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RESEARCH ARTICLE **Open access**

Karyological studies of four agamid lizards from Semnan province of Iran

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Abstract
Iran possesses about 241 species of reptiles, which 55 species of them (22.8%) are endemic to Iran. Agamidae is the important family of reptile in Iran with 22 species, which is poor in terms of chromosomal studies. In this paper, karyological survey was made for four species of the family Agamidae by bone marrow cell preparations. Karyotype of male and female of *Laudakia caucasia* (2n=34) was consisted of 6 pairs macro and 11pairs of microchromosomrs. Karyotype of *Laudakia nupta nupta* (2n=36) was including of 6 pairs of macro and 12 pairs of microchromosomes. Karyotype of *Phrynocephalus scutellatus* (2n=46) was consisted of 22 macro and 24 microchromosomes, which is reported here for the first time. Also, new cytotype of *Traplus agilis agilis* (2n=49) is reported here for the first time. Karyotype of this species was consisted of 21 large acrocentric and 28 microchromosomes, which one of the acrocentric chromosomes may be a sex chromosome.

Key words: *Agamid, Chromosome, Iran, Karyotype, Lizards.*

INTRODUCTION

Agamidae is the fourth largest family among lacertilians and distributed from Africa thought Asia to Australia. According to Mozaffari *et al.* (2016) Iran possesses about 225 species of reptiles including 18 species of Agamidae family. In recent years, several new species have been described and new records published. As a result, the number of reptile species in Iran is increasing very rapidly, 31 new species have been added between 2000 to 2014 (Safaei-Mahroo *et al.*, 2015). According to Safari-Maroo *et al.* (2015) Iran has about 241 species of reptiles which is 55 species (22.8 %) of them are endemic and also including 22 species of Agamidae family. The first described reptile chromosomes were from the sand lizard (*Lacerta agilis*), which was reported by Tellyesniczky (1897). Existence of microchromosomes in iguanind and teiid lizards reported for the first time by Painter (1921). As the discipline of reptile cytogenetics grew over the last century, it became clear that reptiles are an exceptional group in which to study chromosome evolution, as they display a high level of diversity in chromosome number and morphology (Olmo, 2008), differ in the absence or presence of microchromosomes, and have diversity in sex determination systems and sex chromosomes (Ezaz *et al.* 2009; Pokorná *et al.*, 2011; Gamble *et al*, 2015). There are diploid chromosome numbers range from 2n = 20 in a lizard (Rampholeon *spectrum*) to 2n = 68 in a freshwater turtle (twist-neck turtle, *Platemys platycephala)*. In this paper karyological studies of four species of Agamidae are presented.

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MATERIAL AND METHODS

Karyological analyses were carried out on four species of agamids, which are collected from Semnan province of Iran (Table 1). They were intraperitoneally injected with 0.1 ml of phytohemaglutinin (PHA) per gram body weight for 24 h and with 0.1 ml colchicine solution (2mg/ml) per gram body weight for 5 h before sacrifice. The bone marrow cells were treated with 0.075M KCl for 20 min and fixed in acetic acid-methanol (1:3) solution. Mitotic chromosome preparations were made by an air dry method and stained by the Geimsa solution. The karyotype was determined for each specimen on the basis of comparing photographs of 10 metaphase cells. The photographs of chromosomes enlarged were measured and numbered. Calculation for centromeric index and arm ratio on each chromosome is used accordingly to Levan *et al.*, (1964).

TABLE 1. Summary of the information on sampling lizards for this study

Species	Geographic Coordinates	Altitude (m)	Locality
Paralaudakia caucasia	53°37′E, 35°42′N	1662	Semnan: neck of Ahovan
Laudakia nupta nupta	55°47′E, 36°46′ N	1180	Semnan: Kharturan National Park
Phrynocephalus scutellatus	54°25′E, 35°38′N	1134	Semnan: Moaleman 56 Km towards Damghan.
Traplus agilis agilis	54°20′E, 35°53′N	1107	Semnan: Damghan,35 Km towards Moaleman

RESULTS AND DISCUSSION

Family Agamidae

Laudakia caucasia (Eichwald 1831)

Laudakia of Iran has been studied by Anderson (1963, 1974); Clark *et al.,* (1966); Schleich (1979) and Natalia et al. (2020). Also, Iranian *Laudakia* was studied by Rastegar-Pouyani & Nilson (2002); Faizi & Rastegar-Pouyani (2007). *Laudakia* has recently been divided into three genera *Stellagama, Paralaudakia* and *Laudakia* (Baig *et al.*, 2012) which *Laudakia caucasia placed* in the genus *Paralaudakia.*

The Caucasian agama, *Paralaudakia caucasia*, is known from Turkey, Transcaucasia, Iran, Afghanistan, Pakistan, India, Turkmenistan, Tajikistan, and Uzbekistan (Ahmadzadeh *et al.*, 2008). In Iran, *P. caucasia* occurs from sea level to about 4000 m in the mountains of the northern and eastern Central Plateau (Anderson, 1999). *Paralaudakia caucasia* has been collected in the northern parts of Kermanshah province, along the Zagros Mountains (Rastegar- Pouyani, 2002).

