A morphology-based taxonomic revision of *Laudakia* Gray, 1845 (Squamata: Agamidae)

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> **Abstract**

The former genus *Stellio* has already been partitioned into *Laudakia* Gray, 1845 and *Acanthocercus* Fitzinger, 1849 on the basis of several pieces of evidence. The main objective of this study is to revise *Laudakia* which recently includes 20 species: *L. agrorensis*, *L. badakshana*, *L. bochariensis*, *L. caucasia*, *L. dayana*, *L. erythrogaster*, *L. fuscus*, *L. himalayana*, *L. lehmanni*, *L. melanura*, *L. microlepis*, *L. nupta*, *L. muristanica*, *L. pakistanica*, *L. papenfussi*, *L. sacra*, *L. stellio*, *L. stoliczkana*, *L. tuberculata*, and *L. wui*. More than 600 specimens have been studied with reference to 54 morphological characters which resulted in a detailed descriptive account for each taxon. *Agama isozona* is recognized as a synonym of *L. bochariensis*. The latter species itself has been placed in a supraspecific complex consisting of *L. himalayana*, *L. badakshana* and *L. bochariensis*. *Laudakia caucasia* which has been lowered and raised several times since its appearance is again identified as a monotypic species by placing *L. caucasia triannulata* as synonym under *L. microlepis*. *Laudakia fusca* was described as a variety of *L. nupta* but subsequent herpetologists synonymized it or recognized it as full species. According to this study *L. fusca* should be recognized again as subspecies of *L. nupta* pending more detailed further research. Moreover, several previous works have indicated that *Laudakia* is paraphyletic and therefore two new genera are described herein encompassing the *stellio*- and *caucasia*-groups.

> **Key words**


**Prologue**

The present paper is based on the PhD thesis of the late Dr. KHALID JAVED BAIG who passed away through a tragic accident on November 11th, 2006 (see the obituary for him in the Russian Journal of Herpetology 14 [1], 2007). KHALID had been awarded with a fellowship by the German Academic Exchange Service (DAAD) from October 1990 to March 1992 at the Herpetology Section of the Zoologisches Forschungsmuseum A. Koenig in Bonn, Germany. During this time he prepared and finished his thesis [supervised by the fourth author (WB)]. It was defended subsequently at the University of Islamabad, in his home country Pakistan. We think that KHALID J. BAIG’s thesis is a very important contribution to the knowledge of agamid lizards, particularly of the whorl-tailed agamas of the genus *Laudakia*. Therefore, we decided to complete and update the manuscript after some years with the most important data and references published in the meantime, wishing to prevent this major contribution from suffering the same fate of another famous thesis on agamid lizards (MOODY 1980) that unfortunately remained unpublished until today. The third author (NBA) was also cooperating with KHALID and still is a dedicated researcher on agamids. This is also true for the second author (PW) who organized the first international symposium on agamid lizards in Bonn, DeAgamis I, in 2008 which was followed in 2010 by DeAgamis II in St. Petersburg, organized by NBA. Both these meet-
ings could have been even more productive if the late KHALID J. BAIG could have participated. We hope and expect that the publication of his updated thesis will, besides advancing the subject, further demonstrate that he was a very capable and promising herpetologist whose early death is still a great loss for the herpetological community.

Introduction

General Introduction

Taxonomically, the history of Laudakia dates back to 1758 when the first member of this group was described as Lacerta stellio by LINNAEUS. At that time knowledge of systematics was not that advanced and the morphological and behavioral similarities of agamids and iguanids misled many herpetologists to confuse their affiliations. As an example, the aforementioned species was also described as Iguana cordyline by LAURENTI in 1768. These systematic anomalies were even greater concerning iguanids. The present Phymaturus pallima (Molina, 1782) was identified by its author as Lacerta in 1782 but placed in Stellio in 1801. Microlophus peruvi anus (Lesson, 1830) was firstly described as Stellio in 1830 whereas Uracentron azureus was first described as Lacerta azurea by LINNAEUS (1758) and was placed in Stellio in 1801. Likewise, Tropidurus torquatus was described in 1820 as Stellio torquatus (Burt & Burt 1931).

BOULENGER (1885) resolved many discrepancies at least at family level and fixed several taxa into their respective families and genera. Among the Agamidae, which is the fourth largest family among lacertilians and distributed from Africa through Asia to Australia, Stellio has long been a controversial group. Many herpetologists considered it as part of the African genus Agama DAUDIN, 1802 (e.g. BOULENGER 1885; SMITH 1935; WERMUTH 1967). Although the name Stellio LAURENTI, 1768 was made unavailable by STEININGER’s (1936; see also Henle 1995) action of selecting the non-identifiable Stellio saxatilis as the type species, several herpetologists kept it alive. More recently MOODY (1980) resurrected six distinct genera from the collective genus Agama, including Stellio. Moody (1980) placed 22 species into the genus, including several African taxa. Since then, successive herpetologists have largely accepted the importance and individual status of this group. Some of them recognized it as an independent genus Stellio (ANANIEVA & ATAEV 1984; ANANIEVA & DANOV 1990; ANANIEVA et al. 1990, 1991; OSNEGG 1989; JOGER & ARANO 1987) while others treated it as an informal group within Agama (BAIG & BOHME 1991a, b; BOHME 1981; JOGER 1991). BAIG (1992) and BAIG & BOHME (1997) partitioned Stellio (sensu MOODY 1980) into the genera Laudakia GRAY, 1845 and Acanthocercus FITZINGER, 1849. Their morphological analysis was based on 54 characters and incorporated anatomical, karyotypic and biochemical evidence from relevant literature.

In previous years various aspects of this group have been worked out. JOGER & ARANO (1987) and JOGER (1991) tried to resolve the confusion among the African and Asian agamid lizards through their biochemical studies. They also presented phylogenetic relationships among several agamid taxa. Other studies are mostly region-oriented. NIKOLSKY (1915), TEREVENT & CHERNOV (1949), ANANIEVA & ORLOVA (1979), PETERS (1971), ANANIEVA et al. (1981), and ANANIEVA & PETERS (1982) published on the species found in former USSR. Laudakia of Iran has been studied by ANDERSON (1963, 1974), SCHLEICH (1979), CLARK (1991) and CLARK et al. (1966), ANDERSON & LEVITON (1969) and CLARK (1990) reported on laudakias from Afghanistan. The European member of this genus, L. stellio, has been studied by DAAN (1967), BEUTLER & FRÖR (1980), BEUTLER (1981) and OSNEGG (1989). Some forms of this species, which extends into Arabia and North Africa, were commented by FLOWER (1933), SCHMIDT & MARX (1956) and ALM OG et al. (2005). The herpetology of Pakistan has also been studied (SMITH 1935; MINTON 1966; MERTENS 1969; KHAN 1977, 1980; KHAN & BAIG 1988), but most of their work concerned the southern parts of Pakistan. More recent studies in northern Pakistan extended the distribution range of several species (BAIG 1988a, 1990). Iranian Laudakia were studied by RASTEGAR-POUYANI and colleagues (RASTEGAR-POUYANI & NELSON 2002; FAIZI & RASTEGAR-POUYANI 2007; AGHILI et al. 2010).

A genetic study of the entire genus is lacking and is now under the focus of the authors. However, some groups of Laudakia are comparatively well studied, e.g. the Laudakia caucasia species group (MAC EY et al. 1998, 2000b) and species of Central Asia (MELVILLE et al. 2009), or laudakias were used to solve zoogeographical questions (MAC EY et al. 2000a).

However, one of these studies (MAC EY et al. 2000a) has shown that Laudakia, as recently recognized, is paraphyletic. They recognized the L. caucasia group as sister taxon to a clade containing some Phrynocephalus species and Laudakia stellio, whereas the L. tuberculata group is basal to this entire clade (see fig. 1). Even if these bootstrap values (see fig. 1) are not all highly significant, the results are supported by Wagner (2010) who also recognized Laudakia as paraphyl-
the same groups as mentioned above are in distinct clades, which is supported by some morphological characters (BAIG 1992). Very recently, EDWARDS & MELVILLE (2011) published a study including mtDNA analyses showing Laudakia as monophyletic and sister taxon to Phrynocephalus (fig. 2). Also here L. stellio is isolated and sister to the L. caucasia group, while the L. tuberculata group is basal to the previous groups. In all these different studies the same groups are supported, but there is evidence of a paraphyly of the genus. Therefore, we decided to classify the different species groups in distinct genera.

**Previous Works**

Karyotypic studies on agamids have been carried out by HALL (1970), GORMAN & SHOCHAT (1972), GORMAN (1973), SOKOLOVSKI (1974), KUPIYANOVA (1984). In addition, MOODY & HUTTERER (1978) and WITTEN (1978) described karyotypic formulas for several agamids. These studies suggest that Laudakia possess 2n = 36, a pattern considered ancestral for all lizards on the basis of its occurrence in nearly all lizard fami-
lies (William & Hall 1976), a finding which is also observed in Uromastyx, Leiolepis, Physignathus and Acanthocercus.

Cranial morphology and dentition was studied by Camp (1923) who reviewed a number of useful morphological characters that vary at the subfamilial and generic levels, but he examined few agamids. Jollie (1960) succinctly reviewed the head skeletons of several lizards, including agamids. However, both authors relied largely on German-speaking morphologists, primarily Siebenrock (1895) who had depicted skulls and mandibles of several agamid species including L. himalayana and L. tuberculata. Moody (1980), using 78 characters, emphasized the skeletal characters in building phylogenetic relationships among genera of the Agamidae. Ananjeva (1980) published structural characteristics of the skull, dentition and hybrid of L. caucasia, L. erythrogaster, L. himalayana, L. lehmanni, T. ruderatus and Trapelus sanguinolentus. Besides El-touBi (1947) and Duda (1966) who studied L. stellio and L. tuberculata respectively, other information about this group is scattered and mostly concerned with non-Stellio (sensu Moody 1980) members of Agamidae (Smith 1935; Barri 1953; George 1955; Harris 1963). Also Ananjeva (1980) studied skull and associated structures of six agamids, with four belonging to the stellio-group.

The agamids are conventionally characterized as the lizards with acrodont teeth (Romer 1956). This characterization is too general and partly false (see Moody 1980; Smirna & Ananjeva, 2007). Agamid teeth are heterodont i.e., comprise more than one form of teeth, viz. anteriorly pleurodont and posteriorly acrodont. Description of agamid dentition has also been given by several authors (Edmund 1969, Cooper et al. 1970, Presch 1974, Robinson 1976) but Moody’s (1980) point of view seems to be more reasonable. Moody (1980) explains the differential tooth size from anterior to posterior by stating that anterior acrodont teeth are ankylosed juvenile teeth which could not increase in size. The pleurodont teeth at the tip represent an intermediate evolutionary step to higher forms because they do not undergo replacement at regular intervals (except in case of accidental loss) and have partial basal ossification. Siebenrock (1895) reported two pleurodont teeth in Agama hispida, Laudakia himalayana, Laudakia stellio, Trapelus mutabilis pallidus and Trapelus sanguinolenta, and three in Laudakia tuberculata, but only one in Agama atra and Agama agama. Ananjeva (1980) mentioned two in Trapelus ruderatus (now recognized as T. lessonae fide Rastegar-Pouyani 2000) and variably two or three in Trapelus sanguinolenta, L. caucasia, L. lehmanni and L. erythrogaster. Duda (1965) and Baig (1991) confirm the tooth count given by Siebenrock (1895) for L. tuberculata.

Siebenrock (1895), Duda (1965) and Ananjeva (1980) categorized the teeth as incisors, canines and molars, whereas Moody (1980) referred to the anterior pleurodont teeth as canines and the posterior acrodont teeth as molars. The first three authors invariably reported one incisor and one canine in each quadrant of the maxilla and dentary in all species of the genus Agama at this time (sensu Wermuth 1967).


Behavioural patterns of agamids are very similar to those of iguanids and until we have more information on the social behaviour of additional species of agamids, the possibility of significant differences between the social behavioral patterns of these two families remains an open area of investigation (Blanc & Carpenter 1969). Brattstrom (1971) described some 73 behavioral postures and positions for Australian bearded dragon, based on observations made in the field and the laboratory. Information regarding agamid spacing systems is sparse, but the few studies carried out suggest that agamids are remarkably similar in habits and social structure to iguanids (Stamp 1977). Smith (1935), Harris (1964), Schmidt (1966), Blanc & Carpenter (1969), Brattstrom (1971), Carpenter (1978), Schleich (1979), Orlova (1981a, b), Beutler (1981), Daniel (1983) and many others have suggested territorial behavior in agamids. These authors mostly attribute territoriality to the males. Only Schmidt & Inger (1957), Madel & Klockenhoff (1972) and Langerwerf (in Orlova 1981a) observed it in female agamids as well. Moreover, Panov & Zukova (1995) studied the variability and differentiation of e.g. home ranges in populations of L. caucasia.

Material & Methods

Material

Pakistan Museum of Natural History, Islamabad and Zoologisches Forschungsmuseum Alexander Koenig,
Bonn are the primary sources of information for the present study, but in addition almost all other major Museums of Europe and one in the USA have been visited to examine the material deposited there. The list of these institutes with their acronyms (used to quote these institutions in the following text) is as follows:

- BMNH: British Museum of Natural History, London
- UF: Florida State Museum, University of Florida, Florida
- MNHN: Museum National d’Histoire Naturelle, Paris
- NMW: Naturhistorisches Museum Wien, Wien
- PMNH: Pakistan Museum of Natural History, Islamabad
- RMNH: Naturalis, Leiden (former Rijks Museum von Natuurlijke Historie)
- SMF: Senckenberg Naturmuseum, Frankfurt
- SNSD: Senckenberg Naturhistorische Sammlungen Dresden (former Staatliches Museum für Tierkunde, MTKD)
- ZISP: Zoological Institute, Russian Academy of Science, St. Petersburg, Russia
- ZMA: Zoologisch Museum of the University of Amsterdam, Amsterdam
- ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn

We have studied almost all related material housed in these institutes. The selected number was only studied when there were several specimens from the same locality. The data have been compiled based on 54 morphological characteristics found important for the comparison of the different members of this group (see Baig 1992). Of these, 22 are morphometric, 7 quantitative numeric and 25 qualitative (see Baig 1992). Measurements were taken nearest to the 10th of a millimeter with the help of a vernier calliper. The scales on the different parts of body are counted using Stereomicroscope. All statistical data has been analysed on the computer using Microsoft Excel (see Baig 1992).

**Cranial morphology and dentition**

Four species, *L. agroensis* (PMNH 363, see fig. 3a), *L. caucasia* (without collection number, see fig. 3a), *L. himalayana* (PMNH 212, not shown), *L. paksistani ca* (PMNH 157, see fig. 3a), *L. stellio* (without collection number, see fig. 3a) and *L. tuberculata* (PMNH 121, see fig. 3b), have been collected from the northern mountain region of Pakistan. Skeletons were prepared through maceration technique. They were examined to demonstrate different elements of cranium and dentition, and important skulls are presented as drawings, which were made with the help of a camera lucida.

**Results**

**General Morphology**

There is no significant difference between the number of supralabials and infralabials in all members of *Laudakia*. In some taxa, e.g. *L. stoliczkana*, there are slightly more supralabials, whereas *L. stellio vulgaris* shows more infralabials. Most species have nine to twelve supralabials. However, *L. nupta* and *L. erythrogaster* have higher numbers. The lowest number of supralabials is represented in *L. sacra* and *L. agroensis* some of whom have below nine.

In general the number of lamellae under the third finger is smaller than under the fourth toe. In most taxa this difference is approximately five scales, but in *L. dayana, L. stoliczkana, L. erythrogaster, L. himalayana* and *L. nuristanica*, it is higher. The highest numbers can be found in *L. dayana* and *L. nuristanica*. Under the third finger the number usually remains smaller than 20 and under the fourth toe smaller than 25. Specimens of *L. tuberculata, L. nuristanica* and *L. dayana* may exceed 30 and sometimes reach even 35 subdigital lamellae.

In some cases the number of scale rows around midbody is an important character to distinguish different of the herein mentioned taxa. Laudakian species mainly stay within the range of 100–150 scale rows around midbody. However, the minimum numbers (i.e. less than 100) are recognized in *L. nupta, L. erythrogaster* and *L. lehmanni*, whereas the highest numbers in *L. nuristanica*. This latter species shows more than 200 scales around the body. Among others especially *L. tuberculata, L. microlepis* and *L. s. picea* also show a fairly high number of scales rows around midbody.

In some cases the number of pericaudal scales reflects a similar pattern as the number of scales around the body. *L. nuristanica, L. tuberculata, L. stoliczkana*, who all have a high number of scales around midbody, also show a high number of pericaudal scales, while in *L. s. picea* has low numbers in both characters. The largest caudal scales can be found in *L. melanura*, but also *Laudakia s. cypriaca* and *L. nupta* show relatively large scales.

