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TOOTH REPLACEMENT IN AMPHIBIANS AND REPTILES.

By

J. S. Cooper

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Most amphibians and reptiles are polyphyodont, that is their teeth are replaced again and again throughout life. The maintenance of both the number and sharpness of the teeth is of great importance to animals which use their dentition to catch and hold fast-moving, live prey. If all the teeth were to be replaced simultaneously, there would be phases of toothlessness in which the animal would be at a serious disadvantage. There is, in fact, an orderly pattern of replacement along the rows of teeth, which ensures that no toothless phases occur, and that an efficient dentition is always present, but although the arrangement has attracted attention for well over a century, its complexity has defied understanding until recently.

Knowledge concerning tooth replacement has been contributed by histologists, palaeontologists and embryologists over a long period, but the work of Edmund (1960) finally pointed out the underlying principles.

The teeth arise from a structure called the dental lamina which is formed by an infolding of the epithelium of the mouth on the inner side of the jaw bones (Fig. 1). Formation of the lamina in the embryo commences at the anterior end of the jaws and proceeds backwards, and similarly the teeth are formed in a sequence, along the edge of the lamina, beginning anteriorly and progressing backwards. This sequence of tooth formation is preserved in post-natal life; once formed, each tooth grows and moves towards the crest of the jaw bone, and in doing so, erodes the base of its predecessor, ultimately causing it to be shed. Then the growing tooth erupts through the soft tissues into the mouth, becomes fused to the jaw bone, and assumes its function. This cycle is repeated again and again at each tooth position, for the germinal material at the edge of the lamina produces continuous streams of tooth buds, or "tooth families" each generation of which replaces its predecessor (Fig. 1).

The way in which the pattern of replacement is built up along the whole row of teeth can best be appreciated with the aid of the diagram in Fig. 2.

The two growth processes already mentioned must now be considered again. These are the front-to-back sequence of teeth arising along the edge of the lamina, and the migration of the teeth from the edge of the lamina towards their functional positions at the crest of the jaw. Thus in Fig. 2, the first tooth of the dentition is formed at position 1 and has moved a little way across the lamina by the time the second tooth forms at position 2. These two teeth both continue to move across the lamina and the third forms at position 3, and so on. In this way, an oblique row of teeth at successive stages of development is formed on the lamina, and further similar rows,* marked by continuous lines in Fig. 2, follow one behind the other until the whole dentition is built up. Not only are these overlapping, oblique rows a feature of every dentition, but the spacing between them is

*These rows are known by the German term, *Zahnreihen*, in the literature on tooth replacement.

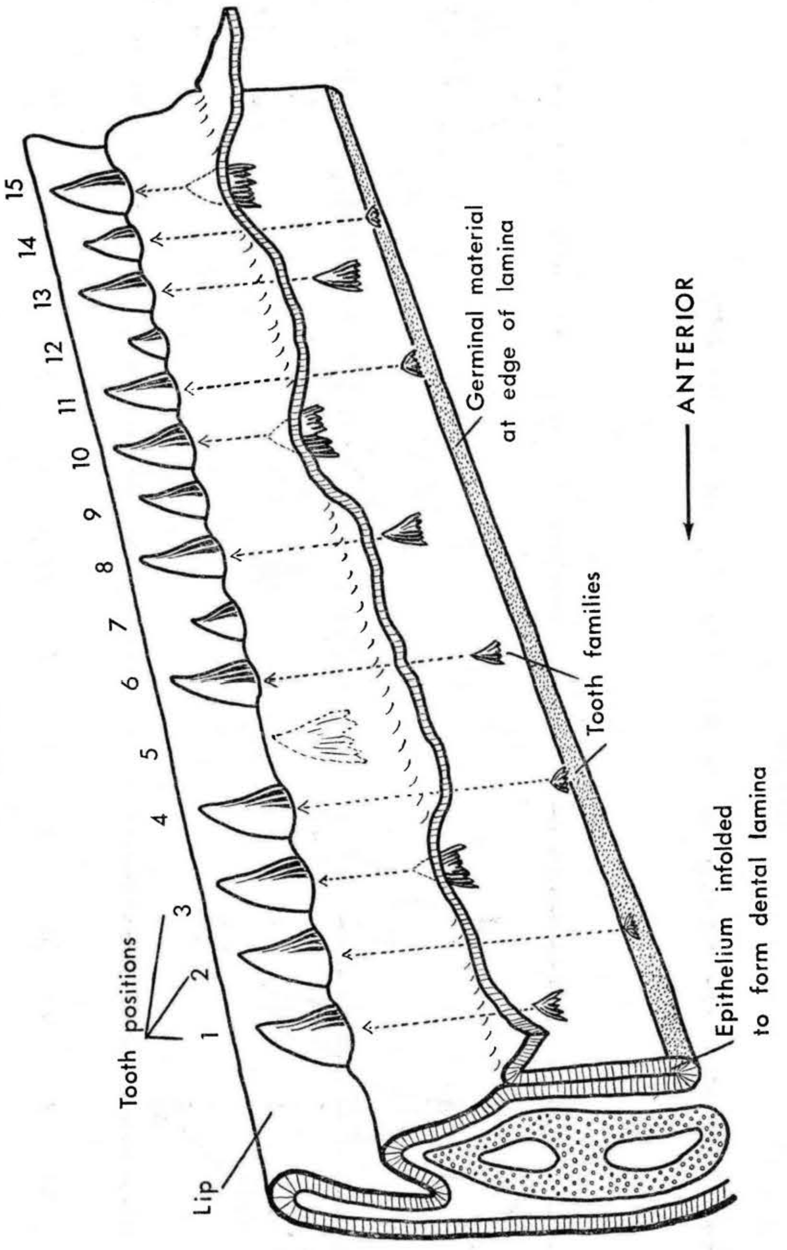

Fig. 1
A portion of a representative reptilian jaw

of great significance. For instance, inspection of the arrangement in Fig. 2 reveals other characteristics of the pattern. If either the odd-numbered or the even-numbered teeth are examined, sequences can be found decreasing in size and age towards the front of the jaw. One such sequence is marked in black in Fig. 2 and the teeth would clearly erupt in the order 14, 12, 10,

