

Taxonomic Diversity of Agamid Lizards (Reptilia, Sauria, Acrodonta, Agamidae) from China: A Comparative Analysis

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Abstract Results of the analysis of taxonomic diversity and representation of different evolutionary lineages of agamid lizards (Reptilia, Sauria, Agamidae) are provided in this article. For comparison with the fauna of China, the following territories were selected: North Eurasia, Iran and different countries of South and Southeast Asia. There are 49 agamid species in China, comprising 12 genera and 4 subfamilies. Annotated check-list and identification keys to genera are provided. Among the 49 species of agamids present in China, the percent of endemic species is relatively high (22 species; 45%). Endemic species refer to 4 genera with the genus *Japalura* having the most, 10 of 14 species, proceeded by members of Tibetan Plateau lineage of *Phrynocephalus*, 8 of 12 species, and *Calotes* with 1 species and *Laudakia* with 3.

Keywords Agamidae, China, taxonomy, biogeography, geographic distribution

1. Introduction

Studies of mitochondrial DNA for acrodont lizards (Honda *et al.*, 2000; Macey *et al.*, 2000; Ananjeva, 2004) has allowed the phylogenetic reconstruction for squamate taxa comprising the clade Acrodonta, whose main evolutionary lineages were associated in their origin with the fragmentation of Gondwana into separate tectonic plates. Within Acrodonta, there are 7 monophyletic lineages: 1) *Chamaeleo* (Chamaeleonidae), 2) *Uromastix*, 3) *Leiolepis*, 4) *Hydrosaurus*, 5) Southeast Asian group of genera, 6) Afro-southwest-Asian group of genera, and 7) Australo-New Guinean group of genera (including *Physignathus cocincinus*). Such interpretation is based on the results of the integration of morphological (Moody, 1980) and molecular data (Macey *et al.*, 2000). Within the family Agamidae there are six major clades (subfamilies): 1) Uromastycinae Theobald, 1868 with the genus *Uromastix*; 2) Leiolepidinae Fitzinger, 1843 with genus *Leiolepis*; 3) Amphibolurinae Wagler, 1830 with all Australian and New Guinean species as

well as *Physignathus cocincinus*; 4) Hydrosaurinae Kaup, 1828 with the genus *Hydrosaurus*; 5) South Asian and Southeast Asian Draconinae Fitzinger, 1826 with numerous Indian and Southeastern genera (mostly arboreal or semiarboreal); 6) Afro-west Asian Agaminae Spix, 1825.

We made an attempt to analyze the taxonomic composition and representation of different evolutionary lines (Amphibolurinae, Leiolepidinae, Draconinae and Agaminae) in the fauna of Asian agamid lizards. For comparing agamid lizard species diversity from China, Iran, and North Eurasia (former Soviet Union + Mongolia), different regions of South and Southeast Asia were selected. Differentiated diagnoses of agamid lizards of China are provided which allow to identify their taxonomic position at generic level. We use our own data as well as published results from studies on Oriental and Palearctic agamid lizards (Moody, 1980; Zhao and Adler, 1993) to develop a dichotomous key of the genera *Acanthosaura* (Orlov *et al.*, 2006; Ananjeva *et al.*, 2008; Wood *et al.*, 2009, 2010), *Draco* (Inger, 1983; Musters, 1983; McGuire and Heang, 2001), *Japalura* (Ota, 1989, 1991, 2000a, b; Ota *et al.*, 1998), *Calotes* (Hallermann, 2000; Ota and Hikida, 1991, 1996; Vindum *et al.*, 2003; Zug *et al.*, 2006), *Pseudocalotes* (Hallermann and Böhme, 2000; Hallermann and McGuire, 2001), *Ptyctolaemus* (Ananjeva and Stuart, 2001; Schulte II

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et al., 2004), *Laudakia* (Ananjeva *et al.*, 1990; Zhao *et al.*, 1999), *Phrynocephalus* (Peters, 1984; Ananjeva *et al.*, 2006; Barabanov and Ananjeva, 2007; Dunayev, 2008), and *Trapelus* (Ananjeva *et al.*, 2006; Macey and Ananjeva, 2004). The identification key published in older monographs and field guides (Boulenger, 1885; Smith, 1935; Taylor, 1963) did not include diagnoses for the genera *Bronchochoela* and *Pseudocalotes* as they were at the time included in the collective genus *Calotes* prior to the phylogenetic work of Moody (1980). We used the recent data on the faunas of North Eurasia (Ananjeva *et al.*, 2006), Iran (Anderson, 1999), China (Zhao and Adler, 1963; Zhao *et al.*, 1999), Vietnam (Ananjeva *et al.*, 2007), Myanmar (<http://www.calacademy.org/research/herpetology/myanmar>), Thailand (Taylor, 1993, with addition), South Asia (Das, 1996), and the Sunda Archipelago (Manthey and Grossmann, 1997) for comparative analysis of taxonomic composition and presentation of different subfamilies in the fauna of Asian agamid lizards.

This paper is an attempt to comparatively analyze the agamid lizard fauna from China, and present a modified translation of the paper of Ananjeva and Wang (2008) with the additional data. An annotated list of agamid species from China was prepared on the basis of the fundamental monographs on amphibians and reptiles of this country (Zhao and Adler, 1993; Zhao *et al.*, 1999).

2. Material and Methods

Data for this study of agamid lizards were compounded from both field and laboratory work in different regions of Northern Eurasia, China, Vietnam, Sri Lanka and Iran through a collaboration on several projects to study the biodiversity of amphibians and reptiles from these countries.

Specimens deposited in the following museums were examined: Zoological Institute, St. Petersburg (ZISP), Chengdu Institute of Biology, Chengdu (CIB), Zoological Museum, Moscow State University (ZMMGU), Natural History Museum, [former British Museum (Natural History)], London (NHM), Muséum National d'Histoire Naturelle, Paris (MNHN); Zoological Museum Hamburg (ZMH), Naturhistorisches Museum of the Humboldt University, Berlin (ZMB), Zoological Forschungsinstitut and Museum, Koenig (ZFMK), United States National Museum, Washington, (USNM), Field Museum of Natural History, Chicago (FMNH); Royal Ontario Museum, Toronto (ROM). Standard morphological characters were used (Ota 1989, 1991; Ota *et al.*, 1998; Hallermann, 2000;

Hallermann and Böhme, 2000; Hallermann and McGuire, 2001; Vindum *et al.*, 2003; Zug *et al.*, 2006; Orlov *et al.*, 2006). Indexes of Syorensen-Chekanovsky were calculated as $2c/N1+N2$ (Pesenko, 1982); program Excel 2003 was used to construct diagrams.

