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# Contributions to the Herpetology of South-Asia (Nepal, India)

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**Herausgeber:**
**Prof. Dr. H. Hermann Schleich/ARCO-Nepal, München**

**Online Version, 2017, unverändert, ISBN 978-3-947497-01-0**

**Eds.: Schleich, H.H. & Kästle, W., Druckversion 1998**

**Veröffentlichungen aus dem Fuhlrott-Museum**

**Herausgeber: Prof. Dr. H. Hermann Schleich**

**Bd. 4: 1-322; Wuppertal, März 1998**

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Veröffentlichungen ARCO, 2017 -online
ISBN 978-3-947497-01-0

Veröffentlichungen aus dem Fuhlrott-Museum Wuppertal

ISSN 1434-8276
ISBN 3-87429-404-8

Herausgeber: Prof. Dr. H. Hermann Schleich

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# Studies on *Tylototriton verrucosus* (Amphibia: Urodela)

## Contributions to the Biology of *Tylototriton verrucosus* Anderson, 1871 from East Nepal (Amphibia: Caudata, Salamandridae)

Christiane C. Anders*, H. Hermann Schleich**
& Karan B. Shah ***

**Key words:** Zoology, morphology, anatomy; ecology, habitats; *Tylototriton verrucosus*; East-Nepal

**Abstract:** Data on the biology of *Tylototriton verrucosus* from East Nepal are given and compared with other distributional records. Five different localities were sampled and analysed. Morphological and biometrical investigations were carried out on locally different populations, and their colourations are described. The urogenital system of both sexes is described and illustrated, seasonal dynamics in the sex ratio are supposed. Sexual dimorphism and oophagy in this salamander species is reported. Food composition and stomach contents are analysed. Statements on research and conservation status are given.

### Introduction

Regarding the quotations on the biology of *Tylototriton verrucosus,* there are many contradictions presented in the different publications. The breeding behaviour, the reproductive mode and the distribution (esp. Nepal) is discussed controversial, or is uncertain in the available literature. Furthermore the conservation status of *T.verrucosus* for Nepal is reported as unknown (Shah, 1995), whereas in India the newt is treated as an endangered species (Dasgupta, 1990). One of the causes for taxonomical confusions surely were the former description of two colour morphs, now recognized as different species. This concept was recognized and worked out by Nussbaum et al. (1995) with the designation of a new species for the orange-patterned form (now: *Tylototriton shanjing* Nussbaum et al. 1995) and restriction of *T. verrucosus* to the westernmost distributed brownish form. Further information concerning possible differencies in the behaviour between the two species, a detailed delimitation of the species range and a verification of the data for each locality record of *T.verrucosus* are still lacking.

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The first notice for the occurence of *Tylototriton verrucosus* from Nepal was given by Soman (1966), and subsequent publications were only provided by Shresta (1981, 1984, 1989 & 1994). A most recent publication (Gruber, 1996) states that the record and description of *T. verrucosus* from Nepal is still lacking. Thus, numerous questions still exist particularly regarding the populations from Nepal, and their comparison with neighbouring populations from the adjacent Darjeeling region. Due to Nussbaum et al. (1995) the possibility should not be disregarded, that *T. verrucosus* contains more than one subspecies, because of the morphometric variation within that species. It is one of the aims of the present paper to report on all available informations we collected on the biology of *T. verrucosus* during field activities in May to June 1996 in East-Nepal.

## Historical review

The original description by Anderson (1871) and repetitive summaries by Boulenger (1882,1890) and Smith (1924) were the few mentionable publications on *Tylototriton verrucosus* for nearly a century. Thorn (1968) provided a clear summary of the genus. Nussbaum & Brodie (1982) divided the genus into *Tylototriton* and *Echinotriton*. Zhao & Hu (1988) gave a new definition for *Echinotriton* as a subgenus, but later Zhao (1990) recognized the generic status of *Echinotriton*.

Descriptions of the reproductive behaviour were given in Annandale (1907,1908), Shresta (1989,1994) and Scholz (1993) as well as in publications concerning animals from pet trade like Mudrack (1969, 1972), Rehberg (1986), Nietzke (1989), Menzer (1991) and Raaijmakers (1992). Information regarding parental care were mentioned by Dasgupta (1984) and Shresta (1989,1994). Observations on the larval stages of *Tylototriton verrucosus* were supplied by Boulenger (1920), Smith (1924), Shresta (1989) and Dasgupta (1988). Further data on general ethology were provided by Wongratana (1984), Brodie et al. (1984) and Shresta (1989). Habitats were described by Chaudhuri (1966), Shresta (1984) and Dasgupta (1990). Investigations concerning the status as an endangered form were made by Shresta (1989,1996a), Dasgupta & Dasgupta (1990) and Dasgupta (1990, 1993, 1994).

Accounts of climatic conditions in the habitats, as well as a report on the accompanying flora and fauna, the description of larvae and some Protozoan blood parasites of *Tylototriton verrucosus* from Darjeeling (N. India) is presented with the Ph. Dissertation of Dasgupta (1994). Investigations on the ecology of populations from Darjeeling were made by Kuzmin et al. (1994). An important survey on the feeding ecology of adult *T. verrucosus* from Darjeeling was published by Dasgupta in 1996. Recently the species was treated as *Pleurodeles verrucosus* by Dutta (1992 &1997), following the publication of Dubois (1987), who stated the genus *Pleurodeles* for *Tylototriton verrocosus*.

## The genus *Tylototriton* in South-East Asia

## Distribution (fig. 1) and Taxa

### *Tylototriton* Anderson, 1871

**Type species**: *Tylototriton verrucosus* ANDERSON, 1871, by monotypy.

According to the partitioning of the genus and the placement of two species (*andersoni* and *chinhaiensis*) in the genus *Echinotriton* gen. nov. by Nussbaum & Brodie,1982 and the taxonomic review of *T. verrucosus* with the description of the orange-patterned form as a new species T. *shanjing* sp. nov. by Nussbaum et al., 1995, the genus consists of

following five extant species:
*T. asperrimus* Unterstein 1930,
*T. kweichowensis* Fang & Chang 1932,
*T. shanjing* Nussbaum et al. 1995,
*T. taliangensis* Liu 1959,
*T. verrucosus* Anderson 1871.

Zhao & Hu (1988) considered *Echinotriton* Nussbaum & Brodie, 1982 as a subgenus. But in 1990, Zhao recognized the generic status of *Echinotriton* and according to this, the genus exists of three species (Duellmann, 1993): *T. verrucosus* Anderson, 1871, *T. kweichowensis* Fang & Chang, 1932 and *T. taliangensis* Liu, 1950. Adding the recently described *T. shanjing* Nussbaum et al. 1995, there are four South Asian species of *Tylototriton*, because *T. asperrimus* was placed by Zhao (1990) in the genus *Echinotriton.* This was declined by Nussbaum et al. (1995), who replaced the species into *T. asperrimus*.

**Fossils**: According to Estes (1983), salamanders of the genus *Tylototriton* were of early and mid-Cenozoic occurence in Europe, with nowadays withdrawn to the Oriental Region. For systematic discussion by means of osteology we refer to the following paper, same vol. by Haller-Probst.

**Distribution**: China; northern Vietnam; Tailand; Myanmar; India and East-Nepal.

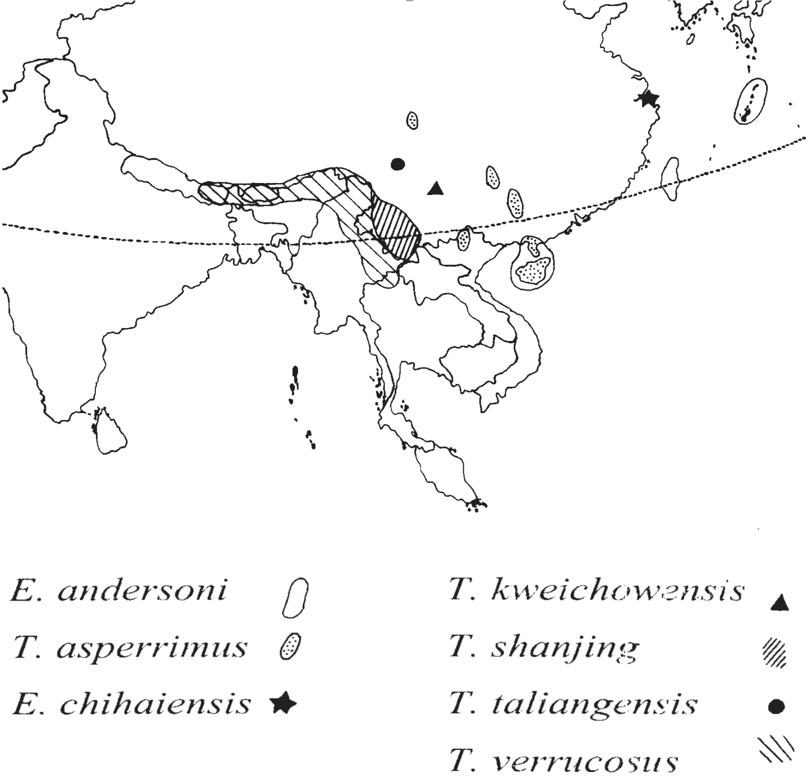

**Fig. 1.** Distribution and range of the different species of the genus *Tylototriton* and

*Echinotriton* (modified after Zhao & Hu, 1988).

## *Tylototriton verrucosus* ANDERSON, 1871.

**Types**: Types not designated and unknown
Syntypes: including BMNH 1874.6.1.3.
Neotype: KIZ 74 II 0061 VI.16, adult male, collected 16.6.1974 at Gongwa, 1600 m elevation, Longchuan County, Yunnan, Province, People‘s Republic of China, by native collectors.
Topotypes: KIZ 74 II 0067 VI.16; UMMZ 189647-8; UTA 27588-9.

**Type locality**: “Nantin, Momien, and Hotha valleys, Western Yunnan, China.”

**Range**: Yunnan, China to northern Myanmar, hills of Arunachal Pradesh, Sikkim, Darjeeling, Manipur and Meghalaya in India, Buthan, and eastern Nepal; Chieng Dao, northern Tailand; and northern Vietnam (Frost, 1985). According to Nussbaum et al. (1995) all specimens outside of China and the specimens from the type locality in extreme western Yunnan (China) are *T. verrucosus*. *T. shanjing* Nussbaum et al. 1995 is only reported for Yunnan.

**Distribution in Nepal** (fig. 2): East Nepal: Dingla (Soman,1966); Chulachuli hills, Mai River Valley, Hile, Dhankuta, Mai Pokhari (Shresta, 1984, 1989); Hurhure (Dr. D.R.Edds, pers. comm. 1996); Mac Valley, Rautac Khola (Dutta, 1997).
Own records of the newt were made for Hans Pokhari, Phikkal, Mai Pokhari, Champgairi and Baglehore in East Nepal. In the area of Hile and Dhankuta (mentioned by Shresta, 1984, 1989) no *T. verrucosus* could be found by us and also local people in that region were not familiar with the occurence of a newt.

**Altitude**: Between 4.000 and 6.000 feet (1220-1830 m, Annandale in Smith,1924), 1.200 and 2.200 m (Thorn, 1968), 1.500 and 2.200 m (Dasgupta,1993), 5.000 and 7.400 feet (1.525-2.250 m, Chaudhuri,1966). Own records were made in an altitude between 1.580 and 2.150 m. Dutta (1997) mentioned for Ukhrul, Manipur, India a vertical range of 8.000-11.000 ft. (2.440-3.350 m).

**Size**: Mudrack (1969): 150-180 mm total length and 70-90 mm SVL. Shresta (1984) mentioned five specimens measuring from 130-200 mm total length and 59-105 mm SVL.

**Ethymology and common names**: The species name is derived from Latin *verrucosus* = full of warts (*verruca* = wart). Nepali: Pani gohora (water monitor), Pani kukur (water dog), long-ling (animal with a long tail); Thai (Wongratana, 1984): Mah-nam (water dog), Kra-taang nam (water lizard), Jing-jok nam (water wall-lizard), Jora-ke-nam (water crocodile); English: Burmese Newt, Himalayan Newt, Crocodile Salamander, Indian Salamander ; German: Rauhhäutiger Wassermolch, Krokodilmolch, Geknöpfter Birma-Krokodilmolch, Geknöpfter Wassermolch, Warziger Krokodilmolch.

**Ethnological usage/treatment**: For Thailand, Wongratana (1984) reported that local people used to collect, kill and sun-dry the animals for mixing with roots of herbs and use in curing fever. Shresta (1984) mentioned dried and smoked preparation of the newt used by witch doctors as a cure for typhoid and gastric ailments. Our own investigations, respectively queries to the local people could not proof paramedical or any other usage of *T.verrucosus* in East Nepal. Dasgupta (1990) reported the capture of *T. verrucosus* from India for illegal export.

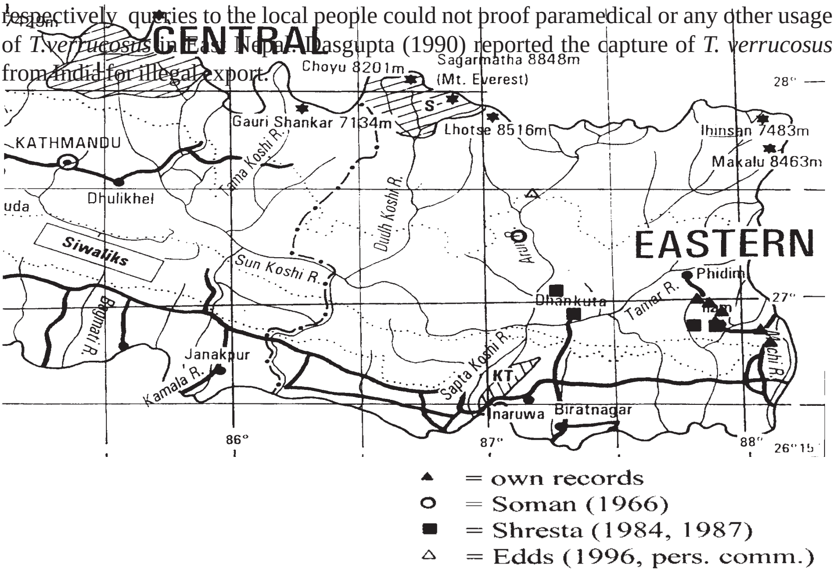

**Fig. 2.** Records of *Tylototriton verrucosus* in Nepal.

## Methods and Abbreviations

Specimens with the code VW-KTM were deposited in the ”Volkswagen collection” of the Natural History Museum, Tribhuvan University, Kathmandu, Nepal and specimens with VW-D are stored in the Institut of Palaeontology and hist. Geology of the University of Munich, Germany. Other museum codes used for types are: BMNH (British Museum, Natural History, London, G.B.), KIZ (Kunming Institute of Zoology; People‘s Republic of China), UMMZ (University of Michigan, Museum of Zoology; USA) and UTA (University of Texas at Arlington; USA).

## Habitats

**General Habitats**: During the non-reproductive period the newts are terrestrial (Zhao & Hu, 1988). During this phase they could be found hidden under stones, shrubs and wood, on humid places in more or less dense forests. During the breeding season they stay in pools, small ponds and ditches. With commencing breeding season they were found after the first monsoon rains nearly in every small pond or even large puddles of rain water. According to Shah (1996, pers. comm.) during October 1996 not a single *Tylototriton verrucosus* was seen in any of the ponds examined in Mai / June. Fully grown postlarvae and adults were found under dry leaves in a maize field and hidden below small bushes inside the forest.

**Study sites**: We could prove the occurence of *Tylototriton verrucosus* for five different localities in Ilam district, East Nepal. The study sites are located along the connecting route between Birtamod (Terai) and Phidim (Mahabharat). All sites were stagnant stretches of water, several of them only filled or flooded by precipitations.

**Fig. 3.** Habitat of *Tylototriton verrucosus*; Phikkal, E-Nepal.

**Fig. 4.** Habitat of *Tylototriton verrucosus*; Champgairi, E-Nepal.

**Fig. 5.** Habitat of *Tylototriton verrucosus*; way to Mai Pokhari, E-Nepal.

Listing of localities:

Hans Pokhari (N 26° 49‘44.7 / E 88°04‘18.2) is situated at an altitude of 1.580m. This habitat consists of a nearly 15 m long and 10 m broad pond near midway between Charali and Phikkal. The depth is approximately 0.05 m at the shore, and up to 0.70 m in the middle. This very flat body of water has no other water supply than meteoric precipitation, mainly the monsoon rains. The pond vegetation appears only sporadically and mainly consists of *Persicaria hydropiper* and grasses. The surrounding subtropical hill forest is dominated by *Schima wallichii* and *Albizzia* sp. along with *Sauraria nepalensis*, *Rubus ellipticus* and *Eupatorium adenophorum* (Singh, 1996). At the ponds edge 6 big agglomerations of Anura-larvae and also a single carnivorous anuran larva could be observed. Furthermore 2 specimens of *Atretium schistosum* were collected, one snake feeding on larvae in the water and the other hiding below the shore vegetation of the pond. On June 13, 1996 we counted about 30 - 40 specimens (all males) from this locality.

Phikkal, Locality near Ph. (N 27°03‘26.2 / E 87°50‘20.6; 1680 m ). The small pond (5 m long, 2.5 m broad, 0.6 m deep) lies in the middle of a tee plantation (fig. 3). The vegetation at this elevation consists mainly of *Thea sinensis* but also of *Cryptomeria japonica*, *Datura* sp. and *Elettaria cardamomun*. The plant species in the pond are *Polygonum plebeium* and grasses. Besides some adults of *Tylototriton verrucosus*, foam nests and single larvae of Rhacophorids (probable *Polypedates leucomystax*) also occur in the small ditch. At June 8, 1996 we counted four specimens in this artificial pond.

Champgairi (N 26°54‘37.7 / E 87°55‘51.3) a monsoon floated pond behind a small dam, en route the way from Ilam to Mai Pokhari (fig. 4). The forest at this altitude of 1820 m is dominated by *Schima wallichii* mixed with *Alnus nepalensis* and *Cryptomeria japonica*. Singh (1996) determined plant species as *Nymphea*, *Persicaria hydropiper*, *Persicaria posambu* and grasses growing in the pool. Along its edges *Potentilla* sp., *Eupatorium adenophorum*, *Plantago lanceolata* etc. are present. On June 1, 1996, 20 foam nests of Polypetatids were scattered over the 20 m long and 15 m broad pool.

Mai Pokhari (N 27°00‘25.7 / E 87°55‘55.1; fig. 5). The main lake lies at an elevation of 2100 m. Due to anthropogeneous release of *Carassius auratus*, not a single *Tylototriton verrucosus* could be observed in the lake itself. In spite of the unfourtunable situation to breed in the lake itself, there were plenty of them in surrounding bodies of water, like ditches, pools (with an average depth of 0.15 - 0.2 m) and monsoonal floods. An estimation of the population density on June 1, 1996 yielded about 80 - 100 specimens of *Tylototriton* for a 35 $m^2$ sized pond. The vegetation is dominated by *Sphagnum* moss and *Nymphaea stellata*. The forest surrounding is of the *Castanopsis* type with *Castanopsis indica* and *Castanopsis tribuloides* as the dominant species.

Baglehore (N 27°00‘25.7 / E 87°55‘52.6; 2150 m). In the 1.5 m long, 1 m broad and 0.4 m spring puddle 12 adult specimens, and four larvae of *Tylototriton* were collected on 1996. Also rhacophorid foam nests, larvae of *Bufo*, *Rana* and some juvenile *Bufo himalayanus* were observed. The common natural vegetation at this altitude is composed by *Castanopsis* and *Quercus*. The vegetation around the pool includes *Alnus nepalensis*, *Sauraria nepalensis*, *Edgeworthia gardneri*, *Aconogonum capanulatum* var. *molle*, *Berberis asiatica*, *Persicaria hydropiper* and *Eupatorium adenophorum* (Singh, 1996).

The average precipitation values for the studied localities (Ilam district) are 2000 - 2500 mm per year. The town of Ilam has an average of 76 to 125 rain days and a single dry period per year. At the elevation of Mai Pokhari and Baglehore snow persists for two

| Locality | date/time | T°C air/water | pH | ORP (mV) | diss.solids (µs) | oxygen (%)/(mg/l) |
|---|---|---|---|---|---|---|
| H. Pokhari | 06/13; 13,30h | 23.4/24.8 | 6.3 | 61 | 107 | 11 / 0.9 |
| Phikkal | 06/08; 8,30h | 18.1/16.6 | 6.1 | 138 | 352 | 31 / 2.3 |
| Champgairi | 06/01; ——— | ——— | 6.6 | 84 | 39 | 42 / 3.6 |
| Mai Pokhari | 06/01; ——— | 17.3/20.6 | 5.5 | 174 | 21 | 24 / 2.1 |

**Tab. 1**. Water analysis of four collecting sites of *Tylototriton verrucosus.*

month (January/February respectively February/March) with a snow cover measuring up to 0.3 m (Dobremez, 1976).

For four of the five habitats of *Tylototriton verrucosus,* water samples were taken and analysed. The examined main parameters of these water samples were temperature, pH, oxidation-reduction potential (ORP), dissolved solids content and content of oxygen; they are listed in tab.1 on the following page.

Own results agree with Shresta (1989) that the water in the breeding pools, mostly resulting from spring rain and melting snow, tend to be rather acidic due to the accumulation of humic acids. The analyses yielded very low pH rates in a range from 5.5 - 6.6. The higher values of dissolved solid contents from the small pond in the tea plantation at Phikkal point to a considerable contamination by feces and urine, both from humans and domestic animals or still more propable the pollution by pesticides from the plantations. The value shows a nearly 17x increased rate of dissolved solids content comparing the pool of the tea plantation with the habitat at Mai Pokhari.

## Systematic descriptrion of *Tylototriton verrucosus* from Nepal

**Diagnosis**: *Tylototriton verrucosus* is distinguished from the other members of the genus by an entirely brown dorsum in combination with strongly developed cranial crests and cranial boss.

**Description**: As *T. verrucosus* was reviewed most recently (Nussbaum et al. 1995), we try to give the most relevant diagnostic features in accordance with our own studies:

- Snout-vent length of adult newts between 59 - 105 mm.
- Total length 129,9 - 200 mm.
- Head flat, with strongly developed cranial crests and cranial boss.
- Nostrils close to the tip of the broad and rounded snout.
- Eyes of moderate size with large, granular upper eyelid.
- Prominent glandular vertebral ridge.
- Dorsolateral row of warts on each side of the body and anterior tail.
- Fingers (4) and toes (5) free, not webbed.
- Skin tubercular.
- Paratoids large and distinct, slightly concave.
- Gular fold present.
- Tail laterally compressed.
- Uniformly brown coloration on dorsum and venter. Tail and soles of hands and feet lighter brown than body. Ventral ridge of tail paler, sometimes yellow or orange.

We add the following features of the examined Nepalese populations which are not conform with the descriptions of Anderson (1871) and Boulenger (1890):
- head always longer than broad.
- tail always shorter than snout-vent length.

## Morphology and biometry

Specimens of *Tylototriton verrucosus* from all mentioned localities,were examined. The determination of the individual‘s sex was possible by external examination of the cloaca in living specimens or by examination of the gonads in preserved specimens, if doubtful.
All measurements were made with callipers according to fig. 6. The following morphometric features were examined and are listed in table 2 : SVL (snout-vent length / tip of the snout to the posterior edge of the cloacal opening), TL (tail length / posterior edge of cloacal opening to the tip of the tail), TW (tail width / at the anterior part of the tail, directly behind the cloaca), TTL (total length / tip of snout to tip of tail), HL (head length / tip of snout to gular fold), HW (head width / at the angle of the upper jaw), IOD (inter-orbital distance / between anterior angles of eyes), IND (inter-narial distance / between the two narial openings), END (eye-naris distance / between the right narial opening and anterior angle of the right eye), ED (eye diameter / between anterior and posterior angle of the right eye), AGD (axilla-groin distance / with fore- and hindlimbs extended at right angle), LF (length of forelimb / extended), LH (length of hindlimb / extended), CL (length of cloaca / anterior to posterior end of the swollen cloacal range), CW (maximum width of cloaca) and BW (number of body warts of the right body side, inclusive the number of warts of the anterior tail).

| Habitat | Hans Pokhari | Phikkal | Mai Pokhari | Champgairi | Baglehore |
|---|---|---|---|---|---|
| sex ratio | 13 m : 0 f | 3 m : 1 f | 34 m : 1 f | 2 m : 0 f | 12 m : 0 f |
| n | 13 | 4 | 35 | 2 | 12 |

size range and (MV) mean value in mm

| | | | | | |
|---|---|---|---|---|---|
| SVL | 72 / 91 (79.92) | 76 / 95 (81.75) | 68 / 89 (81.95) | 76 / 77 (76.5) | 76 / 88(81.29) |
| TL | 64 / 83 (74.23) | 70 / 84 (77.75) | *42 / 81(74.77) | 72 / 73 (72.5) | 64 / 78 (69.08) |
| TW | 10 / 12 (10.46) | 9.5 / 10 (9.63) | 7 / 12 (9.73) | 9 / 9 (9) | 8.5 / 11(9.66) |
| TTL | 141/174(159.7) | 146/175(157.8) | *120/170(154.6)1 | 49/149(149) | 141/166 (150.4) |
| HL | 19 / 22 (21.1) | 19 / 21 (20.8) | 19 / 23 (20.9) | 19 / 20 (19.5) | 19.5 / 21(20.5) |
| HW | 17 / 23 (19.3) | 17 / 19 (18.3) | 15 / 21(18.4) | 17 / 18(17.5) | 16 / 18.5(19.04) |
| IOD | 5.5/ 7 (5.8) | 5 / 7 (6.5) | 4.5 / 6.5 (5.8) | 5 / 5.5 (5.25) | 6 / 8.5 (6.6) |
| IND | 6 / 7 (6.4) | 5 / 6 (5.5) | 4 / 7 (5.9) | 5 / 6 (5.5) | 5 / 7 (6.7) |
| END | 4 /5 (4.7) | 3 / 5 (4.5) | 3.5 / 5 (4.2) | 4 / 4 (4) | 3.5 / 5 (4.1) |
| ED | 4.5 / 5 (4.7) | 5 / 5 (5) | 4 / 5 (4.7) | 4.5 / 5(4.8) | 4 / 6(5) |
| AGD | 36 / 46 (41.3) | 36 / 48 (42.3) | 31 / 48 (38.2) | 36 / 37(36.5) | 36 / 47 (39.6) |
| LF | 19 / 20 (19.7) | 19 / 25 (20.5) | 19.5 / 26( 22.0) | 24 / 26(25) | 22 / 27(24) |
| LH | 20 / 21(19.9) | 20 / 26(20.4) | 20 / 28 (22.3) | 25 / 26 (25.5) | 23 / 29 (26.5) |
| CL | 10 / 13 (11) | 9 / 10 (9.3) | 9 / 13 (10.8) | 10 / 10.5 (10.3) | 8 / 12.5 (10.4) |
| CW | 8 / 12 (9.6) | 7 / 9.5 ( 8.3) | 6.5 / 11 (9.0) | 9 / 9 (9) | 8 / 10 (9.3) |
| BW | 12 / 14 (13.7) | 13 / 14 (13.8) | 12 / 15 (14.6) | 13 / 14 (13.5) | 13 / 16 (14.4) |

**Tab. 2.** Measurements of *Tylototriton verrucosus*.- Abbreviations given above; all measurements (beside BW) in mm; BW = number of warts; * = minimum values very low, because of an animal with tail anomaly, f = female, m = male, n = number of collected *T.v.*

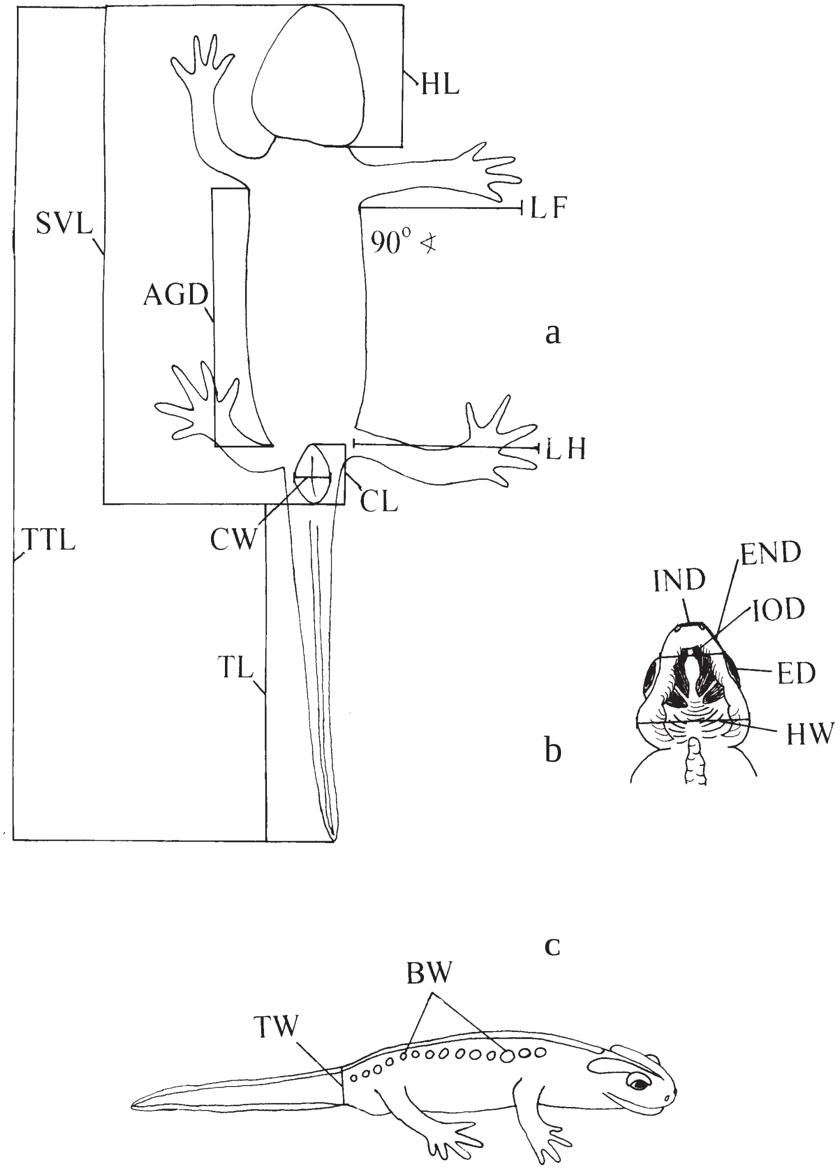

**Fig. 6.** Measurements: a- ventral aspect, b- dorsal aspect of head, c- lateral aspect. Abbreviations are given above.

The tail of *Tylototriton* is almost always longer than the snout-vent length, whereas in *Echinotriton* it is opposite (Nussbaum & Brodie, 1982). In contrary to this, Zhao & Hu (1988) mentioned that the relation of TL/SVL is characterized for *T. verrucosus* by a shorter tail. These latter observations were confirmed by Kabisch et al. (1994) in examining 13 animals from pet trade with a TL/SVL relation of 87,7%. With only one exception (specimen with TL = SVL) we can record a distinctly larger body length in the relation TL/SVL for all examined *T. verrucosus* (n = 66) from East Nepal.

**Colouration** (fig. 7-9)

Concerning the description of the colouration there exists great confusion and a lot of contradictions in the literature because of the two former colour types. By the revision of Nussbaum et al. (1995), *T. verrucosus* is restricted to the brown form, and the orange-marked form was described as a new species (*T.shanjing*). The basic colour of *T.shanjing* is dark brown to black with contrasting orange colour on the head, including the parotoid glands. The dorsal glandular ridge, the rows of lateral warts, the entire tail and the entire legs are also orange (Brodie et al., 1984). According to the first description of Anderson (1871) *T. verrucosus* (brown form) is uniform blackish brown, paler on the lips, snout, chin, throat, and ventral surface of the limbs, all of which are of a brownish-olive tinge, and the surface of the tail is dull orange-yellow, fading to lightish brown on the sides. All recorded and examined specimens of *T. verrucosus* from East Nepal followed the general colour description by Anderson (1871) and therefore agree with the brown form (*T. verrucosus*) for Nepal sensu Nussbaum et al. (1995). Rehberg (1986) describes a wide range in colour differences in juvenile newts of his captive bred specimens (orange -patterned form) and therefore concluded that there is no reason to treat this form as a different species. Besides, there is an interesting tendency of slight colour differences between the specimens of the five habitats. Comparing the intensity of the uniform brown colouration from the different study sites it is interesting that the animals from Hans Pokhari and Phikkal (1.580-1.680 m altitude) showed altogether a somewhat paler ligth greyish brown. The brightest individuals were found at Phikkal. Contrarily, the newts of Baglehore (2.150 m elevation) and Mai Pokhari, both from higher altitudes were accentuated by a darker chocolate blackish-brown.

**Sexual dimorphism** (fig. 10)

Despite only rare remarks regarding sexual dimorphism e.g. Menzer (1991) assumed that males of *T. verrucosus* have distinctly longer tails than females, there are only few facts known and Shrestha (1989) even states the lack of sexual dimorphism in *T. verrucosus*.As mentioned in Kabisch et al. (1994) for *T. taliangensis*, we state that in *T. verrucosus* during the breeding season the cloaca of females is more conical in shape than in males, and that the morphological development of the cloacal zone is relatively week compared with other salamandrids. The small amount of females (n = 2) which are at our disposal exclude a statistical evaluation of the morphometric data to demonstrate sexual dimorphism whithin the nepalese populations. Yet the conical shape, together with a different form of the cloacal opening (fig. 10), at least during the reproductive period, offers the possibility to distinguish female and male. Adding the highly distended venter in females during the breeding season (Shresta, 1989), and the fact that females are 10-20% longer than males (Dasgupta, 1996), the sex of the newts should be easily recognizable. At least during the reproductive period sexual dimorphism seems to be evident in *T. verrucosus* concerning the cloacal size and differentiation. According to Nussbaum et al. (1995) differences between sexes within populations exist for several characters, but they are not corresponding among populations.

**Fig. 7-9.** Different views of different specimens of *Tylototriton verrucosus*.

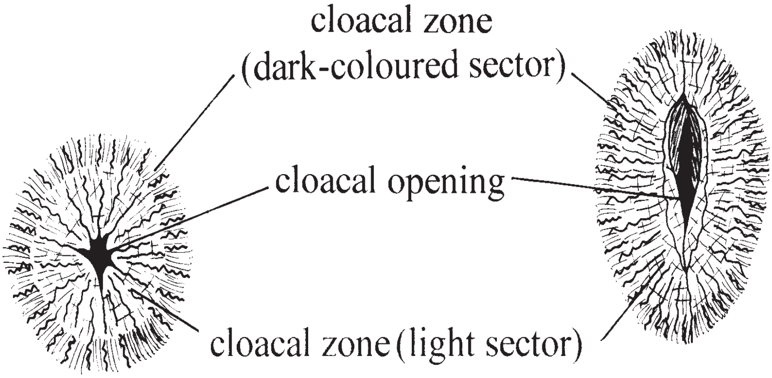

**Fig. 10.** Cloacal opening of female (left: VW/D 96-1/I) and male (VW/D 96-1/V) *Tylototriton verrucosus* during reproductive period.

## Morphology of the urogenital system (fig. 11-13)

The urogenital systems of one female (VW KTM 96- 16/I) and one male (VW D 96-1/III) *T. verrucosus* were examined and described:
During the reproductive periode the ovaries of a female are strongly developed and fill nearly the whole body cave. The examination showed both ripe and developing eggs in different stages. There is a small lobate fat body in a reduced form (fig. 11). The oviduct is convoluted and terminates at its anterior end with a funnel-shaped infundibulum lying at the same level with the posterior tip of the lung. The posterior part of the oviduct is not extended (as in viviparous species). The Wolffian duct first passes along the lateral margin of the kidney and than descends forming a bow to the ventral side. Numerous short collecting ducts are visible joining the Wolffian duct. The thin walled urinary bladder is visible as a ventral outgrowth of the cloaca. On both sides, right and left of the mouth of the intestine into the cloaca are the openings of the oviducts, and dorsally there are the smaller apertures of the Wolffian ducts.
The testis consist of several lobes. Their number, shape and connection differ from one individual to the other (fig. 13). Just as for *Salamandra salamandra* (Dehn v.,1975; Duellmann & Trueb,1986) the number of the lobes of the testis might increase with the age and successive annual breeding cycles of the male *T. verrucosus*. In some cases the lobes are connected by a longitudinal duct. The left testis is slightly posterior to the right one. A longish fat body is adjacent to each testis (fig. 12). The efferent ductules run from the testis to the anterior part of the kidney. The Wolffian duct lies laterally of the elongated kidney. The persisting rest of the Mullerian duct is visible anterior of the Wolffian duct. The male cloaca receives the collecting ducts of the kidney and the Wolffian ducts dorsally.
The examined structures of the urogenital system of *Tylototriton verrucosus* correspond to general construction patterns in salamanders.

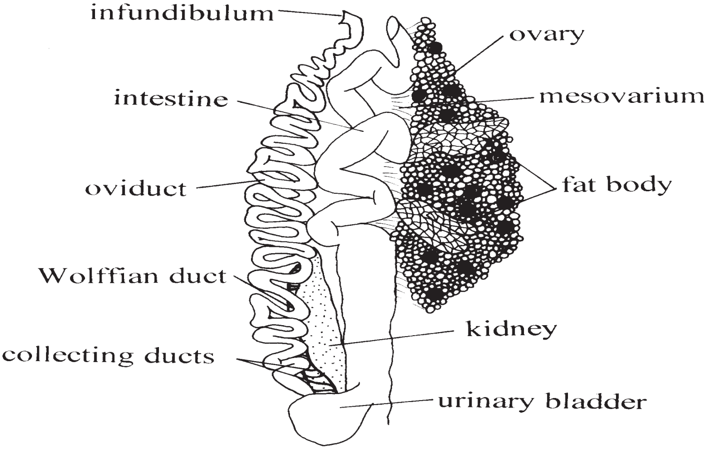

**Fig. 11.** Urogenital system of a female *Tylototriton verrucosus* (VW/KTM 96- 16/I). Right ovary and left oviduct and kidney were omitted.

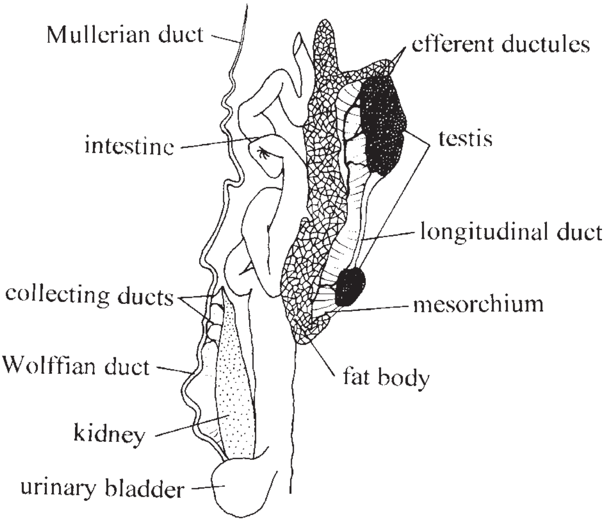

**Fig. 12.** Urogenital system of a male *Tylototriton verrucosus* (VW/D 96- 1/III). Right testis and left kidney were omitted.

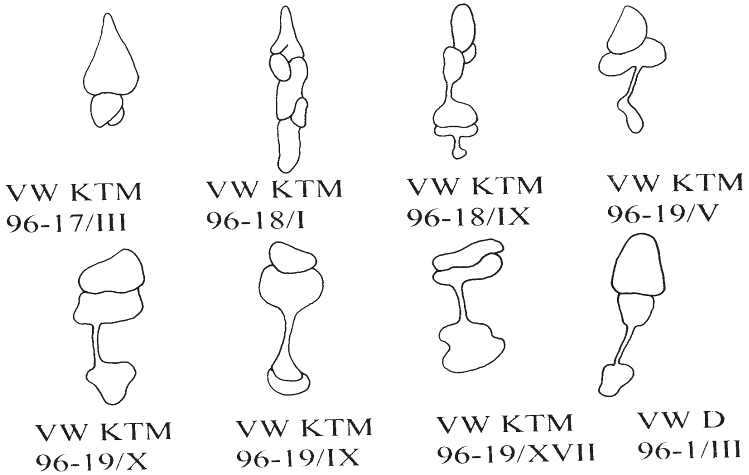

**Fig. 13.** Morphological diversity of testes of different individuals.

## Osteology

See following paper contributions (same volume by Haller-Probst).

## Reproductive Biology (fig. 14)

As soon as the first spring showers fall in March or April the adult newts enter the water and the females begin to lay their eggs shortly afterwards.The breeding season probably continues throughout the rainy season and the adults leave the water by beginning of october (Annandale in Smith,1924). Dasgupta (1993) differentiates three culminations within the breeding season namely in April/Mai, in June/July (courtship and egg-laying period; both sexes migrated into water) and in August/September (post-breeding period; males move back to land, while females still remain in water). He also describes a nuptial dance and a ventral amplexus during the copulation, which is mostly carried out during the night by *T. verrucosus* from north India. Rehberg (1986), Menzer (1991) and Shresta (1994) agree in the observation of a nuptial dance, and Boulenger (1920), Nietzke (1989), Dasgupta (1984) and Shresta (1989) describe an amplexus. Scholz (1993) compares the behavior of *T. verrucosus* with that of *Pleurodeles* and concludes that obviously the perhaps facultative amplexus was simply not observed, or that within single taxa the amplexus lacks. Rehberg (1986) reports that he could never observe an amplexus (*T. shanjing*, China), but on other occasions he records an amplexus of specimens from northern Tailand (*T.verrucosus*). He concluded that if the chinese orange-patterned form differs in its reproductive behavior from all other *T. verrucosus* the establishment of a new species would be nescessary. Annandale (1908) reports, that during his field trip at the beginning of July he could only collect females and he did not see a single male at that time. Menzer (1991) supposed that there could be a correlation between the time of egg laying and the lunar phase (full moon). Maturity of *T. verrucosus* is reached with an age of 2 years (Shresta, 1989) and a total length of 150-200 mm in males and 120-180 mm in females. The age of sexual maturation according to Kuzmin et al. (1994) is with 3-5 years and the maximum age was estimated to be 11 years. Shresta (1989) supposed that females frequently mate more than once in a breeding season. His conclusion is based on the examination of the ovaries of breeding females.

**Fig. 14**. Population density in a monsoon flooded puddle near Mai Pokhari, drawn from a photograph. At this early time of the breeding season mainly males were found in water.

**Eggs**

Very contradictory informations on eggs are presented by different authors . *Tylototriton* deposits small sized eggs singly or in pairs in standing water (Chaudhuri,1966; Gyi,1969; Smith,1924; Wolterstorff & Herre,1935). Smith (1924) described that the eggs are slightly attached, singly to weeds etc. and that they are large although somewhat variable in size (between 6 and 10 mm in diameter when the gelatinous envelope is fully distended by the developing embryo). Dasgupta (1993) mentioned that the eggs are laid singly, not especially on specific weeds, and that the clutch size varies between 15 and 30. He also submits the only known information that *T. verrucosus* from the Darjeeling region mostly deposits its eggs somewhat above the water level and that they only are submerged when the level rises after the onset of monsoon rains. He assumed that this late inundation into water is necessary for the development of the larvae. Annandale (1907) reported, that the eggs were attached together in pairs, each pair being separated from the others and that they are not fixed to any object. As measurements of the eggs he mentioned approx. 10 mm in diameter and a spherical shape. Annandale (1908) added that the eggs of *T. verrucosus* are sometimes also laid singly on the bottom of the pools and sometimes they occasionally were attached to vegetation. Nietzke (1989) observed that a female from pet trade laid soon after copulation about 90 eggs singly on land respectively on objects swimming on the surface of the water. For the deposition of eggs by two females (pet trade) Rehberg (1986) counted 291 respectively 240 eggs with an average diameter of 7 mm. The single laid eggs were put on different objects at, below and above water level and only a few eggs, finding no support, sank to the bottom of the water. Menzer (1991) mentioned an average diameter of 7 mm for the eggs too. According to Mudrack (1972) the clutch size is about 90 eggs, each of an average diameter of 10 mm. Zhao & Hu (1988) stated that in the genus *Tylototriton* (in contrary to *Echinotriton* ) the egg diameter is less than 2.5 mm and that they are deposited in water. Shresta (1989) mentioned spherical and demersal eggs (with an average diameter of 10-15 mm, if freshly laid), laid in groups, attached to leaves, stems and roots of submerged plants, particularly *Polygonum* spp. He counted 40 eggs as average clutch size (maximum 90 eggs) in 1989, in 1994 he reported of about 200 fertilized eggs per female. Investigations made in an aquarium by Dasgupta (1984) shows that the way of laying eggs may change and correlate with the phase of reproductive cycle. He mentioned that in the beginning of May single eggs were laid on land, while at the end of May they were laid in clusters within tunnels and burrows, and that in the (artificial) case of absence of land female newts also accept the back of a toad to attach their eggs. As predators of single eggs and egg-clutches introduced fresh water fish, especially carp is reported by Duellmann & Trueb (1986) and Dasgupta (1988). Their observation was also confirmed in the present study. In the lake of Mai Pokhari the common carp was introduced during the last years for pisciculture and since that time the population became extinct. Shresta (1989) reported the occurence of *T. verrucosus* for the natural lake of Mai Pokhari. Our recent investigations proved the absence of newts in the main lake and confirmed that their occurence is limited to surrounding small water wholes and ditches.

| author | egg ∅ size(mm) | clutch size | single eggs / or in pairs | form | substrat / place |
|---|---|---|---|---|---|
| Annandale (1907) | 10 | — | attached in pairs | spherical | small pools, not fixed |
| Annandale (1908) | — | — | singly, sometimes in pairs | — | bottom of pools occasionaly attached to blades |
| Smith (1924) | 6-10 | — | singly | | slightly attached to weeds |
| Wolterstorff & Herre (1935) | — | — | in pairs, attached | — | rain pools |
| Mudrack (1972) | 10 | ca.90 | singly | — | on land and in water |
| Nussbaum & Brodie (1982) | ”small” | — | singly or in pairs | — | in standing water |
| Dasgupta (1984) | — | — | singly begin of May; in clusters at end of May | spherical | on land and in water |
| Rehberg (1986) | 7 | 291/240 | singly | — | on land and in water |
| Shresta (1989) | 10-15 | 30-60 | in groups (ca.40) | spherical | attached on submerged plants e.g. *Polygonum* |
| Zhao & Hu (1988) | ≤2.5 * | — | — | — | deposited in water |
| Nietzke (1989) | — | ca.90 | singly | — | on land and on objects swimming in water |
| Menzer (1991) | 7 | 15 | — | — | on land |
| Raaijmakers (1992) | 10 | ca.100 (perhaps of 2 females) | in pairs | — | on land |
| Dasgupta (1993) | — | ca.15-30 | singly in a clutch | — | mostly somewhat above water level, no specific plant preference |
| Present investigation | 7.5 | 36 | singly | spherical | in linnen bag after transport |

**Tab. 3.** Characteristics of egg size / number, compared from different literature sources.- * = valid for all species of *Tylototriton*.

## Larvae

The period (d = days) between egg laying and hatching of the larvae, respectively the length (= l) of emerging larvae is described in literature as following:

Annandale (1907): l = 9 mm; Smith (1924): l = 11 mm; Mudrack (1972): d = 16-30; Dasgupta (1984): d = 20; Rehberg (1986): d = 13-19, l = 13 mm; Nietzke (1989): d = 15-30; Shresta (1989): l = 6-10 mm; Menzer (1991): d = 12-15; l = 12 mm; Raaijmakers (1992): d = 13-22; l = 10-12 mm.

The larvae of *T. verrucosus* show the typical morphology of the pond type (Valentine & Dennis, 1964 in Duellmann & Trueb, 1986), with bushy gills (three pairs of external gills (Ferrier,1974; Smith,1924)), adapted to a lower oxygen content of the water, with well-developed balancers and with thin and deep dorsal and ventral caudal fins. Typical for pond-dwelling larvae is, that they stay in their early life periode on the bottom of the pond (Duellmann & Trueb, 1986 and Rehberg, 1986). A description of the larvae is given in Smith (1924) and Boulenger (1920). Dasgupta (1993) observed that the behavior of the larvae is territorial and very agressive against each other, and that they are hiding in the ground to avoid predation. The life-history and especially the development of the larvae is recorded comprehensively in Shresta (1989) and in Dasgupta (1988). Smith (1924) distinguished two developmental stages, whereas Shresta (1989) divided the development into three stages plus the young newt. Finally Dasgupta (1988) distinguished six stages including the post-metamorphic juvenile and stated in agreement with Smith (1924), that the metamorphose of larvae of ”late- egg clutches” is not finished before the first winter, but is completed at end of the following October. The two larvae observed in a pool by us, in the first week of June (measuring 60 and 62 mm) seem to be hatchlings from the preceeding year. The length of metamorphosed newts varies from 43 mm (Menzer, 1991), 49-58 mm (Rehberg, 1986), 65-73 mm (Mudrack, 1972), 52-75 mm (Smith, 1924) to 90 mm (Annandale in Smith, 1924). Possible predators of larval newts might be water beetles, larval odonates and large spiders (Dasgupta, 1988).

| Locality | Baglehore | | Hurhure |
|---|---|---|---|
| Code | 21/V | 21/VI | DE-N-313 |
| SVL | 38 | 35 | 24 |
| TL | 22 | 27 | 18.5 |
| TW | 5 | 4 | 4 |
| TTL | 60 | 62 | 42.5 |
| HL | 10 | 10 | 9 |
| HW | 8.5 | 8 | 7.5 |
| IOD | 4 | 3.5 | 2.5 |
| IND | 2.5 | 2.5 | 2.5 |
| END | 3 | 2 | 1.5 |
| ED | 3 | 2.5 | 1.5 |
| AGD | 20 | 18 | 13.5 |
| LF | 9 | 9 | 7 |
| LH | 10 | 10 | 5 |

**Tab. 4.** Measurements of larvae of *Tylototriton verrucosus*.- Code = Code number of the VW-KTM collection 1996 resp. collection of NHM, Kathmandu; all measurements in mm; abbreviations given in chapter Morphology and Biometry.

## Courtship behaviour and Parental Care

First records of courtship behaviour in *T. verrucosus* were given by Chaudhuri (1966). Captivity observations made by Dasgupta (1984) in an aquarium showed, that females were seen coiling around eggs, respectively sitting on them and standing in the vicinity of the eggs not before the emergence of larvae. Kuzmin et al. (1994) mentioned a tendency of *T. verrucosus* towards terrestrial reproduction accompanied by parental care.

Shresta (1989) discussed, that according Dunn (1923) *T. verrucosus* is a salamandrid with fewer, larger eggs deposited in hidden nest sites in water but that by own observations no parental care was to observe in this species. Concerning parental care, Shresta (1994) also added, that emerging tadpoles of *T. verrucosus* swim directly towards their parents and climb abroad for protection and uptake of food.

### Sex Ratio

In the course of our examinations, the sex ratios of *T. verrucosus* from east Nepal could also be determined. During the investigations at end of May and beginning of June hardly any female newt could be found at the study sites Hans Pokhari, Champgaire and Baglehore. Only one female was found at Phikkal and one at Mai Pokhari. Altogether the sex relation at our five study sites was 64 males : 2 females. Annandale (1908) mentioned for his observations in the Darjeeling region at the beginning of July that there was an abundance of females and that he could find a single male. Kabisch et al.(1994) observed for *T. taliangensis* a relation of 10 males : 3 females during their excursion to southwest China in June. Faber (1996) observed seasonal dynamics for the sex ratio for *Triturus alpestris* during aquatic life circle. For the beginning and the end of the aquatic phase (immigration phase, post-spawning phase), he found that males were more numerous than females, whereas the females outnumbered the males during the mating and spawning season. For *T. verrucosus* from Nepal we suppose seasonal dynamics in the sex ratio, but further investigations at different reproduction periods and sites are still desirable.

### Behaviour

A great diversity of antipredator behavior of *T. verrucosus* (orange-patterned form, now *T. shanjing*) is described and photographed in detail by Brodie et al. (1984). Wongratana (1984) remarked a short low noise while snapping its jaws when being seized and also while snapping at an earthworm. Shresta (1989) reported a low *twak*, *twak*, *twak* as the call from *Tylototriton verrucosus*. During the breading season the newt is also active at daytime but during his land phase it is crepuscular respectively nocturnal (Nietzke, 1989).

### Food Patterns and Stomach Analyses

Informations based on food acceptance of animals from pet trade are reported as follows:

Mudrack (1969): newts only accept food in water, mainly earthworms and sometimes small slugs.

Nietzke (1989) records earthworms and small slugs, also wood-lice, mosquito larvae and caterpillars.

Rehberg (1986) mentioned for captives chopped meat, larvae of meal-beetle, earthworms and slugs.

Shresta (1984): zoo-benthos, mushrooms (!), aquatic insects and tadpoles as main food items for the newts.

Shresta (1994): water insects, beetles and algae.

For *T. taliangensis*, Kabisch et al. (1994) proved different Spheriidae, Dytiscidae, water beetles and decomposed vegetable fragments as food content.

Food reported for larval *T. verrucosus*, as a predominantly bottom-feeder (Dasgupta, 1988) consists of mosquito larvae, microcrustaceans, chironomids and various other benthic prey items.

Dasgupta (1988, 1996): the later larval stages (IV and V) avoid microcrustaceans, prey on aquatic insects and syntopic crabs, whereas stage VI (post-metamorphic juvenils) feed upon small bivalves (*Sphaerium indicum*) and more terrestrial food as collembola, larval

| Locality | Phikkal | | | Hans Pokhari | | | | | Mai Pokhari | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Code | 16/I | 16/II | 16/III | 17/II | 18/I | 18/IX | 19/I | 19/V | 19/X | 19/XI | 19/XIII | 19/XV | 19/XVII |
| Sex | f | m | m | m | m | m | m | m | m | m | m | m | m |
| Insects | | | | | | + | | | + | + | + | | |
| % | | | | | | 41.8 | | | 44.3 | 28.9 | 23.8 | | |
| Bivalves | | | | + | + | + | | + | | + | | | |
| % | | | | 61.2 | 85.7 | 58.2 | | 100 | | 38.4 | | | |
| Plants | | | | | | | | | + | + | + | | |
| % | | | | | | | | | 30.1 | 32.7 | 68.3 | | |
| Sand / stones | | | | + | + | | | | | | | | |
| % | | | | 38.8 | 14.3 | | | | | | | | |
| cannabalized eggs of *T.v.* | | + | + | | | | + | | + | | + | + | + |
| % | | 100 | 100 | | | | 100 | | 25.6 | | 7.9 | 100 | 100 |
| n | | 12 | 7 | | | | 9 | | 6 | | 2 | 11 | 2 |
| Remarks: | | | | | | | | | | | | | |
| Parasites | | + | | + | + | | + | + | + | + | + | | + |

**Tab. 5.** Composition of diet content in adult *T. verrucosus*.- Code = Code number of the VW-KTM collection 1996; f = female; m = male; % = percent of dry-weigth digestive tract content; + = proved content; Parasites = Nematodes.

lepidoptera, larval diptera and isopods.
Halder (pers. comm. in Dasgupta, 1990) listed:
termites, wood-lice and corprophilous insects. Dasgupta (1990) summarized for the time during breeding season/monsoon time: algae, water beetles and bugs, tadpoles of *Polypedates leucomystax*, snails, slugs, earthworm and insect larvae. Dasgupta (1996): diet of *T. verrucosus* is highly variable, depending on study site and comprised of
aquatic and terrestrial components during reproductive periode. Our own investigations of stomach contents showed a diet comprised of aquatic and terrestrial insects, bivalves of the family Pisidiidae (fig. 15), cannibalized eggs of *T. verrucosus* and also a high percentage of herbivorous material. We can add to the prey list of Dasgupta (1996) following:

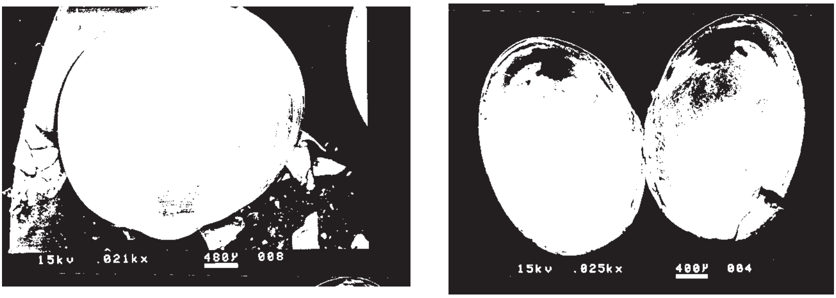

**Fig. 15.** Pisidiids from stomach content of *T.verrucosus* (Ilam, 1996)

Coleoptera (larvae and imagines)-Elateridae,
Homoptera-Anchenorrhyncha, Odonata (larvae)-Libellulidae.
Analysis of stomach contents at different habitats in East-Nepal, yielded several specimens with eggs of the own species. There is some evidence in literature concerning oophagy in other salamanders too. Kuzmin et al. (1994) reported egg cannibalism in *T. verrucosus* and more recently Dasgupta (1996) observed oophagy being restricted to females as he found no male with swallowed eggs. In contrast to him we stated oophygy in males, too. The different contents of the alimentary system found during our investigations (May/June 1996) for adult *T. verrucosus* is presented in the preceding table 5.

## Discussion

### Herbivory

Concerning the common fact, that adult salamanders, like all adult amphibians are carnivorous (Duellmann & Trueb, 1986), the high percentage of vegetal content in the diet of three animals was very surprising to us. The stomach of one animal contained up to 68,3 % vegetal items and in another case the portion of plants (32.7%) passed that of insects. We tend to interprete, that depending on the habitat (herbivorous diet is only reported for Mai Pokhari) also plant material is accepted as food. From one locality (Pacheng, Darjeeling) Kuzmin et al. (1994) report intestinal filling with plant material but it was not considered as food items by these authors. In a detailed report on the feeding ecology of *T. verrucosus* from Darjeeling (Dasgupta, 1996), there is no evidence, even for (partial) herbivory, but adult diet was found to be highly variable depending on the study site. In the case of other amphibians, Ultsch (1973) reported that observations indicate an amount of non animal material even for an excess of 75 % for *Siren*, an aquatic salamander and he added that captive *Siren* also feed on *Elodea*. Dunn (1924) suggested that *Siren* might be a herbivorous salamander but this idea was refuted by Scroggin & Davis (1956 in Ultsch, 1973) who especially refer to its short digestive tract typical for carnivores. KABISCH et al. (1994) list in an analysis of faeces of *Tylototriton taliangensis* besides animal material also heavily decomposed plant fragments. This rises the question, how accidently swallowed herbivorous material could be utilized in such an effective way. Shresta (1994) reported the acceptance of mushrooms as food in captive *T. verrucosus*. We agree with Ultsch (1973) that only physiological studies concerning the digestion of salamanders with high percentage of vegetal food can solve this question finally. We summarize that *Tylototriton verrucosus* from East-Nepal could be, perhaps depending on habitats, an opportunistic omnivorous salamander.

### Oophagy in *Tylototriton verrucosus*

In seven of thirteen digestive tracts of *T. verrucosus* cannibalized spawn of the own species was recorded. The fact of oophagy in salamanders is well known and a detailed review is given in Dasgupta (1996). He considered oophagy in *T. verrucosus* as sex-specific, due to the fact that only female newts were found in Darjeeling with ingested eggs. Own observations on populations from Nepal showed, that oophagy is also practiced by males. Our only examined female had no eggs in its digestive system. In five of seven by dissected males eggs were the only content of the digestive tract. This seems to support our thesis, that eggs are swallowed during opportunistic feeding in times of or at places with insufficient food. The fact, that our investigations were carried out during May and June, while Dasgupta‘s observations are from June to September could point to a seasonally changing of sex-specific oophagy. With the beginning of the mating period in May/June we only found males migrating first to spawning sites, and in these early days the eggs of the fewer females were taken as prey items. It would be important to settle the question whether oophagy in both sexes occurs constantly through the whole periode of spawning. Further investigations are still nescessary, but we consider that oophagy in *Tylototriton verrucosus* is not sex-specific, as oophagy is proved for both, female (Darjeeling) and male (East-Nepal ) newts.

### Coloration

Our observations on a darker coloration of *T. verrucosus* at higher localities could be conform with the general physiological fact, that animals living in higher elevations are darker than those from lower altitudes, due to better protection against ultraviolet radiation. There is also a possibility for intraspecific variation concerning colour developement and the suggestion, that basic coloration is affected by ground colour, illumination and temperature (Duellmann & Trueb, 1986).

### Research and Conservation

According to Dasgupta (1993) the survival of *T. verrucosus* in Darjeeling (India) without distinct protection is doubtful. Therefore local support for the natural habitat of the newt is given in that area by the WWF. Scientific research programs are realized in the zoo of Darjeeling and financial help for protecting is given by the AG Urodela.

In India *T. verrucosus* is recognized as endangered and listed in Schedule I of the Indian Wildlife (Protection) Act of 1972 (Dasgupta, 1990). According to Shresta (1984) the Himalayan newt is on the verge of extinction in Nepal and is scarcely available for detailed studies. In a country report for Nepal, Shresta (1996b) regards *T. verrucosus* of Nepal as rare and being affected by habitat change. Dasgupta (1990, 1993) and Dasgupta & Dasgupta (1990) regard the progressive loss of aquatic habitats and illegal export as primary causes of declining populations of *T. verrucosus* in Darjeeling. According to Shah (1995) the status given by HMG Nepal, IUCN and CITES is unknown for Nepal and *T. verrucosus* is not designated for protection in Nepal under the NRDB status (National Red Data Book). As the Indian/Nepalese border crosses its distribution range, frontier-crossing protective measures would be desirable for the conservation of *Tylototriton verrucosus* in Ilam and Darjeeling.

Our own field data are yet not sufficient enough to make definite statements and suggestions for conservation strategies. As far as it came to our knowledge local inhabitants in Nepals distributional range of *Tylototriton* were not directly disturbing the populations, and many people were even not aware of the newts presence. But the use of puddles and ponds by domestic cattle as well as introduction of fish (e.g,. Mai Pokhari) are first signs of irreversible habitat destructions. Also the use of pestizides around Ilam´s tea plantations might be regarded as steady menace to the species and its habitats. Longterm field studies and reformed legislation should contribute to the knowledge and desirable conservation of *Tylototriton* in Nepal at least to a level similar to neighbouring India.

## Remarks

Shresta (1984) reports that *T. verrucosus* shares its niche with typical mountain brook hylid and rhacophorid frogs, but as far as known to us no evidence for Hylidae is recorded so far for Nepal. Regarding the following locality records Shresta (1989) should be corrected as follows: the Koshi Zone lies in Eastern, not in Western Nepal; the elevation (of the natural lake) of Mai Pokhari lies at 2.100 m (not at 1.300 m) and it should cover 1.75 hectares and not 175 hectares. Surprisingly Shresta (1981) also listed a webbed footed salamander and a caecilian (*Ichthyophis glutinosa*) as recorded for Nepal. As no further information is given the reported salamander is probably from the Arun valley and it could be a species of *Tylototriton*. Although one might expect the occurence of a caecilian for Nepal, we must add, that according to Taylor (1968) and Dutta (1996), *Ichthyophis glutinosus* is an endemic species of Sri Lanka.

## Acknowledgements

We are grateful to the Volkswagen-Stiftung, Germany for financing the present study in the form of the current project ”Natural History of the Amphibians and Reptiles from Nepal”.

Furthermore we thank the DAAD, Germany for providing funds for travel and stay in Nepal, and the University of Munich which provided financial support by granting a scholarship (HSPII,III).

Thanks are also due to Prof. Dr. G. Haszprunar and Prof. Dr. E. Burmeister from the Zoological State Collection Munich, Germany for the identification of stomach contents and to Prof. S. C. Singh from the Natural History Museum Kathmandu, Nepal for determinations of plants.

Furthermore one of us (CCA) ows thank to Prof. Dr. Haszprunar (Zool. State Coll.) for facilities of working place, SEM and library access.

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Veröffentlichungen aus dem Fuhlrott-Museum, 1998, Bd. 4: 27-34

# Studies on *Tylototriton verrucosus* (Amphibia: Urodela)

## Oxyurid Nematode Parasite of the Intestine of *Tylototriton verrucosus* Anderson, 1871

Christiane C. Anders*, Mansur El-Matbouli **
& Rudolf W. Hoffmann **

**Key words:** Parasites, Oxyuridea, *Tylototriton verrucosus*, East-Nepal

**Abstract:** An intestinal mature nematode of the Himalayan newt *Tylototriton verrucosus* from East-Nepal is described. Probably it belongs to the family Oxyuridae. The infestation rate was 69 % in examined salamanders. Data concerning light- and scanning electron microscopy structure are presented.

### Introduction

Fourteen genera of oxyurids have been described from different species of amphibians so far (Yamaguti, 1961). The small-sized helminths develop in the cranial intestine during their immature stages, then migrate into and become established in the large intestine, colon and rectum. Yamaguti (1961) characterized oxyurid nematodes by having an oesophagus with posterior bulbar enlargement, an intestine without diverticula (except in *Cruzidae*) and the caudal tip of females usually prolonged into a pointed tail. For most members of the order Oxyuridae a definite host specifity is characteristic (Frank, 1976). According to this author a greater number of genera was described from lower vertebrates, mostly reptiles but also from amphibians, where the parasites inhabit the large intestine and the rectum in enormous quantities. Although most species cause little or no harm to their hosts, this may happen in the case of a mass-attack. According to Flynn (1973 in Spieler, 1990) such a mass-attack can cause weakness, constipation and peritonitis and therefore can lead to death of the hosts. Very little is known on parasites of the only representant of urodele fauna (*Tylototriton verrucosus*) both in Nepal and India. Dasgupta (1996) reported *Haemogregarine* sp., *Pirhemocyton* and a *Leishmania*- like parasite as protozoic blood parasites of the newt and he also found Collembolan insects (*Hypogastrura* sp., *Seira indica*) and Ostracode crustaceans as parasites of *Tylototriton verrucosus*. Pal & Dasgupta (1980, in Kuzmin et al., 1994) also reported *Balantidium tylototritonis* and *B. rayi* for newts from Darjeeling. As far as known no further investigations concerning endo- or ectoparasites of this salamander have been carried out. The only reported oxyurid parasite (Yamaguti, 1961) for the related genus *Echinotriton* is *Cosmocercoides tridens* Wilkie, 1930 in *Echinotriton andersoni* (the distribution of this newt is restricted to Ryu Kyu-Islands, Japan). In the present report, an oxyurid nematode from the intestine of the Himalayan newt *Tylototriton verrucosus* is described.

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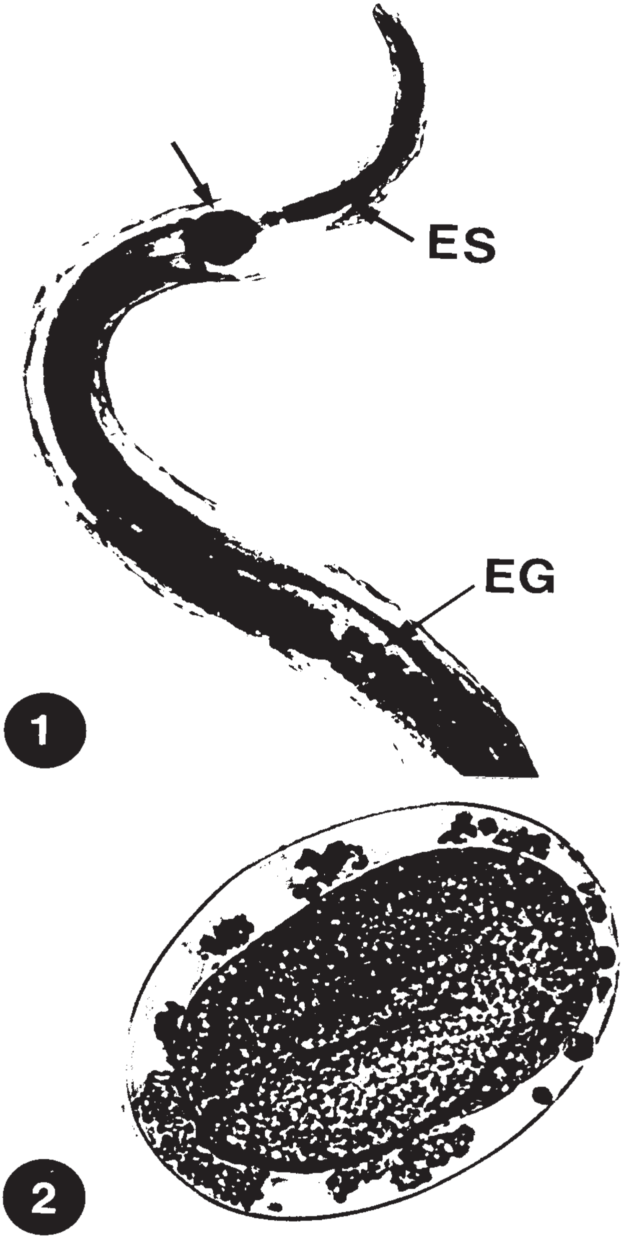

**Fig. 1.-2.** Light micrographs.
1) Adult female oxyurid nematode. Note the long esophagus (ES) with posterior bulb (arrow). (EG) Eggs. Magnification: x50.
2) Isolated, embryonal egg. Magnification: x600.

## Material and Methods

Examining the food of the Himalayan newt *Tylototriton verrucosus* from East-Nepal by studies on the digestive tract (see preceding contributions, same volume by Anders et al.), we found nematodes in the intestine. The present investigation includes examinations of the gastrointestinal tract of thirteen adult newts (12 males, 1 female) collected at the following localities in May / June 1996 : Phikkal (N 27°03‘26.2 / E 87°50‘20.6), Hans Pokhari (N 26°49‘44.7 / E 88°04‘18.2) and Mai Pokhari (N 27°00‘25.7 / E 87°55‘55.1) in the Ilam Province , East-Nepal. The newts were deposited in the Volkswagen Collection of the Natural History Museum, Tribhuvan University, Kathmandu, Nepal (VW KTM 16/I-III; 17/II; 18/I,IX; 19/I,V,X,XI,XIII,XV,XVII). Available endoparasitic specimens were sampled and fixed in 70 % ethanol and examined by light microscopy (LM) and scanning electron microscopy (SEM).

Light microscopy (LM): The morphology of the oxyuridean was observed in fixed unstained mounts, dimensions were determined using an ocular micrometer (Leitz Dialux) assisted by a computer (model PET 300 I; Leitz).

Scanning electron microscopy (SEM): Samples of fixed nematodes were processed through standard techniques for scanning electron microscopy (Dawes, 1971). After liquid dehydration each specimen was subject to critical point drying. After the specimens were mounted, they were coated with a gold CS minicoater sputter apparatus and viewed in a scanning electron microscope (Zeiss, DSM 950) operating at 20 KV. Micrographs were taken at variable magnifications.

## Description of an oxyurid nematode

**Host**: Himalayan newt *Tylototriton verrucosus*.
**Locality**: Province Ilam, East-Nepal, Southeast-Asia.
**Site of infection**: Lumen of the intestine, small and large intestine, rectum.
**Infestation rate**: 9 of 13 host specimens examined.
**Total intensity**: 108 helminths found in 9 hosts.
**Mean intensity**: 12 helminths.
**Maximum intensity**: 33 helminths.
**Minimum intensity**: 2 helminths.

| Locality | — | Phikkal | — | — | Hans Pokhari | | — | — | | Mai Pokhari | | | — |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Code no. VW KTM 96 | 16/I f | 16/II m | 16/III m | 17/II m | 18/I m | 18/IX m | 19/I m | 19/V m | 19/X m | 19/XI m | 19/XIII m | 19/XV m | 19/XVII m |
| Parasites | | + | | + | + | | + | + | + | + | + | | + |
| Intensity | | 7 | | 15 | 2 | | 19 | 4 | 33 | 12 | 5 | | 11 |

**Tab. 1.** Prevalence and intensity of an oxyurid nematode in *T. verrucosus*.- Code No. VW KTM = codes of the deposited newts; f = female; m = male; + = proved infestation; parasites = nematodes; intensity = number of helminths per infected host.

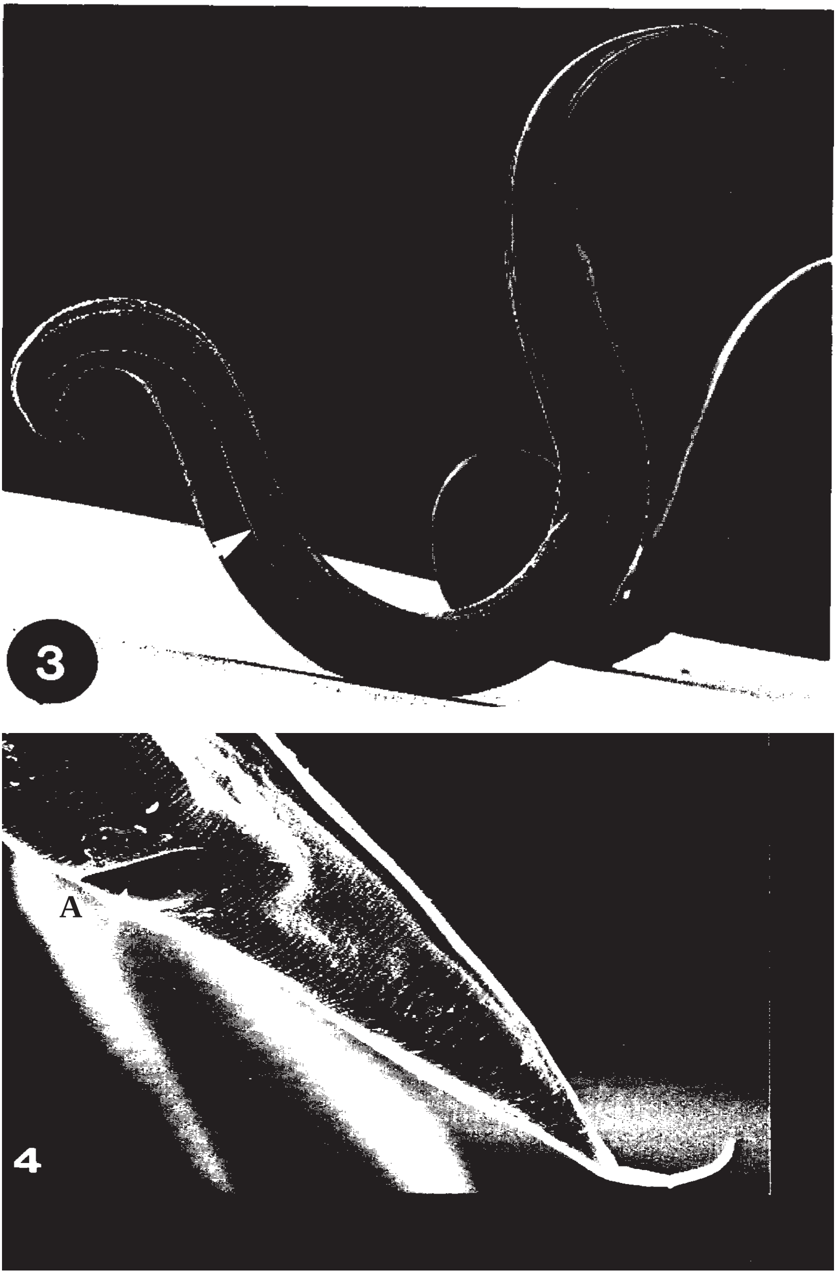

**Fig. 3.-4.** SEM micrograph of oxyurid nematodes.
3) Note the cylindrical shape and the lateral flanges (arrow). Magnification: x60.
4) Posterior region of the female worm (ventral view). Note the long tail, pointed to a fine needle; (A) anus. Magnification x400.

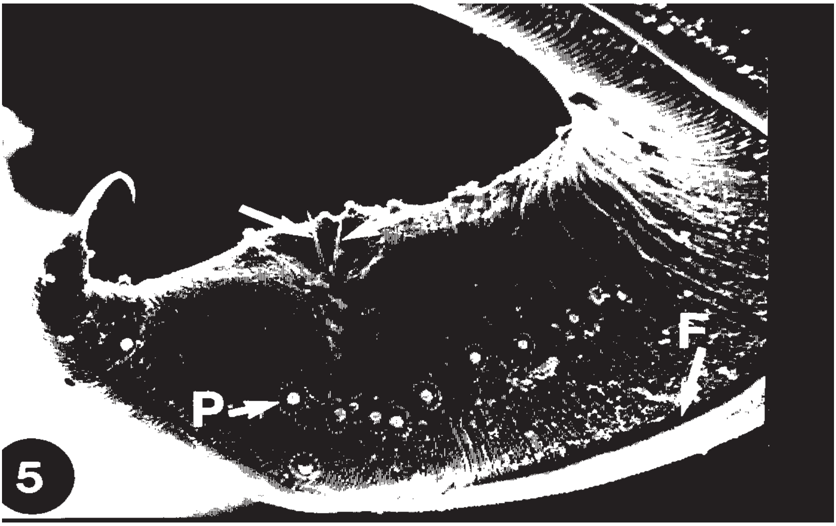

**Fig. 5.** Posterior region of a male worm with slightly ventrally curved tail. Note the false plectanes (P), which consist of large papillae and concentrate in the preanal region. (arrow) double spicules; (F) lateral flanges. Magnification: x340.

**Fig. 6.** SEM of oxyurid nematodes. Anterior end of male demonstrates the three small lips bearing two cephalic papillae each (arrow). Note that 4 of the papillae are distinct and the other two are smaller. Magnification: x2000.

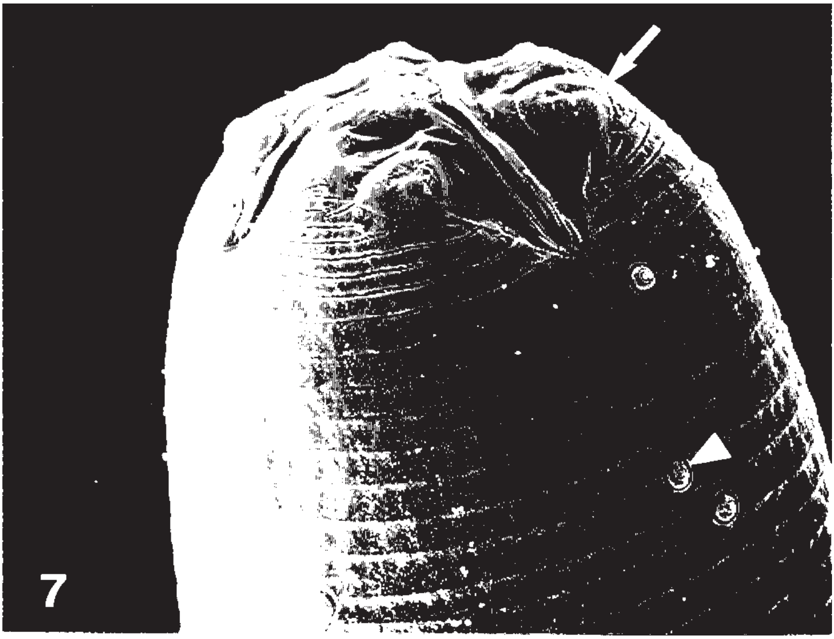

**Fig. 7.** Anterior end of female shows the cephalic papillae (arrow) and other simple papillae (triangle). Magnification x1450.

## Results

### Light Microscopy (LM, fig. 1,2)

Generally: The body is of cylindrical shape, striated and covered with a well-developed cuticle. Total body length varies between 2.8 and 4.0 mm (mean value  = 3.0 mm, standard deviation (SD) = 0.2 mm). The cephalic end with the oral aperture is situated terminally. The digestive system consists of an esophagus with a conical pharyngeal portion at its anterior end which is cylindrical and provided with a posterior bulb (fig.1). The esophagus measures 582 +/- 43µm in length. The intestine is a straight tube, terminating at the anal aperture, which opens ventrally.

Female: (length: 3.6-4.0 mm; width: 0.2-0.3 mm) The genital system consists of two coiling, thin tubular ovaries, each terminating in an uterus. The uteri join in a common muscular vagina, opening ventrally in the genital pore which is in the first third of the anterior half of the helminth. The tail is elongated and pointed at the tip. The eggs of this oviparous nematode are oval (fig. 2), thin-shelled and were embryonated *in utero*. The length of the eggs is 8.2 µm and its width measures 5.2 µm.

Male: (length: 3.0-3.2 mm; width: 0.1-0.2 mm) Posteriorly, the tail is slightly curved to the ventral side and suddenly constricted behind the cloaca to form a terminal spike. There are double spiculae, which are equal in size and sharp-pointed. The genital organs are unpaired, their anterior part forming slender gradually expanding tubules with an intitial filiform portion constituting the testis. Their subsequent large portions form the seminal duct. This duct is terminating with an ejaculating canal into the cloaca.

### Scanning Electron Microscopy (SEM, fig. 3-7)

The cylindrical shape (fig. 3) of this nematode and the tapering posterior end are most clear in the SEM (fig. 4,5). As shown in fig. 6 and 7, the body of the helminths is striated. The mouth cavity of both sexes is very narrow, triradiate and bounded by three small lips. The buccal margin possesses 6 sensile papillae corresponding to the lips (fig. 6,7). The lateral flanges are very distinct and extending throughout the whole length of the body (fig. 3,4). On the ventral surface of the posterior end of the males there is a longitudinal row of 16 false plectanes on each side. Each of this plectanes consists of a large papilla which is surrounded by tubercels. Most of the plectanes are preanal (fig. 5). A number of simple papillae are present on the anterior part of the body of females (fig. 7).

## Discussion

Generally very little is known on parasites of "exotic" animals as *Tylototriton verrucosus*. To our knowlegde Dasgupta (1996) published the first and only information on parasites (Protozoa) of this newt so far. Recent investigations concerning this field of research are rare. On the other hand standard works on nematode systematics as Yamaguti (1961) and Yorke & Maplestone (1962) are from the early sixties. Therefore identification and determination on species level have to be done carefully. According to Spieler (1990) this is extremely difficult with oxyuridean nematodes, and in some cases even the generic rank is unclear or doubtful. Usually identification of nematodes is done by using morphological keys together with light and scanning electron microscopy. Due to the taxonomic importance of external features, such as papillae, alae, striations, boring tooth and oral opening SEM has been a very useful tool (Fredericksen & Specian, 1980; Weerasooriya et al., 1980). According to the above mentioned results and descriptions of LM and SEM investigations we suppose the examined nematode to be a member of the family *Oxyuridae*. For the exact determination of the species, respectively for the description as a probably new species, further examinations as cross sections and different stainings have to be done in combination with further comparison of informations given from the other species of *Oxyuridae*.

## Acknowledgements

The expedition to East Nepal was carried out by the financial help of the Volkswagen foundation. We are grateful to Mrs. H. Schöl, Institute of Tropical Medicine and Parasitology of the University of Munich, for making the scanning electron micrographs. C.C.A. is grateful to the DAAD, Germany for providing funds for travel and stay in Nepal, and to the University of Munich which provided financial support by granting a scholarship (HSP II/ III). Furthermore I (C.C.A.) thank Prof. G. Haszprunar, chief of the Zoological State Collection (ZSM), Munich for providing a working place and the library facilities.

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Veröffentlichungen aus dem Fuhlrott-Museum, 1998, Bd. 4: 35-56

# Studies on *Tylototriton verrucosus* (Amphibia: Urodela)

# Contributions to the Osteology of *Tylototriton verrucosus* Anderson, 1871 and *T. shanjing* Nussbaum et al., 1995 (Amphibia, Caudata: Salamandridae)

**Melitta Haller-Probst***

**Key words**: Caudata, osteology, *Tylototriton verrucosus, T. shanjing*

**Abstract:** Skull and vertebrae of *Tylototriton verrucosus* Anderson,1871 and *Tylototriton shanjing* Nussbaum et al. 1995 are examined, described and compared with different Eurasian urodeles; their osteological correspondences are discussed.

## Contents

## 1. Introduction

Until recently the Southeast Asian salamander genus *Tylototriton* Anderson, 1871 consisted of three species: *asperrimus, kweichowensis* and *verrucosus*. The description of the latter varies in literature. It was often described as a uniformly dark brown animal, with bright orange colouration confined to the ventral edge of the tail, so by Anderson (1871), Fang & Chang (1932) and Rimpp (1978). According to another description it shows a dark brown to black dorsal ground colour with orange dorsolateral warts, an orange vertebral crest, and orange lateral and medial crests on the head, e.g. Chang (1936). In 1995 Nussbaum et al., recognized, that there are obviously two different species. Lack of intergradation in colouration among specimens from Western Yunnan, where both forms occur close together, also suggests that two species are involved.

In this paper this question is discussed from the osteological point of view. Skulls and vertebrae of *T. verrucosus* and *T. shanjing* are figured and compared. In former publications *Tylototriton* has been regarded as closely related to *Salamandrina* and *Pleurodeles* (Bolkay, 1928, Herre, 1933 u. 1941, Laurinat 1955, Estes, 1981). The similarities and differences of these genera are discussed.

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## 2. Material and methods

We prepared and examined the following specimens of *Tylototriton verrucosus* VW-D 96 T1-T12; and *T. shanjing* ZSM.
Abbreviations: ZSM= Zool. State Coll. Munich, Germany; D = Deutschland (Germany); VW= Volkswagen Foundation.

### 2.1 Skull measurements and terminology (fig. 1)

Measured are head length (HL: distance from the anterior end of the upper jaw to the posterior end of the condylus occipitalis), head width (HW: maximal distance between the distal ends of the posterior processes of the maxillae) and quadrate width (QW: maximal distance between the quadrates):

*Tylototriton verrucosus* - Reference specimen:
Material: VW-D 96, Nr. T 11; HL: 14.5 mm, QW: 16.4 mm, HW: 13.3 mm
*Tylototriton shanjing:*
Material: ZSM: HL: 15.9 mm; QW: 15.5 mm; HW:13.2 mm

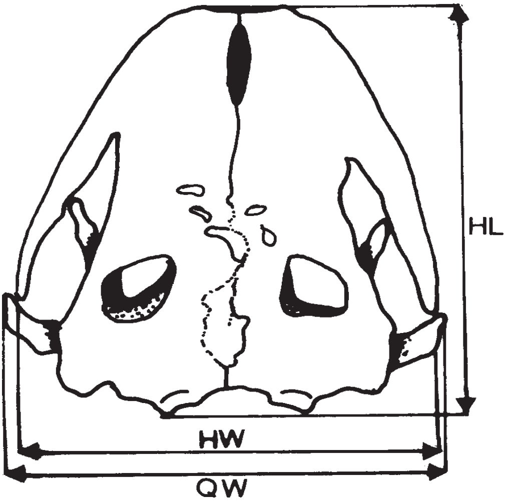


**Fig. 1**. Measurements at the dorsal side of the skull of *Tylototriton*

### 2.2 Terminology of the skull bones (fig. 2,3, sensu Estes, 1981):

### 2.3 Vertebrae measurements and terminology (fig. 4-7)

Measured are total length TL (distance from anterior tip of prae-zygapophyses to posterior end of vertebrae), maximal width of postzygapophyses, PZW (distance between lateral ends of pre- and postzygapophyses; without insertion grooves of the ribs), length of vertebrae centrum CL (anterio-dorsal point of the vertebrae to the caudo-ventral end of the vertebrae) and height of the vertebrae centrum CH (ventro-caudal to dorso-caudal distance at the posterior end of the vertebrae).

1= nasal 2= maxilla 3= prefrontal
4= posterior process of maxilla 5= pterygoid 6= frontal
7= quadrate 8= parietal 9= cavum intermaxillaris
10= sutura sagittalis 11= sutura coronalis 12= orbit
13= tympanic 14= occipital 15= foramen magnum

**Fig. 2.** Skull of *Tylototriton shanjing*; dorsal view, ca. x3.

1= premaxilla 2= maxilla 3= vomeropalatine
4= orbitosphenoid 5= pterygoid 6= quadrate
7= fenestra ovalis 8= apertura nasalis 9= cavum
10= maxillary teeth 11= choane 12= vomeropalatinal teeth
13= foramen 14= parasphenoid

**Fig. 3**. Skull of *Tylototriton shanjing*, ventral view; ca. x3.

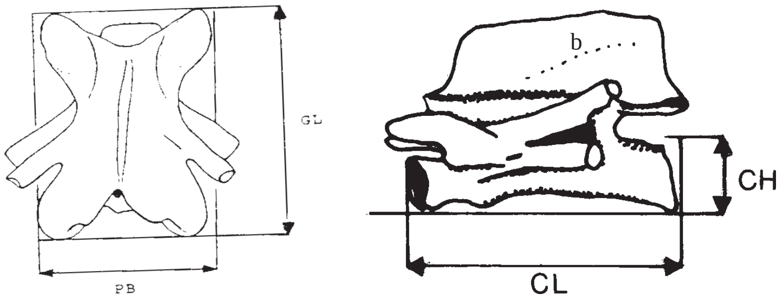


**Fig. 4.** Measurements at the vertebrae of *Tylototriton*. a) dorsal, b) lateral view.

*Tylototriton verrucosus*
Material: VW-D 96, T1-T11; n=187
The range between total lengths (TL) of the smallest and largest praesacral vertebrae in our measured specimens (T1, T2, T3,T4,T11; n=62) are 2,8-4,6 mm, for the atlas (T1, T2, T3,T4,T11; n=5) 2,8-4,0 mm (see tab. 1and fig. 4). The greatest total length in relation to maximal width of the postzygapophyses (CL/PZW) ranges between 1,0-1,6 (n=62), and 0,8-1,4 for the atlas (n=5) (fig. 7).
The relation of CL/PZW shows that the presacralia of *T. verrucosus* are shorter but broader than in *T. shanjing*.

*Tylototriton shanjing*
Material: ZSM; n=17 vertebrae
The range of maximal lengths (TL) for the smallest and largest presacralia (n=16) are 4,7-5,5 mm, the atlas (n=1) measures 3,6 mm. The presacral vertebrae in *T. shanjing* are longer than in *T. verrucosus* (see fig. 6). The range of CL/PZW ratio is between 1.3 and 1.7 and 1.3 for the atlas (fig. 7).

## 2.4 Terminology of the vertebrae

The number of presacral vertebrae varies in different species and genera of Salamandridae, but there is always only one single neck vertebra (atlas). To allow an increasing mobility of the head it evolved a characteristic shape. The atlas never bears ribs, its cranial end is

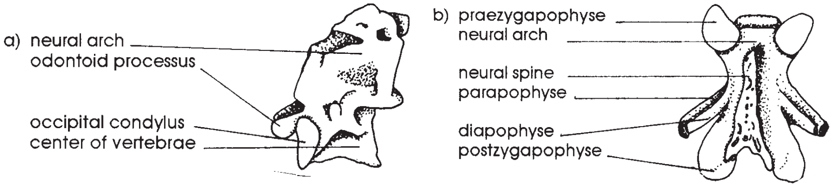


**Fig. 5.** Vertebra lengths of *T. shanjing* and *T. verrucosus*. A= Atlas, 1-16= praesacral vertebrae in natural sequence; solid: *T. verrucosus*, white *T. shanjing*.

connected with the skull by a shovel-like process; additionally there are two lateral articulations with which the atlas contacts with the occipital condyles. The atlas can be recognized easily even in material with isolated vertebrae, which emphasizes its taxonomical value. Therefore it is figured separately in all five different views. The nomenclature of the vertebral structures is taken from Laurinat (1955).

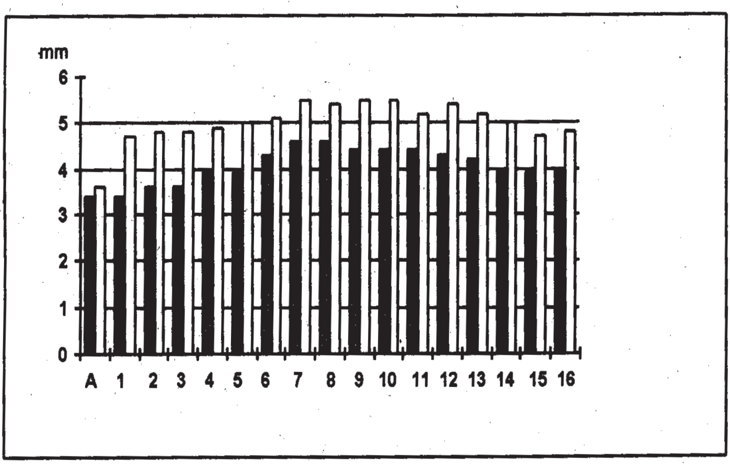


**Fig. 6.** Vertebrae lengths of *T. shanjing* and *T. verrucosus;* A= atlas; 1-16= praesacral vertebrae in natural sequence; solid: *T. verrucosus*, white: *T. shanjing*

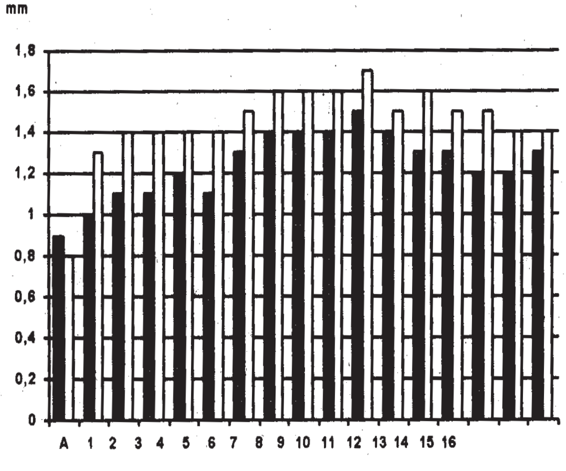


**Fig. 7.** Lengths of praesacral vertebrae and postzygapophyses in *T. shanjing* and *T. verrucosus*, measured in natural sequence; solid: *T. verrucosus*, white: *T. shanjing*

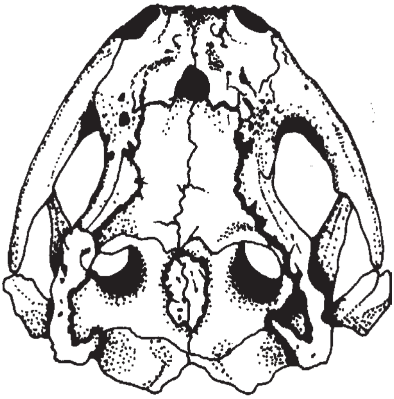
## 3. Description of the skulls

### *3.1 Tylototriton verrucosus* Anderson 1871 (fig. 8-12)

The skull of *T. verrucosus* is very compact, almost as long as broad and has a nearly rounded outline (fig. 8). The skull surface is covered with prominent dorsolateral bony crests and a median crest on the parietalia. As a difference to *T. shanjing*, *T. verrucosus* has no ossified structures at the median part of the frontals.

In dorsal view the apertura nasalis can be seen for about two thirds. The nasals are partly pierced by small foramina and enclose in their posterior part a small nearly round intermaxillar cavity. The frontals are large and widened posteriorly, where they form the main part of the fronto-temporal arch. The latter feature, is similar to *Pleurodeles waltl*. The arch is more diverging caudally than in *T. shanjing*, It looks more angular than curved and bears very strong pustular crests on the lateral areas.

The sickle-shaped, elongated maxillae reach the quadrates. The pterygoids also are in contact with the posterior processes of the maxillae. *T. verrucosus* possesses massive tympanic bones and weakly developed semicircular canals (fig. 8 and 11). The lower jaws, consisting of two dentaries are strong and have a rounded outline (fig. 9).



