

Holaspis, a lizard that glided by accident: mosaics of cooption and adaptation in a tropical forest lacertid (Reptilia, Lacertidae)

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SYNOPSIS. *Holaspis* is the most morphologically apomorphic lacertid taxon with 42 or more derived morphological features arising on its exclusive lineage. Nearly all of these confer advantages in three specialised activities, or ameliorate problems resulting from them. The activities are: climbing on the often vertical open surfaces on tree boles and branches, utilising very narrow crevices in wood and beneath bark, and the ability, unique among lacertids, to glide from tree to tree. Although many of the features related to these activities are likely to result from direct adaptation to the situations concerned, exaptation has been critical in the development of gliding. Two behaviours present in the earliest lacertids have been coopted to this activity: rib spreading associated with basking contributes to an effective aerofoil, and balance control associated with running helps maintain appropriate posture in the air. Features originally developed in the context of crevice use also contribute to the aerofoil and a high surface: weight ratio. So, while natural selection has moulded *Holaspis* for its present activities, multiple accidents of history have also been important, as they also have in the evolution of bird flight.

INTRODUCTION

Sometimes there has been a flurry of adaptation on a lineage after a long period of little or no obvious change. A plethora of apomorphies may have been produced, often in association with shift into a new and demanding niche or a succession of these. For instance, this occurred in the lacertid lizard genus *Meroles* where apomorphies accumulated in a series of increasingly extreme soft-sand environments (Arnold 1990, 1991). In other cases, not all the features that confer performance advantage in such a selective regime necessarily arose by natural selection in its context. In some instances, features developed by natural selection in a different situation or by some other means, and were only later coopted to a new function. Darwin (1872) was aware of this process which was named exaptation by Gould & Vrba (1982). Cases of exaptation are very widespread (Arnold, 1994; Gould, 2002) and contribute to the ability of lineages to enter new selective regimes. Usually, optimum survival in these involves combining exaptations with new features that are built by the new selective regime. Exaptations are typically a small proportion of the necessary features, but there are examples where a number of characters really critical to invading the new regime are exaptations. A case in point is the aberrant lacertid genus, *Holaspis*, the only member of the approximately 1700 species of Scincomorpha known to glide regularly and effectively.

TAXONOMY AND RELATIONSHIPS

Until recently *Holaspis* was regarded as a single species with two well-defined subspecies, but these are now each given species status (Broadley, 2000) as *Holaspis guentheri* and *H. laevis*. *H. guentheri* occurs in Sierra Leone, Ghana, Nigeria, Cameroon, Congo, Uganda, Gabon and Angola, and *H. laevis* in Tanzania, southeast Congo, Malawi and Mozambique. *H. laevis* has six dark longitudinal stripes on the body instead of eight and has on average fewer, larger scales comprising the semitransparent window

present in the lower eyelid which is generally rather better developed than in *H. guentheri*.

Within the Lacertidae, morphology indicates that *Holaspis* is a member of the subfamily Eremiinae (Harris, Arnold & Thomas, 1998) and within this of the Equatorial African clade (Arnold, 1989a, b.), which is relatively basal and has a generally primitive morphology, most of its members not differing much from members of the generally primitive subfamilies, Lacertinae and Gallotiinae. The Equatorial African clade is characterised by the following combination of derived features: pineal foramen lacking; medial area of the clavicle not markedly expanded; only one postnasal scale; parietal scale extending laterally to the edge of parietal table of the skull, and the tympanic scale small. All except *Holaspis* also have the postorbital and postfrontal bones fused, the absence of this condition in *Holaspis* being secondary (Arnold, 1989a). Among the Equatorial clade, morphology suggests *Holaspis* is the sister group of two species of *Adolfus*, *A. africanus* and *A. vauereselli* (Arnold 1989a). Studies of mitochondrial DNA sequence (Harris & Arnold, pers. obs) corroborate this relationship, although with only low bootstrap support.

MORPHOLOGY OF *HOLASPIS*

The following account concentrates on those characters that are peculiar to *Holaspis* and derived within the Equatorial African group, and usually within the Lacertidae as a whole. These autapomorphies are listed in Appendix 1. For illustrations of living *Holaspis* see Schmidt, 1919 (reproduced in Arnold 1989a), Schiötz (1960) and Branch (1998).

Holaspis are small lizards growing to a maximum of only about 53mm from snout to vent and a total length of 130mm. The whole animal is extremely depressed, and more so than any other lacertid. The index, head depth/ head width, measured on alcohol-preserved specimens somewhat exceeds that found in most other flattened lacertids (see for instance Arnold 1998a, p. 344), averaging about 0.54 when measured in adults (n = 10). This however does not give

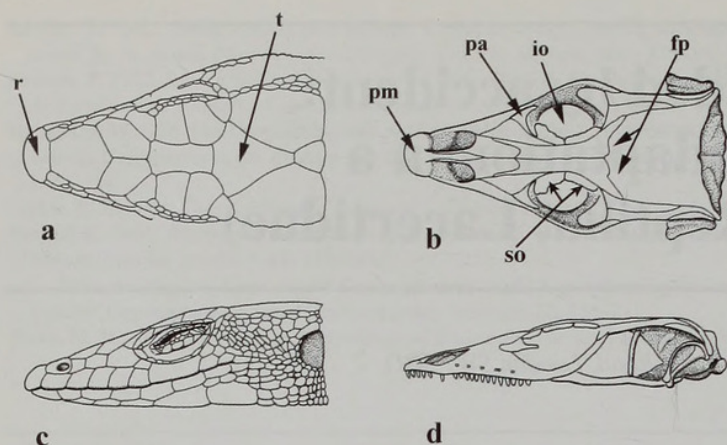


Fig. 1 Head and skull of *Holaspis*. a. Head from above; b. Head from side; c. Skull from above; d. Skull from side. fn frontonasal scale, fp frontoparietal suture, pa palpebral bone, pm premaxilla, r rostral scale, io inferior orbital foramen, so supraocular osteoderms, t triangular scale covering area occupied by interparietal and paired frontoparietal scales in most other lacertid lizards.

a full impression of the extent of the dorsoventral flattening, largely because in fixed material shrinkage of the jaw muscles pulls the kinetic skull into its most retracted position in which the vertical extent is greatest (Arnold 1998a). Also, unlike other lacertids, the whole of the limbs and tail are depressed in *Holaspis*.

