

## Two New Subspecies of *Trapelus agilis* Complex (Sauria: Agamidae) From Lowland Southwestern Iran and Southeastern Pakistan

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**Abstract.**—Based on conducting long-term excursions and carrying out extensive field work in various parts of the Iranian Plateau and studying preserved (museum) material including the syntypes of Olivier's *Agama agilis*, and paralectotypes of Boulenger's *Agama isolepis*, two new subspecies of the wide-ranging Asian ground agamid *Trapelus agilis* complex are described from the lowland southwestern Iran and southeastern Pakistan (and adjoining northwestern India) respectively. The former of the new subspecies has conventionally been considered as belonging to *T. a. agilis*, and the latter to *T. a. isolepis*. They are distinguishable from the other subspecies of *T. agilis* complex by having several distinctive morphological characteristics. The distinctiveness of both subspecies is confirmed according to the author's previous extensive studies on this complex using uni- and multivariate analyses of morphological characters. Both subspecies mainly occur as geographical isolates in the periphery of the main range of the complex, and both have mainly been separated from the central continuum (= *T. a. agilis*) by eco-geographical barriers and are almost entirely restricted in distribution to the lowlands, desert and semi-desert regions with high annual temperature. A taxonomic and biogeographic account as well as a key to subspecies of *T. agilis* complex are presented.

**Key words.**—*Trapelus agilis* complex, *T. a. khuzistanensis*, *T. a. pakistanensis*, New subspecies, Agamidae, Lowland southwestern Iran, Southeastern Pakistan, Systematics, Distribution, Biogeography.

### Introduction

The, taxonomically, controversial ground agamid *Trapelus agilis* is a wide-ranging species complex distributed from extreme southwestern Iran (ca 31° N, 47° E) to eastern Kazakhstan and western China (ca 48° N, 83° E) (Fig. 1), encompassing numerous local populations (Rastegar-Pouyani, 1998). Traditionally, this complex has been divided into three subspecies; *Trapelus agilis agilis* (Olivier, 1804), *T. a. sanguinolentus* (Pallas, 1814), and *T. a. isolepis* (Boulenger, 1885) (e.g., Anderson, 1974; Welch, 1983; Wettstein, 1951). The latter two subspecies are sometimes regarded as full species by some authors (e.g., Ananjeva, 1981; Ananjeva and Tsaruk, 1987; Boulenger, 1885; Moody, 1980; Nikolsky, 1915; Zhao and Adler, 1993). On the other hand, Anderson (in press) places all different forms of *T. agilis* complex under the inclusive name "agilis" and believes that without a firm statistical ground, it is not advisable to divide the complex into separate taxonomic entities.

In a series of studies, using uni-and multivariate statistics, the author analysed geographic variation in *T. agilis* complex, synonymized *T. a. isolepis* (Boulenger) with *T. a. agilis* (Olivier), designated a new type locality as "terra typica designata" (central Iranian Plateau, about 110 km southeast of Esfahan city)

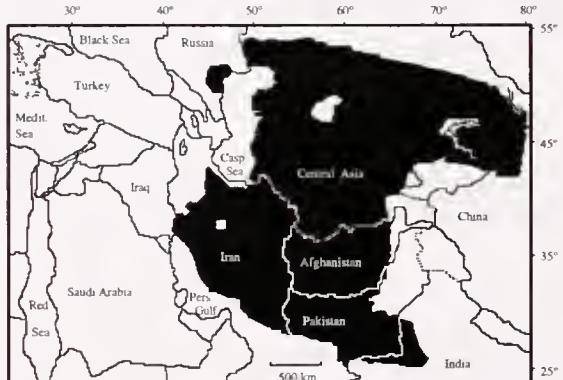


Figure 1. Geographic distribution of *Trapelus agilis* complex. (□) = *Terra typica designata* (central Iranian Plateau, about 110 km southeast of Esfahan city)

(Fig. 1), and showed that *T. agilis* complex consists of four distinct taxonomic entities (subspecies) and that the traditional tri-partite division of the complex, to a great extent, does not portray the actual phenetic patterns of geographic variation (Rastegar-Pouyani, in press, unpublished manuscript). The four distinct subspecies identified are as follows:

*T. a. agilis* (Olivier, 1804) is distributed in the central Iranian Plateau, central and southern Afghanistan, and southwestern Pakistan. Populations of this



Figure 2. *Trapelus agilis khuzistanensis*, holotype (GNHM Re. ex. 5424); A- dorsal view, B- ventral view. Note that almost all dorsal scales are distinctly small and only slightly keeled.

form (as the central core of the complex) are morphologically most similar to the syntypes of Olivier's *Agama agilis*.

*T.a. sanguinolentus* (Pallas, 1814) is the northern representative of the complex, distributed over a wide area from northeastern Iran into the Central Asian countries as far east as western China (Anderson, in press; Rastegar-Pouyani, 1998; Zhao and Adler, 1993). The two other taxa, described in this paper as new subspecies, are geographically isolated, occurring in the southwestern and southeastern margins of the main range of *T. agilis*, and mainly separated from the central continuum (*T. a. agilis*) by eco-geographical barriers. Both new subspecies are morphologically different from the syntypes of Olivier's *Agama agilis* based on several distinguishing characters (Table 1).

Since the subspecific name "isolepis" has been synonymized with "agilis" and is no longer available (Rastegar-Pouyani, in press), new taxonomic names are designated for these two new subspecies.

So, the main objective of this work is to describe and introduce these two new taxonomic entities based on the study of distinguishing morphological characters which make them recognizable from the other subspecies of *T. agilis* complex.

## Material and Methods

I conducted three long-term excursions and carried out extensive field work in various parts of the Iranian Plateau in 1995, 1996, and 1998, collected hundreds of specimens of *Trapelus agilis* and noted the pattern

of adaptation of different populations to the local conditions as well as presence of eco-geographical barriers which have been involved in differentiation and subsequent evolution of all subspecies of this complex. Also I studied preserved materials including the syntypes of *Agama agilis* Olivier, 1804 and paralectotypes of *Agama isolepis* Boulenger, 1885, borrowed from various museum collections around the world (see under "Appendix I, Abbreviations, and Acknowledgments").

In my previous studies, based on examination of about 1000 specimens of *T. agilis* all over the range, I employed uni-and multivariate statistical techniques and explored the patterns of geographic variation in morphological characters within this complex (Rastegar-Pouyani, in press, unpublished manuscript).

Indeed, the present paper is the continuation (and part of the results) of my previous studies concerning taxonomy and geographic variation in *T. agilis* complex according to which both the lowland southwestern Iranian as well as southeastern Pakistani populations do warrant taxonomic recognition.

