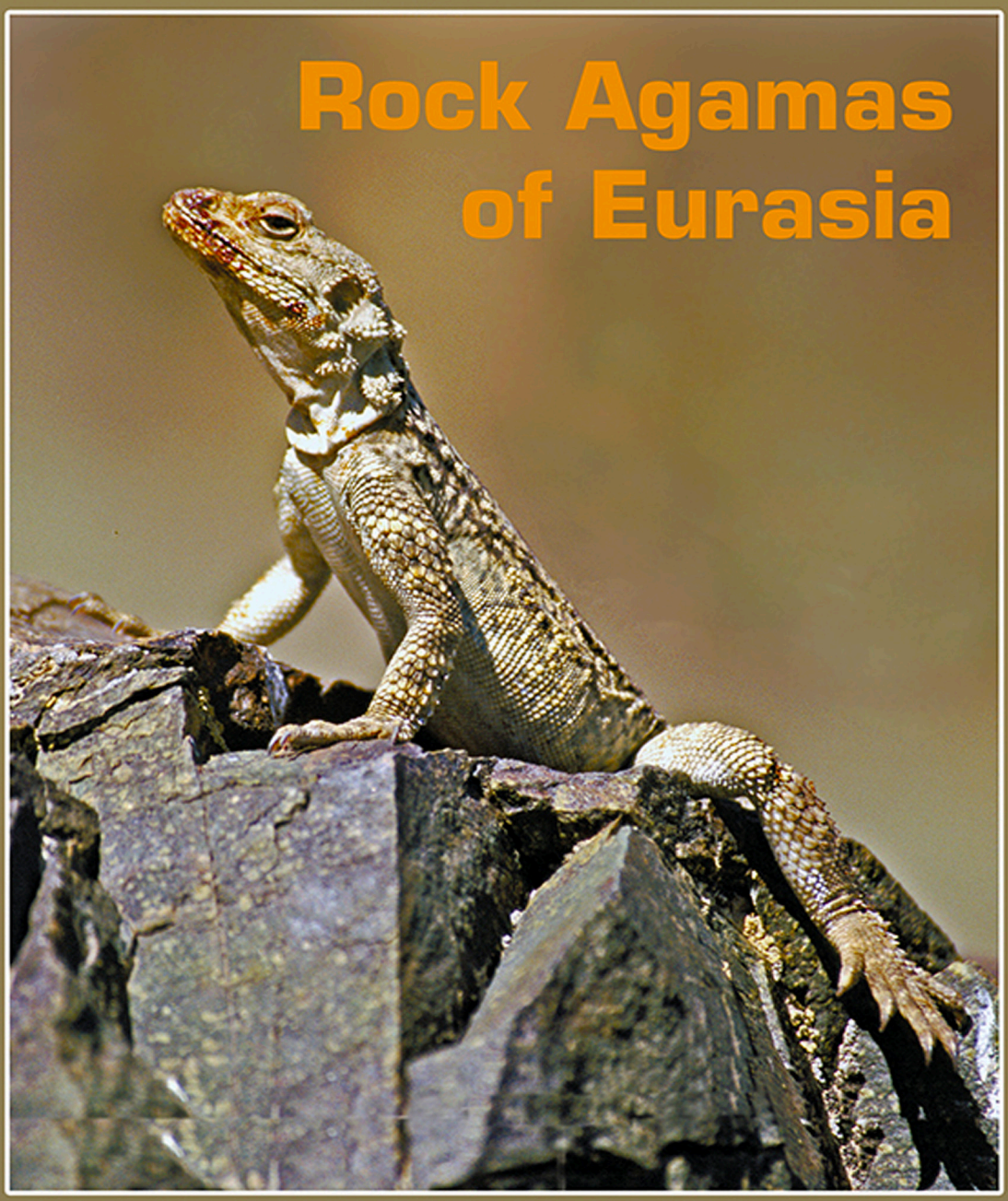
E.N. **Panov**, L.Yu. **Zykova**

Rock Agamas of Eurasia



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Книга представляет собой первый обзор на английском языке систематики и биологии компактного таксона ящериц (около 20 видов), обитающих в пересеченных аридных и высокогорных ландшафтах Евразии и северо-восточной Африки. Эти рептилии в последнее время привлекают пристальное внимание герпетологов из-за своей заметности, обязанной сугубо дневному образу жизни и высокой численности и плотности популяций, характерной для большинства видов.

До сих пор интерес герпетологов был сосредоточен главным образом на систематике и номенклатуре горных агам, а серьезные исследования по их образу жизни, экологии и поведению крайне немногочисленны. В этой книге наряду с обзором наиболее важной опубликованной информацией по изученным представителям таксона дана развернутая картина всех сторон биологии модельного вида – кавказской агамы *Paralaudakia caucasia* и его взаимоотношений с другим – хорасанской агамой *P. erythrogaser*. На протяжении 10 лет полевых исследований прослеживались биографии многих конкретных особей и изучались тонкие детали коммуникативного процесса в нескольких локальных популяциях.

В основу исследования положен анализ социального поведения как фактора, интегрирующего дем в некую общность системной природы. Главной задачей было рассмотреть структуру в ее трансформациях из года в год как процесс изменений в поведении и социальных ролях взрослых особей и детенышей, ежегодно пополняющих контингент дема.

