



HISTORICAL PERSPECTIVE

Sexual Dimorphism in Lizards

 Charles R. Darwin¹

Lacertilia.—The males of some, probably of many kinds of lizards, fight together from rivalry. Thus the arboreal *Anolis cristatellus* of S. America² is extremely pugnacious: “During the spring and early part of the summer, two adult males rarely meet without a contest. On first seeing one another, they nod their heads up and down three or four times, at the same time expanding the frill or pouch beneath the throat; their eyes glisten with rage, and after waving their tails from side to side for a few seconds, as if to gather energy, they dart at each other furiously, rolling over and over, and holding firmly with their teeth. The conflict generally ends in one of the combatants losing his tail, which is often devoured by the victor.” The male of this species is considerably larger than the female³; and this, as far as Dr. Günther⁴ has been able to ascertain, is the general rule with lizards of all kinds.

The sexes often differ greatly in various external characters. The male of the above-mentioned *Anolis* is furnished with a crest, which runs along the back and tail, and can be erected at pleasure; but of this crest the female does not exhibit a trace. In the Indian *Cophotis ceylanica*, the female possesses a dorsal crest, though much less developed than in the male;

and so it is, as Dr. Günther informs me, with the females of many Iguanas, Chamelions and other lizards. In some species, however, the crest is equally developed in both sexes, as in the *Iguana tuberculata*⁵. In the genus *Sitana*⁶, the males alone are furnished with a large throat-pouch (fig. 33)⁷, which can be



Male anoles, such as these Puerto Rican Crested Anoles (*Anolis cristatellus*) erect a dewlap (described by Darwin as a “frill or pouch beneath the throat”) when they court females or engage in territorial conflicts with other males. Dewlap color varies by species and appears to be important in species recognition in many instances. However, dewlap color can also vary by population. The top individual is from Puerto Rico proper, whereas the male below is from the British Virgin Islands. The difference in dewlap color is acknowledged by recognition at the subspecific level (*A. c. cristatellus* in Puerto Rico and *A. c. wileyae* from islands off the eastern coast of Puerto Rico and the Virgin Islands). Top photograph by Fr. Alejandro J. Sánchez Muñoz, bottom photograph by Douglas Bell.

¹ Darwin, C.R. 1871. *The Descent of Man, and Selection in Relation to Sex*. Volume 2. 1st edition. John Murray, London. Pp. 32–37 from Chapter 12: “Secondary sexual characters of fishes, amphibians, and reptiles.” Spelling, punctuation, italics, and nomenclature as in the original text and footnotes.

² The reference to South America is in error, as indicated by its common name, the Puerto Rican Crested Anole (*Anolis cristatellus*) is native to the Puerto Rican Bank and has become established in Costa Rica, the Dominican Republic (Hispaniola), St. Martin and Dominica (Lesser Antilles), and Florida (Kraus, F. 2009. *Alien Reptiles and Amphibians: A Scientific Compendium and Analysis*. Invading Nature: Springer Series in Invasion Biology 4. Springer, New York).

³ Mr. N.L. Austin kept these animals alive for a considerable time; see ‘Land and Water,’ July, 1867, p. 9 (footnote from the original document).

⁴ Albert Günther (1830–1914), a German-born ichthyologist and herpetologist who served as keeper of the zoological collections of the British Museum, founded the *Zoological Record* (the world’s most complete index of zoological literature) and was the first person to realize that *Sphenodon* of New Zealand was not a lizard but the sole living representative of the otherwise extinct order Rhynchocephalia (Adler, K. (ed.). 1989. *Contributions to the History of Herpetology*. Contributions to Herpetology, volume 5. Society for the Study of Amphibians and Reptiles, Ithaca, New York).

⁵ *Iguana tuberculata* is now known to be a synonym of *Iguana iguana* (the Common or Green Iguana).

⁶ Scientific names are italicized or not as in the original document. Fan-throated Lizards in the genus *Sitana* (family Agamidae) derive their name from the brightly colored, extendable throat fans of the males. This genus is endemic to the Indian Subcontinent.

⁷ This and following parenthetical references are to figures in the original document that are included herein under their original numbers.



Male Puerto Rican Crested Anoles (*Anolis cristatellus*) engaged in a territorial struggle. The nuchal and dorsal crests of the male on top in this photograph (the eventual loser) are clearly evident. These are elevated when the lizard is aroused, apparently in order to present a larger, more imposing profile. However, the tail crest is permanently erect (contrary to Günther's information that was cited by Darwin). Photograph by Robert Powell.