Karyotypic studies on agamids have been carried out by Gorman and Shochat (1972), Gorman (1973), Sokolovski (1975) and Kupriyanova (1984). In addition, Moody and 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 families (William & Hall, 1976). The chromosome number of *P. caucasia* (male) was 2n=34. Karyotype consisted of 12 Macrochromosomes and 22 microchromosomes. Macrochromosomes have range in size from 5.36 to 2.06 µm (Table 2). Its metaphase plate of chromosomes and karyotype were shown in Figure (1A, B). Also, the chromosome complements and karyotype of female of this species was similar with male and karyotype consisted of six pairs of macrometacentric and 11 pairs of microchromosomes (Fig.2A, B). This chromosome number and karyotype of this species is in agreements with previous report by Arronet (1965) and differ by Hall (1970) in Moody & Hutterer (1978) which is reported 2n=36. The different is related in numbers of micochromosomes (2n=12 macrometacentric and 24 microchromosomes).

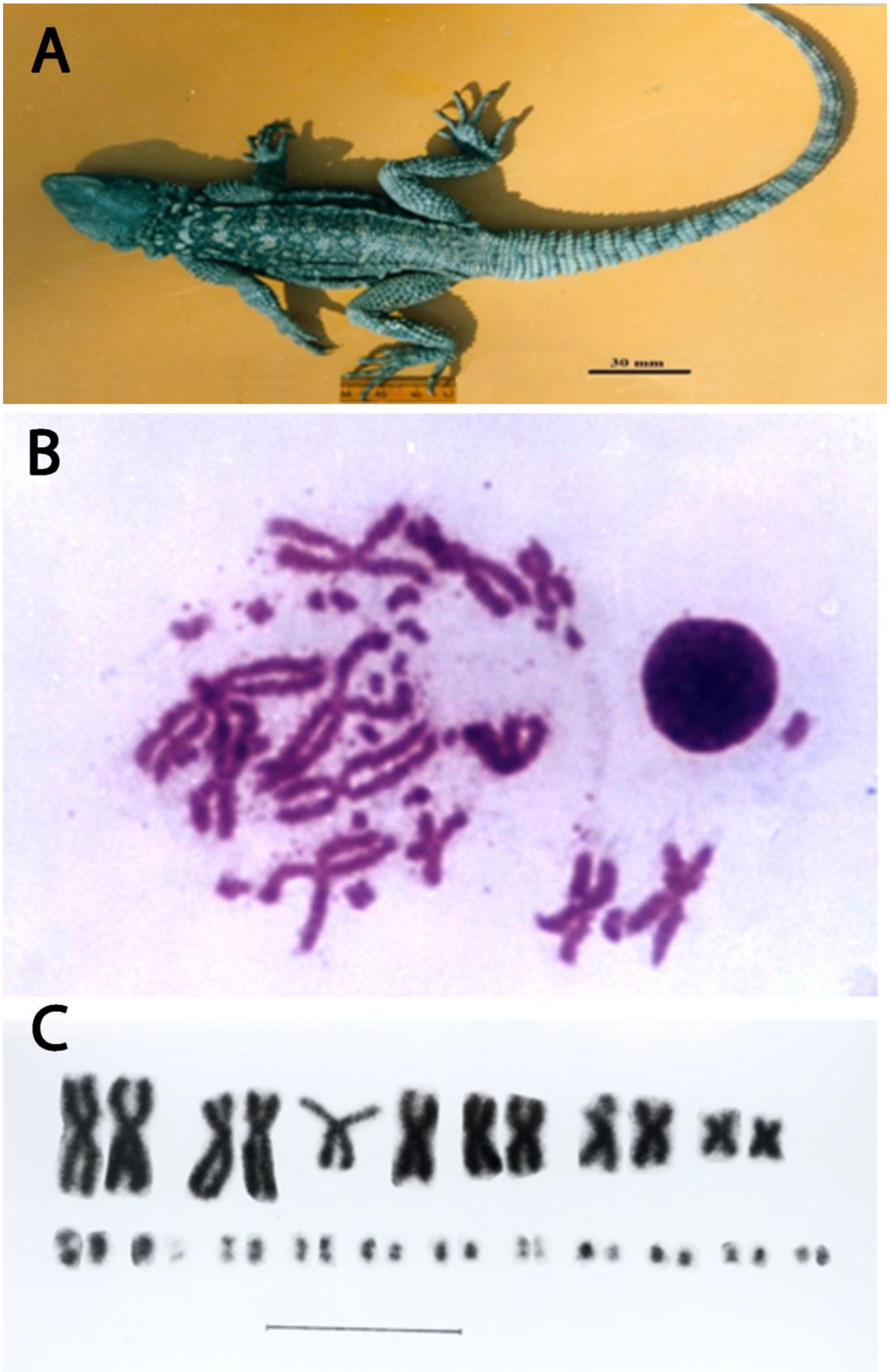

FIGURE 1. *Paralaudakia caucasia:* A, adult (male); B, plate metaphase (2n=34); C, karyotype (6 pairs of macro metacentric + 11pairs of micro chromosomes). Bar=10μm.