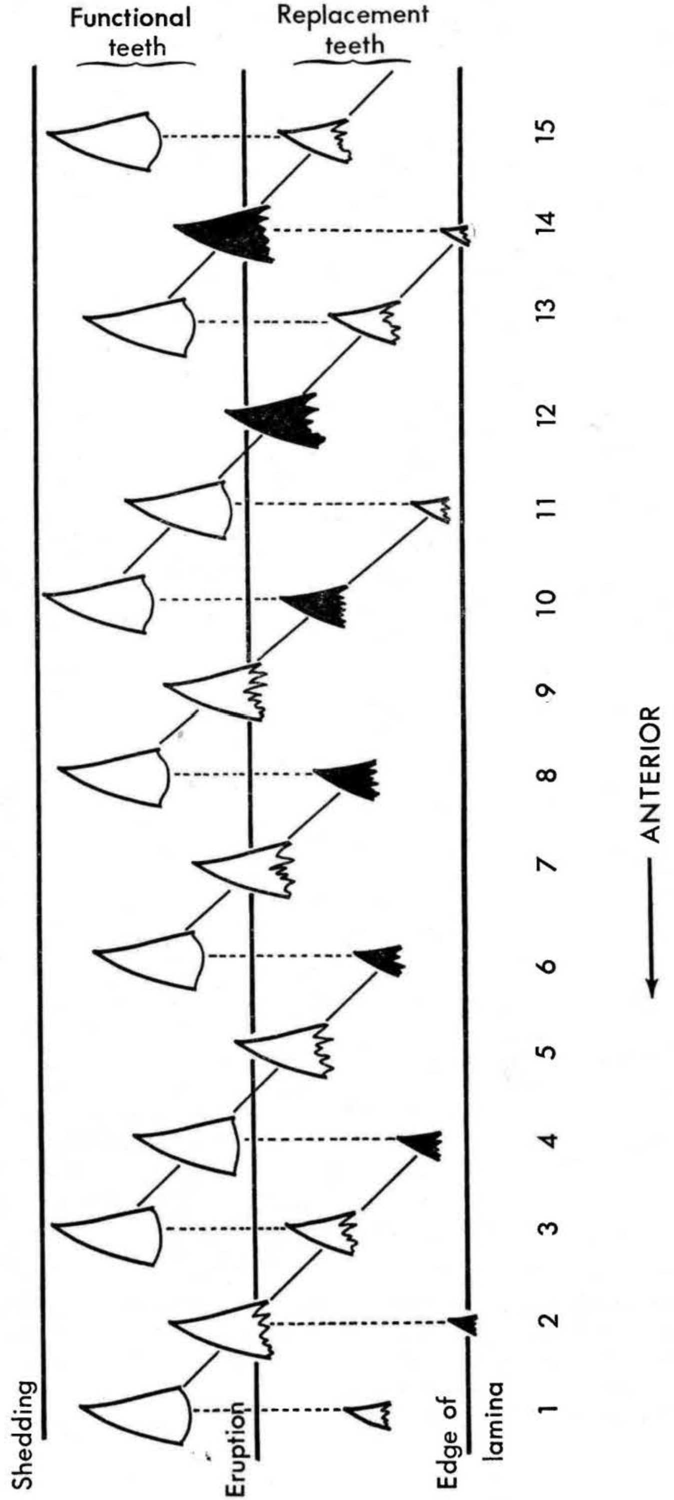

Fig. 2

Diagram of the same jaw showing the oblique rows of teeth on the lamina

8, 6, 4, 2. Tooth 14 is in the process of eruption, 12 is just beginning to erupt, while 2, at the other end of the series, is a tiny germ which has just begun to calcify, deep in the tissues of the jaw. This series can be envisaged as a kind of wave of eruption. Before this wave was complete, however, another similar wave in the odd-numbered series would have begun at places 9, 7, 5, 3 and 1. A number of such waves are usually discernible over the whole length of the jaw at any one time, and these may show great variation in form; for example, they are steeper in some species than in others.

In Fig. 2 the horizontal distance between the oblique rows is about 2.4 tooth positions, and in the case of *Lacerta* forward-moving waves of replacement in the odd- and even-numbered series are produced as described. If the spacing was reduced towards 2.0 the waves of eruption would become longer and their gradients flatter. At a distance of exactly two tooth positions the gradient would be eliminated and there would be simple alternate replacement, all the teeth of each alternate series being replaced at the same time. This, in fact, is almost what happens in the slow-worm (*Anguis*). If the spacing was further reduced, below 2.0, a gradient would re-appear in the waves of eruption, but running in the other direction from front to back. This actually occurs in the elapid snakes. In this way, all the variations in replacement pattern found in nature can be explained.

Edmund has traced the tooth replacement pattern through the fossil record and in numerous living species, and has shown that the dentitions of all vertebrates, including the mammals, are laid down on the dental lamina in a number of oblique rows, and that the principle apparently arose in an ancestral fish of the Devonian period. Thus the process of evolution has acted for over 350 million years on one simple basic design of dentition which is nearly as old as the vertebrate structural plan itself.

Edmund's hypothesis has gained further strength from observations on tooth replacement in living specimens and the methods used for collecting these data have varied according to the size of the animals studied. Large and strong reptiles such as alligators and monitors have been anaesthetised with intra-peritoneal injections of nembutal or with inhaled ether, and radiographs of the jaws taken at monthly intervals (Edmund, 1962, and in current work). For small reptiles including wall lizards (*Lacerta muralis*) and slow-worms (*Anguis*), which can be controlled in the hand and without anaesthetic, two simple methods have been used by the author (Cooper, 1963). The lizard is made to bite on a thin sheet of paraffin wax, leaving impressions of the teeth which can be viewed under a low-power microscope. The tissues of the mouth in many small reptiles are so translucent that it is possible to see the teeth even before their eruption, and in such cases the animal can be examined directly under suitable magnification and lighting. The records must be taken at regular intervals according to the rate of growth and replacement of the teeth, and must be continued over a considerable period. It is then possible to perceive the finer details and variations in all the features of the replacement pattern, to compare the pattern in different species. The effects of various factors, such as temperature, season, disease and even the experimental administration of toxic substances on tooth replacement can then be assessed.

In the past the difficulties of maintaining reptiles and amphibians in captivity and in examining them closely during life has militated against their uses as experimental animals. The information so far obtained by the methods described suggests, however, that further investigation of such material would not only be possible, but profitable.