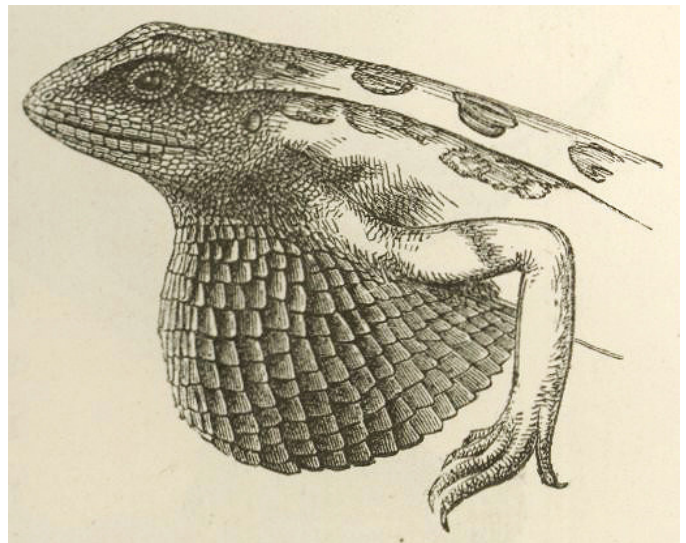


Fig. 33. *Sitana minor*. Male, with the gular pouch expanded (from Günther's 'Reptiles of India.')

folded up like a fan, and is coloured blue, black, and red; but these splendid colours are exhibited only during the pairing-season. The female does not possess even a rudiment of this appendage. In the *Anolis cristatellus*, according to Mr. Austen, the throat-pouch, which is bright red marbled with yellow, is present, though in a rudimental condition, in the female. Again, in certain other lizards, both sexes are equally well provided with throat-pouches. Here, as in so many previous cases, we see with species belonging to the same group, the same character confined to the males, or more largely developed in the males than in the females, or equally developed in both sexes. The little lizards of the genus *Draco*, which glide through the air on their rib-supported parachutes, and which in the beauty of their colours baffle description, are furnished with skinny appendages to the throat, "like the wattles of gallinaceous birds." These become erected when the animal is excited. They occur in both sexes, but are best developed in the male when arrived at maturity, at which age the middle



Both male and female Pygmy Lizards (*Cophotis ceylanica*) possess a dorsal crest, but that of the female (illustrated here) is much smaller than that of the male. Photograph © V.A.M.P.K. Samarawickrama.



Both sexes of Green Iguanas (*Iguana iguana*) have prominent crests, although contrary to Darwin’s report, those of males are more imposing than those of females. This individual is part of an introduced population in Charlotte Amalie, St. Thomas, U.S. Virgin Islands. Photograph by Wilfredo Falcón.



As in most anoles, only male Fan-throated Lizards in the Asian genus *Sitana* have throat-fans or dewlaps. Also like anoles, dewlap colors can vary considerably in many species, such as these *Sitana ponticeriana*. Photographs by Dr. Caesar Sengupta (left) and Dr. J. Subramanean (right).

appendage is sometimes twice as long as the head. Most of the species likewise have a low crest running along the neck; and this is much more developed in the full-grown males, than in the females or young males.⁸

⁸ All these statements and quotations, in regard to Cophotis, Sitana and Draco, as well as the following facts in regard to Ceratophora and Chamaeleon, are taken from Dr. Günther’s magnificent work on the ‘Reptiles of British India,’ Ray Soc., 1864, p. 122, 130, 135 (footnote from the original document).



Lizards in the genus *Draco*, commonly known as “Flying Dragons,” are gliders that employ rib-supported “wings” to “fly.” Appendages on the throat are erected when the animal is excited. They occur in both sexes, but are best developed in mature males. Brilliant colors of the Dusky Gliding Lizard (*D. formosus*; left) are only evident when the “wings” and throat lappets are expanded. Black-bearded Gliding Lizards (*D. melanopogon*) are quite cryptic unless the wings and dewlap are extended. Photographs by L. Lee Grismer.

There are other and much more remarkable differences between the sexes of certain lizards. The male of *Ceratophora aspera*⁹ bears on the extremity of his snout an appendage half as long as the head. It is cylindrical, covered with scales, flexible, and apparently capable of erection; in the female it is quite rudimental. In a second species of the same genus a terminal scale forms a minute horn on the summit of the flexible appendage; and in a third species (*C. Stoddartii*,¹⁰ fig. 34) the whole appendage is converted into a horn, which is usually of a white colour, but assumes a purplish tint when the animal is excited. In the adult male of this latter species the horn is half an inch in length, but is of quite minute size in the female and in the young. These appendages, as Dr. Günther has remarked to me, may be compared with the combs of gallinaceous birds, and apparently serve as ornaments.

