendicular to the current with their mouths open, the lower jaw submerged and the upper jaw above water level. I assume that they are foraging, but I have no evidence of what they catch with this technique.

SUGGESTIONS FOR FURTHER RESEARCH

Much remains to learn about the ecologies of both species of *Paleosuchus*. It is obvious that the habitats of each differ, and that the habitats of both are different from those of other sympatric crocodilians but just which differences are critical remains conjecture. Reasons for habitat segregation could include competition, predation, and behavioral and physiological adaptations. To differentiate the effects of these factors would require large scale experiments, though areas in which sympatric species have been eliminated by overhunting could serve as unplanned manipulations.

P. trigonatus may differ from other crocodilians in its thermal biology because temperatures in its main habitat are moderate, relatively invariant, and opportunities to bask are limited. Zoo animals could serve for the study of the effects of temperature on digestion and metabolic rate.

Field studies will have to focus on populations rather than presence/absence data as has been the pattern in the past. Presence/absence data have raised some interesting questions but to date have been of limited use in providing answers. My as yet unpublished studies indicate that *P. trigonatus* have small home ranges (of the order of 500-1000m small stream) and, if the same proves true for *P. palpebrosus*, long term studies of population dynamics, reproduction and habitat use could be done on marked populations, simply and at low cost. Comparative studies of populations of *P. palpebrosus* living on the high, cold plains of the Brazilian shield, flooded forests of the Amazon system and the lowland floodplains of the Orinoco system would be particularly interesting. Small implanted transmitters could overcome many of the problems associated with difficult habitats and the wariness of the species. Basic data on diet are lacking for *P. palpebrosus* over most of its range and most of the data on the diet of *P. trigonatus* are from a few localities. Stomach contents could be collected by non-destructive means (Taylor et al. 1978) in parallel with other studies.

Schmidt commented in 1928(:212) "It is one of the curiosities of zoological collecting that so little is known of the habits and distribution of these species (*Paleosuchus*)". Sixty years later we know only a little more of their distributions and we have advanced very little in studies of their habits. They remain "one of the most interesting problems in South American zoology" (Schmidt 1928:212).

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