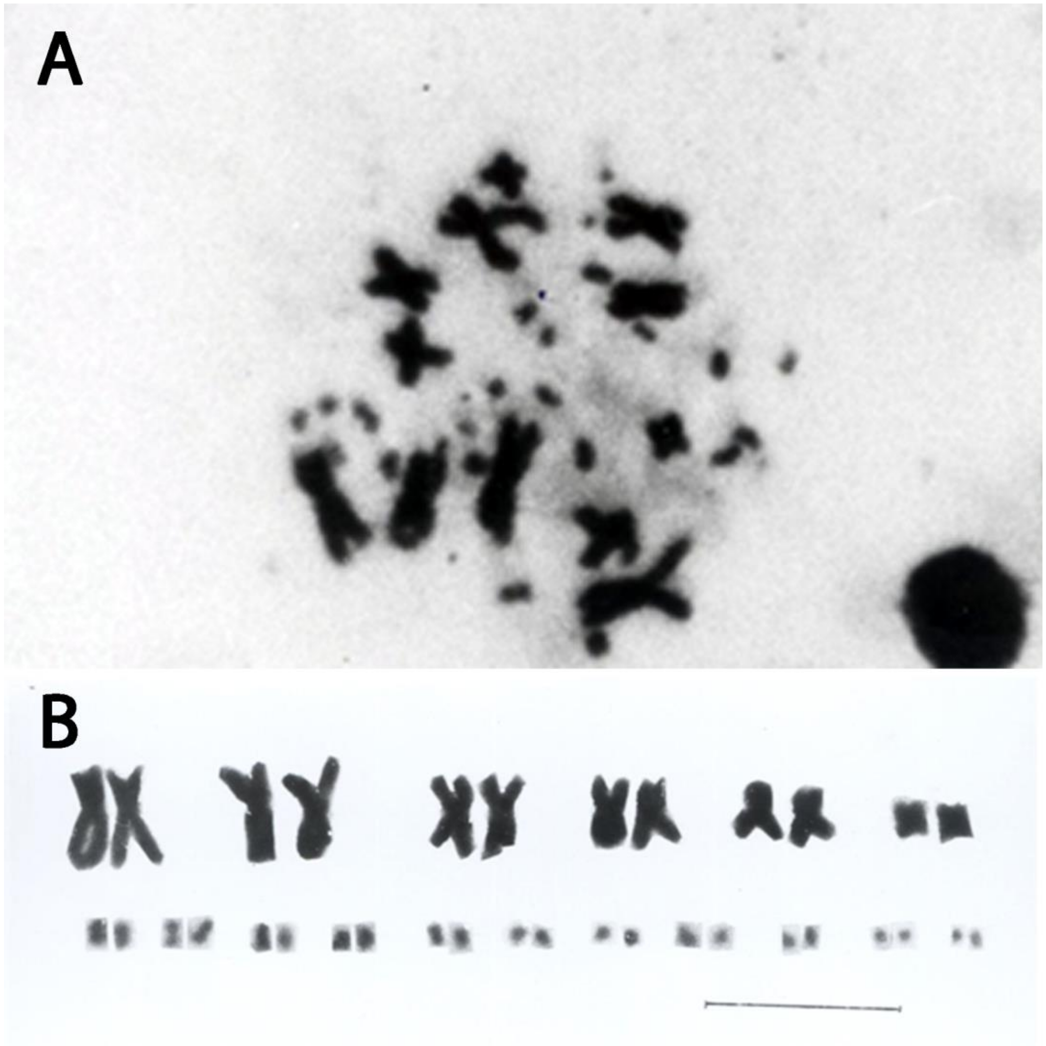

FIGURE 2. *Paralaudakia caucasia* (female): A, plate metaphase (2n=34); B, karyotype (6 pairs of macro metacentric + 11pairs of micro chromosomes). Bar=10µm.

***Laudakia nupta* nupta (De Filippi 1843)**

Khan and Mirza (1977) divided the populations of *L. nupta* in Pakistan into two subspecies*: L. n nupta* and *L.n. fusca*. *Laudakia n. nupta* is one of the largest rock-dwelling aramids occurring in northeastern and eastern Iraq eastwards through Iran, into Afghanistan and Pakistan. According to Anderson (1999), *L. n. nupta* is primarily a species of the southern and southwestern mountains of the Iranian plateau, distributed mainly on the outer slopes of the Zagros Mountains. Rastegar-Pouyani (2002) collected specimens of *L. n. nupta* in the central and east-central regions of Iran. *Laudakia n. nupta* together with *L. caucasia* and *L. stellio* represents the western radiation of the genus. In 1996 an Iranian expedition collected *L. n. nupta* from NE of Semnan province (Rastegar-Pouyani & Nilson, 2002). Previous chromosome information, indicated that *Laudakia n. nupta* has chromosome complement of 2n=36 (Hall, 1970) in Mooy & Hutterer (1975). Our female sample was diploid with 2n= 36 chromosomes. The metaphase plate of chromosomes and karyotype are shown in figure 3. The diploid karyotype consisted of six pairs of macro-chromosomes and twelve pairs of microchromosomes (Fig.3B). Macrochromosomes have range in size from 8.25to 2.62µm (Table 3).