## Subspecies accounts

### *Trapelus agilis khuzistanensis* ssp. nov.1 (Figs. 2-6)

#### Khuzistan Ground Agama

**Holotype and type locality:** adult female, GNHM Re. ex. 5224, collected by the author on 27 July 1996 from Iran, Khuzistan Province, 5 km northwest of Haft-Gel on the road to Shushtar.

**Paratypes:** 14 specimens (ten males and four females) have been designated as paratypes as follows: GNHM. Re. ex. 5225, same information as the holotype; GNHM. Re. ex. 5226, collected by the author on July 28, 1996 from Iran, Khuzistan Province, 38 km south of Masjid-e-Suleiman, Golgir village; CAS 86342, 86346, 86390, Iran, Khuzistan Province, Tul-i-Bazum [31° 55' N, 49° 25' E], about 500 m elevation, collected by S. C. Anderson on 17 April and 22 May 1958; CAS 86403-6, Iran, Khuzistan Province, along road to lake east of Haft-Gel, about 300 m elevation, collected by S. C. Anderson on 23 May 1958; CAS 86418-19, Iran, Khuzistan Province, along road between Haft-Gel and Masjid-Suleiman, by S. C. Anderson on 23 May 1958; CAS 86556, Iran, Khuzistan Province, Haft-Gel (on golf course) [31° 28' N, 49° 30' E], about 300 m elevation, by S. C. Anderson on 5 October 1958; CAS 86464, Iran, Khuzistan Province, along road south of Shushtar, by S. C. Anderson on 18 July 1958; FMNH 170936, Iran, Khuzistan Province, 85 km southeast of

Table 1. legend. Main morphological differences between *T. a. khuzistanensis*, *T. a. pakistanensis*, and the Olivier's syntypes (*T. a. agilis*).

Characters	<i>T. a. agilis</i> (n = 2) (Olivier's syntypes)	<i>T. a. khuzistanensis</i> (n = 97) (ssp. nov. 1)	<i>T. a. pakistanensis</i> (n = 32) (ssp. nov. 2)
- Reverse imbrication of head and neck scales	—	+	—
- Upper head scales	smooth	rugose and keeled	smooth or slightly rugose
- Dorsal sculation	subequal to homogeneous	subequal to heterogeneous	subequal to homogeneous
- Dorsal scales shape	distinctly keeled and mucronate	weakly to moderately keeled and mucronate	distinctly keeled and mucronate
- Ventrals	weakly keeled	smooth or weakly keeled	distinctly keeled in males
- Body	moderately depressed	moderately depressed	sometimes spindle-shaped and compressed in males
- Head	subcordiform	often roundish	subcordiform and more pointed
- Tail	round or weakly compressed	often distinctly compressed in males	strongly compressed in males
- Preanal callose scales	two well developed rows	often one row (in the case of two, the second undeveloped)	almost always one row in males, absent in females
- Nuchal crest	absent	absent	often present
- Background coloration	olive-grey	yellowish-grey-cream	often sandy-grey
- Scales around body	79-88	80-97	67-83
- Supralabials	17-19	15-18	13-16
- Infralabials	17-20	14-19	12-16
- Subdigital lamellae under fourth toe	24-26	16-20	22-28

Ahwaz, Meshrageh, collected by D. Womochel and A De Blase on 20 October 1968.

**Diagnosis:** *Trapelus agilis khuzistanensis* differs from all other subspecies of *T. agilis* in its higher number of scales around body (80-97); subequal and almost heterogeneous dorsal sculation with distinctly small dorsals and ventrals; a shorter head and neck; significantly lower mean number of subdigital lamellae under the fourth toe; reverse imbrication of the posterior head and anterior neck scales; keeled or rugose upper head scales; usually one, and sometimes two rows of callose preanal scales (absent or slightly developed in females); strongly compressed tail in males of most populations; and an exclusive dorsal coloration (yellowish-grey-cream with weak or without reddish-brown cross bars).

**Description of holotype:** an adult female, preserved in 70% ethyl alcohol in good condition; head short but longer than broad with very convex forehead, its length 0.26 of body length and 0.19 of tail length; canthus rostralis more or less continued as a supraciliary ridge; nostril on, or, barely, above the canthus, pierced in a flat shield and posteriorly directed; 3 internasals in a transverse row; upper head scales heterogeneous, keeled or rugose, imbricate and subimbricate; supraciliary ridge strongly developed, composed of 9 scales on each side; 17-18 upper- and



Figure 3. *T. a. khuzistanensis*, holotype (GNHM Re. ex. 5424); neck and head regions with reversely-imbricated scales.

17-17 lower labials; tympanum horizontally elliptical, smaller than orbit, partly covered above by 4-5 small spinose scales; scales of posterior part of head and anterior part of neck distinctive in that their imbrication is reversed (i.e., towards the head) and the posterior border of reversely-imbricated scales is defined by a single large and pointed scale; gular pouch moderately developed; gular region covered by small, imbricate, slightly keeled or smooth scales; gular fold and a fold in front of shoulder strongly developed; body and head moderately depressed; limbs rather slender; dorsal scales subequal to unequal, small, imbricate, slightly keeled and mucronate; median dor-



Figure 4. *T. a. khuzistanensis*, one of the male paratypes (FMNH 170936). Note the presence of a strongly compressed tail and relatively heterogeneous dorsal scalation.



Figure 5. *T. a. khuzistanensis*, posterior ventral region of a male paratype (GNHM. Re. ex. 5426) with one row of callose preanal scales.



Figure 6. Habitat and type locality of *T. a. khuzistanensis*, 5 km northwest of Haft- Gel on the road to Shush-tar, Khuzistan province, southwestern Iran. In the foreground the author is attempting to capture the holotype from inside of its underground hole.

sals relatively larger, grading into distinctly smaller scales of dorsolateral region which are only slightly keeled and mucronate; 94-95 scales round middle of body; scales of upper surface of limbs larger than median dorsals, distinctly keeled, slightly mucronate; lower surface of digits covered by bi- or tri carinate lamellae, 18-19 under the fourth toe; ventral scales almost as large as median dorsals, imbricate, very slightly keeled or smooth, 84-85 scales in a single row from gular fold to the anterior edge of anus; callose preanal scales in one row, slightly developed, consisting 10 scales; caudal scales larger than median dorsals, strongly keeled, distinctly mucronate, 34-36 around base of tail just behind vent; tail weakly compressed at base, distinctly so towards the tip, its length 1.39 of body length.