HEAD. The parietal area of the head (Fig. 1a, b) is flat and unarched and the snout is flattened above, being wedge-shaped in lateral view. The rostral shield is large, extending far on to the top of the snout and contacting the frontonasal scale very broadly. The nostrils are placed on the sides of the snout and are set well back from its tip. The area of the top of the head usually occupied by the interparietal and paired frontoparietal scales in other lacertids is covered in *Holaspis* by a single large triangular scale. The lower eyelid has a 'window' composed of enlarged semi-transparent scales. In *H. guentheri* these number 1–5 (mean 3.5, $n = 15$) while in *H. laevis* there are usually 2–4 (mean 2.3, $n = 8$) that are sometimes black-edged. The scales on the temporal area vary in size: dorsally and posteriorly they are typically large and polygonal, whereas anteriorly they are much smaller and diagonally elongated, running backwards and downwards from behind the eye in irregular lines that are separated by somewhat expansible hinge regions.

The low skull (Fig. 1c, d) is more delicately constructed and thin-boned than in any other lacertid lizard and the roof of the parietal region is so flexible in alcohol-preserved material that it can easily be deflected downwards. As in other lacertids, comparatively immobile sutures in the skull, such as that between the frontal and nasal bones, show a considerable overlap between the elements involved, giving a measure of rigidity in spite of the thinness of the components. In contrast, the frontoparietal suture, one of the main sites of

cranial kinesis, is a relatively simple abutment without the complex interdigitation found at this site in other lacertid lizards.

The body of the premaxilla is peculiar in forming a broad semicircular boss that is convex above and supports the extensive rostral scale. The nasal openings of the skull are situated posterior to this boss and are extremely large. They extend backwards so that the primary nasal cavities are broadly exposed dorsally. Of the bony elements normally roofing the orbits of lacertid lizards, only the palpebral bone is present in its entirety. The usual array of four supraocular osteoderms is greatly reduced; the first being absent and the others only present in adults, where they are limited to a narrow medial fringe. The inferior orbital foramen is very large. Pterygoid teeth are absent. The mandibles are slender and shallow and their retroarticular processes are directed somewhat ventrally.

SCLERAL OSSICLES. In the eye, the scleral ossicles are reduced, from the usual lizard number of fourteen that is present in all other lacertids, to twelve. This is by the loss of two out of the sequence made up of ossicles 5 to 9 (Fig. 2b). The twelve ossicles present are so shaped and arranged that the scleral ring is incomplete peripherally. Instead of extending from the area of the pupil to the vertical equator of the eye, the ring is strongly emarginated above and below. Dorsally this emargination is produced by the loss of the two ossicles, their neighbours extending across the gap so formed and overlapping only in the pupillar region. The ventral gap in the outer part of the ring is largely a result of the peripheral, radially directed part of ossicle 14 being missing but the peripheral sections of ossicles 1 and 13 are also skewed away from the gap thus increasing its extent.

BODY. The neck of *Holaspis* is dorsoventrally flattened, with the skin at the sides forming a prominent sharp-edged flap in many preserved specimens that is also visible in live animals (Fig. 2, Schiøtz, 1960). The flap apparently gains some support from the first branchial and hyoid horns of the hyoid apparatus and its edge is sometimes marked by a longitudinally oval area of somewhat enlarged scales. In other preserved material, in which the pharyngeal cavity is expanded dorsoventrally, the flaps are barely apparent, suggesting that they are homologous with the slight skin folds which occur in this region in many lacertid lizards and which are necessary for pharyngeal enlargement.

The body is strongly depressed and arched in transverse section, being convex above and flat beneath. Posterior to the sternally connected ribs, the trunk has an elongated oval outline when viewed from above and the lateral edges of the body form distinct ridges. The dorsal integument consists of two very different types of scaling (Fig. 3a). Running along the vertebral region from nape to tail is a band of enlarged, broad plates. These are arranged in two longitudinal series, which are slightly staggered relative to each other. Each plate slightly overlaps the one immediately behind it and also, medially, the plate diagonally posterior to it in the other row. The hinge regions between the plates allow flexibility in the vertical plane but do not permit the plates to move much relative to each other in the plane of the integument.

The lateral areas of the dorsal integument are made up of small granular scales. At the broadest part of the dorsum, there are 30 to 41 of these on each side, between the vertebral and ventral plates. These small scales often show a differentiation in arrangement between the anterior and posterior regions of the back. On the neck and shoulders, they are non-imbricate and firmly bonded together so that they can only move slightly relative to one and other. Further back they may gradually alter, so that beyond the sternally connected ribs the scales are completely different in character. Here, they are lined up in two directions: they are arranged in rows running steeply

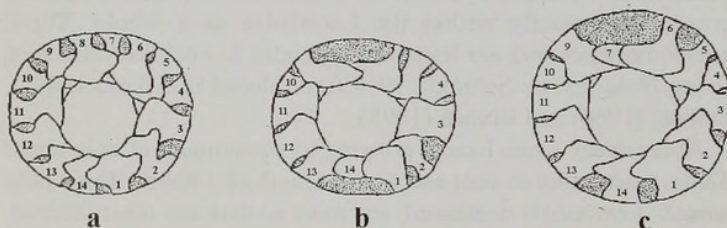


Fig. 2 Scleral ossicles of left eye of lizards. a. Typical lacertid lizard; b. *Holaspis*; c. *Platysaurus* (Cordylidae). Ossicles are numbered according to the system of Gugg (1939); see Underwood (1970).

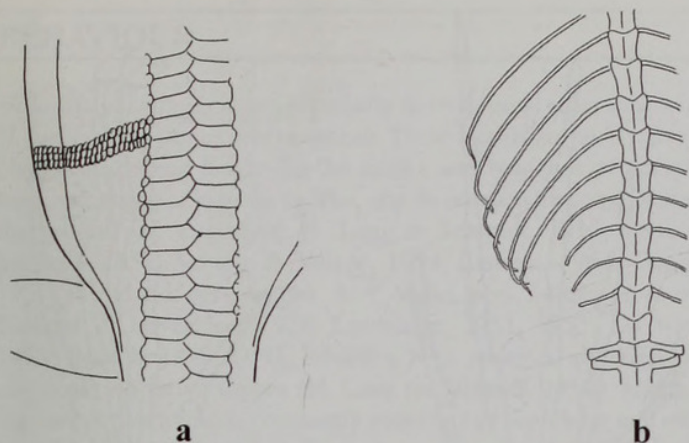


Fig. 3 Dorsal views of the left posterior trunk of *Holaspis*. a. Skin, showing double vertebral band of enlarged scales and small lateral scales (only three rows shown). b. Skeleton showing elongated anterior free ribs with long cartilaginous tips; the tips usually overlap each other to form a continuous edge to the ribs, but in this cleared and stained specimen they have become partly separated.