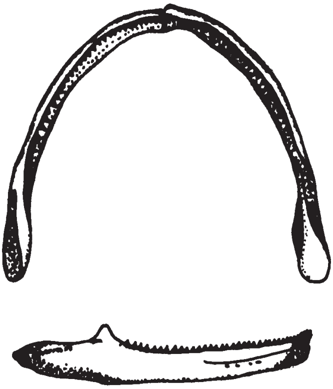


**Fig. 8** (left). Skull of *Tylototriton verrucosus* in dorsal view; ca. x3.
**Fig. 9** (right). Dentaries of *Tylototrtion verrucosus*, a) dorsal, b) lateral view; ca.x3.

On the ventral side of the skull a pair of praemaxillae and a pair of vomeropalatines surround a semi-oval cavum. (fig. 10). The teeth of the vomeropalatinum nearly reach the cavum. The median teeth-bearing part of the vomeropalatines are sligthtly curved and diverging posteriorly more than those of *T. shanjing*. The medial curvature at the caudal end as listed by Bolkay (1928:284) was not to regognize in the specimens.

The wedge-shaped, caudaly broadened and nearly sculptureless parasphenoid (fig. 12) is very similar to that of *Pleurodeles waltl*. There is a clear distance between the parasphenoid and the pterygoid. The latter has a characteristically enlarged cranial arch which touches the processus posterior of the maxilla. The well developed quadrates are in contact with the enlarged posterior maxillar process. In contrast to *T. shanjing* they have no spines.

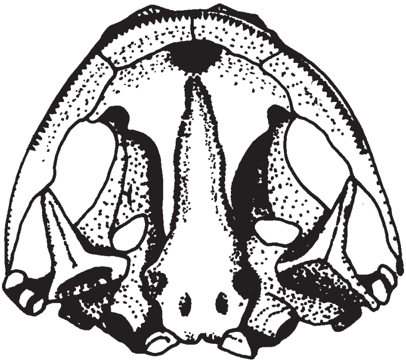


**Fig. 10**. Skull of *Tylototriton verrucosus*. Ventral view, ca. x3

The skull bones which are visible from above are figured in exploded view in fig. 11; the bones, which are only visible from below are shown in fig. 12, their measurements are compiled in tab. 1.

| bone | T1 GLxGW mm | T4 GLxGW mm | T5 GLxGW mm | Range GL-GW mm |
|---|---|---|---|---|
| praemaxilla | 3,6x3,2 | 3,3x3,5 | 3,2x3,4 | 3,2-3,6<br>3,2-3,5 |
| nasal | 3,4x3,3 | 3,2x3,0 | 3,1x3,1 | 3,1-3,4<br>3,0-3,3 |
| praefrontal | 4,8x2,5 | 4,1x2,5 | 4,3x2,1 | 4,1-4,8<br>2,1-2,5 |
| maxilla | 10,3x2,9 | 10,9x3,0 | 9,8x2,7 | 9,8-10,9<br>2,7-3,0 |
| pterygoid | 5,1x3,4 | 5,0x3,4 | 4,0x3,2 | 4,0-5,1<br>3,2-3,4 |
| frontal | 7,9x4,4 | 8,1x5,0 | 7,2x4,2 | 7,2-8,1<br>4,2-5,0 |
| quadrate | 3,2x3,1 | 2,9x2,9 | 2,6x2,7 | 2,6-3,2<br>2,7-3,1 |
| parietal | 4,4x3,3 | 5,0x3,2 | 5,3x3,1 | 4,4-5,3<br>3,1-3,3 |
| tympane | 5,5x4,4 | 5,5x5,0 | 5,3x4,6 | 5,3-5,5<br>4,4-5,0 |
| occipital | 5,6x3,9 | 5,7x4,0 | 5,3x3,9 | 5,3-5,7<br>3,9-4,0 |
| parasphenoid | 9,8x4,3 | 9,1x4,0 | 10,1x4,4 | 9,1-10,1<br>4,0-4,3 |
| vomeropalatinum | 9,1x3,9 | 8,2x4,1 | 7,4x3,6 | 7,4-9,1<br>3,6-4,1 |
| orbitosphenoid | 4,8x1,9 | 4,6x1,8 | 5,0x1,9 | 4,6-5,0<br>1,8-1,9 |
| dental | 12,9x0,9 | 13,3x0,8 | 11,4x0,9 | 11,4-13,3<br>0,8-0,9 |

**Tab. 1.** Skull bone measurements of *Tylototriton verrucosus*; GL = greatest length, GW = greatest width

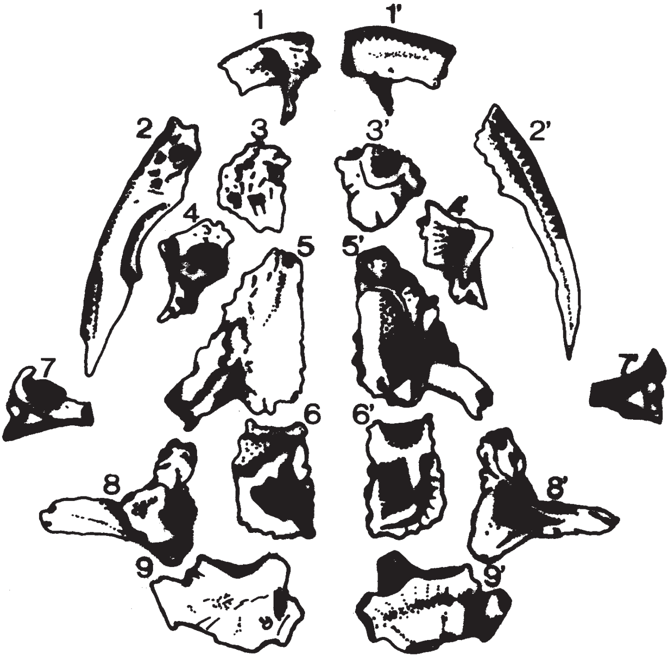


**Fig. 11.** Isolated bones of the skull of *Tylototriton verrucosus* visible from above; ca. x3. 1-9= dorsal, 1´-9´=ventral view: 1)premaxilla, 2) maxilla, 3) nasal, 4) prefrontal, 5) frontal, 6) parietal, 7) quadrate, 8) tympanic, 9) occipital

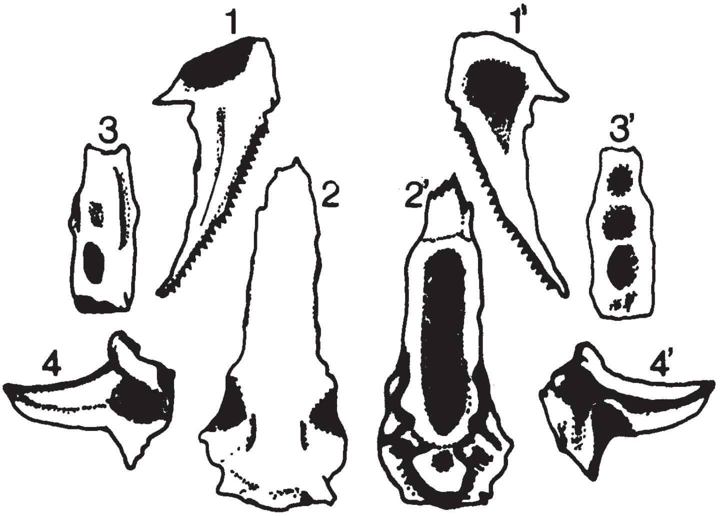


**Fig. 12.** Isolated bones of the skull of *Tylototriton verrucosus* visible from below; ca. x3. 1-4 = dorsal, 1´-4´=ventral view. 1) vomeropalatine, 2) parasphenoid, 3) orbitosphenoid, 4) pterygoid.

The premaxillae are 3,6 mm long and partially visible from above; they show a rough and sculptured surface and a long, spiny posterior process which measures up to 3,5 mm (see tab.1). The nasals are shaped irregularly (size: 3,5x3,4 mm), and also show a surface structure of prominences. Especially the long and narrow prefrontals are strongly crested. They are 4,8 mm long and up to 2,5 mm in width. Their shape is irregular. The strong, toothed maxillae are up to 10,9 mm long and 3,0 mm broad. They are sickle-shaped and smooth, only their anterior part wears minor crest structures. The untextured pterygoids are broad based (size: 5,1 mm x 3,4 mm). The frontals are large, strong and bearing prominent dorsal structures. They are nearly triangular, 8,1 mm long and 5,0 mm broad. The quadrates of *Tylototriton verrucosus* are well developed, also nearly triangular in shape, without crest structures and show a characteristical spine (see fig. 11). They measure 3,3 x 3,1 mm.

The parietals are nearly rectangular and show characteristical bony stuctures and sculptures on their median sides. They are 5,3 mm long and 3,3 mm wide. The tympanics are L-shaped, strongly developed and covered with prominent pustular structures. They measure 5,5 x 5,0 mm. The rectangular occipital measures 5,7 mm in length and 4,0 mm in width.

The parasphenoid is flat, nearly structureless on its surface and has a pointed shape, which is sligthly rounded at the posterior end. It measures 10,1 x 4,3 mm. The vomeropalatines also bear teeth at their median sides. The are nearly triangular with a spiny posterior end. They measure 9,1 mm x 4,1 mm. The long, narrow, rectangular orbitosphenoids are characterized by a big foramen which extends nearly over the whole width (see fig. 12). The measurements are 5,0 mm and 1,9 mm. The dentaries are 13,3 mm long and 0,9 mm in width, smooth, sickle shaped and bearing teeth.

### *3.1 Tylototriton shanjing* Nussbaum et al., 1995

The skull is sligthly longer than broad and bears prominent dorsolateral crests and a middorsal crest along the frontals and parietals. (fig. 2).

The apertura nasalis is covered by the only poorly structured nasals and is not visible from above, but only from below. The bone texture of the small premaxillae is rough. They can be hardly seen from above. The nasals are separated by a long and narrow intermaxillar cavity which ends at the borders of the nasals and frontals. The posterior process of the elongated maxilla almost reaches the quadrate. The pterygoids also contact the posterior processes of the maxillae.

The massive fronto-temporal arch diverges distally less than in *T. verrucosus*. Its shape is more angular than curved, its lateral areas bear numerous crests on a pustular surface, which also can be seen in the live specimen.

*T. shanjing* like the related *T. verrucosus* has strong tympanic bones and weakly developed semicircular ducts. The sutura sagittalis is rather straight. Frontals and parietals are locally covered by prominent pustular crests and therefore not always exposed. The lower jaws are oval and without any striking structures (fig. 13).

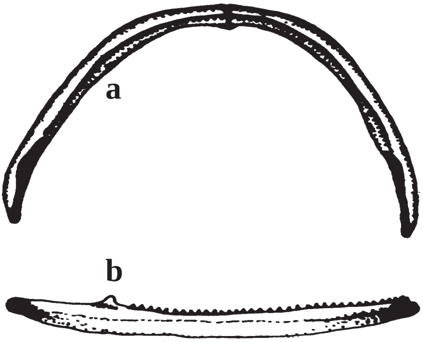


**Fig. 13.** Dentaries of *Tylototriton shanjing;* a) dorsal, b) lateral view; ca. x3.

On the ventral side of the skull a small oval cavity is surrounded by a pair of premaxillae and a pair of vomeropalatines to nearly equal parts (fig. 2). The distance between the anterior margin of the vomeropalatines and the cavity is longer than in *T. verrucosus*. The median toothed parts of the vomeropalatines are slightly curved and posteriorly diverging. The tooth rows are standing closer than in *T. verrucosus.*
The caudaly broadened and nearly sculptureless parasphenoid has irregular margins. The pterygoids posess a characteristically enlarged cranial arch which touches the posterior process of the maxilla.
The quadrates of *T. shanjing* end laterally with a striking curved spine which was supposed to be unique and only present in *Echinotriton* (Nussbaum & Brodie 1982). However, similar structures can also be found in *T. taliangensis* (Kabisch et al., 1994) whilst they are missing in *T. verrucosus.* The lower jaws are strong and without particular features.

## 4. Description of the vertebrae

### 4.4 *Tylototriton verrucosus* Anderson, 1871

The atlas (fig. 14a-e) is short, posteriorly increasing in height and bears well developed occipital condyles. In tab. 2 and 3 measurements of the atlas and the presacral vertebrae (PW) of the two species *T. verrucosus* and *T. shanjing,* are recorded in their original sequence.

The vertebrae are opisthocoelous, shorter and more compact than in *T. shanjing.* The neural spine is high and capped by a caudally broadened, longish to oval plate which bears strong and prominent bony crests and sculptures. (fig. 15a-e). In relation to the vertebrae lengths, the parapophyses are broader than in *T. shanjing* (see tab. 2 and 3). On the ventral side several foramina of different sizes, like in *T. shanjing,* are visible.

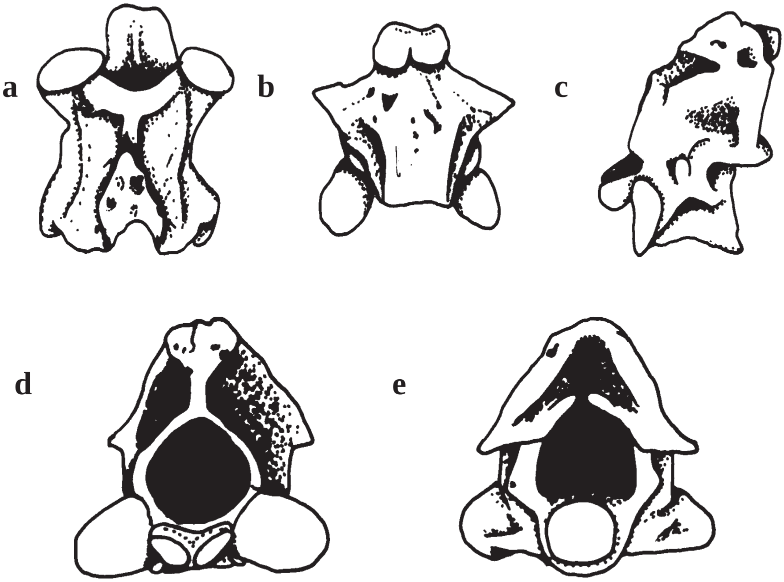
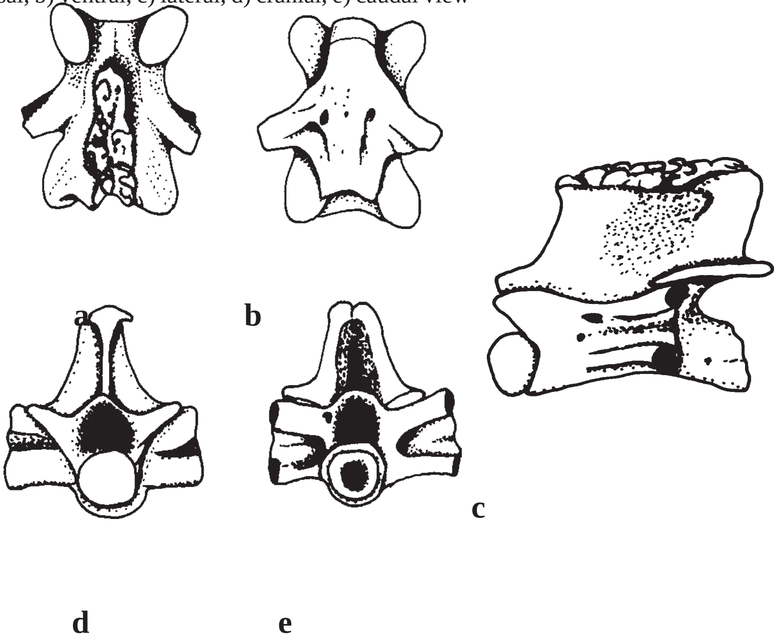
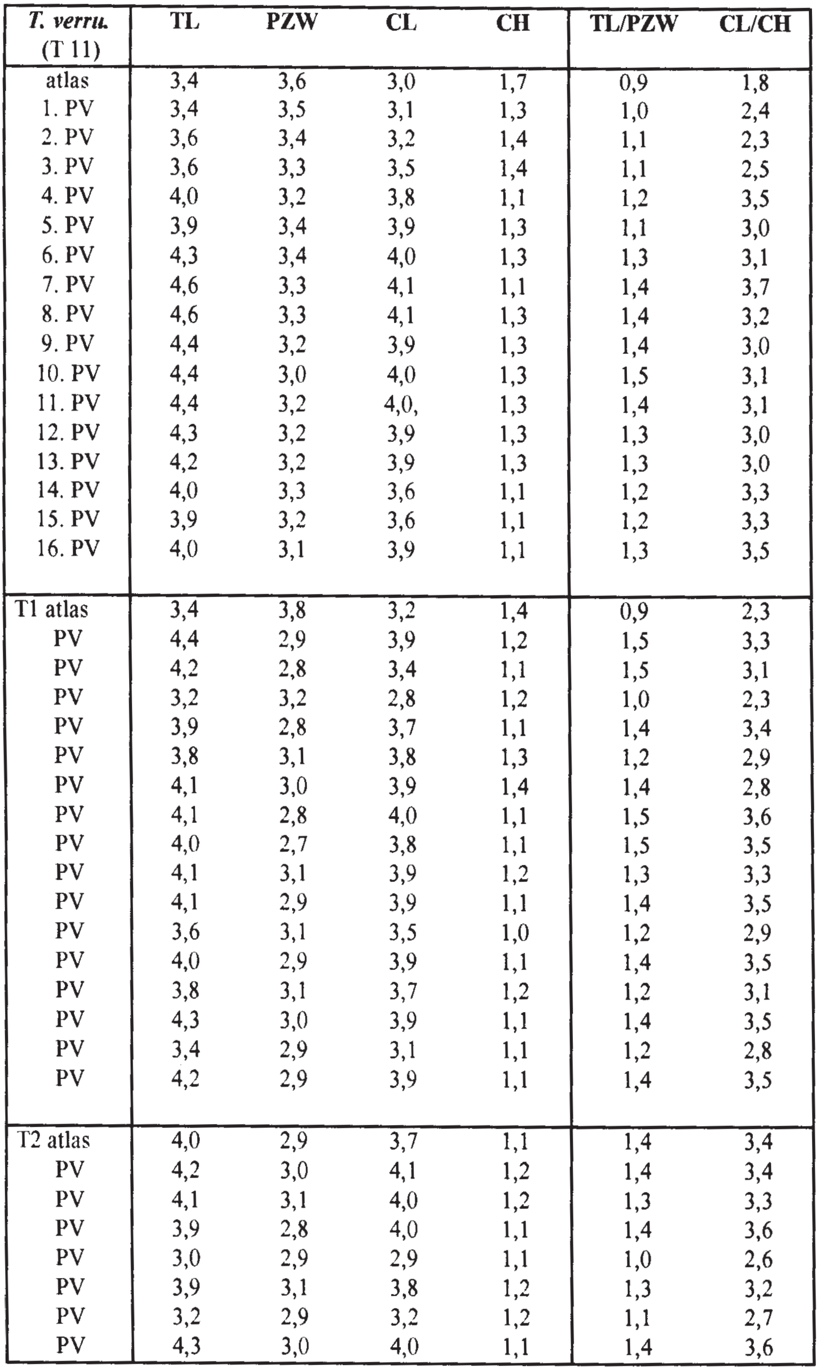


**Fig. 14**. Atlas of *Tylototriton verrucosus*; ca. x6:
a) dorsal, b) ventral, c) lateral, d) cranial, e) caudal view





| *T. verru.* (T 11) | TL | PZW | CL | CH | TL/PZW | CL/CH |
|---|---|---|---|---|---|---|
| atlas | 3,4 | 3,6 | 3,0 | 1,7 | 0,9 | 1,8 |
| 1. PV | 3,4 | 3,5 | 3,1 | 1,3 | 1,0 | 2,4 |
| 2. PV | 3,6 | 3,4 | 3,2 | 1,4 | 1,1 | 2,3 |
| 3. PV | 3,6 | 3,3 | 3,5 | 1,4 | 1,1 | 2,5 |
| 4. PV | 4,0 | 3,2 | 3,8 | 1,1 | 1,2 | 3,5 |
| 5. PV | 3,9 | 3,4 | 3,9 | 1,3 | 1,1 | 3,0 |
| 6. PV | 4,3 | 3,4 | 4,0 | 1,3 | 1,3 | 3,1 |
| 7. PV | 4,6 | 3,3 | 4,1 | 1,1 | 1,4 | 3,7 |
| 8. PV | 4,6 | 3,3 | 4,1 | 1,3 | 1,4 | 3,2 |
| 9. PV | 4,4 | 3,2 | 3,9 | 1,3 | 1,4 | 3,0 |
| 10. PV | 4,4 | 3,0 | 4,0 | 1,3 | 1,5 | 3,1 |
| 11. PV | 4,4 | 3,2 | 4,0, | 1,3 | 1,4 | 3,1 |
| 12. PV | 4,3 | 3,2 | 3,9 | 1,3 | 1,3 | 3,0 |
| 13. PV | 4,2 | 3,2 | 3,9 | 1,3 | 1,3 | 3,0 |
| 14. PV | 4,0 | 3,3 | 3,6 | 1,1 | 1,2 | 3,3 |
| 15. PV | 3,9 | 3,2 | 3,6 | 1,1 | 1,2 | 3,3 |
| 16. PV | 4,0 | 3,1 | 3,9 | 1,1 | 1,3 | 3,5 |
| T1 atlas | 3,4 | 3,8 | 3,2 | 1,4 | 0,9 | 2,3 |
| PV | 4,4 | 2,9 | 3,9 | 1,2 | 1,5 | 3,3 |
| PV | 4,2 | 2,8 | 3,4 | 1,1 | 1,5 | 3,1 |
| PV | 3,2 | 3,2 | 2,8 | 1,2 | 1,0 | 2,3 |
| PV | 3,9 | 2,8 | 3,7 | 1,1 | 1,4 | 3,4 |
| PV | 3,8 | 3,1 | 3,8 | 1,3 | 1,2 | 2,9 |
| PV | 4,1 | 3,0 | 3,9 | 1,4 | 1,4 | 2,8 |
| PV | 4,1 | 2,8 | 4,0 | 1,1 | 1,5 | 3,6 |
| PV | 4,0 | 2,7 | 3,8 | 1,1 | 1,5 | 3,5 |
| PV | 4,1 | 3,1 | 3,9 | 1,2 | 1,3 | 3,3 |
| PV | 4,1 | 2,9 | 3,9 | 1,1 | 1,4 | 3,5 |
| PV | 3,6 | 3,1 | 3,5 | 1,0 | 1,2 | 2,9 |
| PV | 4,0 | 2,9 | 3,9 | 1,1 | 1,4 | 3,5 |
| PV | 3,8 | 3,1 | 3,7 | 1,2 | 1,2 | 3,1 |
| PV | 4,3 | 3,0 | 3,9 | 1,1 | 1,4 | 3,5 |
| PV | 3,4 | 2,9 | 3,1 | 1,1 | 1,2 | 2,8 |
| PV | 4,2 | 2,9 | 3,9 | 1,1 | 1,4 | 3,5 |
| T2 atlas | 4,0 | 2,9 | 3,7 | 1,1 | 1,4 | 3,4 |
| PV | 4,2 | 3,0 | 4,1 | 1,2 | 1,4 | 3,4 |
| PV | 4,1 | 3,1 | 4,0 | 1,2 | 1,3 | 3,3 |
| PV | 3,9 | 2,8 | 4,0 | 1,1 | 1,4 | 3,6 |
| PV | 3,0 | 2,9 | 2,9 | 1,1 | 1,0 | 2,6 |
| PV | 3,9 | 3,1 | 3,8 | 1,2 | 1,3 | 3,2 |
| PV | 3,2 | 2,9 | 3,2 | 1,2 | 1,1 | 2,7 |
| PV | 4,3 | 3,0 | 4,0 | 1,1 | 1,4 | 3,6 |

continue table 2:

| | | | | | | |
|---|---|---|---|---|---|---|
| T3 atlas | 2,9 | 3,7 | 2,9 | 1,2 | 0,8 | 2,4 |
| PV | 3,8 | 2,8 | 3,4 | 1,1 | 1,4 | 3,1 |
| PV | 4,1 | 2,8 | 3,5 | 1,2 | 1,5 | 2,9 |
| PV | 4,0 | 3,0 | 3,7 | 1,1 | 1,3 | 3,4 |
| PV | 4,1 | 3,0 | 3,7 | 1,1 | 1,4 | 3,4 |
| PV | 4,1 | 2,9 | 3,7 | 1,0 | 1,4 | 3,7 |
| PV | 4,1 | 2,8 | 3,7 | 1,1 | 1,5 | 3,4 |
| PV | 3,7 | 2,6 | 3,6 | 1,4 | 1,4 | 2,6 |
| T4 atlas | 2,8 | 3,5 | 2,7 | 1,2 | 0,8 | 2,3 |
| PV | 3,7 | 2,5 | 3,7 | 1,0 | 1,5 | 3,7 |
| PV | 3,8 | 2,7 | 3,6 | 1,2 | 1,4 | 3,0 |
| PV | 3,8 | 2,7 | 3,6 | 1,1 | 1,4 | 3,3 |
| PV | 4,0 | 2,6 | 3,7 | 1,1 | 1,5 | 3,4 |
| PV | 3,8 | 2,6 | 3,7 | 1,2 | 1,5 | 3,1 |
| PV | 4,0 | 2,6 | 3,8 | 1,1 | 1,5 | 3,5 |
| PV | 3,7 | 2,6 | 3,3 | 1,2 | 1,4 | 2,8 |
| PV | 3,8 | 2,3 | 3,6 | 1,1 | 1,6 | 3,3 |
| PV | 3,8 | 2,5 | 3,6 | 1,1 | 1,5 | 3,3 |
| PV | 3,9 | 2,6 | 3,6 | 1,1 | 1,5 | 3,3 |
| PV | 3,1 | 2,6 | 3,2 | 1,0 | 1,2 | 3,2 |
| PV | 3,8 | 2,5 | 3,5 | 1,1 | 1,5 | 3,2 |
| PV | 3,2 | 2,6 | 3,2 | 1,2 | 1,2 | 2,7 |
| PV | 2,8 | 2,5 | 2,6 | 1,1 | 1,1 | 2,4 |
| PV | 3,0 | 2,6 | 2,7 | 1,1 | 1,2 | 2,5 |
| PV | 3,3 | 2,7 | 3,2 | 1,2 | 1,2 | 2,7 |

**Tab. 2**. Vertebrae measurements of *Tylototriton verrucosus*; PV = presacral vertebra, TL = total length, PZW = prezygapophyse width, CL = centrum length, CH = centrum height

**Fig. 15**. Presacral vertebrae of *Tylototriton verrucosus*; ca. x6:
a) dorsal, b) ventral, c) lateral, d) cranial, e) caudal view

### 4.1 *Tylototriton shanjing* Nussbaum et al. 1995

The atlas (fig. 16a-e) is short and caudally rising, with well developed occipital condyles. In tab. 2 and 3 measurements of atlas and praesacral vertebrae (PW) from one specimen each of *T. verrucosus* and *T. shanjing*, are registered in their original sequence.

At the first look, the vertebrae of *T. shanjing* (fig. 17 a-e) are similar to those of *T. verrucosus*. The neural spine is high and capped by a caudally broadened plate which is more triangular than in *T. verrucosus*. The insertion of the parapophyses is less broad than in *T. verrucosus* (see tab. 2 and 3). The hour-glass-shaped structures on the ventral sides of the vertebrae of *Pleurodeles waltl* are scarcely perceptible or totally absent in

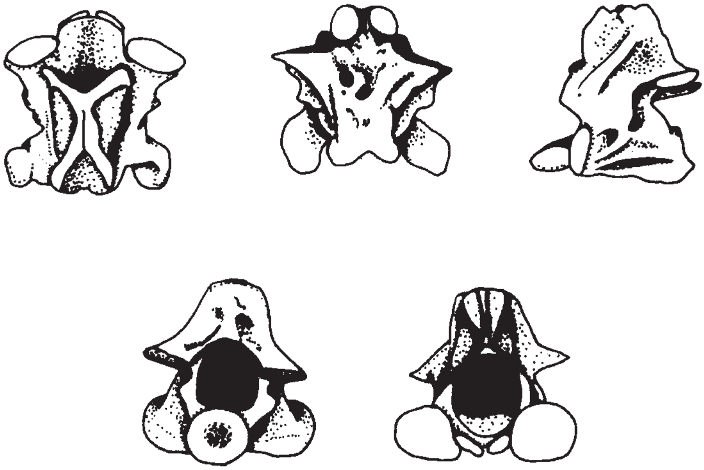


**Fig. 16**. Atlas of *Tylototriton shanjing*; ca. x6:
a) dorsal, b) ventral, c) lateral, d) cranial, e) caudal view

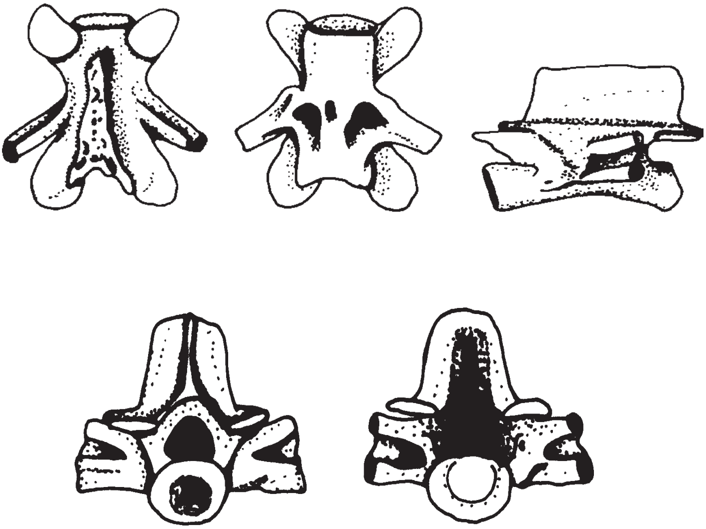
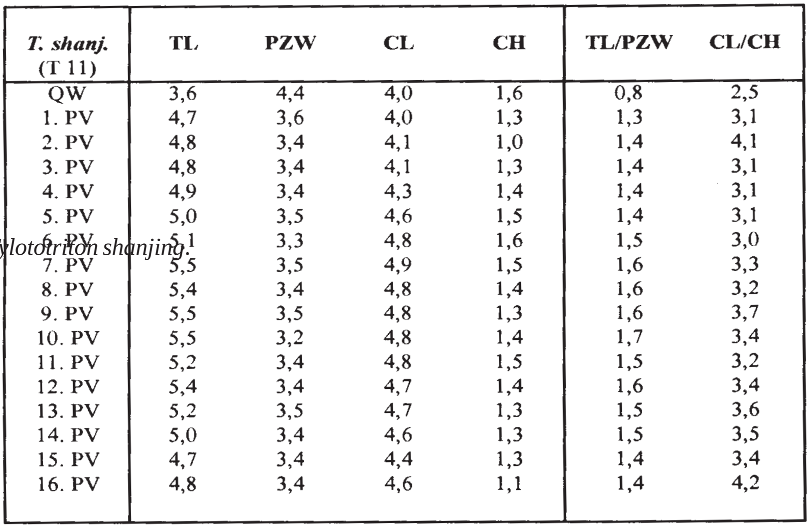


**Fig. 17**. Presacral vertebrae of *Tylototriton shanjing*; ca. x6:
a) dorsal, b) ventral, c) lateral, d) cranial, e) caudal view

Tylototriton shanjing:



| *T. shanj.* (T 11) | TL | PZW | CL | CH | TL/PZW | CL/CH |
|---|---|---|---|---|---|---|
| QW | 3,6 | 4,4 | 4,0 | 1,6 | 0,8 | 2,5 |
| 1. PV | 4,7 | 3,6 | 4,0 | 1,3 | 1,3 | 3,1 |
| 2. PV | 4,8 | 3,4 | 4,1 | 1,0 | 1,4 | 4,1 |
| 3. PV | 4,8 | 3,4 | 4,1 | 1,3 | 1,4 | 3,1 |
| 4. PV | 4,9 | 3,4 | 4,3 | 1,4 | 1,4 | 3,1 |
| 5. PV | 5,0 | 3,5 | 4,6 | 1,5 | 1,4 | 3,1 |
| 6. PV | 5,1 | 3,3 | 4,8 | 1,6 | 1,5 | 3,0 |
| 7. PV | 5,5 | 3,5 | 4,9 | 1,5 | 1,6 | 3,3 |
| 8. PV | 5,4 | 3,4 | 4,8 | 1,4 | 1,6 | 3,2 |
| 9. PV | 5,5 | 3,5 | 4,8 | 1,3 | 1,6 | 3,7 |
| 10. PV | 5,5 | 3,2 | 4,8 | 1,4 | 1,7 | 3,4 |
| 11. PV | 5,2 | 3,4 | 4,8 | 1,5 | 1,5 | 3,2 |
| 12. PV | 5,4 | 3,4 | 4,7 | 1,4 | 1,6 | 3,4 |
| 13. PV | 5,2 | 3,5 | 4,7 | 1,3 | 1,5 | 3,6 |
| 14. PV | 5,0 | 3,4 | 4,6 | 1,3 | 1,5 | 3,5 |
| 15. PV | 4,7 | 3,4 | 4,4 | 1,3 | 1,4 | 3,4 |
| 16. PV | 4,8 | 3,4 | 4,6 | 1,1 | 1,4 | 4,2 |

**Tab. 3**. Measurements on vertebrae of *Tylototriton shanjing*

## 5. Discussion

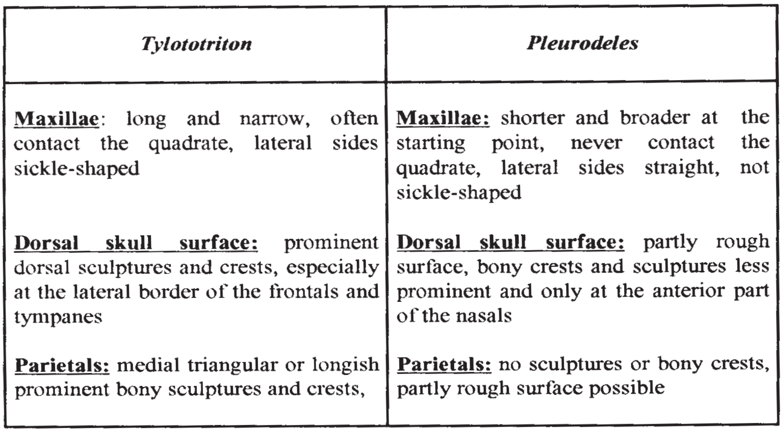
*Echinotriton,* including the species *andersoni, asperrimus* and *chinhaiensis* has recently been seperated from *Tylototriton.* Now the genus consists sensu Nussbaum & Brodie, 1982 of *T. verrucosus, T. kweichowensis, T. shanjing* and *T. taliangensis*. The two genera have several ethological differences, for example in mating behaviour and habitat preferences for egg deposition (Zhao et al., 1988). Important morphological differences also are size and shape of the ribs, egg size and the shape of skull and vertebrae. *Echinotriton* has less developed pustular sculptures on the skull. The anterior processes of the quadrates do not extend as far as in *Tylototriton* compared with *Echinotriton,* and the maxillae and quadrates are more solidly fused in *Echinotriton* than in *Tylototriton* (Nussbaum & Brodie, 1982).

Differences in osteology exist not only at the generic but also on the species level. Skulls and vertebrae from *T. verrucosus* and *T. shanjing* can be clearly distinguished. Important characters are the shape of the skull with its characteristic pustular sculptures and crests, the shape of the cavum intermaxillare, further size and shape of pterygoid, quadrate and maxilla. The vertebrae of these two species also can be distinguished. They have different sizes, as well as neural crests and characteristic dorsal pustular structures. Osteology clearly confirms the separation of *T. verrucosus* and *T. shanjiing* as different species.

The skull of *T. taliangensis* Liu, 1950, described in 1994 by Kabisch et al. differs from the specimens mentioned above, in having prominent angular tympanics, a caudally broadend parasphenoid and shorter vomeropalatines. Apart from these points it is very similar to the skulls of *T. verrucosus* and *T. shanjing*.

The common origin of *Tylototriton*, *Salamandrina* and *Pleurodeles* has been emphasized by numerous authors (Bolkay, 1928; Herre, 1933, 1941; Laurinat, 1955; Rimpp, 1978; Scholz, 1993; Westphal, 1978). Especially many similarities in the courtship of *Tylototriton* and *Pleurodeles*, furthermore the anatomical resemblance and, the absence of dermal crests (Rimpp, 1978:148) seem to prove this. Bolkay (1928) regards the „striking roughness of the skull, the paired intermaxillae and the elongated posterior processes of the maxillae" as a proof for close relationship, although he only examined *T. verrucosus*. Despite Bolkay´s description of very elongated maxillae, the figured specimen (1928: 279, fig. 11), shows rather short maxillae which are neither in contact with pterygoid nor quadrate. The latter is in accordance with our own examined specimens of *P. waltl* (Haller-Probst & Schleich, 1994:41, fig. 18)

Aside from these similarities there are also definite differences which prove the close relationship of *Tylototriton* and *Pleurodeles* but nevertheless characterize them clearly as two different genera. Some important criteria are listed in table 4.



| ***Tylototriton*** | ***Pleurodeles*** |
|---|---|
| **Maxillae**: long and narrow, often contact the quadrate, lateral sides sickle-shaped | **Maxillae:** shorter and broader at the starting point, never contact the quadrate, lateral sides straight, not sickle-shaped |
| **Dorsal skull surface:** prominent dorsal sculptures and crests, especially at the lateral border of the frontals and tympanes | **Dorsal skull surface:** partly rough surface, bony crests and sculptures less prominent and only at the anterior part of the nasals |
| **Parietals:** medial triangular or longish prominent bony sculptures and crests, | **Parietals:** no sculptures or bony crests, partly rough surface possible |

**Tab. 4**. Important differences between the skulls of *Tylototriton* and *Pleurodeles*

The presacral vertebrae of the two genera also show differences: different shapes and sizes of neural arch, neural crest, lateral view and of the insertion point of diapophyses and parapophyses, and in structure of the atlas. *Tylototriton verrucosus* and *T. shanjing* have characteristic pustular sculptures at the dorsal side of their presacralia (see fig. 14-17), whereas *Pleurodeles* has no such structures. The ventral sides of *Pleurodeles* vertebrae are narrowed at half length. The centrum is hour-glass-shaped which is feebly indicated or absent in *Tylototriton*.

The distribution areas of *Tylototriton* and *Pleurodeles* are quite different: *Pleurodeles poireti* and *P. waltl* live in the western part of the Iberian peninsula and along parts of the North African coast (Schleich et al. 1996), all species of *Tylototriton* and *Echinotriton* live in Southeast Asia. In contrast, fossil forms also occured in Europe. Earliest fossil record is *T. weigelti* Herre 1935a, from the Middle Eocene, Geiseltal near Halle a.d. Saale, Germany, followed by specimens from Upper Miocene (Estes, 1981; Herre , 1933, 1935). The fossils only are documented up to the end of the Upper Miocene. No younger fossils of closely related species have been recorded for East Asia. After the obstruction of the Obik seaway and with loss of tropicality in Europe after the Middle Eocene, *Tylototriton* must have migrated to, or become restricted to the Eastern Palearctic Region (Estes, 1981). Populations in Europe evolved into the extinct *Chelotriton* which is closely related to *Tylototriton* (Westphal, 1978).

This close relationship is of interest with regard to the fossil situation. In contrast to the quite different recent disribution areas, records of *Palaeopleurodeles* Herre 1941 and of *Tylototriton* Anderson 1871 are known from the European Tertiary. Sensu Nussbaum & Brodie (1982) the latter is synonymous with *Echinotriton*. There are sktriking similarities in the presacral vertebrae of *Chelotriton paradoxus* and *Tylototriton* (see plates 1,2) from Miocene. The question is if *Tylototriton* is a direct descendent of *Chelotriton* needs further examination.

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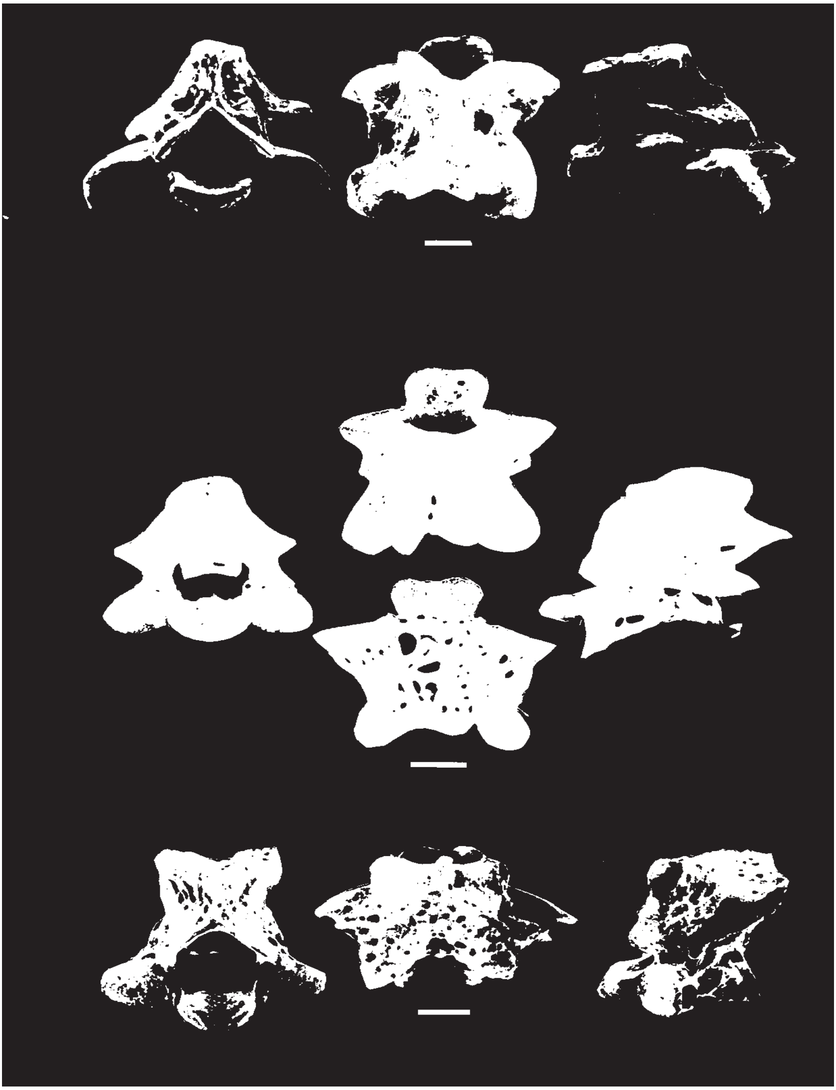

**Plate 1. SEM-Photographs, first vertebra (atlas):**

1. row: *Tylototriton shanjing* Anderson 1871, ZSM/nn
from left to right side: cranial, dorsal, lateral
2. row: *Tylototriton verrucosus* Nussbaum et al. 1995, VW-D 1996, Nepal
left: cranial, middle above: dorsal, middle below: ventral,
right: lateral
3. row: *Chelotriton paradoxus* Pomel 1853,
from left to right side: cranial, dorsal, lateral. Scale = 1 mm

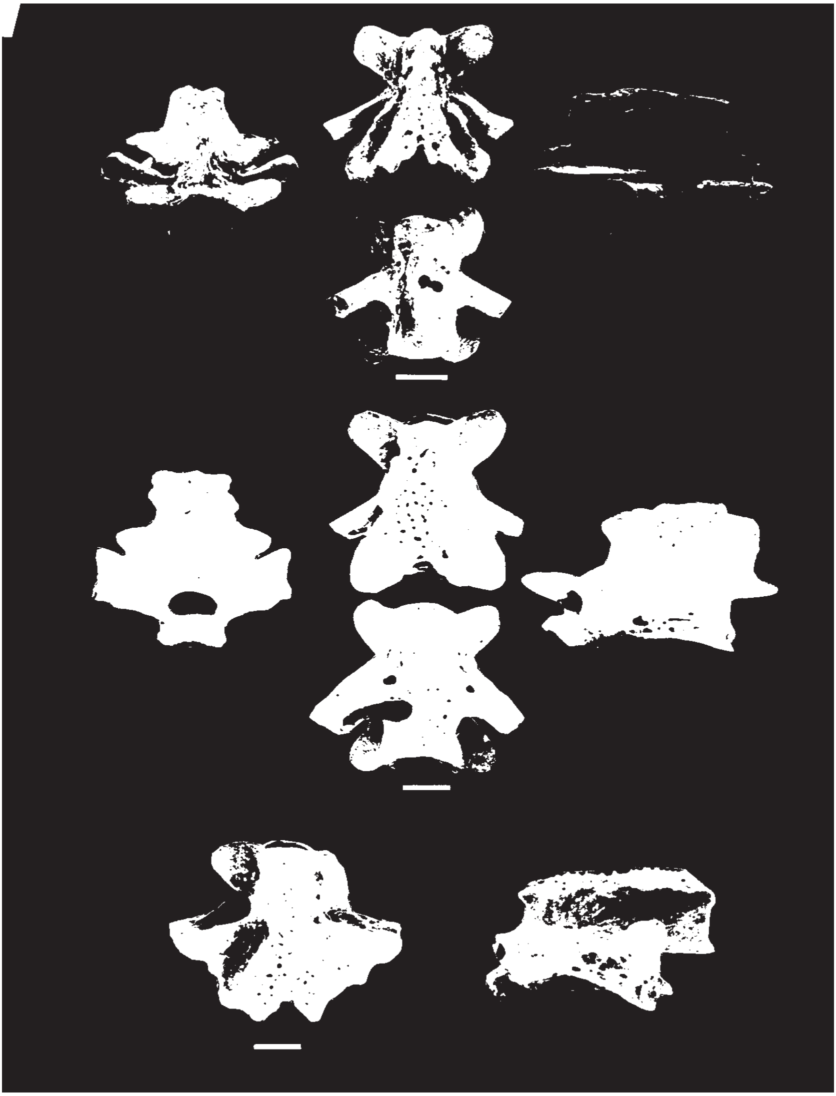

**Plate 2. SEM-Photographs, praesacral vertebra (PV):**

1. row: *Tylototriton shanjing* Anderson 1871, ZSM/nn
left: cranial, middle above: dorsal, middle below: ventral,
right: lateral
2. row: *Tylototriton verrucosus* Nussbaum et al., 1995 VW-MUC 1996, Nepal
left: cranial, middle above: dorsal, middle below: ventral,
right: lateral
3. row: *Chelotriton paradoxus* Pomel 1853, left: dorsal, right: lateral. Scale = 1 mm

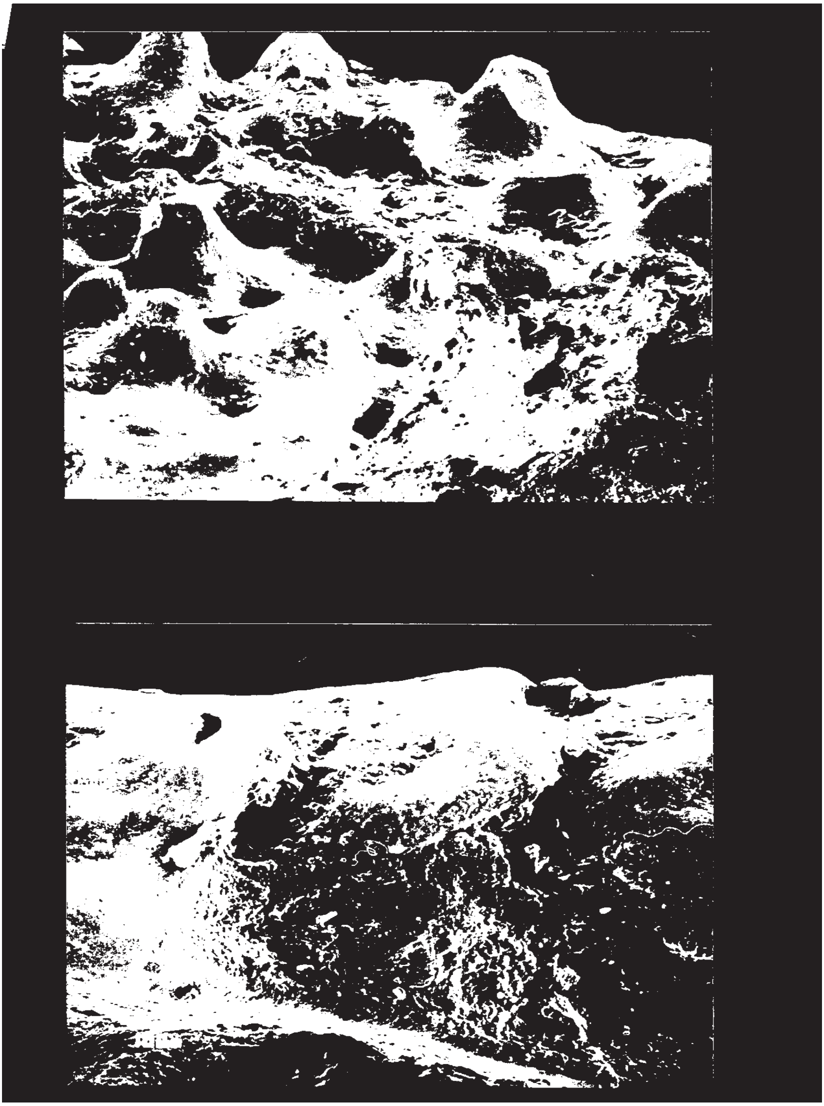

**Plate 3. SEM-Photographs, dorsal structures**

above: Dorsal crest praesacral vertebra *Chelotriton paradoxus* Pomel 1853
below: Dorsal crest praesacral vertebra *Tylototriton shanjing* Anderson 1871

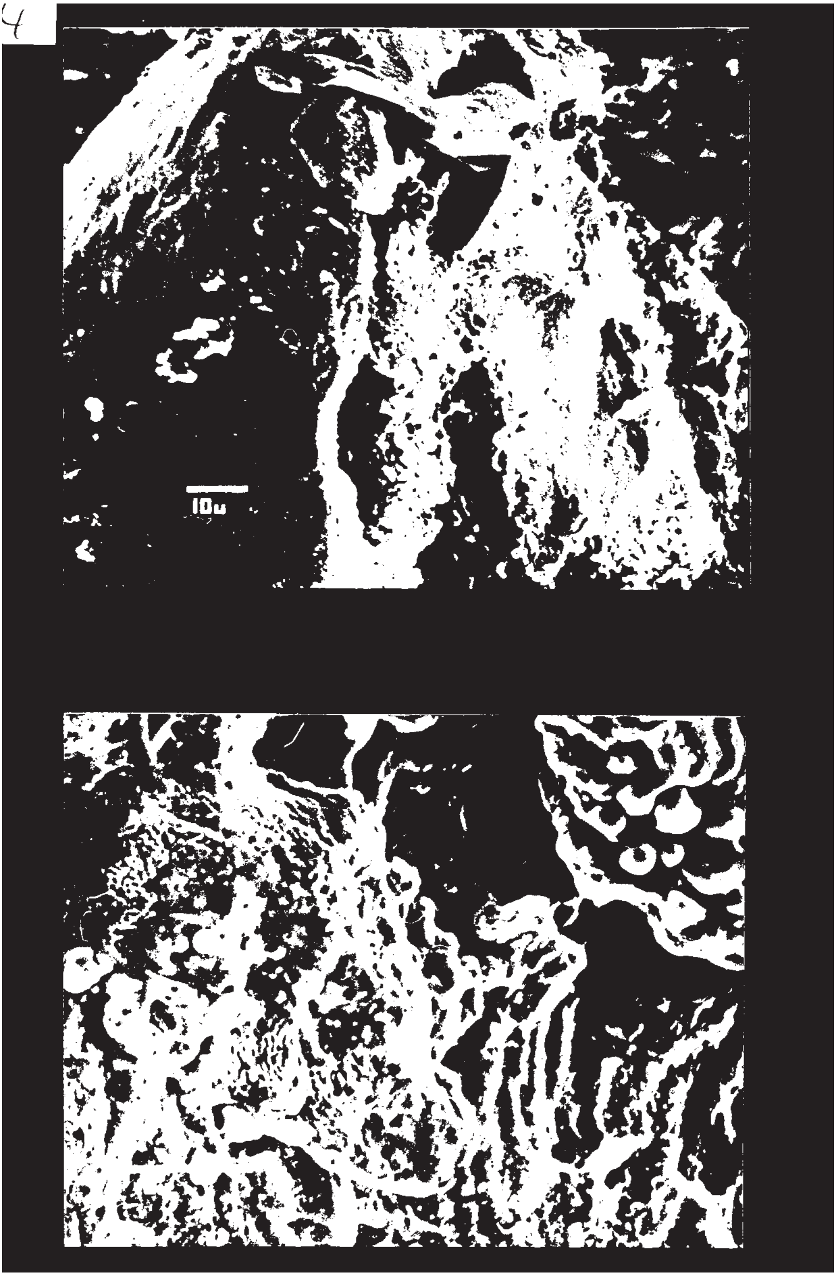

**Plate 4. SEM-Photographs, dorsal ultrastructures**

above: Dorsal crest praesacral vertebra of *Chelotriton paradoxus* Pomel 1853
below: Dorsal crest praesacral vertebra of *Tylototriton shanjing* Anderson 1871

Veröffentlichungen aus dem Fuhlrott-Museum, 1998, Bd. 4: 57-72

# *Tomopterna maskeyi* spec. nov. from Nepal (Amphibia, Anura)

H. Hermann Schleich* & Christiane C. Anders **

**Key words**: Amphibia, Anura: *Tomopterna* spp., *T.maskeyi* sp.n, Asia, Nepal, systematics, morphology.

**Abstract**: Known records as well as the distribution area of *Tomopterna* spp. from Nepal are reported. The distributional ranges of all Asian species of the genus *Tomopterna* are compiled, listed and illustrated. A comparison of the different specific characters of all Asian *Tomopterna* species is presented. Two different, sympatric species of *Tomopterna* were collected and for the first recorded as sympatric during last years´ field activities. *Tomopterna maskeyi* n. sp. is described as a new species for Nepal.

## Introduction

During a field trip to Royal Chitwan National Park in premonsoon 1987, the senior author found several specimens of two sympatric species of *Tomopterna* with the encouraging help of Dr. T. M. Maskey, now DG of the Department of National Parks & Wildlife Services. One species was easily to identify as *T. breviceps*, the other one, here described as new species was not to identify. It was figured for the first time in Schleich & Maskey (1992, fig.10) without specific verification.

Only four species of clear systematical evidence were formerly known for the Asiatic genus of *Tomopterna: T. breviceps, T. rolandae, T. swani* and *T. dobsonii*. Only two of them *T. breviceps* and *T. swani* were reported for Nepal. The description of *T. swani* is based on a single specimen and unfortunately no subsequent report could be made since its first description in 1956. Due to Clarke (pers.comm., 1996) it is extremly unlikely that *T. dobsonii* (only known from two localities: „Mangalore, W-coast of India“ and „S. Canara“) will be found in Nepal. Dutta (1986) suspected another undescribed species within the *T. breviceps* complex. As the specimens from S-Nepal differ in essential morphological characters from other known Asiatic species of *Tomopterna*, we describe *T. maskeyi* n.sp. as a new species.

## Historical review

The genus *Tomopterna* Duméril & Bibron, 1841 was established by subsequent designation of Boulenger (1918) and is based on the African species *Tomopterna delalandii* (Tschudi, 1838).

Boulenger (1890) recognized four Asiatic species: *T. breviceps* (Schneider, 1799), *T. rufescens* (Jerdon, 1854), *T. dobsonii* (Boulenger, 1882) and *T. strachani* Murray, 1884.

During the second half of the last century few papers concerning the Asiatic species of *Tomopterna* were published by Günther, (1858), Anderson (1871), Boulenger (1882) and Murray (1884).

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** Zoological State Collection, D-81247 Munich, Germany

During this century additional four species were described: *T. leucorhynchus* Rao (1937) and *T. parambikulamana* Rao (1937) for India and *T. swani* Leviton et al. (1956) for Nepal. Finally Dubois (1983) described *T. breviceps rolandae*, provisionally treated as a subspecies and later, in 1987, raised to species rank.

Checklists and reviews of *Tomopterna* were made by Kirtisinghe (1957) and Dubois (1983) for Sri Lanka, Minton (1966) and Khan (1976) for Pakistan and Inger & Dutta (1986) for India.

Bhati & Shukla (1975) synonymized *T. dobsonii* with *T. breviceps*. Pillai (1982) provided a key for the identification of the Indian species and recorded *T. dobsonii* for the East-Cost of India. Dutta (1986) resurrected *T. dobsonii* from synonymy with *T. breviceps*. Mertens (1969) and Khan (1976) considered *T. strachani* to be probably a synonym of *T. breviceps*.

The first record of *Tomopterna* in Nepal was made by Bhaduri and Kirpalani (1954) with *T. breviceps*. The results of the Californian Himalaya expedition by Leviton et al. (1956) yielded a second record and *T. swani* as a new species. Swan & Leviton (1962) contributed with a listing to the distribution of these two Nepalese species. Schleich & Maskey (1992) showed for the first time an unindentified species from Royal Chitwan National Park. Numerous publications on Amphibians of Nepal were presented by Dubois, some are also dealing with *Tomopterna* (1974a, 1974b, 1981a, 1981b).

## Systematic account

The systematical status of *Tomopterna* has been a subject of frequent changes in previous times. The generic status was evaluated by Clarke (1981), with the hint on unresolved relationship to other ranids. Dubois (1981a) considered this genus to be a subgenus of *Rana*, closely related to *Euphlyctis* and *Limnonectes*. The subgeneric status was also recognized by Pillai (1982) but refused by Dutta (1986). Dubois (1983) noted that the genus could be divided into two groups, the *Tomopterna rufescens*-group and the *Tomopterna breviceps*-group. In 1987 Dubois refered them to two subgenera, *Sphaerotheca* and *Tomopterna* and finally, in 1992 he proposed the subfamily Tomopterninae.

There are not only difficulties and obscurities linked to the systematical status of the genus, but also concerning probably conspecific species within the Asiatic group of *Tomopterna*. The fact that some of these species are only known from their type locality and sometimes based on single or even lost type specimens, raises problems.

Due to Dutta & Manamendra-Arachchi (1996) some authors confused similar species like *T. breviceps*, *T. rolandae* and *T. dobsonii*. They suspected that previous records of *T. breviceps* are based on specimens of both, *T. breviceps* and *T. rolandae*. These authors also perceived, that Dubois (1983) evidently based his original description of *Rana (Tomopterna) breviceps rolandae* on specimens of both taxa, *T. breviceps* and *T. rolandae*, also that Boulenger (1882, 1890), Bhadhuri & Kirtaplani (1954) and Daniel (1975) confused species. Furthermore, Dutta (1986) argued, that Pillai‘s (1982) description is based on specimens of *T. dobsonii* and *T. rolandae*. The partly contradictory information, given in the various descriptions lead to those conclusions and we herewith follow Dutta & Manamendra-Arachchi (1996).

Being aware of the afore mentioned problems, a new species *T. maskeyi* sp.n. from Nepal is described. It differs in essential morphological characters from all known Asiatic species, including all species previously transferred or treated as conspecific.

**Fig. 1.** Distribution of *T. breviceps*. Hatched areas: countries resp. provinces for which the record of *T. breviceps* is proved.

## *TOMOPTERNA* IN SOUTH-EAST ASIA

### Distribution and Taxa

**Type species**: *Pyxicephalus delalandii* Tschudi, 1838 by subsequent designation of Boulenger, 1918.
*Tomopterna* transferred to Tomopterninae from Raninae Dubois, 1992. Dubois, 1987 recognized two subgenera: *Sphaerotheca* Günther, 1859 (type species: *Sphaerotheca strigata* Günther, 1859 , by monotypy) and *Tomopterna* Duméril & Bibron, 1841 (type species *Pyxicephalus delalandii* Tschudi, 1838 [= *Rana breviceps* Schneider,1799], by subsequent designation of Boulenger, 1918).
According to Duellmann (1993) there are six extant species in the subfamily Tomopterninae, genus *Tomopterna* in south-east Asia:

*T. breviceps* (Schneider, 1799);
*T. dobsonii* (Boulenger, 1882);
*T. leucorhynchus* (Rao, 1937);
*T. rolandae* (Dubois, 1983);
*T. strachani* Murray, 1884 and
*T. swani* (Meyers & Leviton, 1956).

Dubois (1987) transferred *T. rufescens* (Jerdon, 1853) and *T. parambikulamana* (Rao,

1937) to *Limnonectes*. Duellmann (1993) mentions Asian species of Tomopterninae as belonging to the subgenus *Sphaerotheca* in accordance with Dubois (1987).

**Distribution**: India, Sri Lanka, Burma, Nepal and Pakistan.
The general distribution of the different Asian species of the genus *Tomopterna* is given in fig.1-3.

**Fig. 2.** Distribution of Asiatic *Tomopterna* spp. Hatched areas: countries resp. provinces for which the record of *T. rolandae* is proved; star: record of *T. swani*; square: record of *T. strachani*; triangles: records of *T. dobsonii*; circle: record of *T. leucorhynchus*.

## RECORDS OF *TOMOPTERNA* FROM NEPAL

### *Tomopterna breviceps* (Schneider, 1799).
(fig. 5)

**Original name**: *Rana breviceps*.

**Synonymy:** *Rana breviceps* Schneider, 1799:140; Peters,1863:76; Boulenger, 1882:451; Ferguson, 1904:502, Pl. B, Fig. 1.
*Rana variegata* Gravenhorst, 1829:33, pl. 8, fig.1.
*Pyxicephalus fodiens* Jerdon, 1853:534.
*Sphaerotheca strigata* Günther, 1858:20, Pl.2, Fig. A.
*Tomopterna delalandi* (part.) Günther, 1858:129.
*Tomopterna strigata* Günther, 1860:165.
*Pyxicephalus breviceps* Günther, 1864:411; Theobald, 1868:80; Anderson, 1871:200; Murray,1884: 399.

**Type(s)**: Syntypes: including ZMB (2 specimens).

**Type locality**: ”Indes orientales”; ”probablement de Tranquebar (Tamil Nadu; 11°02´N, 79°51´E)” according to Dubois, 1983.

**Distribution**: Reported from Eastern, Central and Western development regions in Nepal (Shah, 1995).

**Range**: Gangetic plain to south India, Uttar Pradesh, Agra (India); Punjab, Sind (Pakistan); upper Burma; Sri Lanka; Nepal.

**Altitude**: According to Shah (1995) *T. breviceps* is reported between elevations of 150 m (Chitwan) to 940 m (Pokhara, Kaski).

**Habitat**: Seems to be restricted to the (sub)”tropical” zone (Shah,1995). Dutta (1996) describes *T. breviceps* from Sri Lanka as a terrestrial species, mainly recorded from arid areas. Specimens found from the senior author were from RCNP only and were active at first pre-monsoon rains in June. The habitat consisted as open patches in Sal forest of RCNP.

**Etymology and common names**: The species name is derived from Latin *brevis* = short and *ceps* = reference to the head. English: Indian Burrowing Frog.

**Status**: Occasional (Shah, 1995).

**Comment**:: In accordance to earlier references we still maintain the systematic position of "*T.breviceps* from Nepal", but it might be suspective for taxonomical changes with further investigations.

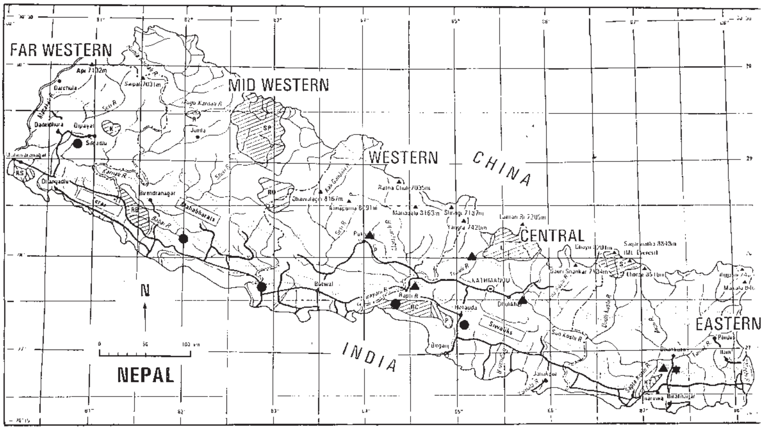

**Fig. 3.** Records of *Tomopterna* spp. from Nepal. Triangles: *T. breviceps*; star: *T. swani* and dots: *T. maskeyi* spec. nov.

### *Tomopterna swani* (MEYERS & LEVITON, 1956)

**Original name**: *Rana swani*.

**Type(s)**: Holotype and only documented specimen: CAS - SU 15371.

**Type locality**: Dharan, East Nepal, at an altitude of 1000 feet (305 m).

**Distribution**: East Nepal.

**Range**: Only known from Nepal, regarded as an endemic species by Shah (1995).

**Altitude**: Between 150 and 305 m.

**Habitat**: Due to Shah (1995) *T. swani* is inhabiting the ”tropical” zone.

**Fig. 4**. Holotype and male paratype of *T. maskeyi* n.sp*;* top- dorsal, center- ventral, bottom- lateral view.

**Etymology**:The species name is an eponym honouring L.W. Swan, who collected the holotype of *T. swani* in 1954 , as participant of the Californian Himalayan Expedition.
**Status**: Categorie S (Susceptible) in the National Red Data Book of Nepal (Shah, 1995).

## ***Tomopterna maskeyi*** **spec. nov.**
**(fig. 4,6-8)**

**Material:** ZSM 106 / 91 - 1-3, 5-7.

**Holotype:** ZSM 106/91-2, a female collected by H.Schleich and T.M. Maskey at Chitwan Jungle Lodge, Royal Chitwan National Park, Central Nepal, at an altitude of approx. 300 m, on July 8, 1991.
**Paratypes**: ZSM 106/91-1, 3, 5- 7. (4 females, 1 male), coll. by Schleich & Maskey.

**Locus typicus**: Chitwan Jungle Lodge, Royal Chitwan National Park, Central Nepal.

**Derivatio nominis**: Dedicated to Dr. Thirta Man Maskey, Director General of the Departement of National Parks and Wildlife Services. Without his engagement neither collection nor possibility for investigation of the new species would have been possible. We also highly esteem the steady help and encouragement of Dr. Maskey supporting research and conservation of wildlife in Nepal
**Status**: Unknown.

**Distribution**: Chitwan, Amlekhganj-Hetauda (Central Nepal), Shivpur, Sakayel-Doti (Western Nepal).
**Range**: So far only reported from Nepal, possibly an endemic species.
Records of *Tomopterna* spp. from Nepal are shown in fig.3.
**Altitude**: Between 200 and 800 m.
**Habitat**: Para-tropical lowlands (Terai) of Nepal. Sympatric with *T. breviceps* in Royal Chitwan National Park.

**Diagnose**: The following combination of characters is unique for the new species:
Dorsum crepe-like without any warts, tubercles or folds and uniform in colour with a single dark triangular mark on the shoulder. The tibio-tarsal articulation reaches the tympanum; an inner metatarsal tubercle is distinctly longer than the first toe; extremities with cross-bars; skin smooth on throat and breast and granular between axilla and groin. Absence of an outer metatarsal- and a tibiotarsal tubercle.

**Features of the holotype:**
An adult female of 47.35 mm snout-vent length. The ultimate phalanges of the first, second and third toes of both the right and the left foot of the holotype are lacking. A 10 mm long section is present on the belly. A sparsely developed vertebral line is present from the triangular marking on the shoulder backwards to the vent. Markings on the sides of the upper jaw are very diffuse, more speckeled than bars. The remaining characteristics correspond to the general description.
**General description:**

**Fig. 5-8.** Different views (a- lateral, b- dorsal, c-frontal) of *Tomopterna* spp. from Nepal
**Fig. 5.** *T. breviceps.*
**Fig. 6,7.** *T. maskeyi* (fig. 7: holotype).
**Fig. 8.** *T. maskeyi* (female, male)

**Morphology**

Body shape globular. Snout-vent length of mature male 41.8 mm, gravid females 46.6 - 53.9 mm. Head distinctly broader than long. Snout not projecting beyond lower jaw, slightly truncate when viewed laterally and rounded when viewed dorsally. Nostril nearer to the tip of the snout than to eye. Internarial width greater than interorbital width. Interorbital distance less than width of upper eyelid. Canthus rostralis indistinct. Loreal region oblique, concave. A small symphysial tubercle on anterior edge of mandible. Upper jaw toothed. Vomerine teeth in two groups. Tympanum distinct, vertically oval. Horizontal diameter equal to the distance between eye and nostril and smaller than the distance between nostrils. Supratympanic fold present, from behind the eye to base of forelimb. Fingers free, moderately thick, tips slightly rounded. 1st finger slightly longer respectively equal in length with 3rd finger, and much longer than 2nd. Second finger equal in length with 4th finger (1.F >/= 3.F; 1.F, 3.F > 2.F; 2.F = 4.F). Subarticular tubercles prominent, conical on fingers; one distinct outer palmar and one indistinct inner palmar tubercle. Webbing is rudimentary, less than one third.

Relative length of toes 1 < 2 < 5 < 3 < 4. Toes with dermal fringes on both sides of 4th toe and inner side of 5th toe. Inner metatarsal tubercle large, longer than 1st toe, shovel shaped, ridged. No outer metatarsal tubercle and no tubercle at the tibio-tarsal articulation present. Tibio-tarsal articulation reaching posterior end of tympanum. Skin dorsally crepe-like; laterally granulated; ventrally granulated only between axilla and groin; few small granules on subsurfaces of thighs and around the cloacal opening. Throat and breast smooth. Male with paired external vocal sacs.

**Colour**

Life: Uniform reddish-brown (between nostrils, upper eyelid and dorsally from the supratympanic fold to the cloacal opening, like a coloured coat) with a prominent dark-brown triangular mark on the shoulder. The dark streak through nostril, eye and along the supratympanic fold is variable in prominence. In some cases the deep black vitta is distinct and in other individuals it is of dark brown-grey and not prominent. Tympanum usually reddish-brown. Three diffuse black bars on each side of the upper jaw. Extremities (dorsal view) of a creme like colour, with dark brownish-grey cross-bars and reddish-brown spots between them. Throat of females is yellowish-white, speckled with dark brown. Throat in males dark bluish black. With or without a fine yellowish-white vertebral line. Laterally creme colour (between axilla and groin) and indistinctly marbled with dark brown.

Preserved: Dorsally reddish-brown with one symetrical dark brown triangular mark on a level with the axilla, forming a chevron. The basic colour is uniform. Dark brown patches on upper lip. Limbs with cross-bars. Inner side of thigh indistinctly speckled cremish-white and brown. Dorsum with or without white vertebral line, mostly commencing slightly anterior of the dorsal patch. Ventral side and underside of thighs yellowish-white. Throat of females scarcely spotted with brown, throat of males including external vocal sacs are of a deep bluish-black colour.

**Sexual dimorphism (see fig. 8)**

Sexual dimorphism is expressed in size differences. SVL of adult females is within the range of 46.6 - 53.9 mm, whereas an adult male, with fully developed and pigmented vocal sacs, measured only 41.8 mm. As in *T. swani* (Leviton et al., 1996), *T. breviceps* and *T. rolandae* (Dutta, 1996) also the male of *T. maskeyi* has paired, bluish-black coloured, external vocal sacs. We could not observe nuptial pads on fingers of males as it is mentioned for *T. rolandae* (Dubois, 1983).

## Methods and Abbreviations

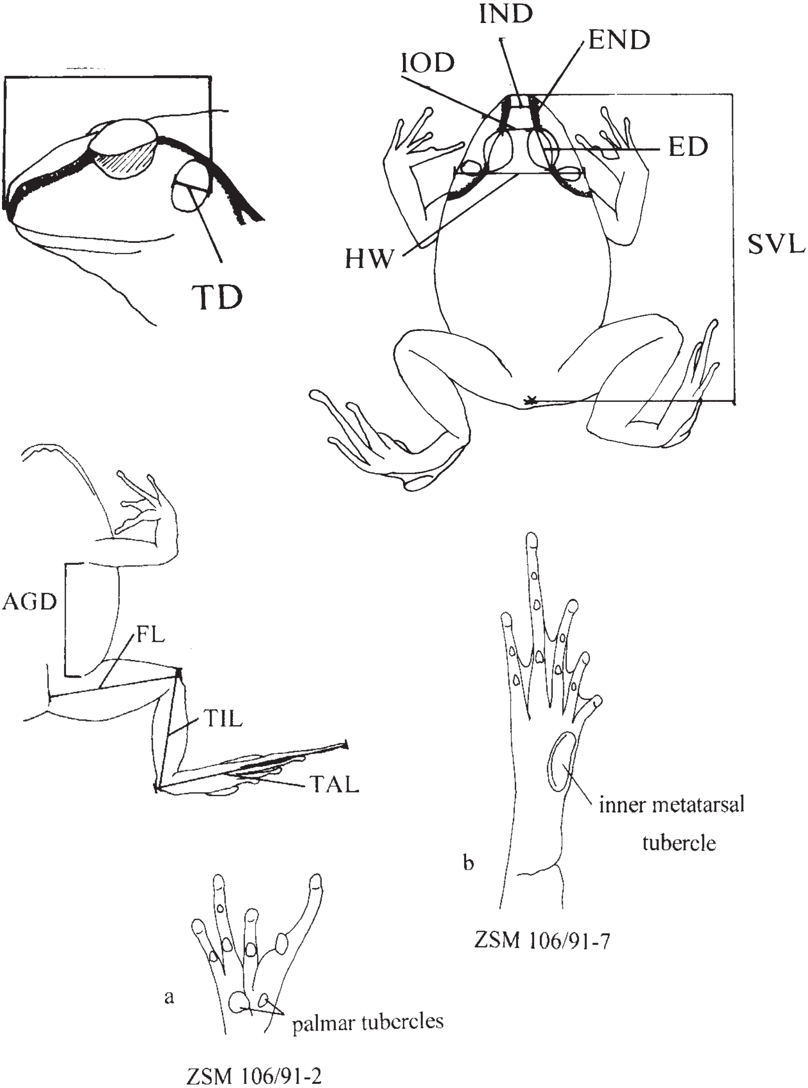

**Fig. 9.** *T. maskeyi* spec. nov. Methods of measurement and ventral aspects of the right hand (a, ZSM 106/91-2) and the right foot (b, ZSM 106/91-7).

**Methods (fig. 9)**: Individuals of both species (*T. breviceps*, *T. maskeyi* sp. n.) collected in Nepal were examined. Sex identification is possible by external characters or internally by the presence of gonads.
All measurements were made with callipers. The following morphometric features were examined and are listed in tab. 1:

SVL (snout-vent length / tip of the snout to the posterior edge of the cloacal opening),
HL (head length / tip of snout to gular fold),
HW (head width / at the angle of the upper jaw),
IOD (inter-orbital distance / between anterior angles of eyes),
IND (inter-narial distance / between the two narial openings),
END (eye-naris distance / between the right narial opening and anterior angle of the right eye),
ED (diameter of eye / between anterior and posterior angle of the right eye),
TD (diameter of tympanum / horizontal diameter),
AGD (axilla-groin distance /fore- and hindlimbs extended at right angle),
FL (length of femur),
TIL (length of tibia),
TAL (length of tarsus, metatarsus incl. toes)
IMT (length of inner metatarsal tubercle / anterior to posterior end of tubercle).

**Abbreviations:** Museum codes used for types are: CAS (California Academy of Science, San Francisco, USA), ZMB (Zoologisches Museum , Berlin/Germany) and ZSM (Zoological State Collection, Munich/Germany).

*T. maskeyi* spec. nov.

| Inv. Nr./ZSM: | 106/91-2 | 106/91-1 | 106/91-3 | 106/91-5 | 106/91-6 | 106/91-7 |
|---|---|---|---|---|---|---|
| Type | holotype | paratype | paratype | paratype | paratype | paratype |
| sex | f | f | f | f | f | m |
| SVL | 53.35 | 53.90 | 46.60 | 47.20 | 47.35 | 41.80 |
| HL | 19.10 | 18.20 | 16.25 | 16.30 | 15.85 | 15.80 |
| HW | 20.25 | 20.45 | 18.35 | 19.45 | 18.50 | 17.65 |
| IOD | 3.85 | 3.85 | 3.40 | 4.35 | 3.65 | 2.20 |
| IND | 5.05 | 5.05 | 4.45 | 4.95 | 5.00 | 4.15 |
| END | 3.00 | 3.50 | 3.15 | 3.00 | 3.00 | 2.25 |
| ED | 8.55 | 7.80 | 7.20 | 7.95 | 7.65 | 7.15 |
| TD | 4.25 | 3.80 | 3.35 | 3.60 | 3.90 | 3.80 |
| AGD | 25.75 | 22.85 | 22.50 | 25.55 | 20.70 | 17.70 |
| FL | 21.15 | 23.50 | 21.80 | 20.05 | 19.70 | 18.70 |
| TIL | 23.00 | 22.90 | 21.55 | 21.55 | 21.45 | 19.00 |
| TAL | 31.00 | 32.90 | 29.55 | 29.10 | 27.95 | 27.90 |
| IMT | 4.65 | 5.30 | 4.90 | 4.90 | 4.90 | 4.40 |

**Tab. 1.** Measurements of *Tomopterna maskeyi* spec. nov. Abbreviations explained in the chapter methods and abbreviations; m = male; f = female.

## Discussion

### Morphological characters

*T. maskeyi* spec. nov. differs from the other Asiatic *Tomopterna* species in having following morphological characters:

1. (from *T. breviceps*) by having a crepe-like dorsal skin without any warts, tubercles or granulae; snout slightly truncate; relative length of toes; relative length of fingers; colouration of dorsum is uniformly reddish grey-brown with one dark triangular marking.

2. (from *T. rolandae*) by having a crepe-like dorsum; relative length of fingers; indistinct inner palmar tubercle; size; colouration of the dorsum; lack of nuptial pads in males.

3. (from *T. swani*) by a head which is distinctly broader than long; diameter of tympanum is about ½ of eye diameter; inner metatarsal tubercle distinct longer than first toe; tibio-tarsal articulation reaching tympanum; dorsum smooth ; venter only granular between axilla and groin and laterally, throat and breast smooth; colouration of dorsum; extremities with cross-bars; no markings on sternal region.
( v. s. *T. swani* diameter of tympanum approx. 2/3 of diameter of eye, length of inner metatarsal tubercle equal to distance from anterior end of tubercle to tip of toe, tibio-tarsal articulation reaching center of eye, extremities without bars or speckles, dorsum without marking, presence of marking on sternal region in male and a coarsely granular skin over the whole venter.

4. (from *T. dobsonii*) by the indistinct canthus rostralis; diameter of tympanum; tibio-tarsal articulation reaching tympanum; temporal streak not covering a portion of the tympanum; dorsum not marbled, only with a single mark.

5. (from *T. strachani*) by having a head distinct broader than long; diameter of tympanum; relative length of fingers; two palmar tubercles; rudimentary webbing; absence of outer metatarsaltubercel; smooth skin on dorsum; single marking on the dorsum.

6. (from *T. leucorhynchus*) by a snout broader than long; relative length of fingers; inner metatarsal tubercle longer than 1. toe, absence of an outer metatarsal tubercle, tibio-tarsal articulation reaching tympanum, absence of inner tarsal fold; absence of an W shaped band between the eyes.

We agree with Dubois (1984) who first considered *T. parambikulamana* as a member of the genus *Rana* and then (1987) changed it to *Limnonectes parambikulamana*. Distinguished from *T. (Limnonectes) parambiculamana* by a totally different habitus, a different relative length of legs and the absence of an outer metatarsal tubercle. From *T. leucorhynchus* it differs by the absence of an outer metatarsal tubercle, an inner tarsal fold and a dark W-shaped band behind the eyes and by a tibio-tarsal articulation not reaching the eye.
Dutta (1990) doubted the systematic position of *T. leucorhynchus* because of the unclear original description by Rao (1937). Furthermore *T. leucorhynchus* is only known from the type locality, and there was no subsequent report of the species so far. There could be the possibility of confusing *T. leucorhynchus* with *T. breviceps* by Rao (1937). Due to Dutta (1996) *T. breviceps* shows a wide range of morphological variation concerning

| Taxon/ | SVL | tymp. | fingers | toes | W | IMT | OMT | TTA | MTT | skin |  |  |  |  |  | colour |  |  |  | E | VL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Author | in mm | Ø ≈ | rel. | rel. |  | rel. to 1. |  | reaching |  | dorsum |  |  |  | venter |  | dorsum |  |  | throat |  | c-b |
|  |  |  | length | length |  | or 2. toe |  |  |  | s | cp | g | st | s | g | u | mb | mk | sp |  |  |
| *T. maskeyi* sp.n. sensu this paper | m 41.8<br>f 46.6-53.9 | 1/2 eye | 1=(≥)3; 1>2; 2=4 | 1<2<5<3<4 | rud. | >1 | - | tymp. | - | - | + | - | - | + | + | + | - | + | + | + | +/- |
| *T. swani* sensu Leviton et al. ,1956 | m 42.3 | 2/3 eye | 1=3; 1>2; 2>4 | 0 | rud. | =1 | - | eye | - | - | + | - | - | - | + | + | - | - | - | - | - |
| *T. dobsonii* sensu Boulenger, 1882 and 1890 | f 54 | 2/3 -3/4 eye | 1>2; 1=3 | 0 | rud. | >1 - ≈2 | - | shoulder - tymp. | 0 | + | - | - | - | - | + | - | + | - | + | + | +/- |
| *T. rolandae* sensu Dubois, 1983 | m 35.4-48.0<br>f 35.3-47.3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| *T. rolandae* sensu Dutta, 1996 | m 32.5-38.5<br>f 33.8-44.5 | 0 | 1<2 and 4; 3 longest | 1<2<5<3<4 | >1/2 | >1 | - | 0 | + | - | - | + | + | 0 | 0 | - | + | - | + | + | +/- |
| *T. breviceps* sensu Boulenger, 1882, 1890 | 63.5 | 1/2 -2/3 eye | 1>2; 1≈3 | 0 | 1/2 | >1 - ≈2 | - | axilla-tymp. | 0 | - | - | + | + | - | + | - | + | - | + | 0 | +/- |
| *T. breviceps* sensu Bhati & Shukla, 1954 | 0 | 1/2-2/3 eye | 1>2; 1=3 | 0 | rud. | 0 | - | axilla-shoulder | 0 | - | - | + | + | - | + | - | + | - | + | + | + |
| *T. breviceps* sensu Kirtisinghe, 1957 | up to 55 | 1/2 eye | 1>2; 1≈3 | 0 | 1/2 | >1 | - | tymp. | 0 | - | - | + | - | - | + | - | + | - | + | + | + |
| *T. breviceps* sensu Dutta, 1996 | m 41.0-55.0<br>f 43.0-57.0 |  | 1<2 and 4; 3 longest | 1<2<3=5<4 | <1/2 | >1 | - | 0 | - | - | - | + | + | 0 | 0 | - | + | - | + | + | + |
| *T. strachani* sensu Murray, 1884 | 0 | ≈ eye | 1=2=4; 3 longest | 5≤3<4 | 1/2 | 0 | + | 0 | 0 | - | - | - | + | 0 | 0 | - | + | - | - | + | 0 |
| *T. leucorhynchus* sensu Rao, 1937 | 35 | < eye | 1>2; 1<3 | 0 | 0 | =1 | + | eye | 0 | + | - | - | - | + | + | + | - | + | - | + | 0 |

**Tab. 2**: Characteristics of *T. maskeyi* sp. n. compared with other Asian *Tomopterna* spp.. Abbreviations: E = extremities; IMT = inner metatarsal tubercle in relation to the length of the 1. or 2. toe; MTT = metatarsal tubercle; OMT = outer metatarsal tubercle; SVL = snout-vent length; TTA = tibio-tarsal articulation; W = webbing; c-b = cross-barrs; cp = crepe-like; f = female; g = granulated with rounded or elongated tubercles or longitudinal folds; m = male; mb = marbled, multiple spots, symmetrically or not; mk = single prominent marking on the shoulder; rud. = rudimentary webbing; s = smooth; sp = throat speckeled with brown in female and bluish-black in male; st = smooth with rounded or elongated tubercles or longitudinal folds; u = uniform; + = present resp. yes; - = absent resp. no; +/-= both presence and absence as well as possible; 0 = no available informations; > = longer or bigger in size; = = equal in length or size; < = shorter or smaller in size.

polychromatism regarding the mid-dorsal stripe. As the type of *T. rufescens* was lost (Dutta, 1985), respectively not stated (Frost,1985), Dubois (1984) erected a neotype for *Rana (Fejervarya) rufescens* and transferred it in 1987 to *Limnonectes rufescens*. Moreover *T. strachani* was reported by Khan (1976) to be closely related to *T. breviceps* and perhaps conspecific with this species. Bhati & Shukla (1975) considered *T. dobsonii* as conspecific with *T. breviceps*, but we agree with Pillai (1982) and Dutta (1986) to consider *T. dobsonii* as a distinct species. Altogether two former Asiatic species of *Tomopterna* were transferred to *Limnonectes* (*T. parambikulamana* and *T. rufescens*), two other species (*T. leucorhynchus* and *T. strachani*) are of a uncertain systematical status or were regarded as conspecific.

**Research and conservation**

Although the investigations for the Biodiversty Profiles Project (1995) were carried out, no further attempt was made to report on the conservational status of *T. breviceps* and *T. swani* in Nepal. *T. swani* is one of nine endemic amphibian species in Nepal (National Red Data Book, 1995) and no subsequent report could be made since its original description in 1956. Therefore this species obtained the status S (susceptible) by Shah (1995). Due to Clarke (pers. comm., 1996) the survival of species as *T. swani* or *T. dobsonii* in the wild will be a matter of conjecture but any newly discovered populations should be carefully monitored. Finally the discovery of *T. maskeyi* should stimzlate further investigations on Nepalese species of *Tomopterna*. Very few is known on the biology of this asiatic genus, due to the secretive way of life. Some rare notes on the biology of *T. breviceps* or *T.rolandae* were given by Kirtisinghe (1957), Minton (1966) and Dutta (1996). It would be of great importance to obtain more information concerning habitat preference, distribution, population density and structure as well as on reproductive biology, food spectrum and predators. More investigations on the biology of *T. maskeyi* are nescessary to estimate its conservational status.

## Acknowledgements

We gratefully acknowledge the Volkswagen-Stiftung, Germany for the present study within the project ”Natural History of the Amphibians and Reptiles from Nepal”.
Furthermore one of us (C.C.A.) thanks DAAD, for providing research funds in Nepal and finally the University of Munich for granting a scholarship (HSP II/III). C.C.A. is grateful to the Zoological State Collection (ZSM), Munich for working facilities including use of library.

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# First record of *Polypedates taeniatus* (Boulenger, 1906) from Nepal (Amphibia, Anura: Rhacophoridae)

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**Key words**: Amphibia, Anura, Rhacophoridae, *Polypedates, P. taeniatus*, morphology, Nepal.

**Abstract:** The rare rhacophorid frog *Polypedates taeniatus* (Boulenger, 1906), hitherto only known from its type locality in Bihar and from Uttar Pradesh, India is recorded for the first time in Nepal. The description is based on six specimens from south Nepal. Information on the habitats in central and eastern Nepal, on sympatric amphibians, and on the natural history of the new species is presented. Morphometric data are given. The different individual dorsal patterns and the ventral aspects of hand and foot of the examined specimens are illustrated. Morphological characters of *Polypedates taeniatus* are discussed.

## Introduction

Two field trips, one to Royal Chitwan National Park (central Nepal) during the monsoon in 1989 and a later one to Koshi Tappu Wildlife Reserve (eastern Nepal) in premonsoon of 1996 yielded three specimens of *P. taeniatus* from each locality. This were the first records of *P. taeniatus* outside of India and the only record of specimens since the description of this species by Boulenger in 1906.

*P. taeniatus* is closely related to *Polypedates leucomystax* (Gravenhorst, 1829) which is widespread and one of the most common south and southeast Asian species of Rhacophoridae (Church, 1963). Though showing striking specific features *Polypedates taeniatus* shares morphological characters with *Polypedates leucomystax*. *P. taeniatus* was classified as a member of the *P. leucomystax* group by Dubois (1987 „1986“). Comparative studies of the type material shall be presented in the PhD thesis of the junior author (Anders, in prep.) on the amphibians of Nepal.

## Historical review

In a comprehenshive work on the *Rhacophoridae* and *Hyperolidae,* Liem (1970) separated the genus *Polypedates* from *Rhacophorus*. The validity of the genus *Polypedates* was later doubted by Dubois (1986; as cited in Das, 1995). Different opinions are discussed not only at the generic level, but also at species and at subspecies level of some Rhacophoridae. Especially the status of *Polypedates leucomystax* subspecies (e.g. *P. l. leucomystax, P. l. megacephalus, P. l. sexvirgatus*) is discussed controversially.

In contrast to the common and intensely studied *P. leucomystax*, only very few information and literature is available on the rare rhacophorid species *P. taeniatus*. In 1906 Boulenger

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described *P. taeniatus* together with *Philautus annandalii* (which is also recorded for Nepal) as two new Indian frog species. Ahl (1931) mentioned *P. taeniatus* in his work on Polypedatidae, presenting a translation of Boulenger‘s original description. Brief remarks of the distribution of *P. taeniatus* are given in Gorham‘s (1974) checklist of the amphibians of the world, in Inger & Dutta‘s (1987) overview of Indian amphibians and in Dutta (1985 and 1997). The first detailed work together with a redescription of *P. taeniatus* was recently presented by Ray (1991) on the basis of new collections in Uttar Pradesh, India.

**Fig. 1.** Habitat at Royal Chitwan National Park.

**Fig. 2.** Habitat at Koshi Tappu Wildlife Reserve.

## Habitats

The first three Nepalese specimens were found at Royal Chitwan National Park on July, 7th 1989, calling in Sauraha on a rainy monsoon night within dense herbs and shrub vegetation (see fig. 1). Accompanying batrachian faunal elements were *Tomopterna breviceps* , *Tomopterna maskeyi*, *Bufo melanostictus*, *Bufo stomaticus*, *Limnonectes limnocharis*, *Euphlyctis cyanophlyctis, Microhyla ornata* and *Polypedates leucomystax leucomystax*. In the headquarters area of Koshi Tappu Wildlife Reserve three more specimens of the arboreal and nocturnal *P. taeniatus* were collected from the vegetation surrounding an artificial pond (6 m x 3 m, with an approximate maximum depth of 1.2 m) (see fig. 2) at 22.30 hrs. on May, 27th 1996. The frogs, all males, could only be located by following their calls. This agrees with the statement of Liu (1950), that at the time of egg-laying male Rhacophoridae croak near or on the banks of pools or on vegetation around their breeding place. They were discovered sitting in a resting position resembling that of *Hyperolius* (see fig. 7) on leafs of shrub vegetation with their venter adpressed to the substrate and their extremities held close along the lateral sides of the body as figured by Stewart (1967). According to Ray (1991) the ventral skin of the abdomen and the thighs act as an adhesive apparatus while *P. taeniatus* sits adpressed to the substratum. At this collecting site *Bufo melanostictus, Bufo stomaticus, Limnonectes limnocharis, Hoplobatrachus tigerinus* and *Euphlyctis cyanophlyctis* were also recorded.

## *Polypedates taeniatus* (Boulenger, 1906)
## (Figs. 3-7)

***Polypedates taeniatus*** (Boulenger, 1906), J. Asiatic Soc. Bengal, (N.S.), 2:385.

**Synonymy:** *Rhacophorus taeniatus* Boulenger, 1906, J. Asiatic Soc. Bengal, (N.S.), 2:385.
*Rhacophorus (Rhacophorus) taeniatus* Ahl, 1931, Das Tierreich, 55:108.
*Rhacophorus (Rhacophorus) taeniatus* Dubois, 1987 „1986“, Alytes, 5:77.
*Rhacophorus taeniatus* Ray, 1991, J. Bombay Nat. Hist. Soc, 88(3):376.

**Types:** Syntype: ZSI No. 15715, designated as paralectotype by Ray (1991) and BMNH 1947.2.26.57, designated as lectotype by Dubois (1987 „1986“).

**Type locality:** „Purneah, Bengal“, now Bihar, India.

**Indian material:** ZSI / NRS-A 188 (3 female, 4 males) and ZSI / NRS-A 189 (4 female, 3 males), collected by Ray on June 11, 1987 respectively on July 21, 1986 in Dudwa National Park, Uttar Pradesh, India.

**Nepal material:** VW-D 1996/11-1,2,3 (3 males), collected by H.H. Schleich and C.C. Anders in the headquarters area of Koshi Tappu Wildlife Reserve (Koshi barrage: 26°37‘10.5 N, 87°01‘55.0 E), east Nepal, at an altitude of approx. 250 m, on May 27, 1996 and ZSM 89/1991-1,2,3 (1 female, 2 males) from Sauraha, Royal Chitwan National Park, central Nepal, collected by H.H. Schleich and T.M. Maskey, on July 7, 1989.
The number of known specimens of *P. taeniatus* is with that collection 22 in total (two syntpes of the type locality, Bihar, India; 14 specimens of Uttar Pradesh, India and additional 6 specimens of central and east Nepal)

**Etymology:** *Taeniatus,* Lat. = striped, banded.

Fig. 3

Fig. 4

Fig. 5

**Distribution in Nepal:** South Nepal (Terai) in Royal Chitwan National Park and Koshi Tappu Wildlife Reserve.

**Range:** *P. taeniatus* is recorded for Bihar (type locality:"Purneah, Bengal") and Dudwa National Park, Uttar Pradesh in India and for Royal Chitwan National Park and Koshi Tappu Wildlife Reserve in Nepal. An additional occurence is stated for Bangladesh (see discussion in this paper and Khan, 1982) and also supposed for West Bengal, India.

## General description

### Morphology

The snout-vent length of the examined mature males attains 31.2 - 35.0 mm, the gravid female measures 40.7 mm. The body is torpedo-shaped. The head is slightly longer than broad; the snout is blunt and projecting beyond the lower jaw. The upper jaw is dentate. The canthus rostralis is distinct. Prominent vomerine teeth are present and situated between the choanae, close to their inner anterior edge. The nostrils are situated nearer to the tip of the snout than to the eyes. The tympanum is distinct, round, close to the eye and about 1/2 to 2/3 of its diameter. A supratympanic fold is lacking. The oval pupils are horizontal. Fingers are free and their relative length is 1<2<4<3. Conical subarticular tubercles are distinct; three palmar tubercles are present. The digital discs are well developed and rounded. The disc of the first finger is much smaller than the others, the disc of the third finger being the largest. The toes are webbed half to two thirds of their length. The subarticular tubercles on toes are distinct and conical. Relative lengths of toes are 1<2<3<5<4 (see fig. 6). The inner metatarsal tubercle is small but distinct and triangular, an outer one is absent. A distinct tibio-tarsal fold is present. The dorsal skin is of crepe-like texture. The venter and the underside of the thighs are granular, chin and throat are smooth.

**Sexual dimorphism:** As reported for the Indian material (Ray, 1991) also the Nepalese specimens show sexual dimorphism concerning size (males are distinctly smaller than females). Ray (1991) also mentioned a subgular vocal sac in males, sexual dichromatism (brighter coulouration of male individuales) and a shorter length of the foot in relation to the length of the tibia in males. The last two characteristics could not be confirmed for the Nepalese material.