**Coloration and color pattern:** upper surface of head and limbs uniformly yellowish-grey, ground color of dorsum yellowish-grey-cream with 5 large, broad, light-brown cross bars from nape to sacrum, interrupted by a series of light, large vertebral ocelli and

two paravertebral rows of smaller ones, proximal upper caudal region with distinct dark-grey bars; ventral surfaces uniformly whitish.

**Measurements (mm):** Total length = 206; Snout-vent length (SVL) = 86; Tail length (TL) = 120; Head length (HL) = 23; Head width (HW) = 19; Head depth (HD) = 12.8; Length of forelimb = 45; Length of hindlimb = 62.

**Variation of the type series:** all paratypes closely approximate the holotype both in morphology and meristics.

The range of the number of scales around body for the whole series ( $n = 14$ ) is 82-97 and the mean 88.5; in all paratypes the number of subdigital lamellae under the fourth toe varies between 16-19; dorsal scales are subequal or heterogeneous (especially in males); there are some differences, however, between male and female paratypes.

- **Male paratypes:** all male paratypes ( $n = 10$ ) are either uniformly yellowish-grey-cream dorsally or with a weakly developed pattern of dark cross bars; as well, the ventral pattern is either uniformly whitish or with distinct pattern of bluish-brown on the gular region, chest and flanks; tail strongly compressed in almost all males; preanal callose scales in one or two rows, in the latter case the second row weakly developed, their number varies from 10-21; dorsal scales more keeled and mucronate and distinctly heterogeneous, approaching *T. persicus* in this respect; ventrals weakly keeled, gular sac distinctly developed; reverse imbrication of the posterior head and anterior neck scales relatively more pronounced and the large scale on posterior end of these reversely-imbricated scales more distinctive and mucronate than in females.

- **Female paratypes:** all female paratypes ( $n = 4$ ) resemble the holotype in almost all pertinent details; the preanal pores are only in one row, weakly devel-

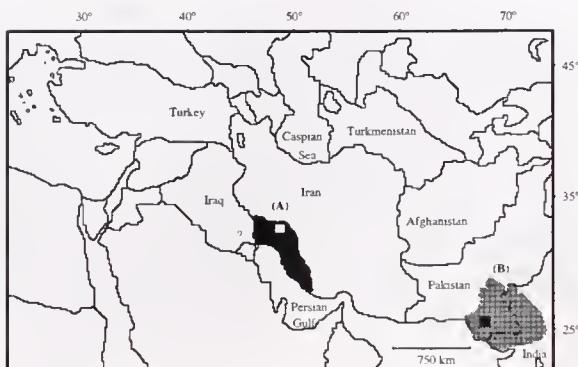


Figure 7. Geographic distribution of *T. a. khuzistanensis* (A) and *T. a. pakistanensis* (B). Squares represent the type localities.

oped, each occupying the tip of a scale, their number varies from 8 to 11; all the dorsal scales weakly keeled and mucronate; tail round or weakly compressed; slight differences in dorsal pattern occur (in some specimens the dorsal cross bars are more intense).

**Habitat:** in lowland southwestern Iran and in the western foothills of the Zagros Mountains, this subspecies mainly occurs on sand dunes, alluvial soils, open plains, low hills, and on dry stream channels (Anderson, 1966a, in press; personal observations). The type locality is specified by numerous low sand dunes as well as gypseous hills imminented with an open plain. The vegetation is sparse, mainly *Artemisia*, *Alhagi*, *Zygophyllum*, and *Euphorbia* association. The climate conditions being harsh, with hot and long summers (about 40°–50°C) and mild, short winters. It seems that this lizard is active throughout the year but Anderson first observed it in the western foothills of the Zagros in early March, becoming numerous by mid-April; both newly hatched and half-grown juveniles were observed in late October and early November (Anderson, 1963: 446).

The holotype and one of the paratypes were collected about 5 km northwest of Haft-Gel on the road to Shushtar. They were active when air temperature was 45°C and the substrate was 49.5°C. When alarmed, unlike most of the central Plateau populations which usually retreat into the base of dense bushes, they retreated into the underground holes; this may be due to vegetation scarcity. Both specimens were captured inside their underground holes (Fig. 6). The third specimen collected near the mouth of an old well in the vicinity of the village of Golgir (38 km south of Masjid-e-Suleiman) while trying to retreat into the well.

**Distribution:** the main distributional range of this subspecies is the Khuzistan Plain which is an extension of the Mesopotamian lowlands (Fig. 7). Also, it penetrates into the western foothills of the Zagros Mountains up to 900 m elevation. It is the westernmost representative of the wide-ranging *T. agilis* species complex. The Zagros Mountains serve as a strong barrier to its further eastward distribution, so it has almost no contact with the central Iranian Plateau nominal subspecies (*T. a. agilis*), except in the southeastern regions of Bushehr province, southern Iran where the two taxa occur as parapatric (Rastegar-Pouyani, Manuscript, a). Its occurrence in the lowland southeastern Iraq is almost unlikely and, so far, there is no proper record inside the Iraqi territory [except the Olivier's original record (1804) which is strongly doubtful]. If it occurs in southeastern lowland regions of Iraq, then the Tigris might have served as an effective barrier to its further westward distribution.

In some areas of lowland southwestern Iran (e.g., 85 km southeast of Ahvaz) it occurs as sympatric with *Trapelus persicus* (Blanford, 1881) but there is no proper record of intergradation, if any, between the two taxa.

**Etymology:** *Trapelus agilis khuzistanensis* is so named as it is mainly restricted in distribution to the lowlands of southwestern Iran, Khuzistan province.

#### *Trapelus agilis pakistanensis* ssp. nov.2 (Figs. 8-9)

##### Pakistan Ground Agama

**Holotype and type locality:** adult male, SMF 63258, collected by M. G. Konieczny on 31 March 1957 from Gaj-River, Kirthar Range, southeastern Pakistan.

**Paratypes (7 specimens):** SMF 63259, 63279, same information as the holotype; SMF 63256, collected by R. Mertens on 1st December 1952 from Sonda, Distr. Thatta, southeastern Pakistan; SMF 63243-4, 63286-7, collected by M. G. Konieczny on 26 April 1961 from Old Airport of Karachi, southeastern Pakistan.