Endemic species are noted by * in the text below.

3. Results and Discussion

3.1 Identification key for the genera of agamid lizards of China

- I Femoral pores present.....Subfamilies Amphibolurinae, Leiolepidinae
 - A. 4-8 femoral pores on each side, tail strongly compressed laterally.....subfamily Amphibolurinae.....genus *Physignathus*
 - B. 13-20 femoral pores on each side, tail roundish, covered with small scales of equal size subfamily Leiolepidinae..... genus *Leiolepis*
- II No true preanal or femoral pores, body mainly laterally compressed, no callose scales.....
 - subfamily Draconinae
 - 1 Ribs much prolonged, supporting a wing-like dermal expansions genus *Draco*
 - 2 No wing-like dermal expansions. Three parallel longitudinal folds on each side of the middle of the throat forming a U-shaped figure.....
 -genus *Ptyctolaemus*
 - 3 (4) Tympanum hidden.....genus *Japalura*
 - 4 Tympanum exposed, visible from outside; spines present behind eye. Tail roundish, length of scales on ventral side smaller than or equal to width
 -genus *Oriocalotes*
 - 5 (7) Dorsal scales normally have different sizes. Tail compressed, length of scales on ventral side larger than width; spines present behind eye and in nape area
 - genus *Acanthosaura*
 - 6 Dorsal scales of equal size, rombic, evenly spaced 7
 - 7 Scales on lateral sides oriented backwards and downwards..... 9
 - 8 Limbs moderately long; adpressed hind limbs do not reaching shoulders, ventral scales not larger than dorsal scales; eggs oval genus *Pseudocalotes*
 - 9 Scales on lateral sides oriented backwards and upwardsgenus *Calotes*
 - III No true femoral pores, body mainly dorsoventrally depressedsubfamily Agaminae
 - 1 Tympanum exposed; males with callose preanal and ventral scales; tail divided into distinct segments,

- each composed of two or more whorls of scales rings, tympanum superficial.....genus *Laudakia*
- 2 Tympanum exposed; no distinct segments of caudal scales which are arranged as oblique rows; tympanum deep with acoustic duct genus *Trapelus*
- 3 Tympanum hidden, no callose scales.....
.....genus *Phrynocephalus*

3.2. Annotated list of agamid lizards of China

Subfamily Amphibolurinae Wagler, 1830

Type genus: *Amphibolurus* J. G. Wagler, 1830. Naturl. Syst. Rept., 145.

Physignathus cocincinus is the sister taxon to the Australo-New Guinean agamids (Macey *et al.*, 2000; Moody, 1993; Schulte II *et al.*, 2003). Previously, a number of Australian species had been considered as sister taxa (Smith, 1935). At present the genus *Physignathus* includes 2 species: *P. cocincinus* and *P. lessueri*. Some authors have provided evidence for a polyphyletic origin of this genus (Macey *et al.*, 2000; Moody, 1993; Schulte II *et al.*, 2003) which represents additional support for the ancient fragmentation of lizard taxa from both sides of Wallace's line (Schulte II *et al.*, 2003); another point of view suggests a much more recent divergence between SE Asian and Australian agamids (around 30 MYA) (Hugall and Lee, 2004; Hugall *et al.*, 2008). Agamids of this subfamily have femoral pores and lens-like skin receptors (Ananjeva, 2004). This group has a Southeast Asian origin (Macey *et al.*, 2000; Ananjeva, 2004).

Genus *Physignathus* Cuvier, 1829

Physignathus G. Cuvier, 1829. Regne Anim., 2nd ed., Paris, 2: 41.

Type species: *Physignathus cocincinus* Cuvier, 1829, Regne Anim., 2nd ed., Paris, 2: 41.

This genus is represented by two species, one of them is distributed in China.

Physignathus cocincinus Cuvier, 1829

Physignathus cocincinus G. Cuvier, 1829, Regne Anim., 2nd ed., Paris, 2: 41.

Lophura cuvieri J. E. Gray, 1831 in Griffiths, Animal Kingdom of Cuvier, 9 Synops. Spec.: 60.

Type locality: Cochinchina, south Vietnam [Cochinchine (Vietnam du Sud)]; coll. Diard.

Distribution: Myanmar, southeastern Thailand, Laos, Cambodia, Vietnam, southern Yunnan and Guandong provinces, China (Smith, 1935; Taylor, 1963; Zhao and Adler, 1993; Zhao *et al.*, 1999).

Subfamily Leiolepidinae Fitzinger, 1843

Type genus: *Leiolepis* G. Cuvier, 1829. Regne Anim., 2nd

ed., Paris, 2: 37.

Study of mt DNA (Macey *et al.*, 2000) and morphological integumentary characters (Ananjeva *et al.*, 2001) supported the monophyly of this lineage, previously combined with *Uromastix* into the subfamily (family) Uromastycinae (-dae) Theobald, 1868 (Moody, 1980; Frost and Etheridge, 1989). These lizards have femoral pores and lens-like receptors without hairs (Ananjeva, 2004; Ananjeva and Stuart, 2001). There are bisexual (*L. belliana*, *L. guttata*, *L. reevesii*, *L. peguensis*) and parthenogenetic (*L. triploida*, *L. guentherpetersi*, *L. boehmei*, *L. ngovantrii*) (Darevsky and Kupriyanova, 1993; Grismer and Grismer, 2010; Hartmann and Böhme, 2010) examples.

Genus *Leiolepis* Cuvier, 1829

Leiolepis G. Cuvier, 1829. Regne Anim. 2nd ed., Paris, 2: 37.

Type species: *Leiolepis guttatus* Cuvier, 1829.

Leiolepis guttatus G. Cuvier, 1829. Regne Anim., 2nd ed., Paris, 2: 37.

This genus includes 7 species, one of which is found in China.