posteriorly, and to a much lesser extent outwards from the vertebral plates, and they also form transverse rows of which there are two or three to each vertebral plate. These rows run slightly posteriorly from their origin, but further out, they curve a little so that they run more or less directly laterally and may turn slightly forwards before they reach the perimeter of the dorsum (Fig. 3a). Each scale in a transverse row strongly overlaps its neighbour on its medial flank, but if the skin is pulled laterally, it stretches easily and extensively, so that each scale is separated from its fellows (Fig. 4). It is then sometimes apparent that the scales are interconnected by 'bridges'. These are often pigmented and not very elastic and apparently contain alpha-keratin, as do the scales. They lie slightly below the level of the scales themselves and fall into two groups. One series runs approximately laterally from the posterior outer border of each scale to insert beneath the inner border of its neighbour. The other runs from the anterior inner border of every scale and joins it to the posterior inner border of the scale which lies in front of it when the skin is unstretched. These longitudinal bridges are the only ones immediately visible in preserved material, the lateral ones being hidden under the imbricating scales. When the skin is not stretched, the bridges are slack and slightly folded. The regions between the scales and their bridges are made up of soft, extensible skin,

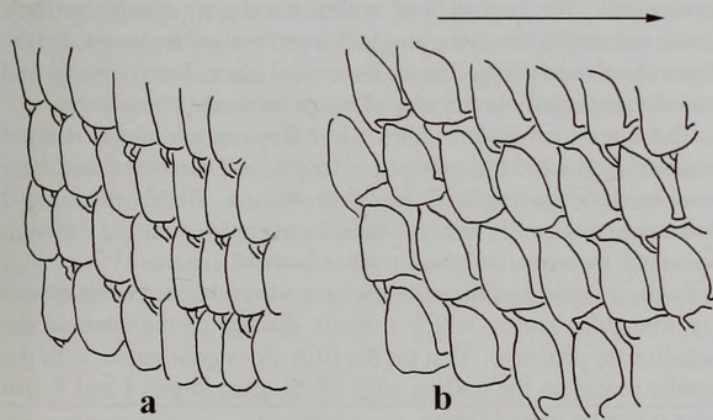


Fig. 4 Scales from right lateral skin of posterior trunk. a. Skin unstretched, scales overlapping medially and longitudinal bridges showing. b. Skin stretched showing lateral and longitudinal bridges and expanded areas between the scales. The bridge system is not always fully apparent. The arrow shows direction of stretching.

presumably consisting largely of beta-keratin. The development of this system of bridges shows very considerable variation among specimens.

When the skin is stretched laterally, each scale moves in a transverse direction, the excursion made by the outer scales being much greater than that made by the inner ones. This results in the originally curved transverse rows approximating more closely to a straight line. These movements can produce at least 50% increase in the area of skin. This ability of the skin to expand is not so highly developed as in many snakes, but it is certainly unique among the Lacertidae and probably among other lizard groups.

The dorsolateral skin, when unexpanded, has one or more longitudinal folds on either side. The whole of the dorsal integument is rather loosely attached to the underlying musculature by connective tissue, as in other lacertids. The area of granular scales passes round the sharp-edged lateral border of the body to contact the ventral plates. These are large and arranged in six longitudinal rows, as in many other lacertids, and are rectangular showing little imbrication. The collar is straight-edged and again not strongly overlapping.

Holaspis has 25–26 presacral vertebrae in males and 25–27 in females. These numbers are unexceptional for lacertids in which the majority of species have 25–29 presacrals with extremes of 23 and 33 and show sexual difference in average number of dorsal vertebrae. The vertebrae of *Holaspis* differ from those of other lacertids in being distinctly depressed with virtually no neural crest or spine.

In most lacertid lizards the dorsal ribs can be divided into three groups: 1. the thoracic ribs attached to the sternum and xiphisternum; 2. the anterior free dorsal ribs which are unattached distally and have prominent cartilaginous extensions at their tips; and 3. the posterior free dorsal ribs which are usually about two-thirds the length of the more anterior ribs and have no cartilaginous extensions. In *Holaspis*, there are 7–8 anterior free ribs in males and 8–9 in females. They are markedly elongate compared with those of other lacertids, being considerably longer than the thoracic ribs and about twice as long as the posterior free dorsal ones. Their cartilaginous extensions are also exceptionally long and are turned backwards, each extending beneath the next posterior rib and running parallel with its own cartilaginous process (Fig. 3b). These overlapping processes are bound together by loose connective tissue and form a smooth border to the series of elongated ribs. It is this border which forms the prominent edge of the body that runs slightly ventrally and backwards to terminate just in front of the anterior border of the hind leg. The termination is enclosed in a fold of loose skin that connects it to the underside of the thigh.

The sternum of *Holaspis* has an extremely large central fontanelle that occupies most of its area, and the scapulocoracoid plate has two foramina compared with one in other lacertid lizards.

Holaspis is peculiar among lacertid lizards in having prominent slips of the *intercostalis scalaris* muscle (Maurer 1896) running from the tips of the anterior free ribs forwards and somewhat inwards to insert on the upper surface of the *rectus abdominis* muscle above the outer edge of the second row of ventral scales. The muscle fibres to the more anterior free ribs form a single block but those to the more posterior ones comprise separate slips.