Другие важные темы, затронутые в книге — это разнообразие носителей коммуникативной информации (оптическая, химическая, тактильная) у модельного и ряда других видов, а также характер взаимоотношений между близкородственными формами в зонах их контакта.

К книге прилагается цифровой диск с многочисленными видеозаписями поведения 12 видов ящериц.

On the front cover: Caucasian Rock Agama *Paralaudakia caucasia*.
SW Turkmenistan. Photo by E.N. Panov

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Chapter 1.

GENERAL INFORMATION ON EURASIAN ROCK AGAMAS

The genus *Laudakia* sensu lato comprises 19 or 20 species (according to Baig *et al*., 2012 and Hoser, 2012, respectively). However, we will not mention *L. dayana*, *L. papenfussi* and *L. wui* so as not to replicate potentially erroneous information. Our review is based on the materials on the 16 relatively well studied forms of the species status as understood by Hoser (2012) (Table 1.1).

Rock agamas are a young group in the evolutionary respect. Agamids appeared in Africa and Eurasia *ca.* 190 Myr ago (Evans *et al*., 2002). *Laudakia* sensu lato began to diverge as late as 24 Myr ago, with the age of the youngest sister species being estimated at *ca.* 18 Myr (Fig. 1.1).

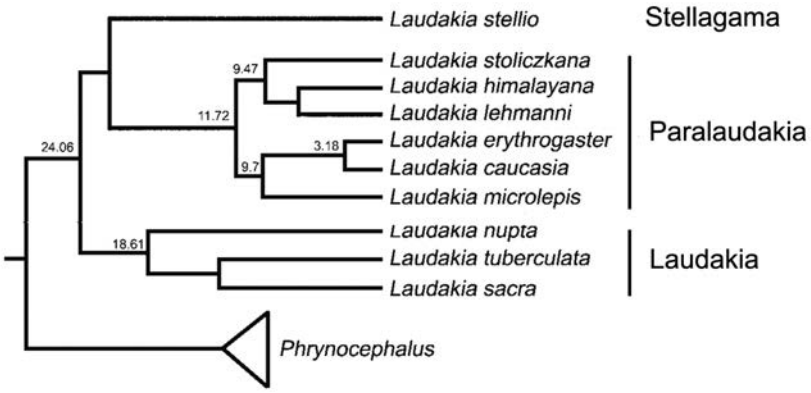

FIG. 1.1. Revision of the genus *Laudakia* s.l., based on comparative mtDNA. Node ages are shown in Mya. After Melville *et al*., 2009 modified by Baig *et al*., 2012.

The distribution area of the genus *Laudakia* sensu lato embraces the central part of the Alpine-Himalayan belt. This is a blanketed folded terrain formed during the Caenozoic. In the west the distribution area of these lizards coincides with the mountain systems passing along the Adriatic Sea across the Dinaric Alps and Hellenic mountains and the Crete crossing the Aegean Sea. Further to the east these mountain ranges continue into the Taurus in the south of Anatolia and the Zagros mountains in the south-west of Iran. Two other branches of the mountain ranges are represented by the Greater Caucasus and the Pontic mountains of the north Anatolia transiting into the Lesser Caucasus and Alborz Mountains in the north of Iran. Still further to the east the latter join the Kopet Dag to form the Turkmenistan-Khorasan Mountain Range. The easternmost part of the distribution area of rock agamas is confined to the mountain systems of Altay in the north and the Baluchistan chains of Pakistan and the Himalayas (Fig. 1.2, 12.12).

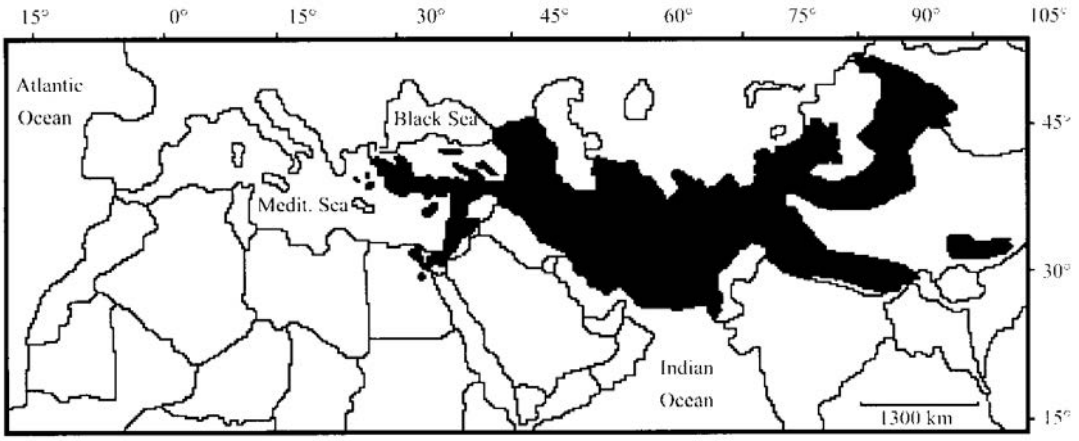

FIG. 1.2. Range of rock agamas *Laudakia* s. l. After Rastegar-Pouyani and Nilson, 2002.

Table 1.1.