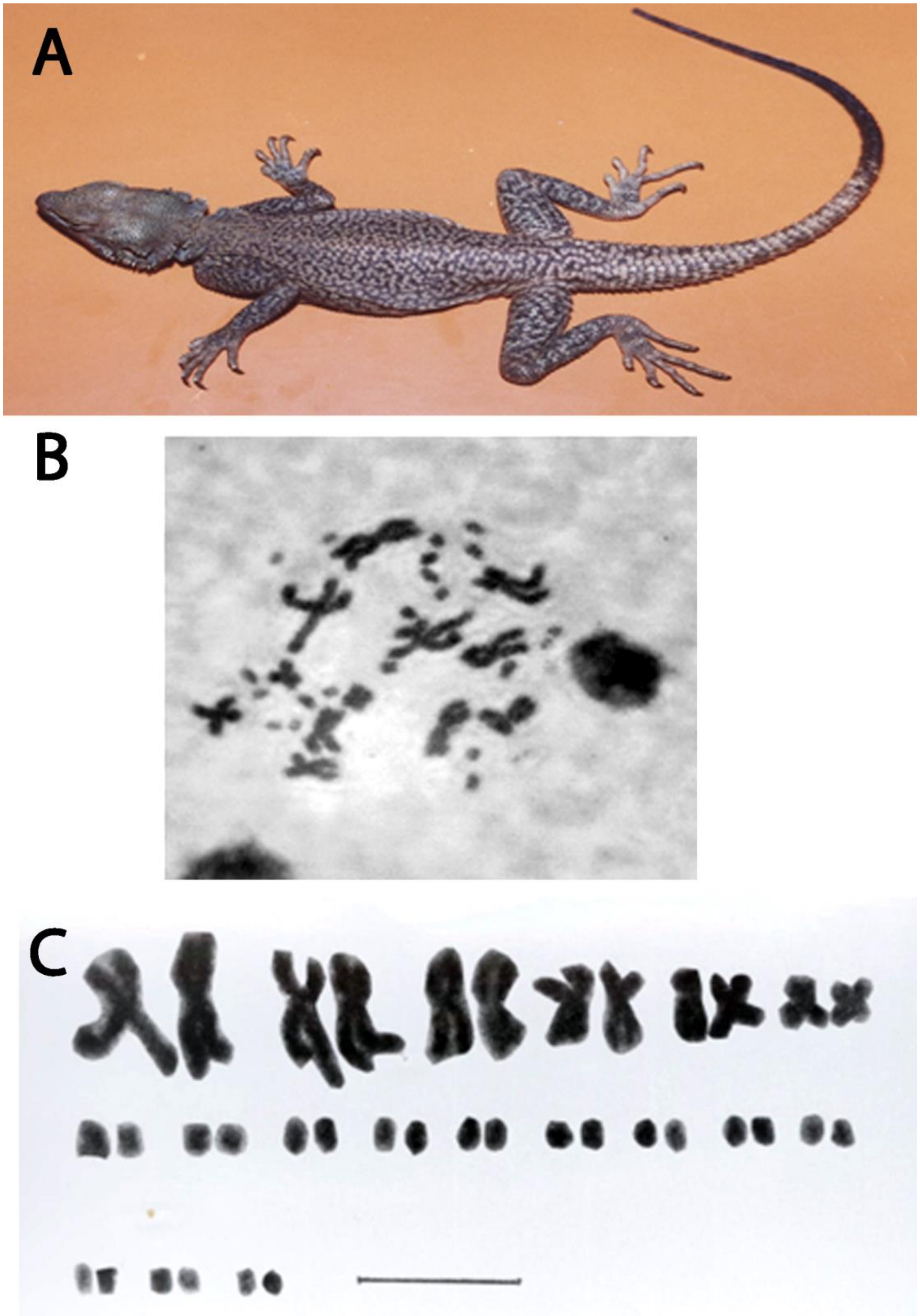

FIGURE 3. *Laudakia nupta nupta.* A: adult female; B: metaphase plate (2n=36); C: Karyotype (6 pairs of macrochromosomes + 12 microchromosomes). Bar=10µm.

TABLE 2. Measurements of macrochromosomes of *Paralaudakia caucasia*.

No. of chromosome	long arm (µ)	short arm (µ)	Arm ratio L/S= r	L+S
1	2.73	2.63	1.03	5.36
2	2.46	2.05	1.2	4.51
3	1.81	1.79	1.01	3.6
4	1.57	1.57	1	3.14
5	1.28	1.16	1.1	2.44
6	1.03	1.03	1	2.06

TABLE 3. Measurements of macrochromosomes of *Laudakia nupta nupta*.

No. of chromosome	Long arm (µm)	Short arm (µm)	Arm ratio	L+S
1	4.7	3.55	1.32	8.25
2	3.88	2.73	1.42	6.61
3	2.85	2.85	1	3.7
4	2.5	2.37	1.05	4.87
5	2.47	1.4	1.76	3.87
6	1.33	1.29	1.03	2.62

***Phrynocephalus scutellatus* (Olivier, 1807)**

The genus *phrynocephalus* Kaup, 1825 encompasses from 28 to 42 species distributed from China to the western side of the Caspian Sea and Southward to the Arabian Peninsula (Anderson, 1999; Guo & Wang, 2007). There are about 10-12 species of this monophyletic genus in desert regions of Iran (Ebrahimpour et al. 2022). The Gray Toad-headed Agama *Phrynocephalus scutellatus* occurs in Iran, Pakistan and Afghanistan. In Iran, the species is mainly found in desert, semi desert and plain areas covered with dispersed vegetation cover (Anderson, 1999). According to Solovyeva *et al.*, (2018) *Phrynocephalus* contained three main clades: (I) oviparous species from south-western and Middle Asia; (II) viviparous species of Qinghai–Tibetan Plateau (QTP); and (III) oviparous species of the Caspian Basin, Middle and Central Asia. The reconstruction of ancestral areas indicated that *Phrynocephalus* originated in Middle East–southern Middle Asia (Solovyeva *et al.*, 2018). The genus *Phrynocephalus* has a three range of chromosome numbers: 2n=44, 46 and 48, which more of them have 2n=48 (Sokolovsky, 1974; Manilo *et al.*, 1991; Zeng *et al.*, 1997; Malino, 2000). An analysis of 50 well-spread metaphase plates from different somatic tissue of two male specimens revealed a diploid chromosome count of 2n=46 comprising 22 macrochromosomes and 24 microchromosomes (Fig.4B, C). Macro chromosomes have range in size from 5.27 to 1.08µm (Table 4). Karyotype formula of our specimens was similar with karyotype formula of three species (P. *przewalskii*; *P. fontalis*; *P. guttatus*) which is reported by Zeng *et al.* (1997) from China. According to the literatures this is the first chromosome number report for this species.