Leiolepis reevesii (Gray, 1831)

Uromastix reevesii J. E. Gray, 1831. In: E. Griffith and E. Pidgeon (eds), Anim. Kingd., London, 9: 62.

Leolepis reevesii J. E. Gray, 1845, Cat. Spec. Liz. Coll. Brit. Mus: 263.

Type locality: China (Boulenger, 1885).

Distribution: Nominative subspecies is known from southern China, including Macao, Guangdong, Guangxi, Hainan Island, and also Vietnam.

Subfamily Draconinae Fitzinger, 1826

Type genus: *Draco* Linnaeus, 1758 (not *Draco* Oken, 1815 = Reptilia, Serpentes). Syst. Nat., Ed. 10, 1: 199

This subfamily is the most diverse group among those genera of arboreal and semi-arboreal agamids with a high percentage of endemics (Moody, 1980). Among them, there are monotypic genera (*Lophocalotes*, *Mantheyus*, *Mictopholis*) or those represented by 2–3 species (*Aphaniotis*, *Cophotis*, *Otocryptis*, *Ptyctolaemus*), and genera with high species diversity (*Draco*, *Gonocephalus*, *Japalura*). Draconine agamids exhibit very high degrees of diversification at the generic level (25 genera in South Asia and 24 genera in Southeast Asia). Agamids of this subfamily have no femoral pores (except the genus *Mantheyus*) and skin receptors with hair (Ananjeva, 2004). Phylogenetic studies conducted in the recent decades have improved our knowledge about the composition and phylogeny of the subfamily. Some problems still exist

relating to newly described or re-studied species in certain genera (Manthey and Grossmann, 1997; Macey *et al.*, 2000; Ananjeva and Stuart 2001; Schulte II *et al.*, 2004).

Fauna of China includes 8 genera of this subfamily as follows:

Genus *Acanthosaura* Gray, 1831

Type species: *Acanthosaura armata* Hardwick et Gray, 1827. Zool. J., London, 3: 216.

This genus presents an interesting example of cryptic taxonomic diversity (Ananjeva *et al.*, 2006; Wood *et al.*, 2009, 2010). Presently, it combines 9 species from which one is distributed in China. *Acanthosaura armata* was recorded in China but was not found during our surveys, nor from the examination of other museum collections and genetic identification (Kalyabina-Hauf *et al.*, 2004; Ananjeva *et al.*, 2006, 2008).

***Acanthosaura lepidogaster* Cuvier, 1829**

Acanthosaura lepidogaster G. Cuvier, 1829. Règne animal, Ed. 2, 2: 39.

Type locality: CochinChina (=Vietnam).

Distribution: *Acanthosaura lepidogaster* is distributed in southern China (Guangxi, Fujian, Guangdong, Yunnan, Hainan Island), Thailand, Laos, Vietnam and Myanmar. It is the widest distributed species of the genus *Acanthosaura* and it occupies the most northern part of the genus' range.

Genus *Calotes* Rafinesque, 1815

Calotes C. S. Rafinesque, 1815. Anal. Nat.: 75.

Type species: *Calotes calotes* (Linnaeus, 1758). Syst. Nat., Ed. 10, Stockholm, 1: 207.

This genus includes more than 20 species, 6 of which are recorded in China.

***Calotes emma* Gray, 1845**

Calotes emma J. E. Gray, 1845. Cat. Spec. Liz. Brit. Mus., London: 244.

Calotes alticristatus K. P. Schmidt, 1925, Amer. Mus. Nov, 175: 2.

Type locality: Afghanistan / East India.

Distribution: India (Assam), Myanmar, China (Guangdong and Yunnan), Laos, Thailand, Cambodia, Vietnam, and western provinces of Malaysia.

***Calotes jerdoni* Günther, 1871**

Calotes jerdoni A. Günther "1870" (1871). Proc. Zool. Soc. London, 1870: 779

Type locality: Assam, India.

Distribution: India (Assam), Myanmar, China (western Yunnan and Tibet).

***Calotes kingdonwardi* Smith, 1935**

Calotes kingdonwardi M. A. Smith, 1935. Fauna Brit. India, Rept. Amphib., London, 2: 188.

Type locality: Adung valley, Tibet-Burma border.

Distribution: China (western Yunnan and Tibet), Myanmar.

****Calotes medogensis* Zhao et Li, 1984**

Calotes medogensis E. M. Zhao et S. Q. Li, 1984. Acta Herpetol. Sinica, Chengdu [new ser.], 3(4): 77.

Type locality: Yarang, Medog County, Tibet, China.

Distribution: Species is known only from its type locality.

***Calotes mystaceus* Dumeril et Bibron, 1837**

Calotes mystaceus A. M. C. Dumeril et G. Bibron, 1837. Erpetol. Gen., Paris, 4: 408. (Guibé, 1954).

Type locality: Myanmar (Birmanie).

Distribution: China (Yunnan), India (Andaman and Nikobar Islands), Myanmar, Thailand, Cambodia, Laos, Vietnam.

***Calotes versicolor* (Daudin, 1802)**

Agama versicolor F. M. Daudin, 1802. Hist. Nat. Gen. Rept., Paris, 3: 395.

Type locality: Not designated by the author of description. Afterwards Smith (1935) designated the type territory as Pondicherry, India.

Distribution: Iran, Afghanistan, Pakistan, Nepal, Bhutan, India, Sri Lanka, Myanmar, southern China (Yunnan, Hainan Island, Hong Kong), Laos, Thailand, Vietnam, Singapore, western Malaysia, Indonesia (Sumatra).

Genus *Draco* Linnaeus, 1758

Draco C. Linnaeus, 1758. Syst. Nat., Ed. 10, Stockholm, 1: 199.

Type species: *Draco volans* C. Linnaeus, 1758. Syst. Nat., Ed. 10, Stockholm, 1: 199.

This genus comprises approximately 20 species, 2 of which are recorded in China.

***Draco blanfordii* Boulenger, 1885**

Draco blanfordii Boulenger, 1885. Catal. Liz. Brit. Mus., London, 1: 76.

Type locality: Tennaserim, east from Tavoy.

Distribution: Southern China (southwestern Yunnan), Thailand, Myanmar, Malay Peninsula.

***Draco maculatus* (Gray, 1845)**

Dracunculus maculatus J. E. Gray, 1845. Cat. Liz. Brit. Mus., London, 262.