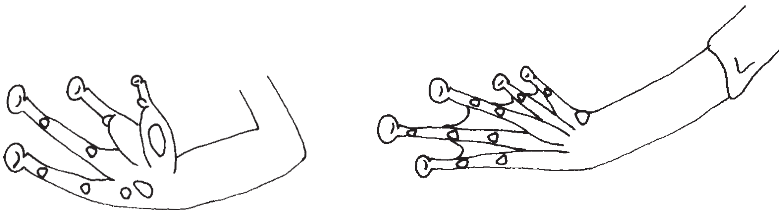

**Fig. 6.** *Polypedates taeniatus,* ventral aspect of right hand and foot of VW-D 1996/11-2.

left:
**Fig. 3, 4.** *Polypedates taeniatus* from Sauraha, Royal Chitwan National Park
**Fig. 5.** *Polypedates taeniatus* from Koshi Tappu Wildlife Reserve

### Colour

The venters of live specimens are uniform creamish-white. The background colour of the dorsum and the dorsal sides of the extremities is a dull reddish to hazelnut brown. There are six dark brown longitudinal bands. They decrease in intensity and width from lateral to dorsal, being hardly visible in the middorsal region. Laterally a broad dark brown band extends backwards from the nostrils to the anterior edge of eye, continuing on the posterior edge of the eye, totally covering the tympanum and reaching the groin. Two additional narrow longitudinal bands run from the eyelids to the lumbar region. Between these bands and the lateral ones the skin is creamish-white. Two faint median stripes run from the tip of the snout to the lumbar region. These two more or less visible lines are individually different and consist of many small spots or stipples (see Fig. 7). The extremities are bordered by an indistinct slender ridge extending from the elbow to the outer side of the 4th finger and on the tibia. The colour of this ridge is dark brown with a parallel white line.

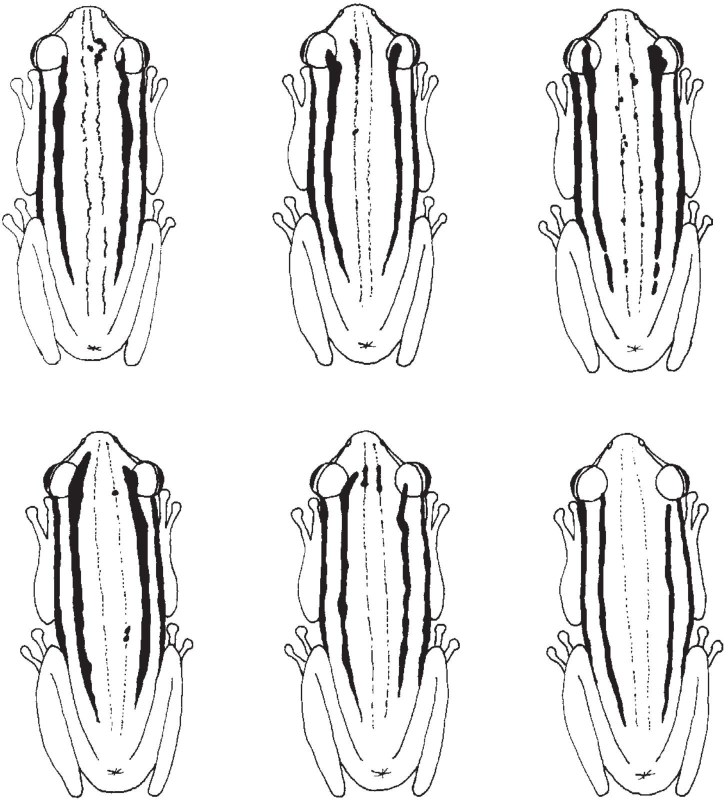

**Fig. 7.** *Polypedates taeniatus.* Dorsal aspects and individual variability of the longitudinal stripes. Top: specimens from Koshi Tappu Wildlife Reserve, Nepal. Bottom: specimens from Royal Chitwan National Park, Nepal.

## Methods and Abbreviations

### Methods

All measurements were made with dial vernier callipers. The following morphometric measurements were made and are listed in Tab. 1:
SVL (snout-vent length: from tip of the snout to the posterior edge of the cloacal opening),
HL (head length: from tip of snout to the gular fold),
HW (head width: at the angle of the upper jaw),
IND (inter-narial distance: between the two narial openings),
IOD (inter-orbital distance: between the anterior angles of eyes),
END (eye-naris distance: between the right narial opening and the anterior angle of the right eye),
ED (diameter of eye: between the anterior and the posterior angle of the right eye),
TD (diameter of tympanum: horizontal diameter),
AGD (axilla-groin distance: between the axilla and the groin when the fore- and hindlimbs are extended at right angles to the body),
FL (length of femur: distance between cloaca and knee),
TIL (length of tibia: distance between knee and heel with both tibia and tarsus flexed) and
TAL (length of tarsus, metatarsus incl. toes: from the heel to the tip of the longest toe).
Sex identification was checked internally by the presence of gonads.

**Abbreviations:** VW-D (Volkswagen Collection, Germany), ZSM (Zoological State Collection, Munich, Germany), ZSI (Zoological Survey of India, Calcutta, India) and BMNH (British Museum Natural History, London, Great Britain).

Measurements of *Polypedates taeniatus* from Nepal.

| | Koshi Tappu | | | Chitwan National Park (Sauraha) | | | |
|---|---|---|---|---|---|---|---|
| VW-D 1996 | 11-1 | 11-2 | 11-3 | ZSM 89/ | 1991-1 | 1991-2 | 1991-3 |
| Sex | m | m | m | | f | m | m |
| SVL | 34.0 | 33.0 | 31.5 | | 40.7 | 35.0 | 31.2 |
| HL | 10.5 | 11.0 | 11.0 | | 13.0 | 11.0 | 10.0 |
| HW | 9.0 | 10.0 | 9.5 | | 11.1 | 9.8 | 9.0 |
| IND | 3.2 | 3.0 | 3.4 | | 3.9 | 3.5 | 3.1 |
| IOD | 6.0 | 6.1 | 5.6 | | 7.6 | 6.5 | 6.2 |
| END | 2.7 | 2.9 | 3.1 | | 3.5 | 3.2 | 3.1 |
| ED | 3.2 | 3.6 | 3.5 | | 5.0 | 4.0 | 3.8 |
| TD | 2.2 | 2.1 | 2.1 | | 2.7 | 2.0 | 2.1 |
| AGD | 16.5 | 17.1 | 16.0 | | 18.5 | 16.1 | 15.6 |
| FL | 13.5 | 13.2 | 12.5 | | 16.5 | 17.0 | 16.0 |
| TIL | 15.0 | 15.0 | 15.0 | | 17.5 | 17.0 | 17.0 |
| TAL | 17.5 | 18.1 | 18.3 | | 21.5 | 20.5 | 17.8 |

**Tab. 1.** Measurements of *Polypedates taeniatus* from Nepal. All measurements in mm; m = male; f = female.

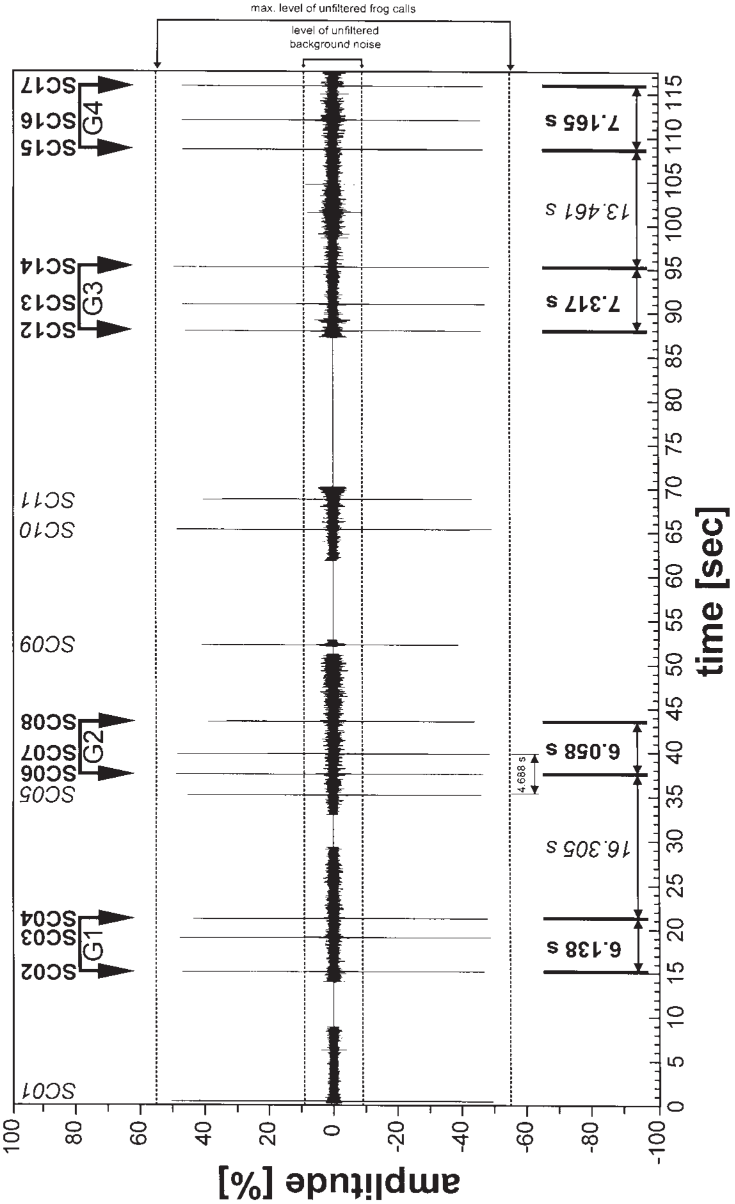

**Fig. 8.** Digitalized and filtered oscilloscope display of *Polypedates taeniatus* male advertisement calls. Single calls appear as high amplitude peaks in low amplitude background noise. In the sections with zero amplitude the background noise (e.g. speech) was totally silenced out. Remarkable is a possible combination of three calls into four groups (G1 to G4) with rather same duration.

## Sound analysis of male advertisement calls

Sounds of calling males were recorded at the headquarters of Koshi Tappu Wildlife Reservat on May 26, 1996 at 22.30h local time and on may 27th between 20:30-23:30 at 28.2 °C with no rain on both days.

The device employed for the sound recording (OLYMPUS Pearlcorder S926) only works reliably between 700 Hz and 4900 Hz. In fig. 10 this section is characterized as „SLR“ (section of „linear“ recording). At lower and higher frequencies the device is by far lesser sensible and an analysis of the sound pattern is much more problematic. Using a filter the noise overlaying the frog calls (tape and background noise) was reduced by approx. 12 to 15 dB, in that case with a minimal influence on the main signal. For the frequency analysis (fig. 10a,b) a 1024-point Blackmann-Harris Fast Fouriere Transformation (FFT) was used. The sound sequence to be analyzed is 117.711 seconds long and contains 17 different frog calls (SC01 to SC17). Peaks of high amplitude (fig. 8), can mostly be arranged into groups of three:

Group 1 (G1) with the calls SC02 to SC04, group 2 (G2) with the calls SC06 to SC08, group 3 (G3) with the calls SC12 to SC14 and group 4 (G4) with the calls SC15 to SC17. Although the calls SC05 to SC07 are suitable to be combined, a group SC06-SC08 is the more probable one, because a duration of 6.058 seconds it is much closer to the comparative values of G1 (6.138 s), G3 (7.317 s) and G4 (7.165 s).

To measure the distance between the calls, the temporal difference between the maximum relative amplitudes of two unfiltered signals was measured. Since 5 calls can not be put into this pattern, a final statement on the basis of the present data is not possible. The amplitude of an individual signal shows a quite characteristic shape and is organized into 3 sections (S1, S2 and S3; fig. 9).

A tripartition (SC 16) of this kind is evident in fig. 2a. Although this basic pattern can be recognized still in other calls, a clear differentiation of the sections S2 and S3 is rather difficult (fig. 9b). As a rule the peaks from S2 amplitude show relative values of more than 40%, but in S3 only peaks up to 35% are to observe. In addition to the problems of the internal subdivision, difficulties occur with the determination of call duration. The reasons herefor lie in the shortness of the signals and in the limited quality of the sound record. However, by the combination of different filters a mean value of 112 msec (± 8 msec SDev) could be determined for the duration of an individual signal.

A characterization of the frequency structure meets similar difficulties as the analysis of the amplitude pattern. The spectrograms of the single calls (fig. 10a) show a rather uniform structure with a frequency of approx. 3000 Hz. Above 3000 Hz a decrease of intensity is observed and above 5600 Hz no more significant frequency pattern can be proved. The lack of signals is observed clearly already below 4900 Hz, and it can be concluded, that a limited sensitivity of the recording device cannot explain this observation. As all individual signals show an approximately equal basic frequency structure, it makes sense to analyse them as a whole in order to manage a broader data base for statistical evaluation. The shape of the graph in fig. 10b confirms basically the impressions from fig. 10a. Here only a small decrease of intensity (approx. 5 dB) can be observed up to 2500 Hz. Between 2500 Hz and 3900 HZ, the intensity of the signals decreases drastically with to 10 dB and up to 5000 Hz the intensity decreases to about 11 dB. The drop of intensity between 5000 Hz and 7500 Hz amounts to about 12 dB. At the present state of knowledge farther trials of interpretation do not make much sense.

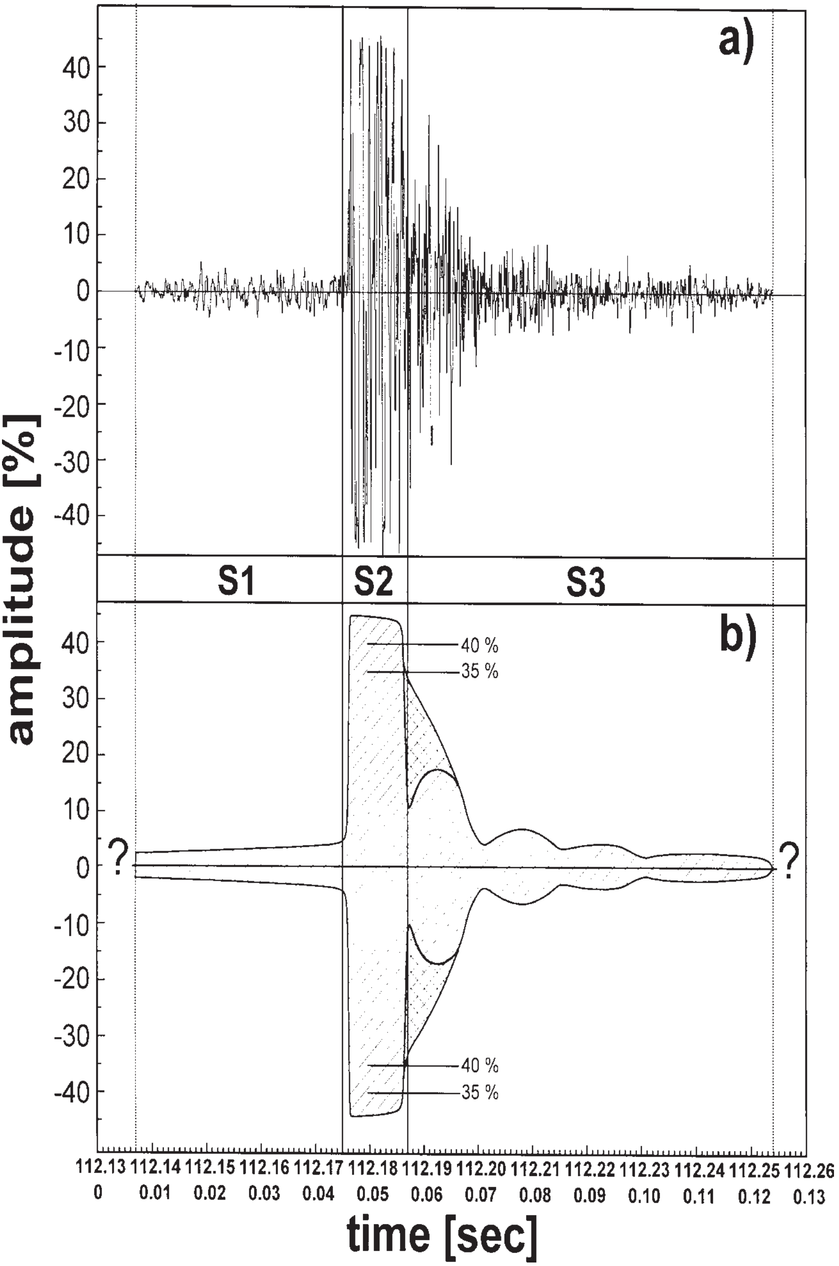

**Fig. 9.** Oscillogram of the filtered individual signal SC16 (a) and the model developed from this (b). In the case of some calls the shown separation of S2 and S3 is less obvious (crosshatched fields). However, S2 consists usually of a dense sequence of amplitudes above 40%. In contrast to this S3 shows amplitude values below 35%.

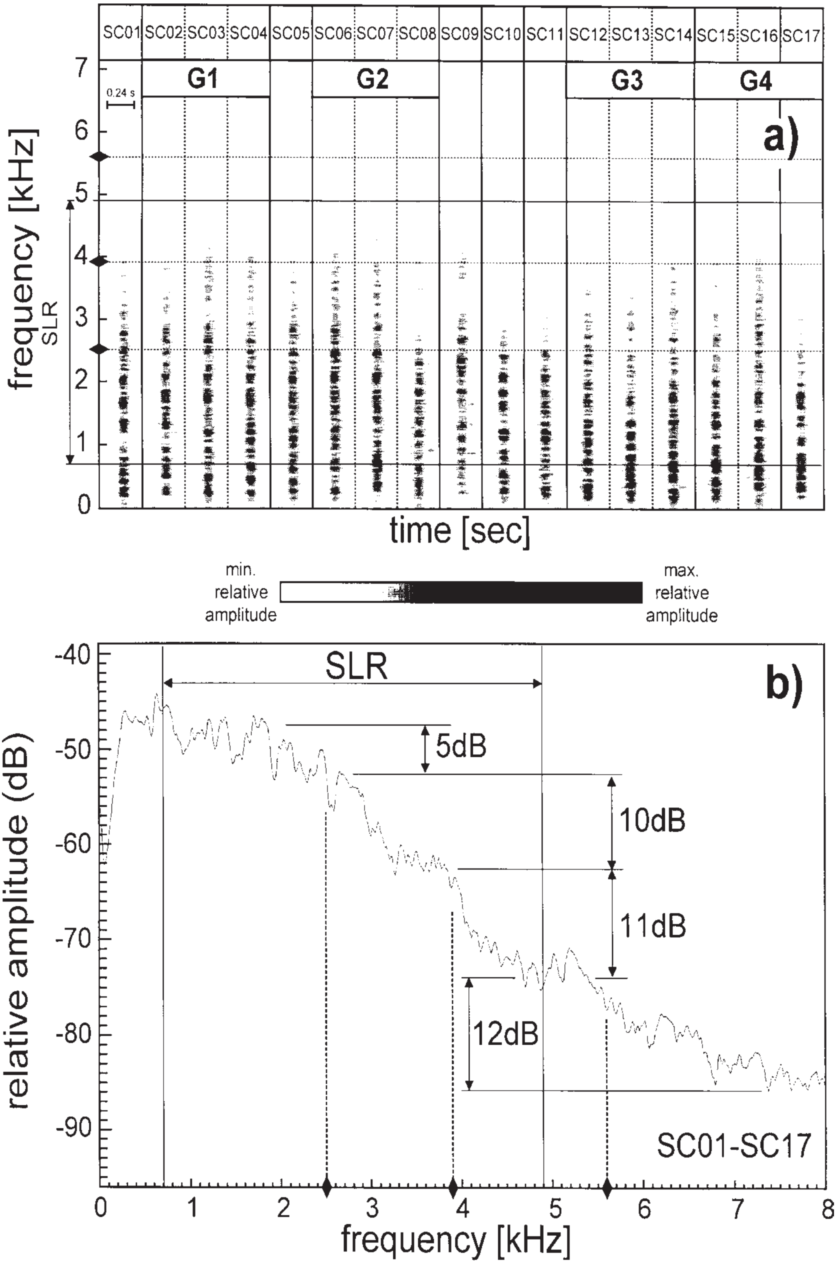

**Fig. 10.** The upper plot (a) shows the filtered spectral data of all frog calls (SC01-SC17) over time with the amplitude shown in shades of grey (spectrogram). In fig. 10b a two-dimensional plot of the spectrum is shown. In order to manage a broader data base for the statistical evaluation the 17 single calls were analyzed as a whole.

Superimposed variations of 3-5 dB being observed in the entire graph, can not be evaluated as a characteristic feature of the calls. Variations in this order of magnitude also can be caused by the recording device and/or the used noise filters. From the above given interpretations one might deduct that no significant frequency patterns are probably above 8000 Hz. However, results must be confirmed by analysing a qualitatively better sound record.

## Discussion

### Morphological characters

Many characters of *P. taeniatus* correspond to the description of *Polypedates leucomystax sexvirgatus* by various authors (Günther (1858), van Kampen (1923), Liu (1950), Taylor (1962), Inger (1966) and Okada (1966)). These are e.g.: disposition of vomerine teeth, obtuse snout projection beyond lower jaw, distinct large tympanum, relative length of fingers and toes, size of digital discs, dimension of webbing on toes, ventral aspects of hand and foot with subarticular tubercles, shape and size of the inner metatarsal tubercle, texture of skin, slender coloured ridge on extremities and dark longitudinal bands on the dorsum. In the original paper Boulenger (1906) mentioned that *P. taeniatus* differs from the related *P. maculatus* and *P. leucomystax* by a narrower head with vertical lores, smaller digital discs and free fingers.

Striking differences between *P. taeniatus* and *P. l. sexvirgatus*:
- Liu (1950) mentioned a small, but distinct outer metatarsal tubercle for *P. l. sexvirgatus* which is absent in *P. taeniatus*.
- According to Inger (1966) *P.l. sexvirgatus* has no dark lateral stripe covering the tympanum. This is in contrast to *P. taeniatus* which shows a totally dark tympanum.
- Differences are also recognizable concerning size. Okada (1966) mentioned two specimens of *P. l. sexvirgatus* with a SVL of 58.0 respectively 60.0 mm and the illustration in original size of van Kampen (1923) measures 65.0 mm. Own measurements on *P. taeniatus* yield a SVL from 31.2 to 35.0 mm for mature males and 40.7 mm for a gravid female. Ray (1991) gives an SVL of 35.0 to 38.0 mm for males and 42.0 to 45.0 mm for females of the Uttar Pradesh populations. In Boulenger (1906) a SVL of 47.0 mm is mentioned for a specimen which, regarding its size, must be considered a female..
- According to Anderson (1871), Liu (1950), Taylor (1962) and Inger (1966) *Polypedates leucomystax sexvirgatus* shows dark cross-bars on the legs and arms, and bars or spots on fingers. None of our specimens possesses such markings. The extremities are of a uniform brown basic colour, scarcely spotted with a somewhat darker brown. Furthermore Liu (1950) described the posterioventral area of the thighs, as intensely marbled with yellowish brown, a character lacking in our specimens.
- The absence of a supratympanic fold in *P. taeniatus* is striking. For *Polypedates leucomystax sexvirgatus*, Liu (1950) mentioned a sharply defined skin fold, van Kampen (1923) described a fold above the tympanum, Inger (1966) reported of a narrow dermal fold running horizontally from the eye above tympanum to behind the arm, and Okada (1966, fig. 51b) illustrated a distinct, well developed supratympanic fold.

### ”Striped” form occuring in Bangladesh

Of great interest for the present investigations is a frog mentioned in the report on the

„Wildlife of Bangladesh“ by Khan (1982). In his checklist Khan (1982, pl.10 h) shows a picture of a frog which belongs without doubt to the same species (*P. taeniatus*) which was collected by Maskey, Schleich and later on by Schleich and the author in Nepal. The illustrated frog is identified as „*Rana tytleri* (cf with *R. temporalis*)“ by Khan (1982) and a common status and a wide distribution is also mentioned for it. As to my knowledge Frost (1985) and Duellmann (1993) supply the most comprehensive species list but even there an amphibian species with the valid scientific name *Rana tytleri* could not be found. Boulenger (1882 and 1890) mentioned *Rana tytleri* for Burma and Bengal and described two distinct metatarsal-tubercles (the inner one prominent and large) and transversely barred legs. This is clearly distinct from the present material. Some years later Sclater (1892) synonymized *Rana tytleri* with *Rana nigrovittata* (Blyth, 1856) after examinations of the type of *Limnodytes nigrovittatus* Blyth, 1856. Due to morphological characters the present Nepalese material can clearly be distinguished from *Rana nigrovittata* using the original description and that of Manthey & Grossmann (1997). Khan`s (1982) „*Rana tytleri*“ is regarded as an misidentification of *P. taeniatus*. Therefore the range of this species probably extends to Bangladesh.

## Conservation

Ray (1991) recommended the inclusion of *P. taeniatus* into Schedule I of the Wildlife (Protection) Act of India. Regarded as dangerous for the populations of this rare rhacophorid is the destruction of wet grassland areas by conversion into agricultural land, and the practices of burning dry grassland during summer. The fact that Ray (1991) could record specimens only in the Dudwa National Park, India and the present Nepalese material originating from Royal Chitwan National Park and Koshi Tappu Wildlife Reserve shows that this rare species seem to take refuge in protected areas as National Parks and Wildlife Reseves of these countries. This indicates the importance of those areas not only for endangered spectacular mammals, but also for the more neglected but nevertheless severely endangered amphibian fauna. Protection measures are also required for the Nepalese populations of *P. taeniatus*.

## Acknowledgements

The Volkswagen-Stiftung, Germany is gratefully acknowledged for financing the field activities of the project ”Natural History of the Amphibians and Reptiles of Nepal”. Furthermore C.C. Anders thanks the DAAD, Germany, for providing funds for travel and stay in Nepal, and the University of Munich which gave financial support by granting a scholarship (HSP II). C.C. Anders is also grateful to the Zoological State Collection (ZSM), Munich for having a working place and access to the library.

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# Studies on the Biology of the Genus *Sitana* (Sauria: Agamidae)

## Description of *Sitana sivalensis* spec. nov. from South Nepal

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**Key words**: Reptilia, Agamidae, *Sitana*, Nepal.

**Abstract:** A new form of the agamid genus *Sitana* with a very small gular fan is described. Only adult males can be readily identified as their enlarged midgular scale row does not reach the venter. This morphological character contrasts with all other *Sitana* forms hitherto known and shows that the signal structures within the genus have evolved in a very different degree. This is the first confirmed record of a *Sitana* for Nepal.

The genus *Sitana* is not monotypic as is emphasised in most revisions of agamids. This wrong point of view is due to the great variability range of head and body pholidosis which makes conventional methods rather inapproriate to separate the different forms. But head scale counts show that *Sitana minor* Günther, 1864 is different from other forms of the *Sitana ponticeriana* complex.

### Introduction

Up to our days (Manamendra-Arachchi & Liyanage, 1994; Erdelen, 1996) the genus *Sitana* is mostly considered as monotypic, with *Sitana ponticeriana* Cuvier, 1829 as the only recognised species, in spite of the fact that additional species have already been described in the last century: *Sitana minor* Günther, 1864 and *Sitana deccanensis* Jerdon, 1870. But Boulenger (1885) lumped them into one species.

One reason for the difficulties of intrageneric taxonomy in *Sitana* is the great variability of pholidotic characters even within one population. The two new Nepalese forms described in this volume are separated from „*S. ponticeriana*“ beyond any doubt as their males have tiny gular fans. But it is impossible to separate them from their large-fanned „*ponticeriana*“ congeners by simple pholidotic characters others than the gular scalation. As a consequence only males can be identified.

The observations on *Sitana fusca* (same volume), the second small-fanned Nepalese form, have shown that morphologically similar forms can differ essentially in social behaviour which evidently evolved more rapidly than pholidotic characters.

For practical reasons we still use the denomination „*Sitana ponticeriana*“ being aware that in reality we have to do with a badly studied complex of several forms.

Since Swan & Leviton (1962) listed *Sitana ponticeriana* in their herpetology of Nepal as occurring in „adjacent plains“ (p. 138) and „possible for West, Central and East Nepal", the

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genus *Sitana* appears, mostly in brackets (Schleich 1993), as a constituent of the Nepalese herpetofauna. The quotation of „adjacent plains“ means that a species was found in the North Indian plains within 50 miles from the Nepalese borders. Moody (1980) also includes southern Nepal in the range of this species. Swan (1993) mentions it for the Darjeeling - Sikkim region.

There is still no record of *Sitana ponticeriana* for Nepal, probably because its biotope - dry lowland regions with partially open ground - is missing, but two new species which undoubtedly belong to the same genus were found at the extreme north of the Gangetic plain and are described in this paper (parts 6 and 9).

During an excursion of the Institut für Paläontologie and Historische Geologie of the Munich University and Nat. Hist. Mus. (Technical University of Munich, sponsored by Volkswagen) a series of small agamids was caught. The absence of fifth toes and the typical dorsal pattern of triangle pairs at once revealed them as members of the genus *Sitana*. The tiny body size with a snout-vent length scarcely depassing four centimetres and the small gular fan of males (fig. 1) undoubtedly allowed to recognise them as members of a new species.

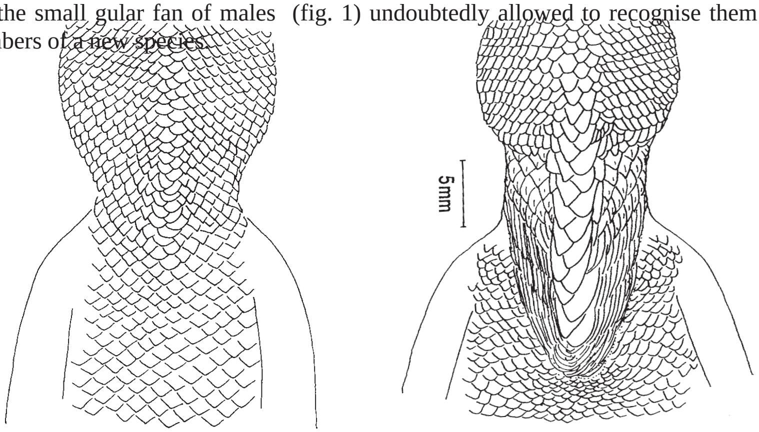


**Fig. 1.** Gular pholidosis of the small-fanned *Sitana sivalensis* male (holotype, left) compared with a large-fanned form (*Sitana minor*). The enlarged alternating fan margin scales form a midventral series. They attain the foreleg insertion in *S. sivalensis*, but midventer in *S. minor*. In the latter species they are much longer and form a fringe around the ventral side of the expanded fan (see also following article, fig. 13-15).

## Material and Methods

From seven juveniles caught near the Suraj Khola (khola = river), West Nepal, five could be reared to adulthood and successfully bred. Their offspring of five females was again reared to adulthood, thus enabling us to record much of the social behaviour, reproductive biology and ontogenesis of the new species (see following article).

Type material: Fuhlrott-Museum, D-Wuppertal; holotype adult male (VW/D- 95/1), paratypes 1 adult male, 5 adult females (VW/D- 95/2-7). More topotypes are deposited in the Natural History Museum (TU) at Kathmandu (VW/KTM).

**Systematic account**

Type locality (fig.2): Along the road (near the margin of Light Sal Wood vegetation) between Shivpur (Shivapur) and Bankas near the Surai Khola in southern West Nepal (Lumbini Zone, Kapilbastu District).

Geographic coordinates (by GPS): N 27°43’17" / E 82°50’40" ; 316 m above sea level (note discordance with contour lines on map!).

The coordinates of the Lamaki dry region (see map, upper left) are N 27°51’46" / E 82°38’22"; elevation 316 m.

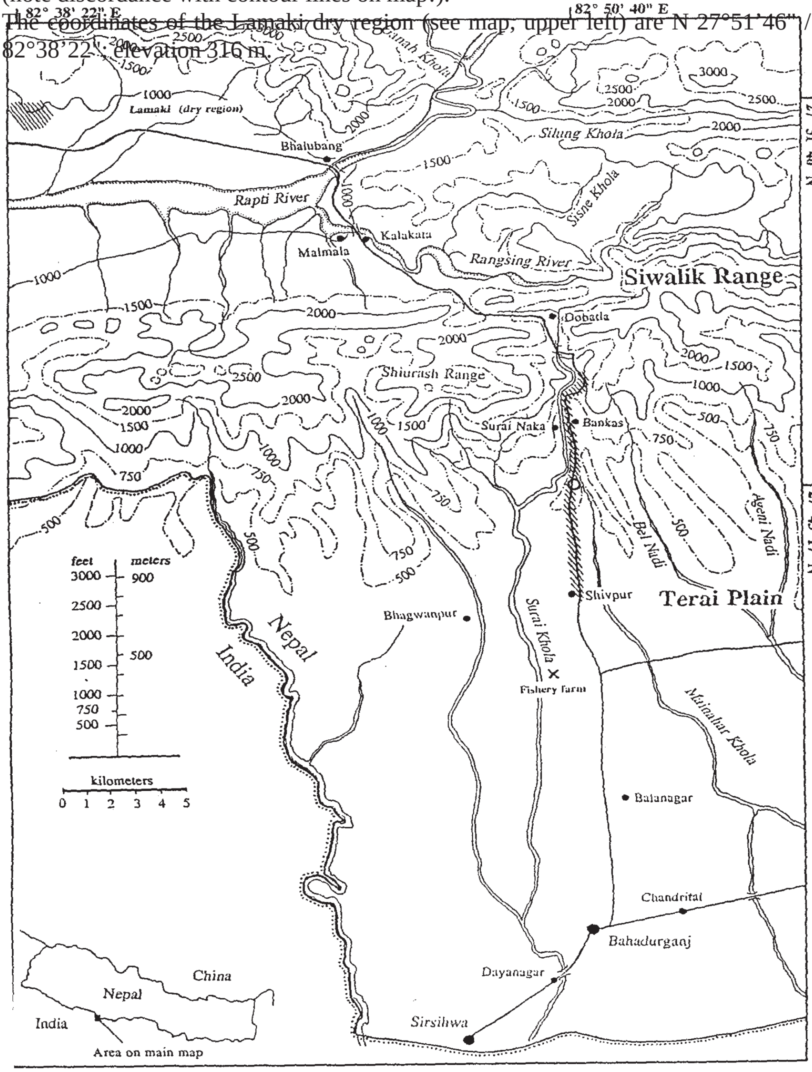


**Fig. 2.** Position of type locality (circle south of Bankas) within the type area along the road north of Shivpur (hatched). Another very sparse population was recorded from the Lamaki dry region (on map at upper left, hatched). Elevations in feet.
Etymology: Named after the Siwalik Range in S Nepal at the southern margin of which the lizards were caught (see Zool. Nom. Code: the ending „-ensis“ is used for the latinized indication of provenience). The name *Sitana* is related to Hindu mythology as Sita is the wife of Lord Rama.

Diagnosis: A tiny *Sitana* species with a snout-vent length of little over four centimetres. The very small gular sac of males ends between the forelegs and not in midventer as in the hitherto known *Sitana* species.

## Description

The holotype, an adult male, was caught as a juvenile at an age of at most one month in September 1994. When he died on July 4, 1995 his age can be estimated at 11 months. The six paratypes, one male and five females, died at estimated ages from at least one year to two and a half years (male paratype).

Biometry of types (the numbers refer to the material in Germany inventarized with VW (=Volkswagen) access dates:

Explanations for measurements:

Head length: snout tip to posterior border of tympanum
Head width: at largest temporal region
Forelimb length: axilla to tip of longest finger without claw
Hindlimb length: groin to tip of longest toe without claw
Foot length: heel to longest toe without claw

| | Holotype male | Paratypes females | | | | | male |
|---|---|---|---|---|---|---|---|
| VW/D | 96/1 | 96/2 | 96/3 | 96/4 | 96/5 | 96/6 | 96/7 |
| Snout-vent length (SVL, mm): | 39.45 | 44.5 | 39.1 | 38.4 | 40.5 | 37.5 | 38.3 |
| Tail length (mm): | 80.3 | 77.9 | 73.9 | 70.55 | 73.5 | - | 84.2 |
| Relation tail length : SVL: | 2.035 | 1.75 | 1.89 | 1.84 | 1.81 | - | |
| 2.20 | | | | | | | |
| Head length (mm): | 10.25 | 11.5 | 10.71 | 10.7 | 11.5 | 10.6 | 11.5 |
| Relation SVL : head length: | 3.84 | 3.87 | 3.65 | 3.59 | 3.52 | 3.54 | 3.33 |
| Head width (mm): | 7.5 | 8.7 | 7.4 | 7.8 | 8.6 | 7.5 | 8.3 |
| Relation Head length : width : | 1.36 | 1.32 | 1.78 | 1.37 | 1.33 | 1.41 | 1.39 |
| Forelimb length (mm): | 16.5 | 16.5 | 15.1 | 16.0 | 16.6 | 14.9 | 16.6 |
| Hindlimb length (mm): | 31.9 | 37.8 | 35.5 | 34.2 | 35.6 | 28.3 | 34.7 |
| Relation hindlimb:forelimb length: | 1.93 | 2.29 | 2.35 | 2.14 | 2.14 | 1.90 | 2.09 |
| Relation SVL : hindlimb length: | 1.24 | 1.17 | 1.1 | 1.12 | 1.13 | 1.33 | 1.10 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Foot length (mm): | 14.8 | 14.3 | 13.9 | 14.6 | 13.4 | 12.6 | 13.8 |
| Heel to 2nd. longest toe (mm): | 10.5 | 9.4 | 10. | 9.45 | 9.8 | 9.0 | 10.4 |

| **Body/leg proportions:** | **holotype** | **paratypes** | | | | | |
|---|---|---|---|---|---|---|---|
| | male\| VW/D | females | | | | | male |
| | 95/1 | 95-2 | 95-3 | 95-4 | 95-5 | 95-6 | 95-7 |
| If the forelimb is plied forward | | | | | | | |
| most finger insertions reach the snout | X | | | | | X | |
| two longest fingers depass the snout | | X | X | | | | X |
| the longest finger reaches the snout | | | | X | X | | |
| If the forelimb is plied backwards | | | | | | | |
| the longest fingers reach the groin | X | | X | | | | X |
| the claw of longest finger is 1 mm from groin | | X | | | X | | |
| the claw of longest finger is 2 mm from groin | | | X | X | X | X | |
| If the hindlimb is plied forward | | | | | | | X |
| the longest toe depasses the snout | | | | | | | |
| the longest toe reaches the nostril | X | | X | | | | |
| the longest toe reaches between eye and nostril | | X | | | | | |
| the claw of longest toe does not depass the orbit | | | | X | X | X | |

**Pholidosis**

Pileus (fig. 3,8):

Scales feebly imbricate, unequal, rounded polygonal, obtusely keeled, normally with one keel, parietal with two; arrangement irregular; 11-12 scales between orbits (between supraoculars); 8 scales between parietal (small scale with parietal eye) and supraocular; 12 scales between rostral and parietal ; no distinct occipital spines, but several occipital scales are conical.

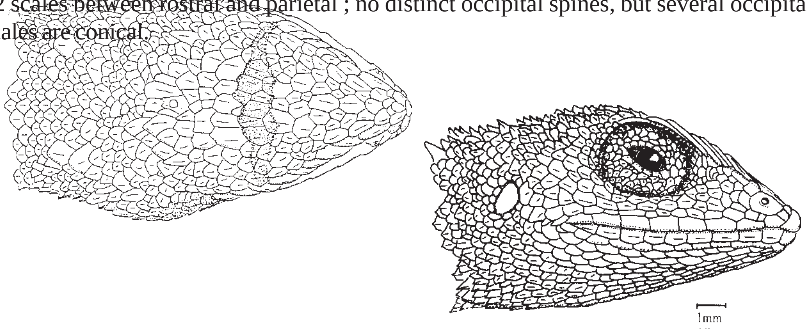


**Fig. 3.** Head pholidosis of *Sitana sivalensis*, holotype male.

Head sides: (fig. 3, 4):

Anterior part of nasal in contact with first supralabial; three rows of elongate scales between orbit and supralabials; supralabials (left/right): 8/8; infralabials: 8/9; 6 large scales counted in one row between orbit and tympanum.

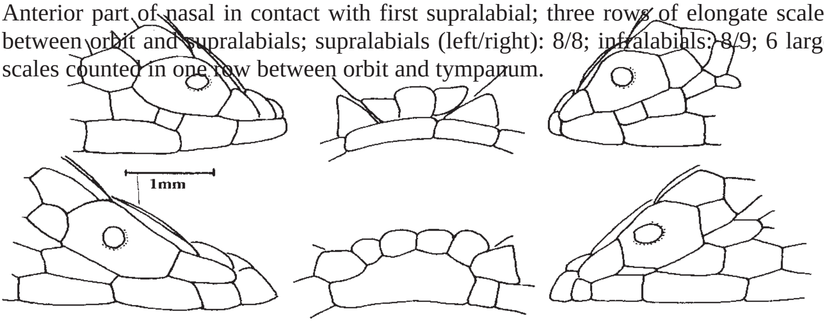


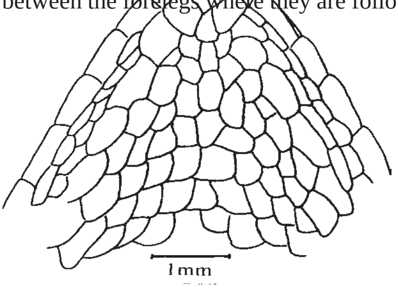
**Fig. 4.** *Sitana sivalensis*, pholidosis of nasal and rostral regions, above holotype male, below a topotype female. Note the intraspecific variability and the asymmetries of the head sides.

Ventral side of head (fig. 5):

A pentagonal mental is followed by three postmentals, the central one smaller; 1-2 rows of elongate scales between infralabials and larger gulars.

All scales of the gular fan keeled (fig. 6), gradually increasing towards the midgular line, where they largely overlap. The enlarged gular fan scales end abruptly between the forelegs where they are followed by those of the smaller ventrals.

**Fig. 5** (at left). *Sitana sivalensis*, pholidosis of the mental region (holotype).



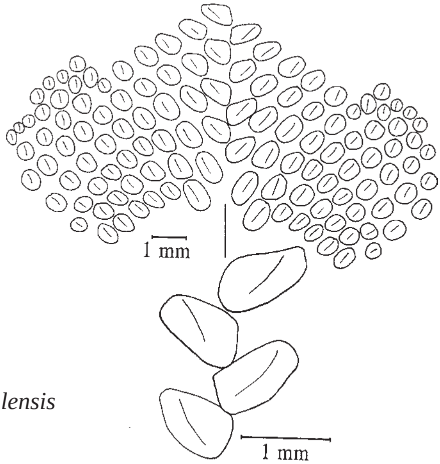


**Fig. 6** (at right). Fan scales of *Sitana sivalensis* male in a skin shedding stretched flat.
It shows the pholidosis of both fan sides

in distended state with the skin between the scales visible. In the living male the vertical midventral line forms the margin of the expanded fan.

Body scalation (fig. 7):

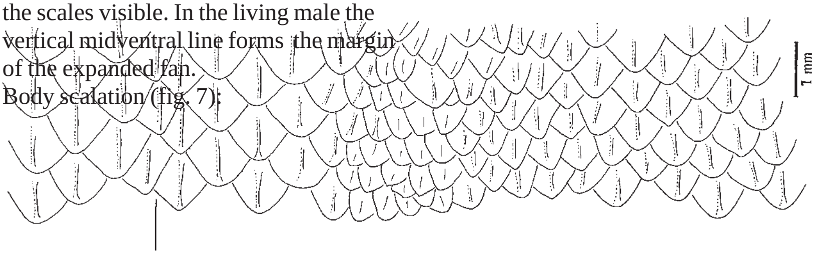


**Fig. 7.** Body scalation of *Sitana sivalensis* holotype male at midtrunk around the right body side from middorsum (marked by line) to the ventral region. Note the very irregular lateral scalation and the gradual transition from lateral to ventral scales

Nuchal crest (roach) faintly indicated; no dorsal crest.

Dorsalia (fig. 7) subtriangular, rounded with sharp keels, not mucronate, regularly arranged, in 8-9 longitudinal rows. Most of the scales in the two median (vertebral) rows are smaller than the lateral ones.

The lateral scales are, in contrast to the dorsals, irregular, of very unequal size, most of them much smaller than the dorsals, oval and obtusely keeled.

Interspersed larger scales are of threefold length and width, with prominent keel.

Ventralia regular, obtusely keeled, with indistinct transition zone to lateralia. The scale form varies between „triangular with straight sides and rounded tip“ and „ subtriangular with rounded sides“.

Limbs: The scales on the ventral side of feet - from heel to toe tip - bear sharp tips which must be interpreted ad scansorial adaptations. This fact indicates an arboreal origin of the genus, which was also concluded by Moody (1980).

Tail: The scales around the thickened tail base have rounded apical ends, those from the rest of the tail have triangular tips. All scales are sharply keeled with the keels of subsequent scales forming continuous ridges along a part of the tail. With decreasing tail circumference the number of ridges diminishes.

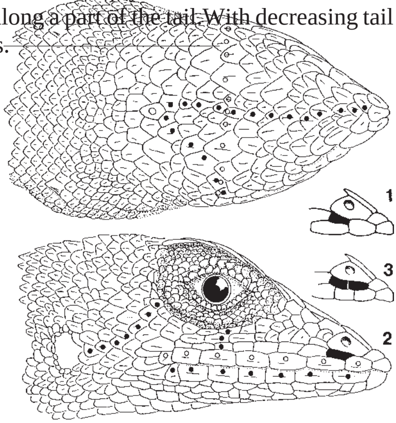


**Fig. 8.** Scale counts used in following table :

1. Scales between supraoculars (lowest number counted, small circles)
2. Scales between parietal and supraocular, left / right (dot row)
3. Scales between parietal and rostral
4. Number of supralabials, left / right
5. Number of infralabials, left / right
6. Number of scale rows between supralabial and orbit, left / right
7. Number of large scales between tympanum and orbit, left / right

8. Contact between nasal and 1st supralabial: 1 total; 2 partial; 3 separated, left/right
9. Dorsalia longitudinal rows (lowest number counted at midtrunk)

| | holotype<br>(male)<br>VW96/1 | paratypes<br>(females)<br>96/2 | 96/3 | 96/4 | 96/5 | 96/6 | (male)<br>96/7 |
|---|---|---|---|---|---|---|---|
| 1. orbit - orbit | 12 | 11 | 12 | 12 | 12 | 13 | 11 |
| 2. parietal - orbit | 8/7 | 6/6 | 7/7 | 7/7 | 8/8 | 6/6 | 6/6 |
| 3. parietal - rostral | 12 | 11 | 11 | 12 | 12 | 11 | 13 |
| 4. supralabials | 8/8 | 8/8 | 9/9 | 9/8 | 9/10 | 9/9 | 10/9 |
| 5. infralabials | 8/9 | 8/9 | 9/8 | 9/9 | 9/9 | 9/8 | 10/8 |
| 6. supralabial - orbit | 2/3 | 3/2 | 3/2-3* | 3/3 | 3/3 | 3/3 | 3/3 |
| 7. tympanum - orbit | 8/8 | 7/7 | 8/7 | 8/8 | 8/7 | 6/7 | 7/7 |
| 8. nasal - supralabial | 2/1 | 1/1 | 1/2 | 1/1 | 1/2 | 1/1 | 1/1 |
| 9. dorsalia rows | 8 | 8 | 10 | 8 | 8 | 11 | 8 |

* means at an intermediate state

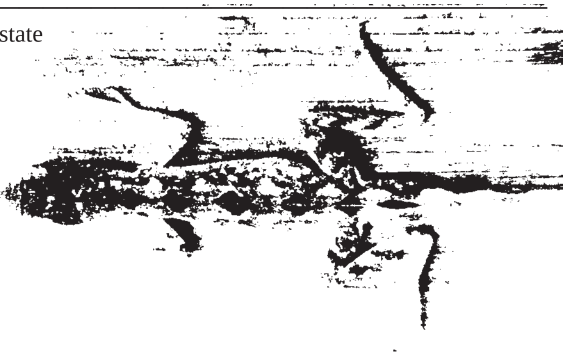


**Fig. 9.** Holotype male, dead from social stress.

## Colour pattern

As the male died during the reproductive phase from social stress its colour pattern (fig. 9) is different from the normal state, at which both sexes resemble each other (fig. 12; see also part 8, paragraph 3.1). The basic pattern corresponds to the standard of the whole genus and comprises the following elements:

1. A dorsal pattern of five dark rhombi (one each at the limb insertions and three between them) which are more or less divided lengthwise by a narrow light vetrebral line.
2. A light line on each side which delimits the dorsal region. It runs inside the outer margin of the dorsalia scales.
3. A dark prefrontal (interocular) triangle the base of which faces forward
4. A light triangle at each hindleg insertion in the angles between the femurs and the tail for which the term „inguinal mark“ is proposed.

With the exception of the inguinal marks all these pattern elements are present in slightly altered form in the related *Otocryptis wiegmanni* (according to Moody, 1980, *Otocryptis* is a sister genus to *Sitana*) and must therefor be considered as phylogenetically old.

Head: Upper side of anterior head sepia brown with the prefrontal (interocular) triangle almost black and bordered with a faint light line. Eyelids whitish gray with large diffuse spots of ultramarine blue. The same vivid colour forms a vertebral streak within the first dorsal rhombus and divides it lengthwise.
When the nuchal roach of the animal is erected the ultramarine streak runs along its upper

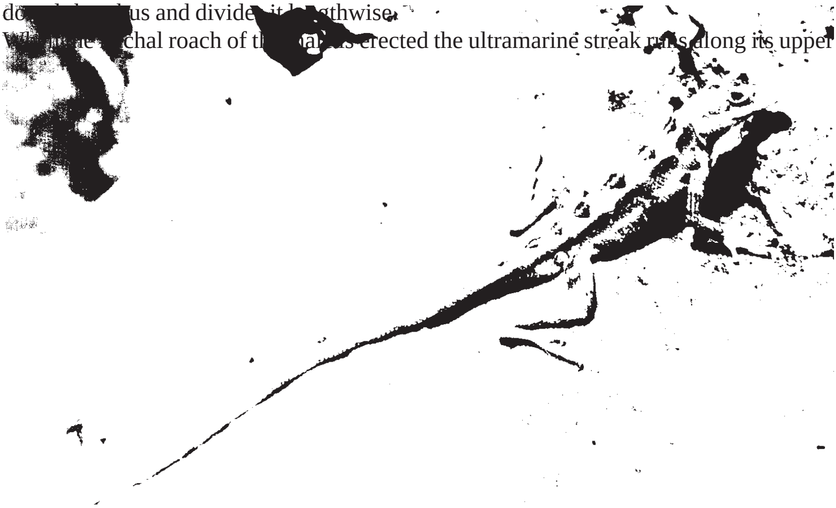


**Fig. 10.** Alert male in the biotope; note the bluish gray eyelids.

rim. Anterior to it the interstices between the dorsal scales are marked as faint blue lines. The dark sepia colour of the head becomes lighter towards the occiput and the upper lips. The supralabials are marked with a dark brown spot each. In the regions anterior and posterior of the tympanum groups of scales are of a diffuse white.

Upper side of body: The dorsal rhombi are dark sepia brown with light ochre margins which partially lack. A light brown vertebral line divides the rhombi into two isosceles triangles with exception of the first one, which is divided by the ultramarine line as mentioned above. The lateral angles of the rhombi are marked with diffuse gray which is most extended at the third rhombus.
The dorsal region between the dark triangles and the upper flanks is of a grayish brown which towards the venter gradually fades into a grayish white. Diffuse ochre dorsolateral patches are located at the interstices between the triangles. The enlarged flank scales are grayish white over most of their surface. This colour changes into pure white towards the scale keels, rims and tips.

Limbs: Their upper sides are grayish brown with proximal patches of ochre and with darker transverse bands which become pale and narrow towards the fingers and toes. The inguinal mark at the angle between the hindlegs and tail base is light grayish brown.

Tail: The middorsal rhombi are replaced by oblong patches, the first of which is dark and bordered with light ochre. The subsequent ones are lighter and less contrasting, fading towards the middle of the tail. The interstices between the dark spots are diffuse light ochre, flanked by light gray.The posterior half of the tail shows a faint dark and light annulation which fades towards the tip.

Ventral side: A dark gular streak of different width runs from the chin backwards to level of the foreleg insertion where the gular fan ends (fig. 11). The white gular sides are dotted with grayish brown.
A clo[illegible] shows th[illegible] dark stre[illegible] is com[illegible]
da[illegible] ari[illegible] blue[illegible] rply de[illegible] Poste[illegible]
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**Fig. 11a.** Throat region of male with dark streak. **11b.** Male with extended throat fan.

blotch which extends backwards between the forelegs. When the fan is extended (fig. 11b) a compact blue streak marks its anterior margin, while the brownish colour appears in dots on the [illegible] epa[illegible]
network of the extended interscala[illegible]
The venter is uniform white.

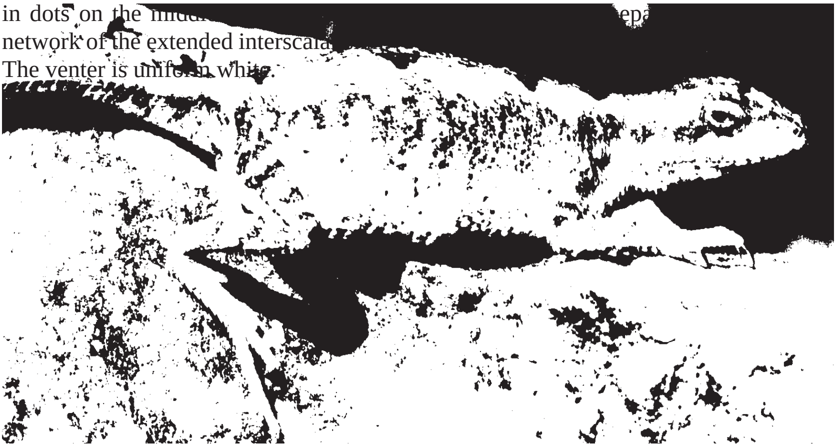

**Fig. 12.** *Sitana sivalensis,* gravid female.

## Description of paratypes VW/D 96/2-7

### Pholidose:

Individual variability is moderate on the body parts with a rather homogeneous pholidosis, e.g. on the dorsal field; it is strongest where the pholidosis is extremely heterogeneous, e.g. on the head and flanks. The variability around the nasal or rostral region (fig. 4) is so divergent that in other lizard genera the differences would be sufficient to characterise different species. No pholidotic character besides gular scalation was found which allows to separate *S. sivalensis* and *S. fusca* females without any doubt.

Within the dorsal field the scalation of the vertebral rows varies between „single small scales“, over „mostly a double row of small scales“ to „a complete double row of small scales“, a condition which seems to prevail in juveniles.

The ventral scalation is never absolutely uniform and changes from “triangular with rounded tips“ to „rounded“ with all intergrades.

**Colour pattern** (fig. 10,12):

The basic pattern elements are principally the same as in the holotype, but the colour pattern is rather plain in shades of brown. The basic colour of the pileus, the back and flanks as well as of the upper side of the tail is light grayish brown. The somewhat darker brown dorsal rhombi are not composed of triangles as in the holotype male (no reliable sex character) but consist of V-shaped halves, the interior of which is somewhat lighter.The brown prefrontal triangle is framed by a light line which is bolder on the posterior margin. The prefrontal bar and the dorsal rhombi are generally subject to great individual variability (following p. 121, fig. 6,7), but do not change their colour. They can be arranged symmetrically and asymmetrically. The halves of the dorsal rhombi can be angular or, much rarer, bell-shaped with a rounded tip. There are intermediary forms of both types, also combinations of both in one lizard. In cases of strong asymmetry there can be small rudimentary, eventually surplus marks (see following article, fig. 6).

The light grayish brown vertebral line is weakly expressed over all of its length. The light gray dorsolateral lines are widened where they approach the lateral angles of the rhombi.

The dorsal sides of the limbs are light brown with darker transverse bands.

On the dorsal side of the tail oblong dark spots fade until they disappear halfway to the tip. In its posterior half the tail bears light annuli.

The white ventral side shows some blackish spots which are smaller than the extent of a scale.

Examples for major individual variabilities: A female had large orange dorsolateral blotches (see article p. 121, fig. 11b,c) which were much more intensely coloured than in the other females.

Another captivity-bred female was always much darker than her siblings. When they reached adulthood the difference disappeared. This change was independent of the social status, which remained the same superior one all the time.

## Comparison with *Sitana ponticeriana*

The classic taxonomy which is mainly based on the evaluation of pholidotic characters is an inadequate tool to handle the forms which until today are collectively called *Sitana* *ponticeriana*. But striking differences in body size and gular fan morphology contradict today's view which assumes a single species with several subspecies. Therefore we think it necessary to mention the collection locality, if possible, in the following text.

## Systematic evaluation of pholidotic characters

Scale morphology and counts seem of limited use to separate *Sitana* forms for the following reasons:

1. Scale counts (number of longitudinal dorsalia rows, of enlarged lateral scales and of occipital spines) and morphology (expressivity of keels, scale form, size differences between small and large scales, fig. 15) vary between members of the same population.
2. Even *Sitana sivalensis*, which is doubtlessly a separate species, has most of its pholidotic characters in common with the species of the *S. ponticeriana* group.
3. The form of head scales changes strikingly from the hatchling to the adult state (see also part 7) so that age classes have different pholidotic characters!

Comparison of some pholidotic data of *Sitana* forms (counts and numbers corresponding to those in fig. 8):

| *Sitana* forms | *sivalensis* | *fusca* | *ponticeriana* | | *minor* |
|---|---|---|---|---|---|
| | | | Ceylon | Orissa | Madras |
| | | | (Palatupana) | fig.13 | fig. 14 |
| 1. orbit - orbit | 11-13 | 10-13 | 10-11 | 11-13 | 10-**18** |
| 2. parietal - orbit | 6-8 | 5-7 | 5-8 | 5-8 | **9** |
| 3. parietal - rostral | 11-13 | 10-12 | 10-13 | 10-14 | 12-**16** |
| 4. supralabials | 8-10 | 7-9 | 7-9 | 7-9 | 8-**12** |
| 5. infralabials | 8-10 | 7-9 | 7-10 | 8 | 7-**12** |
| 6. supralabial - orbit | 2-3 | 2-3 | 2-3 | 2 | 3 |
| 7. tympanum - orbit | 7-8 | 5-7 | 5-7 | 7-8 | **10** |
| 8. nasal - supralabial | 1-3 | 1/2 | 2/3 | 2 | **3** |
| dorsalia rows | 8-11 | 8-9 | 8-10 | 8-11 | **7-13** |

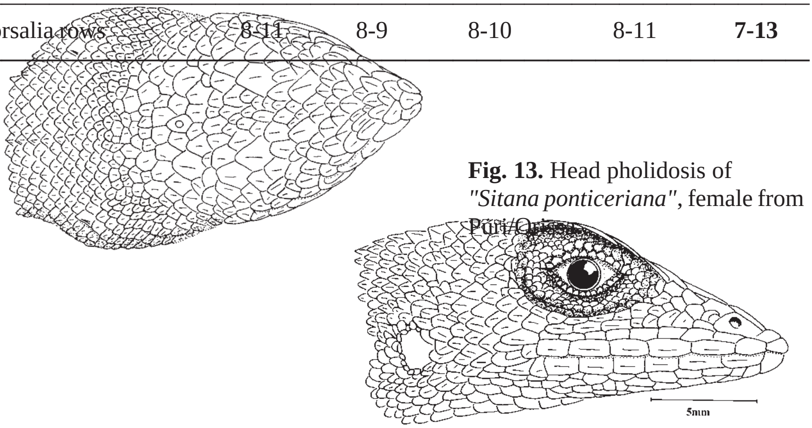

**Fig. 13.** Head pholidosis of *"Sitana ponticeriana"*, female from Puri/Orissa.

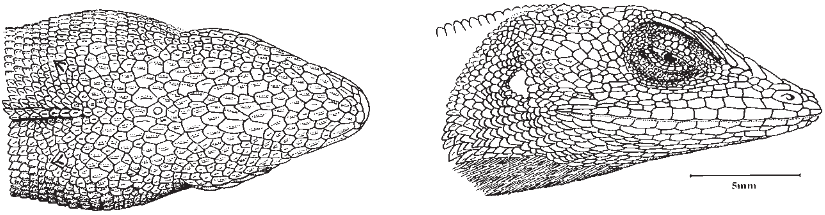

**Fig. 14.** Head pholidosis of *Sitana minor* (male) with markedly higher scale counts. The species is very robust in comparison with other Sitana forms (male, BMNH 1946.8.27.4)

As this comparison is based on a few specimens, methods of statistical analysis cannot be applied.

But the broad overlaps of scale counts show that they are useless to identify single specimens with the exception of *Sitana minor* which me must considered a taxon which is distinctly separated from the rest of the *ponticeriana* group.

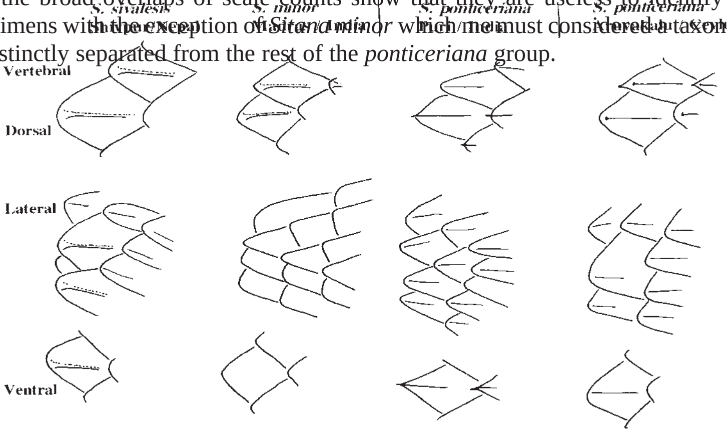

**Fig. 15.** Dorsal, lateral and ventral scales of different *Sitana* forms. The apparent interspecific differences are in reality individual variations.

## Discussion:

The discovery of *Sitana sivalensis* has shown the inadequacy of scale morphology and counts as tools for the intrageneric taxonomy of the genus *Sitana*. Evidently these characters are rather irrelevant for selection, and speciation within the genus may have been rather rapid and recent. As part 8 on the biology of this species will show, the communication system evolved in striking divergence within the genus. Courtship signals and mating behaviour play an essential role as reproductive isolating mechanisms, and the study of signal organs (structure and colour pattern of the gular fan) and signal acts could become useful tools to deal with *Sitana* taxonomy.

Under these circumstances it is highly recommendable in future studies on the *S. ponticeriana* - complex to take the morphology of the gular fans and - as far as possible

- signal behaviour into consideration. Morphologically well characterised forms e.g. „*Sitana ponticeriana minor*" Günther, 1864 are candidates for a re-evalidation as full species.

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# Studies on the Biology of the Genus *Sitana* (Sauria: Agamidae)

## SEM Studies on the Morphology of *Sitana sivalensis* spec. nov. and *Sitana ponticeriana* Cuvier 1829

H.Hermann Schleich* & Werner Kästle**

**Key words**: Reptilia, Agamidae, *Sitana*, pholidose, dentition, eggshell structure.

**Abstract:** Scale surfaces show the alveolar microstructure which has been found in all agamids studied hitherto. During adolescence the alveoles retain their original diameter of about 20 μ, but increase in number. The head pholidose undergoes an ontogenetic change from imbricate rounded scales to juxtaposed polygonal plates. The heterodont dentition consists of pleurodont conical incisoroids and caninoids which are replaced, and of permanent subpleurodont („acrodont“) tricuspid molariforms. Five of them are of a premolaroid type in the *S. sivalensis* hatchling. During juvenile development others which are distinctly larger are added posteriorly. The structure of the *S. sivalensis* eggshell is described.

**Pholidose** (pl. 1-7)
The microstructures on scale surfaces have been extensively studied (for literature see Limberger, 1985; Schmidbauer, 1993) and were termed microornamentation, microdermatoglyphs or microarchitecture. Discussion on their ecological role (e.g. for water permeability, Lillywhite & Maderson, 1982) has partially remained speculative, but their systematic relevance has been clearly demonstrated.

The microstructures are renewed during each shedding cycle and are formed at the contact zone between the oberhäutchen (outermost homogeneous keratinized layer) and the „clear layer“ which forms the lowermost zone of the shedding. Oberhäutchen and clear layer originate as simple cell layers, but their cellular character is lost before shedding: The oberhäutchen cells form a syncytium with the underlying multi-layerd β-cells and then keratinizes; the clear layer cells lose their nuclei and also keratinize.The splitting zone which allows moulting runs between them.

The process of microstructure formation is still unknown in detail. It is accompanied by an interdigitation of oberhäutchen and clear layer, with processes of the Oberhäutchen jutting into the clear layer (Maderson, 1985). The shaping of the microstructures is thought to be influenced by at least two factors: the arrangement of epidermal cells and their surface sculpturing (Peterson, 1984).

The alveolar (honeycomb) pattern is present on most studied *Sitana* scales and was found in all agamids investigated hitherto: *Aphaniotis fusca,Ceratophora stoddarti, Cophotis ceylanica, Japalura tricarinata, Otocryptis wiegmanni, Phrynocephalus theobaldi,*

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*Pogona vitticeps, Sitana ponticeriana, Uromastyx acanthinura* (Schleich & Kästle, 1979, 1982). But this type of microstructure is by no means restricted to that family. Similar structures appear in genera of a series of squamate families (Anguidae, Gekkonidae, Helodermatidae, Iguanidae, Lacertidae, Scincidae,Teiidae, Varanidae; Elapidae, Viperidae) (Schmidbauer, 1993) where the alveoles may be very flat, oblong or tilting.

Limberger (1985) has already shown that ontogenesis has little influence on scale microstructures. Size increase does not alter the diameter of honeyomb alveoles (15-20 µ), but their number per scale increases proportionally to scale size. In comparison with the adult state the embryonal alveoles are very flat (pl. 1,2).

Gular scalation (pl. 3)

The highly evolved fans of the *ponticeriana* group (for morphology and function see following article, p.121) bear two types of enlarged scales: elongate marginal scales and broad surface scales. Both are very thin and translucent.

In the plied state of the fan all of its scales are stacked upon each other. The two median rows form an alternating double series of lanceolate marginal scales (fig. 7). When the fan is stretched the stack distends, and each scale performs a rotation of 90° to the left resp. right with the scale surfaces alternatingly facing opposite sides (for details see article on p. 121). The lateral fan scales also form stack rows in which normally only the margin of each scale is visible (at right in fig. 7). In the left half of the same figure the stack is torn apart and more of scale surfaces is visible. When the fan is expanded the two scales of fig. 8 are drawn headward (to the right) until their keels are in vertical position, and they are pulled apart, being connected only by a very thin skin. Both scales belong to two successive scale rows of the expanded fan.

The lack of alveoles on most of the surface in the normal gular scales (fig. 9) is perhaps connected with their reflexivity which is mentioned in the article on p.121 (fig. 22).

Ontogenetic change of head pholidose (fig. 10, 13, 14, 16, 19)

The change of rounded and largely overlapping scales into plates calls to mind Ernst Haeckel's „Biogenetic Law“ („ontogenesis recapitulates phylogenesis“).

In the hatchling most head scales are elongate with rounded tips, and distinctly imbricate with overlapping margins. During juvenile development the free posterior borders disappear, and the margins become subimbricate to juxtaposed. The scales are transformed into polygonal plates.

Finger pholidose of late embryo (fig. 20, 21)

In contrast to the embryonal body scalation (pl. 2) the finger pholidose appears rather advanced and similar to the adult state with very strong terminal spines and strong keels with an alveolar microstructure.

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**Plate 1.** Lateral scalation, *Sitana sivalensis.*

**Fig. 1.** Heterogeneous scalation of body sides..
**Fig. 2.** Detail from fig. 1: alveolar microstructure which lacks on the keels.
**Fig. 3.** Detail from fig. 2: surface alveoles filled with dirt particles.

# Plate 1

fig. 1

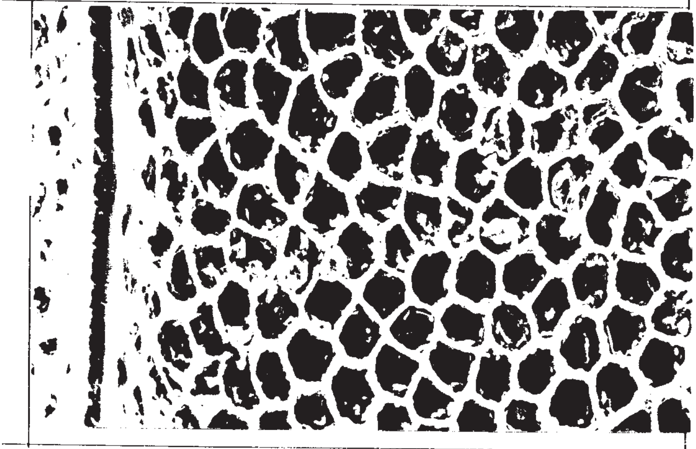

fig. 2

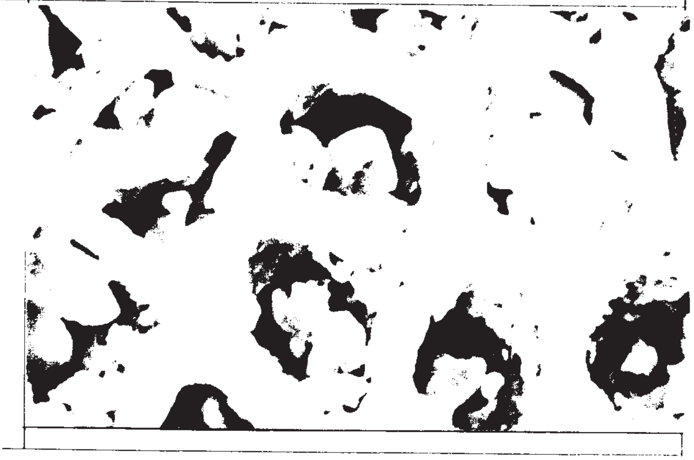

fig. 3

**Plate 2.** Scalation of late embryo, *Sitana sivalensis*.

**Fig. 4.** Regular middorsal scalation.
**Fig. 5.** Detail from fig. 4: the bristles of the tactile papillae near the scale tips are still lacking.
**Fig. 6.** Heterogeneous scalation of body sides with one large gibbous granule.

**Plate 3.** Gular scalation, *Sitana ponticeriana*, adult male.

**Fig. 7.** Double row of enlarged midgular scales which form the fringe when the fan is expanded.
**Fig. 8.** Detail from fig. 7: large and extremely thin lateral fan scales largely overlapping in resting position.
**Fig. 9.** Gular scales (not belonging to the fan) which partially lack the alveolar microstructure.

**Plate 4.** Head scalation, *Sitana ponticeriana*, adult male.

**Fig. 10.** Mouth cleft from left side with supra- and infralabials. The tips of the tricuspid maxillary teeth are partially visible.
**Fig. 11.** Detail from fig. 10: infralabial scute with four tactile papillae.
**Fig. 12.** Detail from fig. 11: insertion of the tactile bristle.

**Plate 5.** Head scalation, *Sitana ponticeriana*, adult male.

**Fig. 13.** Detail from fig. 10: most head scales are keeled and bear at least one tactile papilla.
**Fig. 14.** Parietal plate at center with the parietal organ indicated by a hump. The head scales are not fully symmetrical.
**Fig. 15.** Detail from fig. 14: center of the parietal plate with fading alveolar structure.

**Plate 6.** Head scalation of late embryo, *Sitana sivalensis*.

**Fig. 16.** Mouth cleft from left side. In contrast to the adult condition ( plates 4, 5) the scales are largely overlapping.
**Fig. 17.** Detail from fig. 16: As the alveoles are of equal absolute size in neonates and adults, they are relatively large in this stage of development.
**Fig. 18.** Detail from fig. 17: Note the clean state of embryonal alveoles in contrast to fig. 3.

**Plate 7.** Late embryonal scalation, *Sitana sivalensis.*

**Fig. 19.** The left tympanum is completely covered with alveoles.
**Fig. 20.** Hand from below, with different scale types.
**Fig. 21.** Detail from fig. 20: While parts of the body scalation may become mucronate at a more advanced age, the spines of hand scales are already well developed.

## Plate 2

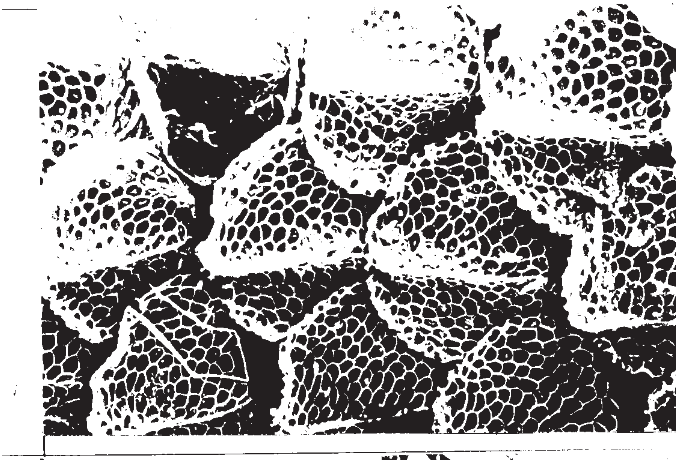

fig. 4

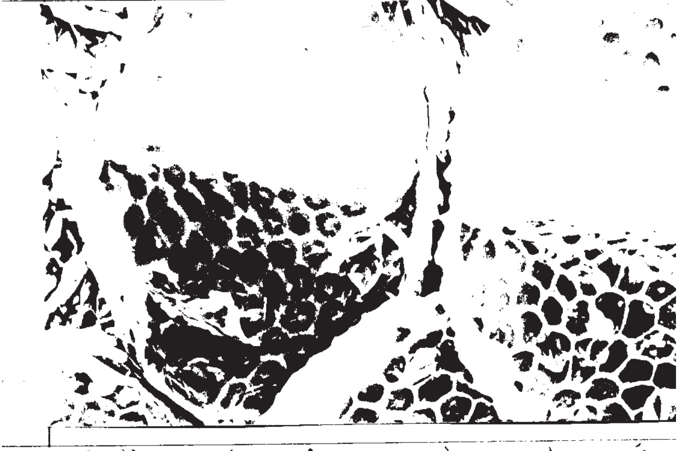

fig. 5

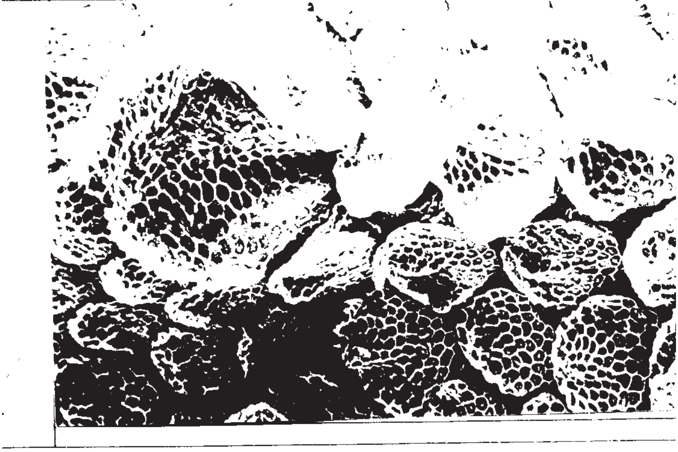

fig. 6

## Plate 3

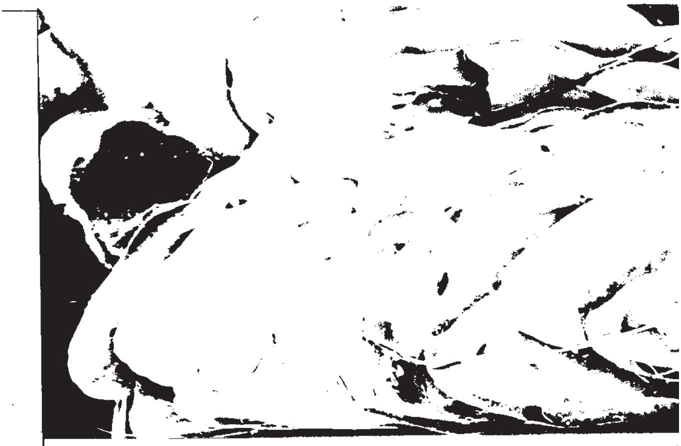

fig. 7

fig. 8

fig. 9

## Plate 4

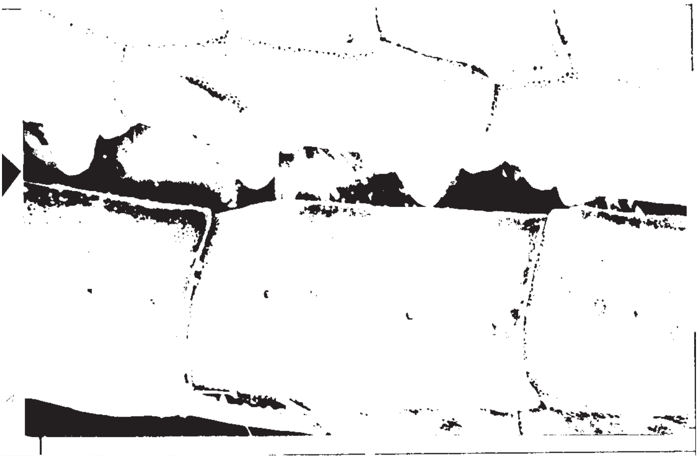

**fig. 10**

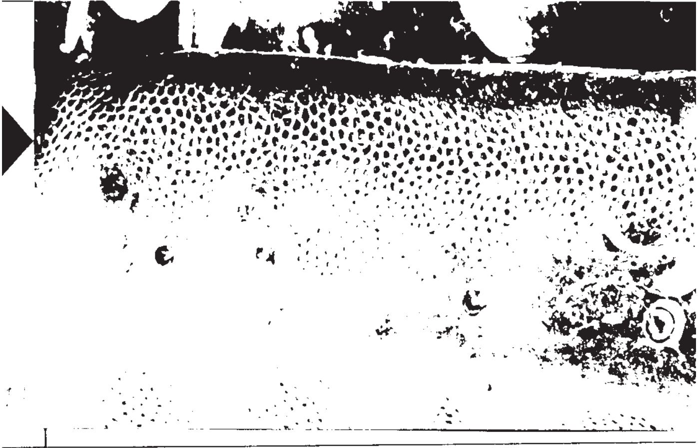

**fig. 11**

**fig. 12**

## Plate 5

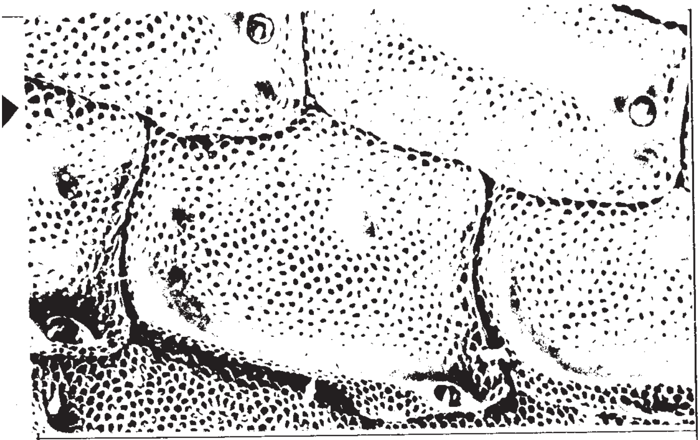

fig. 13

fig. 14

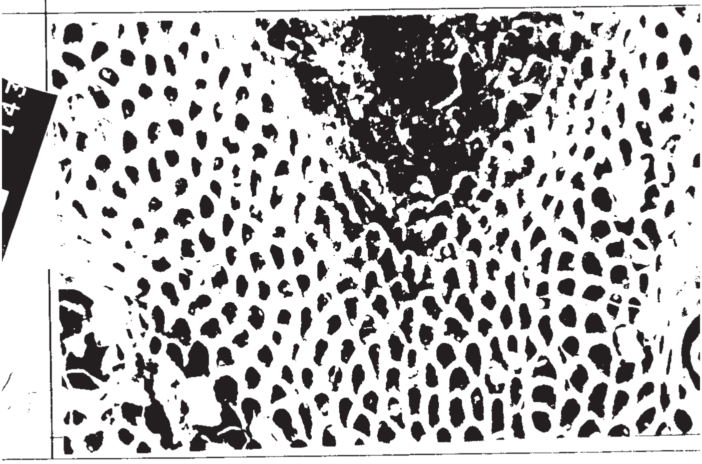

fig. 15

## Plate 6

fig. 16

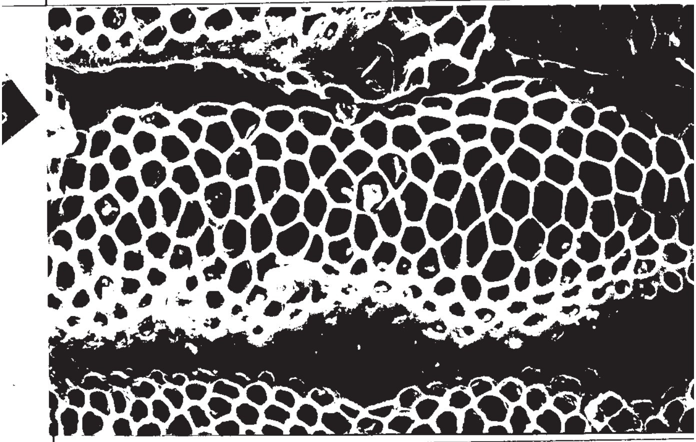

fig. 17

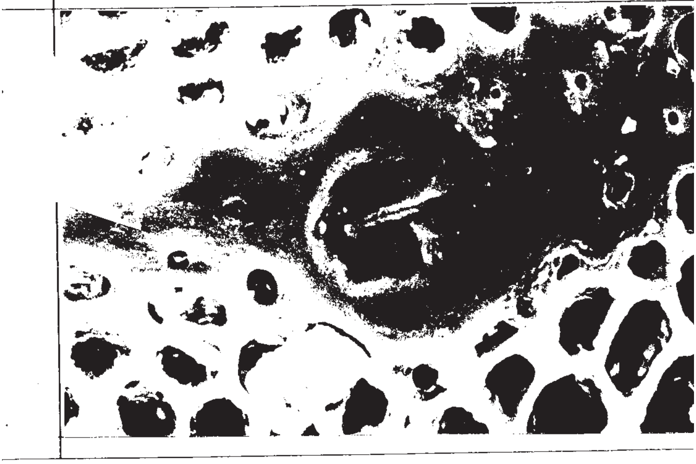

fig. 18

## Plate 7

fig. 19

fig. 20

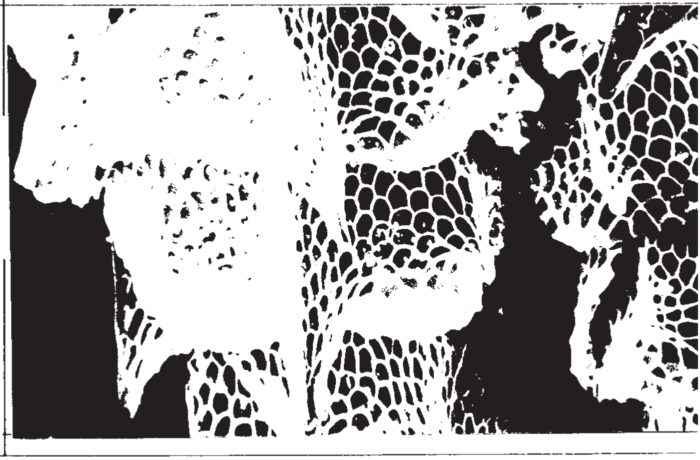

fig. 21

**Dentition** (fig. 22, pl. 8-10)

The dentition of most agamids is heterodont (fig. 22) as a few of the anterior teeth differ in size, shape and function from the rest, reminding the heterodont dentition of mammals.The smaller upper incisoroids are attached to the premaxillae and the anterior end of the maxillae.They are followed by longer caninoids and a series of larger laterally compressed and tricuspid molariforms. The differentiation of teeth on the dentary is similar. Incisoroids and caninoids are subpleurodont and subject to replacement while the tricuspid molariforms are mostly called acrodont and serve for the whole lifetime or are worn down to the bone, which then can serve as a cutting edge. Edmund (1968) and Moody (1980) have emphasized that the acrodont condition of agamids should better be called subpleurodont as the position of teeth is shifted toward the dental gutter on the lingual side of the jaw bones.

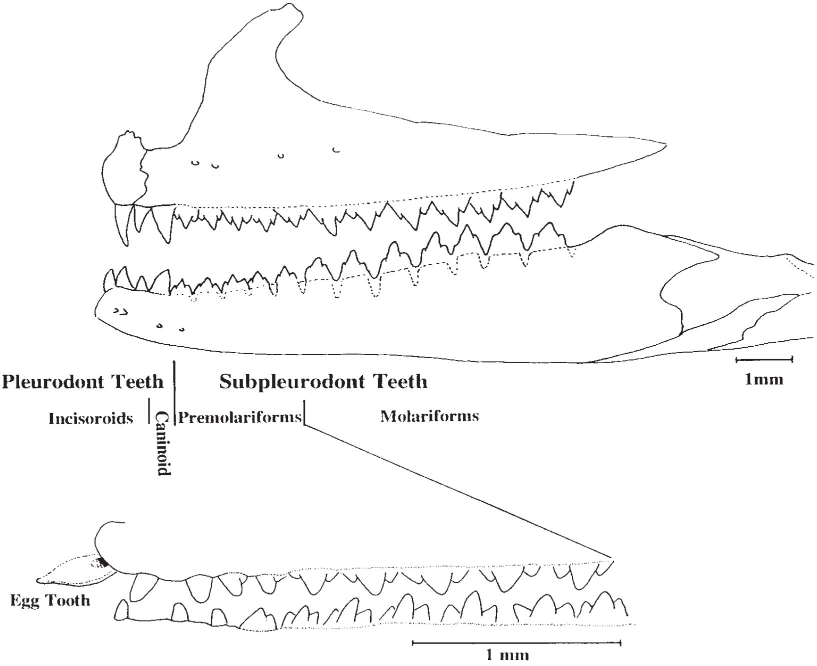

**Fig. 22.** Dentition; above: adult *Sitana ponticeriana* from Puri, below *Sitana sivalensis.* hatchling with the prominent egg tooth and the molariforms still lacking.

In *Sitana* all tricuspid teeth are heavily ankylosed to the jaw bone and among each other by a mass of enamel (fig. 23, 24, 26, 27, 30, 31), which can be discerned from the bome by its glossy appearance. As the whole row of premolariforms and molariforms forms a single solid mass the replacement of a single tooth is impossible. If the jaw bones are dissolved e.g. by a heated alkaline solution the entire tooth row can be isolated as a whole.
The lateral teeth are distinctly subdivided into two groups: smaller „premolariforms“ which are followed by the larger molariforms (fig. 22,23). The premolariforms represent the hatchling's dentition (plate 10) which persists into adulthood and is supplemented posteriorly by the successive addition of molariforms. Each new tooth becomes ankylosed to the one in front of it and to the jawbone.

Premolariforms and molariforms of maxillaries and dentaries are tilted in labial resp. lingual direction, causing a shearing overbite of the maxillary teeth. The upper rims of the dentary are exposed to the bone and subject to heavy wear by the tips of the interlocking maxillary teeth which leave deep furrows (fig. 27).

As we could not sacrifice an adult *Sitana sivalensis* to study its dentition the SEM photos were taken from a *Sitana ponticeriana* from Puri/Orissa while the hatchling dentition is from *Sitana sivalensis*. This methodically unhappy comparison leaves many questions open. Besides the lacking molariforms (which are added posteriorly during adolescence) the dentition of the *sivalensis* hatchling shows no differentiation between incisoroids and caninoids, and large gaps between the front teeth.The number of premolariforms is higher in the hatchling.

Further studies are necessary to show if these differences are due to age, specifity or individual variability.

Note on the photos of the hatchling dentition (plate 10) that pleurodont and subpleurodont teeth are not neatly monocuspid resp. tricuspid, but some of the pleurodont teeth have a small second cusp. The egg tooth is anchored in the intermaxillary and has the form of a horizontal lanceolate blade. In the hatchling a tiny tip of it protrudes from the mouth cleft below the rostral.

---

**Plate 8.** Dentition, *Sitana ponticeriana*, adult male.

**Fig. 23.** Right upper jaw, lingual view showing the heterodont condition (see fig. 22). The anterior incisoroid is broken.
**Fig. 24.** Detail from the same jaw, but in labial view.
**Fig. 25.** Detail from fig. 24 showing the tooth cavity and the trabecular structure of dentine.

**Plate 9.** Dentition: *Sitana ponticeriana*, adult male

**Fig. 26.** Fused maxillary molariforms which are anchylosed to the bone.
**Fig. 27.** Fused dentary molariforms with deep wear marks between them.
**Fig. 28.** Anterior end of left lower jaw with incisoroids and caninoid.

**Plate 10.** Dentition, *Sitana sivalensis*, late embryo.
The v-shaped arc of the jaw bones has been stretched.

**Fig. 29.** Upper jaw with the lanceolate egg tooth .
**Fig. 30.** Lower jaw. Note the different size of the premolariforms.
**Fig. 31.** Lower jaw. In the first premolariform the tricuspidity is but faintly indicated.

# Plate 8

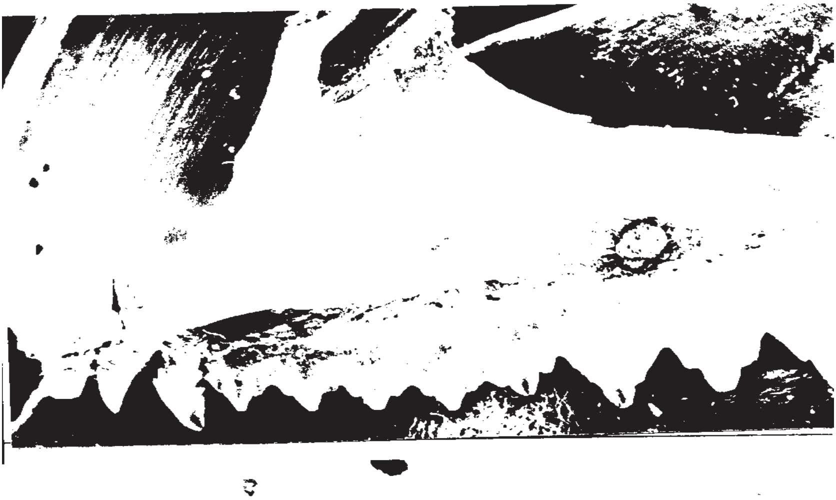

fig. 23

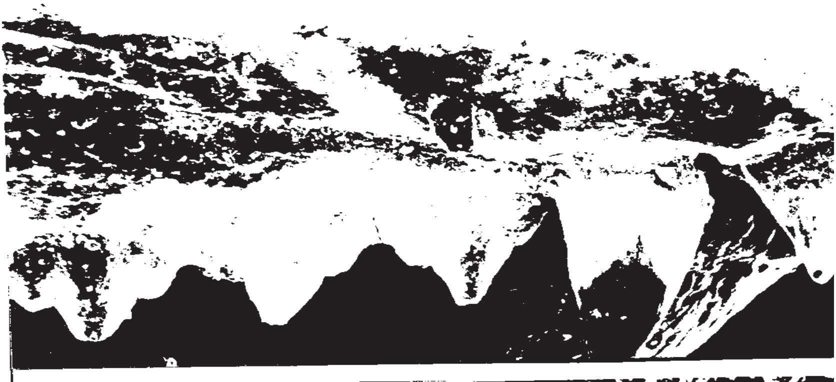

fig. 24

fig. 25

## Plate 9

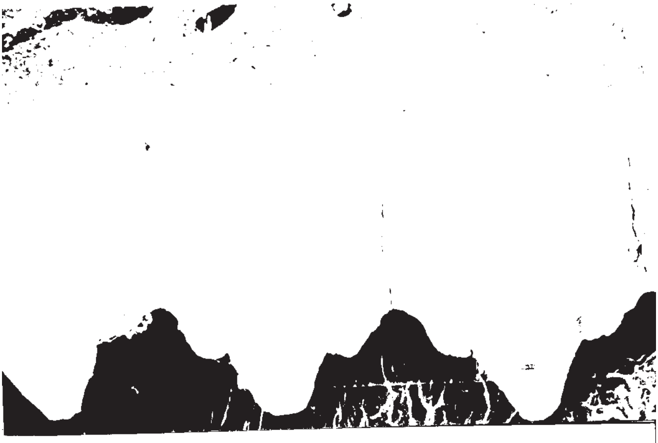

**fig. 26**

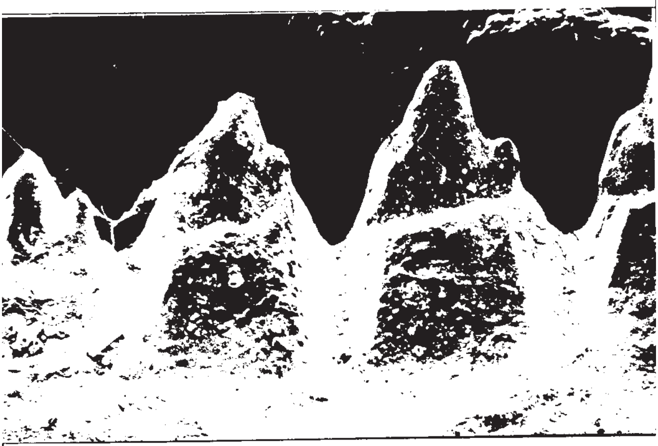

**fig. 27**

**fig. 28**

**Plate 10**

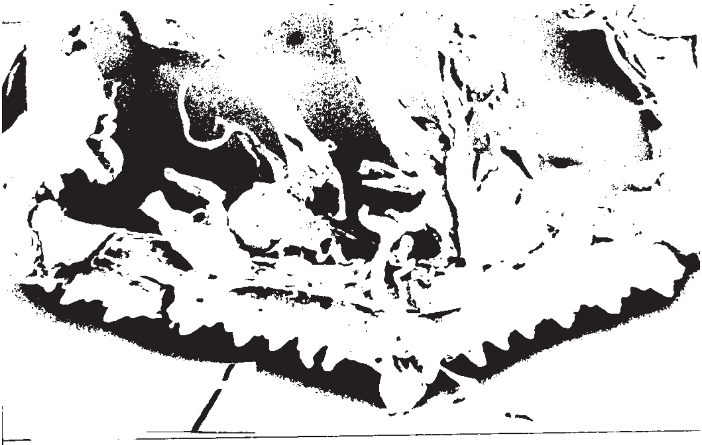

fig. 29

fig. 30

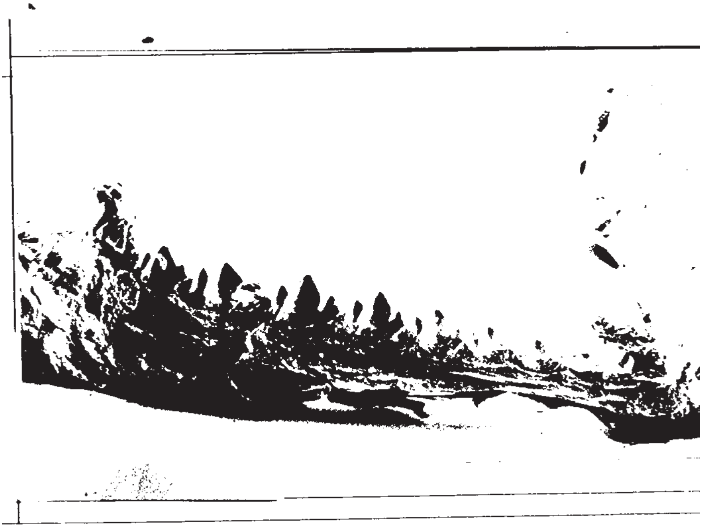

fig. 31

## **Eggshell structure *of Sitana sivalensis*** (pl. 11, 12, fig. 32)

Egg quality: Oval, flexible-shelled, white. For data of egg size see next article, p.121, paragraph 3.6.9.
Preparation: Hatched in captivity, dried.