***Traplus agilis agilis* (Olivieri 1807)**

Trapelus agilis is a species of agama found in Central, West and South Asia, in Iran, Pakistan, India, Russia, Turkmenistan, Tajikistan, Uzbekistan, Kazakhstan, China, possibly Iraq, and Afghanistan. The genus *Trapelus* consists of 13 species (Uetz, 2019), which are distributed from northwestern Africa, along the Saharan border, through the near East to southwest and central Asia (Rastegar-Pouyani, 1999; Rastegar-Pouyani, 2005; Wagner, 2006; Wagner & Crochet, 2009). *Trapelus agilis* is distributed on the Iranian Plateau and in adjacent regions of southwestern Asia (Šmíd *et al.*, 2014). Rastegar-Pouyani (1999) reported four subspecies within this complex group: the nominal subspecies *T. agilis agilis*, occurring on the central and southern Iranian Plateau; *T. a. pakistanensis*, restricted to the lowland and semi desert regions of southeastern Pakistan and to adjoining Indian territory; *T. a. sanguinolentus*, occupying the northern Iranian Plateau, vast areas of central Asia and westward into southeastern Europe, and *T. a. khuzestanensis* occurring in the southwestern area of the Iranian Plateau and possibly in neighboring regions of Iraq (Rastegar-Pouyani, 1999). According to literatures (Gorman & Schochat, 1972; Moody &

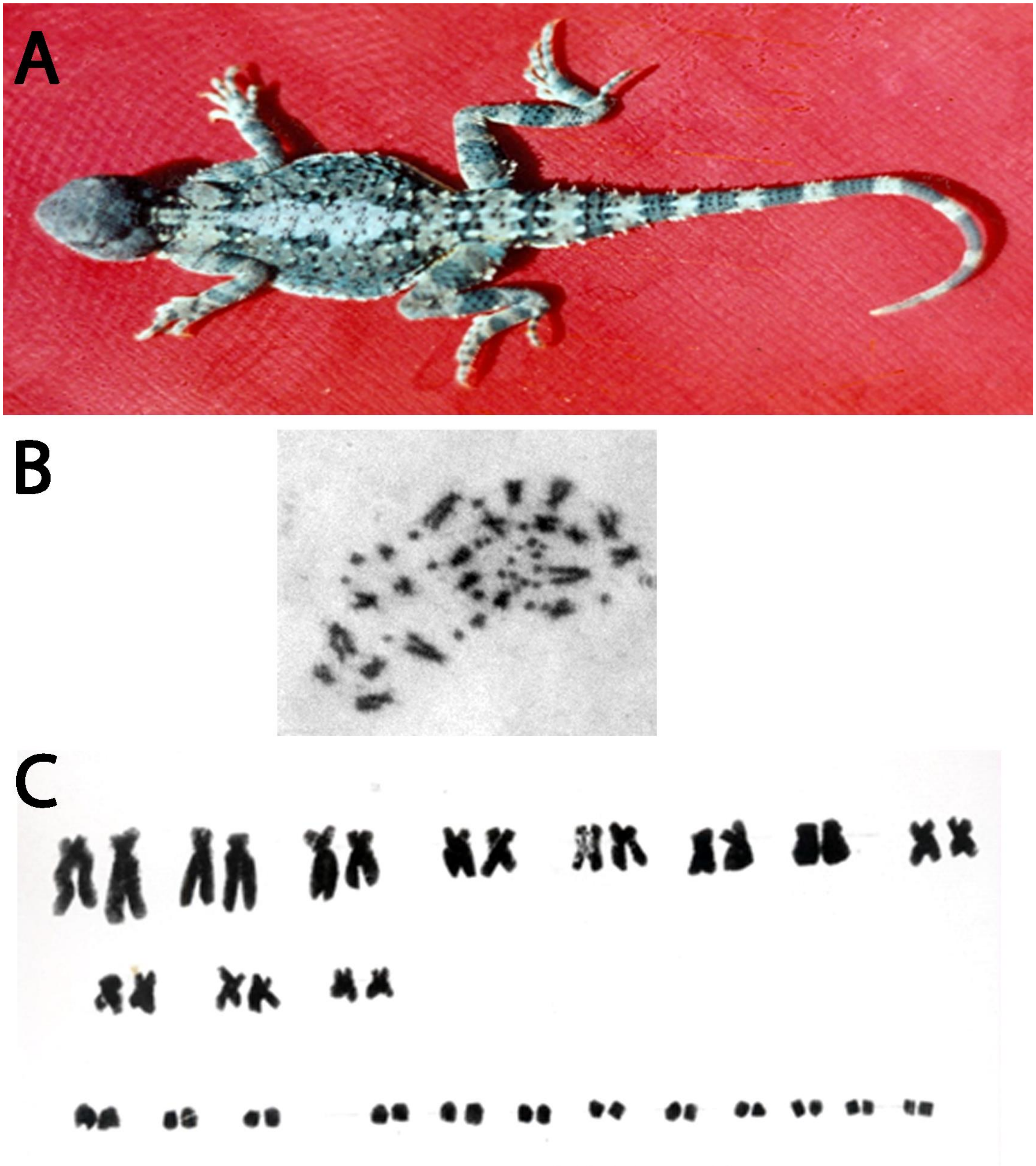

FIGURE 4. *Phrynocephalus scutellatus*. A: adult male. B: Metaphase plate (2n=46).C: karyotype (12 pairs of macro chromosomes+ 11 microchromosomes). Bar=10µm.