List of taxa of the species level within the genus *Laudakia* sensu lato

Genus	Scientific names	Common names	Number of subspecies	Range
Stellagama	*S. stellio* (Linnaeus, 1758)	Hardun, Hardim, Star Lizard, Starred Agama, Sling-tailed Agama, Roughtail Rock Agama	5–6	Eastern spurs of Balkhans, islands of Aegean Sea, Cyprus, Asia Minor, Near East, northeastern Africa
Laudakia[1]	*L. agrorensis* (Stoliczka, 1872)	Agror Agama		Southern Hindu Kush, western Himalayas
	L. fusca (Blanford, 1876)[2]	Yellow-headed Agama	–	Hindu Kush
	L. melanura (Blyth, 1854)	Black Agama	2	Southeastern and eastern parts of the Iranian Plateau
	L. nupta (De Filippi, 1843)	Large-scaled Rock Agama	2	The Zagros Mountains, southern parts of the Iranian Plateau
	L. nuristanica (Anderson et Leviton, 1969)	Leviton's Rock Agama	–	Hindu Kush
	L. pakistanica (Baig, 1989)	Pakistan Rock Agama	2	Western Himalayas
	L. sacra (Smith, 1935)	Sacred Rock Agama	–	Southeastern Tibet
	L. tuberculata (Hardwicke et Gray, 1827)	Kashmir Rock Agama		Hindu Kush and The Himalayas (eastern Afghanistan, northwestern Pakistan, Kashmir, parts of Uttar Pradesh, India, southwestern Nepal.

Table 1.1.

Paralaudakia	*P. caucasia* (Eichwald, 1831)	Caucasian Rock Agama	1 (2?)	Caucasus and South Caucasus, Alborz, Kopet Dag, Iranian Plateau (mainly its northern parts)
	P. erythrogaster (Nikolsky, 1896)	Redbelly Rock Agama	1 (2?)	Eastern Kopet Dag, northwestern Hindu Kush
	P. badakhshana (Anderson et Leviton, 1969)[3]	Badakhshan Rock Agama	–	Hindu Kush
	P. bochariensis (Nikolsky, 1897)[3]	Bukhara Rock Agama	–	Kugitangtau, Pamiro-Alay
	P. himalayana (Steindachner, 1869)[3]	Himalayan Rock Agama	–	Kugitangtau, Pamiro-Alay, southwestern Tien Shan, Hindu Kush, western Himalayas
	P. lehmanni (Nikolsky, 1896)	Turkestan Rock Agama	–	Kugitangtau, Pamiro-Alay, western Tien Shan
	P. microlepis (Blanford, 1894)	Small-scaled Rock Agama	–	Iranian Plateau (mainly its southern parts)
	P. stoliczkana (Blanford, 1875)	Mongolian Rock Agama	2	Eastern Tien Shan, Mongolian Altay, Gobi-Altay

Underlined are the names of species with restricted ranges of the relict type.
[1] Forms *dayana*, *papenfussi* и *wui* regarded by us as doubtful are not mentioned.
[2] Cheatsazan *et al*. (2008) suggest: 'Based on the co-occurrence of these subspecies in Kuh-e-Bang and morphological clues for their reproductive isolation at this site, they are recognised as full species. But Baig *et al*. (2012) consider it as subspecies of *L. nupta*. They wrote: '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-Pouyani and Nilson (2002) could indicate an initiating speciation'.
[3] These three forms are treated by Baig *et al*., 2012 as belonging to the superspecies *P. himalayana*.

A relatively young evolutionary age of rock agamas is also indicated by the fact that the distribution of most species is allopatric (Fig. 1.3) and the species themselves are usually monotypic.