Fibrillar and granular (but no globular) elements are discernible as in other soft-shelled squamate eggs . On the shell surface the fibrils are deformed and fused. The shell thickness may be estimated at 30-50µ.

3.1 Shell surface
3.1.1 Surface gross morphology (fig.33 - 35): Broad, but very flat and indistinct furrows run predominantly in longitudinal and transverse direction.
3.1.2 Surface fine morphology (fig. 37, 38): The rough aspect at higher magnification is caused by granules and fibril ends on the egg surface. More or less large plaques are formed by the fusion of these elements. They are divided by numerous irregular fissures

3.2 Cross section (fig.34, 36 - 38): Only the upper half of fig. 36 presents the eggshell. Several extra-embryonic membranes (chorio-allantois) are attached below it. By far the greatest part of the shell consists of fibrillar layers, the uppermost of which merges into the covering layer (fig. 37, 38) while the lowest one is fixed to the scarcely discernible boundary layer.

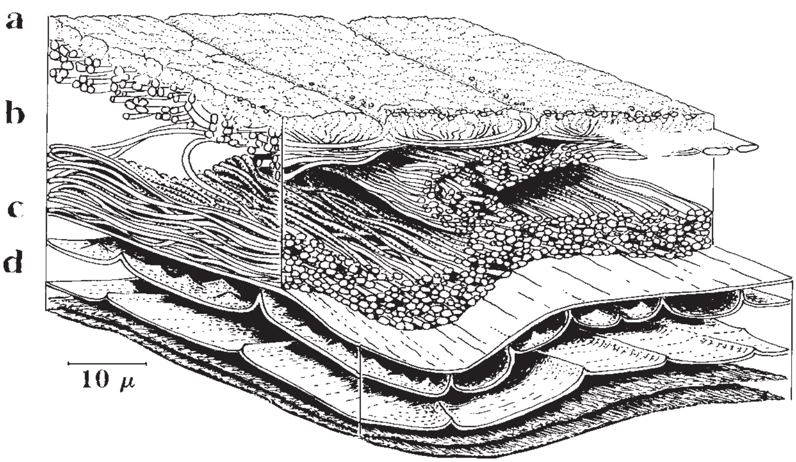

**Fig. 32.** Egshell structure of *Sitana sivalensis.*

# Plate 11

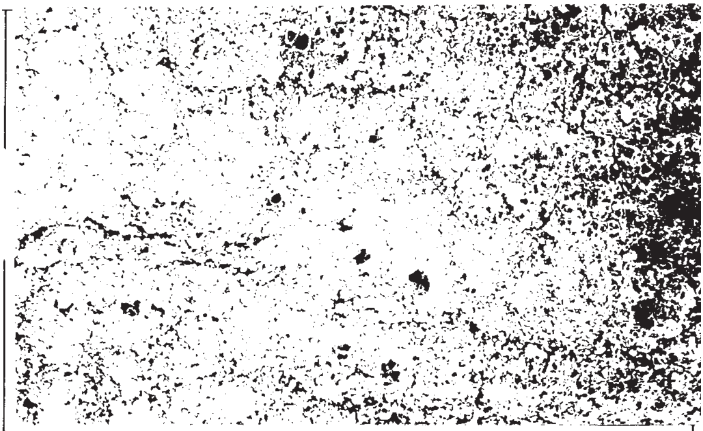

**fig. 33**

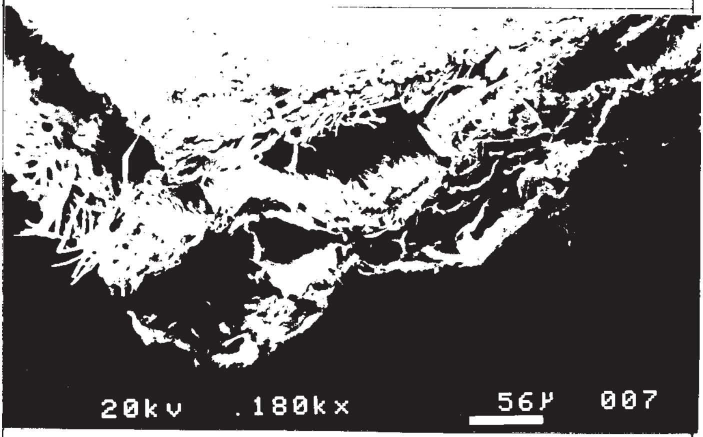

**fig. 34**

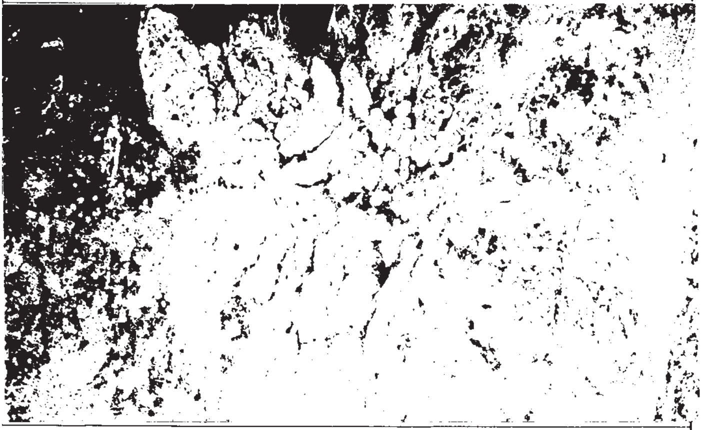

**fig. 35**

On the surface the structural elements form a mass of fully or partially fused granules and fibers which may appear more or less homogeneous in cross section (fig. 37, 38). As fusion is not complete, many interspaces remain as pores or fissures, permitting ample gass and water exchange.

3.2.1 Covering layer (fig.38): This 11-13 µ thick hull consists of two crossed fibrillar layers: A superficial one of fused elements which form a system of branched ribbons (fig. 37), and an inferior one of straight and parallel fiber bundles which are fixed to the upper stratum at their ends and hang down like garlands (fig. 36, 38).

3.2.2 Deep fibrillar layer (fig. 34, 36): With 10-20 µ in cross section (1-3 fibrils on top) this stratum is rather thin. Again its fibers run crosswise to the overlying ones (fig. 36).

All fibrillar strata are interconnected by single fibrillae.

3.3 Boundary layer: The fibrillar shell described above is in narrow contact with a very thin and apparently homogeneous sheet (fig. 36). As several extra-embryonic membranes adhere to the shell base, we can not differentiate if there is only one boundary layer or several of them.The membranes - at least six of them are discernible - are by no means plane, but at least some of them bear tips and folds protruding upwards and forming contacts between the membranes.

The normal fibrils are 0.9-1.7 µ thick, round or polygonal in cross section (fig. 38) and often packed into tight parallel bundles.

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**Plate 11.** Eggshell, *Sitana sivalensis*.

**Fig. 33.** Surface layer of more or less dense concretions.
**Fig. 34.** Transverse section of eggshell and adhering layers of extraembryonal membranes.
**Fig. 35.** Crystal concretion on shell surface.

**Plate 12.** Eggshell, *Sitana sivalensis*.

**Fig. 36.** Cross section with fibril layers running in different directions and torn apart by preparation. As in fig. 34 several extraembryonal layers adhere to the shell.
**Fig. 37.** Upper layer of fibrils which fuse into a solid mass at the shell surface,
**Fig. 38.** On an other part of the shell surface the concretions are rather thin. below them run fibrils which were hit in cross section.

## Plate 12

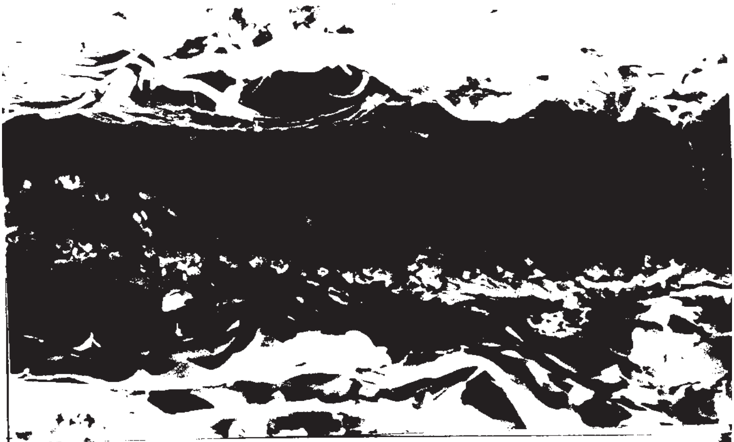

fig. 36

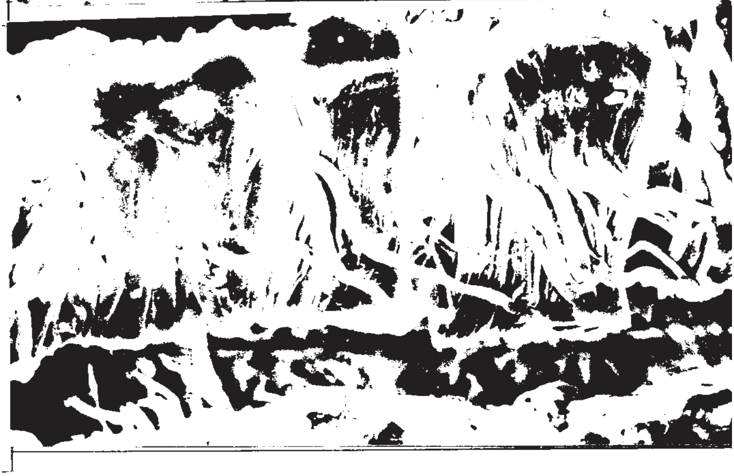

fig. 37

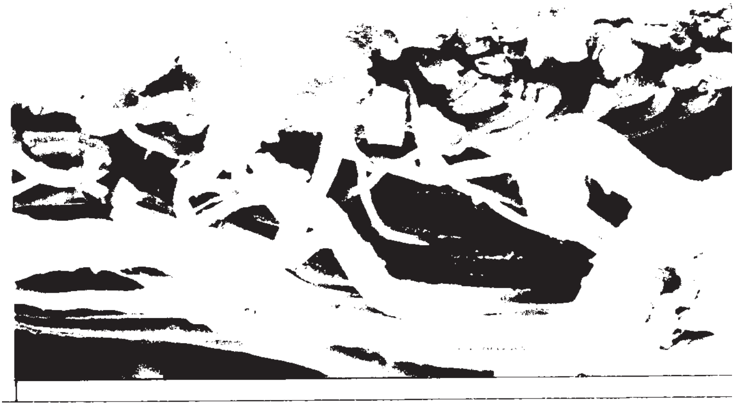

fig. 38

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Veröffentlichungen aus dem Fuhlrott-Museum, 1998, Bd. 4: 121-206

# Studies on the Biology of the Genus *Sitana* (Sauria: Agamidae)

## Studies on the Ecology and Behaviour of *Sitana sivalensis*

Werner Kästle*

**Key words:** Reptilia, Agamidae, *Sitana sivalensis*, ecology, ethology, communication system, reproduction.

**Abstract:** *Sitana sivalensis* differs from the *Sitana ponticeriana*- complex by a communication system which appears less differentiated. The signal system of *S. sivalensis* is described and compared with that of the *S. ponticeriana* group. Trends of signal evolution within the genus *Sitana* comprise important morphological changes of the gular fan as well as a considerable increase in display diversity.

*Sitana sivalensis*, like forms of the *ponticeriana* group, is a thermoconformer which spends the cold months in a state of brumation. Copulation is characterised by the very short duration of the neck bite hold, and postcopulatory torpor in males. Nest digging techniques are apparently identical within the genus, as is a high reproductive rate combined with a very low annual survival rate. The new species lays fewer eggs while egg size is not much different from that of larger congeners.

Long-time observation of captives allowed to collect data on the ontogenesis of act systems.

### Introduction

The members of the genus *Sitana* are highly specialised herbicole to terrestrial agamids which at the first glance, as to general body proportions, remind of the mostly arboreal anoles. Another convergence with this iguanids is the development of a large gular fan. Besides the gular appendage other structures which increase body outline during lateral presentation have evolved in *Sitana* as another parallel to anoles, namely a nuchal crest (roach) and a dorsal crest in the *ponticeriana* group only), which can be erected during challenge display. A third parallel to the anoles is the evolution of ritualised motions which enhance the effect of the appendages and serve as specific signals. In *Sitana ponticeriana* these stereotyped display forms are among the most complicated hitherto observed in a lizard, comprising about 25 acts and act combinations, most of them released during challenge (see appendix). In anoles the problem of display diversity has been intensely studied and discussed by Jenssen (1977).

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The discovery of a *Sitana* with a small gular fan in eastern Nepal by Schleich and Shah ( see preceding article) arose the question about the communication systems of *Sitana* species. As their gular fans differ drastically in conspicuousness, dissimilarities in display actions were also probable. As the communication system in *Sitana ponticeriana* is extremely differentiated (Kratzer, 1980 and own observations), a more primitive state of signal evolution was thought possible. For this reason prolonged observation (September 1994 into summer 1996) of the new species was performed. The authors are much obliged to Regine Seitz who took care of the precious and irreplaceable animals during our absence.

Contents:

## 1. Material and methods

*Sitana sivalensis* was collected near the Surai Khola in western Nepal in Oct. 1994 (see preceeding article, p. 87), and 7 juveniles, caught as hatchlings were raised in captivity without special problems until adulthood was reached.

The following conditions seem essential for successful husbandry:
Diurnal illumination with combination of halogen lamps (35W or 50W) and a mercury lamp (HQL, 100W). Below the lamps the ground (at a distance of 12 cm) consisted of sand covered with a flat stone and some dry fern leaves. The agamas liked to lie flat on the sand or dig into it, often partially hidden below the leaves and resting there for hours.
Local illumination created a temperature gradient between ca. 40° on the stone and 25° in the opposite corner by day. During the night the terrarium cooled to room temperature of about 18°C in summer and 8°C in winter.

Some very thin branches served for roosting at night and as a lookout during the day.
A bunch of grass with living and dry leaves in a flat pot stood in the cool and shady corner and played an important role as a refuge for sleeping and during days of inactivity.
A flat food dish kept Wax moth larvae exposed for some time. The sitanas drank drops from the grass leaves which were intensely sprinkled in the morning, later they readily licked from the water dish.

Providing the sitanas with the necessary trace substances means to grope in the dark. We neither have an idea which minerals they need, nor which organic substances they take with their food insects. The ideal food - varied small insects from a biotope which is not contaminated with pesticides - is often not to provide. We try to administer the vital substances by several ways:

1. Nutrients are added to the drinking water: To 100 ml of water (we take tap water, mineral water is perhaps better) we add five drops of a water soluble multivitamin preparate (Multibionta Merck reg. Nr. M 1093), one small drop of an iron chloride solution and a small calcium tablet for teething children .
2. Wax moth larvae are fed with a solid mixture of honey, milk powder and wheat germs (to buy as health food). Before feeding them to the sitanas they a powdered with a calcium preparate for veterinary use.
3. Crickets are fed with wheat germs to which some powdered lava (used for gardening) was added. As vegetable food they get green plants, e.g. salad or dandelion.
4. Small bits of eggshell which are carefully licked up from the ground provide another source of calcium.

Nevertheless the maintenance conditions were apparently defective. In the first year three females died from egg retention and many eggs were laid without regular nesting and had insufficiently calcified shells. The following generation did not produce viable eggs.
The embryonic development was disturbed and the sitanas perforated the eggshell one or two weeks before the yolk was absorbed, dying before hatching.
Evidently our knowledge in maintaining these lizards is fragmentary. Typically, the rearing of young *Otocryptis wiegmanni* is also extremely problematic. Buhle (after Rogner, 1992) did not succeed to keep a single of his 22 hatchlings longer than nine months in spite of providing them with calcium and a mixture of vitamins.

On warm and sunny days the terrarium is exposed to the sun and open air. Otherwise it is irradiated with ultraviolet light for 15-30 min each day.

As bases for comparison with different forms of the ***Sitana ponticeriana*** **group** the following references were used:
1. The unpublished work of W. Kratzer (1980) containing a wealth of field observations from the coastal dunes of **Palatupana/ SE-Ceylon**, near Ruhunu (Yala) National Park.
2. Unpublished captivity observations by W. Kästle during 1965 on captives from the animal trade (unknown provenience) including a film on display types.
3. Unpublished field and captivity observations by H.- H. Schleich & W. Kästle on animals from **Puri /Orissa**.
4) Data on reproduction and development from **Poona /Maharashtra** (Chopra 1964a,b, 1967).
5) Data on different aspects of biology including population biology from **Tirupati/Andhra Pradesh** (Subba Rao & Rajabai 1972a,b, 1973, 1974, 1976; Subba Rao, 1983).

Results:
In order to facilitate comparison the observations on *Sitana sivalensis* are directly confronted with data on *Sitana ponticeriana*. If not indicated otherwise the data refer to the adult state which in captivity was reached with end of June.

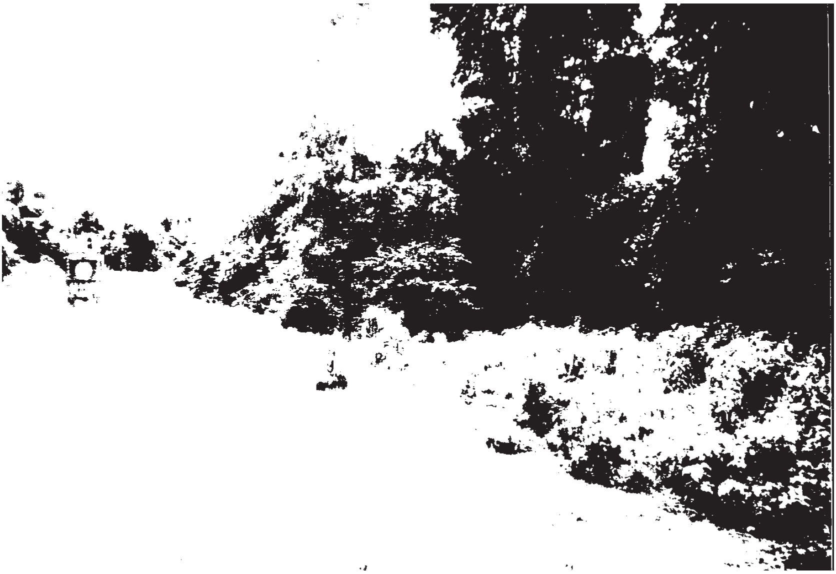


**Fig. 1.** Secondary biotope of *Sitana sivalensis* along the road north of Shivpur (see map part 6 fig. 2).

## 2. Ecology

### 2.1 Biotope (fig. 1-4)

On open patches in Monsoon woods with low vegetation: road embankments along open Sal wood forest with adventitious vegetation, predominantly *Eupatorium adenophorum*, an introduced tropical weed which grows about one meter high; degraded fields; probably also around fallen trees (not found there in spite of search).
Temperature (meteorological station, see fig. 3): Average temperature: 24°; average temperatures of coldest and hottest month: 16° - 30°
Annual precipitation 1500 mm.

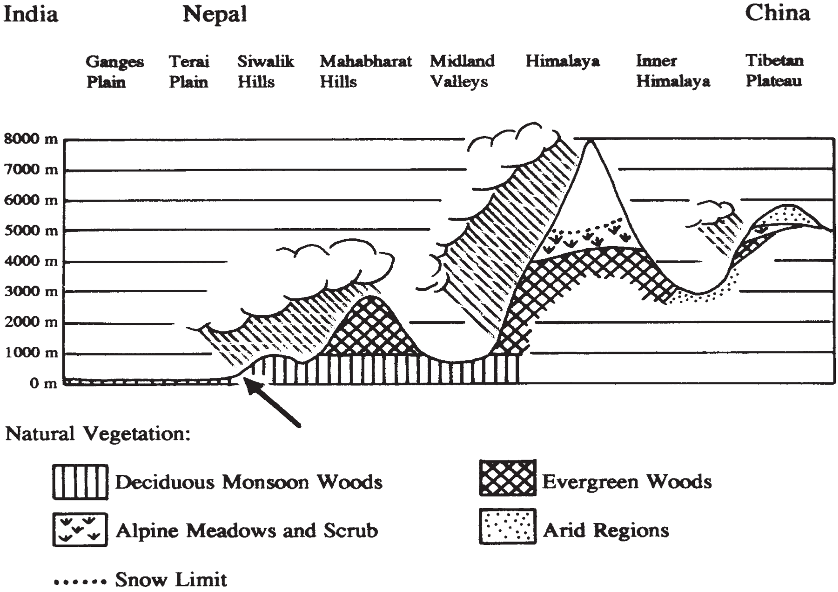


**Fig. 2.** Vegetation zones of Western Nepal with the record locality of *Sitana sivalensis* indicated by the arrow.

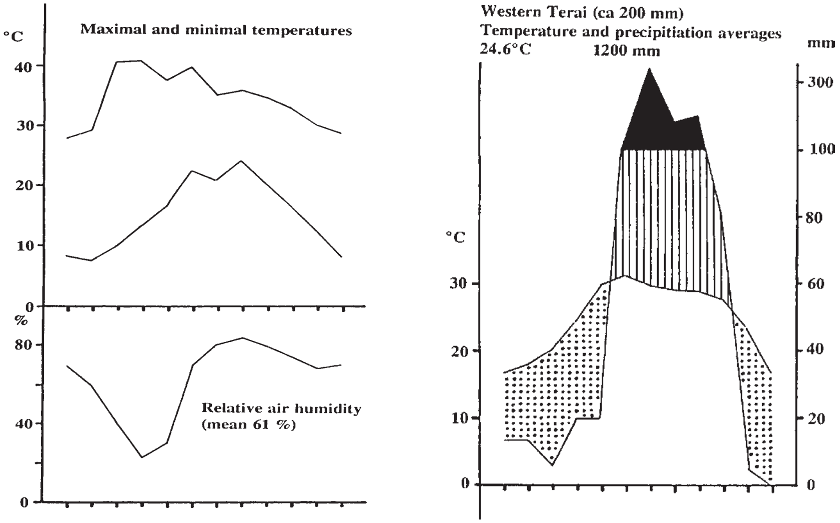
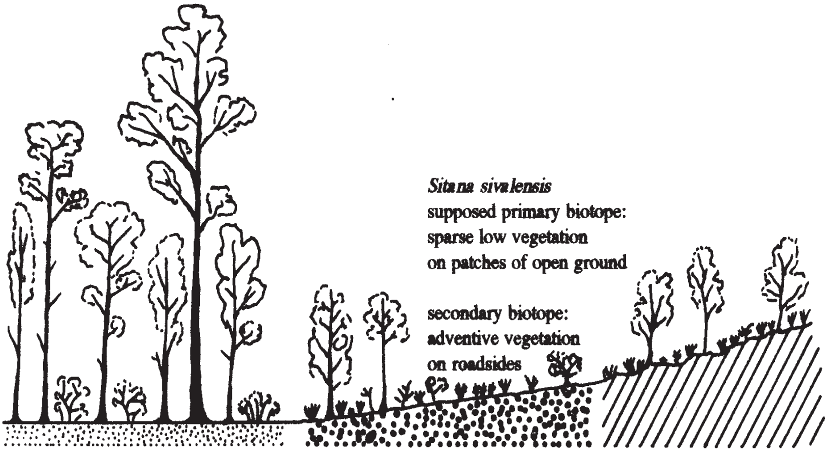


**Fig. 3.** Climatic graphs for the western Terai region, data compiled from Dobremez, 1976: monthly average temperatures for Bhairawa (140 m); precipitation for Nepalganj (190 m): they are about 200 mm higher for the Shivpur region; maximal and minimal temperatures for Butwal.
Dotted: dry period. hatched: wet period.

| **South** | | | **North** |
|---|---|---|---|
| | **Terai Plain** | **Piedmont scree deposits** | **Siwalik hills** |
| **Elevation above sea level:** | 150 m | up to over 300 m | up to 2000 m |
| **North-South extension:** | 300 km | 2 - 10 km | 40 . 80 km |
| **Soil type:** | fine-grained alluvial | debris | rock |
| **Plant society:** | **Tropical** | **Deciduous** | **Forest** |
| | **Terai Sal Forest** (now almost entirely replaced by cultures) | **Light Sal Forest** | **Siwalik Forest** |
| Maximal tree hight: | 30-35 m | 10 m | 10 m |



| | | | |
|---|---|---|---|
| **Plant species diversity:** | high | low | low |
| Dominant trees: | *Shorea robusta* | *Anogeissus latifolia*,<br>*Terminalia tomentosa* | *Anogeissus latifolia* |
| **Vegetation layers:** | High trees,<br>low trees, bushes,<br>no undergrowth | low trees with undergrowth of grasses up to 1.2 m high<br>many xerophytes<br>(dry vegetation frequently destroyed by forest fires) | |
| **Light penetrating to ground:** | 2% | in *Sitana* biotope up to 100 % | 30-40% |

**Fig. 4.** Vegetation zones around the *Sitana sivalensis* habitats (Dobremez, 1976; Dobremez & al., 1984) in a cross section with the Ganges Plain at left and the Nepalese mountain ranges at right.
Characteristic, but with different dominance in the three forest types are: *Shorea robusta* (Sal tree), *Anogeissus latifolia, Terminalia tomentosa.*
Other tree components are: *Acacia gageana, Bauhinia valhii, Bauhinia malabarica, Buchanania latifolia, Butea monosperma, Caesaria tomentosa, Erhetia laevis, Dalbergia acuminata, Ficus semicordata, Ficus subincisa, Firmiana colorata, Glochidion acuminatum, Hollarhena antidysenterica, Ichnocarpus lutescens, Indopiptadenia oudhensis, Lagerstroemia parvifolia, Lannea grandis, Mallotus philippinensis, Mitragyne parvifolia, Murraya koenigii, Phoenix humilis, Sabia paniculata, Schleicheria trijuga, Semecarpus anacardium, Spondias pinnata, Wendlandia exserta.*

***Sitana ponticeriana***

**Palatupana** (Kratzer 1980): Elevation: Sea level. Sandy plots on the landward side of dunes with scarce vegetation on the coast or inland on dry palm leaves (*Borassus flabellifer*); on the seaward side of dunes among more or less dense growth of *Spinifex* grass (*Spinifex ceylanica*) and cushions of other herbs (*Hydrophylax maritima, Ipomoea pes-caprae, Pogostamon* spec.); on open sands of the landward dune side with single bushes of *Cassia auriculata* and *Dichrostachys cinerea* (2.5 m high, in groups 5-10 m distant) .The sitanas prefer a low scrub (ca. 40 cm) of these species.
Air temperature: annual average 27°C
Minimum and maximum during the observation period (March - July): 25° - 39.5 °C
Sand surface temperature during the same period: 25° - 52° C
Annual precipitation: 750 mm.

**Tirupati** N of Madras (Subba Rao & Rajabai, 1972a; Subba Rao, 1996): On degraded land with herbs (*Zornia diphylla*) and single shrubs (*Barleria noctiflora, Randia dumetorum*).
Temperature:Absolute minimum/maximum: 16° - 40° C.
Annual precipitation: 984 mm.

**Puri** / Orissa (Schleich, personal observation): Elevation: sea level; on coastal sands .

***Sitana mucronata*** from **Hiniduma**, S-Ceylon (Deraniyagala, 1957): Elevation: 600m. On rocks near streams in cool and humid surroundings.
Temperature: 23° C.
Annual precipitation: 375-400 mm.

## 2.2 Population biology

### 2.2.1 Population density

Beginning with September 19, 1994 three adulti and 20 juveniles of *Sitana sivalensis* were caught on a plot of 0.1 ha (100 m x 10 m). The resulting theoretical density of 30 adulti plus 200 hatchlings and juveniles from the same year per ha (0.03 respectively 0.2/m²) is certainly too low because of the cryptic habits of this species and the very small size of juveniles. The difficulty of collecting the lizards becomes evident from the fact that 2-3 people searched 3-4 days for them.

***Sitana ponticeriana*:**
Annual biotope shifts observed by Kratzer (1980) cause massive changes in density.
Palatupana (Kratzer, 1980): Highest on dry leaves of Palmyra palms (*Borassus flabellifer*) and dense growth of *Spinifex ceylanica*: 1-2/m². On open sands with single *Cassia auriculata* and *Dicrostachys cinerea* bushes: 0.1-0.2/m². On open sands with patches of *Spinifex* grass and herbs: 0.05-1/m².

Tirupati (Subba Rao & Rajabai, 1972a): In the site controlled over three years the calculated densities were lower by several orders of magnitude: 0.00373/m² (=37.3/ha: 9.9 juveniles, 14.3 males, 13.1 females).

### 2.2.2 Population turnover

The presence of small juveniles from at least two successive clutches (hatchlings with 14 mm and others with up to 23 mm snout-vent-length) and the extreme rarity of adulti in mid-September gives clear evidence that oviposition in this population starts in early summer. Among the three captured adulti were two pregnant females, and oviposition certainly continues into late September.

As the juveniles are much more difficult to discover than their parents, the latter had probably died after reproducing with an age of about one year.

***Sitana ponticeriana***

Tirupati (Subba Rao & Rajabai, 1972a): Of 175 marked lizards only 3.5% (1.5% males, 2% females) survived after one year.

The rapid population turnover might create conditions under which *S. ponticeriana* is in advantage over *S. sivalensis*: Each death of a resident male is followed by a displacement of others and causes great instability. The animals have to reorganise their social system and to found new territories. Perhaps the highly developed signal system of this species is connected with its colonising abilities. Males with larger fans and a more diverse display repertoire are at advantage in attracting females and fending off rivals.

Another point of view which is connected with a rapid population turnover is presented by Jenssen (1978 p.285): "Species which are territorial and sexually active throughout most of the year but are short lived would tend to experience a rapid turnover in nearest neighbours, especially if population densities are high. The frequent territorial interactions with unfamiliar conspecifics would be more tenable if the species' agonistic repertoire contained a number of display types. This would permit ritualised escalation and place a greater reliance on bluff than on fighting to maintain territories. Risk of injuries should be decreased with a large display repertoire."

### 2.2.3 Reproductive strategies

Observations by several authors lead to the conclusion that *Sitana* species are rather typical r-strategists sensu Pianka (1970). According to Wilson (1975) the correlates of these forms contrast with their "antipodes", the K-strategists in the points listed below (incomplete).

In many regards the r-concept fits the whole genus *Sitana* (see notes in brackets), and *S. fusca* (see part 9) apparently comes closest to it.

| Correlate | r-strategists | K-strategists |
|---|---|---|
| Climate | Variable and/or impredictable: uncertain (in monsoon regions) | fairly constant and/or predictable, |
| Mortality | Often catastrophic, non-directed, density-independent | More directed, density dependent |
| Population size | Variable in time, non equilibrium; | Fairly constant in time, equilibrium, |
| | recolonization each year | no recolonization necessary |

| | | |
|---|---|---|
| Intraspecific and interspecific competition | Variable, often lax (no vehement interactions of *Sitana ponticeriana* observed in the field. *S. sivalensis* fight in confinement, but *S. fusca* seems totally tolerant) | Usually keen |
| Attributes favoured by selection | 1. Rapid development (*S. sivalensis* mature with 11 months) | Slow development |
| | 2. High r max. - reproductive rate (in *S. sivalensis* 3 x 6-8 eggs per season, in *S. ponticeriana* at least 36) | |
| | 3. Early reproduction | Late reproduction |
| | 4. Small body size (especially in *S. sivalensis:* SVL 4 cm | Larger |
| | 5. Single reproduction (most females die after one egg-laying season) | Repeated reproduction |
| length of life | Short, usually less than one year<br>(in both species groups only few specimens survive) | Longer, usually more than one year |
| Emphasis in energy utilisation | Productivity | Efficiency |
| Colonisation ability | Large: (*S. sivalensis:* on recently opened patches of open ground in woods)<br>(*S. ponticeriana*: change between coastal biotopes from dry to monsoon season) | Small |
| Social behaviour | Weak, mostly schools, herds, aggregations<br>(*S. fusca* forms colonies) | Frequently well developed (in *S. ponticeriana* still more than in *S. sivalensis*) |

The following arguments support the opinion, that a strong tendency towards r-strategy is typical for the genus *Sitana*:

1. Rapid population turnover: Adulti were rare in the population of *Sitana sivalensis* observed by Schleich in October 1994 .
Subba Rao & Rajabai (1972a) recaptured only 3.5 % of 175 marked *ponticeriana* specimens after one year.
2. A high colonising ability was deduced by Kratzer (1980) when he observed that during June/July 1980 the population density on the seaward side of the coastal dunes dwindled to 1/50 of its original value. Heavy winds had moistened the site with salty froth and blown parts of the insects inland. Apparently most of the sitanas moved behind the dunes.

## 3. Behaviour (ethology)

Sexual dimorphism: Adulti are very different in shape: Males have a distinctly enlarged tail base and a gular fan, Adult females are very thick during pregnancy and entirely lack a gular appendage. During the reproductive season their venters show a pattern of brown streaks while that of active adult males is uniform white.

The easiest character to sex an adult male is the double midgular row of enlarged fan scales and the dark streak along the middle of the throat. It is intense in sexually active animals but can become much weaker and fade to a light gray, but is nevertheless still distinct.

## 3.1 The communication systems of *Sitana sivalensis* and *Sitana ponticeriana*

### 3.1.1 Morphological differences

### 3.1.1.1 Colour pattern:

In all taxa of the genus *Sitana* there are stable and changeable pattern elements, the former ones being almost identical in all species.

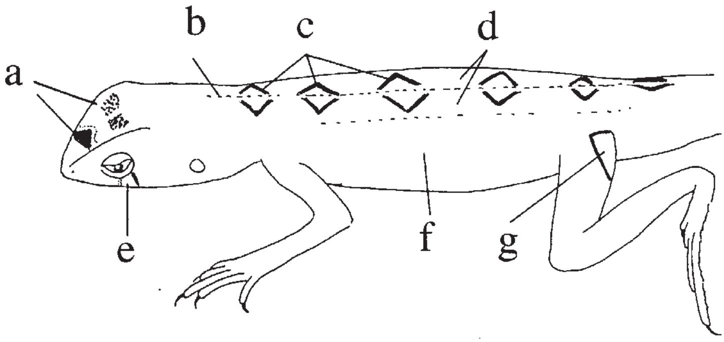


**Fig. 5.** Stable pattern elements present in both sexes: a) prefrontal transverse bar followed by diffuse patches; b) light vertebral line; c) chevron pairs; d) dorsal field often lighter than the lateral (f) one; e) light subocular patch; (g) inginual mark which never changes its colour of beige.

### 3.1.1.1.1 Stable pattern elements (fig. 5):

They are conservative within the genus. Therefore *Sitana sivalensis* looks like a small *Sitana ponticeriana*. The most striking stable elements seen in dorsal view are the chevron pairs (c) and the prefrontal transverse bar (a). Both show remarkable individual variability (fig. 6,7) and are possibly characters which play a role in individual recognition. Both physiological stability and individual variability are needed for this function.

Field observations by Kratzer (1980) have shown that dominant males and females tolerate subordinate specimens within their territories and distinguish them readily from intruders. In *Sitana sivalensis* many reactions as courtship, flight or male rejection behaviour were released at the mere sight of a conspecific without any display. A rival male was recognised by his head alone which peeped out of a bunch of grass.

The chevron pairs (c ) consisting of dark triangles are arranged along the vertebral line, one of them anterior to the foreleg insertion, three anterior to hindleg insertion, and they continue in decreasing size on the tail. Mostly the dorsal triangles are exactly opposite and form rhombi which are most time divided by the light middorsal line. Sometimes they are shifted against one another or there are additional ones.

The delimitation of the dorsal and the lateral fields is marked by enlarged scales, and forms a sharp ridge during lateral display (see paragraph 3.1.2.6).

In both sexes the general body hue may change from dark to light grayish brown with heating. But there are, at least in juveniles, specimens which are exceptionally light or dark.

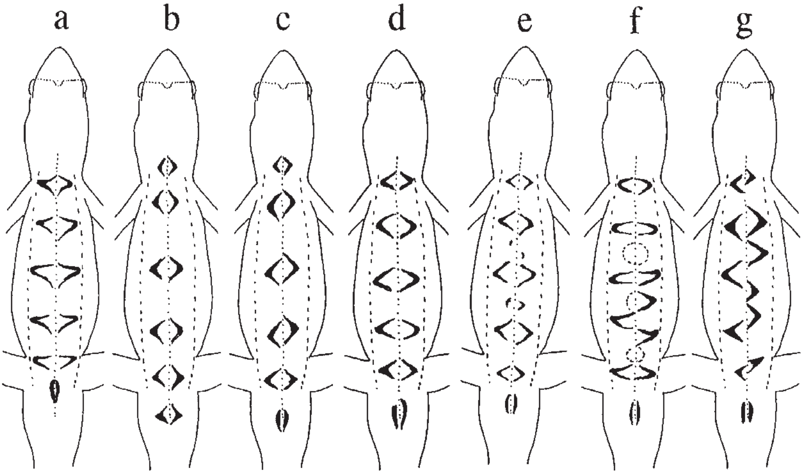


**Fig. 6.** Individual variability of the chevron pattern: symmetrical arrangement (a,b), asymmetry of single or several chevron pairs (c,d), additional chevrons in traces (e,f) or fully developed (g).

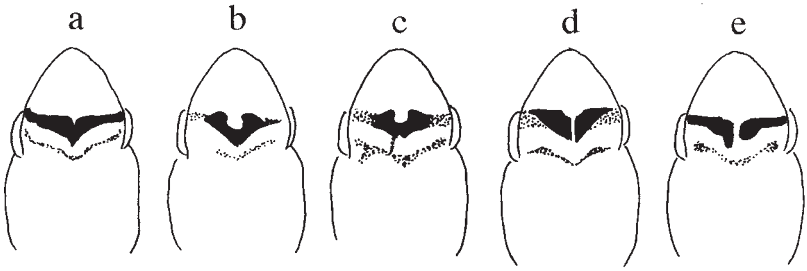


**Fig. 7.** Individual variability of the prefrontal transverse bar: a-c symmetrical and undivided, d,e divided.

3.1.1.1.2 Changeable elements in *Sitana sivalensis* males (fig. 8):
Compared with females the males show a wider range of colour change with the following elements appearing in definite situations:
a) gray upper head region. b) blue nuchal stripe in front of and between the first chevron pair. Its colour changes together with the upper lids; c) light brown or cinnamon coloured dorsolateral patches of different extent and contrast; d) upper eyelids which can be light

blue in sexually active males and fade to light gray during the inactivity period; e) the margin of the throat fan is deep indigo blue in excited specimens but fades to gray in inactive ones; f) The grayish brown posterior part of the gular fan is subject to little colour change but can become lighter if the lizard is not excited; g) white spots appear at the locations of the enlarged lateral scales during rival behaviour. They were also present in the type male dead from social stress (see preceeding article p.87, fig. 9).

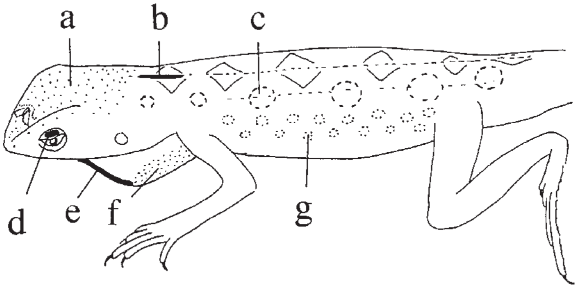


**Fig. 8.** Changeable pattern elements in the male:
a) a grayish hue of the of the upper head and nape region
b) a nuchal streak (which eventually widens over the whole surface of the erected nuchal roach) can change from gray over bluish gray into a greenish blue.
c) a more or less distinct row of dorsolateral blotches which are lighter than their surroundings.
d) upper eyelids changing from gray to light blue in subadults, constantly blue in alert adults.
e) a blue streak on the anterior margin of the gular fan
f) a gray posterior gular region resp gray sides of the gular fan
g) a more or less regular rows of white spots covering the enlarged flank scales
h) a ventral pattern of brown lengthwise streaks with an especially conspicuous midventral line (fig. 12).

Factors releasing colour change in males (fig. 9):

1) During many activities as basking, sand bathing, feeding or observing (without seeing a conspecific) the male pattern is identical to that of females (see article on p. 87, fig. 12) with eventually the only exception of a faint grayish gular streak (a).The plain pattern is also typical for losers in a rival combat.

2) In any state of social arousal the dark blue gular streak and gray gular region appear while the nape streak grows more intense (b). Note that these pattern elements are present in all of the following states.

3) During challenge behaviour (c) the white spots on the flanks appear. After the end of a fight they may persist for some minutes in the winner but disappear in the looser as soon the fight is going to be decided.

4) Directly after a fight the winner’s head turns light grayish and the nape stripe becomes vivid greenish blue.

5) Once superiority is attained the high-ranked male retains his grayish head and bluish nuchal streak. The gular region is marked with a dark gray longitudinal streak (d; fig. 10). This pattern is independent of the presence of conspecifics.

6) A male dead from social stress (article on p.87, fig. 9) showed the whitish lateral spots typical for rival combat (e). Upper eyelids and nuchal stripe were blue.

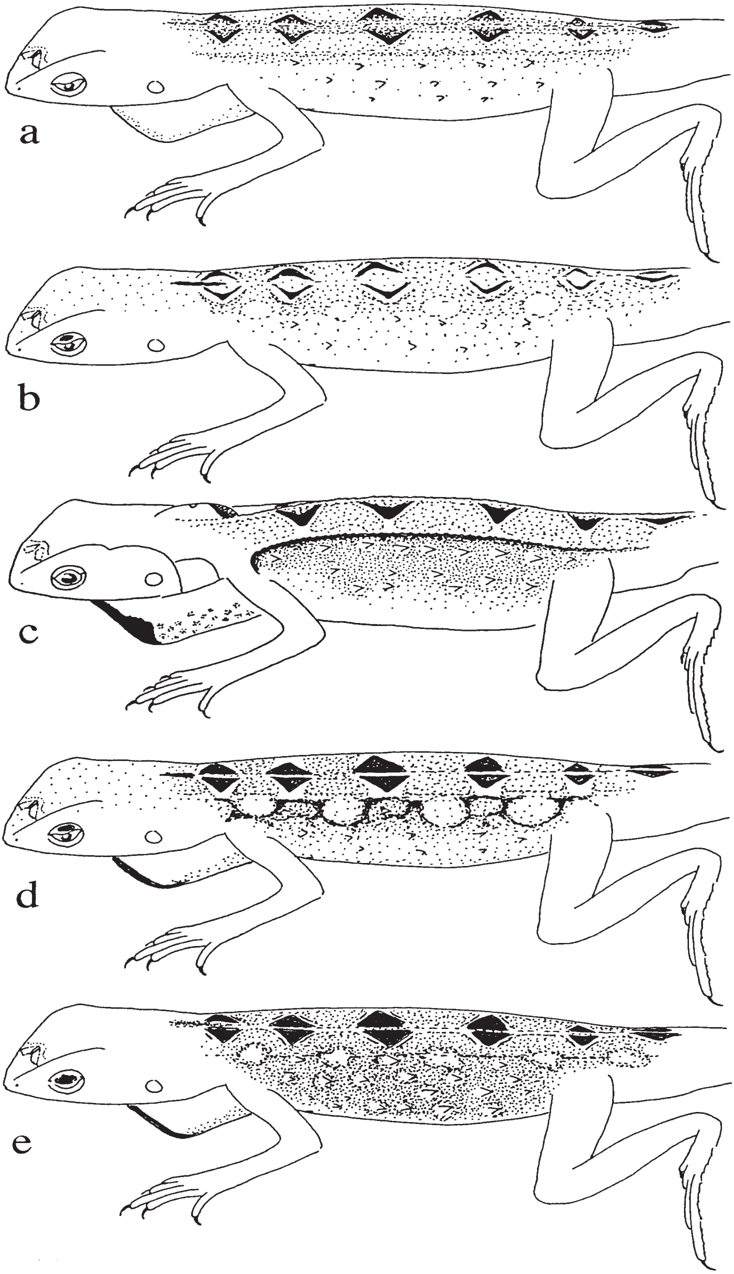


**Fig. 9.** Male pattern types in different situations: a) normal, b) social arousal, c) challenge, d) dominant, e) dead from social stress.

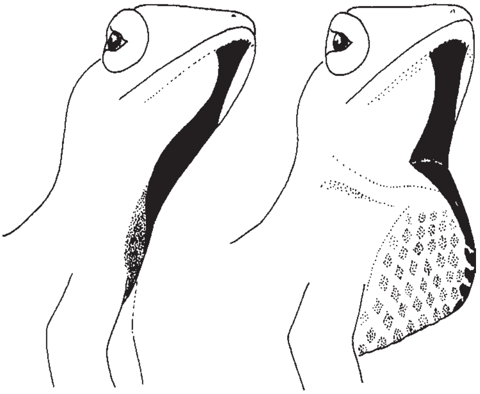


**Fig. 10.** Folded and distended *S. sivalensis* fan with a dark blue margin and grayish brown dots on lateral surfaces.

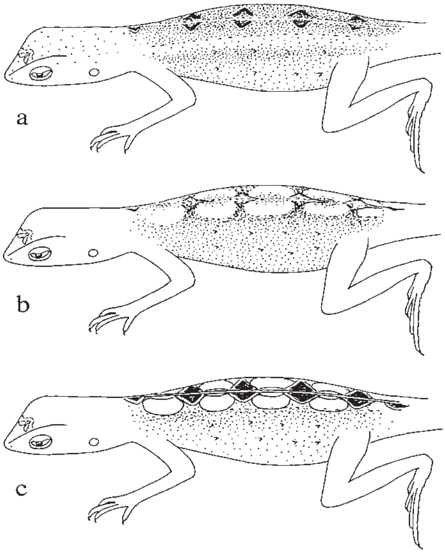
3.1.1.1.3 Changeable elements in the colour pattern of *Sitana sivalensis* females (fig. 11): Normally the females show different hues of brown (a, see also part 6, fig. 13).
In a bathing female (see 3.4.5) the normally weakly defined brownish spots which alternate with the dorsal triangles widened to sharply defined orange transverse blotches on a dark background which made the dark triangles almost disappear (b). During gravidity the same female developed sharply contrasting kidney-shaped spots while basking in the morning (c).

**Fig. 11.** Female pattern types in different situations:

a) normal,

b) individual variation with kidney-shaped dorsal spots: bathing,

c) the same animal basking.



### 3.1.1.1.4 Ventral pattern (fig. 12):

The ventral pattern changes from white to dark brown and shows a high degree of individual variability. It consists of longitudinal streaks which disappear during the white and the darkest phase. Many specimens have a pronounced midventral stripe and a gular region with stripes converging towards the middle of the throat.

During the warm season the white phase (a) can show single dark dots and is typical for highly active juveniles and males as well as most sleeping females and some dead specimens. The dark phase (d) was only observed in blackish juveniles. The longitudinal lines are very intense and broad, and even their lighter brown interspaces are intensely covered with dark dots.

The patterns b) and c) are normal for active females, wintering males and normal juveniles.

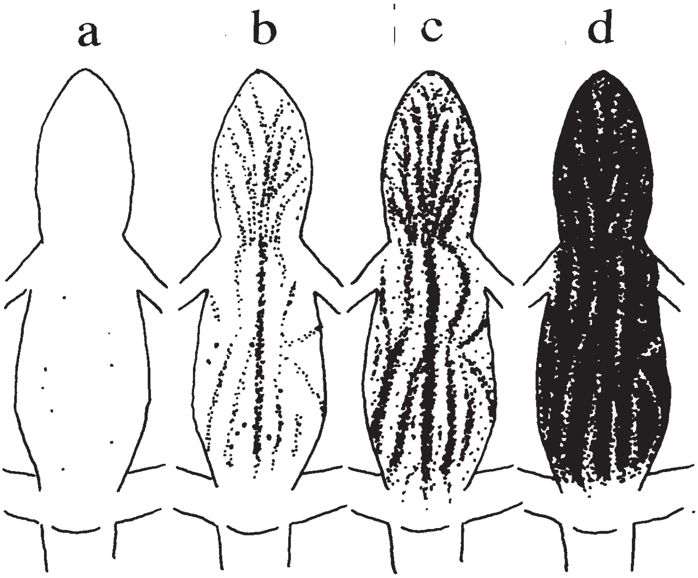


**Fig. 12.** Colour change of the abdominal pattern of one specimen. Generally the pattern consists of longitudinal streaks with the midventral one especially distinct (b,c). Coloration ranges from white with single dots (a) to dark brown with some traces of white (d).

### 3.1.1.1.5 Comparison with ***Sitana ponticeriana***

The sharply contrasting white stripe along the upper lip and along the neck sides lacks in *S. sivalensis*.

In *Sitana ponticeriana* the changeable gular pattern is also differentiated into a middle streak accompanied by a lateral coloured zone, but both are of a metallic blue, very dark in the middle line and with a purple hue on the sides.

There is no grayish or bluish colour in the nape region. Nape and dorsal crests are of the same colour.

During challenge behaviour there are also white spots on the body sides, but relatively smaller than in *Sitana sivalensis*. Additionally there are red ones from the flanks up into the nuchal and dorsal crests.

### 3.1.1.2 . Gular fan

To emphasise the differences between the structures of small and large *Sitana* fans we also present the fan of *Sitana ponticeriana* (fig. 13), one of the most complex signal structures to be found among reptiles.

As to terminology we propose to distinguish between three forms of gular appendages in lizards:

1. Gular pouch (gular sac, German: Kehlsack) : a broad appendage formed by the gular skin which is often differentiated by its colouration and pattern. It is extended by means of the hyoid apparatus (mostly not "inflated")
2. Gular fan (German: Kehlfächer): a flat median skin fold which mostly bears a specific colour pattern and is normally contracted. In extreme cases, e.g. in *Sitana ponticeriana*, its posterior margin may reach backwards to the ventral region. The fan is spread by means of the hyoid skeleton. A thin bone, the processus retrobasalis (basibrachiale) is moved anterio-ventrally by a lever mechanism which in *Sitana ponticeriana* has been studied by Gnanamuthu (1930).
3. Dewlap (German: Kehlwamme) could be applied to flat but rather immobile appendages as in *Iguana iguana*.

This classification disregards the existence of intermediate forms e.g. rather flat pouches. Gular fans evidently come close to the "ideal signal". Their colour patterns are simple, conspicuous and unmistakable (at least in sympatric forms), they allow additional information by motion, emit directed messages by adequate orientation, and the sometimes huge appendage is easily stowed away. The essential information emitted by fans regards species, sex as well as motivations and their gradedness.

Fans are an example for convergent evolution (fig. 14) in several genera of the families Agamidae (*Sitana, Otocryptis*, *Gonocephalus*, *Draco*) and Iguanidae (*Anolis*, *Norops, Chamaeleolis*).

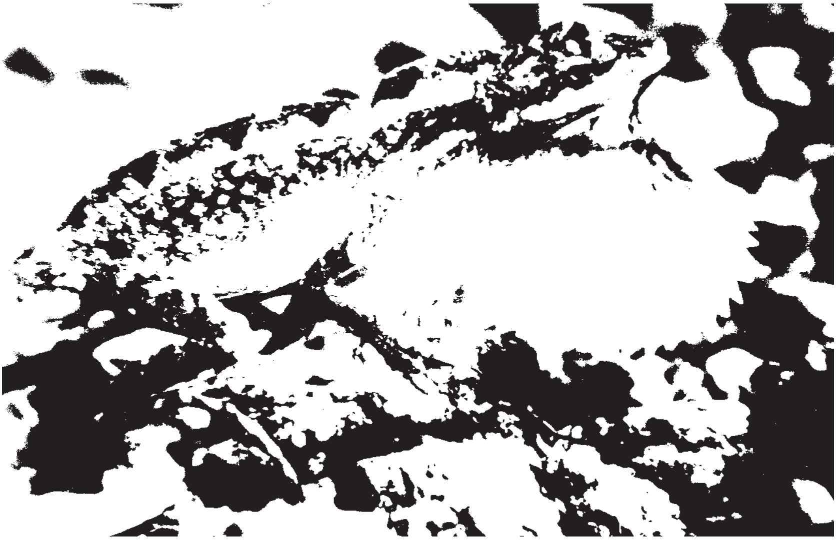


**Fig. 13.** *Sitana ponticeriana* male from Puri with fully extended fan. Note the lanceolate marginal scales.

Large gular fans must be "stowed away" during most of the time as they are a hindrance during locomotion and easily perceptible by visually oriented predators. The packaging problem can be solved in three ways: (fig. 14):
1) The skin forms one longitudinal fold along which the fan is plied together (in the genus *Draco*). The skin between the gular scales is not extended.
2. The very elastic skin between the fan scales is stretched/ respectively contracted (*Anolis* mechanism). On the extended fan the scales form isolated rows.
3. In *Sitana ponticeriana* the fan scales are very large and hamper a normal contraction. They lie flat on the extended fan but rotate into a vertical position if the fan is at rest. In the stowed state the scales are strongly imbricate with the ventral ones covering their dorsal neighbour. Only the midgular scales (which lie at the margin of the extended fan) can be seen entirely. From those at their left and right only the dorsal margins are visible in longitudinal rows (see article on p. 87, fig. 1; p. 101, fig. 7).

### The specific structure of the gular fan in *Sitana*

As the fan scales of *S. ponticeriana* are white, large and translucent their rapid rotation produces a strange flickering effect (the term "flicker" was used by Deraniyagala 1953) similar to a rotating mirror, making the *Sitana* fan one of the most advanced and effective signal organs in reptiles.

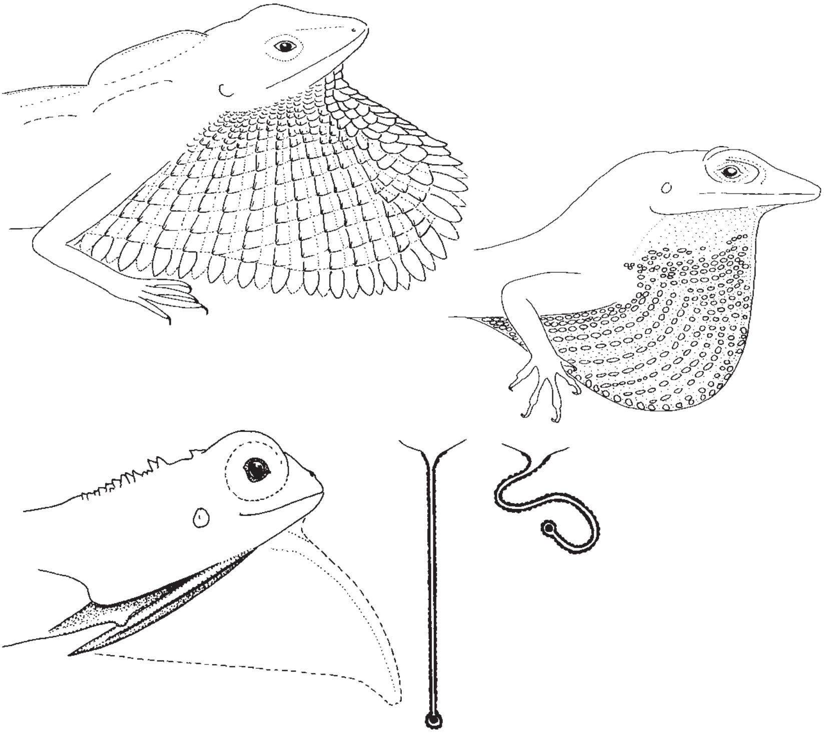


**Fig. 14.** Convergent evolution of large fans in agamid and iguanid lizards: *Sitana ponticeriana* (left) and *Anolis roquet* (right, after Henderson & Schwarz, 1985), *Draco volans* (bottom) with extended and folded fan in cross section.

**The folding mechanism of the gular fan in *Sitana ponticeriana*** (fig. 15, 16):

In the *Sitana ponticeriana* fan the large size and high degree of differentiation needs a special mechanism for folding and spreading. Structures and function can be explained using a Japanese fan as a model (fig. 16). It consists of a sector of paper or fabric (which is often decorated) which is glued to and supported by long lamellae of wood, turtleshell or other solid material. The lamellae of the model correspond to the rows of rigid scales, the sheet between them represents the soft skin between the scale rows. When the fan is folded, the lamellae are pulled to one side (backwards in the *Sitana*) and stacked with the soft skin between them. the opposite fan surface (the left one in fig. 16) corresponds to a second Japanese fan, a mirror image of the first one, with the fabric facing the reader. But this fan is shifted so that the lamellae of the right and left side alternate (see fig. 15 upper half, cross sections).

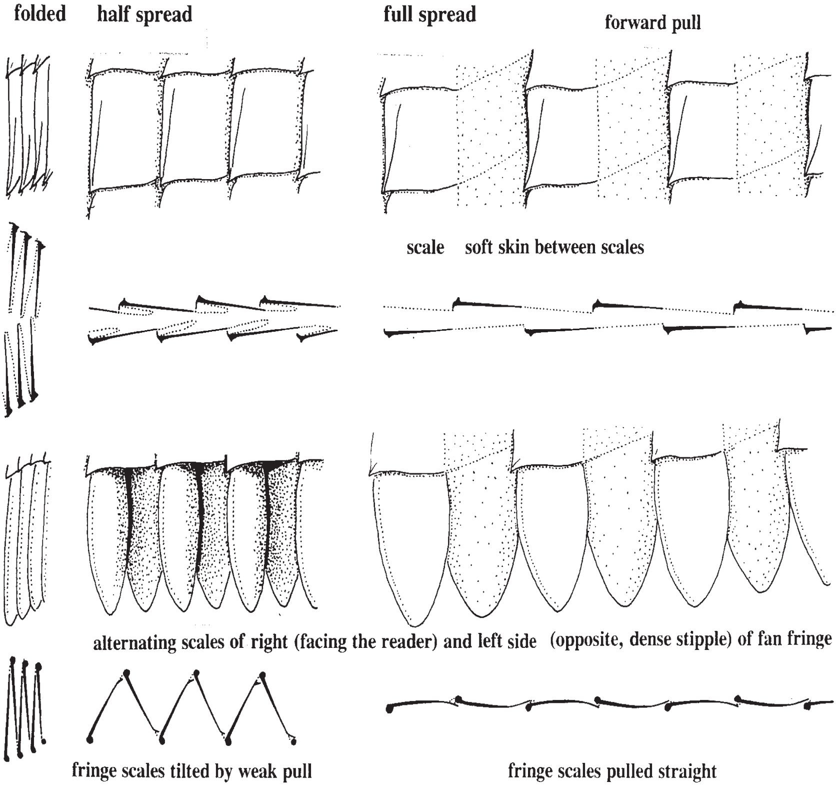


**Fig. 15.** Scale arrangement on a *Sitana ponticeriana* fan in different stages of fan spreading. Upper half: fan surface scales in lateral view and cross section; lower half: scale fringe scales in lateral view and cross section.
Note the alternating scale positions on both sides of the fan in the cross sections.

The model of the *Sitana ponticeriana* fan margin (same fig. 16, bottom) may be imagined as a long rectangular piece of fabric which is folded lengthwise at first (with the free margins upwards) and in a zigzag way afterwards. In the model drawing half the number of the elongate seam scales were omitted to show the skin fold to which they are attached. In reality the fringe scales alternate on the right (simple hatching) and left side (interrupted hatching) of the duplication. (the alternating position of marginal scales of the left and right body side is principally the same as in *Sitana sivalensis*, (see article p. 87, fig. 6, midventral line). When the zigzag structure is pulled straight the fringe scales form an uninterrupted series. They are in line with the anterior and posterior lamellae, as indicated by the fat resp thin broken connecting lines. The folding and unfolding of the zigzag structure is easily understood, but here are difficulties at the junction of the two systems where fan and zigzag structure meet. They are attached to one another but fold in different ways. The soft skin which connects both systems absorbs the strain which is caused by their different senses of rotation, and there are definite folding lines.

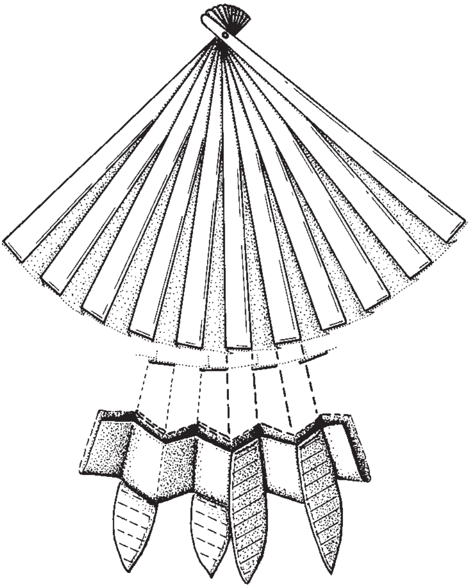


**Fig. 16.** "Japanese fan model" of the *Sitana ponticeriana* fan. For explanations see text.

Our model forms two stacks when folded: One of the Japanese fan and another one of the zigzag fringe lamellae.

The *Sitana ponticeriana* fan is still more complicated than our simplistic model as there is not only one pivot point for the scale rows (as is for the Japanese fan lamellae) but they are attached in a line reaching from the throat to the midventral region. Secondly the scale rows are of increasing length, with exception of the last ones. For this reason the folded fringe scales do not form a simple stack, but they form a midventral double row (article on p. 101, fig. 7) with left and right elongate scales alternating. Below them the lateral fan scales are tightly stacked with only their margins visible. During fan extension the lateral scales are drawn apart and off their stack, and the skin from both sides is drawn toward the midventral line.

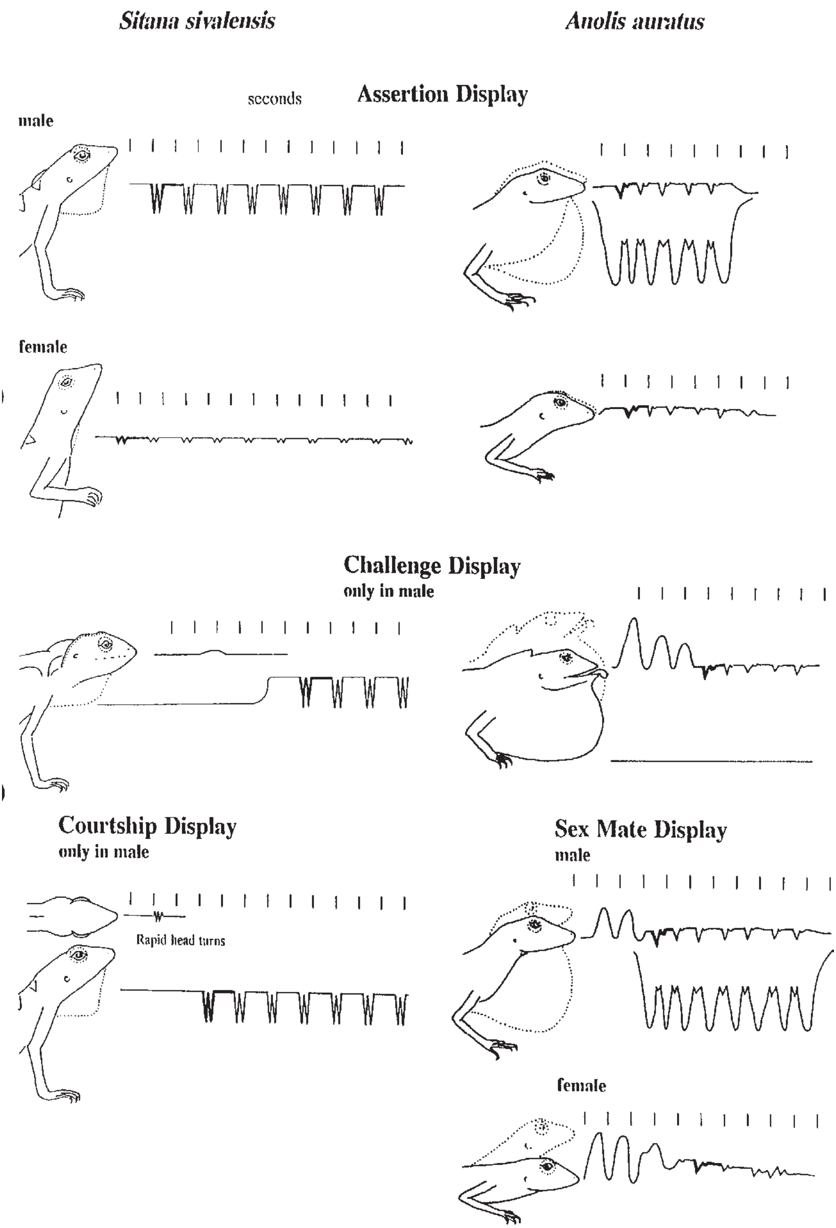


**Fig. 17.** Displays of different function are "tagged" with signature sequences which are marked as bold lines. In *Sitana sivalensis* signature units consist of double flickers of the gular fan, in *Anolis auratus* (after Kästle, 1963) they consist of rhythmical head nods. The kind of record used here is called DAP (display action pattern)-graph.

3.1.1.3 Nuchal and dorsal crests:

During challenge display both *S. sivalensis* and *S. ponticeriana* erect a short nuchal crest (roach, fig. 30 ff) by contracting the nape skin into a small fold. *Sitana ponticeriana* is capable of erecting a much longer dorsal crest which is separated from the roach by a gap.

3.1.2 Social behaviour

(Act systems directed against and released by conspecifics)

The following scheme shows the observed types of interaction between conspecifics:

**juvenile**——————————————————**juvenile**
very scarce hostile interactions; frequent body contact during rest

courtship and mating, frequent body contact →
**male**——————————————————**female**
| ← mating posture, rejection behaviour, rarest short attacks|
| |
| challenge display and fighting, fleeing, | rare short attacks,
| eventually subordination | frequent body contacts
| body contact avoided |
| |
**male** **female**

In *Sitana sivalensis*, much more than in *S. ponticeriana*, the simple schematic classification of main display types which were originally described for iguanids (Carpenter & Ferguson, 1977) is suitable. In males we can distinguish assertion, courtship and challenge display, each of which can contain a sequence of signature display (see next paragraph). Females perform different types of rejection displays against courting males which are difficult to interpret. Female assertion (fig. 19) is only performed under exceptional conditions.

In adults the only spontaneous signal act is assertion, a combined signal consisting of exposed position, elevated posture and signature display.

Note that the rapid head turns which are typical for courtship never appear in combination with threat acts. The signalling of non-aggressivity by the male is an important function of courtship and one prerequisite to inhibit the female's flight when the male approaches.

### 3.1.2.1 Signature display

Species-specifity is one of the most important qualities of display actions, above all if the ecosystem comprises several similar sympatric species. A lot of work has been dedicated to species-unique display types in anoles (Carpenter & Ferguson, 1977) where signature normally consists of stereotypic gular fan and body motions. If a species' display system has evolved towards signal diversity (e.g. assertion, courtship, challenge), specifity can be guaranteed by using a common "tag" (drawn in bold line for *Anolis auratus*, fig. 17) which can be added to different display forms and is called signature display in allusion to the signature of a letter which allows to identify its sender.

The signature display of *Sitana sivalensis* is of a very simple type and consists of two short extensions of the gular fan for which we propose the term "double flicker" (fig. 17, 18,19). In contrast to many iguanids and other agamids body motions like pushups or nods are lacking during assertion, but are a component of challenge. Double flickers are constituents of assertion, courtship and challenge display. In contrast to *S. ponticeriana* the amplitude of gular fan extension remains rather constant in adult males. Signature display lacks entirely in *Sitana ponticeriana*. Its gular motions look like random sequences. The following table shows the role of *Sitana sivalensis* signature display as a constituent of display types. At the same time it gives an idea of their complexity:

| | Position | Orientation | Posture | Signal motions |
|---|---|---|---|---|
| Assertion | exposed | random | erect | only signature |
| Courtship | near female | versus female | erect | rapid head turn<br>+ signature |
| Challenge | near rival | parallel or antiparallel | threat | slow pushup<br>+ signature |

Counts of flickers per sequence are somewhat arbitrary as the flicker series are sometimes interrupted by short pauses of one or a few seconds. These interruptions were neglected and the whole number of flickers was counted. The maximal number was recorded in a threatening juvenile of four months with 31 signature double flickers in one series.

We made no records on the number of units in flicker sequences during assertion, courtship and threat/challenge display, but the sequences are apparently much longer during threat (average about 16 flickers) and attain but half the counts which were observed during assertion or courtship.

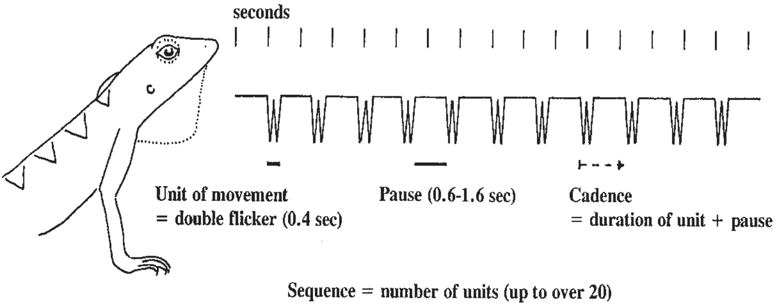


**Fig. 18.** Record of a signature flicker sequence in a male *Sitana sivalensis* (terminology after Carpenter, 1962). Motions during male assertion is identical with signature and performed in an exposed position and elevated posture.

### 3.1.2.2 Assertion

An asserting male informs his conspecifics of a territorial *Sitana*'s presence and this is the only display type which is released spontaneously i.e. without the presence of a conspecific. Assertion can change into courtship and challenge as soon as a female or rival is detected. Assertion display is performed in an exposed position, on a stone, branch or bunch of herbs with the male taking an elevated posture with high forebody (fig. 18). Short sequences of double flickering alternate many times with pauses of some seconds in which the lizards looks around, turning its head one or two times. Assertion may be interrupted by long pauses of many minutes or by a change of position. In captives with established social order only the high-ranked male performed typical assertion and was visible, mostly in exposed position, during his entire activity period while females remained much less mobile and exposed. The inferior male once (04.01.95) performed double flickers in unexposed position with horizontal body. Later in the year assertion seemed totally suppressed in this male.

As the asserting animals are not always in a state of social arousal any colour pattern of the gular fan may be lacking in young males, but the blue streak persists, sometimes faint, in adult ones.

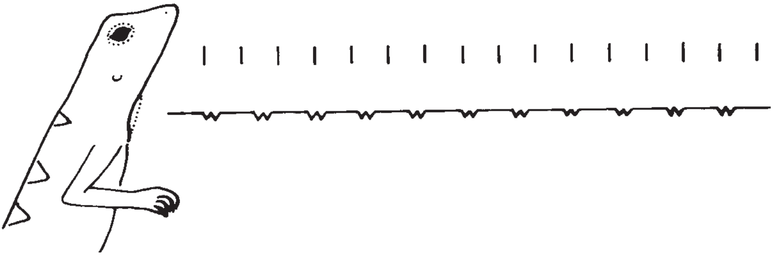


**Fig. 19.** Assertion in a female is only observed in the absence of a male.

Assertion in females (fig. 19)

During more than a year of our observations we believed that assertion lacks entirely in females. Finally we saw this behaviour in a group of five females without a male. Evidently the presence of a mature male inhibits female assertion (fig. 61), which has otherwise many similarities with the corresponding behaviour of males:

1. Long series of double flickers - up to 24 - were counted as a maximum
2. Exposed position e.g. on a branch
3. Elevated posture with stretched forelegs and lifted chin
4. During very intense female assertion even rapid head turns like those in male courtship were observed.

Between display sequences the high-ranked female often sat with a bulging hyoid apparatus which characterised her gular profile.

Assertion makes "lonely" females spectacular and might serve to attract males.

In ***Sitana ponticeriana*** males the gular flickers are totally irregular in an impredictable sequence. Their role in different *S. ponticeriana* forms has not been studied.

### 3.1.2.3 Courtship

In *Sitana sivalensis* courtship is often released by the locomotion of a female, e.g. in connection with her feeding. In its typical form it consists of three parts: Rapid head turns, signature display and neck bite hold.

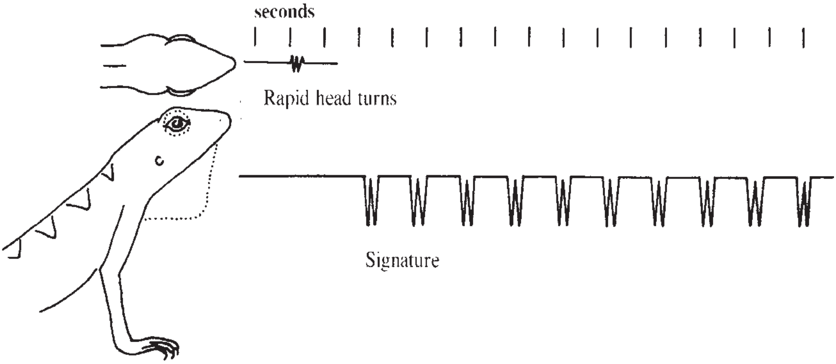


**Fig. 20.** Composed courtship of a *Sitana sivalensis* male.

1) Head turn display (fig. 20) is performed in a similar posture as during assertion: The head turns rapidly three to five times from side to side with a wide amplitude. The male takes an elevated posture with his chin turned towards the female. The dark gular stripe becomes intense and strongly contrasting with the white throat.
This display can be performed on the ground and on plants.
2) The following sequences of signature display (double flickers) are longer than during assertion and may increase in length with ongoing courtship, e.g. starting with 5 and ending with 21 consecutive double flickers.
3) Neck bite courtship (or its intention movement) may follow the rapid head turns and is a first step towards copulation. It is regarded as a part of courtship here as it serves to test the female's reaction, and the interaction is often interrupted here when the male is rejected. During this part of courtship the female normally sits on the ground.

The components of courtship display may appear isolated or in different combination. They are subject to remarkable changes during the reproductive season: In males which are not yet sexually mature courtship consists only of rapid head turns plus signature display. With beginning sexual maturity the neck bite hold is often added. Later in the summer with increasing individual acquaintance the sequence is simplified and one or both introductory parts can be omitted. The following stages which do not follow a strict temporal regime can be observed:

| | |
|---|---|
| 1) Rapid head turn + signature | in spring, no copulations |
| 2) Rapid head turn + signature + neck bite | fully developed in early summer |
| 3) Rapid head turn + neck bite | late summer |
| 4) Neck bite only | maximally reduced, immediate copulation possible. |

In ***Sitana ponticeriana*** (male from animal trade) courtship is similar to that of *S. sivalensis*, but the ritualization of head turn display has gone much farther: The elevated posture has become vertical and the gular flickers have changed into pulsations in which the hyoid apparatus moves in anterior and posterior direction (fig. 21 left, 22). This act is apparently lacking in the form from Palatupana (Kratzer, 1980; fig. 21 right) and Puri (own observation). Similar motions were observed as intention movements of flickers in juvenile *S. sivalensis* males. In spite of the reduction of motion amplitude the pulsations are very evident because of the shimmering light reflections of the bluish gular scales (fig. 22).

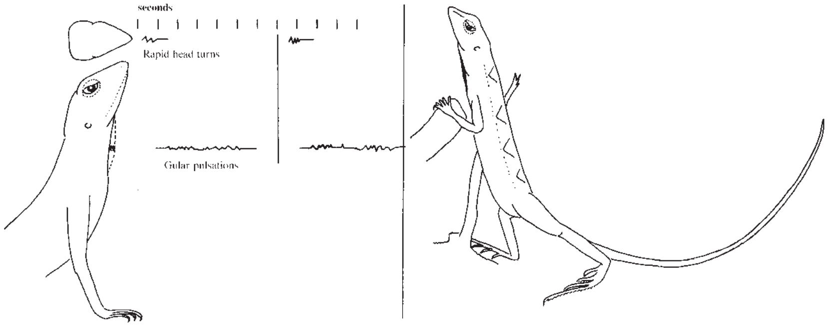


**Fig. 21.** Courtship in two forms of *Sitana ponticeriana*: In the male from animal trade (left) it consists of rapid head turns followed by gular pulsing (two sequences); the Palatupana male (right) remains in upright posture exposing his dark blue gular streak.

### 3.1.2.4 Female reaction to courtship

Courtship sequences were observed as early as mid April, but the first copulation was recorded in end June (fig. 25).

The reactions of reproductive females to courtship display are ambiguous and anything else but a simple receptivity / rejection alternative as in *Pogona (Amphibolurus) barbata* or *Agama agama* (Carpenter & Ferguson, 1977, fig. 10 b,c). The difficulties of interpretation result from the observations that non-receptive females react to courtship in different ways (fig. 24), and female submissive behaviour can release copulation or not. This act system is highly ritualised and combines lowered head, arched back (both similar to the mating posture of *Agama agama,* Harris, 1964) and an alternating wipe with the hindlegs on the substrate which is characterised by its rapidity and low amplitude similar to that at the begin of sand-bathing (shimmy-burying). The wiping lasts about one second and is not repeated while the arched-back posture is kept for about 5 seconds.

Non-receptivity in non-gravid young females mostly leads to simple evasive reactions as fleeing, hiding or struggling loose from the neck bite hold. Flight behaviour is often reduced to an intention movement as it may cover only a few centimetres. In one case the cover under which the female hid was the male’s venter!

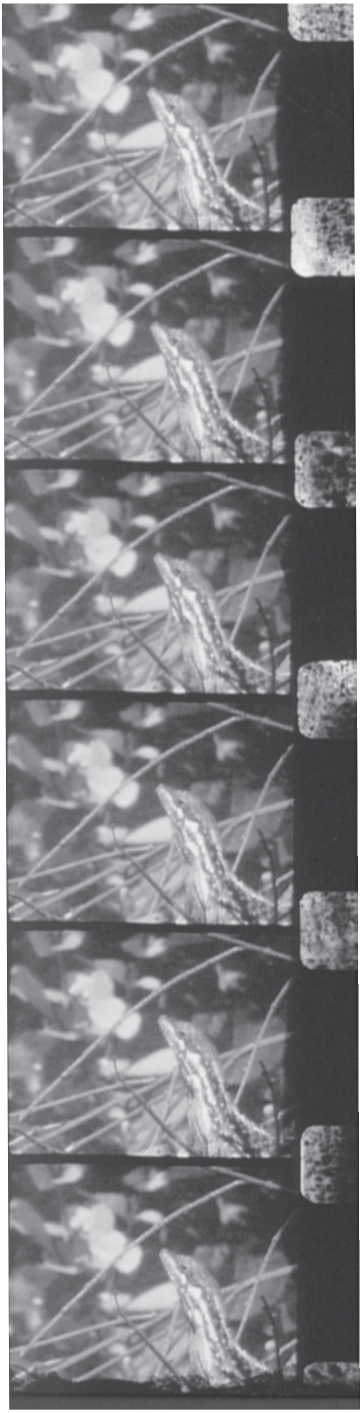
Reactions of gravid females are graded from total passivity over flattening on the substrate with body wriggling similar to sand bathing, but also submissive behaviour with arched back with or without hindleg wiping. The full rejection act system may even be released by a “neutrally” approaching male which jumps after an insect near the female.

In case of rejection the males leaves after a few seconds, resumes assertion behaviour or returns to court.

### 3.1.2.5 Mating (fig. 24-28)

In *Sitana sivalensis* the mating sequence as a whole is very complicated and somewhat plastic, but is always performed on the ground. This regards male neck bite courtship as well as female submissive or rejection behaviour (see preceding chapter). In captivity where the animals live relatively close together in many cases courtship display was omitted and the male ran directly towards the female trying the neck bite hold.

The mating sequence is characterised by the fact that the male's neck bite hold lasts only a few seconds until cloacal contact is attained, and that the position of the two animals changes during copulation from parallel to almost antiparallel position.



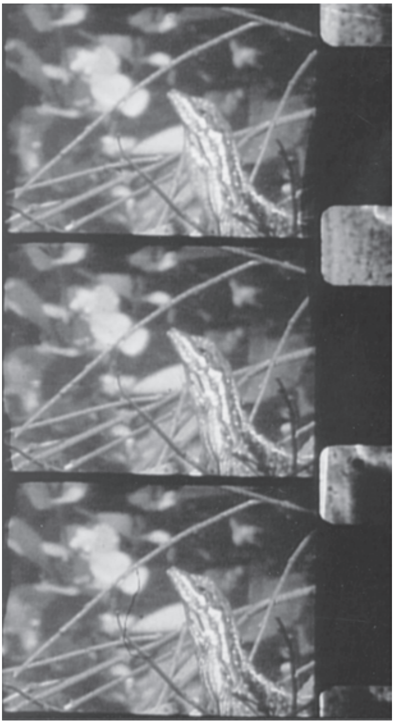


**Fig. 22.** Gular pulsation causes moving light reflexes on the gular scales of a courting *Sitana ponticeriana* male (from animal trade). Sequence from 8 mm film.

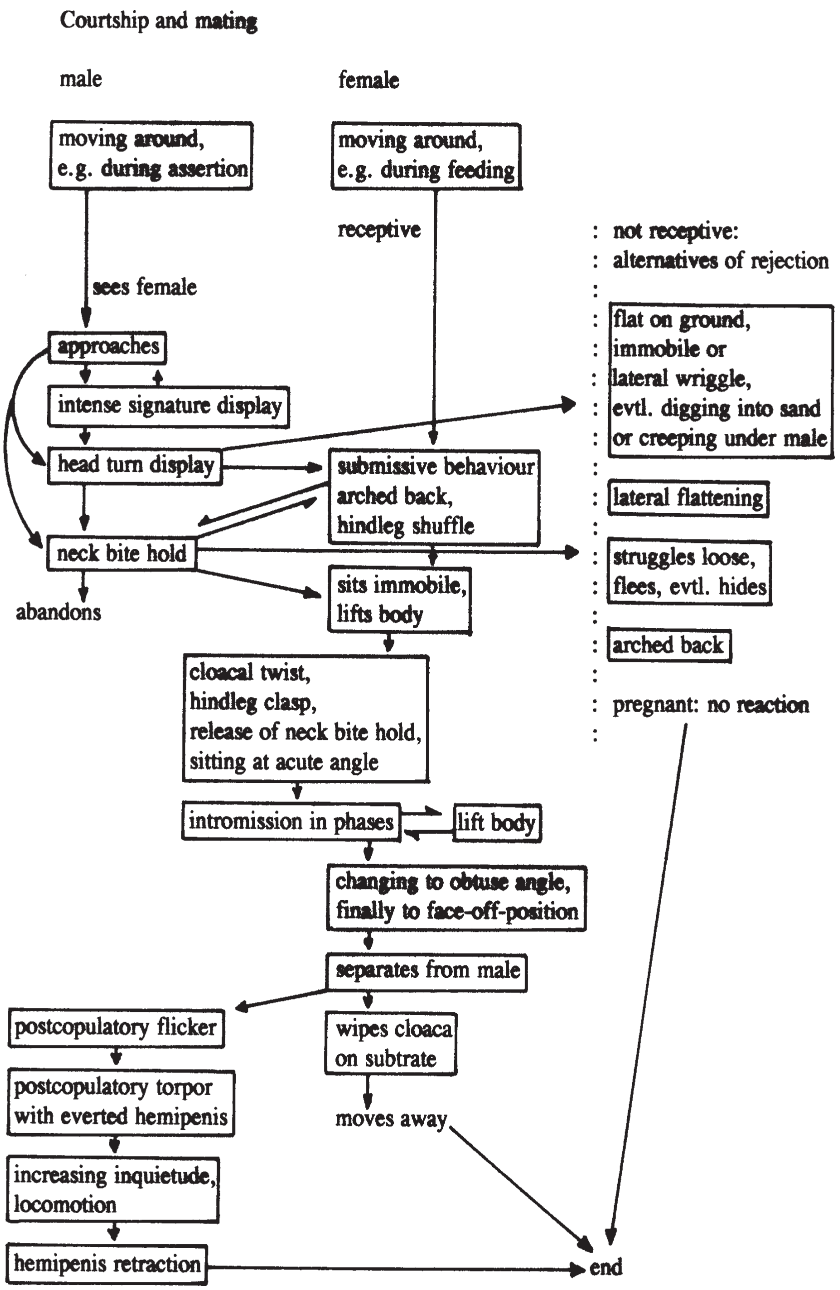


**Fig. 23.** *Sitana sivalensis*: flow diagram of reproductive activities

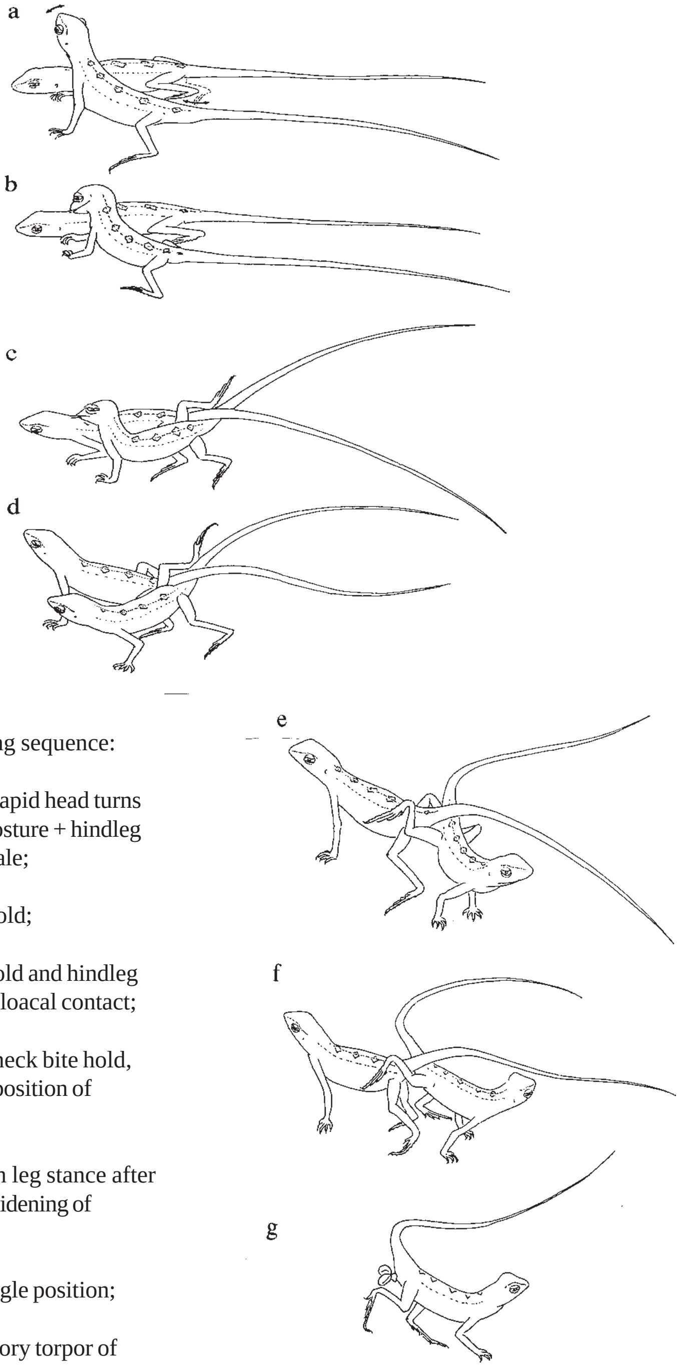


**Fig. 24**. Mating sequence:

a. Courtship: rapid head turns in male, flat posture + hindleg shuffle in female;

b. Neck bite hold;

c. Neck bite hold and hindleg grip of male, cloacal contact;

d. Release of neck bite hold, narrow angle position of mates;

e. Female high leg stance after intromisson, widening of position angle;

f. Stretched angle position;

g. Postcopulatory torpor of male with everted hemipenis.

The following phases can be distinguished (fig. 25):

| | | duration |
|---|---|---|
| 1 | Courtship | |
| 1.1 | Head turn display | |
| 1.2 | Neck bite hold courtship | a few sec |
| 2 | Neck bite hold and cloacal contact | 2-3 sec |
| 3 | Copulation | |
| 3.1 | Release of neck bite hold and intromission | 3 min |
| 3.2 | Immobility phase in narrow angle position | 10 min |
| 3.3 | Stepwise widening of angle | 20 min |
| (3.4) | Long sequence of double flickers; copulation 29.07. 1995) | |
| 4. | Separation | |
| 5. | Postmating behaviour | |
| 5.1 | Male postmating display | 5-15 sec |
| 5.2 | Male postmating immobility | 7 min |
| 5.3 | Male postmating mobile phase | 10 min |
| 5.4 | Hemipenis retraction | 2 sec |

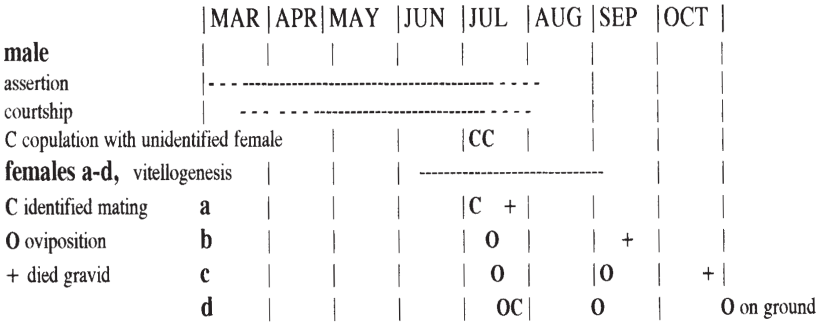


**Fig. 25.** Temporal survey of reproductive activities
Note the early beginning of male reproductive behaviour. In two of the four observed copulations the females were not identified.
Of the four females only female d survived three ovipositions, but did not deposit her third clutch normally.

1. Courtship display differs from assertion by its orientation versus a female and by the strongly ritualised lateral head movements (fig. 20,24a). Its most advanced state is characterised by short attempts of neck bite hold. The receptive female may react by lying flat on the ground with lowered head and slightly arched back and perform rapid shuffling motions with her hindlegs (like those observed during bathing in sand or wet grass). Even then the male often quits, but may start another attempt within a few minutes.

2. If the male was able to fix a firm neck bite hold (fig. 24b) he puts a hindleg over the female's pelvic region (fig. 24c), clasping around the female's tail base and taking a firm hold there. The initial mating posture is similar to that of most other lizards, but lasts only a few seconds.

3. Copulation

3.1 The neck bite hold is released as soon as abdominal twist and cloacal contact are performed (fig. 24d) with the female standing in elevated posture now. Both mates are fixed in mating position by the male's hindleg passing above the female's tail base. Then intromission begins, on which the female reacts by stretching her hindlegs five times for about one second in intervals of 4-6 seconds. The intromitted hemipenis is on the body side the hindleg of which is lifted.

The following phases of copulation are characterised by the fact that the angle between the bodies of the mating animals remains constant for about 10 min and then widens successively until it is more or less stretched.

3.2 During the subsequent immobility phase the mates remain subparallel or at an acute angle with only a few isolated double flickers of the male.

3.3 A stepwise widening of the angle between the bodies (fig. 24e,f; 26) may follow small motions of the female: short lifts of the tail or a hindleg. But mainly the male is responsible for the changes which even can lead to the head-off-position. During that time the male exerts single signature displays or short sequences for about 3 min.

4. Separation can be induced by any of both mates.

5. Postmating behaviour

5.1 Postmating display consists of a few double flickers which can be preceded by a gular spread. In one case the first gular spread lasted 6 sec and was followed by four double flickers; a second spread of five sec was again followed by four double flickers.

5.2 During postmating immobility the male remains on the place in high stance with everted hemipenis (fig. 24g,27).

5.3 The male postmating mobile phase includes several bouts of locomotion which may consist in forward jumps or hopping on a twig with the hemipenis still everted. During this phase the male reacts to approaching females with assertion displays.

5.4 Hemipenis retraction may take place as late as 23 min after separation and lasts only 2-3 seconds. On his way from the copulation locality the male may wipe his cloaca on the substrate.

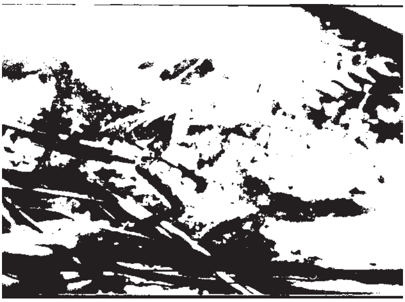


**Fig. 26.** *Sitana sivalensis*, copulation phase e.

**Fig. 27.** Mating phase g.

Protocol of a mating sequence from July 29, 1995 (fig. 28; hours in summer time):

Courtship :

13:45 After courting with some rapid head turns the male quickly approaches the female which lies flat on the ground and shuffles with her hind legs. Lateral neck bite hold after some seconds.

Neck bite hold and cloacal contact:

The bite hold changes to the dorsal neck region. The female changes to a high-legged stance while the male establishes cloacal contact and fixes it with the hindleg clasp. Immediately after this the neck bite hold is released.

Intromission:

The female lifts her hindbody five times in distances of 4-6 sec

13:48 A three min long sequence of double flickers begins. The mates stand at an angle of about 40°

Changes of angle:

13:51 Another short series of double flickers.
13:55 The males changes position; the enclosed angle is now 45°.
13:56 The female moves her tail
13:59 The female lifts her hindbody.
14:02 Another lift of the female's hindbody; the males turns to a 120° position.
14:04 The female moves to 135°
14:08 The male pulls and changes to 160°.
14:14 A long series of double flickers.
14:16 The female terminates the copulation by moving away. She wipes her cloaca on hard substrate and starts basking.

Postcopulatory behaviour of the male:

After some more double flickers he sits immobile.

14:23 He jumps 3 cm forward.
14:25 Another small jerky forward motion.
14:27 Moves 2 cm forward.
14:29 Another 3 cm movement.
14:30 He performs some double flickers versus a close by female and jumps on a branch (with hemipenis still partially everted), basks.
14:34 More double flickers versus the female.
14:36 Double flicker and a small motion forward.
14:39 The hemipenis is quickly retracted. The male jumps from the branch.

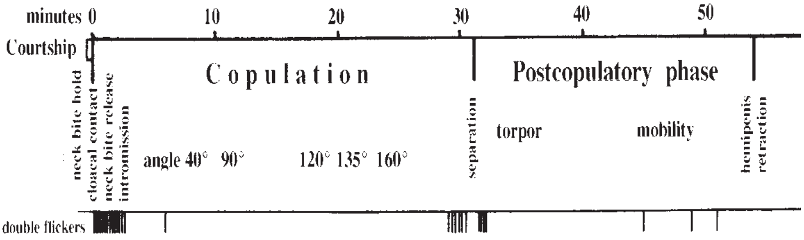


**Fig. 28.** Temporal sequence of mating phases: Note the very short duration of courtship. The final neck bite hold directly leads to cloacal contact and is at once released as soon as the hindleg clamp forms a firm hold. The angle between mates enlarges stepwise until the mates look in opposite directions. The female leaves the male which stays in torpor. Prolonged double flickers of the female are typical for the beginning and end of copulation.

***Sitana ponticeriana*** from Tirupati (Subba Rao & Rajabai, 1972b; Subba Rao, 1983): Females become mature with a snout-vent length of 36 mm and attain a maximum SVL of 52 mm. The average size of mature females is 48 mm while mature males measure 42-56.5 mm.
Vitellogenesis takes place from April to September, ovipositions from July to October.