TAIL. In nearly all lacertid lizards, the tail is cylindrical and at most slightly flattened dorsoventrally at its base. It is covered by whorls of numerous subequal scales there being two whorls to each caudal vertebra. Deviations from this pattern are usually slight but *Holaspis* differs radically. Its tail (Fig. 5) is somewhat dorsoventrally compressed and above has a double row of broad plates, which is a direct continuation of the series on the body. These enlarged scales differ from those on the back in being arranged in simple

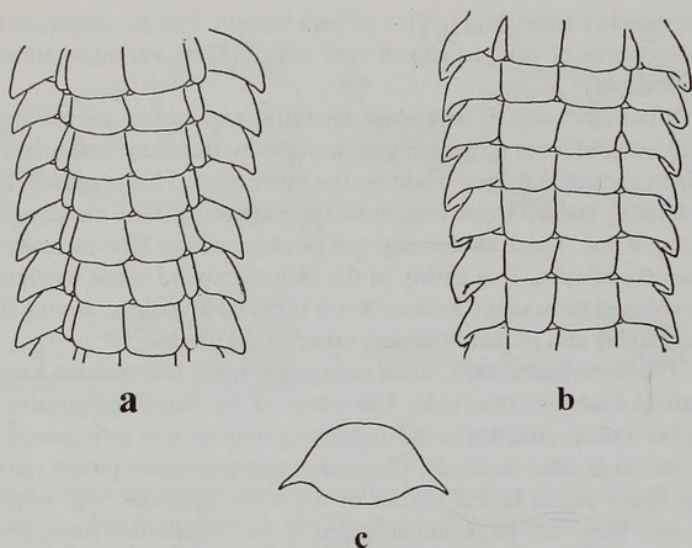


Fig. 5 Tail of *Holaspis*. a. Proximal segment from above; b. Proximal segment from below; c. Transverse section.

lateral pairs instead of being staggered. The plates each have several sense organs on their posterior border and, as the usual number of sense organs per dorsal caudal scale in other lacertid lizards is one, it is likely that the plates have replaced a number of smaller scales. The wide double band is flanked by one or two (rarely three) longitudinal rows of narrower scales, one row being frequent in *H. laevis* and one or two in *H. guentheri*. The number of rows sometimes increases anteriorly and these scales are replaced by granules on the tail base. The median part of the ventral surface of the tail is formed by another row of wide, paired plates, again replacing multiple small scales in other lacertid lizards.

The lateral edges of the tail are serrated and consist of a single row of strongly modified scales. In transverse section, each of these scales is more or less triangular, the broad base joining the tail, the apex pointing outwards; in this plane, the lateral scales curve downwards. Viewed from above, these scales are again approximately triangular, the point being directed obliquely backwards. Proximally, the longitudinal axis of these scales is parallel with that of the whole tail; distally, their anterior edges tend to be twisted downwards so that their longitudinal section here runs backwards and slightly upwards. Each lateral scale is capable of some movement since it is connected with contiguous scales in its whorl by flexible hinge regions. However, the motion is limited by the scale interlocking with its anterior and posterior neighbours. On the underside of each of these scales, parallel with and close to the trailing edge, is a slit-shaped cavity. The anterior portion of the following scale projects into this, giving the lateral fringes considerable stiffness.

LIMBS. The spans of the fore and hind limbs approach equality more closely than in any other lacertid lizard, the index, forelimb span/hindlimb span, being 0.85 in males ($n = 3$), and 0.85 in females, ($n = 4$) while the total range for the Lacertidae is 0.53–0.85 (Arnold 1998b).

The forelimbs are rather flattened and the single band of enlarged scales, present on the anterior surface of the upper limb of most lacertids, occurs in *Holaspis* too. However, instead of being continued as a single band on the lower limb, it is replaced by two parallel ones, one dorsal, the other ventral with their zig-zag line of contact forming a forwardly directed edge that may sometimes be quite acute.

The hind leg is similarly markedly depressed and the proximal, femoral segment has large plates above and below the leading edge;

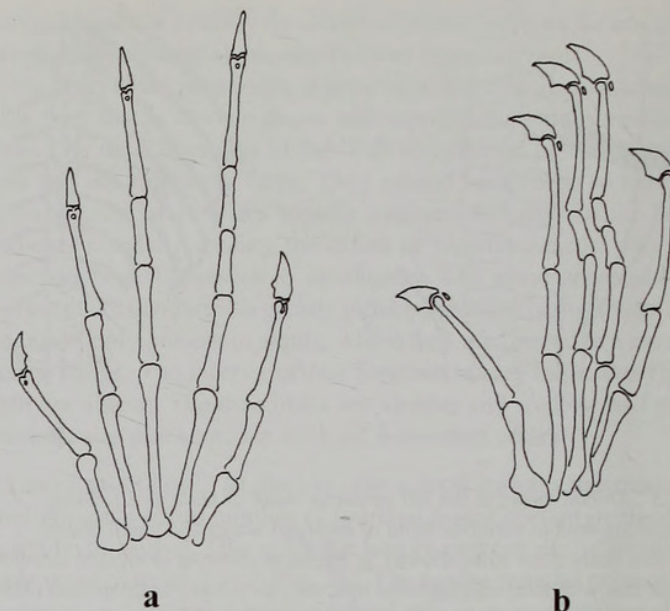


Fig. 6 Right manus of lacertid lizards. a. A form frequently climbing on steep open surfaces (*Lacerta oxycephala*); b. *Holaspis guentheri*.

only the lower series reaches the front of the crus. The greater part of the trailing area of the hind leg is formed by a web of loose elastic skin, which becomes taut when the leg is partly extended. This 'patagium' is continuous with a series of about four large sharp-edged, sometimes interlocking, scales which make up the trailing edge of the crus. These scales are generally similar in construction and arrangement to those on the lateral edges of the tail

The manus and pes of *Holaspis* show strong development of a syndrome of features characteristic of lacertid lizards that climb on continuous open surfaces (Fig. 6; Arnold, 1998b) and many features are better developed than in other forms. The longest digit is number 4 and all digits are strongly latero-mesially compressed; some digits are flexed downwards at the articulation of phalanges 1 and 2 and in most there is upward flexure at the penultimate articulation. Phalanges are very slender, the penultimate ones being very long and markedly curved downwards. In the manus intermediate phalanges of digits 3 and 4 are shorter than the ones bordering them and the same is true of intermediate phalanges of digits 3 and 4 of the pes. The final phalanx of each digit and the claw that covers it is short, deep and recurved. The large ventral digital tendons are offset from the articulations in the regions where digits can be abruptly flexed downwards. The articulations within the digits, except the most distal, are simple involving single cup and ball arrangement and the digits are abruptly flexed in the horizontal plane, both mesially and laterally, especially in the area of the penultimate articulation.

The manus of *Holaspis* has the following additional derived features. Digits 2–5 are subequal in length, and numbers 3 and 4 are conjoined for the length of their first phalanx. The shortening and downward flexure of phalanx 2 digit 3 and phalanges 2 and 3 of digit 4 is much more marked than in other lacertid lizards.