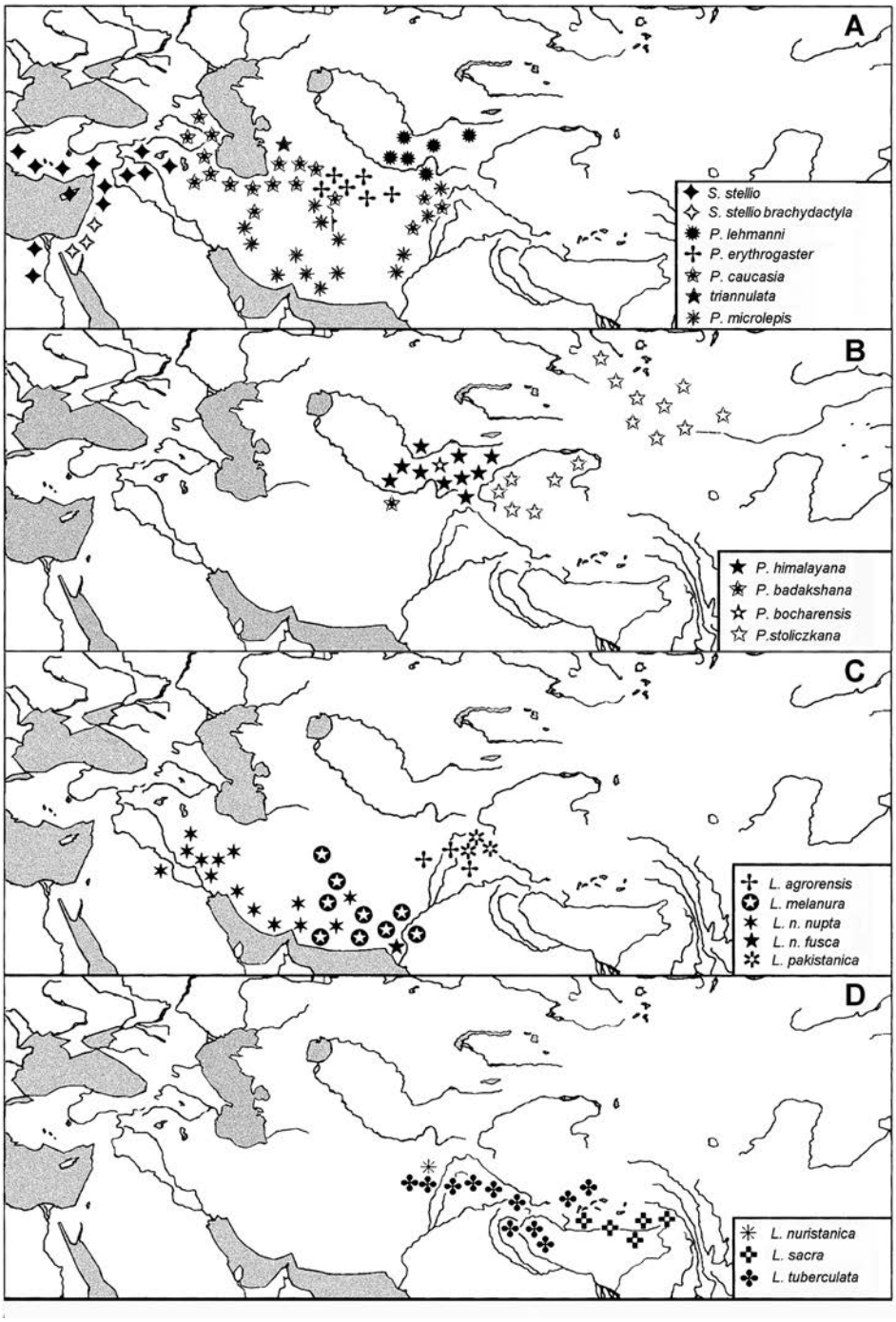

FIG. 1.3. Tentative scheme of the rock agamas genera *Stellagama*, *Paralaudakia* and *Laudakia* s. str. distribution. Original.

1.1. MORPHOLOGICAL FEATURES

1.1.1. General characteristic

Eurasian rock agamas are medium-sized lizards. The body mass of the mature males varies in different species between 60–140 g and that of females, between 30–130 g. Smaller species are few. General appearance and body proportions are rather uniform across all species (Fig. 1.4). Rock agamas have flat bodies and a triangular head, making up *ca.* 35% of the body length. Legs are not long, forelegs make up some 50% of body length, while hind legs are longer: 66–76% in the males of different species and 64–70% in the females (Ananjeva *et al*., 1990).

The usual locomotion type is running and the main allure is fast trot. Rock agamas may run very fast. The maximum speed of the Hardun, for instance, makes up 2.3–2.7 m/s, positively correlating with the body mass and body temperature (Hertz *et al*., 1983; Van Damme and Vanhooydonck, 2001).

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Toes are comparatively long, with strong claws. In hind legs the fourth toe is much longer than the others. Tail is somewhat flattened at its base, towards the tip it has a round profile. In most species the tail is much longer than the body and the head taken together (1.3–2.5 times longer in different species). It is relatively short (<110% of the body with the head) only in a few species. These proportions vary with age and sex and show geographic variation across all the species for which sufficient morphological data are available (Table 1.2).

The cranium of rock agamas is flat and the surface of frontal and parietal bones is nearly smooth. Eurasian rock agamas differ from the closely related *Trapelus* and *Phrynocephalus* agamas by the details of maxillae and dental bones (Ananjeva, 1992). The nostrils, cut on the side surface of the inflated naricorn, are invisible from above. Their openings may be round (*S. stellio* subsp., *L. nuristanica*, *L. melanura*, *L. agrorensis*, *L. tuberculata*) or oval (*L. sacra*, *P. himalayana*, *P. bochariensis*), being elongated along the cranial-caudal axis (Ananjeva *et al*., 1990).

Some species have a parietal foramen in the occipital scutum. The eyes are covered with movable lids and the iris is round. The eye sockets are depressed and covered from above by a lateral projection of the supraorbital tuber, so that the eyes are almost invisible from the above. The tympanum is located more or less superficially. Behind tympanum on the sides skin's fold is of neck a well-defined. Its bulge is covered by large cone-shaped scales, with the spikes on them being developed in varying degrees in different species. The skin of the lower part of the head forms the so-called gular fold (Plate IX). When an animal is agitated, the skin of the ‘chin’ is lowered down by a hyoid apparatus forming a small bulge the size of which varies in different species. At least in one form [*S. stellio brachydactyla*] this bulge is shaped similarly to the typical gular sac of some *Trapelus* species (in particular, the Steppe Agama *T. sanguinolentus*).