In body proportions, the longest tails can be found in *L. dayana* and *L. melanura*, whereas the short-
Fig. 3a. Skulls of *L. pakistanica*, *L. agrorensis* and *L. stellio*. Left column: dorsal view of the skull; middle column: ventral view of the skull; right column: lower jaws from above and left. *L. pakistanica* and *L. agrorensis* are originally published in BaiG (1992), whereas *L. stellio* is obtained from El-Touh (1947a).
Peter is unique in that the distance between eye-tympanum indicates that eyes are always at least relative head height. The width of head is more or less one and half times that of its height in most species. The other taxa in which tail width exceeds one half times the tail height are L. melanura and L. bochariensis. In all other taxa the ratio is reversed. In case of limbs, although the longest heads can be found in all subspecies of L. stellio. The other species show more or less the same range regardless the head length. Laudakia tuberculata, L. agrorensis and L. pakistanica show the least relative head height. The width of head is more or less one and half times that of its height in most taxa, although L. agrorensis shows the highest proportion. The ratio of the snout length to the distance between eye-tympanum indicates that eyes are always located more towards tympanum. In L. agrorensis, L. dayana, L. nuristanica and L. tuberculata the eye is closer to the tympanum than in the other members of Laudakia. The ratio eye-width to tympanum diameter is unique in L. melanura and L. nupta, where eye-width is smaller than tympanum diameter. In all other taxa the ratio is reversed. In case of limbs, although the tendency is more or less similar to head length, L. stoliczkana altaica, L. lehmanni and L. sacra show relatively shorter limbs than other taxa. The ratio of forelimb to hindlimb is almost uniform in all members of Laudakia. In all species, the tail width exceeds tail height. Laudakia s. picea has the most depressed tail, where the height of the tail is about half of its width. The other taxa in which tail width exceeds one and half times the tail height are L. agrorensis, L. bochariensis, L. caucasia, L. melanura, L. microlepis, L. pakistanica, L. s. stellio and L. tuberculata. The least depressed tail have been found in L. s. cyprica, L. lehmanni and L. nupta. The proportional length of the upper arm (humerus) is always higher than the lower arm (radius and ulna). With reference to the hand, the humerus is only slightly longer in L. melanura, L. nupta and L. stellio picea and almost equal in L. s. brachydactyla and L. erythrogaster. In all other species, the hand is longer than the humerus. The hand is always longer than the lower arm, although L. melanura and L. nupta show a relatively longer lower arm compared with other Laudakia species. The ratio of hand length to the length of the third finger and the ration of foot length to the length of the fourth toe do not show any significant variation among all the taxa. In the Hindlimb the thigh is always longer than the shank, but with reference to hand it is equal or more in L. melanura, L. nupta, L. s. picea and L. s. stellio. In all other taxa, the foot is longer than the thigh. The shank is always shorter than the foot, but again L. melanura and L. nupta show relatively longer shanks as compared to other members of Laudakia.
Cranial Morphology

Variation among different bony elements are generally noticeable and significant at the generic or suprageneric level. Specific level is typically too low to contribute something significant in this regard. However, to demonstrate different elements and features of the skull and associated structures, drawings of some specimens are being presented (figs. 3a, b). The skull of *Laudakia* is depressed and triangular when viewed from above. From the dorsal side three pairs of openings or vacuities are visible, i.e. nasal openings, orbital openings and temporal openings. The nasal openings are small and lead through the olfactory chamber to the buccal cavity. They are separated from each other by the premaxilla and bordered laterally by the maxilla and posteriorly by the nasal bones. The premaxilla is a single midline bone bearing only pleurodont teeth. It is T-shaped with an arching denticulate margin and a long internarial shaft that forms an arching buttress of the snout and a firm overlapping joint with the compressed anterior process of the nasals. The maxilla is the major tooth-bearing element of the cranium. The anteriormost two teeth are enlarged and pleurodont. The remainsders are acrodont. The maxilla continues posteriorly to the last tooth as a sharp process, dorsally sueret by the jugal and medially overlapped by the ectopterygoid. The palatal portion of the maxilla comprises a narrow shelf that expands anteriorly to form a suture at the midline and overlap the palatal portion of the premaxilla. The nasals are invariably paired and in contact along the midline. Posteriorly, they overlap the frontal. Laterally, as a thin process, they overlap the dorsal process of the maxilla and border the prefrontal. The two orbital openings are separated by a median frontal bone. Their anterior border is formed by the prefrontal bone, a small lacrimal bone and the maxilla, whereas their posterior border by the postorbital and jugal bones. The frontal is posteriorly broad, due to the lateral processes that extend to the postorbital. The suture with the parietal is thus broad and straight and bends slightly posterior at the midline where it forms the anterior margin of the parietal/pineal foramen. Anteriorly, it is doubly fork-shaped. A midline process separates the nasals posteriorly and contacts the internarial process of the premaxilla beneath the nasal and lateral processes. On both sides it separates the prefrontal and nasal. The prefrontal bones are robust and form much of the anterior rim and wall of the orbit. The dorsolateral corner of the prefrontal is the apex of the dorsal and lateral surfaces of the snout, and it is also the posterior culmination of the rostral canthal ridge. The lacrimal forms the anteroventral margin of the orbit and a small portion of the posterolateral snout region. It is a thin plate without firm functional articulation with surrounding elements and provides principal support for the lacrimal duct. The base of the lacrimal is more robust, not visible externally and firmly sutured between the palatine and maxilla in the anterior orbital floor.

The postorbital is large, forms much of the posterior margin of the orbit and lies in a horizontal plane with a slight ventrolateral tilt. It forms the temporal arch and, together with the squamosal, the lateral margins of the supratemporal fossa. The dorsoanterior margin of the postorbital defines the posterior apex of the orbit. Here, it articulates with the lateral processes of the frontal and parietal. The jugal forms the entire ventral margin of the orbit without any participation of the maxilla. It has a strong dorsal process that forms much of the anteroventral part of the temporal arch and acutely inserts between the postorbital and squamosal. The third pair of skull opening, the temporal openings, are each surrounded by the postorbital that forms much of the posterior margin of the orbit, parietal, supratemporal and squamosal bones. A single parietal bone covers most of the upper skull. The pineal foramen is near the anterior border of the parietal bone whereas at its posterior border two long supratemporal-parietal processes pass back diagonally towards the squamosal and quadrate. The origins of the supratemporal processes are widely separated and project posteriorly, curving only slightly below the horizontal plane. A downwards projection of the anterior base of the supratemporal process of the parietal produces a partial lateral wall to the cranial case.

The supratemporal is a small splint that closely adheres to the ventrolateral edge of the parietal process and articulates by means of a triangular-shaped head with the dorsoanterior surface of the quadrate, paroccipital process and the squamosal. It completely separates the last two elements from mutual contact. The squamosal is the posterior element of the temporal arch. It forms an overlapping joint with the postorbital and jugal anteriorly and a hinge joint with the dorsal head of the quadrates posteriorly. The foramen magnum, through which the spinal cord passes, is surrounded by four bones: dorsally by the supraoccipital, ventrally by the basioccipital and laterally by two exoccipital bones. The supraoccipital is a broad, hour-glass shaped and fused midline element which continuously contacts the posterior cranial wall of the parietal. The basioccipital forms the posterior floor of the brain-case and contributes to the basal portion of the occipital condyle.

The exoccipital bones are paired elements lying on either side of the foramen magnum contributing to the occipital condyle. The palatal region comprising denticulate and non-denticulate elements and is observable from the ventral view of the skull. Anteriorly, there are two crescent shaped openings, the internal nares,
leading from the nasal cavity, separated by the vomers and bounded at their hind end by the palatine. The palate itself is bounded at its anterior tip by the single premaxilla and along its lateral border by the maxilla. These two bones constitute the denticulate elements of the palate and have already been described under the heading of nasal openings. Vomer, palatine, pterygoids and ectopterygoids are said to be non-denticulate elements of the palate. Vomers are thin anterioirmost elements of the palate and lie between the internal nares. The latter are paired and their medial and lateral borders turn dorsally. The palatines are the middle elements of the palate and form most of the medial margin of the fenestra. The posterior part of the internal narial margin is formed by the palatine. The suture with the vomer is transverse and lies more closely to the posterior margin of the internal nares. The palatines are paired and form a loose ligamentous contact along the midline. The palate is not a flat roof of the mouth but instead bends midway along the palatine to form a horizontal anterior margin. The floor of the nasal capsule comprises the vomers and anterior palatines. The pterygoids constitute the largest element of the palate. The posterior process connects with the quadrate and the braincase via the basisphenoid. The anterior palatal portion is firmly sutured with the palate and adjacent centrum. A ventrally projecting process has sliding contact with the coronoid process of the mandible. The pterygoid do not suture on the midline, however, a membranous contact across the interpterygoid space is very likely. The medial margin of the pterygoid, which lies on the floor of the palate, is divergent posteriorly. The suture between the pterygoid and palatine is firm. The pterygoid forms a strong downward projecting process, which articulates in a sliding manner with the coronoid process of the mandible. The ectopterygoids bridge the pterygoid, the posterior part of the maxilla and the anterior part of the temporal arch. Along the internal margin of the posterior wall of the orbit, a dorsal process of the ectopterygoid contacts a ventral process of the postorbital. The medial process of the ectopterygoid overlaps the pterygoid dorsally. The ectopterygoid forms the posterior margin of the palatine fenestra and also part of the lateral margin due to the anterior process running medially to the infraorbital process contributed by the jugal.

**Mandible**

Seven bony elements, namely the dentary, angular, supraangular, articular, prearticular, splenial and coronoid, constitute the mandible and may also be termed as mandibular elements. The dentary is the largest of these bones and extends labially to the posterior coronoid process and almost reaches the articular. Lingually it is larger than the small splenial and the splint-like angular which curves along the ventral margin of the Meckelian groove to the ventral edge. The dental gutter in which the dental papillae are situated does not extend very deeply along the lingual surface of the dentary and is nearly straight. Posteriorly, the dentary strongly overlaps the supraangular as a sharply pointed dorsal and ventral process. Within the acute notch formed by these processes lies the anterior supraangular foramen. In all examined material the angular is always large and contains an angular foramen medially. The foramen is located below the anteromedial coronoid process. The supraangular is visible labially where it is overlapped by the dentary and forms an acute margin and suture with the angular. An anterior foramen is present in the apex of the notch produced by the dentary process. Lingually, the supraangular can be seen forming the internal wall of the mandibular fossa. The articular is the only endochondral bone of the mandible. It is indistinctly fused with the dermocranial prearticular bone. It forms the articulating facet for the quadrate and the retroarticular process on which the depressor mandibularis musculature inserts. The prearticular is on the lingual surface of the mandible and extends from the articulating surface of the articular to the anteromedial process of the coronoid. It forms the lingual or internal wall of the mandibular fossa. Ventrally, it forms an acute border with a distinct suture to the angular. The splenial is present as small bone flakes. It is flat, thin and roofs the posterior part of the Meckelian canal. It overlaps the dentary, the anteromedial process of the coronoid, the prearticular and the angular. The large coronoid has a prominent dorsal process which articulates as a sliding joint to the opposing coronoid process, formed by the pterygoid and ectopterygoid. The wide coronoid dorsal process curves slightly posteriorly. The lingual surface of the coronoid is an inverted V with well defined anterior and posterior medial processes. The anterior process is flat and overlapped by the dentary and the splenial. The posterior process is ridged and compressed in a transverse plane near the tip which overlaps the prearticular.

**Dentition**

Two types of teeth can be found among species studied in this publication. The acrodont tooth has a broad and slightly swollen basal portion which is ankylosed against the medial wall and floor of the shallow dental gutter. The shearing portion is triangular and compressed laterally, with the labial surface more flattened than the lingual surface. The pleurodont teeth are large and conical. The premaxilla has three teeth in *L. agrorensis* and *L. pakistanica* and apparently two
in *L. himalayana*. The maxilla carries anterior two pleurodont teeth behind which the number of acrodont teeth ranges from 12–14. The dentary shows a similar pattern of pleurodont and acrodont teeth. The number of pleurodont teeth varies between two and three. There are two in *L. pakistanica* and *L. himalayana* and three in *L. agrorensis*. The number of acrodont teeth (molars) ranges between 14–15.

**Species Accounts**

The systematic account of the species, based on all 54 morphological characteristics analysed by *Baig* (1992), has been given separately for each species. It begins with the synonymy of each taxon, followed by diagnosis, description and distribution. Important aspects of previous studies, together with own observations and comments, have been included in ‘Remarks’ at the end of each taxon chapter. *Murthy* (2010) published a book about the reptiles of India, classifying *Brachysaura minor as Laudakia*. However, he only mentioned the species in a checklist and a short species account, but he failed to explain his re-classification. Therefore, we still recognize this species as *Brachysaura* and further research will show the correct position of this taxon.

In general, all herein mentioned lizards can be characterized as diurnal, conspicuously active occupants of terrestrial mountainous habitat (with the exception of *L. stellio*), and are visually oriented in feeding and social behavior. In morphology, physiology, and behavior they show several characteristics which may be observed in other agamids and iguanid taxa. *Laudakia* lizards possess a head and body more or less depressed; tympanum distinct, diameter half or more than that of eye; groups or series of spinose scales on neck and around tympanum; nuchal crest absent or represented by a row of spinose scales; gular sac absent (some species show slight tendency); gular pli cate; head scales heterogeneous; vertebral scales usually enlarged; femoral glands absent; callous glands present in males (in some species also in females); tail oval in cross section; and caudal scales form distinct annuli. As typical agamid lizards they have strong limbs which aid efficient in running on the ground and climbing on the rocks and long, slender, oval, tapering tails which is not capable of autotomy like in lacertid lizards. However, it may be regenerated in case of accidental loss, regenerated mostly clubshaped, but sometimes bifurcated (*Baig* 1988b; *Ananjeva & Danov* 1990) or elongated (*Wagner* et al. 2009). They may use the tail for defense during fighting with one another. Most members of this group are semiherbivorous, feeding on insects and plants (*Moody* 1980), though *L. stellio picea* is largely herbivorous (*Parker* 1935). The herein mentioned lizards have a Palearctic distribution and contribute significantly to the lower terrestrial vertebrate fauna throughout this range. High speciation events of this group seem to occurred in northern Pakistan and northern Afghanistan, as this is the diversity hotspot of the entire species group.

**Stellagama gen. n.**

1768 *Stello laurenti*, Synops. Rept.: 56.
   Type species: *Stello saxatilis laurenti*, 1768 (nomen dubium).

**Type species. Lacerta stellio Linnaeus, 1758**

**Diagnosis.** Tail arranged in distinct segments of two scale whors, sometimes three in distal half. Vertebral scales heterogeneous, irregular, keeled, often larger than other dorsals scales. Gular scales keeled. Tail length about one and half times the distance of snout-vent.

**Etymology.** The chosen nomen is a composition of the nomina *Stello* (as allusion of the formerly used name of the genus) and *Agama* (to show the affiliation to the Agamidae). But ‘*Stella*’ is also the latin word for star which refers to the English common name ‘starred agama’.

**Distribution.** Southeastern Europe, western Asia and northeastern Africa.

**Stellagama stellio** (*Linnaeus, 1758*)

   Type locality restricted by neotype (*Crochet et al. 2006*): “Delos Island, Cyclades”.

1768 *Iguana cordylina laurenti* (fide Bouleneger 1885), Synop. Rept.: 47. Type locality: “America”.


Fig. 4. *S. s. stellio*: left from Tinos, Greece; right from Delos, Greece (type locality). *S. s. daani*: left from Rhodos, Greece; right from Samos, Greece (type locality). *S. s. brachydactyla*: both from Mitspe Ramon, Israel. *S. s. picea*: from an unknown locality, Israel. *S. s. salehi* from Sinai mountains, Israel.
**Taxonomy.** Daan (1967) and Beutler & Frör (1980) compared different populations of *S. stellio*. Beutler & Frör (1980) used biochemical methods and described the new subspecies *S. stellio daani*, from Ikaaria. Unfortunately, their sample size was too small and included too few populations to reach any conclusion. The most extensive morphological study of the different subspecies of *S. stellio* was conducted by Daan (1967). Present studies largely agree with his observations and recognize the complexity of the nominate form. Clark & Clark (1973) noticed colour differences among the different populations in Turkey. Despite these studies, more extensive work is still required before splitting the *S. stellio* complex. Genetic comparisons in addition to morphological studies may should resolve this issue. Despite the lack of complete information concerning this topic, Baig (1992) placed *L. stellio daani* under the nominate form pending further studies. This point of view was corroborated by Bohme & Wiedl (1994). However, their study has shown that the remaining six taxa *S. s. brachydactyla*, *S. s. cyprica*, *L. stellio daani*, *S. s. picea*, *S. s. salehi*, and *S. s. vulgaris* are quite distinct subspecies.

*Stellagama s. picea* is the smallest among all subspecies and it is unique in its black colour with yellow dots. *S. s. vulgaris* is a medium sized lizard of the group and may be differentiated from other members by being dull brown in colour with broken vertebral patches and having a segmented tail with two whorls anteriorly and three posteriorly on the dorsal side, while two whorls occur ventrally. The complete change from two to three whorls per segment is characteristic for *S. s. cyprica*. Daan (1967) mentioned that *S. s. brachydactyla* was the largest but observations made by Osenegg (1989) and Baig (1992) prove *S. s. cyprica* as the largest subspecies. *Stellagama s. brachydactyla* is unique in its wide vertebral zone of similarly sized scales and is usually bright in colouration, sometimes with a reddish tinge.

Despite the efforts of many herpetologists, the taxonomic status of different populations of *S. stellio* is still unclear. Flower (1933) was the first who identified three different populations in the Egyptian-Palestinian region. Haas (1951a) mentioned striking geographical differences and later he described (Haas 1951b) a new subspecies of *S. stellio* from the Negev (southern Israel). Parker (1934), Daan (1967) and Beutler & Frör (1980) subsequently described new races of *S. stellio* whereas Baig (1992) recognized only four subspecies in addition to the nominate form.

**Remarks.** The groups of the whorled agamas are distributed mainly an Asia while *S. stellio* is the only species occurring in southern Europe, northern Africa and on several different islands. All subspecies are primarily rock dwelling (some go on trees and buildings) at quite low elevations.

A fair amount of work has already been conducted focusing on this species. Biochemically, it was compared with other members of, at this time, *Laudakia*, *Acanthocercus* and *Agama* species by Jogger (1991) and Jogger & Arango (1987). Morphological and cytogenetical studies of the blood were made by Erfati et al. (1970), while serum proteins were studied by Hussein & Al-Badry (1968). Osteology was examined by El-Toubi (1947a, 1947b) and Eyal-Giladi (1964, 1965), chromosomes by Gorman & Shochat (1972) and morphology by Flower (1933), Parker (1934), Haas (1951), Schmidt & Marx (1956), Daan (1967), Beutler & Frör (1980), Moody (1980), and Osenegg (1989). Panov & Zykova (1979a, 1979b) studied behavioural aspects of *S. stellio* in addition, Clark & Clark (1973) also made observations along with studying habitat requirements and morphological features.

**Stellagama stellio brachydactyla** (Haas, 1951)


**Diagnosis.** Head slightly depressed; wide band of enlarged vertebral scales, enlarged body scales heterogeneous, irregular, usually smooth, transverse rows of enlarged scales hardly distinguishable; usually 5–7 yellowish vertebral bloches; tail segment of two whorls which may contain a third in distal half; 3–5 rows of callous precoxal glands and a stripe at abdomen in males only.