In the genus *Chamæleon*¹¹ we come to the climax of difference between the sexes. The upper part of the skull of the male *C. bifurcus*¹² (fig. 35), an inhabitant of Madagascar, is produced into two great, solid, bony projections, covered with scales like the rest of the head; and of this wonderful modification of structure the female exhibits only a rudiment. Again, in

⁹ Horned Agamas (genus *Ceratophora*, family Agamidae) are endemic to Sri Lanka. The common name is derived from the nasal appendages of the males, which vary by species.

¹⁰ Specific epithets derived from proper names once were capitalized. This is no longer done; consequently, the proper form of the name for this species would be *Ceratophora stoddartii*.

¹¹ Chameleons (family Chamaeleonidae) once were placed in a single genus, but recent analyses have led to the recognition of about a dozen species in two subfamilies.

¹² This name is now considered a synonym of *Furcifer bifidus*, a chameleon endemic to Madagascar.

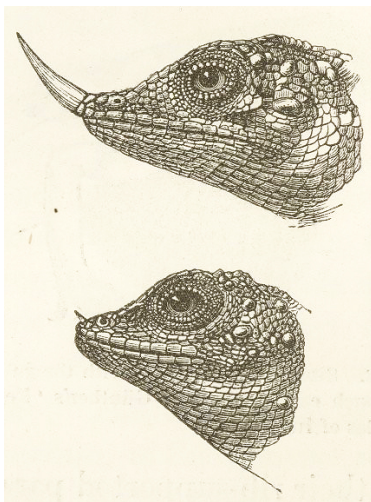


Fig. 34. *Ceratophora Stoddartii*.
Upper figure, male; lower figure, female.

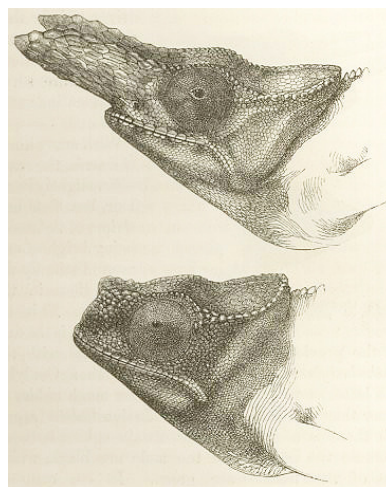


Fig. 35. *Chamæleon bifurcus*.
Upper figure, male; lower figure, female.

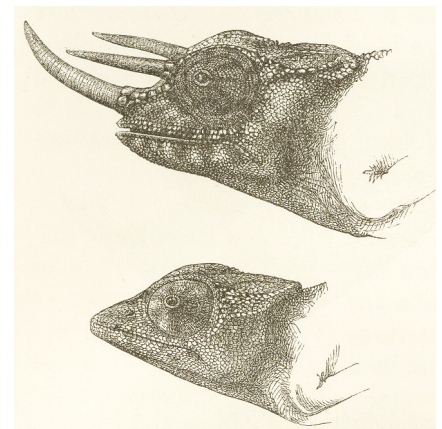


Fig. 36. *Chamæleon Owenii*.
Upper figure, male; lower figure, female.

*Chamaeleon Owenii*¹³ (fig. 36), from the West Coast of Africa, the male bears on his snout and forehead three curious horns, of which the female has not a trace. These horns consist of an excrescence of bone covered with a smooth sheath, forming



Although fundamentally similar in appearance, male Smith's Sand Lizards (*Meroles ctenodactylus*; Darwin's "*Acanthodactylus capensis*") differ slightly from females in color, with the "tints and stripes of the males being brighter and more distinctly defined than in the females." Photograph by Johan Morais

part of the general integuments of the body, so that they are identical in structure with those of a bull, goat, or other sheath-horned ruminant. Although the three horns differ so much in appearance from the two great prolongations of the skull in *C. bifurcus*, we can hardly doubt that they serve the same general purpose in the economy of these two animals. The first conjecture which will occur to every one is that they are used by the males for fighting together; but Dr. Günther, to whom I am indebted for the foregoing details, does not believe that such peacable creatures would ever become pugnacious. Hence we are driven to infer that these almost monstrous deviations of structure serve as masculine ornaments.