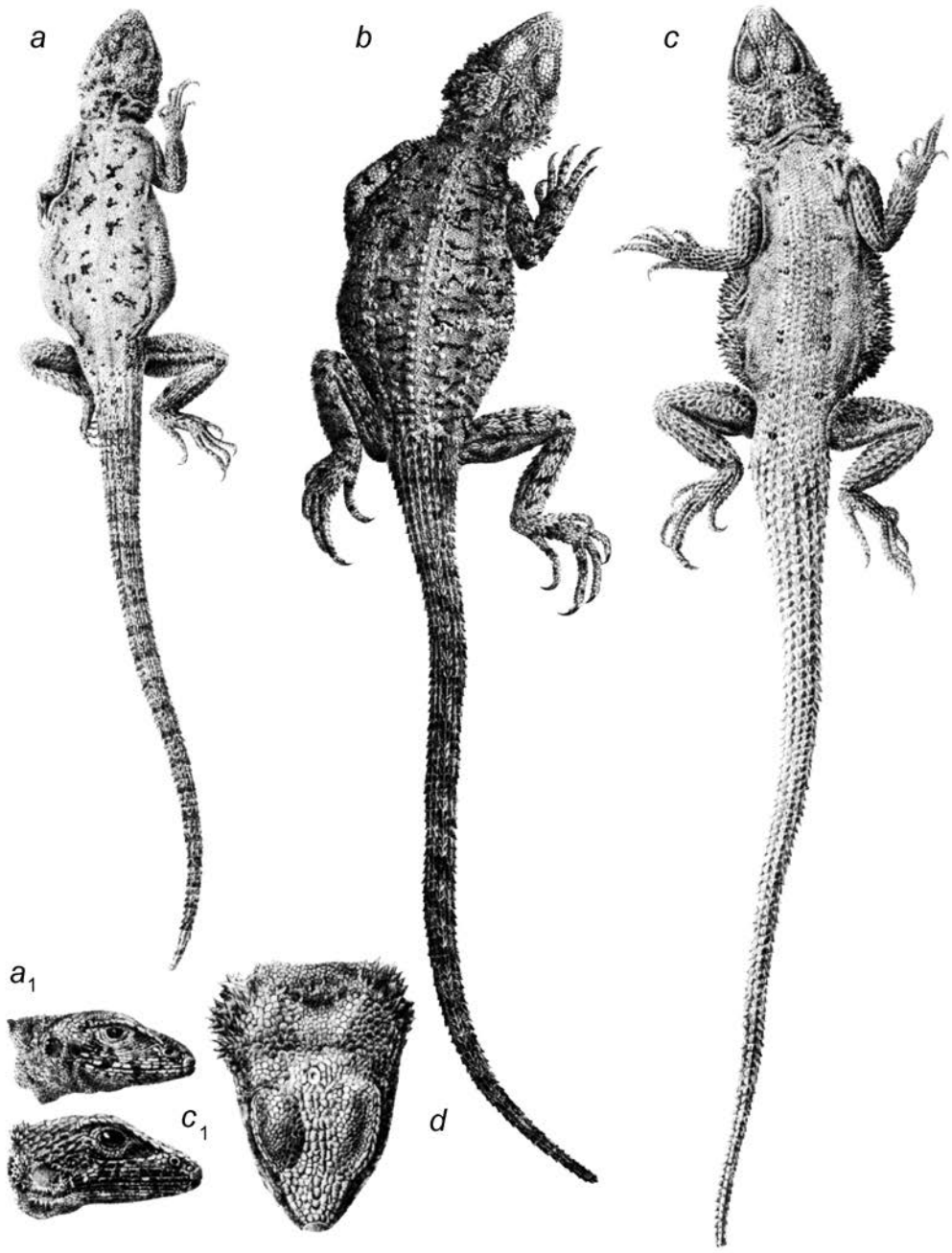

FIG. 1.4. Variants of external morphology in some representatives of the genus *Paralaudakia. a* — Himalayan Rock Agama *P. himalayana*, a_1 — its head; *b* — Turkestan Rock Agama *P. lehmanni*; *c* — Bukhara Agama *P. bochariensis*, c_1 — its head; *d* — head of the Mongolian Rock Agama *L. stoliczkana.* After Bedryaga, 1907.

Table 1.2.

Size of eggs and indivudials of different ages in some *Laudakia* s. l. species.

Species	Egg length (mm)	Egg width (mm)	Egg weight (g)	SVL (mm), shortly after hatching	Egg weight (g) shortly after hatching	SVL (mm), after first Molt	Weight (g) juv after first winter	SVL max. (mm), males ad.	Weight max. (g), males ad.	SVL max. (mm), females ad.	Weight max. (g), females ad.
stellio ssp.	24–27 19	15 11	–	32	–	–	–	120	–	112	–
caucasia[1]	19–26 (**22.7**)*	11–15 (13.3)	0.3–3.0 (**1.8**)	38–46 (**43.3**)	1.9–3.6 (**2.4**)	57	–	138	70	135	58
erythrogaster	19–25	9–14	–	45	3,3	–	–	154	143	148	129
himalayana	16–22	10–12	–	35–39	–	63–70	8,5	108	60	96	30
lehmanni [2]	19–21[2] (**19.6**) 15–19 18–19	12–14 (**13.5**) 9–12	0 . 8–1 . 2	35–37	2–7	46–66 35–65 (**49**)	3–10	150	128	140	118
tuberculata	21–23 (**21 . 8**)	–	–	35	–	–	–	140	88	138	84

[2] According to different sources.
* Means.