**Description.** Head moderately heavy, less depressed; snout longer than the distance eye-tympanum or eye width; tympanum exposed, more than half of eye width; nostril pierced below canthus rostralis, equal or less than half of the size of the nasal scale, touching rostral or sometimes interrupted by one scale; no true gular pouch but occasionally displays a tendency especially in males; gular strongly plicate; upper head scales heterogeneous, subequal, usually smooth above but may be rugose posteriorly; labials 10–14 (12 ± 1.0); groups of spinose scales present on the neck and sides of head especially around tympanum; very wide vertebral zone of enlarged scales, vertebral scales heterogeneous, irregular, usually smooth or weakly keeled, larger than other small dorsals, not differentiated into mid-vertebral and those of transverse series of highly enlarged mucronate scales; no true patch of enlarged
munronate scales on flanks but groups of spinose scales randomly present over the sides of body; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral; gular scales mucronate or spinose; total number of scales around midbody 108–153 (126 ± 13.1), mostly between 110–140; limbs very strong, covered with enlarged mucronate scales, hind-limb slightly longer than distance between gular fold and cloaca; fingers and toes compressed, 14–17 (15 ± 0.8) lamellae under 3rd finger and 18–24 (20 ± 1.4) under 4th toe. Tail moderately depressed, oval in cross section; distinct tail segments, each consists of 2 whorls of enlarged mucronate scales but may display a third in terminal part of tail; 22–28 (25 ± 2.0) scales in first complete whorl around the tail; 3–5 rows of callous glands present at males at precloacal position and 2–3 scale wide stripe at abdominal position.

It exhibits very bright colouration and sometimes in life shows a reddish tinge. It is yellowish brown with bright yellow vertebral blotches and a banded pattern on tail.

**Distribution.** Jordan, Saudi Arabia, Northern Sinai and southern Israel.

**Stellagama stellio cypriaca (Daan, 1967)**


**Diagnosis.** Head only slightly depressed with swollen cheeks; vertebral scales heterogeneous, irregular, keeled, larger than other dorsal scales, mid-vertebral scales moderately large and sometimes interrupted by transverse rows of highly enlarged mucronate scales; tail at least one and half times the distance of snout fold and cloaca; fingers and toes compressed, 17–21 (18.8 ± 1.3) lamellae under 3rd finger and 20–27 (24.2 ± 1.6) under 4th toe. Tail almost rounded; each tail segment consists of two whorls of enlarged mucronate scales which change into three in the distal half; 20–26 (23 ± 2.0) scales in first complete whorl around the tail. Callous glands present in males at precloacal and also at abdominal position, number of rows at precloacal position 3–5. A very narrow, 2–3 scales wide patch on abdomen. Head ash grey; gular also grey, rarely with few black scales or faded pattern; belly pale yellow but may be speckled; yellow vertebral blotches hardly visible in grown specimens but may be visible in juveniles, generally space between transverse enlarged scale rows filled with black, otherwise grey; enlarged transverse vertebral scales and other groups of enlarged scales light; tail light in proximal half and cross-banded distally.

**Distribution.** Endemic to Cyprus.

**Habitat.** According to Baier et al. (2009) a variety of dry habitats like stone walls, rocks, walls of old houses or on trees.

**Stellagama stellio daani (Beutler & Frör, 1980)**

Diagnosis. Larger size than other subspecies; head
and body moderately depressed, head dorsally col-
oured like back or darker, not distinctly coloured
from back; back with usually 4 – 5 yellowish verte-
bral blotches on dark grey ground color, belly whit-
ish, throat whitish ground colour, spotted dark usually
over half of the area; vertebral scales heterogeneous,
irregular, keeled, larger than other small dorsals, mid-
vertebral moderately large and interrupted at regular
intervals by transverse series of highly enlarged mu-
cronate scales; 3 – 5 rows of precoacal callous glands
with more than 30 scales; tail segment of two whorls,
tail length about one and half times the distance of
snout-vent.

Description. Head and body moderately depressed;
snout longer than the distance between eye-tymanum
or eye width and more than twice that of tympanum
diameter; tymanum exposed, more than half of eye
width; nostril pierced below canthus rostralis, less
than half of nasal scale in size, touching rostral; no
gular pouch, gular plicate; upper head scales heteroge-
neous, subequal, smooth or carinated; gular scales het-
erogenous, mucronate to spinose; groups of spinose
scales present on the neck and sides of head especially
around tymanum, in groups; narrow vertebral zone of
enlarged scales in up to six rows, vertebral scales het-
erogenous, irregular, keeled, larger than other dorsal
scales, mid-vertebral moderately large and interrupted
at regular intervals by transverse rows of enlarged
mucronate scales, these rows are interrupted by 5 to 6
rows of granular scales; ventral scales smooth, smaller
than vertebral and flank scales; limbs strong, covered
with enlarged mucronate scales, hind-limb slightly
longer than distance between gular fold and cloaca;
fingers and toes compressed, lamellae 16 – 23 (19.7)
under fourth toe; tail moderately depressed, oval in
cross section; each tail segment consists of two whorls
of enlarged mucronate scales; callous glands present
in males at precoacal and also at abdominal position,
number of rows at precoacal position 3 – 5.

Colouration characterized as head coloured dark
grey to black and not distinct in colouration from back;
gular spotted or speckled with black, usually over half
the area; belly whitish and pale speckled; 4 – 5 yellow
vertebral bloches on dark background, white spots on
the flanks; tail whitish below, dark grey and and yel-
low bandes above.

Taxonomy. The status of Stellagama s. daani was un-
clear, because of doubts presented by BAG (1992), but
the study of AMOG et al. (2005) clearly shows signifi-
cant differences in morphology between this subspe-
cies and the nominate form. Also the different coloura-
tion of the head, in comparison to S. stellio, indicates
at least a subspecific differentiation.

Distribution. Central Macadonia, central Cyclades,
Saloniki, islands in the Aegean Sea and Turkey.

Studies by BUTLER & FRÖR (1980) and AMOG et
al. (2005) were uncertain concerning this range
boundary. AMOG et al. (2005), BARAN & ÖZ (1985), BARAN
& ATATÜR (1998) and GÖÇMEN et al. (2003) accepted
the occurrence of this subspecies in western Anatolia
but assigned the population of south-eastern Anatolian
cost to S. s. stellio. However, because they did not
report the typical yellow to red head colouration of the
nominate form and because AMOG et al. (2005) did
not find significant differences between these popula-
tions and S. s. daani, the status of these populations
remains open. The eastern boundary of the range re-
 mains open.

Habitat. According to FRANZEN et al. (2008) exposed
rocks, walls or screes from coastal to montane areas.

Stellagama stellio picea (PARKER, 1935)

1935: 137; pl. 1. Type locality: "Black Lava Desert
of Transjordania (32° 10' N × 36° 40' E)."

Diagnosis. Smaller size than other subspecies; head
and body much depressed; colour black; vertebral
scales heterogeneous, irregular, keeled, larger than other
small dorsals, mid-vertebral moderately large
and interrupted at regular intervals by transverse rows
of enlarged mucronate scales; tail segment of two
scale whorls , tail length about 20% more than the
distance of snout-vent.

Description. Head and body much depressed; snout
longer than the distance eye-tymanum or eye width
and about twice that of tymanum diameter; ty-
panum exposed, almost equal to eye width; nostril
pierced on edge of canthus rostralis, less than half of
nasal scale in size, directed outward and backward;
no gular pouch, gular plicate; upper head scales het-
erogeneous, subequal, mostly carinated; upper labials
10 – 15 (12 ± 2.1) and lower 12 – 13 (13 ± 1.0); groups
of spinose scales present on the neck and sides of head
especially around tymanum, in groups; narrow ver-
tebral zone of enlarged scales, vertebral scales heter-
ogeneous, irregular, keeled, larger than other small dor-
sals, mid-vertebral moderately large and interrupted
at regular intervals by transverse rows of highly enlarged
mucronate scales, transverse rows therselfs may not
be regular; no true patch of enlarged mucronate scales
on flanks but these scales are randomly present over
the sides of body, sometimes in groups; other small
dorsals distinctly smaller than enlarged ones; ventral
scales smooth, smaller than enlarged vertebral & flank scales; gular scales very small, spinose; total number of scales around midbody 184–194 (190 ± 3.9); limbs strong, covered with enlarged mucronate scales, hind-limb slightly longer than the distance between gular fold and cloaca; fingers and toes compressed, 15 lamellae under 3rd finger and 18–21 (19.8 ± 1.3) under 4th toe. Tail very depressed, oval in cross section; tail segment distinct, each segment consists of two whorls of enlarged mucronate scales; 21–27 (24 ± 3.0) scales in first complete whorl around the tail; 5 rows of callous glands present in males at precloacal and a narrow stripe at abdominal position.

Males jet black above with traces of yellowish spots on some dorsal scales, on the toes and on the back; chin and throat black, other lower parts brownish grey. Females are also black with yellow spots on head and body, those on the body are arranged in rather irregular transverse rows; tail banded in both sexes, anterior one or two bands are broken; gular reticulate; belly yellow speckled with black.

**Distribution.** Black Lava Desert of Jordan, Syria and Saudi Arabia.

**Stellagama stellio salehi (Werner, 2006)**


**Diagnosis.** Broad band of enlarged vertebral scales, body scales heterogenous, tail segment of two scale rows. Differs from the similar *S. s. vulgaris* as follows: band of somewhat enlarged vertebral scales with transverse rows of greatly enlarged scales, separated by smaller scales, enlarged scales on the left and right side: longer toes with an average of 18.5 subdigitalia; dorsal colouration with light markings forming numerous narrow transverse bars. This taxon differs from *Stellagama s. vulgaris* in having dorsal enlarged scales over the pelvis juxtaposed in transverse rows.

**Description.** Head moderately heavy, less depressed; snout longer than the distance eye-tympanum or eye width; tympanum exposed, more than half of eye width; nostril pierced below canthus rostralis, equal or less than half of the size of the nasal scale, touching rostral or sometimes interrupted by one scale; no true gular pouch but occasionally show some tendency, especially in males; gular strongly plicate; upper head scales heterogeneous, subequal, usually smooth above but may be rugose posteriorly; labials 9–13 (11.6 ± 0.91); groups of spinose scales present on the neck and sides of head especially around tympanum; vertebral zone of enlarged scales, vertebral scales heterogeneous, irregular, usually smooth or weakly keeled, larger than other small dorsals, 16–19 transverse rows of enlarged mucronate scales between axilla and groin; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral; gular scales mucronate or spinose; limbs very strong, covered with enlarged mucronate scales, hind-limb slightly longer than the distance between gular fold and cloaca; fingers and toes compressed, 16–23 lamellae under 4th toe. Tail moderately depressed, oval in cross section; distinct tail segment, each consists of 2 whorls of enlarged mucronate scales but may be mixed with a third in the terminal part of the tail; 3–5 rows of callous glands with 25–60 femoral pores present in males at precloacal.

Ground-coloured grey, mid-dorsal enlarged scales orange, remaining enlarged scales metallic bluish grey, clusters of tubercles at the flanks cream-yellow, earhole and eye framed orange, hindlimbs and tail cross-banded yellow. Females lacking the bluish component of the enlarged dorsal scales.

**Distribution.** Southern Sinai and southernmost Israel.

**Remarks.** This recently described subspecies was recognized by biometric studies of the hardun in the Sinai and Negev deserts. The results indicated that the Sinai population differs from other populations and it was thus described as a new subspecies by Werner (in Lachmann et al. 2006). This distinction coincides with biogeographic breaks in other taxa, such as Mesalina bahaezini, Eirenis coronella ibrahimi and Hemidactylus mindiae.

**Stellagama stellio stellio (Linnaeus, 1758)**


**Diagnosis.** Head moderately depressed; vertebral scales heterogeneous, irregular, keeled, larger than
other small dorsals, mid-vertebral moderately large and interrupted at regular intervals by a series of transverse highly enlarged mucronate scales (this pattern is almost unique among all populations of *S. stellio*, as usually the vertebral band interrupts the transverse rows tubercles); tail segment of two whorls, tail length about one and half times the distance of snout-vent; colouration highly variable (usually 4–5 yellowish vertebral bloches on dark grey ground color); 3–5 rows of precloacal callous glands and small stripe at abdomen in males. Males possessing yellow to red heads during nuptial conditions.

**Description.** Head and body moderately depressed; snout longer than the distance eye-tympanum or eye width and more than twice that of tympanum diameter; tympanum exposed, more than half of eye width; nostril pierced below canthus rostralis, less than half of nasal in size, touching rostral; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, smooth or carinated; labials 10–13 (11±0.8); groups of spinose scales present on the neck and sides of head especially around tympanum, in groups; narrow vertebral zone of enlarged scales, vertebral scales heterogeneous, irregular, keeled, larger than other small dorsals, mid-vertebral moderately large and interrupted at regular intervals by transverse rows of highly enlarged mucronate scales; no true patch of enlarged mucronate scales on flanks but these scales are randomly present over the sides of body, sometimes in groups; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral & flank scales; gular scales keeled, mucronate or spinose, those in the middle slightly enlarged; total number of scales around midbody 122–190 (148.5±15.6); heterogeneous vertebral zone and groups of enlarged scales on lateral sides present difficulties in counting; limbs strong, covered with enlarged mucronate scales, hind-limb little longer than distance between gular fold and cloaca; fingers and toes compressed, lamellae 13–18 (15.5±1.1) under 3rd finger and 18–25 (20.5±1.6) under 4th toe. Tail moderately depressed, oval in cross section; each tail segment consists of two whorls of enlarged mucronate scales; 22–28 (25±1.7) scales in first complete whorl around the tail; callous glands present in males at precloacal and also at abdominal position, number of rows at precloacal position 3–5 and very thin, 2–3 scales wide patch on abdomen. A wide variation of colour combinations, sometimes because physiological color change, is presently associated with the nominate form and future studies are required to reach any conclusions. However, the subspecies may be characterized, in preserved state, as head pale yellow to brownish grey; gular may or may not spotted or speckled with black; belly pale yellow but may be speckled; 4–5 yellow vertebral bloches on dark background, enlarged transverse dorsal rows and other groups of enlarged scales usually yellow; tail light in proximal half and cross-banded distally. During breeding time or while defending territories the males possess typical yellow to red heads.

**Distribution.** Greece, several islands of Cyclades, Turkey, Syria, Lebanon, Israel (excluding southern part) and western mountain regions in Jordan.

**Habitat.** Clark et al. (1973), in their herpetological studies of Turkey, said that it is an inhabitant of rocky places, either natural or artificial (stone walls, bridge parapets, ancient buildings). However, they also observed them in a few unusual habitats: around holes in an earth ditch by the roadside, the base of bushes, and even more surprisingly between Gazipasa and Anamur several of them were seen up in olive trees in a field.

**Stellagama stellio vulgaris** (Soninni & Latreille, 1802)


**Diagnosis.** Medium size; head and body depressed; dull brown color, vertebral bloches broken and indistinct; vertebral band of enlarged scales narrow; tail segment of two whorls.

**Description.** Head and body depressed; snout longer than the distance eye-tympanum or eye width and at least twice that of tympanum diameter; tympanum exposed, almost equal to eye width; nostril pierced below canthus rostralis, less than half of the size of the nasal scale, directing backward; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, smooth or carinated; upper labials 9–11 (10±0.6) and lower 10–12 (11±1.0); groups of spinose scales present on the neck and sides of head especially around tympanum; narrow vertebral zone, vertebral scales heterogeneous, irregular, keeled, larger than other dorsal scales, mid-vertebral moderately large having highly loose transverse series of enlarged mucronate scales, deviating from usual *S. stellio* patterns; no true patch of enlarged mucronate scales on flanks but a few groups or small series of enlarged mucronate scales are randomly present over the sides of body; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral; gular scales very small, spinose; total number of scales around midbody 150–168 (161±6.0); limbs moder-
ately strong, covered with enlarged mucronate scales, hind-limb slightly longer than the distance between gular fold and cloaca; fingers and toes compressed, 15–19 (17.3±1.1) lamellae under 3rd finger and 21–24 (22.7±1.0) under 4th toe. Tail depressed, oval in cross section; tail segment distinct, each segment consists of two whorls of enlarged mucronate scales, in distal half changes in to three on dorsal side but two remain ventrally; 24–28 (26±2.0) scales in first complete whorl around thwe tail; 2–3 rows of callous glands present in males at precloacal and a small stripe at abdominal position.

Colour dull brownish grey, pattern of vertebral blotches is present in juveniles but in adults it mostly fades away and may be represented by some broken, irregular whitish spots; gular region dark grey with yellow ocelli which are more concentrated near tip or below the labials; belly yellowish brown and may be spotted.

Distribution. Northeast Egypt, in and around Alexandria and Cairo, and probably coastal Sinai.

Remarks. This Levantine lizard is referred to as the Starred agama by Flower (1933) and is identified as “Hardum” in Egypt. Among all Laudakia in the old sense this is the first to be described by herpetologists.

**Paralaudakia gen. n.**

Type species. *Stellio caucasius* Eichwald, 1831

**Diagnosis.** Tail arranged in distinct whorles of usually three, only sometimes two or four scale annuli. Gular scales smooth. Vertebral scales larger than other dorsal scales, body scales heterogeneous, irregular and keeled. Tail length about two times of the snout-vent length or longer.

**Etymology.** The chosen name refers to *Laudakia* (as allusion of the formerly used name of the genus) and *para* [greek for ‘next to’] (to show the relation between the two genera).

**Paralaudakia caucasia** (Eichwald, 1831)

1814 *Lacerta muricata Pallas* (non *Lacerta muricata Shaw*, 1801 = *Amphibolurus muricatus*), Zoog. Rosso-asiat 3: 20, plate 4 fig. 1. Type locality: “in deserto Mogano.”


**Diagnosis.** Medium to large size; head and body depressed; olivaceous above with black rimmed yellow ocelli; vertebral enlarged scales keeled; flanks with enlarged mucronate scales; tail segment of two; callous glands present.