Digits 3, 4 and 5 of the pes each have a lateral fringe of interlocking triangular scales, which extends distally to the base of the penultimate phalanx. That on the fifth toe is continuous with the similar scales on the trailing edge of the crus. Digits 4 and 5 also have a similar mesial fringe.

COLOUR IN LIFE. In life, *Holaspis* is blue-black with several longitudinal pale stripes on the dorsum, the two on the vertebral plates being tinged blue posteriorly. The tail has a series of large, light, intensely blue spots on its upper surface and its lateral fringes are yellow, while the belly is red.

BEHAVIOUR

Holaspis guentheri occurs especially in rain-forest situations while *H. laevis* also extends into savannah. These lizards are nearly always observed at some height on the trunks and branches of standing trees, occurring at least up to 30m, and do not usually come down to the ground (*H. guentheri*: H. Lang in Schmidt, 1919; Perret & Mertens, 1957; Schiøtz & Volsøe, 1959; Laurent, 1964; Dunger, 1967; P. Agland, pers. comm. A. P. Mead, pers. comm. *H. laevis*: Barbour & Loveridge, 1928; Loveridge, 1951, 1953; De Witte, 1953; Branch, 1998; D. G. Broadley pers. comm.), although they can occur on fallen timber (H. Lang in Schmidt, 1919). *Holaspis* spp. are active hunters, constantly moving and searching and often investigating crevices (P. Agland, pers. comm.) in which they also frequently hide when disturbed and at night (H. Lang in Schmidt, 1919; Loveridge, 1951; Laurent, 1964; pers. obs. on captive animals). They are extremely agile, moving with ease on vertical and overhanging surfaces (H. Lang in Schmidt, 1919). *Holaspis* appear to thermoregulate and at times basks in patches of sunlight for at least up to ten minutes (Dunger, pers. comm.; P. Agland, pers. comm.). As in many other basking lacertid lizards, the body is spread and flattened by the dorsal ribs being rotated forwards and in *Holaspis* the body becomes as flat and round as a coin (Dunger pers. comm., P. Agland pers. comm.).

Holaspis is unique among lacertid lizards in being able to glide between trees. This behaviour was first formally reported in *H. guentheri* in Ghana by Schiøtz & Volsøe (1959) and subsequently confirmed by P. Agland in Cameroun and A. P. Mead in Nigeria (pers. comms). Earlier reports also provide some collaboration. C. J. P. Ionides (quoted by Loveridge, 1955) noted that in Tanzania *H. laevis* covers long distances in leaps between trees and Laurent (1964) reported that local people in northern Angola said that *H. guentheri* can fly. According to Schiøtz & Volsøe (1959), this lizard starts from a head-downwards position, high on a tree trunk from which it leaps outwards and glides steeply downwards. The trajectory later becomes shallower, and just before the lizard alights, it turns slightly upwards. For most of the glide, the lizard is orientated with its sagittal axis along the direction of motion, but towards the end this becomes perpendicular to it, the lizard stalling and reducing speed by this means. In one measured leap a lizard travelled 10.5m horizontally while dropping 9m, an overall angle of about 42° from the horizontal. *Holaspis* appears capable of selecting a target before launching itself, and of changing direction in mid-flight.

Among the *H. guentheri* observed by P. Agland (pers. comm.) one glided 30m at an angle of 10–20°, another travelled 25m and a third 6m. Motion was fast and straight and again appeared to be directed. In some cases there was an initial drop before the trajectory levelled out but in one instance a lizard running horizontally on a branch launched itself into the air without much fall before stabilising its flight path. At the end of a dive animals again alighted head upwards, landing very fast and sometimes immediately running upwards. *Holaspis* clearly has the ability to maintain its belly-downwards posture in the air with limbs spread and to change orientation as appropriate.

FUNCTIONAL ANATOMY

In this section an assessment is made as to whether particular morphological apomorphies of *Holaspis* could have evolved through direct adaptation by natural selection in connection with one or more of its special behaviours: frequent locomotion on very steep often

vertical open surfaces, use of very narrow crevices, and gliding. Assessment is made on two criteria: 1. perceived functional benefit of the apomorphies in the activities concerned; and 2. whether similar apomorphies have appeared independently in other lizards that have evolved similar behaviours. The second criterion is most convincing if there are multiple independent origins of the apomorphy and if these origins are correlated with appearance of the relevant behaviour on the lineages of the taxa concerned. Even if there is a *prima facie* case for functional advantage of an apomorphy in connection with a particular behaviour, its absence in forms that have evolved the behaviour independently raises the possibility that it is not connected with the activity concerned. Alternatively, it may represent one of several strategies with other taxa gaining similar advantages in different ways.

LOCOMOTION IN TREE BOLES. The functional advantages of near-equality in fore and hind limb spans, and of characteristic foot architecture, in climbing on steep open surfaces has been discussed elsewhere (Arnold 1998b). These features are particularly well developed in *Holaspis* and presumably related to the abundance of such surfaces in its environment. The unique manus features of *Holaspis* suggest the forelimbs are sometimes used in parasagittal planes (Arnold, 1998b). This may be when the lizard launches itself from a head-downwards position on a steep surface. Extending the forelimbs at this time would push the foreparts of the body out into a more horizontal position, putting it closer to its orientation when gliding and making an outward leap easier.

USE OF CREVICES. Features that confer advantages in crevice use and the functional basis for this has already been surveyed (Arnold 1998a). Many derived features of *Holaspis* occur in other lacertids that use rock crevices, having developed independently at least once in archaelacertas (*Lacerta* spp.), and in *Omanosaura cyanura* and some populations of *Podarcis hispanica*. These forms show many apomorphies similar to those of *Holaspis* although the features are less developed than in this form, especially the degree of flattening of the head, body and limbs. These low vertical dimensions enable lizards to enter narrow crevices and a variety of cranial features (Appendix 1, numbers 4, 6, 7, 8, 10 and 12) results in a deformable skull that can be inserted into irregular spaces. Increased cranial kinesis enables the skull to be flattened further by protraction on entering a crevice and locked into place by subsequent retraction. As a result of flattening of the skull, the eyes, which are large, project well above it during normal activities and this potentially impedes entry into crevices. However, in lacertids including *Holaspis* each eye is pushed downwards as the lizard enters a crevice by contact with the crevice roof so that its lower surface deflects the flexible membrane crossing the greatly enlarged inferior orbital foramen. This enables the lower part of the eye to project into the buccal cavity, so that it can be housed within the depth of the head. Reduction of the supraocular osteoderms increases the flexibility of the skin over the eyes so that its geometry can alter during their depression. Reduced overlap of collar and belly scales increase smoothness enabling lizards to move easily both forwards and backwards in crevices. Some or all these features are paralleled in many non-lacertid crevice users including skinks (such as *Mabuya laevis* and *M. sulcata*), xantusiids (*Xantusia henshawi*), geckos (*Afroedura*) and iguanids (*Sauromalus*, *Oplurus*).