With many kinds of lizards, the sexes differ slightly in colour, the tints and stripes of the males being brighter and more distinctly defined than in the females. This, for instance, is the case with the previously-mentioned *Cophotis* and with the *Acanthodactylus capensis* of S. Africa.¹⁴ In a *Cordylus* of the

¹³ This name is now considered a synonym of *Triceros oweni*, a chameleon endemic to west-central Africa.

¹⁴ These lizards are no longer assigned to the genus *Acanthodactylus* and are instead placed in the genus *Meroles* (Sand Lizards); the name used by Darwin is now in the synonymy of *M. ctenodactylus* (Smith's Sand Lizard).



In Asian Black-lipped Agamas (*Calotes nigrilabris*), "the lips of the male are black, whilst those of the female are green." Photograph by Ken Preston-Mafham / Premaphotos Wildlife.



In addition to colors and patterns in males being brighter and more distinctly defined than in females, in the European Viviparous Lizard (*Zootoca vivipara*), “the under side of the body and base of the tail in the male are bright orange, spotted with black; in the female these parts are pale greyish-green without spots.” Photograph by Matt Wilson.

latter country, the male is either much redder or greener than the female. In the Indian *Calotes nigrilabris* there is a greater difference in colour between the sexes; the lips of the male are black, whilst those of the female are green.¹⁵ In our common little viviparous lizard (*Zootoca vivipara*)¹⁶ “the under side of the body and base of the tail in the male are bright orange, spotted with black; in the female these parts are pale greyish-green without spots.”¹⁷ We have seen that the males alone of *Sitana* possess a throat-pouch; and this is splendidly tinted with blue, black, and red. In the *Proctotretus tenuis*¹⁸ of Chile the male alone is marked with spots of blue, green, and coppery-red.¹⁹ I collected in S. America fourteen species of this genus, and though I neglected to record the sexes, I observed that certain individuals alone were marked with emerald-like green spots, whilst others had orange-coloured gorges; and these in both cases no doubt were the males.

In the foregoing species, the males are more brightly coloured than the females, but with many lizards both sexes are coloured in the same elegant or even magnificent manner; and there is no reason to suppose that such conspicuous colours are protective. With some lizards, however, the green tints no doubt serve for concealment; and an instance has already been incidentally given of one species of *Proctotretus* which closely resembles the sand on which it lives. On the whole we may conclude with tolerable safety that the beautiful colours of many lizards, as well as various appendages and other strange modifications of structure, have been gained by

the males through sexual selection for the sake of ornament, and have been transmitted either to their male offspring alone or to both sexes. Sexual selection, indeed, seems to have played almost as important a part with reptiles as with birds. But the less conspicuous colours of the females in comparison with those of the males cannot be accounted for, as Mr. Wallace²⁰ believes to be the case with birds, by the exposure of the females to danger during incubation.

¹⁵ Both the scientific name (*nigrilabris*) and common name (Black-lipped Agama) reflect the black lips and cheeks of the males.

¹⁶ The Common or Viviparous Lizard of northern Eurasia has the distinction of ranging farther north than any other species of lizard, with populations occurring well north of the Arctic Circle in Scandinavia and Russia.

¹⁷ Bell, ‘History of British Reptiles,’ 2nd edit. 1849, p. 40 (footnote from the original document).

¹⁸ This species is now assigned to the genus *Liolaemus* (family Liolaemidae).

¹⁹ For *Proctotretus* see ‘Zoology of the Voyage of the “Beagle:” Reptiles,’ by Mr. Bell, p. 8. For the Lizards of S. Africa, see ‘Zoology of S. Africa: Reptiles,’ by Sir Andrew Smith, pl. 25 and 39. For the Indian *Calotes*, see ‘Reptiles of British India,’ by Dr. Günther, p. 143 (footnote from the original document).

²⁰ Alfred Russel Wallace (1823–1913), British humanist, naturalist, geographer, and social critic, became a public figure in England during the second half of the 19th century. He was known for his courageous views on scientific, social, and spiritualist subjects. His formulation of the theory of evolution by natural selection predated Charles Darwin’s published contributions (and many authors credit his letter to Darwin on the subject for prompting Darwin to publish the first edition of *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* in 1859. Wallace’s work on biogeography has led some historians to call him the “father of biogeography” (modified and amended from the Britannica Online Encyclopedia, www.britannica.com/EBchecked/topic/634738/Alfred-Russel-Wallace).