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NOTES ON FERTILISATION, THE INCUBATION PERIOD AND HYBRIDISATION IN *LACERTA*

By

J. S. COOPER

The following observations have been made upon lizards of the genus *Lacerta,* kept in outdoor vivaria which provide near-natural surroundings.

In *L. muralis* and *L. viridis* mating and egg-laying occur regularly during the summer, the eggs being buried in the soil or under large stones. In the outdoor reptilium of the Bristol Zoo, where some dozens of these lizards are kept, literally hundreds of eggs are laid every year, yet none have ever been known to hatch even in the best seasons. The embryos do, however, reach an advanced stage of development before perishing. It is interesting to note that the eggs of *L. agilis,* in the same outdoor vivarium conditions, hatched after a normal incubation period of 60 days.

Introduced colonies of *L. muralis* and its subspecies now exist in South Devon, the Isle of Wight and Surrey (Taylor 1963, Frazer 1964). The latter colony was started over twenty years ago and breeding is said to occur regularly (Smith, 1954). Such colonies are of special interest since vivarium experiments indicate that hatching of the eggs under natural conditions in this country is unlikely.

THE INCUBATION PERIOD.

Eggs of *L. muralis,* maintained at different temperatures, and in conditions otherwise similar (Cooper, 1958) have indicated that the rate of development is affected directly by temperature and can vary widely :—

Incubation temperature	*Incubation period*
65–70°F by day, 55 at night	122 – 160 days.
70°F by day, 60 at night	78 – 92 days.
75°F by day, 60 at night	51 – 53 days.
80°F day and night	46 days.

It seems improbable that sufficiently high natural soil temperatures to hatch the eggs would be found, and incubation periods of over five months would certainly be too long for our seasons.

FERTILISATION.

There is strong evidence that in *L. muralis* (and others of the genus) the eggs are carried for almost exactly one month after fertilisation. The figure of one month is affected only slightly by weather conditions, which is surprising, since the incubation period of the eggs is so markedly affected by temperature. During a fine season in this country, a mature female

L. muralis produces up to three clutches of eggs at monthly intervals. Always sexual activity ceases abruptly after fertilisation has occurred and is resumed immediately after the eggs have been laid. For instance, a female *L. muralis* laid eggs on May 16th, June 18th and July 18th, and mating was observed within two days after each laying. Separate fertilisation for each clutch also seems necessary. Females without a mate often lay eggs at the normal intervals, and such eggs are invariably infertile. Furthermore, if a female lays a normal first clutch, and is then deprived of a mate, later clutches are infertile. It appears that delayed fertilisation does not occur in *L. muralis,* though it is known to occur in many reptiles.

The male *L. muralis* can fertilise numerous females and a ratio of one male to seven females has been known to produce thirteen clutches of fertile eggs in a season.

HYBRIDISATION.

Numerous instances of cross-breeding among reptiles are on record, but few references to the genus *Lacerta* can be found. Rollinat (1934) described unsuccessful attempts at breeding between *L. agilis* and *L. viridis,* in which mating was observed, but all the eggs proved to be infertile.

The following two hybrids have been produced between subspecies of *Lacerta.*

L. muralis nigriventris and *L. muralis brueggemanni.*

These subspecies are so closely related that cross-breeding is not surprising. A female *L. muralis brueggemanni,* which had already bred with a male of the same subspecies, produced two clutches of eggs by a male *L. muralis nigriventris* and one of the resultant young is still alive, aged two years. Its colouration and markings could identify it with either parent since the subspecies in question intergrade in this respect.

L. lilfordi lilfordi and *L. lilfordi brauni.*

These subspecies interbred during the seasons of 1958 and '59, despite the great differences in their appearance. Two eggs were produced on each occasion, and the resultant hybrids were male and female in each case. Their colouration and markings showed features which are interesting.

Male parent, *L. lilfordi brauni.* Greenish grey dorsal surface with a pronounced pattern of dark markings including longitudinal lines and discrete spots. Pale greenish grey ventral surface, including the throat, without markings.

Female parent, *L. lilfordi lilfordi.* Jet black dorsal surface and brilliant deep blue ventral surface.

HYBRID YOUNG.

	Dorsal surface	*Ventral surface*	*Throat*	*Tail*
Male	Rich brown with markings as male parent, spots predominating.	Pale blue	Intense blue	Bright green
Female	Paler brown with markings as male parent. Longitudinal stripes predominating.	Pale blue	Pale blue	Bright green

Bright colouring of the tail is common in the young of many species in the family Lacertidae (Boulenger, 1920) and the colour usually fades with increasing age.

In many lizards, longitudinal stripes are more pronounced and common in the female, and vivid colouration of the throat is more common in the male. In the hybrids described, these sexual differences became marked, although they did not occur in either parent.

One of the hybrids, a female, lived for three years, but no opportunity arose to assess its fertility.

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HERPETOLOGICAL NOTES ON RHODES

By

J. F. D. FRAZER

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Rhodes is an island in the eastern Mediterranean, approximately 100 miles to the north-east of Crete, and a mere 15-20 miles from the western part of the south coast of Turkey. Politically, its history has been varied: originally the site of three Greek cities (Lindos, Rhodes and Kamiros) which were merged two thousand years ago in the major one of Rhodes itself, it was at that time famous for one of the Wonders of the World, the Colossus, a gigantic bronze figure said to have stood by the entrance to the old harbour of Mandraki.

In A.D. 1306, the island was sold by the governor to the Knights of St. John, who built the present fortifications around the city of Rhodes, so that it became renowned at that time as the best fortified city in the world. Here the knights held out as a bastion against the forces of Islam, until after a long campaign the island finally fell (as the result of treachery) to Suleiman the Magnificent in the year 1522. After this, it remained in the hands of the Turks until 1912, when it was taken by Italy, and only in 1948 was it handed over again to Greece.