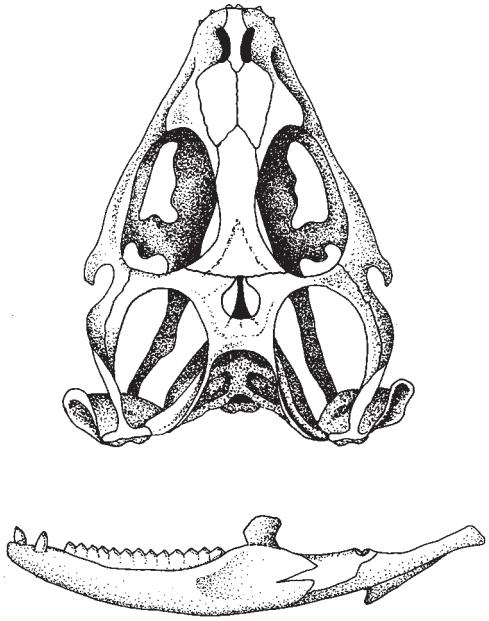

FIG. 1.5. Scull (from above) and lower jaw of the Caucasian Rock Agama *P. caucasia.* After Orlova, 1981.

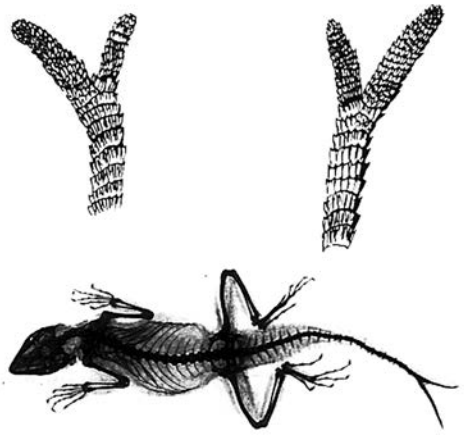

FIG. 1.6. Bifurcation of the tail distal portion during its regeneration in Caucasian Rock Agama. Bottom — radiograph of this individual. After Ananjeva and Danov, 1991.

The dental system is usually well differentiated. Usually two or three teeth are located on premaxilla, while 12–15 (rarely up to 18) triangular acrodont teeth are positioned on maxilla and the dental bone. Each side of both the maxilla and the mandible bears an 'incisor', a 'fang' and 12–15 broader 'molars', named by analogy with the heterodont teeth of mammals (Ananjeva, 1992; Fig. 1.5). Rock agamas chew hard food items by moving their jaws. A large agama can bite quite hard. A lizard imprudently offered a finger, holds on to it with an iron grip. The only way to get rid of it is to stand completely still for several minutes. The tongue is thick and fleshy, not bifurcated.

Skin receptors are goblet-shaped and submerged. The signal is perceived by a thin papilla ('hair') which goes from the body of the skin receptor and protrudes through a microscopic opening in the scale. In all species studied the number of receptors per scale is usually greater on the dorsal side (up to 2–4 vs. solitary receptors on ventral scales). However, due to the larger number of small scales on the ventral side the total number of receptors there is1.2–1.9-fold greater than on the dorsal side (Ananjeva *et al*., 2000). In *P. caucasia* and *P. lehmanii* the highest density of skin receptors is recorded on the jaws, up to 6–9 on each scale. In *P. erythrogaster* the papillae of these receptors form structures similar to mammals' eyelashes around the eyes (Ananjeva *et al*., 2000). Skin receptors are very similar in the Himalayan Agama and the Bukhara Rock Agama, differing from those in all the other Eurasian rock agamas studied (Ananjeva, 1992; Ananjeva *et al*., 2000).

Old receptors are lost during each Molt, and new ones develop. The function of skin receptors in rock agamas remains obscure. It is assumed that they are mechano- or thermoreceptors (Ananjeva, 1992; Ananjeva *et al*., 1991;

Matveyeva and Ananjeva, 1995). However, they might also function as chemoreceptors (Panov and Zykova, 1999).

A characteristic feature of rock agamas is their ability for tail autotomy (the break occur between the vertebrae) and regeneration of the lost tip, which may bifurcate (Fig. 1.6). In some species (*P. caucasia*, *P. stoliczkana*, *L. agrorensis*, *L. nupta L. tuberculata*) up to 80% of individuals have autotomised tails. These species can regenerate their tails, but this ability is most pronounced in some species of the '*himalayana*' group (*P. himalayana*, *P. bochariensis*), in which the regenerated portion may reach 90 mm. On the other hand, in the Turkestan Rock Agamas *P. lehmanni* the regeneration ability is practically lacking (Ananjeva, 1992).

The flattened body, the spiky scales with caudally directed spikes and the ability for autotomy are considered as adaptations for using narrow cracks in rocky surfaces as shelters. Indeed, a rock agama cannot be pulled from such a crack by the tail. In such situations these reptiles invariably resort to autotomy, even though a quite significant pulling force is often necessary to break the caudal part of the spine.

1.1.2. Size and proportions

Rock agamas are typical K-strategists, which means, in particular, that they live for a long time in the wild: definitely up to 7 years and up to 12–13 years according to some data (Zykova and Panov, 1991). In *Stellagama stellio* SVL ranged between 90.05–133.14 mm (mean: 109.58 ± 10.26) in males and 86.24–130.43 mm (mean: 105.83 ± 10.68) in females. The age ranged between 2–9 (mean: 5.34 ± 1.63) in females and 3–10 years (mean: 5.72 ± 1.82) in males. No significant difference in terms of age and SVL between sexes was found in this species (Ergül *et al.*, 2014).

Intersexual differences in body size were male-biased (SDI= – 0.03) but this relation was not statistically significant. A significant difference between the lowland (below 800 m) and mountain (above 800 m) populations was found in respect of SVL, with mountain individuals being larger than the lowland. However, the age difference between lowland and mountain populations appears to be not significant. A significant positive correlation was found between the age and SVL both in males and females. Individuals reached maturity between 2 and 3 years (Ergül1 *et al*., 2014).