TABLE 4. Measurements of macrochromosomes of *Phrynocephalus scutellatus*.

No. of chromosome	long arm (μ)	short arm (μ)	Arm ratio = r	L+S
1	4.08	1.19	3.42	5.27
2	3.12	1.19	2.62	4.31
3	3	1.28	2.34	4.28
4	2.12	1.07	1.98	3.19
5	1.56	1.26	1.23	2.82
6	1.45	1.18	1.22	2.63
7	1.64	0.76	2.15	2.4
8	1.49	0.87	1.71	2.36
9	1.4	1.36	1.02	2.76
10	1.34	1.14	1.17	2.48
11	1.02	1.02	1	2.04
12	1.08	-	-	1.08

TABLE 5. Measurments of macro- acrocentric chromosomes in *Traoelus agilis agilis.*

No. of chromosome	Chromosome type	Long arm (μ)
1	Acrocentric	3.94
2	Acrocentric	3.72
3	Acrocentric	2.94
4	Acrocentric	2.61
5	Acrocentric	2.52
6	Acrocentric	2.34
7	Acrocentric	2.26
8	Acrocentric	2.21
9	Acrocentric	1.87
10	Acrocentric	1.3
11	Acrocentric	1.11
12	Acrocentric	0.91
13	Acrocentric	0.89
14	Acrocentric	0.77
15	Acrocentric	0.76
16	Acrocentric	0.71

Hutterer, 1975; Sokolovsky, 1975; Solleder & Schmid, 1988) from a total of 13 species of the genus *Trapelus*, eight of them were counted in chromosome number which seven of them have 2n=46 and one has 2n=44 chromosomes. Previous chromosome count for *Trapelus agilis* by Hall (1970) in Moody & Hutterer (1978) indicated that this species has karyotype that consisted of 24 acrocentric and 22 microchromosomes. Our male specimen was a new cytotype with karyotype including 21 acrocentric and 28 microchromosomes, which one of the acrocentric chromosomes may be sex chromosome (Fig. 5C) Macro acrocentric chromosomes have range in size from 3.94 to 0.71μm (Table 5).

ACKNOWLEDGMENTS

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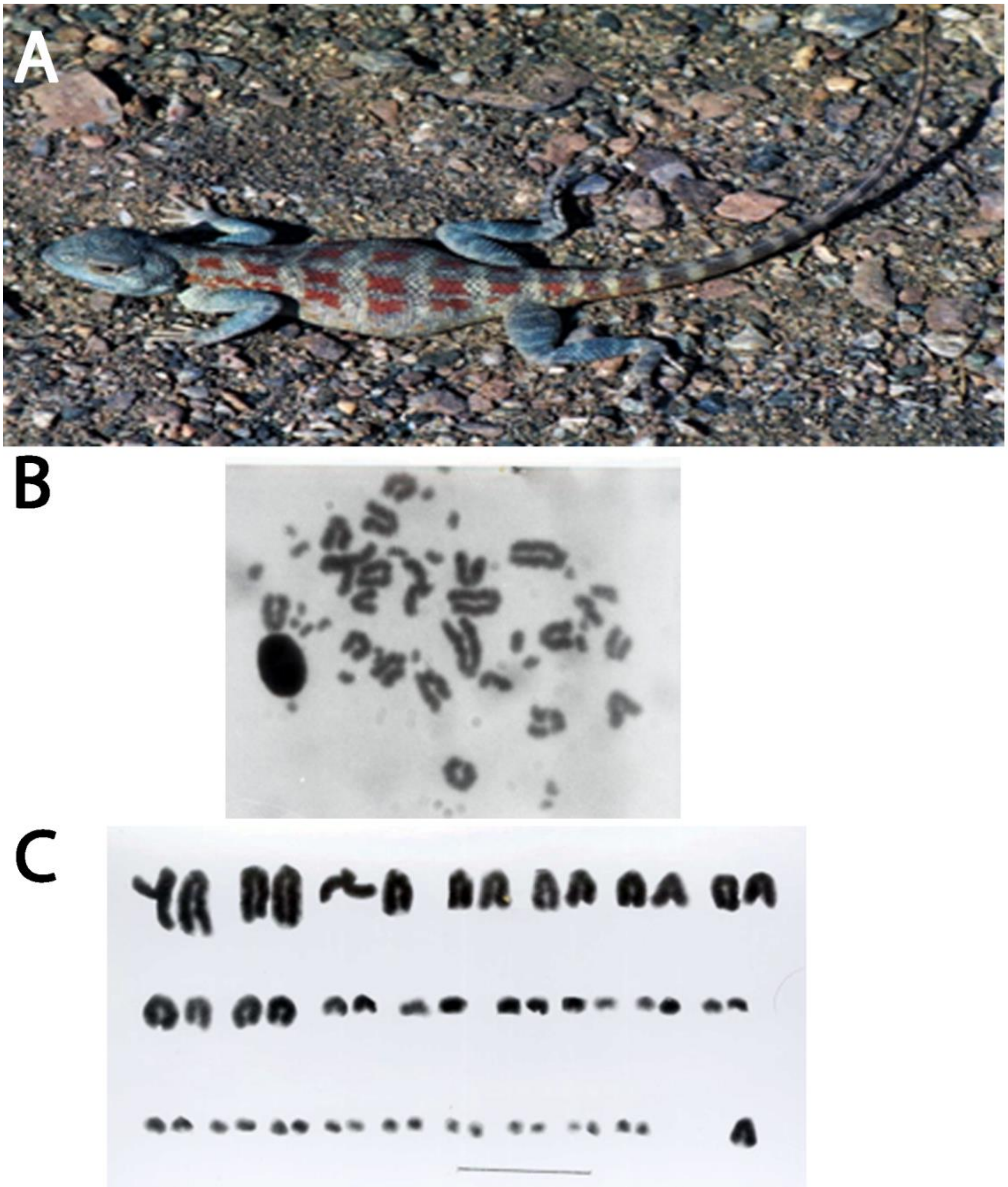