Two matings were observed, one of them on Aug. 28, at 15:30 . The male grasped the female and their tails twisted together for 2 min 5 sec. The male took a firm hold and twisted his cloaca against that of the female. Copulation lasted about 2-3 min. The authors remark that the action sequence was the same as in *Calotes nemoricola*. Typical acts recorded from *Sitana sivalensis* as neck bite release, hindleg hold or postcopular torpor are not mentioned.

### 3.1.2.6 Challenge and aggressive behaviour, territoriality

While the challenge behaviour of adult males is highly ritualised the aggressions of females generally lack any form of display. They simply serve to fend off approaching conspecifics. In most cases these were coming too close while catching prey. They are chased away with a short launch with open mouth but without biting. Courting males are never attacked this way. Only on one occasion a female reacted aggressively to an approaching male which chased an insect.

**Fig. 29.** Threatening male with temporal ridge, a character of the threat face.

The full challenge repertoire of adult males appears with sexual maturity. They show the threat posture with half or full gular extension over several seconds, plus signature displays. Besides short sequences of double flickers the act systems were identical with those observed in many other lizard families. During lateral threat a sort of slow pushup can be seen occasionally. It may be followed by a sequence of double flickers.

Rival behaviour is distinctly graded and shows the following steps:
1. Lateral flattening with elevated stance and transverse orientation. By contraction of skin muscles a nuchal roach and dorsolateral ridges are formed. This way the dorsal region takes the shape of a roof which juts a little over the flanks.

A very peculiar trait which perhaps is unique for this species, but lacks in *S. ponticeriana* is the "threat face" with a temporal ridge bent downwards from the orbital region (fig. 29-31). Apparently this skin fold is formed in a similar way as the nuchal ridge by the contraction of subdermal muscles. A facial threat expression seems rather unique among reptiles and is probably an autapomorphy of *S. sivalensis*.

The eyes are widely opened with the lid opening no more forming a slit but a circle.
2. An additional gular spread
3. A single slow up-and down pushup (fig. 30), eventually double flickers
4. An additional gape with protruded tongue.

If the rival responds the challenge both males orient themselves in antiparallel (fig. 31) or parallel position. With increasing fighting motivation both contestants approach each other for a close threat and finally change from threat to damaging fight (fig. 32).

In contrast to challenge display fights are a very rare event and were observed only in a short period from June 24, to July 27. The rivals tried to take a bite hold on flanks or limbs, holding firm for about one minute. One single fight apparently decided the social position of both males and established it until the looser died, possibly from social stress one week later.

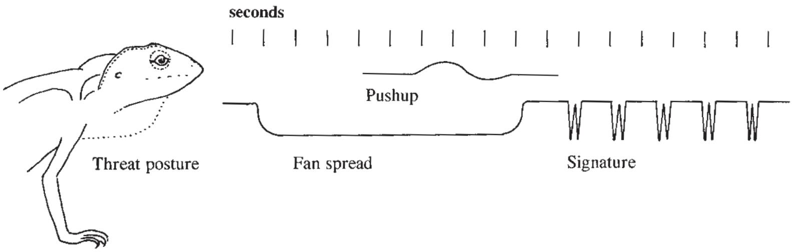


**Fig. 30.** Challenge with fan spread and pushup in *Sitana sivalensis*.

The record of social disputes among males covers over one month:

May 29: The two males perform assertion displays in a distance of 8 cm without reacting to one another.

June 6: The two males rest on top of each other without any hostilities.

June 9: Repeated short threats and attacks with open mouth against the smaller male when it chases a cricket.

June 13: The two rivals sit closely together without interactions.

June 16: The smaller male chases a cricket, approaches the larger one. He is heavily threatened, and attacked with open mouth. He flees.

June 17: Several short chases of the males.

June 18: The males sit closely together, ignoring one another's assertion. Only a short challenge display of both.

June 19: Rivals threatening against one another without further interaction.

June 23: Repeated challenges followed by short bite attacks, mostly against the dorsal region. No bite holds.

June 25: Repeated challenges with parallel or antiparallel position at a distance of up to 20 cm distance followed by bite attacks and clinches during the whole morning. Records from 8:30, 8:55, 10:35. Only one male takes a hold. Once a rival lay on its back with the adversary biting into his flank. Fights are interrupted by threats at close distance with open mouth. The superior male changes to a bright coloration.

June 26: In the morning the superior male attacked the awakening rival's head peering out between plants.

June 27: Prolonged challenge displays and damaging fights beginning at 8:30. A rank order is established.

July 1: No more fights but evident behavioural differences proving dominance (see top of following page).

July 2 and 3: Inferior male hides or flees and is no longer attacked.

July 4: At 7:30 hemipenis eversion of inferior male. At 9.30 the inferior flees immediately after being threatened, dies 13:30 evidently from social stress. This mortal event was certainly caused by the spatial restriction in which the captive males were forced to live.

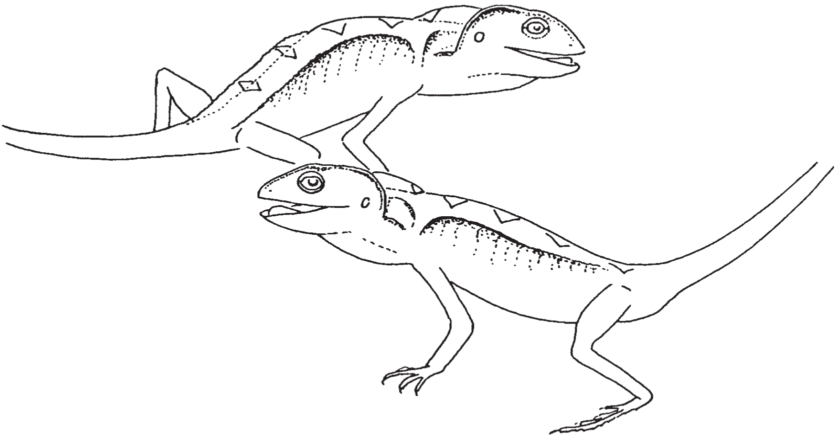


**Fig. 31.** Challenge display in *Sitana sivalensis* : antiparallel (head off) position during close-range threat. Note the lateral head ridge, a trait lacking in *S. ponticeriana*.

After a damaging fight ending with established dominance (June 27) both contestants show typical signals:

In the winner the eyelids and nuchal roach are bluish green, the upper head is gray. In the looser all these parts of the head are brown. During the following days the bright colours of the winner fade somewhat.

Dominance of one male influences behaviour as follows:

| **superior male:** | **inferior male:** |
|---|---|
| frequent change of perch | mostly immobile |
| exposed seat during the activity period | stays hidden |
| frequent assertion display | no assertion |
| courtship and mating activities | no sexual activities |
| attack without preceding challenge | fleeing without preceding challenge |
|  | death, probably from social stress |

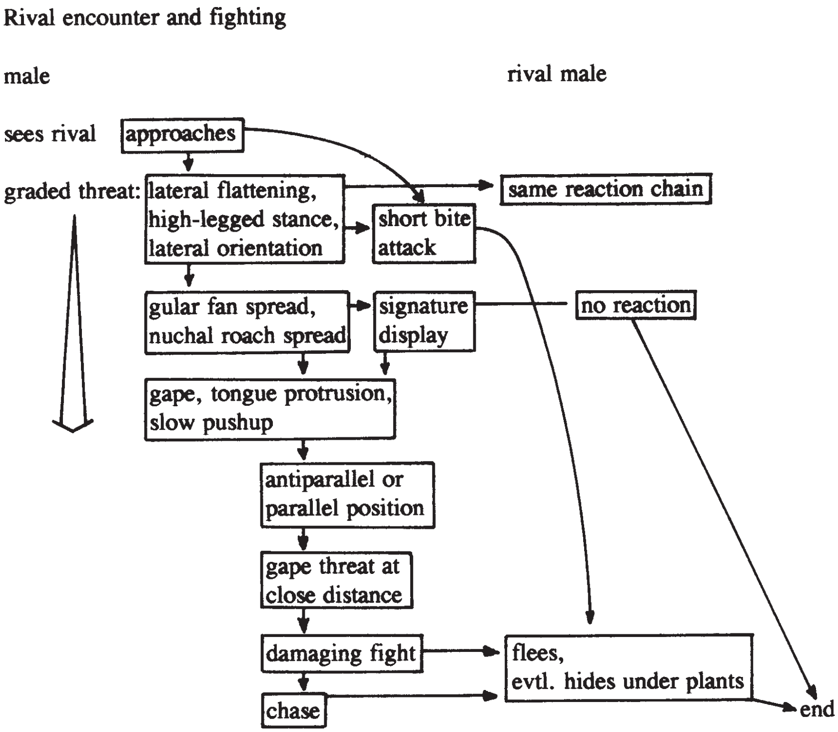


**Fig. 32.** Flow diagram of rival behaviour in *Sitana sivalensis*.

In ***Sitana ponticeriana*** there are differences from *S. sivalensis* in threat posturing and display motions.

Both species can erect a nuchal crest (roach) and dorsolateral ridges. The latter are continuous in *Sitana sivalensis* but interrupted in *S. ponticeriana*. But *S. ponticeriana* cannot erect a temporal ridge.

The challenge repertoire is characterised by a remarkable increase in challenge display diversity (fig. 33, 34), where neutral acts as hindleg rise (= bipedal stance, a special case of bipedalism), jump or chew have additionally been ritualised into threat signals. Gradedness is less conspicuous than in *S. sivalensis*, and the single forms of aggressive display follow each other at random.

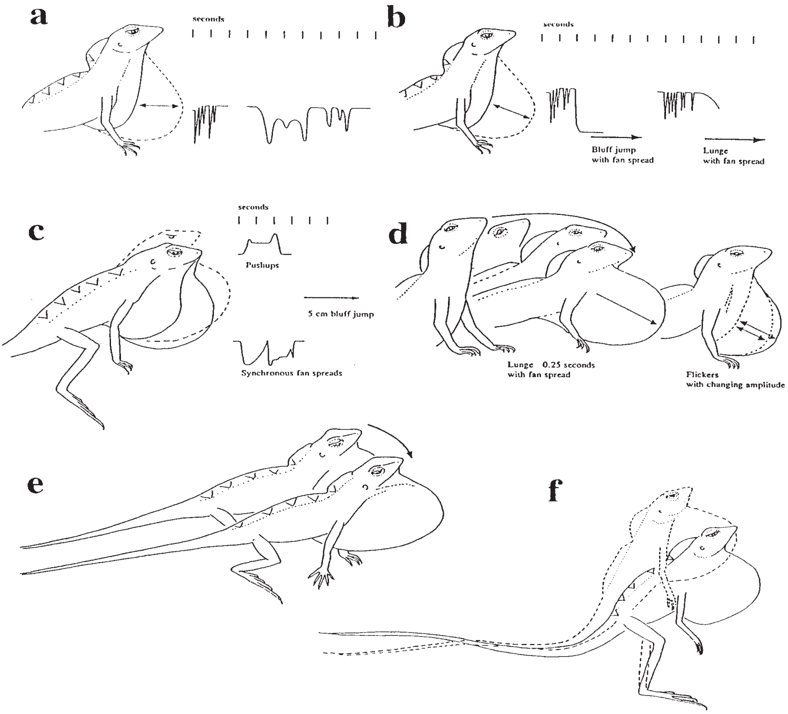


**Fig. 33.** Challenge acts and their combinations observed in *Sitana ponticeriana* from animal trade (unknown provenience) observed during challenge behaviour toward the mirror image: a) Irregular fan flickers and slow irregular fan spreads.
b) Irregular flickers and subsequent jump forward resp. a lunge towards the mirror image. c) Irregular pushups and simultaneous slow fan spreads. d) Lunge towards mirror image with simultaneous fan spread and subsequent irregular flickers.
e) Lateral jump towards mirror image with full fan spread. f) Raising into bipedal stance with fan fully spread.

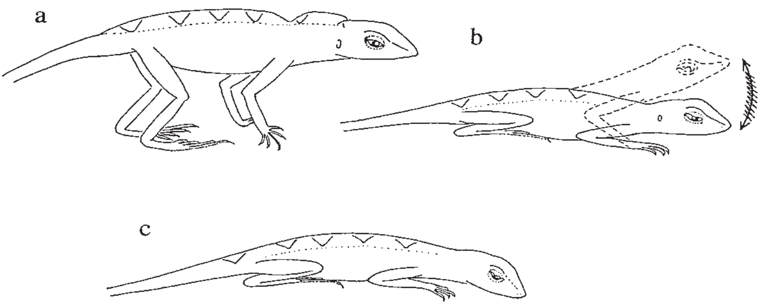


**Fig. 34.** Acts recorded during social encounters in *Sitana ponticeriana* from Palatupana (Kratzer, 1980):
a) Four-legged high stance in a challenging male. b) Pushups with rapid lateral head motions are observed in both sexes in a state of high aggressivity. c) Ducking which signals submission in both sexes.

Threat acts are not totally equal in all *S. ponticeriana* forms (see appendix 1). This is one of the main arguments to consider it rather a species complex than a "classic" species. Tail wave which is a very frequent conflict reaction in other lizards is not common in both *Sitana* forms. This may be due to the fact that the *Sitana* tail is rather rigid, but it is often bent upward in both species as a sign of alertness.

Territoriality in ***Sitana ponticeriana***

**Palatupana** (Kratzer 1980):Territories were inhabited by one dominant male, inferior males and several females (up to seven specimens). Territories were smallest (1-2 m²) in sections with the highest population density. The largest territories (rather home ranges) measured 50 - 100 m².

Subba Rao (1996) measured activity ranges from 20 - 200 square feet, which corresponds to 1.8 - 18.5 m².

## 3.2 Activity patterns

Characteristic for the strictly diurnal *Sitana sivalensis* are pronounced annual and diurnal inactivity phases. Type, intensity and extent of activities differ with sex, season and time of the day.

### 3.2.1 Annual cycle

3.2.1.1 Correlations of developmental phases with the seasons

In the natural biotope adulti were a rarity by the end of September (3 out of 20 specimens caught), and a survival into the second year seems to be exceptional. Most specimens encountered in the field belong to the same age-group. From the three clutches which apparently each female is theoretically able to lay, the first one has the greatest chances to produce a new generation. This is due to the facts that climatic conditions (humidity and warmth) become more unfavourable towards autumn when the second and third clutches should be deposited, and as the time proceeds a considerable number of females probably dies from predation and emaciation in gravid state. During the following seasons the mass of hatchlings which appear in September moves through the following phases:

1. Autumnal growth phase
2. Winter with a high inactivity rate (see following paragraph): In the natural habitat the main climatic changes are
   a. reduced insolation
   b. lowered temperatures (8°C minimum against 22-24° in summer, 26° maximum against 36° in summer)
   c. lower precipitations (almost zero in January against 380 mm in August).
3. Main growth rate in spring: Developing an astonishing appetite the lizards should be fed at least twice a day. During this period the secondary sex characters and forms of social interactions develop; against its end growth slows down.

Intense feeding continues into the following phase.

4. Period of intense social interactions and first clutch in early summer: Dominant males spend most of the day with advertising, eventually courtship and challenge. Female activities are characterised by receptivity. As the vitellogeneses of the first and second clutch overlap, the females are still rather thick after their first oviposition, but they terminate to replete food storage by the middle of August.
5. Reduced activity, second and third clutch phase in late summer.

### 3.2.1.2 Winter inactivity (brumation, fig. 35)

Gregory (1982) admits that a definition for hibernation (winter dormancy) of reptiles is rather difficult and somewhat arbitrary. It includes non-emergence, inactivity, aphagia and metabolic depression under marginal temperatures.
For a number of reasons the term "hibernation" cannot be applied for the wintering state of *Sitana sivalensis*, which might better be called brumation, a term which Auffenberg applied for *Varanus bengalensis* (1994 p. 145). Activities of *S. sivalensis* were recorded over one winter for a couple of adults, over two winters for five resp six juveniles. The state of inactivity was pronounced in the adults while among the juveniles a changing minority remained active.

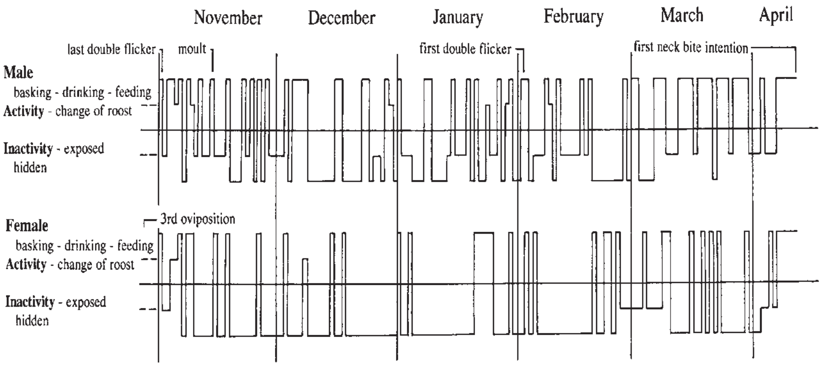


**Fig. 35.** Activity states in a captive male and female recorded during winter. The two steps above the basal line represent two levels of activity, those below the line are levels of inactivity (explanation see bottom of next page).

It is not recommendable to remove captive animals from their terraria for wintering as they continue using their resting places. When the sitanas reduced their activities the daily illumination period was slowly reduced from 13 hrs in summer to 11 hrs in November and 9 hr in December. The acrylic glass cover on the mesh wire lid was partially opened to lower the air temperature to 22° by day (it was much warmer under the lamps). During the night the air temperature fell to about 10°C in cold winter nights.

The main aspects in which the wintering of *Sitana sivalensis* differs from true hibernation is that they use the same resting places as in summer, do not fall into a cold torpor and continue basking, drinking and feeding, but at a reduced rate. Low temperature does not play an outstanding role to induce the resting state.
The shift from normal activity to brumation is by no means abrupt. Already as early as in late August the lizards become more secretive. Some of them reduce their daily activity period to a few hours around noon, or they remain entirely hidden for one or two days. On

the other hand the resting state in winter is often interrupted by changes in position without leaving the site.

Inactivity was considered as interrupted when the sitanas left their resting places, often to bask several hours under a lamp.

The couple of adults entered their inactivity phase during the first week of November when noon temperatures in the terrarium still rose to 25°C. They withdrew into the plant thicket to relatively dark and moist places and even slept free on twigs. Their posture was tilted to almost vertical with much contact to surrounding plants, in sleeping or resting (with open eyes) posture. Changes of resting places occurred from one or two times a day to every few days. In early winter they became active once or several times per week, drank eagerly but took no food. The dark ventral pattern of males is typical for the wintering state as is the white one for the summer activity period.

Full winter inactivity was recorded beginning with Nov. 8. It is characterised by the following change in behaviour recorded for a male and a female.

1. Diurnal activities are omitted for prolonged periods of up to 16 days, but the lizards may keep their eyes open for hours.
2. During the rare activity periods the animals quit their resting places relatively late at 10:00 and returned soon at about 16:00 .
3. They use much of their activity period for basking under a lamp.
4. They feed almost regularly during their activity phases
5. They strictly return to the resting places of which the male had two: An exposed branch which he also preferred in summer, and the narrow space between a flower pot and a window pane. The female chose a totally different locality: Most of the time she hid under a dry fern leaf lying on the sand below the 35 W halogen lamp. This place warms up to 23° by day and was used for sand bathing in summer.
6. Temperature oscillations at the resting sites were measured at the end of January with minima in the early morning and maxima in the early afternoon:

| | | |
|---|---|---|
| Near branch chosen by the exposed male | max. 20 °- 21°C | min. 11.5° - 12°C |
| In a bunch of grass preferred by both | 18.5°- 18.6°C | 11.4 °- 11.9°C |
| On sand surface as described under 5.: | 20.8°- 22.2°C | 10.0 °- 11.5°C |

As our graph (fig. 35 ) renders only the activities of two specimens it is impossible to distinguish if the differences between both animals are correlated with their sex or some other individual factor. In the drawing two steps for activity and inactivity are indicated by different levels above and below the basal line:

Step two (high level activity): basking, drinking, feeding
Activity Step one (low level activity): change of resting place without further actions

Inactivity Step one (weak brumation): exposed on branches or in a bunch of grass
Step two (deep brumation): hidden in bunch of grass or under dry leaves on the ground

Survey of winter activities of two specimens (the same as in fig. 35) with a comparison of mensual data.

| | | NOV | DEC | JAN | FEB | MAR | Total |
|---|---|---|---|---|---|---|---|
| 1. n resting days | male | 16 | 19 | 20 | 23 | 11 | 89 |
| | female | 21 | 27 | 23 | 23 | 23 | 117 |
| 2. n resting periods per month | male | 10 | 5 | 8 | 6 | 5 | 34 |
| | female | 6 | 4 | 3 | 6 | 6 | 25 |
| 3. max.resting period (days) | male | 3 | 7 | 6 | 8 | 4 | |
| | female | 7 | 13 | 16 | 14 | 6 | |
| 4. Average duration of resting periods (days) | male | 1.8 | 3.8 | 2.9 | 2.6 | 2.0 | 2.62 |
| | female | 3.8 | 6.2 | 7.1 | 4.3 | 3.2 | 4.68 |
| 5. Percentage of deep brumation (hidden) | male | 37.5 | 84.2 | 60,0 | 43.5 | 45.5 | 55.1 |
| | female | 90.5 | 100 | 86.9 | 78.3 | 69.6 | 85.5 |

If a resting period extends from one month into the next one it is counted for the month in which it lasts longer. For the case of equal duration in two successive months it is counted for the first of both.

A high number of resting periods (2.) does of course not automatically mean a total of more resting days as the resting periods can be very short.

The average duration of resting periods per month (4.) is the quotient from number of resting days (1.) and the number of resting periods (2.)

The percentage of deep brumation (5.) refers to the total of resting days. The value of 100% (female in Dec.) means that the female spent all her inactivity days during this month in the hidden state.

Results:

Brumation was less pronounced in November and March, but appeared deepest in December and January.

The female's brumation was more intense than the male's: She had the larger total of resting days, higher absolute and average duration of resting periods and a higher percentage of hidden inactivity.

Annual activity of ***Sitana ponticeriana*** (Subba Rao & Rajabai, 1972 a) from Tirupati. Activities in summer and winter are high, and there is no evidence of an inactivity phase during the dry season. The authors do not mention a seasonal shift of age groups due to a population turnover.

### **3.2.2 Diel activities** (fig. 36; see also 3.3.1 - postures)

As the preceding paragraph shows, the complexity and intensity of diel activities change markedly with annual periods. During the low-activity periods the elevated activity states are mainly limited to the time around noon. The decrease of sand bathing (almost exclusively females) during late summer may be connected with the lower metabolism rate of the females at the end of the reproductive period.

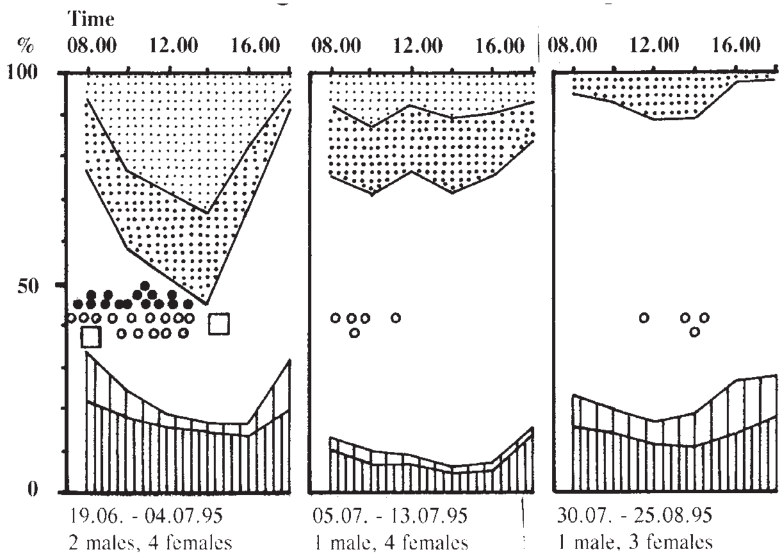


**Fig. 36.** Activity records (in percent of all animals) for captive *Sitana sivalensis* during three summer months. Wide and narrow hatching: half and fully hidden in plants; white: exposed, without thermoregulatory activities; heavy dots: basking under lamps; light dots; sand bathing; full circles: challenge activities; open circles: courtship; squares: matings (total of 715 observations).

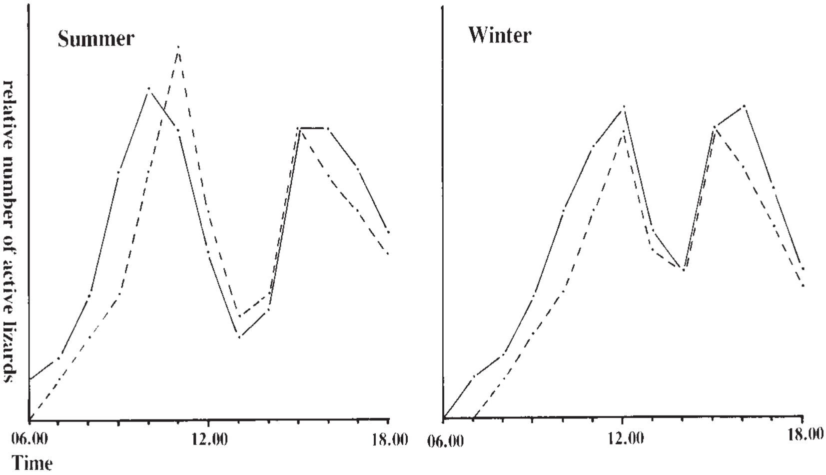


**Fig. 37.** Activity records for *Sitana ponticeriana* from Tirupati during sunny (continuous lines) and overcast (broken lines) weather (after Subba Rao & Rajabai, 1976).

***Sitana ponticeriana*** from Tirupati (fig. 37; Subba Rao & Rajabai 1972a, 1973): On clear days the animals are active from 9-12 h and 15-17 h. The graphic presentation of the activity estimates shows bimodal curves in summer and winter. In both seasons activities are reduced around noon, evidently because of the high temperatures. This is shown by the fact that under laboratory conditions with a constant temperature of 30°C locomotor activity was monophasic. Under these conditions illumination is considered the most important temporal cue (zeitgeber), as activity readily shifts with the light regime.

In the field the animals sleep at the bases of bushes, dug flat into the sand; sometimes they rest on tree trunks.

## 3.3 Multipurpose behaviour

### 3.3.1 Postures (fig. 38, 39)

*Sitana sivalensis* descends to the ground for basking, sand bathing, feeding, defecating, mating, rival combats and eventually fleeing. Males in their passive phases and females spend most time in the low vegetation sleeping or resting and observing. Much of the males' assertion, courtship and challenge display is performed from perches which are not too steep (from horizontal to an angle of 60°). Vertical ones are accepted for sleeping and resting. Often the females hide in grass tufts with ventral, lateral and dorsal body contact with the surrounding blades. The lizards keep themselves on the plants mainly with their sharp foreclaws while one or both hindlegs hang loose or find a support with the scansorial scales of the metacarpal or carpal sole region.

The different states of arousal appear without a change in position and with little difference in posture. In the morning their sequence with increasing alertness is:

1. Eyes closed, head on substrate
2. Eyes open, or closed for phases of several seconds, head on substrate
3. Eyes open, or closed for several seconds, head lifted about one mm above substrate (normal state of females)
4. Eyes open, forebody lifted several mm from substrate (normal state of alert males).

### 3.3.2 Locomotion

In spite of the fact that *S. sivalensis* spend most of their time in low vegetation they are poor climbers. Most locomotion on plants is performed by asserting males which jump over distances of up to 5 cm between twigs, stalks and leaves. The relatively heavy and clumsy gravid females rarely change position.

On the ground bipedal locomotion - which is often mentioned for *Sitana ponticeriana* - was not observed, but on one occasion a specimen sat upright with both forelegs lifted off the ground.

Digging with legs never served to excavate burrows for resting and lacks in the normal locomotion repertoire. Its onset in females is a doubtless sign of imminent nesting and oviposition.

Shimmy-burying with rapid lateral body motions similar to those observed in bathing specimens (see 3.4.4) is observed during thermoregulation (see 3.4.3), hiding for a rest, and escape behaviour (see 3.5.2).

**Fig. 38.** Postures of resting males, frequently exposed on twigs and grass blades. One hindleg is often hanging free.

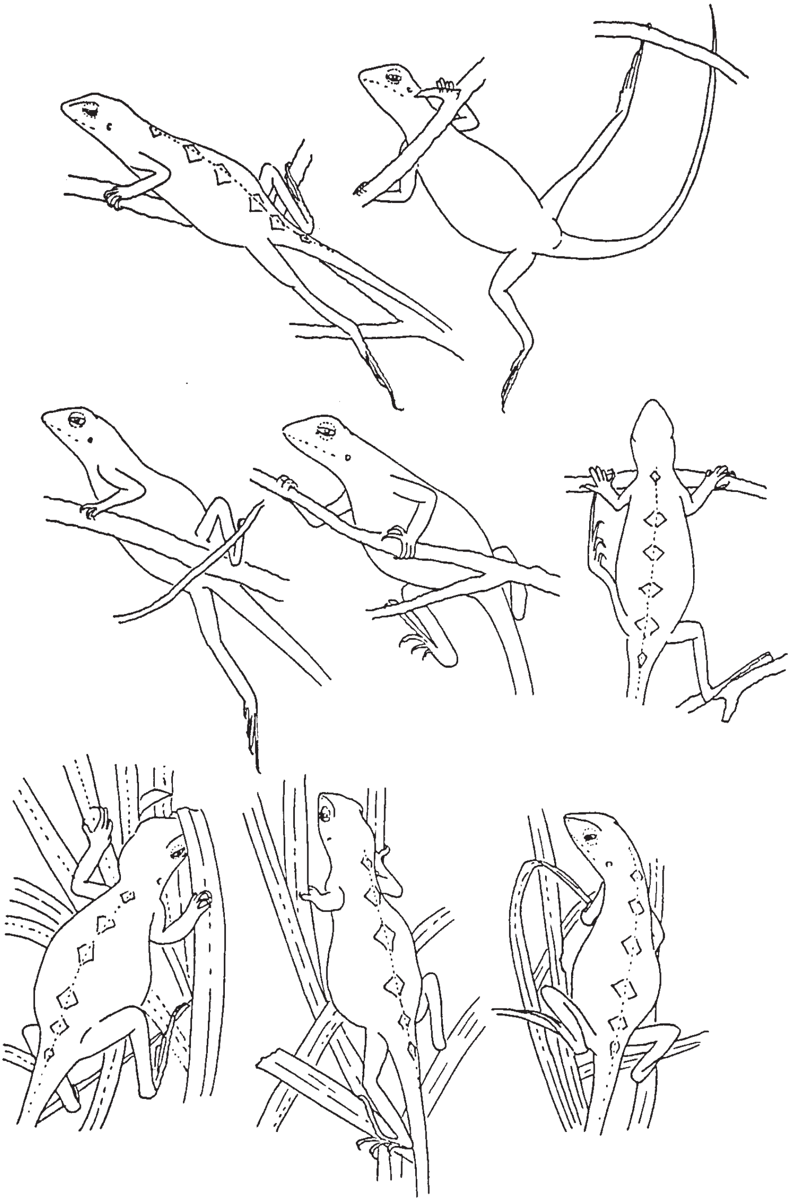


**Fig. 39.** Postures of gravid females, which often rest hidden in grass bunches.

In ***Sitana ponticeriana*** Subba Rao & Rajabai (1972a) observed an average speed of running males (n=12) of 172 cm/sec, in one running female they measured 170.7 cm/sec, which corresponds to 6.1 km per hour. But of course the lizards are obliged to rest aft a few seconds.

The occurrence of bipedal locomotion is apparently more complicated than most authors accept, and probably lacks in several forms of this complex. Commonly *S. ponticeriana* is mentioned to run bipedally at high speeds (Smith, 1935; Deraniyagala, 1953; Kratzer, 1980; Christian & al., 1994; Erdelen, 1996). But Schleich could not observe this during hours of chasing them on the beach of Puri / Orissa. Subba Rao (1996) who has been observing *Sitana* for two decennia states briefly, "they show quadrupedal locomotion".

3.3.3 Observational behaviour (visual survey).

*S. sivalensis* which observe their surroundings intensely do not move their eyelids, as many agamid species do, but only their heads which are turned, lifted or rotated over relative small angles of 30°. Such movements are frequent in males but rare in saturated gravid females which doze over many hours with their eyes closed over phases from 10-20 sec.

## 3.4 Maintenance behaviour

3.4.1 Feeding (fig. 40)

Feeding strategies are presented in a flow diagram which shows their great plasticity in hunting and handling prey of very different agility and from a minimal length of 2 mm up to a maximal one of 12 mm.

The most impressive hunting performance is the capture of low-flying House flies from the air, which has a high failure rate.

Key stimuli for prey catching are locomotion, low distance and relatively small size of prey. Myrmecophagy (eating of ants), which plays a very important role in the *Sitana ponticeriana* complex (see below), is obviously lacking. When captives were offered ants (*Tetramorium caespitum*) they refused them totally or ate only one. Eventually they opened their mouths for a few seconds, evidently irritated by the formic acid of the prey.

Feeding is strongly inhibited if the prey is close to a conspecific (ca 5 mm or closer). In this case the sitana often observes the prey but does not dare to approach it. Another effect under these circumstances is the failure of prey catching. The lizard has to repeat its attempt two or three times before seizing a small caterpillar as the act of snapping is inhibited by the close vicinity of a conspecific.

This inhibition helps to avoid a misinterpretation by the approached lizard which might take this a an attack. On the other hand such "wrong" reactions are not rare, with the approached sitana biting at the animal coming too close, and a short fight may follow. In one case a male even attacked an approaching female.

Chewing motions released by moving prey and interpreted as vacuum activities were observed under two conditions: If the prey was not close by, but in a distance from 10-15 cm, and if the sitanas were saturated.

Captives were fed with small crickets (*Achaeta domestica*), larvae of Wax moths (*Galleria mellonella, Achroea grisella*), larvae of *Alphitobius diaperinus*, flies (*Musca domestica*), small grasshoppers, small sowbugs (*Porcellio, Oniscus*). As they are not specialised, they certainly accept many other insects. Wax moth larvae (they are eaten greedily) should not

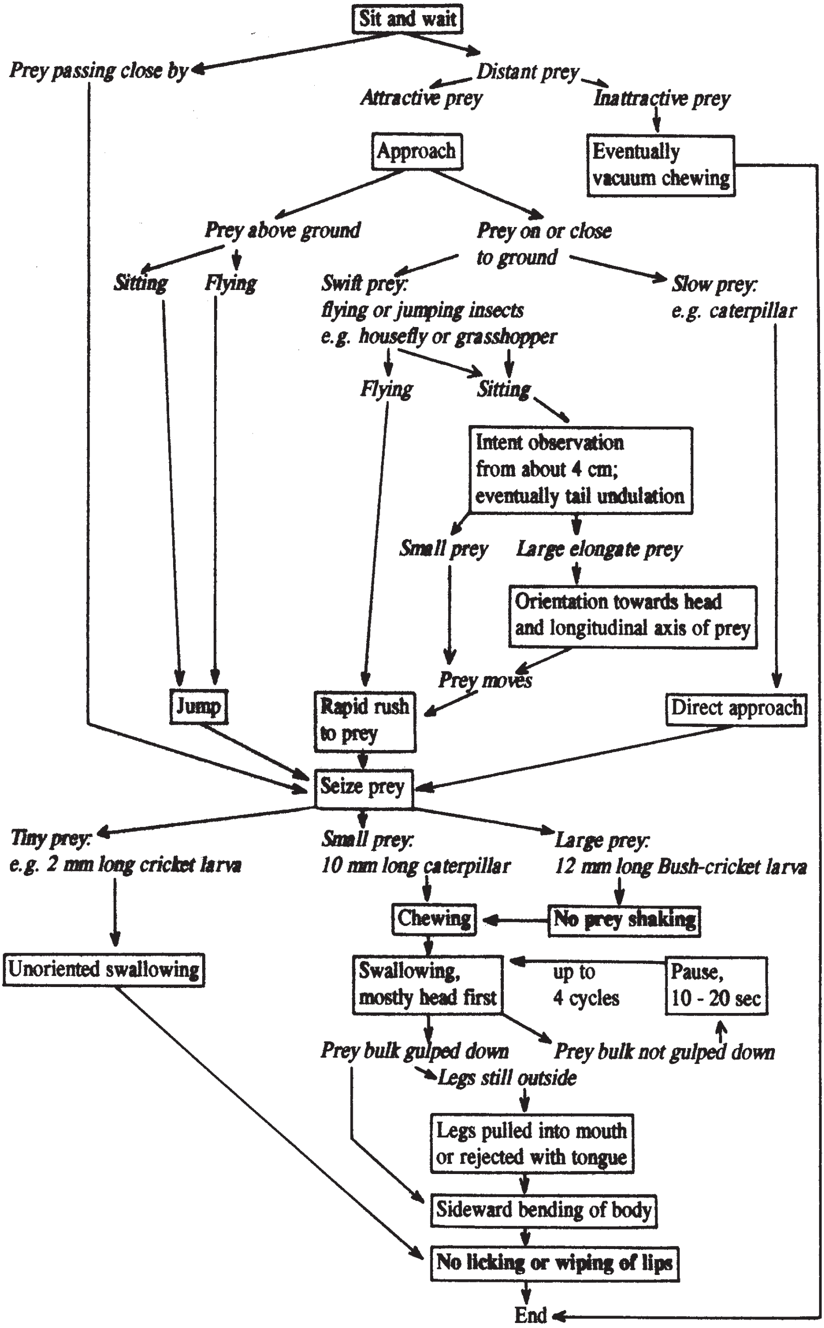


**Fig. 40.** Flow diagram of feeding behaviour.

form the main diet, as the lizards are prone to fattening.
For defecation (fig. 41) the sitanas always come down to the ground.

***Sitana ponticeriana*** from Tirupati (Subba Rao & Rajabai, 1972a): This form also applies a sit-and-wait strategy, perceiving a termite at a distance of 20 cm. Food consists of 65% termites (*Heterotermes indica*), 25% Red ants (*Solenopsis geminata*) and a rest of unidentified insects.

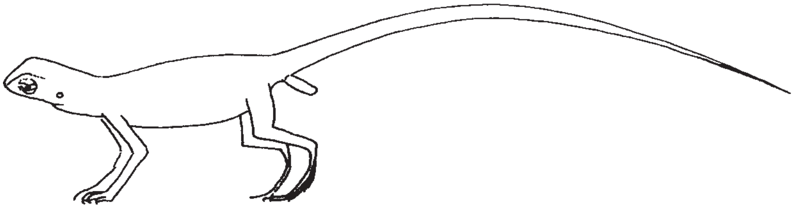


**Fig. 41.** Defecation posture. The fecal pellets are always deposited on the ground.

### 3.4.2 Drinking

The sitanas lick drops of water from leaves but also learn to drink from a dish holding their snout into the water as long as they drink, or dipping it into the water, swallowing and repeating the process several times.
In contrast to other agamids the head is not lifted afterwards. At the water dish they have occasional difficulties finding the open water and sometimes start licking moist stones which arehalf submerged.

### 3.4.3 Thermal behaviour

Over much of their diurnal activity period the sitanas behave as thermoconformers with an air temperature between 25° and 27°C at their preferred resting sites. This is in accord with their stationary and cryptic habits which avoid locomotion except in active territorial males. Social interactions increase markedly between 25° and 30°C.
Thermoregulatory activities consisted of basking under the lamps, sand bathing and gaping (panting). Basking lasted from a few minutes up to several hours (in gravid females) and was very rarely accompanied by special posturing or by a change in body shape (dorsoventral flattening).The intensity of irradiation was regulated by partially hiding below dry leaves. Semiadults repeatedly spread their gular fans while basking.
Panting as a method of thermoregulation was observed twice in a high-ranked semiadult female which sat high on a branch close to the lamp with the body temperature rising to about 40°C. For several seconds she gaped while the tongue was curved upwards. Curiously, both times panting was followed by a sequence of signature display.
In one case a specimen in a cage exposed to the sun fell into heat torpor near 45°C and lay immobile on its side, but recovered in a few seconds in cool surroundings.

***Sitana ponticeriana* group:** Animals from the Tirupati region (Subba Rao & Rajabai, 1972a) showed to be thermoconformens as their body temperatures lay only up to 1°C above or below the air temperature (mostly below it) over the whole range from 25-38°C. Thermoregulatory activities are limited and mainly consist of shuttling into and out of the shadow.
The main thermal set points were recorded as follows:
Activity range: 34.1-37.5°C
Voluntary minimum: 22.0-25.5°C
Voluntary maximum 37.6-39°C
Preferred temperature 35.5°C
Critical thermal maximum 46.5°C
Lethal maximum 47.0°C.

In a more recent statement Subba Rao (1996) calls *S. ponticeriana* "a true heliothermic basker" with "preferred temperatures at 46.5° and 47° respectively", which corresponds to their lethal maximum (see Subba Rao & Rajabai, 1972a).

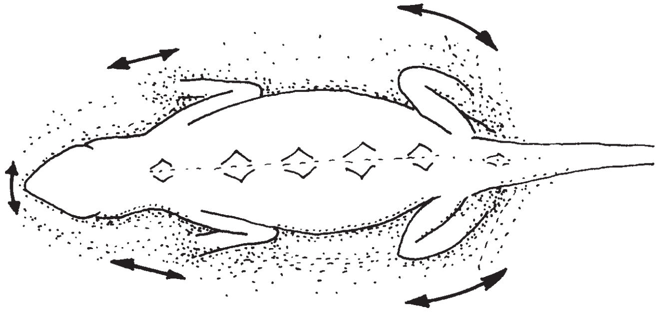


**Fig. 42.** Digging into the sand with shimmy motions.

3.4.4 Sand bathing (fig. 42)
Regularly single (above all gravid females) specimens were observed to dig into the warm sand surface below the lamps (preferably the 50W halogen lamp) for several daytime hours and/or over night.
The digging action lasts only a few seconds and starts with a flat dive of the forebody during which the lizard performs rapid lateral "shimmy" undulations and rapid hindleg scratching motions very similar to those of females reacting to courtship. Lateral body motions persist for 1-1 1/2 sec until the lizards is covered with sand, with only the tail, the back and the upper part of the head with eye and ear openings showing.
Preferred are spots where warm and loose sand is bordered by a stone and partially hidden under plant cover.
Sand bathing disappeared completely after the first oviposition and was only exceptionally observed in males.

### 3.4.5 Bathing in wet plants

#### 3.4.5.1 The bathing act system

Bathing sitanas wriggle jerkily (shimmy motions) through wet plants, repeatedly change directions for several minutes rubbing their heads laterally on leaves and stalks and oaring with their hindlegs. With exception of the head rubbing this act system is similar to sand bathing. They search maximal contact with the wet plant parts, either with throat and venter or, creeping below plants, with their backs.

After leaving the bunch of wet grass females (twice) and a male (once) huddled into the water dish with lateral body undulations and short synchronous pushes of hindlegs. The male even dipped his head below the water surface.

In one case (20.09.1995) the female violently tried to escape through the glass pane of the terrarium after filling the nest pit. Sprinkled with water she at once ceased these attempts and performed intense bathing motions oaring with her limbs, and with lateral undulations, at first on a stone, then in the wet sand. Finally she wriggled through the narrow space under a twig lying on the sand. After these activities striking brown patches showed on her back in the interstices between the dark triangles (fig. 11b).

#### 3.4.5.2 Releasing factors

Water is the main external stimulus to release bathing behaviour. Repeated sprinkling intensifies the oaring and shimmy motions.

Besides water on leaves, in wet sand, on a stone or in a dish, there are several additional priming factors which lower the releasing threshold of this act system.

1. Gravidity: in 16 of 32 recorded bathing events gravid females were involved.
2. Nesting: bathing was recorded seven times in females immediately after nesting and/or the following morning.
3. Five observations show that social stimulation plays an important role during mass performances with two or all (gravid) females and once even the male (who never bathed alone!) involved.
5. Hatching: During a single performance all six hatchlings in a cage - most of them three days old - took place in a common bathing performance.
6. Bathing was observed between April and the end of October (when monsoon rains cease in the natural habitat).
7. In one case bathing followed after drinking from a water dish.

#### 3.4.5.3 Function

The function of this act system might be to clean the skin, which is especially evident after nesting when the female’s head is dirty with earth and sand particles, or after hatching when the skin is covered with the dried egg fluid.

### 3.4.6 Moulting

The entire moulting process can last several days and starts with the head, followed by the body, hind- and forelimbs and finally the tail. The skin loosens in shreds with only a few regular rupture lines.

The moult usually starts with the upper head. “Eye protrusion” (fig. 43) during which both eyeballs are pressed out of their cavities for several seconds up to one minute seems to be a comfort behaviour which sometimes, but not always, accompanies the moult of the head. Its sheddings may rupture at the snout edges and fall off in three pieces: the pileus and the head sides. After this the skin loosens along the infralabials and is rubbed away on solid objects or by creeping under plants or even conspecifics. The neck and body skin is loosened by lateral windings and by spreading of the gular region.

The body moult always starts with the dorsal region, often with one rupture along the vertebral line, or two dorsolateral ones. In the latter case the dorsal shedding falls off as a broad strip. Additional rupture lines run crosswise behind the forelimbs and anterior to the hindlimbs. The venter is the last body region to shed its skin.

Most of the body, limb and tail shedding is torn off with the mouth and swallowed. The sitanas perceive even small shedding remnants and make efforts to reach and remove them neatly.

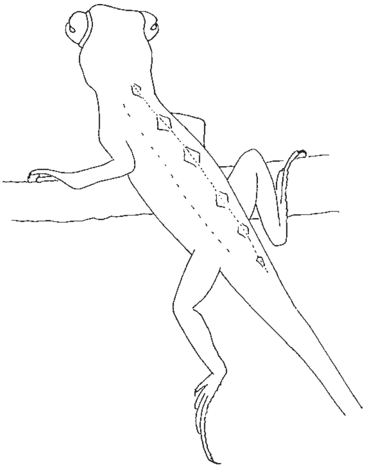


**Fig. 43.** Eye protrusion, probably a sort of comfort behaviour, observed also during the moult.

3.4.7 Hemipenis eversion

On the day of his death the inferior male everted one hemipenis for at least 13 minutes while sitting on a twig with his hindlegs hanging free. A small bit of skin was adhering to the copulatory organ. This reminds of similar observations on *Plica plica* (Köster & Böhme, 1975).

Normally hemipenis eversion is observed in *Sitana sivalensis* during the mating sequence after copulation.

## 3.5 Antipredator behaviour

3.5.1 Cryptic behaviour

The rarity of encounters with sitanas in the field is due to their camouflaging coloration, their reduced mobility and their preference of plant growth, in the densest parts of which inactive animals hide over much of the day. Basking and sand bathing places below dry plants on the ground are well concealed. The lizards rather tolerate to be carried away with the plants than to leave them.

3.5.2 Escape behaviour

The typical fleeing reaction of *Sitana sivalensis* in the field is the “jump-and-huddle” method. When approached they remain sitting on low plants until a fleeing distance of about 30 - 50 cm is reached. Then they suddenly jump to the ground and run for the nearest cover of plants lying on the earth. Quickly they bury themselves into the loose soil or under plant debris with shimmy motions identical to those during sand bathing (3.4.4). In this new location their fleeing distance shrinks to zero. It is very difficult to discover them, even if the exact location of their disappearance has been observed.

There are no data concerning predation on *Sitana sivalensis* in the natural biotope, but we found there juvenile and adolescent *Calotes versicolor*. Even larger juveniles of this species try to swallow smaller conspecifics, and adulti are very voracious predators.

Captive *Sitana sivalensis* do not react to the presence of an observer, nor are they disturbed by a quick approach. Adpressed to the ground they even tolerate being seized.

Predation on ***Sitana ponticeriana*** from Tirupati (Subba Rao & Rajabai, 1972a): Rats (Gerbillus spec.), Birds (*Milvus* spec., *Neophron* spec., *Gyps* spec.), snakes (*Naja* spec.), lizards (*Mabuya beddomi, Mabuya carinata*)

### 3.6 Nesting behaviour

Gravid females are very critical in the acceptance of laying sites. The high rate of egg retention in captive females is perhaps - at lest partially - due to insufficiency of environmental conditions for nesting. These might include soil type, humidity, temperature, presence of plants or other cover, and insolation.

The terrarium was provided with three boxes planted with grass and containing a 5 cm high filling of moist vermiculite / sand mixture. These were not accepted as nesting places, but the first nesting female started do dig below a 50 W halogen lamp on one of the warmest spots of the ground with a surface temperature of 31°C. As the sand was only 2 cm deep at that place the *Sitana* reached the terrarium bottom within one minute. Immediately the sand filling was raised to 5 cm. A small pit impressed with the finger tip was readily accepted as a digging site by the returning female.

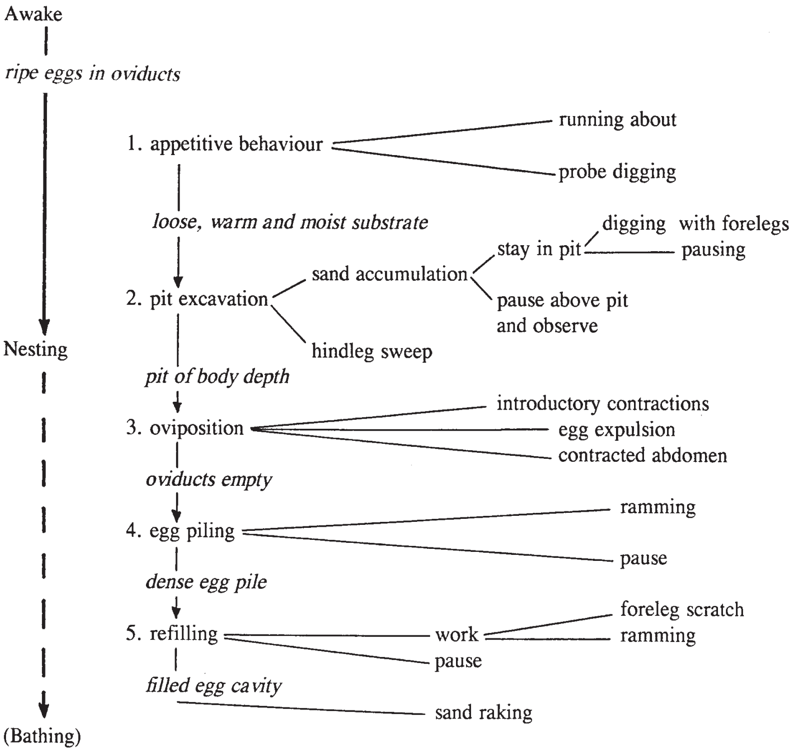


**Fig. 44.** Hierarchical organisation of oviposition activities. The important motivating (priming) factors in italics. The nest excavation activities are organised in repetitive cycles which are represented in fig. 49, 51).

The second female nested one day later at the same place. The third one started scratching on the bottom of a plastic food dish near by. After being carefully pushed to the prepared laying site, where the finger tip trick was repeated, she began to dig without further problems. Another female laying her 2nd clutch had to be poked away from the food dish two times before she started nesting in the prepared thick sand layer.
The eggs were transferred to an incubator the following morning.

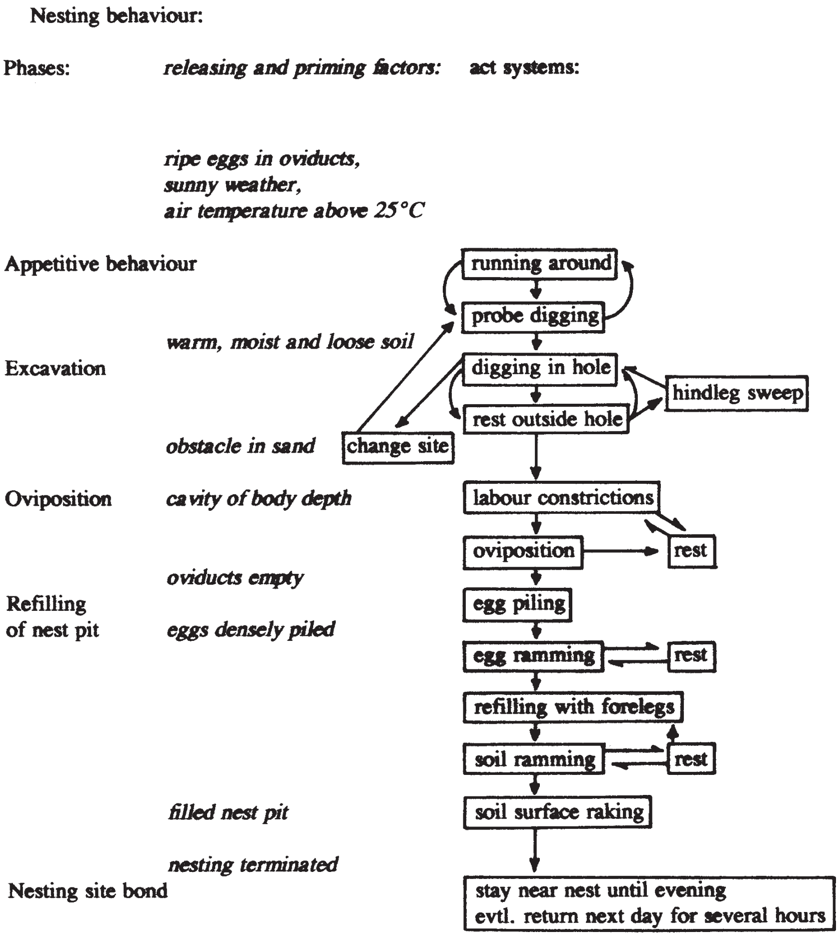


**Fig. 45.** Flow diagram of nesting behaviour

The complete nesting activities could be observed four times, on July 14, 15, 23, and September 1, 1995. During the nesting of July 15 as much as possible timings were taken with a stop watch in order to get some idea of its temporal organisation. Nesting starts in the forenoon after the sitana warmed up and proceeds after a rather rigid scheme with the single phases clearly delimited (fig. 44-46):

3.6.1 Appetitive behaviour
3.6.2 Excavation of nest pit
3.6.3 Oviposition
3.6.4 Egg piling and ramming
3.6.5 Refilling of egg pit
(3.6.6 Bathing in wet plants)
(3.6.7 Nesting-site bond)

The hard work of digging and egg expulsion lays an extremely heavy burden on the females' metabolism. Crudely estimated 9/10 of nesting time is spent with resting in order to oxidate the products of anaerobic energy release. For this reason all phases consist of short working and long resting periods which are repeated in cycles.

3.6.1 Appetitive behaviour for nesting starts when the air has warmed to above 25°. The female begins to run about in different parts of the cage and scratches the ground with her forelegs, even at totally hard places e.g. the bottom of a plastic dish. If loose ground is found the sitana stops moving about and concentrates its probing at a warm and moderately moist place. Monsoon rains create ideal conditions as moisture is not only indispensable for egg development but also softens the otherwise hard soil. Within a few minutes the digging activities are restricted to a spot where rapid scratching deepens the hole down to one centimetre. If a solid layer is encountered at a depth of less than four cm the locality is abandoned and a new one is selected.

If the sandy soil is dry the sitana cannot dig a narrow shaft as the loose material slides down at the edges to form a wide crater. In this case the excavation activities stop and may be interrupted until next day or even later.

3.6.2 Excavation of nest pit (timings from July 15, 1995)

Almost the whole work of digging is performed with rapid motions of the forelegs while the head is propped against the ground (fig. 46a) and soon becomes dirty from the moist substrate. The foreleg of one side scratches 3-7 times in rapid sequence and then the animal pauses for about half a second. Work is resumed with the same or the opposite foreleg and this may be repeated up to four times.

As soon as the sitana's head disappears in the pit which is about 1 cm deep she interrupts her work in irregular intervals (3-107 sec, average 28.4 sec) to appear at the surface, rest and observe the surroundings (fig. 46d), disappearing again in the pit after 51-106 sec (average 69.4 sec).

Only sometimes - at the end of a rest on the surface outside the pit - the sitana sweeps the sand near the pit opening away with a rapid alternating motion of the hindlegs (fig. 46e) which are otherwise not engaged in digging. Foreleg motions are vehement and throw the sand up to 10 centimetres into the periphery of the pit.

As the lizard always digs with her back facing the same direction, and loosens the sand on its lateral and ventrolateral side the pit soon becomes approximately crescent-shaped in cross section (fig. 46b). Its rounded horns mark the furrows scratched by the left and right foreleg. The soil below the venter is not discarded and forms a flat ridge. The furrows at its

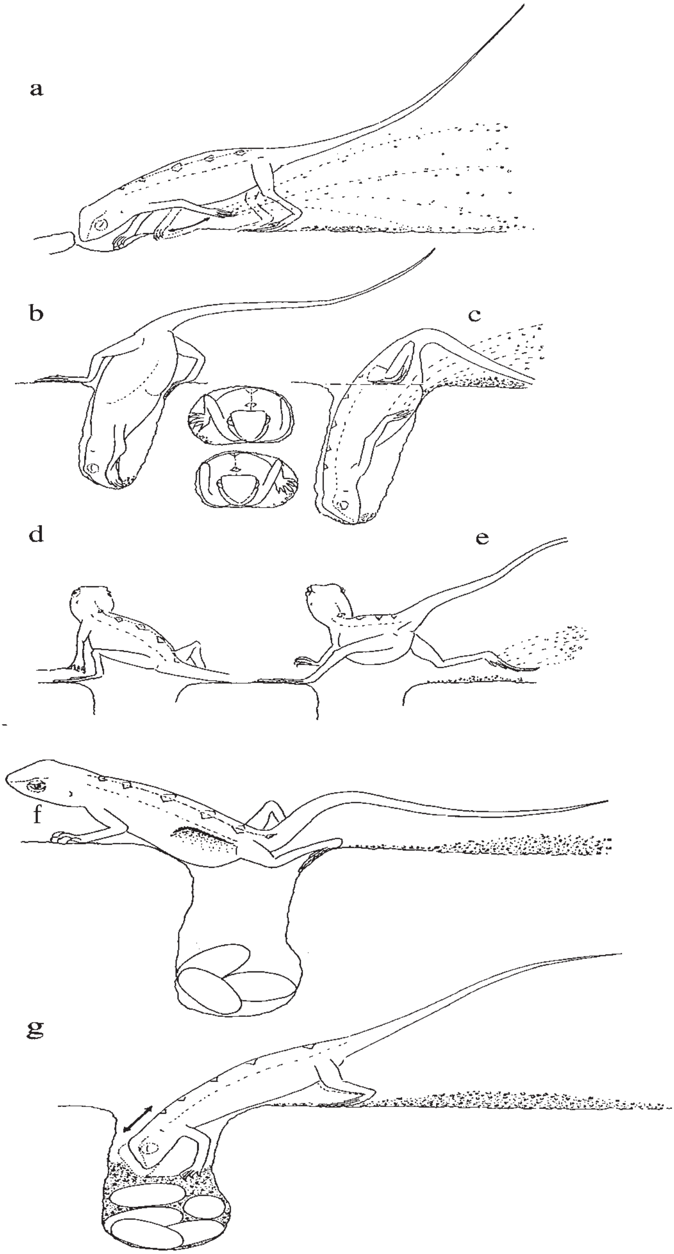


**Fig. 46.** Nesting: a-c: successive stages of excavation. Note different posture of hindlegs with increasing depth. The transverse sections between b) and c) show the sideward shift of the lizard when forelimbs alternate in digging; d) rest and outlook; e) hindleg scratch; f) oviposition with abdomen contracted by labour; g) sand ramming after piling the eggs and some refilling.

side serve as channels to throw out the loose sand and are used alternatingly. While digging with one foreleg the sitana presses her body towards the opposite shaft wall which is used as a support for the hard work of scratching. By this lateral motion the channel on the working side is widened thus facilitating sand ejection. When the other foreleg is used the body changes to the opposite side. If the forelegs would work alternatingly (left - right - left - right...) such side shifts would be too frequent and troublesome.

With increasing depth of the pit the lizard moves into a vertical position, clinging to the upper rim of the shaft with the long toes of its hind feet (fig. 46c; 47,48). When no more sand can be thrown out in this posture the construction of the nesting pit is terminated.

The construction of a vertical shaft seems an ideal way for a small lizard to dig down into deeper layers with the least possible amount of work.

Extremely long stays of up to over three minutes in the pit announce the termination of this phase which lasted 1h 40 min in one case.

The figures 49 and 50 give an idea of the temporal sequence of the digging activities in different time scales.

The organisation of the excavation phase in repetitive cycles merits special attention and is rendered in figure 51: The scheme should be read from the centre outward and starts with the shortest and most rapid circle, namely retraction and protraction of forelegs. Foreleg motions alternate with pauses in the pit. several stays in the pit again alternate with a rest outside.

Sand accumulation alternates with hindleg sweeps every 4-27 min, and the excavation phase consists of ca 12 of such cycles.

**Fig. 47.** Gravid female digging nest shaft.

**Fig. 48**. In a later phase the hindlegs form a right angle.

### 3.6.3 Oviposition (timings from July 15, 1995)

During this phase the sitana sits on the ground with the cloaca above the pit (fig. 46f; 52). Abdominal contractions start after a few minutes and are repeated in intervals of 10-47 (average 21.5) seconds. After eight initial constrictions the phase of egg expulsion labour starts. The abdomen contracts vigorously in intervals of 40-90 (average 73.7) sec and two eggs at the beginning, one each at the following times plop out of the cloaca in fractions of a second.

When the last egg has left the oviduct the female's abdomen is still totally contracted, but relaxes in the course of the following five minutes.

The emptiness of oviducts probably induces the change to the next act: The sitana leaves her position above the pit and at once enters the pit with her head.

### 3.6.4 Egg piling and ramming (fig. 46g)

The following treatment of the freshly laid eggs is astonishingly rough and serves to pile them densely on the bottom of the pit. In short phases of a few seconds the *Sitana* jostles her eggs towards the bottom of her shaft. Further dense piling is achieved by very short and quickly repeated head jerks in anterio-ventral direction. These bouts were interrupted by long pauses of 15-50 (average 37) sec and in one case were repeated 13 times until the eggs were fixed in the loose soil and refilling starts. The egg piling and the sand ramming (see following paragraph) motions are identical. The tight contact in the nest cavity transfers motions of hatchlings to neighbouring eggs and evidently stimulates and synchronises the hatching process of the whole clutch (see 3.7.1.1).

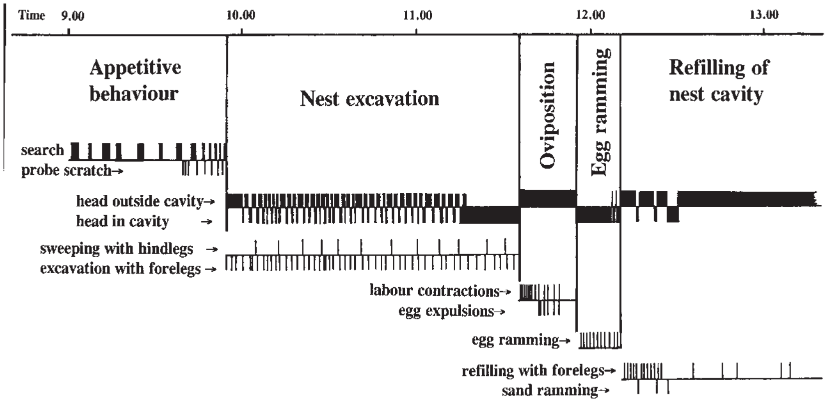


**Fig. 49.** Temporal sequence of nesting activities with cyclic activities indicated by vertical bars. Excavation and refilling motions are identical but oriented away from respectively towards the nest cavity. Ramming movements serve to pile the eggs after oviposition or to tap the sand during early phases of refilling.

### 3.6.5 Refilling of egg pit

The acts - foreleg scratching and head ramming - used during this phase appeared in previous phases namely during excavation and immediately after oviposition but are now slightly altered. Foreleg scratching is oriented towards the pit and less vigorous so that the loose material simply falls down into it. Ramming alternates with several scratching phases but it is this time directed towards the filling material in the pit which must be fastened. During the ramming phases the *Sitana* digs her forelegs somewhat into the sand and this way anchors her body for the tapping. After three phases of ramming a foreleg digging phase follows. Due to the increasing exhaustion of the *Sitana* the pauses become longer, and the lizard even starts to gape from heavy respiration. Scratching phases with long pauses between them may continue into the evening.

On one occasion (17.08.96) a female terminated refilling at 12:30 and returned at 16:00 to continue scratching for several minutes.

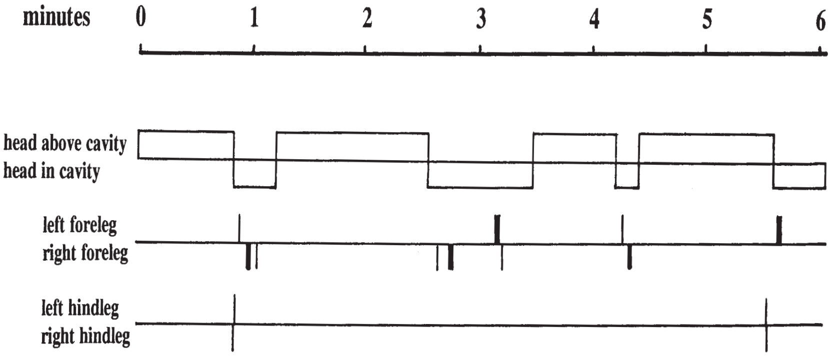


**Fig. 50.** Enlarged section from digging phase of the preceding figure with the activity phases drawn approximately to temporal scale. Foreleg digging is restricted to a few seconds of the "head in cavity" phases. Hindleg sweeps terminate resting phases with head above cavity. Physical work is indicated by the vertical bars and limited to a fraction of time.

(3.6.6 Bathing in wet plants, facultative, see 3.4.5)
It was observed in seven cases.
In the two cases of continuous observation intense dew bathing was released by sprinkling the cage. During this process the females cleaned their heads and bodies from adhering mud particles but the head of one animal was still smeared and grayish during the following weeks.

### 3.6.7 Nesting-site bond?

After most ovipositions the females returned several times to the egg-laying site in spite of the fact that nesting was completely finished and the pit refilled. The term "guarding" can not be applied as no female showed the least hostile reaction against approaching conspecifics and the stays near the nest never continued longer than the day after oviposition. In one case a female even tolerated another female do dig her egg pit in immediate vicinity of her nest from the previous day. At 14:00 the female was seen scratching at her old nesting site and then quit without paying further attention to it.

Another female had finished nesting at 14:50 and left the site. She returned for a short period at 18:30 , scratched a little and left again. At 19:15 she was back again, scratched and finally slept the whole night on her laying site. Next morning she was gone but returned at 8:15 and stayed until 10:30 sitting inactively on the spot. After this she resumed her normal activities.

After the oviposition of September 1 (second clutch) the female rested several times during the refilling phase. Each time she huddled under a stone half dug into the sand (fig. 53). The following night she slept there. Next morning she left for about one hour (the eggs were recovered by this time) and returned at 8:30 staying at the spot without further activities.

On August 17, 1996 the female had finished refilling at 13:30 and returned at 16:00 to scratch around the laying site.

Increased appetite during the following week quickly restored the girth, and the females appeared gravid again.

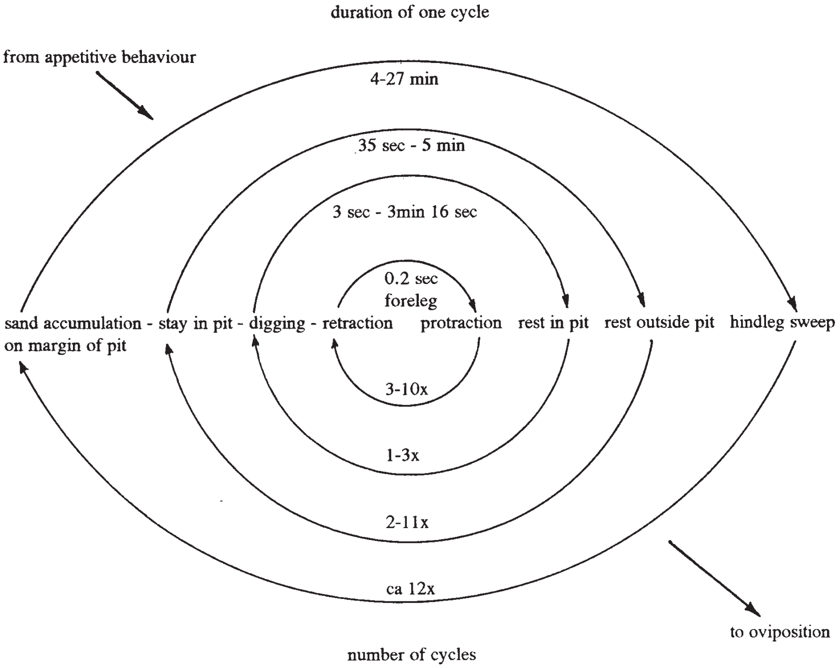


**Fig. 51.** Interlocking hierarchical cycles during nest excavation (total duration 1 h 40 min). Each of the larger cycles encloses several repetitions of the next smaller subordinate one. For explanation see text.

One of the females died pregnant. In the preceding days she had differed from the other females by her grayish hue. Seven eggs were dissected from the oviducts and had a very weakly calcified and translucent shell which made look the eggs not white but brownish yellow with a reddish spot (blastodisc) where embryonic development had started. With the exception of one juvenile which hatched after 45 days all the other embryos had died with a yolk reserve for about another week. They had punctured their eggshells at the end of their normal incubation period.

### 3.6.8 Temporal variations of nesting behaviour

Data on five clutches show some of the plasticity of the nesting time schedule, above all in the length of the excavation phase. Appetitive behaviour becomes evident as soon as the lizard begins probe diggings.

**Fig. 52.** Female during oviposition squatting above the shaft hole.

| Nesting date | first probe diggings | duration of excavation | oviposition | ramming | end of refilling |
|---|---|---|---|---|---|
| 15.07.95 | 09:40 | 100 min | 20 min | 16 min | 15:30 |
| 23.07.95 | 12:30 | 46 min | 19 min | 2 min | 19:45 |
| 01.09.95 | 11:45 | 62 min | 29 min | 2 min | 18:15 |
| 02.09.95 | 13:00 | 68 min | 18 min | 10 min | 17:45 |
| 27.07.96 | 09:10 | 10 min | 21 min | 8 min | 14:00 |

**Fig. 53.** Female resting near the nest and interred into the sand.

In all cases the nesting behaviour began in the first half of the day and was terminated the same day during the afternoon.

The prolonged duration of the refilling phase is caused by many rests, and in September was terminated by sunset.

On September 27 the refilling ended prematurely when a small pit was still visible. The sitana terminated nesting with a disoriented ramming of the sand several centimetres away from the laying site. The clutch failed to develop.

***Sitana ponticeriana*** from Tirupati (Subba Rao & Rajabai, 1972b, Subba Rao, 1983): Nesting takes place after the soil was soaked by rain. To dig the nest pit the female selects a grassy place with roots near by. The role of fore- and hindlegs during the excavation (lasting 48 min) is identical with *Sitana sivalensis* (fig. 54) as are outside rests alternating with working phases and the basic plan of the nest. The nest is 6 cm deep with a 2.3 cm wide shaft.

Oviposition lasted 5 min 45 sec with intervals between eggs between 40-45 sec. The nest was refilled in 34 min 45 sec and the loose soil tapped with head and hind limbs (the latter act was never observed in *S. sivalensis*).

### 3.6.9 Clutches and incubation

The *S. sivalensis* eggs normally have white calcified and soft shells. Seven clutches contained 6 - 10 eggs (see the following table), average value 6.86. The minimal distance between two clutches was 47 days. The maximal performance were three clutches deposited within 96 days.

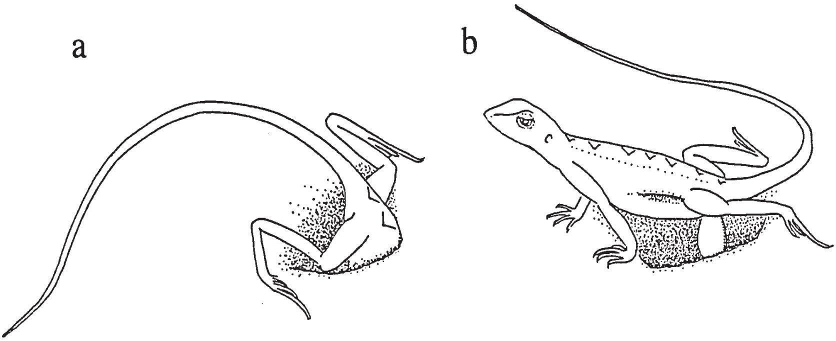


**Fig. 54.** Nest excavation and oviposition in *Sitana ponticeriana* from Tirupati (Subba Rao & Rajabai, 1972a).

At oviposition the eggs measured 8.1- 9.5 x 4.4 - 5.2 mm.

Average values from four clutches were: 8.33 x 4.71 mm; 8.37 x 4.97 mm; 9.28 x 4.86 mm; 8.28 x 4.86 mm.

The length : width ratio in the four clutches were after oviposition 1.77 : 1; 1.68 : 1; 1.9 : 1. and 1.70:1.

During 30 days of incubation the last clutch enlarged to an average size of 12.1 x 6.9 mm while the length : width ratio became 1.75 : 1.

The eggs were incubated at 26°C and hatched after 36 - 45 days.

The apparently abnormal and short incubation period of 36 days was recorded from an egg which was not laid with normal nesting (deposition on ground from 28.10. in following table) from a clutch which was apparently retained too long in the oviducts. Egg retention (and incomplete calcification of the eggshell) from unknown causes was still a frequent disorder in the following generation.

Survey of clutches laid during 1995 from four (a-d) wild caught females (parental generation) reared in captivity and 1996 from a surviving female (d: same female as 1995) and from females of the $F_1$-generation (e,f).

| 1st clutch | | 2nd clutch | | 3rd clutch | |
|---|---|---|---|---|---|
| year: 1995 | | | | | |
| date | number of eggs | date | number of eggs | date | number of eggs |
| a) 13.07. | 7, dissected from dead | | | | |
| b) 14.07. | 7, normal nesting | 15.09. | 6, on ground, | died 10.10.with retained eggs | |
| c) 15.07. | 6, normal nesting | 02.09. | 6, normal nesting | 25.10. | died gravid |
| d) 23.07. | 7, normal nesting | 01.09. | 7, normal nesting | 28.10. | 8 on ground. |
| year: 1996 | | | | | |
| d) 16.07. | 9, dissected from dead | | | | |
| $F_1$ - generation: | | | | | |
| e) 27.07. | 9, normal nesting, not fertilised | | | | |
| f) 17.08. | 10, normal nesting, not fertilised | | | | |

The very high mortality rate (three of four females) is probably due to already mentioned maintenance deficiencies. As an autopsy by Anders & Schleich (same vol.) showed, the females had also abnormally large fat bodies and a fatty degeneration of the liver, possibly from eating a too high quantity of Wax moth larvae. None of the third clutches was laid with normal nesting. In one case the clutch was totally retained (25.10.), in another female (10.10.) a part of the eggs was laid on the ground. The third female (28.10.) laid the whole clutch on the ground and started winter inactivity one week later.

***Sitana ponticeriana*** from Tirupati (Subba Rao & Rajabai, 1972b, Subba Rao, 1983): The clutches contain 8-13 (average 11.2) eggs. One female produced three clutches with 11, 12 and 13 eggs within 41 days. *Sitana sivalensis* is much less productive and needed more than the double span (96 days) for three clutches (with 7, 7 and 8 eggs).

The eggs measure 8.2 - 8.8 x 4.6 - 5.9 mm at oviposition, 10.4 x 7.4 mm with ten days, and 12.0 x 9.3 mm with 30 days. During this time their length:width ratio changed from 1.47 : 1 to 1,129 : 1, i.e. they become more rounded.

With 42.2-43.2 days (no data on incubation temperature) the incubation period was about as long as in *Sitana sivalensis*.

Clutches of *Sitana sivalensis* do not only contain fewer eggs (average 8.2 against 11.2), but these are relatively longer (length : diameter = 1.76 : 1).

## 3.7 Juvenile development

All data are based on records from captive animals

### 3.7.1 Hatchlings and their behaviour

#### 3.7.1.1 Hatching

The hatching process within one clutch is timed with an astonishing precision and in one case took about two hours. An observation on hatchlings which were one day old furnishes important information about this event. Several tiny lizards were sitting on a heap of dry grass separated by only a few centimetres of distance. When one of the animals moved, all the others made abrupt jerky lateral motions. As the eggs are densely piled any heavy motion inside will cause tactile stimulation of the neighbours which also start moving. As soon as there is a slit in the shell the snout is poked through. Rotating and undulating motions help to leave the egg. A longer pause is made with the head showing.

***Sitana ponticeriana*** from Tirupati (Subba Rao & Rajabai, 1972b; Subba Rao, 1983): Hatching (from shell slitting to shell leaving) lasted 4hr 20 min. The hatchlings carried yolk remnants for 3-7 days (not observed in *Sitana sivalensis*).

#### 3.7.1.2 Hatchlings:

Snout-vent length 13 - 15 mm, tail length 17 - 20 mm.

During the late embryonic phase and in hatchlings the dorsal pattern consists mainly of dark lines: The dark dorsal triangles are tiny and rather light, and at their place there are bifurcating transverse lines which insert at right angles at a middorsal line (fig. 55c).

***Sitana ponticeriana*** from Tirupati (Subba Rao & Rajabai, 1972b, 1983): With a snout-vent length of 16.55 - 16.96 mm (average 16.96 mm) and a tail length of 30.25 - 32.55 mm (average 31.7 mm) the hatchlings are considerably longer than those of *Sitana sivalensis*.; an essential difference is their high relative tail length (1.87 x snout-vent length against 1.3 x SVL in *Sitana sivalensis*). Their weight was 0.166 - 0.178 g (average 0.173 g).

#### 3.7.1.3 Maintenance of juveniles

Containers for neonates should not be provided with a sand or earth filling, as small food items (wax moth larvae) might escape into the ground, and moist soil particles can stick to the lizards, above all after sprinkling.

Additionally the neonates might ingest soil particles together with the food. A mixture of sand and plaster (equal amounts are mixed before water is added) cast semiliquid into a small plastic aquarium (base 15 x 20 cm) proved to be practical. The plaster ground can addditionally serve to embed a small water dish and a flower pot which are used later and for the present are filled with sand when the neonates are housed. Their needs for hiding, climbing and drinking can easiest be satisfied if the only equipment consists of a small bunch of dry grass which can be sprinkled in the morning. If they are available the hard dry leaves of the fern *Pteridium aquilinum*, a common weed on pastures, can be used as it is much hardier than grass. Drying the plaster in a warm place before using the terrarium is recommendable as surplus water from sprinkling is instantly absorbed and cannot endanger the tiny hatchlings. A (halogen) lamp of 20 - 50 W - depending on its distance from the cage - provides light and heat. When tiny crickets are fed they must be carefully controlled. Otherwise some of them escape predation, grow too large and attack sleeping juveniles. As the hatchlings dehydrate rapidly it should be controlled if all of them drink regularly.

After a month a bunch of grass can be planted into the pot. A tangle of thin twigs serves for climbing, and the water dish can be filled after putting a stone as a rescue island into it. A small funnel, which also can be glued together from a rolled-up stiff plastic foil and glued into an opening of the mesh wire lid is practical for feeding.

### 3.7.1.4 Development of the basic act systems repertoire during the first days

First observations, mainly on maintenance and multipurpose act systems, are enumerated day by day:

1st day: Resting flat on ground; jerky lateral motions (see hatching) released by moving siblings; wipe head with hindleg, prolonged bathing in wet grass.
2nd day: Sitting erect or flat on ground, some hiding in dense grass; moving prey is fixed but not caught; some sleep on branches with extended hindlegs.
3rd day: Observational behaviour (visual survey) pronounced; first feeding on small wax moth larvae, prey shaking; grooming with tongue (a bit of dirt near the cloaca: jumping upwards on a twig, siblings stimulate others to do the same.

4th day: Drinking drops from leaves
5th day: Running around
6th day: First defecation,
11th day: Pieces of eggshell eaten
13th day: Tail curls up if excited, social contact during sleeping
25th day: First moult
28th day: Still some difficulties when hunting small crickets: The sitanas sometimes dash too far and overrun the prey.

### 3.7.1.5 Colour change in juveniles (fig. 55)

While the stable pattern elements are identical with those of adults, the general body colour range is much wider, from light gray to dark brown.

Colour change is mainly induced by heating and wetting.

In a light brown hatchling the enlarged scales appeared very prominent (a) possibly by contractions of parts of the skin.

In b) the juvenile was irritated. Faint dots and streaks show on the light brown back, and the chevrons are rather indistinct.

c) and d) represent the most frequent grayish or brown pattern of hatchlings.

In an older juvenile with 23 mm snout-vent length small white spots regularly appeared during the dark state (e). They were located on the tips of the enlarged flank scales in two series on each side, and in the temporal region.

In the darkest phase the dorsal pattern becomes almost invisible and the flanks are blackish (f).

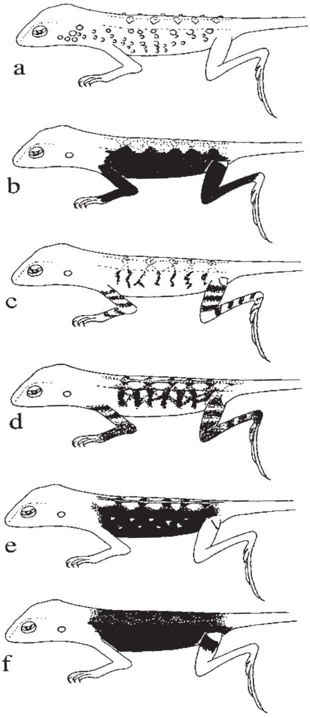


**Fig. 55.** Colour change in Juveniles: a) prickly phase when wet; b) light with faint pattern; c-f) darkening to almost black. For details see text.

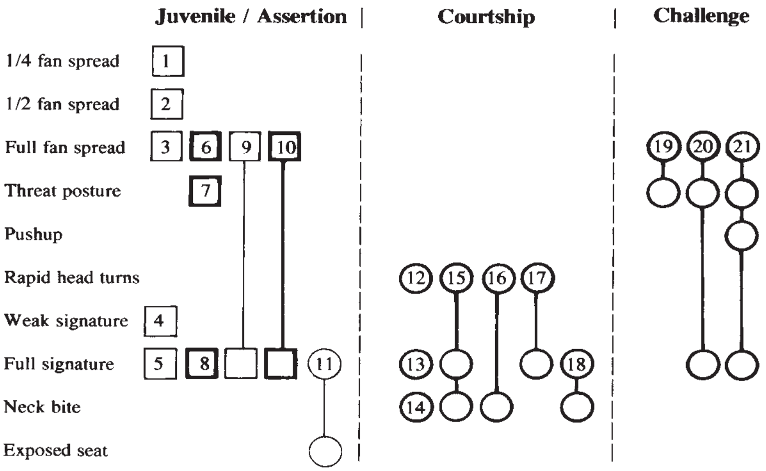


**Fig. 56.** Signal acts and their combinations (connected by vertical lines): Squares refer to juvenile behaviour, circles to adult behaviour, which is eventually anticipated in juveniles. Thin frames symbolise spontaneous behaviour, bold ones mark acts which are released by exterior stimuli. The temporal sequence of composed acts must be read downwards. The 21 acts and act combinations reappear in the following figure.

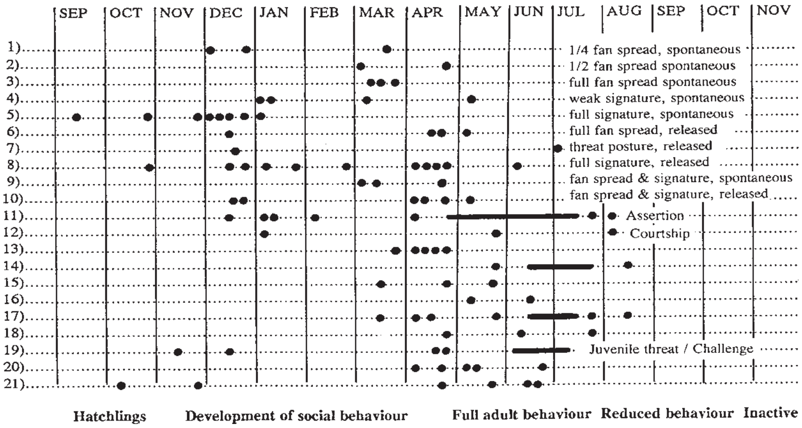


**Fig. 57.** Temporal record of acts and act combinations during ontogenesis. Numbers at left refer to the preceding figure.

This coloration was constant in sick juveniles which very probably suffered from a severe vitamin A deficiency. They had great trouble with opening their eyelids and remained in the sleeping posture for most of the day.

In both dark brown phases even the very stable light subocular spot darkens. Only the inguinal marks remain light brown. The ventral coloration also becomes darkest (fig. 12d).

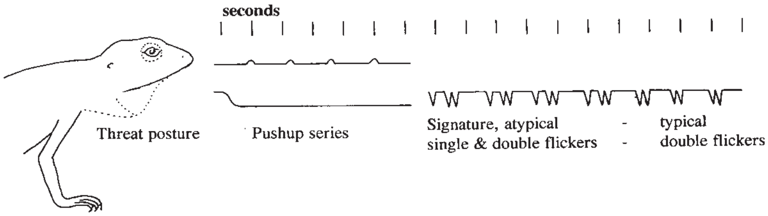


**Fig. 58.** Irregular threat behaviour of a juvenile female.

3.7.2 Ontogenesis of the communication system in *Sitana sivalensis* (fig. 56-58)
Observations on juveniles caught in the wild and reared from eggs showed that the development of the communication system is a complicated and prolonged process of maturation, and even in adult specimens the communication acts are by no ways totally stereotyped and predictable. Schematically there are five stages of development, the last of which coincides with the reproductive period. The reduction of display behaviour from late summer on is treated in chapter 3.1. The developmental stages are recorded in fig. 56 and 57.

3.7.2.1 Ontogenesis of signal acts

A. Hatchlings without social interactions. Social contact is avoided. This phase lasts from birth to the third week.

B. Isolated signature, independent of sex, appears very early and can be observed from the third week. Records are very sporadic.

C. Isolated juvenile aggressivity appeared in both sexes during the 6th week. The short bite attacks never turned into damaging fights, and no hostile interactions were observed during the following weeks.

D. Transition phase with a great number of isolated, spontaneous and unusual combinations (e.g. weak gular spread, spontaneous gular spread + atypical signature, fig. 58; weak signature). Acts which are typical for this phase appear in number 1-10 of figure 56. Almost all of these acts are connected with fan or gular spreads.

There are also intention movements of gular flickers which are similar to the gular pulsation of *Sitana ponticeriana* (fig. 21 left, 22).

The transition phase coincides with the final development of the throat fan which attains its size and pattern during these months. The multitude of irregular reactions suggests a maturation process which involves changes in the “releasing mechanism” and its neural connection with the developing fan.

Regardless of their sex the juveniles do not avoid direct contact and often form resting or sleeping aggregations with the sitanas sitting on top of each other (fig. 59).

E. Fully developed, with stabilised and "correct" communicative interrelations between conspecifics. Forms of juvenile display became rare by the end of April. Signature display appears as a regular constituent of assertion, courtship and challenge.
Assertion becomes extremely frequent in males, courtship can be observed several times a day and challenge behaviour (as described in paragraph 3.1.2.6) with fighting is performed until superiority is established between the rivals.
The end of this phase in late August is characterised by a drastic diminution of the male's assertion behaviour, which normally continues over much of the day.

**Fig. 59.** Aggregation of resting three months old juveniles.

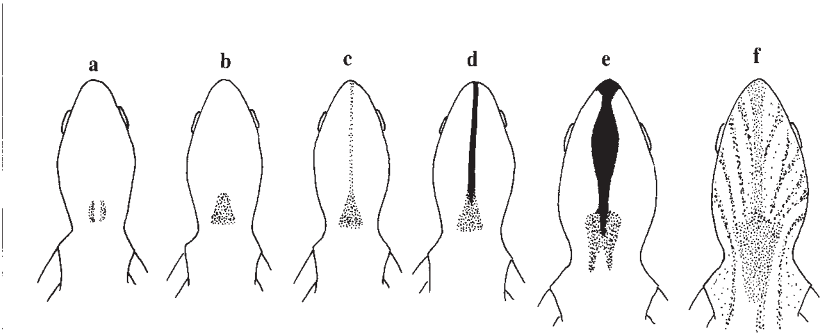


**Fig. 60.** Development of the male throat pattern starts with about three months in the posterior gular region and continues over almost half a year; f: female pattern.

### 3.7.2.2 Gular fan and Nuchal crest

In its complete form the gular pattern consists of a longitudinal blue streak and adjoining gray triangle, both of which are subject to colour change.

Its ontogenesis (fig. 60) starts with about three months at the future location of the triangle with two small oblong grayish patches at both sides of the posterior gular fan end (a).

Two weeks later the patches have fused and enlarged forming a single triangle (b).

After another 12 days the first trace of the longitudinal streak appears as a grayish line (c).

In another three weeks it grows blue on its anterior part (d).

Another month later the blue line is terminated by a blackish wedge within the gray triangle. The latter becomes large and rather diffuse, extending towards the foreleg insertions until June (e).

The male’s characteristic bluish gray nuchal streak at the location of the future roach (nuchal crest) appears relatively late with about six months.

Ten days later a tiny crest of about 0.5 mm height appears for the first time.

One week later the roach could be folded up to the final height of about 1 mm.

During rival combats at an estimated age of nine months the nuchal streak turned light bluish green (together with the upper eyelids) for the first time in the winning rival.

### 3.7.2.3 Signature and assertion behaviour

Double flickering is the first signal act to appear during ontogenesis. A juvenile of 17 days performed it while sitting in outlook posture with its tail end turned upwards as a sign of alertness.

Assertion - regular repetitions of double flickers at intervals of 10-15 sec - were first recorded with about 6 months (March 11). One month later (April 9) a male was seen on an assertion tour from branch to branch with repeated double flickering at every perch.

### 3.7.2.4 Courtship and mating behaviour

A three months old female flees from a flickering male (December 26).

With four months a male performs rapid sideward head motions in upright posture (January 1).

At five months (March 19th) a complete courtship with rapid head motions, double flickers and neck bite was recorded.

### 3.7.2.5 Ontogenesis of social interactions (fig. 61)

An involuntary experiment helped to solve the question why signature display and assertion behaviour is normally limited to the males.

The early appearance of signature display in juveniles of both sexes and its absence in adult females arises the question for its regulation.

The theory that signature flickers are primed in juvenile females by male sex hormones is not probable. But it might be suppressed by female hormones after the onset of maturity. The latter possibility was contradicted by our observations: When the juvenile group reared in early 1996 approached the adult stage it became evident that all of them were females. None of them showed the typical secondary male sex characters: gular fan, dark stripe on throat, slender body and thickened tail base. But at least two of them repeatedly showed signature displays with double flickers. One of them even performed prolonged assertion display with exposed high position, elevated posture and long series of double flickers (fig. 19).

Evidently the presence of a male normally inhibits female displays, and the following stages can be observed in a mixed group of juveniles (fig. 61):

1. no signature display in hatchlings
2. different types of fan flickers in juveniles of both sexes
3. rare social interactions
4. unstable social system

5a. The signals emitted by sexually mature males inhibit gular flickers of females.
5b. Alternatively: if no males are present the females continue flickering.

When an adult male was added to the group the female at once ceased her double flickering.

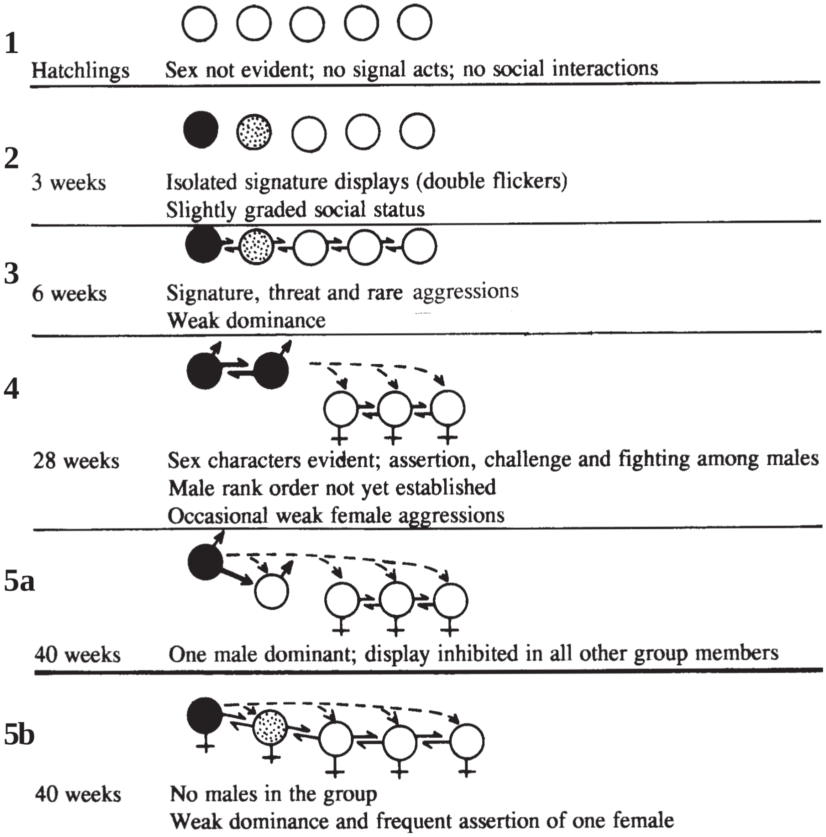


**Fig. 61**. Ontogenesis of signature display within the social system:
Graded darkening symbolises the frequency of display activities.
Continuous arrows symbolise strong (between males) resp weak (between females) aggressivity; broken arrows mark the inhibition of display acts in conspecifics by the dominant male or (in its absence) female.

## 4. Discussion - The evolution of the communication system in the genus *Sitana*.

### 4.1 Basic principles (see Wilson, 1975)

According to the ethological concept of animal behaviour genetically programmed acts and releasing mechanisms which serve communication are subject to selection and evolution as are morphological structures. Therefore the homology principle can be applied to them in a similar was as in morphology. The evolutionary changes of structures and motions into signals are dealt with by the principles of **semanticisation** and **ritualization**.
Signalling in *Sitana* is almost exclusively optical with the exception of a few tactile stimuli during copulation, e.g. neck bite hold and cloacal contact. The number of known **simple signals acts** is limited to a few dozens (see appendix), but this number is considerably enlarged by signal **diversification: gradedness, combinations** and **disruption**. The signals of *S. sivalensis* are adapted to **close-range communication**: the fan is small and inconspicuous, as are the blue eyelids and the threat face of males. A close-range signal of *S. ponticeriana* is throat pulsing (during courtship) with a small amplitude of the gular skin. The large fan of the latter group has evolved parallel with **long-range communication**.
The principle of **antagonism** - contrasting information is conveyed by "opposite" signals- is realised in the submissive ducking of *S. ponticeriana* (fig. 34c) as a contrast to threat with elevated body.

### 4.2 The evolution of the *Sitana* fan.

4.2.1 Hypotheses

The presence of at least two very distinctly separated *Sitana* groups with signal organs and motions of different complexity arises the question if one of them can be regarded as more advanced in signal evolution. If one considers the ethology of the *Sitana sivalensis* group the differentiation of its communication system is relatively modest compared with the *Sitana ponticeriana* group. The small gular fan, its unspecialized scalation and the low number of challenge display acts suggest a rather primitive state, perhaps close to a fanless ancestral form. But we must not disregard the opposite possibility of fan reduction which was e.g. postulated for the small *Anolis bahorucoensis* (fig. 62; Fitch & Henderson, 1987). The authors have shown that a modest gular fan and display repertoire must by no means be primitive but can be interpreted as the result of a selection for inconspicuousness and an adaptation to avoid predation by larger forms.