**Description.** Head and body depressed; snout longer than the distance between eye-tympanum or eye width and more than twice that of tympanum diameter; tympanum exposed, more than half of eye width; nostril pierced below canthus rostralis, equal or more than half of nasal, separated by 2–4 scales from rostral, directing backward; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, usually carinated, on posterior margin mucronate; labials 10–16 (13±1–0); groups of spinose scales present on the neck and sides of head especially around tympanum, post-auricle patch usually larger than the others; vertebral scales irregular, but sometimes constitute oblique rows, usually keeled, larger than other small dorsals; small patch of enlarged mucronate scales on flanks; groups of enlarged scales which may be spinose present on the sides of body; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral; gular scales small, smooth; total number of scales around midbody 112–160 (138±11.8; population of Turkey lie on the lower range); limbs strong, covered with enlarged mucronate scales, hind-limb slightly longer than the distance between gular fold and cloaca in males but in females this may be shorter; fingers and toes compressed, lamellae 13–20 (15.8±1.5) under 3rd finger and 18–26 (21.1±1.7) under 4th toe. Tail depressed, oval in cross section; tail segment distinct, each segment consisting of two whorls of enlarged mucronate scales; 22–32 (28±3.0) scales in first complete whorl around the tail; 4–5 rows of callous glands present in males at precloacal and large patch at abdominal position, not represented in females.

Colour yellowish brown above, vertebral zone usually yellow, sometimes with distinct lateral exten-
Fig. 5. *P. microlepis*: both from Khorasan Province, near Birjand, Iran. *P. lehmanni*: both from Feyzabad, Afghanistan. *P. s. stoliczkana*: left from southwestern Mongolia; right from south of Bayan-Khongor aimal, Mongolia. *P. caucasia*: both from Khosrov Nature Reserve, Armenia.
sion; yellow ocelli or transversely expanded yellow spots with black border on the lateral sides of body with black specklings, pattern of yellow ocelli or spots sometime not distinct and black spots form a network; gular region reticulated but not necessarily extensively and in some cases only few bars can be observed mainly towards tip; belly pale yellow and sometimes with black spots, breeding males have bluish grey wash ventrally.

**Taxonomy.** Annanjeva & Orlova (1979) compared different populations of *P. caucasia* using several morphological characteristics and suggested a splitting of the species into eastern and western groups. Unfortunately, they did not include a population from Tadjikistan in their comparison. However, they identified two populations from Turkmenia where one is comparatively longer and with higher scale counts as the other one. Later, Annanjeva & Ataev (1984) described a new subspecies as *Stellio caucasius triangularis* from Turkmenia and distinguished it from the nominate form by the forementioned characters and in addition by up to three whorls per tail segment. Bagh (1992) placed this subspecies to *P. microlepis*, because of the higher scale counts (a diagnostic character of *P. microlepis*) and the relatively larger size in comparison to *P. caucasia*. Nevertheless, he (Bagh 1992) also noted that further studies and molecular analysis are required to support this taxonomic conclusion. And later, Macev et al. (1998) recognized *P. microlepis* and *P. caucasia* as different evolutionary lines. Annanjeva & Kalyabina-Hauf (2006) analysed the relationships between *P. caucasia* and *P. microlepis* on the basis of molecular and morphological data and placed the subspecies *triangularis* in synonymy of *P. caucasia*. However, we suggest that the aforementioned population of Turkmenia with long body length and high scale counts together with the subspecies described by Annanjeva & Ataev (1984) should be both included in *P. microlepis*.

**Distribution.** Transcaucasia, Turkey, northern Iran, northern Afghanistan, Turkmenia, Uzbekistan, and Tadjikistan. Khan (2002) also recognized the species from Waziristan and northern Baluchistan in Pakistan. Southern parts of Iran, Pakistan and Afghanistan are occupied by *P. microlepis*.

Because of its wide range, *P. caucasia* is probably the most studied taxon among its genus. Nikolsky (1915), with reference to previous publications and museums records, mentioned several localities including Transcaucopian Territory, Baku, Tbilisi, Kirovabad, Araks, Sevan Lake, Lenkoran, Khurasan and Kopet Dagh. Annanjeva & Orlova (1979) thoroughly reviewed this species and added two new territorial records, the Black Sea coast of Caucasus and southern Tadjikistan. Smith (1935) and Terentev & Chernov (1949) also expanded its distribution range. They included NE-Turkey, almost all of Iran, Afghanistan, Pakistan, the mountains of southern Turkmenia, southern Uzbekistan, and southern Tadjikistan in addition to the Caucasus Mountains and the Transcaspian territory.

Clark et al. (1969) identified some Afghan specimens with very high scale counts and showed their concern about *S. microlepis*. Even later, Clark (1990) casted doubts about some specimens from north of Hindu Kush. Bagh (1992) also studied several specimens from Afghanistan and was convinced that both *P. caucasia* and *P. microlepis* exist there. However, it has yet to be determined whether they live in true sympatry or if they inhabit separate biotops in the same locality. Unfortunately, no specimens of *P. caucasia* or *P. microlepis* from Tadjikistan were represented in the study made by Bagh (1992) and also Annanjeva & Orlova (1979) did not give any detailed account of these populations. It appears that *P. caucasia* and *P. microlepis* are sympatric in some parts of Turkmenia and northeastern Afghanistan. This is one of the reasons not to consider them as taxa of the same species, despite the fact that they share some common characteristics.

**Habitat.** The Caucasian agama lives on rocks, screes, and clay slopes up to 3000 m elevation (Terentev & Chernov 1949). Clark & Clark (1973) also confirmed its existence in mountain habitats and its absence from open plains. They further stated that it is so habitat specific that the exact limit of its range could be accurately predicted with the change of habitat.

**Remarks.** The lizards are known to hibernate in large groups of several hundred individuals. They mainly feed on insects when they are abundant in spring and early summer, but in autumn they switch to feeding more on vegetation (Nikolsky 1915).

The recent study on the *P. caucasia* complex made by Panov & Zakova (1995) and an earlier work by Panov et al. (1987) present an intriguing hypothesis. They believe that the northerly distributed *P. caucasia* and the southerly distributed *P. microlepis* have reached the species level of divergence. In the zones of secondary contact interbreeding takes place among them. They identified different population groups in this area and believed that populations from lower Sumbar Valley and Meshad Sands were of hybrid origin. They also observed a high level of divergence among different populations of *P. caucasia*.

Growth pattern of the Caucasian agama has been studied by Zakova & Panov (1991). They determined the age of individuals with sizes up to 92 mm with the accuracy of up to one year, those with sizes of up
to 116 mm to two years and the bigger ones with the accuracy of up to three years or more. They believe the lizards continue growing during their whole life which may be 12–13 years. Panov & Zakova (1995) studied also the social organization and demography in this agama. They found that populations were stable with low turnover. They attribute delayed reproduction, longevity and a sedentary life style as the most plausible explanations for this observation. Older age classes dominated the age structure of all the subpopulations studied. They further mentioned that it is a good example of lizards practicing a K-strategy.

**Paralaudakia erythrogaster (Nikolsky, 1896)**


**Diagnosis.** Head and body depressed; olivaceous with irregular black spots; scales on the body and tail with strong ridges and spines, even ventral scales may be carinated; several scattered enlarged mucronate scales may constitute a patch on flanks; dorsolateral-fold marked with groups of enlarged spinose scales; tail segment distinct, each segment consists of two whorls of enlarged mucronate scales; 24–29 (27±2.0) scales in first complete whorl around the tail; 3–5 rows of callous glands present in males at precloacal and large patch at abdominal position, also represented in females (not always) but only at precloacal position.

Colour pale brown above with irregular dark brown scales which are sometimes arranged in transverse series; head yellow and may be speckled with black; transverse stripes on the upper parts of legs and tail; under parts yellow, gular may show black marmoreal pattern but breeding males may be almost black ventrally; in life displays orange shade ventrally.

**Taxonomy.** Tuniyev et al. (1991) described the subspecies *P. erythrogaster nurgeldievi* but its validity was questionable and it is herein placed in the synonymy of the nominate form. The description is based on morphological differences, but Macey et al. (1998) did not found any considerable differences using mtDNA and also recognized it as synonym. The nomen ‘gaster’ is a noun and not flexible. Therefore, the name ‘erythrogaster’ stays as masculine noun also with feminine *Laudakia*.

**Distribution.** Northeastern Iran, mainly around Mashhad, some parts of Turkmenia and Afghanistan. In Turkmenistan the species is recognized from Badkhyz and Karabil in the south of the Tejen-Murgab rivers interstream area as well as in eastern Kopet Dag. Its supposed subspecies (see taxonomy) was known only from eastern Kopetdag. Clark (1991) reported *P. erythrogaster* from Torbat-i-Jam (el. 1120 m) and an area about 60 km S.E. of Mashhad (1380 m) in Iran. Previously it was thought that it is restricted to northeastern Iran and southeastern Turkmenia at an elevation of 1000–1700 m, but reports by Anderson & Leviton (1969), Clark (1991) and Baig (1992) indicate its presence also in Paktaia and Paghman of eastern Afghanistan. The elevation records of Anderson & Leviton (1969) have expanded the vertical range of this species up to 2440 m.
Habitat. Contrary to other *Paralaudakia* it lives in clay and sandy-loamy soils, mainly in areas with colonies of *Rhombyomys Wagner*, 1841 (Rodentia: Muridae), and it avoids vertical slopes (Terent’ev & Chernov 1949). Clark et al. (1966) found them on man made rock piles in Iran, but Clark (1991) characterized the habitat as deep holes and crevices in earth banks, cliffs, and piles of stones.

Remarks. Terent’ev & Chernov (1949) and Ananjeva et al. (1998) mentioned that *P. erythrogaster* uses rodent burrows as hideouts and feeds on insects, mainly beetles and caterpillars, and plants. Anderson & Leviton (1969) examined stomach contents of this species and found no plant material.

*Paralaudakia (himalayana) badakshana* (Anderson & Leviton, 1969)

1969 Agama badakshana Anderson & Leviton, Proc. Calif. Acad. Sci., 4th ser. 37: 33; Fig. 6, 7. Holotype: FMNH 161108. Type locality: “Mazar-i-Sharif; northern Afghanistan, 36°34’N, 67°05’E; elevation 457 m.”

Diagnosis. Head and body depressed; tail not more than twice that of SVL; distinct patch of highly spinose scales on flanks and several groups of spinose scales on neck, shoulder and sides of head; three whorls of enlarged spinose scales in each segment; callous glands in both sexes.

Description. Head and body depressed; snout longer than the distance between eye-tympanum or eye width; tympanum exposed, slightly less than eye width; nostril below canthus rostralis, less than half of nasal, pointing backward, separated usually by one scale from rostral; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, flat, obtusely carinated on tip and low spinose at posterior border; labials 10–13; groups of spinose scales present on the neck, shoulders and sides of head especially around tympanum, preauricular in series otherwise in groups; enlarged vertebral scales flat or keeled, in 8–12 straight or slightly oblique rows converging towards mid vertebral line; distinct patch of enlarged mucronate scales on flanks; other small dorsals distinctly smaller than enlarged vertebral or flank scales; ventral scales smooth, smaller than enlarged vertebral and flank scales but larger than gular and other small dorsal scales; gular scales very small and smooth; skin of lateral sides loose forming a dorsolateral fold; total number of scales around midbody 112–132; limbs strong, covered with enlarged mucronate scales, hindlimb slightly longer than the distance between gular fold and cloaca; fingers and toes compressed 18–19 lamellae under third finger and 23–27 under fourth toe, fourth toe considerably longer than third, extremity of the claw of the latter does not reach the base of the claw of former. Tail depressed, oval in cross section; each tail segment consists of three complete whorls of enlarged (largest of all body scales), spinose scales; 26–32 scales in first complete whorl around the tail; callous glands present in both sexes, in males 3–5 rows at precloacal and a large patch at mid abdominal position, in females up to two rows at precloacal and rarely possess a small patch at abdomen. Head olive or grey with black spots over it; gular grey with or without yellow specks or reticulation; chest and belly pale yellow, in males with grey wash; vertebral stripe usually grey; olive grey above with dark rimmed yellow ocelli, males usually do not show bright and marked pattern; tail with dark spots which sometimes gives the impression of cross bars.

Taxonomy. Anderson & Leviton (1969) described this species from the material collected by the Street Expedition to Afghanistan. Bag (1992) identified it as a distinct taxon but showed his suspicion in believing of a correct type locality (reasons are given under himalayana). We suppose that the types were somehow mislabelled before reaching the authors.


Habitat. Sparse information is available about the habitats of *P. badakshana*, which are reported as dry, steppe, or montane areas along watercourse.

*Paralaudakia (himalayana) bochariensis* (Nikolsky, 1897)


Diagnosis. Head and body depressed; tail longer, two or more than two times that of SVL; patch of strongly mucronate scales on flanks and groups of spinose scales on neck and sides of head; three whorls of en-
larged spinose scales in each segment; callous glands only in males.

**Description.** Head and body depressed; snout longer than distance between eye-tympanum or eye width; tympanum exposed, more than half of eye width; nostril below canthus rostralis, half or less than half of nasal, pointing outward or outward & backward, separated usually by two scales from rostral; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, flat, obtusely carinated on tip and low spinose at posterior border; labials 9–11 (10±1); groups of spinose scales present on the neck and sides of head especially around the tympanum, preauricle in series otherwise in groups; vertebral scales always keeled, distinctly larger than other small dorsals, in 6–8 straight rows; distinct patch of enlarged mucronate scales on flanks; other small dorsals distinctly smaller than enlarged vertebral or flank scales; ventral scales smooth, smaller than enlarged vertebral & flank scales but larger than gular & other small dorsal scales; gular scales very small, smooth; skin of lateral sides lose forming dorsolateral fold; total number of scales around midbody 102–120 (115±5.73); limbs less strong, covered with enlarged mucronate scales, hindlimb slightly longer than distance between gular fold and cloaca; fingers and toes compressed 17–23 (20.1±2.3) lamellae under third finger and 23–30 (26.3±2.37) under the fourth toe, fourth toe longer than third, the extremity of the claw of the latter may reach the base of the claw of former. Tail depressed, oval in cross section; each tail segment consists of 3 complete whorls of enlarged, spinose scales; 22–27 (25±2.0) scales in first complete whorl around the tail; callous glands present in males, 3–5 rows at precloacal and a large patch at mid abdominal position may/ may not present. Head olive brown or grey with dark spots over it; gular reticulated; chest and belly pale yellow, in males contains blue or grey wash; vertebral stripe pale yellow or silver grey, irregular dark spots form festooned band on each side of vertebral line; olive grey or light brown above with dark rimmed yellow ocelli; tail with dark spots which sometimes gives the impression of cross bars.

**Taxonomy.** Ananjeva et al. (1981) described a new species as Agama chernovi from Tadjikistan. They compared the species with *P. himalayana* and *P. badakshanensis* and found several dissimilarities from the mentioned species. Unfortunately, they did not compare their specimens with *Agama isozona*, which was also described from the same area before. An examination of the type specimen of the latter taxon, deposited at the Natural History Museum in Vienna, shows marked differences to *P. himalayana*, to which it was synonymised by Smith (1935). Simultaneously, it has been indisputably observed that *A. chernovi* and *A. isozona* both differ from *P. himalayana*, but they hardly show any dissimilarity with one another. Ananjeva et al. (1981) distinguished *A. chernovi* from *P. himalayana* and *P. badakshanensis* by having a relatively longer tail, always keeled enlarged vertebrae, fewer number of enlarged vertebral rows, and more rows of callous precloacal scales. However, all these have been proved true with respect to *A. isozona*. Type material of *P. bochariensis* was not examined but the description given by Nikolsky (1915) shows several common characteristics similar to *A. isozona* and *A. chernovi*. Moreover, all three (*P. bochariensis*, *A. isozona* and *A. chernovi*) had been described from areas in close proximity to one another. It is therefore, suggested that *A. chernovi* and *A. isozona* should be considered as a junior synonyms of *P. bochariensis*.

**Distribution.** Tadjikistan and Uzbekistan (western side of Pamir).
very small, smooth; skin of lateral sides loose forming
dorsolateral fold; total number of scales around mid-
body 122–166 (132 ± 8.35); limbs less strong, cov-
ered with enlarged mucronate scales, hindlimb little
longer than distance between gular fold and cloaca;
fingers and toes compressed, 16–23 (19.7 ± 1.73) la-
mellae under third finger and 24–32 (27.3 ± 1.93)
under fourth toe, fourth toe considerably longer than
third, extremity of the claw of the latter does not reach
the base of the claw of former. Tail moderately de-
pressed, oval in cross section; each tail segment (in-
distinct) consists of three complete whorls of moder-
ately enlarged spinose scales; 26–43 (35 ± 5.0) scales
in first complete whorl around the tail; caudal glands
present in males only at precloacal position, number of
rows at precloacal position never exceed three.

This species exhibits sexual dimorphism in color
pattern, which is more sharply demarcated in females
as compared to males. Females have silver grey or
olive ground color versus a dull brown or yellowish
brown in males. Head shows dark spots over light
ground; gular reticulated; chest and belly pale yellow
in females and juveniles but is blue or a grey wash in
males; vertebral stripe grey, irregular black spots form
festooned band on each side of vertebral line; olive
grey above with dark rimmed yellow oceli along the
entire vertebral length in females, in males these oceli
are mainly concentrated on neck region; tail with dark
spots which sometimes gives the impression of cross
bars, the banded pattern is usually seen in females or
juveniles. Females are clearly distinguishable from
males by the presence of a red or bright orange collar
region; juveniles have this female pattern.

**Taxonomy.** Together with *P. bohariensis* and *P.
badakshana* this species constitutes a sub-group
within *Paralaudakia* and is being recognized as su-
praspecies complex. The group may be characterized
as small *Paralaudakia* lizards whose SVL rarely ex-
ceeds 90 mm. However, Ananieva et al. (1981) re-
ported the range of *A. chernovi* (recognized as syno-
nym of *P. bohariensis*) as 80–120 mm, but without
presenting information about the measured specimens.
Therefore, Baig (1992) studied several specimens of
*A. chernovi* including a type specimen and none were
found longer than 90.00 mm (with the exception of
ZMB 46603 which was 96.00 mm). There are also
some few specimens of *P. badakshana* from Kabul,
Afghanistan which have a range of 90–92 mm, but all
other examined specimens belonging to this group
were measured with a SVL of 90 mm or below. In par-
cular, *P. himalayana* does not even reach 90 mm and
females are even shorter than males.