To a chequered political history may be added ecological changes which have left their mark on the island. Volcanic in origin, it has been severely weathered in recent millenia. Pine forests have been denuded, and woodland is now very rare in the northern part of the island. Great rivers have obviously run in former times from the now bare mountain tops (rising to 3,000 ft.), and apart from the season of the autumn rains their valleys exist as dry wadis with an occasional trickling stream or shallow pool of permanent water. The deepest of these pools are only a foot or so in depth. The land is arid, and by the month of May the level of the permanent water may be as much as 20 ft. below the surface of the river-bed. Wells are dug in this and the water pumped up (often by the use of windmills), both for direct irrigation along permanent channels and by means of small tanks which contain standing water to a depth of 6 ft. or so.

Not only is the climate a dry one, with the main rains in the autumn, but it is warm and sunny. Mean temperatures vary from 55°C in January to 83°C in August. Grain crops, oranges and tomatoes are already being harvested by May, and later crops include grapes, melons, figs and olives. While some areas in the north of the island are relatively bare, with an aspect reminiscent of Aden or Ingleborough, in this part other areas are well-wooded, with natural regeneration of pine occurring. Elsewhere, the slopes are covered with a maquis type of prickly scrub, very floriferous, but remarkably free of insects, save for aphids and whiteflies, with a varied hymenopterous fauna and a large number of robber-flies. In places, grass-hoppers of various types are abundant.

Cultivation occurs not only on the slopes and in the flatter enclosed fields, but in the outlying parts of the dry river wadis, where the presence of orchards or young plantations suggests that the peripheral floodplain is no longer subject to any major water flow. On the flatter lands, cultivation is fairly continuous in small fields, frequently protected from the wind by brushwood or even fences of bamboo. On the slopes, crops are grown briefly, and the land then reverts to the maquis. Orchards of olives or figs make a type of parkland, where the grazing asses, ponies, sheep or goats are tethered, or the orchards may carry grain or other crops, even close against the trees. Hedges as such are non-existent, but scrub and bushes are plentiful, such species as oleander (*Nereus oleander*) being especially abundant in the dry river wadis and along their edges.

Walls are a particular habitat to be found among both modern and ancient sites. Either type of place may have close-set stones with little mortar between them, or rough drystone walling with plenty of crevices which can give shelter to lizards. Vegetation may cluster round the foot of these, or the wall may more rarely be clear of it. Many of the former Italian houses and farmsteads are now tumbling into ruin, and form a similar habitat.

Little appears to have been published about the herpetology of Rhodes, though in ancient times it was particularly known as the Island of Serpents, and was also notorious as a haunt of lizards. Both these are said to have diminished in recent times, presumably with the increasing dryness of the climate and the increase in land reclamation by man. An opportunity was taken to make a somewhat cursory examination of the reptile and amphibian fauna during the course of an entomological expedition to Rhodes in 1964.

Wetland habitats.

In the drier parts of river wadis the Green Lizard (*Lacerta viridis meridionalis*) was found commonly, especially around the vegetation massed along the banks, though occasionally well out into the wadi. Adults could be found as little as 10 yards apart, and occasionally in pairs together. Another lizard (*Mabuya vittata?*) could also be found in similar terrain. Both species are very shy, and retreat rapidly through the dead leaves and bushes as soon as they are aware of human presence. On the bushes may sometimes be seen treefrogs (*Hyla savignyi*). On one occasion, a snake (*Natrix natrix persa*) was found proceeding in the full heat of the afternoon along a completely dry wadi.

The wetter parts of the wadis are inhabited by terrapins (*Clemmys caspica rivulata*) and by edible frogs (*Rana esculenta*). The former may be found in the pools or even the shallows, basking or hiding under debris. As they are an article of food for the human population, their shyness is understandable. One was discovered on land in a narrow wadi near the water. The frogs may occur in an atypical habitat for the species: in this land where deep pools are scarce, they are found in and near the verges of even shallow water, and may remain unmoved while a human passes by. When disturbed, they sometimes enter water which is deep enough, or jump into the shallows and then out again, as if conscious of the inadequacy of their refuge. The largest frog seen was about 4 inches long, and all were a mottled brown in colour. Frogs as small as three inches would call from two inches of water in the sun. In contrast, a small one was seen to dive into the depths of an irrigation tank from its shallow margin. Large tadpoles (1½ inches long) were seen on one occasion in May, in addition to smaller ones.

As well as being found on the vegetation by day, treefrogs (*Hyla savignyi*) were also calling by night from both foliage near the irrigation tanks and from rockwork at water level, as well as floating in the water of an artificial pool a foot deep. Green toads (*Bufo viridis*) were both found by night in this pool, and during May in the form of newly metamorphosed young in the damp sand by flowing water in the river wadis.

Near the mouth of one river in western Rhodes, there was a "slack" not more than thirty yards from the sea, whose water was almost certainly brackish. Both terrapins and edible frogs were seen in this. In the dry sand nearby, a specimen of the ocellated skink (*Chalcides ocellatus*) was captured.

Dry habitats.

Stone walls form a particular type of habitat, and were inhabited particularly by the agamid *Agama stellio* and a lacertid lizard (*Lacerta danfordi pelasgiana*). Four or five of the agamas might be found in about 30 yards of wall, while the lacertids occasionally occurred, sometimes in pairs. On white walls they were represented by a particularly pale form. In the hotter summer months, their tails take on a striking blue coloration. Both species retire rapidly into crevices when disturbed. In addition to these, a single snake was observed at the base of a wall below the ancient ruins of Kamiros. This had the markings of a grass snake (*Natrix natrix*), but seemed abnormally thin for a length of 2 feet, if of this species. It may, however, have been *N. natrix persa*. One other species of snake was also seen, on dry earth in an area of walls, retiring down a hole after a threat display. It was probably the sand viper (*Vipera ammodytes meridionalis*).

While no particular species were noted in the pinewoods of the south of the island, the same lizard (*L. danfordi*) was seen both there and among the hardwood trees in the Petaloudes valley, in each case retiring up the trunk of a tree when disturbed. Although none were present in the actual woodlands, green lizards (*L. viridis trilineata*) were found in some abundance in suitable terrain just outside. Edible frogs were present in the woodland pools, and treefrogs were to be found on the bushes.

Although the maquis appeared suitable terrain for tortoises, none was found, and no reptiles or amphibians were noted in this, save where bare rock protruded through the scrub, and such species as *L. viridis* could be found. Orchards and cultivated fields were not searched, but lizards (especially *L. viridis, M. vittata?* and *A. stellio*) were present along the field boundaries.