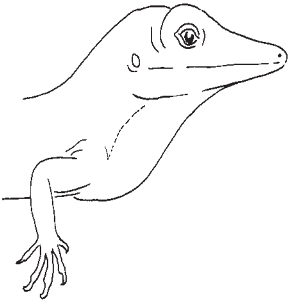


**Fig. 62.** Fan reduction in *Anolis bahorucoensis*, a species heavily predated by larger congeners (after Schwarz & Henderson, 1985).

A central role in our arguing plays the sister genus *Otocryptis* (Moody, 1980) in which, similar to *Sitana*, forms of very different fan size occur. In the larger species *Otocryptis wiegmanni* (fig. 63) the fan has about the same relative size as in *Sitana ponticeriana*, in *Otocryptis beddomi* the males have no gular appendage at all.

**Fig. 63.** Left: *Otocryptis wiegmanni* male, asserting. Right: *Otocryptis wiegmanni,* structure of gular fan.

If the common ancestor had a small fan or a gular pouch (fig. 64A), *O. beddomii* and *S. sivalensis* could be regarded as primitive. If the common ancestor of both genera had a large fan (fig. 64 B ) then the gular appendage was secondarily reduced in *Otocryptis beddomii* and -separately- *Sitana sivalensis* (a really unlikely case!). Expressed in phylogenetic terminology the question is, if large-sized *Sitana "ponticeriana"* and *Otocryptis wiegmanni* fans are autapomorphies or synapomorphies - evolved twice and separately (A) or phylogenetically old and inherited from a common ancestor (B). If the synapomorphy hypothesis is confirmed, the ancestral *Sitana* form had a large gular fan with similarities both to *Otocryptis wiegmanni* and *Sitana "ponticeriana"*, and the reduced communication system of *Sitana sivalensis* could represent a derived state (comparable to *Anolis bahorucoensis*) and not a primitive one.
Hypothesis B has the great handicap that it postulates fan reduction - which is evidently rare - twice independently in closely related forms.

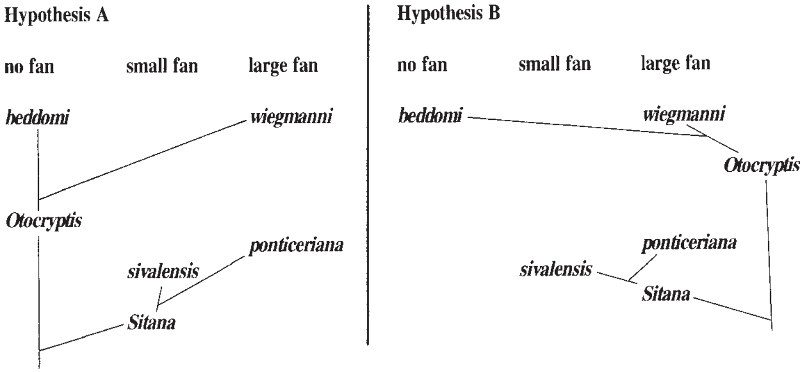


**Fig. 64.** Hypotheses for the origin of the small-fanned *S. sivalensis* and the large-fanned *S. ponticeriana* groups illustrated by phylogenetic trees.
A: The small fan as a primitive character; independent evolution of large fans in the genera *Sitana* and *Otocryptis.*
B: The small fan as a derived character, the common ancestor of both genera having a large fan.

### 4.2.2 The common ancestor of *Sitana* and *Otocryptis*

Morphological comparison based on more than 120 characters lead Moody (1980) to the conclusion that *Sitana* and *Otocryptis* are sister genera and were primarily arboreal (p. 110). He compared skeleton preparates of *Sitana ponticeriana* and *Otocryptis wiegmanni* and was convinced, that *Sitana* was a monotypic genus. The second *Otocryptis* species *O. beddomii* (which is a rarity in collections) was X-rayed, but apparently not used to construct the phylogenetic trees.

As it was Moody's aim to elucidate phylogenetic interrelations between the agamid genera, but not within them he did not discuss the state of both *Otocryptis* species. While relationships of *Otocryptis wiegmanni* and *Sitana* are well funded, the state of *Otocryptis beddomii* needs to be reconfirmed. This species is characterised by a relatively short tail, shorter hindlegs in relation to body length and to foreleg length. Moody's statements on interrelations between the *Otocryptis* species are only indirect and support the standpoint that *O. beddomii* is closer to the common ancestor:

In his evaluation of morphological "character states" which Moody used to calculate phylogenetic interrelations the increase of relative hindleg length (character number 107) is interpreted as evolutionally derived.

According to both of these arguments the fanless *O. beddomii* is closer to the common ancestor.

**Fig. 65.** Stacking of fan scales in *Sitana ponticeriana* (right) and *Otocryptis wiegmanni*. The hollow circle symbolises the processus retrobasalis of the hyoid skeleton in transverse section.

Considering the common characters of both genera and the advanced ones which lack in one of them (as the hidden tympanum of *Otocryptis* or the reduced 5th toe in *Sitana*), the common ancestor of both genera might have shown the following traits:

An unspecialized insectivorous subarboricole woodland lizard, sit-and-wait strategist of small size which occasionally comes down to the ground to seize prey, with a slender body, a long tail, long hindlegs and a very small 5th toe. The tympanum is visible, the body scalation heterogeneous. Its general colouration is brown, with a light dorsal field and a pattern of five chevrons (three of them between fore- and hindlegs). Some enlarged lateral scales bear light tips. There is a dark prefrontal transverse bar and a light subocular spot.

The lizard is capable of colour change (including the gular region) and can erect a nuchal roach and probably also a low dorsal one. During threat it can lower a gular pouch and perform a gape-and-tongue display with slow nods. During assertion it remains in elevated posture.

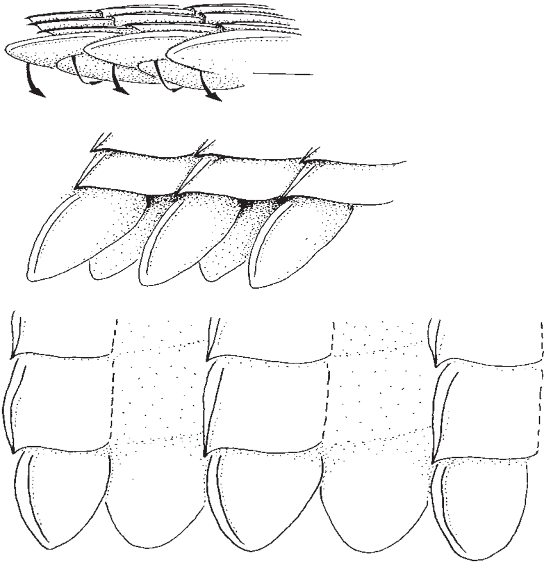


**Fig. 66.** *Sitana ponticeriana*: scale rotation during fan spreading. Orientation as in fig. 15 with the head facing right.

### 4.2.3 The fans of *Otocryptis* and *Sitana*

We try to solve the autapomorphy / synapomorphy question of the large *Sitana ponticeriana* and *Otocryptis wiegmanni* fans by studying details of their epidermal structures:

1. The most striking aspect in this regard is that the enlargement of scaled skin surface is achieved by two contrary methods: In *S. ponticeriana* the size of fan scales has enormously increased while their number remains rather low. *Otocryptis wiegmanni* has gone the opposite way with rather small but very numerous scales.
2. In *S. ponticeriana* the fan scales are extremely thin, translucent and nearly quadrangular (fig. 15); those of *O. wiegmanni* rounded and massive (fig. 63, 65 left).
3. In the folded *S. ponticeriana* fan the scales are stacked like two folders and form a flat ridge along the gular region. In *O. wiegmanni* they are arranged in a rounded bulge (fig. 65).
4. The scales and the skin between them are of very similar texture and colouration in *S, ponticeriana*, but contrasting in *O. wiegmanni*.
5. Only *S. ponticeriana* developed a pliable fringe of enlarged scales. This structure contributes efficiently to fan enlargement, but folding and unfolding demand an extremely complex system of “skin hinges”(fig. 66).

Apparently both large fans are the result of a divergent evolution of their scalation (fig. 67) with that of *S. ponticeriana* being more specialised. This supports hypothesis A (paragraph 4.2.1) which considers the large fans in the genera *Otocryptis* and *Sitana* as autapomorphies, postulates a fanless ancestor of both genera, and regards the state of the *S. sivalensis* fan as intermediary on the way to the complicated signal structure of *S. ponticeriana*.

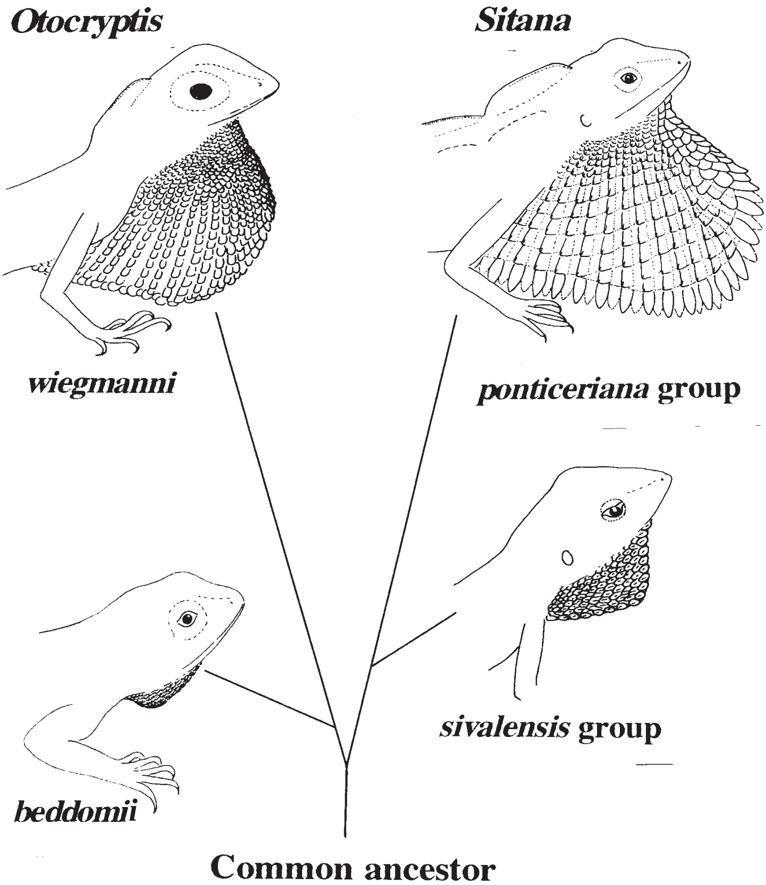


**Fig. 67.** Evolutive stages of gular appendages in *Otocryptis* (left) and *Sitana*.

## 4.3 Evolution trends in signals

### 4.3.1 Semanti(ci)sation

Semantisation - the evolution of signal structures - is characterised by morphological changes of organs (mostly epidermal structures) which widened their original function as “tools” like the normal body cover, but acquire a “secondary value” as information transmitters. They are often of striking appearance of size, shape and colouration as are for example the gular pouches, fans, crests, roaches, helmets, rostral appendages, frills etc. Up to the middle of our century zoologists had difficulties to interpret these partially very lavish structures. Mertens (1946) termed them “aposematic” (intimidating) structures which were used for warning and threat reactions. The ethological concept regards them as optical signals which evolved during speciation processes (Hillenius, 1959; Rand, 1961; Rand & Wiliams, 1970). The signal function of a rostral appendage has been proved experimentally in chameleons (Parcher, 1974).

Semanticisation (evolution of morphological signals) of the gular fan in both "models"

| | *sivalensis* | *ponticeriana* |
|---|---|---|
| Fan size | small | very large |
| Scale size | small | very large |
| Basic colour | whitish | yellow |
| Colour change | white or blue gular anterior margin | white or blue anterior margin |
| Pattern | brown scales appearing as dots | black, yellow, orange or red pattern elements,<br>evidently specific characters |
| Marginal scales | not differentiated<br>no stacking problems | lanceolate<br>rotate during fan spread (fig. 66) |
| Scale rotation | insignificant | pronounced |

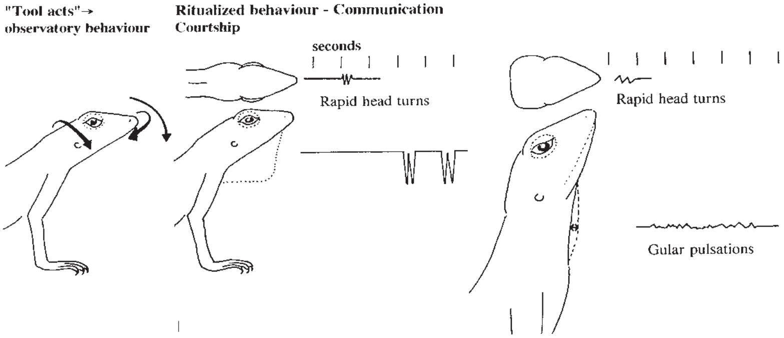


**Fig. 68**. Theoretical origin of ritualised courtship: Observatory head movements gave origin to rapid head turns which are in turn combined with flickers (*S. sivalensis*) or pulsations (*S. ponticeriana* from animal trade).

### 4.3.2 Ritualization

Ritualization - the evolution of signal actions (and corresponding releasing mechanisms)- is characterised by the functional change of acts from "tool actions" (Jenssen, 1977, calls them "utilitarian source behaviour") into (often optical) signals.

We may use the head and gular motions during courtship display in *S. sivalensis* as an example (fig. 68). The originary "tool acts" are the slow obervational turns of the head. In courtship display the head is tilted upwards and its turns become so rapid and are of such a small amplitude that an observation of the surroundings becomes impossible. Double signature flickers are combined with this signal.

In *Sitana ponticeriana* ritualization is still more advanced as the almost vertical head moves with minimal amplitude and high frequency. In this posture the reflecting and brightly coloured gular scales become exposed. Instead of flickers there are low amplitude gular pulsations. These can be interpreted as ritualised weak flickers (as are actually observed in juvenile *S. sivalensis*). This ritualization is connected with a corresponding semantisation: The "normal" lateral gular scales of *S. ponticeriana* are reflecting. During gular pulsation in the sun, sparkling light reflexes move on the throat (fig. 22).

Eibl-Eibesfeldt (1972 p. 129) characterises some typical traits of ritualised actions (reference to the rapid lateral head motions during *Sitana* courtship display in brackets):
1. functional change (from observational motions to courtship)
2. special motivation (in reproductive males only)
3. mimically exaggerated motion (rapidity of lateral head motions)
4. change of orientation (the gular region is oriented towards the female)
5. stereotypy (independent of the female's position the male's posture and motions remain constant)
6. simplified motions (real observational motions are irregular and comprise complicated eye and head turns in several directions)
7. parallel development of signalling structures - corresponding semanticisation - (gular fans, gular coloration, reflecting gular scales in *Sitana ponticeriana*).
8. "freezing" of postures (in contrast to observation the male's posture remains unchanged)

Typical for ritualised acts is their integration into an other functional system, e.g. from the multipurpose to reproductive behaviour.

Often the ritualised acts are not derived from a full "tool action", but from their intention movements which are frequent in conflict situations. The *S. sivalensis* females perform intention movements of digging into the sand as a male rejection act (see fig. 23).

Attempts to explain the origins of the commonest signal motions in agamids are as follows:

1. Up-and-down motions (ritualised into → nods → pushups) originate from a conflict between aggressiveness and fear, an oscillation between postures of dominance and submission (Greenberg, 1978).
2. Gular motions (ritualised into → gular pouch spread → fan spread → repeated slow fan motions → flickers) may be derived from a simple lowering of the hyoid apparatus as an intention movement for biting. The bite intention can be ritualised into a gape (eventually with a coloured mouth mucosa as a colour signal - blue in *S. ponticeriana* from Ceylon, Deraniyagala, 1953) or into a static or dynamic gular display with a parallel evolution of fan structures (see paragraph 4.3.1).

Flickers versus nods

Flickers as a peculiar type of fan display are evidently a synapomorphose of all known *Sitana* forms, but evidently lack in close relatives as *Otocryptis*. The poor notes on display behaviour of *Otocryptis wiegmanni* (Matuschka, 1978) as well as own observations have shown that in this species flickers are apparently lacking, and the large gular fan is never rapidly extended and folded during threat reactions against rivals and non-conspecifics. In *O. wiegmanni* gular spreading is sometimes accompanied by pushups, which are very common in agamids. Additionally nod sequences of a complicated rhythm serve for intraspecific communication.

Evidently the new signalling tactic of flickering has largely replaced the more primitive and widespread nods. Flickers with large gular fans have evolved at least twice within agamids. The other case is the genus *Draco*, the specimens of which signal from one tree trunk to an other. In *Draco volans* a sequence consists of the gular spreads: of a middle - long - very short duration (flicker). The rapid flicker - comprising fan extension and folding - lasts about 0.12 sec - about as long as in *Sitana*. The mechanism of fan folding works without stretching of the interscale skin, with the fan forming two large folds (fig. 14) which can be unfolded rapidly.

One cause for the evolution of flickers as a new form of display could be signal diversification within the agamids. South Asia evidently was an evolution centre of this family (Moody,

1980) and is inhabited by numerous genera which had to develop specific recognition signals. This reminds of the multitude of structural signals (crests, horns, nasal processes, casques etc.) which the former genus *Chamaeleo* (now *Chamaeleo*, *Bradypodium*, *Calumna* and *Furcifer*) evolved. The highest number of such structures is to be found in East Africa, the supposed evolution center of this genus (Hillenius, 1959). Rand (1961) has a first suggested their role as specific signals, and Parcher (1974) proved the significance of rostral processes experimentally.

### 4.3.3 Enrichment devices and display diversification

With a small set of basic acts a species can attain great display diversity by three ways: their grading from zero to maximal, the combination of several signals into a complex one, and signal disruption - the evolution of several signals out of a common root.

#### 4.3.3.1 Gradedness

A wide range of behavioural states can be expressed by gradually changing the parameters of signals:

1. Colour patterns: The gular streak of males can fade from deep blue to pale grayish; their upper eyelids change from grayish brown to light blue.
2. Postures: gradedness concerns e.g. lateral flattening, throat spread, nuchal roach erection.
3. Gradedness of actions are e.g. the flicker amplitude, the duration of flicker series or fan spreads.

The opposite of a graded signal is a discrete one which exists only in the “off” and “on” state - in *Sitana* rather an exception. One of the rare examples is the challenge pushup (fig. 30).

#### 4.3.3.2 Signal combinations

Many agamids get along with a rather simple signal system comprising a spread of the gular pouch and one or two types of nods and pushups. These are restricted to challenge behaviour in *Sitana*, and there is only one simple type of pushup in the repertoire of *S. sivalensis*.

Signal combination also plays a role in what Wilson (1970) calls “evolutionary turnover in signals: “As old signals decline, perhaps in competition with new displays that are more efficient in conveying the same information, they can be expected to become linked as a component with another display....”

The threat pushup of *S. sivalensis* seems to be such a relictary act, while pushups play still a most important role in many agamid genera.

Ideal signals are conspicuous, unambiguous and simple. Display diversity is in a certain contrast to the basic attribute of simplicity, but the combination of simple signals is an elegant solution to convey detailed information with a small set of basic units. Signal combinations can be simultaneous or successive. Examples for both methods are illustrated in fig. 33 and 56.

#### 4.3.3.3 Signal disruption (fig. 69)

The disruptive evolution of one signal act into several “sibling signals” shows some similarities with the divergent genetically programmed specialisation of homologous structures for different functions, e.g. arthropod legs, mammal teeth or bird’s feathers which evolved from the same origin, but are now different in shape and function.

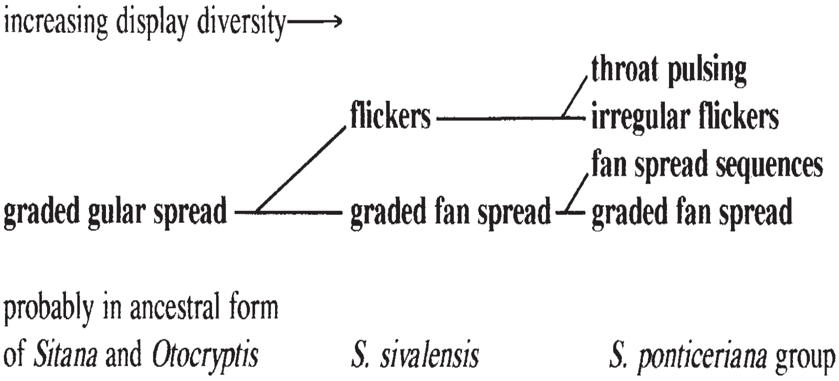


**Fig. 69.** Signal disruption of fan motions in *Sitana* forms with a low resp high degree of signal diversification.

The high evolutive significance of gular motions against vertical head or body movements in the genus *Sitana* is shown by the fact that there are four (homologous) types of them in *S. ponticeriana* display: continuous gular spread, slow spread sequences, flickers and pulsations (fig. 21 left, 22, 33). Typically, three of them are used during challenge. The two latter ones can be easily recognised as closely related homologues as both of them show very similar temporal patterns. The flickers serve for long-range communication and challenge, while pulsations are used in close-range communication during courtship.

Again this type of diversification is poorer in *S. sivalensis* with only two forms of gular motion.

We can try to design a phylogenetic tree, arranged according to morphological similarities, with the state of *S. sivalensis* closer to the base than the *ponticeriana* group.

### 4.3.3.4 Evolution of challenge display

This most complicated functional system in the behaviour of *Sitana* demonstrates all methods of signal evolution which were discussed in the preceding paragraphs.

Challenge display is less specific than assertion and courtship (which apparently play a more important role as isolating mechanisms) and in many regards identical in both *Sitana* groups. Many components are even common to many agamids or belong even to a **common stock of saurian act systems**. They are printed in bold in the following comparison and are evidently **plesiomorphies** - phylogenetically old characters which are common to many related systematic units, in our case many saurian families namely Agamidae, Chamaeleonidae, Iguanidae, Lacertidae, Varanidae.

Static signals appear in normal print, dynamic ones (motions) in italics.

In conformity with the general diversification of signal evolution, in *Sitana ponticeriana* many additional acts developed and make the threat repertoire of this forms more complicated.

Comparison of the challenge act systems of *Sitana sivalensis* and the *S. ponticeriana* group.
New acts on the right side are possibly derived from ancient forms at left (for combinations see fig. 33, 56)

| *S. sivalensis + S. ponticeriana* basic generic threat repertoire | additional threat acts in *S. ponticeriana* group, autapomorphies of *S. ponticeriana* forms |
|---|---|
|  | hindleg stance |
|  | *sideward bluff jump* |
| ***lunge towards rival*** | *forward bluff jump* |
| ***slow pushup*** | *pushup sequence* |
| *rapid gular flicker* | *slow gular motions* |
| **static gular spread** |  |
| erect nuchal roach |  |
| dorsolateral folds |  |
| **gape** |  |
| **tongue protrusion** |  |
| **elevated forebody** | high four-legged stance |
| **lateral compression** |  |
| **lateral orientation** |  |
|  | autapomorphy in *Sitana sivalensis*:<br>threat face with temporal fold (fig. 29) |

The lack of a dorsal crest in *Sitana sivalensis* may be due to reduction, as a dorsal crest can also be erected by males of *Otocryptis wiegmanni*.

As Jenssen (1977) has argued, a random performance of different display forms during challenge is more efficient than the repetition of the same threat act, which leads to habituation. Thus the diversification of challenge behaviour helps to prolong ritualised threat and evites or postpones damaging fights between rivals.
A similar argument has been used by Frankenberg (1975) to explain distress call diversity in geckos (*Stenodactylus sthenodactylus*). Display diversity and its random use might evoke a “surprise effect” in the addressee, a real or possible predator.
This strategy is especially valuable if territorial males are repeatedly confronted with unknown neighbours, as is above all the case in short-lived species with high colonising abilities (r-strategists, see 2.2.3). Field observations by Kratzer (1980) have shown that the superiority/ inferiority state of territorial *S. ponticeriana* males is established by extended display duels and not by real fights. Bites serve only to chase an inferior rival away when the social rank is already established.
The theory works convincingly as Kratzer could observe damaging fights between females, which have only a very limited display repertoire.
Challenge display diversity does not increase the transmitted information rate but is rather a combination of bluff actions aiming at chasing a rival with a minimum of risk.
Jenssen (1977) who worked with anoles - iguanid lizards from temperate and tropical America- found many parallels with *Sitana* displays:

1. the important role of lateral display during challenge
2. the evolution of structures which enlarge the lateral outline of lizards
3. the differentiation of vertical head and body motions
4. the diversification of challenge acts.

Evidently selection worked parallel in both groups, anoles and sitanas, and the more complicated system of *S. sivalensis* shows more convergence to the anoles than to the closely related *S. sivalensis*.

4.3.4 Progressive and conservative character states in *Sitana*.

The species groups of the genus *Sitana* do not only offer a prime example for signal evolution, but also for different evolutionary speed.

As has been shown in the article on p.87, it is extremely difficult if not impossible to discern the forms of the *sivalensis* and *ponticeriana* groups by classic pholidotic characters and counts, or by pattern elements (with exception of the fan and mouth mucosa). Evidently most of the external morphology has remained unchanged during the processes of speciation, while the communication system has evolved rapidly.

As Lorenz (1964) has argued, intraspecific selection alone (without environmental selection as a counterweight) can lead to the evolution of "exaggerated" signal structures (he cites the classic examples of the Great argus ,*Argusianus argus*, and the subfossil Giant deer, *Megaloceros giganteus*).

The large fan of *S. ponticeriana* could present a similar case, as males with a larger fan (acting as a "super-decoy") and a more efficient challenge repertoire had greater chances to occupy a larger territory and to mate with the females which dwell within it. The mating success of subordinate males (Kratzer, 1980) is unknown.

Wilson (1970) alludes to the same problem saying: "Display phenomena are among the most evolutionary labile of all phenotypic traits."

Another factor which could have speeded up the evolution within the genus *Sitana* is the rapid (annual) sequence of generations with a recombination of genes.

### 4.4 Ecological implications - evidence from climatology

The discovery of the *S. sivalensis* group stimulates speculations on the origin and migration routes of the species. As the hitherto known record localities of *S. sivalensis* and *S. fusca* are widely separated, marginal and outside of the *S, ponticeriana* range, one might think of a relictary distribution pattern of the small-fanned forms.

One of the most important factors in the evolution of the genus might have been the drastic climatic change which is postulated by Quade & al.(1989) and based on analyses of soil carbon isotopes from Pakistan (outside the range of the genus *Sitana*). The isotopic composition changed rather abruptly during latest Miocene, 7.5-5 Mio yr. before present, and the authors interpret this shift as caused by a massive change of the vegetation cover from tropical woodland to grassland. They also see a connection with a strong increase of the monsoon system. This argumentation is supported by the marine fossil record, in which diatom assemblages typical for monsoon circulation appear 10-11 Mio yr. ago and increase markedly at 7.3 Mio yr.

The authors remark that already anterior to the great climatic change the forest canopy was locally broken and allowed the growth of grassland patches. The subsequent extensive replacement of forest by grassland is brought in connection with the increase of the dry seasons of the monsoon climate.

The change from a balanced tropical climate to the monsoon system could have been the key event in the evolution of *Sitana ponticeriana* while *S. sivalensis* remained restricted to the shrinking woodlands as its close-range signalling system is inferior to *S. ponticeriana* in the open landscape. Whether the subsequent expansion of *S. ponticeriana* lead to an almost total extinction of *S. sivalensis* is unknown.

The drastic climatic oscillations during the Pleistocene with at least four cool periods at the Himalayan foothills created the scenario for a repeated separation and fusing of populations and probably induced processes of microevolution and speciation.

The evolutionary record of the genus may read as follows:

1. Disruption of the common wood-inhabiting and subarboreal *Otocryptis / Sitana* stock in South India (area of the most primitive *Otocryptis*).

2. Expansion of a primitive small-fanned *Sitana* with colonising abilities over light forest and glades all over India to the Himalayan foothills

3. Climatic change during latest Miocene with partial replacement of woodland by open vegetation - disruption of *Sitana* into a small-fanned woodland (*sivalensis*) and an open-ground (*ponticeriana*) stock. Evolution of a far-distance signalling system in the latter.

4. Microevolution induced by climatic oscillations during Pleistocene

5. Extinction of the *sivalensis* group over much of its area ?

The advanced development of the communication system in *S. ponticeriana* could be connected with a larger spacing of the animals in a drier biotope and with communication over greater distances. The evolution of light reflecting devices in the gular region of *S. ponticeriana* (fig. 22) is favoured by the heavy insolation in its biotope.

A comparison of field data (paragraph 2.2.1) shows that a low population density is not a specific character, but lies within the variability range of this form. Myrmecophagy (feeding on ants) is another outstanding character of *Sitana ponticeriana*. In its open, sandy and very sunny biotopes ants and termites are by far the most numerous insects.

The intermediary position of the *S. sivalensis* group in the evolution of the genus could be seen as follows:

| | Common ancestor | *S. sivalensis* | *S. ponticeriana* |
|---|---|---|---|
| Climate | humid | subhumid | semiarid |
| | stable | monsoon | monsoon |
| Biotope | woods | woodland border, | open landscape |
| | | open patches | coast, treeless habitats |
| soil | litter | litter | open ground |
| perch | low stems | low plants, | low plants |
| | feeding on ground | hiding, feeding on ground | mostly on ground |
| food | diverse insects | diverse insects | termites and ants |
| ambient | stable | unstable | unstable |
| territory | | small | small to very large |

Appropriate open natural habitats for the *sivalensis* group are evidently scarce within forests and often created by catastrophes on small scale: the felling of large old trees during storms, or their destruction by fires. Alluvial riverine sands might form another biotope. All of these have in common that they are soon reconquered (within one monsoon season?) by a dense plant cover which forces the sitanas to emigrate and recolonize. The natural population size of these lizards is probably very small and their natural habitats have remained hitherto unknown. The creation of vast treeless secondary anthropogeneous habitats by the extensive destruction of the Terai forests during the last decades has evidently lead to a demographic explosion which greatly facilitated their discovery.

### 4.5 Outlook

Much of the preceding discussion had to remain speculative, as our knowledge about *Sitana* complexes is rudimentary. The “classical” concept of *Sitana* as a monotypic unit has blocked further systematic studies, which are additionally hampered by the fact that the fans - which present perhaps the most important morphological clue for speciation - loose most of their colouration in preserved specimens. Besides the colour patterns even simple structural characters of fans have remained unknown as the fans of hardened collection species are difficult to unfold and to study.

The easiest enterprise in this regard would be the checking of herpetological collections for small-fanned forms which are easily to recognise even in juveniles which represent a high percentage of the preserved material. It is highly improbable that the only recent members of relictary small-fanned forms are limited to two localities in the Nepalese Terai region.

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# Appendix:

1 Stereotyped behavioural patterns in *Sitana ponticeriana* and *Sitana sivalensis*
2 Terminology

## 1 Stereotyped behavioural patterns in *Sitana sivalensis* and *Sitana ponticeriana*

(numbers after Carpenter & Ferguson, 1977; data on *Sitana ponticeriana* also from Subba Rao 1970, 1982).
Note that not only simple acts (as "compress laterally", "flicker" or "leg bite") are listed but also combined ones (as "assertion", "courtship" or "challenge display").

| Behaviour | *S. sivalensis* | *S. ponticeriana* | | |
|---|---|---|---|---|
| | | Palatupana (Kratzer 1980) | animal trade | Puri (and Tirupati) |
| Maintenance behaviour: | | | | |
| hindleg scratching | + | | | |
| eye protrusion | + | | | |
| defecation posture | + | | | |
| basking | + | | + | +(Tirupati) |
| move into shade | + | | | +(Tirupati) |
| select sleeping site | + | | + | |
| sleeping posture | + | | + | |
| rest with open eyes | + | | + | |
| body winding + extended gular fan | + | | | |
| eat skin shedding | + | | | |
| sand bathing | + | | | +(Tirupati) |
| bathing in wet plants | + | | | +(Tirupati) |
| Multipurpose behaviour: | | | | |
| alertness posture | + | | + | |
| observational behaviour | + | | + | |
| bipedal locomotion | | ? | | |
| 155 colour change | + | + | + | + |
| Aggression and fighting: | | | | |
| 2. dominance | + | + | + | |
| 6. gape | + | - | + | |
| 8. fight | + | + | + | |
| lunge | + | + | + | |
| 16. leg bite | + | | | |
| 19 chase | + | + | | |
| 34 challenge display | + | + | + | + |
| 35 assertion display | + | + | + | |
| signature flicker | + | - | - | |
| throat pulsation | - | - | + | |
| 38 display site selection | + | + | + | + |
| 40 posture | + | + | + | + |
| 41 four-legged high stand | + | + | + | |
| aggressive lift of pelvic region | - | + | | |

| | Behaviour | *S. sivalensis* | *S. ponticeriana* | | |
|---|---|---|---|---|---|
| | | | Palatupana (Kratzer 1980) | animal trade | Puri (and Tirupati) |
| 43 | front leg rise | + | | + | |
| | stand on hindlegs | - | - | + | |
| 49 | display chin | + | + | + | |
| | rapid head turns | + | + | + | |
| 50 | compress laterally | + | + | + | + |
| 57 | extend gular fan | + | + | + | + |
| | flicker gular fan | + | + | + | |
| 62 | protrude tongue | + | | + | - |
| 65 | erect roach (nuchal crest) | + | + | + | + |
| | erect dorsal crest | - | + | + | + |
| | erect temporal crest | + | - | - | - |
| 66 | lateral presentation | + | + | + | + |
| 67 | face off position of rivals | + | | + | |
| | parallel positions of rivals | + | | | |
| 73 | pushup | + | + | + | |
| | pushup with lateral head motions | - | + | - | |
| | aggressive displacement chewing | - | + | - | |
| | curl tail | + | + | + | |
| | submissive ducking | - | + | | |
| 95 | horizontal tail wave | + | | | |
| | females fighting | - | + | | |
| 98 | Courtship: | + | + | + | |
| 116 | female rejection behaviour: | + | + | + | |
| | arched back | + | - | | |
| | hindleg sweeping | + | - | | |
| | fleeing from male | + | + | | |
| | hiding from male | + | - | | |
| Mating: | | | | | |
| 126 | leg hold | + | | | |
| 129 | neck bite hold | + | | | |
| | release neck bit while mating | + | | | |
| | mating posture of female | + | | | |
| | change orientation while mating | + | | | |
| | postmating display | + | | | |
| | postmating immobility | + | | | |
| Nesting: | | | | | (Tirupati) |
| | dig nest with forefeet | + | | | + |
| | dig vertical shaft | + | | | + |
| | sweep sand with hindfeet | + | | | + |
| | rest outside shaft | + | | | + |
| | oviposition on shaft opening | + | | | + |
| | push eggs with snout | + | | | |
| | ramming sand | + | | | + |

## 2 Terminology (ethological)

| | |
|---|---|
| Appetitive behaviour | Search for key stimuli which start an act system |
| Assertion | Spontaneous (not released) static or dynamic display of males to advertise conspecifics of their presence |
| Autapomorphy | Phylogenetically new character restricted to a few or one species |
| Challenge | A male's ritualised threat against a rival |
| Display | Signal behaviour by which an animal becomes more conspicuous |
| Disruption | Phylogenetic process by which selection favours the evolution of two divergent forms by eliminating intermediate ones. |
| Dynamic display | Display with motions, e.g. with body, head or gular appendage |
| Flicker | Rapid extension and contraction of the gular fan in a fraction of a second |
| Functional system | Group of acts with similar task or function, e.g. locomotion, reproduction |
| Gradedness | Quality of a signal which can be emitted in different intensities which are continuous from zero to a maximal value |
| Gular fan | Appliable flat gular appendage serving for display |
| Gular pouch | Voluminous gular appendage which is formed by the expansion of the gular skin by the hyoid apparatus |
| Intention movement | Incomplete act, normally marking only the start or preparation for a full action |
| K-strategy | For explanation see paragraph on reproductive strategies (2.2.3) |
| Key stimulus | Stimulus or stimulus combination which is needed to trigger or maintain an innate act system |
| Male rejection | Rejection of a courting male by a female which is not motivated to mate |
| Nod | Ritualised vertical head motion |
| Plesiomorphy | Old phylogenetic character common to a greater systematic unit |
| Pulsation | Minimal rapid dorsoventral movement of the gular skin caused by repeated protractions of the hyoid apparatus |
| Pushup | Ritualised vertical motion of the forebody in which the forelegs are involved |
| r-strategy | For explanation see paragraph on reproductive strategies (2.2.3) |
| Releasing threshold | Minimal quantity of a stimulus which is needed to trigger a reaction. |
| Ritualization | Evolutive process by which motions and postures of other functional systems (e.g. multipurpose or maintenance behaviour) are transformed into signals |
| Semanti(ci)sation | Evolutive process by which morphological structures (very often of the integument) are transformed into signal structures. |
| Signature | Species-specific display, in *S. sivalensis* the double flicker, which serves to specify assertion, courtship and challenge |
| Static display | Display by posturing alone, opposite to dynamic display |
| Stimulus "summation" | Reciprocal support of several key stimuli which release the same action |
| Synapomorphy | New phylogenetic character present in several related species |
| Threat | Any ritualised behaviour serving to fend off a facultative predator or a conspecific. |

## Literature for terminology

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# Contributions to the Biology of the Genus *Sitana* (Sauria: Agamidae)

# *Sitana fusca* spec. nov., a further Species from the *Sitana sivalensis* Complex

H. Hermann Schleich* & Werner Kästle**

**Key words:** Reptilia, Agamidae, *Sitana fusca*, *Sitana ponticeriana*-complex, *Sitana sivalensis*-complex.

**Abstract:** The description of a second small-fanned form, *Sitana fusca,* from a locality 300 km east of the type locality of *Sitana sivalensis* shows that the genus *Sitana* consists at least of two groups: the large-fanned *S. ponticeriana* and the small-fanned *S. sivalensis* -complexes. The latter seems restricted to marginal areas while the *ponticeriana* group inhabits most of the Indian subcontinent.

*Sitana sivalensis* and *S. fusca* are closely related and their separation by polidotic characters is nor easy. During the mating season *fusca* specimens are generally almost black with exception of the dorsal region and some light marks. Fully grown males of this species have much longer heads and bodies than S. sivalensis.

In contrast to *sivalensis* they can evidently not erect a nuchal roach and never have their upper eyelids and nuchal streak coloured blue.

Both *S. sivalensis* and *S. fusca* perform double flickers with their gular fans. The communication system of *S. fusca* has perhaps undergone fundamental changes to reduce intraspecific aggressivity, especially between males.

**Contents**

## 1. Introduction

As it is very improbable that the area of *Sitana sivalensis* is restricted to a few localities H.-H. Schleich searched intensely for *Sitana* during his stay in East Nepal in June 1996. 300 km eastward from the *Sitana sivalensis* locality and 90 km SSE of Kathmandu he found several specimens of a form with a small fan in a biotope similar to that of *S. sivalensis*. It was evident that the animals were much darker. First observations on captives showed that both forms are closely related, but differ fundamentally in the organisation of their signal systems, social organisation and at least some aspects of their ecology. Thus their separation as different species is justified.

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## 2. Materials and methods

Our studies are based on six living (four males, two females) and seven preserved (one male, four females) adult specimens from one population. All females were pregnant when captured. We are greatly indebted to Christiane Anders for collecting the living ones. Her engagement helped us to observe the animals in captivity and compare their behaviour with *S. sivalensis*. Additionally eight hatchlings could be observed since the end of October 1996.

The conditions of maintenance and observation were identical to those for *S. sivalensis* (same vol., preceeding article) and the animals accommodated themselves quickly. They began to feed immediately after leaving their transport cloth bag. The first mating was observed on the 4th of June, five days after their arrival.

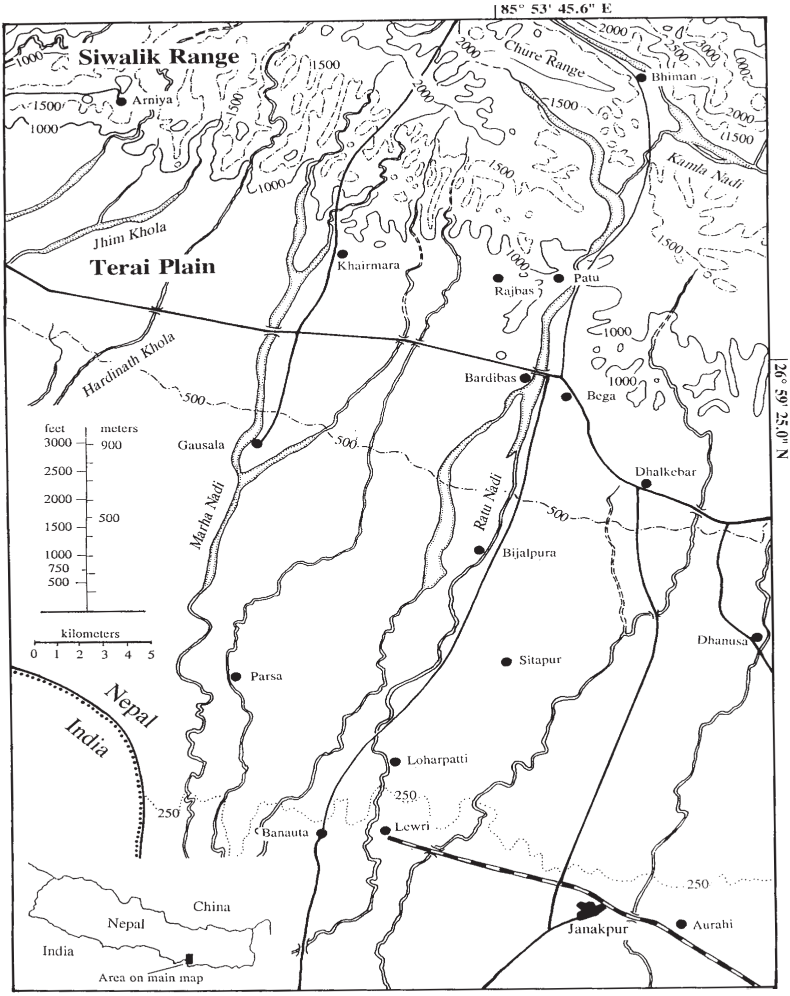

**Fig. 1.** Position of the type locality (circle near Bardibas). Elevations in feet.

Nevertheless it was apparently very difficult to provide optimal keeping condition, and the following disturbances were recorded: total egg retention; partial egg retention; egg deposition on the ground; interruption of nesting, unfertilised eggs. One late embryo punctured its eggshell in time after 46 days of incubation, with yolk for 1-2 weeks remaining, and died The three ovipositions obtained up to date from two wild caught females occurred without regular nesting. In spite of the fact that the terraria were provided with a variety of nesting facilities - moist sand and earth of different temperatures, stones, leaf cover and grass bunches under which to dig - the females laid their eggs on leaves or below them on moist sand where they rapidly dry if not put into an incubator.

## Comparison of both species of the *Sitana sivalensis* group

It is much easier to distinguish both forms in the field. The dark brown general, coloration changes (for reasons unknown to us) to greyish brown under captivity conditions. Specimens preserved in alcohol additionally lack the orange inguinal spots.

| | *Sitana sivalensis* | *Sitana fusca* |
|---|---|---|
| Last enlarged fan scales | much larger than ventrals<br>broad and rounded | very similar to ventrals<br>triangular |
| Scalation of dorsal field | regular | partially irregular |
| Body size and shape: | | |
| Snout in males | high | depressed |
| in both sexes | not jutting over mental | prominent |
| Coloration: | | |
| Normal body colour in the field! | light brown | very dark brown to blackish |
| Dorsal pattern mainly of | triangles | bell-shaped patches |
| Male in reproductive phase: | | |
| Upper eyelids | blue | dark |
| Nuchal streak | blue | lacking |
| Venter | white | brownish, spotted with dark |
| Behaviour: | | |
| Double flickers | during assertion, courting and threat | seen only during excitement |
| Assertion | dynamic:<br>posturing with flickers | static:<br>only posturing |
| Nuchal crest (roach) | erected during challenge | never observed |
| Rival tolerance | very low | very high |
| Threat nods | single | long series with up to 7 units possible |

## 3. Description

### Systematic account

Type material: Fuhlrott-Museum, Wuppertal: two subadult males (holotype, VW-D 96/21; paratype 96/22) and four adult females (paratypes, 96/23-27). Six specimens are still living in captivity. More topotypes are deposited in the Museum of Kathmandu, eight hatchlings are being reared.

Type locality (fig. 1): East Nepal, Ghauri Dhara Road Camp 0.8 km north of the road Janatir - Bardibas. Geographic coordinates: N26° 59'25.0" / E 85° 53'45.6" by GPS

Etymology : from lat. fuscus = dark brown. In the field the lizards showed a much darker coloration than Sitana sivalensis

Diagnosis : A small *Sitana* species which is closely related with *Sitana sivalensis* (fig. 2). In the field it differs by its much darker colour in life. Preserved females are difficult to distinguish from *S. sivalensis*, but males have a very pointed and depressed snout. jutting over the mental region (fig. 3 ). In *Sitana sivalensis* the mental plate is surrounded by four or five scutes (two infralabials and two or three postmentals), in *S. fusca* apparently always by five. In this species the first infralabials are rather long, and the connection lines of their posterior borders (dotted in fig. 4) divides the lateral postmentals approximately into halves, while in *S. sivalensis* this line transsects their anterior part. In *sivalensis* males the outline of the head is more oval (fig. 5) while the snout appears triangular in *fusca*.

The last fan scales are - in contrast to *S. sivalensis* - very similar to the ventrals (fig. 6). In the reproductive phase *S. fusca* males lack the blue colour on the eyelids and the nuchal crest . Their venter never becomes pure white.

The scales of the dorsal field are partially irregular in shape and size (fig. 7 ) and, in contrast to *S. sivalensis*, the longitudinal keel rows are frequently disturbed.

The behaviour of *S. fusca* is characterised by the tolerance between males and a reduced challenge behaviour.

**Fig. 2.** Holotype specimens of *Sitana sivalensis* (darker!) and *S. fusca* (VW-D 95/1; 96/21).

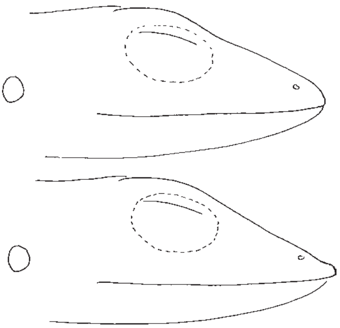

**Fig. 3.** Head profiles of *S. sivalensis* (above) and *S. fusca* males.

**Biometry of the types**

| | holotype | paratypes | | | | | |
|---|---|---|---|---|---|---|---|
| | male | male | females | | | | |
| VW-D | 96/21 | 96/22 | /23 | /24 | /25 | /26 | /27 |
| Snout-vent length (mm): | 39,0 | (41,1) | 47,7 | 42,1 | 42,0 | 42,5 | 41,5 |
| Tail length (mm): | 86,2 | — | 77,9 | — | — | — | — |
| Relation tail length : SVL | — | (2,1) | — | 1,85 | — | — | — |
| Head length (mm): | 11,4 | (10,8) | 11,1 | 11,05 | 10,8 | 10,9 | 11,6 |
| Head width (mm) : | 7,6 | 8,15 | 7,4 | 8,2 | 8,2 | 8,0 | 8,3 |
| Relation head length : width : | 1,5 | (1,33) | 1,5 | 1,35 | 1,3 | 1,36 | 1,40 |
| Forelimb length (mm): | 16,6 | 16,3 | 14,3 | 13,8 | 14,3 | 14,1 | 14,6 |
| Hindlimb length (mm): | 32,5 | 35,0 | 35,8 | 30,25 | 32,1 | 33,9 | 32,2 |
| Hindlimb length : forelimb length: | 1,95 | 2,14 | 2,50 | 2,13 | 2,24 | 2,40 | 2,20 |
| Relation SVL : hindlimb length: | 1,2 | (1,17) | 1,33 | 1,39 | 1,31 | 1,25 | 1,29 |
| Foot length (mm): | 15,5 | 14,8 | 14,1 | 14,5 | 14,6 | 13,85 | 13,5 |
| Heel to second longest toe (mm): | 10,2 | 10,4 | 13,0 | 10,6 | 9,9 | 10,3 | 9,9 |

Measurements in brackets refer to the paratype male with a defect snout.

**Body/leg proportions:**

| | holotype | paratypes | | | | | |
|---|---|---|---|---|---|---|---|
| | males | | | females | | | |
| If the forelimb is plied forward | | | | | | | |
| four fingers tips surpass the snout | | X | | | | | |
| the three longest fingers surpass snout | | | | X | | | X |
| the two longest fingers surpass snout | X | | | | X | | |
| the two longest fingers reach snout | | | X | | | X | |
| If the forelimb is plied backwards | | | | | | | |
| two longest fingers reach the groin | X | X | | | | | |
| claw of longest finger is 2 mm from groin | | | | X | | | X |
| claw of longest finger is 4 mm from groin | | | X | | X | X | |
| If the hindlimb is plied forward | | | | | | | |
| longest toe surpasses the snout | | X | | | | | |
| longest toe reaches betw. eye and nostril | X | | | X | | | |
| claw of longest toe reaches the orbit | | | X | | X | X | X |

As in *S. sivalensis* the males have higher averages in limb length, but there is some overlap. The relatively longer bodies of *S. fusca* females causes a wider gap between the forelegs plied backwards and the groin, and a relatively short reach of the hindlimbs plied forward.

Even if we admit faulty measuring from the preserved and hardened material the body proportions of our small type series show a considerable variability range. At present it can be doubted if measurements and scale counts can serve to separate specimens of *S. fusca* from *sivalensis*.

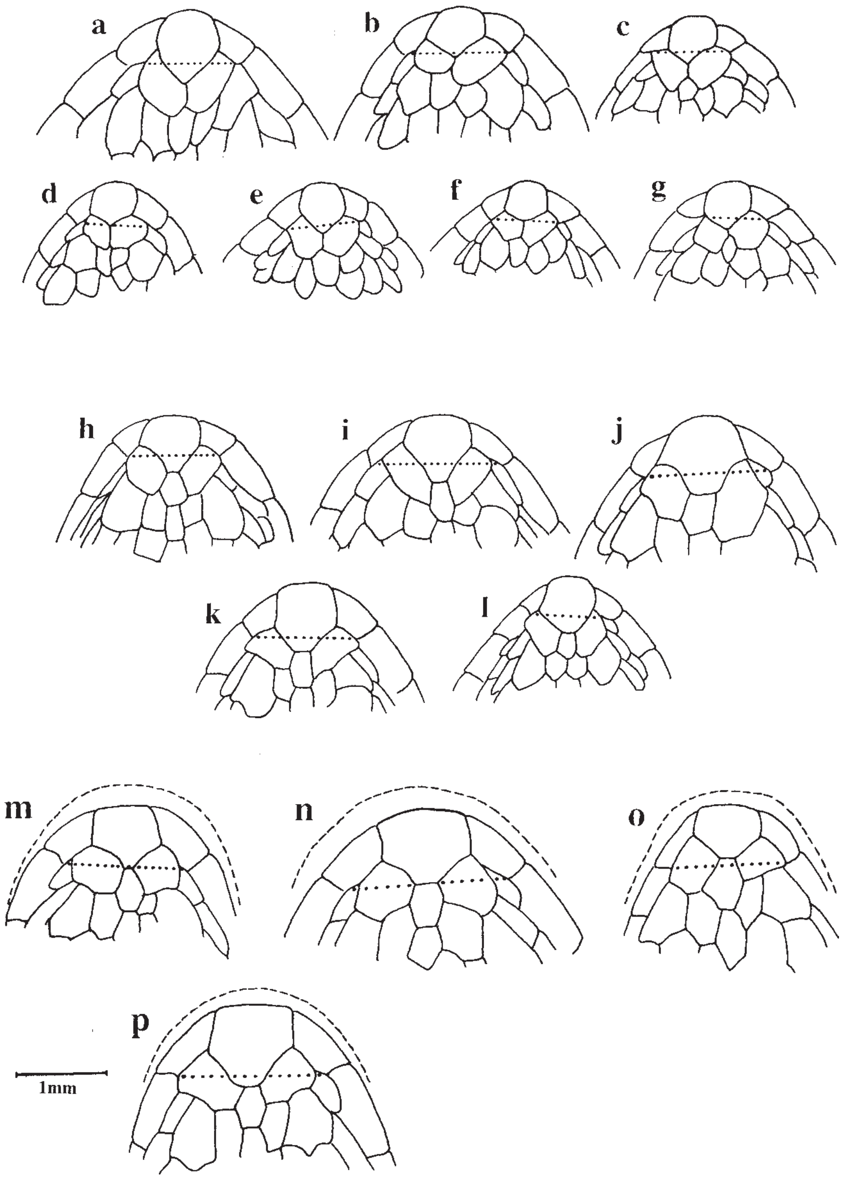

**Fig. 4.** Mental region of *S. sivalensis* (a-l) and *S. fusca* (m-p). The broken line indicates the jutting rostral. The dotted line connects the posterior ends of the first supralabials.

Comparison of body proportions (averages for females if several data are available)

| | *S. fusca* | | *S. sivalensis* | |
|---|---|---|---|---|
| | male | female | male | |
| female | | | | |
| Tail length : snout-vent length | 2,1 | 1,85 | 2,0 | 1,82 |
| Snout vent length : head length | 3,42 | 4,0 | 3,8 | 3,66 |
| Head length : head width | 1,33 | 1,38 | 1,36 | 1,45 |
| Hindlimb length : forelimb length | 2,05 | 2,29 | 1,93 | 2,23 |
| Snout-vent length : hindlimb length | 1,20 | 1,31 | 1,24 | 1,13 |

In both species the males have relatively longer tails and hindlimbs. The strikingly low quotient for snout-vent length : head length in the *S. fusca* male is caused by the considerable head length in this species which shows a striking sexual dimorphism (fig. 8,9).

**Fig. 5.** Ventral head sides of *S. sivalensis* (left) and *S. fusca*. The dark gular streak of *S. fusca* faded in captivity.

### Pholidosis of holotype and paratypes

Pileus (fig. 10):
The scalation is similar to the general situation in *Sitana* with irregularities in scale size and symmetry. In the internasal region many scutes are not polygonal, but rounded and more like scales. This character lacks in most paratypes.

Head sides (fig. 10,11):
On the acuminate snout the prenasal scute is more elongate (in the holotype, but not in all paratypes) than in *S. sivalensis*. The pholidosis between the nasals and the supralabials is often asymmetrical on both head sides (fig. 11) and shows a large variability range e.g. in the shape of rostrals and nasals, or in the intercalar scales between nasals and supralabials.

Mental region:
The mental is rather broad and not bulging forward between the first supralabials. As in many *S. sivalensis* it is surrounded by five scales (fig. 4m-p).

Gular region:
The change from enlarged midgular fan scales to ventrals of small size is abrupt in *S. sivalensis*, but gradual in *S. fusca* (fig. 6, at right). In *S. sivalensis* the last midgular fan scales are very broad, rounded and without a tip. In *S. fusca* they are rounded triangular and similar in size to the adjoining ventral scales. This character is present in the holotype as well as the paratype male and perhaps reliable for separating *S. fusca* from *S. sivalensis*. Additionally the longest median fan scales show a greater overlap in *S. sivalensis* (fig. 6 left).

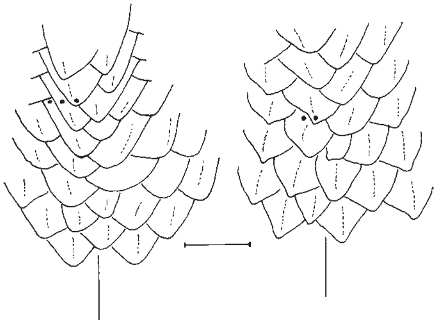

**Fig. 6.** Comparison of the gular scalation: In the *S. sivalensis* type (left) the enlarged fan margin scales abruptly border on the much smaller ventrals; in the *S. fusca* type there is a transition zone. In *S. sivalensis* three long median scales overlap (dots), in *S. fusca* only two.

The weak difference between the fan scales and the subsequent ventrals (fig. 12) is perhaps due to a lower degree of differentiation, which could be interpreted as a more primitive character state. The fan is of equal size as in *S. sivalensis* (fig. 13).

Body scalation (fig. 14):
Due to irregularities in scale size, shape and arrangement the dorsal scale keel rows are frequently interrupted. There are small additional scales inserted between the regular rows, and even in regular scale rows the orientation of the keels may vary. The double vertebral row consists of distinctly smaller scales.

Comparison of some pholidotic data from the type specimens
The rounded form of the pileus scales in the holotype is due to intraspecific variability and not present in all paratypes-

1. Scales between supraoculars (lowest number counted)
2. Scales between parietal and supraocular, left/right
3. Scales between parietal and rostral
4. Number of supralabials, left / right
5. Number of infralabials, left / right
6. Number of scale rows between supralabial and orbit, left / right
7. Number of large scales between tympanum and orbit, left / right
8. Contact between nasal and supralabials: 1 total; 2 partial; 3 full contact, left / right
9. Dorsalia longitudinal rows (lowest number counted at midtrunk)

| | holotype | paratypes | | | | | |
|---|---|---|---|---|---|---|---|
| | VW-D 96/21 | 96/22 | /23 | /24 | /25 | /26 | /27 |
| | male male | females | | | | | |
| 1. orbit - orbit | 13 | 11 | 10 | 11 | 11 | 11 | 12 |
| 2. parietal - orbit | 7/7 | 6/7 | 7/7 | 5/5 | 5/5 | 7/6 | 7/7 |
| 3. parietal - rostral | 12 | 11 | 10 | 11 | 10 | 11 | 11 |
| 4. supralabials | 8/9 | -/8 | 7/7 | 9/8 | 9/9 | -/- | 8/8 |
| 5. infralabials | 9/8 | 7/7 | 7/7 | 7/6 | 7/6 | 8/- | 9/9 |
| 6. supralabial - orbit | 2/2.5* | 2/2 | 2/3 | 2/2 | 2.5/2.5* | -/2.5 | 2/2 |
| 7. tympanum - orbit | 6/6 | 6/6 | 7/7 | 7/6 | 7/6 | 5/6 | 7/6 |
| 8. nasal - supralabial | 2/1 | -/2 | -/2 | 2/2 | 2/2 | 2/2 | 2/2 |
| dorsalia rows | 8 | 8-9 | 9 | 9 | 9 | 8 | 8 |

*two broad rows and a very narrow one.

In comparison with *Sitana sivalensis* some scale counts are slightly lower, e.g. for the interorbital scales, infralabials, rows between supralabials and orbit, finally tympanum - orbit. A total contact of the nasal with supralabials (1) is frequent in *S. sivalensis* but was not observed in *S. fusca*. Nevertheless the counts between both species are widely overlapping.

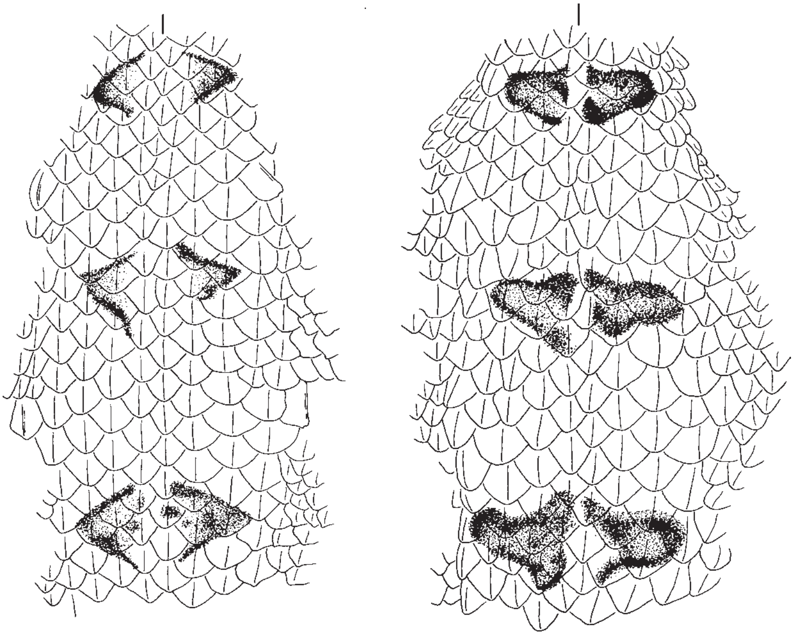

**Fig. 7.** Pholidosis of the dorsal field in *Sitana sivalensis* (left) and *S. fusca*. In the latter there are more irregularities of scale size and shape which interrupt the longitudinal keel rows.

## Colour pattern

The general pattern elements are identical with those of *S. sivalensis* except the blue stripe on the nuchal roach and the blue spots on the upper eyelids. As sexual dichroism lacks in this species. The patterns of males and females are identical with the only exception of the dark gular streak which can totally fade (fig. 5, 13).
Mostly there are no dorsal rhombi which are composed of two isosceles triangles as in *S. sivalensis,* but the dorsal marks are - with rare exceptions - composed of two bell-shaped or u-shaped spots (fig. 7,15 ). Totally asymmetric patterns with small additional elements as in *Sitana sivalensis* (se preceding article, fig. 6 f,g) were not observed.

As the preserved specimens lost their typical dark brown basic coloration we describe the pattern of specimens under natural conditions which was documented with photographs (fig. 16, 17):
Head, flanks, most of the limbs and the posterior part of the tail are brownish black. The head shows only a few light spots on the superciliary ridges; the dark pileus pattern as well as the light subocular spot disappears under the dark hue. The black colour of the flanks

can extend towards the dorsal rhombi and fuses with them (fig. 16). The light vertebral streak persists only within the rhombi. Light tips of the enlarged lateral scale are a common trait with *Sitana sivalensis*.

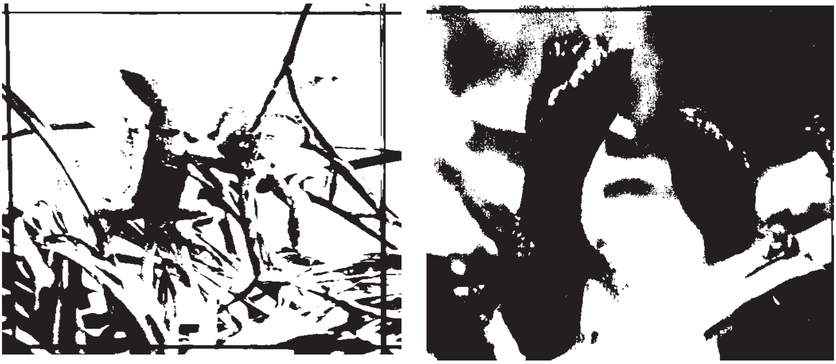

**Fig. 8.** *Sitana fusca*, male and female.
**Fig. 9.** *Sitana fusca*, heads of male and female.

In a somewhat lighter colour phase (fig. 17) the dark flanks do not reach the lateral tips of the rhombi. These appear in sharp outline as the adjacent dorsal field is light.

In contrast to the brown middorsal field the orange dorsolateral patches are very persistent against darkening and never disappear entirely. In animals with a maximal darkening they are enclosed in oval "eyespots" (fig. 18) which perhaps have signal character as they are sharply delimited and contain a dark centre contrasting with light brown.

The same function can be supposed for the inguinal marks (fig. 18) which are of a constant light orange and contrast most effectively in the darkest colour phase.

We could not make out any difference in the gular patterns of *S. fusca* and *sivalensis*. In both species a deep blue streak is followed by a greyish brown blotch.

While in *S. sivalensis* the venter can turn white in both sexes (in females they are mostly spotted), they are always marked with brown in *S. fusca* (fig. 19).

As the ranges of colour change overlap *S. fusca* in its light phase is difficult to discern from *S. sivalensis* in its dark phase.

Coloration of preserved specimens:

In alcohol the orange inguinal marks and the brown ventral pattern fade. As a part of the brown pigments is dissolved the specimens turn greyish with the dorsal rhombi almost black. Preserved *S. sivalensis* are distinctly lighter and brownish.

**Biological function of the dark colour phase**

In captives the typical blackish basic coloration faded after a few days to a greyish brown (fig. 20, 21). Evidently *Sitana fusca* is the only species of the genus which is capable to turn to an almost total black overall colour. We can only speculate about the biological function of this evidently derived character, nor can we explain its disappearance within a few days.

A connection with heat absorption and heliothermy apparently lacks, and no specimen in the sun, under halogen or ultraviolet lamps ever turned dark.

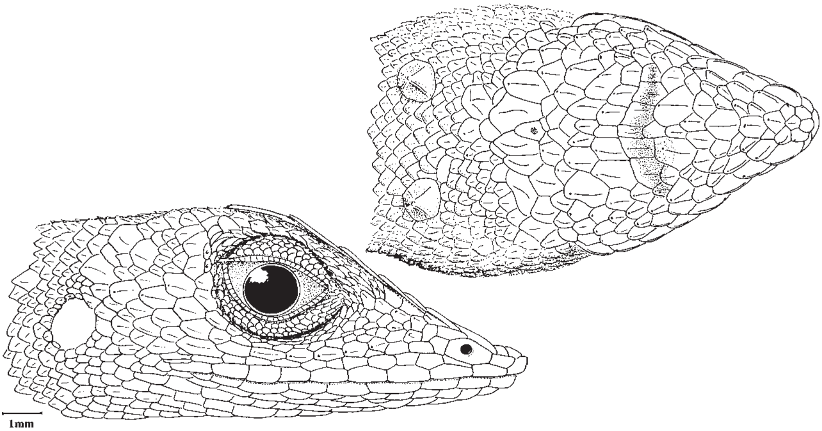

**Fig. 10.** Head pholidosis of *Sitana fusca* holotype (VW-D 96/21).

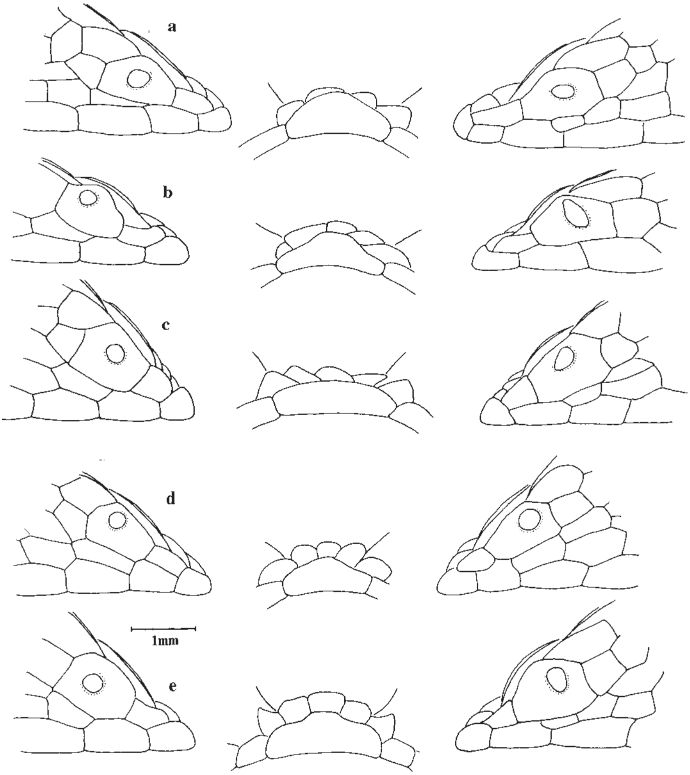

**Fig. 11.** *Sitana fusca*, pholidosis of nasal and rostral regions. As in *S. sivalensis* the intraspecific variability and the asymmetries are striking. a. holotype male; b-e females (paratypes 96/23, 24, 26, 27).

A signal function was not confirmed, but there are two arguments for it:

1. The dorsal eyespots and the inguinal marks are most striking during the dark phase of the lizards.
2. Together with the dark coloration the dark gular streak of males disappeared totally.
3. Within five days after their arrival the single and last mating was observed on June 23rd 1996.
4. At the same time the assertive posturing of males ceased.

We therefore propose a preliminary interpretation of the dark phase as a nuptial coloration. Paradoxically the hatchlings turn almost black when wet. As the coloration is - in contrast to *S. sivalensis* - equal in both sexes other signals are necessary for sex recognition. As to our observations flickers are very rare in *S. fusca*, but the species shows a very pronounced sexual dimorphism, which eventually compensates the lack of male colour signals - a case of "stimulus summation".

This concept is applied if several key stimuli work in combination to trigger some form of innate behaviour, e.g. the receptivity of females. Far from a simple addition of key stimuli (as the term could make believe) the releasing threshold of an action needs a certain total of stimuli, the components of which can partially replace each other. *S. fusca* has fewer colour signals, but additional morphological cues for sex recognition.

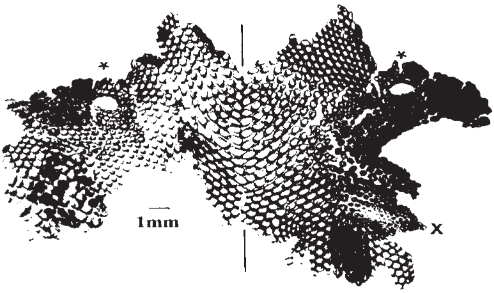

**Fig. 12.** Gular skin shedding of *S. fusca* male with the midgular line marked. The alternating and weakly enlarged scales along it form the fan margin. The positions of the eardrums are indicated with asterisks. The * marks the granular scalation of the armpit.

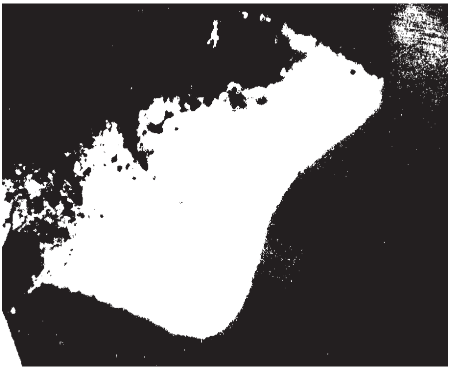

**Fig. 13.** *S. fusca* male with fully expanded fan.

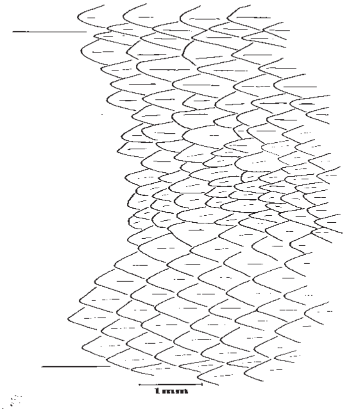

**Fig. 14.** *Sitana fusca*, pholidosis of right body side; middorsum and midventer are marked with a line.

The light brown captives did not turn dark again, independent of illumination, plants in the terraria (green or dry), moisture, food (including "wild" insects, or number of animals in the cages. The general effect of stress from captivity and confinement can perhaps be eliminated when we succeed to rear captivity-bred juveniles.

A rather simple but unconfirmed explication of the fading dark colour is the supposition that the mating season was over by the end of June. But the effect of defective maintenance conditions cannot be ruled out and is supported by the fact that none of the clutches was deposited with normal nesting behaviour.

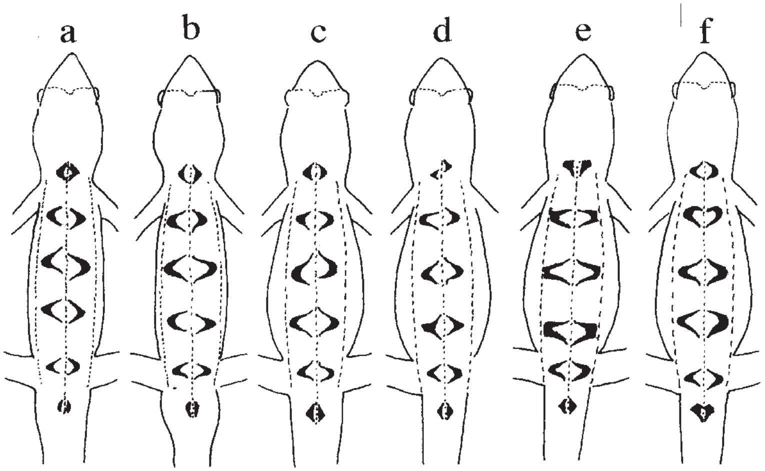

**Fig. 15.** *S. fusca,* dorsal patterns mostly composed of symmetrically arranged bell-shaped elements (a: holotype; b-f paratypes 96/22,24-27).

## 4. Biology

### 4.1 Biotope

While *S. sivalensis* was found in roadside condition, *S. fusca* lived in abandoned fields (fig. 22). Again the main herb was the introduced *Eupatorium (odoratum?)* between isolated *Dalbergia sissoo* and *Acacia* trees. They are a relict of the deciduous monsoon woods which in the past decades have been destroyed and replaced by extensive paddy fields. On the plots with *Sitana fusca* the ground was dry and sandy.

**Fig. 16.** Female *Sitana fusca* in the habitat.

### 4.2 Population biology

#### 4.2.1 Population density:

In a vast stretch of low and dry *Eupatorium* growth the only population which could be discovered lived in an area of 500 m². The population size was estimated at 15 adult specimens and no juveniles, which might result in a theoretical density of 300 adult specimens / ha. But they formed a colony (in French literature the term “noyau” was proposed for this type of inhomogeneous distribution, which was also observed and described for *Phrynocephalus helioscopus* by Schleich). It consisted of two aggregations about 20 m apart within a rather homogeneous habitat, and social attraction evidently prevented their wider dispersal. The formation of colonies is perhaps favoured by the lack of male rival hostilities which is one outstanding characteristic feature of the species.

#### 4.2.2 Population dynamics:

The presence of half grown and fully adult specimens of *S. fusca* in May and June suggests a prolonged reproductive season similar to that of *Sitana sivalensis* (see preceding article, paragraph 2.2.3)with the earliest hatchlings (from July) attaining maturity in less than one year.

**Fig. 17.** Female *Sitana fusca* in the habitat; lighter colour phase.

**Fig. 18.** Female *Sitana fusca* with strikingly coloured inguinal marks and dorsal eyespots.

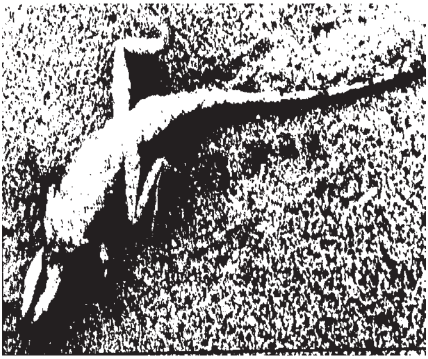

**Fig. 19.** *Sitana fusca* male, ventral colour pattern.

**Fig. 20.** *Sitana fusca* male in grey colour phase.

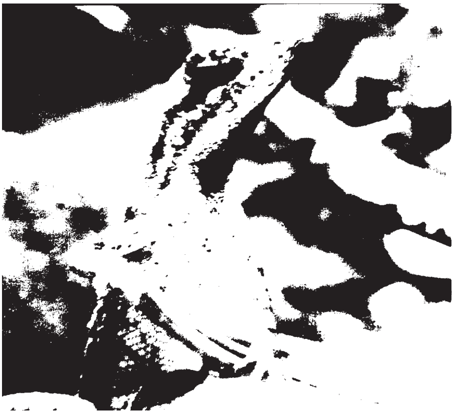

**Fig. 21.** *Sitana fusca* male in grey phase, gular pattern.

**Fig. 22.** Habitat near Bardibas, in an abandoned field with dry *Eupatorium* weed.

### 4.3 Behaviour:

When this manuscript was finished observations on the social behaviour of this species were still fragmentary. But some behavioural differences between *S. fusca* and *S. sivalensis* are so striking that they must be mentioned here as they support their description as separate species:

1. In *S. fusca* double flickers - which play an essential role during assertion, challenge and courtship of *S. sivalensis* - are largely lacking. While a recently matured *S. sivalensis* male performs them during the reproductive period hundreds of times per day, they can be observed in *S. fusca* only on very rare occasions: in very excited males e.g. when they were released from the transport bag or when their terrarium was transported to a place in the sun to take fotos. In both cases very short series of two or three double flickers were preceded by two or three rapid turns of the head similar to courtship in *S. sivalensis*. From two males in a terrarium only the smaller one performed flickers. In the subsequent months the undisturbed males stayed rather cryptic and their display behaviour ceased totally.

2. Flickers were not recorded with a camera, but seemed slower in *S. fusca*, where one unit lasts about 0.8 sec against 0.5 sec in *S. sivalensis*.

3. Male assertion seems to be entirely static, not dynamic with ritualised motions as in *S. sivalensis*. The male sits exposed in upright posture with the head in one line with the trunk.

4. No male rival behaviour was observed. We saw neither threat posturing (gape, fan extension, lateral flattening, pushups or transverse orientation) nor fights. The male even sat in body contact over many minutes.

5. Mechanisms helping to reduce intraspecific aggression

Some special features of the species can be interpreted as adaptations to reduce intraspecific aggression, especially rival behaviour between males: Signal structures which in *Sitana sivalensis* release challenge and aggression in males were not observed in all our captive *S. fusca* males and are evidently lacking: The erectile nuchal crest (roach) and the blue colour on roach and upper eyelids. The blue gular streak is mostly not as dark as in *S. sivalensis*.

If there is any correlation between reduced signalling and the contracted distribution pattern of *S. fusca* in its habitat must remain a matter of speculation.

As some male sex characters - as blue eyelids and nuchal line as well as assertion flickers - are lacking other traits of sexual dimorphism have evolved: The males have a distinctly larger head and longer neck.

6. Interspecific threats between *Sitana fusca - S, sivalensis*

The evident incompatibility of their communication systems makes normal challenge duels between males of both taxa impossible.

Method: Two adult *S. fusca* males were kept together with and adult *S. sivalensis* male and several females of this species. For six weeks the males of both species did not show any hostile behaviour. After six weeks one of the *S. fusca* males began to interact with the *sivalensis* male, but only incomplete and low-graded threat behaviour was elicited on three successive days:

a) Each time the reaction chain started when the *fusca* male began his static assertion behaviour with upright head, showing his ventral side in a colour pattern which is very different from a displaying *sivalensis* male: The dark gular streak lacked, the infralabials were dark brown and the venter was light brown with dark spots.

The sight of the *sivalensis* male at a distance from 10 to 20 cm irritated the *fusca* male and released a few double flickers (a sign of general arousal in this species, but a normal constituent of assertion in *sivalensis*).

b) The *sivalensis* male reacts with low intensity threat. The *fusca* male lacks essential releasers for normal challenge behaviour: the blue eyelids and nuchal crest, the dark gular streaks and the white ventral side. Additionally his flicker series are very short.

c) The weak threat of the *sivalensis* male is answered by the *fusca* males with a reaction never released by conspecifics of this apparently very pacific species: full fan spread, lateral flattening and a series (up to seven) slow nods.

d) Fan spread is "understood" by the *sivalensis* male which attacks, but did not start fighting as the adversary lacks important cues for full challenge behaviour: those mentioned above plus the threat face and dorsolateral ridges.

e) The *fusca* male invariably fled in spite of his somewhat superior size as he is evidently not "programmed" for fighting.

On one occasion the *sivalensis* male followed his adversary, approached to a distance of 1 cm and then scrutinised him for 4 min until he jumped away without further interactions.

f) Nevertheless he sometimes resumed static assertion within a few minutes with the whole sequence repeated.

The following survey compares the normal challenge behaviour of a *sivalensis* male against a conspecific rival (left side) with the low level reaction released by a *fusca* male (right side).

| Intraspecific challenge against *sivalensis* rival | Interspecific threat against *fusca* male |
|---|---|
| full challenge display (see preceeding article): | low threat steps: |
| a) gular spread | gular spread |
| b) lateral flattening | lateral flattening |
| c) transverse orientation | transverse orientation |
| d) nuchal crest | - |
| e) threat face | - |
| f) dorsolateral ridge | - |
| g) antiparallel position and circling | - |
| damaging fight with firm bite hold | short attack |
| subordination of inferior rival (see preceeding article) | no fundamental change of behaviour |

To his own mirror image the same *sivalensis* male responded with full challenge repertoire.

8. Digging into the sand surface was never, and bathing was only once observed. Even when the lizards hid under dry leaves or twigs they never dug into the sand surface neither spent the night there.

Apparently bathing in wet plants has a high releasing threshold. The single observation on this activity of a pregnant female was made when the terrarium was sprinkled in the morning. At this time four females and seven males had been kept for over three months.

9. Three days old hatchlings showed prolonged and very intense phototactic locomotion towards light sources of high intensity - a neighbouring cage or (in case of sunshine) the window. This type of behaviour appeared in “bouts” of several minutes during which they most vehemently struggled against the plastic panes of their cage. Often several siblings were stimulated. On the fourth day the bursts of locomotion had completely ceased. The social stimulation reminds of the observations made by Burghardt & al. (1977) in an *Iguana iguana* rookery and shows that posthatching activities in lizards with large clutches are worth being studied more intensely
One adult male needed several months to learn that a glass pane is an impenetrable obstacle.

## 5. Discussion

The morphological differences alone are not sufficient to separate *S. sivalensis* and *fusca* as full species. The fan patterns are identical, The basic body coloration of light *fusca* and dark *sivalensis* specimens are principally the same, and the alternative of bell-shaped spots versus triangles as components of the dorsal rhombi is not an absolute one.
The regularity of the dorsal field scales in *S. sivalensis* has its exceptions.
What induced us to describe *fusca* as a separate species are its behavioural specialisations, above all the absence of male hostilities, and - connected with this - the lacking ability to interpret the signals of the other species.

The discovery of a second small-fanned *Sitana* form which additionally reveals its close relation to *S. sivalensis* by its signature display of double flickers suggests that the genus *Sitana* consists of at least two complexes - a small-fanned and a large-fanned one with several species each. They may be named the *sivalensis* - and the *ponticeriana*- complex. The apparently very limited distribution area of small-fanned *Sitana* forms suggests a relictary situation caused by the expansion of the more modern *ponticeriana* group. If this point of view is correct further small-fanned forms will be found in marginal (moister and/ or cooler?) biotopes.

The reason why the small-fanned forms escaped discovery is due to the fact that their females and juveniles are scarcely to distinguish from those of the *ponticeriana*-complex, and their males were taken for juvenile *ponticeriana*. Both *S. sivalensis* and *S. fusca* inhabit open ground with low vegetation, conditions which were extremely rare in the original deciduous monsoon woods of the Terai lowland in Nepal . Only in the last decades the eradication of malaria caused a wave of intense colonisation with a rapid increase of population and heavy deforestation. The latter factor evidently favoured the founding of the once probably much rarer small-fanned *Sitana* populations. Typically both *S. sivalensis* and *S. fusca* were found in anthropogeneous biotopes - roadside respectively between cultures - with an adventive vegetation of low *Eupatorium* (*odoratum*?) weed.

Our knowledge on *Sitana* behaviour is still too fragmentary to draw solid conclusions on the direction of evolutive changes in display acts. But as intense male aggression, above all during the reproductive season, is the rule in agamids, especially in all other *Sitana* forms which were studied hitherto, we can conclude that “the peaceful male” is a highly derived state evolving towards an advanced r-strategy (see preceding article, paragraph 2.2.3) . The vehement phototactic locomotion of the hatchlings might be in connection with colonising abilities, as light guides them towards clearings with an open forest canopy, their only biotopes in their natural surroundings. The further study of this second small-fanned *Sitana* species with a very different level of aggression promises more insight into the evolution of communication and social systems within the genus *Sitana*.

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# Contributions to the Biology of the Genus *Sitana* (Sauria: Agamidae)

## Brief Notes on the Anatomy of the Female Urogenital Tract of *Sitana sivalensis*

Christiane C. Anders* & H.Hermann Schleich**

**Key words**: *Sitana sivalensis*, anatomy, female urogenital tract, Nepal.

**Abstract**: The urogenital system of a gravid female *Sitana sivalensis* is described and illustrated. Intraoviducal eggs are analysed. An overview of the opened pleuro-peritoneal cavity is given. Measurements of the position of following organs, relative to the tip of the snout, are mentioned: fat bodies, liver, kidneys and ovaries. Furthermore the different parts of the digestive tract are measured.

### Introduction

Most of the investigations concerning anatomy of lizards are given in still valid standard works from the last century. Many of previous papers deal with more physiological than anatomical aspects of reproductive systems in reptiles. Due to Childress (1970), reproductive data on Old World agamids are scarce in comparison to those of New World lizards.

Investigations on the reproductive biology of agamid lizards, containing informations on number and size of both ovarian and oviducal eggs are given by Childress (1970) and Vitt (1973).

General anatomical informations on lizards are presented in Gans & Parsons (1977). Guidance for dissection of *Agama agama* is provided by Renner (1984) and for *Lacerta viridis* by v. Dehn (1975). A comprehenshive description of agamid anatomy is given by Harris (1963) on *Agama agama.*

### Material and Methods

One female specimen of a captive population of the new species *Sitana sivalensis* (see preceeding paper contributions, same volume by Schleich & Kästle ) probably died from egg retention. The present investigation includes examination of the urogenital tract of this gravid female agamid. The dissection of the body was accomplished under water and details were observed with a binocular microscope. All measurements were made with callipers.

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## RESULTS

Species: *Sitana sivalensis* Schleich & Kästle, 1996
Sex: female
Age: mature, gravid
Snout-vent length (SVL): 38 mm
Total length (TL): 106 mm

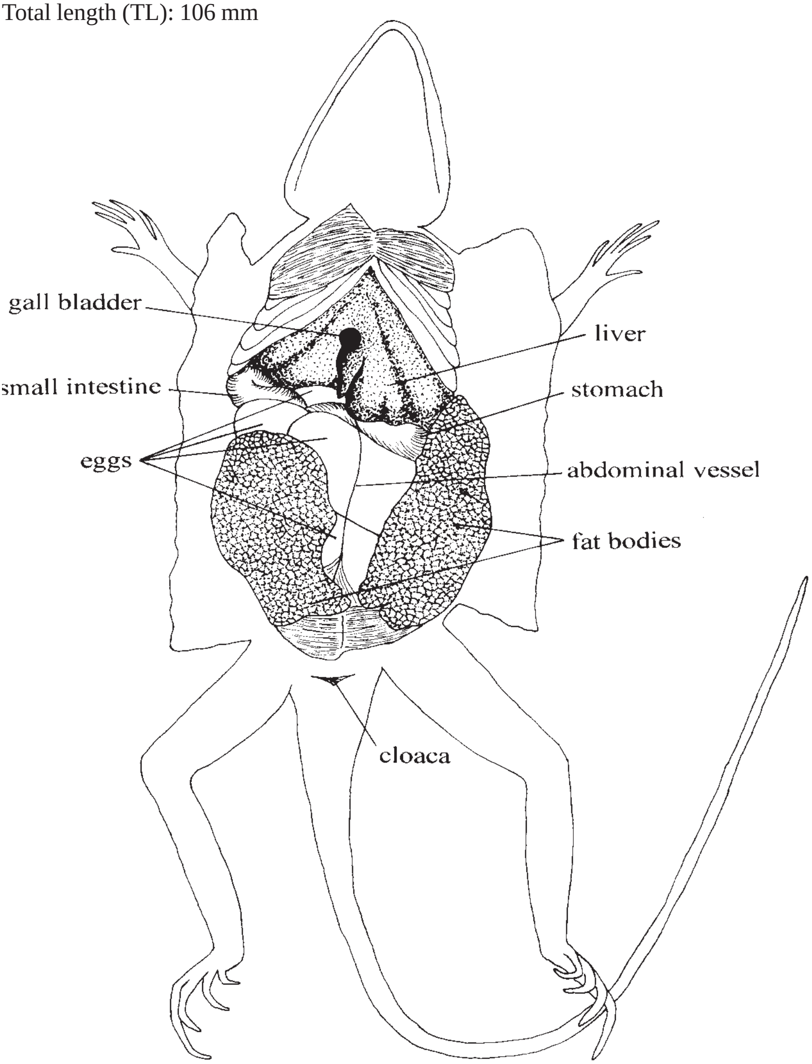

**Fig. 1.** Dissected *Sitana sivalensis* female with most of the abdominal organs covered by

the large fat bodies.

**Body cavity** (see fig.1)

Opening the body cavity by cutting through skin, abdominal musculature, body wall and by ligaturing the anterior abdominal vessel, the following anatomical situation could be observed: Striking were the dimensions of the paired fat bodies, covering nearly 1/3 to 1/2 of the body cavity. In their posterior and lateral parts, the fat bodies were covered by the strongly pigmented peritoneum. The left fat body was smaller and longer in dimension (max. width 5 mm / max. length 16 mm), whereas the right organ measured 6.5 mm in width and 11 mm in length. The distances from the tip of the snout to the anterior verge of the fat bodies were 19 mm for the left and 23 mm for the right one.

After opening the thorax and removing the ribs, the heart, liver and gall bladder were visible. The liver was of an unusual pale, cream colour. Embedded in the liver, the gall bladder was situated on the verge of the ventral lobe, nearly in the middle of this organ. Shape and dimensions of the liver are given in fig.2. The position of the liver, in relation to the tip of the snout extended from 11.5 mm (anterior end of ventral lobe) to 26 mm (posterior pointed end of mid-dorsal lobe).

After pinning the anterior part of the liver down at the right body side and the fat bodies to both sides, the body cavity seemed to be completely filled up with numerous ripe eggs. Parts of the digestive tract (oesophagus, stomach) and the lungs seem to be displaced because of the enormous dimensions of the eggs.

To describe the urogenital tract the complete digestive tract had to be removed. The rectum was cut through close to its mouth into the cloaca. The parts of the alimentary canal measured: oesophagus 10 mm, stomach (cardiac and pyloric part) 12.5 mm, small intestine 32 mm, large intestine 14,5 mm and rectum 5 mm. A horn-shaped caecum (length: 4 mm) was also present at the passage from small to large intestine.

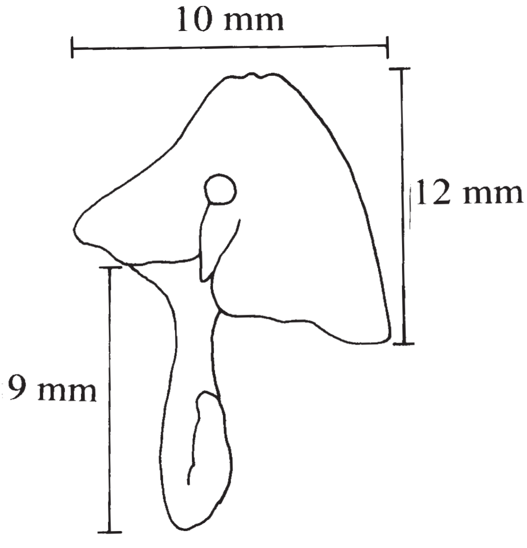

**Fig.2**. Shape and dimensions of the liver of *Sitana sivalensis;* female.

**Urogenital system** (see fig.3)

To expose the whole urogenital system, especially the kidneys, it was necessary to remove the ventral part of the pelvic girdle. Previously also the ventral part of the pectoral girdle was cut through and the following organs were removed respectively pinned down: fat bodies, digestive tract, liver, heart and lungs.

The ovaries lay nearly attached to each other, but not at the same level, in about the middle of the abdominal cavity. The right ovary is positioned more anteriorly than the left one and grew together with the dorso-median lobe of the liver. The adrenal bodies were visible laterally near the anterior ends of the ovaries. The female gonads were of a grapelike structure, containing rounded respectively a few ovoid oocytes in various stages of developement. Their colour varied from whitish, opaque to a transparent grey and they measured from min. 0.9 mm to max. 2.3 mm in diameter. The right and the left ovaries contained about the same number of oocytes (right: 15, left: 14). This agrees with the investigations of Childress (1970) on female *Agama stellio picea*. The relation of the distance from the tip of the snout to the anterior verge of the ovaries were 26 mm for the left and 23 mm for the right one.

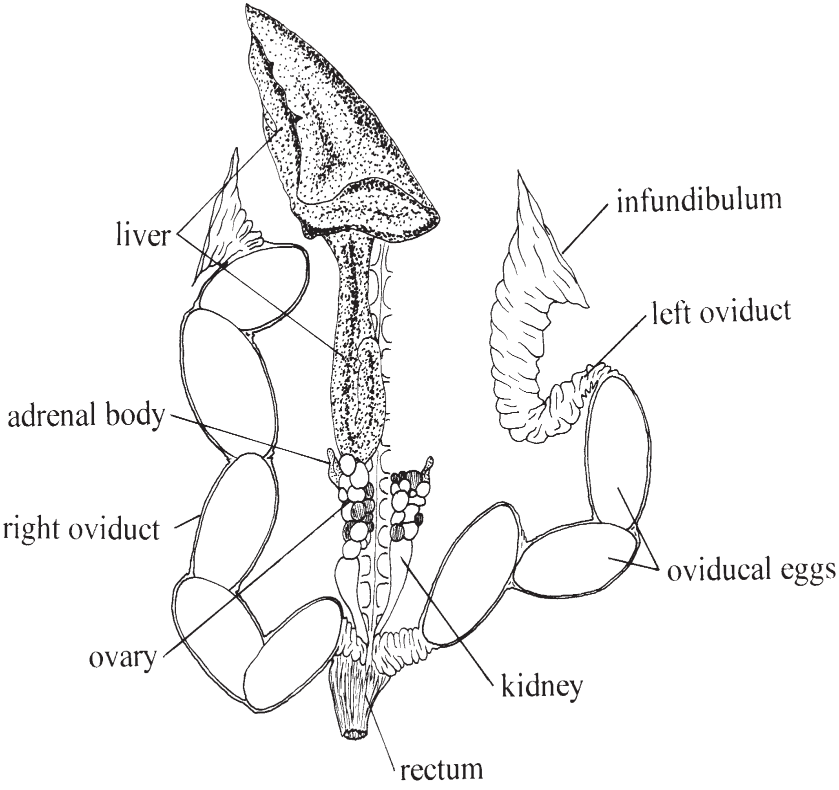

**Fig. 3.** Urogenital system of a gravid female *Sitana sivalensis*

The paired, thin-walled oviducts begin with wide anterior oviducal funnels (extending about 6 mm), on a level with the posterior ends of the lungs. The number of oviducal eggs in the two oviducts varied on both sides. The right oviduct contained 5 eggs, so that the whole oviduct was filled with eggs up to the opening of the infundibulum. The left oviduct contained 3 eggs, and between them and the infundibulum the oviduct was densely convoluted for a shorter fragment. This is in agreement with the observations of Vitt (1973), on the anguinid lizard *Gerrhonotus coeruleus princips*, that usually the right oviduct contained a larger number of eggs than the left one. Harris (1963) reports that gravid *Agama agama* usually carry 2 or 3 eggs in each oviduct. The size of the oviducal eggs is presented in tab.1. The oviducts open into the cloaca through the dorsally situated genital papillae.

The compact, slightly drop-shaped kidneys lied far behind in the pelvis. The left one is to a little anterior to the rigth one. The distance from the snout to the verge of the right kidney was 32 mm and to the left one 29 mm. Dorsally of the cloaca they are fused. As mentioned in Harris (1963) the two ureters open into the cloaca by two urinary papillae.

| | | right oviduct (length x width in mm) | left oviduct (length x width in mm) |
|---|---|---|---|
| egg | 1 | 8 x 4.5 | 10 x 5 |
| | 2 | 9 x 5 | 9 x 4 |
| | 3 | 8.5 x 4.5 | 10 x 5 |
| | 4 | 8.5 x 4.5 | ——— |
| | 5 | 9 x 5 | ——— |

**Tab. 1.** Size of oviducal eggs of *Sitana sivalensis*. - egg 1 = the posteriormost egg in the oviduct, near the cloaca, egg 3 resp. 5 = the anteriormost egg in the oviduct, near the infundibulum.