**Distribution.** Southern Pamir, Wakhan Corridor in
Afghanistan, mountain ranges of Karakoram, Ladakh
and Himalaya up to Tibet. Khan (2002) documented
the species from Gilgit and Chitral in the remote areas
of northern Pakistan at elevations between 3000 and
3200 m.

All the three forementioned species are distributed
at an elevation range of about 1000–3500 m a.s.l. *Pa-
ralaudakia (himalayana)* himalayana mostly remains
over 2000 m. Baig (1992) showed doubts about the
type locality of *P. badakshana* (Mazir-i-Sharif, NW-
Afghanistan), but however the localities mention-
ed by Anderson & Leviton (1969) for the paratype
series are very likely. The suspicions about Mazir-
i-Sharif as type locality are mainly because i) the
locality is far from the main distribution area of this
group, and ii) the elevation of the area (about 360 m
a.s.l.) is unbelievable for either of *P. badakshana,
P. bohariensis* or *P. himalayana.*

**Habitat.** Baig (1992) collected several specimens of *P.
himalayana* in the northern mountain areas of Pakistan
where cliffs and boulders are avoided. It was found
running on the sandy bank of a river or away from the
riverside among small stones which are used for hid-
ing. The lizards were taking shelter in the crevices of
stone walls along the river or road-side, or underneath
larger stones or slabs of stones. Their larger number
along the watercourse may be related with the avail-
ability of food, otherwise they are not found close to
this habitat.

**Remarks.** The distribution ranges inhabited by the
taxa of the superspecies complex apparently lie
quite close to each other within an intricate system
of mountain ranges. These ranges sometimes attain
heights well above 5000 m a.s.l. Several peaks re-
main under snow throughout most of the year, form-
ing impassable barriers for these lizards and dividing
them into many disjunct populations. It appears that
speciation of this group occurred at Pamir Knot where
Pamir, Karakoram, Hindukush and Himalaya meet
each other. *Paralaudakia himalayana* went into the
eastern side and is presently distributed in southern
Pamir, Wakhan, and mountain ranges of Karakoram,
Ladakh and Himalaya up to Tibet. *P. bohariensis* fol-
lowed a northwestern route and is presently distrib-
uted at different biotops on the western side of Pamir
in Tajikistan and Uzbekistan. The southwestern
side along the Hindukush range was followed by *P.
badakshana* which is now found in Badakshan, Kabul
and Ghazni provinces of Afghanistan.

Ananieva et al. (1981) observed *P. himalayana*
at one locality of Zeravshan mountain range. Baig
(1992) also came across with two specimens (ZFMK
32157–58) from Schador (Tajikistan). All remaining
records from Tajikistan and Uzbekistan do not show
*P. himalayana* in the west or northwest of Pamir. The
nearest record of *P. himalayana* is Sarhad (Wakhan, Afghanistan), south of Pamir. The locality of Schador close to Wakhan makes the presence of *P. himalayana* observed by Ananieva et al. (1981) further west or northwest of Pamir even more doubtful. Except for the aforementioned records, all other records of *P. himalayana*, *P. badakshana* and *P. bochieriensis* (together with *A. izoona* and *A. chernovi*) are allopatric. However, populations of *P. himalayana* in Chitral (Pakistan) represent an intermediary position and show resemblance with *P. badakshana* in some characteristics (e.g. number of scales around the body). We assume that the records of *P. himalayana* from Afghanistan (Anderson & Leviton 1969) might belong to a aforementioned Chitral population. Presence of *P. himalayana* in an unidentified area in Schador, observations regarding the sympatry of *P. himalayana* and *A. chernovi* (Ananieva et al. 1981), and an intermediary population of Chitral do not allow us to consider these three taxa (*P. himalayana*, *P. badakshana* and *P. bochieriensis*) as subspecies. Therefore, we recognize them in a superspecies complex as follows: Paralaudakia (himalayana) himalayana, Paralaudakia (himalayana) bochieriensis, and Paralaudakia (himalayana) badakshana.

**Paralaudakia lehmanni** (Nikolsky, 1896)


1907 Agama borchstewskij Elpatjeewsky & Sabanejew (fide Nikolsky 1915), Zool. Jb. Syst., Jena, 24: 250; pl.18, fig.2. Type locality: “Buchara region.”

**Diagnosis.** Head and body depressed; flower-shaped formation of enlarged scales on anterior side of head; olivaceous with irregular black spots; scales on the body and tail with strong ridges and spines, several vertical rows of highly enlarged spinose scales; no patch on flanks; dorsolateral-fold marked with enlarged spinose scales with distinct high ridges; tail segment of three; callous glands present.

**Description.** Head and body depressed; snout longer than the distance between eye-tympanum or eye width and more than twice that of tympanum diameter; tympanum exposed, deep, more than half of eye width; nostril pierced below canthus rostralis and cannot be viewed dorsally, equal or more than half of nasal, separated by 1–2 scales from rostral, directing backward; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, usually carinated except sub-
previously published record from Afghanistan, however they reported the presence of this species from Mazar-i-Sharif (Afghanistan) at an elevation of 457 m. The material studied by BAIG (1992) shows its presence in Badakshan (NE-Afghanistan) from an elevation of 1600 m.

**Habitat.** According to TERENT’EY & CHERNOV (1949) and ANANIEVA et al. (1998) it is a mountain lizard, present at an altitude up to 2600 m above sea level. It can be found on rocks and stones of steeples, slopes of canyons, and on more or less gentle slopes covered with coarse disintegrated rock formations. Additionally, sometimes near mountain rivers and creeks. In some places they have also been found near mountains in loessy hills. The space underneath or between stones, or the fissures in rocks or slopes serve as their hideouts.

**Remarks.** Eggs were laid not earlier than end of June, or the first half of July. One female lays two to three eggs. Eggs were laid not earlier than end of June, or the first half of July. One female lays two to three eggs. Eggs were laid not earlier than end of June, or the first half of July. One female lays two to three eggs.

**Paralaudakia microlepis** (BLanford, 1874)


**Diagnosis.** Size relatively large; head and body depressed; olivaceous or bluish grey with yellow ocelli; vertebral enlarged scales smooth or feebly keeled; flanks with or without any enlarged mucronate scales; body scales very small; tail segment of two whorls; callous glands present in both sexes.

**Description.** Head and body depressed; snout longer than the distance between eye-tymanum or eye width and more than two times that of tymanum diameter; tymanum exposed, more than half of eye width; nostril pierced below canthus rostralis, equal or less than half of nasal, separated by 1–2 scales from rostral, directing outward; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, mostly smooth, on posterior margin mucronate; upper labials 12–16 (13±0.9), lower labials 12–17 (14±1.0); groups of low spinose scales present on the neck and sides of head especially around tymanum; vertebral scales usually smooth or weakly keeled, moderately enlarged and usually constitute a narrow band with or without lateral extensions; enlarged mucronate scales on flanks totally absent or a few vertical series may present; groups of enlarged scales marked with yellow may be present on the sides of body; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral; gular scales small, smooth; total number of scales around midbody 150–212 (180±19.7); limbs strong, covered with enlarged mucronate scales, hind-limb about equal to the distance between gular fold and cloaca or may be even shorter in both the sexes; fingers and toes compressed, lamellae 13–20 (16.1±1.6) under 3rd finger and 18–23 (21.3±1.28) under 4th toe. Tail depressed, oval in cross section; tail segment distinct, each segment consists of two whorls of enlarged mucronate scales; 26–33 (30±2.0) scales in first complete whorl around the tail; 3–5 rows of callous glands present in males at precloacal and large patch at abdominal position, also represented in females (but not always) at both precloacal and abdominal positions (may be as large as in males).

Colour is highly variable in different populations. Generally olivaceous above with vertebral zone usually yellow, sometimes with distinct lateral extension and yellow ocelli or transversely expanded yellow spots with black border similar to *P. caucasia* but some of Afghan specimens are bluish grey with yellow ocelli or spots usually distinct in upper half; gular region may be reticulated; belly pale yellow and may sometimes have black spots; under parts of forementioned grey Afghan specimens were also grey with some yellow blotches on the throat.

**Distribution.** Southern Iran, southern & western Pakistan, Afghanistan and some parts of Turkmenia.

ANDERSON (1974) thought that *P. microlepis* is a distinct population of *P. caucasia* only and assigned a subspecific status. The same author also expanded the range from the type locality to central and south eastern parts of Iran up to Afghanistan and Baluchistan. MINTON (1966) and MERTENS (1969) studied the herpetology of Pakistan and were unable to find *P. microlepis*. They identified the Pakistani population as *P. caucasia*, which is contrary to BAIG (1992) later. Although most of the material from Pakistan which is included in BAIG (1992) was identified as *P. microlepis*. However, some records show that *P. caucasia* is present in northwestern Pakistan, while Baluchistan and southern parts of the country are occupied by *P. microlepis*. BAIG (1992) has extended the range of *P. microlepis* by including some localities in western and
southwestern Pakistan, almost all of Afghanistan (at several places together with *P. caucasia*), and southwestern Turkmenia.

**Remarks.** *Paralaudakia microlepis* was largely neglected or less attended by herpetologists in the past. It was described in 1874 by **Blanford** from southern Iran, north of Shiraz. In subsequent publications it was accordingly mentioned, but records were largely based on the original description, except for **Clark et al.** (1969).

**Panov** et al. (1987) and **Panov & Zykova** (1995) studied populations of rock agamas from Transcaucasia, Middle Asia, Iran and adjacent regions and mentioned that populations (especially in and around SW Turkmenia) showed marked differences. They suspect that some of them are a product of secondary contact between *P. caucasia* and *P. microlepis* because they exhibit hybrid characteristics.

**Paralaudakia stoliczkana altaica** *(MunkhBayar & Shagdarsuren, 1970)*


**Diagnosis.** Differs from the nominate form mainly by having tail segment of 3 whorls; slightly less number of scales around tail and body; scales generally more carinated; relatively shorter hind-limbs; callous glands present in males only at the precloacal position but rarely females also display this character.

**Description.** Head and body depressed, covered generally with small scales; snout longer than the distance between eye-tympanum and by eye width; tympanum exposed, in adults usually half or less than half of eye width; nostril pierced below canthus rostralis, less than half of nasal, separated by 1 or 2 scales from rostral, directing outward and backward; no gular pouch, gular plicate; upper head scales heterogeneous, smooth; labials 10–14 (12 ± 1.0); groups of spineose scales present on the neck and sides of head especially around tympanum; nuchal not marked with rows of enlarged scales; vertebral scales keeled, moderately enlarged arranged in about 12 vertical rows, but may have lateral transverse extensions of enlarged scales; no true patch of enlarged mucronate scales on flanks but sometimes enlarged, spineose scales over there give impression of it; other small dorsals smaller than enlarged vertebral; ventral scales smooth, larger than gular scales; gular scales smooth, those close to gular fold may be mucronate; total number of scales around midbody 130–150 (139±5.0); limbs strong, covered with enlarged mucronate scales, hind-limb usually equal or less than distance between gular fold and cloaca in adults; fingers and toes compressed, lamellae 18–24 (21±2.1) under 3rd finger and 24–30 (27.8±2.2) under 4th toe. Tail moderately depressed, oval in cross section, two, or more than two times the distance between gular fold and cloaca; tail segment distinct; each segment consists of three complete whorls; 30–39 (35±2.0) scales in first complete whorl around the tail; four or five rows of callous glands present in males only at precloacal position, in females apparently absent but some females weakly display callous glands at precloacal position.

The colouration of this form is speckled with black on pale or lemon yellowish ground; head lemon yellow with several black spots; yellowish lateral extensions from vertebral line more distinct in anterior half which itself is darker than posterior part; gular dark grey with yellow spots or reticulated in juveniles; belly pale yellow with black spots; chest dark grey; tail light in proximal part and shows indistinct banded pattern and is dark distally.

**Taxonomy.** In all recent publications **Peters** (1971) is mentioned as author of this subspecies. However, he mentioned himself that **MunkhBayar & Shagdarsuren** (1970) described the same taxon under the same name some months before and therefore, **Peters** (1971) created a primary homonym. The original description by **MunkhBayar & Shagdarsuren** (1970) is based on a holotype (no. 611) and 30 paratypes (fig. 6), all collected in the area of the source of Uliastajn [=Uliastai] River (Khovd district) from 1964–1970 (see below). The holotype (no. 611) was originally deposited at the herpetological laboratory of the “State University for Education of Mongolia”. Later it was transferred to the University of Tashkent in 1970 and is today most probably lost (pers. com. Kh. **MunkhBayar**, March 2011). Moreover, there are two paratypes in the latter mentioned collection, one paratype in the collection of the “Zoological Museum of the Mongolian State University” and three paratypes in the biological collection of “School numer 33”. All remaining paratypes are still at the collection of the “State University for Education of Mongolia”. Currently, one of these
Fig. 6. A–C = paratypes of Paralaudakia stoliczkana altaica (A = no. 1518; B = no. 1516; C = no. 1666); D = living specimens of Paralaudakia stoliczkana altaica from Mongolia: Gobi-Altai aimak. Erdengiin-Nuru mountain range, 1950 m.
paratypes was gratefully donated to the authors by Kh. Munkhbayar and is now present in collection of the Museum Koenig in Bonn (ZFMK 93007). The authors described the holotype as an adult specimen with a SVL of 113mm and a tail length of 181mm. The tail is arranged in whorls of three scale rings each, having 121 scale rings together.

One year later, Munkhbayar (1971) placed altaica as subspecies to P. stoliczkanus. This was in accordance with Peters (1971) who identified the taxa as distinct subspecies, but published his description about a year after the original description. Peters (1971) compared populations of P. stoliczkanus from four different localities of Central Asia and found populations of Gobi-Altai and Mongolian-Altai as different. He distinguished his P. s. altaica by having a shorter tail and hind limb as compared to the nominate form. These characters have been later corroborated by Baig (1992).

Distribution. Mongolian and Gobi Altai area. Munkhbayar (1971) mentioned some detailed localities within the Altai area: Tsagaan Burgas, Shar Khuls, Atas, Ya. Eglon at Altan Uul mountain, at river Bulgan Gol, Uushgiin Ulaan, Aj Bogd, Takhin Shar Khuruu, Atas, Nemegt tost and in the Edren mountains. Munkhbayar & Shagdarsuren (1970) mentioned the river Uliastain in their description. This subspecies not only marks the northern limit of the species, but also the northeastern end of the genus Paralaudakia and extends its range into Mongolia.

Paralaudakia stoliczkanus stoliczkanus
(Blanford, 1875)


Diagnosis. Head and body dorsolaterally depressed; head covered with smooth scales; nostril on edge of canthus rostralis; low spinose scales on the sides of head; vertebral enlarged scales smooth or weakly keeled; no patch of enlarged mucronate scales on flanks; tail segment consists of 4 complete whorls but not marked; callous glands present in males only at precloacal position.

Description. Head and body depressed, covered generally with small scales; snout longer than the distance between eye-tympanum and of eye width; tympanum exposed, more than half of eye width; nostril pierced below or on edge of canthus rostralis, more than half of nasal, separated by 2 scales from rostral, directing outward and backward; no gular pouch, throat plicate; upper head scales heterogeneous, smooth; upper labials 12–14 (13±0.8), lower labials 11–13 (12±1.0); small groups of spineose scales present on the neck and sides of head especially around tympanum; nuchal not marked with rows of enlarged scales; vertebral scales smooth or very weakly keeled, moderately enlarged arranged in about 12 vertical rows; no patch of enlarged mucronate scales on flanks; other small dorsals smaller than enlarged vertebral; ventral scales smooth, larger than gular scales; gular scales smooth; total number of scales around midbody 134–154 (141±6.7); limbs strong, covered with enlarged mucronate scales, hind-limb usually greater than the distance between gular fold and cloaca; fingers and toes compressed, lamellae usually 20–24 (21.4±1.4) under 3rd finger and 28–32 (30±1.57) under 4th toe. Tail moderately depressed, oval in cross section, more than two times the distance between gular fold and cloaca; tail segment feebly distinct; each segment consists of four complete whorls; usually 30–46 (39±6.0) scales in first complete whorl around the tail; 4 or 5 rows of callous glands present in males only at precloacal position.

The colouration of this species is generally similar to P. caucasia. Olive yellow above; head and body speckled with black, may have pale yellow ocelli especially in anterior half; gular yellow or in males grey with yellow spots; belly pale yellow but males have grey wash; tail light in proximal part and may show banded pattern whereas it is dark distally.

Taxonomy. Although this species was described in 1875 from central Asia it has attracted very little attention from herpetologists. Zugmayer (1909) very superficially described a new species as Agama tarimensis from Mongolia and both taxa were mentioned in subsequent literature until 1971. At this time Peters (1971) compared P. stoliczkanus and A. tarimensis and carried out a morphological analysis of the material from Central Asia. He divided the material into four groups according to the different geographical localities viz. Kashgar, East Tien-Shan, Gobi-Altai and Mongolian Altai.

Regarding colouration Peters (1971) found no differences within populations of P. stoliczkanus and A. tarimensis from the western side among the Kashgar and Tien-Shan. However, he did find differences within Mongolian populations which have a dark chin, throat, neck and chest with light spots. Moreover, he noticed that males show a more contrasting pattern by having more melanin as compared to females and secondly, northern Mongolian lizards exhibit more in-
tensive pattern than southern (Kashgar and Tien-Shan) ones. The light ground colour in the lizards has different shades and is rather individual or locality-oriented. The yellowish green spots of *A. tarimensis* mentioned by *Zugmayer* (1909) were not seen by *Peters* (1971). He observed no difference in colour pattern between *P. stoliczkana* and *A. tarimensis*, but found differences in the number of scales at different body parts. However, he attributed these differences to be clinal and suggested *A. tarimensis* as junior synonym of *P. stoliczkana*.

**Distribution.** Mongolia, China (Kashgar, Tien Shan and southern Gobi; see Ananjev et al. 1997).

**Laudakia Gray, 1845**


**Type species.** *Agama tuberculata* HARDWICKE & GRAY, 1827

**Diagnosis.** Head and body depressed; head scales smooth or rugose; no gular pouch; usually no patch of enlarged or spinose scales on flanks (but present in some species); gular scales smooth; ventral scales smooth; vertebral scales enlarged, sometimes with median rows of small scales; groups of spinose scales on neck and sides of head; tail segment of two to four whorls, usually three to four.