FIGURE 5. *Traplus agilis agilis*. A: adult female. B: Metaphase plate (2n=49).C: karyotype (21 macro acentric chromosomes + 28 microchromosomes). Bar=10µm.

LITERATURE CITED

Ahmadzadeh, F., Kiabi, B.H., Kami, H.G., Hojjati, V., 2008. A preliminary study of lizard's faunaand their habitats in the northwest of Iran. Asiatic Herpetological Research 11,1–9.

Anderson, S.C., 1963. Amphibians and Reptiles from Iran. Procceedings of the California Academy of Science 31 (16), 417 – 498.

Anderson, S.C., 1974. Preliminary key to the turtles, lizards and amphibianains of Iran Fieldiana Zoology 65(4), 27 – 44.

Anderson, S. C., 1999. *The Lizards of Iran.* Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri, 442 p.

Arronet (Kulikova), V. N., 1965. Description of the karyotypes of Agama caucasica and Phrynocephalus helioscopus (Agamidae, Reptilia). Tsitologiya 7, 237-239.

Baig, K. J., Wagner, P., Ananjeva, N., Böhme, W., 2012. A morphology-based taxonomic revision of *Laudakia* Gray, 1845 (Squamata: Agamidae). Vertebrate Zoology 62 (2), 213–260.

Clark, R., 1991. Contribution to the reptiles fauna of northern Iran. British Herpetological Society Bulletin 35, 36 – 46.

Clark, J., Clark, D., Anderson, S.C., 1966. Reports on two small collections of reptiles from Iran. Occasional Papers of the Callifornia Academy of Science 55, 1 – 9.

Deakin, J. E., Ezaz, T., 2019. Understanding the evolution of reptile chromosomes though applications of combined cytogenetics and genomics approaches. Cytogenetic and Genome Research 157, 7-20.

Ebrahimipour, F., Rastegar-Pouyani, N., Rastegar-Pouyani, E., 2022. Systematics and distribution of the genus Phrynocephalus Kaup, 1825 (Sauria: Agamidae) in the Iranian Plateau: A Review. Journal of Wild Life Biodiversity 6(x), x-x. DOI: https://doi.org/ 10.5281/zenodo.6502821

Ezaz, T., Sarre, SD., Meally, D., Marshall Graves, JA., Georges, A., 2009. Sex chromosome evolution in lizards: independent origins and rapid transitions. Cytogenetic and Genome Research 127, 249–260.

Faizi, N., Rastegar-Pouyani, N., 2007. Further studies on the lizards cranial osteology based on a comparative study of the skull in *Trachylepis aurata transcaucasica* and *Laudakia nupta* (Squamata: Sauria). Russian Journal of Herpetology 14(2), 107 – 116.

Gamble, T, Coryell, J., Ezaz, T., Lynch, J., Scantlebury, DP., Zarkower, D., 2015. Restriction site-associated DNA sequencing (RAD-seq) reveals an extraordinary number of transitions among gecko sex-determining systems. Molecular Biology and Evolution 32, 1296–1309.

Gorman, G.C., 1973. The chromosomes of the reptilia, a cytotaxonomic interpretation. In: Chiarelli, A.B., Capanna, E. eds. Cytotaxonomy and vertebrate evolution. Academic Press, London, pp. 349 424.

Gorman, G.C., Shochat, D., 1972. A taxonomic interpretation of chromosomal and eletrophoretic data on the agamid lizards of Israel with notes on some East African species. Herpetologica 28, 106 – 112

Guo, x. g., Wang, y. z., 2007. Partitioned Bayesian analyses, dispersal-vicariance analysis, and the biogeography of Chinese toad-headed lizards (Agamidae: *Phrynocephalus*): A revaluation. Molecular Phylogenetics and Evolution 45 (2), 643–662

Khan, M. S., Mirza, M.R., 1977. An Annotated Checklist and Key to the Reptiles of Pakistan, Part II: Sauria (Lacertilia*).* Biologia 23(1), 41-64.

Kupriyanova, L.A., 1984. Karyotypes of 3 species of agamid lizards – Ecology and faunistic of amphibians and reptiles of USSR and adjacent countries. Procceedings of the Zoological Institute of the Academy of Sciences USSR, 124, 115 – 118.

Levan, A., Fredga, K., Sandberg, A.A., 1964. Nomenclature for centromeric position on chromosomes. Hereditas 52, 201-220.

Moody, S.M., Hutterer, R., 1978. Karyotype of the agamid lizard Lyriocephalus scutatus (L. 1758), with a brief review of the chromosomes of the lizard family Agamidae. Bonner Zoologische Beiträge 29,165-170.