## Acknowledgements

We are gratefull to the DAAD, Germany for providing funds for travel and stay in Nepal and the University of Munich which facilitated financial support by granting a scholarship (HSP II).

Furthermore I (C.C.A.) thank Prof. G. Haszprunar, head of the Zoological State Collection (ZSM), Munich for providing working facilities.

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Veröffentlichungen aus dem Fuhlrott-Museum, 1998, Bd. 4: 233-246

# Studies on the Systematics and Biology of the Genus *Japalura* (Sauria: Agamidae)

## Notes on Comparative Ethology and Taxonomy of the Genus *Japalura*

Werner Kästle* & H. Hermann Schleich**

**Key words**: Reptilia, Agamidae, *Japalura*, *Oriotiaris*, comparative ethology, systematics

**Abstract**: The species of the genus *Japalura* are partially difficult to separate because of unstable key characters and a wide intraspecific variability. The additional use of male signal structures and acts appears promising and allows some intrageneric grouping. There is an evident, but not absolute, correlation between a covered tympanum, a coloured gular region, the absence of dorsal chevrons, and the presence of an erectile nuchal fold with large spines. The assertion behaviour of this group is a rather static „pouch and roach display". These combination of morphological and behavioural characters lacks in *Japalura tricarinata* and its closer relatives (*Japalura kumaonensis*, *Japalura major*) which are characterized by a dynamic diplay with simple nod sequences. They probably form a phylogenetic unit for which a re-evalidation of the generic name *Oriotiaris* Günther, 1864 is proposed.

**Contents**

### 1. Introduction

After Malcolm Smith (1934) a *Japalura* is an agamid, the body of which is compressed or not at all; which has a low nuchal crest or not; a dorsal crest which is feebly denticulate or absent; a gular sac which is small or absent and a tympanum which is concealed or naked. The obvious lack or instability of reliable key characters has led to frequent changes of the denomination: Members of today's genus Japalura have been classified as *Acanthosaura (dymondi, kumaonensis, major, varcoae, tricarinata), Biancia (B. niger = J. variegata), Calotes (tricarinatus), Diploderma (polygonatum), Oreocalotes (major), Oriotiaris (elliotti = J. tricarinata), Pelturagonia, Phoxophrys (grahami), Tiaris (ellioti = J. tricarinata).*

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The genus *Japalura* ,which now comprises about 23 species, is by no means stringently characterised as the above definition by Smith (1934) shows. This handicap becomes evident in keys for agamid genera which contain a certain element of vagueness. Smith (1934, p. 134/135) uses character combinations rather than simple alternatives. The character „dorsal crest a mere denticulation" may be correct for most preserved specimens, but not for living *J. variegata* or *polygonata* males which can erect crests of considerable (up to 1 cm in *variegata*) height.
In the key presented by Zhao & Adler (1993, p. 80) the body of *Japalura* is characterized as „not depressed". This is certainly correct for arboreal forms as *J. szechwanensis* or *J. splendida*, but very dubious for ground-dwelling forms as female *J. tricarinata*.In his dissertation on agamid phylogeny Moody (1980) studied osteological preparates of five, and X-ray plates of 12 *Japalura* species. Because of the homogeneity of the studied morphological characters he used only data for *J. polygonata* and *J. variegata* for his phylogenetic trees. According to this author the genus *Japalura* is a monophyletc unit which is rather close to the common ancestor of the related genera *Salea, Acanthosaura, Phoxophrys, Sitana* and *Otocryptis*. From the two *Japalura* species taken into account by Moody *J. polygonata* is considered more advanced, but the difference concerns only one out of 122 character states (no. 69), as *J. polygonata* has a reduced number of „pleurodont" lateral teeth (four instead of five) in one row.

Apparently the genus *Japalura* has undergone a vivid radiation into morphologically badly defined species in which individual variability may attain the level of interspecies differences. Maybe the situation becomes still more confusing with increasing material available as is shown by specimens from Nepal. The evolutionist is prone to regard the Himalaya region of S- and SE-Asia as an ideal stage for the speciation of montane forms, but nevertheless in Taiwan four species: *J. brevipes, makii, polygonata* and *swinhonis* occur in a relatively limited area. In this study we try to cast some light on the intrageneric relations and take into account the correlation of morphological with beavioural traits.

## 2. Material and methods

A total survey on the behaviour of all known *Japalura* forms is a hopeless enterprise. On the other hand, even data on a few species might allow some insight into basic trends within the genus.

**Colour photographs of following pages:**

**Fig. 1**. *Japalura polygonata*, male.
**Fig. 2**. *Japalura splendida*, female.
**Fig. 3.** *Japalura splendida*, male with arched back, rejecting a courting male.

**Fig. 4.** *Japalura tricarinata*, couple; note the pronounced sexual dimorphism between the smaller green male and the much larger brown female.
**Fig. 5.** *Japalura tricarinata*, male.
**Fig. 6.** *Japalura tricarinata*, male threatening against a human.

**Fig. 7.** *Japalura tricarinata*, female in leaf litter.
**Fig. 8.** *Japalura tricarinata*, female.
**Fig. 9**. *Japalura variegata*, displaying male.
**Fig. 10.** *Japalura variegata*, female.

**Fig. 1**

**Fig. 2**

**Fig. 3**

Fig. 4

Fig. 5

Fig. 6

**Fig. 7,8**

**Fig. 9**

**Fig. 10**

As prolonged field observations were impossible we studied captive animals, some species over several months up to years: *J. polygonata* Hallowell, 1860 (evidently *J. polygonata polygonata* according to the key in Ota, 1991) (fig. 1) and *J. splendida* Barbour and Dunn, 1919 (fig. 2,3 ), were acquired from the animal trade. Three Nepalese species were caught in the biotope: *J. tricarinata* Blyth, 1854 (fig. 4-8), from Mt. Phulchoki, 30 km SE of Kathmandu. *J. kumaonensis* (Annandale, 1907) (see following article, this volume) from extreme Western Nepal between Dhangadi and Dandeldura. *J. variegata* Gray, 1853 (fig. 9,10), from Ilam district in E Nepal.

There are no special difficulties to maintain Japaluras in captivity, provided they are not forced to live in narrow confinement. A small greenhouse (see Kästle & al. 1993) is ideal and if the lizards cannot be exposed to solar radiation at least artificial light with mercury lamps is urgently recomended to avoid a decrease in vitality that otherwise threatens due to poor illumination in German cloudy and rainy summers. An essential factor in accustoming japaluras to captivity conditions is their greediness, and even recently caught specimens start feeding without difficulty. Observation from close distance was no problem.

An important base of reference for comparative ethology is the article of Wei & Lin (1981) on the behaviour of *Japalura swinhonis* (evidently *J. s. formosensis*), written in Chinese. It was translated for us by Mrs. Wenyu Wu, Inst. of Paleontology, Academia Sinica, Beijing. There are some difficulties to match the rather brief enumeration of acts with the ethological standard concept.

As Wilson (1975) has emphasized, behavioural evolution - especially intraspecific communication - may proceed at a much faster pace than normal morphological changes and therefore is an especially sensible indicator for phylogenetic changes. Even species which are very difficult to discern by morphological traits can show fundamental behavioural differences, as is shown by *Sitana sivalensis* and *Sitana fusca* (see preceeding articles, this volume).

Selection pressure is especially high on signals which are connected with speciation processes and isolating mechanisms, as are e.g. the species-specific nod and pushup rhythms of many iguanids or fan colour patterns of anoles (Carpenter & Ferguson, 1977). Other signal acts need less specification and are of a more general and widespread use as are the basic forms of assertion (static or dynamic), the gular colouration (present or lacking) or the presence of erectile nuchal and dorsal crests. While the first group of signals is an indicator for speciation, the second one might offer cues to characterize species groups.

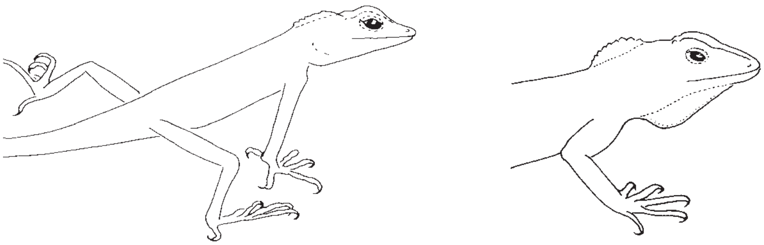

**Fig. 11.** Static pouch and roach display in *Japalura polygonata* (above) and *J. splendida* males.

## 3. Observations on *Japalura splendida* Barbour & Dunn, 1919

The area of this species comprises SW China, extending eastward to the province of Hunan, northward to Henan and Gansu (Zhao & Adler, 1993) with a climate similar to that of Kathmandu with average winter temperatures of about 10°C and monsoon rains from May to October.

### 3.1 Static assertion (fig. 11 right)

The performance was similar to that observed in *Japalura polygonata* (Kästle & al., 1993): The exposed and otherwise immobile male erected his nuchal roach and extended his black and yellowish gular pouch.

The fact that static display was but rarely seen in the males can be explained with the relatively small cage where the constant close vicinity of the females frequently released courtship behaviour.

### 3.2 Courtship with lateral head motion (fig. 12)

While nods and pushups belong to the basic stock of display acts in agamids and iguanids, lateral display motions are exceptional and should be regarded as phylogenetically new. The courtship display sequence of a *Japalura splendida* male is a combination of vertical and horizontal head motions in a rather strict sequence: An initial sideward head motion (a) is followed by two separated nods of different amplitude. After a few seconds the first unit (1) is soon followed by a second one (2) and so on over many minutes. The lateral head jerk is often directed versus the female. As the repeated subsequent lateral jerks can gradually shift the head position to one side, others in the opposite direction may follow. But there is no strict alternating sequence of left or right head motions.

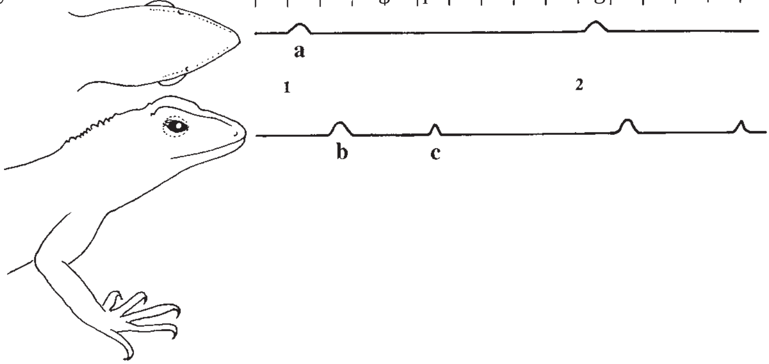

**Fig. 12.** Display-action-pattern graph of complex courtship motions in a *Japalura splendida* male with lateral (a) and vertical (b, c) head motions. The display sequence consists of many successive units of which two (1, 2) are represented.

### 3.3 Male rejection with arched back

The female reacted to the intensely courting male by arching her back (fig. 3), a signal act which is widespread among agamids (*Sitana sivalensis*, see article p. 121) and iguanids, but not in other *Japalura* species.

## 4. Observations on *Japalura variegata* Gray, 1853 (fig.9,10)

This species from W Nepal and the Darjeeling-Sikkim region (southwards to Jalpaiguri) is one of the large japaluras, attaining a snout-vent length of up to 110 mm and a total length of over 300 mm.With an altitudinal distribution from 300 m to over 3000 m it reaches elevations in which hibernation is obligatory.

*Japalura variegata* looks very robust and shows a very pronounced sexual dimorphism: the males possess a nuchal and dorsal crest of prolonged spines. Displaying males can erect nuchal and dorsal skin folds up to a height of about 10 mm. At the same time they spread their gular pouch which turns dark blue at its posterior end, surrounded by pink (fig. 9,13). The species ows its specific name to a drastic colour change from almost blackish (a sign of disturbed state from cold, wettening or bad state of health) to vivid yellowish green (mostly seen in displaying males). A pattern of dark chevrons is distinct in certain colouration phases, but can be partially overlaid by whitish lateral stripes.

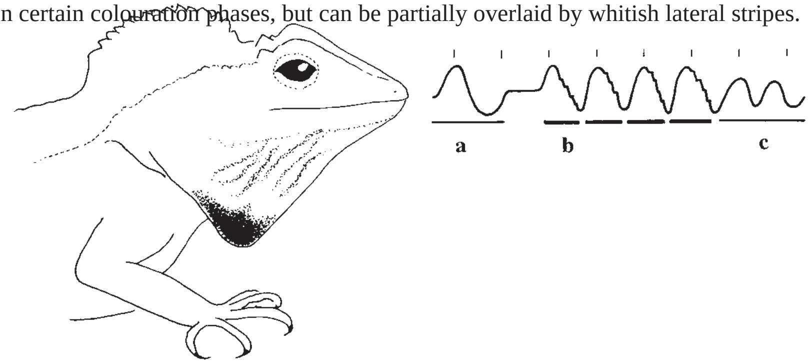

**Fig. 13.** Graph of step-nods in *J. variegata* directed against a conspecific. Introductory and terminal nods are simple.

### 4.1 Static assertion

While the females spend most of their time hidden in plants and observing, the males start their static assertion display with beginning insolation, They move to an exposed position on a branch or rock, spread their dorsal skin folds and gular pouch (posture as in fig. 13), and change to their most vivid colouration. During this static assertion the lizards remain largely immobile and only start display movements when a conspecific approaches. In summer the displaying males withdraw into the shade with increasing heat and do not start advertizing again for the rest of the day. Advertizing neighbourts are tolerated if they come not too close (limit at about 70 cm). Rivalries between males normally end with a rush of the larger lizard towards the smaller one, which immediately flees. In spite of the fact that at least five males were in the 3 m long greenhouse, no damaging fight was recorded.

### 4.2 Step-nods

A displaying male's normal response to an approaching conspecific (challenge or courtship situation) is a nod sequence which is characterized by several short stops during the downward motion of the head, giving the display-action pattern graph the aspect of several steps. The nod sequence consists of three parts (fig.13):

a) a few simple up-and-down motions of the head
b) several step-nod sequences
c) simple terminal nod of a primitive type.

The whole unit can be repeated several times, forming a long display sequence, until the conspecific runs away or is approached by the displaying male in order to copulate with a female or to chase the rival.

## 5. Synthesis

### 5.1 Display forms in the genus *Japalura*

With some data on the behaviour of five *Japalura species* at hand we try to deduce some general principles of signal evolution within the genus:

Data are from Wei & Lin (1981, *Japalura swinhonis*), Kästle & al.(1993, *Japalura tricarinata, J. polygonata*) and unpublished observations by Schleich & Kästle on *J. splendida and J. variegata*.

Data on display behaviour and morphological signals were used to design a survey (fig. 14) which also includes a series of other *Japalura* species for which no ethological records were available and for which only morphological data are listed.

**Discriminating character states in *Japalura* species**

The following group characters often represent different evolutive levels. Their classification into primitive and advanced ones is suggested. The numbers refer to the survey in fig. 14.

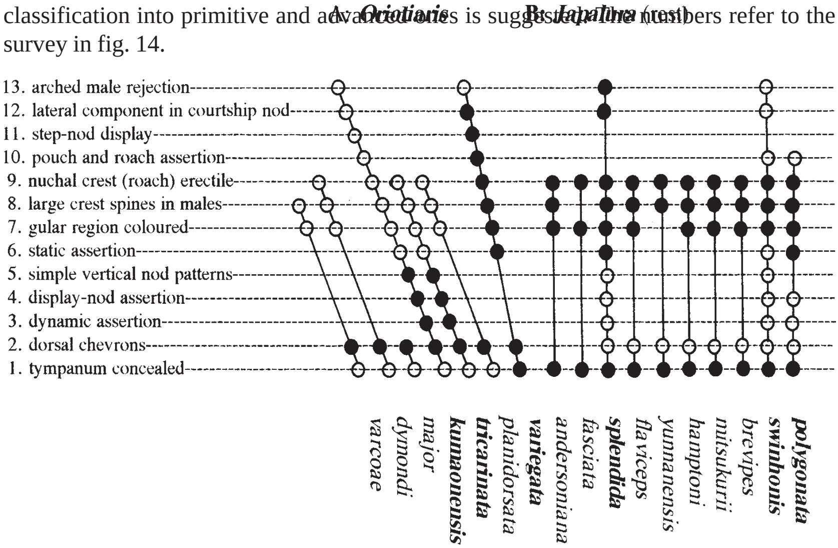

**Fig. 14.** Survey of signal structures and acts in *Japalura* species. Observed characters are indicated with a black dot, lacking ones with a circle. No marks indicate the absence of observations.

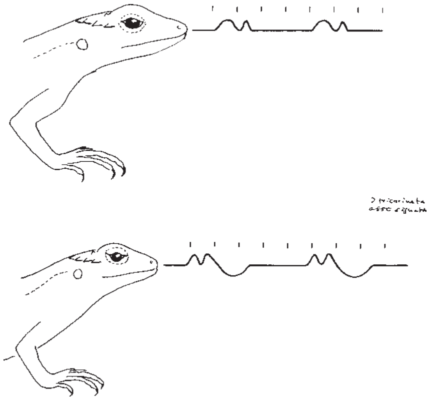

**Fig. 15.** Simple assertion nod patterns in *J. tricarinata*: male (above) and female.

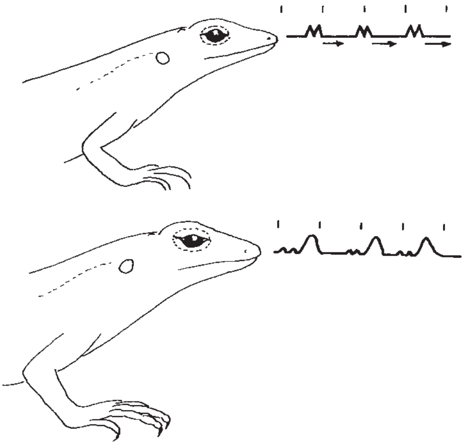

**Fig. 16.** Simple assertion nod patterns in *J. kumaonensis* males: above double-nod march during approach versus a female; below triple-nods during strong social arousal.

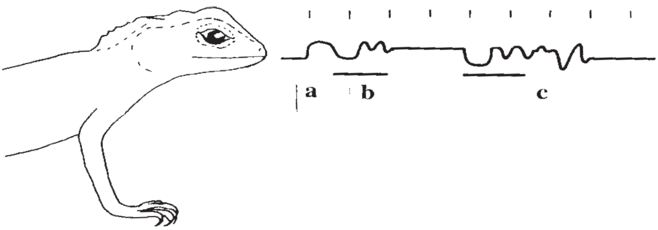

**Fig. 17**. In *J. swinhonis* sequences of simple nod patterns are a typical male display form, the social context of which has remained unclear (graph from Wei & Lin, 1981): between a simple initial and terminal nod a basic unit (underlined) is repeated twice.

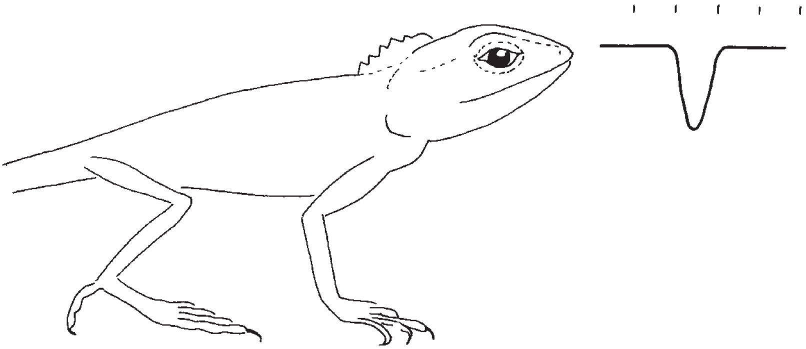

**Fig. 18**. Simple nod of *J. polygonata* male.

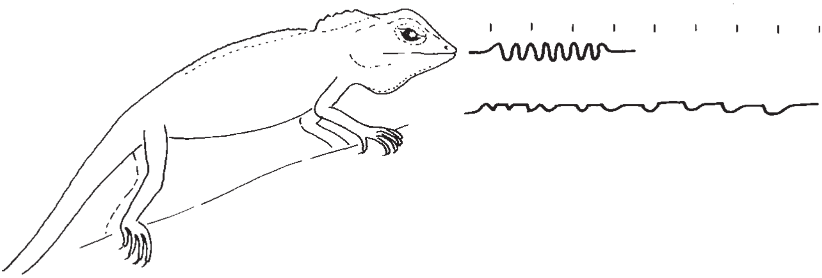

**Fig. 19**. Repeated uniform nods of *Japalura swinhonis* males (after Wei & Lin, 1989)

1. There are three different states of the tympanum. It can be naked, covered with scales or totally hidden under the skin. The first two states can even occur in one specimen, therefore bear little on taxonomic conclusions and are disregarded here.

2. One of the morphological signals listed in the scheme are the dorsal chevrons (fig. 4-10) which are characteristic for a group of agamid species. We consider this relatively complex pattern element as primitive as it is also found in other genera as *Otocryptis* and in the form of rhombi in *Sitana*. The probability that this pattern type originated several times independently during agamid evolution is extremely low. *Japalura* chevrons and *Sitana* rhombi have the following characters in common:

a) Number and arrangement of pattern elements within the dorsal field: one above the fore- and hindlimb insertions and three between them.

b) Similarity in size and shape

c) A dark margin: In *Sitana* the anterior and posterior margins are mostly of the same intensity, in the chevron patterns the anterior margin is weak and may be absent (e.g. by colour change).

d) The margin may be doubled with a light zone.

e) The halves of the pattern elements can be shifted against each other.
f) The pattern elements can disappear by mutation, and the dorsal field becomes more or less uniform. For *Sitana* this is shown in a photo by Chopra (1964), for *Japalura tricarinata* by photos in Kästle & al. (1993).
The replacement of chevrons by dorsal blotches or other pattern types e.g. broad lateral bands or a „ladder“ pattern is regarded as progressive.

3. Dynamic assertion, includes locomotion during inspection tours within the home range during which the male often stops and nods. When sitting quiet the lizards are rather inconspicuous, without roaches and crests, but with bright general colouration.
Generally, assertion behaviour serves to signal the presence of a territorial male to its conspecifics.

4. The display nods during dynamic assertion consist of vertrical head or forbody motions and are probably primitive.

5. The graphs of simple nod patterns (fig. 15-17) consist of vertical oscillations of different frequency and amplitude.
There are short ubits which are often repeated. Lateral head motions and complex nods are lacking.
Threat nods (fig.18,19) are of no use for our classification as they seem to consist of single
or repeated primitive up-and-down motings in all species.

6. Static assertion (fig. 11) consists merely of selecting an exposed site, posturing and eventually colour change.

7. Coloration and pattern of the gular pouch (fig. 1,13) may serve as releasers and isolating mechanisms. They are therefore subject to a relatively rapid evolution.

8. Crest and spines are regarded as large if they at least double all dimensions of their lateral neighbours.

9. Species in which the nuchal crest is erectile have long nuchal spines set on a distinct skin fold. All these characters are apparently advanced.

10. During the „pouch and roach assertion“ (fig.11) the gular appendage and the nuchal crest are not spread maximally as during challenge.

11. The step-nod display (fig. 13) until now seems specific for both sexes of *Japalura variegata* and restricted to this species within the genus.

12. A lateral component combined with the courtship nod was exclusively observed in *J. splendida* (fig. 12).

13. Only in a non-receptive *J. splendida* female the arched-back posture (fig. 3) was seen as an answer to courtship during the non-reproductive phase.

## 6. Discussion

Speciation and display diversity

In the survey (fig. 14) species with morphological similarities were grouped together. The character states used for the arrangement were the numbers 1, 2 and 7 which are rather strictly correlated. A bipartition in two groups becomes evident:

Group A with the combination: exposed tympanum - chevron pattern - lacking long dorsal spines - gular pouch without a striking colouration or patter.

Group B with the combination: hidden tympanum - lacking or indistinct chevron pattern - long dorsal spines in the male - gular pouch with striking colouration and eventually pattern.

Additionally within group A the assertion behaviour is dynamic and includes simple nod patterns, while for group B the static „pouch and roach display“ seems typical.

As the comparison shows, *J. kumaonensis* and *J. tricarinata* can be considered as closely related. *J. major* is morphologically very similar to *J. kumaonensis,* and the three species can be set apart from the rest of the genus *Japalura*. This unit can be denominated *Oriotiaris,* a name proposed by Günther (1864) for *Japalura tricarinata*. The states of the morphologically similar *J. varcoae, dymondi* and *planidorsata* remain still questionable.

There are some irregularities which show that our simplistic bipartition is not ultimate: In *J. variegata* both sexes perform step nods. In the same species dorsal chevrons (a character of the A-group) are often distinct. *J. swinhonis* males. - in addition to their pouch and roach display - often change their perches during assertion which therefore cannot be called static in this species (Wei & Lin, 1981).

Other specific characters of *Japalura* species can not yet be considered as group characters, as the singular type of male rejection (arched back) and courtship (lateral head jerks) in *J. splendida,* the step-nods of *J. variegata.* The striking sexual dichroism of *J. tricarinata* (not listed in our comparison) is limited to this single species.

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Veröffentlichungen aus dem Fuhlrott-Museum, 1998, Bd. 4: 247-268

# Studies on the Systematics and Biology of the Genus *Japalura* (Sauria: Agamidae)

## Contributions to the Biology of *Japalura kumaonensis* (Annandale, 1907)

Werner Kästle * & H.Hermann Schleich**

**Key words:** Reptilia, Agamidae, *Japalura kumaoensis*, ecology, behaviour

**Abstract:** With an altitudinal distribution between 1700 and 2100 m *Japalura kumaonensis* inhabits similar colline and montane biotopes as the closely related *Japalura tricarinata* which lives at an altitude of 1800 - 2800 m in an area which is situated more towards the east.

Both species are similar in size (snout-vent lengths 4-5 cm) and ecological demands, but show striking differences in sex characters:

In *J. tricarinata* sexual dimorphism is very marked and probably connected with somewhat different ecological niches of males and females. *Japalura kumaonensis* needs a close look to distinguish the sexes. The annual and diel activity cycles of *Japalura kumaonensis* are characterised by a relatively long and facultatively interrupted hibernation and by prolonged resting periods in summer, even during warm weather. Activity temperatures are strikingly low, and the lizards start feeding even immediately after emergence and without basking.

The display repertoire is very conservative, and hostile interactions are weak.

As successful breeding was achieved, data on oviposition and incubation are presented.

**Contents**

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## Introduction

*Japalura kumaonenis* is named after the Indian Kumaon region close to the western Nepalese border. Together with *Japalura major* its area extends into the north-western Himalayas (fig. 1). The westernmost record for *Japalura kumaonensis* is from Mussoorie, 250 km west of Nepal, while the area of *J. major* extends another 300 km to the west into the “Chamba region” around the Ravi river. Differences in the ecological demands of both species are not exactly known, but *J. major* evidently prefers higher altitudes up to over 3600 m. There are no reports on sympatry of both species.

The only Nepalese records of *Japalura kumaonensis* are from the Extreme West (Doti District), while *J. major* is also known from several localities in Central Nepal (Annapurna Massive N of Pokhara).

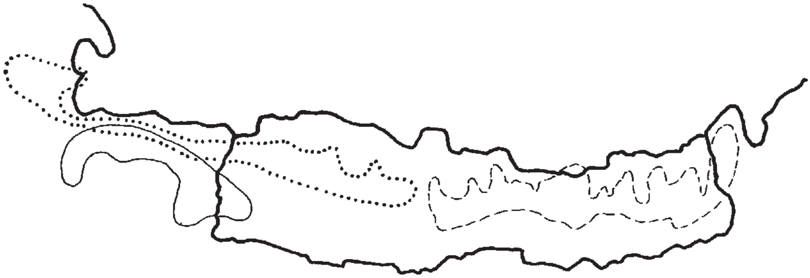

**Fig. 1.** Roughly estimated ranges of *Japalura kumaonensis* (continuous line), *J. major* (dotted line) and *J. tricarinata* (broken line).

## 1. Material and methods

The lizards were collected by H. Schleich and K.B. Sah during field studies for a VW (Volkswagenstiftung) project. In September 1995 the research team crossed extreme Western Nepal from Dhangarhi (Dangadhi) to Dandeldhura where the lizards were frequent in roadside biotopes along forests. Most specimens were half grown, three were hatchlings, two of which could be reared to adulthood, as well as the only hatchling from captive breeding.

Husbandry

The terrarium should at least measure 50 x 40 x 30 cm (L x W x H), but continued and obstinate trials of the lizards to escape through the glass panes make larger terraria advisable. Their standard outfit should include:

1. Branches, 1-2 cm thick, which serve as sites for basking and male display.
2. Some potted plants (e,g, evergreen grasses) offer some hiding possibility, help to increase air humidity and can be sprayed to provide occasions for licking drops.

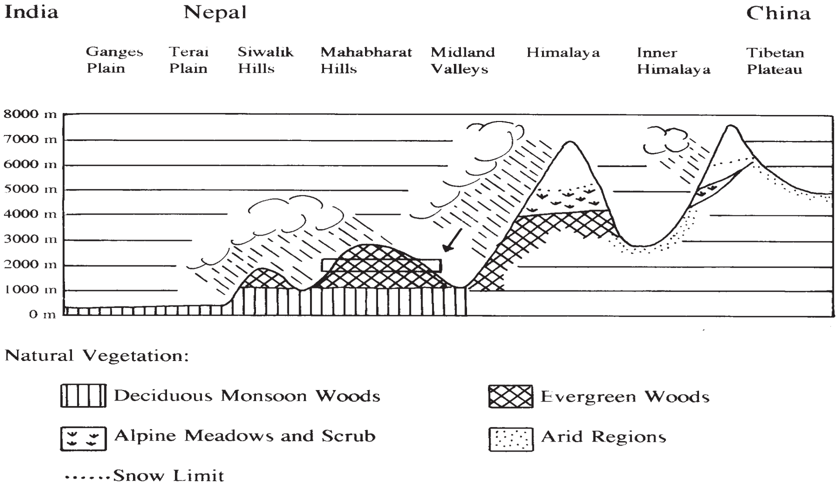

**Fig. 2.** Cross section of Nepal with main vegetation zones. The area of *J. kumaonensis* is framed.

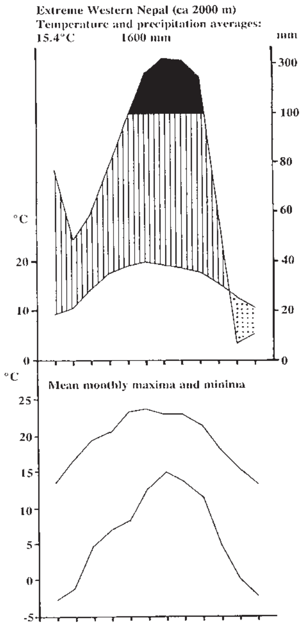

**Fig. 3.** Annual climatic changes in Extreme Western Nepal. The surplus of precipitation is indicated by the hatched area. The dry period (dotted area) is very short.

3. A 10 cm high heap of dry grass in a darker and cooler corner is a very helpful hiding place for sleeping and during other periods of rest. Females retire into it when molested by courting males.
4. A heap of moist sand in another corner, at least 7 cm high, offers an appropriate nesting site. It should be readily accessible to recover the eggs, placed in a corner and covered with a flat overhanging stone to facilitate the start of digging activities.
5. A water dish, eventually with a flat stone in it which emerges above the water level. Water dropping on the stone facilitates drinking for animals which are still unaccustomed to drink from a dish.

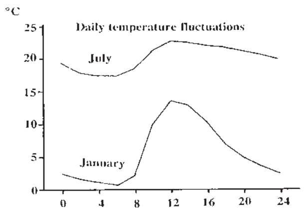

**Fig. 4.** Daily temperature fluctuations differ markedly between summer and winter. Noon temperatures of 15° in January were recorded at a height of 2 m above the ground. The soil surface exposed to insolation reaches much higher values and permits activities of *J. kumaonensis* around the year.

6. A food dish, where besides slow food as mealworms and their pupae crushed eggshell is steadily offered to furnish calcium
carbonate.
7. The very positive results during many years of herptile husbandry suggest not only for *Japalura* but for all other helio- and thermophilous reptiles the use of mercury lamps (e.g. Osram HQL or HQI) as a unique source of illumination or in combination with other lamps. The HQL/HQI lamps of 50, 80 and 120 W can be used with normal sockets. HQI lamps with 160 W for bigger enclosures can be used directly, without transformer.

More adequate to their biological requirements the animals are kept in a larger terrarium or a small greenhouse, where their maintenance is not problematic during the warm season and where they can hibernate with temperatures around 5°-8°C. As the above mentioned type of artificial illumination contains a high percentage of ultraviolet and closely resembles daylight in its composition it helps to avoid skeletal degenerations and stimulates activity.

Illumination and temperature regime
Temperature requirements are rather low. Over the whole year the terraria stood near a westward window in an unheated room. By day they were illuminated and heated by a 50W halogen lamp. The lizards could bask close to them on the branches.

Feeding
*Japalura kumaonensis* is by no means very selective. As standard food served: crickets, wax moth larvae, mealworms and their pupae, and flies.
Individual feeding with crickets which were dusted with calcium carbonate powder (optimally enriched with provitamin D3) is no problem. The japaluras readily catch crickets out of a low plastic box which is held in front of them.

Drinking
Drinking water was steadily enriched with a vitamin mixture (Multibionta, Merck, drops) in a relatively high concentration of one drop to 100 $cm^3$. As the real vitamin requirements of reptiles are unknown we are groping in the dark, and probably many other water soluble multivitamin preparates will do just as well.

For hibernation see Activity phases (paragraph 3.2.1).

## 2. Ecology

### 2.1 Biotope (fig. 2, 5, 9)

2.1.1 Climate (fig. 3, 4)
Climatic records from the region are insufficient to design a climate diagram. Fig. 3,top is based on a compilation and interpolation of data taken from DOBREMEZ (1976) and DOBREMEZ & JOSHI (1984). The climate diagram tries to visualise above all one climatic peculiarity of Extreme Western Nepal, namely the absence of a prolonged dry period and the two peaks of the precipitation curve. While in East Nepal the precipitations are limited to the summer monsoon period, the Far West receives "Mediterranean" rain with western winds during early spring, and the arid season is restricted to November and December. The lack of a severe and long dry period puts no restriction on the annual activity cycle of *J. kumaonensis* which is mainly influenced by temperature.

### 2.1.2 Plant Society

*Japalura kumaonensis* inhabits the evergreen vegetation belt in which oaks and rhododendrons play a predominant role. Further data, also for adjoining vegetation belts, see fig. 5.

| Elevation in meters | Vegetation level | | Plant Communities |
|---|---|---|---|
| 3000 —— | Montane | | 2450 - 2900 m. Evergreen mesophytic montane Oak *(Quercus semicarpifolia)* - Rhododendron *(R.arboreum)* forest |
| | Colline | | 1850 - 2400 m. Evergreen collinean Oak *(Quercus incana, Q. lanata)* forest with *Rhododendron arboreum, Lyonia ovalifolia*, mostly on southern slopes |
| | | II | |
| 2000 —— | | II | |
| | | II | 1400 - 1900 m. Mixed Chir pine *(Pinus roxburghii)* - Oak *(Quercus incana, Q. lanata)* forest with *Rhododendron arboreum, Lyonia ovalifolia, Inula cappa, Campylotropis macrostyla* |
| | | II | |
| | Subtropical | | |
| | | | 900 - 1900 m. Chir pine *(Pinus roxburghii)* forest with grasses and *Engelhardtia*, often mixed with Sal in lower parts and broad-leaved trees in upper parts |
| 1000 —— | | | |
| | Upper Tropical | | 600 - 1000 m. Deciduous Sal *(Shorea robusta)* forest with *Terminalia tomentosa* |

For the Evergreen Collinean Oak Forest, the main biotope of *J. kumaonensis* in the region, Dobremez (1976) enumerates 13 species of trees. From the 35 species of bushes we mention only those which belong to genera which are perhaps known to most biologists: *Berberis wallichiana, Cornus oblonga, Cornus macrophylla, Cotoneaster bacillaris, Corylus colurna, Deutzia corymbosa, Deutzia staminea, Hypericum patulum, Jasminum humile, Jasminum officinale, Morus serrata, Philadelphus coronarius, Philadelphus tomentosus, Pistacia integerrima, Pyracantha frenulata, Rhamnus purpureus, Rhamnus virgatus, Rhus cotinus, Rhus punjabensis, Rhus succedana, Rhus wallichii, Ribes glaciale, Sorbaria tomentosa, Spiraea canescens, Spiraea hypoleuca, Spiraea sorbifolia, Staphylaea emodi, Syringa emodi, Viburnum stellulatum.*

From the poor herbaceous layer we mention: *Euphorbia pilosa, Athyrium odontoloma, Scutellaria scandens, Viola pilosa, Adiantum venustum*and other ferns, a multitude of mosses and lichens, epiphytes.

**Fig. 5.** Vertical vegetation levels in western Nepal (data from Dobremez & Damodar Prashad Joshi, 1984). The vertical bar indicates the distribution of *J. kumaonensis*).

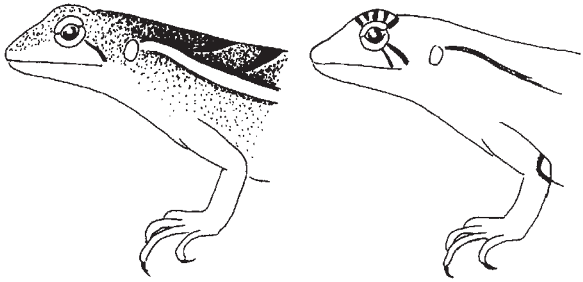

**Fig. 6**. Forebody pattern of *Japalura kumaonensis* (left) and the closely related *J. tricarinata*.

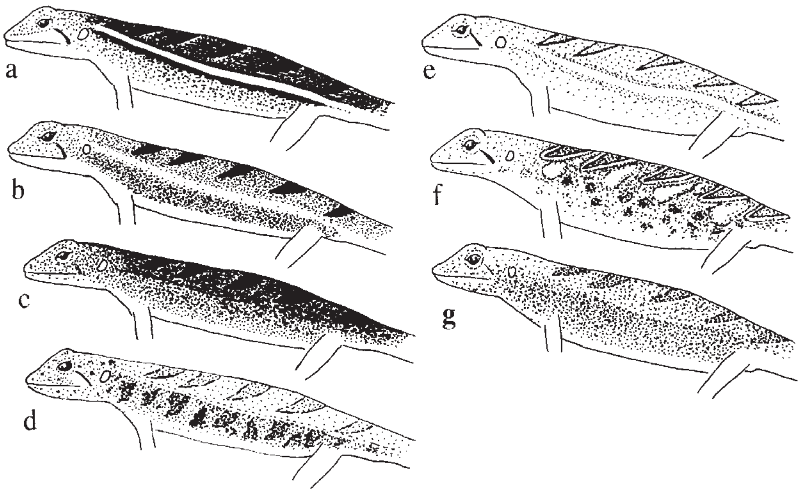

**Fig. 7.** Colour change of *J. kumaonensis* males (a-d) and females (e-g):. a: brilliant coloration; b: neutral colouration; c: “wet and cold” coloration; d: irritated while chaing a rival.
e: Brilliant colouration; f: irritated by a courting male ; g: neutral pattern of brown hues in a resting female.

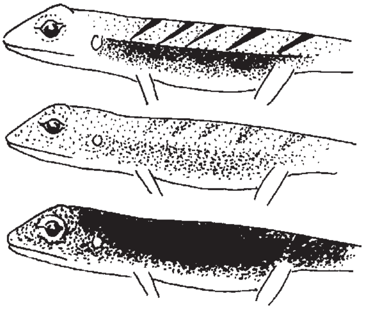

**Fig. 8.** Colour change in juveniles. Above: contrasting pattern while basking; centre: neutral pattern; below: “wet and cold” pattern.

## 2.2 Population biology

### 2.2.1 Population density

In the biotope the distribution of the lizards is mainly linear along the margins of woodland, e.g. near roads. They were encountered at distances from 15 to 2 metres. Compared to the population density of *Japalura variegata* in East-Nepal, *J. kumaonensis* was less frequently to encounter and we only found single specimens along roadside clearings mainly on southwest exposed slopes at altitudes between 1700 and 1850 mtrs.

**Fig. 9.** Roadside biotope of *Japalura kumaonensis* at an elevation of 1870 m between Dangadhi and Dandeldura, Far Western Nepal.

### 2.2.2 Population dynamics

An adult female can produce at least two clutches per year, each with up to 14 eggs .

Because of their long inactivity phases in winter and during bad weather in the warm season, predation pressure is low and many specimens survive for several years.

*J. kumaonensis* needs at least two years to attain full size. Adults which were caught at this age were still alive after two years in captivity, and the maximal age amounts to at least four years.

Adults were much more frequent than juveniles in September and it can be concluded that many of them hibernate.

## 3 Behaviour (Ethology)

## 3.1 The communication system

Signal structures and act systems involved in intraspecific display are not highly specialised, but a combination of rather common features which can also be found in other Agamidae as head nods, spreading of gular pouch, high stand, lateral flattening. The three “classic” display categories of assertion, courtship and challenge are present, but not strictly stereotyped.

#### 3.1.1 Signal structures

Body structures serving as signals are: the colour pattern which is subject to change in both sexes and all life phases, as well as a gular pouch and dorsal crest in the male.

##### 3.1.1.1 Colour pattern and colour change

The basic pattern elements show similarities with those of *Japalura tricarinata* (fig. 6) and we use the same terminology to denominate them.

1. The relatively light dorsal region, which is in some colour phases separated from the body sides by light stripes.
2. Dark chevrons which can become indistinct or disappear when the background darkens. Often they are bordered with dark brown or black.

In most specimens there is one chevron each above the foreleg and hindleg insertion and three on the body between them. This arrangement of dorsal marks seems to be widespread among agamids and appears in other *Japalura* species as well as in all or some members of the genera *Otocryptis, Sitana, Calotes, Tympanocryptis, Diporiphora* and *Lophognathus*.

3. Light dorsolateral stripes which are typical for the states of assertion and arousal.
4. Body sides which as a rule are somewhat darker than the dorsal region and can show a pattern of darker spots on a gray, reddish brown or brown basic colouration which can be mottled with green.
5. A light upper lip which is posteriorly bordered by a dark subocular streak
6. Dark marks on legs and tail.

With the exception of no 6 all the elements are subject to a vivid colour change. Light pattern elements show shades of brilliant white (dorsolateral stripe in males), yellowish olive (dorsolateral stripes and chevrons in females) and light gray (dorsal region). Intense black is typical for the dorsal region of asserting males. Both sexes become dark brown when they are wet and cold. In this state sexual dichroism is minimal.

The differences between the *Japalura kumaonensis* and *J. tricarinata* males are evident in all colour phases with exception of the darkest one: Asserting males of *Japalura tricarinata* become almost entirely green, their dorsal chevrons disappear, and their light dorsolateral lines are reduced.

The more stable markings of both species differ in the following points (fig. 6):

1. The radiating stripes above the eye lack in *J. kumaonensis.*
2. The elbow spot also lacks in this species

Colour change

Juveniles and adults of both sexes have in common that they change to a sombre brown hue in moist and cold surroundings (fig. 7,8). Their colouration is most brilliant when they are warmed up and undisturbed. In this state the colouration of males and females become most different (fig. 7a,e). Fundamentally this scheme can be observed in other *Japalura* species (Kästle & al., 1993).

Colour change in males (fig. 7, a-d)

a) Brilliant colouration (fig. 16): This phase is shown by alert males which advertise (see 3.1.2.2) and are ready to court. The dorsal region as a whole looks black with the jet-black chevrons still a hue darker than the rest. The dorsolateral stripes are splendid white and contrast vividly with the adjacent back. The flanks are uniform brown.

b) “Emergence” before starting to bask: the dorsolateral stripes are less brilliant and

contrasting than in a). The dorsal region is not black as in a) but greyish brown.
c) "Wet and cold" coloration, which is similar in both sexes and juvenile: The light dorsolateral lines have disappeared and the black chevrons show little contrast to the dark brown general colour.
The change from a) to c) can be promptly triggered by sprinkling the lizards and lasts about one minute. In a young male which became frightened by the food dish held in front of it the change lasted only a few seconds.
d) Irritation pattern after chasing a rival. The chevron margins are contrasting and the flanks show a pattern of irregular dark spots.

Colour change in females (fig. 7,e-g)
e) In the brilliant colouration of females olive pattern elements (fig. 17) play an essential role. The olive chevrons are delimited by a contrasting brown margin. The dorsolateral stripe is yellowish olive, but not sharply delimited. The dorsal region and the body sides are light grey.
f) In an irritated female the chevrons show a double (light and dark) margin and are separated by light wedges. The flanks are mottled with dark spots.
g) In the neutral and inconspicuous colouration the pattern elements are all grey or brown with exception of the slightly darker chevrons. The dorsolateral stripe is slightly indicated. Back and flanks are greyish, the latter with a tinge of brown.

Colour change in juveniles (fig. 8)
The range of colour change in juveniles is definitely smaller than in adults. Above all the brilliant contrasts of white, black or olive are lacking. Shades of grey and brown are prevailing (fig. 20). Sprinkling with water causes a sudden darkening which makes the anterior chevrons invisible. Intense irradiation evokes a contrasting pattern.

In both sexes and all age classes the colour range of the venters covers the shades from pure white over cream to beige with brown streaks and dots.

All the above mentioned forms of colour change take a few seconds to several minutes. But there are strong arguments for a long-time change which depends probably on ambiental humidity: In the field most females show a yellowish or greenish hue along their flanks (fig. 17). After some months of captivity these colours disappeared entirely, changing to grey or reddish brown (fig. 18,19).

#### 3.1.1.2 Gular pouch

The gular pouch is not differentiated from the general scalation and colouration of the ventral side. It is erected during threat behaviour, rarely during courtship. It forms a rounded triangle (fig. 12) and cannot be rapidly extended and folded .

#### 3.1.1.3. Dorsal crest

There is a serrated uninterrupted crest from the nape to the lumbar region which is not much different in both sexes and about 1 mm high. Excited males are capable to heighten the crest somewhat by a slight contraction of the dorsal skin.

### 3.1.2 Social behaviour - pushups and nods (fig. 10,11)

Typical exclusively male acts are the spread of the gular pouch, erection of the dorsal crest, threat pushup and the double-nod march . In captives the level of aggressivity was low. Several males were kept in a group without severe hostile interactions.

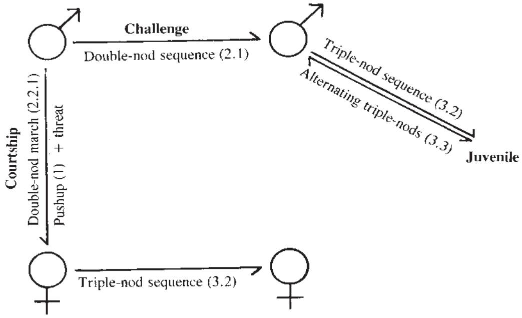

**Fig. 10.** Nod and pushup signals during social interactions.

Vertical head motions serve as signals in both sexes and juveniles, but are most frequent in males. They can be grouped into several types, but there is a lot of variability. They are most frequent during sunny weather.

Our classification of pushups and nods into single pushups, double-nods, triple-nods, multiple-nods and uncommon nods (fig. 11) is highly artificial but of some use in their interpretation. The uncommon nods are especially variable, rather rare, and typical for juveniles. Some characteristics of the four common forms are compared in the following table:

| Head motion type | single pushup | double-nod | triple-nod | multiple nod |
|---|---|---|---|---|
| Basic unit | up and down | pairs of equal amplitude | two low+one high | low in series |
| Gradedness | amplitude | amplit., sequence length | sequ. length | sequence length |
| Combinations | gular pouch<br>threat posture | series only<br>with march | series or single<br>and alternatin | different duration<br>and repetition |
| Age and sex | males | males | ad. and juv. | ad.and juv. |
| motivation | threat | threat and courtship | social arousal | irritation |

During social interactions (fig. 10) double- and triple-nods are most frequently observed. It seems that the double-nod march and the triple-nod are closely related. Both can be deduced from the fundamental double-nod to which a pace is added in the first case, and another nod with higher amplitude in the second case.

Nods stimulate conspecifics, and even three specimens are sometimes engaged in nod displays simultaneously.

### 3.1.2.1 Signature display

A definite species-specific display form is lacking, but double and triple nods are most frequent. They can already be observed in hatchlings and are common in females and males. They demonstrate a “general state of arousal” during encounters with conspecifics or after prey detection.

### 3.1.2.2 Assertion (males only)

Position, posture and colour pattern are characteristic in an asserting male: he sits high on a perch, mostly along a branch, holds his head elevated and shows a brilliant contrasting pattern (see 3.1.1.1, fig. 16) with the dorsal region dark brown to black and the dorsolateral stripes in contrasting white. The low dorsal crest becomes more prominent. This display type is static, and assertion posturing is maintained over the greatest part of the day. Head

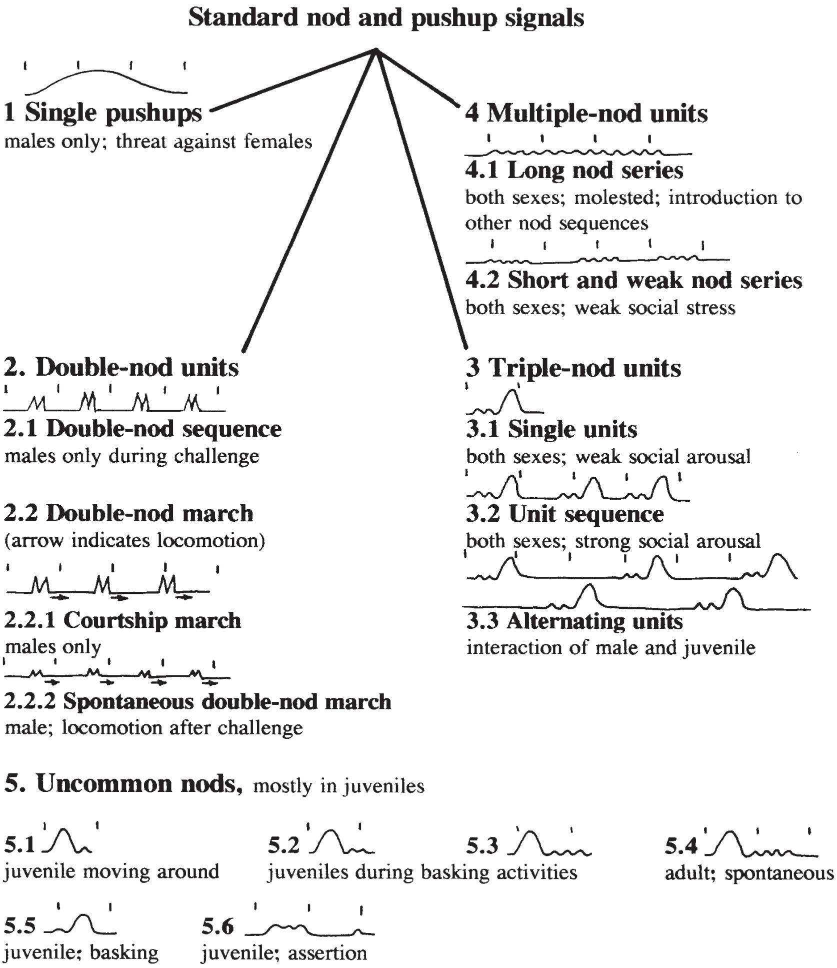

**Fig. 11.** Nod and pushup signals during social interactions.

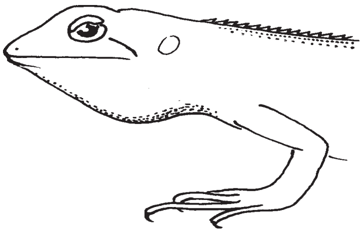

**Fig. 12.** Gular poach of threatening male.

nods are not an obligatory constituent of assertion, but they are released by approaching conspecifics.

### 3.1.2.3 Sexual maturity and courtship

At least in males maturity is attained in their second spring at an age of about 18 months, after the emergence from their second hibernation.

The sexes can be best distinguished if the cloacal regions are compared in lateral view. In females there is a distinct step behind the cloacal slit (fig. 13) while in males the transition from the cloacal region to the thinner tail is continuous.

Courting is released by the sight of a female, above all when she moves. It is even triggered if the female is almost completely hidden between plants with only a part of her head visible. Many times courtship starts as soon as the female changes position, e.g. when hunting pray. A male which approaches a resting female starts a peculiar march with a sequence of double nods each of which is followed by forward motion (fig. 11:2.2.1). Each time the male moves one or two centimetres towards the female and he repeats this until he is up to a distance of 5 centimetres.

At close distance the male does not approach further, but nods on the spot, but now with his gular pouch spread and presented to the female in lateral view. The male takes a bite hold at the female's neck during the forward motion of a triple nod and then tries to attain cloacal contact, twisting his hindbody. Sometimes the male seizes the female's tail.

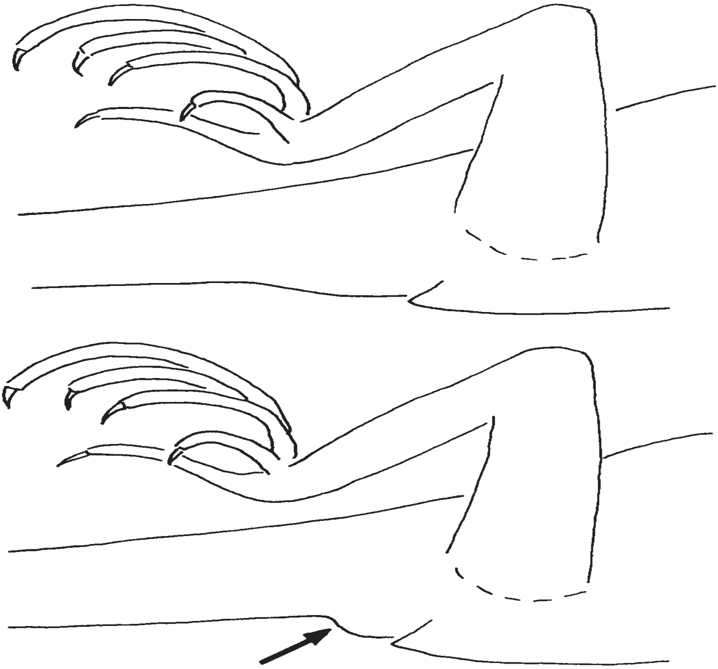

**Fig. 13.** Sex differences: in *Japalura*: in the male (top) the narrowing from the cloacal region towards the tail is continuous; in the female there is a step (arrow) behind the cloacal cleft towards the much thinner tail.

#### 3.1.2.4 Female response to courtship

While at least one male continued courting into November, no female was motivated to mate at this time of the year.

Rejecting females flee from courting and approaching males under cover and/or crouch flat on the ground. Crouching is even released if a male moves around vehemently close to a female. Or they move up to the cage lid where they hang with the head downwards. In this position they are of no more interest to a male.

A female which was suddenly seized at the neck side by a male simply turned on her back with the male still clinging to her. In this position he gave up his mating attempts.

#### 3.1.2.5 Mating

In spite of prolonged phases of intense courting, no complete mating could be observed. The reason of this failure is unknown to us.

#### 3.1.2.6 Challenge and aggressive behaviour

Males threaten one another at close distance, but were never seen gaping or engaged in damaging fights. Nevertheless dominance is established.

In a dominant male challenge behaviour can readily be released by his mirror image. It comprises the "standard threat posturing" of many lizards: high stance, lateral flattening and lateral orientation. Additionally a long series of double-nods is released (about ten or more units in sequence, with intervals of about one second).

An intention movement of fleeing was observed in a mall male which sat close to the dominant one. The small specimen moved its head laterally with small amplitude away from the conspecific and back again, then fled.

#### 3.1.2.7 Social structure

When several males and females were enclosed in a relatively small cage a young male established despotism without heavy aggressions, after six weeks. Between the other specimens no rank order was evident. Their behaviour is characterised by the following traits:

1. They stay on the ground, often with lowered head, show a tendency to hide, and have relatively short activity periods.
2. Their pattern is less contrasting than in the dominant male, the dorsal chevrons are brown, not black, and the light dorsolateral stripe is only distinct in its anterior part up to the foreleg insertion., similar to fig. 7b
3. They show prolonged phases of fleeing attempts through the glass panes of the terrarium.
4. Otherwise locomotion is reduced, sometimes they hang suspended in cataleptic state from a branch.
5. Head nods are much rarer than in the dominant lizard.

The despot showed the following behavioural traits:

1. Exposed stay under the heating lamp with prolonged signature display
2. Contrasting pattern: the dorsal chevrons become almost black, and the white lateral stripe is ventrally lined with contrasting dark (fig. 7a).
3. Chases and short bite attacks at conspecifics of both sexes.

### 3.2 Activity pattern

A strong tendency towards prolonged resting periods during hibernation as well as in summer is typical for the species.

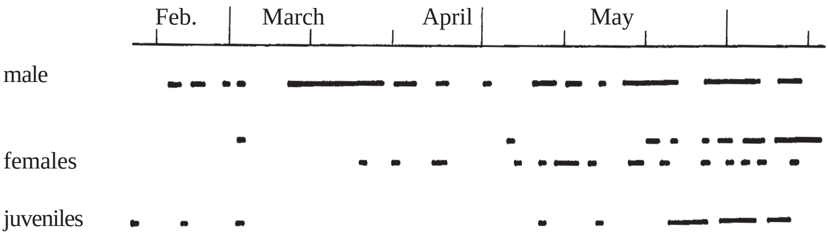

**Fig. 14.** Interrupted hibernations in four *J. kumaonensis* specimens:- one male, two females and one juvenile - in late winter 1995; Activity periods are indicated by bold lines.

### 3.2.1 Annual cycle

Information about a snow cover of several weeks in the biotope caused us to try a cold hibernation during the first winter of captives. A three months' stay in a room with 4°C led to the death of several lizards, evidently from dehydration. Others were very weak and thirsty after emergence, but recovered. During the next winter the lizards stayed in a weakly heated room (night temperatures down to 10°C) with the terrarium illumination reduced down to nine hours minimally, with night temperatures down to 10°C. Under these conditions, with temperatures between 11°C and 17°C at the hiding places, the japaluras showed individually very different activity cycles: almost regular activity in the male, but weeks of dormancy in females (fig. 14). One female which had laid a clutch in autumn emerged rather frequently and ate remarkable quantities of food each time. Another female remained hidden from Dec. 2 to March 17.

After their transfer into a greenhouse which was heated just to avoid temperatures below 6°C from autumn on, the japaluras no more interrupted their hibernation phase. In the end of October they abruptly disappeared within a few days between the rocks and did not reappear until the end of February when a young male appeared during sunny weather and an air temperature above 20°C.

The evidently high adaptability of hibernation strategies to ambiental conditions is essential during changing weather conditions and for populations which live at different altitudes.

### 3.2.2 Diel cycle

*Japalura kumaonensis* prefers dark retreats. In a terrarium with branches and plants they withdrew into the darkest corner for the night, but as soon as a heap of dry grass was put into a corner it was readily accepted by most of them. Occasionally a lizard slept clinging to the wire netting of the terrarium lid or crouched on a branch with the hindlegs stretched along the tail, as is typical for many arboreal agamids.

A specific trait of females are inactivity periods in summer, even during sunny weather, when some of them disappear for several days while others remain fully active.

## 3.3 Multiple-purpose behaviour

### 3.3.1 Postures

In some specimens there is a pronounced tendency to rest in a hanging position with the head downward. They do so when resting at the underside of the cage lid, to catch flies or to escape mating attempts. Without effort a single toe claw can support a hanging female for several minutes.

#### 3.3.2 Locomotion

Digging seems restricted to the nest excavation and could never be observed under other conditions.

#### 3.3.3 Observational behaviour

In contrast to *Japalura tricarinata* in *J. kumaonensis* the observatory motions of eyes and head are less conspicuous. This may be due to the fact that in J. tricarinata the eye opening seems to be a little smaller, so that searching eye motions similar to those of a chameleon become necessary.

In unknown surroundings (a new terrarium) objects are frequently probed with the tongue during locomotion.

### 3.4 Maintenance behaviour

#### 3.4.1 Feeding

The optic sense is leading during predation, e.g. mealworm pupae are scarcely taken when they are immobile, but readily seized if they move. The lizards have prolonged activity phases if they are confined to a narrow cage. Those living in the greenhouse were rather sedentary and behaved as ambush hunters. Prey distance is an essential cue for feeding: A caterpillar which released only fixation at a distance of 20 and 10 cm was instantly seized at 5 cm. Eventually the lizards try to jump and seize a prey insect above their head. They even show surprising skill to catch flies in a sudden dash. One specimen caught about fifteen Bluebottle flies (*Calliphora vomitoria*) one after the other in a small terrarium.

The appetite of females in gravidity and after oviposition is enormous, and they eat several medium-sized crickets (up to eight) in a few minutes.

The low activity temperature permits feeding at early hours (07.30 summer time) and directly after emerging from the retreat.

#### 3.4.2 Drinking

The lizards lick water from hanging drops or when running down a surface. They also drink from a dish with their snout remaining submerged.

#### 3.4.3 Thermal behaviour.

*Japalura kumaonensis* is a thermoconformer which occasionally basks. In captives the repeated shift between the radiation beam of lamps and rather cool places in the terrarium is evident. When sitting unexposed the females escape constant courting and mating attempts. Gravid females have a higher temperature preference and start to bask intensely one week before nesting.

The handicaps of rapid emergence from retreats are lacking in this species. The lizards do not need a basking period before full mobility is attained, and prey is hunted with a body temperature of 14°C. This low voluntary temperature is remarkable in comparison with the European and Tasmanian species in which Spellerberg (1976) studied adaptations to cold. Most of them have voluntary minima above 20°C.

#### 3.4.4 Moulting

During the moult of the head one or both eyes may be protruded for several minutes. The mouth opens wide, and the head sides are rubbed on the substrate.

3.4.5 Bathing

A five months old juvenile once entered the water dish, diving its head several times below the surface.

## 3.5 Antipredator mechanisms

### 3.5.1 Cryptic behaviour

The low temperature requirements make long exposures to insolation unnecessary and allow a prolonged stay in retreats if the lizards are not hungry or about to reproduce. This fact reduces the exposure to predators.

### 3.5.2 Escape behaviour

In the field the lizards flee at a distance of 1-3 meters if approached by a human. During bad weather and with low body temperatures the fleeing distance is higher. Normally they stay close to a hiding place and flee into a hole between rocks or roots, or below plant matter on the ground. On open soil they move running or in jumps.

The fleeing distance can be altered by a learning process, and captives loose their shyness in a few days. Due to their greediness they take food insects from pincers . In the greenhouse they were not deranged by the presence of an observer.

### 3.5.3 Defence behaviour

When handled the lizards gape and eventually bite vigorously. Only once a loud peeping was emitted with a low body temperature of 5°C. Similar vocalisation has been known from *J. tricarinata* and *polygonata* (Kästle & al. 1993).

### 3.5.4 Catalepsy (fig. 15)

An adult lizard which had escaped from the terrarium was caught by a domestic cat which apparently played with it over several minutes, pawing it and carrying it about without any lesions being visible. The lizard fell into a cataleptic state, resting immobile with limbs adpressed to the ground, eyes half closed and no respiratory movements . Its body was strongly inflated. After 90 minutes the lizard regained its mobility, but nevertheless died the following day.

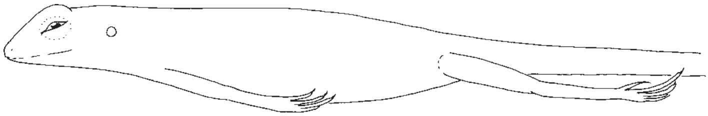

**Fig. 15.** *J. kumaonensis* female in cataleptic state.

## 3.6 Female reproductive behaviour

Females can lay up to two clutches per year. The minimal distance of two clutches was from 12. 11. 1995 to 08.06. 1996.

During the last week before nesting the gravid female entirely changed her activity cycle and basked intensely for many hours daily under the lamp, starting at 9 h in the morning.

### 3.6.1 Nesting

Nesting behaviour can be subdivided into:

1. Appetitive behaviour which consists of the search of an appropriate nesting site and probe digging. It can completely lack or last up to several days.

2. Digging of the nest tunnel

3. Oviposition

4. Egg ramming, refilling of the nest tunnel.

As an “ideal” nesting site had been prepared in the terrarium (see paragraph 1.4), the females normally lost not time in digging at other sites of the terrarium.
The nesting female digs a horizontal or weakly downward tilted gallery until the body has entirely disappeared in the hole. This takes a minimal time of one hour. For oviposition she turns round with the head showing towards the entrance. The exact duration of oviposition is difficult to measure as the periods of expulsion labour and of rest cannot be discerned as only the head of the *Japalura* is visible. The whole phase may be estimated at 45 minutes including long pauses of rest before, during and after egg expulsion.
As in many (all?) agamid species the phase following oviposition is characterised by refilling and head ramming. The rapid head thrusts serve at first to pile the eggs. After this the refilling material is raked into the hole with the forelegs and condensed by identical head motions. Refilling usually lasts much longer than excavation, ending usually in the evening. Typical are disoriented phases of scratching with activities in the vicinity of the nest, but also in some distant corner of the terrarium.

One nesting event (12. 11. 1995) was recorded from its beginning. The female started digging in a sand layer under a stone at 09.30, interrupted the activities soon and started again at 11.15. She dug a horizontal gallery of 8 cm length. At 14.30 egg laying was terminated and the female started to ram (eggs and/or sand) with rapidly repeated head thrusts. Refilling and raking the sand in the surroundings of the nest pit continued with long interruptions until 17.30. When the eggs were recovered the next day, one of them was damaged by the digging female and had shrunk.

In another female the probing phase lasted over a week with the proper nesting process (June 6, 96) taking only a few hours:

| | |
|---|---|
| May 28 | Some probe digging at the prepared nesting site, interrupted by intense basking |
| June 3+4 | Strikingly high activity level of the gravid female which runs about. |
| June 5 | Starts digging at 12.30 and continues until 19.00 with long pauses |
| June 6 | Interrupted digging from 13.00 to 17.00 |
| June 7 | Some digging at the same hole |
| June 8. | Intense digging starts at 12.15; oviposition at about 17.00; refilling the pit until 20.00; running about still at 20.30. |

### 3.6.2 Clutches and incubation

Survey of obtained clutches:

| Date of oviposition | egg number | egg dimensions (mm) | average (mm) |
|---|---|---|---|
| 19.05.1995 | 11 | 4 viable eggs: 11.5 x 6 | 11.5 x 6 |
| 13.09.1995 | 9 | all eggs spoilt when laid | |
| 12.11.1995 | 9 | 10 - 11 x 6 - 7 | 10.88 x 6.62 |
| 16.05.1996 | 9 | all eggs spoilt when laid | |
| 08.06.1996 | 14 | 9.5 - 11.5 x 6.5 - 7.35 | 10.49 x 6.9 |

The four viable eggs of the first clutch enlarged from 11.5 x 6 mm to 13 x 10 mm during the incubation period. At an incubation temperature of 26° C one hatchling appeared after 50 days. The other eggs had slits, but the hatchlings were too weak to leave the shell.

## 3.7 Juvenile development

### 3.7.1 Maintenance of juveniles

Housed in a small cage with principally the same outfit as for adulti the juveniles are not difficult to rear. We did not risk a long hibernation, but continued to keep them in a still heated and illuminated cage during winter. A darker and cooler corner behind a bunch of grass provided a refuge for longer phases of inactivity. The length of the light phase was reduced to ten hours.

3.7.2 Growth: Two fully developed juveniles which opened their eggshell but could not hatch measured 17.85 + 28.6 mm resp. 18.8 + 30.9 mm (snout-vent + tail length). Juveniles grew to a snout-vent length of 25 - 27 mm (tail 45 mm) in four months and to a snout-vent length of 39 mm with 5 months.

### 3.7.3 Ontogenesis of the communication system

The following data are based on three juveniles. Two of them were caught with an age of at most one month in July 1994. The other hatched in captivity on July 8, 1995. The classification of display nods (partially in brackets) follows fig. 11.

1 day: Very shy, flees in panic at the slightest cause; eats small wax moth larvae; drinks from a moist stone.
6 days:: First nods in excitement, irritated by other lizards
1 month: Double-nod (5.1) during climbing locomotion
2 months: Triple-nod (3.1)
3 months: Triple-nod (3.1) while seeing caterpillar, which was afterwards eaten
Short and weak series (4.2) when landing near another lizard after a jump
4 months: Uncommon nods (5) while basking
During basking a mixture of different nods: 4.1 (1x); 5.2 (2x); 3.1 (1x); 5.5 (1x) with pauses of 5-10 sec.
Uncommon nods (5.3) during assertion, sitting exposed, with expanded gular pouch . Threat against other juvenile with spread gular pouch.
Alternating nods (3.3) with another juvenile
6 months: Threat against mirror-image with double-nod sequence (2.1)
7 months: Alternating double-nods with adult male
18 months: Full threat repertoire with slow pushup against approaching female
18 months: Triple-nods against moving female (3.1; 3.2)
Courtship behaviour in second spring after hatching.

### 3.7.4 Additional remark

A juvenile housed together with several adult *Sitana sivalensis* in a terrarium became extremely excited when one of them began to dig a nest pit. The *Japalura kumaonensis* stayed close by and nodded over and over again recording the event as something quite unusual. It had to be put into a neighbouring cage to avoid disturbance of the nesting. After this the hatchling tried several hours to get back into its former cage through the window pane.

## 4. Discussion

Low thermal demands and weak sexual dimorphism (more contrasting pattern in displaying males) of *Japalura kumaonensis* are keys to essential traits of its behaviour. Compared with the closely related *Japalura tricarinata* (Kästle & al., 1993), which occupies a similar ecological niche, *J. kumaonensis* mostly lacks a pronounced sexual dichroism. (see following article, same volume). The striking sexual contrast in *Japalura tricarinata* is evidently connected with some ecological diversification: the brown females are mainly found in the leaf litter, while the green males often sit in low bushes. The striking frailness of captive males may be connected with some special ecological demand.

As stated in the paragraph on thermal behaviour (3.4.3) *J. kumaonensis* behave in captivity largely as thermoconformers and start feeding at relatively low temperatures (14°C) without a preceding basking period. Switching from an inactivity phase to activity is correlated, but not stringently, with ambiental temperature, and there are no grave problems of emergence from cold torpor which are often fatal to other species. The reduction of basking time diminishes the danger of being predated, and females which are unmotivated to mate escape continuous courting. This female tactic is partially compensated by the very low releasing threshold for courting in males, which is already triggered by the partial sight of a female's head. Speculations on correlation between thermal behaviour and rank order (paragraph 3.1.2.7) are misplaced as despotism was established under highly unnatural conditions.

During gravidity the body temperature is kept at a higher level, and the females bask regularly and extensively. Contrarily, during digestion no higher body temperature is established in contrast to many other species (Huey, 1982). This fact supports the view, that the species is a low-temperature lizard rather than a generalist (same author), as its thermal set values (activity temperature range, mean activity temperature) have at least partially shifted towards lower temperatures.

Inactivity periods of indvidually variable length are normal in winter and summer, even during sunny weather. Reduced activity diminishes the frequency of social encounters, perhaps one reason why intraspecific agressivity can be kept at a low level. There are too few data on rival behaviour in the genus *Japalura*, but as much as is known, even males seem to be rather tolerant. In the greenhouse there were no open rival attacks between *J. polygonata* (Kästle & al., 1993), and several adult *J. variegata* males mostly tolerated each other at distance, with occasional short chases (recent observation).

In *J. kumaonensis* open attacks on rivals are exceptional. The mirror-image is threatened, but was never attacked. Nevertheless a rank order is established if several males are confined close together, and the inferior males stay more hidden and display less frequently.

Display behaviour shows little sexual differentiation and is simple but variable in different social situations. Only the double-nod march and the pushup are restricted to males. The other forms of nods can be sorted out into frequent and rare types, but the correlation between the various nods and the lizard's state of arousal is uncertain, with the only statement that weak reactions may consist of low-amplitude nods in shorter sequence. Alternating nods during encounters (fig.11:3.3) play a similar appeasing role as e.g. “treteln” (a rapid up-and-down motion of the forelegs accompanied by head nods) in Lacertidae which can be considered, anthropomorphized. as a form of “greeting” after which both conspecifics continue their routine activities.

Considering the genus as a whole, low thermal requirements are apparently a main factor for the speciation process. With exception of a few species from Taiwan and neighbouring Islands (Ryukyu) the majority of about 20 forms - which are partially very difficult to keep apart - inhabits mountain regions of SE Asia northward to the Shaanxi Province, Central China. If terrestrial and arboreal forms live together in the same biotope is unknown. But there are no studies on sympatric forms, and the distribution pattern of species rather suggests a disruption of a common stock into isolates due to elevated temperatures in the lowland. All recent records are from cool refuge areas where concurrence from other lizards is restricted mainly to scincids, which are still more secretive and reach much higher elevations (*Scincella ladacensis* at 4590 m, Nanhoe & Ouboter, 1987).

## 5. Literature

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**Fig. 16.** *Japalura kumaonensis* male in splendid coloration.

**Fig. 17.** *Japalura kumaonensis* female with partially green flanks.

Next page:

**Fig. 18.** *Japalura kumaonensis* female with light brown hue.
**Fig. 19.** *Japalura kumaonensis* female with reddish brown hue.
**Fig. 20.** *Japalura kumaonensis* juvenile.

**Fig. 18**

**Fig. 19**

**Fig. 20**

# Description of *Gonydactylus nepalensis* spec. nov. from the Inner Terai of Far West Nepal (Reptilia: Sauria: Gekkonidae)

H. Hermann Schleich* & Werner Kästle**

**Key words**: Herpetology, Nepal, *Gonydactylus nepalensis* spec. nov.

**Abstract**: A new species of cyrtodactylid gecko from the Terai region of Far Western Nepal is described. This is the first gecko of this group recorded from this country. The new species seems closely related to *Gonydactylus fasciolatus* from the highland regions of the western Himalaya. The affilation of the new form to the genus *Gonydactylus* must remain preliminary until a revision of the whole complex of cyrtodactylid geckos is at hand.

## Introduction

On 28, April 1994 H.-H. Schleich discvovered a cyrtodactylid gecko in the village of Sakaye, 20 km off Silgadhi in Dipayl/Silgadhi district, Far Western Nepal (fig. 1 foto of area where the new species was recorded). As no other similar gecko had been recorded from Nepal hitherto, the importance of the finding was at once recognised and a premium promised to the villagers for more specimens. The result was another gecko of the same species found by Schleich at the police station of Sakaye. Both animals were males kept in captivity. Because of their cryptic habits the death of one specimen remained unobserved and the carcass was lost, being completely destroyed by food crickets in the cage. For this reason this description is based almost exclusively on the holotype. As photos of the lost specimen were available, additional data on body pattern and characters of the original tail could be added.

Acknowledgement: One of the authors (Schleich) is grateful to K.B. Shah who helped to catch the first specimen at midnight on his family house.

~~**Fig. 1.** Area of~~ type locality of *Gonydactylus nepalensis* spec. nov.

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**Fig. 2.** *Gonydactylus nepalensis* spec. nov., holotype.

**Fig. 3.** *Gonydactylus nepalensis* spec. nov., holotype.

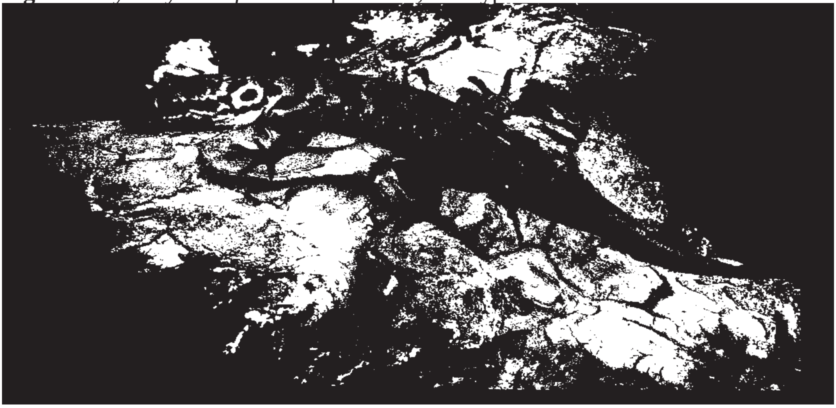


**Fig. 4.** *Gonydactylus nepalensis* spec. nov., holotype.

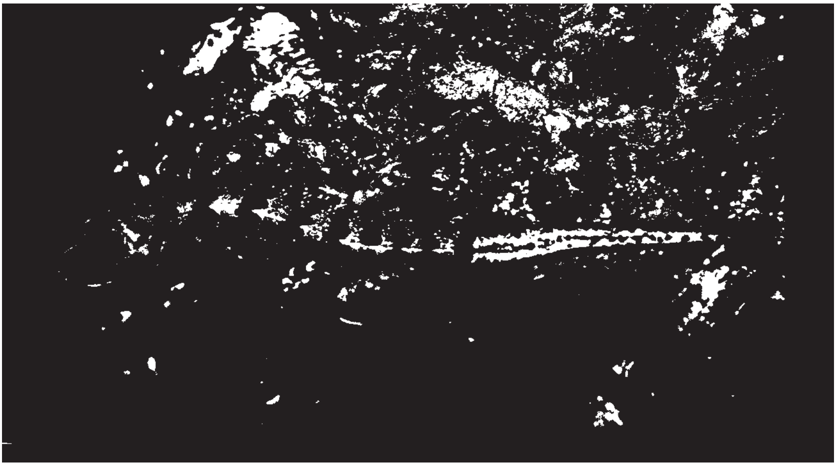


**Fig. 5**. *Gonydactylus nepalensis* spec. nov., holotype.

**Fig. 6**. *Gonydactylus nepalensis* spec. nov., lost specimen.

**Fig. 7**. *Gonydactylus nepalensis* spec. nov., lost specimen.

Material: Holotype male, Fuhlrott-Museum Wuppertal, VW-D 94/14; additionally a series of photos of a lost specimen.

## Systematic account

Type locality (fig. 1): Sakaye, a small village with a new police station, close to Dipayal. The locality data were taken by GPS (Garmin, GPS 75): N 29° 18´ 37.6 – E 80° 43´ 10,6, the elevation was given with 745 mtrs.

Etymology: The Latin termination -ensis indicates the provenience.

Diagnosis: A rather large and slender angular-toed gecko (fig. 2-7) with a rather blunt snout, the distance from snout to eye being longer than the distance from eye to ear opening. The nostrils lie in a depression behind the rostral and are directed laterally. A longitudinal furrow on the forehead begins behind the nostrils and ends between the eyes. There is no ventrolateral fold discernible in the preserved and injected specimen, but it was distinct in the living animal. Sparse round and flat tubercles are irregularly distributed over the dorsal surface from the posterior head to the tail base. The back bears a bold pattern of dark wavy transverse cross bars. The upper head shows an irregular pattern of diffuse dark marks. Tail distinctly longer than snout-vent length and marked with transverse bands.

Measurements (mm):
Total length (tail regenerated): 131
Snout-vent length: 72,6
Length of body between axilla and groin: 32,5
Head length (snout to posterior margin of tympanum): 19,7
Largest head width: 14,7
Head height: 9,8
Snout - orbit distance: 8.5
orbit - ear distance: 6.5
Diameter of eye: 4,3
Foreleg length (axilla to tip of longest finger without claw): 23,3
Hindleg length (groin to tip of longest toe without claw): 36,9
Length of a median dorsal tubercle: 0,6 mm.

Body proportions:

| | |
|---|---|
| Relation snout - vent length : head length: | 3,69 |
| Relation snout - vent length : hindleg length | 1,98 |
| Relation hindleg : foreleg | 1,58 |

Pholidosis:
Head (fig. 8): The upper side of the head is covered with small rounded to hexagonal granules which are largest in the loreal region, above all at the contact zone with the supralabials. Behind the eyes the small scales become intermixed with round and flat tubercles which from there backward are irregularly distributed on the dorsal side down to the flanks. The parietal tubercles are surrounded by 7-9 granules.
Rostral (fig. 9 top) very broad, bipartite in its upper half, its upper margin contacting

two large internasals. Behind the rostral the nasal region is laterally compressed so that the nostrils are located in a small pit and lie almost vertical.

Nostril (fig. 9 bottom) surrounded by the rostral, the first infralabial, the internasal and two or three small nasals. The ear-opening is oval, oblique and much smaller than the eye

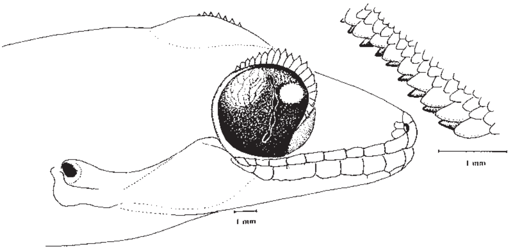


Fig. 8.

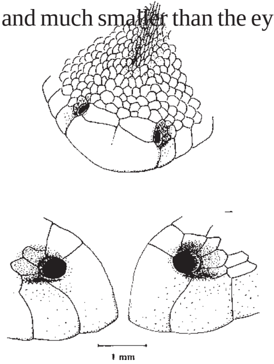


Fig. 9.

**Fig. 8.** *Gonydactylus nepalensis* spec. nov.: holotype, head; as the snout is not viewed at a right angle it appears shorter than the eye - ear distance. The inset shows a dorsal view of the supraciliary region.

**Fig. 9**. *Gonydactylus nepalensis* spec. nov. holotype, nasal region, right and left nostril.

Number of supralabials left 10/ right 10; Number of infralabials left 8/ right 7. As one of the right infralabials (the 5th) appears exceptionally long it must be supposed that the 5th and 6th have fused on one side of the head.

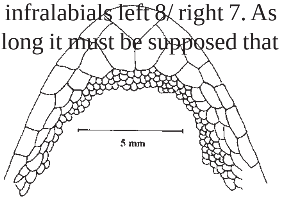


**Fig. 10**. *Gonydactylus nepalensis* spec. nov. holotype, mental region.

Mental region (fig. 10): Mental triangular; there are three pairs of enlarged postmentals. The first pair is in contact behind the mental and forms a suture which is shorter than the mental. Ventrally from the supralabials run 2 - 3 rows of oblong scales which merge into the gulars.

Body (fig. 11): The dorsal side is covered with small rounded and juxtaposed to subimbricate granules which are sparsely intermixed with rounded tubercles of double to fourfold granule diameter which neither on the back nor on the tail form regular transverse or longitudinal rows. The middorsal tubercles are surrounded by 9-11 granules and separated by 2 or 3 granules. The middorsal tubercles are rather round, many of them flat, but the highest of them form a flat asymmetrical cone the round apex of which lies towards the posterior border.

Towards the flanks the tubercles become more sparse and do not reach the lateral fold. The latter is seamed by somewhat larger scales which are smaller than the ventrals. On the flanks the granules show a tendency to form parallel vertical rows, and where a furrow between such rows reaches the posterior margin of a tubercle the latter may become truncate.

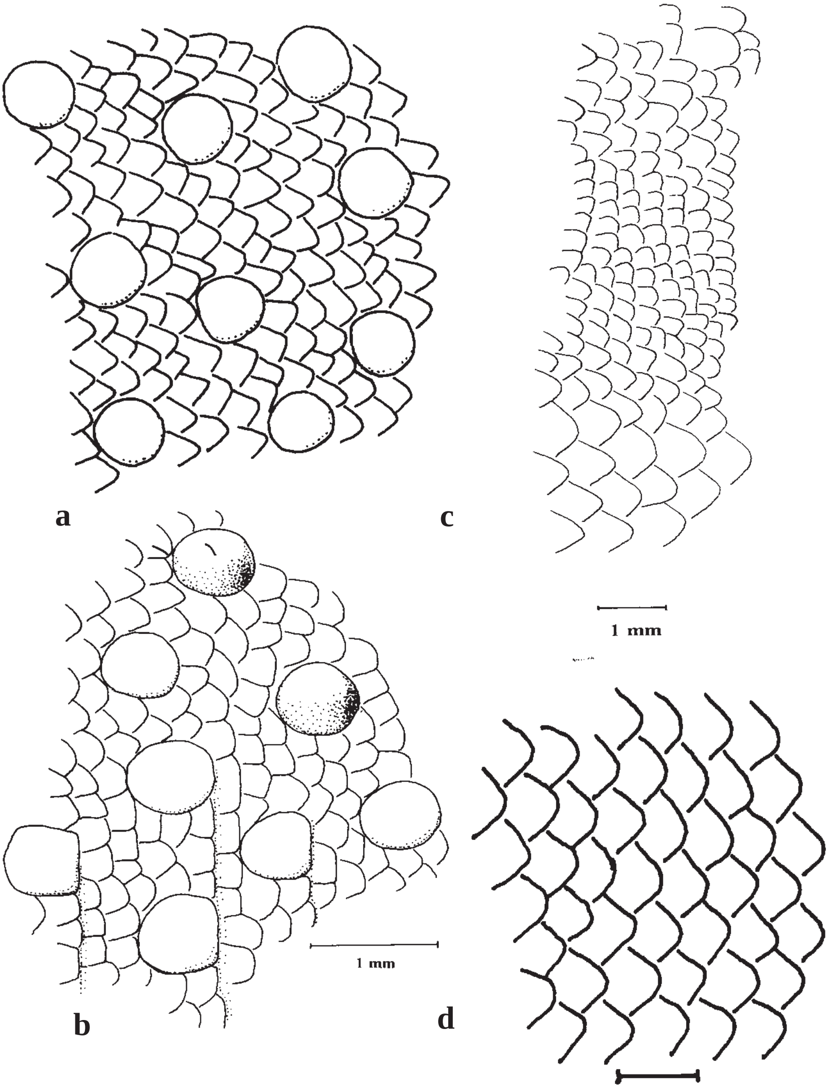


**Fig. 11**. *Gonydactylus nepalensis* spec. nov. holotype, body scalation: middorsal, dorsolateral (left bottom), ventrolateral (right top), ventral.

The ventrals are rounded imbricate and arranged in very regular rows.

There are two supraanal tubercles on each side (fig.12c). Preanal perforated scales are weakly differentiated, four on the right an six on the left side (fig. 12a,b). They are in line with enlarged subfemoral scales (fig.12b). The total count of preanal plus subfemoral scales on each side is 18.

Limbs: They are covered with subtriangular and subimbricate granules. Flat round tubercles are present on fore- and hindlimbs except the forarms, hands and feet. The sudigital lamellae are large and overlapping (fig.12e).

The tail of the holotype specimen is regenerated, but in the lost specimen it was intact.The ventral side of the regenerated tail is covered with irregular broad scales (fig. 12d).

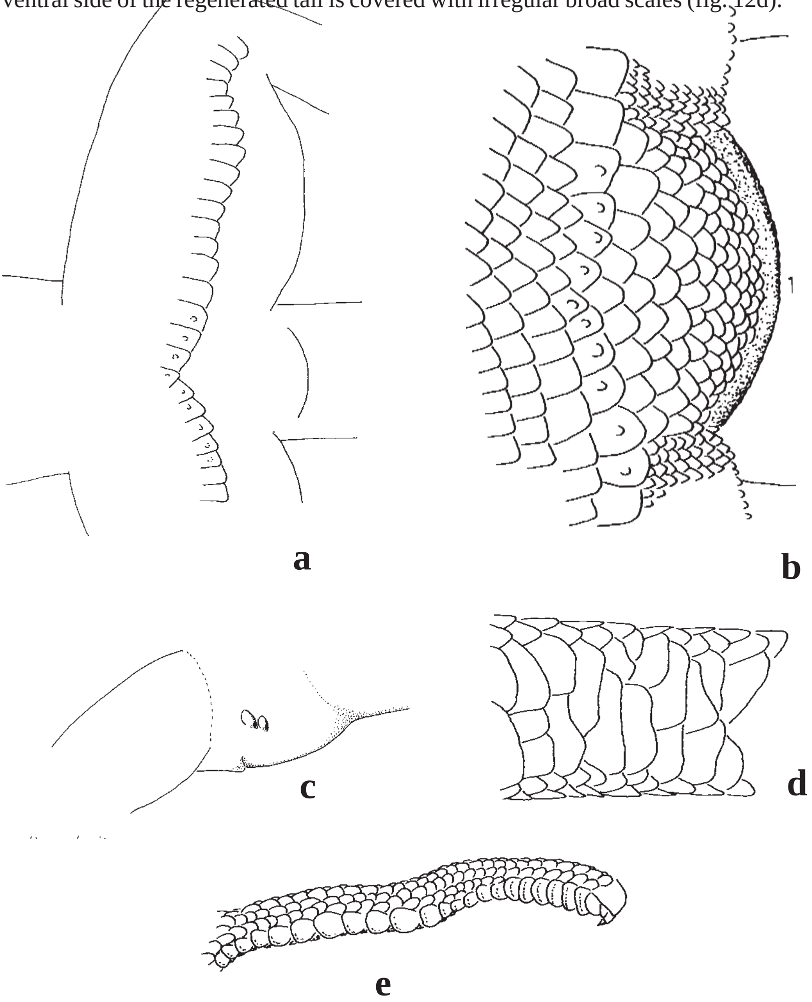


**Fig. 12**. *Gonydactylus nepalensis* spec. nov., holotype.
a) row of preanal and femoral scales
b) anal region with indistinct preanal pores
c) supraanal tubercles (left side)
d) ventral side of regenerated tail
e) 4th toe of right pes.

Summary of pholidosis
interorbital scales: 52
scales between nostrils: 2 internasals

| | | |
|---|---|---|
| scales around the nostrils, | left: 6 | right: 5 |
| supralabials, | left: 10 | right: 10 |
| infralabials, | left: 8 | right: 7 |
| dorsal tubercles | | |
| transverse count at midbody: | 14 | |
| paravertebral longitudinal count: | 34-36 | |
| granules around midback tubercles: | 9-11 | |
| granules between midback tubercles: | 2-3 | |
| ventral scales across mid-abdomen: | 24 (lowest count) | |
| scales from mental to anal: | about 152 (70 midgular, 76 ventrals, 6 preanals) | |
| preanal pores (indistinct) | left: 4 | right: 6 |
| subdigital lamellae | | |
| under fourth finger, | left: 20 | right: 20 |
| under fourth toe, | left: toe lacking | right: 23 |

Hemipenis structure (fig. 13): The hemipenis is bilobed a shows a variety of longitudinal folds. As no material for comparison is available the taxonomic relevance of hemipenial structures must be left out of consideration.

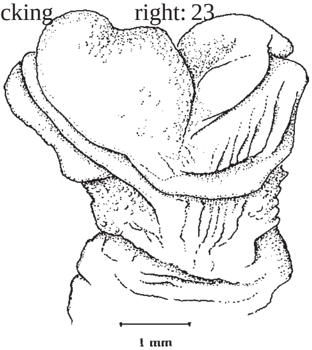


**Fig. 13**. *Gonydactylus nepalensis* spec. nov., holotype, right hemipenis

Coloration, colour in life (fig.2-7,14,15 left)
The dorsal basic coloration is light reddish ochre from which the deep purple brown wavy transverse bands stand out. They are larger than their interspaces. Their anterior and posterior margins are undulated and contrast sharply with the adjacent ground colour. The central part of the bands is somewhat lighter. Some of them bifurcate on the flanks, on which brilliant white tubercles are dispersed. There is a strong tendency of the bands to become interrupted in the vertebral region. Most halves are still joined there by a dark pigmentation. On the flanks the ends of the bands merge into a vague longitudinal stripe.
The most striking colour marks are the two light blue supraocular spots. Other head pattern elements are diffuse dark patches on the pileus and a pattern of dark bars and spots between occiput and eyes.
The regenerated tail shows the same colours as the body, but bears a longitudinal pattern of irregular stripes.
The limbs show dark transverse stripes.

Colour of the preserved specimen: The vivid colours fade into a light and a dark brown, but the markings are not changed in shape. The blue supraocular spots disappear. The venter is white, probably by extraction of the light purplish pigments which can be recognised on photos of the holotype.

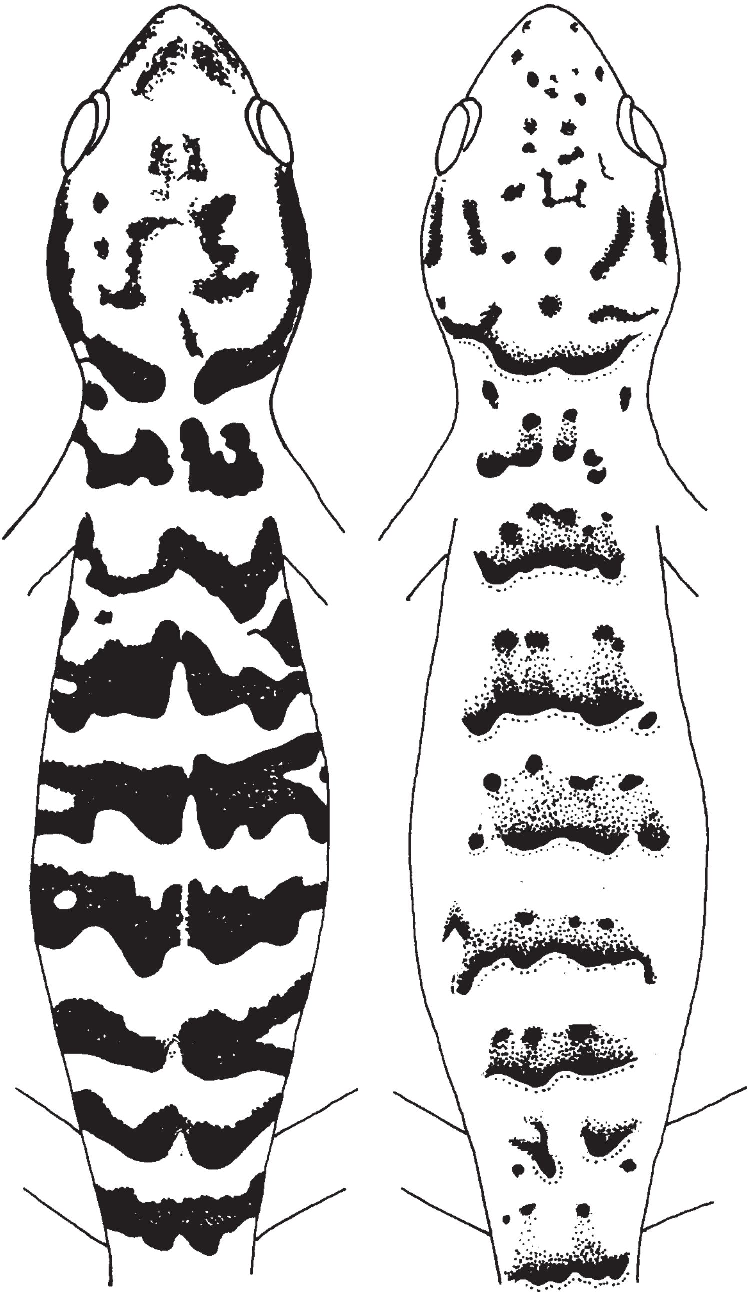
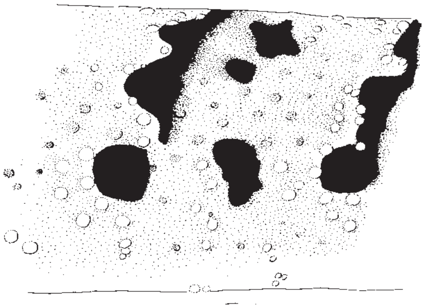


**Fig. 14**. *Gonydactylus nepalensis*, types of dorsal pattern, holotype (left) and lost specimen.

## Additional data from the photos of the lost specimen

The intact tail of this specimen is much longer than snout-vent length and the proportion tail length : SVL was estimated at about 1,3.