Type locality: Penang, Malaysia.

Distribution: Southern China (Guangxi, Yunnan, Hainan Island, Tibet), Myanmar, Laos, Thailand, Vietnam, western Malaysia.

Genus *Japalura* Gray, 1853

Japalura J. E. Gray, 1853. Ann. Mag. Nat. Hist., London, ser. 2, 12: 387.

Type species: *Japalura variegata* Gray, 1853. Ann. Mag. Nat. Hist., London, ser. 2, 12: 388.

This genus includes 24 species, 14 of which live in China. According to the data of molecular analysis (Macey *et al.*, 2000; Zug *et al.*, 2006; Ota and Honda, 2010), this genus is not monophyletic and is represented by at least two evolutionary lineages (the Himalayan lineage and Indochina lineage).

***Japalura andersoniana* Annandale, 1905**

Japalura andersoniana N. Annandale, 1905. Jour. Proc. Asiatic Soc. Bengal, Calcutta, new ser., 1: 85.

Type locality: Dafla hills, border between Bhutan and Assam, India.

Distribution: Southern Tibet (Medog County) of China, Arunachal Pradesh (India, border between Buthan and India).

***Japalura brevipes* Gressitt, 1936**

Japalura brevipes J. L. Gressitt, 1936. Proc. Biol. Soc. Washington, 49: 117.

Type locality: Bukai, central Taiwan of China.

Distribution: Live only in Taiwan, China.

****Japalura dymondi* (Boulenger, 1906)**

Acanthosaura dymondi G. A. Boulenger, 1906. Ann. Mag. Nat. Hist., London, ser. 7, 17: 567.

Type locality: Donguan-Fu (= Dongchuan City), Yunnan, China.

Distribution: Southwestern China (Yunnan and northwestern Sichuan).

****Japalura fasciata* Mertens, 1926**

Japalura fasciata R. Mertens, 1926. Herp. Mitt., Senckenbergiana, 8 (3-4): 146.

Japalura szechwanensis Hu and Zhao, 1966. Acta Zool. Sinica, Peking, 3(2): 158.

Type locality: Tonkin (north Vietnam).

Distribution: North Vietnam, Lang Son Province (Maoson), central and southern China (Sichuan, Guizhou, Guangxi, Hunan). Mertens described *J. fasciata* from Tonkin in 1926. In 1966 *J. szechwanensis* Hu and Zhao was described from Sichuan which was synonymied with *J. fasciata* (Ota, 2000a). Further records made a wider distribution range in China.

****Japalura flaviceps* Barbour et Dunn, 1919**

Japalura flaviceps T. Barbour et E. R. Dunn, 1919. Proc. New Engl. Zool. Club, Cambridge, 7: 16.

Type locality: Bank of the Tung River (Dadu River),

western Sichuan, China.

Distribution: Western China [western Sichuan, eastern Xizang (= Tibet), Qinghai, Gansu, Shaanxi, Shanxi, northern Yunnan].

****Japalura grahami* (Stejneger, 1924)**

Japalura grahami L. Stejneger, 1924. Occas. Pap. Boston Soc. Nat. Hist., 5: 120.

Type locality: Sui-fu (= Yibin City), Szechuan (= Sichuan), China.

Distribution: Sichuan (China).

***Japalura kumaonensis* (Annandale, 1907).**

Acanthosaura kumaonensis N. Annandale, 1907. In G. A. Boulenger, N. Annandale, F. Wall, et C. T. Regan, Rec. Indian Mus. Calcutta, 1: 152.

Type locality: Naini and Massuru rivers valley, Nepal.

Distribution: Xizang (= Tibet, China) and Nepal.

****Japalura makii* Ota, 1989**

Japalura makii H. Ota, 1989. Copeia, Gainesville, 1989: 570.

Type locality: Chitou, Nantu, Taiwan (China).

Distribution: Central Taiwan (China).

****Japalura micangshanensis* Song, 1987**

Japalura micangshanensis M. T. Song, 1987. Acta Herpetol. Sinica, Chengdu, (New ser.), 6(1): 59.

Type locality: Qingmuchan, Ningqiang County, Shaanxi (China).

Distribution: Species is known only from its type locality.

***Japalura polygonata* (Hallowell, 1861)**

Diploderma polygonatum E. Hallowell, "1860" (1861). Proc. Acad. Nat. Sci. Philadelphia, 12: 490.

Type locality: "Amakarima" Island (= Kerama Shima), Ryukyu Archipelago.

Distribution: North part of Taiwan (China) and islands of Ryukyu Archipelago (Japan).

****Japalura splendida* Barbour et Dunn, 1919**

Japalura splendida T. Barbour et E. R. Dunn, 1919. Proc. New Engl. Zool. Club, Cambridge, 7: 18.

Type locality: From the gorge of the Yangtze River near Ichang (= Yichang City), Hupeh (= Hubei Province) of central China.

Distribution: Southwest China, eastwards to Hunan and northwards to Gansu.

****Japalura swinhonis* Günther, 1864**

Japalura swinhonis A. Günther, 1864. Rept. Brit. India, London: 133.

Type locality: Formosa (= Taiwan, China). Restricted to Tamsui, Formosa (= Taiwan, China) by Stejneger, 1907.

Distribution: Taiwan (China).

****Japalura varcoae* (Boulenger, 1918)**

Acanthosaura varcoae G. A. Boulenger, 1918. Ann. Mag. Nat. Hist., London, Ser. 9, 2: 162.

Type locality: Yunnan-fu (=Kunming City) and Wuting chu (=Wuding County) in Yunnan, China.

Distribution: Western Yunnan, Guizhou (China).

****Japalura yunnanensis* Anderson, 1879**

Japalura yunnanensis J. Anderson, "1878" (1879). Anat. Zool. Res.: Zool. Result. Exped. West Yunnan, London.

Type locality: Neighborhood of Teng-yue-chow (=winth in Tengchong), Momein (= Tengchong County) in Yunnan, China.

Distribution: Yunnan (China).

Data on distribution of this species in Vietnam and Cambodia were disproved by Ota (2000b), who showed that the information on record in Vietnam is erroneous. He restricted its distribution to Yunnan in China. The synonymy of the name *Japalura yunnanensis popei* is known from Cambodia with *Japalura swinhonis*.