**Diagnosis:** *Trapelus agilis pakistanensis* differs from the other subspecies of *T. agilis* complex by having a combination of distinctive characters; body and head sometimes compressed (not depressed) in males; males almost always with one row of callose preanals (rarely a second undeveloped row may be present); females without callose preanals; dorsal scales relatively flat, subequal to homogeneous, distinctly keeled throughout and mucronate, grading into small dorsolaterals rather abruptly (especially in males), 67-83 around body; ventral scales also often distinctly keeled in males; body and limbs often strongly slender and head distinctly pointed (in adult males); tail

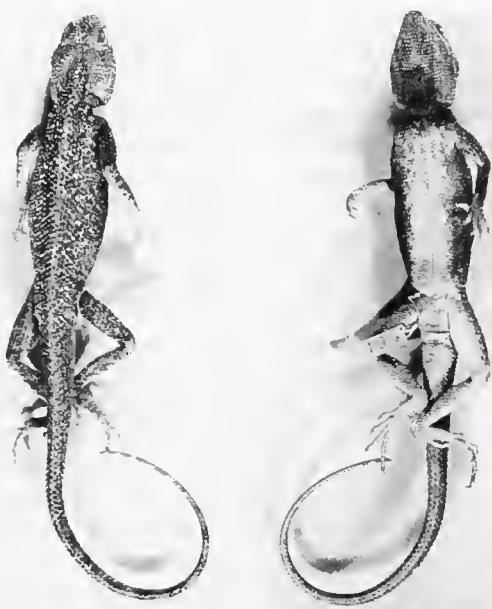


Figure 8. *T. a. pakistanensis*, holotype (SMF 63258); A- dorsal region, B- ventral region. Note the presence of a strongly compressed tail, and pointed and slender body and head.

often strongly compressed in adult males, its length more than 1.55 of body length; the mean number of supra- and infralabials significantly lower than those of the other subspecies; a rudimentary nuchal crest often present.

**Description of holotype:** an adult male, preserved in 70% ethyl alcohol in good condition; head pointed with a slightly convex forehead, its length 1.36 of its width and 0.27 of body length and 0.15 of tail length; canthus rostralis continued as a supraciliary ridge which is rather strongly developed, composed of 7 scales on each side; nostril as a horizontal slit, slightly above canthus rostralis, pierced in a triangle-shaped scale, posteriorly directed; 4 internasals in a single transverse row; upper head scales subequal, smooth, or slightly rugose, imbricate and subimbricate; 14-14 upper- and 13-13 lower labials; tympanum horizontally elliptical, smaller than orbit, partly covered above by 6-8 spinose scales; no reversal imbrication of scales on the posterior part of head and anterior part of neck; a rudimentary nuchal crest composed of 6-7 spinose scales; gular sac moderately developed and rather pointed posteriorly; gular region covered by large and small, imbricate, and slightly keeled scales intermixed; gular fold and a fold in front of shoulder strongly developed; body slender and distinctly compressed laterally, a prominent vertebral ridge throughout the dorsum; limbs distinctly slender; dorsal scales subequal to homogeneous, rather large,



Figure 9. *T. a. pakistanensis*, holotype (SMF 63258); posterior ventral region. Note the presence of only one row of callose preanal scales and distinctly slender hindlimbs.

imbricate, almost entire individual scale distinctly keeled (unlike the eastern populations of *T. a. agilis* in which only the proximal part of scales are keeled) and mucronate; median dorsals larger, grading into distinctly smaller scales of dorso-lateral region which are only slightly keeled and mucronate; 72-73 scales round the widest part of body; ventral scales rather distinctly keeled, imbricate, large, but slightly smaller than median dorsals, 70-71 in a single longitudinal row from gular fold to the anterior edge of anus; scales of upper surface of limbs almost as large as median dorsals, strongly keeled and mucronate; lower surface of digits covered by bi- and tri-carinate keeled lamellae, 24-25 under the fourth toe; preanal callose scales only in one row, not exceptionally developed, encompassing 8 scales; all caudal scales distinctly keeled and larger than median dorsals, 33-35 around base of tail, just behind the vent; tail long and strongly compressed throughout, its length 1.81 times of body length.

**Coloration and color pattern:** upper surface of head yellowish-grey; dorsum uniformly sandy-grey with numerous light scales scattered throughout; upper surfaces of limbs olive-brown; upper caudal region as dorsum in coloration with barely distinct dark-brown rings; gular region, chest, and flanks heavily suffused by lavender-blue; other ventral surfaces yellowish-white; no black patch on the shoulder fold.

**Measurements (mm):** Snout-vent length (SVL) = 101.6, Tail length (TL) = 184, Head length (HL) = 28.2, Head width (HW) = 20.7, Head depth (HD) = 13.5, Length of forelimb = 50, Length of hindlimb = 73.

**Variation of the type series:** all paratypes are similar to the holotype both in morphology and meristics. In all specimens nostril is almost above the canthus rostralis and a rudimentary nuchal crest, more or less,

developed. The range of scale counts around body for the whole series ( $n = 7$ ) is 69-81 (mean 74.42). The range of ventral scales from gular fold to the anterior edge of anus (in a single longitudinal row) varies from 67-77 (mean 74.57). In all paratypes the number of subdigital lamellae under the fourth toe varies from 22-26 (mean 23.85). The number of supra-and infra labials varies from 13-16 (mean 14.55) and 12-16 (mean 14.25) respectively. Dorsal scales being homogeneous or subequal and, more or less, set off from the small dorsolaterals.

However, there are some differences in morphology between males and females:

**- Male paratypes:** all male paratypes ( $n = 4$ ) resemble the holotype in almost all relevant details; the mean SVL = 90.5 mm, TL = 155 mm; mean TL 1.71 times as mean SVL; the preanal callose scales almost only in one row (in the case of two, the second row rarely developed), encompassing 10-11 scales (mean 10.4); median dorsal scales enlarged, homogeneous, distinctly keeled throughout and mucronate, forming distinct ridges along dorsum, grading, rather abruptly, into small dorsolaterals which are weakly keeled and mucronate; all ventral scales, as in holotype, more or less keeled, rather large, but smaller than median dorsals; tail strongly keeled in almost all specimens, although body not as strongly compressed and pointed as in the holotype; color pattern almost as in holotype.

**- Female paratypes:** in females ( $n = 3$ ), the body and tail are normal (neither distinctly compressed nor slender), the dorsal scales are moderately keeled and mucronate and median dorsals are not clearly set off from the small dorsolaterals; as well, ventrals are slightly keeled and distinctly smaller than the median dorsals; callose preanal scales absent; gular sac not as well developed as in the holotype; in color pattern some of them are rather different from the holotype in the presence of, more or less pronounced, dark cross bars and a series of vertebral light ocelli and in the absence of ornamentation in the lower parts of body; ventral surfaces being uniformly whitish.

**Habitat:** the habitat of this subspecies is characterised by flat alluvial plains as well as some high slopes. The vegetation consists of some grass, herbs, and stunted shrubs. Some populations occur on the lowlands around Karachi, and the eastern part of the range is a typical desert known as Thar Desert in eastern Sind extending into adjacent northwestern India (the great Indian Desert). This desert mainly consists of sandy hills which vary from small dunes to hills with 100-150 m elevation. In summer, dust storms are the main feature of the area (Khan, 1980).