In summary, the island of Rhodes is an arid land containing a number of habitats which are filled by relatively few reptiles and amphibians, even though these are more varied than those comprising our own fauna. Species seen or collected are listed below, but stress must be laid on the inadequacy of this list, in view of the very brief investigation carried out.

SALIENTIA.

Ranidae.

Rana esculenta. Occurs in even the smallest trickle of water. Small size, mottled grey colouring. Calls by day. Large (1½ inch) tadpoles seen in May could only have belonged to this species.

Bufonidae.

Bufo viridis. Found in suitable moist places, both by day and by night.

Hylidae.

Hyla savignyi. Common. On foliage by day, and in breeding congregations by night during May These would start calling an hour or more before dark.

SQUAMATA.

SAURIA.

Lacertidae.

Lacerta viridis trilineata. Found around bushes in dry habitats especially along dry river wadis, but also on road margins, etc.

L. danfordi pelasgiana. On and near walls, retiring to holes in these when disturbed. In the Petaloudes Valley this species completely ignores the warningly coloured Jersey Tiger moth (*Callimorpha quadripunctaria*) which is abundant there, though cryptic moths are eagerly taken (M. Rothschild, pers. comm.).

Amphisbaenidae.

Blanus strauchi. Said to occur on Rhodes (Hellmich, 1962) but not seen there by us.

Scincidae.

Mabuya vittata (?). In the same habitat as *L. viridis*, but not so abundant.

Chalcides ocellatus. Only found once, in sand on the seashore in western Rhodes, but probably frequent in suitably sandy places.

Agamidae.

Agama stellio. Plentiful on walls everywhere. Often seen while crossing roads.

SERPENTES.

Colubridae.

Natrix natrix persa. Found in a dry riverbed below Petaloudes. Possibly seen at Kamiros.

Viperidae.

Vipera ammodytes meridionalis. A snake seen on one occasion in north-west Rhodes (M. Rothschild, pers. comm.) may have been of this species.

TESTUDINES.

CHELONIOIDEA.

Cheloniidae.

Clemmys caspica rivulata. Apparently abundant everywhere in suitable moist habitats.

I am greatly indebted to Miss Miriam Rothschild, who financed and organised this expedition. My thanks are also due to Mr. J. W. Steward for assistance in identification of the various species and sub-species.

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TERRITORIAL BEHAVIOUR IN THE WALL LIZARD *LACERTA MURALIS*

By

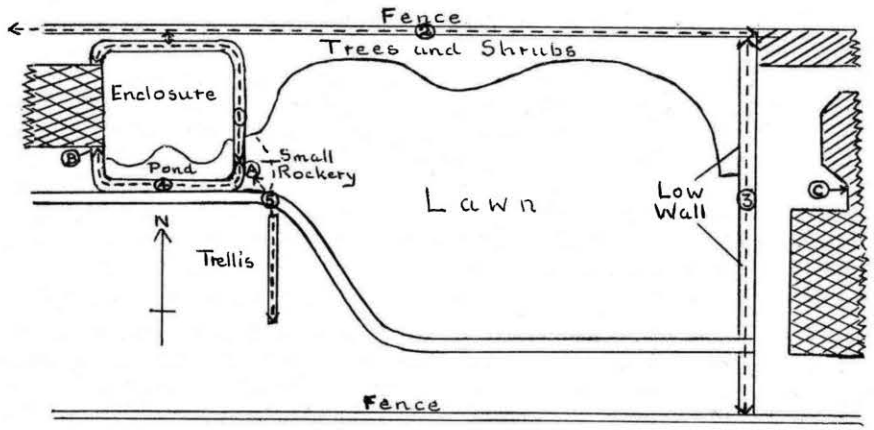
J. W. STEWARD

Some Wall Lizards of the species *Lacerta muralis* and *L. sicula* were released in 1960 in a walled enclosure some 25 feet square in my garden. Most remained there, but an occasional specimen of *Lacerta muralis*, which is a better climber than *L. sicula*, has managed to negotiate the overhanging edge of the wall and escape. One such specimen, a male *L. m. brüggemanni*, took up residence in the spring of 1962 in a small rockery immediately outside the wall, and I allowed him (personal pronouns will be used for ease of reference later) to remain there in the hope that he would stay long enough to provide some observations on a free-living specimen of this species. He actually remained free in the garden until August 1964, since when he has not been seen.

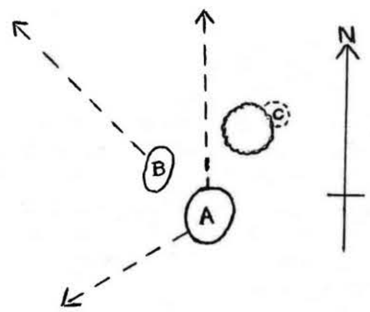
During the winters of 1962/3 and 1963/4 he hibernated under a fairly large rock in the centre of the small rockery (Point "A" in Sketch 1). For two or three weeks after first emerging in spring, he remained near the rock, retiring under it after sunset and during dull weather. As the days became warmer, he commenced a long series of perambulations away from and back to the rock, and it was noticeable from the start that these sallies were rigidly limited to a precise route. This was at first confined to the flat top of the enclosure wall along the east and north sides (Route 1 on the sketch). In early summer 1962, he extended the route by climbing a distance of about 18 inches through a bush on to a fence running parallel with the north wall of the enclosure. This fence is of conventional construction with overlapping vertical boards nailed to two long runners supported at intervals by posts. The posts and runners are on my side of the fence, and the lizard invariably climbed up to the higher runner, about 9 inches below the top of the fence, and used it as a runway along the fence. He progressively extended his journeys in both directions along the fence until he had reached both ends (Route 2), but did not descend from the runner at any point other than that immediately adjacent to the enclosure wall where he crossed from the one to the other.

In early June, 1963, an additional extension was made, in that when he reached the east end of the fence he climbed down and ran part of the way along a very low wall bordering the east edge of the lawn. Over the next week or two he gradually extended this route until he had reached the opposite fence at the south end of the low wall (Route 3). By late June he had found his way over this fence and between then and early August, on almost every sunny day when observation was possible, he was seen to

make a regular journey along Routes 1, 2 and 3 to disappear into the next garden. Towards late afternoon he would return and retrace the same path back to point "A".