Genus *Pseudocalotes* Fitzinger, 1843

Pseudocalotes L. J. Fitzinger, 1843. Nat. Syst. Rept., 1: 15, 46.

Type species: *Pseudocalotes tympanostriga* (Gray, 1831). In Griffith, Animal Kingdom Cuvier, 9 Synops. Spec. 56. This genus includes approximately 11 species, 3 of which are found in China.

***Pseudocalotes brevipes* (Werner, 1904)**

Calotes brevipes F. Werner, 1904. Zool. Anz., Leipzig, 27: 462.

Type locality: Tonkin (Vietnam).

Distribution: North Vietnam and south China (Guangxi).

***Pseudocalotes kakhensis* (J. Anderson, 1879)**

Oriocalotes kakhensis J. Anderson, 1879. Zool. Res. W-Yunnan: 806; Taf. 76, Figure 1

Type locality: Ponsee(= Pengxi) in western Yunnan, China.

Distribution: South China (western Yunnan), Myanmar (= Burma) (east of the Irrawadi River), India, northern Thailand.

***Pseudocalotes microlepis* (Boulenger, 1887)**

Calotes microlepis G. A. Boulenger, 1887. Ann. Mus. Civ. Stor. Nat. Genova, 2(5): 476.

Type locality: Pla-pu, Burma and west of Mt. Muleyit, N. Tenasserim

Distribution: Vietnam, India (Assam), Myanmar, China (Guizhou and Hainan Island).

Genus *Oriocalotes* Günther, 1864

Oriocalotes A. Günther, 1864. Rept. Brit. India, London: 146.

Type species: *Calotes minor* J. Gray, 1845 (= *Oriocalotes paulus* M.A. Smith, 1935). Catal. Spec. Liz. Coll. Brit. Mus., London: 244.

It is a monotypic genus.

***Oriocalotes paulus* M. A. Smith, 1935**

Oriocalotes paulus M. A. Smith, 1935. Fauna Brit. India, Rept. Amphib., London, 2: 166

Type locality: Khasi Hills, Sikkim (?)

Distribution: India (east Himalaya, Khasi Hills, Sikkim ?), China (Xizang = Tibet)

Genus *Ptyctolaemus* Peters, 1864

Ptyctolaemus W. Peters, 1864. Monatsber. Königl. Preuss. Akad. Wissensch. Berlin, 1864: 386.

Type species: *Otocryptis (Ptyctolaemus) gularis* W. Peters, 1864. Monatsber. Königl. Preuss. Akad. Wissensch. Berlin, 1864: 386.

This genus includes 2 species, 1 of which is recorded in China.

***Ptyctolaemus gularis* (Peters, 1864)**

Otocryptis (Ptyctolaemus) gularis W. Peters, 1864. Monatsber. Königl. Preuss. Akad. Wissensch. Berlin, 1864: 386.

Type locality: Calcutta (in error).

Distribution: Northeast India (Assam; Khasi hills; Arunachal Pradesh), Bangladesh, China (Xizang = Tibet), Myanmar (Kachin, Chin)

Subfamily Agaminae Spix, 1825

Type genus: *Agama* Daudin, 1801. Hist. Nat. Rept., 3: 333.

This subfamily consists of approximately 115 species distributed mainly in Asia and Africa. In comparison with the Draconinae subfamily, the Agaminae is characterized by low generic diversity (number of species in parentheses) – 7 genera in total: *Acanthocercus* Fitzinger, 1843 (about 10 species), *Agama* Daudin, 1802 (about 30), *Phrynocephalus* Kaup, 1835 (40), *Pseudotrapelus* Fitzinger, 1843 (1), *Laudakia* Gray, 1845 (16), *Trapelus* Cuvier, 1817 (12), *Xenagama* Boulenger, 1895 (2). Three genera (*Laudakia*, *Trapelus*, *Phrynocephalus*) live within the territory of China.

Genus *Laudakia* Gray, 1845

The Asian rock agamids of the genus *Laudakia* Gray, 1845 includes 16 species distributed in mountain rock landscapes from Greece and the Nile River delta on the

west through Middle East and Central Asia to Gobi Altai on the northeast and the Bramaputra River on the east. The mountain ring-tailed agamas belonging to this genus were considered for a long time as a part of the genus *Agama* Daudin, 1802 (Boulenger, 1885). After Moody's revision (1980) they were referred to a distinct genus *Stellio* Laurenti, 1768. The subsequent study of the whole complex of mountain ring-tailed agamas showed that it is a paraphyletic group (Joger and Arano, 1987; Ananjeva *et al.*, 1990; Joger, 1991). Taking into consideration of these data and some nomenclatural suggestions of some authors (Leviton *et al.*, 1992), the generic name *Laudakia* Gray, 1845 for Asian rock agamids and for the Afro-Arabian group of species the generic name *Acanthocercus* Fitzinger, 1843 was adopted. Species inhabiting China occupy the eastern part of distribution range of this genus. Data from mtDNA phylogenetic analyses (Macey *et al.*, 2000, 2006) support that the genus *Laudakia* is represented by two distinct evolutionary lineages.

Type species: *Laudakia tuberculata* (Hardwick et Gray, 1827), T. Hardwick et J. E. Gray, 1827. Zool. J. London, 3: 218.

Six species are included in fauna of China.

***Laudakia himalayana* (Steindachner, 1869)**

Stellio himalayanus Steindachner, 1869. Reise österreich. Freg. Novara, Rept.: 22. Taf. 1. Fig. 8.

Type locality: Lei and Kargill, Ladakh-Province, Kashmir, India.

Distribution: China (Xinjiang, Tibet), mountain ranges of Himalaya and Transhimalaya, southeastern Tyan-Shan, southern Pamir and Karakorum in Nepal, northern India, northern Pakistan, eastern Afghanistan, western Tajikistan and western Kirgizstan.

****Laudakia sacra* (M. A. Smith, 1935)**

Agama himalayana sacra M. A. Smith, 1935. Fauna Brit. Inida, Rept. Amph. 2: 214.

Type locality: Lhasa, Tibet, China.

Distribution: China (Xinjiang, Tibet),

***Laudakia stoliczkana* (Blanford, 1875)**

Stellio stoliczkana W. T. Blandford, 1875. J. Asiatic Soc. Bengal, Calcutta, New ser., 44(2): 191.