**Distribution:** *Trapelus agilis pakistanensis*, as the southeasternmost subspecies of *T. agilis* complex, is restricted in distribution to the lowland and semi-desert regions of Sind province, southern Punjab, and some regions of eastern Baluchistan (southern and southeastern Pakistan), from around Hab River in the west through Karachi and Thatta to the vicinity of Hyderabad and Mirpur Khas eastward into the Indian Desert (Fig. 7). Biswas and Sanyal (1977) recorded this lizard inside the Indian territory (from Jaisalmer, Kolayat, Pugal, Phalodi and some other localities in Rajasthan Desert, northwestern India); to the north, it is distributed along the Kirthar Range up to the areas south of Khuzdar (south-central Pakistan). Apparently the Hab River serves as a barrier for further distribution of this taxon towards the west; however it is parapatric with its *T. a. agilis* in the eastern regions of Baluchistan province. In the east, it goes up to the Nagaur District, Rajasthan, northwestern India.

**Etymology:** *Trapelus agilis pakistanensis* is so named as it is restricted in distribution to the lowland and semi-desert regions of southeastern Pakistan and adjacent northwestern India.

#### Taxonomic and biogeographic account

Detailed discussion concerning systematics and patterns of geographic variation in *Trapelus agilis* complex is presented elsewhere (Rastegar-Pouyani, Manuscript a-b) and here is not dealt with in details. As a brief account, however, it can be mentioned that I classified all populations of *Trapelus agilis* complex throughout the range into four distinctive taxonomic entities (and as the most parsimonious definition= subspecies): *T. a. agilis* (Olivier, 1804), *T. a. sanguinolentus* (Pallas, 1814), *T. a. khuzistanensis* ssp.nov.1, and *T. a. pakistanensis* ssp.nov.2.

An ANOVA-based pairwise comparison showed that in most metric and meristic characters these four taxonomic entities are significantly different ( $P < 0.05$ ) (Rastegar-Pouyani, Manuscript, a). Also employing multivariate statistical techniques (principal component analysis, canonical variate analysis, and cluster analysis), to a great extent, showed the objectivity of these four distinct groups within *T. agilis* complex and re-confirmed my previous taxonomic decisions (Rastegar-Pouyani, Manuscript, b). Of the four subspecies of *T. agilis*, the nominal form (*T. a. agilis*) occurs in a wide range of habitats, shows higher degree of morphological variability, occupies the central and southern parts of the species range (these regions might have served as a refugia during intervals of unfavorable and cold climatic conditions in the Tertiary and Quaternary), and consists of two western and eastern

groups of populations (clines) (Rastegar-Pouyani, in press, unpublished manuscript). With regard to these factors, it could be logical if we consider this form as the central core of the complex and as the parental population from which the other subspecies have been derived. So, preliminarily, I propose the following scenario for origination and subsequent evolution of the three marginal subspecies which occur in the periphery of the main range of the complex being parapatric with the central continuum (= *T. a. agilis*):

It seems that *T. a. sanguinolentus*, in spite of being distributed over a very wide area, is the most recently-evolved group, originated from the parental populations in the southern parts of the range (apparently) in the very Late Pliocene and Pleistocene (2-1.2 MYBP = millions of years before present), invading towards the northern and northeastern regions during intervals of favorable climatic periods. The very low degree of variability observed in this subspecies is indicative of its recent history. *Trapelus a. pakistanensis* separated from the central continuum in the southeastern parts of the range (probably by dispersal or, less likely, due to a vicariant event) distributed towards the east and reached as far east as northwestern Indian desert. This invasion might have taken place in the Pliocene (5-1.7 MYBP). In the southwestern part of the range, a drastic vicariant event (the huge orogeny of the Zagros) separated the southwesternmost populations from rest of the complex and from the parental populations. These isolated populations served as founders and, with further divergence, gave rise to *T. a. khuzistanensis*. Apparently, this vicariant event has taken place in the Late Miocene or early Pliocene (7-4.5 MYBP). Therefore, we can say that both dispersal and vicariance have been involved in radiation and subsequent evolution of various subspecies of *Trapelus agilis* complex though the role of dispersal in evolution of *T. a. sanguinolentus* and *T. a. pakistanensis*, and vicariance in evolution of *T. a. khuzistanensis* are more prominent.

*Trapelus agilis* (Olivier, 1804) is the easternmost representative of an essentially homogeneous and similar group of about five species complexes which also include *T. persicus* (Blanford, 1881) in the Mesopotamian Plain and lowland southwestern Iran, *T. flavimaculatus* Rüppell, 1835 in Saudi Arabia, *T. savignii* (Dumeril and Bibron, 1837) in Israel and eastern Egypt, and *T. turnevillei* (Lataste, 1880) in north Africa (north of Sahara). Although the monophyly of *Trapelus* has been shown by Moody (1980) with a morphological approach and by Joger (1991) using molecules (neither Moody nor Joger studied all the species of *Trapelus*) but, so far, no comprehensive

revisionary study has been done on all species of this genus and this is mainly because of political instability of the region and difficulties in collecting proper material throughout the range. Furthermore, even in a few studies done on a limited number of *Trapelus* species, the results obtained by morphological and the other approaches (e.g., immunological) were contradictory (e.g., Anderson, in press; Joger and Arano, 1987; Rastegar-Pouyani, in press, unpublished manuscript).

*Trapelus* is mainly Saharo-Sindian in distribution, often associated to the lowlands, desert, and semi-desert regions with high annual temperature.

### Key to the subspecies of *Trapelus agilis* complex

- 1a. Tail almost always round, two (or more) rows of callose preanal scales ..... 2
- 1b. Tail often compressed, often only one row of callose preanal scales, in the case of two, the second undeveloped (preanals absent or weakly developed in females). ..... 3
- 2a. Body size variable; 65-91 scales around body; dorsal scales subequal, weakly to moderately keeled, often strongly mucronate; ventral scales smooth or weakly keeled; usually 2, sometimes 3 (rarely 4-5) rows of callose preanals; background coloration variable; central Iranian Plateau, central and southern Afghanistan, southwestern Pakistan. . . *Trapelus agilis agilis* (Olivier, 1804).
- 2b. Body stout; 52-73 scales around body; all dorsal, ventral, and gular scales larger in size, homogeneous, strongly keeled and mucronate; almost always 2 (rarely 3) rows of callose preanals; background coloration of males often dark sandy-grey; northeastern Iran, northern Afghanistan, Central Asian Republics, western coast of the Caspian Sea (Daghestan), western China. . . *Trapelus agilis sanguinolentus* (Pallas, 1814).
- 3a. Body and limbs smaller than those of the other subspecies and sometimes relatively slender, not compressed; head and neck distinctly short; all body scales smaller than those of the other subspecies; dorsal scales subequal to unequal (heterogeneous), weakly to moderately keeled, weakly mucronate; 80-97 scales around body; ventral scales slightly keeled; scales of posterior part of head and anterior part of neck reversely imbricated; upper head scales keeled or rugose; often 14-19 upper- and lower labials; background coloration often yellowish grey-cream; lowland southwestern Iran (0-900 m elevation) ..... *Trapelus agilis khuzistanensis*, ssp. nov.1