Sketch 1



Sketch 2

One day in early August, 1963, I was surprised to see a strange wall lizard on top of the south wall of the enclosure. This proved to be a female *Lacerta m. muralis*, and I assumed it to be one which escaped from a cage in the house during the summer of 1962. She disappeared into a crack under a loose brick in the wall at point "B", and it was obvious after a few days that this was her normal retiring place for the night. Similar development of routes was observed. The first was along the south wall of the enclosure as far as the small rockery (Route 4). Within a few days, she was seen in company with the male lizard, who started to accompany her along Route 4, which he had not before been seen to use. This accompaniment consisted of keeping close to the female but a little behind her.

When she stopped, so did he, and when she moved on, he followed. They still retained their individual retiring places at points "A" and "B", and met somewhere along Route 4 in the mornings, the female at such times showing the normal reaction of shaking the front feet up and down.

During the next week or so, the female kept to Route 4, and the male did likewise but with the occasional excursions along Route 1, though no further. By early September, 1963, however, they had mutually developed a new route, leading from the small rockery obliquely across a narrow path to a tall rose-covered trellis (Route 5). This short additional route was probably chosen because at that time of the year the west side of the trellis caught the last rays of the sun, and it became customary for both to climb up into the trellis during the afternoons and bask together. The male, more active at all times than the female, would sometimes go for a walk along Route 1, but always returned after a short while, crossing the small path at exactly the same place each time, to rejoin the female.

By the middle of October, both had disappeared into hibernation, the male presumably under his rock at point "A" (next to which he reappeared the following spring), but the whereabouts of the female were unknown. The small exposed cranny at point "B" did not seem a suitable place for hibernation and examination showed that she was, in fact, not there. When she reappeared next spring, it was inside the enclosure, and she must have climbed down into it to hibernate under the rocks there. After emerging in April, 1964, she remained inside the enclosure for about a week, and was then seen back on the south wall of the enclosure.

During the spring of 1964, both lizards confined themselves to Routes 1 and 4; Route 5 was apparently forgotten. With warmer weather in early summer, they were seen less and less in each other's company, the female still keeping to Routes 1 and 4, but the male once again spending most of his time on Routes 2 and 3. The female was never seen on either of these routes, but one day in July, 1964, was seen on the wall of the house at point "C". The next day she was back on the enclosure wall, and did not seem to leave it again, but from this time on the male, though occasionally seen somewhere on Routes 2 or 3, no longer seemed to return to point "A" at night. If seen late in the afternoon, he was usually heading away from point "A", and the impression was gained that he had established a new retiring place in the next garden.

The last time the male was seen was at the beginning of August, 1964. The female was still around when I went on holiday in the middle of August, but since my return in September has been seen no more.

The main interest of these observations has been the surprising rigidity which the lizards showed in their territorial wanderings. Apart from the two minor aberrations on the part of the female (hibernation in the enclosure and single appearance at point "C"), several hundred sightings of the lizards never once found them anywhere but on one or other of their habitual routes. It would seem that these lizards find their way about their territory entirely by means of such learned routes, and rely very little on any sense of direct orientation. When, for example, the male returned from his trips into the next garden, it could be foreseen that he would finally reach point "A" via Routes 3, 2 and 1, although he could have got there by crossing the lawn in about half the distance. Even the single

appearance of the female at point "C" could possibly be put into this picture of remembered routes, since it was immediately next to the door through which she must have originally escaped.

Lizards living in the enclosure showed similar rigidity of movement, each individual maintaining a specific retiring place for long periods and following the same routes day by day, but even though the enclosure is fairly large (some 25 feet square), their movements must have been affected by the overall limitation in area. The observations on the free-living lizards, which as far as I know are unique over such a period of time, showed that the behaviour of the lizards in the enclosure was typical though restricted in space. The free-living lizards followed even more rigid a system of movements, but extended it (in the case of the male) to regular return journeys of well over 120 feet each way.

What also seemed clear was that the choice of route was decided by the facilities available. Having selected their bases at points "A" and "B" (two of the sunniest spots in the garden), the lizards extended their range along routes with certain features in common. These routes were all either along the top of a wall, or along horizontal wooden railings in the fence or trellis. All offered an easy route free from encumbrances, with plenty of cover close to hand from bushes and shrubs but otherwise open to the sun. Open spaces at ground level were almost completely avoided, the only exception being the narrow path between the small rockery and the trellis, and this was always crossed at a fast run.

Feeding took place along the routes, and it almost seemed that one reason for walking the routes was to look for food. Deviations from the route to chase insects were frequent, but rarely exceeded a foot on either side, and were followed by an immediate return to the route proper. Otherwise, the only deviations ever seen were on three occasions when a lizard alarmed by a bird or cat dashed into the nearest cover, and remained there for perhaps 5 to 10 minutes before returning to the route.

The lizards in the enclosure frequently drank from a pond there. The free-living lizards had no water available other than rain and dew. In hot weather, they would readily drink water sprinkled near them, but there was no indication that they ever entered the enclosure to drink or otherwise tried to find water.

Males of *Lacerta muralis* and *L. sicula* in the enclosure rarely tolerated each other in close proximity, but one would chase the other away vigorously. It was found in practice that in the 25 feet square area of the enclosure the maximum number of males that could be kept at one time, if constant chasing was to be avoided, was three. Even with this small number, a rough division of territory took some time to achieve, and the introduction of a new male could upset the balance for quite a while. This always surprised me, as local populations of both species in the wild appear to reach much greater concentrations. The system of fixed routes could perhaps provide the explanation. Each lizard, or at least each male, would develop routes which constituted his territory. If a route came to coincide in part with that of another male, in due course the two lizards would meet and a chase would ensue. The dominant lizard would retain the route, the other would have to find another. This would result in a network of routes which might frequently cross each other, but rarely have any lengths in common.

Under certain circumstances, this would enable a number of lizards with otherwise divergent territories to include in them a common local area with some periodic advantage. An obvious example could be a rock face which catches the sun at a certain time of day, or even some local and temporary source of food such as winged ants emerging from a nest or caterpillars dropping from a tree. This suggestion can be put forward all the more readily because it fits in with many observations of wall lizards of various species in the wild. It is in fact quite normal to find that a given rock or wall is visited by a number of lizards each day at about the same time, and this is often what gives the impression of large local populations. It is exceptional, however, to find two male lizards really close to each other, even though many may be present in a small area.