Type locality: plains of Eastern Turkestan (= including part of Xinjiang), China.

Distribution: China (Xinjiang, Gansu), western Mongolia.

***Laudakia tuberculata* (Hardwick et Gray, 1827)**

Agama tuberculata T. Hardwick et J. E. Gray, 1827. Zool.

J. London, 3: 218.

Type locality: India; restricted to Bengal by Smith 1935.

Distribution: India (west Himalaya, Kashmir, Punjab, Jammu, Uttar Pradesh, Himachal Pradesh), Nepal (Katmandu, Chitlong), east Afghanistan, China [Xizang (= Tibet)].

****Laudakia papenfussi* Zhao, 1998**

Laudakia papenfussi Ermi Zhao, 1998. Zool. Res., Kunming, 19 (5): 401-404.

Type locality: Mayang River Valley between Mayang Village and Diya Village, Zanda Co., Xizang Autonomous Region; 3300 m elevation.

Distribution: China (Xizang).

****Laudakia wui* Zhao, 1998**

Laudakia wui Ermi Zhao, 1998. Acta Zootaxon Sinica, Beijing, 23 (4): 440-444.

Type locality: Yi'ong, Bomi County, Xizang Autonomous Region; 2350 m elevation.

Distribution: China (Xizang).

Genus *Trapelus* Cuvier, 1817

This genus includes 12 species distributed across the arid belt of southeastern Europe, southwestern Asia, Middle Asia, China, Iran, Afghanistan, Northern Africa and Arabian Peninsula. Within the genus *Trapelus*, specific status of *Trapelus agilis* and *T. sanguinolentus* (Macey *et al.*, 2000, 2006) was confirmed based on analysis of mt-DNA.

Type species: *Trapelus mutabilis* (Merrem, 1820). Tent. Syst. Amph.: 50.

One species is recorded in the fauna of China.

***Trapelus sanguinolentus* (Pallas, 1814)**

Lacerta sanguinolenta Pallas, 1814. Zoogr. Rosso-Asiat., 3: 23, Tab. 4, Figure 2.

Type locality: Terek River Valley. "Hügelland Kum-Ankatar am Terek-Fluss, Kaukasien".

Distribution: Russia (Dagestan), Ciscaucasus, Kazakhstan, Kyrgyzstan, Uzbekistan, Turkmenistan, Tajikistan, Kazakhstan and southward to north Iran and north Afghanistan, northwestern China (western Xinjiang).

Genus *Phrynocephalus* Kaup, 1825

This genus includes approximately 40 species distributed across the arid belt of southeastern Europe, Middle Asia, western China, Iran, Afghanistan, Pakistan, northern Africa and Arabian Peninsula. These lizards represent the core fauna of the Palearctic deserts together with the lacertid lizards of the genus *Eremias*. It is one of the most taxonomically complicated groups among Palearctic lizards. Methods and approaches of taxonomic and

phylogenetic study of Chinese species of this genus are in focus of the research that leads to many taxonomic and nomenclature changes. We try to provide general ideas about species richness of this group of lizards within China (Zhao and Adler, 1993; Zhao *et al.*, 1999; Pang *et al.*, 2003; Wang and Fu, 2004; Barabanov and Ananjeva, 2007; Ji *et al.*, 2009).

Type species: *Phrynocephalus guttatus* (Gmelin, 1789)

Fauna of China includes at least 11 species. Detailed information about type specimens, type localities, synonyms and distribution of forms known during all history of study is presented by Barabanov and Ananjeva (2007). Phylogenetic relationships within clade of Tibetan Plateau (subgenus *Oreosaura* Barabanov et Ananjeva, 2007) are discussed in papers of Pang *et al.* (2003) and Guo and Wang (2007). According to the opinion of the authors of the last monograph on the fauna of China (Zhao *et al.*, 1999), with addition of newly described species there are 20 species as follows:

1) *Phrynocephalus albolineatus* Zhao, 1979, K. T. Zhao, 1979. Acta Univ. Inner Mongolia, Huhhot, 1979 (2): 113. According to Barabanov and Ananjeva (2007), it is junior synonym of *Ph. guttatus melanurus*.

Type locality: Ural Desert, Kazakhstan.

Distribution: China (northern Xinjiang), Russia, Kazakhstan.

2) *Phrynocephalus axillaris* Blanford, 1875, W. T. Blanford, 1875. J. Asiatic Soc. Bengal, Calcutta, New ser., 44 (2): 192.

Type locality: Eastern Turkestan (=southern Xinjiang), China.

Distribution: Xinjiang and Gansu, China.

3) *Phrynocephalus erythrurus* Zugmayer, 1909, E. Zugmayer, 1909. Zool. Jarb., Syst. Geogr. Biol. Tiere, Jens, 27: 504. According to Barabanov and Ananjeva (2007), it is junior synonym of *Ph. theobaldi*.

4) *Phrynocephalus forsythii* Anderson, 1872, J. Anderson. 1872. Proc. Zool. Soc. London, 1872: 390. Type locality: Yarkand (=Shache, Xinjiang Auto Reg), China.

Distribution: Xinjiang, China.

5) *Phrynocephalus fronalis* Strauch, 1876. In N. Przewalski, Mongol Strana Tangut, St. Petersburg, 2(3): 15. According to Wang and Fu (2004), Barabanov and Ananjeva (2007) as well as Gozdzik *et al.* (2009), it is junior synonym of *Ph. przewalskii*

6) *Phrynocephalus grumgrzimaloi* Bedriaga, 1907, J. von Bedriaga, 1907. Wissensch. Result. Przewalski Central-

Asien Reisen, Zool., St. Petersburg, 3(1): 420. According to Barabanov and Ananjeva (2007), it is junior synonym of *Ph. guttatus melanurus*.

7) *Phrynocephalus guttatus* (Gmelin, 1789). J. F. Gmelin, Linn. Syst. Nat., Ed.13, Leipzig, 1: 1078.

Type locality: Ural Desert. Kazakhstan.

Distribution: China (Xinjiang), Russia, Kazakhstan.

8) *Phrynocephalus helioscopus* (Pallas, 1771), P. S. Pallas, 1771. Reise versch. Prov. Russ. Reichs, St. Petersburg, 1: 457.