3b. Body and limbs often distinctly slender, sometimes compressed in males; dorsal scales subequal to homogeneous, distinctly keeled and mucronate, usually clearly set off from small dorsolaterals; 67-83 scales around body; ventrals distinctly keeled in adult males; no reversal imbrication of head and neck scales; upper head scales often smooth; 12-16 upper- and lower labials; background coloration often sandy-grey; southeastern Pakistan and adjoining northwest-ern India . . . *Trapelus agilis pakistanensis*, ssp. nov.2

### Abbreviations

BMNH = British Museum (Natural History; (London, UK), CAS = California Academy of Sciences (San Francisco, USA), FMNH = Field Museum of Natural History (Chicago, USA), GNHM = Göteborg Natural History Museum (Göteborg, Sweden), MNHN = Museum National d'Histoire Naturelle (Paris, France), MZLS = Museo Zoologico de "La Specola" (Firenze, Italy), NMW = Naturhistorisches Museum Wien (Vienna, Austria), SMF = Museum und Forschungsinstitut Senckenberg (Frankfurt, Germany), SMNH = Swedish Museum of Natural History (Stockholm, Sweden), ZFMK = Zoologisches Forschungsinstitut und Museum Alexander Koenig (Bonn, Germany); ZISP = Zoological Institute St. Petersburg (St. Petersburg, Russia), ZMUC = Zoological Museum University of Copenhagen (Copenhagen, Denmark).

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## Appendix 1. Material examined

### *Trapelus agilis agilis* (n =541)

MNHN 5708 (2) = 1994. 1178 (2) (Olivier's syntypes):

170987, FMNH 170988: Iran, Gilan prov. 4.2 mi N of Tukestan (Zanjan prov. Takestan?). NMW 33166-1, Iran: Fars prov. 9 km N of Abadeh. NMW 33167, NMW 33085-2: Iran, Hormozgan prov. 14km E Bandar-Abbas. NMW 7276-1, NMW 7276-2: Iran: Kerman prov.? Sabzewan. NMW 7276-3: Iran: Kerman prov.? Rigmati, 150 km SE of Sabzewan. NMW 7276-4: Iran, Esfahan prov. 135 km N of Esfahan. NMW 33159-3, NMW 33159-4, NMW 33159-5, NMW 33165-1: Iran, Esfahan prov. Murcheh-Khurt, N of Esfahan. NMW 33165-2, NMW 33165-3, NMW 33085-1: Iran: Esfahan prov. 4 km SE Robat-Tork (165 km NW of Esfahan). NMW 33085-3: Iran, Zanjan prov. 26 km SE Ghazwin. NMW 33083-1, NMW 33083-2, NMW 33083-3: Iran, Zanjan prov. 41 km SE Ghazwin. Elev: 1380 m. NMW 33164: Iran, Tehran prov. 60 km S of Tehran. NMW 33084-3: Iran, East Azarbaijan prov. 42 km SE Mianeh. Elev: 1200 m. NMW 33166-1: Iran, Kerman prov. 15 km SE Kerman. SMNH 3139-1, SMNH 3139-2, SMNH 3139-3, SMNH 3139-4, SMNH 3139-5, BMNH 85. 5. 27. 14, BMNH 85. 5. 27. 15, BMNH 85. 5. 27. 16, BMNH 85. 5. 27. 17, BMNH 85. 5. 27. 18, BMNH 85. 5. 27. 19: Iran: Tehran (exact locality?). GNHM. Re.ex. 4437, GNHM. Re.ex. 3324, GNHM. Re.ex. 4395-1: Iran, Gilan prov. 65 km SSW of Rasht. GNHM Re.ex. 4395-2: Iran, Tehran prov. 150 km S of Tehran, Siah-Kuh, Shah-Abbas post. GNHM Re.ex. 4396-1, GNHM. Re.ex. 4396-2: Iran, Mazandaran prov. 150 km E of Gorgan, Golestan Park. La Specola 30584, La Specola 30585: Iran, Tehran prov. 50 km S Qum? BMNH 1920. 3. 20. 1: Iran, Hamadan prov. Hamadan, Jinjan? BMNH 1936. 10. 12. 1: Iran, Kerman prov. N. Of Kerman, Sekonj. 7000 ft. BMNH 1934. 12. 16. 3, BMNH 1936. 12. 16. 4: Iran, Sheakuh, seat (Salt?) desert. BMNH 1912. 3. 26. 13, BMNH 1912. 3. 26. 14, BMNH 1912. 3. 26. 15, BMNH 1906. 8. 10. 25, BMNH 1900. 5. 9. 9, BMNH 1900. 5. 9. 10, BMNH 1900. 5. 9. 11, BMNH 1900. 5. 9. 12, BMNH 74. 11. 23. 104, BMNH 74. 11. 23. 105, BMNH 74. 11. 23. 106, BMNH 74. 11. 23. 107, BMNH 74. 11. 23. 108, BMNH 74. 11. 23. 109, BMNH 74. 11. 23. 110, BMNH 74. 11. 23. 111, BMNH 74. 11. 23. 112, BMNH 74. 11. 23. 113: Iran, Sistan-Baluchestan prov. BMNH 1951. 1. 6. 50, BMNH 1951. 1. 6. 51-2, BMNH 94. 11. 13. 4, BMNH 94. 11. 13. 5: Iran, Hormozgan prov. BMNH 87. 12. 20. 1: Iran, Hormozgan prov. Kishim (=Gheshm?) Island, Persian Gulf. BMNH 79. 8. 15. 10-15: Iran, Fars prov. Dehbid, north of Shiraz. BMNH 1903. 3. 14. 1: Iran, Bushehr prov. Bushehr. BMNH 1933. 4. 1. 20-22: Pakistan, Waziristan, N. W. F. P. BMNH 86. 9. 21. 17, BMNH 86. 9. 21. 18, BMNH 86. 9. 21. 23, BMNH 86. 9. 21. 24, BMNH 86. 9. 21. 25: Afghanistan: Helmand. ZMUC R36133, ZMUC R36149-54, ZMUC R36160, ZMUC R36204-5: Afghanistan: Seistan prov. Faisabad (south of Afghanistan). ZMUC R36155-9, ZMUC R36145-8, Afghanistan, Seistan prov. Baqrabad. ZMUC R36161: Afghanistan, Seistan prov. Faisabad-Farah. ZMUC R36206: Afghanistan, Kandahar prov. Przadah, W of Kandahar. ZMUC R36208-9: Afghanistan, Kabul prov. near Kabul? ZISP 7361: Afghanistan: Harat. NMW 33170-12: IRAN, East Azarbaijan, 42 km SE Mianeh. NMW 33173-1-2: IRAN, Zanjan prov. 26 km SE Qazwin. NMW 33170-1:

IRAN, Tehran prov. 95 km S Tehran. NMW 33148-1-10: IRAN: Tehran prov. Zaveyeh, 80 km SW Tehran. NMW 7276-5-6: IRAN, Kerman prov. Sabzewan. NMW 33175-5, NMW 33170-5, NMW 33170-6, NMW 33170-7: Iran, Esfahan prov. NMW 33172-3-4: IRAN; Kerman prov. 138 km S Rafsanjan. NMW 33172-5: IRAN: Kerman prov. 29 km SE Sirjan. NMW 33165-4: IRAN, Kerman prov. 110 km SW Kerman. NMW 33172-2, NMW 33175-6, NMW 33175-7: Iran: Yazd prov. 200km SE Yazd. NMW 33174-1-8: IRAN, Khorasan prov. 15-25 km S Qayen. NMW 33163: Pakistan: Nepandgur (where?). NMW 33162: Pakistan: Delbandin. NMW 33161-1-2: Iran, Shirgesht Beiteabas. NMW 33161-3: Iran, eastern Iran, Ozbak-Kuh. NMW 33172-6: Pakistan, Baluchestan prov. 50 km W Nushki. NMW 33150-9: Iran W Sangbast. NMW 24763-1-3: Iran, N Persian, Kuh Daschteh (Taj-abad). NMW 24767: Iraq, Baghdad? (Paris Museum). CAS 120280-1: Afghanistan, 10km NE Darweshan (Central Afg.). CAS 84642-45: Afghanistan, 35 mil. down stream from Girishk, Dasht-e-Margo area, Chah-e-Angir, (Central Afg.). CAS 120242-4 Afghanistan, 12 km S Lashkargah (near Girishk), 2700ft. CAS 97990: Afghanistan, 20 mil. SE Kandahar, 31 23 N, 65 53 E, 3800 ft. CAS 90762-9: Afghanistan, Sharisafa, 60 km NE Kandahar, 1400m. CAS 90777: Afghanistan, Tarnak river, 75 km NE Kandahar, 1405m. CAS 120276-9: Afghanistan, 30km S Ghazni-Qalat 7100ft. FMNH 20987-1-10: Iran, Esfahan prov. Yazd-e-Khash. FMNH 20985-90: Iran, Esfahan prov. FMNH 20988-1-2: Iran, Daria-Masila. FMNH 245507-10: Pakistan, Baluchestan prov. SMF 63226-37, SMF 63262, SMF 63285, SMF 63255: W-Pakistan, Siah-Kuh, S Delbandin. BMNH 1951.1.6.54: Iran, Bandar-e-Lengeh. BMNH 1919.5.2.2-3: Iran, Fars prov. Abadeh. BMNH 1936.10.12.3: Iran, Fars prov. between Quatrue-Chah Salz to Neiriz road. BMNH 1966-355-57: Iran, Kerman prov. 148 km E Neiriz on Zaidabad road to Sirjan. BMNH 1951.1.2.20-22: Iran, Kerman prov. 20 mil. S of Kerman. Jupar. BMNH 1951.1.6.45-48: Iran, Sistan prov. Khash, SE Iran. BMNH 1940.3.1.19-24: Afghanistan, Ghazni, (E Afg.). CAS 141028: Iran, Kerman prov. 17km SSE Minab on inland road to Jask. CAS 141020: Iran, Kerman prov. 13 km E of Eastern edge of city of Kerman. CAS 141051: Iran, Kerman prov. 19km SE Shagu on road to Minab. CAS 141027: Iran, Kerman prov. 21 km N Rudan on road to Jiroft. CAS 141097: Iran, Sistan prov. 10km SW Hirmand, abandoned village, SE of road from Zabol to Dust-e-Mohammad Khan. CAS 141065: Iran, Baluchestan prov. 13km southerly of Zahedan on road to Khash. CAS 102484-90: Iran: Sistan prov. 15 mi SW Zabol. CAS 102491-2: Iran, Fars prov. Ahram. CAS 141149: Iran, Fars prov. 5km northerly from Dalaky on road to Shiraz where foothills begin. CAS 96270: Iran, Khorasan prov. Tayebat, about 10 mi from Afghanistan border. NMW 33150-1-6: Iran, Khorasan prov. 5 km N Taybad. NMW 33166-1: Iran: Kerman prov. 15 km SE Kerman.

### ***Trapelus agilis sanguinolentus* (n = 238)**

GNHM Re.ex. 4396 (1-2): Iran: Mazandaran prov. 150 km E of Gorgan, Golestan Park. GFN 40: Turkmenistan, Lowland steppe, East Kopet Dagh. GNHM. Re. ex. GFN 41: Turk-