Since these conclusions were based largely on the behaviour of only two lizards, I have endeavoured to check them against behaviour of wall lizards in the wild. The best opportunities were with *Lacerta hispanica* and *Psammodromus algirus* in north-east Spain, and the results confirmed that a given lizard could be seen about the same time each day at precisely the same spot. In three cases (two *L. hispanica* and one *P. algirus*) it was possible to work out at least part of a regular individual route by plotting the places in which a recognisable lizard appeared repeatedly. Most significant of all was the possibility of confirming that certain small areas were used regularly by more than one lizard, without their ever coming into close contact. The best-observed example involved three specimens of *P. algirus* which could be seen on most mornings on a group of isolated rocks on a steep slope facing east. The lizards were easily identifiable as individuals—one had a large scar on the back, one had very distinct dorsolateral stripes, and the third was a particularly large specimen with a re-grown tail. The locality was visited on nine days out of fourteen in August/September, 1962, between 7 and 8.30 in the morning and on six days out of the same fourteen at some time during the afternoon. Out of the nine morning visits, on six occasions all three lizards were seen among the group of rocks, on two occasions two were seen, and on one occasion one. In each instance each lizard was occupying the same individual spot —the scar-backed lizard on top of a large boulder, the bright-striped one on a small flat rock about two feet from the boulder, and the very large specimen in a patch of dead grass at the foot of a bush roughly three feet from both the boulder and the flat stone (see Sketch 2). The lizards were watched from a distance through binoculars and not disturbed. On four occasions the first lizard was seen to approach or leave the boulder, three times along a route leading from the boulder to the south-west and once directly north, passing between the flat rock and the bush. The second lizard was twice seen to arrive on the flat rock from the north-west. The third lizard moved twice into the bush but no route could be worked out. During the afternoon visits, only once was one of the lizards seen in position, this being the large lizard by the bush. The general area was carefully searched on several other afternoon visits, but only once was one of the lizards sighted in another spot. This was when the scar-backed lizard was seen basking on a patch of granulated limestone among low vegetation some 35 feet south-west of the boulder, almost exactly in line with the route it took when leaving and approaching it. No other lizards of any kind were at any time seen within 100 feet of the small group of rocks.

In another place, some dozen lizards (*P. algirus*) were present each afternoon in a small area of sand-dunes sloping south-west to sea-level, but as the dunes were fairly thickly covered with bushes and tall grass, it was difficult to locate them without disturbing them. It was, however, noticeable that at the most only one or two lizards were to be found in the same area in the mornings.

SUMMARY.

Close observation of two specimens of *Lacerta muralis* living free in a garden over a period of nearly 2½ years, together with more generalised observation of the habits of wall lizards in captivity and the wild, suggests that in this species and probably in other species of wall lizard, individual territories are developed, not as compact areas but as a system of routes built up over a period and kept to more or less rigidly. Males may tolerate females on their routes and even actively accompany them at times, but may be expected to defend their routes against other males. The foot-shaking reaction of the females when meeting other lizards suppresses antagonism in the males. The system of routes facilitates greater concentration of lizards in periodically favourable areas than would be possible in more compact territories.

11 Churchill Road, St. Albans, Herts.

VERY LARGE ENGLISH SLOW-WORM

By

R. A. FAIRFAX

A blue-spotted male slow-worm (*Anguis fragilis*) caught at Portsmouth, Hampshire, measured 489 mm. (19¼ inches) in length. M. Smith (The British Amphibians and Reptiles, 1964, Collins, 3rd ed.) gives 460 mm. as the length of the two largest British specimens he had seen. Is the Portsmouth specimen the largest yet found in this country?

9 Bolingbroke Grove, London, S.W.11.

SLOW-WORM EATING COMMON LIZARD

By

H. ASHLEY BEST

On the evening of March 29th, 1965, a captive female slow-worm (body-length 180 mm.) was found eating an almost full-grown common lizard (*Lacerta vivipara*) of about 100 mm. total length. The lizard had been seized by the head, possibly by accident, and was consumed about 20 minutes later. The effort caused the slow-worm to water at the eyes but there were no apparent ill-effects; three days later it fed again on earthworms. The reptiles had hibernated together in the same cage and had emerged about three weeks before the events described.

Limericks, Stonecourt Lane, Pembury, Kent.

LIVING ECTOPIC EMBRYO IN COMMON LIZARD

By

SUSAN V. POYNTZ

St. Mary's Hospital Medical School, London

Dead, encapsulated ectopic embryos in *Lacerta vivipara* have been described by J. P. Dufaure (1964) and L. H. Matthews (1965) in recent numbers of this Journal (Vol. 3 : No. 6, p. 165 and No. 8, p. 207). In the course of dissecting a number of freshly killed common lizards I have found a single ectopic egg containing a living embryo. This was at a late stage of development and showed advanced skin pigmentation. It was lying quite free in the coelomic cavity, on the left side of the liver and anterior to the left oviduct. The chorio-allantois of the egg was covered by a thick membrane. This may have consisted partly of the thin shell membrane which is normally present, but it seems likely, as Matthews suggests, that a pinched-off portion of the oviduct also formed part of the covering. Four other eggs containing living embryos at the same stage were found in each oviduct. Those in the left oviduct were attached to each other, apparently by fusion of the adjacent areas of their shell membranes. Probably the ectopic embryo would ultimately have died without being able to emerge from its coverings, and remains of it would be likely to persist into or beyond next year's breeding season, in the manner suggested by the authors above. Another lizard was found to contain a single, apparently infertile ectopic egg, and six living embryos within the oviducts.

DUPLICATION OF TAIL IN SMOOTH NEWT

By

M. DAVIES

A subadult specimen of *Triturus vulgaris vulgaris* with a double tail was found under a brick, near Wollaton, Nottingham, on the 13th June, 1964. One of the tails, clearly the abnormal one, was growing from the dorsum of the normal tail at an angle of about 45°, and was about half the length of the latter. No signs of scarring were present, but it is possible that the abnormality was due to some injury to the dorsum of the normal tail. The newt was kept alive in the writer's collection for 11 months. A comparable case is recorded by W. G. Lynn (Herpetologica, 1950, 81).