Type locality: Deserti australois (= Inderskaya Steppe), Kazakhstan.

Distribution: China (Xinjiang, Inner Mongolia), Turkey, Iran, Armenia, Kazakhstan.

9) *Phrynocephalus hongyuanensis* Zhao, Jiang et Huang, 1980, E-M Zhao, Y-M Jiang et Q-Y Huang, 1980. Acta Zool. Sinica, Beijing, 26: 178. According to Guo and Wang (2007) as well as Jin *et al.* (2008), it is junior synonym of *Ph. vlangalii*.

10) *Phrynocephalus immaculatus* Zhao, 1995, K. T. Zhao, 1995. In Zhao Er-mi (Ed.): Herpetological Series (8), Amphibian Zoogeogr. Division of China: 47-56. According to Barabanov and Ananjeva (2007), it is junior synonym of *Ph. versicolor versicolor*.

11) *Phrynocephalus kozlovi* Bedriaga, 1906, J. von Bedriaga, "1905" (1906). Ann. Mus. Zool. Acad. Imper. Sci. St. Petersburg, 10: 162. According to Barabanov and Ananjeva (2007), it is junior synonym of *Ph. axillaris*

12) *Phrynocephalus mystaceus* (Pallas, 1776), P. S. Pallas, 1776. Reise versch. Prov. Russ. Reichs, St. Petersburg, 3: 702.

Type locality: Arenosis Naryn.

Distribution: China (Xinjiang), Russia, Middle-Central Asia.

13) *Phrynocephalus nasatus* Golubev et Dunayev, 1995, M. L. Golubev et E. A. Dunayev, 1995. Russ. J. Herpetol., 2(1): 5-9. According to Barabanov and Ananjeva (2007), it is junior synonym of *Ph. axillaris*

14) *Phrynocephalus przewalskii* Strauch, 1876, A. Strauch, 1876. In N. Przewalski, Mongol Strana Tangutov, St. Petersburg, 2(3): 10.

Type locality: Alashan Desert, Ordos Desert, China.

Distribution: Inner Mongolia, Ningxia, Gansu, China.

Note: Zhao and Adler (1993) described the distribution of *P. przewalskii* including Qinghai, which was not correct according to Zhao K. T. 1979.

15) *Phrynocephalus putjatia* Bedriaga, 1907-1909. In Wissenschaftliche Resultate der von Przewalskii N. M. nach Central-Asien unternommenen Reisen. Ann. Zool. Mus. Acad. St. Petersburg Zoologischer, III.

Type locality: Guide, China.

Distribution: Qinghai, Gansu, China.

Note: According to Wang *et al.* (2002), *P. putjatia* was a valid species.

16) *Phrynocephalus theobaldi* Blyth, 1863, E. Blyth, 1863. J. Asiatic Soc. Bengal, Calcutta, 32: 90.

Type locality: Lake Chomoriri (= Tso Moriri, Kashmir)

Distribution: China (Xizang), India (Kashmir), Nepal.

Note: Zhao and Adler (1993) described the distribution of *P. theobaldi* as including Xinjiang to be incorrect as stated in Zhao K. T. 1979.

17) *Phrynocephalus versicolor* Strauch, 1876. A. Strauch, in N. Przewalski, Mongol. Strana Tangutov, St. Petersburg, 2(3): 18.

Type locality: Alashan Desert, China.

Distribution: Xinjiang, Gansu, Inner Mongolia, Ningxia, China.

18) *Phrynocephalus vlangalii* Strauch, 1876. A. Strauch, in N. Przewalski, Mongol. Strana Tangutov, St. Petersburg, 2(3): 20.

Type locality: Kuku-noor (=Qinghai Lake), China.

Distribution: Qinghai, Xinjiang, Sichuan, Gansu, China.

19) *Phrynocephalus zetagensis* Wang *et al.*, 1996, Wang, Zeng *et al.*, 1996. Zool. Res., Kunming, 17(1): 27-29. According to Guo and Wang (2007), it is junior synonym of *Ph. theobaldi*.

20) *Phrynocephalus guinanensis* Ji, Wang *et al.*, 2009, X Ji, Y-Z Wang & Z Wang, 2009. Zootaxa, 1988: 61-68.

Type locality: Guinan, China.

Distribution: Only found in its type locality.

According to the list of species in the genus *Phrynocephalus* (Barabanov and Ananjeva, 2007), within the territory of China 12 species occur and they are:

Phrynocephalus axillaris Blanford, 1875

Phrynocephalus forsythii Anderson, 1872

Phrynocephalus guttatus (Gmelin, 1789) (*Ph. g. alpherakii* Bedriaga, 1905 and *Ph. g. melanurus* Eichwald, 1831)

Phrynocephalus helioscopus varius Eichwald, 1831

Phrynocephalus mystaceus (Pallas, 1776)

Phrynocephalus przewalskii Strauch, 1876

Phrynocephalus putjatia Bedriaga, 1909

Phrynocephalus roborowskii Bedriaga, "1905" 1906

Phrynocephalus theobaldi Blyth, 1863

Phrynocephalus versicolor Strauch, 1876

Phrynocephalus vlangalii Strauch, 1876 (*Ph. v. vlangalii* Strauch, 1876 and *Ph. v. hongyuanensis* Zhao, Jiang *et al.* Huang, 1980)

Phrynocephalus guinanensis Ji, Wang *et al.* Wang, 2009

Comparison of these lists of species confirms that the study and clarification of taxonomic status of species of complexes (*guttatus-versicolor-melanurus*) and (*frontalis-przewalskii*) taking in account the newly collected specimens from type territories of all species ever described is especially important and complicated goal.

Thus, recently the taxonomic diversity of agamid lizards in China is estimated as 49 species belonging to 12 genera and four subfamilies.

4. Discussion

4.1 Taxonomic diversity and species richness of agamids from China

Fauna of agamids of China has a complicated origin and is represented by the species from four evolutionary lineages (subfamilies) (Ananjeva, 2004), among which the subfamily Draconinae (7 genera, 28 species) reaches maximal generic and species richness. Three genera with 19 species (among them 12 species in *Phrynocephalus*) refer to the subfamily Agaminae, whereas the subfamilies Amphibolurinae and Leiolepidinae are represented by 1 genus and 1 species each.