Holaspis has other features not found in other crevice-using lacertids but present in the most extremely flattened exploiters of rock crevices in other families, such as *Platysaurus* (Cordylidae) and *Tropidurus semitaeniatus* (Iguaninidae, Tropidurinae) and probably functionally associated with such strong depression. Among these is modification of the scleral ossicles, so that there is one or

more windows in the scleral ring (Fig. 2). These enable the eyeballs to distort and flatten, so they can be housed in the narrow space available within the head. Other shared features, which also contribute to low vertical dimensions, are depression of the body vertebrae and reduction of the crests on their neural arches.

Shortening and consequent decrease in mass of the adductor muscles associated with reduction in head height probably plays a critical role in facilitating the evolution of this cranial morphology. Curtailed mass reduces the power of the muscles, so a particularly strong, thick arched parietal area of the skull is no longer necessary to resist their action, and this also permits the posterior skull roof to become thin and flat. Similarly the mandibles are subjected to reduced forces in biting and can consequently be more slender with smaller vertical dimensions. However, such shortening of the muscles carries penalties in terms of reduced efficiency in biting and prey handling (Arnold, 1998a). Change in geometry of the skull during the retraction phase of cranial kinesis ameliorates this effect by improving their angle of action on the jaw and the length of their excursion. This phenomenon is prominent in *Platysaurus*, which has an expansion area in the skin on the anterior cheek that accommodates the changes involved in the substantial kinetic movement. The similarly orientated hinge regions of *Holaspis*, between the small scales found in this region, indicates that its skull is similarly highly mobile, as does the simplified fronto-parietal suture.

The downward flexion of the retroarticular process of the mandible may permit a longer and more efficient *depressor mandibulae*, in spite of the flattened head, although this feature is not paralleled in other very flattened crevice users. Other characteristics of *Holaspis* could also plausibly be considered as adaptations to crevice use, but are not repeated in functional analogues. Thus, the large plates along the back which might possibly increase smoothness and so ease mobility within crevices; although neither *Platysaurus* or *T. semitaeniatus* have this feature. The enlarged sternal fontanelle could similarly be thought to increase flexibility in this region, but *Platysaurus* has no fontanelle at all.

Another complex of *Holaspis* features may also be related to use of crevices, specifically those beneath bark. This involves the snout which is wedge shaped in lateral view (unlike that of rock crevice dwellers), with the bizarre flattened boss formed from the premaxilla, and nostrils set back from the snout tip and low on its sides. Such features are not found even in extremely flattened lizards using rock crevices, but they do occur in the flattened lygosomine skink *Aulacoplax*, which habitually conceals itself in the narrow interstices between the bases of the fronds of screw pines (*Pandanus* spp.) (Brown and Fehlmann, 1958). This arrangement may enable the skink to enlarge interstices so they are broad enough to take the rest of the animal as it moves forwards. *Holaspis* may possibly do the same when pushing beneath flexible pieces of loose bark. The frequent presence of longitudinal scratches on the dorsum of the head suggests this may be the case. Fusion of the frontoparietal and interparietal scales may increase strength and smoothness of the head surface but has no parallels elsewhere.

GLIDING. Since *Holaspis* descends through the air in a controlled way at relatively shallow angles it glides rather than parachutes. Gliders depend on the possession of an aerofoil which extracts a lift component as the animal moves through the air, the lift counteracting the force of gravity. For gliding at shallow angles to be possible, the ratio of surface: body weight needs to be high. Some other gliding lizards have a specialised lift surface that provides this. In the agamid *Draco*, this is formed from a membrane supported by the

elongated abdominal ribs while in the gecko *Ptychozoon* there are flaps attached to the sides of the belly that fold out, increasing surface area. In *Holaspis*, it is the whole body that acts as an aerofoil and some features that also confer performance advantage in using crevices contribute to its formation. This is particularly true of dorsoventral compression, but low ossification of the skull must help increase the surface: weight ratio. Other features appear to be specifically associated with gliding and are not found in crevice dwellers, although they may occur in other gliders. Included here is low ossification of the pectoral girdle and perhaps that of the sternum and depression of the legs and tail. This last feature, together with development of distinct trailing edges on the limbs, also occurs in *Draco* and *Ptychozoon*, which do not enter very narrow crevices. Surface area is further increased by the lateral flaps on the neck and the webs of skin that form the trailing edge of the proximal hind legs, both features again found in *Draco* and *Ptychozoon*. The modified scales on the sides of the tail, on the trailing edge of the crus and on the hind digits also increase surface very efficiently, forming stiff lateral fringe-like extensions with little increase in weight. They are exactly paralleled in structure and function by scales on the hind side of the thigh and tail base in *Draco*, while *Ptychozoon* has analogous cutaneous extensions along the length of the tail.

Holaspis is able to produce further temporary increase in surface area by lateral expansion of the abdominal region so that this becomes almost disc-like. The increase in surface area is brought about by the long free dorsal ribs being rotated forward around their articulations with the body vertebrae, so that instead of being directed diagonally backwards they project more laterally. In *Holaspis*, the gain in surface area this produces is large because the ribs are long. The overlapping flexible rib tips form a continuous lateral edge to the area supported by the ribs and this maintains its continuity and longitudinal orientation in spite of the movements of the ribs themselves. The rotation of the ribs is presumably partly brought about by the intercostal muscles, as seems to be the case in *Draco* (Colbert, 1967). But it is likely that the well-developed slips of the *m. intercostalis scalaris* also play a part. As they run somewhat diagonally outwards and backwards from the *m. rectus abdominis* to the rib tips, their contraction would also help swing the ribs forwards; at the same time the ribs would tend to bow laterally and bend distally downwards. The contraction would also raise the *m. rectus abdominis* and with it the ventral integument which is closely attached. These movements would produce a more aerodynamically efficient transverse section in which the dorsal surface was more strongly convex and the belly flat or slightly concave.