Rock agamas grow each year until their death. This explains the fact that the body size varies broadly in each population. The length of the body with the head (SVL) of an adult rock agama may exceed 300% of this value for a newly hatched individual from the same population.

Actually, lizards younger than 1.5 years and those that have survived more than three winters, can be considered as two different life forms. They have very different foraging and spatial strategies, avoid predators differently and exhibit different social behavior. In different populations of the same species with the same starting body size of hatchlings, growth rate may differ. Therefore, the body size of the lizards of maximum age in such populations is also significantly. It is these maximum size values rather than the means for samples of males or females that should be considered as the characteristic features of a local population, a geographic race or a species (Zykova and Panov, 1991).

The varying growth rate, the fixed maximum attainable size of adults and a similar size of hatchlings are probably stable population-specific characteristics. In species with large and small maximum size of adults egg size is very similar (Table 1.2). The same can be said of lizards at early stages of post-hatching development. Unfortunately, the scarcity of the data on early ontogenetic stages precludes statistical comparisons of the data summarised in Table 1.2.

The size of closely related species is sometimes comparable (*P. himalayana – P. bochariensis – P. badakhshana*). However, this is not always so (cf. data on *P. himalayana* and *P. stoliczkana*). Therefore, the maximum size can hardly be used for verifying genealogical relationships between species. There may be distinct differences in the general size even when two forms exchange genes in the zone of parapatry, e.g. *S. stellio brachydactyla* vs. 'Near East rock agama' *S. stellio* ssp. (Panov and Zykova, 1997). The degree of size variation between species from the genera *Laudakia*, *Paralaudakia* and *Stellagama* can be assessed using the data in Table 1.3. This table also gives the values of ratio 'tail length / SVL', which may be used as a morphological character for taxonomic purposes.

Table 1.3.

Maximum size and proportion tail length/SVL in some rock agama species

Taxon	SVL max (mm)		Tail length: SVL		Sources
	Males	Females	Males	Females	
S. stellio brachydactyla	148	141	1.2	1.2	Panov and Zykova,1997
S. stellio subsp.	120	112	1.5	1.4	Panov and Zykova,1997
L. agrorensis	92	90	2.3[1]		Boulenger, 1885 Anderson and Leviton, 1969
L. melanura	142	130	2.3–2.7[1] 2.1 1.9		Minton, 1966 Anderson, 1999
L. nupta nupta	151	148	1.8–2.2[1]		Minton, 1966
L. nupta fusca	162	140	1.8[1]		Minton, 1966
L. nuristanica	131	93[2]	2.0	1,9	Anderson and Leviton, 1969
L. pakistanica	150, 156	124	2.1–2.4	2.1–2.3	Baig, Bohme, 1996
L. tuberculata	140	138	2.0	1,9	Waltner, 1991
L. sacra	147	130	1.6	1.5	Ananjeva *et al*., 1990
P. badakhshana	82[3]	80[3]	1.7	1.7	Anderson and Leviton, 1969
P. bochariensis	120	95	1.8–2.2		Ananjeva *et al*., 1981
P. caucasia	139–174[4]	135–158[4]	1.4	1.3	Panov and Zykova,1995
'*triannulata*'	159	158	1.5	1.5	Ananjeva and Ataev , 1984
P. erythrogaster	150	145	1.1	1.0	Panov and Zykova,1996
P. himalayana	85[3]	78[3]	1.9–2.0	1.6–1.7	Yakovleva, 1964
	108	96	1.5	1.4	Ataev, 1985
	–	–	1.7–2.0	1.4–1.6	Ananjeva *et al*., 1981
P. lehmanni	143	140	1.5	1.4	Ataev, 1985
P. microlepis	133	149	1.13[5]	–	Anderson, 1999
P. stoliczkana stoliczkana	144[1]		1.6[1]		Ananjeva, 1997
P. stoliczkana altaica	150[1]		1.4 –1.6[1]		Ananjeva, 1997

[1] Both sexes pooled.

[2] On examination of single specimens (eggs in oviducts).

Sex-related variation is apparent not only in the general size but also in the relative tail length[1]. Males usually have longer tails than females; however, this may be true for some populations of a given species but not for the others (Panov and Zykova, 1995). The yearlings of the Caucasian Rock Agama have longer tails than the adults (Panov and Zykova, 1995). The same is true of the Kashmir Rock Agama *L. tuberculata*, in which the tail growth rate declines with sexual maturity (in males to a lesser degree than in females). This difference is not statistically significant, however, so that the adult males and females have similar 'tail : SVL' ratio.

Interestingly, in this species tail grows faster at low altitudes as compared with high-altitude populations within the same region, so that the former have relatively longer tails. Besides, toes are longer in low-altitude Kashmir Rock Agama populations, and in both low and high-altitude populations the fourth hindleg toe is significantly longer in males than in females of the same age (Waltner, 1991).

The relative size and and shape of the head is also sex-biased: it is longer and higher in males. Head : body ratio (expressed as percentage) in males and females varies in different populations of *S. stellio* between 31–33 and 29–30, respectively; in *P. caucasia*, between 24–27 and 24–25; and in four species of the so-called '*himalayana*' group, between 26–28 and 25–26 (Daan, 1967; Ananjeva *et al*., 1990; Panov and Zykova, 1995). In the Caucasian Rock Agama the relative growth rate of the head decreases with age: in yearlings it makes up 27–30% body length (Panov and Zykova, 1995).