Methodology of phylogenetic analysis (Moody, 1980), as well as approaches and methods of molecular analysis (Honda *et al.*, 2000; Macey *et al.*, 2000; Ananjeva, 2004) contribute greater clarity to understanding of the composition of genera of agamid lizards. However, the problem of revealing phylogenetic evaluation of morphological characters remains to be still actual as well as the construction of identification keys. Modern results from DNA analyses (Macey *et al.*, 2000, 2006) allow the reconstruction of further divisions within the genera *Japalura* and *Laudakia*, reflecting distinct evolutionary lineages.

4.2 Zoogeographic Analysis of the Fauna of Agamids in China

The list of specified Chinese agamids was compared with those of several regions of Eurasia, including South Asia (Das, 1996), Southeast Asia [Myanmar, Thailand, Sunda region (Manthey and Grossmann, 1997; Zug *et al.*, 2003; [www.http://www.calacademy.org/research/herpetology](http://www.calacademy.org/research/herpetology))], Vietnam

(Ananjeva *et al.*, 2007; Nguyen *et al.*, 2009)], Iran (Anderson, 1999) and North Eurasia (Ananjeva *et al.*, 2006a). Comparison shows maximal genera and species diversity of agamids in South Asia and the Sunda Archipelago. The fauna of China demonstrates the highest phylogenetic variety (four subfamilies whereas other regions have no more than three subfamilies), and it shows third highest species richness among the compared territories. The agamid fauna of Indochina (Vietnam, Myanmar, Thailand) is represented by 3 subfamilies with 10 genera, and their species richness varies from 25 to 28 species. The oriental fauna of China (without Palearctic species) is similar in its composition with the fauna of Vietnam (index of similarity -0.39), i.e., the highest among the regions compared with China (Ananjeva *et al.*, 2007). The Palearctic fauna of China is presented by one subfamily and 3 genera, its species richness accounts for about 40% all the agamid species in China. The oriental (Indomalayan) fauna of China has many common species together with the fauna of Vietnam (Ananjeva *et al.*,

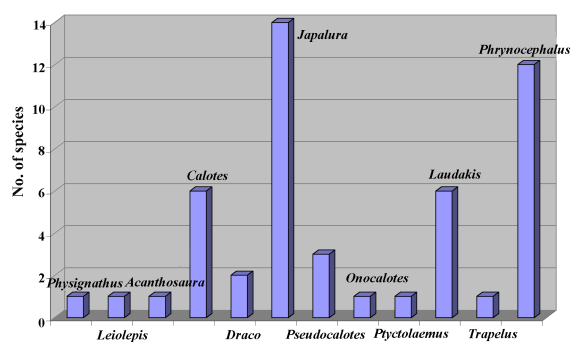


Figure 1 The composition of the fauna of agamid lizards of China.

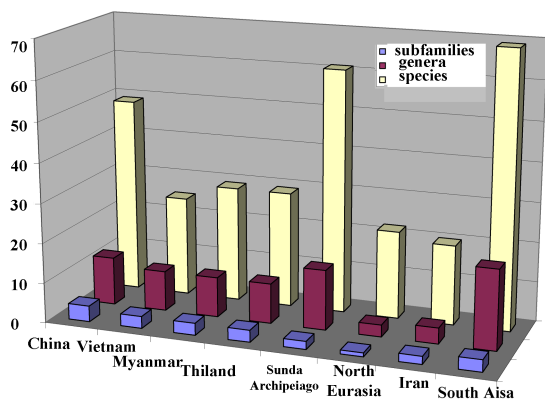


Figure 2 Comparison of the subfamilies, genera and species of agamids among different regions of Eurasia.

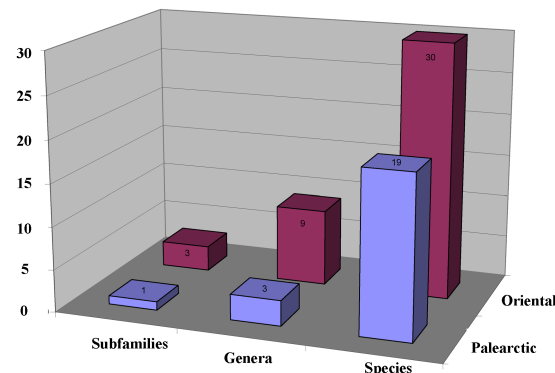


Figure 3 Value of Palearctic and Oriental elements in the fauna of the Agamas of China.

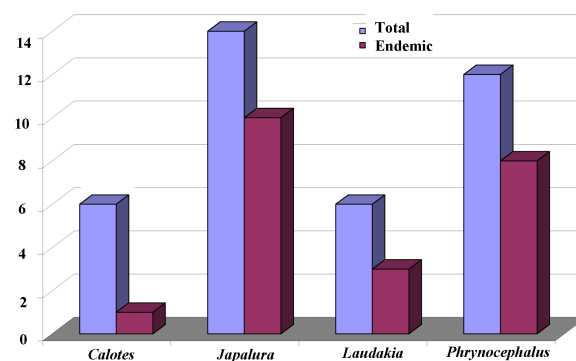


Figure 4 Endemic species of the agamid lizards in the fauna of China.

2007). Those common species are widely distributed, belonging to the genera *Calotes*, *Draco* and *Leiolepis*, with the most widely distributed species being the genus *Acanthosaura* (*A. lepidogaster*), *Japalura fasciata* and *Pseudocalotes brevipes*.

Two widely distributed species of the genus *Calotes* (*C. emma*, *C. versicolor*) and *Physignathus cocincinus* (typical for all Southeast Asia except Sunda Archipelago) are all found living in China. Among the palearctic agamids there are also some widely distributed Eurasian species, such as *T. sanguinolentus*, *Ph. mystaceus*, *Ph. helioscopus* and *Ph. guttatus*.

Among the 49 species of agamids of China (see annotated list), 22 species (45%) are distributed exclusively within the territory of this country. Endemic species refer to 4 genera, with the most belonging to the genus *Japalura* (10 of 14) and being the members of phylogenetic lineage from the Tibetan Plateau (8 of 12) in the genus *Phrynocephalus*. These data testify a great importance of biodiversity conservation in western

provinces of China which is already included into the list of Priority regions of planet.

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