Tail: feebly imbricate subquadrangular scales (fig. 10b) which form regular or irregular transverse rows. Neither the arrangement or size of scale rows nor the position of tubercles indicate any verticillation or segmentation of the tail.



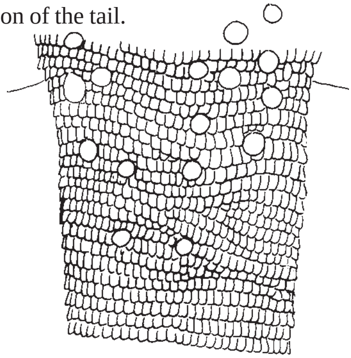


**Fig. 15** (left). *Gonydactylus nepalensis*, detail from body pattern (right flank). Note that two of the spots are still united with the subsequent bar by dark pigmentation.

**Fig. 16** (right). *Gonydactylus nepalensis* n. sp. dorsal pholidosis of tail base.

Colour pattern:

Body: A light beige basic coloration bears a bold dorsal pattern of six dark brown sinuous transverse bars which alternate regularly with dot rows of the same colour (fig. 9). This pattern type can easily be derived from the holotype's: The undulated dark posterior margin remained stable, the zone anterior to it became light, and the dark anterior zone was split into a row of dots. Shades of dark pigment still connect the former posterior and anterior margins (fig 10c).

The bars are much narrower than the interspaces. The last one in the pelvic region is divided into two large patches. Some of the bars break up into dots at their ends. The anterior borders of the bars are often connected by darker pigmentation with the dots ahead of them while their posterior margins are strongly contrasting and set off from the basic colour with a diffuse light line.

Many dorsal tubercles, including those on the head, show a colour contrast with their surroundings: Those within the brown bars are very dark, those on the beige skin are lighter than their surroundings.

Tail: The pattern of the dorsal tail surface has some resemblance with the dorsal one and consists of twelve pairs of dark, narrow bars. These form pairs which include a diffuse lighter interspace. Each pair is separated from the subsequent one by the light basic colour. The dark bars are partially bordered with white. Near the tail base the anterior one of each pair is shorter and/or shows a tendency to break up into dots. Towards the tail end the pairs are no more clearly separated and fuse. The tail end is uniform beige.

The pattern differences between the holotype and the lost specimen could be significant enough for seducing a rash herpetologist two describe two different species. Some theoretical possibilities, which cannot be proved, could be:

- The patterns represent the range of normal colour change.
- They are due to intraspecific variability.
- The coloration of the lost specimen is a juvenile pattern.

## Differential diagnosis

The cyrtodatylid geckos are a heavy challenge to taxonomists (Szczerbak & Golubev, 1986). As many of the Himalayan species are only known from very few specimens there are almost no data on their intraspecific variability. This lead to the description of numerous new species the validity of which was later abandoned as it was recognised that the "new" form fits still into the variability range of another species with priority of name.

As the dorsal patterns seem to be relatively unstable they should not be used as the main or exclusive discriminating characters in a key.

Comparison with the other angular-toed geckos of the region:

While a number of new species have been described from Pakistan, Jammu and Kashmir during the last decades (Duda & Sahi, 1978; Khan, 1991, 1993; Khan & Tasnim, 1990), only two species were recorded since the last century from the Kumaon region:

*C. lawderanus* (Stoliczka, 1871): W-Himalaya, close to the western Nepalese border

*C. fasciolatus* (Blyth, 1860): W-Himalaya, close to the western Nepalese border.

Their separation from *C. nepalensis* n.sp. is not difficult (key after Boulenger, Smith, Tikader & Sharma):

*Gonydactylus himalayanus* which is recorded for Western Nepal on a distribution map in Szczerbak & Golubev (1986, p. 200) can be omitted here, as this species is restricted to the Jammu and Kashmir region and the map entry is erroneous.

1 Intact tail shorter than snout - vent length; tubercles on body and limbs rather small and not very contrasting with granules; no enlarged subfemoral scales: *Gonydactylus lawderanus.*

1’ Intact tail distinctly longer than snoutvent-length; a row of enlarged subfemoral scales: ....2

2 Dorsal tubercles triangular; mental followed posteriorly by 2 pairs of medially contacting large postmentals: *G. fasciolatus*

2’ Dorsal tubercles rounded, rarely truncate posteriorly; mental followed posteriorly by 1 pair of medially contacting large postmentals: *G. nepalensis*

Summary of discriminating characters:

| *Gonydactylus fasciolatus* | *Gonydatylus nepalensis* n. sp. |
|---|---|
| ear diameter about half of eye diameter | much smaller |
| dorsal tubercles (sub)trihedral | round or truncate behind |
| tubercles on tail base arranged in regular transverse rows | irregularly arranged |
| ventrals across midbody 28-34 | 24 (lowest count) |

| | |
|---|---|
| an uninterrupted band from the eyes across the occiput | no continuous dark band between the eyes |
| 2 pairs of large postmentals | 1 pair of large postmentals |
| a highland form known from Almorah and the vicinity of Simla (Subathu), 1500 - 2100 m | in tropical Terai lowland 745 m |

**Remarks on ecology and general behaviour**

Habitat: In a village between houses in the tropical Terai zone.

Altitudinal distribution: 745 m.

Activity pattern, diel: In the field the species is strictly nocturnal, and its activity period starts with darkness. The two specimens were caught at 23.40h and 01.30 h respectively. The captives regularly left their hiding places after sunset when the room was still weakly illuminated.

Thermal behaviour: Apparently a thermoconformer and never seen basking.

Locomotion: Slowly walking on the ground and climbing on rough substrate.

Population biology: Population density evidently extremely low as in spite of a very intense search no more specimens could be recovered.

Feeding strategy: The geckos forage until prey comes in sight. It is carefully approached and suddenly seized.

Food spectrum: The captives took wax moth larvae and small crickets as a standard food.

Antipredator behaviour: The species is rather fast moving and very secretive. Taken by hand it turns round and tries to escape from a firm grip.

Geographic range:

Nepal: Hitherto known only from the type locality.

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Veröffentlichungen aus dem Fuhlrott-Museum, 1998, Bd. 4: 281-290

# Necessity for a Turtle Conservation in Nepal

H. Hermann Schleich* & Tirtha M. Maskey**

**Contents**

## Introduction

One of the authors (H.S.) is linked for more than ten years to scientific projects and field research activities in a survey of the Nepales herpetofauna. Particular interest was shown to the turtle fauna as there were hardly any proved records documented by preserved specimens or reliable photographs. In January 1997 the ministry of soils and forest conservation allowed the inition of a turtle conservation project. To gain more interest, collaboration and sponsoring from potential partners we are publishing our project plan for the study on systematics, biology and conservation of the turtles from Nepal. For the same purpose we also founded **ARCO Nepal** (= **A**mphibian and **R**eptile **C**onservation **o**f **N**epal) to allow sponsors and donators to raise funds for the project.

## Status Quo

All turtles are under tremendous pressure from professional fishermen, tribal people, children and cursorial collectors collecting fish, snails and turtles. The latter are used for their meat, as pets or for shell preservation.

## Action Plan

The development of an action plan requires the coordinated effort on the part of many people. Primary objectives of the turtle action plan are:
(1) identification of the most pressing issues currently threatening turtle survival and
(2) development of projects/actions necessary to diminish those threats. This action plan will be a dynamic document that will be revised as projects are completed, as our knowledge increases, and as the survival status of populations changes.
We hope that the action plan will serve to focus international efforts on behalf of turtles and to present an unified appeal for the financial support necessary to complete these projects.

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## Threats to the survival of turtles

Human impact has affected the survival of turtles since prehistoric man hunted them and gathered their eggs. Originally, the effect of human activities on the turtle populations was essentially limited to direct exploitation, and turtle products played important roles as food, medicines, tools and ornaments in cultures throughout the world. More recently, turtle populations have come under additional threats as a result of human activities not directed at turtles, particulary from habitat degradation, pollution and debris, and capture in fisheries. In some areas direct take of turtles has increased as a result of higher human predation rate and more efficient capture techniques. While direct take can be estimated, other factors for the decline of species and specimen number are more difficult to control and to quantify. Habitat degradation is an ongoing threat to the survival of turtles. Degradation of nesting areas can better be documented than degradation of foraging habitats because of the greater visibility of nesting areas to humans. Nesting areas can be completely destroyed by monsoon floodings e.g. when too much of the sand bars is removed. The degradations of foraging habitats, although less obvious than the degradation of nesting areas, are serious threats to turtles as the human population continues to grow, particularly near water bodies which provide food and facilitate irrigation.

These threats to the survival of turtles are great, not only because of the magnitude of the pressure, but also because of the biology of turtles. As mentioned (in the section on turtle biology), turtles are characterized by slow rates of population growth as a result of slow individual growth rates, slow sexual maturation, and high natural mortality and predation, especially in the early stages. These demographic characteristics impose real constraints on the ability of turtles to sustain exploitation. It is clear that most turtle populations can only substain relatively low levels of human-inducted mortality.The present high level of mortality by human impacts may meet or exceed the substained level and thus preclude any direct harvest of turtles.

Better quantification of demographic parameters - including both natural and human- inducted mortality - is required before we can effectively evaluate sustainable utilization of turtles. As migrations and distribution patterns of turtles in large water bodies are still poorely understood the census of populations is rather difficult.

## Records of turtles from Nepal being proved during last years´ field activities

In a previous listing (Schleich, 1993) of the herpetofauna of Nepal based mainly on literature, the applicant tentatively reported 15 turtles to occur in Nepal. Due to last years´ (incl. 1996) field activities at least the following 11 species have been recorded hitherto.

Emydidae
    *Kachuga smithi, Kachuga tecta ssp., Kachuga tentoria flaviventer, Melanochelys trijuga, M. tricarinata, Morenia petersi*
Testudinidae
    *Indotestudo elongata*
Trionychidae
    *Aspideretes gangeticus, A. hurum, Chitra indica, Lissemys punctata*

Amongst the above listed forms, only *Indotestudo* and *M. tricarinata* are terrestrial while the remaining ones are strictly bound to lacustrine water bodies. The situation for the whole turtle fauna of Nepal is an extremely bad one. In Far West as well as in East Nepal we observed, that all species are collected mainly for food by local people from the Terai. Records of *Indotestudo* became extremely rare. *Morenia* is only recorded by a single shell collected from local people in West Nepal. All softshells suffer heavy persecution by fishermen mainly at Koshi river but also in all other wetlands. The realisation of the presented master plan, supported by H.M.´s National Parks & Wildlife Service is urgently needed for the necessary turtle conservation.

## Nescessity for a turtle conservation in Nepal

Two different types of habitat are used by the turtles in Nepal. Viable terrestrial habitats mainly exist in natural forests of the lowlands and may contain two species, *Indotestudo elongata* and *Melanochelys tricarinata*. Although latter one is not mentioned by any conservation categories (IUCN, Red Data Book) it became already rather rare in Nepal. The *Indotestudo* in fact became so rare, that we only could get hints on its existance by broken shell fragments shown to us by local people in the Terai (*Indotestudo* is registered under CITES 1 and listed in the Red Data Book as being endangered or close to extinction). From own field activities throughout the whole range of South Nepal we obtained the information that all turtles are collected by local people, almost all of them are eaten for their meat, and also the shells are being ground down for paramedical purpose.

-In the Koshi Tapu area fishermen catch turtles and sell them on the market. According to information obtained there, turtles are also exported to West Bengal and Bangladesh. There was a rather high catching rate to observe at the Koshi Barriage in July 1996 when we just spent one week there in Koshi Tappu Wildlife Reserve. About 3-5 turtles/day were caught and offered on the market. Extrapolating this figure one can estimate an annual catching - or killing rate of 1000 to 1500 turtles in a size class of mature, thus reproductive stock. The practices of fishermen to handle live turtles are not applicable to any vertebrate caught to be slaughtered and die on their long way to other distributors and the final consumer. We obtained reports of turtles caught last year weighing up to 45 kg. Prices range for 40-80 Rs /kg on the local market.

-Confiscation of turtles is not practiced yet as a method of law enforcement in Nepal, but it came to my knowledge that a few years ago a truckload of turtles on the East-West-Highway in Terai with unknown destination was brought to Kathmandu for rectification.

-Turtle masks are sold on the market to tourists, mainly in Kathmandu. This unnecessary souvenir production and trade contributes definitely to sustain a hidden market supplied with turtles which were killed by fishermen.

## Natural history of turtles in Nepal and adjacent areas

Nepal´s lowland comprises the Terai and the Siwaliks. The latter range from Pakistan to India and the central parts around Nepal bear one of the most spectacular fossil reptile faunas of the world.

The palaeontological records that document the evolution of Nepals countryside and animal life are only a few million years old.

Most spectacular amongst those fossil findings are the biggest crocodile (*Rhamphosuchus*) and the biggest tortoise ever existing on earth (*Colossochelys atlas*).

Such fossils were studied in detail by one of the authors (H.S.) and the systematic description may provide an interesting insight in the evolution of the extant turtle fauna.

To describe the extant turtle fauna of Nepal is not an easy task, especially as there are many forms regarded close to extinction according to international regulations by IUCN or CITES. The available taxonomic information was in most of the cases rather tentative and speculative. Neither references in literature nor records by the staff from national parks and protected areas are yet reliable for a taxonomical identification of turtles. Really confirmed records are extremely rare, those from earlier publications must be taken cautiously. Sightings of turtles are rare, mostly due to their cryptic life as, e.g. in softshells, but also due to heavy overharvesting by humans.

The few species recorded so far were rarely encountered by direct closeups, but more likely by viewing them from far distances of several up to tens of meters.

Thus, the publications containing listings on Nepal‘s turtle fauna are almost exclusively based on informations coming from neighbouring countries like India, Pakistan, Myanmar and Bangladesh where species have been studied better. What makes things still worse is that formerly the records were never documented by good photographs or deposition in museum collections.

This project plan contains now colour photographs of turtles recorded by the senior author during last years. For the moment we only can roughly estimate to have 2 terrestrial and approx. 10 aquatic species in Nepal.

## Turtle distribution and habitats in Nepal

Turtles are restricted in their distribution to special habitats and climates. Most of them depend on subtropical and tropical conditions as they are found in the Siwaliks and the lowlands of the Terai.

We regard altitudes of 1000 or 1500 m as the maximum in altitudinal distribution for turtles in Nepal, but all confirmed records originate from elevations below 1000 m.

Thus, only the paratropical Terai, the Siwaliks and the Gangetic Plains contain the important habitat areas for turtles. Here we have to subdivide them into two groups: Species bound to terrestrial life are *Indotestudo elongata* and *Melanochelys tricarinata*, both occuring in woodland, riverine vegetation and in rarer cases also migrating into agricultural land. *Indotestudo* is also kept in temples in Kathmandu for worshipping, but according to own observations they are suffering there very much being unprotected in cold winter and kept on bare rock ground with inadequate food.

As aquatic species or forms living in wetland areas we find *Melanochelys trijuga* in palustrine habitats in the Terai, in lakes and ponds e.g. in Royal Chitwan National Park, or in Suklaphantah Wildlife Reserve. A most recent record provided by K.B. Shah (Natural History Museum, TU) via local fishermen proves the existence of *Morenia petersi* in South-West Nepal by a collected shell.

*Kachuga smithi* and *Kachuga tecta* are recorded representatives of the roof shelled turtles occuring in deeper rivers of the lowland. The first record of *Kachuga tentoria flaviventer* was brought by K. Ernst (Hamburg) at premonsoon 1997 from Koshi river. Other species like *Kachuga dhongoka* and *Hardella thurjii* are mentioned in literature but not yet confirmed by identifiable photographs or museum specimens.

During the last years we could record four softshell turtle species from natural habitats like rivers, ponds and lakes but also from fishery farms into which they might have migrated with monsoon floodings. These are the rather secretive *Aspideretes gangeticus*, *Aspideretes hurum* and the peculiar *Chitra indica*. All of them are listed in CITES and IUCN as threatened or close to extinction, but heavily hunted in Nepal for food. There are still only very few informations on their biology. The same must be said for *Lissemys punctata*, the Flap winged softshell with its beautiful yellow dotted markings on the shell. It is still more common than the afore mentioned species and it enters a higher variety of habitats, from paddy fields, to rivers, ponds, lakes, ditches and other wetlands areas. But its persecution is also extremely high, and our knowledge on the biology of this equally CITES bound species is still extremly poor.

## Own activities

During the last 10 years, field studies on the herpetology of Nepal were carried out by one of the authors (H.S.) together with members from National Park and Wildlife Department, King Mahendra Trust and Natural History Museum.

During several expeditions to far West and far East Nepal (Terai and Siwaliks) we tried to cover all National Parks and Wildlife Reserves but also other accessable areas including adequate habitats for turtles and other reptiles. A further aim was to confirm taxonomically all records by high quality photographs providing views on dorsal, ventral and lateral sides of the studied specimens together with correlated biometrical data. In a few cases species are already close to extinction and only some bony shell elements obtained from local people could serve for identification. A recentmost listing of proved species known to occur in Nepal was presented in August 1996 at the International Conference on the Biology and Conservation of the South Asian Amphibian and Reptiles in Sri Lanka (see lit.).

During last years´ field activities some turtles could be aquired from local fishermen and were handed over to National Parks or Wildlife Reserves in the Terai for seminatural breeding purposes.

As there is no particularly trained staff available yet, breeding should be organized in a proper way to optimize possibilities for biological observations in seminatural circumstances, to breed and to study reproductive biology, to raise offspring and stocking for release to the wild.

An adequate locality for the realisation of the project could be Koshi Tappu Wildlife Reserve,that is easily accessible, and there are great chances to protect specimens from being slaughtered by purchasing them from the local market. Capture techniques and rates can be studied there in detail and information on the biology of the concerned species can be obtained from the local people and from captivity observations at Koshi Tapu Wildlife Reserve.

A detailed stocking, tagging, breeding and release program may be applied after further research in Koshi Tapu until the end of this year.

At Royal Chitwan National Park and Bardia Wildlife Reserve small scale breeding centers may be established for the locally available specimens to assure species survival and to train park personnel monitoring wild turtles in future.

## Master Plan

Evaluation of Situation in Parks and Protected areas:

The study will characterize turtle populations by species, size distribution, sex ratio, abundance, seasonality, and different habitat utilization

Koshi Tapu Wildlife Reserve

The area is now under tremendous pressure from fisheries based outside the parks. A thorough study shall be the basis to start the proposed project.

Parsah Wildlife Reserve

Due to the Park´s nature only terrestrial turtles are to expect. Data are deficient.

Royal Chitwan National Park

RCNP bears several habitats feasible for terrapins and tortoises. There are records for Emydids and for the testudinids but detailed studies are lacking. The stations in RCNP provide good basic possibilities for further elaborations. The park´s head quarter station could provide good facilities for investigations, training and breeding.

Bairdia Wildlife Reserve

BWR bears several habitats appropriate for terrapins and tortoises. Emydids, possibly a testudinid, and trionychids seem to be prooved but detailed studies are lacking. The park´s headquarter station could provide good possibilities for investigations, training and breeding.

Suklaphantah Wildlife Reserve

SWR is utmost interesting for its still unstudied turtle fauna, being situated in the extreme West of Nepal and thus possibly contributing to the biogeography of Testudines in S-Asia.

Godha Godhi Tal

Yet not established by Nepal´s government but an extremely valuable wetland area that needs most urgently protection status and scientific investigation.

## Brief account of the Master Plan

Biological Studies:

The following biological studies shall be carried out within the frame of the project (dissertation of K. Ernst, others are possible) to collect data and basic knowledge on the biology of the concerned species. It is noteworthy to say that e.g. actually no details are known on the biology of *Chitra indica,* just giving one example as reference for the situation as a whole.

Development and reproductive biology:

- cytology and development of spermatozoa and oocytes, studied in dead caught (fish market) animals
- functional morphology and histology of the reproductive tracts of the concerned turtle species

Knowledge of the function of the reproductive tract of an organism is basic for an understanding of its reproductive output. Studies of the functional morphology and histology of the reprocuctive tracts will yield information on the factors which potentially limit the reproductive output.

- Diet and feeding ecology

There is a considerable lack of information concerning the distribution and abundance of potential food items, detailed analysis of feeding patterns, habitat use and role of the lacustrine system community. Basic information on prey and predation of the concerned species is necessary to evaluate their position in food chains.

Foraging: Diet of the species will be determined by examination of stomach contents obtained from dead caught animals and by stomach flushing of living specimens only if necessary. Data will be analyzed quantitaively and qualitatively to assess the effect of seasonality as well as for turtle size (and sex) on diet. Once the primary food resources are identified, the resources will be mapped.

- Captivity breeding and release into natural enviroments:

We propose to start the project with a study of the reproduction of these turtles in captivity (protected breeding centers in seminatural conditions) and by this way to secure survival of species and organize restocking possibilities.

Captive stocks exist at Bardia WR, Royal Chitwan NP and Koshi Tapu WR. In Royal Chitwan NP considerable success in raising crocodiles and gharials has already been attained, and similar efforts will be made to secure turtle reproduction and restocking. Their biology will be studied in seminatural outdoor enclosures.

Funds are needed to feed, maintain and monitor captive populations until the best time for release comes.

Sex in turtles might be determined by the temperature of the nest during the incubation. Studies on hatchlings and sex ratios in different groups of reptiles have shown that sex rates strongly skewed toward one sex or the other.

- Biogenetical investigations shall document the phylogenetical relations of different populations from East to West Nepal. Genetic analyses using mitochondrial DNA and allozyme electrophoresis techniques shall help to identify the genetic stock within the concerned regions.
- Tagging and marking

To enhance recovery and monitoring efforts, long term tag- and -recapture studies are needed on land and in the water. These studies will investigate species composition, stock identity, seasonality, population structure, sex ratios, growth rates, habitat use and migration. They aid management efforts by:

1. defining important habitats
2. identifying genetic stocks and life history stages
3. determining the location of distant foraging grounds and developmental habitats of turtles
4. promoting insight into population dynamics of turtles
5. identifying the impact of actual rural development, pollution, and other human activities

Fishery activities offer an inexpensive method for a sampling of populations: Size composition, sex ratios, maturity status, reproductive and activity cycles, and genetic composition of populations could be determined from turtles captured by the fishermen.

Survey of turtle eggshell structure using scanning electron microscopy

This study will determine the ultrastructure and composition of turtle eggshells at different stages of development.

Using scanning electron microscopy (SEM) to examine the crystalline and membrane structure of eggshells of different species, it will be possible to define variations between different species but also to get information on the physiology of mature females. Knowledge is lacking about the mineral interaction between the eggshell and the nest enviroment. Evaluation of structural alteration from fresh to weathered eggshell, their trace element content, and nest sand composition will clarify some aspects of the physical and chemical processes during incubation. The results will be compiled in a structural atlas and identification guide to turtle eggshells.

All these aforementioned studies would take advantage of current research programs for turtles in any other country concerning tortoises, terrapins and softshells.

## Protection and conservation

Legislation:

International laws and national legislation should ban the trade and capture of the turtle species from Nepal and enhance the need for governmental protection - as crocodiles, tiger and rhino already do have. Therefore we apply and kindly request support from all concerned authorities to ban turtle catching and killing in Nepal for whatever reason of trade and consumption, but for scientific investigations only until knowledge is extended and completed.

Threat and Overexploitation:

Inland and foreign demand for eggs, meat, shells and other turtle products is high and increasing. One result will be the decimation of local turtle populations due to overharvesting. It is clear that in areas of intensive use (such as the main rivers and their tributaries), turtle populations have been seriously depleted. The results may be the total destruction of these resources.

There is an active turtle fishery in the region by which turtles are captured in nets and with spears or hooked lines and brought to several towns in the vicinity and neighbouring countries to be butchered.

Trade and products:

The goals of this study are to identify: the actual turtle population exploited; the numbers killed in each size class; the average weight of shell obtained from each turtle; the amount of shell used for domestic consumption vs. the quantity exported; the financial dependence of turtle fishermen on this trade; and the trade routes used.

## Management Plan

Population monitoring programm:

The conservation status of these populations will be evaluated and monitored. Necessary management measures are promoted, within the context of a national strategy.

Study of growth rates and population structure:

Growth rates and age at sexual maturity are important parameters for understanding population demography and developing management plans. Using a method recently developed, scute size could also be used to collect data on the size distribution of harvested animals.

Protection of nests; breeding and hatcheries:

In this project, nests will be located and protected against predators and inudation either in situ or by relocation to hatcheries. These must be planned to fulfil the main task of protecting eggs and hatchlings.

Hatching success in hatcheries commonly averages about 50% and is quite variable.

A breeding/hatching program would benefit from a once-a-month visit by a technical expert with the following objectives:

1. Evaluate hatchery procedures and advise on modifications to optimize hatching success.
2. Evaluate incubation temperature and sex ratio of hatchlings and advise on modifications to ensure adequate production of both male and female hatchlings.
3. Evaluate current threats on the shores and develop strategies to protect nests both in situ and ex situ.
4. Train local personnel to continue these evaluations.

The transfer of turtle eggs to a hatchery building or to protected alternative sites on the shores to enhance reproduction may be a suitable management practice for many years. Nest protection programs should be evaluated, and a technical manual produced for the Terai.

## Education and training for public awareness

Education:

A multi-media, culturally adapted enviromental education progam is needed to promote the concept of stewardship of natural resources using turtles as a model. Development of this program will be through cooperative efforts of the National Parks and Wildlife Services and by Universities and the concerned departments of education .

One final goal can be a number of videos describing the life history characteristics of turtles as well as various threats faced by the local turtle populations.

Such a program will also hint at solutions to these threats and show how local students and residents can be involved.

Turtle education media already available should be adapted to Nepal and distributed throughout the school districts. A program to stimulate enviromental awareness among rural school children in concerned areas can be monitored, too. Education manuals should be developed which are concerned specifically with the enviroment in which rural children live.

Nepal´s Wildlife and Park Systems include nesting areas of some of the rarest ( CITES, IUCN) turtle populations in the world.There is great need that the guards in the parks are educated in turtle conservation and management. One or more of the parks of Nepal which enclose turtle habitats could provide valuable education grounds for the park guards.

This programe can benefit from periodic visits by turtle experts who have evaluated the program, recommended improvements, assisted with data analysis, trained local personnel, and assisted in the development of a draft National Turtle Management Plan.

Technical advice at that time may center on the instruction and training of new personnel, conduct training, coordinate data analysis, continue the refinement of the National Management Plan, evaluate all aspects of the programm, and make recommendation that will maintain the program.

Local inhabitants are aware that turtles are becoming rare. They must participate in the development of a conservation program.

The progam will attempt to incorporate turtle fishermen into a turtle conservation program.

Fishermen will be hired to tag turtles, protect nests and record data.

Enviromental education will be provided on a continuous basis for the local people.

Tagging projects should be continued, and an educational campain is needed to secure the cooperation of fishermen who catch the turtles but do not return the tags for fear of penalties.

Technical Training and Information Exchange

The methodology will accompany the one developed on nesting grounds, in which fishermen and biologists work together to protect the turtles.

Fishermen who usually set nets at lakes or rivers can be hired to rescue the turtles and, if necessary, to change the position of their nets.

Fishermen will work as local guards, and the programe will also train local university students.

A technical workshop is needed which involves appropriate government officials from all concerned representatives of the fishing industries, forest industries, the Department of Biology the University and the National History Museum and National Parks and Wildlife Reserves.

Increased communication among peolpe who work with turtles in South Asia shall be one of the final aims of the project. A conference of such persons would increase the effectiveness of turtle management in the region.
We propose to convene at a conference, to which representatives from India, Bangladesh, Myanmar and Pakistan would be invited.

Collaborations with other scientists:
Nominations will be recommended after approval of the project.

Acknowledgements

We are grateful to Mrs. K. Ernst for discussions and contributions.

# Disastrous Impact of Intestinal Infection in Captive Bred Gharial Hatchlings

**Maskey, T.M*., Kölle, P**., Hoffmann, R**., Anders, C.C.*****
**& Schleich, H.H.******

**Key words**: *Gavialis gangeticus*, Parasites, Nepal

## Material and observations

Since 1978 gharials (*Gavialis gangeticus*) are bred under seminatural conditions in the Royal Chitwan National Park, South Nepal. The aim of the breeding program is to assure a self-sustaining stock of wild gharial populations in the main river systems of Nepal where gharials were almost completely extinct by human impacts, mainly the construction of barrages and dams. Furher information about the situation of the gharial in Nepal is given by Maskey (1989) and Maskey & Schleich (1992).

The first batch of artificially raised gharial hatchlings were released into the Narayani River in 1981. Later, more than 400 hatchlings were released in the different river systems of Nepal as Koshi, Kali Gandaki, Narayani, Babai and Karnali rivers. During last three years gharials were bred successfully in captivity at Royal Chitwan National Park. Between 25 and 80% of the captive gharial hatchlings died within the first year of their life (Maskey, 1989). Most of the hatchlings (12-36%) died within three months. In the nursery the major causes of mortality of the neonates were necrotizing skin desease (Jacobson, 1982), neurological disorders, bloated stomach and prolapse of the rectum.

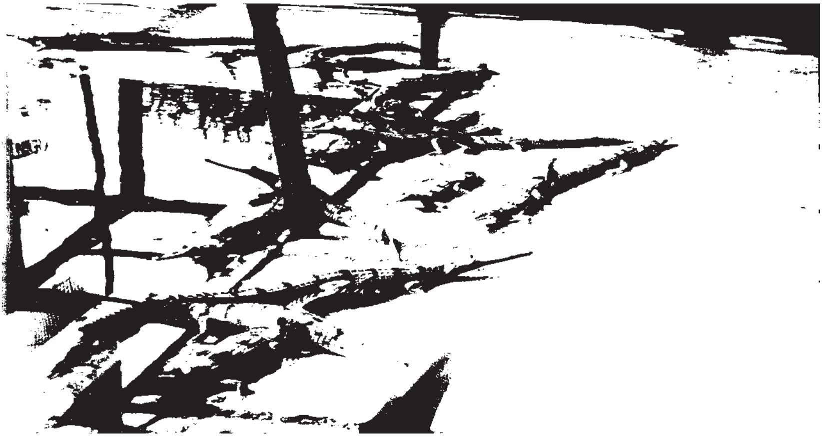

**Fig. 1.** Gharial hatchery in Royal Chitwan National Park, Nepal.

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Some of the last year´s hatchlings were observed carefully to study the causes of death. Postmortem they were dissected and studied. The first symptoms in the neonates arose some weeks after hatching and the juvenile gharials began to suffer from starvation and developed other unspecific symptoms, became apathetic and finally died.

An examination of the last perished specimen in January 1997 yielded the following results:
The male hatchling had a total length of 41.5 cm and weighed 55 g. The dissection showed mainly submiliar white stipples in the myocard and plenty of approximately 5 mm long white nematodes in the parenchyma of the heavily swollen kidneys. The liver was of olive colouration and of rather tough consistency. The pulmonary walls seemed to be thickened.

The histological examination showed a myodegeneratio cordis with swelling of myocytes and hyperchromatic or fragmented nuclei, pulmonary oedema, a fatty degeneration of the liver which was irregularly infiltrated by melanomacrophages especially around blood vessels and iliary ducts.

The bacteriological investigation proved *Flavobacterium indologenes* and *Citrobacter freundii* which have to be considered as only facultatively pathogenic germs. They also are found often in clinically healthy or unaffected animals.

The resistance test with antibiotics yielded highest effectivity of Enrofloxacin. Surprisingly massive resistances against other common antibiotics e.g. Tetracycline, Chloramphenicol and Neomycin existed yet. Whether the germs posess already a high natural resistency, as it is known eg for *Pseudomonas* spp., or whether this is already due to previous treatment with antibiotics is difficult to decide without knowing about earlier medication.

## Discussion

Myodegeneratio cordis in vertebrates is very often caused by deficiency of vitamin E not rarely in combination to lack of selenium. This could have been provoked by feeding with fat or /and rotten food fish. The results found for the liver also support this view. On the other side, the high amount of melanomacrophages in the liver indicates a chronic process including infections or parasitic invasions. The documented nematodal invasion could be an explanation for this reaction.

The still unidentified nematodes in the kidneys cause also local inflammations, hampering the function of the organs.
It is unknown if the nematodes are transmitted directly between the gharials or more probably by an intermediary host (e.g. fishes). Affected animals can be treated with a nematocide (e.g. Levamisol) and injections of vitamin E.
An appropriate prophylaxis is of greatest importance. Only fresh, if possible live and not too fat fish should be used as food. In order to interrupt a direct transmission of parasites between conspecifics food fish should be caught in waters where no gharials live.

Interesting to our results seem further mentionworth the following references:

| **author** | **crocodile/host** | **organs** | **parasites** |
|---|---|---|---|
| **Helminthic diseases** | | | |
| Maplestone (1930) | *Gavialis* | stomach | *Multicaecum* sp. |
| Maplestone (1930) | *Gavialis* | intestine | *Polycaecum gangeticum* |
| Maplestone (1930) | *Gavialis* | stomach | *Goezia gavialidis* (perhaps accid. in gharial, = fish parasite) |
| Baylis (1923)* | *Gavialis* | —— | *Dujardinia woodlandi* |
| Baylis & Daubney (1922)* | *Croc. porosus* | stomach | *Dujardinia helicina* |
| Bhalerao (1935)* | *Croc. porosus* | stomach | *Multicaecum agile* |
| Linstow (1906) | *Gavialis* | mesentery | Filaria: *Micropleura vivipara* LINST. |
| | | stomach | Resorbentes: *Typhlophoros lamellaris* LINST.<br>*Ascaris* indet. |
| | | trachea/lungs | Linguatulidae: *Porocephalus indicus* LINST. |
| **Bacterial diseases** | | | |
| Jacobsen (1982)* | *Gavialis* (hatchling) | —— | *Clostridium* sp. |
| Report Vet.College,* Bhubaneswar | *Gavialis* | skin | *Klebsiella* sp.<br>*Staphylococcus* sp.<br>*Escherichia coli* |
| Arora & Kumar (1985-90)* | *Gavialis* (hatchling) | skin | *Aeromonas hydrophila* |
| Arora & Kumar (1985-90)* | *Gavialis* (hatchling) | digestive system | *Corynebacterium bovis*, *Pseudomonas aeruginosa*, *Escherichia coli* |
| Arora & Kumar (1985-90)* | *Croc. porosus* | oral cavity | *Aeromonas salmonicida* |
| **Mycotic diseases** | | | |

| | | | |
|---|---|---|---|
| Parihar (1979)* | *Gavialis* (hatchling) | skin | *Trichophyton mentagrophytes* |
| Arora (1987)* | *Gavialis* (hatchling) | buccal<br>snout | *Aspergillus flavus*<br>*Aspergillus niger* |

* = source: Arora (1994).

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# Fossil Microreptiles from Pliocene Siwalik Sediments of lndia

Rajeev Patnaik* & H.Hermann Schleich**

**Key words**: Fossil Squamates, Pliocene, Palaeoecology, Siwaliks-India

**Abstract**: Jaw fragments belonging to agamid and possibly scincid lizards have been recovered from Pliocene Siwalik sediments exposed near Chandigarh. Except *Uromastyx*, this is the first report of fossil agamids and scincids from the Indian subcontinent. Based on their present distribution and habitat it is presumed that these lizard bearing Pliocene sediments were deposited under semiarid to arid conditions.

## Introduction

Our studied collection of microreptlies comes from four localities in the Upper Siwaliks being exposed in the Chandigarh-Nahan Area (Fig.1). Palaeomagnetic studies have been carried out in Markanda and Nadah sections (Aziaroli and Napoleone, 1982). Extrapolating from ages of tuffaceous mudstones palaeomagnetic dates and sedimentation rates Kanthro, Ghaggar and Nadah localities have been considered here to be around 2.5, and 1,8-2 m.y old respectively.

Based on faunal similarity with Ruscinian deposits of Afghanistan an Upper Ruscinian age (3.5-4.5 m.y.) is assigned to the Moginand locality (Patnaik, in press).

The mudstone layers at GI and GII (Ghaggar section) have yielded evidence for pedogenic modifications under arid conditions. They lack organic matter, contain calcareous concretions and at places are intercalated with carbonate rich bands. The sediments of Ghaggar river section have heen compared with recent deposits of arid Central Australia on the bases of presence of high percentage of overbank deposits in individual cycles, lacking vegetal matter, organic poor palaeosol and abundance of syngenetic CaCO3 (Kumar and Tandon, 1985). The microvertebrate yielding beds at Nadah have been placed in 'Bluish grey mudstone facies' of Kumar and Tandon (1985). These grey mudstones contain ferrugenous and calcareous nodules, molluscan shells, bioturbation products and are capped by around 15 cm thick nodular calcium carbonate band indicating presence of shallow seasonal pools of limited lateral extent. Occurrence of tabular, variegated colored units with wide aerial extent, general absence of bedding, presence of microtopography at their contacts, Fe, Ca, AI rich nodules, mottling and bioturbation products at Kanthro and Moginand localities has been interpreted as pedogenic modifications (Patnaik, 1995).

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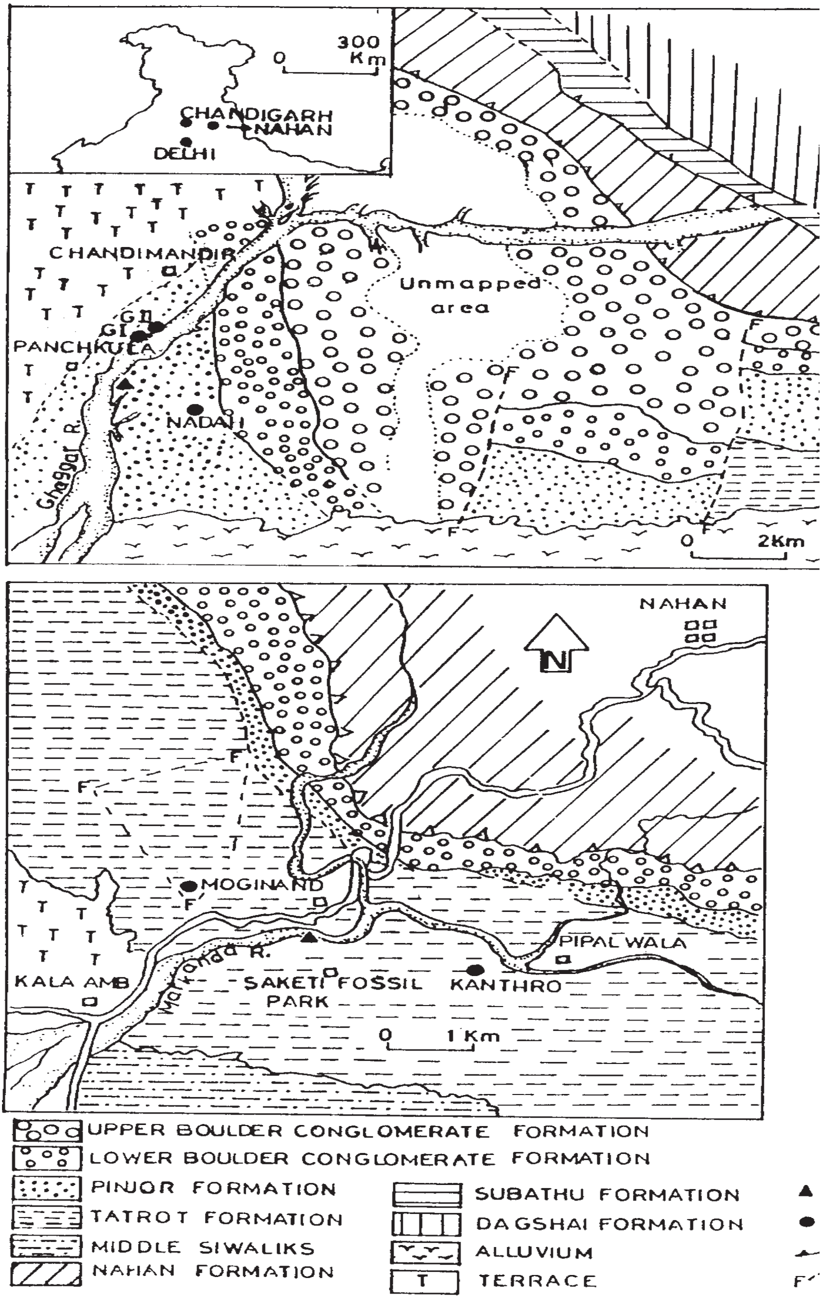

**Fig. 1a**. Geological maps showing fossil localities E of Chandigarh and SW of Nahan; modified from Kumar & Tandan (1985) and Patnaik (1995).

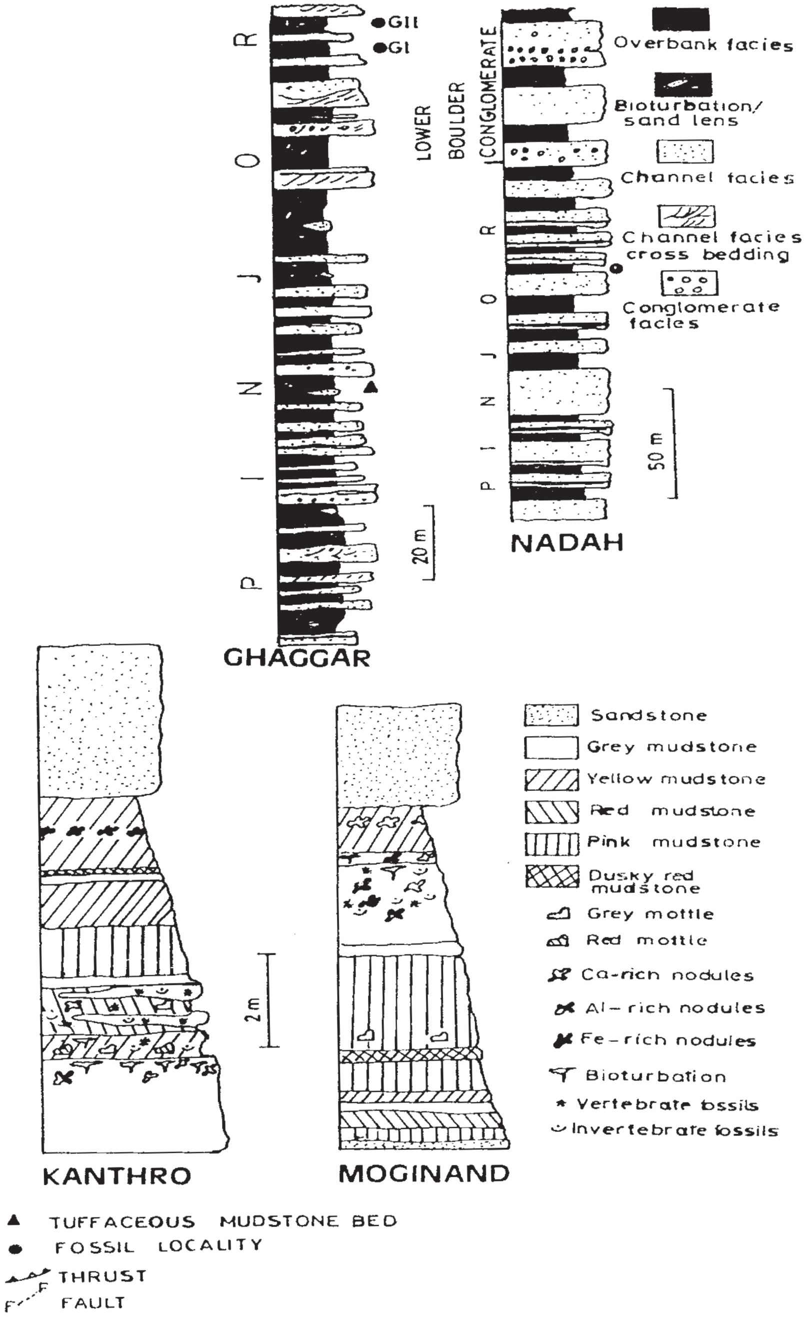

**Fig. 1b.** Geological sections showing fossil bearing horizons E of Chandigarh and SW of Nahan; modified from Kumar &Tandon (1985) and Patnaik (1995).

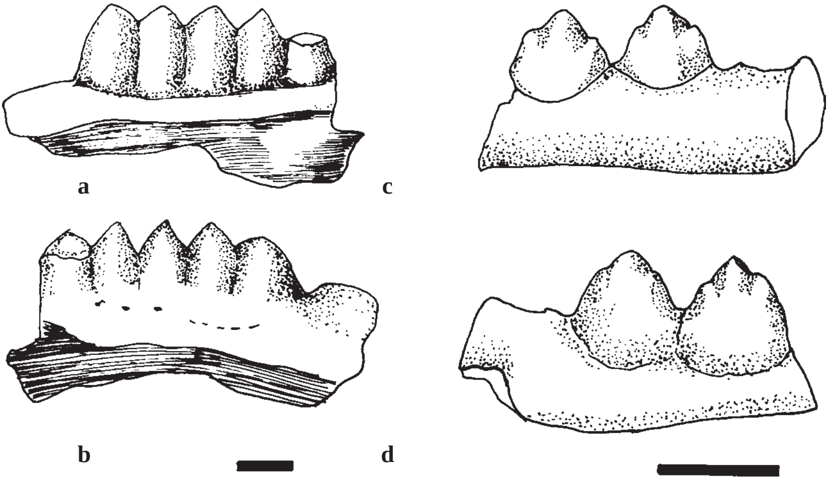

**Fig. 2 a,b**. Labial and lingual views of mandible of *Uromastyx* sp.(VPL/RP-L1) C&D, (VPL/RP-L2), labial and lingual views of mandible of *Calotes* sp. Bar represent 1 mm.

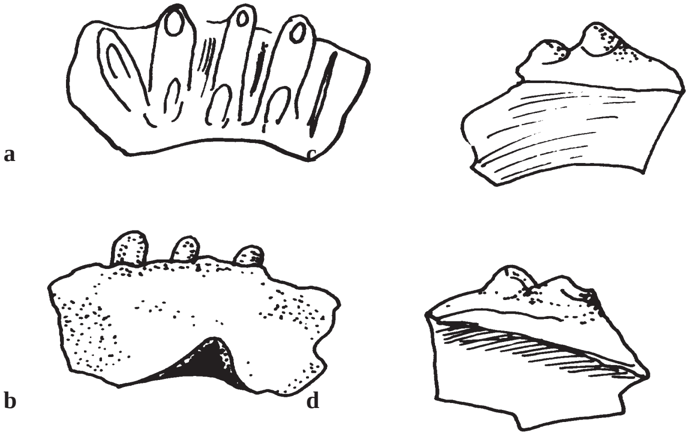

**Fig. 3 a,b.** Lingual and labial view of maxillae of Scincidae indet (VPL/RP-L$).
**c,d**: labial and lingual view of mandible of an agamoid lizard. Bar represents 1 mm.

## Systematic Identification

### *Uromastyx* spec. indet.

Compared with jaw material of extant *Uromastyx hardwicki* in fig. 2a/b is shown a broken fragment of a dextral maxillary. There are four complete and one broken tooth on the jaw fragment. The material is stored at Centre of Advances studies in Geology, Panjab University, Chandigarh (Coll. Nr. VPL/RP-L1)

### *Calotes* spec. indet.

The specimen from fig. 2c/d allows a taxonomic approximation to *Calotes* sp. indet. The fossil bears only two teeth on a fragmerntary jaw bone not to identify whether it was a maxillary or dentary. The way how the lateral accesorial lobes or cusps are arranged aside the central cusp makes this determination rather probable.

### ?Scincidae indet.

We would tend to interprete the fargmentary premaxillary bone with unicuspid teeth propably belonging to a scincid lizard.

There is also much uncertainty whether the illustrated jaw fragment (fig. 3c,d) might belong to an agamid or chamaeleonid lizard. Several other teeth fragments are due to its bad state of preservation not further to identify.

## Discussion

This fossil record of a *Uromastyx* is the second one from India. Another jaw was described by Raghavan (1991) as a new species. We think the study of latter material does not rectify a new taxon. *Uromastyx*.

For the genus *Calotes* we are not aware of any other fossil records hitherto known in its distributional range.

The occurence of both taxa still extant in India allow to interprete palaeoecologically rather dry semidesert to desert areas with scarce vegetation.

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Veröffentlichungen aus dem Fuhlrott-Museum, 1998, Bd. 4: 301-306

# Late Cretaceous Gekkonid Egg Shells from the Deccan Intertrappeans of Kutch (India)

Sunil Bajpai*, Ashok Sahni** & H.Hermann Schleich****

**Key words**: Fossil Eggshells, Reptilia-Squamata, Gekkonidae, India

**Abstract**: The Deccan intertrappeans of Kutch have yielded the remains of dinosaurs (skeletal elements, teeth and eggshells) as well as the remains of gekkonid eggshell fragments along with pelomedusid turtle material. The present paper describes the lizard material in the context of existing stratigraphic constraints.The gekkonid eggshell material is preserved and documents the earliest records of geckonids from the Upper Maastrichtian. The eggshells show characteristic wedge-shaped spheroliths which have been documented for the eggshell fragments of Nagpur. Pore canals are not very common but individual pores are fairly frequent on the outer surface and in the upper part of the eggshell and are circular in shape. The wedge-like spheroliths extend throughout the whole shell and are characterised by horizontal accretion lines. A mammillary layer is well developed and shows the presence of numerous mammillae.

## Introduction

The Kutch intertrappeans represent the westernmost extension of the Deccan-volcano-sedimentary sequence of the Deccan Trap Province of India. In general these outcrops were poorly known and have been studied more intensively only recently by Ghevariya & Srikarni (1990,) and Bajpai (1990ff). Recent work has demonstrated (Bhandari et al. 1995, 1996) the presence of an iridium anomaly at the Anjaar section in southern Kutch. The iridium anomaly in conjunction with radiometric dating based on Ar40/Ar 39 data suggests that the Anjaar section is close if not coincident with the Cretaceous-Tertiary Boundary and may indicate one of the last records of dinosaurs in India. In fact, teeth and eggshell fragments of ornithischian dinosaurs have already been reported (Bajpai et al., 1990). Here we report the presence of lizard eggshells which are of fairly common occurrence along with the eggshells of ornithischian or avian morphostructural types.

There are four intertrappean sections which have been studied in detail (Bajpai 1990ff). Several hundred kgs of sediment was screen-washed to recover microvertebrates including the gekkonid eggshell fragments described here. The principal localities are at Kora, Lakshmipur, Dayapar and Anjaar, the stratigraphic and geographic details having been given by Bajpai et al (1990).

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## Systematic description

Lizard (gekkonid eggshell fragemnts)

In 1984, Sahni et al. described the presence of thin eggshell fragments from the Takli Formation at Nagpur representing the first report of thin eggshell fragments from the Latest Cretaceous of India. While some of the described eggshell morphotypes were assignable to the dinosaurs, others were of uncertain affinity.These latter kind of eggshells were tentatively related to the gekkonids by Hirsch & Packard (1987). The present work conclusively demonstrates their lacertilian (gekkonid) affinities by comparing their morphostructure to their modern-day counterparts. It is worthy to note that in the microvertebrate assemblages recovered by screen-washing from the Kutch intertrappean localities, several associated elements of lacertilia (skull fragments, jaws and vertebrae) have beeen found. The presence of lacertilian eggshell fragments in the intertrappean sediments is therefore not unexpected.

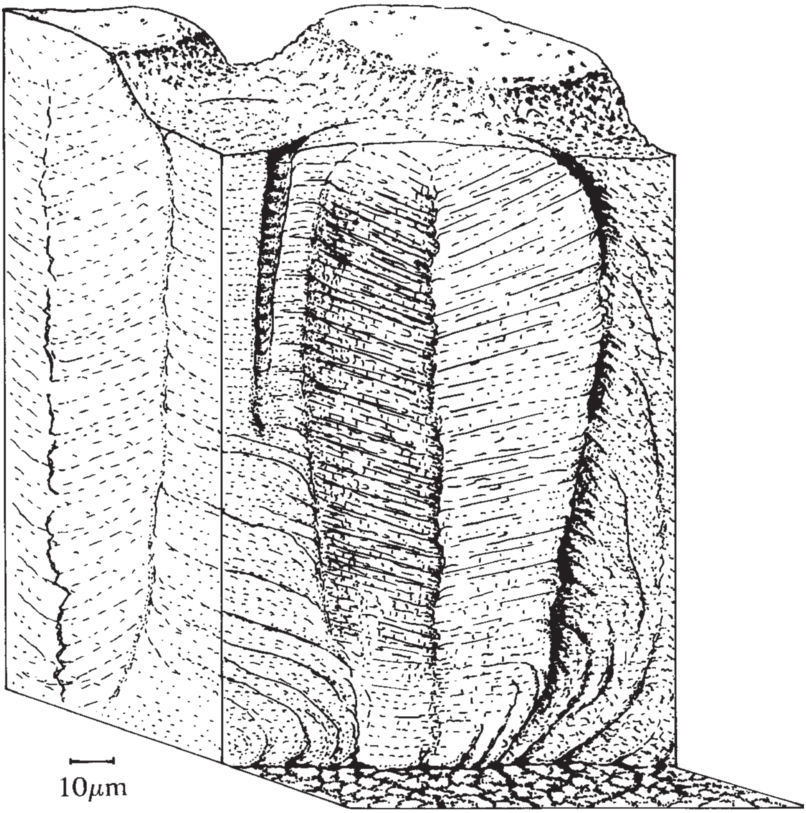

**Fig. 1.** Cross section of gekkonid eggshell from Kutch

**Fig. 2**

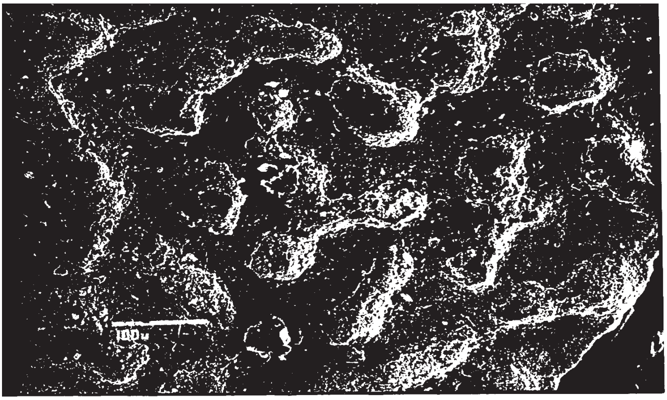

**Fig. 3**

**Fig. 4**

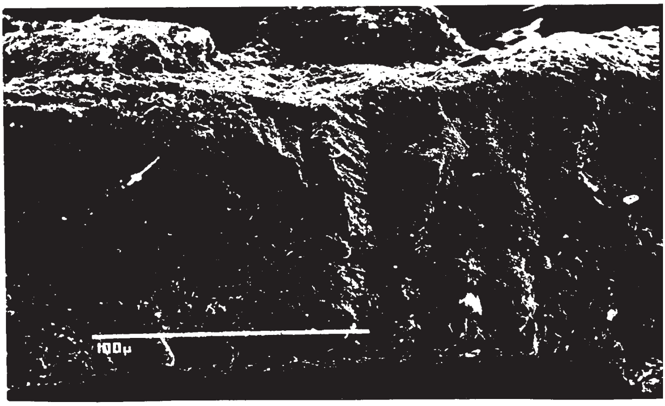

**Fig. 2.** Outer shell surface; x 210.SEM photographs (figs. 2-7)
**Fig. 3.** Inner shell surface; x 2000.
**Fig. 4.** Cross section; x 560.

**Fig. 5**

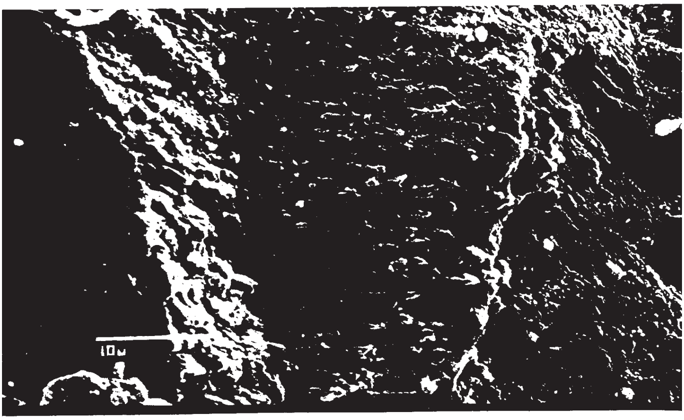

**Fig. 6**

**Fig. 7**

**Fig. 5.** Detail of cross section, outer range; x2800.
**Fig. 6.** Detail of cross section, middle part; x2300.
**Fig. 7.** Deatil of inner surface; x2700.

The outer surface is ornamented, this feature being in contrast to most modern lizards (see Schleich & Kästle, 1988) which have a smooth surface. It was this character which hindered the identification of the eggshell material from India for a long time. However, ornamentation is only one feature which has to be considered together with several others for making a taxonomic assignment. The ornamentation is best illustrated in (fig.2). It consists of isolated and coalescing tubercles surrounded by a fairly flat matrix. Usually the isolated tubercles may vary in size from about lesss than 100 μ to over 200 μ in diameter. The coalesced tubercles form ridges comprising either two or more tubercles which can be observed by their more rounded outlines. The coalescing tubercles may be 300 μ or longer and are somewhat curved in orientation. The groundmass has pores of variable density (more than 20 pores/100 $\mu^2$). This number is estimated on the lower side as the matrix may cover more pores. A close-up of the pore distribution of the outer surface shows the presence of densely spaced pores of apparently different diameters though in general these tend to be circular and 1μ or less in diameter. At least on the surface, the pores seem to be interconnected (fig.3). Some small pores can be seen at the bottom right of the micrograph. A radial section across one of the isolated tubercles again demonstrates the interconnected nature of the pores (fig. 4).

One of the most characteristic features of gekkonid eggshells (Schleich & Kästle, 1988, Schleich unpubl.) are the wedge-shaped spheroliths which extend radially from the mammillary surface outwards. The shell thickness inclusive of the tubercles ranges around 170 μ while along the smooth outer surface it is about 130-140 μ. Usually the spheroliths from the Kutch intertrappeans are about 20-30 μ in width but towards the outer surface may be double this size.

The material is well preserved and allows a detailed analysis of the structural blocks: the principal mineral is calcite though it cannot be determined whether this is a diagenetic effect or this represents the original constituent of the eggshell. The crystallites are tabularly arranged in rows about 3-4 μ apart. The pores are clearly visble on this surface as well and suggest the well aerated and spongy nature of the spheroliths. (figs. 5, 6).

The mamillary layer is developed only on the inner surface and consists of rounded mammillae of variable size (fig. 7).

A schematic sketch showing the structure of the Late Cretaceous Kutch gekkonid eggshell is given in fig. 1.

## Remarks and conclusions

Eggshells, both recent and fossil are becoming better known and provide useful information on the taxonomic affinities of those animals that produce calcified eggshells. They can also be used for palaeoecological reconstructions because thin eggshells cannot be transported over great distances and therefore their presence indicates the suitability of nearby nesting environments. Rösler (1995) lists the following modes of oviposition for modern gekkonid taxa: eggs are interred into sand or earth; they can be deposited on the ground below stones or logs, or laid into fissures of rocks or bark. Gluing eggs to the rock or wood substrate is considered the most advanced method. *Tarentola* species combine two methods: sand grains are glued to the hardening, freshly laid eggs, which are then covered with sand.

A correlation between egg-laying mode and shell thickness has been noted in a few studied species the interred eggs had thinner shells than exposed ones.

It must be mentioned that several gekkomorph taxa lay soft-shelled eggs: Eublepharidae and Pygopodidae including Diplodactylinae. The only Lepidosaurian family with hard-shelled eggs besides the Gekkonidae are the insufficiently studied Dibamidae which today are limited to the Indo-Australian region.

The presence of gekkonid eggshells along with other thin shells of the ornithischian or avian type suggests that small reptiles were fairly common components of the Latest Cretaceous intertrappean faunas.

Acknowledgements: The authors are grateful to Dr. W. Kästle for drawing the cross section of fig. 1.

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# Reptilia from the Intertrappean Beds of Bombay (India)

Swaran D. Singh*, Ashok Sahni**, Eugene Gaffney***
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**Key words**: Reptiles, Cretaceous, Deccan Intertrappean, Pelomedusid, crocodile egg shell

**Abstract:** Fossil record of pelomedusid turtles is extremely rare in India. Recent systematic investigations of Deccan volcano-sedimentary sequences exposed at Malabar and Worli Hills and Amboli Quarry, Bombay have yielded a well preserved turtle skull, few crocodilian eggshell fragments and fragmentary teeth from tuff beds. Crocodilian eggshell fragments are described for the first time from any intertrappean locality of peninsular India. These elements are found associated with fossil frogs and ostracodes in the Late Cretaceous (Maastrichtian) intertrappean beds rich in pyroclastic material.

## Introduction

The Bombay Deccan basalts and the fossiliferous intertrappean beds have excited interest for nearly a hundred and fifty years. Of late, there has been a sudden revival of interest in various aspects of this volcanic activity such as its age, duration and paleoenvironment primarily due to the consideration that the Deccan volcanism might have played a major role in the Late Cretaceous mass extinctions (Officer and Drake, 1983, 1985; Courtillot et al., 1986; Courtillot, 1990). The crucial paleontological evidence in this regard is provided by the fossil biota recovered from the sedimentary sequences, infratrappean and intertrappean, associated with the Deccan volcanic flows, now collectively termed as Deccan volcano-sedimentary sequences (Sahni et al., 1994).

The Bombay traps represent the waning phase of the Deccan volcanic activity, and the contained intertrappean beds, unlike their counterparts in the other infra- and intertrappean localities of peninsular India such as Jabalpur, Nagpur, Asifabad, Kutch, Gurmatkal etc., are rich in pyroclastic material suggesting their proximity to the volcanic source. The intertrappean beds exposed at Malabar and Worli Hills and at Amboli Quarry are represented by lithic and vitric tuffs and black carbonaceous shales deposited under alkaline marshy conditions (Singh, 1995).

There are differing views regarding the age of Bombay trapps and the contained intertrappeans. Chiplonkar (1940) assigned an Early Eocene age to the intertrappean beds of Worli Hills containing fossil frogs. Mathur (1968) based upon a lone specimen of *Scylla serrata* (supposedly from an intertrappean derived boulder) assigned a much

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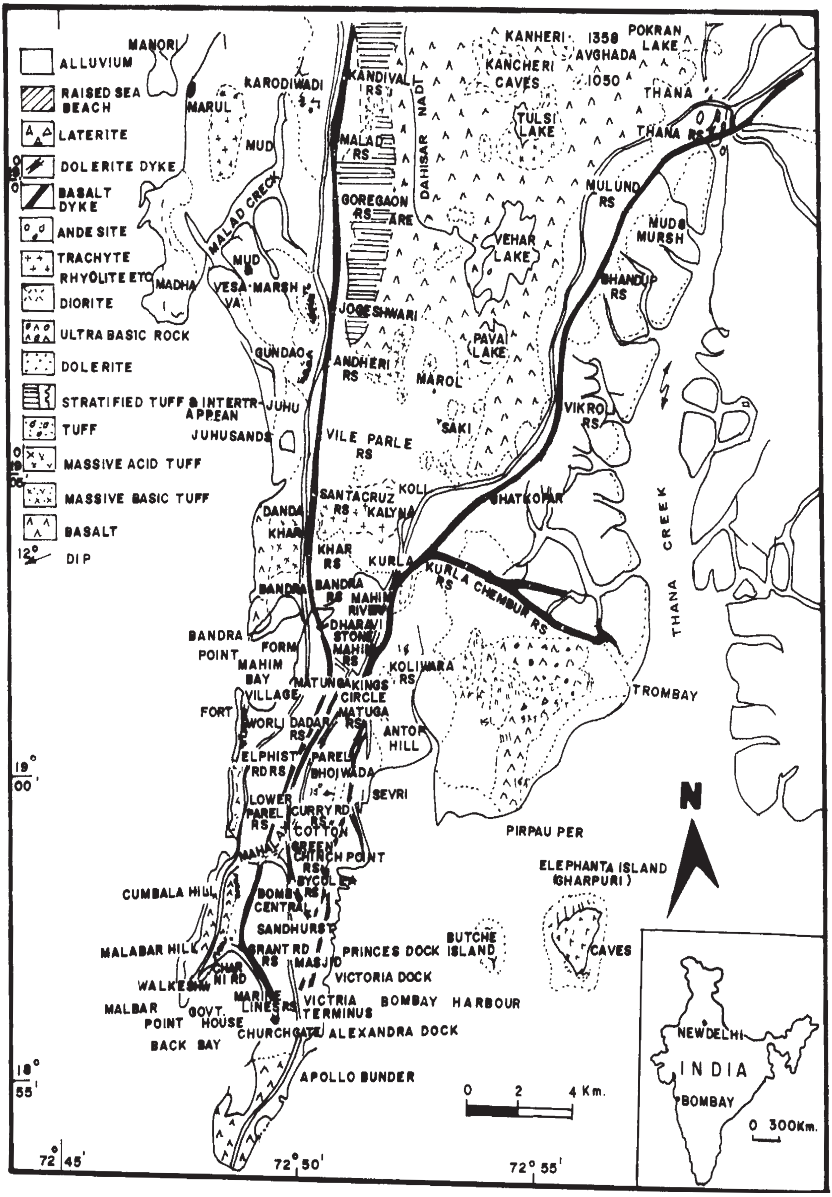

**Fig. 1.** Geological map of the fossiliferous outcrops around Bombay area

younger age to these beds since *Scylla serrata* has a range from Oligocene to Recent. Recently, Singh & Sahni (1996) reported an ostracode assemblage: *Altanicypris-Cyprois-Cypridea* (*Pseudocypridina*)- *Mongolianella-Timiriasevia* from the intertrappean beds of Bombay and assigned a Late Cretaceous (Maastrichtian) age to these beds.

Work on the intertrappean beds of Bombay area was initiated in the mid nineteenth century with the report of a fossil frog *Rana pusilla* by Owen (1847) from the Worli Hills. Later investigations of intertrappean beds of Bombay led to the reports of ostracodes, a turtle skull and fossil frogs from these beds (Carter, 1852; Noble, 1930; Chiplonkar, 1940; Williams, 1953; Verma, 1965 and Singh and Sahni, 1996). The present paper deals with a turtle skull, crocodilian eggshell fragments and fragmentary teeth recovered as a part of the research program initiated around ten years back which led to a large collection of fossil frogs, ostracodes and turtle carapace fragments along with these elements from the intertrappean beds of Bombay (Fig. 1). The entire collection is housed at the Vertebrate Paleontology Laboratory, Centre of Advanced Studies in Geology, Panjab University, Chandigarh, India.

## Systematic description of the fossils

Class Reptilia
Subclass Archosauria
Order Crocodylia
Suborder Eusuchia
Family Crocodylidae Cuvier, 1807

### Gen. et sp. indet.

Material: SDS/VPL 1101, a broken crocodilian tooth fragment (Pl. 1, fig.a)
Horizon and locality: Green tuff bed of the Worli Hill Section, Bombay.

Description: SDS/VPL, 1 101, a conical tooth of crocodile is broken with only the basal part presented (Plate la). The surface of the tooth bears longitudunal striations which are parallel to each other. Basal section of the tooth is circular. The diameter near base is 6.0 mm. It is possible that the tooth with identical morphological features previously referred to the shark genus *Oxyrhina* (Sukheswala, 1953: fig. 15) is actually crocodilian.

### Crocodylia indet.

Crocodilian eggshell fragments (Pl. 1, fig. b-f; Pl. 2, fig. a-c)

Eggshell fragments of crocodilian affinity are hardly reported from India. Recently, Patnaik and Schleich (1993) reported some crocodilian eggshell fragments from Upper Siwalik sequences of Saketi and Moginand along the Markanda River in Himachal Pradesh, India. Records of crocodilian eggshells from the other parts of the world are also very scarce. Heller (1931) reported crocodilian eggshells from the Eocene Soft Coal Beds in Geiseltal (Halle, Germany). Erickson (1978) described an eggshell of crocodilian affinity from the Upper Cretaceous of Wyoming, USA. Hirsch (1985) described four crocodilian eggshells from the Eocene of Colorado, USA and erected a new genus and species *Krokolithus wilsoni*. Hirsch & Quinn (1990) reported an eggshell fragment of doubtful crocodilian affinity from the Upper Cretaceous, Two Medicine Formation of Montana, USA. Present investigations of Bombay intertrappeans have yielded around 16 eggshell fragments from Malabar and Worli Hill localities. Some specimens have been studied using scanning electron microscopy.
Material: Figured specimens SDS/VPL 1201 to 1206 and ten other well preserved eggshell fragments.

Horizon and locality: Green and greyish tuff beds of the Malabar Hill Section and green tuff bed of the Worli Hill Section, Bombay.

Description:
The average thickness of crocodilian eggshell fragments recovered from the two localities, Malabar and Worli Hills, Bombay is 350 µ. In general the eggshell fragments are well preserved, whitish in colour and in some cases have undergone some degree of calcitic recrystallization. The internal surface of the eggshell is composed of discrete mammillae (Plate 1: b, c, d, e), and the external surface of the eggshell fragments is smooth marked by shallow pits, and in some cases shows dissolution structures (Plate 1: f). The pits are circular and show resolution of the tabular crystallites leading at places to a localised rough and reticulate ornamentation. The diameter of the pits is about 4 µ.

Most of the Bombay crocodilian eggshell fragments have a similar morphology. Towards the external side the spheroliths coalesce to from a very distinct, fine horizontal banding, and towards the external mammillary side the spheroliths appear to be more distinct and diverging (Plate 2: a, b, c). The fine horizontal layering consisting of fine, tabular crystallites is clearly visible. The tabular structure can be traced over large distances of the eggshell structure especially near the external surface. At places (Plate 2b), there appears to be a superposition of calcitic overgrowth with layers intersecting at angle which approximately corresponds to that of the calcite cleavage suggesting a certain degree of recrystallization.

In general, the width of the fine layers is 1,0 µ. The horizontal tabular zone constitutes nearly one third of the entire thickness of the eggshells. The upper zone leads internally to distinct spherolitic structures again composed of tabular crystallites (Plate 2: a, b, c). The spheroliths are broadly wedge-shaped and distinct from one another, coalescing at approximately one third of the thickness of the eggshell. At the point where adjacent spheroliths intersect, a small fine canal occurs (pl. 2: c). This fine canal may extend externally and link up with the larger pore canal represented by a pit on the external surface.The average width of spheroliths is about 75 µ.

## Order Cheloni

Family? Bothremydidae
Genus indeterminate

Material: SDSNPL 1125, a dorsoventrally flattened skull (Pl. 2, fig. e,f)

Horizon and locality: Green tuff bed of Amboli Quarry, Jogeshwari, Bombay.

Description: The dorsal view of the skull shows extensive temporal emargination which seems to be original. An undescribed bothremydid turtle (fig. 2-3) from the Kalamedu Formation also shows extensive temporal emargination, but most other bothremydids are well roofed. The characteristic bothremydid anterior-facing stapedial canal is not determinable.
In ventral view the triturating surfaces have a well developed labial ridge with two accessory ridges. This condition is not found in any shweboemydines nor in any other bothremydids. *Podocnemis* has a large labial ridge with accessory ridges but the skull is much narrower.

There is no medial expansion forming a secondary palate as in shweboemydines. The large internal nares are visible at the anterior part of the palate rather than being extensively covered by the palatines and pterygoids as in shweboemydines. The processus trochlearis oticum is preserved on both sides, demonstrating that the skull is a pelomedusoid (formerly Pelomedusidae). The enlarged carotid/pterygoideus chamber of Podocnemididae appears to be absent, although the area is crushed. The position of the foramen posterius canalis carotici interni is not deterninable.

## Discussion

Due to poor preservation, certain key characters defining the various pelomedusoid groups are not determinable. However, the palate and skull roof strongly suggest the Bothremydidae. If this is the case, the triturating ridge arrangement and skull proportions are unlike any described form and the skull may represent a new species. An undescribed skull from the Kalamedu Fonnation shows that the Bothremydidae were present in India.

The material described as „*Carteremys (Testudo) leithii*“ no longer exists as far as anyone can tell. The available descriptions of the skull are too vague to be useful in modern systematics. The shells of pelomedusoids are notoriously conservative and rarely reveal characters useful above the species level. Consequently, „*Carteremys leithii*“ should be considered a nomen dubium, and ignored.

## Conclusions

A turtle skull is being reported after having been discovered nearly a century and half ago from the Late Cretaceous (Maastrichtian) intertrappean beds of Bombay. The only other turtle find from the intra- /intertrappean beds *Shweboemys pisdurensis* originates from the Late Cretaceous Pisdura sediments of Central India. Living pelomedusids are restricted to South America, Sub-Saharan Africa and Madagascar. Extant pelomedusids are confined to fresh-water however, the previous fossil record shows that they inhabited marine, fresh water and terrestrial environment. The intertrappean beds of Amboli Quarry, Bombay yielding our fossil turtle remains might indicate a marshy environment of deposition for these beds.

## Pelomedusidae indet.

## Description of a fossil pelomedusid shell from Worli Hills, Bombay

Material: Sarketi Fossil Park; cast is deposited at Inst. Palaeontology, Univ. Munich.

The shell is extremely flattened due to diagenetic processes, and with a crack running across its full posterior width. Due to this compaction the areas of the axillary and the inguinally buttresses are rather disturbed and thus hinder a thorough description. Also the peripherals (between those buttresses) of the bridge are lacking.

The general habitus is of pelomedusid type. The description uses german terminology of shields and plates.

### Carapax (fig. 6)

The general shape of the carapax is oval, slightly widened at the height of peripheral 7. The distal margin of the posterior peripherals might have been slightly undulated. Pleurals 6-8

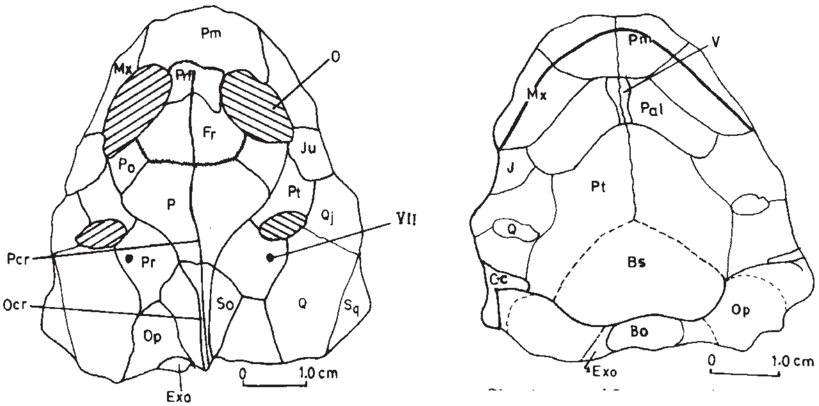

**Fig. 2,3**: ?Bothremydidae indet., view of skull (SDSNPL 1125) from Bombay; left (fig. 2) dorsal, right (fig. 3) ventral.

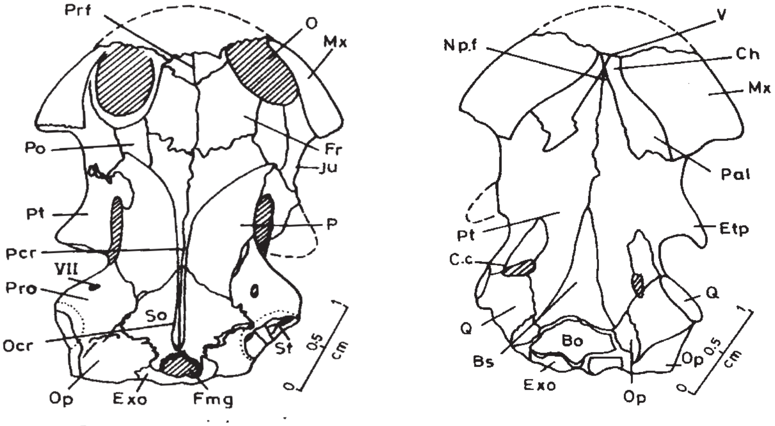

**Fig. 4,5**: *Carteremys pisdurensis*, skull, holotype (ISI R 200) from Pisdura, India (after Jain, 1977); left (fig. 4) dorsal view, right (fig. 5) ventral view.

Abbreviations used in Figs. 2-5:

| | | | | | |
|---|---|---|---|---|---|
| Bo | Basioccipital | Bs | Basisphenoid | Cc | Carotid canal |
| Exo | Exoccipital | Fmg | Foramen magnum | Fr | Frontal |
| Ju | Jugal | Ch | Choana | Etp | Ectopterygoid process |
| Mx | Maxilla | Np. f | Nasopalatine foramen | O | Orbit |
| Ocr | Occipital crest | Op | Opisthotic | P | Parietal |
| Pal | Palatine | Pcr | Parietal crest | Prf | Prefrontal |
| Pm | Premaxilla | Po | Postorbital | Pr | Prootic |
| Pt | Pterygoid | Q | Quadrate | QJ | Quadratojugal |
| So | Supraoccipital | St | Columella auris | V | Vomer |
| VII | Foramen for stapedial artery | | | | |

are in direct contact, without intercalated neurals. The first pleurals contact each other and also the nuchal directly. The first neural is intercalated between pleurals 1 and 2. There exist 4 neurals of that typical elongate hexagonal shape with shorter lengths at their anterior sides. Neural 5 might already have been the last one and is placed between pleurals 6 and pleurals 7.

### Scalation

It is difficult to say whether a cervical was developed, but it can be assumed that there was a small one. The central 1 is bowl-shaped, without corners. Centrals 2-4 must have been very typically shaped. It looks as if the following centrals were laterally distinctly pointed and reaching very far over the corresponding pleurals, thus furcating Y-shaped with the laterals and deeply penetrating into the anterior section of pleurals 2 and 3. The shape of the centrals might be compared to the schematized outline of a butterfly.

The marginal sulci of the first three peripherals reach up to their middle or even upper third. The posterior marginals furrow the peripherals in their upper third. Neural 5 is more or less rounded and small.

The morphometrical data of straight length measurements (in cm) are given below; values in () are reconstructed:

max. length of fossil: 19.6 width at Peripherals 7/8: 14.2

max. length x ant. width of Neurals:
N1 19.2 x 12.6 N2 (19.3) N3 16.7 x 13.0
N4 (15.3 x 10.x) N5 (10.0 x 10.5)

max. length x width of centrals:
C1 35.6 x 38.4 C2 (27.5 x 61.4) C3 (34 x 55)
C4 (-- x 56.8) C5 - x -

### The plastron (fig. 7)

A fragmentary plastron front lobe is broken and lacking its sinistrolateral posterior part. As bone sutures are difficult to recognize it remains speculative whether the extended dextroposterior end might be (part of) a mesoplastral plate. The front lobe is generally well rounded, showing a slight protrusion of the flat gular beak. The entoplastron is very large, in ventral view of triangular shape with a frontal bow. Its visceral view shows widely extended lateral wings and an anterior buckling. A V-shaped serration situated in the middle of the plastron is another characteristic visceral feature. The epiplastra are sickle-shaped having about the same anteriomedian and posteriolateral lengths. The Haustsaumrinne (s. Schleich, 1981) is weakly marked. There are hardly any relief-like structures but those serrations on the epiplastron to recognize.

The scalation shows a vase-shaped central gular part, two small v-shaped intragulars which are not reaching the entoplastron, a gular furrow reaching up to the posterior third of the entoplastron. The humero-pectoral furrow is rather straight in the frontmost part of the hyoplastron. The latter is very elongate and has only a slightly curved pectoral/abdominal furrow.

Diagnostic features or apomorphies might be: visceral and ventral shape of Entoplastron.

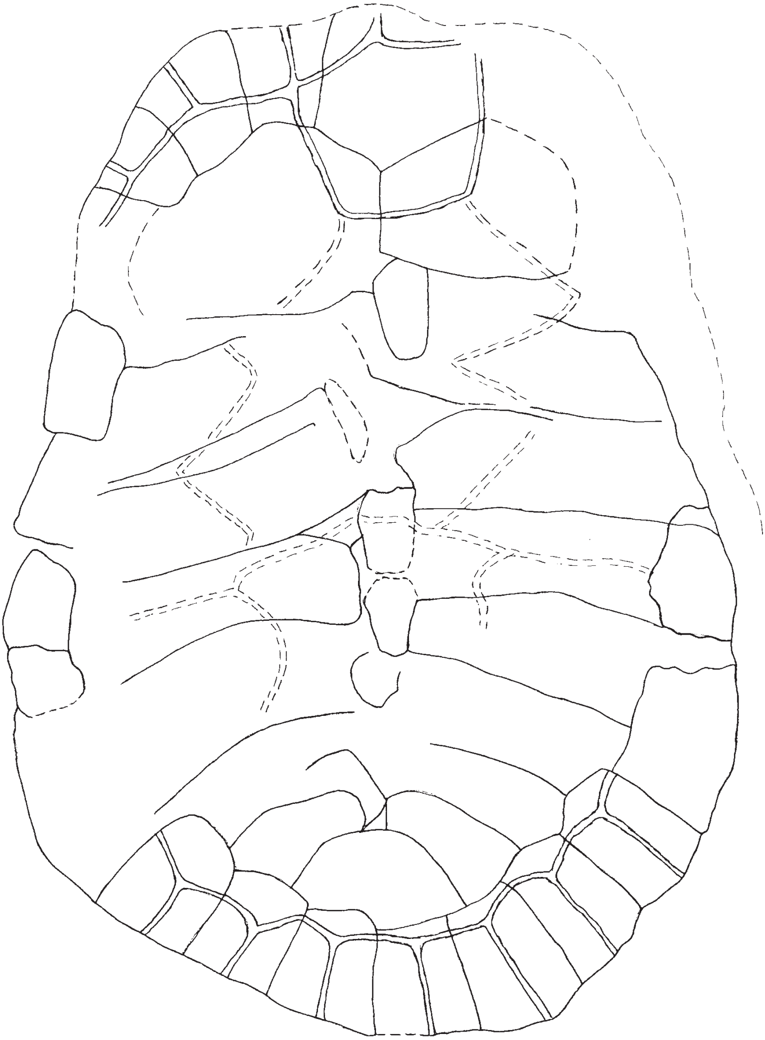

**Fig. 6.** Carapace of Pelomedusidae indet.

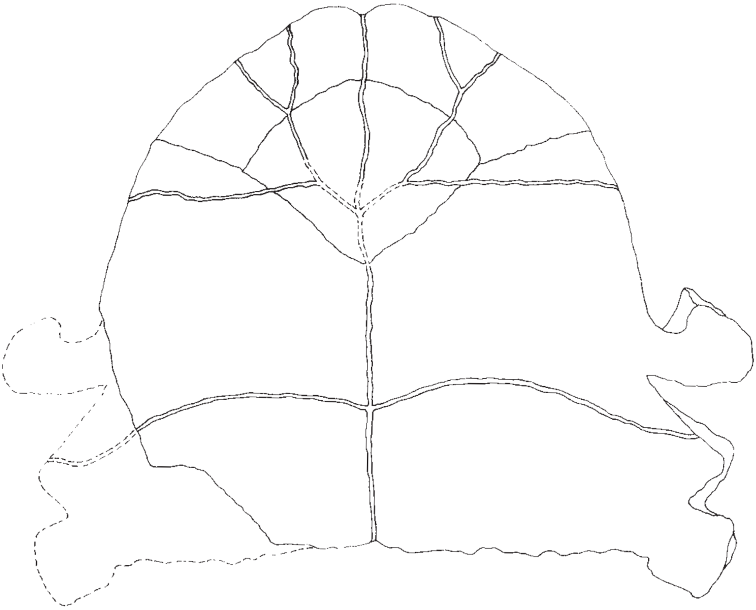

**Fig. 7a.** Pelomedusidae indet.; Plastron front lobe, ventral view

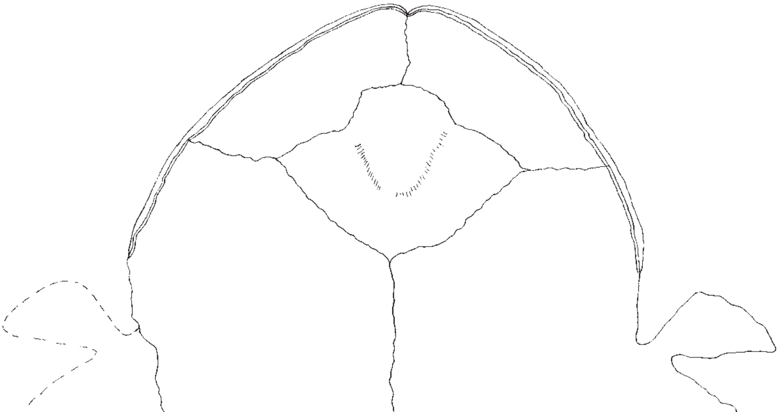

**Fig. 7b.** Pelomedusidae indet.; Plastron front lobe, visceral view

Morphometrical measurements (in cm) :

|  |  |  |  |
|---|---|---|---|
| front lobe med. length x max width (of fossil): |  | 15.0 x 18.2; ventral. |  |
| Entoplastron max. length x max. width : |  | 52.5 x 68.2; ventral. |  |
|  |  |  | 55.5 x 67.1; visceral. |
| Epiplastron (visceral): | med. length | 22.5 | post. length 25.1 |
|  | straight marginal length |  | 67.8 |
| Hyoplastron med. length | 72.5 | lat. length 110.4 |  |

Acknowledgements
The authors are grateful to Prof. S.L. Jain, Lucknow, India for his critical review of the manuscript, many useful suggestions and generous loan of literature. One of the authors (SDS) is thankful to Dr. V. Narayanan, Head, Regional Geology Laboratory, ONGC, Bombay, India for his help and encouragement during the course of the study.

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## PLATE 1

### Crocodylidae, Gen. et. sp. indet.

a) SDS/VPI, 1101, a broken tooth.

Crocodilian eggshell fragments

b) SDS/VPL 1104, inner surface with mammillae
c) SDS/VPL 1204, enlarged mammilla
d) SDS/VPL 1204, enlarged mammillae
e) SDS/VPL 1205, mammillary view showing well-separated individual mammillae
f) SDS/VPL 1204, external surface showing dissolution surface and pore in a pit.

## PLATE 2

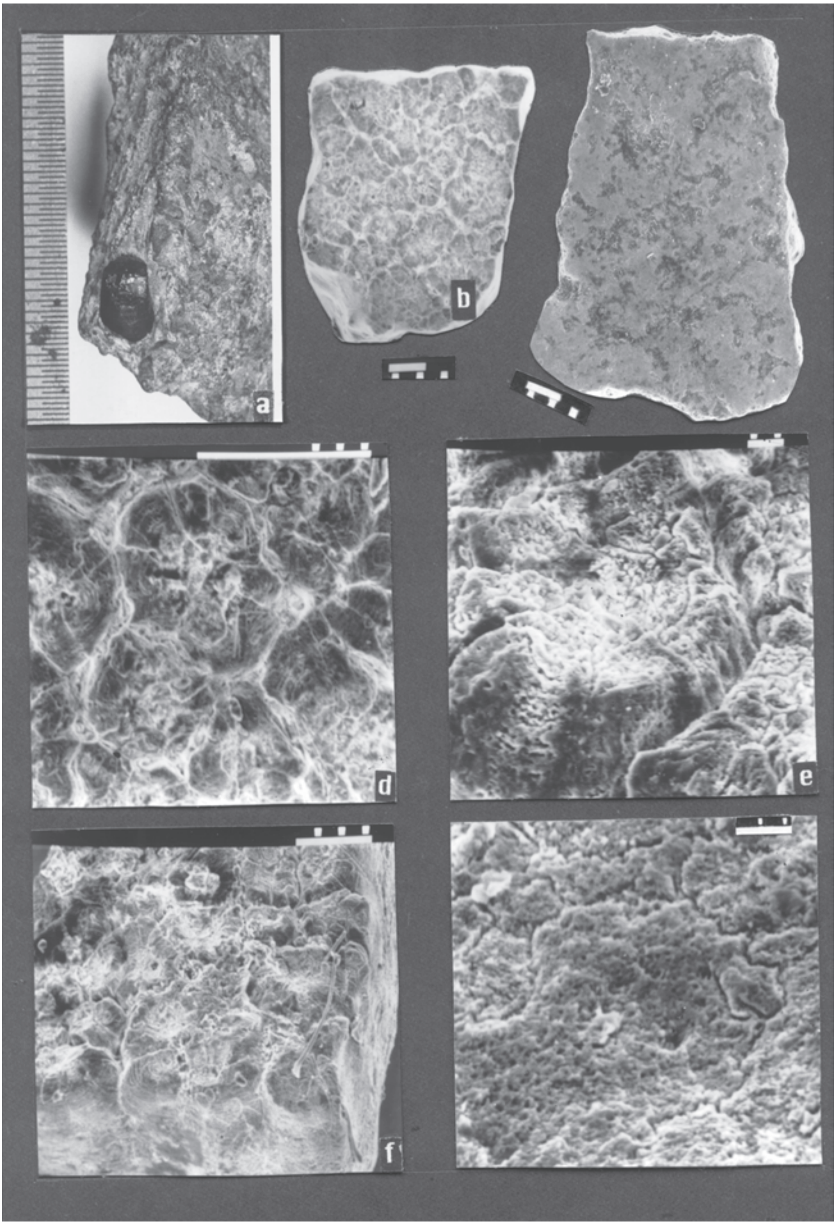
Crocodilian eggshell fragments

a) SDS/VPL 1203, cross-section showing wedge-shaped spheroliths,
b) SDS/VPL 1206, cross-section showing wedge-shaped spheroliths and fine horizontal layers,
c) SDS/VPL 1206, magnified cross- section showing wedge-shaped spheroliths with fine canals on both sides, and fine layering.

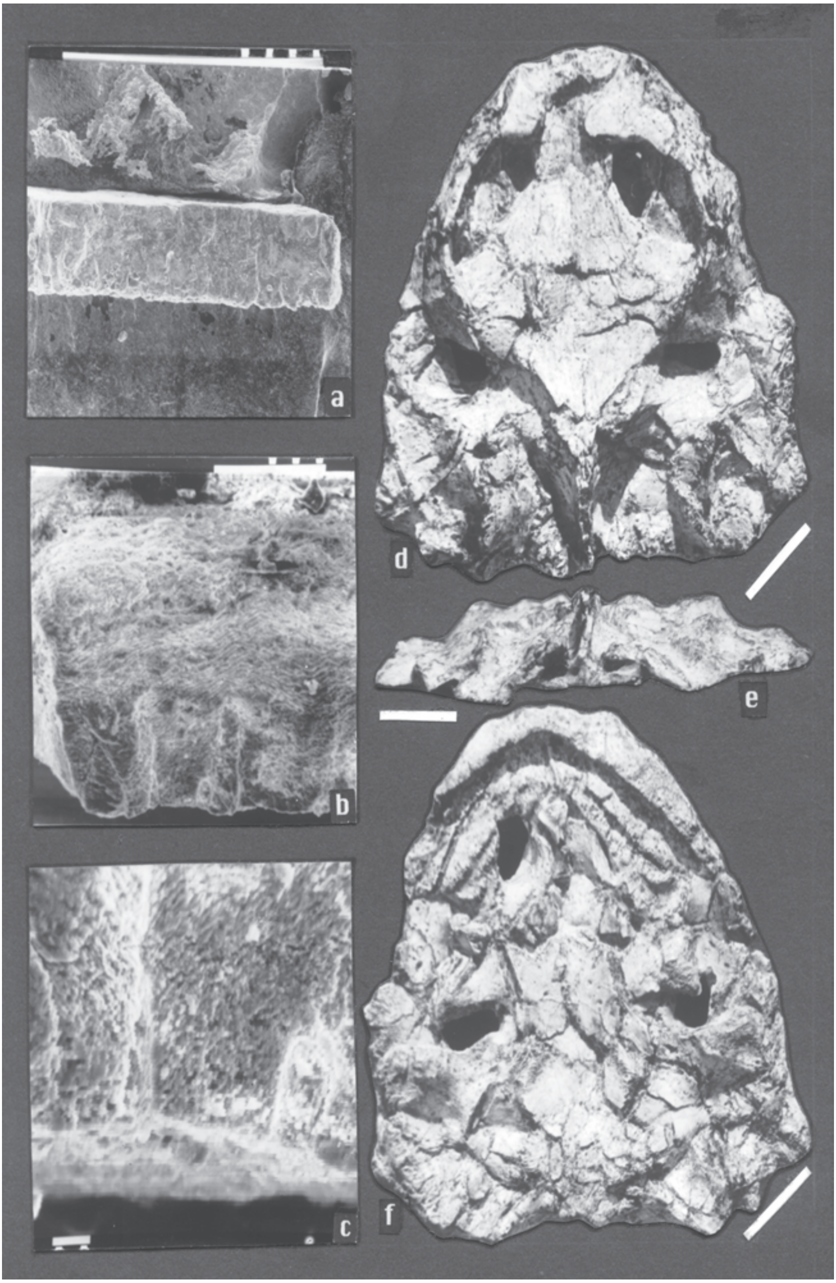
?Bothremydidae indet.; SDS/VPL 1125 skull
(bar length in all cases 10 mm)

d) dorsal,
e) posterior,
f) ventral view.

# Plate 1



## Plate 2



Veröffentlichungen aus dem Fuhlrott-Museum, 1998, Bd. 4: 321-322

# ARCO-Nepal

(registered society)
www.arco-nepal.de

The recently founded international sponsoring society **ARCO-Nepal** (**A**mphibian and **R**eptile **Co**nservation of **Nepal**) is concerned with the promotion of herpetological knowledge. Its main field of activity is to enhance the knowledge on the biology and systematics and the conservation of amphibians and reptiles in Nepal.

Name and symbol of the new conservation society use the English abbreviation to employ the official language of Nepal and to emphasise the necessity of international orientation and collaboration. Arco also means “the bow”, in our case the rainbow which as a symbol for nature, ambient and ecology should span and shelter our efforts.

The predominant task of our society is the support of the turtle conservation project (Systematics, Biology and Conservation of the Turtles of Nepal) which was approved by the Nepalese government in January 1997. Besides the urgently needed initiation and realisation of this conservation project there is great need to record the hitherto largely unexplored amphibian and reptile fauna of Nepal.
The ARCO Nepal society is intended to arouse interest in the actual problems and the planned measures. Talks, events and publications will inform members, but also interested non-members and guests, on project development, progress of official and practical conservative measures as well as the latest scientific results concerning the herpetology of Nepal. Seminars and guest lectures are intended to arouse interest in this field of knowledge.

Research work (projects, dissertations for diplomas and doctorates) has already started successfully but should still be intensified and widened in the fields mentioned above.

ARCO-Nepal welcomes all interested persons and of course, new members. With a single annual membership fee several meters of fencing for an observation or breeding station in a Nepalese national park can be paid. Information on membership and collaboration can be obtained from the Fuhlrott-Museum, which also welcomes any kind of suggestion.

The turtle conservation project needs a lot of idealism, engagement and recruitment of new members. It is a long-term enterprise with a great aim.

As a part of public communication the contents of the project are exposed in the exhibition ”Das andere Nepal” at Fuhlrott-Museum Wuppertal.

Further information get from:

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www.arco-nepal.de
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