The skin must stretch to allow for the increase in lateral area that the rib movements produce. Its distinctive structure permits this, for expansion occurs not only at the longitudinal lateral skin folds but also at the extensible areas between the scales. The bridges that often join the scales limit the direction and extent of expansion; they also help distribute it evenly throughout the skin, discouraging wrinkling and so contributing to a smooth surface. The looseness of the connection between the skin and underlying structures usual in lizards is also important in allowing skin tension to be evenly distributed.

It is probable that the band of large broad plates in the vertebral region also has a function in producing as good an aerofoil as possible. As the hinge regions between the plates are virtually inelastic, the whole area can be regarded as a single lamina which is firmly fixed at the occiput and at the tail base. When such an elongate lamina is stretched over a flat or convex surface, and placed under tension, it becomes very resistant to lateral deformation. This

effect is increased when the tension is both along and across the lamina. It can be demonstrated by placing a strip of paper on plane surface and putting it under longitudinal tension, after which displacing the intermediate area laterally, even to a small extent, becomes very difficult.

Such rigidity appears to be developed in the vertebral area of *Holaspis*, which extends over the convex dorsum of the body. Tension is generated by the lateral skin being pulled outwards during rib spreading. This movement distorts the large plates and their hinge regions slightly, so that there is a small widening and longitudinal contraction of the vertebral band. As this is firmly attached at the occiput and the tail, tension within it is thereby increased. The slight movements of the plates exhaust the very limited internal mobility of the band, increasing its lateral rigidity further. These processes can be discerned in the detached dorsal skin of an alcohol-preserved *Holaspis*. Lateral tension alone, produces a longitudinal contraction of the vertebral band whereas, if it is applied when the ends of the band are fixed to the substrate, the band becomes laterally rigid.

The rigid vertebral band ensures that the extended lateral skin is spread evenly on both sides of the body, again helping to avoid the tendency of the tense skin to wrinkle. It may also act to keep the body straight during gliding by restricting lateral bending. This effect can be simulated by attaching a strip of adhesive paper tape along the side of an elongate rubber balloon. When this is inflated, the stretched wall of the balloon exerts tension on the paper strip, which represents the vertebral band of *Holaspis* and the air pressure provides support for this in an analagous manner to the body of the lizard. A balloon modified in this way is substantially harder to bend sideways than an unmodified one.

When the lateral skin of *Holaspis* is unstretched, the vertebral band is slack and capable of rucking upwards at its hinges. This permits the lizard a normal amount of lateral movement, when for instance walking rather than gliding, since the band now lacks lateral rigidity.

The surface: weight ratio ('wing'-loading) of *Holaspis* was roughly assessed on the assumption the whole animal acts as an aerofoil. Area was found by placing straightened preserved lizards belly downwards on squared paper and tracing their outline; maximum lateral extent of the body was then estimated by comparison with photographs of animals basking with their bodies fully expanded, and by stretching the lateral skin. Weight was calculated on the assumption that live lizards weigh 10% more than alcohol preserved ones (Colbert, 1967). The loadings for four individual adult *Holaspis* varied between 0.26 and 0.37 gm/cm². These are relatively small figures when compared with those for *Draco* (Colbert, 1967). Such low loading is probably necessary to compensate for the relatively poor general aerodynamic shape of *Holaspis*.

FUNCTIONAL SIGNIFICANCE OF OTHER CHARACTERS. A minority of derived features of *Holaspis* are not functionally associated with its main distinctive behaviours. The presence of a window in the lower eyelid has developed in a wide range of small lizards that bask directly in the sun in relatively dry microclimates (Arnold, 1973; Greer, 1983). This means that such lizards can reduce the extensive water loss associated with these situations by closing their eyes but still retain vision to detect predators, passing food items etc. In agreement with this explanation, the window is better developed in *H. laevis* which extends into relatively dry savannah, than in *H. guentheri* which appears to be confined to forest. Loss of pterygoid teeth in lacertids tends to correlate with the general reduction in ossification found in *Holaspis* and may be a concomitant of this.

EVOLUTION OF *HOLASPIS*

The order in which new features develop and the situations in which they do so can often be reconstructed by examining states on side branches on the lineage of the taxon concerned. This cannot be done with many features of *Holaspis* as they have evolved within its exclusive lineage, which by definition lacks side branches, so other cues have to be used for these autapomorphies. However examination of the relatives of *Holaspis* does give some information. Thus, a degree of climbing is widespread in lacertids as is a modest amount of crevice use. This makes it most parsimonious to assume these behaviours precede gliding, which is unique to *Holaspis*. These activities and the morphological adaptations associated with them are better developed in *Holaspis* itself. Improvement in climbing modifications may possibly have begun first, as climbing steep tree boles and branches must precede exploiting crevices in them.

Animal gliders and fliers can be stable or unstable. In stable ones, there is a long lift surface behind the centre of gravity. This means that, as an animal glides, any tendency to pitch in the sagittal plane around the centre of gravity is self-correcting. In pitching, the long posterior lift surface will rise or fall, but the air pressure produced by forward locomotion will return it and the animal as a whole to its original orientation. Unstable fliers with short lift surfaces behind the centre of gravity gain in manoeuvrability but do not self-correct and so require sophisticated neurological mechanisms to maintain appropriate posture in the air, something that is unnecessary in stable forms (Smith, 1952). Unsurprisingly, stable forms evolved before unstable ones in most of the main groups of flying animals, namely insects, pterosaurs and birds, and possibly bats too (Smith, 1952).

As might be expected from this, *Holaspis* is a stable glider. The centre of gravity of preserved *Holaspis* appears to be just behind the midpoint between the two pairs of legs. There is therefore a considerable area of lift surface posterior to the centre of gravity, made up of the hind body, hind limbs and tail. Experiments were conducted with models made out of laminated cardboard and weighted to give a wing loading and weight distribution similar to that of *Holaspis*. When gently launched in the appropriate position, these glided well, confirming that a glider of the dimensions and shape of *Holaspis* is stable.