menistan, Murgab River, 150 km S of Marv (Mary). GNHM. Re. ex. GFN 42-50: Turkmenistan, Sahra-Bairam-Ali, 45km NW of Marv, Kara kum desert. CAS 185104-9, CAS 185134-5: Turkmenistan, Ashgabad region [38 00 N, 58 00 E]. CAS 184570-6: Turkmenistan: Krasnovodsk region [39 45 N, 54 33 E]. GNHM. Re. ex. GFN 35: Turkmenistan, Archenjan village. GNHM. Re. ex. GFN 36: Turkmenistan, Krasnovodsk region [39 45 N, 54 33 E]. GNHM. Re. ex. GFN 43 (1-2): Turkmenistan, Kaka. GNHM Re. Ex 10622-3: Kazakhstan, at the lake (artificial) at Illi River, near village Bokter [43 54 N, 77 16 E]. ZISP 5109, 13701-15 Kazakhstan, E. Kazakhstan, Illi River, near border of China. ZISP 5796: Kazakhstan, Tardski, Dshungaria, between Kazakhstan-China. ZISP 20298 (7745-79): Kazakhstan, near Ilisk city, Illi River. E. Kazakhstan. ZISP 15143, 17329, 13695, 1168: Kazakhstan, near Ilisk city, Illi River, E. Kazakhstan. ZISP 11070 (1-12): Kazakhstan: , Illi River, E. Kazakhstan, close to lake Balkhash. ZISP 19115 (7643-84): Uzbekistan, Vicinity of Nucus city, Caracal, near Aral sea. ZISP 19398 (7428-48): Uzbekistan-Tajikistan, Fergan Valley. ZISP 15803 (1-15): Tajikistan, Fergan Valley. ZISP 20097(371-87), 10715 (3-13): Tajikistan-Afghanistan border. Termez. ZISP 13588, 13590 (1-12), 13592, 6914 (1-10): Kazakhstan-Uzbekistan, between Aral Lake and Caspian Sea. ZISP 19392 (1-24): Russia (west of Caspian Sea), Daghestan. ZISP 15753: Iran, Astarabad (= Gorgan?). CAS 183032-39: Russia, Chechen-Ingush Autonomous Republic, the lowland between Terek-Kuma Rivers [43 21 N, 46 06 E]. CAS 120249-50: Afghanistan, 30-70 km E of Herat 3700-5350 ft. CAS 115922-3: Afghanistan, Maimana, 35 54 N, 64 43 E. 884m. CAS 120280-1: Afghanistan, 10km NE Darweshan (Central Afg.). CAS 120275: Afghanistan, 25 km E Khanabad (between Mazare-Sharif-Faizabad), 2400ft. CAS 115920: Afghanistan, northeastern Afghanistan, 64 mi by road E Faizabad, 37 05 N, 70 40 E. CAS 115921: Afghanistan, Paghman Vicinity, 34 36 N, 68 56 E. 2440m. CAS 120251: Afghanistan, 25km NW Pul-e-Khumri, 2400ft.(near Mazar-sharif?). CAS 120255: Afghanistan, 20 km E Mazar-e-Sharif. CAS 120253: Afghanistan, 10 km W Tashkurgan, Near Mazar-Sharif? CAS 120256-8: Afghanistan, 20-50 km E Mazar-e-Sharif. CAS 120259-61: Afghanistan, 45 km W Mazar-e-Sharif, 1500ft. CAS 120273: Afghanistan, 50 km W Mazar-e-Sharif. FMNH 161197-9: Afghanistan, Maimana, 35 54 N, 64 43 E 884 m. FMNH 161133: Afghanistan, 64mil E Faizabad, 35 05 N, 70 40 E. FMNH 161191-2: Afghanistan, Paghman vicinity, 34 36 N, 68 56 E. 244m. FMNH 141399: Iran, Mazandaran prov. 1 mi N of Pahlavi Dezh.

#### ***Trapelus agilis pakistanensis* (n =97)**

GNHM. Re. ex. 5424 (holotype): Iran, 5 km NW Haft-Gel on the road to Shushtar. GNHM. Re. ex. 5425 (paratype): Iran, Khuzistan prov., 5 km NW of Haft-Gel on road to Shushtar. GNHM. Re. ex. 5426 (paratype) : Iran, Khuzistan

prov., 38 km S of Masjid-e-Sulaiman, Golgir village. CAS 86403-6, 86418-19 (paratypes) : Iran, Khuzistan prov. along road to lake east of Haft-Kel. CAS 86464 (paratype): Iran, Khuzistan an prov. along road south of Shushtar. CAS 86556 (paratype): Iran, Khuzistan prov. Haft-Kel (on golf course) [31 28 N, 49 30 E]. CAS 86342, 86346, 86390 (paratypes): Iran, Khuzistan prov. Tuli-Bazum road [31 55 N, 49 25 E]. FMNH 170936 (paratype): Iran, Khuzistan prov. 53 mi SE Ahwaz , Mashrageh. CAS 86341, 86343-72, 86374-89: Iran, Khuzistan prov. Tuli-Bazum road [31 55 N, 49 25 E]. CAS 86320, 86323-28: Iran, Khuzistan prov. Masjid-Suleiman [31 57,N, 49 16,E]. CAS 86322: Iran, Binak, near Persian Gulf at foot of Kuh-e-Bang [29 44,N, 50 19,E]. CAS 86338-51: Iran, Khuzistan prov. along old Masjid-Suleiman and Ahvaz road [32 N, 49 11,E]. CAS 86251: Iran, Khuzistan prov. Masjid-i-Suleiman [31 57 N, 49 16 E]. CAS 86373: Iran, Khuzistan prov. road south of Shushtar. CAS 102491-2: Iran, Fars prov. Ahram. CAS 86625: Iran, Khuzistan an prov. Binak, on Persian Gulf at foot of Kuh-i-Bang, north of Ganaweh. [29 44 N, 50 19 E]. CAS 86487: Iran, Fars prov. Agha Jari. [29 48 N, 49 46 E]. FMNH 141392-3, 141395-6, 141398: Iran, Fars prov. Ahram. ZISP 10335: Iran, Kochrud, Irak-Adschemi (exact locality?) (Nikolsky's Type of *Agama kermanensis* , var. *brevicauda* ). ZISP 9321: Iran, Kochrud, Irak-Adschemi (exact locality?) (Nikolsky's Type of *Agama kermanensis* ). ZISP 9889: Iran (exact locality ?).

#### ***Trapelus agilis pakistanensis* (n =32)**

SMF 63258 (holotype), 63259, 63279 (paratypes): Pakistan, Gaj-River, Kirthar Range. SMF 63256 (paratype): Pakistan, Sonda Distr.Thatta. SMF 63236: Pakistan. Old Airport of Karachi. 63243-4 and 63286-7 (paratypes): Pakistan, Old Airport of Karachi. SMF 63239, 63264: Pakistan, Hab River at Goth Mauladad. SMF 63263: Pakistan, Jati, Sind. SMF 63276: Pakistan, Karangee at Karachi. SMF 63265: Pakistan, Karachi. SMF 63267: Pakistan, Karachi area. FMNH 224946: Pakistan, Sind Prov. Dadu dist. Ranicot. FMNH 244977: Pakistan, Sind Prov. Karachi Dist. Malir, contonment. FMNH 244948: Pakistan, Sind Prov. Karachi Dist. Malir, contonment. BMNH 1933.7.8.23: Pakistan, Salt Range, Punjab. BMNH 74. 4. 29. 1432. 80. 11. 10. 25: Pakistan, Sind area. BMNH 98. 12. 22. 7-8: Pakistan: Kurrachee (karachi). BMNH 1964-271: Pakistan, Mirpur Khas. BMNH 1933.12.7.1: Pakistan, Sind area.