A faster growth of the head with increasing age in males as compared to females has been reported in *L. tuberculata* (Waltner, 1991). Daan (1967) suggested that a similar pattern exists in *S. stellio*.

Species of rock agamas sometimes differ by the skull height, which is estimates as head breadth : head height ratio. The difference is usually small (1.7–2.0 within the genus) and not statistically significant. *P. erythrogaster*, *P. lehmanni* and *L. sacra* are 'high-headed' species (Ananjeva *et al*., 1990). However, this viewpoint needs to be clarified. In one Caucasian rock agama population the yearlings had significantly higher heads than the adults. Adult males tend to have higher values of this parameter than adult females.

1.1.3. Pholidosis

Scales significantly differ in different parts of of the body. Their arrangement is in general species-specific, even though most characters vary broadly within species. The most important species-specific character is the overall number of scales on the surface of an individual. A proxy for this character is the number of elements on the line drawn around the middle part of the body. The mean values vary between 87–92 in the Redbelly Rock Agama *L. erythro-*

[1]A series of recent publications on sexual dimorphism in different species of rock agamas (Cheatsazan *et al*., 2006, Cheatsazan *et al*., 2008, Heidari *et al*., 2010, Aghili *et al*., 2011) is beneath criticism. Sample sizes of males and females are either too small (the minimum of 9–12 individuals) or, on the contrary, inflated by including the individuals from younger age groups. The failure to reveal statistically significant difference between the size characters of males and females is apparently due to these drawbacks in two cases out of four.

[3] Possibly on immature individuals.

[4] For different populations (see Chapters 2 and 3).

[5] On examination of a single specimen, tail may be broken (see Boulenger, 1885: 366).

Table 1.4.

Some features of pholidosis in rock agamas

Taxon	Scales around midbody	Scales number across vertebral band	Scales of vertebral band	Posterior edge of vertebral band scales are jagged vertically	Lateral extensions of vertebral band	Spiny scales on flanks	Whorls number in tail segment	Scales number around the tail	Upper labials	Lower labials	Nuchal crest
1	***2***	***3***	***4***	***5***	***6***	***7***	***8***	***9***	***10***	***11***	***12***
S. stellio brachydactyla	97–127 (**119**)	5–7	Strongly spined	+[1]	+++	++	2(1)	12–14	10 –14 (**12 ± 2.1**)	12–13 (**13 ± 1.0**)	–
S. stellio subsp.	116–147 (**132**, **137**)[2]	1+(3–5)+1	Keeled with strong spines	–	+++	++	2(3)	12–13	?	?	–
L. agrorensis	106–130	8–12	Distinctly keeled	–	Sometimes	++	3	28–33 (**30 ± 2**)	?	?	+
L. melanura	120–130	6–11[3]	Distinctly keeled with spines	+	–	–	Segment s inconsistent, starts with 2–3 whorls and gradually changes into 5, sometimes 6 in terminal part	18–28 (**21 ± 5**)	12–15 (**14 ± 1**),	13–14 (**13 ± 1**)	+
L. nupta nupta	75–106 (**92**)	15–18 (cover most parts of the dorsal surface)	Slightly keeled with spines	+	–	–	Only little away from pelvic, each segment consists of 3 whorls, but occasionally may be 4 in terminal end	18–28	12–18 (**15 ± 1**)	12–17	+
L. nupta fusca	max. 180	13–16	Strongly mucronate	–	–	–	As in the nominate form	13–22	?	?	–

Table 1.4.

1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
L. nuristanica	230–248	10–12	Strongly spined	–	–	–	4	43–48 (**46 ± 2**)	11–13 (**12 ± 0.8**)	10–12 (**11 ± 1.0**)	–
L. pakistanica	146– 178 (**154, 157, 171**)	8	Keeled	–	+?	++	starts with 3, but from mid of the tail changes into 4	31–36	11–13	11–13	Rudi-mentary
L. tuberculata	134–221 (**171**)	11–16[3] (**12**)	Slightly keeled	–	–	–	4, but 3 on ventral side	28–46 (**36 ± 4**)	8–12 (**10 ± 1**)	8–12	–
L. sacra	230–247 (**240**)	6–7[3]	Slightly keeled	+	–	+	4, but 3 on ventral side	30–32 (**31± 1.0**)	9–10 (**10 ±0.4**)	9–10	–
P. badakshana	112–132	6–8 [3]	Smooth to weakly keeled	–	–	++	3	26–32	10–13	10–13	–
P. bochariensis	98–112 (**105**)	7–8	Keeled	–	+	+++	3	22–27 (25 ± 2)	9–11	9–11	–
P. caucasia	125–150 (**149–133**)	5–10 (**6–7**)	Smooth to distinctly keeled with spines in different populations (character is very variable)	–	Sometimes	+ *only at few sectors*	2[4]	18–21 (**20**), in Pakistan 25–30	10–16	10–16	–
'*triannulata*'	167–208 (**190**)	– (**7, 9**)		–	–	++	3	20–26 (**23**)	12–15	2–15	–
P. erythrogaster	80–118 (**87–94**)	7–16 10–12	Distinctly enlarged, almost equal in size, strongly keeled and spined	+	+++	+++	2	24–29 (**27 ± 2**)	13–15	13–15	–