Given inherent stability, gliding ability seems to require only an aerofoil and ability to reach and maintain an appropriate belly-down posture with limbs slightly raised, as well as some ability to trim, at least initially. In tree frogs Cott, (1926) found adoption of initial posture very critical: *Phrynohyas venulosa* spread its limbs and glided when dropped whereas *Hyla arborea*, which is morphologically similar, dropped vertically with legs flailing. It might be expected that the ability to adopt the appropriate posture would be confined to *Holaspis* among lacertids as it is the only known glider, but when tests were carried out on a number of lacertids this propensity was found to be widespread, being present in completely terrestrial lizards such as *Lacerta agilis* and *Acanthodactylus erythrurus*, as well as climbing ones (Arnold, 1989a). The wide distribution of this ability suggests it confers advantage in another more general context and may have arisen there. This context may be terrestrial locomotion. Certainly running lacertids seem to have to continuously adjust their body positions and, at some points in the stride cycle, they may be balanced on only a single toe (Arnold 1998b), so good neurological control of posture seems to be essential in this activity.

The production of an aerofoil is likely to largely result from direct adaptation, as many of the features of *Holaspis* appear to confer advantage only in gliding. However rib spreading, like balance, is

coopted from an earlier activity. All lacertids, including *Holaspis*, appear to spread their ribs when basking in relatively cool conditions, increasing surface area and rate of heat intake.

Permanent depression of the head, body and limbs of course also contributes to the aerofoil and we can ask whether this is a special feature of gliding or whether it is coopted from crevice use. As already noted there is some phylogenetic evidence of its earlier origin for crevice use, something that has occurred in many independent lineages.

Modifications for gliding in *Holaspis* are quite extensive, several organ systems being involved. It is therefore rather surprising that *Holaspis* has not developed a more efficient aerofoil such as occurs in *Draco*. However to do this would probably involve the development of a delicate patagium or extensive lateral skin flaps. It is likely that such structures would interfere with the lizard's ability to enter and move in the narrow crevices it regularly utilises. Consequently *Holaspis* is restricted to using means of broadening the body that do not project exteriorly.

As a stable glider, *Holaspis* is very dependent on its long tail, but this can break easily, even close to its base where loss might make it unstable in the air and reduce its ability to control its glide path. Nonetheless the tail is lost and often regenerated in many individuals (Arnold, 1984). This emphasises the importance of tail loss as an antipredator device and suggests the cost: benefit ratio still favours frequent tail loss in *Holaspis* even though locomotory costs may well be high.

It might be thought that cases like *Holaspis*, where entrance into a new life mode has been dependent on multiple exaptations, are rare. But this phenomenon occurs in another instance where aerial locomotion has been attained, that of birds where feathers and the complex mechanism of wing folding arose long before gliding or active flight (Gauthier & Gall, 2001).

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Appendix 1

Derived features of *Holaspis* not found in immediate relatives in the paraphyletic genus *Adolfus*. Most features are unique in the Lacertidae as a whole and these are denoted by *. Separate postorbital and postfrontal bones are primitive in the Lacertidae but fusion is the usual condition in the African Equatorial group and separation in *Holaspis* is a reversal (Arnold, 1989a). Most features appear to confer a performance advantage in one or more of the characteristic behaviours of *Holaspis* or ameliorate a problem associated with them. The behaviours concerned are designated as follows: L – locomotion on steep surfaces, C – use of crevices, G – gliding. Brackets indicate a relatively minor role.

Proportions

- | | |
|---|----|
| 1. Head, body, limbs and tail extremely depressed* | CG |
| 2. Snout sharply wedge-shaped in lateral view* | C |
| 3. Fore and hind limbs approach equality in length* | L |

Skeleton and musculature

- | | |
|---|------|
| 4. Skull light and very thin-boned with some deformability* | CG |
| 5. Premaxilla forming a large semicircular boss* | C |
| 6. Nasal openings of skull very large and widely expose primary nasal chambers | C(G) |
| 7. Fronto-parietal suture a simple abutment, not strongly interdigitated*. | C |
| 8. Postorbital and postfrontal bones separate | C |
| 9. Supraocular osteoderms very reduced* | C(G) |
| 10. Inferior orbital foramen extremely large | C |
| 11. Pterygoid teeth absent | |
| 12. Increased cranial kinesis | C |
| 13. Ring of scleral ossicles reduced to twelve and emarginated above and below* | C |
| 14. Retroarticular process of mandible directed somewhat ventrally* | C |
| 15. Dorsal vertebrae depressed with very reduced neural spines* | C |
| 16. Anterior free ribs elongated with long cartilagenous extensions at their tips* | G |
| 17. Coracoid plate with an extra fontanelle* | CG |
| 18. Sternal fontanelle very large* | CG |
| 19. <i>M. intercostalis scalaris</i> well developed, consisting of slips originating on tips of anterior free dorsal ribs | G |

and running forwards and medially to insert on upper surface of *m. rectus abdominis*, above outer margins of second row of ventral scales*

- | | |
|---|---|
| 20. Manus and pes have syndrome of features associated with climbing on continuous open surfaces very pronounced*. | L |
| 21. Length and downward curvature of penultimate phalanges of digits better developed than in other lacertids* | L |
| 22. Digits 2–5 of manus subequal in length* | L |
| 23. In manus, shortening and downward flexure of phalanx 2 of toe, 3 and phalanges 2 and 3 of toe 4, very pronounced* | L |

External features

- | | |
|---|------|
| 24. Rostral scale very large, extending on to top of snout with broad frontonasal contact* | C |
| 25. Nostrils set back, on sides of snout* | C |
| 26. Interparietal and paired frontoparietal scales all replaced by a single triangular scale* | C |
| 27. A window in the lower eyelid made up of 1–5 enlarged semitransparent scales | |
| 28. Temporal scales differentiated with anterior ones arranged in diagonal lines* | C |
| 29. Neck with sharp-edged flap on each side when pharynx not expanded* | G |
| 30. Cross section of body convex above and flat below | G |
| 31. A double series of very large flat scales along vertebral region of body* | (C)G |
| 32. Dorsal scales on sides of posterior trunk laterally expandable* | G |
| 33. Lateral dorsal scales on posterior trunk sometimes joined by a system of bridges* | G |
| 34. Collar and belly scales with very reduced imbrication | C |
| 35. Tail with two longitudinal rows of broad enlarged scales above and below, the former with multiple sensory pores* | G |
| 36. Tail with lateral fringes of interconnected pointed scales* | G |
| 37. Two rows of large scales on front of forelimbs* | CG |
| 38. A patagium behind the knee* | G |
| 39. A row of flat triangular scales on trailing edge of crus* | G |
| 40. Second and third fingers of manus conjoined at base* | L |
| 41. Digits 3–5 of pes with a fringe of interlocking pointed scales* | G |
| 42. Distinctive colouring* | |



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