Manilo, V.V., Golubev, M.L., Sattorov, T., 1991. Karyotype of *Phrynocephalus helioscopus saidalievi* (Sauria, Agamidae) from Fergana Valley. Vestnik Zoologii 2, 79–81.

Manilo, VV., 2000 Description of karyotypes of some species and subspecies of the genus Phrynocephalus (Sauria, Agamidae) from Central Asia. *Vestnik Zoologii*, 34(6),113–118.

Mozaffari, O., Kamali, K., Fahimi, H., 2016. The Atlas of Reptiles of Iran. Department of the Environment, Tehran, pp.361.

Natalbia, B., Ananjeva, Konstantin, D., Milto, Andrei, V., Barabanov, Angeny, A., Golynsky, 2020. An annotated type catalogue of amphibians and reptiles collected by Nikolay A. Zarudny in Iran and Middle Asia. Zootaxa DOI: 10.11646/ZOOTAXA.4722.2.1

Sokolovsky, V. V. (.1974) Comparative caryological study of the lizards Agamidae. I. Chromotype of eight species of Phrynocephalus. Cytology 16(7), 920 – 925.

Olmo, E., 2008. Trends in the evolution of reptilian chromosomes. Integratve and Comparative Biology 48, 486–493.

Painter T. S., 1921. Studies in Reptilian spermatogenesis. I. The spermatogenesis of lizards. Journal Experimental Zoology 34, 281-327.

Pokorná, M., Giovannotti, M., Kratochvíl, L., Kasai, F., Trifonov, VA., 2011. Strong conservation of the bird Z chromosome in reptilian genomes is revealed by comparative painting despite 275 million years divergence. Chromosoma 120,455–68.

Rastegar-Pouynai, N., Nilson, G., 2002. Taxonomy and biogeography of the Iranian species of *Laudakia*. Zoology of the Middle East 26, 93 – 122.

Rastegar-Pouyani, N., 1999. Analysis of geographic variation in the Trapelus agilis complex (Sauria: Agamidae). Zoology in the Middle East 19,75 –99.

Rastegar-Pouyani, N., 2005. A multivariate analysis of geographic variation in the Trapelus agilis complex (Sauria: Agamidae). Amphibia-Reptilia 26,159–173

Safaei-Mahroo, B., Ghaffari, H., Fahimi, H., Broomand, S., Yazdanian, M., Najafi Majd, E., Hosseinian Yousefkhani, S. S., Rezazadeh E., Sadat Hosseinzadeh, M., Nasrabadi, R., Eajabizadeh, M., Mashayekhi, M., Motesharei, A., Naderi, A. & Kazemi, S., 2015. The Herpetofauna of Iran: Checklist of Taxonomy, Distribution and Conservation Status. Asian Herpetological Research 6(4), 257–290

Schleich, H.H., 1979. Feldherpetologische Beobachtungen in Persien, nebst morphologischen Daten zu den Agamen, *Agama agilis*, *Agama caucasica* and *Agama erythrogaster*. Salamandra 15(4), 237 – 253.

Šmíd, J., Moravec, J., Kodym, P., Kratochvíl, L., Hosseinian Yousefkhani, SS., Frynta, D., 2014. Annotated checklist and distribution of the lizards of Iran. Zootaxa 3855,1–97

Sokolovsky, V. V. (.1974) Comparative caryological study of the lizards Agamidae. I. Chromotype of eight species of Phrynocephalus. Cytology 16(7), 920 – 925.

Sokolovskii, V.V., 1975. A comparative karyological study of the lizards of the family Agamidae. Part II. Karyotypes of the five species of the genus *Agama*. Tsitologiya 17, 91 – 93.

Solleder, E., Schmidt, M., 1988. Cytogenetic studies on Sauria (Reptilia). I. Mitotic chromosomes of the Agamidae. Amphibia-Reptilia 9, 301-310.

Tellyesniczky, K., 1897. Über den Bau des Eidechsenhodens. Mathematische Naturwissenschaftliche Berichte Ungarn 13,303–342

Uetz, P., Freed, P., Hosek, J., 2019. The Reptile Database, http://www.reptile-database.org

Wagner, P., 2006. A new species of the genus Trapelus Cuvier, 1816 (Squamata: Agamidae). Bonner Zoologische Beitraege 55,81–87.

Wagner, P., Crochet, PA., 2009. The status of the nomina Trapelus savignyi Audouin, 1827 and Agama savignii Duméril & Bibron, 1837 and the valid nomen of the Savigny s Agama (Sauria: Agamidae). Zootaxa 2209,57–64.

William, E.E., Hall, W.P., 1976. Lizard karyotypes from the Galapagos Island: Chromosomes in phylogeny and evolution Part II. Primitive karyotypes. Breviora 441,6 – 18.

Witten, G.J., 1978. A triploid male individual *Amphibolurus nobbi nobbi* Witten (Lacertilia: Agamidae). Australian Zoology 19, 305 – 308.

Zeng, XM., Wang, YZ., Liu, ZJ., Fang, ZL., Wu, GF., Papenfuss, TJ., Macey, JR., 1997. Karyotypes of nine species in the genus *Phrynocephalus*, with discussion of karyotypic evolution of Chinese Phrynocephalus. Acta Zoologica Sinica 43,399–410.

Zug, G R., Vitt, LJ., Caldwell, JP., 2001. Herpetology: an introductory biology of amphibians and reptiles, 2nd edition, Academic press, New York.