10c Tevery Close, Stapleford, Nottingham.

SURVEY OF BRITISH AMPHIBIANS AND REPTILES

During the period 1947-1963, R. H. R. Taylor undertook the task of systematically collecting together all available information on the distribution of Reptiles and Amphibia in the British Isles. The results of his labours have recently been published in map form in this Journal (Vol. 3, No. 5, 1963). The degree to which it was possible to complete the maps varies considerably. Whereas little remains to be added to the maps of the rare species like the Natterjack, *Bufo calamita*, or the Sand Lizard, *Lacerta agilis*, this is certainly not true of the maps of the more common species. For instance, the large areas left blank on the map of the common frog, *Rana temporaria*, are due to lack of observations, not of frogs.

A survey at the present time of the distribution of the British reptiles and amphibians would be of considerable help in studies being made by the Nature Conservancy on the effects of certain persistent organo-chlorine pesticides on wild vertebrates. Work so far carried out, in co-operation with the British Trust for Ornithology and the Royal Society for the Protection of Birds, has been concentrated on birds. This work has demonstrated, however, that some freshwater habitats have been contaminated by these chemicals and residues of them have been taken up along the food chain by water birds such as the Heron, Kingfisher, Goosander and Great Crested Grebe. It is possible, for example, that amphibians could have accumulated residues in a similar manner in some areas. Where large quantities of these pesticides are used, the residues may reach sufficient levels to kill animals or inhibit their breeding, as is thought to have occurred in some bird species. There is a widespread belief that the frog is disappearing in Eastern England, but there is no real evidence against which to test this belief.

To meet the needs of conservation and to arrive at a more accurate understanding of the distribution of the reptiles and Amphibia of this country it is proposed to carry out an intensive survey during the next five years. The Nature Conservancy has promised its full support with this survey in processing the data and preparing the maps.

All that is required is that every active herpetologist should collect, and encourage others to collect, information on the presence or absence of the reptiles and amphibians which are to be found in the 10 km. squares of the National Grid. Record Cards and instructions will be provided to all volunteers, who will be asked to take on particular areas. Every effort must be made to ensure that the survey is as complete as possible, and the Nature Conservancy has agreed to enlist the support of general naturalists in this work, many of whom must know with certainty the common animals like the frog, toad, grass snake and viper: the species most in need of attention. Nevertheless this is surely a challenge to which every herpetologist must respond with enthusiasm: we must be prepared to collect the greater part of the information required, particularly as far as the newts are concerned.

Volunteers are asked to write to :—

Dr. F. H. Perring,
Biological Records Centre,
Monks Wood Experimental Station,
Abbots Ripton, Huntingdonshire.

SOME RECENT HERPETOLOGICAL PAPERS

Accounts are given of breeding behaviour in pit vipers (Petzold, 1963) and in Surinam toads (*Pipa pipa*) and *Hymenochirus boettgeri* (Rabb & Snedigar, 1960; Rabb & Rabb, 1963a, b). The new salamanders *Bolitoglossa epimela* (Wake & Brame, 1963) and *Plethodon longicrus* (Adler & Dennis, 1962) are described.

Tumour production in *Xenopus laevis* is covered in a series of papers by Balls (1963, 1964a, b) and the subject reviewed by Balls & Ruben (1964). Ippen (1964) gives a detailed account of the pathology of mycobacterial infection in poikolotherms.

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E. Elkan.

REVIEWS

PHYSIOLOGY OF THE AMPHIBIA. Edited by John A. Moore.

Academic Press, 1964. Price $18.—

No comprehensive work on amphibian biology has appeared since Noble's classic of 1931. The results of countless experiments on Amphibia, performed by physiologists all over the world, are hidden in a multitude of journals. If, as Dr. G. W. Brown says, there are 'some ten thousand original papers' dealing with amphibian metabolism alone, the editor of the volume under review really deserves our thanks for presenting us with a skeleton and a condensation of present day knowledge of amphibian physiology.

The contributors to this book are, with the exception of G. E. H. Foxon, all Americans. The bibliographies however—perhaps the most important part of a book like this—embrace all countries where important work on poikilothermic physiology has been published. Chapters are divided as follows: Metabolism (G. W. Brown), Digestion (W. G. Reeder), Blood and Respiration (G. E. H. Foxon), Heart (A. J. Brady), Water Balance and Kidney (I. J. Deyrup), Muscle (B. C. Abbott and A. J. Brady), Endocrinology (A. Gorbman), Metamorphosis (W. Etkin), Development (L. Jaeger Barth), and Regeneration (S. M. Rose). Amphibian genetics, which would probably fill a book by themselves, are not included. The book is well indexed as to authors, species and subjects, a great help to those who will want to use it.

The only criticism that can be made of a book like this is that it is too short. The gamut of our knowledge on amphibian physiology is too large to be presented in one volume of 654 pages and the degree of condensation and the almost complete elimination of illustrations gives us more of a guide to amphibian physiology than a complete textbook on the subject. Even as an introductory guide, however, the book will be of great value to those who wish to acquaint themselves with our present day state of knowledge in any branch of amphibian physiology. Let us hope that the publishers, having dealt with the physiology of fishes and amphibians, will follow this up with a physiology of the last remaining group of lower vertebrates, the reptiles.

E. Elkan.

DICTIONARY OF HERPETOLOGY: by James A. Peters. Hafner Publishing Company, New York and London. 1964. 392 pp. + preface + 30 figs. + blank pages for notes. $11.50, £4 12s. 0d.

An extremely useful compendium of terms used in herpetological work. Many of them are concerned with anatomy and physiology, and there is excellent coverage of such topics as the skeleton, pigment cells and venoms. Names of animals and animal groups (e.g. *Rana*, Anura) are not listed; to have included them would have been a staggering task, requiring an enormous volume. This book, the first of its kind, is a most welcome addition to the literature.

LIZARDS WANTED

Dr. A. Bellairs would be most grateful if anyone who might be able to supply him with common lizards next summer would write to him (St. Marys' Hospital Medical School, London, W.2.).

WANTED

THE BRITISH JOURNAL OF HERPETOLOGY

Volume I. Nos. 1 to 5 inclusive.

The Linnean Society of London, Burlington House, Piccadilly, London, W.1.