**Laudakia agrorensis (Stoliczka, 1872)**


**Diagnosis.** Head scales strongly carinated; tail twice or more than SVL; 8–10 rows of strongly keeled vertebral scales; distinct patch of strongly mucronate scales on flanks; tail segment of three whorls; callous glands present in both sexes.

**Description.** Head very depressed; snout longer than the distance between eye-tymanum; tymanum exposed, diameter less than eye width; nostrils pierced below or on the edge of canthus rostralis, pointing outward and more or less backward, less than half of nasal which touches rostral; upper head scales heterogeneous, subequal, strongly carinated, sometimes with sharply lifted margin; groups of spinose scales present on the sides of the head and neck; nuchal row of small spinose scales (sometimes very weak); supralabials 9–11 (9.8 ± 0.6), infralabials 8–11 (10.0 ± 1); no gular pouch; throat plicate; gular scales small and smooth. Body depressed; skin on lateral sides of body loose, forming a dorsolateral fold; dorsal scales imbricate, strongly keeled or mucronate, 105–130 (117 ± 7.3) around middle of the body; 8–10 rows of enlarged, strongly keeled vertebral scales with sharp lifted margin, median two rows may be of relatively small scales; a distinct patch of enlarged mucronate scales on flanks; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral and flank scales but larger than gular and other small dorsal scales. Limbs moderately strong, hind-limb longer than distance between gular fold and cloaca; fingers and toes long and compressed, 18–24 (22.2 ± 1.59) lamellae under third finger and 26–32 (29.5 ± 1.8) under fourth toe. Tail depressed, oval in cross section, forming very distinct annuli, each tail segment consists of three complete whors; 28–33 (30 ± 2) scales in distal whorl of first proximal segment of the tail, scales on dorsal and lateral sides strongly mucronate. Callous glands present in both sexes, 3–4 rows at precloacal and small patch at mid abdominal position in males and similar patches in females where the number does not go beyond 3 at precloacal position and abdominal patch less often present.

Olive grey, variegated, spotted with yellow, juveniles and young with dark and light longitudinal stripes which may be broken, central light stripe continues on to the tail; throat with dark reticulation; belly yellowish white; tail generally light in proximal half and dark distally and shows light and dark transverse bands especially in young specimens. Rarerly exceeds 100 mm in SVL but never goes beyond 110 mm.

**Distribution.** Northern Punjab and northwestern Frontier Province in Pakistan, Kashmir (at least the part now associated with Pakistan) and Afghanistan.

In Pakistan and Kashmir it occurs in the Lesser Himalayas at a low elevation of approximately 700–1300 m a.s.l. Although there is only one record from Afghanistan, but its presence in Arandu (Chitral, Pakistan) within a mountain range which spread into Afghanistan suggest the presence of the species also in eastern parts of this country. There is an interesting pattern of the vertical distribution together with *L. tuberculata* in Pakistan and Kashmir. In these mountain areas *L. agrorensis* and *L. tuberculata* are distributed...
parallel, with *L. agrorensis* at low (700–1300 m) and *L. tuberculata* at relatively high (1200–2200 m) elevation. These upper and lower limits vary slightly in different areas within their specified ranges, but occasionally they are found in sympatry. *L. agrorensis* may also be found in sympatry with another agamid, *Calotes versicolor* in Pakistan.

**Habitat.** *Laudakia agrorensis* is a mountainous species and occurs in low mountain areas with vegetation cover. Several individuals were found basking or running on rocks, mostly along water streams. Availability of food (insects) is the most probable reason for their presence in that habitat. Instead of single or solitary pairs, large groups of individuals were usually seen. Except the studies of callous glands (Baig & Böhme 1991b) and some morphological comparisons, other aspects of this species are largely unexplored.

**Remarks.** Among the specimens housed in different museums, BMNH 1933.4.1.39 differs from *L. agrorensis* in several characteristics which are diagnostic for *L. pakistanica* and therefore the specimen is re-identified as the latter species.

**Laudakia dayana** (Stoliczka, 1871)


1935 *Agama tuberculata* Smith, Fauna of brit. India including Cylon and Burma. (in part).

**Diagnosis.** Head and body depressed; head scales carinate; patch of enlarged, mucronate scales on flanks, similar scaled scales on body; groups of low spinose scales on neck and sides of head; tail segment of four whorls dorsally becoming three ventrally; callous glands in males, very rarely occurring in females.

**Description.** Head and body depressed; snout more than one and half times that of the distance between eye-tympanum or eye width and more than twice the tympanum diameter; tympanum exposed, more than half of eye width; nostril pierced on or below canthus rostralis, less than half of nasal, pointing outward and backward, touching rostral; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, carinate; upper labials 9–13 (11 ± 1), lower labials 9–11 (10 ± 1.0); groups of low spinose scales present on the neck and sides of head especially around tympanum, preauricle in series otherwise in groups; vertebral scales keeled, larger than other small dorsals, 10–12 oblique rows of strongly keeled scales; patch of enlarged mucronate scales on flanks and similar scales scattered over the sides of body; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral and flank scales but larger than gular and other small dorsal scales; gular scales granular, smooth; skin of lateral sides loose forming a dorsolateral fold; total number of scales around midbody 102–130 (118 ± 8.43); limbs strong, covered with enlarged mucronate scales, hind-limb slightly longer than distance between gular fold and cloaca; fingers and toes compressed, 20–30 (26.5 ± 2.1) lamellae under third finger and 27–37 (34.9 ± 2.2) under 4th toe. Tail depressed, oval in cross section; each tail segment consists of 4 whorls of enlarged mucronate scales with three remaining on the ventral side; 26–33 (29 ± 2.0) scales in first complete whorl around the tail; callous glands present in males at precloacal and also at abdominal position, number of rows at precloacal position 4–6 and an oblong patch on abdomen; very rarely represented in females at precloacal position in three or less rows.

Head pale yellow; gular spotted or speckled with black, males marked with blue, in juveniles reticulated; chest and belly pale yellow but may be speckled with age, males with blue or grey wash; numerous yellow spots on dark slate background, sub-adults have irregular pattern; tail light in proximal half and dark distally, young or juveniles sometimes show faded pattern.

**Taxonomy.** Baig (1992) studied several specimens from different localities, including typematerial of *L. tuberculata*, *L. sacra*, *B. sykesii* and *L. dayana*, and found several dissimilarities among specimens from western mountain ranges. However, on the eastern side of their distribution, up to Sikkim, all material is more or less similar to *L. tuberculata*.

The types of *B. sykesii* are dissimilar. BMNH 1946.8.28.16 from Ladakh belongs to *L. dayana*, whereas BMNH 1946.8.28.60 (without locality) was identified as *L. tuberculata*. The types of *L. dayana* and few more specimens from the same locality are clearly distinct from *L. tuberculata*. They show a strong carination, quite distinct tail segments and patches on the flanks. Therefore, as recognized by Baig (1992), *L. dayana* should be recognized on species level, while *B. sykesii* can partly be identified as *L. tuberculata* and *L. dayana*.

**Distribution.** Ladakh Range (Kashmir), Hardwar, and upper Simla.

In Simla, *L. dayana* occurs at an elevation of 3000 m, while *L. agrorensis*, if allopatrically distributed, occurs at lower elevations of about 1300 m a.s.l.
Nothing is known about the vertical distribution pattern between *L. tuberculata* and *L. dayana* in Kashmir (the part presently under the administrative control of India). Future studies proving allopatric distributions of these two species may identify them as two distinct populations of the same species only, but at the moment both are recognized as full species because of distinct morphological characters.

**Remarks.** In scolation and colour pattern this species also resembles *L. agroensis*, which is relatively smaller, possess three whorls per tail segments and shows a different arrangement of callous glands.

**Laudakia melanura melanura** BLYTH, 1854


**Diagnosis.** Size large; head and body dorsolaterally depressed; nostril on canthus rostralis; spinose scales on the sides of head greatly reduced; vertebral enlarged scales smooth or keeled; no patch of enlarged mucronate scales on flanks; tail long; tail segment inconsistent, starts with 2–3 whorls and gradually changes into 5, sometimes 6 in terminal part; callous glands present in males both at precloacal and abdominal positions.

**Description.** Head and body depressed, triangular when viewed from above; snout longer than the distance between eye-tympanum, about twice eye width; tympanum exposed, large, equal or more than that of eye width; nostril pierced on canthus rostralis, more than half of nasal, separated by two scales from rostral, directing outward; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, usually smooth, those on posterior margin transversely keeled, those on tip sometimes carinated; upper labials 12–15 (14±1.0), lower labials 13–14 (13±1.0); groups of low spinose scales present on the neck and sides of head especially around tympanum; nuchal marked with rows of slightly enlarged scales; vertebral scales smooth or keeled, distinctly enlarged arranged in 8–10 vertical rows; no patch of enlarged mucronate scales on flanks; other small dorsals distinctly smaller than enlarged vertebral; ventral scales smooth, smaller than enlarged vertebral; gular scales about the size of ventrals but distinctly larger than neck scales, smooth; total number of scales around midbody 120–156 (137±13.4); limbs strong, covered with enlarged mucronate scales, hind-limb usually greater than the distance between gular fold and cloaca; fingers and toes compressed, lamellae 17–19 (17.8±1.0) under 3rd finger and 22–27 (24.3±1.8) under 4th toe. Tail moderately depressed, oval in cross section, distally rounded, much longer, usually 2.5 times or greater than the distance between snout to vent; tail segment becomes distinct slightly distal to its origin, not consistent in number of whorls in each segment, 2–3 whorls in each segment but gradually changes into five (sometimes six) in terminal part of tail; mucronate scales in proximal part of tail have very low ridges; 18–28 (21±5.0) scales in first complete whorl around the tail; 4 or 5 rows of callous glands present in males at precloacal and a patch (sometimes small and rounded like *P. nupta* and sometimes broad and rectangular) at abdominal position. Colour of this species is highly variable. Those in Salt Range have light brown head with reddish tinge on posterior side; rest of the body olive brown with several yellow spots all over the body; under parts pale yellow, gular reticulated; tail light brown in proximal half and black in distal half.

Smith (1935) mentioned five specimens collected at Ladha (Waziristan) by Capt. Ingoldby as dark brown all over dorsally. According to Stolickzka (1872) juveniles are olive above, yellowish white below; entire head, including chin and front breast, reticulated with black; neck, body, limbs and base of tail above with numerous small black and interspersed yellow spots; eyelids and supraciliary ridge yellow; tail dusky black toward tip. The adults are more brownish olive, with dark reticulation on the upper head less distinct, the black spots on the body small and more or less confluent, but the yellow spots are more brightly coloured and larger in size; tail pale yellowish at the base but for the greater part of length entirely black. In spring males are more or less jet black, usually on the tail and posterior portion of the back (Blanford 1876). Minton (1966) mentioned that adult males are sooty black above and black to dark grey beneath; adult females dark brownish grey with traces of paler dorsal spots, light grey to dull white tail at the base and underside of thighs; juveniles dusky grey, with faint dorsal spots, belly white, throat mottled with grey. He also observed colour differences among members of the same sex but of different age groups in Ormara (Mekran Coast).

In general this species resembles *L. nupta*, and in some localities of southern Pakistan both of them are found together. However, they are distinguished by several morphological characteristics. *Laudakia* species have a tendency to change the number of whorls in caudal segments from the anterior to posterior region, but the difference never exceeds one whorl and
it usually occurs only on the dorsal part of the tail. Accordingly, this species, because of its inconsistency of tail segments, is unique and distinguishable from all other members of the previously collective genus *Laudakia*. Secondly, the callous abdominal patch is usually oblong or a thin longitudinal stripe in *Paralaudakia* or *Laudakia*, but it is rectangular, much wider than long, in some specimens of *L. melanura* (BMNH 76.10.13.1, 98.6.29.1 and PMNH 368).

**Taxonomy.** Blanford (1876) described *Stellio liratus* from Baluchistan and later BoulenGER (1885) distinguished it from *L. melanura* as having partly keeled head scales, six or seven rows of keeled vertebral scales and by the absence of caudal rings. Smith (1935) synonymized it with *L. melanura* and mentioned specimens with smooth enlarged vertebral scales from the northern range while specimens from the southern part have them more or less keeled. This might be partly true with respect to some ranges, but Baig (1992) examined specimens with keeled enlarged vertebrals (but with very low ridges) and transversely keeled head scales near the nuchal end of head also in the northern part of the range (Salt Range, Pakistan), and smooth vertebral scales in specimens from southern parts of Sind and Baluchistan. Therefore, this is not a consistent character within the species and either habitat or age might have some influence on it. Mertens (1969) again resurrected *L. lirata* as a subspecies of *L. melanura* on the basis of carinated scales and colouration. However, both of these characters are apparently inconsistent and therefore should not be considered as sufficient evidence to split both taxa on subspecies level.

**Distribution.** Mainly in Pakistan (Salt Range in northern Punjab, Waziristan in NW Frontier province and western parts of Sind and Baluchistan provinces), some parts of southeastern Iran and some localities of southeast Afghanistan.

**Habitat.** It inhabits cliff and rocks of low mountain ranges. Smith (1935) found it on rocks and shrubs. In the Salt Range it was found among rocks and on clay vertical slopes around bushes.

**Remarks.** Heidari et al. (2010) comment on the weakly expressed sexual dimorphism in this species (named still *L. m. lirata*) and explain it by the lack of territoriality, i.e. lacking defense of territory and harems. However, as callous abdominal patches of scales are present in both sexes, this species could also belong to those agimid species living in pairs rather than in harems, with females defending their own territories (e.g. *L. pakistamica*, see Bose & Baig 1991b).

Breeding apparently takes place during early spring and the young begin to appear in June (Minton 1966). According to Smith (1935) and Minton (1966), it is herbivorous.

**Laudakia melanura nasiri Baig, 1999**


**Diagnosis.** Medium size, head and body greatly depressed, vertebral scales enlarged, number of scales rows around midbody more than 150, no patch of spinose scales at the flanks, tail segmented, each segment with 2 to 4 rings.

**Description.** Head triangular, snout longer than the distance between eye and tympanum. Nostril on canthus rostralis, directed backward, more than half of nasal. Tympanum exposed, smaller than the eye, small group of spinose scales around tympanum. Upper head scales heterogenous, subequal and smooth. Supralabials range between 12 and 14, infralabials between 12 and 14. Gular pouch absent, gular-fold present. Vertebral scales smooth, enlarged, arranged in 8 rows, remaining dorsals small. No patch of spinose scales at the flanks. Ventral scales smooth, gular scales smaller than ventrals. Total number of scale rows around midbody higher than 150, up to 180. Limbs strong, covered with enlarged mucronate scales, hind-limb length less than the distance between gular fold and cloaca. Tail depressed, tail segments not consistent, vary from two to four rings, distinct only in the middle, pericaudal scales in the first complete whorl 26.

Color is grayish brown with yellow spots all over the body, including head but excluding tail. Under parts yellowish gray with yellow speckling, which are prominent at chest, gular region and chin. Proximal part of the tail yellowish gray, distal dark brown.

**Distribution.** Only known from its type locality (Tanishpa, Dist. Killa Saifullah, Toba Kakar Range, Baluchistan, Pakistan; 31° 12’ N, 68° 28’ E, elevation 2320 m a.s.l.).

**Laudakia nupta fusca** *(Blanford, 1876)*

Diagnosis. Size large; head heavy; nostril on canthus rostralis; body moderately depressed; absence of a nuchal fold across the neck; vertebral enlarged scales strongly mucronate and cover most of dorsal part of body; no patch of enlarged mucronate scales on flanks; tail long and has segments of three whorls; callous glands present mostly in males.

Description. This taxon differs from the nominate form by some slightly expressed characters, and the colouration of adult males. The striking character is the absence (sometimes rudimentary obvious) of the nuchal fold across the neck. It usually has less than 90 scale rows along the midbody, but other characters are often shared by both taxa and only lower or stronger expressed in this subspecies: tufts of spiny scales around the ear and on the sides of the neck large and broad posteriorly; no patch of enlarged mucronate scales on flanks; tail long and has segments of three whorls; callous glands present mostly in males.

Adult males with an entirely carany-yellow head, especially during the breeding season; body, limbs and tail dark brown to black above; belly, underside of legs and tail black sparsly speckled yellowish; callose ventral and precloacal scales amber. Females brown, speckled yellowish; distal part of the tail black. Juveniles more similar to females than to males; with a greyish, yellow body colouration with an irregular pattern of brownish crossbars or reticulated pattern; head black, often with yellow chevrons and yellow spots on the upper head; tail banded with a black tip.

Distribution. The subspecies is only known from southeastern Iran, Pakistan. It was collected in the Baluchistan Province at Kalagan and near Jalk by BLANFORD (1876). MINTON (1966) recognized it from southern and southwestern Pakistan (near Khadeji Falls, 30 miles NE of Karachi; near Diwana on the upper Hab River; southern part of Pab Hills). KHAN & MIRZA (1977) also found it in southwestern Baluchistan. ANDERSON (1999) mentioned a specimen from Binak at the Persian Gulf coast also belonging to L. n. fusca. According to MINTON (1966) the subspecies is known from elevations up to 2000 m a.s.l.

Habitat. A shy and secretive lizard, only found in rocky areas with vertical or nearly vertical surfaces that provide shelter. According to RASTEGAR-POUVANI & NELSON (2002) also the type of vegetation has an effect on the distribution range of the subspecies.

Laudakia nupta nupta (De Flippi, 1843)


Diagnosis. Size large; head heavy; nostril on canthus rostralis; body moderately depressed; yellowish or reddish brown; vertebral enlarged scales strongly keeled and cover most of dorsal part of body; no patch of enlarged mucronate scales on flanks; tail long and has segments of three whorls; callous glands present mostly in males.

Description. Head quite heavy, only moderately depressed, subtriangular when viewed from above; body not too depressed but rather slender; snout longer than the distance between eye-tympanum, about twice that of eye width; tympanum exposed, large, equal or more than that of eye width; nostril pierced on canthus rostralis, more than half of nasal, separated by two scales from rostral, directing outward; neck narrow; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, mostly smooth, on posterior margin rugose; labials 12–17 (15 ± 1.0); groups of highly spinose scales present on neck and sides of head especially around tympanum; vertebral scales strongly keeled, distinctly enlarged and constitute a very broad band of 16–18 scales which cover most parts of the dorsal body and resemble a flask, narrow near neck and broad posteriorly; no patch of enlarged mucronate scales on flanks; other small dorsals distinctly smaller than enlarged vertebral; ventral scales smooth, smaller than enlarged vertebral; gular scales about the size of ventrals, smooth; total number of scales around midbody usually 75–106 (92 ± 9.09); limbs strong, covered with enlarged mucronate scales, hind-limb usually greater than the distance between gular fold and cloaca; fingers and toes compressed, lamellae 15–18 (16.8 ± 0.9) under 3rd finger and 19–24 (21.3 ± 1.5) under 4th toe. Tail moderately depressed, oval in cross section, distally rounded; first tail segment distinct, only little away from pelvic, each segment consists of three whorls of enlarged mucronate scales but occasionally may be four in terminal end; 16–29 (23 ± 3.0) scales in first complete whorl around the tail; 3 or 4 rows of callous glands present in males at precloacal position and a small patch at abdominal position, may be represented in females but very rarely.

Colouration is predominately uniform yellowish, reddish brown or may be speckled; head dark brown or blue in males; tail yellowish brown in proximal half
and black distally; in one specimen Baig (1992) observed entire black tail; under parts yellowish brown and may contain reddish or grey wash.

**Taxonomy.** BLanford (1876) identified two distinct varieties within the species and subsequently BoulenGer (1885) recognized them as races and distinguished the *L. n. fusca* from the nominate form by having longer spinose scales on the sides of the head and neck. Later, Smith (1935) did not find any significant difference between *L. n. nupta*, *L. n. fusca* and *Stellio carinatus* and thus placed all three together under *L. nupta*. Anderson (1963) gave a very good account of this species and said that tufts of long spiny scales on the sides of the head and neck were ontogenetic. He observed the absence of these scales and differences in colour pattern in young specimens. Minton (1966) and Mertens (1969) again resurrected *L. n. fusca* because of the characters already described by Anderson (1963) as age related. Anderson (1974) differentiated both taxa by the absence or presence of a transverse fold across the nape, which was supported by Khan (2002). Although the trinomial status has been adopted by several authors, Baig (1992) recommended the point of view adopted by Smith (1935) and found additional support from the observations made by Anderson (1963). However, Rastegar-Pouriani & Nilson (2002) also found good differences between the taxa and followed authors like Minton (1966) and Mertens (1969). More recently, Cheatsazan et al. (2008) while analysing 16 specimens, including four juvenils, recognized both taxa on species level. Most probably Smith (1935) and Baig (1992) are correct in treating *L. n. fusca* as synonym, but until further research the taxa should be recognized as subspecies. Morphological differences are clearly not distinct enough to recognize them as full species like Cheatsazan et al. (2008) did, but the small differences recognized by Rastegar-Pouriani & Nilson (2002) could indicate an initiating speciation.

**Distribution.** E-Iraq, Iran, Pakistan and Afghanistan.

**Habitat.** This species is abundant in foothill regions, inhabiting rock outcrops with deep crevices. It is common on artificial walls, cement monuments, and buildings (Anderson 1963). Clark et al. (1969) mentioned that adults usually remain on the cliff faces with crefts and large boulders and seldom more than two are found together. Smith (1935) reported its abundance in the mountains of Baluchistan (Pakistan) at an elevation of about 1000 m a.s.l.

**Remarks.** This is an extremely wary species, which retreats quickly into a crevice when alarmed. Observations (particularly of those living near build-

ings) indicate that the area of activity of an individual generally has a radius of less than fifteen meters. The basking area, as indicated by the distribution of fecal pellets, is usually not more than two to three metres (Anderson 1963).

Anderson (1963) noticed shift in the periods of activity from February through the summer. In late February and March individuals were observed only at midday and early afternoon while basking on rocks and exposing maximum surface area to the direct sunlight during air temperatures of about 30 °C. In the afternoon they were raised on their forelegs, facing the sun that the sunlight strikes the head and belly, and the angle of reflection from the surface of the rock exposed them to maximum radiation. Later spring, basking was initiated progressively earlier in the day and continued later into the afternoon. In summer the lizards retired during the hottest hours, and their activity was restricted to the earliest daylight hours and late afternoon in July and August. Additionally, Anderson (1963) measured a cloacal temperature of 27.2 °C of a basking individual during an air temperature of 22.4 °C. The critical maximum temperature in this species was recognized between 43.8–48.5 °C.

Analysis of stomach contents shows both insects (mostly beetles) and plant material. Females containing gravid eggs were collected in March, August and October, indicating that eggs are laid at least in the spring and in the autumn in Iran region (Anderson 1963).

**Laudakia nuristanica** (Anderson & Leviton, 1969)

1969 *Agama nuristanica* Anderson & Leviton, Proc. Calif. Acad. Sci., 4th ser. 37: 39–42; Fig. 8. Type locality: “Kamdesh, eastern Afghanistan, 1342 metres elevation.”

**Diagnosis.** This form is very close to *L. tuberculata* and may be distinguished by having a higher number of scales around the body and tail, indistinct tail segment, and a unique type of scattered, enlarged conical, spinose scales over the limbs and body.

**Description.** Head and body depressed; nostrils roughly round, less than half of nasal, below canthus rostralis, pointing outward and backward; upper head scales heterogeneous, subequal, flat (on posterior parietal region low spinose); upper labials 11–13 (12±0.8) and lower labials 10–12 (11±1.0); groups of spinose scales present on the neck and sides of head especially around the tympanum; vertebral scales keeled, enlarged vertebrals start from postshoulder
level and gradually increase in size from anterior to posterior, 7–9 enlarged keeled scales in transverse row; median two may be relatively small, do not constitute vertical rows; no patch of enlarged mucroneate scales on flanks; scattered, enlarged, conical and spinose scales over body and limbs; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral & flank scales but larger than gular & other small dorsal scales; skin of neck and lateral sides loose forming gular and dorsolateral folds respectively, dorsolateral fold marked with enlarged, strongly mucronate scales at least in posterior half; total number of scales around midbody 216–274 (242 ± 15.8); limbs strong, covered with heterogeneous scales above and flat scales below, hindlimb longer than distance between gular fold and cloaca; fingers and toes compressed 25–32 (28 ± 2.2) lamellae under third finger and 32–39 (35.9 ± 2.8) under fourth toe. Tail depressed, oval in cross section; each tail segment consists of four complete whorls but may not be distinct in the proximal portion; 43–48 (46 ± 2) scales in first complete whorl around the tail; scales on dorsal and lateral sides strongly mucronate but mucrone hardly extends beyond posterior margin of the scale. Callous glands present in males only, six rows at precloacal and a large patch at mid abdominal position.

Colouration is dark grey or brown marblings on pale brown ground colour; vertebral stripe is pale yellow; head dusty brown with dark brown specklings, three supraciliary dark bars; throat brown or silver grey with yellow oceli which are more concentrated near tip; distal part of tail dark while proximally it is pale brown; belly and under parts pale yellow.

**Taxonomy.** The species is very close related to *L. dayana* and *L. tuberculata*. ANDERSON & LEVITON (1969) compared it with material of *L. tuberculata* from Nepal and found several striking dissimilarities. BAIG (1992) suggested that it undoubtedly differs from *L. tuberculata*, but it is more similar in some characters (e.g. number of scales around the body, scattered enlarged scales on flanks, rugose head scales) to western populations as to Nepalese populations of *L. tuberculata*. In tail characters it differs both from *L. tuberculata* and *L. dayana* by having four complete whorls around the tail. The arrangement of the scales over the limbs is unique i.e. enlarged conical scales among other very small scales.

**Distribution.** Eastern Afghanistan and Northwestern Pakistan.

The species was previously known only from Afghanistan, but BAIG (1988a) recognized its presence in the Chitral district of Pakistan. This mountain range streaks from Afghanistan into Pakistan therefore a wider distribution range within in Pakistan is very likely.

**Habitat.** ANDERSON & LEVITON (1969) described the habitat as montane area with conifer and evergreen oak woodlands along watercourse.

**Laudakia pakistanica auffenbergi**

**BAIG & BÖHME, 1996**


**Diagnosis.** This form is very close to the nominate form in certain characteristics but quite distinguished by being dull dark brown to grey in colour with white transverse bands across the body and having a fewer number of scales around the body.

**Description.** Head triangular when viewed from above, depressed; nostrils roughly round, on edge of the canthus rostralis, pointing outward and backward; upper head scales heterogeneous, subequal, flat (on posterior parietal region low spinose); upper and lower labials 11; groups of spinose scales present on the neck and sides of head especially around tympanum, those at subauricle level arranged in two distinct horizontal rows, neck scales are relatively low; vertebral scales mucronate, enlarged vertebrals start from postshoulder level and gradually increase from anterior to posterior, eight rows of mucronate scales, median two rows are of relatively small scales which may overlap; a patch of enlarged, closely arranged and few scattered, mucronate scales on flanks; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral and flank scales but larger than gular and other small dorsal scales; skin of neck and lateral sides loose forming gular and dorsolateral folds respectively, dorsolateral fold marked with enlarged, strongly mucronate scales in posterior half; total number of scales around midbody 152; limbs strong, covered with mucronate above and flat scales below, hindlimb longer than distance between gular fold and cloaca; 22 lamellae under third finger and 30 under fourth toe. Tail depressed, oval in cross section, each tail segment consists of three whorls but the tendency of 4th whorl is evident, approximately from mid of the tail and in distal part changes into four, except on ventral side where it remains of three; 36 scales in first complete whorl around the tail; scales on dorsal and lateral sides strongly mucronate, ven-
tral scales smooth. Callosous glands present, six rows at precloacal and a large oblong patch at mid abdominal position.

Colouration is a dull dark brown (in formalin has changed into dark grey) with distinct white cross bands; head and distal part of tail black; limbs show highly indistinct pattern; gular region bluish black with irregular pale yellow blotches; chest, belly and under parts of limbs pale yellow with thick black reticulation.

**Distribution.** Mansehra Besham and Kohistan districts, Northwestern Frontier Province, Pakistan.

*Laudakia pakistanica* was previously considered to be restricted to a small radius of about 40 km around Gilgit, Pakistan (BAIG 1989), but the description of two new subspecies considerably enlarged the distribution range. BAIG (1992) suggests that *L. pakistanica* is widely distributed along Indus from Gilgit down to the Mansehra district of Pakistan. The previously defined range is occupied only by the nominate form and the subsequently defined range extensions are inhabited by different populations of *L. pakistanica* (BAIG & BÖHME 1991a).

**Habitat.** It is restricted to montane regions and can easily observed on cliffs or while basking on rocks during daytime. The habitat of all three taxa within *L. pakistanica* is typified by barren rocky mountain with very sparse vegetation. However, the southern limit contains more green eco-zones, but the species itself remains restricted to unvegetated rocks. More frequent presence is generally witnessed along the water course.

**Remarks.** In early afternoon, when temperature rises up to or above 40°C individuals were often found on the shaded side of the rocks. Even that the mentioned habitat are rocky areas with sparse vegetation, individuals can be observed in vegetated area or on river or stream banks, presumably for insect hunting. Analysis of the gut contents shows that it is an omnivorous species, feeding on insects (mostly beetles) and herbs (BAIG 1989).

BAIG (1989) described it as a non gregarious species, always found them solitary or in pairs, which is supported by the presence of callosous glands in females as reported by BAIG & BÖHME (1991). The subspecies appears unique among all members of *Laudakia* in having 100% callosity irrespective of sex, and provides indirect evidence linking territorial behavior and callosity. However, further studies are still required to support or disprove this hypothesis.

**Laudakia pakistanica khani**

**BAIG & BÖHME, 1996**

1996  *Laudakia pakistanica khani* BAIG & BÖHME, Russ. J. Herp. 3: 1–10. Type locality: “Hadar (Chilas), Federal Administered Northern Areas, Pakistan. 32°25’ N / 74° E; altitude 945 m.”

**Diagnosis.** This form is very close to the nominate form but having fewer scales around the body and a more mosaic-like in colouration.

**Description.** Head triangular when viewed from above, depressed; nostrils oval, touching edge of canthus rostralis, pointing outward and backward; upper head scales heterogeneous, subequal, flat; upper labials 11 and lower labials 11 to 12; groups of spinose scales present on the sides of the head and neck, those at subauricular level arranged in two distinct horizontal rows; vertebral scales strongly mucronate, enlarged vertebrals start from postshoulder level and gradually increase from anterior to posterior, eight rows of strongly mucronate scales with sharp lifted margins, median two rows consist of relatively small scales which may overlap in posterior half of body; a distinct patch of enlarged, distantly arranged, spinose scales whose lifted margin is broken into sharp spiny border, other small scales spinose or multispinose; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral and flank scales but larger than gular and other small dorsal scales; skin of neck and lateral sides loose forming gular and dorsolateral folds respectively, posterior half of dorsolateral fold marked with enlarged, strongly mucronate scales; total number of scales around midbody 164; limbs strong, covered with strongly mucronate above and flat scales below, hindlimb longer than distance between gular fold and cloaca; 21 lamellae under third finger and 27 under fourth toe. Tail depressed, oval in cross section, each tail segment consists of three complete whors; 34 scales in first complete whorl around the tail; scales on dorsal and lateral sides strongly mucronate and spinose, spine extends little beyond posterior margin of scale; ventral scales smooth. Callosous glands present, six rows at precloacal and 2–3 scale wide small patch at mid abdominal position.

Colouration is a black mosaic on silver grey ground, head black with scattered light colour scales; forelimbs, shank and foot show banded pattern; thigh and proximal part of tail possess scattered black scales; distal 2/3 of tail black; gular region with yellow blotches on black ground; chest, belly and lower parts of limbs pale yellow with irregular dark spots.

**Distribution.** In and around Chilas, Federal Administered Northern Areas, Pakistan.
**Laudakia pakistana pakistana (BAK, 1989)**


**Diagnosis.** It is very closely related to *L. agrorensis*. The jet black colour, larger size (SVL), number of labials, flat head scales, and other body and callous scatation distinguish it from *L. agrorensis*.

**Description.** Head triangular when viewed from above, depressed; nostrils oval, touching edge of canthus rostralis, pointing outward; upper head scales heterogeneous, subeual, flat; labials 11–13; groups of spinose scales present on the sides of the head and neck, those at subauricular level arranged in two horizontal rows; vertebral scales spinose, enlarged vertebraals start from postshoulder level and gradually increase from anterior to posterior, 8–10 vertical rows of spinose scales (with sharp lifted margin), median two rows are of relatively small size scales which may overlap in posterior half of body; presence of a distinct patch of enlarged, distinctly arranged, spinose scales whose lifted margin is broken into sharp spiny border on flanks, other small scales spinose or multispinose; other small dorsal scales distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral and flank scales but larger than gular and other small dorsal scales; skin of neck and lateral sides loose forming gular and dorsolateral folds respectively, posterior half of dorsolateral fold marked with enlarged, strongly mucronate scales; total number of scales around midbody 168–178 (mean 171.3); limbs strong, covered with strongly mucronate above and flat scales below, hindlimb longer than distance between gular fold and cloaca; 22–26 lamellae under third finger and 26–31 under fourth toe. Tail depressed, oval in cross section, forming very distinct annuli, each tail segment consists of three complete whors; 33–40 scales in first complete whorl around the tail, scales on dorsal and lateral sides strongly mucronate and spinose, spine extends slightly beyond the posterior margin of scale; ventral scales smooth. Callous glands present, six rows at precloacal and 2–3 scale wide small patch at mid abdominal position in males and similar patches present in females but does not extend beyond three rows at precloacal position and rarely possess an abdominal patch.

Colouration is a jet black above; under parts speckled with yellow or orange. However, young and juvenile specimens may show some faded pattern above and less black underneath. This indicates that colour variations in the nominate form are somehow related with age.

**Distribution.** In a radius of about 40–50 km around Gilgit (Federal Administered Northern Areas of Pakistan).

**Laudakia papenfussi ZHAO, 1998**


**Diagnosis.** This species is very similar in morphology to *Laudakia tuberculata*, with the latter differing from this species in the nostril being situated in the enlarged portion of the pear-shaped nasal, directed outwards; having two supranasals; having the superciliary ridge well developed, with a sharp free margin which is slightly everted upwards; and dorsum and flanks are scattered with many orange-yellow, round spots, there is a large conic scale corresponding to each spot or one large conic scale surrounded by a circle of small scales.

**Description.** Body depressed, head slightly triangular and 1.33 times longer than wide. Nasal elliptic, nostril situated in the center. Nostril elliptic, directed outwards and rearwards, on the canthus rostralis; one supranasal; nasal separated from rostral by a small scale. Eye moderate with a rounded pupil; eyelids covered with scales; a row of large, keeled scales arranged in a curve below the lower eyelid, separated from supralabials by three rows of small, smooth, slightly bulging scales tympanum large, slightly smaller than the eye, slightly rounded, superficial, columella auris visible; tympanum bordered with conic scales, patches of these scales also on side of neck; scales between eye and tympanum large and keeled on upper part, small and keeled on anterior lower part, granular on posterior lower part; rostral scales broad and low, upper margin of scales straight; scales on top of the head heterogeneous, large on snout, slightly large, bulging and smooth on fronto-parietal region, small on supraocular region distinctly keeled on occiput. Superciliary ridge poorly developed, its margin blunt and not everted upwards; 10 supralabials, 11 infralabials on each side, mental large, triangular, 4 or 5 rows of long and narrow scales parallel to the infralabials; gular pouch absent, gular fold present, rudimentary nuchal crest. Vertebral scales slightly large, keeled and obliquely towards the midline on sacrum, in 10 to 12 longitudinal rows; remaining dorsal scales small and keeled, among with scattered with large, conic scales; ventral scales smooth, or slightly keeled, slightly larger than
vertebrals; limbs stout, longest toe of hind limb reaches the tympanum, back of limbs covered with large, strongly keeled scales, scales of inner side of upper arm small, fingers and toes well developed, claws compressed and sharp. Tail cylindrical, slightly depressed at the base, covered with large, strongly keeled scales, scales of lower surface largest, scales are arranged in segments, each segment with three rings of scales.

**Distribution.** Only known from the type locality (Mayang River Valley between Mayang Village and Diya Village, Zanda County, Xizang Autonomous Region, China at 3300 m a.s.l.).

**Remarks.** The description of the species is based on the holotype, the only available voucher of the taxon (fig. 8).

**Laudakia sacra** (Smith, 1935)

1935 *Agama himalayana sacra* Smith, The Fauna of Brit.India, vol II (Sauria): 214. Type locality: “near Lhasa, Xizang [Tibet], Autonomous Region, China.”

**Diagnosis.** Comparatively large; head and body depressed; head scales mostly smooth; no enlarged, mucronate scales either on flanks or on body; higher number of scales around mid body; groups of low spinose scales on neck and sides of head; distinct tail segment of four whorls above becoming three below; callous glands both at precloacal and abdominal position.

**Description.** Head and body depressed; snout more than one and half times the distance between eye-tympanum or eye width and more than two times that of tympanum diameter; tympanum exposed, more than half of eye width; nostril pierced on canthus rostralis in the form of unique diagonal slit like aperture, more than half of nasal, pointing outward and backward, touching rostral; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, mostly smooth; labials 9–10 (±0.4); groups of low spinose scales present on the neck and sides of head especially around tympanum, preauricle in series otherwise in groups; nuchal dentition clearly visible; vertebral scales keeled, larger than other small dorsals, arranged in 14–16 rows of keeled scales; complete absence of any enlarged scales on the lateral sides of the body or flanks; other small dorsals distinctly smaller than enlarged ones; ventral scales smooth, smaller than enlarged vertebral; gular scales granular, smooth; skin of the lateral sides does not form distinct dorsolateral fold; total number of scales around midbody 180–196 (±6.0) (according to Ananjeva et al. 1990, up to 239 scales); limbs strong, covered with enlarged scales, over thighs mostly smooth and weakly keeled except those on the posterior border of thigh, hind-limb little longer than distance between gular fold and cloaca; fingers and toes compressed, usually 21–27 (23.6±1.99) lamellae under 3rd finger and 28–32 (30±1.4) under 4th toe. Tail depressed, oval in cross section; each tail segment consists of 4 whorls of enlarged mucronate scales but only 3 on the ventral side, not marked in proximal part; 30–32 (31±1.0) scales in first complete whorl around the tail; callous glands present in males at precloacal and also at abdominal position, number of rows at precloacal position 4–6 and an oblong patch on abdomen.

Colouration in preserved specimens is a dull grey or brownish speckled with dark spots forming a very indistinct pattern; gular spotted or reticulated; tail light in proximal half and dark distally.

**Taxonomy.** On the basis of i) the much larger size, and ii) the presence of large patches of callous scales at precloacal and abdominal positions, Smith (1935) described *L. sacra* as a subspecies of *L. himalayana*. All subsequent authors (e.g. Anderson & Leviton 1969, Ananjeva et al. 1981) followed this taxonomic conclusion and recognized *L. sacra* as subspecies. However, Ananjeva et al. (1990) realized the complexity of the situation, found striking dissimilarities between *L. sacra* and *L. himalayana*, and raised it to full species level. Unfortunately, they compared it extensively with *L. himalayana*, but failed to include *L. tuberculata* in their comparison. Although some differences are obvious, Baig (1992) suggests that it should be placed in the *L. tuberculata* group because of the similarity in major characteristics (e.g. size, number of scales around body, tail segment, callousity). This is recently supported by Macey et al. (2000) who recognized *L. sacra* as the sister taxon to a clade containing *L. nupta* and *L. tuberculata*.

**Distribution.** Restricted to the river drainage of the Yarlung Zangbo in Lhasa Valley, Xizang (Tibet), Autonomous Region, between elevations of 3000–4000 m a.s.l.

Previously it was only known from the type locality, but Ananjeva et al. (1990) recognized it from several other localities and extended the range to Bomi (29°50’N, 95°45’E). The distribution range lies quite close to the eastern limit of *L. tuberculata* and includes an area where both species are allopatric. *Laudakia sacra* inhabits an isolated area in southeastern Tibet. The elevational range is given by Ananjeva et al. (1990) as 3000–4000 m a.s.l., which is apparently the highest among all *Laudakia* species and the species also marks the southeasternmost limit of the genus.
Laodakia tuberculata (Hardwicke & Gray, 1827)  


1853 *Stelvio indicus* Blyth (fide Smith 1935; non *Agama indica* Gray = *Calotes versicolor*), J. Asiat. Soc. Bengal, Calcutta, 22: 647. Type locality: “Mirzapore [= Wazirabad, upper Hindistan].”  

1860 *Barycephalus sykesii* Günther (fide Smith 1935), Proc. zool. Soc. London, 1860: 150; pl. 25, fig. A. Type locality: “Simla, Himalaya, 2500 feet above sea level; Simla, Himalaya, 7200 feet above sea level; Gahrwál, Himalaya, 8200 feet above sea level; Balti, Tibet, 6100 feet above sea level; Ladak, Tibet, 15,250 feet above sea level,” interpreted as “Simla, Himalaya” by Smith 1935.  

**Diagnosis.** Head and body depressed; head scales smooth or rugose; no patch of enlarged, mucronate scales on flanks; only scattered, enlarged, mucronate scales present on body; groups of low spinose scales on neck and sides of head; larger number of scales around body; tail segment of four whorls which remain of three below, indistinct proximally; callous glands in males only.  

**Description.** Head and body depressed; snout one and half times or more the distance between eye-tympanum or eye width and more than twice that of tympanum diameter; tympanum exposed, more than half of eye width; nostril pierced on or below canthus rostralis, less than half of nasal, pointing outward and backward, touching rostral; no gular pouch, gular plicate; upper head scales heterogeneous, subequal, smooth or posteri orly slightly rough; labials 8–12 (10 ± 1); groups of low spinose scales present on the neck and sides of head especially around tympanum, preauricle in series otherwise in groups; vertebral scales keeled, larger than other small dorsals, 12–14 oblique rows of keeled scales; no patch of enlarged mucronate scales on flanks, enlarged mucronate scales scattered over the sides of body; other dorsals smaller than enlarged ones; ventral scales smooth, smaller than enlarged ventral but larger than gular and other small dorsal scales; gular scales granular, smooth; skin of lateral sides loose forming dorsolateral fold; total number of scales around midbody 134–221 (171 ± 22.3); limbs strong, covered with enlarged mucronate scales, hind-imb slightly longer than distance between gular fold and cloaca; fingers and toes compressed, 20–30 (24.8 ± 2.49) lamellae under third finger and 26–37 (31.5 ± 2.6) under fourth toe. Tail depressed, oval in cross section; each tail segment consists of 4 whorls of enlarged mucronate scales but remain 3 on ventral side; 28–46 (36 ± 4) scales in first complete whorl around the tail; callous glands present in males only at precloacal and at abdominal position, number of rows at precloacal position 4–6 and an oblong patch on abdomen.  

Head pale yellow or grey, sometimes speckled, on the sides black bar between eye and tympanum; gular spotted or speckled with black, males marked with blue, in juveniles reticulated; chest and belly pale yellow but may be speckled with age, males with blue or grey wash; body colour highly variable, sometimes dust brown or grey without any noticeable pattern, may be olive brown mottled with black and yellow, yellow spots may be of different sizes, the bigger ones are sometimes arranged in transverse series; another pattern which is generally observed in females is characterized as olive brown, light vertebral stripe with lateral extensions which are bordered by black and several other light and dark spots and specks, sub-adults have irregular pattern; tail shows indistinct banded pattern but when the specimen itself lacks any pattern on the body, the tail is also devoid of it.  

**Taxonomy.** Duda (1966, 1972, 1974) carried out morphological and anatomical studies, while Böhme (1988) found strong differences in hemipenes morphology of *L. tuberculata* (the type species of *Laodakia*) as compared to *Paralaudakia himalayana* and *P. lehmannii*. These hemipenial differences support the distinct character of *Laodakia* and *Paralaudakia*.  

**Distribution.** Eastern Afghanistan, northwestern Pakistan, Kashmir, some parts of Uttar Pradesh, India, and southwestern Nepal.  

*Laodakia tuberculata* has a very wide distribution. In 1827 it was originally described from Bengal, without specifying any precise locality. At that time Bengal was a very large province and as *L. tuberculata* is a mountain dwelling species, it is very likely that the type series was collected in northern parts of the province. Boulenger (1885) synonymized *Barycephalus sykesii* and *Stelvio indicus* with *L. tuberculata*, including several new localities (Tibet and Bengal (?) in the East, Simla, Kashmir, Ladakh, and Murree in the West). *Laodakia tuberculata* is widely distributed in Pakistan and the Kashmir area now associated with Pakistan. Its presence in eastern Afghanistan is very likely because of a continuous mountain range which spreads from Pakistan into Afghanistan.  

The presence of both *L. tuberculata* and *L. dayana* is known from the Simla area of India, but it is recently unknown if both species are in true sympathy in this area. Because of altitudinal distributions in mountain areas, the presence of two taxa does not necessarily imply a sympatric occurrence. It can be supposed that in Simla area *L. tuberculata* is distributed in lower
Laudakia wui Zhao, 1998

Type locality: “Yi’ong, Bomi County, Xizang [Tibet] Autonomous Region, China; altitude 2350 m.”

**Diagnosis.** Closely related in morphology to *Laudakia sacra* but the latter taxon has the lateral scales uniform in size and not intermixed with large scales.

**Description.** Body depressed, head slightly triangular, longer than wide. Nasal elliptic, connected with the rostral and first supralabial, nostril in the center, directing outwards, nostril large, oval, just below the canthus rostralis, 4 to 5 small scales between posterior margin of nasal and supraciliary ridge. Superciliary ridge not well developed. Eye moderate with round pupil, upper and lower eyelids covered with scales, altitudes while *L. dayana* occupy higher elevations. Specimens (e.g. ZMA 11636) identified as *L. dayana* were collected from the bank of Sutlaj River in upper Simla at an elevation of 3000 m a.s.l. while *L. tuberculata* is known from elevations between 1200–2200 m in Pakistan and Kashmir.

WALTNER (1991) studied the altitudinal ecology of *L. tuberculata* in the Uttar Pradesh state of India and found several dissimilarities among the populations living at different altitudes. However, it could be possible that one population belongs to *L. tuberculata* while others to *L. dayana*, but that has yet to be examined.

WALTNER (1991) defined the eastern distribution limit up to Kathmandu (Nepal), but the records show the presence up to Sikkim. Few specimens of *L. tuberculata* have been reported from Singapur (BMNH xxiii. 536) and Burma (ZMB 6052), but these are doubtful.
Fig. 8. A = syntypes of *Laudakia wui*; B = holotype of *Laudakia papenfussi*. 
scales behind the eye slightly enlarged and keeled. Tym-
panum elliptic, slightly smaller than the eye, superfi-
cial, columella auris visible, upper margin with a row
of large, keeled scales, comparable in size to scales
of temporal region, anterior margin also with large,
keeled scales, lowest one is the largest and is conic;
scales on top of head heterogenous, slightly large
and bulged on snout, remaining scales small and smooth,
parietal organ indistinct, visible as a small white spot;
angle of mouth and neck with patches and rows of
conic scales; 8 supralabial and 11 infralabial scales on
each side, two rows of long scales parallel to infralabi-
al scales, mental triangular; gular pouch absent, gular
fold present, one or two large spinose scales before
the fold in front of the shoulder; rudimentary nuchal crest
present; vertebral scales slightly large and keeled, re-
maining dorsal scales small; curved skin-fold on each
side of back from shoulder to groin, scales below the
skin-fold intermixed with large, conic scales, arranged
in two parallel, longitudinal, discontinuous rows; ven-
tral scales as large as the vertebral scales, arranged in
longitudinal rows; limbs moderate, the longest toe of
hindlimb reaches the armpit of shoulder, back of limbs
with large, strongly keeled scales. Tail cylindrical,
slightly depressed at the base, covered with large,
strongly keeled scales, scales arranged in segments
and each segment in three rings.

Distribution. Only known from the type locality
(Yi’ong, Bomi County, Xizang Autonomous Region,
China, at an elevation of 2350 m a.s.l.).

Remarks. The description of the species is based on
the type material, the only available vouchers of this
taxon (fig. 8).

Key to the Species

1 Tail segment consists of two whorls ............. 2
   Tail segment consists of more than two whorls... 7
2 Enlarged vertebral scales heterogeneous, keeled
   or mucronate, irregular with vertebralateral trans-
   verse series ........................................ 3
   Enlarged vertebral scales homogeneous, smooth or
   keeled, may or may not arranged in oblique rows
   .................................................................. 5

3 In posterior half of tail caudal segment completely
   changes into three whorls ........... S. stello cytriaca
   Caudal segment may rarely be contaminated with
   3rd whorl only on lateral side, otherwise remains
two ......................................................... 4

4 Colour jet black with or without yellow spots, size
   small, number of scales around the body usually
   more than 180 ........................................ S. stello picea
   Size medium, vertebral band of enlarged scales nar-
   row, vertebralateral series broken, indistinct verte-
   bral bones on dull ground colour
   ...................................................................... S. stello vulgaris
   Size relatively large, colour bright with distinct yel-
   low blotches, usually more than four, vertebral band
   of enlarged, weakly carinated scales broad, dorsally
   transverse rows of enlarged scales merge medially
   with the broad continuous vertebral band similar en-
   larged scales, scales around mid-body less than 150
   ...................................................................... S. stello brachydactyla
   Size relatively large, colour bright with metallic bluish
grey tubercles, narrow vertebral band of en-
   larged, weakly carinated scales, dorsally transverse
   rows of enlarged scales almost always separated by
   the narrow continuous vertebral band of small scales
   ...................................................................... stello salehi
5 Number of scales around the body usually more
   than 160 (up to 220) ..................................... 6
   Number of scales around the body less than 100, all
   scales of the body are very strongly mucronate or
   spinose ................................................. P. erythrogaster
   Number of scales around the body 110–160, en-
   larged vertebral scales keeled ......... P. caucasia
6 Vertebral scales flat or weakly carinated, enlarged
   mucronate scales less often present on the flanks,
   usually as short vertical series .......... P. microlepis
   Tail segment consists of three whorls .......... 8
7 Tail segment consists of more than three whorls
   .................................................................... 16
8 Size (SVL) of mature specimens usually remain
   under 100.0 mm ......................................... 9
   Size of mature specimens exceeds 100.0 mm ... 11
9 Enlarged vertebral scales more than 10 in transverse
   row, those on mid-vertebral line smooth and
   bordered by weakly keeled scales .................... 10
   Enlarged vertebral scales in less than 10 verti-
   cal series, all keeled, 3–5 rows of callous scales at
   precloacal and sometimes a patch on belly
   .................................................................... P. bochariensis
10 Vertebral rows of enlarged scales more than 12, 2–3
   rows of only callous precloacal scales, no patch of
   enlarged mucronate scales on flanks
Distinct patch of enlarged spinose scales on flanks, males with 3–5 rows of callous precloacal scales, and a patch on belly .................. P. badakshana

Callous glands present in males only at precloacal position .................................................. 12

Callous glands present both at precloacal and abdominal positions ........................................... 13

Mid-vertebral scales only moderately enlarged, no enlarged mucronate scale on flanks or sides of the body .................................. P. stoliczkanala altaica

Vertebral scales heterogeneous, 2 vertical rows of distinctly enlarged, highly ridged scales on either side of mid-vertebral line and similar scales randomly scattered on the body ........ P. lehmanni

Size of specimens does not exceed 120.0 mm, number of scales around the body usually less than 130, a distinct patch of enlarged mucronate scales on flanks, large dorsal scales, larger than ventrals ...................................................... L. agroensis

Size of specimens may exceeds 150.0 mm ...... 14

Nuchal fold across neck present, mid-dorsal scales highly enlarged, in 16–18 rows, usually more than 90 scale rows along the body, groups of high spinose scales around tympanum, number of scales around body less than 110, no patch of enlarged mucronate scales on flanks .................. L. nupta nupta

Nuchal fold across neck absent, , mid-dorsal scales highly enlarged, in 13–16 rows, usually less than 90 scale rows along the body ........... L. nupta fusca

Mid-dorsal scales highly mucronate, in 8–10 rows, number of scales around body more than 140, head with smooth scales, distinct patch of highly spinose scales on flanks ............................................... 15

Jet black colour ........... L. pakistanica pakistanica

Mosaic colour ................... L. pakistanica khani

White transverse stripes on dull brown ........................................... L. pakistanica auffenbergi

Tail segment is inconsistent and changes from three to five and sometimes six from anterior to posterior side; vertebral scales smooth to keeled; less than 150 scales rows around midbody .................................. L. melanura melanura

Tail segment is inconsistent and changes from three to five and sometimes six from anterior to posterior side; vertebral scales enlarged, smooth; more than 150 scales rows around midbody ..................................................... L. melanura nasiri

Tail segment consists of 4 complete whorls ...... 17

Tail segment consists of 4 whorls on dorsal and lateral side and 3 on ventral side ..................... L. nupta fusca

Enlarged mucronate scales on the limbs are surrounded by very small scales, groups of conical scales on the flanks, number of scales around body more than 200 ............................. L. nupta fusca

No enlarged mucronate scale on flanks, vertebral scales moderately enlarged, number of scales around body 130–160 ............. P. stoliczkanala stoliczkanala

No enlarged scale on flanks or side of body, number of scales around mid-body more than 18 ........ L. sunda

Lateral scales heterogeneous, intermixed with large scales, arranged in two rows; dorso-lateral skinfold present ................................. L. wui

Several enlarged mucronate scales scattered on the sides of body, largest dorsal scales smaller than ventrals, number of scales around body more than 130 ...................................................... L. tuberculata

One supranasal, superciliary ridge not well developed; no sharp, free, slightly everted, upwards margin .................................. L. papenfussi

Distinct patch of enlarged mucronate scales on flanks in addition to scattered enlarged scales, scales around body 100–130 .............. L. dayana

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